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Using plant functional distances to select species for restoration of mining sites

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Abstract

1. Plant facilitation, an ecological interaction that benefits at least one species without harming the other, is increasingly used as a restoration tool. To restore degraded habitats under a facilitation framework, practitioners must correctly select both the benefactor (nurse) and the beneficiary (facilitated) species.
2. Based on community assembly and species coexistence theory, we propose selecting plant species that largely differ in a suite of functional traits so that competition is minimized and facilitation maximized due to functional complementarity. To apply this guideline in a pilot restoration experiment performed in metalliferous mine tailings in South-Eastern Spain, we first built the plant–plant facilitative interaction network naturally occurring in a set of 12 tailings. After characterizing each species with 20 morphological and physiological traits, we verified that facilitative interactions were predominantly established between functionally distant species.
3. Then, we designed a sowing experiment combining 50 nurse-facilitated species pairs separated by a wide range of functional distances. The success of seedling establishment significantly increased with the functional distance between the nurse and the facilitated plant species.
4. *Synthesis and applications*. We encourage the use of ecological facilitation together with trait-based species selection to design restoration programmes based on the principle of increasing functional distance between target species. This method may not only promote the restoration of the plant cover but also impact paramount ecosystem functions, thus being an efficient low-cost restoration practice in abiotically stressful ecosystems.

KEYWORDS
abiotic stress, community assembly, dryland, ecological facilitation, heavy metal, mine tailing, nurse plant, plant trait

1 | INTRODUCTION

Ecological interactions, either negative (e.g. competition) or positive (e.g. facilitation), are important mechanisms underlying the assembly of plant communities (Bruno, Stachowicz, & Bertness, 2003; Callaway, 2007). Traditional restoration programs tried to avoid competitive exclusion by planting target plants in isolation after eliminating pre-existing vegetation (Castro, Zamora, Hódar, & Gómez, 2002). Since the beginning of the XXI century, however, the literature on ecological restoration is providing with compelling evidence that planting species together does not result in competitive exclusion but in benefits for the target plant in terms of establishment, survival and reproduction (Castro et al., 2002; Gómez-Aparicio et al., 2004; Padilla & Pugnaire, 2006). Based on this evidence, facilitation, in which one species(nurse) ameliorates the microhabitat and allows the establishment of second (facilitated) species, has been tested as a restoration tool in a wide range of ecosystems for the past two decades (Gómez-Aparicio et al., 2004; Padilla & Pugnaire, 2006). In these assays, target plants were planted close to neighbour species (potential nurses) or in gaps. Target species were selected mainly following successional or technical criteria (traditional forestry species, woody species), whereas nurses were chosen mainly due to their perennial character and colonization ability. Studies focusing on the outcome of species interactions in restoration and afforestation programmes have traditionally put the focus on the life-form of the nurse and the target plant, while competition mainly occurs between species with similar life-forms, and facilitation is primarily detected between species showing contrasting life-forms (Gómez-Aparicio, 2009; Verdú, Gómez-Aparicio, & Valiente-Banuet, 2012). This idea can be traced back to Darwin (1859), who was the first to hypothesize that functionally similar species tend to compete more than different species do. We now know that indeed functionally different species tend to be involved in positive interactions, like facilitation (Valiente-Banuet & Verdú, 2013).

The selection of adequate plant species is crucial to guarantee the success of restoration programs, especially in stressful habitats (Bainbridge, 2007). When the niche requirements of the species are not very well known, practitioners may resort to biological indicators of species performance. Plant traits are any morphological, physiological or phenological features that determine where a species can live, how it interacts with other species or how it contributes to the functioning of ecosystems (Cadotte, Carscadden, & Mirotchnick, 2011; Violle et al., 2007). Traits have been shown to be convenient predictors of the functional role of plant species in ecological restoration (Pywell et al., 2003). Efficient species selection would be ideally based on plant traits that maximize the establishment of a highly diverse plant community where ecological interactions are also restored (Forup, Henson, Craze, & Memmott, 2008).

The mining industry has widespread impacts on the environment world-wide. More than 700 MT of metalliferous mine wastes are annually deposited in tailings (Warhurst, 2000). Metalliferous mine tailings are extremely stressful habitats because of their high content of heavy metals and salinity, lowpH and high erosion risk (Conesa & Schulin, 2010; Dudka & Adriano, 1997). Toxicity poses a serious hazard not only for biological communities but also for human health, and restoration practices are, therefore, urgent to alleviate such an environmental and public problem (Conesa, García, Faz, & Arnaldos, 2007). In Europe, less than 5% of the closed-down mine tailings have been restored (Panagos, Liedekerke, Yigini, & Montanarella, 2013). Hard-engineering restoration techniques such as capping, excavation and chemical stabilization have been used occasionally, but their tremendous economic costs and environmental impacts discourage their use compared to other more environmentally friendly techniques like phytoremediation (Mendez & Maier, 2008). The use of plants for the stabilization of mine wastes represents a soft (less dependent on heavy machinery and extensive applications) and cheaper restoration method, particularly for those tailings embedded into natural areas that are located far from urban areas and do not show high risk of structural collapse (Navarro-Cano, Verdú, & Goberna, 2018).

The selection of functionally complementary species to establish facilitation-based experiments is a promising tool to restore degraded habitats under extreme environmental stress like mine tailings (Gastauer et al., 2018). Here, we try to validate this restoration guideline in the Cartagena-La Unión Mining District (SE Spain), a traditional metalliferous mining area under semi-arid conditions. In this area, plant colonization in abandoned mine tailings is filtered by three main abiotic stress factors: soil toxicity (by heavy metals, pH and salinity), water limitation and negligible fertility (Conesa & Schulin, 2010; Navarro-Cano et al., 2018). These systems behave as micro-deserts where functional traits related to plant architecture, metabolism, physiology, above- (leaf) and below- (root) ground resource acquisition and reproduction are potentially relevant for the establishment of facilitative interactions (Butterfield & Callaway, 2013). By collecting information on 20 plant features covering these different trait dimensions in 151 plant species, we aimed to validate the selection of target species for restoration whose traits maximize their functional distances to nurses established in the studied mine tailings. We then performed an extensive field sampling to test whether large functional distances among plant species are indicative of successful establishment and persistence of facilitative interactions. Finally, we developed a pilot restoration experiment where target species with varying functional distances to the nurses were sown in the mine tailings, to test if increasing the functional distance between the nurse and facilitated species promotes seedling establishment. The outcome of both observational and experimental analyses can help to understand the mechanisms assembling plant communities under extreme conditions and improve plant and microsite selection based on functional complementarity for plantation in restoration programs.

2 | MATERIALS AND METHODS

2.1 | Study system

The Cartagena-La Unión Mining District (Murcia, Spain; 30S689151E, 4164433N) ranges 5,000 ha of a <400 m a. s. l. coastal mountain range. Climate is semi-arid Mediterranean (17.9°C average annual temperature, 316.3 mm rainfall and 762.2 mm evapotranspiration). Important ores of iron, lead, zinc and copper have been historically exploited in the area. The beginning of open cast mines and the use of aggressive refining technologies during the second half of the 20th century left around 89 mine tailings up to the cessation of mining activities in 1991 (Conesa & Schulin, 2010). In these waste deposits, primary succession is hindered by severe abiotic stress. Acidic to neutral pH, high salinity and heavy metal contents, as well as extremely low fertility are general soil properties in the tailings (Conesa, Faz, & Arnaldos, 2006; Navarro-Cano et al., 2018). A low-cover patchy vegetation currently occupies most of the tailings, with a variable plant cover ranging from 0% to 25%. Dominant plant species are mainly perennial grasses (*Lygeum spartum*, *Piptatherum miliaceum* and *Hyparrhenia syanica*), shrubs (*Atriplex halimus* and *Salsola oppositifolia*), some trees (*Pinus halepensis* and *Tamarix canariensis*) and some perennial herbs such as *Zygophyllum fabago*. Nevertheless, the diversity of annual and short-life species in these artificial habitats has not been adequately addressed. Some of the perennial plants have been identified as nurses, as they usually colonize barren soils and promote the formation of plant patches and essential ecosystem functions related to soil fertility and microbial productivity, as well as the softening of temperature, radiation and water stress (Navarro-Cano et al., 2018).

2.2 | Field sampling of plant communities in mine tailings

Twelve mine tailings that hold the majority of plant species colonizing these ecosystems and occupy a total of 38 hectares were sampled in 2015. Plant communities were sampled considering plots shaped by two microsites: plant patches (hereafter “patches”) and adjacent open areas (hereafter “gaps”). Patches were defined as clustered plant communities growing beneath the canopy of one of the 13 perennial plants that were previously identified as nurse species by Navarro-Cano et al. (2018) in tailings from this mine district. Gaps were defined as pioneer plant communities growing on open spaces adjacent to each patch, where only isolated individuals grow and no adults of potential nurse plants are observed (Figure S1). Nurses are species able to recruit on gaps and promote seedling establishment of beneficiary species by relaxing the abiotic filter imposed by high soil toxicity, physical instability and/or water and temperature stress in the mine tailings. A mininum number of 30 patches per potential nurse species were randomly selected in each tailing, except for *Pinus halepensis* (n = 7–16), *Tamarix canariensis* (n = 8–18) and *Osyris lanceolata* (n = 9–16), that have larger growth forms and are less abundant in the tailings. Each sampled patch had an adjacent gap, which was delimited with a similar area and shape and systematically placed west at a distance equal to the mean canopy diameter of the corresponding patch. This strategy aimed at avoiding the assymetric modification of soil properties that plant patches can induce in their surroundings, as well as avoiding root or canopy influence on gap communities.

A total of 1,758 patches and gaps were sampled. Nurse plants spanning a wide range of sizes were included in each tailing. The abundance of seedlings, juveniles and adults of each species was recorded for every patch and gap (Figure S1). Seedlings were defined as recently established plants that still showed cotyledons or inmature leaves and soft stems. Juveniles were plants with adult leaves that had not reached the reproductive stage at the sampling season and did not show clues of flowering during the previous year. Adults were plants with evidence of past, present or coming reproduction.

We determined if the plants growing within a patch were actually facilitated by a nurse by calculating the relative interaction intensity index (RII; Armas, Ordiales, & Pugnaire, 2004):

$$\mathrm{RII} = \frac{B_w - B_o}{B_w + B_o}$$

where B_w and B_o denote the number of contact points below the nurse and in the open spaces respectively. Positive values of RII are indicative of facilitation.

We separated seedling facilitation from juveniles and adults in our analysis to determine whether initial facilitative interactions (i.e seedlings) persist overtime (i.e. juveniles and adults). To visualize the facilitative interactions, we built plant–plant interaction networks using the plotweb function in the *bipartite* package *version* 2.0.8 for R (Dormann, Gruber, & Fründ, 2008). A dynamic version of these networks was built as Sankey diagrams with the help of the *bipartiteD3* Package for R (Terry, 2018).

2.3 | Functional distance between nurse and facilitated species

To characterize the functional strategies of each species detected in the field sampling, we selected a set of traits that are relevant to the species life span, morphological and canopy structure, colonization ability, soil exploration and resistance to erosion, photosynthetic efficiency, tolerance to salinity, high temperatures and drought and ability to regrow after disturbance. We specifically gathered information on 20 above- and below-ground traits for 151 out of 162 species. The remaining 11 species were excluded as they could not be characterized for some of the traits analysed. We included 13 morphological traits (specific life-form, bud height, plant height, leaf length, leaf area, leaf thickness, leaf weight, seed size and dispersal, root length, root depth, root laterality and root weight). We also included seven ecophysiological traits (photosynthetic metabolism, flowering phenology and span, halophytism, xerophytism, sclerophytism and resprouting ability). Mean trait values were either obtained from five adult plants per species that were fully harvested above- and below-ground in the tailings or from the literature. Information on the measurement and specific role of each trait is summarized in Table 1.

We computed the pairwise functional dissimilarities (distances) between species using the *daisy* function and the Gower's distance, which allows for simultaneous use of nominal, categorical and continuous variables(Kaufman & Rousseeuw, 2009). This distance ranges from 0 to 1, zero indicating the total similarity between two species. Analyses were run in the *cluster* package *version* 2.0.7 for R (Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2017; R Core Team 2018).

2.4 | Seed sowing experiment in a mine tailing

We performed a seed sowing experiment beneath natural patches from five of the studied nurse species present on a mine tailing and their adjacent gaps (Navarro-Cano et al., 2018). UTM coordinates

TABLE 1 Plant functional traits studied to assess the functional distance between nurse and facilitated species in mine tailings. D: discrete qualitative variables; C: continuous quantitative variables. The trait value range or the percentages for each level within a qualitative variable are shown

Trait	Measurement (unit)	Trait values	Related to	Ref.
Specific life-form	D: Annual = 0, Perennial = 1	A: 44%; P: 56%	Life span	1, 2, 3
Bud height	D: **B**elow-ground buds, **S**oil surface buds, **L**ow buds (up to 10 cm height), **M**edium buds (10–50 cm), **H**igh buds (>50 cm)	B:4%; S:22%; L:59%; M:5%; H:10%;	Raunkiaer's life-form and morphological structure	1, 2, 3
Plant height	C: Total above-ground height (cm)	2.8–300	Morphological structure	1
Leaf length	C: Fresh leaf length (mm)	1.2–345.6	Canopy structure	1
Leaf area	C: Fresh leaf area (mm^2)	1.0–24262.2	Canopy structure	1
Thickness	C: Fresh leaf thickness (mm)	0.03–3.31	Canopy structure	1
Leaf weight	C: Dry leaf weight (mg)	0.1–5564.0	Canopy structure	1
Seed size	C: (Larger length + minor length)/2 (mm)	0.3–10.5	Seed dispersion and colonization ability	1
Seed dispersal	D: **S**hort distance (<1 m), **M**edium (1–10 m), **L**ong (>10 m)	S: 27%; M: 50%; L: 23%	Seed dispersion and colonization ability	1
Root length	C: Fresh root length (cm);	1.6–172.5	Soil exploration and erosion resistance	1, 4, 5
Root depth	C: Fresh root depth (cm);	1.3–50.0	Soil exploration and erosion resistance	1, 4, 5
Root laterality	C: Fresh root laterality (cm)	0.8–217.0	Soil exploration and erosion resistance	1, 4, 5
Root weight	C: Dry root weight (g)	0.001–237.030		1, 4, 5
Metabolism	D: C3 = 0, C4 or CAM = 1	C3: 95%; C4 or CAM: 5%	Photosynthetic efficiency under high temperature and water stress	2, 6
Flowering phenology	D: **W**inter, **Sp**ring, **Su**mmer and **A**utumn	W: 20%; Sp: 64%; Su: 11%; A: 5%	Physiological activity periods	1, 7
Flowering span	C: Number of months	2–12	Physiological activity period	1, 7
Halophytism	D: Yes = 1, No = 0	Y: 13%; *N*: 87%	Functional trait syndrome for high salinity tolerance	1, 7
Xerophytism	D: Yes = 1, No = 0	Y: 75%; *N*:25%	Functional trait syndrome for tolerance to high temperature and water stress	1
Sclerophytism	D: Yes = 1, No = 0	Y: 11%; *N*: 89%	Functional trait syndrome for tolerance to mid temperature and water stress	1
Resprouting ability	D: Yes = 1, No = 0	Y: 39%; *N*: 61%	Ability to regrow after disturbance by activation of dormant vegetative buds	1, 3

Note: 1: Own data based on observations and measurements from this study; 2: Cornelissen et al. (2003); 3: Paula et al. (2009); 4: Guerrero Campo (1998); 5: De Baets et al. (2007); 6: Pyankov, Ziegler, Akhani, Deigele, and Lüttge (2010); 7: Mateo and Crespo (2014).
Bold letters in Measurement are used as initials in Trait values.

of the tailing are 30S 690898E, 4164216N. Environmental and soil characterization of the tailing and the microsites shaped by the nurses and their adjacent gaps is shown in Table S1. The tailing has similar pH values to the surrounding *P. halepensis* forest soils that are not directly affected by mining, but higher total metal concentrations, salinity and lower total organic carbon and total nitrogen (Párraga-Aguado, González-Alcaraz, Álvarez-Rogel, Jiménez-Cárceles, & Conesa, 2013). We selected a set of 10 target species for sowing so as to include a large range of trait values (Table S3). We chose local species with contrasted life-forms, belonging to eight families. The functional distances between the 10 target species and the five nurses, which were calculated as above, averaged 0.21 ± 0.09 and ranged from 0 to 0.38. These values fall well within the range of observed functional distances for wild plants in the study site (see Results) and allowed to test for 50 different nurse-facilitated species pairs.

Seeds from the 10 target species selected for the sowing experiment were collected in the surroundings of several mine tailings in the Cartagena-La Unión Mining District in Summer–Autumn 2015. The sowing experiment was launched without any seed pretreatment on December 2015. We defined a plot as shaped by two microsites: a patch and its adjacent gap. Ten patches, each one shaped by an adult nurse, and their adjacent gaps were selected and labelled for sowing, thus making a total of 50 patches (5 nurses × 10 patches) and 50 adjacent gaps. We delimited with nails a sowing frame (25 × 25 cm) beneath each patch and gap (100 frames in total). Each frame consisted of four parallel and equidistant grooves, on which a mixture of seeds belonging to 10 species were sowed (10 species × 50 seeds = 500 seeds per frame). The seeds were manually sown at approximately 0.5 cm depth. No watering was carried out along the experiment. The sowing frames were inspected every 2 weeks during the emergence season for 2 years and all seedlings recorded (Figure S2). Mean annual rainfall during the monitoring time was 45% lower (172 ± 10 mm) than the mean annual rainfall of the previous decade (316 ± 149 mm). Total seedling emergence was calculated for statistical analyses.

2.5 | Statistical analyses

In the observational study, in order to determine which trait values are key determinants of the nurse-facilitated interaction outcome, we tested the role of functional traits on the RII of the 151 sampled species. All trait values were reduced by PCA including quantitative and qualitative variables with the *PCAmixdata* R package (Chavent, Kuentz, Labenne, Liquet, & Saracco, 2014). We used the first and second dimensions as predictive variables in generalized linear models (GLMs) with RII as the dependent variable. All analyses were performed with R 3.1.3 (R Core Team, 2018).

Then, we compared the average functional distance observed between nurses and facilitated species with that expected under a null model averaging distances between pairs of randomly selected species. The same number of random pairs as those observed in the studied tailings was used in the null model to average each functional distance. We built 999 iterations to test whether the observed average was below 2.5% or above 97.5% of the random mean values, respectively indicating that facilitative interactions either occur between functionally similar (low plant–plant functional distance) or dissimilar species (high distance). This procedure was repeated to compare the functional distances between each nurse and its facilitated species both at a seedling stage, and at juvenile plus adult stages.

In the seed sowing experiment, to determine whether nurses facilitate the establishment of the target sowing species, we built a generalized linear mixed model (GLMM) with a binomial error distribution. Seedling emergence was the dependent variable and the microsite (patch vs. gap) the independent variable. As each nurse had an adjacent gap within a plot, we considered plot as a random factor in the model.

We then tested whether seedling emergence depends on the functional distance between the sown species and the nurse species through a GLMM with a binomial error distribution. In this case, only seedling emergence beneath the nurses was considered, and so we used the sown species, nested within the nurse species, as random factors in the model. Overdispersion was tested with *overdisp_fun* function. The variance explained (conditional R^2) by the GLMM was calculated through the *theoretical* method for binomial models with the r.squared GLMM function in the R package *MuMIn*. All GLMMs were performed with the g*lmer* function in the R package *lme4*.

3 | RESULTS

3.1 | Facilitation and functional distances naturally occurring in the mine tailings

We detected a total 162 plant species naturally growing in the mine tailings (Table S3). We registered 15,637 seedlings from 124 species, most of which predominantly established underneath nurse plants (11,476 seedlings in patches vs. 4,161 in gaps; χ^2 = 3,422; $p < 0.0001$; Table S3). Such a strong spatial association was still detected within the category "juveniles and adults", with 13,104 versus 5,461 individuals of 155 species growing in patches and gaps respectively (χ^2 = 3,147; $p < 0.0001$; Table S3).

Among all 162 species, we identified 104 species that grew preferentially beneath the 13 nurse species based on their significant (or marginally significant) and positive RII considering seedlings, juveniles and adults altogether (Table S3). The remaining 58 species were found to either grow preferentially isolated in the gaps (significantly negative RII), to be indifferent to the microsite (RII close to 0) or not abundant enough so as to statistically determine their ecological preferences.

We detected a complex facilitation network among the nurses and their facilitated species in the seedling stage, which accounted for 26.6% of all potential interactions (411 observed vs. 1,547 possible interactions between 13 nurses and 119 facilitated species). The involvement of each nurse in the total number of interactions observed varied substantially, from 0.3% (*T. canariensis*) to 25.8% (*H. sinaica*; Figure S3). Five nurse species were responsible for ca. 85% of all interactions observed (*H. sinaica*, *Helichrysum stoechas*, *P. miliaceum*, *Paronychia suffruticosa*, and *A. halimus*). Juveniles and adults of 151 species were associated with the same 13 nurses in a total of 552 interactions (28% of all potential interactions between 13 nurses and 151 species in juvenile or adult stages). Also in this case, nurse contributions to observed interactions varied substantially (from 0.5% *T. canariensis* to 25.7% *P. miliaceum*) and the same five species listed above explained ca. 73% of all interactions (Figure S4).

The reduction of 20 traits of 151 species by PCA yielded a first dimension (Dim1) that explained 22.3% of the variance and was positively correlated mainly with all the root attributes and the bud height, and secondarily with the specific life-form, the height, the sclerophytism and the resprouting ability (Figure S5). The second dimension (Dim2) explained 10.9% of the variance and was positively associated with leaf traits (leaf area, dry leaf weight and leaf size) and seed size. Thus, Dim1 would be higher in species with larger above- and below-ground trait values, mainly perennial species able to resprout after severe ecological disturbances. Dim1 significantly and positively explained both the relative interaction intensity (RII) among seedlings and nurses (Estimate ± *SE* value of the linear model; 0.07 ± 0.02; $t = 3.8$, $p < 0.001$) and the RII among the juvenile + adults and nurses (Estimate ± *SE* value of the linear model; 0.03 ± 0.01; $t = 2.3$, $p = 0.02$), whereas Dim2 did not show any significant effect on RII.

The mean functional distance separating two randomly selected species in the community was 0.19 ± 0.08 (mean ± *SD*; 95% CI [0.18, 0.20]) (Figure 1). The functional separation between nurse and facilitated plants was significantly higher than expected by chance (i.e. not overlapping random CI values) both for seedlings (0.25 ± 0.09) and juveniles and adults (0.32 ± 0.11) (Figure 1).

3.2 | Functional distances among nurse and sowed facilitated species in a mine tailing

Seeds experimentally sown under nurses had significantly higher emergence than those sown on the bare ground (Estimate ± *SE* = 1.52 ± 0.05; $z = 26.5$; $p < 0.0001$; GLMM). This facilitative effect was consistently significant for nine out of the 10 target species (all $p < 0.0001$) and its magnitude was dependent on both the nurse and the target species identities (Figure 2). *Z. fabago* was the only species that significantly emerged better in the gaps (Estimate ± *SE* = −1.03 ± 0.2; $z = -5.04$; $p < 0.0001$; GLMM).

The functional traits harboured by both nurse and the facilitated plants explained the variation in the magnitude of seedling emergence, because the emergence success significantly increased with the functional distance between the target and the nurse species (Estimate ± *SE* = 5.15 ± 2.47; $z = 2.08$; $p = 0.03$; GLMM) (Figure 3). The GLMM explained 39.6% of variance.

4 | DISCUSSION

Restoration based on the use of facilitative plant–plant interactions requires an appropriate selection not only of the target species, but also of the nurse from which it is expected to benefit. Functional traits can provide clues of whether a species can act as a nurse or a facilitated species (Butterfield & Callaway, 2013; Soliveres et al., 2014). In facilitative interactions, functional complementarity is expected to promote plant coexistence, since harbouring different traits might decrease niche overlap and divert resource usage (Cadotte et al., 2011; Loreau, 1998; Valiente-Banuet & Verdú, 2013). Here, we validate this premise by (a) performing an extensive field sampling of 34,202 plant individuals belonging to 162 species that have naturally colonized an abandoned mining area based on facilitative interactions, (b) collecting data of 20 above- and below-ground traits of the same species to evaluate if the intensity of natural facilitative interactions increases with the functional distance between the nurse and its beneficiaries and (c) experimentally testing whether seedling establishment increases with the functional distance between selected adult nurses and sowed target species. Our approach strongly suggests that functional traits should guide the selection of pairs of species. We also conclude that maximizing the functional distance between benefactor and beneficiary species can be an efficient option to restore extremely degraded ecosystems.

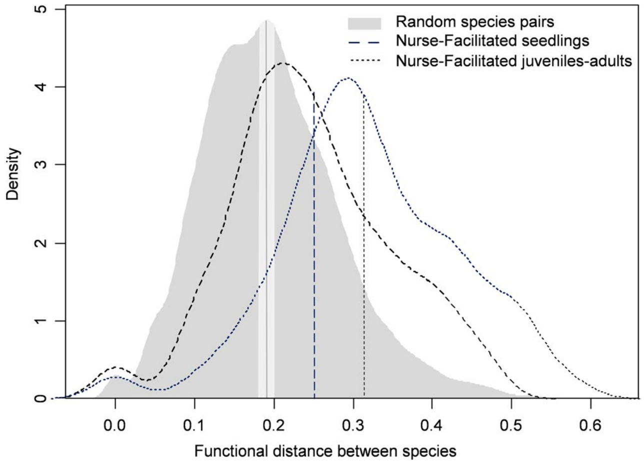
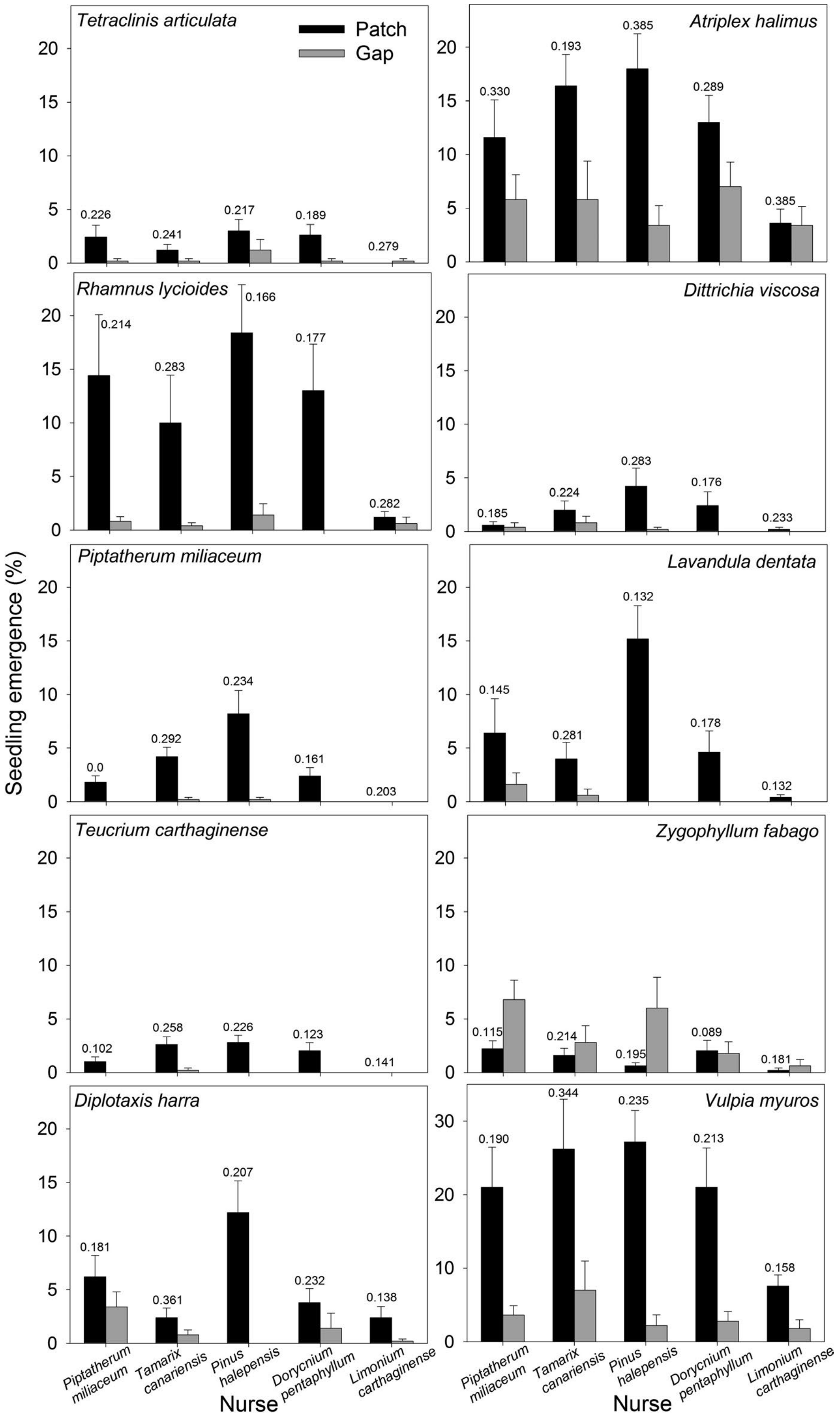


FIGURE 1 Distribution of the functional distances separating randomly selected pairs among all species in the community (shaded area) and all observed pairs of nurse and their facilitated seedlings (dashed line) or juveniles and adults (dotted line).The vertical solid line and the light grey-coloured area depict the mean functional distance and 95% CI for randomly selected pairs of species. Note that the mean distances of both nurse-facilitated seedlings (vertical dashed line) and juveniles–adults (dotted vertical line) do not overlap with the CI for randomly drawn species pairs. Functional distance was calculated based on 20 above- and below-ground traits (see main text for details)

Facilitation is a prominent assembly mechanism that shapes plant communities during the colonization process of barren areas (Callaway, 2007). We built the plant–plant interaction network naturally configured in patchy plant communities that grow on abandoned mine tailings. We detected a complex network that was based on the nursing ability of only 13 species that determined plant community reassembly by facilitating almost 120 other species. The number of realized (among all potential) interactions, varying between 26.6% and 28% for seedlings and juveniles–adults, falls within the range observed in other plant communities shaped by facilitation (15.7%–34.7%; Verdú & Valiente-Banuet, 2008). We detected a remarkable variation in the extent of involvement of the nurses in the interaction network, which correlates well with the idea that a nurse species is not necessarily a good benefactor for any facilitated species (Landero & Valiente-Banuet, 2010; Paterno, Siqueira Filho, & Ganade, 2016). Instead, there is a species-specificity in the nursing effect that hampers the selection of the appropriate nurse-facilitated species pair (Lortie, 2017). Despite the variation in the frequency of interactions supported by each nurse, five nurse species alone accounted for the great majority (85%) of facilitative interactions, regardless of the developmental stage of facilitated species (Figures S3 and S4). This observation suggests that these five species (*H. sinaica*, *H. stoechas*, *P. miliaceum*, *P. suffruticosa* and *A. halimus*) are ideal candidates to restore ecological interactions and trigger community reassembly in these and likewise mining areas. It is worth emphasizing that all listed nurses are shrubs, dwarf shrubs and perennial grasses, adding up to evidence that challenges the traditional clearing of short vegetation before reforestation and the extended use of trees in restoration programmes (Castro et al., 2002; Gómez-Aparicio, 2009). By studying the network of interactions, we also provide a tool for the taxonomy-based selection of those facilitated species that are more likely to succeed if planted beneath each of these nurses.

Plant species involved in facilitative interactions were functionally more distant than expected by chance based on the species pool registered on the mine tailings. This result supports our expectation that the intensity of natural facilitative interactions increases with functional distance between the nurse and its beneficiaries.

FIGURE 2 Seedling emergence (±*SD*) of 10 target species experimentally sown under five nurse species and on adjacent bare gaps. The 50 nurse-sowed pairwise functional distances are sowed on each patch column



We defined the functional distance in terms of a suite of 20 above- and below-ground traits that encapsulate architectural, morphological and physiological dimensions ensuring the exploration of different temporal (e.g. phenology) and spatial (i.e. root length) niches, and promoting coexistence (Thorpe, Aschehoug, Atwater, & Callaway, 2011). Nurses have been traditionally considered to bear stress-tolerance traits that allow them to establish and thrive under abiotically harsh conditions, while facilitated plants are seen as less stress-tolerant (Brooker et al., 2008). Butterfield and Briggs (2011) refined this view, proposing that colonizers have opportunistic strategies to cope with fluctuating microenvironments, whereas facilitated species show conservative functional strategies aiming at persistant dry and low light conditions. In the same line, we detected that beneficiaries showing the most intense facilitative interaction (i.e. highest RII values) had traits conferring resilience to disturbance. That is to say, these were perennial plants with larger

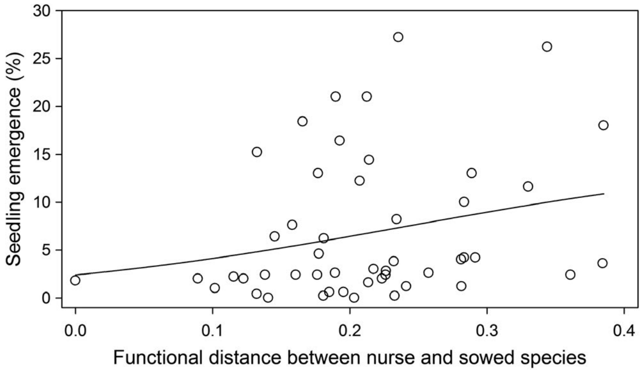


FIGURE 3 Effect of the functional distance between 10 species and five nurses on the seedling emergence of the target species experimentally sowed beneath the nurses' canopy. A logistic fit is depicted. The results of the GLMM are showed in the main text

root weight, with longer, deeper and/or more laterally spread roots, as well as resprouting ability. Below-ground traits informing on root size and structure are surrogates of ecological strategies related to tolerance to chemical and physical stress owing to infertility, erosion, thermal and water limitation (De Baets, Poesen, Knapen, Barberá, & Navarro, 2007; De Bello et al., 2010). The type of root system is also fundamental to understand community assembly, since functionally complementary roots allow a higher shared efficiency in the use of soil resources (Blignaut & Milton, 2005). Our results also emphasize the power of most root traits for the selection of plant species in restoration programmes. However, logistical sampling limitations, or perhaps unconscious underestimation of hidden traits, have led to the underuse of root traits in studies on community assembly and ecosystem functioning(Kattge et al., 2011; Weiher et al., 1999). By recording seedlings, juvenile and adult plants growing preferentially beneath nurse species, we could also determine that the coexistence of functionally distant species is not an ephemeral attribute in the community but persists over long-term coexistence. Indeed, the functional distances between each nurse and its facilitated species increased with beneficiaries' age. This pattern is similar to that detected in facilitation networks from Mexican deserts, where the most phylogenetically (and therefore functionally) distant species were those that maintained long-term facilitation interactions (Valiente-Banuet & Verdú, 2008). Thus, another convenient result of maximizing plant functional distances in restoration schemes could be the long-term maintenance of restored ecological interactions.

Mimicking the facilitation process that takes place in nature, a practitioner should plant the target species under a functionally distant nurse species. We experimentally confirmed this guideline by sowing 50 nurse-facilitated species pairs encompassing a wide range of functional distances. We verified that the probability of seedling establishment significantly increases with the functional distance between the target plant and its corresponding nurse. Using functional distances between species not only increases the success of plant establishment but may have derived consequences on essential ecosystem properties. Functionally diverse neighbourhoods provide elevated rates of ecosystem processes related to primary productivity, soil fertility, nutrient cycling, resistance to invasion or recruitment of new plant species (Díaz & Cabido 2001; Funk, Cleland, Suding, & Zavaleta, 2008; HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012). Indeed, we have previously shown that some of the five nurse species used in this experiment have morphological and physiological traits that not only facilitate the establishment of other plants, but also induce a faster recovery of soil fertility, rates of organic matter decomposition and nutrient cycling or resistance to erosion (Navarro-Cano et al., 2018). This opens up the possibility to restore not only species populations and ecological interactions, but also relevant ecosystem functions (Navarro-Cano, Goberna, Valiente-Banuet, & Verdú, 2016). As information on plant traits is abundant and publicly available in scientific databases (Cordlandwehr et al., 2013), using plant functional distances to design plantations based on the principle of increasing functional distance between target species may be viewed as an efficient low-cost restoration practice (Montoya, Rogers, & Memmott, 2012). Our results provide empirical support to a recent review on new ecological approaches for mine land rehabilitation, which demands the use of functional and phylogenetic information not only for species selection and plantation design but also for monitoring the rehabilitation success (Gastauer et al., 2018). Moving from pairs of target species to functionally diverse complex communities following a full trait-based restoration approach must focus our next efforts. On this subject, Laughlin (2014) suggested to manage community-level functional traits through manipulating relative species abundances as the easier way to provide practitioners and land managers with practical tools for restoring specific ecosystems. Ultimately, the satisfactory establishment of functionally diverse species assemblages will ensure the provisioning of a wide range of ecosystem functions, fulfilling the restoration goals of maintaining biological diversity and its associated ecosystem services (Cadotte et al., 2011).

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AUTHORS' CONTRIBUTIONS

All authors conceived the study. J.A.N.-C. and M.G. collected data. J.A.N.-C. analysed data and wrote a draft of the manuscript to which all authors made significant contributions and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data used in this study are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.gn52t27 (Navarro-Cano, Goberna, & Verdú, 2019).

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