RESEARCH ARTICLE

Additive effects of nurse and facilitated plants on ecosystem functions

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Abstract

1. Nurse plants drive the assembly of facilitated communities and commonly promote plant–soil feedbacks, and are thus recognized as key engineers in abiotically stressful ecosystems. The literature neglects; however, the role of the communities which benefit from the presence of the nurse as contributors to soil ecosystem functions. We hypothesized that the nurse and its beneficiaries synergistically enhance essential ecosystem functions mediated by soil microbiota.

2. To track how plant–plant facilitation impacts plant–soil feedbacks, we selected three nurse species in semi-arid mine tailings and defined three microsites (open space, nurse canopy and nurse + facilitated canopy). In each microsite, we quantified 18 abiotic and biotic variables associated with four functions: reduction in climatic stress, reduction in edaphic stress, soil fertility and soil microbial productivity (decomposition and nutrient cycling).

3. Litter biomass increased from open spaces to the microsite beneath the nurses, and further beneath the nurses and their beneficiaries. Litter biomass was a good predictor of both the reduction in climatic stress and increase in edaphic stress (likely owing to metal bioaccumulation). We attributed increments in soil organics and heterotrophic respiration beneath the nurses and their beneficiaries, compared to nurses alone, to biomass effects through increased litter deposition. Variation in fertility and microbial productivity among microsites shaped by the nurses and their facilitated communities was attributed to both diversity and biomass effects. In particular, fertility was promoted beneath phenotypically diverse facilitated communities, as inferred from ten above- and below-ground traits. However, microbial productivity increased at low levels of root biomass likely due to reduced plant–microbe competition for nutrients.

4. *Synthesis*. Our results show that facilitated plant communities sheltered by nurse species relieve local abiotic stress and promote plant–microbe interactions, both through biomass and biodiversity effects. These observations shift the conception of facilitated species from simple beneficiaries of the nurse's effects to co-drivers of essential ecosystem functions.

KEYWORDS
leaf litter, mine tailing, nutrient cycling, organic matter decomposition, phylogenetic diversity, plant traits, root biomass, soil microbes

1 | INTRODUCTION

Many plant species work as engineers that shape new microhabitats beneath their canopy and facilitate the establishment of other species in stressful ecosystems worldwide (Callaway, 2007; Jones, Lawton, & Shachak, 1997). These engineers, often referred to as nurse plants, have stress-tolerance traits that allow them to establish on barren soils. Nurse plants locally soften abiotic stress – related to water availability, UV radiation and temperature fluctuations – and benefit other species with more stringent abiotic niche requirements (Graff & Aguiar, 2017; Maestre, Callaway, Valladares, & Lortie, 2009). This process generates patchy vegetation patterns that are the quintessential characteristic of facilitation-driven ecosystems (Callaway, 2007; Navarro-Cano, Verdú, García, & Goberna, 2015). The plant neighbourhood of nurse species tends to be functionally diverse, since functional differences among facilitated plants allow their coexistence through niche segregation (Danet, Anthelme, Gross, & Kéfi, 2018; Navarro-Cano, Goberna, Valiente-Banuet, & Verdú, 2016; Valiente-Banuet & Verdú, 2007). High functional diversity is often mirrored in phylogenetic diversity (Valiente-Banuet & Verdú, 2013), because evolutionary related taxa tend to be functionally similar based on niche conservatism (Blomberg, Garland, & Ives, 2003; Prinzing, Durka, Klotz, & Brandl, 2001). In addition, plant assemblages composed of distantly related species use the overall resource more efficiently, ultimately maximizing plant biomass (Cadotte, 2013; Cadotte, Cardinale, & Oakley, 2008). Such an increase in plant productivity can augment the supply of plant litter and rhizodeposits to soils, which are the fundamental resources for heterotrophic microbes (De Deyn & Van der Putten, 2005). Increased plant biomass at high plant diversity can impact not only the levels of soil organics but also bacterial and fungal diversity (Pérez-Valera, Verdú, Navarro-Cano, & Goberna, 2018), eventually determining the rates of microbial processes such as organic matter decomposition and nutrient cycling (Navarro-Cano et al., 2014; Zak, Holmes, White, Peacock, & Tilman, 2003). These microbial processes are considered fundamental ecosystem functions (Hooper et al., 2005), which feed back into the performance of plant communities (Rodríguez-Echeverría, Lozano, & Bardgett, 2016). This linkage among primary producers and decomposers is paramount to the functioning of ecosystems (van der Putten et al., 2013; Wardle et al., 2004).

Plant colonization of barren lands that have experienced natural or human-induced disturbances (e.g. landslides, lava flows, desertified areas, mined sites) allows tracking how facilitation assembles plant communities (Walker & del Moral, 2003). These systems are also ideal to understand how plant–plant facilitation impacts the feedbacks between plants and soil microbes with essential consequences for ecosystem functioning (Navarro-Cano, Verdú, & Goberna, 2018). We have previous indirect evidence suggesting that nurse species and their beneficiaries contribute additively to promote soil fertility and microbial productivity, in terms of microbial biomass, organic matter decomposition and the rates of carbon, nitrogen and phosphorous cycling (Navarro-Cano et al., 2015). In that study, the effects of the nurse age and the plant cover of

facilitated communities on ecosystem functions in gypsum outcrops were decomposed by regression commonality analysis. However, the identities of facilitated species were not taken into account, and neither plant traits nor organic supplies were assessed as drivers of soil changes. As far as we know, there is no evidence based on the collection of field data at the proper scale to separate the contribution of nurse plants and their facilitated species to microbially driven ecosystem functions. Here, we test the synergistic role that facilitated species play to improve key ecosystem functions related to the promotion of soil fertility, microbial productivity and reduction in abiotic stress beneath three nurse species. We selected an extremely anthropogenic ecosystem under semi-arid conditions that was recently created from metal mining wastes. We hypothesized that, beyond simply occupying the less-stressful microsites created by the nurses, facilitated species significantly contribute to locally improving soil properties by supplying additional litter and root exudates proportionally to their biomass (mass-ratio effect sensu Grime, 1998). Moreover, functionally diverse plant communities might produce a more diverse set of organic chemicals that increase microbial resource usage (Eisenhauer et al., 2017; Steinauer, Chatzinotas, & Eisenhauer, 2016), the so-called biodiversity effect. Thus, we expect that facilitated plants promote a fine-tuned mosaic of improved soil microsites and enhanced below-ground ecosystem functions, which adds to the coarse mosaic shaped by the nurses (Figure 1). We aimed to assess whether facilitated plants exert positive effects on climatic and edaphic stress, soil fertility and microbial productivity that add to the shifts promoted by the nurse plants. Furthermore, in order to achieve a mechanistic comprehension of these plant–soil feedbacks, we linked the shifts described to: (a) the amount of plant litter and root biomass and (b) the functional diversity of the facilitated community using a combination of ten above- and below-ground traits. As we assume that many other (unmeasured) functional traits could be relevant for ecosystem functioning, we also used phylogenetic diversity as a reasonable proxy of the overall functional diversity (Cadotte, Cavender-Bares, Tilman, & Oakley, 2009). Our additive approach can help better linking positive plant–plant interactions with microbially mediated soil ecosystem functions that are key pieces in community structure and ecosystem dynamics (Wardle et al., 2004). Such an approach may also help discern between diversity and mass effects to mechanistically explain how facilitation drives ecosystem functions. Our study may eventually result in a more comprehensible and profound inclusion of facilitation into the ecological theory (Bruno, Stachowicz, & Bertness, 2003).

2 | MATERIALS AND METHODS

2.1 | Study site and species

The study site is located in the Cartagena-La Unión Mining District (SE Spain; 30 S 689151 E, 4164433 N), which ranges 5,000 ha. of a coastal mountain range where metamorphic nappes alternate with limestones and igneous rocks. Climate is semi-arid Mediterranean
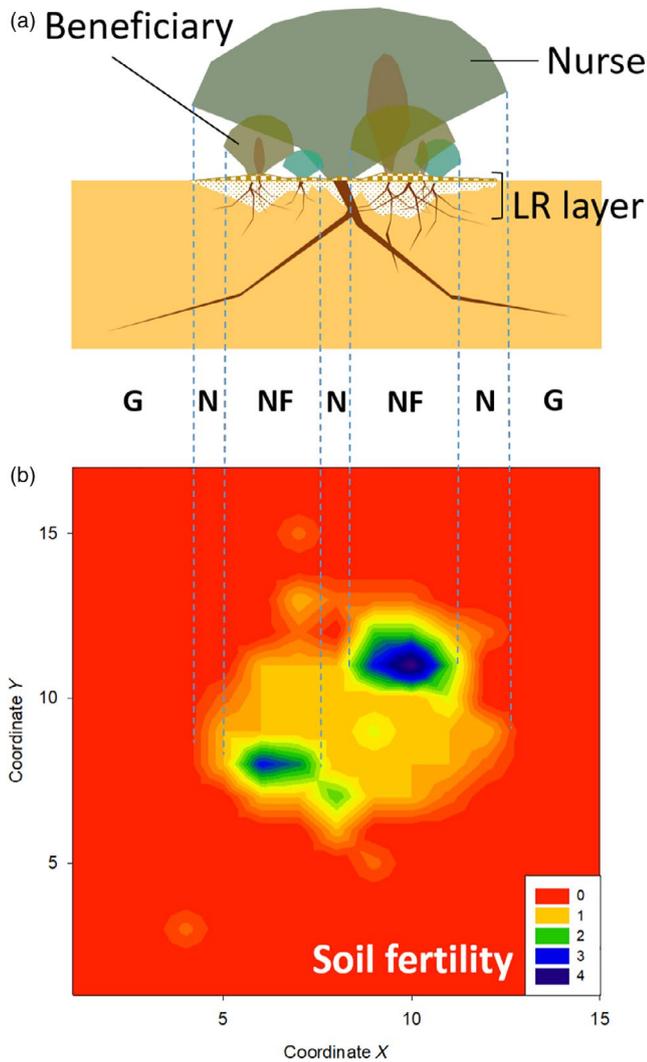
FIGURE 1 Schematic model to integrate the role of plant–plant interactions on micro-scale changes in soil ecosystem functions in facilitation-driven ecosystems. (a) Side view showing above- and below-ground plant structure and (b) vertical view of topsoil fertility for a hypothetical plant patch and the surrounding bare soil. LR layer is the leaf litter (above-ground) plus the main rhizodeposits layer (below-ground) beneath the patch canopy. Dashed vertical blue lines are the projections of the plant canopy on the soil surface. The three microsites studied according to the canopy structure are depicted: G = gap; N = beneath the nurse canopy; NF = beneath facilitated plants below the nurse canopy. Red to deep blue colours indicate growing levels of fertility in (b)

tailings, and shape facilitation-driven communities (Navarro-Cano et al., 2018).

We selected three mine tailings that were active from the 1960s to the 1980s, which are now covered by patchy plant communities with c. 20% plant cover and dominated by different nurse species (Figure S1): *Pinus halepensis* (tree), *Osyris lanceolata* (shrub) and *Atriplex halimus* (shrub). These species are early- (*P. halepensis* and *A. halimus*) or late-colonizers (*O. lanceolata*) of disturbed semi-arid Mediterranean ecosystems. Moreover, *A. halimus* has a C4 metabolism and is able to grow on unflooded saline soils. These species colonized the polluted barren tailings around 1999 (*P. halepensis*), 1986 (*O. lanceolata*) and 2001 (*A. halimus*). Their ability to facilitate second species in the same tailings was verified by Navarro-Cano et al. (2018). The barren substrates of the three tailings show total organic carbon contents <0.5% and high concentrations of As, Cd, Cu, Pb and Zn (Table S1), which are highly above the regional thresholds (Conesa & Schulin, 2010).

2.2 | Experimental design and sampling

In spring 2016, we randomly selected five mature nurse plants among those with the largest canopy diameters in each tailing. We took canopy diameter as a surrogate of age. Average (±*SD*) diameters were 431 ± 148 cm for *P. halepensis*, 499 ± 187 cm for *O. lanceolata* and 372 ± 68 cm for *A. halimus*. We defined three microsites for each plant, namely: Gap (G); Nurse (N) and Nurse + Facilitated (NF). G corresponds to the barren soil located in the open area adjacent to the nurse at a distance equal to the nurse diameter. N and NF are two microsites beneath the nurse canopy. N is the space that is not shared with any facilitated plant species, while NF is shared with at least one facilitated species (Figure 1).

Plant litter and topsoil samples (0–5 cm) were independently collected in each microsite. N samples were taken at a distance half of the nurse radius. NF samples were collected beneath the canopy of facilitated plants placed roughly half of the nurse radius. G samples were taken out of the nurse canopy at a distance equal to the nurse radius. Four 10 × 10 cm quadrat subsamples were collected per microsite and nurse plant. Subsamples were distributed in the four cardinal points of the area occupied by each nurse, and similarly in its adjacent gap. By collecting soil in the cardinal points, we aimed to capture microenvironmental heterogeneity and avoid biasing our sampling towards enriched or impoverished spots. Subsamples were bulked into single composite samples, making one litter sample and one soil sample per microsite and nurse individual (*n* = 5 L samples and five soil samples per microsite and nurse species). Thus, we collected a total of 45 L and 45 soil samples (3 microsites × 3 nurses × 5 replicates). Samples were refrigerated and transported to the laboratory.

2.3 | Plant litter and soil analyses

Litter samples collected from the soil surface were oven-dried at 65°C for 48 hr and weighed to estimate the litter dry weight. Soil

with 17.9°C mean annual temperature, 316.3 and 762.2 mm mean annual precipitation and evapotranspiration respectively. The area includes ores of iron, lead and zinc among other metals, which have been exploited for over 2,000 years until 1991 (Navarro-Cano et al., 2018). Eighty-nine mine tailings generated from the refining process show substrates with high metal and metaloid concentrations, high electrical conductivity, negligible organic matter and occassionally acidic pH, which hamper plant recolonization and restoration (Conesa & Schulin, 2010). Nowadays, stress-tolerant plants from the surrounding natural areas are colonizing the abandoned mine

samples were sieved through a 1 mm mesh to separate roots or finely broken litter and soil, thus avoiding an artificial overestimation of organic C and nutrients in the mineral soil (Pansu & Gautheyrou, 2007). Finely broken litter obtained from the topsoil layer was treated as surface litter samples and total litter biomass calculated as the sum of both litter components. To estimate the root biomass, we manually separated all roots and dried them as above (although thick roots required longer drying times until weight stabilized).

Soil samples were stored at 4°C until analysed using standard procedures (see details in Navarro-Cano et al., 2015). We measured variables informing on soil fertility, soil microbial productivity, reduction in climatic and edaphic stress, which play an important role as ecosystem functions (sensu Hooper et al., 2005). Variables informing on soil fertility were Total Organic Carbon (TOC), Total Nitrogen (TN), P, K and Gravimetric Humidity (GH). Climatic stress was analysed through the surface soil temperature (T) and radiation (Rad). Edaphic stress was estimated by measuring total As, Cd, Cu, Pb, Zn, pH and electrical conductivity (EC). High T and Rad are limiting factors for many physiological processes, whereas high heavy metal concentrations and salinity, or low pH in soils might have toxic effects on organisms as they interfere with metabolic processes related to nutrient acquisition (Walker & del Moral, 2003). Soil microbial productivity was estimated through variables indicative of total microbial activity (microbial basal respiration, BR), carbon, phosphorus and nitrogen cycling (β-glucosidase, alkaline phosphatase and urease activities respectively).

2.4 | Functional and phylogenetic diversity of facilitated plant communities

We calculated the functional diversity of the facilitated community growing beneath each nurse individual based on ten above- and below-ground traits. This includes seven morphological traits (life form, leaf area and weight, root depth, length, laterality and weight) and three eco-physiological traits (halophytism, root C and N concentrations), whose specific role is summarized in Table S2. Trait values were either obtained from five adult plants per species that were dug up and collected in the tailings or from the literature (Table S2). We estimated the functional distance among facilitated species using the Gower distance of all traits, which accounts for categorical and continuous variables, with the *daisy* function in the *cluster* package for R (Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2018).

The Standardized Effect Size of the Mean Functional Diversity (SES_{MFD}) was estimated as the abundance-weighted mean pairwise functional distances between co-occurring facilitated species standardized against a null model, as follows:

$$SES_{MFD} = \frac{MFD_{obs} - \text{mean}\left(MFD_{null}\right)}{\text{sd}\left(MFD_{null}\right)}$$

where MFD_{obs} refers to the Mean Functional Distance observed among the species coexisting underneath the same nurse individual and MFD_{null} refers to each of the 999 values of MFD obtained after randomly reshuffling distance matrix labels (across all taxa included in distance matrix). This standardization procedure allowed us to compare the mean functional diversities across treatments, despite the fact that the plots had different numbers of species and individuals. Abundance weighting allowed taking into account the large effect of some trait expressions from the abundant species (Ochoa-Hueso et al., 2018). We used as a null model the independent-swap algorithm that randomizes the community data matrix keeping species occurrence frequency and sample species richness (Gotelli, 2000; Kembel et al., 2010). This algorithm has been shown to be adequate to test the phylogenetic structure of ecological communities under a wide range of scenarios (Hardy, 2008; Kembel, 2009).

We estimated the phylogenetic distances among the facilitated plants growing beneath each nurse by reconstructing a phylogenetic tree based on a checklist of the local flora (authors' unpublished data) with the program Phylomatic, implemented in PHYLOCOM v4.2 (Webb, Ackerly, & Kembel, 2008) and BEAST 1.5.4 (Drummond & Rambaut, 2007; for a similar procedure see Navarro-Cano et al., 2014). The topology of the community phylogeny was assembled with Phylomatic by matching the species family names in the local flora with those contained in a backbone phylogeny, which is the megatree based on the Angiosperm Phylogeny Group (APGIII, 2009). This tree contained 55 polytomies that were randomly resolved while dating the tree. Chronological information of to date nodes in the resulting tree was obtained from Wikström, Savolainen, and Chase (2001). Then, we estimated the age of the undated nodes by fitting a birth-death model with uniform priors for both the mean growth rate and relative death rate parameters, with the help of BEAST (Drummond & Rambaut, 2007) and the PolytomyResolver script (Kuhn, Mooers, & Thomas, 2011). Markov Chain Monte Carlo analyses were run for 10^6 iterations and trees were sampled every 10^3 iterations. A 25% burn-in was discarded and the maximum clade credibility tree recovered with the help of the TREEANNOTATOR v1.5.4 software (Drummond & Rambaut, 2007). From this phylogenetic tree, we constructed a phylogenetic distance matrix among all the facilitated species growing underneath each nurse individual and calculated a standardized phylogenetic diversity index (SES_{MPD}), following the same procedure as for functional diversity. The *picante* package for R (Kembel et al., 2010) was used to calculate functional and phylogenetic diversities.

2.5 | Statistical analyses

2.5.1 | Testing the existence of microsite effects

We performed four principal component analyses (PCAs) to reduce 18 soil variables to single variables (PCs). First, we reduced T and Rad in a single PCA. PC1 explained 89% of the total variance and was negatively correlated with both variables (Table S3, Figure S2), thus we interpreted it as a gradient of decreasing microclimatic stress. Second, PCA of As, Cd, Cu, Pb, Zn contents, pH and EC generated a PC1 (37%) that negatively correlated with all variables except pH, and was interpreted as a gradient of decreasing soil metal concentration. PC2 (22%) had strong negative correlations with Cd, Zn and pH, and a positive correlation with EC (Table S3, Figure S2). Third, TOC, TN, P, K

and GH were reduced in a single PCA. PC1 (57%) positively correlated with all variables and was interpreted as gradient of increasing soil fertility. PC2 (19%) positively correlated with GH and negatively with P and K (Table S3, Figure S2). Four, we reduced BR together with β-glucosidase, phosphatase and urease activities. PC1 (52%) positively correlated with the levels of BR, C and P cycling, while PC2 (25%) increased with decreasing N cycling (Table S3 and Figure S2). We used PC1 and PC2 of all PCAs as single response variables in the linear mixed effects models described below.

We assessed whether the microsite shaped by the facilitated community provides the soil with extra organic supplies (i.e. litter and root biomass), and further exerts positive effects on soil variables that add to the shifts promoted by the nurse plants. To do so, we used linear mixed effects models fit by maximizing the restricted log-likelihood (GLMM). For each GLMM, the random effects were set on the intercept in a random intercept model. These models had a fixed part (with the intercept and the coefficient of the explanatory variables as parameters) and a random part (with the variances as estimated parameters). First, we ran four models in which the dependent variables were the first two principal components of each of the four PCAs performed on soil variables associated with (a) reduction in climatic stress, (b) reduction in edaphic stress; (c) soil fertility and (d) soil microbial productivity (see PCA description above). We used the "microsite" as a fixed factor with three levels (G, N and NF). Differences in the values of the dependent variable between these three levels were tested through paired contrasts. We included two random factors in the models: (a) the "nurse species" (*P. halepensis*, *A. halimus*, *O. lanceolata*) to account for site effects, as nurses grow on different tailings; and (b) the "nurse individual" (nested within the "nurse species") to account for the lack of independence of the microsites sampled to characterize each nurse individual. The random effects were set on the intercept of the model to allow each nurse species or individual to have its own intercept, thus capturing possible species (or individual)-specific effects. The dependent variables were log-transformed in all models to stabilize the variance. Second, to further scrutinize the effect of the microsites on the four ecosystem functions studied, we performed models with the same structure as above, but taking every soil parameter individually as a dependent variable. Third, we assessed in two separate models whether (log-transformed) litter and root biomass differed across microsites, including two random factors as above. Finally, we used litter and root biomass as predictors of the reduction in climatic stress, reduction in edaphic stress, soil fertility and microbial productivity in four GLMMs with the same random factors. We log-transformed the dependent variables in all GLMMs and the independent variables in the model predicting the reduction in climatic stress to account for nonlinear relationships.

2.5.2 | Testing biodiversity and biomass effects of beneficiary species on ecosystem functions

We evaluated which mechanisms – biodiversity and/or biomass effects – underlie the hypothesized additive effects of nurse and facilitated species on soil ecosystem functions. To do so, we used biodiversity and biomass variables to explain the increment in NF compared to N in two variables that are widely used proxies of soil fertility (TOC) and microbial productivity (BR). TOC is a measure of the total pool of oxidizable soil carbon available for heterotrophic respiration, and is the key property influencing physical and chemical soil fertility. BR quantifies the potential rate of heterotrophic respiration and is a general indicator of soil microbial activity (Nannipieri, Grego, & Ceccanti, 1990). We ran two linear mixed effects models in which we used as dependent variables the increments of either TOC or BR in microsite NF compared to N. The increments were calculated as the value of each variable in NF minus the value of the same variable in N, divided by the value in NF. In both models, we included four predictive variables: the increments of all functional diversity, phylogenetic diversity, litter biomass and root biomass as predictive variables. We also included the nurse species as a random factor.

Finally, we explored the existence of biodiversity and/or a biomass effects on ecosystem functions within the NF microsite, to test their predictive power on the variability generated by the facilitated community. We ran four linear mixed effects models with the NF data only, including functional diversity + phylogenetic diversity + litter biomass + root biomass as predictive variables. We also included the nurse species as a random factor, and the reduction in climatic stress, reduction in edaphic stress, soil fertility and microbial productivity as response variables. All models were performed with the *lme* function in the package *nlme* of ʀ v3.1.3 (R Core Team, 2015).

3 | RESULTS

3.1 | Testing the existence of microsite effects

Climatic stress significantly decreased from gaps (G) to nurses (N), with no significant differences between N and nurse + facilitated (NF) microsites (Figure 2). Edaphic stress did not show significant changes among the microsites (Figure 2). Both soil fertility and microbial productivity increased from G to N and from N to NF, indicating an additive effect of facilitated communities on the nurse effect (Figure 2). In all models, random effects were significant for the nurse species. Nurse individual nested within species was not significant in any case, but for edaphic stress.

Considering individually the parameters used to evaluate climatic stress, only radiation showed a significant pattern G > N > NF (Figure S3), whereas temperature decreased from G to N, with no significant differences between N and NF. The abiotic variables used to estimate edaphic stress did not show significant differences excepting electrical conductivity, which had higher EC in G than in N and NF (Figure S3). Seven out of nine variables that we used to estimate soil fertility (TOC, TN, K and GH) and microbial productivity (BR, C and P cycling activities) showed individually an increase from G to NF. We found additive effects from N to NF in TOC, K concentration, microbial basal respiration, as well as carbon and phosphorus cycling activities (Figure S4).
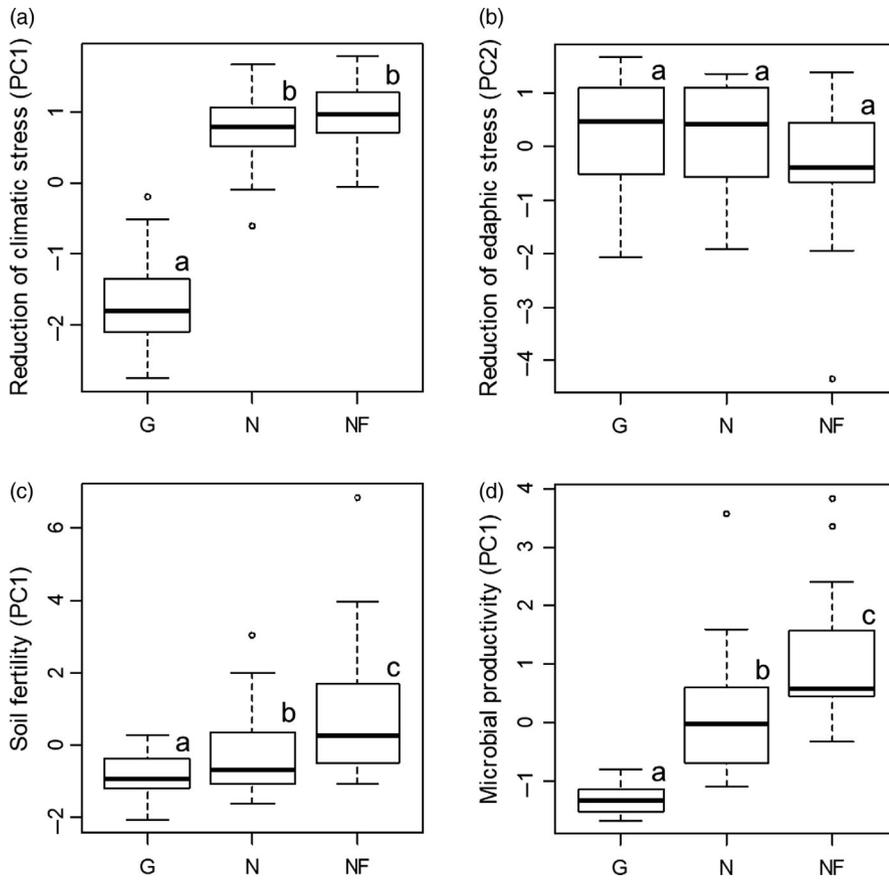
(a)
(b)

FIGURE 2 Effects of the microsite (G, N or NF) on the reduction in climatic stress (a), reduction in edaphic stress (b), soil fertility (c) and microbial productivity (d) beneath the three nurse species. Reduction in climatic stress was the first component (PC1) of the PCA to reduce T and Rad. Reduction in edaphic stress was the PC2 of the PCA to reduce As, Cd, Cu, Pb, Zn, pH and EC. Soil fertility was defined as the PC1 of the PCA used to reduce TOC, N, P, K and GH. Microbial productivity was the PC1 of the PCA to reduce BR, β-glucosidase, alkaline phosphatase and urease activities. See the text and Figure S2 for interpretation of each PC. Different letters indicate significant differences across microsites (GLMM, $p < 0.05$). Variables were log-transformed prior to analyses

Leaf litter biomass significantly increased from G to N and from N to NF (Figure 3), suggesting an additive contribution of the facilitated community to the nurse's organic inputs. Root biomass was larger in N and NF than G, with no significant differences between N and NF. Litter and root biomass were not correlated (*Pearson r* = 0.07, *p* = 0.64). Considering jointly litter biomass and root biomass as explanatory variables of ecosystem functions, plots with high values of litter biomass significantly decreased PC1 climatic stress (Figure S2a; estimate ± *SE* = 0.246 ± 0.032; t_{28} = 7.7, *p* < 0.001) but increased PC2 edaphic stress (Figure S2b; −0.001 ± 0.001; t_{28} = −2.1, *p* < 0.05). This observation indicates that more abundant litter layers reduced the radiation that reached the soil surface, as well as temperature and EC, but increased pH, Cd and Zn concentrations. Moreover, larger amounts of

litter translated into more fertile soils (estimate ± *SE* = 0.003 ± 0.001; t_{28} = 4.2, *p* < 0.001), which had higher microbial productivity (0.003 ± 0.001; t_{28} = 9.3, *p* < 0.001). Root biomass also exerted a significant positive effect on microbial productivity (0.02 ± 0.01, t_{28} = 2.59, *p* < 0.05). The individual relationships among litter biomass, root biomass and ecosystem functions are depicted in Figures S5 and S6.

3.2 | Testing biodiversity and biomass effects of beneficiary species on ecosystem functions

We tested the existence of plant biodiversity effects (functional diversity and phylogenetic diversity) and biomass effects (litter and root biomass) on soil ecosystem functions. The increment in
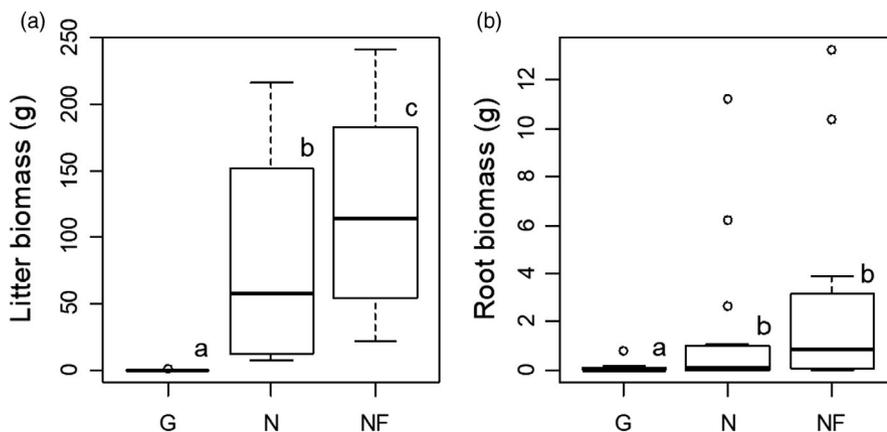
(a)
(b)

FIGURE 3 Effects of the microsite (G, N or NF) on the amount of leaf litter (a) and root biomass (b) in the three mine tailings. Different letters indicate significant differences across microsites (GLMM, *p* < 0.05). Variables were log-transformed prior to analyses

litter biomass in NF compared to N was the only predictor that significantly explained the increments of both TOC (0.46 ± 0.16, t_8 = 2.87, $p < 0.05$) and BR (log-transformed; 1.80 ± 0.72, t_8 = 2.50, $p < 0.05$).

Finally, we analysed the variation within the NF microsite only. A positive relationship between functional and phylogenetic diversity was observed (*Pearson r* = 0.60; t_{13} = 2.72, $p = 0.017$). The analyses to jointly test the biodiversity and biomass effects on the four ecosystem functions within NF are given in Table 1. The reduction in edaphic stress was more pronounced beneath phylogenetically diverse facilitated communities due to a drop of the As, Pb, Cu and Cd contents, whereas root biomass had the opposite effect (Figure S2). The largest increases in soil fertility, mainly through rises in TOC, TN, K and humidity, occurred underneath functionally diverse facilitated neighbourhoods (Figure S2). Soil microbial productivity was, however, promoted within NF at lower levels of root biomass, mostly through increased BR, carbon and phosphorus cycling (Figure S2).

4 | DISCUSSION

Facilitation-driven ecosystems are often conceived as being fully dependent on the dynamics of nurse plants, which improve the abiotic conditions at the microhabitat scale and allow the secondary assembly of a community of facilitated species. Here, we redirect the attention to the hardly assessed role of the facilitated community to improve fine-scale below-ground ecosystem functions. Our results indicate that the nurse influence goes beyond the mere assembly of a facilitated community and prompts microbial activity, thus fostering ecosystem functions through plant–microbe feedbacks. This effect is nurse-specific since the nurse identity had a significant effect in all soil functions analysed, as expected based on the differential above- and below-ground functional traits of the studied nurses (Navarro-Cano et al., 2018). Most importantly, we found evidence of additive effects of nurse and facilitated species on all the reduction in climatic stress, and increase in fertility and microbial productivity in extremely degraded soils.

TABLE 1 Effects of plant diversity and biomass of facilitated communities on the reduction in climatic stress, reduction in edaphic stress, soil fertility and microbial productivity in the studied mine tailings

Response variable	Log reduction in climatic stress (PC1)			
Predictor	**Value**	**SE**	**t**	**p**
Functional diversity	0.046	0.271	0.170	0.869
Phylogenetic diversity	0.125	0.619	0.201	0.845
Litter biomass	0.004	0.004	1.143	0.286
Root biomass	−0.088	0.071	−1.233	0.253
Response variable	**Log reduction in edaphic stress (PC1)**			
Predictor	**Value**	**SE**	**t**	**p**
Functional diversity	−0.089	0.082	−1.094	0.306
Phylogenetic diversity	0.537	0.187	2.877	**0.021**
Litter biomass	−0.001	0.001	−0.037	0.971
Root biomass	−0.070	0.022	−3.270	**0.011**
Response variable	**Log soil fertility (PC1)**			
Predictor	**Value**	**SE**	**t**	**p**
Functional diversity	0.557	0.222	2.513	**0.036**
Phylogenetic diversity	−0.402	0.631	−0.637	0.542
Litter biomass	−0.006	0.004	−1.363	0.210
Root biomass	0.058	0.079	0.739	0.481
Response variable	**Log soil microbial productivity (PC1)**			
Predictor	**Value**	**SE**	**t**	**p**
Functional diversity	0.086	0.074	1.162	0.279
Phylogenetic diversity	0.122	0.206	0.592	0.570
Litter biomass	0.002	0.001	1.413	0.195
Root biomass	−0.070	0.026	−2.738	**0.026**

Note: Functional diversity + phylogenetic diversity + biomass litter + biomass roots were jointly used as predictors in four GLMMs testing effects on the four above mentioned response variables. These response variables are respectively the first principal components of four PCAs that reduce groups of variables to orthogonal variables (see the text, Figure S2 and Table S3 for interpretation of each PC1. Significant p-values ($p < 0.05$) in bold. Dependent variables were log-transformed.

The main environmental change produced by nurse plants is the reduction in abiotic stress in terms of temperature and radiation (Callaway, 2007). We also detected this common pattern at the microsite level. More interestingly, we demonstrated that such a reduction in climatic stress, at least regarding radiation, was potentiated within the facilitated microsites beneath the nurse canopy (NF). Having a special photosynthetic metabolism (C4 or CAM) to cope with abiotic stress, as is the case of the nurse *A. halimus* and some of our facilitated species (e.g. *Salsola genistoides*, *Fagonia cretica* or *Hyparrhenia sinaica*), might also increase water use efficiency at high temperatures (Pyankov, Ziegler, Akhani, Deigele, & Lüttge, 2010). The establishment of plants with these abilities might increase the subcanopy cover beneath the nurse, thus contributing to the observed reduction in radiation. This response shows a saturative relationship for the effect of litter biomass on the reduction in climatic stress (Figure S5), likely because radiation is mostly filtered by the nurse canopy.

The responses of edaphic stress, contrarily to those of climatic stress, were not so straightforward. The microsite determined by facilitated communities beneath the nurses reduced salinity compared to the gaps. However, facilitated microsites induced just slight effects on edaphic stress variables compared to the nurse microsite. In metal mining ecosystems, as ours, plant species able to cope with high soil concentrations of toxic elements (heavy metals, metalloids, salts, etc.) are often reported (Parraga-Aguado, González-Alcaraz, Álvarez-Rogel, & Conesa, 2014). Metal bioaccumulation both above- and below-ground could help explain the increase in metals in the topsoil layer through litter decomposition and rhizodeposition (van der Ent, Baker, Reeves, Pollard, & Schat, 2013). In contrast to the accumulators, other species are able to exclude high metal levels, thus developing litter layers with lower levels of stressors. Here, plant species show low abilities to extract, accumulate, or contrarily, exclude trace elements or salts from soils. Working in the same study system, Parraga-Aguado et al. (2014) found very contrasted As concentrations, ranging from 1.8 to 31.6 mg/kg in leaves or shoots of species that grow as beneficiaries of our nurses (*Dittrichia viscosa*, *Helichrysum decumbens*, *Piptatherum miliaceum* and *Pistacia lentiscus*). Similar patterns were described for Cd and Pb. These data suggest that the specific composition of the facilitated community could determine contrasted abiotic properties associated with edaphic stress. Our analyses aimed at splitting the biodiversity and biomass effects of facilitated communities within the NF microsite indicate that phylogenetically diverse neighbourhoods drop some metal concentrations. Such a pattern is counterbalanced by high levels of root biomass, which exerted the opposite effect. These results suggest that a diverse set of plant traits that are evolutionarily conserved can shift soil concentration of key metal stressors. Nevertheless, these traits seem to be missing within our studied set, since we failed to relate functional diversity to edaphic stress.

Multispecific plant patches triggered by nurse plants have been usually described as "islands of fertility" in facilitation-driven ecosystems (Callaway, 2007; Ochoa-Hueso et al., 2018). We found

here that nurse plants increased soil fertility, as expected. Most importantly, such an improvement was reinforced when the canopy of the nurse and its facilitated species juxtaposed, where we detected the highest levels of litter and root biomass. The increment in litter biomass beneath the canopy of nurse and facilitated species, compared to the nurse alone, significantly explained the increment in soil organic carbon. This result suggests that the mass-ratio effect (Grime, 1998) is a fundamental mechanism by which facilitated species enhance soil fertility at the microsite scale. It could be alternatively interpreted that facilitated plants establish on fertile and less-stressful spots within a heterogeneous soil beneath the nurse canopy. Indeed, El-Bana, Nijs, and Kockelbergh (2002) reported the existence of enriched spots beneath *Retama raetam* in the sandy Nebkhas associated with mound formation through airborne particle trapping. Mounds beneath our nurses were <0.45 m average height compared to the average 0.86 m of those in El-Bana et al. (2002). In addition, our sampling was designed to avoid possible edge effects and to minimize the biased collection of fertile and less-stressful spots. It can be reasonably argued that a manipulative experiment controlling species establishment to spatially separate nurse and facilitated species would be necessary to formally demonstrate their individual effects on soil properties. However, facilitated species are, by definition, rare out of the vegetated patches in facilitation-driven ecosystems, and so, the results of such an experiment would not correspond with realistic patterns in nature.

Soil fertility promotes microbial productivity, in terms of mineralization rates and enzymatic hydrolysis of organic matter (Navarro-Cano et al., 2015). Leaf litter and root chemistry are species-specific traits that determine decomposition rates (Gallardo & Merino, 1993; Jo, Fridley, & Frank, 2016). Thus, different facilitated plant species will deliver distinct substances to the soil that will decompose at unlike rates. We found that microbial productivity increases from open spaces to soils underneath adjacent nurses, and further to the microsite defined by nurses and their beneficiaries. Similar to soil organic carbon, the increment in total heterotrophic respiration from N to NF was attributed to a mass effect through increased litter deposition beyond the facilitated community. This result suggests that the organic matter delivered by facilitated plants to the soil in the form of leaf litter, which is the main organic linkage among plant and microbial communities (De Deyn & Van der Putten, 2005), provides additional resources for soil microbes that are relevant enough so as to impact decomposition and nutrient cycling.

On top of mass effects, which drove the synergistic action of nurses and their beneficiary species, we detected that both diversity and mass effects explain the spatial variation in soil fertility and microbial productivity within NF. Diversity and mass effects, however, did not act in a concerted manner. The functional diversity of facilitated species in NF showed a positive relationship with soil fertility, suggesting that facilitated neighbourhoods with complementary traits yield more fertile microsites. Phenotypically dissimilar communities can potentially supply more assorted organics to the

soil through leaf litter and rhizodeposition (Eisenhauer et al., 2017; Spehn, Joshi, Schmid, Alphei, & Körner, 2000; Steinauer et al., 2016). Moreover, functionally complementary root systems (e.g. spreading at different depths) can reduce the interspecific competition due to a shared efficiency in the use of resources, thus promoting a biodiversity effect (Blignaut & Milton, 2005). It could be subsequently expected that the high variety of organics delivered by a diverse plant community could trigger microbial productivity through the more efficient resource use by a large array of soil microbial decomposers with complementary niches (Steinauer et al., 2016). Such a complementarity effect has been supported by manipulative inter-trophic experiments (Naeem, Thompson, Lawler, Lawton, & Woodfin, 1995; Zak et al., 2003). We detected, however, no diversity effect on the variation in soil microbial productivity within NF, but a negative below-ground mass effect. Specifically, microbial productivity was promoted beneath NF at low levels of root biomass, which might be the result of the intense competition between roots and soil microorganisms for mineral nutrients in depleted soils (Wei et al., 2017; Zhu, Riley, & Tang, 2017). The fact that a mass-ratio effect drives soil shifts at the patch scale (N vs. NF), whereas both mass and diversity effects explain soil variability within the facilitated microsite (NF) could seem contradictory. However, both results are compatible because they inform on different processes. A mass-ratio effect comparing NF versus N highlights the amount of litter that the facilitated community adds to the vegetated patch compared to the nurse litter alone. However, the positive role of phylogenetic and functional diversity within the NF microsite indicates the relevance of species and trait composition of facilitated plants as a source of variation of soil conditions.

Our study adds to the few surveys that jointly analyse biomass and biodiversity effects of plants on ecosystem functions (as reviewed by Dias et al., 2013), and suggests that both mechanisms operate (sometimes in opposite ways) to explain plant–soil feedbacks in facilitation-driven ecosystems. Our results depict a facilitation-driven cascade triggered by nurse plants that initially benefits second plant species beneath their canopy. Moreover, we show that both nurses and their beneficiaries synergistically impact below-ground communities of microbial decomposers and nutrient cyclers. In turn, microbial communities return bottom-up fluxes of matter and energy that promote the ecosystem dynamics through complex inter-trophic feedbacks (Scherber et al., 2010; Wardle et al., 2004). These findings shift the conception of the community of facilitated plant species from mere recipients of the positive influence of the nurses, to relevant drivers of ecosystem functions. The micro-scale top-down effects that we describe here can be directly applied to ecological restoration programs, which can make use of facilitative interactions between plant species (Gómez-Aparicio, 2009). We emphasize that planting assemblages of facilitation-driven species following functionally and/or phylogenetically informed models can promote key plant–soil feedbacks. Such an approach might help embarking degraded ecosystems upon a positive trajectory towards increasing resilience to degradation factors (Clewell, Rieger, & Munro, 2005; Navarro-Cano et al., 2018).

AUTHORS' CONTRIBUTIONS

J.A.N.-C. conceived and designed the study; J.A.N.-C., B.H. and M.G. collected and processed data; J.A.N.-C. analysed the data and wrote a draft of the manuscript to which all authors made 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.qd753bg (Navarro-Cano, Horner, Goberna, & Verdú, 2019) and in the Supporting Information.

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