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Plant phylodiversity enhances soil microbial productivity in facilitation-driven communities

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Abstract The classical relationship between biodiversity and ecosystem functioning can be better understood when the phylogenetic component of biodiversity is considered. We linked plant phylodiversity and ecosystem functioning in a water-limited gypsum ecosystem driven by plant facilitation. We tested whether (1) plant facilitation relaxes the abiotic filter imposed by gypsum, allowing the establishment of non-gypsophyte plant species, and consequently increasing plant phylodiversity, and (2) plant phylodiversity influences soil microbial productivity. Our data revealed that the gypsophyte *Ononis tridentata* spatially determines a macrophytic mosaic, ameliorates the microenvironment, and maximizes plant richness and phylodiversity through facilitating non-gypsophyte species. Beyond the direct effect of the nurse plant on soil microbial biomass, activity, and respiration, the analyses suggest a direct effect of plant phylodiversity (MPD) on these general indicators of soil microbial productivity. Plant diversity (Shannon index) neither correlated with the mentioned parameters nor with specific indicators of C, N and P cycling. This is the first report of a relationship between producer phylodiversity and decomposer productivity, which supports phylogenetic diversity as a relevant player of the ecosystem functioning.

Keywords Ecosystem functioning · Microbial biomass · Nurse plant · Phylogenetic diversity · Regeneration niche

Introduction

Linking biodiversity with ecosystem functioning has been traditionally explored by tackling the relationship between plant species richness and plant productivity (Balvanera et al. 2006). This topic has been recently revived to integrate new facets of biodiversity such as genetic and

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phylogenetic diversity (Cadotte et al. 2008, 2009; Srivastava et al. 2012). The measurement of ecosystem functioning has also been broadened to incorporate trophic levels other than producers (Zavaleta et al. 2010), assuming that plants operate on ecosystem productivity via multitrophic feedbacks (Wardle et al. 2004). Among all organisms, the decomposers are the main drivers of the global biogeochemical cycles and energy fluxes (Wardle et al. 2004; Van der Heijden et al. 2008). Thus, soil microbial biomass and activity have long been used as indicators of ecosystem functioning (Nannipieri et al. 1990; Sinsabaugh 1994; Wardle and Ghani 1995; Zak et al. 2003; Goberna et al. 2012). These indicators inform on: (1) general microbial activity, such as soil ATP content and microbial respiration, and (2) specific processes, such as enzymatic activities involved in main steps of the nutrient cycles (e.g., β-glucosidases and ureases, which break down C and N organic substances, respectively). However, surveys assessing the link between plant biodiversity and soil microbial productivity are still a minority (Hooper et al. 2005; Van der Heijden et al. 2008). Some authors have observed a positive correlation between plant richness and both single microbial parameters (Zak et al. 2003; Balvanera et al. 2006), and an index combining nutrient pools and microbial variables (Maestre et al. 2012). The influence of biodiversity on productivity has been primarily attributed to a higher efficiency in resource usage owing to increased niche complementarity (Hooper et al. 2005). Nevertheless, it remains unexplored whether plant phylodiversity, as an integrative measure of plant functional complementarity (Webb et al. 2002), can shed light on the relationship between biodiversity and decomposer-based ecosystem functioning.

Plant facilitation provides a convenient scenario to test the relative contribution of different facets of biodiversity to ecosystem functioning, since facilitation increases both plant species diversity (Brooker et al. 2008) and phylogenetic diversity (Valiente-Banuet and Verdú 2007). Facilitation assembles ecological communities through the opening of microscale spatial windows for the establishment of plant species (Brooker et al. 2008). One of the most widely studied types of facilitative interactions in plants refers to the nursing effect. The nurse species relaxes the environmental stress expanding the microsites that fulfill the regeneration niche requirements of the facilitated species (Valiente-Banuet et al. 2006), this niche determining the main demographic bottleneck for plant population dynamics (Harper 1977). A common characteristic of ecosystems governed by facilitation is the formation of discrete multispecific vegetation patches surrounded by a low-cover matrix or open space. The spatial heterogeneity derived from this two-phase mosaic determines water and soil nutrient redistribution from gaps to patches (Aguiar and Sala 1999). This positive feedback promotes plant abundance and biomass in the patches (Aguiar and Sala 1999). However, this starting beneficial nurse effect can turn into competitive exclusion due to shifts in the ontogenetic niche of interacting species (Valiente-Banuet and Verdú 2008). Current research suggests that species coexistence in the patches can be determined by the phylogenetic relationships between all community members in such a way that co-occurrence is maximized under phylogenetically diverse neighborhoods (Webb et al. 2006; Castillo et al. 2010). This responds to the fact that distantly related taxa are generally more dissimilar ecologically than closely related taxa, since phenotypic traits tend to be evolutionarily conserved (Pausas and Verdú 2010). Hence, the net effects of facilitative and competitive interactions in patchy ecosystems can be successfully assessed by using the mean phylogenetic distance across species as a simple and integrative index (Valiente-Banuet and Verdú 2008; Soliveres et al. 2012).

Here, we explore the linkages between plant biodiversity and ecosystem functioning, in terms of soil microbial productivity, in a community organized by facilitation in a stressful habitat of gypsum soils dominated by *Ononis tridentata* L. Gypsum soils occupy <1 % of the terrestrial ecosystems but their stressful physical–chemical properties added to their dryland-associated geographic distribution act as a double abiotic constraint promoting plant speciation and exclusive vegetation communities (Parsons 1976). Gypsum filters plant communities mainly through: (1) its chemical properties, due both to the toxic concentration of sulphate ions and the ion imbalance caused by the excess sulfur and calcium that saturate the exchange positions resulting in nutrient limitation (Merlo et al. 2011); and (2) its physical properties, mostly the formation of sealing crusts that limit seedling establishment and root penetration (Pueyo et al. 2011). Moreover, water stress owing to the climatic conditions limits seed germination in gypsum soils (Escudero et al. 1997). *O. tridentata* is a strict gypsophyte legume associated with N-fixing rhizobial bacteria (Rincón et al. 2008) that usually recruits on bare gypsum soils creating shrubby patches in arid- to semi-arid Mediterranean areas from the Iberian Peninsula (Mota et al. 2009). *O. tridentata*-dominated patches ameliorate thermal and water stress and constitute both resource islands and hotspots of microbial activity (Goberna et al. 2007). All these traits suggest that *O. tridentata* is a nurse plant able to act as an ecosystem engineer in these stressful environments.

We speculate that facilitation via nursing relaxes the abiotic filter imposed by gypsum, allowing the establishment of functionally complementary (i.e. non-gypsophyte) plant species. This, consequently, increases plant diversity and/or phylodiversity, which may ultimately influence soil microbial productivity. We sequentially tested whether: (1) facilitation expands the regeneration niche of non-gypsophyte

plant species promoting their abundance; (2) facilitation increases plant species diversity and phylogenetic diversity; (3) plant diversity and/or phylodiversity correlate with soil microbial productivity; and (4) a direct effect of plant biodiversity on soil microbial productivity exists, beyond the nurse-mediated effect on the soil properties. Based on the key role that plant attributes play in the producer–decomposer linkages (Wardle et al. 2004; van der Putten et al. 2007), we discuss how plant facilitation can have a synergistic effect on ecosystem functioning due to the amelioration of the stressful microenvironmental conditions and the promotion of plant diversity.

Materials and methods

Study area and characterization of patches and gaps

The study site was located in Serra de Crevillent (Alacant, SE Spain; UTM 30N 689062, 4238201). Climate is semi-arid Mediterranean with a mean annual rainfall of 240 mm in <40 days and mean annual temperature around 20 °C. Hills are steeply sloping (40 %) and are located at an average 350 m a.s.l. Soils are Typic Xerorthents developed on gypsum and covered with a patchy shrub-steppe dominated by the gypsophyte *O. tridentata*. Plant patches cover 25 % of the landscape. Inter-patch areas are mostly covered by sealing crusts (Goberna et al. 2007) where only some dwarf shrubs as *Helianthemum squamatum* (L.) Dum. Cours., *Herniaria fruticosa* L. and *Teucrium libanitis* Schreb. are frequent.

The study system was divided in two environments. "Patches" were defined as groups of plants growing underneath the canopy of an *O. tridentata* individual. On May 2010, 15 patches separated by an average distance of 11 m were selected along two parallel transects. Transects were delineated along the slope to capture the soil variability derived from the slope position of the patch. The first transect was located randomly and the second transect was delineated roughly 20 m apart. The area of each patch was estimated by calculating that of the geometric shape bearing the closest resemblance, and averaged 2.4 ± 1.1 m^2 (mean ± SD). "Gaps" were defined as the open space adjacent to each patch, at the same slope position and located 1 m west beyond the vertical projection of the patch canopy. The sampled area and geometric shape of each gap corresponded to that of the adjacent patch.

To analyze the effects of the nurse plant on the microenvironmental conditions, soil samples (0–2 cm) were collected from patches and gaps after removing the litter layer, when present. Five sub-samples (ca. 100 g) were collected randomly from the area of each patch or gap and then bulked into a single composite sample. Soil samples were transported to the laboratory, refrigerated, and immediately sieved through a <1-mm mesh. Soil samples were stored at 4 °C for subsequent analyses. Soil physical and chemical properties were measured using standard procedures, as in Goberna et al. (2012). Plant patches and gaps significantly differed in all soil properties analyzed (except for the nitrate content). Most importantly, plant patches were more fertile and had higher water availability than gaps (Table 1). To discard the possibility that improved conditions under patches were the cause and not the effect of the presence of *O. tridentata,* we randomly sampled soils below the canopy of 10 *O. tridentata* seedlings (average ± SD plant height: 10.1 ± 5.8 cm) and in their neighboring gaps. We found no significant differences between both microsites in any of 27 soil variables measured, including gravimetric humidity, total and organic carbon, and macro- and micro-nutrients (Online Resource Table 1). Altogether, these results clearly indicated that *O. tridentata* establishes on infertile soil and modifies it subsequently.

Table 1 Soil physical and chemical properties in *Ononis tridentata* patches and gaps

Soil property	Patch[a]	Gap[a]	*t* value[b]	*P* value
pH	7.09 ± 0.03	7.30 ± 0.03	−4.3	**<0.001**
Electrical conductivity (dS m^{-1})	3.06 ± 0.06	2.50 ± 0.02	11.6	**<0.001**
Total organic C (g kg^{-1})	93.6 ± 5.1	19.8 ± 0.7	23.6	**<0.001**
Pyrophosphate extractable C (g kg^{-1})	3.2 ± 0.2	0.3 ± 0.1	14.7	**<0.001**
Water-soluble C (mg kg^{-1})	454 ± 47	63.2 ± 3.4	16.0	**<0.001**
Water-soluble carbohydrates (mg kg^{-1})	62.9 ± 5.9	27.2 ± 3.0	5.6	**<0.001**
Carbonates (%)	22.3 ± 0.8	15.1 ± 1.3	6.0	**<0.001**
Total N (g kg^{-1})	6.2 ± 0.4	1.1 ± 0.1	24.7	**<0.001**
Ammonium-N (mg kg^{-1})	26.0 ± 3.8	1.4 ± 0.1	5.9	**<0.001**
Nitrate–N (mg kg^{-1})	10.6 ± 4.6	4.5 ± 0.6	0.5	0.635
Gravimetric humidity (%)	4.2 ± 0.2	1.6 ± 0.1	10.4	**<0.001**

Significant differences between both environments are indicated in bold (paired *t* test; $P < 0.05$)

[a] Average ± SE for $n = 15$. All data are given on an oven-dried weight soil basis

[b] Data were log-transformed prior to statistical analyses

Plant facilitation and regeneration niche expansion

Plant abundance in the patches and gaps were registered using the point contact method. A spiral-shaped transect was delimited in the area of each patch and gap with a tape

measure. Along each transect, 100 evenly distributed points were marked. In each point, a metal stick (3 mm diameter) was projected downwards until it reached the ground at an angle of 90° to the vertical. All the contacts of the vegetation with the stick were recorded by species, regardless of the number of hits. In cases of no contacts with live vegetation, bare ground was registered.

We quantitatively estimated the facilitation by *O. tridentata* for each species by calculating the relative interaction intensity (RII; Armas et al. 2004):

$$\mathrm{RII} = \frac{B_\mathrm{w} - B_\mathrm{o}}{B_\mathrm{w} + B_\mathrm{o}}$$

where B_w and B_o denote the number of contact points below *O. tridentata* and in the open spaces, respectively. Positive values of RII are indicative of facilitation (Armas et al. 2004).

We qualitatively defined the regeneration niche of each sampled species as 'gypsophyte' or 'non-gypsophyte' according to Mota et al. (2009). Gypsophytes are species which exclusively inhabit gypsum soils while non-gypsophytes are species which are also able to live in other soils. This single trait captures the main genotypic and phenotypic features that condition the demographical success of a plant species to establish on gypsum soils, which turn into ecophysiological and morphological adaptations to water and to osmotic and ionic stress (Merlo et al. 2011).

Statistical analysis of facilitation by *O. tridentata* was assessed by Chi square tests to explore whether plant abundance (total number of contact points) was higher in patches than gaps for all sampled species excepting the nurse plant. To assess whether facilitation was higher between species with complementary regeneration niches, we performed a generalized linear model (GLM) using RII as response variable and the regeneration niche 'gypsophyte' or 'non-gypsophyte' as factor. As we hypothesized that the nurse effect of *O. tridentata* is to expand the regeneration niche of non-gypsophyte species, we expected facilitation to be higher in non-gypsophytes.

Plant diversity and phylogenetic diversity

Plant richness was calculated as the total number of species in each patch and gap. The Shannon diversity index was calculated with the R package vegan (R Development Core Team 2011). Plant phylodiversity was quantified as the abundance-weighted mean pairwise phylogenetic distance (MPD) between co-occurring plant species (Webb et al. 2008). To compute MPD, plant abundance was estimated as the number of contact points of each species per 100 points and the phylogenetic tree was constructed as explained below. To test whether (1) gypsum, by imposing an abiotic filter to the species from the regional flora, reduces the phylogenetic diversity of the plant community, and (2) the facilitative role of *O. tridentata* relaxes such a filter and increases the phylogenetic diversity, we used the Net Relatedness Index (NRI), a standardized measure of MPD, which was calculated as follows:

$$\mathrm{NRI} = -(\mathrm{MPD} - \mathrm{MPDrnd})/\mathrm{sd}(\mathrm{MPDrnd})$$

where MPDrnd and sd(MPDrnd) are the average and the standard deviations, respectively, of 999 MPDs obtained after randomly reshuffling the species across the phylogenetic tree. To obtain a phylogenetic tree, we first constructed a list of the regional flora by applying geographic and bioclimatic filters to the checklist of Mateo and Crespo (1990). This resulted in 818 species, including semi-arid to dry, and thermo- to meso-Mediterranean plant communities. We obtained the phylogenetic tree of this community with the help of the programs Phylocom 4.2 (Webb et al. 2008) and BEAST 1.5.4 (Drummond and Rambaut 2007). The topology of the community phylogeny was obtained with Phylomatic by matching the family names of the species in the regional flora with those contained in a backbone phylogeny, which is the megatree based on the work of the Angiosperm Phylogeny Group (APGIII 2009). We simultaneously resolved polytomies and adjusted branch lengths with the help of BEAST (Drummond and Rambaut 2007) and the PolytomyResolver script (Kuhn et al. 2011). This branch length adjustment procedure uses an evolutionary, birth–death model, and is more realistic than traditional non-model-based approaches, like that used by the Bladj algorithm in Phylocom (Webb et al. 2008), which assigns branch lengths by evenly distributing the undated nodes between the known parent age and the known daughter age. The use of evolutionary models to resolve and date community phylogenies is needed because ecological communities are not only the product of ecological assembly processes but also a framework in which diversification occurs (see Roquet et al. 2013 for a review of polytomy resolution methods, and Verdú and Pausas 2013 for a case study). The PolytomyResolver script indicates to the BEAST program the chronological and topological constraints as well as the specifications of a birth–death tree prior. We defined chronological constraints for 42 nodes following the ages estimated by Wikstrom et al. (2001), and the remaining nodes were left to be dated by BEAST using the default settings specified in the PolytomyResolver script. We ran Markov Chain Monte Carlo (MCMC) analyses for 10^6 iterations, sampling trees every 10^3 iterations, discarded a 25 % burn-in, and randomly selected 100 fully-resolved dated trees. These 100 trees were used in subsequent analysis to account for the topological and chronological uncertainty associated to the phylogenetic tree.

Abundance-weighted metrics of plant diversity (Shannon index) and phylodiversity (NRI) were compared in

patches and gaps under Bayesian GLMs, using each patch–gap block as a random factor. To accommodate phylogenetic uncertainty, we ran 100 Bayesian GLM models with the phylodiversity calculated from the 100 phylogenetic trees. Then, we integrated over the posterior samples by drawing 1,000 random samples across models. The models were run with the help of MCMC techniques as implemented in the MCMCglmm package for R (R Development Core Team 2011). We used the default priors and ran 13.000 MCMC iterations with a burn-in period of 3.000 iterations. Convergence of the chain was tested by means of an autocorrelation statistic. The statistical significance of the factors in the model was estimated by calculating the 95 % credible interval of their posterior distribution.

Soil microbial productivity

We quantified six soil microbial parameters indicative of microbial biomass (microbial biomass carbon), general activity (ATP content and respiration), as well as carbon, phosphorous, and nitrogen cycling (β-glucosidase, alkaline phosphatase and urease activities), and calculated two simple indices reflecting the microbial efficiency to utilize organic resources (microbial and metabolic quotients; see details below).

Microbial biomass carbon (MBC) was determined by chloroform fumigation extraction (Vance et al. 1987) with minor modifications, as in Goberna et al. (2007). The microbial quotient, i.e. the ratio between MBC and total organic C (MBC/TOC), was calculated as an index reflecting the conversion efficiency of organic carbon into microbial carbon. The ATP content was extracted from soils under field moisture conditions (Webster et al. 1984) including slight modifications, as in Goberna et al. (2007). The ATP content was quantified in a luminometer (Optocom 1; MM Instruments). The CO_2 evolved under controlled conditions during an aerobic incubation was determined to estimate the soil's potential to mineralise organic C (Nannipieri et al. 1990). Soil samples (10–15 g) were moistened to 60 % water-holding capacity prior to incubation at 28 °C in 125 cm^3 air-tight containers. The CO_2 (%) evolved in the containers was measured over 23 days at 3- to 4-day intervals with an infrared analyser (CheckMate II; PBI Dansensor). After each measurement, stoppers were removed for 1 h to balance the atmosphere inside and outside the bottles. Basal respiration was calculated as the average C content respired daily per kilogram soil. The metabolic quotient (qCO_2) was calculated as the cumulative CO_2-C production during the whole incubation period divided by MBC. This index declines as the soil microbiota becomes more efficient at conserving C (Wardle and Ghani 1995).

Soil β-glucosidase (GA), alkaline phosphatase (PA), and urease (UA) activities were used as indicators of microbially mediated biogeochemical ecosystem functions (Sinsabaugh 1994). β-glucosidases break down the β-glucoside bonds of carbohydrated chains. Phosphatases hydrolyse phosphoric esters rendering an alcohol and orthophosphoric acid, thus replenishing the soil pool of inorganic P. Soil GA and PA were determined colorimetrically as the amount of *p*-nitrophenol (PNP) produced after incubation of 0.5 g of soil (37 °C, 1 h) in 2 mL of modified universal buffer (MUB; pH 6) and 0.5 mL of 0.025 M *p*-nitrophenyl-β-D-glucopyranoside or MUB (pH 11) and 0.025 M *p*-nitrophenyl-phosphate, respectively (Eivazi and Tabatabai 1988; Tabatabai and Bremner 1969). Soil UA, which catalyzes the conversion of urea into carbon dioxide and ammonia, was quantified colorimetrically as the NH_4^+ produced after incubating (37 °C, 2 h) 1 g of soil in 4 mL borate buffer (pH 10) and 0.5 mL of 0.48 % urea (Kandeler and Gerber 1988).

The effect of facilitation on the soil microbial productivity (biomass and activity) and metabolic efficiency was assessed by performing Bayesian GLMs with each microbial parameter used individually as the dependent variable and plant diversity (Shannon index), phylodiversity (MPD), and the environment (patch vs. gap) as independent variables in the same model. Phylogenetic uncertainty was also included in the GLM models as explained above. All variables excepting BR, qCO_2, and ATP required log-transformation to improve normality. BR and ATP were binary coded and analyzed with a binomial error structure.

In order to quantify the relative effect of significant factors on soil microbial productivity, we used structural equation models (SEM) as confirmatory analyses. SEMs allow the quantification of the percentage of variance explained by each explanatory variable independently (Pugesek et al. 2003). Based on the results of the Bayesian GLMs analyses, we built a model reflecting the relationships between the plant community variables that were significant in explaining soil microbial productivity. General indicators of microbial biomass, activity, and metabolic efficiency were reduced through a principal component analysis (PC) to a single variable explaining 72 % of the variation and describing a gradient from low to high MBC and RB (loadings: qCO_2 0.14; MBC/TOC 0.46; ATP 0.48; RB 0.52; MBC 0.52). Similarly, specific indicators of C, N, and P cycling were reduced to a single variable explaining 94 % of the variance and defining a gradient between low and high PA and GA (loadings: UA 0.57; PA 0.58; GA 0.59). Both variables were considered as endogenous variables in the SEM. The overall goodness of fit of the model, significance at a confidence interval of 95 % of each path, and direct and indirect effects of relevant plant community properties on these two variables were calculated using a bootstrap of 200 replicates. We assessed the sensitivity of the results to the use of different phylogenies repeating

the SEM analyses with 10 different plant phylogenies. SEM analyses were performed using the AMOS module of PASW statistics (v.18.0; SPSS, Chicago, IL, USA).

Results

Plant facilitation and regeneration niche expansion

O. tridentata acted as a nurse plant in the study system. Plant abundance beneath *O. tridentata* patches was significantly higher than out of the patches ($\chi^2 = 455.989$; $P < 0.0001$). Patches accumulated 82 % of total scored contact points, whereas 18 % was scored in the gaps. Individually, out of 43 plant species recorded, five had RII <0, one was equally abundant below *O. tridentata* and in open spaces (RII = 0) and 37 showed RII >0 (Table 2). Nevertheless, due to the low abundance of some species, the absence of facilitation could only be statistically confirmed in three out of five species with RII <0, whereas facilitation was tested in 15 out of 37 species with RII >0 (Table 2). Facilitation was not restricted to any particular clade but dispersed along the phylogenetic tree of the plant community (Online Resource Fig. 1).

Gypsophily had a significantly negative effect on RII (estimate = −0.78 ± 0.29, $t = -2.77$, $P = 0.009$). Plants that are not strict gypsophytes preferentially grew below *Ononis*. Conversely, those species that are more gypsum stress-tolerant did not thrive below *Ononis*, but in open spaces.

Plant richness and phylodiversity

Plant richness was significantly higher in patches than gaps [MCMCglmm; post-mean estimate = 0.590; (0.417, 0.744) 95 % credible interval]. Patches and gaps had (average ± SD) 14 ± 3 and 7 ± 2 species, respectively. In contrast, the Shannon index was not significantly different between both environments [0.1; (−0.1794, 0.3598)].

The plant community sampled on gypsum soils constituted a random subset of the regional flora [NRI = 0.01 (−0.386, 0.209)]. When we analyzed patches and gaps separately, patches were significantly overdispersed (−0.491 [−0.731, −0.180]), whereas gaps were clustered [0.584 (0.235, 0.897)]. Thus, and similarly to plant richness, plant phylodiversity was higher in patches, as reflected by the significantly lower NRI values in patches compared to gaps [−0.99 (−1.359, −0.654)].

Soil microbial productivity

Both general and specific indicators of soil microbial productivity were significantly larger in patches compared to gaps (Fig. 1). Differences were one or more orders of magnitude larger in patches for microbial biomass C, basal respiration, β-glucosidase activity, phosphatase activity, and urease activity (Table 3). When the effects of plant diversity, phylodiversity,and the environment (patch vs. gap) on soil microbial productivity were tested in a single model, we found that plant diversity had no effect on any of the microbial indicators (Fig. 1). In contrast, plant phylodiversity had a significant positive effect on all general indicators of microbial biomass (MBC), activity (ATP and basal respiration), and efficiency to convert organic C into microbial C (MBC/TOC). Phylodiversity had a negative effect on the metabolic quotient (qCO_2; Fig. 1), which is inversely related with the microbial efficiency to use C substrates. In contrast, no effect of phylodiversity was detected on the specific indicators of C, P, and N cycling (β-glucosidase, phosphatase, and urease activities; Fig. 1).

The proposed SEM (Fig. 2) explained 96 % of the variation in the general indicators of microbial activity, and 93 % when considering specific indicators. The overall fit of the model was good as there were non-significant differences between the variables correlation matrix proposed in the model and the observed structure ($n = 30$, $\chi^2 = 1.20$, $df = 1$, $p = 0.27$; all the results were consistent when different phylogenies were used, i.e. p range 0.26–0.28; hereafter, only the values for one representative SEM are presented). The model had a high goodness-of-fit index (GFI) of 0.98 (index ranges from 0 to 1; Byrne 2009) and a root mean square error of approximation (RMSA) of 0.08. The model showed significant direct effects of environment (patch vs. gap) on both general [standardized direct effect (SDE) = 0.89 (0.81, 0.96)] and specific [SDE = 0.98 (0.97, 0.99)] indicators of microbial productivity. Independently, plant phylogenetic diversity, considered as MPD between plant species in a patch, also showed a significant direct effect on general indicators of microbial productivity [SDE = 0.17 (0.07, 0.27)]. The direct effect of phylodiversity on microbial general indicators was reinforced by the fact that the fit of the model is very poor when we remove this relationship ($\chi^2 = 12.73$, $df = 2$, $p = 0.001$). The Akaike's Information Criterion also supported the model with effects of phylodiversity on microbial indicators (AIC = 19.2) compared to the model without these effects (AIC = 28.6).

Discussion

Our results show that *O. tridentata* acts as a nurse species enhancing microenvironmental conditions and spatially organizing semi-arid plant communities thriving on gypsum into a patch–gap mosaic. This process ultimately conditions plant diversity, phylodiversity, and the community

Table 2 Relative interaction intensity (*RII*) of each plant species with *O. tridentata*

Species	Regeneration niche	RII[a]	No. contact points		χ^2	*P* value
			Patch	Gap		
Centaurium quadrifolium	ng	−1.00	0	4		
Reseda phyteuma	ng	−0.85	0	1		
Herniaria fruticosa	g	−0.78	2	16	10.89	**<0.001**
Globularia alypum	ng	−0.69	2	11	6.23	**0.012**
Teucrium libanitis	g	−0.47	17	47	14.06	**<0.001**
Helianthemum squamatum	g	0	6	6	0	1
Fumana thymifolia	ng	0.14	8	6	0.29	0.59
Helianthemum syriacum	ng	0.16	40	29	1.75	0.18
Fumana ericoides	ng	0.40	47	20	10.88	**<0.001**
Dorycnium pentaphyllum	ng	0.44	23	9	6.12	**0.013**
Atractylis humilis	ng	0.50	3	1		
Launaea nudicaulis	g	0.50	6	2		
Coris monspeliensis	ng	0.60	4	1		
Helichrysum stoechas	ng	0.62	60	14	28.59	**<0.001**
Thymus moroderi	ng	0.70	91	16	52.57	**<0.001**
Stipa offneri	ng	0.78	120	15	81.67	**<0.001**
Fagonia cretica	ng	0.92	23	1	20.17	**<0.001**
Hyparrhenia hirta	ng	0.93	26	1	23.15	**<0.001**
Rhamnus lycioides	ng	0.94	34	1	31.11	**<0.001**
Sedum sediforme	ng	0.97	70	1	67.06	**<0.001**
Linum strictum	ng	1	4	0		
Diplotaxis lagascana	ng	1	9	0	9	**0.003**
Anagallis arvensis	ng	1	2	0		
Asparagus horridus	ng	1	9	0	9	**0.003**
Pallenis spinosa	ng	1	2	0		
Asterolinon linum-stellatum	ng	1	1	0		
Brachypodium retusum	ng	1	239	0	239	**<0.001**
Carduus valentinus	ng	1	5	0		
Carrichtera annua	ng	1	1	0		
Cuscuta epithymum	ng	1	11	0	11	**<0.001**
Dipcadi serotinum	ng	1	0	0		
Echium creticum	ng	1	0	0		
Eryngium campestre	ng	1	5	0		
Euphorbia sulcata	ng	1	1	0		
Launaea fragilis	ng	1	10	0	10	**0.002**
Phagnalon saxatile	ng	1	0	0		
Plantago albicans	ng	1	0	0		
Polygala rupestris	ng	1	3	0		
Reichardia tingitana	ng	1	1	0		
Reseda paui	ng	1	4	0		
Sonchus tenerrimus	ng	1	1	0		
Stipa tenacissima	ng	1	23	0	23	**<0.001**
Teucrium pseudochamaepitys	ng	1	2	0		

Results of Chi square tests to assess the strength of facilitation by the nurse species are shown for those species with sufficient sample size for testing. Significant differences between both environments are indicated in bold (χ^2; $P < 0.05$). The regeneration niche of each species (*g* gypsophyte, *ng* non-gypsophyte) is also shown. Species authority can be consulted in Mateo and Crespo (1990)

[a] *RII* <0 denotes absence of facilitation; *RII* = 0 implies no effect; *RII* >0 denotes facilitation by the nurse (Armas et al. 2004)

assembly patterns. Plant phylodiversity, but not diversity, is shown to be directly related to the soil microbial productivity. Overall, our data confirm that facilitation can have a synergistic effect on ecosystem functioning due to the independent and direct effects of microenvironmental conditions and plant phylodiversity on soil microbial productivity. So, our results build on the growing evidence that claims phylodiversity to be a good proxy of overall

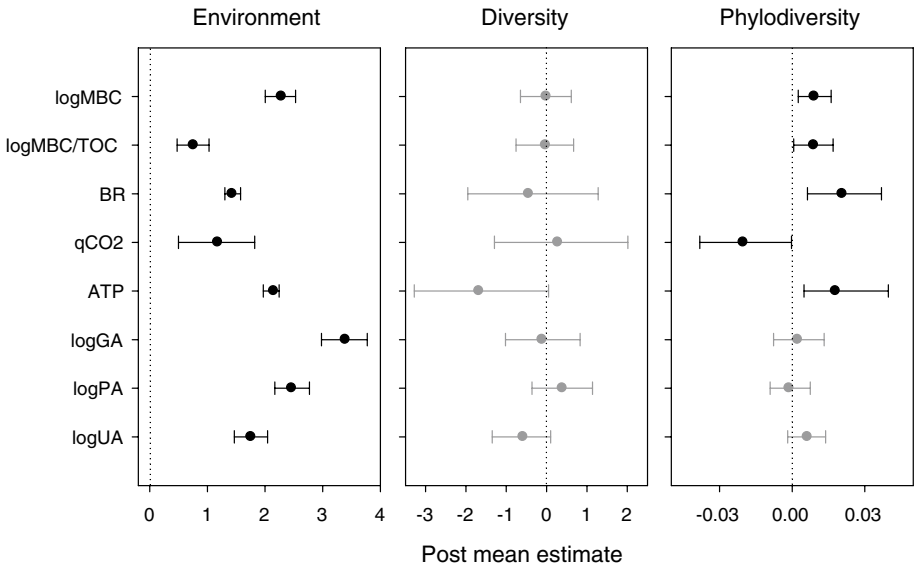

Fig. 1 Bayesian post-mean estimates and their expected 95 % credible intervals for the effect of the environment (patch vs. gap), plant diversity (Shannon index), and phylodiversity (MPD) on the eight soil microbial indicators. The Bayesian GLMs were carried out with the patch–gap block as a random factor. The credible intervals for the effects of diversity and phylodiversity on BR and ATP were divided by 10 and 100, respectively, for graphical representation. Effects with intervals not including zero are significant (*black* intervals), whereas those including zero are not significant (*gray* intervals)

Table 3 Soil microbial productivity indicators in *O. tridentata* patches and gaps

Variable	Patch[a]	Gap[a]	*t* value[b]	*P* value
General indicators				
Microbial biomass C (mg C kg^{-1})	2,458 ± 225	205 ± 20	21.1	**<0.001**
MBC/TOC (%)	2.7 ± 0.9	1.0 ± 0.4	7.0	**<0.001**
Basal respiration (mg C-CO_2 kg^{-1} d^{-1})	136 ± 11	8 ± 1	19.4	**<0.001**
qCO_2 (μg C-CO_2 mg^{-1} MBC h^{-1})	2.6 ± 0.3	1.8 ± 0.2	2.5	**0.024**
ATP content (ng g^{-1})	614 ± 31	196 ± 77	8.2	**<0.001**
Specific indicators				
β-Glucosidase activity (μmol PNP g^{-1} h^{-1})	10.7 ± 1.1	0.34 ± 0.03	19.8	**<0.001**
Phosphatase activity (μmol PNP g^{-1} h^{-1})	28 ± 2.5	2.4 ± 0.2	20.2	**<0.001**
Urease activity (mg NH_4^+-N g^{-1} h^{-1})	3.3 ± 0.2	0.6 ± 0.1	14.0	**<0.001**

Significant differences between both environments are indicated in bold (paired *t*-test; $P < 0.05$)

[a] Average ± SE for $n = 15$. All data are given on an oven-dried weight soil basis

[b] Data were log-transformed prior to statistical analyses

ecosystem functioning, but differ from previous studies by linking producer's phylodiversity and decomposer's productivity. We discuss the possible mechanisms explaining the observed pattern below.

Plant facilitation and regeneration niche expansion

Gypsum limited the establishment of many species, but these restrictions were overcome in the presence of *O. tridentata,* which facilitated the recruitment of most of the species in the community, leading to increased plant richness in the patches. Facilitation was likely both direct, since experimental data show higher seed emergence under *O. tridentata* compared to open ground (J.A Navarro-Cano et al., in preparation), and indirect, owing to passive propagule trapping (Caballero et al. 2008). Our results agree with many studies on the positive effect of nurse species on plant richness under abiotic stress conditions (Brooker et al. 2008). In our system, the gypsophyte *O. tridentata* facilitated ecologically complementary species (i.e., non-gypsophytes). Facilitation between species differing in their regeneration niches has been observed in other desert and Mediterranean plant communities (Valiente-Banuet and Verdú 2007, 2008; Verdú et al. 2009). However, individual cases showing facilitation between species with similar regeneration niches have also been reported on gypsum soils (Caballero et al. 2008; Quintana-Ascencio et al. 2009; Soliveres et al. 2011). The importance of niche complementarity for community assembly was highlighted by manipulative experiments using an aphid-parasitoid–producer system (Finke and Snyder 2008). In addition, phylogenetic distance, used as a proxy of niche complementarity, was found to be a good predictor of fungal coexistence in an experimental mycorrhiza–plant system (Maherali and

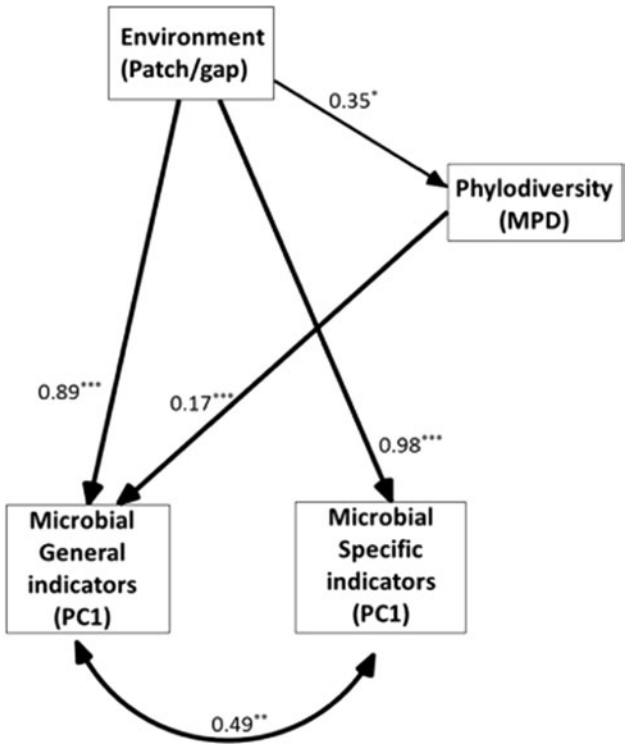

Fig. 2 Structural equation model proposed to test for plant community effects on soil microbial productivity. Standardized direct effects of the presence of patch versus gap (*Environment*), and the mean phylogenetic distance between pairs of plant species within a patch (*MPD*) on soil microbial productivity are presented. The significance of each path is indicated as ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$. Microbial general indicators represent the first principal component axis considering: qCO_2, MBC/TOC, ATP, BR, and MBC, and specific indicators considering: UA, PA, and GA

Klironomos 2007). Similarly, we found that facilitated species coexisting under *O. tridentata* formed a phylogenetically diverse neighborhood. These results agree with experimental findings showing that plant co-occurrence in nurse-created patches is maximized under phylogenetically diverse neighborhoods, indicating that coexistence is strongly determined by the evolutionary relationships among species (Castillo et al. 2010). This ultimately supports the notion that facilitation increases phylodiversity (Valiente-Banuet and Verdú 2007).

Soil microbial productivity

The nurse *O. tridentata* established on infertile soils and enhanced the microenvironment. This plant created resource-rich patches that increased plant richness and phylodiversity, while significantly promoting soil microbial productivity, activity, and metabolic efficiency. Our data suggest that *O. tridentata* was mainly responsible for shifts in general and specific microbial indicators (89 and 98 % of explained variance in SEM, respectively). In addition, the increased plant phylodiversity induced by *O. tridentata* had an independent effect on microbial general indicators, although this effect explained a lower portion (17 %) of the variance. Plant phylodiversity, but not diversity, had a positive effect on microbial biomass, total activity, and respiration, as well as on the efficiency of the soil microbiota to utilize organic C resources. However, neither plant phylodiversity nor plant diversity explained the variation on the specific indicators of microbial activity linked to C, P, and N cycling. These data added to those of Naeem et al. (1995) show that individual indicators of ecosystem functioning respond differently to changes in biodiversity. The observation that patches and gaps present contrasting microbial biomass and total and specific activities has been reported before in this ecosystem, not only for the growing season, as was the case here, but throughout the year (Goberna et al. 2007). This indicates that the mechanisms linking facilitation and soil microbial productivity might be consistent across time.

Positive or neutral effects of biodiversity on productivity have been the most frequently reported in the literature, whereas negative patterns have been rarely observed (Hooper et al. 2005; Balvanera et al. 2006). Positive relationships have been traditionally explained by at least two different mechanisms. First, there is the selection effect, according to which the probability of including very productive taxa in the community increases with the total number of taxa (Hooper et al. 2005). Second is the complementarity effect, by which productivity is maximized when the existence of positive interactions and/or the absence of niche overlap allow a more efficient use of the overall resource (Hooper et al. 2005). Authors focusing on the producer–decomposer interaction have usually alluded to the importance of the complementarity effect (Loreau 2001). Naeem et al. (1995) constructed multitrophic communities bearing from 6 up to 30 species of plants, herbivores, and soil invertebrates. They observed that higher species richness is associated with faster rates of overall community respiration, plant productivity, and soil P and K accumulation, which was attributed to the complementarity of the functional groups. Zak et al. (2003) found a positive effect of plant species richness on soil microbial biomass, activity, and composition in experimental communities ranging from 1 up to 16 plant species. They speculated that richer systems might be more productive owing to niche complementarity. Also, Maestre et al. (2012) hypothesized that the complementarity in the use of resources might underlie the correlation that they detected between plant species richness and an index integrating 14 soil variables informing on the cycling and storage of C, N, and P in drylands. However, the authors highlighted that species richness explained a small fraction of the

variance ($R^2 = 0.03$). Our results confirm the importance of the complementarity effect since *O. tridentata* facilitated ecologically complementary plant species. Patches of increased phylodiversity accumulated more organic C resources, which entered the soil through litter deposition and root exudation. Such conditions significantly increased the abundance of Proteobacteria and Actinobacteria compared to those in the gaps (unpublished results). These bacterial phyla include hundreds of fast-growing and highly productive taxa in terms of growth response to labile C substrates, such as those found in rhizosphere exudates (Goldfarb et al. 2011). Our line of reasoning on the effects of producer phylodiversity on decomposer productivity is consistent with the idea that plant–microbe interactions controlling ecosystem functioning are more top–down than bottom–up driven (Wardle et al. 2004; van der Putten et al. 2007). This is attributed to the limited food specificity and great functional redundancy of decomposers (Van der Putten et al. 2007). Still, factors governing multitrophic interactions are poorly understood, and above/belowground feedbacks might be context-dependent (Wardle et al. 2004). Manipulative experiments are needed in order to formally demonstrate our observation that plant phylodiversity has a direct effect on soil microbial productivity.

We found that plant phylodiversity, rather than plant diversity, is a good proxy of ecosystem productivity quantified in terms of soil microbial biomass, activity, and efficiency. Our findings agree with previous studies that estimated ecosystem productivity through plant biomass. Cadotte et al. (2008) reviewed manipulative experiments controlling plant diversity in grasslands to infer that phylodiversity can predict plant biomass better than functional diversity or species richness. Cadotte et al. (2009) argued that this relates to the fact that plant phylodiversity integrates all functional traits that contribute to ecosystem productivity. They added that phylodiversity is more accurate and easy to measure than functional parameters to describe ecosystem functioning. This is also supported by Srivastava et al. (2012), who discussed how phylodiversity incorporates an evolutionary approach to community ecology.

Beyond the basic understanding of the ecosystem functioning, our results are relevant for applied restoration ecology. Gypsum lands are biodiversity hotspots (Mota et al. 2004) which have been severely damaged due to the industrial use of gypsum as a raw material. We propose that managing and restoring gypsum areas requires combining soft tools, such as the use of nurse plants, seeding (Barberá et al. 2006), and the selection of complementary species to accelerate the formation of a patch–gap mosaic that recovers biodiversity and ecosystem functions (Verdú et al. 2012).

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