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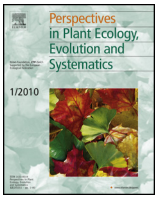

Research article

Nurses experience reciprocal fitness benefits from their distantly related facilitated plants

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ABSTRACT

It is well known that many plants benefit from growing beside a nurse plant of another species, but the possibility that the nurse also benefits has been rarely studied. We hypothesize that positive interactions are maintained not only because of the recruitment benefits for the facilitated plants but also because of fitness benefits for the nurse plant. We tested this hypothesis by comparing seed production, seed predation and seed viability of a dominant nurse plant species (*Mimosa luisana*) when growing alone and in patches surrounded by its facilitated species. We also tested whether fitness of the nurse species is dependent on the phylogenetic neighborhood formed by their facilitated species using an analysis that accounted for the abundance and pairwise phylogenetic similitude of all species in each patch. Nurses growing associated to their facilitated species produced more seeds (1.86 times) and these seeds were more viable (1.47 times) than those of nurses growing alone. Seed predation did not alter these fitness differences. Seed number and viability increased in phylogenetically diverse neighborhoods. We conclude that distantly related partners are more likely to cause reciprocal increases in fitness, and that such effects contribute to species coexistence.

Introduction

The recent interest in the role of facilitation in plant communities has helped redress an undue emphasis upon antagonistic interactions, though some crucial topics are still poorly covered (Brooker et al., 2008). Thus, while the relationship between facilitation and competition has been extensively analyzed, the relationship between facilitation and mutualism has practically been unexplored (Bronstein, 2009).

Under the dominant influence of the competition paradigm, many studies using pairs of species have shown that facilitation may turn gradually into competition as plants grow larger (Miriti, 2006). For example, Miriti et al. (2001) showed a negative impact of adult neighbors upon population growth rates of *Ambrosia dumosa.* Asymmetric responses in the facilitation–competition balance have also been found, with consequences that were harmful for the facilitated species but harmless for the nurse (Verdú et al., 2004). Similarly, competitive interactions have been found to prevail in many observational and experimental studies that considered several facilitated species growing with a nurse plant (Schöb et al., 2014). However, a search of the literature indicates that in semiarid communities positive interactions are more likely to persist. Thus, a shift from facilitation toward competition was reported in only 43% of cases, while facilitative effects persisted in 57% of cases (Valiente-Banuet and Verdú, 2008).

It is generally supposed that species coexistence is primarily a consequence of niche differentiation, and that this tends to be greater between more distantly related species (Valiente-Banuet and Verdú, 2007; Soliveres et al., 2010, 2012 but see Cahill et al., 2008; Mayfield and Levine, 2010). In many ecosystems, facilitation leads to the formation of discrete, multi-specific vegetation patches surrounded by open space, although the significance of these has been largely overlooked (Prentice and Werger, 1985; Eccles et al., 1999; Castillo et al., 2010). Furthermore, the few experimental studies performed in such vegetation have shown that facilitated species benefit more in phylogenetically diverse neighborhoods

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(Castillo et al., 2010). Similarly, the richness of facilitated species tends to have positive effects on nurse fitness, indicating that the costs and benefits of harboring associated species depend on the composition of the plant assemblage (Schöb et al., 2014). In such cases, we might expect any benefits to the nurse species to depend upon its evolutionary relationships to its neighbors. Improved plant performance in phylogenetically diverse neighborhoods has been interpreted as indicating reduced competition between distantly related species (Castillo et al., 2010). However, it is tempting to hypothesize that indicates mutualism between distantly related plants (Valiente-Banuet and Verdú, 2013). For example, a distantly related plant can be more helpful to a neighbor if it provides functionally complementary fungi to the mychorrizal network (Beltrán et al., 2012; Montesinos-Navarro et al., 2012a).

A demonstration of non-random association of species together with physiological and growth benefits for the nurse species (Pugnaire et al., 1996) would provide valuable evidence about the mutualistic nature of facilitation. However, to demonstrate such a mutualism, it is ultimately necessary to measure a fitness component like reproductive success and compare it with the fitness of individuals that are not involved in facilitation (Bronstein, 2009). Fitness benefits for associated individuals may arise via different mechanisms, including microclimatic amelioration, associational defense and shared mutualists (Callaway, 2007; Bronstein, 2009; Beltrán et al., 2012). For example, nurses might benefit from their facilitated plants if these reduce direct insolation, or reduce soil erosion, or increase fertility by providing organic matter (Pugnaire et al., 1996). Associational defenses and shared mutualisms are biotic mechanisms to improve the microenvironment where plants coexist. Mycorrhizal fungal networks have shown to provide these functions in the facilitation interactions because nurse and facilitated plants can help each other by sharing mycorrhizal fungi that enhances nutrient supply and protect against pathogens (Selosse et al., 2006; Van der Heijden and Horton, 2009).

Here we hypothesize that positive interactions within a vegetation patch are maintained not only by providing recruitment benefits for facilitated plants but also by improving the performance of nurse species. We specifically determined whether the shrub *Mimosa luisana*, a key nurse species forming multi-specific patches through the facilitation of 86% of species in Mexican deserts (Supplementary Material Fig. S1), has higher reproductive success when growing in these patches than when it grows alone. We subsequently tested whether the fitness benefits for *M. luisana* increase with increasing phylogenetic distance of the facilitated species.

Materials and methods

Study area and species

This study was conducted in the semiarid Valley of Zapotitlán (18° 20′N, 97° 28′W), a local basin of the Tehuacán-Cuicatlán Valley in the state of Puebla, Mexico. This region owes its aridity to the rain shadow produced by the Eastern Sierra Madre (Valiente-Banuet et al., 2000). It has an annual average rainfall of 380 mm, most of which falls during the summer months, and an annual mean temperature of 21 °C with rare frosts (García, 1988). Specifically, the study site is located inside the Botanical Garden "Helia Bravo Hollis", a natural unmodified protected area located approximately 30 km south of Tehuacán city in which the vegetation is a xeric shrubland dominated by the columnar cactus *Neobuxbaumia tetetzo*, and the species such as *M. luisana, Mascagnia seleriana, Ipomoea arborescens, Aeschynomene compacta, Caesalpinia melanadenia, Calliandra eryophylla, Zapoteca formosa, Senna wislizenii, Agave marmorata*, *Agave macroacantha*, *Jatropha neopauciflora*, among other taxa (Valiente-Banuet et al., 2000). Most of the species that have been recorded in this community (48 out of 56) appear to depend upon *M. luisana* plants for recruitment. These include species of several functional groups – shrubs, succulents plants such as *Agave* and cacti, perennial climbing vines, and perennial herbs (Verdú and Valiente-Banuet, 2008) – which together form discrete patches of vegetation. The area occupied by a vegetation patch ranges from 1 to 5 m^2 and corresponds to the vertical projection of the canopy of an adult individual of *M. luisana*. We regard facilitated plants as being those restricted to the subcanopy of the focal *M. luisana* individuals. In addition, isolated individuals of *M. luisana* can also be found.

M. luisana is a deciduous spiny shrub reaching heights up to 2.2 m. Plants reach reproductive maturity when they are ca. 0.80 m tall. The pink, hermaphrodite flowers occur in spike-like inflorescences and are produced during July at the beginning of the rainy season. Seeds are produced within a spiny brown legume. Seeds have a hard, wax-covered coat and scarification is needed to break dormancy and germination occurs after few days (Camargo-Ricalde et al., 2004). Seed predation rates by the bruchids *Acanthoscelides mexicanus*, *A. chiricahuae*, and *Stator pruininus* range between 30 and 75% (Camargo-Ricalde et al., 2004; Romero-Nápoles et al., 2005). Pods and seeds are eaten by mammals such as horses (*Equus caballus*), donkeys (*Equus africanus*) and goats (*Capra hircus*). At present goats have been eliminated from the study area, as well as the white-tailed deer (*Odoicoleus virginianus*) considered as the native main possible seed disperser. Although a high proportion of seeds consumed by goats, the remaining seeds germinate in a higher proportion after gut passage than control treatment (47.5 vs. 5.83% respectively; Giordani, 2008). Goats, horses, and donkeys are efficient dispersal agents for the seeds of *M. luisana*, carrying seeds considerable distances and depositing their feces in open areas that are suitable for germination.

Fitness estimation

Three components of *M. luisana* fitness were estimated: (i) seed production, (ii) seed predation and (iii) seed viability. Seed production was estimated by counting the total number of seeds produced by the shrub *M. luisana* in patches with and without neighbors. A total of 90 reproductive *M. luisana* individuals (>80 cm height) growing alone ($N = 25$) and growing associated to other species ($N = 65$) were randomly selected. This unbalanced design corresponded to the natural distribution of isolated and associated individuals. The size of shrubs was estimated as the volume of an inverted cone with an elliptical base by measuring the height and two perpendicular diameters of the canopy cover (Supplementary Material Table S1). Seed predation was estimated by counting the number of seeds with the exit hole done by bruchids in random samples of 300 seeds obtained from each *M. luisana* individual growing without or with neighbors ($N = 17$ and $N = 29$ respectively). Seed viability was estimated as the proportion of non-preyed seeds that were able to germinate. Seeds were scarified with sandpaper to reduce the thickness of the testa, and germinated in Petri dishes with filter paper at 25 °C in 12 h. light/dark in a growth chamber.

A potentially confounding factor in the relationship between nurse fitness and coexistence with facilitated plants may be microclimatic variation. For example, a very rich microhabitat may independently support the establishment of multiple species and enhance *M. luisana* fitness. For this reason, it is important to ensure that there is a nursing effect of *M. luisana* on the rest of species and the association is not merely the response of plants to a resource-rich patch. To check that this was not the case, we randomly sampled soils to a depth between 0–10 cm below the canopy of

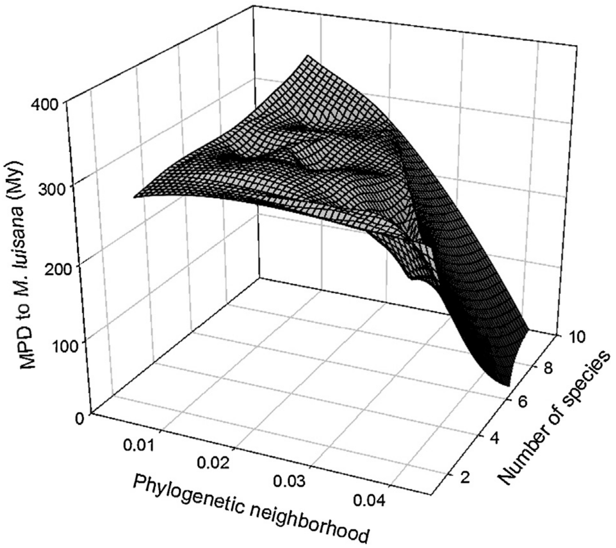

Fig. 1. Relationship between the phylogenetic neighborhood metrics (Pillar and Duarte, 2010) and both the number of species and the mean phylogenetic distance of associated species to *Mimosa luisana* in each vegetation patch. High phylogenetic neighborhood values occur when the abundance of species closely related to *M. luisana* in the patch is high whereas low values occur in patches with distantly-related species to *M. luisana*.

20 young *M. luisana* plants (ca. 10 cm height) and compared it to soil collected in their neighboring gaps.

To test whether nurse benefits could result from micro-environmental amelioration produced by an increasing number of their facilitated plants, we measured soil fertility (pH, electrical conductivity, organic matter, total N, total P and total K, olsen P, N-NO_3^-, N-NH_4^+, $CaCO_3$) physicochemical structure (cation exchange capacity, % sand, silt and clay) and water availability (gravimetric humidity and water holding capacity) in soils of 14 patches and correlated with the number of facilitated species in the patch (0–7).

Phylogenetic neighborhood calculations

The phylogenetic neighborhood of *M. luisana* in each patch was characterized following the framework for meta-community analysis of phylogenetic structure developed by Pillar and Duarte (2010). In contrast to other widely used metrics such as Mean Phylogenetic Index (MPD) or Mean Nearest Neighbor Distance (MNND), Pillar and Duarte metrics incorporates the identity of coexisting plant species. For example, a patch where *M. luisana* coexists with both a distant and a closely related species (300 and 10 My respectively) will have the same MPD than a patch where *M. luisana* coexist with two species with intermediate (150 and 160 My respectively) phylogenetic distances. However, Pillar and Duarte metrics will score each patch with different values by characterizing the phylogenetic structure of a given patch taking into account the abundance and the pairwise phylogenetic similitude of each species with the rest of the species in the community. A matrix (P matrix) containing the composition of the patches is calculated by fuzzy weighting of species abundance by the species phylogenetic similarities (see Pillar and Duarte, 2010 for the mathematical explanation). Each element of the P matrix represents the phylogenetic neighborhood of a focal species in a given patch. We used the elements of the P matrix corresponding to *M. luisana* to characterize its phylogenetic neighborhood in each patch. This metric of phylogenetic neighborhood is correlated with both the species richness and the mean phylogenetic distance of *M. luisana* to all its neighbors in the patch (Fig. 1). More specifically in our system, vegetation patches with many closely-related species to *M. luisana* have high scores of phylogenetic neighborhood while patches with distantly-related species to *M. luisana* have low values (Fig. 1).

The phylogenetic similarity matrix was obtained from the community phylogeny generated with the help of the program Phylomatic as implemented in 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 our study species with those contained in a backbone phylogeny, which is the megatree based on the work of the Angiosperm Phylogeny Group 3 (Stevens, 2005). We then resolved the phylogenetic relationships at the species level of the Fabaceae, Cactaceae and Agavaceae families based on published phylogenies of Good-Avila et al. (2006), Simon et al. (2009), and Hernández-Hernández et al. (2011). Our final tree was fully resolved with the exception of two polytomies (Supplementary Material Fig. S2). We simultaneously resolved these 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 is based on an evolutionary, birth-death model and has been shown to be more realistic than traditional non-model-based approaches, like that used by the bladj algorithm in phylocom (Webb et al., 2008) which assign branch lengths by evenly distributing the undated nodes between the known parent age and the known daughter age. 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% of the node ages on the basis of published chronograms (Wikstrom et al., 2001; Good-Avila et al., 2006; Simon et al., 2009; Arakaki et al., 2011; see Supplementary Material Fig. S2 for node ages), 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% burnin, and randomly selected 100 fully-resolved dated trees. We used these 100 trees in the subsequent analysis to account for the topological and chronological uncertainty in our phylogenetic tree.

Data analyses

We first compared the three fitness components for *M. luisana* individuals growing alone and in association with other species using a Bayesian Generalized Linear Model with different distributions of errors (Poisson for seed production and binomial for seed viability and seed predation). The size of each *M. luisana* individual was also included in the model because large individuals may have more seeds than small ones.

Second, we tested whether the three *M. luisana* fitness components depended on its phylogenetic neighborhood as well as on its size by means of the same Bayesian Generalized Linear Models. Bayesian models allow different sources of uncertainty to be accommodated in the model. More specifically, we integrated topological and chronological uncertainty associated with phylogenetic reconstructions. To do this, we ran 100 Bayesian GLM models with the phylogenetic neighborhood scores calculated from the 100 phylogenetic trees. Then, we integrated over the posterior samples by drawing 1000 random samples across models (Longdon et al., 2011). The models were run with the help of MCMC techniques as implemented in the MCMCglmm package for R (Hadfield, 2010; R Development Core Team, 2011). We used the default priors and ran 13,000 MCMC iterations with a burn-in period of 3000 iterations. Convergence of the chain was tested by means of an autocorrelation statistic. The statistical significance of the factors in the model was

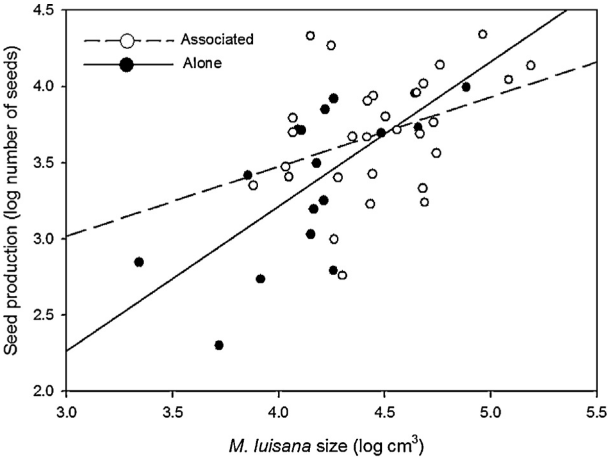

Fig. 2. *Mimosa luisana* shrubs produced more seeds when growing associated with other species (dashed line) than when growing alone (solid line) in small and medium sized shrubs but not in large shrubs.

estimated by calculating the 95% credible interval of their posterior distribution. Means are shown with standard errors throughout the manuscript.

Results

Microhabitat characteristics

Soils samples taken from under young *M. luisana* individuals (ca. 10 cm height) were not significantly different from those taken in open areas for any soil fertility measures (Supplementary Material Table S2). This suggests that improved soil conditions under *M. luisana* adults was not a cause of initial recruitment in the most fertile microhabitats.

The microhabitat amelioration produced by *M. luisana* adults did not change with the number of facilitated species in the vegetation patch (Supplementary Material Table S3)

Fitness estimates of M. luisana with and without neighbors

The mean number of seeds produced by *M. luisana* shrubs associated with other species was significantly higher (1.86 times greater) than by shrubs growing alone (Table 1; Fig. 2). The number of seeds increased significantly with shrub size and there was a significant although weak negative interaction between shrub size and the association condition of the shrub (associated vs. alone) (Table 1). This interaction occurred because the seed production benefits of growing associated with other species was evident in small and medium shrubs but not in large ones (Fig. 2).

Seed predation rate did not differ between individuals of *M. luisana* living with and without neighbors (0.22 ± 0.01 and 0.17 ± 0.03 respectively; Table 1). Seed predation was also independent of shrub size and the interaction between association condition and size (Table 1).

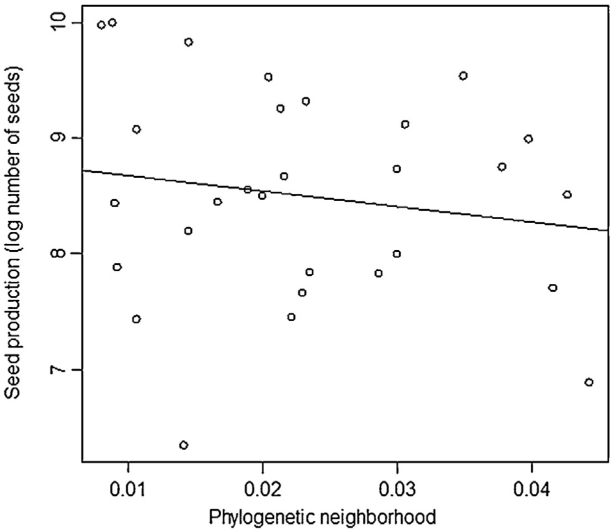

Fig. 3. Number of seeds produced by *Mimosa luisana* as a function of its phylogenetic neighborhood. The fitted line is drawn to illustrate the trend, but the appropriate statistical model can be seen in the Results section.

Mean seed viability differed significantly for *M. luisana* individuals growing with and without other species, being 1.47 times higher for shrubs associated with other plants (0.62 ± 0.03 and 0.42 ± 0.04 respectively; Table 1). This difference was independent of shrub size and the interaction between association condition and size Table 1).

Taking together these results, it can be estimated that *M. luisana* living with neighbors have 2.7 times (1.86 × 1 × 1.47) the fitness of individuals living alone.

Fitness estimates of M. luisana as a function of its phylogenetic neighborhood

The mean number of plant species associated with *M. luisana* was 3.7 ± 0.3 (range 1–10) species, and the mean number of individual plants was 6.8 ± 0.9 (range 1–42). *M. luisana* did not coexist with close relatives such as *A. compacta*, *Z. formosa*, *C. melanadenia* and *C. eryophylla* unless species of other families (Cactaceae, Asteraceae, Agavaceae, Acanthaceae, Bromeliaceae) were also present in the patch.

The number of seeds produced by *M. luisana* growing in vegetation patches varied according to the phylogenetic composition of the patch (Fig. 3), being high in patches with distantly related species and lower in patches harboring many closely-related neighbors (Fig. 3; Table 2). Interestingly, this correlation was independent of shrub size as there was no significant interaction between phylogenetic neighborhood and size (Table 2), indicating that seed production dependence on phylogenetic neighborhood was similar across all the shrub sizes.

Seed predation of *M. luisana* growing in vegetation patches was independent on its phylogenetic neighborhood, its size and

Table 1
Bayesian Generalized Linear Models testing for the effects of growth condition (without or with neighbors) and shrub size on three different fitness components of *M. luisana* individuals (seed production, seed predation and seed viability). Post-mean estimates are shown with their 95% credible intervals.

	Seed production	Seed predation	Seed viability
Intercept	3.64 [2.00, 5.17]	−1.23 [−1.77, −0.76]	−0.04 [−1.09, 0.21]
Condition	2.65 [0.91, 4.72]	0.45 [−0.18, 1.05]	0.96 [0.06, 1.77]
Size	1.1e−04 [4.3e−05, 1.8e−04]	1.67e−05 [−6.46e−07, 3.42e−05]	2.53e−06 [−2.05e−05, 2.77e−05]
Condition X size	−8.3e−05 [−1.5e−04, −1.1 e−05]	−1.73−05 [−3.63e−05, 1.83e−06]	−2.86e−06 [−3.18e−05, 1.96e−05]

Table 2

Bayesian Generalized Linear Model testing for the effects of phylogenetic neighborhood and shrub size on three different fitness components of *M. luisana* individuals (seed production, seed predation and seed viability). The model accommodates the phylogenetic uncertainty by integrating over the posterior samples of 100 models in which the phylogenetic neighborhood were calculated from 100 different phylogenetic trees. High phylogenetic neighborhood values occur when the abundance of species closely related to *M. luisana* in the patch is high. Post-mean estimates are shown with their 95% credible intervals.

	Seed production	Seed predation	Seed viability
Intercept	9.39 [6.61, 12.3]	−0.38 [−2.4, 2.0]	2.14 [0.80, 3.54]
Phylo neighb	−1.14e02 [−2.24e02, −1.54e01]	25.9 [−56.5, 121.1]	−47.89 [−111.85, −2.43]
Size	−3.14e−05 [−1.2e−04, 4.4e−05]	1.2e−05 [−4.7e−05, 7.1e−05]	−2.42e−05 [−6.77e−05, 1.11e−05]
Phylo neighb *size	2.7e−03 [−7.8e−04, 6.5e−03]	−7.2e−04 [−3.5e−03, 2.1e−03]	1.0e−03 [−6.98e−04, 2.83e−03]

from the interaction between phylogenetic neighborhood and size (Table 2).

Seed viability was high in patches with distantly related neighbors and lower in patches harboring many closely-related neighbors (Fig. 4). This relationship was significant and independent of shrub size. Also, there was no significant interaction between phylogenetic neighborhood and size (Table 2), indicating that seed viability dependence on phylogenetic neighborhood was similar across all the shrub sizes.

Discussion

Our study shows that the fitness of the key nurse in this semi-arid community, *M. luisana*, is higher when growing associated with their facilitated species than when growing alone. Contrary to the common finding that facilitation turns into competition with time (Miriti, 2006), we show that *M. luisana* continues to benefit in terms of its reproductive output, although the effect is less strong for large plants. The appearance of competitive effects only under the largest *M. luisana* shrubs is consistent with the results described for the columnar cactus *Neobuxbaumia tetezo* recruiting beneath *M. luisana* in our study system (Flores-Martínez et al., 1994). However, by moving beyond pairwise interactions, we find that the fitness of the nurse *M. luisana* is positively affected by the presence of several, distantly-related neighbors, and that this benefit applies for shrubs of all sizes. These results have implications for understanding species coexistence in communities by extending the concept of facilitation, which is usually considered to be an asymmetrical effect, to include mutualism, where both facilitated and nurse species benefit.

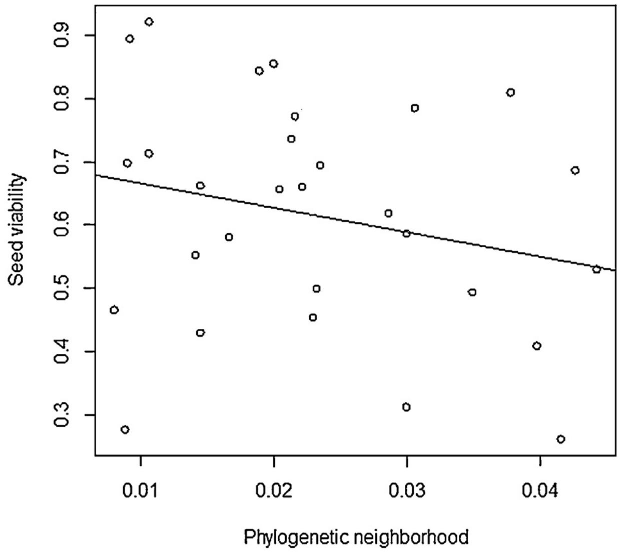

Fig. 4. Seed viability of *Mimosa luisana* as a function of its phylogenetic neighborhood. The fitted line is drawn to illustrate the trend, but the appropriate statistical model can be seen in the Results section.

In our system, the nurse *M. luisana* establishes in the open ground and ameliorates the microhabitat, enabling other species to establish and ultimately resulting in the formation of multi-specific patches (Valiente-Banuet and Verdú, 2008). Facilitated species increase their fitness through high seedling survival under *M. luisana*, where temperatures and evaporative demands are lower than in open ground and where no seedlings can survive (Valiente-Banuet and Ezcurra, 1991). Here, we demonstrate that fitness of nurse plants is also enhanced by the presence of neighbors, suggesting that plants may be helping each other. Nurses might be benefitting from the microclimatic amelioration produced by their facilitated plants, as occurred for example with *Retama sphaerocarpa* nurses benefitting from the soil improvement produced by their facilitated plants, ultimately resulting in higher biomass, total nitrogen content and higher water potentials (Pugnaire et al., 1996). However, in our study the number of facilitated species had no influence upon soil fertility or water availability, indicating that it was not these abiotic factors that caused the observed fitness effects upon *M. luisana*. However, micro-environmental amelioration via biotic factors can also be produced. Growing evidence exists that mutual benefit among neighboring plants may occur through the establishment of a common mycorrhizal network that enables resources to be shared (Selosse et al., 2006; Simmard et al., 2012). In our study area, this network is not random but is phylogenetically structured in such a way that closely related fungi tend to interact with the same plant species (Montesinos-Navarro et al., 2012b). Among all the plants in the network, *M. luisana* is a key species acting as a mycorrhizal and nutrient “resource island” from which a range of plants associated with it may benefit (Camargo-Ricalde and Dhillion, 2003; Montesinos-Navarro et al., 2012b). Once the mycorrhizal network is established, *M. luisana* may benefit from its facilitated plants by sharing their resources (Selosse et al., 2006). Unpublished experiments with fungicides show that the disruption of this mycorrhizal network significantly decreases the number of seeds (from 1014 ± 241 to 511 ± 132) and the leaf dry-matter content (from 18.1 ± 0.2% to 17.1 ± 0.3%) of *M. luisana* (L. Sortibrán, M. Verdú, M. & A. Valiente-Banuet, unpublished). These results suggest that resource sharing among plants is the mechanism underlying the higher fitness of *M. luisana* in vegetation patches. We have also shown that growing with neighbors allows *M. luisana* not only to produce more seeds but also more viable seeds, which is consistent with higher resource availability provided by multiple neighbors. The demographic fate of these seeds is not jeopardized by seed predators because the predation rate is unaffected by the presence of neighbors. The main predators of *M. luisana* seeds are bruchids, which feed exclusively upon legumes (Johnson and Siemens, 1995; Camargo-Ricalde et al., 2004; Romero-Nápoles et al., 2005); since closely related legumes were almost absent from the vegetation associated with *M. luisana*, they had no effect upon predation rates.

In short, contrary to the commonly reported outcome that facilitation turns into competition with time (Miriti, 2006; Schöb et al., 2014), we find mutually positive interactions that allow the nurse shrub to increase its fitness. But not all the neighbors are equivalent for a given plant species. For example, the performance of facilitated seedlings is dependent on the identity of the nurses (Castillo and Valiente-Banuet, 2010; Castillo et al., 2010). Such specificity has a strong phylogenetic component because closely related facilitated species tend to recruit under the same nurses, indicating that seedlings completely depend on the regeneration niche provided by specific nurse species (Verdú et al., 2010). Of these, *M. luisana* is a hub in the facilitation network that may facilitate up to 48 species in the community we studied (Verdú and Valiente-Banuet, 2008). We found that the fitness of the nurse *M. luisana* was higher when the neighboring plants were distantly related to it. This demonstrates that lifetime fitness is affected by the species that become established. As most mutualisms, facilitation would be a diffuse mutualism involving multiple species interacting (Palmer et al., 2003). Contrary to the traditional approach to mutualisms, which considers interactions between pairs of species in isolation, our results suggest that fitness is affected by multiple partnerships, as has also been shown in other systems (Palmer et al., 2010). To unambiguously assess that facilitation is a mutualism, the genetic basis of relevant traits associated to facilitation should be identified. Although we do not have such evidence, promising new evidence indicates that phenotypic differences in facilitative effects of a nurse species have a genetic basis (Michalet et al., 2011).

Three non-exclusive mechanisms potentially explaining why distantly related species enhance fitness of *M. luisana* are (i) competition release, (ii) resource sharing, and (iii) enemy escape. Competition is reduced when niches of coexisting species do not overlap. As functional and ecological similarities are usually shaped by patterns of common ancestry, phylogenetic unrelatedness is a good proxy of ecological differentiation (Wiens and Graham, 2005; but see Cahill et al., 2008; Mayfield and Levine, 2010). Consequently, more distantly related species in the vegetation patch would reduce niche overlap, reducing at the same time competition (Valiente-Banuet and Verdú, 2008). In our case, the reduction of competition in phylogenetically diverse neighborhoods may allow *M. luisana* to increase its reproductive output. Competition release in the presence of distantly related partners may also explain why close relatives of *M. luisana* only coexisted with it in the presence of other, unrelated species. In an adjacent community, Castillo et al. (2010) also reported indirect effects through distantly related species to explain the coexistence of close relatives within the same vegetation patch. However, it should be noted that competition release cannot explain why the lowest fitness was detected in nurses growing alone. As our results clearly indicate that living with other species enhances nurse fitness, we should move from explanations based only upon competition to consider the possibility that plants are helping each other.

The idea that resource sharing can be maximized in phylogenetically diverse neighborhoods would explain why *M. luisana* reproduced best when associated with less related species. There is growing evidence that belowground process involving plant–mycorrhizal interactions might be operating in the facilitation processes (Van der Heijden and Horton, 2009; Van der Putten, 2009; Selosse et al., 2006; Montesinos-Navarro et al., 2012a,b; Simmard et al., 2012). Specifically, the existence of a phylogenetically and therefore functionally diverse rhizosphere has been shown to contribute to a high plant productivity (Bever, 2002; Maherali and Klironomos, 2007). Interestingly, *M. luisana* belongs to a family that benefits more than most others from mycorrhizal fungi, because of the high phosphorus requirement of leguminous plants to support symbiotic nitrogen fixation (Scheublin et al., 2007). In the extremely low-resource environment we studied (e.g. low rainfall and low P content in soils), the benefits from sharing a mycorrhizal network with facilitated, distantly-related species may be particularly high.

Enemies may also be avoided in a diverse phylogenetic neighborhood. Although we have shown that this is not the case for seed predators, other enemies like pathogens may infect a set of more closely related hosts because of their shared phylogenetic predilections (Webb et al., 2006; Yguel et al., 2011). Therefore, phylogenetically distant plant species can promote an increase of fitness by decreasing the presence of plant pathogens (Van der Putten, 2009). Future research on the effects of other enemies on the fitness of the *M. luisana* living in different phylogenetic neighborhoods will help to understand the selective pressures favoring the reciprocation of benefits between plant species we have detected.

Although these ideas seem plausible, the observational nature of our study means that we cannot exclude the possibility that other factors were responsible for the observed benefits to *M. luisana* of growing in species-rich patches. In principle, one could study the fitness effects of experimentally removing neighbors. However, below-ground interactions, which may be responsible for the observed patterns, might respond very slowly to such perturbations, with the established soil community persisting for years or even decades after individual plants had been removed (Van der Putten, 2009). One potentially confounding factor in the relationship between *M. luisana* seed production and coexistence with other plants is microclimatic variation. For example, *M. luisana* colonizing stressful microclimates would have limited both its seed production and the coexistence with other species due to resource competition. In contrast, in less stressful microclimates seed production may be higher and the coexistence with other species allowed due to the lack of resource competition. However, we have discarded this confounding effect by showing that microhabitat amelioration is a direct effect, and not the cause, of nurse establishment. Furthermore, that confounding effect could not explain why nurse fitness increases with phylogenetic distance to its neighbors.

Community ecology implications

In contrast to theoretical models showing that communities driven by positive interactions tend to extinction (Kefi et al., 2008 and references therein), our results support the view that mutualistic interactions minimize competition and increase biodiversity (Wilson and Nisbet, 1997; Okuyama and Holland, 2007; Bastolla et al., 2008). We have shown that living in diverse neighborhoods produces fitness benefits for the nurse plants, though we know little about the demographic consequences of this effect. One possible consequence might be mediated through increased herbivory, since seeds of *M. luisana* germinate more readily after passage through the gut of a herbivore such as a goat (Giordani, 2008). Since these mammals defecate in open spaces and away from the mother plant, the only suitable sites for seedling establishment, they act as efficient seed dispersers, which may have a positive demographic effect on *M. luisana* populations. Patch-specific matrix models to test the influence of the phylogenetic neighborhood on the demography of nurse plants (Miriti et al., 2001) could help to understand the evolutionary potential of facilitation as a mechanism allowing the populations to escape extinction (Valiente-Banuet et al., 2006).

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ppees.2014.07.001.

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