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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