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Nurse effect and soil microorganisms are key to improve the establishment of native plants in a semiarid community

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ABSTRACT

Facilitation by the nurse effect can occur through an amelioration of environmental stress. Plant-microorganism interaction, however, is another key facilitation mechanism of the nurse effect, but is by far the least documented. Here we tested if microclimatic mitigation and soil microorganisms isolated from the root-zone of the nurse shrub *Porlieria chilensis* can increase the establishment of other native plants in a semiarid community. We conducted field and greenhouse experiments to evaluate the direct and indirect effects of the presence of *P. chilensis* on the survival and growth of three native plants. In the field experiment, we compared the survival and growth of transplanted individuals beneath nurses and outside of them in pots filled with soil from both microsites (beneath and outside nurses). Finally, in the greenhouse experiment we grew native plants in soil taken from both microsites (below and outside nurses) and with and without soil microorganisms (sterilization process). We found a clear and significant nurse effect of *P. chilensis* on the tested species through of amelioration of climatic (air temperature, soil moisture, and solar radiation) and edaphic (nitrogen availability) conditions, increasing the performance of these native species. Moreover, performance and establishment were enhanced when soil was kept with microorganisms. Thus, nurse effect mediated by microclimatic amelioration, edaphic improvement and presence of soil microorganisms could be key mechanisms to increase the establishment of native plant species in semiarid communities of central Chile.

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1. Introduction

The nurse plant syndrome occurs when a plant generates microclimatic conditions less stressful for other plants compared with open spaces, enhancing the survival or performance of these last (see Flores and Jurado, 2003). This interaction is now a well-documented phenomenon in a broad range of habitats like arid and semi-arid (Tewksbury and Lloyd, 2001; Good et al., 2014), alpine (Cavieres et al., 2005; Badano et al., 2015), coastal dune (Shumway, 2000; Tirado and Pugnaire, 2003), Mediterranean (Verdú and García-Fayos, 2003; Armas et al., 2011), and Antarctic (Molina-Montenegro et al., 2013) ecosystems.

The nurse plant syndrome seems to be critical in dry habitats. Significant amount of the reported examples in the literature come from such environments (see, Flores and Jurado, 2003; van Zonneveld et al., 2012; Good et al., 2014), supporting the general hypothesis that facilitation increases in importance with increasing environmental severity (Bertness and Callaway, 1994; Brooker and Callaghan, 1998; but see Michalet et al., 2014). In semi-arid environments, facilitation usually involves increased water or nutrient availability (Holzapfel and Mahall, 1999; Tracol et al., 2011). The soils under nurse plants commonly have a higher nutrient content, for example, organic matter, nitrogen and potassium (Pugnaire et al., 2004), than the surrounding open areas, and thus induce a relative increase in seedling growth (Pugnaire et al., 1996, 2004;

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Tirado and Pugnaire, 2003). In addition, the shade from nurse plants reduces thermal amplitudes and decreases soil water evaporation (Domingo et al., 1999), which may further facilitate germination of seeds and growth of seedlings.

Arid and semi-arid environments are characterized by low water availability, and usually low nutrient content in the soil. The water (osmotic) stress is mainly due to low precipitation and in some place to high salinity, and the low nutrients could be attributed to low N-fixing activity, also related to water availability in the soil (see Divito and Sadras, 2014) as well as to other factors related with soil type and parental material. In these stressful environments, the association with microorganisms seems to be essential for plant survival and growth (Aguilera et al., 1999; Bashan and de-Bashan, 2010; Armada et al., 2014). For instance, it has been reported that the presence of species of family Fabaceae that usually associate with N-fixing bacteria will locally increase N availability, promoting its uptake and the growth of other species. Moreover, there is an increasing of water availability, commonly found for nurse species, and this situation can also increase the activity of N-fixing bacteria (Divito and Sadras, 2014). On the other hand, association with microorganisms, such as mycorrhizae, could enhance water uptake and thus reducing water stress (Ortega et al., 2004; Smith and Read, 2008; Harris-Valle et al., 2009). In addition, fungal hyphae provide plants with a wide network in the soil and improve the water status with little cost to the host plants (Smith and Read, 2008).

It is well known that most of the plant species tend to associate with microorganisms especially from the soil (see, Smith and Read, 2008). This symbiotic association usually results in several ecological benefits to the plant such as increased tolerance to abiotic conditions (Harley and Smith, 1983; Steinfeld et al., 2003; Ortega et al., 2004; Atala et al., 2012), improved nutrients content or uptake (Simard and Durall, 2004), and also protection against pathogenic fungi and bacteria (Newsham et al., 1995). Other, but less studied, aspect of plant–microbial interaction is the indirect facilitating effect mediated by microorganisms on plants. It has been found that below certain nurse species, a greater abundance and diversity of beneficial microorganisms can be found compared to bare ground (Casanova-Katny et al., 2011; Molina-Montenegro et al., 2015). Evidence for facilitation via microorganisms has been documented in stressful environments such as Alpine environments (Molina-Montenegro et al., 2015), tundra (Ruotsalainen et al., 2010), and semi-arid formations (Horton et al., 1999). All these environments have in common the presence of water stress and low nutrient availability, both aspects improved by the association with microorganisms (Harley and Smith, 1983; Steinfeld et al., 2003; Smith and Read, 2008; Atala et al., 2012).

Porlieria chilensis I.M. Johnst. (Zygophyllaceae) is a vulnerable endemic shrub that grows in Chile between ~30 and 34°S (Marticorena and Rodríguez, 2011). It can be found from the coastline to about 800–1000 m a.s.l. in stony and exposed sites (Gutiérrez et al., 1993; Riedemann and Aldunate, 2014). It can reach 4 m high and 3 m wide with a canopy of small composite leaves that folds in the afternoon and unfolds in the morning (Gutiérrez et al., 1993; Riedemann and Aldunate, 2014). In Coquimbo region in Chile (~30–32°S), *P. chilensis* is found in semi-arid communities dominated by Cactaceae, and native shrubs. It has been shown that this shrub increase the soil water availability in soils under their canopy (Muñoz et al., 2008). In addition, Gutierrez et al. (1993) demonstrated that *P. chilensis* accumulate six times more nitrogen, three times more organic material, and two times more phosphorus under their canopy compared with surrounding open areas. Thus, *P. chilensis* has been considered as a nurse plant for other vascular plants inhabiting the arid and semi-arid ecosystems of Chile (Gutiérrez et al., 1993).

Here we tested the direct and indirect nurse effect of the shrub *P. chilensis* on native plant species *Flourensia thurifera* (Asteraceae), *Puya berteroniana* (Bromeliaceae), and *Senna cumingii* (Fabaceae) in a semi-arid community in northern Chile. We selected these species because all of them possess high abundance in the study site and are distributed both beneath and outside of nurses of *P. chilensis*. Specifically, we assessed if: *i*) microclimatic modifications induced by the presence of *P. chilensis* nurses improve the survival and growth of these native plant species and *ii*) the presence of soil microorganisms from *P. chilensis* improve the survival and growth of these native plant species.

2. Methodology

The study was conducted in the Parque Nacional Bosque Fray Jorge (30°S), IV Región de Coquimbo, Chile. The study site was located in an interior valley at 300 m a.s.l, about 6 km east of the Pacific coast, on the eastern side of the coastal mountain range. The study area is a transitional zone between the central Mediterranean region and the hyperarid Atacama Desert to the north of Chile. The climate is semiarid Mediterranean, with 145 mm of annual precipitation falling mainly in the austral-winter months, while austral-summer months are warm and dry but fog contributes significant with additional inputs of moisture during many months (Kummerow, 1966; Tracol et al., 2011). The maximum daily temperature is 24 °C in summer and the minimum daily temperature is 4 °C in winter (Tracol et al., 2011).

The xerophytic plant community is characterized by spiny drought-deciduous (sclerophyllous) and evergreen shrubs 2–3 m in height, with an herbaceous understory and low vegetated sandy areas. Major species of shrub layer include *P. chilensis*, *Proustia cuneifolia* (Asteraceae) and *Adesmia bedwellii* (Fabaceae), which form the characteristic vegetation pattern of the “matorral” (Gutiérrez et al., 1997). The herbaceous layer corresponds mainly to an ephemeral community, with annuals, geophytes and several perennial species (Gutiérrez et al., 1993).

2.1. Microclimatic and edaphic measurements

To assess whether *P. chilensis* nurses ameliorate microclimatic and edaphic conditions beneath their canopies, we measured temperature, soil moisture, nutrient content, and solar radiation beneath and outside of them. We recorded temperature on twenty randomly selected nurses and on twenty points on bare ground adjacent to each nurse. At each selected point, temperature was measured at 10 cm above substrate with a WK072 non-contact infrared thermometer (0.1 °C resolution). Measurements were taken between 12:00 and 16:00 h, and were made simultaneously in the two microhabitats (nurses and surrounding bare ground). Soil moisture (soil matric potential) was measured in ten randomly selected nurses of similar size (1.8–2.4 m diameter of protected canopy) and in ten points on the bare ground adjacent to each nurse. At each sampling point, a soil tensiometer (2725 series Jet Fill Tensiometer; Soil moisture equipment Corp., Santa Barbara, CA, USA) was dug into the soil at 10–12 cm depth. Tensiometers were placed at 12:00 h and, after a stabilization period of 1 h, the soil matric potential was recorded. We also compared nitrogen availability in the soil between ten *P. chilensis* nurses and ten randomly selected points on the bare ground. A soil sample at 15–20 cm depth (ca. 300 g) was taken beneath nurses and on bare ground. For nitrogen availability, soil samples were stored in hermetic plastic bags and sent for analyses to determine the concentration of nitrate (NO_3^-) and ammonium (NH_4^+) following the colorimetric techniques proposed by Robarge et al. (1983) and Longeri et al. (1979), respectively. We measured photosynthetic active radiation (PAR) in

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