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Factors affecting cactus recruitment in semiarid Chile: A role for nurse effects?

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A B S T R A C T

The nurse-protégé hypothesis states that adult plants of one species provide micro-environmental conditions that favor the establishment of seedlings of a second species with no effect for the first species. Several studies suggest this effect should be prevalent in arid and semiarid zones as adult plants often provide shelter from low moisture and high temperature. *Echinopsis chiloensis* and *Eulychnia acida* are endemic columnar cacti that inhabit the arid and semiarid zones of Chile. In this study, we examined the pattern of recruitment of both cactus species at Reserva Nacional Las Chinchillas, located ~60 km east from the Pacific coast. We determined number, growth and survivorship of young cacti (<30 cm height) through biannual monitoring between 2009 and 2012 in microhabitats that strongly differ in their abiotic variables (minimum and maximum temperature and mean relative humidity, moisture content, and physical and chemical soil characteristics), under five different shrub species and in open spaces, and examined the association of these cacti with potential nurse plants. Most young cacti occurred under shrubs, the microhabitat having the lowest mean and maximum temperatures and the highest relative humidity. In particular, *E. chiloensis* and *E. acida* were found under the shrubs *Flourensia thurifera* and *Bahia ambrosioides*, respectively, in a higher frequency than expected by chance, suggesting that these shrub species behave as nurse plants through species-specific effects than are not accounted for by differences in soil nutrients.

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Introduction

The local abundance of cactus populations depends in a large extent on their seed germination and seedling survival (Godínez-Álvarez et al., 2003). During the early stages of the life-cycle, cactus seedlings are often exposed to extreme environmental conditions such as drought, hot soil temperatures and low moisture content. This makes this stage one of the most critical to maintain viable populations (Valiente-Banuet and Ezcurra, 1991). The establishment of seedlings under the canopy of other plant species (Flores and Jurado, 2003) may counteract the negative effect imposed by desiccation and high soil temperatures. For instance, several studies have reported that nurse plants are important for seedling establishment and recruitment of cacti (e.g., Franco and Nobel, 1989; Mandujano et al., 1998; Turner et al., 1966; Valiente-Banuet and Ezcurra, 1991; see review in Rojas-Aréchiga and Vázquez-Yanes, 2000) and other plants in arid habitats (e.g., Sanjerehei et al., 2011). Although many authors suggest diverse benefits provided by nurse plants, such as (i) protection against direct solar radiation (Valiente-Banuet et al., 1991a, 2002), (ii) reduction of daytime high soil surface temperatures (Franco and Nobel, 1989), (iii) reduction of night-time and winter heat loss beneath their canopy (Nobel, 1980), (iv) reduction of wind (Drezner, 2006), (v) addition of nutrients to the soil (Franco and Nobel, 1989) and (vi) protection against herbivores (Muro-Pérez et al., 2011), studies are rarely the result of experimental work, which implies that the mechanisms by which nurse plants benefit cactus recruitment remain poorly understood.

In spite of the potential importance of nurse plants for cactus recruitment and conservation (Guerrero et al., 2012), empirical evidence is almost entirely restricted to the arid zones of North America (see review in Godínez-Álvarez et al., 2003; Muro-Pérez et al., 2011; Suzán-Azpiri and Sosa, 2006; Valiente-Banuet et al., 1991b). Examples of this association for North American cacti are: (i) the cactus *Carnegiea gigantea* (Engelm) Britton and Rose (Cactaceae) and its nurse plants *Ambrosia deltoidea* Torr. (Asteraceae), *Cercidium microphyllum* (Torr.) Rose and I. M. Johnst (Fabaceae), *Encelia farinosa* Torr. and A. Gray (Asteraceae), *Larrea tridentata* (DC) Coville (Zygophyllaceae), *Olneya tesota* A. Gray (Fabaceae) and *Prosopis juliflora* (Sw) DC (Fabaceae), which offer shade (Turner et al., 1966), frost protection (Hutto et al., 1986) and predation avoidance (Franco and Nobel, 1989), and (ii) the

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cactus *Neobuxbaumia tetetzo* (Coulter) Backeberg with *Mimosa luisana* Brandegee (Mimosaceae) as nurse plant, which offers shade (Valiente-Banuet and Ezcurra, 1991) and increases the availability of soil nutrients (Carrillo-García et al., 2000). Even though the stressful environmental conditions observed in South American arid regions suggest that nurse effects favoring cactus recruitment may not only occur in North America, there is a conspicuous lack of knowledge of this phenomenon in the southern hemisphere (but see Larrea-Alcázar and Soriano, 2008; López and Valdivia, 2007).

The richness in columnar cacti species of Chilean arid and semi-arid zones is relatively low as compared to Mexico and Argentina (Ortega-Baes and Godínez-Álvarez, 2006), being *Echinopsis* and *Eulychnia* the most diversified genera (Hoffmann and Walter, 2004; Medel et al., 2010). *Echinopsis chiloensis* (Colla) Fried. and Rowl. and *Eulychnia acida* Phil., are two widely distributed endemic columnar Cactaceae species that inhabit mainly equatorial-facing slopes in semiarid Chile (Medel, 2000). Currently, the two species do not present important conservation problems (Hoffmann and Walter, 2004), being categorized as of "least concern" according to Hunt (2006). According to Ortega-Baes and Godínez-Álvarez (2006), Chile has a very high proportion of endemic cactus species, which corresponds with a general richness in endemic species of the country, relative to its area. Regarding potential nurse species facilitating establishment of cactus seedlings, several shrub species may, in principle, provide good quality shade due to their architecture and highly dense canopy (Gutiérrez and Squeo, 2004), which can act as a collecting trap for organic debris carried by the wind, as it is, e.g., reported for the shrub *Porlieria chilensis* Johnst. (Zygophyllaceae) in semiarid Chile (Gutiérrez et al., 1993). Several other drought-deciduous shrub species that inhabit the semiarid region of Chile might play as well an important role for cactus seedling establishment and recruitment. Notwithstanding, one of the most abundant native shrub species in these semiarid environments, *Flourensia thurifera* (Molina) DC., Asteraceae, has been reported to reduce plant species richness (e.g., forbs, grasses, and other shrub species) in the surroundings, due to the presence of allelopathic compounds in its leaves and stems (Fuentes et al., 1987; Faini et al., 1997); therefore, a multi-factorial approach should be considered when studying the role of putative nurse plants in arid and semiarid Chilean communities.

In this study, we examine the association of *E. chiloensis* and *E. acida* with different shrub species in an attempt to identify potential nursing effects on cactus recruitment. To gain insight into the mechanisms involved, we record abiotic variables among microhabitats. More specifically, we attempted to answer the following questions: (i) Do *E. chiloensis* and *E. acida* show a different pattern of recruitment under shrub species and in open spaces? (ii) Do abiotic conditions differ among microhabitats? (iii) Do cactus growth and mortality show correlations to the microhabitat under which the seedlings occur? These questions relate to the more general one, (iv) Is there evidence suggesting a role for nurse effects in the establishment and survival of cacti in Chile?

Materials and methods

Study site

This study was carried out at the Reserva Nacional Las Chichillas (31°30′ S, 71°06′ W), a protected area located ~60 km east from the Chilean Pacific coast. The climate of the study site is of a semiarid Mediterranean-type with most rainfall concentrated between June and August (di Castri and Hajek, 1976). Mean annual precipitation is 185.0 mm, with ample variation across

years, alternating between long droughts and unusual years of high rainfall which latter seemingly are associated to El Niño events (di Castri and Hajek, 1976). The vegetation is characterized by thorny shrubs (Luebert and Pliscoff, 2006) mainly represented by the shrub species *Flourensia thurifera*, *Bahia ambrosioides* Lag. (Asteraceae), and *Porlieria chilensis* (Medel et al., 2004). The cactus species consist on the columnar *E. chiloensis* and *E. acida*, and the spherical *Cumulopuntia sphaerica* (C.F. Först.) E.F. Anders. and *Eriosyce aurata* (Pfeiffer) Backeb (Hoffmann and Walter, 2004; Martínez del Río et al., 1995; Medel et al., 2002; Medel, 2000).

In the Reserve area, the reproduction of *E. chiloensis* and *E. acida* is relatively synchronous with the blooming season extending from early September to mid-November, and the fruiting season from mid-October to late December or mid-January (Medel, 2000). *E. chiloensis* presents arborescent growth with basitonic structure, being generally very branched or with several trunks emerging near the base (Medel, 2001). *Eulychnia acida* presents arborescent growth with mesotonic structure, branched and usually with only one trunk (Hoffmann, 1989). Scarce information has been provided about demography and growth of columnar cacti, but Hoffmann (1989) suggests that natural regeneration may be difficult and growth rate can be extremely low.

Recruitment of young cacti

In May 2009, we sampled 131 young cacti (<30 cm height) of *E. chiloensis* and *E. acida* at north-facing slopes of the Reserve. We measured the height of each young cactus with a tape (0.1 cm precision). The microhabitat was categorized according to the shrub species where young cacti were found or as open spaces. The recruitment was defined by the total number of young cacti found under the different species of shrubs and in the open spaces, respectively. In addition, in the same north-facing slopes, we set ten 50 m line transects to estimate the relative microhabitat availability and the relative abundance of every shrub species in the study site. Shrub species comprised *Adesmia microphylla* Hook. and Arn. (Fabaceae), *Cordia decandra* Hook. and Arn. (Boraginaceae), *Ephedra chilensis* K. Presl. (Ephedraceae), *Krameria cistoidea* Hook. and Arn. (Krameriaceae), *Senna cumingii* Hook. and Arn. (Fabaceae), *B. ambrosioides*, *Bridgesia incisifolia* Bert. ex Cambess. (Sapindaceae), *F. thurifera*, *Heliotropium stenophyllum* Hook. et Arn. (Boraginaceae), and *P. chilensis*.

Abiotic conditions

At each microhabitat where young cacti were found (below five different shrub species and in open spaces), we recorded the temperature and relative humidity using data-logger sensors (HOBO Pro v2/U23-002) placed at ground level during 24 h ($N = 9$ replicates per microhabitat). The variables were recorded every 30 min during January.

In addition to the overall characterization of microhabitats, we collected soil samples under the canopy of the shrub species and in the open sites to quantify the water content gravimetrically ($N = 5$ samples per microhabitat, 30 in total). Samples were weighed *in situ* (0.1 g precision) and stored in sealed plastic bags. At the laboratory, soil samples were dried at 70 °C during 72 h and weighed again. Additional soil samples were collected ($N = 5$ samples per microhabitat, 30 in total) to carry out basic chemical and physical analyses (INIA, 2006). Specifically, we characterized pH, using a combined electrode and pH-meter, in the undiluted extract of the wetted soil sample. Then, each sample was extracted with water at 20 °C ± 1 °C in a soil:water ratio of 1:5 to dissolve salts. Electrical conductivity of the filtered extract was measured. To quantify total nitrogen, we used the Kjeldahl digestion, and the "P-Olsen"

method to measure phosphorus. Cation determination (Na$^+$, K$^+$, Mg^{2+} and Ca^{2+}) was performed by Ion-Exchange High Performance Liquid Chromatography (IE-HPLC).

Growth and survivorship assessment of young cacti

We tagged and geo-referenced 131 young cacti to estimate growth (by quantifying the height of each young cactus with a tape measure, 0.1 cm precision) and survivorship in a three-year period (from May 2009 to May 2012). Additionally, we recorded by inspection the potential cause of cactus mortality such as desiccation, herbivory, parasitism or fungal infection.

Statistical analyses

The probability of occurrence of young cacti under a particular shrub species and in open spaces was compared by likelihood-ratio G-tests of goodness of fit, using the relative availability of the microhabitats (shrub species and open spaces) in the field as expected values under a random recruitment process (Sokal and Rohlf, 1995).

The abiotic conditions (temperature and relative humidity) of microhabitats were compared using one-way ANOVA with *a posteriori* Tukey test. Data were log-transformed to fulfill the requirements of parametric statistics (Sokal and Rohlf, 1995). The water content and ionic composition of the soil (each soil parameter separately) were compared using Kruskal–Wallis tests with *a posteriori* multiple comparisons of mean ranks for all groups to detect specific differences among microhabitats (Sokal and Rohlf, 1995).

The growth of young cacti was analyzed for each cactus species by one-way ANOVA, using microhabitat type as the fixed factor. Data were log-transformed to fulfill the requirements of parametric statistics. The mortality of young cacti for each cactus species was compared using Fisher's exact test (Sokal and Rohlf, 1995).

Table 1
Relative abundance of the shrub species and open spaces in the study site, and occurrence (%) of *E. chiloensis* and *E. acida* in each microhabitat.

Microhabitat	Relative abundance (%)	Occurrence of *E. chiloensis* (%)	Occurrence of *E. acida* (%)
Open spaces	57.3	39.4	27.0
F. thurifera	32.7	48.9	56.8
B. incisifolia	8.9	6.4	5.4
P. chilensis	0.8	3.2	0
B. ambrosioides	0.3	1.1	10.9
H. stenophyllum	0	1.1	0

Results

Recruitment of young cacti

Results from transects showed that open space was the microhabitat with the highest relative representation of young cacti, followed by the shrubs (Table 1). Overall, most recruitment of young cacti occurred under the shrub *F. thurifera*, in part resulting from the high relative abundance of this species in the field, followed by open spaces and by the other shrubs (Table 1). Considering the relative abundance of microhabitats it becomes obvious that some shrub species must have had influenced the chance of recruitment beyond their availability in the study site. For example, young *E. chiloensis* were associated with *F. thurifera* more frequently than expected by chance (Fig. 1), which suggests that this shrub species might act as nurse plant for *E. chiloensis*. Similarly, although the occurrence of young *E. acida* under *B. ambrosioides* was relatively low, *E. acida* was observed under this shrub in a higher proportion than expected by chance. On the contrary, the percentage of occurrence of young *E. chiloensis* under *B. incisifolia* was lower than expected by chance, suggesting some kind of inhibitory process (Fig. 1).
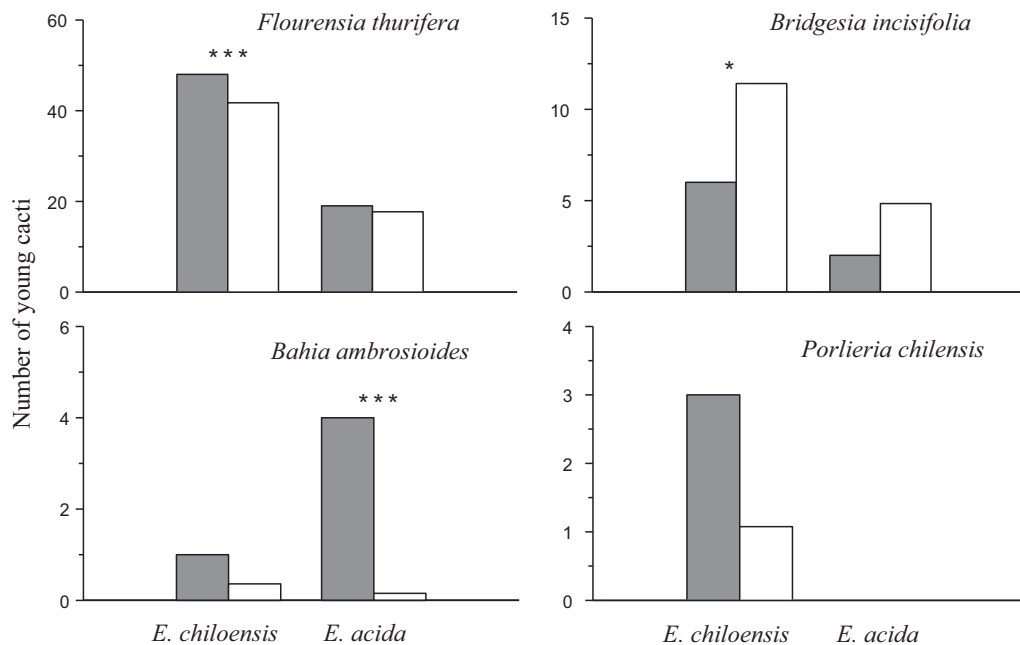

Fig. 1. Number of young cacti of *E. chiloensis* and *E. acida* found in association with shrub species. Dark bars represent the observed number of young cacti under shrubs. White bars indicate the expected number of young cacti under shrubs based on the relative abundance of the shrub species in the field. ***$P < 0.001$, *$P < 0.05$.

Table 2
Abiotic conditions (mean ± SE) in the microhabitats. T: temperature, RH: relative humidity. Results from one-way ANOVA (*F*, *P*) with *a posteriori* Tukey tests. Different letters indicate significant differences at $P < 0.05$.

Abiotic variable	Under *F. thurifera* canopy	Under *B. ambrosioides* canopy	Under *P. chilensis* canopy	Under *B. insicifolia* canopy	Under *H. stenophyllum* canopy	In open spaces (unshaded)	$F_{5,48}$	P
Min T (°C)	17.5 ± 0.5	17.4 ± 0.8	16.2 ± 0.8	16.7 ± 0.6	17.9 ± 0.7	16.8 ± 0.4	0.97	0.448
Max T (°C)	49.8 ± 2.9[a]	45.0 ± 1.8[a]	44.5 ± 2.7[a]	43.2 ± 1.6[a]	46.7 ± 1.9[a]	60.1 ± 1.4[b]	7.54	<0.001
Mean T (°C)	28.2 ± 0.7[ab]	26.7 ± 0.4[ab]	25.5 ± 1.0[a]	26.8 ± 0.5[ab]	28.6 ± 1.2[b]	32.8 ± 0.5[c]	11.37	<0.001
RH (%)	39.2 ± 1.2[ab]	41.0 ± 1.9[ab]	45.3 ± 1.9[a]	41.7 ± 1.6[a]	41.7 ± 4.5[ab]	33.3 ± 1.9[b]	3.61	0.007

Table 3
Parameters of physical and chemical characteristics of soil samples (mean ± 1 SE, $N = 5$) collected under different shrub species and in open spaces. EC: electric conductivity. Results of phosphorus, total nitrogen, Na⁺, K⁺, Mg²⁺ and Ca²⁺ are expressed in mg kg⁻¹.

Variable	*F. thurifera*	*B. ambrosioides*	*P. chilensis*	*B. incisifolia*	*H. stenophyllum*	Open spaces
EC (μS cm⁻¹)	115.8 ± 14.1	158.0 ± 25.9	268.7 ± 116.5	106.0 ± 42.4	172.2 ± 78.2	51.6 ± 17.7
pH	7.2 ± 0.1	6.9 ± 0.1	7.1 ± 0.2	6.8 ± 0.2	7.0 ± 0.1	7.1 ± 0.3
Phosphorus	38.9 ± 1.9	36.2 ± 3.4	51.1 ± 9.9	31.0 ± 4.5	43.1 ± 7.3	23.3 ± 3.6
Total nitrogen	392.5 ± 119.9	672.7 ± 196.2	1548.9 ± 408.8	544.7 ± 215.8	789.9 ± 220.1	226.8 ± 73.7
Na⁺	31.8 ± 14.4	39.9 ± 16.5	65.9 ± 45.8	12.9 ± 5.8	125.7 ± 91.9	25.0 ± 10.5
K⁺	75.1 ± 31.8	114.3 ± 59.3	34.5 ± 20.4	7.5 ± 1.9	27.5 ± 18.2	23.8 ± 11.0
Mg²⁺	13.8 ± 4.3	21.2 ± 4.4	48.0 ± 28.2	12.8 ± 3.7	28.0 ± 12.7	8.5 ± 4.1
Ca²⁺	38.9 ± 9.4	48.6 ± 10.5	31.2 ± 11.4	22.5 ± 11.2	11.5 ± 2.6	21.6 ± 9.2

Abiotic conditions of microhabitats

The microhabitats differed in their abiotic conditions. Overall, lower temperatures were recorded under shrubs than in open spaces (Table 2). The highest mean temperature was recorded in open spaces, where maximum temperatures up to 60 °C were recorded. Under the shrub canopies temperatures did not exceed 50 °C. In addition, relative humidity was significantly lower in the open (Table 2).

The soil water content significantly differed among the microhabitats ($H_{5,30} = 11.45$, $P = 0.043$). This was most obvious under *B. incisifolia* compared to open spaces, with a significantly higher soil water content under the shrub (*post hoc* test, $P = 0.038$). The physical and chemical characteristics of soil samples (Table 3) showed slightly significant differences among microhabitats in phosphorus ($H_{5,30} = 10.82$, $P = 0.055$) and total nitrogen ($H_{5,30} = 10.71$, $P = 0.057$). The marginal effect in phosphorous amount resulted primarily from the difference between *P. chilensis*-affected soil and samples from open spaces (*post hoc* test, $P = 0.06$). Also the differences in total nitrogen were most obvious in comparisons between *P. chilensis* and open space samples (*post hoc* test, $P = 0.034$).

Growth and survivorship of young cacti

In the three-year period, the height of *E. chiloensis* and *E. acida* increased (mean ± SE) 7.6 ± 0.5 cm and 6.7 ± 0.7 cm, respectively. Due to the low number of young cacti under some shrub species, which prevented assessment of species-specific associations, young cacti were grouped into three microhabitats for statistical analyses: open spaces, under *F. thurifera* and under the other shrub species. No significant difference in growth was detected among microhabitats for both cactus species (Table 4).

During the monitoring period, only six young cacti (three *E. chiloensis* and three *E. acida*) died due to herbivory, probably by rodents, and desiccation. Therefore, in the three-year period mortality reached to 3.3% and 8.8% for *E. chiloensis* and *E. acida*, respectively. Because few cacti were found dead, mortality analyses

are based on two only categories, open spaces and all shrub species combined. Mortality did not differ significantly between the microhabitats for both *E. chiloensis* ($P = 0.341$) and *E. acida* ($P = 0.624$).

Discussion

In this study we examined the pattern of occurrence of young cacti under different shrub species in arid Mediterranean-type habitats in Chile. In other countries, several studies have shown the importance of favorable microhabitats for cactus germination success and seedling establishment, suggesting the importance of nurse plant – seedling relationships (Flores and Jurado, 2003; Franco and Nobel, 1989; Rojas-Aréchiga and Vázquez-Yanes, 2000; Turner et al., 1966; Valiente-Banuet and Godínez-Alvarez, 2002). The observation that the young cacti of *E. chiloensis* and *E. acida* occurred more frequently than expected by chance under *F. thurifera* and *B. ambrosioides*, respectively, suggests that these shrub species may play a role facilitating cactus recruitment. This is consistent with previous studies documenting a key role of nurse plants for seed germination and seedling establishment in cacti (Godínez-Álvarez et al., 1999; Landero and Valiente-Banuet, 2010; Larrea-Alcázar and Soriano, 2008; Valiente-Banuet and Ezcurra, 1991). Valiente-Banuet et al. (1991a,b) gave evidence for a nurse effect for five cactus species under perennial shrubs, and showed a positive association of young cacti of *N. tetetzo* and *Mimosa luisana*, in the Zapotitlán Las Salinas' Valley, Mexico. In present study, the high proportion of young cacti of *E. chiloensis* and *E. acida* under some of the shrub species of the investigated site suggests also a "nurse plant syndrome" (Turner et al., 1966). The nurse-plant shrubs may act as "seed traps", when seeds are moved by wind or water (Sánchez-Salas et al., 2012) across the soil surface and accumulate under established plants (Flores and Jurado, 2003). Also seed disperser animals, birds perching on branches, could increase seed accumulation under the shrubs, which would explain in part the non-random distribution pattern of columnar cacti that can be observed in regions of high occurrence of them (McAuliffe, 1988;

Table 4
Total growth (cm) of *E. chiloensis* and *E. acida* under *F. thurifera*, other shrubs and in open spaces (mean ± SE). Results from one-way ANOVA (*F*, *P*).

Species	In open spaces	Under *F. thurifera*	Under other shrubs	F	N	P
E. chiloensis	8.17 ± 0.81	7.20 ± 0.62	7.18 ± 1.68	0.95	91	0.39
E. acida	7.00 ± 2.06	6.42 ± 0.74	7.00 ± 1.88	0.07	34	0.93

Sosa and Fleming, 2002). The correlative only evidence of this study, however, does not permit to rule out still other potential explanations for the observed patterns. For example, it is likely that soil conditions under the nurse plant could be more favorable for any plant species growing under the shrub canopy, including the putative nurse plant, and such conditions may have been there even before any putative nurse plant germinated. Also the microtopography may exert some influence on plant distribution in this open vegetation type, if seeds become unevenly distributed across a landscape with uneven surface, which may affect the distribution of both, nurse plant species and protected ones.

Data about the abiotic conditions at our study sites suggest that the climate in open spaces would reduce the chance of successful cactus establishment as compared to more moderate conditions below shrub species, resulting from higher mean (5.7 °C higher on the average) and maximum temperatures (14.3 °C higher on the average), and lower relative humidity (8.5% drier on the average) in the open. Nevertheless, these results do not show specific differences between *F. thurifera* or *B. ambrosioides*, the probably most efficient nurse plants, and the situation under other shrubs. Results from standard soil analyses indicated that phosphorus and total nitrogen availability partly differed among the microhabitats in a significant degree. However, in these differences no separation became obvious between *F. thurifera* and *B. ambrosioides* on the one hand and the other shrubs on the other hand. Therefore, soil physical and chemical characteristics do not seem to play an important role shaping the spatial recruitment pattern of the two cactus species, similarly as it has been reported by Arriaga et al. (1993). *F. thurifera* is a large spineless shrub with leaves that stay on the branches even in the dry season. It provides good quality shade due to its architecture forming a dense canopy. Interestingly, previous studies reported important allelopathic effects of *F. thurifera* on forbs, grasses, and shrubs reducing, in consequence, the local plant species richness in Chilean semiarid ecosystems, and the presence of antifeedant compounds that reduce herbivory by lepidoptera larvae (Fuentes et al., 1987; Faini et al., 1997). Even though we did not detect chemical differences in soil samples from the putative nurse plants and the other microhabitats (i.e., open spaces and the other shrub species), possibly soil chemistry may play a role in the synthesis of allelopathic compounds present in *F. thurifera* and involved in the chemical defence of this species (Faini et al., 1997). Whether *F. thurifera* protects *E. chiloensis* from direct causes of mortality (e.g., dessication, herbivory) and/or reduces the effects of competition with other plants, including *E. acida*, needs to be assessed in future studies.

Species associations in the study site tend to be species-specific (*E. chiloensis – F. thurifera* and *E. acida – B. ambrosioides*). This finding confirms previous suggestions indicating that some plants are probably better nurse plants than others (Callaway and D'Antonio, 1991; Callaway, 1998; Pugnaire et al., 2011). Interestingly, however, young *E. chiloensis* seem to recruit less than expected by chance under *B. incisifolia*, suggesting a potential antagonistic relationship between such species. According to Flores and Jurado (2003), the growth of cacti under shrubs can also be limited by several factors, among which competition for water with the nurse plant is an important one. Experimental studies have demonstrated that the water status and above-ground productivity of plants improve when the neighbors in such competition situations are removed (Franco and Nobel, 1989). Whether competition for water can occur in the association *E. chiloensis – B. incisifolia* must be investigated in further studies.

In summary, in the Reserva Nacional Las Chichillas approx. 2/3 of all young cacti occur under shrubs, the microhabitat where the lowest mean and maximum temperatures, and highest relative humidity were registered. *E. chiloensis* and *E. acida* were found in significantly higher numbers than expected by chance under the shrubs *Flourensia thurifera* and *Bahia ambrosioides*, respectively, which suggests that these shrub species could function as nurse plants through species-specific effects. Experimental studies are needed to evaluate in detail the mechanisms which lead to the specific species associations described here.

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