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Nurse rocks are more important than nurse plants in determining the distribution and establishment of globose cacti (*Mammillaria*) in the Tehuacán Valley, Mexico

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Abstract

While it is widely acknowledged that nurse-plants facilitate the establishment of seedlings in drylands, there are several anecdotal reports on associations between cacti and rocks. We assessed the preference for rocks or shrubs from the spatial distribution of eight cactus species (*Mammillaria* spp.). We experimentally assessed if distribution results from facilitation evaluating the survival of *Mammillaria pectinifera* seedlings growing next to rocks or under nylon sunblockers that simulated shrub shading. We found that more than half of the species avoided shrubs, while 50% of them were positively associated with rocks. Longevity and growth were highest for seedlings placed next to stones, so it may be concluded that the observed association is due to differential survival and not to other processes such as non-random seed dispersal. It is broadly accepted that the association between cacti and shrubs is mainly due to shading, however it may also represent a cost for the seedling in terms of photosynthetically active radiation. Rocks may provide a fresh and moist environment without reducing sunlight. Our results are relevant for conservation and reintroduction programs. It is important to continue the research on stress amelioration in drylands and to consider other kinds of nurse objects besides plant canopies.

Keywords: Facilitation; Restoration; Stress amelioration; Threatened species

1. Introduction

In stressful environments, positive-sign interactions such as mutualisms and commensalisms among plants are very relevant (Aguiar and Sala 1994, 1999; Callaway, 1995; Menge, 2000; Menge and Sutherland, 1987). In many cases, the presence of neighboring plants reduces environmental stress. This seems to be especially

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important throughout germination and establishment of new plants since seedlings have few mechanisms to cope with unfavorable conditions in the environment (Godínez-Álvarez et al., 2003; Harper, 1977; Solbrig, 1980). If seedlings can only get established when individuals from a different species ameliorate environmental stress, then facilitation is said to occur (Connell and Slatyer, 1977). In arid areas, unpredictable rainfall, high predation rates, and dry soils reaching high temperatures (Callaway and Walker, 1997; Franco and Nobel, 1989; Nobel, 1980; Valiente-Banuet and Ezcurra, 1991) hinder seedling establishment. Many plantlets can only survive under the microenvironmental conditions that exist under the canopy of nurse-plants, such as shrubs, grass tussocks, succulent plants, and trees (Armas and Pugnaire, 2005; Barchuk and Díaz, 2005; Carrillo-García et al., 1999; Cavieres et al., 2002; Flores and Jurado, 2003).

In deserts, nurse-plant associations occur in many groups of species. They are very common among cacti (Carrillo-García et al., 1999; Drezner, 2006; Drezner and Garrity, 2003; Flores and Jurado, 2003; Flores-Martínez et al., 1994; McAuliffe, 1984; Shreve, 1931; Valiente-Banuet et al., 1991; Yeaton, 1978; Zúñiga et al., 2005). It has been demonstrated that the association between cacti and shrubs results from the increased survival of the former due to stress amelioration (Drezner, 2006; Drezner and Garrity, 2003; McAuliffe, 1984; Suzán et al., 1994; Valiente-Banuet and Ezcurra, 1991; Zúñiga et al., 2005). Nurse-plants create less stressing conditions of reduced temperature, evaporation, evapotranspiration, incident radiation, and freeze damage (Nobel, 1988; Parker, 1989; Shreve, 1931; Valiente-Banuet and Ezcurra, 1991), while increasing the availability of nutrients, and organic matter; they may also change soil texture, and offer protection against grazing and trampling (Flores and Jurado, 2003; Flores-Martínez et al., 1994; García and Obeso, 2003; Pyke and Archer, 1991).

While the association with shrubs has been widely documented among cacti, other types of stress amelioration have been scarcely studied. The nurse association may be biotic, as with nurse-plants, or abiotic, as with rocks. A microenvironment similar to that found under shrubs can be generated beneath rocks. After a rain event, water on the ground can be available for as long as 19 more days when close to rocks than on the bare soil (Nobel et al., 1992). At a distance of 0.5 cm from a rock, temperature on the ground surface can be as much as 7 °C lower than at a distance of 50 cm (Nobel, 1988; Nobel et al., 1992; Patiño and Martorell, unpublished data). In addition, depending on their shape and on the incidence of solar radiation, rocks may cast dense shade. It has also been suggested that rocks may act as good moisture-collectors (Reyes-Olivas et al., 2002). Cacti and other desert plants vigorously develop their root systems close to rocks (Nobel et al., 1992; Nobel and Zutta, 2005).

Just as in biotic-nurse associations, there are some reports of cacti growing preferentially near rocks. Up to 85% of *Carnegiea gigantea* plants smaller than 1 m tall can be associated with plants or rocks (Parker, 1987). Thirty-two percent of the *Stenocereus thurberi* individuals in the same size class are associated with rocks (Parker, 1989). The cactus *Cereus calcirupicola* preferentially grows associated with limestone fragments (Rizzini, 1986). *Astrophytum asterias* is usually distributed under the partial shade cast by other plants or rocks (US Fish and Wildlife Service, 2003). The roots of *Echinocereus engelmannii*, *Ferocactus acanthodes*, and *Opuntia acanthocarpa* are longer and thicker under stones (Nobel et al., 1992).

Despite evidence about the widespread occurrence of abiotic-nurse associations, it may be inferred from most of the literature that nurse-plant interactions are far more common. Flores and Jurado (2003) report that at least 429 plant species in arid and semiarid areas are associated with nurse-plants. However, very scarce quantitative data are available on the frequency at which associations with rocks occur. This may be the result of nurse rocks receiving less attention from scientists: While there are 158 papers on biotic-nurse associations (Flores and Jurado, 2003), nurse rocks are the main subject of just a small number of papers. Recognizing that sometimes recruitment in drylands takes place without the intervention of nurse-plants, and measuring the frequency with which it occurs, may largely enhance our understanding of subjects that have been suggested to be determined by botanical nursing, such as community structure, population dynamics, dryland conservation, and restoration.

Compared to columnar cacti, globose species appear to depend less on shrubs. Some species, such as *Ariocarpus fissuratus*, *Epithelantha bokei*, *Turbinicarpus pseudopectinatus*, and several *Mammillaria*, have been reported to grow preferentially in the absence of nurse-plants (Godínez-Álvarez et al., 2003). Some of these cacti thrive on stony soils (Valverde et al., 2004; Zavala-Hurtado and Valverde, 2003), which makes them suitable candidates for studying the association with rocks as an alternative to the classical nurse-plant phenomenon.

The fact that a cactus species is distributed close to rocks does not prove that the latter are abiotic nurses. Such spatial relation may be due to seed dispersal or catchment in the vicinity of rocks, and not necessarily to stress amelioration which is a distinctive feature of nurse associations (Godínez-Álvarez et al., 2003; Smit et al., 2006; Withgott, 2000). If distribution next to rocks is due to a stress amelioration process during early growth, then seedlings would be expected to have a greater probability of survival when close to rocks than in other microenvironments.

In this paper we assess the frequency at which biotic- and abiotic-nurse associations occur within a group of threatened species in the genus *Mammillaria* (Cactaceae). We also study whether the association with rocks is a result of enhanced survival by means of stress amelioration. Likewise, we assess if, as in the case of nurse-plants, the shade provided by a rock may explain the association between cacti and rocks. We decided to work with threatened species since knowing their early-growth requirements may be determining for a reintroduction program to succeed.

2. Methods

2.1. Study site and species

The Tehuacán–Cuicatlán Biosphere Reserve, between 17°39′N and 18°52′N, is the southernmost arid area in North America. It lies in the southeast of the State of Puebla and the north of Oaxaca. There are 22 species in the genus *Mammillaria* in the Tehuacán Valley. We worked with eight of these species which are protected by Mexican legislation (Arias et al., 1997). The Tehuacán Valley is a very heterogeneous area, with altitudes ranging from 560 to 2480 m. From data recorded in a total of 52 weather stations within the valley for 10 years or more (IMTA, 2000), mean temperature was 19.4 °C (range 10.8–26.2 °C), and mean annual precipitation was 899 mm (range 368–1572 mm). The studied species grow on a complex vegetation mosaic of xeric scrub, grassland, tropical dry forest, and pine or oak forests.

2.2. Spatial distribution

The study was conducted in 10 localities for each species, with the exceptions of *Mammillaria lanata*, of which only two localities are known, and *Mammillaria supertexta*, of which only one locality where the plant grows out of cliffs is known. In each site, 50 m-long transects where randomly placed. For *Mammillaria pectinifera*, *M. solisioides*, *M. kraehenbuehlii*, *M. napina*, and *M. hernandezii*, the transects were 1 m wide and for *M. dixanthocentron*, *M. lanata*, and *M. supertexta* 4 m wide. The number of transects varied depending on the area and population density. The number of plants associated with a biotic nurse (under a shrub or tree), with an abiotic nurse (at less than 2 cm from a 20 cm diameter rock fixed to the ground), or with no nurse at all, was recorded for each transect.

In order to assess the availability of microenvironments per locality, 60 points along three 50-m-long transects were randomly selected. We assessed if a hypothetical plant growing in each point would show biotic, abiotic, or no association based on the above-mentioned criteria. In order to assess if each *Mammillaria* species prefers a specific type of environment a *G*-test was applied. Expected frequencies were estimated as

$$E_i = \sum_j p_{ij} N_j,$$

where E_i is the number of expected plants in the *i*-type microenvironment, p_{ij} is the fraction of randomly placed points found in the *i*-type microenvironment in the *j*th site, and N_j the total of plants registered in site *j*. Observed frequencies were obtained as the number of plants found in each category summed across all the localities. If it was observed that the plants did not conform to a random distribution, then two separate *G*-tests were applied, distinguishing only two categories in each, shrub vs. non-shrub, and rock vs. non-rock, so as to assess if the original test was significant due to the preference of the cactus for one or for both types of nurse object.

2.3. Survival analysis

This portion of the study was only carried out with *Mammillaria pectinifera*. A factorial experiment was set up in the field with two levels of herbivore exclosure (with wire mesh and insecticide and with no exclosure), three levels of microenvironmental conditions (bare ground, bare ground with artificial shade, and next to a rock of at least 30 cm diameter. These large rocks were used since they cast large shades where a large number of seedlings could be placed), and two age levels (3-day-old and 6-month-old seedlings). Each treatment was replicated three times so as to have a total of 36 experimental units. In the experimental units for the 3-day-old seedlings, 45 individuals were planted, and 35 seedlings were used in the 6-month-old seedling treatments. The seeds were germinated under greenhouse conditions in soil from the locality, and the seedlings were hardened two months prior to transplant by gradually reducing watering. The seedlings were followed-up throughout a year, at the end of which the surviving plants were measured with a caliper. Survival was analyzed through a linear model assuming a Weibull error distribution, which allows the risk of death to change over time depending on age. The model allowed for censored data and was fitted in GLIM 4.0 (Crawley, 1993). Plant sizes after 2 years were compared through an ANOVA.

3. Results

A non-random distribution of cacti in the environment was found for all the species. The association with nurse-plants happened to be scarce within the group; in fact, five of the eight species were found under nurse-plants less frequently than expected by chance alone. Only *M. kraehenbuehlii* was associated with shrubs. The association with rocks was much more common, occurring in half of the cases, while two species avoided it. As for *M. hernandezii* no 20 cm rocks were found, such category was not included in the analysis. It was found that *M. solisioides* and *M. lanata* preferred spots completely devoid of both types of nurse-objects (Table 1).

The shape of the Weibull distribution is defined by a parameter commonly represented by the Greek letter α. If α assumes a value of 1, then the death rate is constant over the full life cycle, if it is larger, then the death rate increases with age, and if it is smaller than one then the young individuals have a larger probability of dying than older individuals (Crawley, 1993). We found that for *M. pectinifera*, the shape-parameter α of the Weibull distribution was 0.87 and it was significantly different from 1 ($\chi^2 = 44.00$, $P < 0.0001$), showing that mortality rate decreases with age (Fig. 1). The age, the nurse-type (shade, rock, or none), the presence of exclosures, as well as the interactions among them had a significant impact on the life expectancy of seedlings in the field. The model explained 51.77% of variation in longevity, being the seedling age at the moment of sowing, followed by the nurse-type what explained most of variation (Table 2). All of the 3-day-old plants died. In most cases, life expectancy was greater within the exclosures and near rocks (Fig. 2), with the exception of

Table 1
Microenvironmental associations of eight *Mammillaria* species

Species	Soil rockiness range (%)	Random distribution		Association with					
		G	*P*	Shrubs	*G*	*P*	Rocks	*G*	*P*
M. dixanthocentron	3–68	114.52	<0.0001	0	0.94	0.3318	+	92.22	<0.0001
M. hernandezii	0	83.80	<0.0001	–	83.80	<0.0001			
M. kraehenbuehlii	8–73	336.49	<0.0001	+	20.70	<0.0001	+	147.73	<0.0001
M. lanata	22–38	171.37	<0.0001	–	83.97	<0.0001	–	82.81	<0.0001
M. napina	0–42	36.91	<0.0001	–	24.18	<0.0001	0	3.17	0.0749
M. pectinifera	14–49	12.70	0.0018	0	0.07	0.7919	+	10.85	0.0010
M. solisioides	0–30	265.91	<0.0001	–	202.22	<0.0001	–	35.30	<0.0001
M. supertexta	0–69	22.92	<0.0001	–	5.23	0.0222	+	20.25	<0.0001

Rockiness is the percent of the soil covered by stones $\geqslant$ 20 cm. The cover for the localities with less and more stones is reported. The first *G*-statistic tests for a non-random distribution of each species among rocks, nurse-plants, and bare soil. The next two tests examine whether there is a positive (+), negative (–), or no association (0) of each species with specific types of nurse objects. No rocks were observed in the area where *M. hernandezii* grows, so the corresponding test could not be performed.

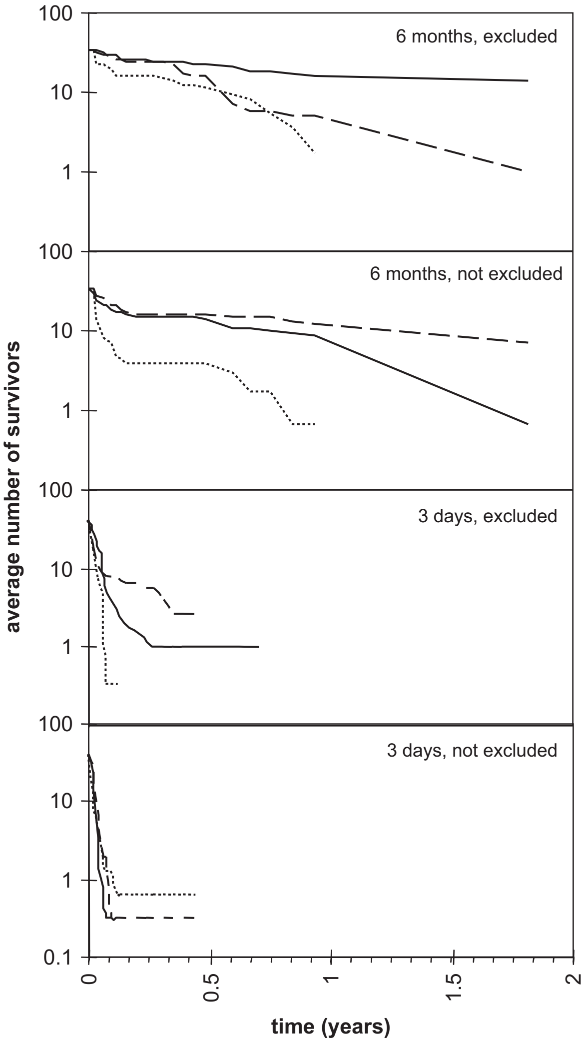

Fig. 1. Number of surviving seedlings of different ages over time in different experimental conditions. Nurse objects are rocks (continuous line), artificial shade (dashed line), or none (dotted line).

Table 2
Deviance analysis of life expectancy of *Mamillaria pectinifera* seedlings under different treatments

Source	χ^2	d.f.	P	R^2 (%)
A	1307.12	1	<0.0001	39.80
E	80.08	1	<0.0001	2.44
N	134.02	2	<0.0001	4.08
A × E	42.76	2	<0.0001	1.30
A × N	13.69	2	0.0011	0.42
N × E	0.24	2	0.8863	
A × E × N	56.55	2	<0.0001	1.72

A: age (3 days or 6 months); E: exclosure (with or without); N: nurse type (rock, shade, or none).

the newly germinated seedlings, for which there were no significant differences in terms of survival among the rock and shade treatments ($\chi^2 = 2.96$, $P = 0.2276$). In the absence of herbivory, the seedlings placed next to rocks had a life expectancy greater than one year.

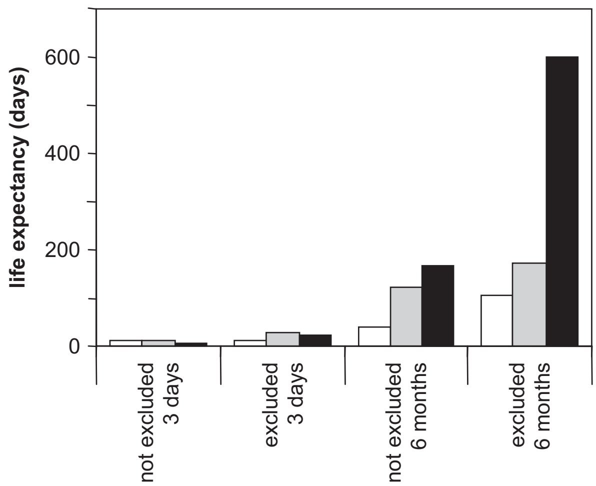

Fig. 2. Life expectancy of seedlings of different age exposed and excluded from herbivores and associated to rocks (black), artificial shade (gray), or none (white).

Due to scarce survival at the end of the year of study, the data were not enough to analyze neither the 3-day-old seedlings nor those without any kind of nurse. Therefore, a two-way ANOVA with the following factors was performed: nurse-type (rock and shade) and exclosure. No significant effects of the interaction nor of the exclosure were found, though the plants were slightly but significantly taller (5.84 ± 0.14 mm, mean $\pm$ S.E.) near rocks than under the shade (5.30 ± 0.18 mm; $F = 5.162$, $P = 0.026$).

4. Discussion

One of the most outstanding results of this study was that abiotic-nurse associations were much more frequent than the classical, biotic ones. *M. kraehenbuehlii* was the only species found in association with shrubs, although apparently rocks could provide more favorable conditions for it, since the associations with the latter are more frequent than with nurse-plants. Moreover, 62.5% of the species preferred shrub-free areas. This result calls for a continued study of facilitation processes in drylands, and requires reconsideration of the relative importance of nurse-plant associations. Botanical nursing is a well-studied phenomenon, and it is certainly very common, but the comprehension of facilitation requires that other stress-ameliorating objects are considered. In some areas and taxa, plants are not even the most important nurse objects.

The results we obtained are similar to those reported in the literature for other species in the genus *Mammillaria* in terms that it is relatively common for them not to be associated with nurses, such as *M. lasiacantha*, *M. mazatlanensis*, *M. magnimamma*, and *M. pectinifera* (Godínez-Álvarez et al., 2003; Reyes-Olivas et al., 2002). Nevertheless, and contrasting to what we found, in a high number of works, positive associations of *Mammillaria* with shrubs have been also reported, such as in the cases of *M. carnea*, *M. casoi*, *M. colina*, *M. dioica*, *M. gaumeri*, and *M. haageana* (Mandujano et al., 2002; Reyes-Olivas et al., 2002; Valiente-Banuet et al., 1991). Some studies account for other genera of globose cacti for which associations with shrubs have not been detected, such as *A. fissuratus*, *E. bokei*, *T. pseudopectinatus*, and *Ferocactus herrerae*. There are even species which are known to avoid the shade cast by other plants, like *Echinocereus sciurus* (Godínez-Álvarez et al., 2003; Reyes-Olivas et al., 2002). Reyes-Olivas et al. (2002) report the evasion of nurse-plants by at least three species of non-globose cacti in a study that found that most of them grew at less than 1 cm off large rocks. Although our results are restricted to a geographical area and to a genus, the absence of the nurse-plant associations seems to be much more common than what is usually presumed.

On the other hand, rocks were found to act as nurse objects in the majority of the species that we studied. Rocks are very conspicuous elements in the areas where most of the species grow (Table 1), providing large amounts of suitable habitat to cacti. Some species are very rarely found growing far from stones. In this study we may have underestimated the importance of nurse rocks, since pebbles having a diameter much smaller that 20 cm may have a large effect on cactus seedlings. Fifty-eight percent of the seedlings of *M. hernandezii* in 2006 were found in areas covered with pebbles (personal observation). Apparently small rocks have the same effect on the seedlings of *Coryphantha werdermannii* (Portilla-Alonso, 2007). Most *M. pectinifera* plants were observed in association with rocks smaller than 20 cm.

However, as for *M. dixanthocentron*, where the analysis suggests an association with rocks, we must be careful because this may result from plants growing on top of rocks (the distance between the cactus and the stone was smaller than the threshold value of 2 cm established by us to consider the occurrence of an association). Said species grows in areas with relatively high water inputs, such as temperate and tropical dry forests. In those places, *M. dixanthocentron* is usually found as epiphyte or saxicole, suggesting a preference for arid microenvironments rather than a process of stress amelioration related to rocks.

The studied species are representative of a very wide environmental and altitudinal gradient, with some of them growing in semiarid, temperate or tropical areas. Thus, it seems that the high frequency of associations with rocks cannot be easily attributed to a specific set of climatic conditions occurring in the Tehuacán Valley. Some species such as *M. hernandezii*, *M. kraehenbuehlii*, and *M. napina* are frequently exposed to frost, which could promote rock nursing because nighttime temperature near stones is milder (Körner, 2003). Nevertheless, only one of these three species was found to be associated with rocks.

To a great extent, the association with nurse-plants is due to the reduction of direct solar radiation and the decline in temperature beneath them (Valiente-Banuet and Ezcurra, 1991), with the consequential decrease in the loss of soil humidity (Flores and Jurado, 2003, and references therein). However, for some cacti, this may have a cost because the shade reduces the amount of Photosynthetically Active Radiation (PAR), which is already a limiting factor for succulents since they have a very low surface/volume ratio (Nobel, 1988). Apparently this is especially relevant for small cacti since, unlike columnar species, they cannot grow and avoid the shade of shrubs. On the contrary, rocks produce less obstruction to solar radiation while providing a fresh and moist environment such as that existing under shrubs (Nobel et al., 1992). The greater survival and growth of the *M. pectinifera* seedlings growing next to rocks, in comparison with those placed under artificial shade, suggest that abiotic nurses may provide these cacti with something else than a reduction in solar radiation.

Four of the species studied (*M. hernandezii*, *M. napina*, *M. pectinifera*, and *M. solisioides*) present a semi-geophytic habit with a very large proportion of the stem covered by the soil, substantially reducing its photosynthetic surface. We have observed that when growing under the shade of a shrub, the stems of these cacti do not get buried but etiolated, a typical behavior of plants which lack solar radiation. All these species preferably grow in exposed areas or associated with rocks but never with shrubs (Table 1). This matches with the above mentioned in terms that the PAR reduction may be a reason for avoiding biotic nurses.

Shade may also account for the observed differences in the behavior of the *M. pectinifera* seedlings based on age. When they have recently germinated, there is no difference between the types of nurse in relation to survival. At this stage, seedlings are devoid of spines so the shade may be important. Apparently, it can equally be provided by a plant or by a rock. In contrast, at the age of 6 months, the plant is already covered by areoles, which perhaps increases its tolerance to radiation (Nobel, 1988). This may account for the greater survival observed in individuals of that age which were next to a rock in comparison with those under the shade.

M. pectinifera was recurrently found in association with rocks. This matches with the results of the reintroduction experiment, where survival and growth were higher when next to stones. The experimental approach enables us to conclude that, just as it occurs in the classical nurse association (Valiente-Banuet and Ezcurra, 1991), it is the differences in survival during the early stages of the life cycle that accounts for the associations observed between cacti and rocks.

Getting to know the environmental requirements of cacti proves to be of particular relevance for the preservation of threatened species. Many globose cacti are threatened as a result of indiscriminate collections, in addition to changes in land use, deforestation, animal husbandry, extensive agriculture, and urban growth (Martorell and Peters, 2005; Oldfield, 1997). Their potential association with rocks may be determinant for a reintroduction program to succeed. Apparently, it is among globose cacti where abiotic-nurse associations are more frequent, suggesting that if a reintroduction of individuals in the field is targeted, using shrubs or artificial shading as nurses may result not very useful or even counterproductive. On the contrary, using rocks seems to be much more effective. The exclosure and the use of grown plants increased the survival, which must be taken into account for a reintroduction program.

There is enough evidence to regard rocks as one of the most important ''nurse objects'' (sensu Parker, 1987) which are capable of ameliorating stress in deserts. The major causes of the association between cacti and rocks are the same (stress amelioration and the resulting decrease in mortality in comparison with exposed areas) as those which account for the association with shrubs. The fact that abiotic nurses may be more common than biotic ones, and that the latter may even be exceptional among some taxonomic groups such as the one we studied, must not be neglected. Focusing on the association with shrubs has resulted in a bias in the study of nurse objects, as well as in the overlooking of other elements such as rocks, crevices, and cliffs (Martorell and Patiño, 2006), in spite of the numerous anecdotal allusions about them made in the literature when discussing facilitation. A full understanding of cactus ecology calls for a more balanced approach to their microenvironmental requirements during early growth.

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