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Columnar cacti-shrub relationships in an Andean semiarid valley in western Venezuela

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Abstract Spatial associations between columnar cacti and mimosoid shrubs were evaluated in an Andean semidesert enclave. An analysis on the capacity of other deciduous shrub species and medium-sized ephemeral plants to modify the spatial distribution of cacti was also included. The number of *Stenocereus griseus* (Haw.) F. Buxb., *Cereus repandus* (L.) Backeb. and *Pilosocereus tillianus* Gruber & Schaftzl that grow below the canopies of perennial plants were assessed and compared with open areas. Comparison of observed and expected number of cactus individuals shows a positive spatial association between *S. griseus* and *Prosopis juliflora* DC. Moreover, abundance of *C. repandus* and *P. tillianus* under the canopies of mimosoid shrubs were not statistically different from what was expected by chance. Positive spatial association between *S. griseus* and *Capparis odoratissima* Jacq., *Cassia emarginata* L., *Cordia curassavica* (Jacq.) Roem. & Schult., *Croton rhamnifolius* H.B.K. and *Jatropha gossypifolia* L. was also found. Evidence suggests that positive columnar cacti-shrub spatial association may occur either in the cactus thickets or in the thornscrubs. Due to the clumped distributions of *S. griseus* beneath *P. juliflora* and other perennial plants, we here postulate that *S. griseus* is the primary nursed columnar cactus of the enclave. The presence of cacti in open areas suggests that facilitation may be less important for establishment of columnar cacti species in this Andean semidesert landscape than in other temperate and tropical semiarid zones. We here discuss the importance of the nurse syndrome phenomenon for recruitment of *S. griseus* and for the conservation of this Andean semiarid environment.

Keywords Andes · Facilitation · Habitat mosaic · Semiarid zone · Spatial associations

Introduction

Positive interactions between columnar cacti and perennial shrubs have been reported from extratropical and tropical arid ecosystems, and have contributed to re-emphasize the role of the facilitation as a driving force of plant communities (Valiente-Banuet and Ezcurra 1991; Valiente-Banuet et al. 1991a, b; Arriaga et al. 1993; Reyes-Olivas et al. 2002; Flores and Jurado 2003; Godínez-Álvarez et al. 2003). The positive effects of nurse plants for cacti have been well documented. Benefactor plants (or species) can influence recruitment, growth and spatial associations

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of beneficiary species through a variety of pathways, both direct and indirect (Valiente-Banuet and Ezcurra 1991; Valiente-Banuet et al. 1991a, 1991b; Arriaga et al. 1993; de Viana 2001; Godínez-Álvarez et al. 2003). Nevertheless, there is little information on the occurrence of the nurse plant phenomenon in the Andean tropical semiarid environments (Larrea-Alcázar et al. 2005; Larrea-Alcázar and Soriano 2006; López and Valdivia 2007; López et al. 2007). Moreover, few authors have examined if the occurrence of the nurse-plant phenomenon varies within a semi-desert plant community which may exhibit different replicates from the same xerophyllous plant community (Pugnaire et al. 1996; Pugnaire and Luque 2001; Tewksbury and Lloyd 2001; Tirado and Pugnaire 2005). If perennial shrubs have consistent positive effects on plant establishment, many beneficiary columnar cacti may depend on these effects throughout their natural regeneration and show positive spatial associations with them.

The Andes of northern South America contain a set of dry valleys that constitute an archipelago of small semiarid enclaves that occur from Cordillera de Mérida (western Venezuela) through Colombia to Ecuador (Sarmiento 1972; Soriano and Ruíz 2002). The prevailing vegetative elements of these semi-arid valleys are thorny mimosoid shrubs and long-lived columnar cacti species, which cover a mosaic of cactus thickets and thornscrubs. The so-called "nurse plant phenomenon" and the effect of these mimosoid shrubs on spatial distribution of the columnar cacti has been demonstrated (Larrea-Alcázar and Soriano 2006). However, studies on local variations of cacti-shrub associations and comparative analysis between both habitats on a local scale are still absent in the Venezuelan Andes and variations in the importance of mimosoid species, as nurse plants for natural regeneration of columnar cacti have not been sufficiently probed. An empirical approach documenting spatial associations between these two life forms should help us to evaluate the importance of facilitation for the natural regeneration of cacti and the structure and functioning of the semi-arid plant communities where they occur.

Here, we have examined the columnar cacti-mimosoid shrub associations in five localities of the Lagunillas semiarid enclave in the Venezuelan Andes to determine if mimosoid shrubs modify the spatial distribution of columnar cacti and, if so, how this effect varies within a mixed mosaic of cactus thickets and thornscrubs. We hypothesize that the facilitation may be the main mechanism to explain the abundance and distribution of cacti in the enclave causing the positive spatial association between columnar cacti and perennial shrubs. In contrast, if competition is the main mechanism to affect the spatial arrangement of cacti, they will not be spatially associated to perennial plants, since to grow below potential nurse plants would be disadvantageous. The objectives of this study were to (1) assess the relative importance of mimosoid plants on spatial distribution of long-lived columnar cacti in cactus thickets and thornscrubs, and (2) to evaluate the capacity of other deciduous shrub species and medium-sized ephemeral plants to modify the spatial distribution of columnar cacti in this habitat mosaic.

Study area

This study was carried out in the Lagunillas semiarid enclave in the Venezuelan Andes (262 km^2, Soriano and Ruíz 2002). Annual rainfall ranges from 450 to 550 mm, with peaks in April–May and September–October. Weather is semiarid and it is characterized by a warm climate with an annual mean temperature of 22°C. The dominant vegetative elements of this semiarid landscape are long-lived thorny shrubs, such as *Prosopis juliflora* DC., *Acacia farnesiana* (Willd.) L. and *A. macracantha* H.B.K.; and fleshy-fruited columnar cactus species, such as *Stenocereus griseus* (Haw.) F. Buxb., *Cereus repandus* (L.) Backeb. and *Pilosocereus tillianus* Gruber & Schaftzl. The thornscrubs are strongly associated with small persistent water bodies of the enclave and contain high abundances of *P. juliflora* (~307 ind/ha), *A. macracantha* (~66 ind/ha), *S. griseus* (~2619 ind/ha) and *P. tillianus* (~396 ind/ha), as well as scarce portions of bare areas (<20%); while the cactus thickets occur mainly on dry uplands and contain high abundance of *A. farnesiana* (~116 ind/ha) and *C. repandus* (~395 ind/ha), together with high portions of bare areas (30–35%). In the thornscrubs, soils are loamy clay with high concentrations of organic matter (4–5%), nitrogen (0.15–0.30%), potassium (0.4–1.1 ppm), magnesium (2.0–5.5 me/l) and calcium (30–45 me/l); while in the cactus thickets, soils are loamy sand with high concentration of phosphorous (30–60 ppm). Both habitats can represent 62% (cactus thicket) and 28% (thornscrub) of the total cover of the enclave (Rico et al. 1996) and there is no difference in annual rainfall between them. Grazing and removal of taller thorny legumes have increased the processes of erosion and desertification in both habitats and the natural vegetation is being slowly replaced by cultivation and by extensive grazing by cows and goats.

The study was conducted in five study sites within the enclave. Two study sites were located close to Caparú Lagoon. These sites were defined as continuum thornscrub and low thornscrub. Long-lived mimosoid shrubs in the continuum thornscrub form a dense thorny scrubland around the lagoon, while the low thornscrub forms a discontinuous thorny landscape and is located to 0.6–0.7 km from the lagoon. Other three sites were located on dry uplands far from any water body. These sites were defined as interrupted cactus thicket, open cactus thicket and interrupted open cactus thicket, which contain a high abundance of columnar cacti as well as high portions of open areas resulting in a dry landscape strongly dominated by cacti. These sites were separated from one another by approximately 10–12 km of distance.

Methods

We assessed the spatial association between columnar cacti and mimosoid shrubs' using eleven to twenty 50 m linear transects, which were randomly installed in each study site. This field sampling does not consider the isolated or clumped condition of perennial shrubs and therefore there is a direct relationship between plant cover and the number of columnar cacti recorded. In each transect, we counted all columnar cacti growing beneath mimosoid shrubs, other perennial plants and in open areas to obtain the observed frequencies and compare them with those expected under the hypothesis of random distribution. We considered all perennial plants with at least 50 cm height, including two cacti of prostrate-erect habit (*Opuntia caribea* Britton & Rose and *O. depauperata* Britton & Rose) and common medium-sized ephemeral plant species. We identified all the shrubs in each transect and obtained their diameter through foliage interception of focal plants along the transects. We estimated plant species cover assuming that all species had circular-shaped crowns. We have used separate Chi-square tests (χ^2) to test the null hypothesis that the number of columnar cacti under each species is proportional to the total area covered by the canopy of each plant species. We assessed the significance of each cell using standardized residuals tests. We assumed that the standardized residuals are normally distributed with a zero mean and unit variance, so that any value greater than 2 was regarded as a significant deviation (Greig-Smith 1983; Valiente-Banuet et al. 1991a). Based on the Pearson's criterion, we do not consider plant species with expected values lower than 5, because that low expected values violate the asymptotic criteria of convergent mean and variance. Finally, in order to determine biotic differences between two conditions (cactus thickets vs. thornscrubs) in terms of composition and abundance of shrubs, we estimated the Jaccard's index between both types of habitats (Gauch 1982)

Results

The area covered by the canopy of *P. juliflora* shrubs was relatively high in all thornscrubs and cactus thickets studied (13.8 [continuum thornscrub]–54.5% [interrupted cactus thicket]; min–max). Moreover, the area covered by *A. macracantha* shrubs was high in both thornscrubs, mainly in the continuum thornscrub (46.8%), whereas the area covered by *A. farnesiana* shrubs was relatively high in all cactus thickets, mainly in the interrupted open cactus thicket (35.1%). We recorded other thorny legume species, such as *Acacia tortuosa* (Willd.) L., *Acacia tamarandifolia* (Willd.) L., *Cassia emarginata* L. and *Leucaena leucocephala* (Lam.) De Wit (exotic species), which we only found in the thornscrubs. The proportion occupied by open areas was relatively low in both thornscrubs (<23%) and ranged from 32.6% to 75.6% in the cactus thickets (Table 1).

Overall, we recorded on 50 m linear transects from 254 to 778 individuals of *S. griseus* (115 [open cactus thicket]–720 cacti [low thornscrub]; min–max), *C. repandus* (16 [low thornscrub]–133 cacti [open cactus thicket]) and *P. tillianus* (4 [interrupted cactus thicket]–42 cacti [low thornscrub]). The total number of *S. griseus* beneath shrubs of *P. juliflora* was

Table 1 Importance of perennial plant cover for the three columnar cactus species in five sites of the Lagunillas semi-arid enclave in the Venezuelan Andes

	Sum of canopy sizes (m^2)	*Stenocereus griseus*			*Cereus repandus*			*Pilosocereus tillianus*			Total		
		Obs.	Esp.	Test	Obs.	Esp.	Test	Obs.	Esp.	Test	Obs.	Esp.	Test
a. Continuum thornscrub													
Acacia farnesiana (Willd.) L.	45.37	5	5.49	−0.21	1	0.61	0.50	0	0.27	−0.52	6	6.38	−0.15
Acacia macracantha H.B.K.	1082.41	91	131.09	−3.50	11	14.51	−0.92	3	6.55	−1.39	105	152.16	−3.82
Capparis odoratissima Jacq.	86.67	6	10.50	−1.39	1	1.16	−0.15	0	0.52	−0.72	7	12.18	−1.48
Prosopis juliflora DC.	862.39	155	104.44	4.95	17	11.56	1.60	10	5.22	2.09	182	121.23	5.52
Open areas	156.24	17	18.92	−0.44	1	2.09	−0.76	1	0.95	0.06	19	21.96	−0.63
Total	2311.96	280			31			14			325		
	$\chi^2 = 57.38$*												
b. Low thornscrub													
Acacia tamarandifolia (Willd.) L.	30.99	13	15.28	−0.58	0	0.34	−0.58	1	0.89	0.12	14	16.51	−0.62
Capsicum frutescens L.	19.07	10	9.41	0.19	1	0.21	1.73	2	0.55	1.96	13	10.16	0.89
Cassia emarginata L.	28.54	22	14.07	2.11	0	0.31	−0.56	0	0.82	−0.91	22	15.21	1.74
Croton rhamnifolius H.B.K.	16.72	14	8.25	2.00	0	0.18	−0.43	0	0.48	−0.69	14	8.91	1.71
Jatropha gossypifolia L.	21.78	27	10.74	4.96	0	0.24	−0.49	1	0.63	0.47	28	11.61	4.81
Lippia aff. *graveolens* H.B.K.	23.27	12	11.47	0.16	0	0.25	−0.50	1	0.67	0.40	13	12.40	0.17
Opuntia caribea Britton & Rose	13.44	3	6.63	−1.41	0	0.15	−0.38	0	0.39	−0.62	3	7.16	−1.56
Prosopis juliflora DC.	960.50	444	473.65	−1.36	12	10.53	0.45	25	27.63	−0.50	481	511.81	−1.36
Open areas	338.68	171	167.01	0.31	3	3.71	−0.37	12	9.74	0.72	186	180.46	0.41
Total	1460.07	720			16			42			778		
	$\chi^2 = 91.48$*												
c. Interrupted cactus thicket													
Croton ovalifolius Vahl.	153.62	20	27.28	−1.39	10	8.88	0.37	0	0.31	−0.56	30	36.48	−1.07
Pereskia guamacho F.A.C. Weber	28.43	1	5.05	−1.80	0	1.64	−1.28	0	0.06	−0.24	1	6.75	−2.21
Prosopis juliflora DC.	1065.49	238	189.21	3.55	75	61.62	1.70	1	2.18	−0.80	314	253.01	3.83
Open areas	637.16	72	113.15	−3.87	24	36.85	−2.12	1	1.30	−0.27	97	151.30	−4.41
Total	1954.01	347			113			4			464		
	$\chi^2 = 52.11$*												
d. Open cactus thicket													
Acacia farnesiana (Willd.) L.	146.62	4	4.99	−0.44	6	5.77	0.10	0	0.26	−0.51	10	11.02	−0.31
Prosopis juliflora DC.	465.33	28	15.84	3.06	13	18.32	−1.24	0	0.83	−0.91	41	34.98	1.02

Table 1 continued

	Sum of canopy sizes (m^2)	*Stenocereus griseus*			*Cereus repandus*			*Pilosocereus tillianus*			Total		
		Obs.	Esp.	Test	Obs.	Esp.	Test	Obs.	Esp.	Test	Obs.	Esp.	Test
Open areas	2553.22	75	86.91	−1.28	104	100.5	0.35	6	4.53	0.69	185	191.95	−0.50
Total	3378.58	115			133			6			254		
	$\chi^2 = 142.93$*												
e. Interrupted open cactus thicket													
Acacia farnesiana (Willd.) L.	497.01	150	110.54	3.75	39	28.42	1.98	4	2.81	0.71	193	141.77	4.30
Capparis odoratissima Jacq.	33.53	15	7.46	2.76	4	1.92	1.50	0	0.19	−0.44	19	9.56	3.05
Cordia curassavica (L.) Roem. & Schult	56.89	30	12.65	4.88	3	3.25	−0.14	1	0.32	1.20	34	16.23	4.41
Croton ovalifolius Vahl.	29.39	1	6.54	−2.17	1	1.68	−0.53	0	0.17	−0.41	2	8.38	−2.20
Lippia aff. *graveolens* H.B.K.	29.24	4	6.50	−0.98	2	1.67	0.25	1	0.17	2.05	7	8.34	−0.46
Prosopis juliflora DC.	213.54	69	47.49	3.12	15	12.21	0.80	1	1.21	−0.19	85	60.91	3.09
Open areas	507.78	33	112.93	−7.52	9	29.04	−3.72	1	2.87	−1.10	43	144.84	−8.46
Total	1416.35	315			81			8			404		
	$\chi^2 = 173.79$*												

Standardized residuals values are shown (Test). Absolute values >2 are significant at 5% of the normal distribution. Based on the Pearson's criterion, plant species with expected values lower than 5 were excluded from table in order to do not violate the asymptotic criterion of convergent mean and variance statistically higher than expected by chance in all cactus thickets (Table 1). This means that *S. griseus* has a clumped pattern under *P. juliflora* in habitats with high portions of open areas. We also found a positive spatial association between *S. griseus* and *P. juliflora* in the continuum thornscrub, suggesting that positive effects of this mimosoid plant as a nurse plant could also be occurring in this habitat kind. In contrast, the number of *S. griseus* individuals underneath shrubs of *A. farnesiana* was statistically greater than expected by chance in the interrupted open cactus thicket. When we compared observed and expected number of individuals of *C. repandus* growing under mimosoid species, we did not find any positive spatial association except for the association between *C. repandus* and *A. macracantha* in the open cactus thicket. Finally, the number of individuals of *P. tillianus* beneath *P. juliflora*, *A. farnesiana* and *A. macracantha* was not statistically greater than expected by chance, suggesting that this cactus species does not grow spatially associated with any other plant species.

We also recorded positive spatial associations between columnar cacti and *Capparis odoratissima* Jacq., *Cassia emarginata* L., *Cordia curassavica* (Jacq.) Roem. & Schult., *Croton rhamnifolius* H.B.K. and *Jatropha gossypifolia* L. (Table 1). Many of these plant species appeared to modify the spatial distribution of *S. griseus*. In the low thornscrub, we found individuals of *S. griseus* spatially associated with individuals of *J. gossypifolia, C. emarginata* and *C. rhamnifolius*, while the number of individuals of *C. repandus* and *P. tillianus* beneath these shrubs was not statistically greater than expected by chance (Table 1). In the interrupted open cactus thicket, we found a positive effect of *C. frutescens*, *C. odoratissima*, and *C. curassavica* on the spatial distribution of *S. griseus* (Table 1). Finally, we obtained a Jaccard's index value of 0.65 which shows that both types of habitats (cactus thickets/thornscrubs) are replicates from the same xerophyllous community type (Gauch 1982).

Discussion

The consistent pattern of the presence of *S. griseus* below mimosoid legumes and other perennial plants suggests that the establishment of this cactus in our study site depend on nurse associations. Positive cactus-shrub spatial relationships were more frequent in the cactus thickets than in the thornscrubs. However, these cacti-shrub associations are not restricted to these cactus-dominating landscapes and do not include all potentially interacting species. In fact, the spatial distribution of columnar cacti does not seem to be associated with mimosoid shrubs, except in the case of *S. griseus*. The density of *C. repandus* and *P. tillianus* beneath mimosoid shrubs was not statistically different from chance, which indicates a random or regular spatial distribution; however, these cacti could have a clumped distribution away from the mimosoid shrubs. Moreover, we found that individuals of *S. griseus* are spatially associated with at least nine perennial plant species, including three mimosoid legume species (*P. juliflora*, *A. farnesiana* and *A. macracantha*). Among these plant species, the spatial distribution of *S. griseus* has a clumped pattern beneath *P. juliflora*, indicating that *S. griseus* is the primary nursed cactus species in the enclave.

Individuals of *C. repandus* and *P. tillianus* were rarely recorded underneath mimosoid shrubs. This suggests that these fleshy-fruited columnar cactus species are not spatially associated with perennial plants and it is likely that they do not require a mimosoid nurse plant for establishment. In contrast, the distribution of *S. griseus* individuals is associated with mimosoid legumes, suggesting that their natural regeneration takes place underneath perennial plants. The clumped pattern of spatial distribution of *S. griseus* suggests that common underlying mechanisms such as post-germination mortality (Godínez-Álvarez et al. 2003, 2005), amelioration of abiotic conditions (Franco and Nobel 1989; Reyes-Olivas et al. 2002) and the possible modifications of soil properties underneath the canopies of mimosoid shrubs (vs. open areas) may be operating. In fact, compared with open areas, higher concentrations of organic matter, nitrogen, phosphorus and potassium have been found in the undercanopy of *Prosopis* species, such as *P. flexuosa* (Rossi and Villagra 2003), *P. glandulosa* (Tiedemann and Klemmèdson 1972) and several *Mimosa* species (Valiente-Banuet et al. 1991a; Camargo-Ricalde et al. 2002). Thus, *P. juliflora* may ameliorate soil nutrient conditions as well as other environmental factors (e.g. lower temperatures, higher humidity and shade producers) under their canopy, creating 'resource islands' (Reynolds et al. 1999; Camargo-Ricalde et al. 2002) that are occupied either by columnar cacti (mainly *S. griseus*) or other plant species.

Although our data suggest that *P. juliflora* is a benefactor plant for the establishment of *S. griseus*, field assessment focused on isolated mimosoid shrubs also shows that individuals of *S. griseus* and *C. repandus* may be spatially associated to *A. farnesiana* (Larrea-Alcázar and Soriano 2006). This suggests isolated *A. farnesiana* individuals may also be important in determining spatial community structure and the establishment of columnar cacti. Isolated individuals and plant cover of *A. farnesiana* tend to be higher in the cactus thickets than in the thornscrubs. In the present study, we found a clumped distribution pattern of *S. griseus* beneath *A. farnesiana* in only one of the cactus thickets studied. This pattern may be explained by the field sampling used, which does not consider the isolated and clumped condition of perennial shrubs and, therefore, reduces the effect of isolated shrubs on the total number of columnar cacti counted (observed values) in the field. However, other mechanisms may be regulating the relationships between cacti and mimosoid shrubs. For instance, ants of the genus *Pheidole* Westwood, *Camponotus* Mayr, *Acromyrmex* Mayr and *Ectatomma* F. Smith are implicated in seed predation of columnar cacti (Ibáñez and Soriano 2005). Some mimosoid shrubs provide critical nesting sites for ground-foraging ants (Bestelmeyer and Schooley 1999), which may favour the presence of nests of these ant species. Nevertheless, it is not known if columnar cacti seeds find more benign conditions for their survival below the canopies of shrubs of *A. farnesiana* and/or shrubs of *P. juliflora*.

Even though *S. griseus* are sometimes spatially associated with many perennial shrub species (mainly *P. juliflora*), the presence of these cacti in open areas, often areas completely lacking vegetation, suggests that some individuals are able to tolerate unprotected conditions. This result implies that these columnar cacti in this Andean region are capable of establishment in open areas, unlike many cactus species from other semi-arid environment which require the moderate conditions existing beneath the canopies of shrubs (Godínez-Álvarez et al. 2003). However, rocks, several surface irregularities or annual plants may act as potential or ephemeral facilitators allowing germination and seedling survival (Nobel et al. 1986, 1992; Godínez-Álvarez et al. 2003). Alternatively, mimosoid plants may be replaced by nursed cacti through interference or competition (McAuliffe 1984; Flores-Martinez et al. 1994, 1998), or there may be removal of thorny legumes by local peasants, which favours the growth of nursed cactus juveniles. Although the elimination of mimosoid plant appears to modify the spatial distribution of *S. griseus*, this conclusion is still far from certain. Until systematic observations of juvenile individuals are conducted, any interpretation of the outcome of competition or anthropogenic disturbance remains strictly speculative.

Potential benefactor plants *J. gossypifolia, C. emarginata*, *C. odoratissima* and *C. rhamnifolius* are shrub species which maintain their leaves throughout the entire year and reach 1.5–4.0 m in height, while *C. curassavica* and *C. frutescens* are small plant species (<1.0 m in height), which drop their leaves early in the dry season. These perennial shrubs, together with *P. juliflora*, may be considered as key plant species for conservation and restoration strategies of this semiarid enclave and the richness and endemism that it contains. Successful field tests in which seeds or cactus seedlings are placed close to these plants may demonstrate the potential of this approach.

In summary, positive spatial associations between columnar cacti and different perennial shrubs occur in the cactus thickets and thornscrubs of an Andean semiarid environment, showing that establishment of some columnar cacti (mainly *S. griseus*) may take place underneath perennial plants in both conditions. Besides, the presence of cacti in open areas suggests that facilitation may be less important for establishment of columnar cacti species in this Andean semiarid landscapes than in other arid zones, such as the Sonoran Desert (Suzán et al. 1996), the Tehuacán Valley of the central Mexico (Valiente-Banuet et al. 1991b) and the Cardones National Park in Argentina (de Viana et al. 2001). Although, these cacti prefer the microhabitat underneath shrubs, they seem to be capable of establishing in areas completely lacking vegetation. Regardless of the precise mechanisms that favour the association between *S. griseus* and *P. juliflora*, our results reveal a highly dynamic nurse-protégé association. By confirming that cactus-mimosoid associations appear to influence present-day plant distributions and plant community structure, this study may provide a foundation for future research that focuses specifically on the competition between columnar cacti and mimosoid shrubs and conservation of the Andean semiarid valleys where they occur.

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