Effects of *Prosopis flexuosa* on soil properties and the spatial pattern of understorey species in arid Argentina

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Abstract. In arid zones dominant woody plants are capable of causing changes in microclimate and soil properties likely to affect species composition, as well as the establishment and spatial distribution of plant species. In North American and European deserts species richness appears to be higher under the canopy of shrubs and trees, in contrast with Chilean deserts where it seems to be lower. Since *Prosopis flexuosa* (*Fabaceae, Mimosoideae*) is the most conspicuous tree in the central Monte desert, Argentina, we analysed the effect of this species on the composition and abundance of the shrub and herbaceous layers and on soil properties. We considered two mesohabitats: 'under *P. flexuosa* canopy' and 'intercanopy areas'. In addition, we analysed the differences between two microhabitats under canopies: 'northern part of the canopy' and 'southern part of the canopy'. Results indicate that species composition and soil properties are affected by both mesohabitats and microhabitats. We found a higher number of shrubs under canopies, whereas that of grasses and perennial forbs increased in intercanopy areas. Concentrations of organic matter, nitrogen, potassium and phosphorus, factors limiting biological productivity in Monte desert soils, were significantly higher under than outside *P. flexuosa* canopies. Electrical conductivity and concentrations of Na^+, Ca^{++}, Mg^{++} were higher in the northern than in the southern microhabitats. No differences in species richness, evenness or diversity were found between mesohabitats or between microhabitats. We conclude that *P. flexuosa* modifies the spatial pattern of plant species in the shrub and herbaceous layers and the chemical conditions of the soil, generating spatial heterogeneity on different scales.

Keywords: Facilitation; Fertility island; Heterogeneity; Interaction; Mendoza; Monte province; Overstorey.

Abbreviations: EC = Electrical conductivity; SAR = Sodium absorption ratio.

Introduction

In arid and semi-arid ecosystems, dominant woody plants are likely to cause changes in microclimate and soil properties by attenuating harsh environmental conditions (e.g. high temperature and radiation) and by modifying soil characteristics, resource availability (e.g. water and nutrients) and spatial distribution of nutrients (Gutiérrez et al. 1993; Callaway 1995). Through these environmental changes shrubs and trees can affect species composition, phenology, productivity and biomass allocation of their understorey, as well as the establishment and, therefore, the spatial distribution of plant species.

When nutrients become limiting to biological productivity a conspicuous concentration of vegetation usually occurs under trees or shrubs where soil nutrient content is higher, resulting in the formation of the so called 'fertility islands' (Barth & Klemmedson 1982; Garner & Steinberger 1989; Pugnaire et al. 1996a). In these islands, species richness appears to be higher than outside the canopy of shrubs and trees and has been observed in North American, European and African deserts (Franco-Pizaña et al. 1995; Pugnaire et al. 1996b; Akpo et al. 1997). In contrast, species richness of annual plants in Chilean deserts appears to be higher in open areas, maybe as a consequence of the increased dominance of some species (Gutiérrez et al. 1993). The spatial heterogeneity of soil resources is the result of a series of interacting physical, chemical and biotic mechanisms such as the relocation of absorbed nutrients under the canopies of woody species and changes in the mineralization rate of nitrogen (Tiedemann & Klemmedson 1972; Barth & Klemmedson 1982; Mazzarino et al. 1991).

As well as generating environments that differ from those in open areas, dominant species can promote different microhabitats under their canopies. These represent small-scale environmental changes that have rarely been addressed. Moro et al. (1997a, b) found differences between microhabitats associated with

distance from the plant trunk and Valiente-Banuet & Ezcurra (1991) found greater establishment of cacti on the northern side of nurse shrubs in northern Mexico (Vizcaino desert). In contrast, Valiente-Banuet et al. (1991) found a random distribution of five cacti species in central Mexico. Latitude seems to account for the different responses on both sites. However, no differences between cardinal directions were found by Franco-Pizaña et al. (Franco-Pizaña et al. 1995) in southern Texas, located at the same latitude as the Vizcaino desert.

The Monte phytogeographical province stretches diagonally across the arid region of Argentina from 24° 35' - 44° 20' S and from 69° 50' - 62° 54' W. Mean annual rainfall is less than 350 mm.yr^{-1} throughout the region. In this area *Prosopis flexuosa* (*Fabaceae*, *Mimosoideae*) is the main tree species, forming open woodlands at sites with a shallow water table (Morello 1958). Studies on other *Prosopis* species provide evidence that, as with other legumes, these plants are important components of the habitat of other species, as they are likely to alter environmental conditions under their canopies in arid and semi-arid ecosystems (Tiedemann & Klemmedson 1972; Mares et al. 1977; Barth & Klemmedson 1982; Bush & Van Auken 1990).

Since *P. flexuosa* is the major tree species in the Monte desert (Morello 1958), the aim of this work was to study the effect of this tree on soil properties and the spatial pattern of other species. We expected *P. flexuosa* to generate spatial heterogeneity at different scales. If so, floristic composition, plant cover, species richness, diversity and soil conditions should be different between undercanopy and intercanopy areas, as well as between microhabitats at different aspects with respect to the trunk as a consequence of the higher radiation levels on the north side and the predominantly SSE winds and precipitation.

Material and Methods

Study site

The study was carried out in the Ñacuñán Biosphere Reserve (12 800 ha), Mendoza Province, Argentina (34° 2' S, 67° 58' W), in the central part of the Monte phytogeographical province. In the reserve, the open woodland of *P. flexuosa* and *Larrea divaricata* represents the most extensive plant community and is characterized by three layers. *P. flexuosa* is dominant in the tree layer, with trees 4-6 m tall and a cover of ca. 20%. The shrub layer is dominated by *L. divaricata, Capparis atamisquea* and *Lycium tenuispinosum*. The herbaceous layer shows predominance of grasses such as *Pappophorum caespitosum*, *Trichloris crinita* and *Aristida mendocina* (Roig 1971).

The climate is dry and temperate and mean annual rainfall is 335 mm (1972-1998). Over 75% of the annual rainfall occurs as torrential events during spring and summer. Winds blow primarily from the south and southeast. An important feature of this region is the unpredictability of precipitation and interannual variation. Soil is silt-sandy. Run-off occurs only during exceptionally heavy rainfall events. As our study was conducted during an exceptionally wet year (summer 1997-1998, 300 mm during the growing season) owing to an 'El Niño' event, we are confident that species composition is adequately represented, including ephemerals and herbs that are absent or poorly represented when rainfall is within or below its normal range.

Vegetation sampling

We sampled the vegetation in different habitats of the open woodland of *P. flexuosa* and *L. divaricata*. We analysed the problem at two different scales: meso-habitats and microhabitats. At the first scale we considered two different mesohabitats: under the canopy of *P. flexuosa* (hereafter 'undercanopy areas') and in adjacent outside the canopy areas (hereafter 'intercanopy areas'). Within the first mesohabitat we studied two micro-habitats: under the northern part of *P. flexuosa* canopies (hereafter 'northern microhabitat') and under the southern part of *P. flexuosa* canopies (hereafter 'southern microhabitat'). We randomly selected six 2 ha plots and, in each plot, we randomly distributed ten 1 m × 1 m quadrats (Kent & Coker 1992) under *P. flexuosa* canopies (five in northern microhabitats and five in southern microhabitats) and another ten quadrats in intercanopy areas adjacent to each selected individual, at least 5 m away from the tree. We selected trees with basal diameters between 15 and 25 cm, which represent the more abundant diametric classes (Villagra & Villalba 2001) and we placed the quadrats ca. 1 m from the trunk in a N or S direction. Floristic composition and cover of plant species were estimated for each quadrat, as well as percentages of litter cover and bare soil (the tree cover under which measurements were taken was not considered). To this end, quadrats were established with four 1 m rules scaled every 10 cm. Each 2-ha plot was regarded as a replicate. We used the mean values obtained from these measurements as a single entry representing the replicate ($n = 6$). We estimated the frequency of each species as the percentage of quadrats where that species occurred in each plot.

The number of species was used as an index of richness and diversity was estimated using the Shannon index (Kent & Coker 1992).

Soil sampling

Within each quadrat, soil samples from the upper 20 cm were collected and oven dried for 72 h at 40°C. Samples of the same microhabitat, taken from each 2 ha plot were pooled. Soil texture was determined by granulometry. The pH was determined in a 1:1 suspension of soil in water using an Orion 501 digital pH meter. Organic matter was estimated by oxidization with dichromate in presence of H_2SO_4. Total nitrogen was determined using the micro-Kjeldahl digestion technique. Potassium was determined with Pratt's method and phosphorus with Jackson's technique (Jackson 1976). The Sodium Absorption Ratio (SAR) was estimated using Na^+ concentration (determined by flame photometry) and Mg^{++} and Ca^+ concentration (determined by EDTA titration). Electrical conductivity (EC) was determined on a saturation extract (Jackson 1976).

Statistical analysis

We performed an ordination of the plots through the Detrended Correspondence Analysis (DCA) to examine their variation and to recognize plot grouping (Kent & Coker 1992). To explore the differences in the cover and frequency of each species between habitats, we used a nested design with microhabitats (southern and northern) nested within mesohabitats (undercanopy and intercanopy areas). Data were analysed with an ANOVA for nested design. As data on plant species cover and bare soil percentage did not meet the assumption of homogeneity of variance, they were transformed using ranks (Conover & Iman 1981).

Results

Species composition, richness and diversity

The ordination performed on the plots clearly separates intercanopy from undercanopy mesohabitats in axis 1 (eigenvalue = 0.63). In contrast, no clear differentiation was found between microhabitats (Fig. 1).

In comparing species cover and frequency between mesohabitats, we found: (a) species exclusively distributed under *P. flexuosa* canopies (e.g. *Ephedra triandra*, *Capparis atamisquea*, *Lycium gillesianum*); (b) species that, although present in both mesohabitats, were more frequent in the shelter provided by these trees (e.g. *Lycium tenuispinosum*, *Setaria leucopila*, *Chenopodium papulosum*); (c) species occurring exclusively (e.g. *Sporobolus cryptandrus*, *Heliotropium mendocinum*) or most commonly (e.g. *L. divaricata*, *Parthenium hysterophorus* and *Pappophorum caespitosum*) in intercanopy
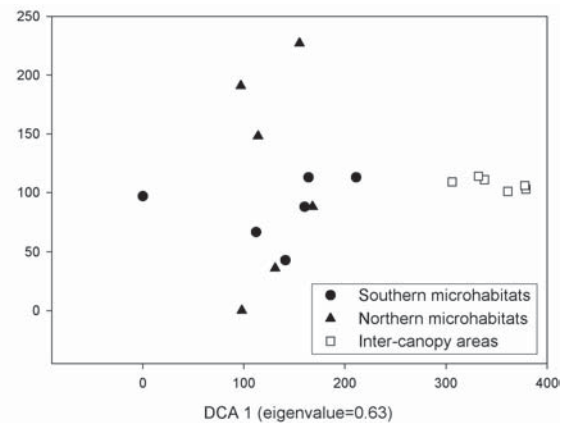

Fig. 1. DCA ordination of the 18 plots in the different habitats analyzed.

areas and (d) ubiquitous species (*Junellia aspera*, *P. flexuosa*) found in both mesohabitats (Table 1). On account of their rarity there were species that, despite occurring only in one of the mesohabitats, did not show significant differences in abundance between mesohabitats.

Among the species most likely to be found under tree canopies, only a few were differentially distributed between northern and southern microhabitats. *Stipa ichu* (a C_3 grass) and *Chenopodium papulosum* were more frequent in southern microhabitats, while *Lycium gillesianun* was mostly found in the northern microhabitats (Table 1). Despite the fact that *Sphaeralcea miniata* was most common in intercanopy areas, when found under canopies it occurred in the northern microhabitats.

There were more shrub species and higher cover under *P. flexuosa* canopies, while grasses had higher species richness and cover in intercanopy areas (Fig. 2). There were more forb species in intercanopy areas but they had higher cover in undercanopy mesohabitats. At the microhabitat scale, shrubs had higher cover in southern, and forbs in the northern microhabitats.

There were no significant differences in total species richness, species per m^2, diversity or total plant cover between mesohabitats or microhabitats. Undercanopy areas showed higher litter cover and a lower percentage of bare soil than intercanopy areas. No significant differences were found between microhabitats (Table 2).

Soil characteristics

Soil samples taken either from undercanopy or intercanopy areas were loamy sand and texturally similar. With respect to soil chemical characteristics, the percentage of organic matter and the concentration of nitro-

Table 1. Comparison of frequency (percentages of the samples where the species occur) and mean cover percentage. Column Meso shows levels of significance between mesohabitats (undercanopy and intercanopy) and column Micro between both microhabitats nested in the undercanopy mesohabitat.

| | Frequency | | | | | Cover (%) | | | | |
| | Undercanopy | | Inter- | P-level | | Undercanopy | | Inter- | P-level | |
	S	N	canopy	Meso	Micro	S	N	canopy	Meso	Micro
Setaria leucopila	65	67	19	**		3.7	6.0	0.6	**	
Lycium tenuispinosum	55	37	19	*		17.1	14.4	3.2	**	
Ephedra triandra	19	13		**		0.9	0.6		*	
Capparis atamisquea	13	17		*		3.3	11.2		*	
Lycium chilense	45	57	24	*		6.0	6.7	1.6	o	
Chenopodium papulosum	74	50	30	*	o	10.1	4.0	2.6		
Lycium gillesianum	3	13		o	o	1.3	7.2		o	o
Stipa ichu	23	3	2	o	*	6.4	0.1	0.4		*
Tweedia brunonis	13	7	2	o		0.04	0.1	0.01	o	
Solanum atriplicifolium	13	20	2	o		1.6	1.1	0.1	o	
Conyza laevigata	3	3				1.1	0.7			
Diplachne dubia	6	3				0.01	0.02			
Cucurbitella asperata	3	3				0.06	0.1			
Bidens subalternans	3					2.6				
Baccharis darwinii		3					0.5			
Pitraea cuneato-ovata		3					0.1			
Echinopsis leucantha		3					0.01			
Amarilidaceae		3					0.01			
Euphorbia ovalifolia		3					0.01			
Trixis papillosa	13	3	2			1.7	0.01	0.1		
Condalia microphylla	13	10	3			2.9	3.2	0.3		
Atriplex lampa	16	10	5			1.9	7.3	0.8		
Allionia incarnata	3		3			0.03		0.3		
Geoffroea decorticans	9	13	14			2.9	7.7	1.2		
Lycium chilense var. *minutifolium*	6	6	2			0.3	0.2	0.2		
Verbesina encelioides	10	10	3			0.5	1.2	0.2		
Prosopis flexuosa	6	7	5			0.06	0.1	0.2		
Chondrosum barbatum		2				2.0				
Munroa mendocina		3				0.02				
Amaranthus standleyanus		2				0.03				
Chloris castilloniana		2				0.03				
Trichocline sinuata		2				0.1				
Pappophorum phillipianum		5				0.5				
Junellia aspera	29	20	34	o		6.5	2.8	3.6		
Sphaeralcea miniata		10	10	o	o	0.04	0.4	*	o	
Cottea pappophoroides	3	24	*			0.2	0.9	o		
Trichloris crinita	35	20	41	o		1.1	0.7	3.7	*	
Aristida mendocina	6	10	25	*		0.1	0.5	3.0	*	
Neobouteloua lophostachya		5	*			0.6	*			
Glandularia mendocina		3	*			0.02	*			
Digitaria californica	23	20	47	*		0.7	0.4	7.5	**	
Acantholippia seriphioides	6	3	34	**		0.3	0.4	3.7	**	
Parthenium hysterophorus	10	7	49	**		0.04	0.07	5.4	**	
Pappophorum caespitosum	13	13	44	**		1.9	0.5	4.2	**	
Larrea divaricata	16	7	75	**		0.9	0.8	22.7	**	
Heliotropium mendocinum		8	**				0.06	**		
Sporobolus cryptandrus		10	**				0.9	**		

** = $P < 0.01$; * = $P < 0.05$; o = $P < 0.15$.

Table 2. Total richness, species per m^2, diversity (Shannon index), evenness and percentage of total cover, litter cover and bare soil in the different mesohabitats and microhabitats. Values represent means (and SD). Column Meso shows levels of significance between mesohabitats (undercanopy and intercanopy) and column Micro between both microhabitats (northern and southern) nested in the undercanopy mesohabitat.

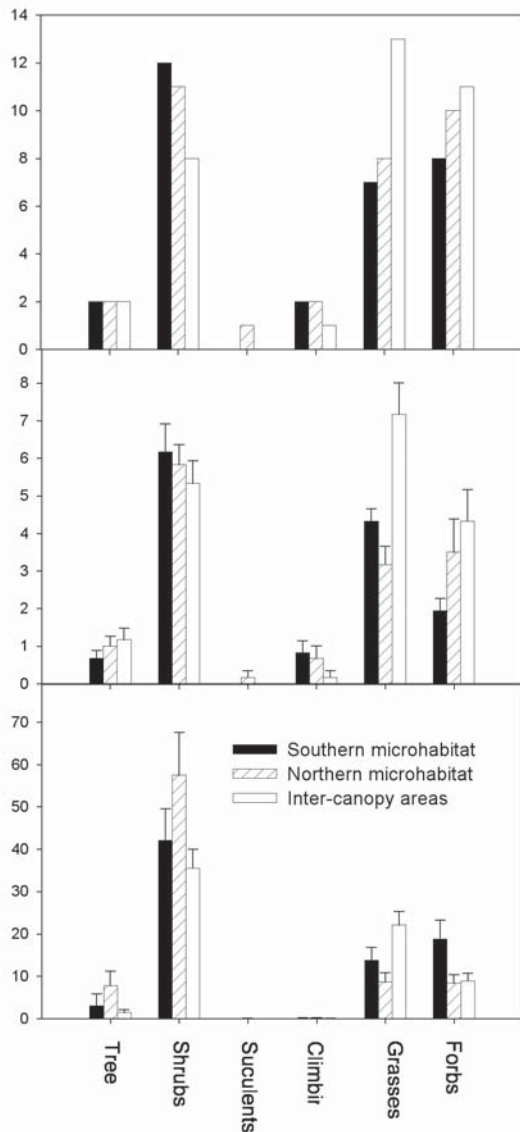| | Undercanopy | | Intercanopy | P-level | |
	southern	northern		Meso	Micro
Total richness	31	34	35		
Species per m^2	5.6 (0.6)	4.9 (0.7)	5.6 (0.9)	0.44	0.11
Diversity	1.95 (0.30)	1.86 (0.27)	1.91 (0.16)	0.98	0.59
Evenness	0.71 (0.1)	0.70 (0.07)	0.72 (0.06)	0.78	0.84
Total coverage (%)	77 (16)	79 (27)	69 (13)	0.38	0.87
Bare soil (%)	1.4 (1.2)	2.5 (2.7)	36 (10)	0.001	0.79
Litter (%)	46 (13)	55 (13)	10.25 (7)	0.001	0.2

Fig. 2. Total number of species, number of species per plot and cover percentage of the different life forms under *P. flexuosa* canopies (northern and southern microhabitats) and in intercanopy areas. Bars represent mean values and vertical lines the standard error.

Table 3. Soil chemical conditions under *P. flexuosa* canopies (northern and southern microhabitats) and in intercanopy areas. Values are means. Column 'Meso' shows levels of significance between mesohabitats (undercanopy and intercanopy) and column 'Micro' between both microhabitats (northern and southern) nested in the undercanopy mesohabitat.

	Undercanopy		Intercanopy	P-level	
	southern	northern		Meso	Micro
Organic matter (%)	1.74	2.37	0.74	0.004	0.16
N (ppm)	1332	1584	851	0.0001	0.12
P (ppm)	7.80	8.27	7.23	0.0005	0.03
K (ppm)	988	954	923	0.04	0.2
Ph	6.73	6.88	6.88	0.60	0.41
Na (me/l)	0.85	3.58	1.11	0.04	0.008
Ca (me/l)	2.7	9.1	2.9	0.004	0.001
Mg (me/l)	0.75	2.03	0.92	0.02	0.001
EC (S)	611	1543	434	0.009	0.002
SAR	0.64	1.6	0.83	0.2	0.04

Discussion

In agreement with the postulated hypothesis, our results show that *P. flexuosa* does modify soil conditions, generating spatial heterogeneity at different scales and the spatial pattern of understorey species. At the mesohabitat scale, this is evidenced by the differences observed in floristic composition, frequency and relative cover of plant species, as much as in edaphic conditions between the areas under *P. flexuosa* canopies and intercanopy areas. Although at the microhabitat scale the ordination of vegetation data showed no separation between the different aspects under *P. flexuosa* canopies, we found differences in the distribution of life forms and some species and in the edaphic conditions.

Differences in floristic composition between sites under shrubs and trees and intercanopy areas have been reported by Mares et al. (1977) and Archer (1988) for other *Prosopis* species, and by Akpo et al. (1997), Pugnaire et al. (1996a, b) and Moro et al. (1997b) for different woody species in other arid regions of the world. In the Monte desert, the change in floristic composition implies replacement of species according to life form since shrubs are best represented in the *P. flexuosa* understorey. Intercanopy areas, instead, exhibit the highest number and cover of grasses, all of these with C_4 metabolism. This replacement is similar to the one proposed by Archer (1995b) for the semi-arid lands of North America.

Furthermore, we found that *P. flexuosa* generates different microhabitats under its canopy in response to different cardinal orientations with respect to the trunk. This agrees with Moro et al. (1997a,b) who suggested that generating spatial heterogeneity by overstorey shrubs and trees is not restricted to canopy-intercanopy, but

gen, phosphorus and potassium were significantly higher under canopies than in intercanopy areas. No differences, however, were found in pH or SAR. Electrical conductivity and concentrations of Na^+, Ca^{++}, Mg^{++} were higher in northern than in southern microhabitats. They were also higher in undercanopy than intercanopy areas, but these differences were due to the high values found in northern microhabitats, because southern microhabitat means were similar to those of intercanopy areas (Table 3).

even promotes the formation of different microhabitats within the undercanopy area, resulting in increasing heterogeneity. Small-scale environmental changes produced under the canopy of trees and shrubs have rarely been addressed. Archer (1995b) and Moro et al. (1997a,b) found environmental differences and associated changes in species composition following a gradient from the trunk to the edge of the canopy. Franco-Pizaña (1995), on the other hand, found no differences in shrub composition between the four cardinal directions.

Pugnaire et al. (1996a,b) and Moro et al. *(*1997a,b) found a conspicuous layer of annual and perennial herbs underneath shrub canopies. We only found a higher cover of forbs in the southern microhabitat where we found the lowest richness. This indicates a high dominance of some annual forbs (e.g. *Chenopodium papulosum* and *Bidens subalternans*) in this microhabitat. Gutiérrez et al. (1993) related the increased dominance of some species to the increased fertility in undercanopy areas. However, in this study we found no difference in N or K concentrations between northern and southern microhabitats and the P concentration is higher in northern microhabitats. Therefore this effect is most likely to be related to water availability or shading.

The mechanisms whereby *P. flexuosa* induces the replacement of species may be attenuation of extreme climatic conditions, reduction in the incidence of sunlight, modification of soil chemical properties and passive facilitation by providing perches for seed dispersing birds (Archer et al. 1988; Archer 1995a; Moro et al. 1997b). Moreover, the higher litter cover and smaller patches of bare soil observed under canopies may contribute to moisture conservation, although litter is likely to have negative mechanical and chemical effects on understorey growth (Facelli & Pickett 1991). Evidently, in the Monte desert these mechanisms do not act homogeneously over the entire undercanopy area. For example, as the reserve of Ñacuñán receives solar radiation predominantly from the North and rainfall and winds from the south-southeast (Estrella et al. 1979), we can expect hotter and drier environments in northern microhabitats as well as different soil conditions. The differences observed in species distribution would be determined by each species' ability, or lack of, to cope with these environmental changes, and would be associated with different requirements for light, moisture and nutrients. For example, C_4 grasses (that are more frequent in intercanopy areas) would benefit from environments with high temperature, high radiation and more limited water supply; *Stipa ichu*, the only C_3 grass in the reserve, would be favoured by more shaded, more humid and cooler habitats (Cavagnaro 1988).

Simpson & Solbrig (1977), Aggarwal et al. (1976) reported higher diversity under *Prosopis* canopies. Akpo et al. (1997), Pugnaire (1996b) and Moro (1997b) attributed increased species richness in the understorey of trees and shrubs in drylands to increased soil fertility. In contrast, Gutiérrez et al. (1993) found that species richness was lower underneath shrubs and that some species had higher densities and/or biomass outside than underneath shrubs, while others showed the opposite trend. In the Monte desert we found no differences in species richness, diversity or total cover between mesohabitats, or between the two cardinal directions considered, which indicates that differences are only the result of a replacement of plant species but not of the enrichment of the generated patches. It is clear, however, that *P. flexuosa* generates patches that can be occupied by species different from those in open areas, contributing to increase the total diversity of the ecosystem.

Interactions among plant species are determined by complex mechanisms that depend on the particular species, life stage, environmental conditions and presence of other species (Callaway & Walker 1997). The effect of plant interaction is the result of combined positive (facilitation) and negative (interference) interactions. Various studies point out that facilitation predominates in more stressful environments while interference prevails in less stressful ones (Callaway 1997; Callaway & Walker 1997; Pugnaire & Luque 2001). The present study was conducted during a particularly wet year. The effect of *P. flexuosa* on other species could be greater in drier years, accentuating the differences between habitats. Likewise, facilitation can assume greater importance in more xeric areas of the Monte desert, i.e. in areas where annual rainfall does not exceed 80 mm.yr^{-1}.

The differences found in soil chemical characteristics show that perennial plants can strongly influence edaphic conditions under their canopies. Soil constraining elements in the Monte desert such as organic matter, and the concentration of N and P were significantly higher under than outside *P. flexuosa* canopies. This agrees with several authors that have reported increased fertility under the canopy of *P. glandulosa* (Tiedemann & Klemmedson 1972, 1977; Barth & Klemmedson 1982; Franco-Pizaña et al. 1995), *P. cineraria* (Aggarwal 1980; Shankar et al. 1976) and other trees and shrubs in arid and semi-arid environments (Garner & Steinberger 1989; Mazzarino et al. 1991; Rostagno et al. 1991; Moro et al. 1997b). Two mechanisms can explain soil nutrient enrichment beneath canopies: first, redistribution of nutrients absorbed by the root system to the area (Tiedemann & Klemmedson 1972; Barth & Klemmedson 1982) and second, biological fixation of nitrogen by symbiotic *Rhizobium* (Geesing et al. 2000).

We also found differences in soil conditions between cardinal directions under the canopy of *P. flexuosa*. Only a few studies analyse the spatial variation in soil

conditions under canopies (Tiedemann & Klemmedson 1977; Moro et al. 1997b). Our results revealed that electrical conductivity and concentrations of P, Na$^+$, Ca^{++}, Mg^{++} were higher in the northern microhabitat. This could be attributed to the direction from which winds and precipitation come (Estrella et al. 1979), since they would have a higher incidence in the southern microhabitat by leaching the soil under trees, and in contrast the northern microhabitat has a higher exposure to solar radiation and therefore higher salt concentration.

In conclusion, the presence of *P. flexuosa* in the desert environmentof the Ñacuñán Biosphere reserve modifies the spatial pattern of plant species in the shrub and herbaceous layers and the soil chemical conditions (and therefore microclimatic conditions), generating spatial heterogeneity at different scales. The differences in floristic composition and in soil conditions are observed not only between the two mesohabitats studied but also between different microhabitats under *P. flexuosa* canopies in response to different aspects. These differences in floristic composition are the result of species replacement rather than species enrichment. It is clear, however, that this replacement contributes to increasing the total diversity of the ecosystem.

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