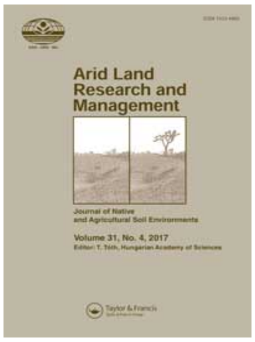

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Ameliorative effects of nurse shrubs on soil chemical characteristics are driven by plant size in the Monte desert

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ABSTRACT

In deserts, shrubs determine landscape structure and influence plant productivity by creating nutrient-enriched environments. Attributes vary among shrub species, thus their contribution to soil characteristics is expected to vary as well, and nutrient input under shrub cover will depend on species attributes. We propose that plant size determines the contribution to soil chemical characteristics. Therefore, the contribution of larger species will be higher than smaller ones. Also, each species will contribute differentially for each chemical parameter. To corroborate these premises, we measured six soil chemical characteristics in areas covered by shrubs and in bare soil, as well as among five nurse species, in four sites of the Monte desert (La Rioja, Argentina). A multivariate analysis of variance (MANOVA) indicated significant variation between cover conditions and locations. Supporting previous studies, the presence of shrubs improved soil properties. Chemical concentration between soils under shrubs and bare soils, respectively, showed as mean and (SD) were: carbon(%): 0.82 (0,47), 0.52 (0.22); nitrates (ppm): 33,33 (67,36), 2.63 (0.56); phosphorous(ppm): 16.76 (25.02), 6.56 (1.92); electrical conductivity (dS m^{-1}): 0.24 (0,43), 0.03 (0,02); pH: 6.93 (0.56), 7.62 (0.53); and water content (%): 3,17 (8.94), 2.47 (9.15). Chemical characteristics also varied according to the nurse species. Larger nurse species affected the ensemble of chemical characteristics, after controlling for cover condition and site. Larger plant species (*Bulnesia retama, Prosopis torquata*, and *Zuccagnia punctata*) were significantly associated with higher carbon and higher nitrates concentration. These results suggest that soil properties are enhanced by the size of nurse plant species.

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Introduction

A major principle of arid land ecology is that the location of perennial plants influences the spatial distribution of microclimate, soil properties, and organisms (Tielbörger and Kadmon 1997; Flores and Jurado 2003; Allen, Steers, and 2011). Plants that facilitate the establishment of other plant species under their canopy or provide protection against herbivores are called nurse plants (Callaway 1995, Gutiérrez and Squeo 2004; Schade

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and Hobbie 2005). Desert plant communities are excellent study systems for examining effects of positive interactions on soils. Knowledge of the natural processes involved in the functioning and establishment of vegetation is important for management, restoration and conservation of arid lands (Castro et al. 2002; Padilla and Pugnaire 2006). In degraded desert areas, the re-establishment of fertile islands is necessary for the initiation of ecosystem recovery (Padilla and Pugnaire 2006; Bonanomi, Incerti, and Mazzoleni 2011). When re-establishing native vegetation as part of ecological restoration, the knowledge regarding which native species to use is a fundamental question (Abella and Smith 2013). In fact, shrubs are determinant of the landscape structure in desert ecosystems and influence plant productivity and biodiversity by creating nutrient-enriched environments. However, given the differences in structural and functional attributes among shrub species, their contribution to soil characteristics is expected to vary.

Soils have been ubiquitously recognized as a critical resource for sustaining productivity, ecosystem functioning, and resilience (Smith et al. 1995; Herrick 2000), particularly in water-limited environments. A distinctive feature of arid ecosystems is the heterogeneity in environmental conditions and soil resources, generated by a patchy plant cover (Noy-Meir 1985; Aguiar and Sala 1999). Briefly, the landscape of these ecosystems is characterized by two phases: one dominated by shrubs and small trees (either isolated or in groups) and the other corresponding to the interspaces between perennial plants, with low to null herbaceous cover (Noy-Meir 1985; Aguiar and Sala 1999; López and Ortuño 2008). The microclimate and soil characteristics associated with both types of microenvironments are often very different (Callaway 1995). In the case of bare soil, extreme environmental conditions (high values of solar radiation, soil temperature, evapotranspiration, and thermal amplitude) prevail and the texture of soils is coarse (Nobel 1984; Titus, Nowak, and Smith 2002; Gutiérrez and Squeo 2004). In contrast, perennial plant canopies create more favorable microenvironmental conditions by providing shade and moderating soil and air temperatures, reducing solar insolation, and decreasing evaporation rates compared to that of the interspaces between perennial plants (Hunter and Aarssen 1988; Franco and Nobel 1989; Valiente-Banuet and Ezcurra 1991). Likewise, litterfall and roots from shrubs contribute to the enrichment of organic matter and nutrient content in the soil (Gutiérrez and Squeo 2004), promoting moisture and mineral concentration and mycorrhizal proliferation (Vitousek and Hooper 1993; Titus, Nowak, and Smith 2002; Celaya-Michel and Castellanos-Villegas 2011). These nutrient-enriched soils are termed "fertility islands" (García Moya and Mickell 1970; Virginia and Jarrel 1983; Schlesinger et al. 1996; Schade and Hobbie 2005; Perroni-Ventura, Montaña, and García-Oliva 2006) or "resource islands" (Reynolds et al. 1999), and have a major role in the dynamics of desert ecosystems (Titus, Nowak, and Smith 2002; Rodríguez-Echeverría and Pérez-Fernández 2003). As a result, in these environments, biota such as soil microbes and annual plants are often more abundant below perennial plant canopies than in the bare soil (Patten 1978; Tewksbury and Lloyd 2001; Su et al. 2012). Resource islands regulate the size and activity of soil microbial biomass through the contribution of litter and roots (Perroni-Ventura, Montaña, and García-Oliva 2006). By promoting better conditions for the growth of soil microorganisms (Carrillo-García et al. 2002; Perroni-Ventura, Montaña, and García-Oliva 2006), resource islands stimulate nitrogen mineralization, increasing nitrogen availability (Bernhard-Reversat 1982). After water, nitrogen is the second most limiting factor of plant productivity in arid environments (Celaya-Michel and Castellanos-Villegas 2011) and is considered a key element in determining community structure and succession (Tilman 1986). Arid regions are generally low in N content compared to other regions and have few nitrogen-fixing plant species (Farnsworth, Romney, and Wallace 1976; Wullstein 1989; Evans and Belnap 1999).

In deserts, woody plants can act simultaneously as barriers and traps for the flow of seeds and organic matter (Giladi, Moran, and Ungar 2013; Filazzola and Lortie 2014). Mulch accumulation under shrubs (dry leaves, thin branches, flowers, fruits, and particulate organic matter) may contribute to a greater flow of nutrients in the soil. The abundance, composition, and characteristics of the mulch depend on the species that produces it. Thus, nutrient input under shrub cover will depend on the attributes of species. Zinke (1962) showed that the effect of the tree canopy on soil properties was proportional to canopy size. This is a simple premise which has been rarely considered as a direct factor in plant facilitation studies (Filazzola and Lortie 2014). We propose that the size of nurse plants determine the level of contribution to soil chemical characteristics. Therefore, the contribution of larger plant species will be higher than that of smaller ones. In addition, the contribution of each species to each chemical parameter may be different.

To test these premises, we conducted an observational study in the Monte desert of Argentina. The Monte desert is one of the largest arid biogeographic regions in Argentina (460,000 km^2), and is characterized by xeric shrub steppes dominated by Zygophyllaceae (Cabrera 1994). Despite the fact that nurse plants can play useful roles in maintaining or restoring arid ecosystems (Padilla and Pugnaire 2006; Gómez-Aparicio 2009), there is little information about nurse-soil interactions in this region. The results of a comparative study conducted in the Monte of Mendoza (Méndez, Guevara, and Estevez 2004) indicate that shrubs significantly increase the content of organic matter, nitrogen and soil moisture. Nurse plant studies in the Monte desert were mostly carried out at the patch scale (i.e., areas with and without shrubs), but there is still no data on the particular effect of nurse species on soil characteristics.

The Antinaco-Los Colorados Valley in the province of La Rioja (northwestern Argentina) is a characteristic area of the northern Monte. The steppe of this valley is dominated by five species of evergreen shrubs: *Larrea cuneifolia* ("jarilla"), *Bulnesia retama* ("retamo"), *Prosopis torquata* ("tinti-taco"), *Tricomaria usillo* ("usillo"), and *Zuccagnia punctata* ("pus-pus") (Varela, Buedo, and Parrado 2015). Because of their abundance and wide distribution in the valley, these species are expected to function as major contributors of organic matter to the soil by providing remnants of leaves, roots, branches, flowers, and fruits. Differences in size among these species (height, crown diameter, crown area, and crown volume; Table 1) may determine different contributions to soil properties, under the assumption that a larger nurse size favors nutrient inputs by means of net

Table 1. Size of nurse plant species (mean ± 1 standard deviation).

Species	Height	Major crown diameter	Minor crown diameter	Crown area	Crown volume
Bulnesia retama (Gillies ex Hook. & Arn.) Griseb.	3.2 ± 0.6	4.9 ± 1.5	4.2 ± 1.5	17.8 ± 12.5	39.2 ± 28.6
Prosopis torquata (Cav. ex Lag.) DC.	2.0 ± 0.4	4.7 ± 1.0	3.9 ± 0.9	15.3 ± 6.0	21.4 ± 10.0
Zuccagnia punctata Cav.	3.1 ± 0.7	4.3 ± 1.5	3.6 ± 1.1	13.3 ± 8.6	29.7 ± 24.0
Tricomaria usillo Hook. & Arn.	1.4 ± 0.3	2.9 ± 0.8	2.3 ± 0.7	5.6 ± 3.6	5.2 ± 3.4
Larrea cuneifolia Cav.	1.7 ± 0.4	2.7 ± 0.5	2.4 ± 0.5	4.7 ± 1.5	5.2 ± 2.2

Note: Species names are ordered from larger to smaller plant size. Data are in meters (height and diameter), squared meters (area), and cubic meters (volume).

trapping of particles and seeds, better conditions for undergrowth biota, and animal refuge; altogether increasing the nutrient input rate. The aim of this study was to evaluate the influence of five shrub species on soil chemical properties in the Monte of Argentina. The following questions are raised: (1) Are chemical soil properties enhanced by the presence of shrubs? (2) Do shrub species contribute differently to soil properties? (3) Is the variation in soil chemical properties associated to shrub size? We expect that if shrubs generate changes in soil chemical properties, soil under shrubs will exhibit better properties than bare soil. We also expect that different shrub species will differentially contribute to soil properties, with larger species having a greater contribution.

Materials and methods

Study area

The Antinaco-Los Colorados valley (28°50′–29°57′S - 67°23′–67°06′W) is a vast plain (≈ 3,000 km^2) that extends longitudinally between the Sierra de Velasco (4,100 m a.s.l.) and Famatina (6,100 m a.s.l.) in the center-west of La Rioja province, Argentina. It presents a continuous and gradual north-south slope, with a maximum altitude of 1,100 m a.s.l. on the northern side, near Antinaco; and a minimum altitude of 660 m a.s.l. in the southern sector, near Los Colorados (Varela, Buedo, and Parrado 2015). The soils correspond to the Order of the Entisols. They are, in general, loose, sandy, or stony loam, very permeable, with variable depth and minimal profile development, structure-less, and poor in organic matter and nutrients. The presence of calcium carbonate is common throughout the soil profile in the driest areas, although the contents are not enough for the formation of a calcic horizon (Regairaz 2000).

According to the classification of Köppen, the climate of the valley is of type (B.S.h.w) desert, dry, warm; with a significant annual temperature range (Rosa 2000). Rainfall is scarce, and 75% is concentrated in the summer (December to March) with a long dry season in winter (Varela, Buedo, and Parrado 2015). Average annual rainfall in Chilecito locality (La Rioja) is 146.7 mm. Maximum and minimum average temperatures are 26.8°C and 11.3°C, respectively (Servicio Meteorológico Nacional 2010). The dominant vegetation is that of a steppe with scattered shrubs, corresponding to the phytogeographic province of Monte (*sensu* Cabrera 1994), dominated by *Larrea cuneifolia* and *Bulnesia retama* (Zygophyllaceae) (Varela, Buedo, and Parrado 2015). Since the second half of the nineteenth century, the north sector of the Monte (Provinces of Catamarca and La Rioja) has undergone remarkable changes in the coverage and use of the soil, driven by emerging activities, such as the rise of metalliferous mining, the arrival of railroads and the demand—mostly extra-regional—of wood products from the native forest (Rojas 2013). Nowadays, agriculture is the main activity (mainly olive orchards and vineyards; Varela, Buedo, and Parrado 2015), but other land uses such as extractions of firewood, sand and gravel, chicken production, and sub-urban buildings also occur.

Field sampling

In order to get a representative sampling of the Antinaco-Los Colorados valley, we selected four sampling sites distributed along the north-south axis of the valley using Landsat satellite imagery. These sites were selected because they represent the different geo-morphological conditions of the valley, and are located 300–500 m from national routes 40 and 74, which run along the center of the valley. From north to south the selected sites were: Capayán (28°59′17,3″; 67°28′47,2″, 1,223 m a.s.l.), San Nicolás (29°06′37,8″; 67°28′11,8″; 966 m a.s.l.), Los Sarmientos (29°09′23,4″; 67°28′09,3″; 1,054 m a.s.l.), and Chilecito (29° 12′07″; 67°29′ 45,3″; 1053 m a.s.l.). During September 2013, we established a linear transect (80 m east-west), with five points at 20-m intervals at each site. At each point, we sampled the nearest shrub of the five most frequent and abundant species of the valley (*Bulnesia retama, Zuccagnia punctata, Prosopis torquata, Tricomaria usillo*, and *Larrea cuneifolia*). For each individual shrub, we recorded height and largest and smallest plant crown diameters using a graduated ruler and a tape measure. Also, at each point we sampled the nearest area of open space that was not covered by shrubs (hereafter "bare soil"). The size of this area was similar to the crown area of each shrub. Distances from sampling points to focal shrubs and bare soils ranged between 1–30 m and 2–20 m, respectively.

Soil sampling and chemical analysis

During September 2013, we extracted soil samples for chemical analysis between 08:00 and 09:00 hours AM to a depth of 10 cm. We obtained the samples from the area under the canopy of the five aforementioned shrub species and from the adjacent bare soil using a cylindrical bore (diameter: 3 cm). Boreholes for soil samples were drilled at 25 cm from the shrub stem (or the center of the point location in the case of bare soils) in each of the four cardinal points. We sampled a total of 20 individuals per shrub species (five individual shrubs per species per site) and 20 bare soil areas (five bare soil samples per site). In the laboratory (National University of Chilecito), we determined the following variables: (1) carbon (%), through the Walkley-Black method. Dry soil sieved at 0.5 mm, weighed with sufficient accuracy in a dry 250-mL conical flask (between 0.5 g and 1 g). We treated each soil sample with 20 mL of concentrated H_2SO_4 and 10 mL of 0.5 M $K_2Cr_2O_7$. The flask was immediately shaken until the soil and the reactants mixed. When the mixture reached room temperature, we transferred the solution to a flask with 100 mL of deionized water. We determined the unreacted $K_2Cr_2O_7$ by titrating with 0.25 M ferrous ammonium sulfate $[Fe(NH_4)_2(SO_4)_2^{*}6H_2O]$, using diphenylamine as indicator. We calculated total organic carbon content as the difference between a blank solution and a soil solution; (2) we determined nitrates (NO_3-, ppm) using a Nitracheck kit; (3) extractable phosphorus (P, ppm) by the Bray and Kurtz method; (4) electrical conductivity of the saturation extract (EC, dS m^{-1}) using a standard electrical conductivity meter that employs a potentiometer and four electrodes (Hanna Instruments); (5) pH on a 1:5 soil:deionized water suspension potentiometrically measured with a glass electrode standardized against a known buffer solution; and (6) soil moisture (H_2O %), by the gravimetric method (difference between wet weight and dry weight obtained by drying the sample in an oven at 105°C for 24 hours; Carter and Gregorich 2007).

Statistical analysis

To corroborate that the five selected shrub species showed differences in size, we applied a linear model (univariate ANOVA) with the factor species (five levels) and plant volume (surrogate of plant size) as the response variables. We estimated volume as the volume of an ellipsoid with the following formula = (4*π)/3)*((height/2)*(major diameter/2)*(minor diameter/2)). We determined the relationships between soil variables through Pearson's correlations, setting the critical value at $p = 0.0033$. For this, we divided the commonly used p-value threshold of 0.05 by the number of possible correlations from the six soil characteristics. Thus, we avoided Type I errors, since when multiple tests are performed, the probability of finding a significant one is greater than when a single test is performed (Rice 1989). Also, given that soil characteristics are bio-geochemically related and that they were measured in the same sampling unit, we applied a multivariate analysis of variance (MANOVA) (Korkmaz, Goksuluk, and Zararsiz 2014). With the MANOVA, we examined the effects of cover condition (bare soil and soil under shrubs), site (four levels), shrub species (five levels), and shrub size (volume) over the six soil characteristics (log-transformed to meet normality assumptions). It is worth remarking that the full model with the factors species and condition shows a correlated structure, due to the fact that the variation associated to the species factor is represented also by the levels of the condition factor. Due to that, and because our design was focused in the variation between species, we took a step-down approach. First, we ran a MANOVA (additive model without interactions) accounting for the variation in soil properties due to site (four levels) and cover condition (shrub cover versus bare soil) effects. In a second step, the residuals of this model were used as the multivariate response variable where the species factor (five levels) was the unique source of variation. Also, and due to the high co-linearity between species and shrub size, we ran another MANOVA model where shrub size (volume) was the unique source of variation. We interpreted these results as the variation in soil properties due to species characteristics and shrub size, after having accounted for the variation due to site and cover condition (shrub cover versus bare soil). Since the MANOVA showed significant effects (see the Results section), we applied a *post hoc* analysis of variance on each soil characteristic. These univariate ANOVAS exhibit the same model structure than the MANOVA. All analyses were performed in R 3.2.4 (R Development Core Team 2016).

Results

The five nurse species varied significantly in size (Table 1; $F_{4,95} = 14.96$, $P < 0.00001$). *L. cuneifolia* and *T. usillo* were significantly smaller than *B. retama, P. torquata*, and *Z. punctata*. Similar results were found for height, major crown diameter, minor crown diameter, and crown area (results not shown). Overall, these results suggest that soil chemical characteristics are associated to plant size.

Soil characteristics varied greatly between bare soil and soil under shrubs (Table 2). As expected, soil characteristics were correlated among each other, with six positive correlations and four significant negative correlations detected (Table 3). The first step of the MANOVA applied to the six soil characteristics revealed that bare soil differed significantly from soil under shrubs (Pillai's = 0.33198, approx. $F_{6,110} = 9.1108$, $P < 0.000001$). Soil characteristics also differed significantly among sites (0.33019, approx. $F_{18,336} = 2.3086$, $P = 0.002024$). *Post hoc* univariate ANOVAs applied on each soil characteristic indicated significant variation between bare soil and soil under shrubs ($P < 0.05$ in all six soil characteristics). In the same way, the site significantly affected the variation in soil characteristics ($P < 0.05$ in all cases, with the exception of phosphorus). Overall, these results

Table 2. Soil chemical parameters (mean ± 1 standard deviation) recorded under five shrub species and in bare soil.

Variable	*B. retama*[a]	*P. torquata*[b]	*Z. punctata*[a,b]	*T. usillo*[c]	*L. cuneifolia*[c]	Bare soil
C (%)	0.96 ± 0.35	0.86 ± 0.69	0.97 ± 0.53	0.64 ± 0.35	0.69 ± 0.26	0.52 ± 0.22
NO_3^- (ppm)	57.4 ± 93.35	26.40 ± 36.40	37.65 ± 73.23	26.85 ± 56.49	18.35 ± 63.92	2.63 ± 0.56
P (ppm)	11.58 ± 6.58	19.51 ± 10.92	11.66 ± 6.41	27.19 ± 52.90	13.88 ± 8.62	6.56 ± 1.92
EC (dS m^{-1})	0.39 ± 0.62	0.13 ± 0.16	0.25 ± 0.42	0.20 ± 0.29	0.24 ± 0.51	0.03 ± 0.02
pH (1:5)	7.15 ± 0.43	6.72 ± 0.60	6.80 ± 0.47	6.98 ± 0.60	7.02 ± 0.61	7.62 ± 0.53
H_2O (%)	2.71 ± 9.18	4.49 ± 10.21	2.17 ± 6.95	1.54 ± 4.20	4.96 ± 12.35	2.47 ± 9.15

Note: Species names are ordered from larger to smaller plant size (significant differences in size are denoted by different letters). C, carbon; NO_3^-, nitrates; P, phosphorus; EC, electrical conductivity; pH, potential of the ion hydrogen; H_2O, soil moisture content; n: 20.

Table 3. Pearson correlations among soil characteristics.

	NO_3^-	P	EC	pH	H_2O (%)
C (%)	**0.479 (0.000)**[a]	0.167 (0.068)	**0.435 (0.000)**[a]	**−0.352 (0.000)**[a]	0.100 (0.276)
NO_3^- (ppm)		0.056 (0.558)	**0.935 (0.000)**[a]	−0.208 (0.023)	0.186 (0.042)
P (ppm)			0.050 (0.589)	**−0.329 (0.000)**[b]	0.015 (0.869)
EC (dS m^{-1})				−0.166 (0.069)	0.205 (0.025)
pH (1:5)					−0.141 (0.126)

Note: The r and probability values (within brackets) are indicated. Significant correlations are indicated in bold, considering a critical value of 0.00333 (0.05/15 correlations). C, carbon; NO_3^-, nitrates; P, phosphorus; EC, electrical conductivity; pH, potential of the ion hydrogen; H_2O, soil moisture content.
[a]$P < 0.0001$.
[b]$P < 0.001$.

provide confirmation of the well-established knowledge regarding the effects of spatial heterogeneity on soil parameters in deserts due to location and nurse plant effects.

The second step of the MANOVA revealed significant variation due to species effects over the six soil parameters (Pillai's = 0.47833, approx. $F_{24,372} = 2.1053$, $P = 0.002032$). Since the MANOVA showed significant differences between species, we performed univariate *post hoc* ANOVAs. Overall, these analyses showed that the factor species generated significant variation in soil characteristics. Particularly, we found significant variation in C and NO_3^- (Table 4). Also, we found significant variation due to shrub size effects over the six soil parameters (Pillai's = 0.13288, approx. $F_{6,93} = 2.3753$, $P = 0.03522$). Since the

Table 4. Summary of the *post hoc* Multivariate Analysis of Variance (MANOVA) for the effects of shrub species on soil characteristics (see the Methods section for details).

Response variable	Source of variation	SS	MS	*F*	*P*
C (%)	Species	2.734	0.684	2.767	0.032
	Error	23.469	0.247		
NO_3^- (ppm)	Species	20.029	5.007	2.857	0.028
	Error	166.499	1.753		
P (ppm)	Species	3.244	0.806	1.178	0.325
	Error	65.030	0.685		
EC (dS m^{-1})	Species	4.689	1.172	0.914	0.459
	Error	121.826	1.282		
pH (1:5)	Species	0.052	0.013	2.207	0.074
	Error	0.559	0.006		
H_2O (%)	Species	2.788	0.697	0.508	0.730
	Error	130.490	1.374		

Note: C, carbon; NO_3^-, nitrates; P, phosphorus; EC, electrical conductivity; pH, potential of the ion hydrogen; H_2O, soil mositure content. Degrees of freedom: 4 (factor), 95 (error); SS: sum of squares; MS: mean squares; *F*: value of the *F* statistic; *P*: probability value.

Table 5. Summary of the *post hoc* Multivariate Analysis of Variance (MANOVA) for the effects of shrub size (volume) on soil characteristics (see the Methods section for details).

Response variable	Source of variation	SS	MS	*F*	*P*
C (%)	Volume	2.611	2.611	10.846	0.001
	Error	23.592	0.241		
NO_3^- (ppm)	Volume	7.467	7.467	4.087	0.046
	Error	179.061	1.827		
P (ppm)	Volume	0.015	0.015	0.021	0.884
	Error	68.239	0.696		
EC (dS m^{-1})	Volume	1.342	1.342	1.050	0.308
	Error	125.174	1.277		
pH (1:5)	Volume	0.003	0.003	0.434	0.511
	Error	0.608	0.006		
H_2O (%)	Volume	0.237	0.237	0.175	0.677
	Error	133.041	1.358		

Note: C, carbon; NO_3^-, nitrates; P, phosphorus; EC, electrical conductivity; pH, potential of the ion hydrogen; H_2O, soil moisture content. Degrees of freedom: 4 (factor), 95 (error); SS: sum of squares; MS: mean squares; *F*: value of the *F* statistic; *P*: probability value.

MANOVA showed significant effects of shrub size, we performed univariate *post hoc* ANOVAs. These analyses showed that the factor shrub size generated significant variation in soil characteristics. Particularly, we found significant variation in C and NO_3^- (Table 5). Overall, this significant variation in soil characteristics is congruent with an increasing gradient of nutrients from smaller to larger nurse species (Table 2).

Discussion

Our findings suggest that shrubs enhance soil chemical properties. Particularly, soil chemical properties were associated to plant size. Larger shrub species enhanced the concentration of carbon and nitrates in comparison to smaller shrub species. Nitrate content was 12.7 times higher in soil under nurse shrubs than in bare soil. A similar trend was observed for EC (7.8 times), P (2.6 times), and C (1.7 times). These changes of magnitude in soil chemical attributes suggest enhanced fertility conditions for plant growth under nurse shrubs and provide new evidence of the benefits of nurse plants in the Monte desert.

Our data are comparable to those obtained in the Monte of Mendoza province by Méndez, Guevara, and Estevez (2004), who have also reported amelioration in soil characteristics due to the effect of shrubs. The difference between soil under shrubs and bare soil areas reported by those authors were 1.8, 4.1, and 1.1 times higher for N, EC, and phosphorus, respectively. Other studies examining the influence of nurse plants on soil characteristics have consistently reported positive effects (Filazzola and Lortie 2014; Verdu, Gómez-Aparicio, and Valiente-Banuet 2015). For example, in arid zones of Chile with similar rainfall patterns (185 mm), soils under shrubs presented higher values of N, P, and EC than in bare soil with a ratio of 3.5, 3.2, and 1.7, respectively (Cares et al. 2013). In desert areas of North America, such as the Mojave Desert, N and P soil levels under the canopy of shrubs was likely 50% higher than in the areas between shrubs (Cares et al. 2013). In general, studies assessing the spatial pattern of soil nutrients in deserts indicate that the average concentration ratios of nitrogen and other nutrients in soils under shrubs and inter-spaces range between 1.3 and 3.0 (Thompson et al. 2005). The causes by which nurse plants enhance soil chemical properties are basically a greater supply of biomass than in bare soils, and a higher flux of nutrients driven by the interaction with fungi organisms and animals that use plants to rest and eat (Méndez, Guevara, and Estevez 2004; Schade and Hobbie 2005; Filazzola and Lortie 2014).

In different types of ecosystems, such as the African savannas (Bernhard-Reversat 1982), Chilean thornscrubs (Gutiérrez et al. 1993) and grasslands and deserts of North America (Barth and Klemmedson 1978, Virginia and Jarrel 1983; Hook, Burke, and Lauenroth 1991), organic matter, nitrogen, and other soil chemical variables were higher under shrubs and trees than in bare soil, suggesting that soil characteristics are strongly influenced by plant canopy (Moro et al. 1997). In this study, the presence of shrubs produced remarkable improvements in soil moisture content compared to bare soil areas. Such differences are expected, due to the poor organic matter content and low water retention capacity that characterize desert soils (Fernández Gálvez 2010; Mazuela Águila 2013). However, in our study the effect of shrub size and species was not significantly different, perhaps because of the high variability of this trait.

Our data support the importance of shrubs as generators of "fertility islands" in deserts (García Moya and Mickell 1970; Charley and West 1975; Virginia and Jarrel 1983; Noy-Meir 1985; Schlesinger et al. 1996; Perroni-Ventura, Montaña, and García-Oliva 2006) and as promoters of heterogeneity in soil properties (Titus, Nowak, and Smith 2002; Thompson et al. 2005). The results also support the hypothesis that differences in plant size among different species (*Bulnesia retama, Prosopis torquata, Zuccagnia punctata, Tricomaria usillo*, and *Larrea cuneifolia*) determine a differential contribution to soil chemical properties. This effect has been frequently observed in arid and semi-arid ecosystems, where isolated trees are found within a herbaceous matrix, and generally consists of an increased content of organic matter, water, and nutrients under canopies (Mordelet, Abbadie, and Menaut 1993; Breman and Kessler 1995). These influences may be due to the fact that larger species might exhibit a greater incidence acting as seed traps (Giladi, Moran, and Ungar 2013), shade and shelter (Filazzola and Lortie 2014), rooting depth, and litter quality and quantity (Gregory 2006) or to secondary effects over soil pH, moisture, and nutrient levels (Lynch and Whipps 1990; Wardle 1992). Different plant species can potentially affect nutrient cycling in a variety of ways, due to differences in uptake, loss, litter quality, and associations with microbes (Hobbie 1992). The variation in nutrient concentration generated by different species may have important implications for the spatial distribution of soil plants and animals (Gallardo 2003). These observations suggest that plant species that differ in their phenotypic traits, specially size, have the potential to alter soil chemical properties, which may, in turn, affect biogeochemical cycling and ecosystem functioning.

In summary, the studied shrub species make a great contribution to the improvement of soil chemical properties and conditions for plant growth. This study supports previous reports documenting the positive effects of nurse shrubs on soil chemical characteristics. The microenvironments created by nurse plants have an important role in the spatial variation of productivity and biodiversity at the local and landscape levels. Our results also provide the first evidence of shrub contribution to soil chemical properties for the five most common species of the Monte desert of La Rioja and contribute to the understanding of the dynamics of this ecosystem. The presence of shrubs in a matrix of bare soil can greatly modify geochemical and biological mechanisms, resulting in different spatial properties of soil nutrients driven by plant size. Therefore, the conservation of these species is expected to contribute to the maintenance and improvement of soil properties in the Monte desert ecosystem.

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