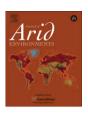
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Spatiotemporal heterogeneity of soil fertility in the Central Monte desert (Argentina)

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ABSTRACT

In arid environments, soil fertility exhibits a high degree of spatial and temporal heterogeneity, which results from high climatic variability seasonally and heterogeneous plant distribution. However, because most desert areas have been altered by human activities, heterogeneous fertility would originate from grazing or logging activities. We evaluated spatial and temporal heterogeneity of soil fertility in cattle-excluded sites under and outside woody plant cover (*Prosopis flexuosa* and *Larrea divaricata*), and in sites disturbed by tree removal during wet and dry season in Nacuñán Biosphere Reserve (Central Monte desert of Argentina). Soil organic matter, fulvic acids, bioavailable organic matter, and nitrate were lower outside plant canopy (8.9 mg g $^{-1}$, 0.03 mg g $^{-1}$, 8.2 mg g $^{-1}$, and 4.17 mg kg $^{-1}$, respectively). Total N, humic acids, and abundance of microbial functional groups did not show differences among sites. Most parameters differed between seasons, tending to be higher in the wet season. Overall soils of Nacuñán Reserve are characterized by: a) more homogenous spatial pattern than expected from woody plant presence; b) very heterogeneous temporal pattern; and c) after two years, tree removal does not seem to induce infertile soil formation.

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1. Introduction

In arid environments, soil fertility is characterized by a high temporal and spatial heterogeneity (Austin et al., 2004: Farley and Fitter, 1999; Maestre et al., 2003). Temporal heterogeneity of soil properties here results from a high seasonal and inter-annual climatic variability, since the amount and frequency of precipitation limit continuous biological activity (Austin et al., 2004; Huxman et al., 2004; Xie and Steinberger, 2001). Spatial heterogeneity of soil properties has been attributed to heterogeneous plant distribution, which creates areas of great nutrient uptake and high deposition of organic residues in the soil (Prescott, 2002; Rietkerk et al., 2004; Rotundo and Aguiar, 2005). Moreover, residue decomposition benefits from improved environmental conditions present beneath the plant cover (moderate temperatures, higher infiltration, greater water-holding capacity, etc.) (Aguiar and Sala, 1999; Farley and Fitter, 1999; Rossi and Villagra, 2003). Thus, many authors define the areas of surface soil beneath plants as "fertility islands", in contrast to highly abundant bare soil areas (Carrera et al., 2003; Gutiérrez et al., 1993; Schlesinger et al., 1996; Stock et al., 1999).

However, because the most desert areas have been altered by human activities, some investigators suggest that spatial heterogeneity originates from the contrast between vegetation cover areas with areas desertified by grazing or logging. Overgrazing induces soil compaction and erosion, and asymmetrical distribution of water and nutrients (Abril and Bucher, 1999; Abril et al., 2005; Mazzarino et al., 1998). Similarly, greater exposure of fertile soils due to woody plant removal promotes soil organic matter loss as a result of both dry climatic conditions and lack of litter deposition (Abril and Noe, 2007; Londo et al., 1999).

Desert soil fertility has been generally defined by the mineral nutrient content available to plants, whereas studies on functional aspects of soil are rare, particularly in the Argentina Monte desert (Aguilera et al., 1999; Bolton et al., 1993; Smith et al., 1994; Titus et al., 2002; Xie and Steinberger, 2001). However, functional parameters, such as evolution of the different fractions of organic matter, nutrient flow, and abundance and activity of soil microorganisms are essential aspects for the understanding of soil fertility dynamics (Abril and Bucher, 2008; Gelsomino et al., 2006; Robertson and Paul, 2000).

Ñacuñán Biosphere Reserve in the Central Monte desert of Argentina, provides the opportunity to evaluate soil fertility heterogeneity under no-grazing conditions because cattle were excluded 30 years ago. Moreover, a logging assay that is being

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conducted in the reserve allows evaluation of soil fertility changes due to woody plant removal.

Here we report the effects of spatial and temporal heterogeneity (due to differential distribution of woody plants and climatic seasonality) in the Central Monte desert on soil functional parameters (organic matter and N fractions, and abundance and activity of soil microorganisms). Also, we evaluated the soil characteristics of sites under and outside woody plant cover and those sites disturbed by tree removal during wet and dry season in Nacuñán Biosphere Reserve

We predicted that soils of the Central Monte desert would have: a) high spatial heterogeneity resulting from the presence of woody plants; b) high temporal heterogeneity; and c) that woody plant logged always leads to the formation of infertile soil areas.

2. Materials and methods

2.1. Study area

The study was conducted in Ñacuñán Biosphere Reserve, province of Mendoza (Argentina) (34°03′S and 67°58′W). The 12,000-ha reserve was created in 1972 as a Forest Reserve; in 1986 it became part of the MAB–UNESCO network. The reserve is situated in a vast plain, 540 m a.s.l., covering an extensive region in Argentina. The deep and sandy soils are of eolian and hydric origin. The climate is temperate and dry, with a seasonal annual precipitation regime concentrated in summer (November–March). Mean annual rainfall is 329 mm (1972–1998 data) with a water deficit throughout the year and marked inter-annual variation. Mean annual temperature is 15.6 °C, with a maximum annual mean of 23.8 °C and a minimum annual mean of 7.6 °C (Claver and Roig–Juñent, 2001).

The area is in the central portion of the Monte desert, which is mainly characterized by an extensive shrubland dominated by *Larrea* spp. interspersed with open forest of *Prosopis* spp. (Cabrera, 1976). The most extensive community in the reserve is the open *Prosopis flexuosa* DC woodland, which also has *Geoffroea decorticans* (Gillies ex Hook & Arn.) Burkart, in the tree layer, and *Larrea divaricata* Cav, *Capparis atamisquea* Kuntze, and *Lycium tenuispinosum* Miers, in the shrub layer. The herbaceous layer is composed of grasses (mainly summer perennial Poaceae C4 species), such as *Pappophorum caespitosum* R.E.Fr. & P. Philippianum Parodi, *Digitaria californica* (Benth.) Henr., *Trichloris crinita* (Lag.) Parodi, *Aristida mendocina* Phil., and *Sporobolus cryptandrus* (Torrey) A. Gray. (Claver and Roig-Juñent, 2001; Marone et al., 2000).

The study was conducted in a forest with a mean density of 40 adult trees ha $^{-1}$, within a matrix of *Larrea* spp. The *P. flexuosa* trees generally have several stems, with a mean height of 3.7 m and an average crown diameter of 7 m. The *P. flexuosa* tree cover is 15–20%, the *L. divaricata* cover is 60% and 15% of bare soils. The grass cover ranges between 25 and 50% among years (Claver and Roig-Juñent, 2001; Marone et al., 2000).

2.2. Experimental design

A total of 30 individuals of *P. flexuosa* 4–5 m high) were marked in ca. 18 ha area. In August 2002, half of the trees were randomly cut (10 cm in height) and the woody debris manually removed. Six composite soil samples (n=6) were randomly taken (0–20 cm) in two sampling dates: August 2004 (precipitation: 5.0 mm; mean temperature: 12.4 °C) and February 2005 (precipitation: 64.5 mm; mean temperature: 20.3 °C) at the following undisturbed sites: a) under the canopy of *P. flexuosa* ca. 1 m from the trunk (Under P); b) under the canopy of *L. divaricata* (Under L), and c) intercanopy areas (Intercanopy), and a disturbed site: gap areas ca. 1 m from the cut trunk of *P. flexuosa* (Gap P). Part of each soil sample was maintained

at 4–5 °C for biological determinations for up to a week and the rest was air-dried and sieved (2 mm sieve) for chemical determination.

2.3. Laboratory analysis

The following chemical parameters were analyzed: a) soil moisture content (SM) by gravimetry; b) total soil organic matter content (SOM) by the wet-digestion method of Walkley and Black (Nelson and Sommers, 1982); c) total N content by micro Kjeldahl; d) nitrate (NO₃) by colorimetric methods (Keeney and Nelson, 1982); d) humic substances (HS) and fulvic acids (FA) following Jouraiphy et al. (2005); e) humic acids (HA), determined as the difference between HS and FA; and f) bioavailable SOM (BOM), determined as the difference between SOM and HS. Soils were characterized according to the following variables: texture, conductivity, and pH using the standard methods recommended by Klute (1986).

The following biological parameters were analyzed: a) total heterotrophic activity by soil respiration through CO2 release method (during 7 days), in the laboratory under standardized soil conditions (28-30 °C - 60% water-holding capacity) (Alef, 1995); and b) abundance of different functional groups of microorganisms by the most probable number (MPN) and direct cell counts by agar plate methods. For the MPN method (three replicates) we used mineral salt basal medium containing: K_2HPO_4 (1.0 g L^{-1}), $MgSO_4 \cdot 7H_2O$ (0.5 g L⁻¹) with selective substrate for each functional group as follows: ammonifiers, mineral media plus asparagine; nitrifiers, mineral media plus ammonium sulphate; and cellulosedegrading bacteria, mineral media plus cellulose strips (Lorch et al., 1995). For agar plate methods we used nitrogen-free basal medium (NFB) for N-fixing bacteria (Döbereiner, 1995). The media pH was 7. Samples were incubated at 28 °C for 5-21 d, depending on the functional group.

2.4. Calculations and statistical analyses

To analyze the dynamics of SOM and N fractions the following indices were estimated: C mineralization index (CO₂-C/SOM-C) (Abril et al., 2005), humification index (HA/SOM), humus type (HA/FA)(González et al., 2003), and available N index (NO₃-N/total N) (Sparling, 1998). To determine spatial and temporal heterogeneity, data from the different sites (Under P, Under L, Gap P, and Intercanopy) and sampling dates (dry and wet seasons) were analyzed statistically using ANOVA and comparison of means by LSD test (p < 0.05). Previously, we tested normality using the Kolmogorov-Smirnov test, and variance homogeneity using the Bartlett test. Chemical and biological data of soils were also analyzed using principal component analysis (PCA). Relationships among samples were evaluated after plotting sample scores on the two most significant principal components dimensions. Correlation analysis was performed to Pearson's test for linear relationships between variables.

3. Results

3.1. Spatial variation

All soils analyzed were characterized as sandy loam, of neutral to slightly alkaline pH and medium salinity. Soils of Intercanopy sites had the most alkaline pH and the lowest conductivity. In Under L sites, conductivity was lower than in Gap P sites and similar to Under P sites (Table 1).

The soil chemical properties showed significant variations among sites (Table 2). The contents of SOM, FA, BOM, and NO₃ were lower in Intercanopy and higher in Under P sites, except SOM and

Table 1 Soil characteristics in the analyzed sites (mean \pm 1 SD of summer and winter data combined). Under P: beneath canopy of *Prosopis flexuosa*; Under L: beneath canopy of *Larrea divaricata*; Intercanopy; and Gap P: under *Prosopis flexuosa* canopy removal. Letters indicate significant differences between sites (LSD test, p < 0.05).

	Undisturbed s	Disturbed sites		
	Under P	Under L	Intercanopy	Gap P
pН	$7.76b \pm 0.23$	$8.00b \pm 0.36$	$8.15a \pm 0.11$	$7.70b \pm 0.57$
Conductivity (dS m ⁻¹)	$7.72ab \pm 1.79$	$4.83b \pm 3.06$	$2.20c \pm 0.91$	$10.96a \pm 5.31$
Texture	Sandy loam	Sandy loam	Sandy loam	Sandy loam

BOM, which were higher in Gap P sites. The more stable soil parameters, such as total N content and HA, did not show significant differences between undisturbed sites (Under P, Under L and Intercanopy). The disturbed site (Gap P) showed higher HA content than the Under P, Under L, and Intercanopy sites, but did not differ from Under P site. Abundance of microorganisms of all functional groups analyzed did not differ among sites, in contrast to soil respiration, which was lower in Intercanopy site.

The dynamics of C compounds was very similar among sites, except for C mineralization index, which was higher in Under L site (Table 3). Available N index was very variable among sites (Table 3); it was higher in Gap P and Under P, and lower in Intercanopy and Under L sites.

3.2. Temporal variation

In all sites, no changes were detected in SOM, BOM, HA content, nitrifiers, N fixers or soil respiration between winter and summer values. Although respiration rates did not differ significantly between seasons, values tended to be lower in the wet season (range $0.12-0.65 \, \text{mg} \, \text{CO}_2 \, 7 \, \text{d}^{-1} \, \text{g}^{-1}$).

Soil moisture (SM) was almost zero in the dry season and higher in summer in all sites. Abundance of cellulolytic microorganisms and FA content followed the same pattern. Ammonifiers and NO_3 were also influenced by moisture content, although ammonifiers were only significantly higher in Gap P and Under P sites, whereas

Table 2 Chemical and biological soil properties in the analyzed sites (mean \pm 1 SD of summer and winter data combined): Under P: beneath canopy of *Prosopis flexuosa*; Under L: beneath canopy of *Larrea divaricata*; Intercanopy; and Gap P: under *Prosopis flexuosa* canopy removal. Letters indicate significant differences between sites (LSD test, p < 0.05).

	Undisturbed si	Disturbed sites		
	Under P	Under L	Intercanopy	Gap P
Soil moisture (SM) (%)	2.83 ± 3.18	3.33 ± 3.50	3.32 ± 3.48	4.29 ± 4.53
Organic matter $(OM) (mg g^{-1})$	$24.01b \pm 9.40$	$18.60b \pm 12.90$	$8.90c \pm 4.50$	$33.50a \pm 9.81$
Bioavailable organic matter (BOM) (mg g ⁻¹)	$20.04b \pm 7.5$	$16.4b \pm 10.9$	$8.2c \pm 5.2$	$27.5a \pm 8.9$
Fulvic acids (FA) (mg g ⁻¹)	$1.88ab \pm 1.90$	$0.80b \pm 1.10$	$0.03c \pm 0.05$	$2.90a\pm2.20$
Humic acids (HA) $(mg g^{-1})$	$1.86ab \pm 1.31$	$1.40b \pm 2.22$	$\textbf{0.70b} \pm \textbf{1.50}$	$3.10a\pm2.00$
Total N $(mg g^{-1})$	2.60 ± 1.60	$\textbf{2.20} \pm \textbf{1.20}$	2.60 ± 2.80	$\boldsymbol{2.70 \pm 0.70}$
Nitrate (NO ₃) $(mg kg^{-1})$	$41.15a \pm 20.14$	$16.54b\pm16.42$	$4.17b \pm 1.23$	$57.81a \pm 44.43$
N fixers $(\log g^{-1})$	$\textbf{6.28} \pm \textbf{0.27}$	$\boldsymbol{6.00 \pm 0.79}$	$\textbf{6.16} \pm \textbf{0.72}$	$\boldsymbol{5.95 \pm 0.53}$
Nitrifiers (log g ⁻¹)	4.67 ± 0.85	4.41 ± 1.02	4.33 ± 0.90	$\boldsymbol{4.59 \pm 0.71}$
Cellulolytics (log g ⁻¹)	$\textbf{6.37} \pm \textbf{3.88}$	$\textbf{6.54} \pm \textbf{4.09}$	$\textbf{7.47} \pm \textbf{4.06}$	$\boldsymbol{6.49 \pm 3.66}$
Ammonifiers $(\log g^{-1})$	$\boldsymbol{9.74 \pm 1.55}$	$\textbf{10.73} \pm \textbf{2.10}$	$\boldsymbol{9.39 \pm 2.57}$	$\boldsymbol{9.09 \pm 2.31}$
Soil respiration $(mg CO_2 7 d^{-1} g^{-1})$	$0.52a \pm 0.3$	$0.57a\pm0.23$	$0.19b \pm 0.14$	$0.6a \pm 0.23$

Table 3

C and N dynamic indexes in the analyzed sites (mean and \pm SD of summer and winter data combined). Under P: beneath canopy of *Prosopis flexuosa*; Under L: beneath canopy of *Larrea divaricata*; Intercanopy; and Gap P: under *Prosopis flexuosa* canopy removal. HA: humic acids; SOM: soil organic matter; AF: fulvic acids. Letters indicate significant differences between sites (LSD test, p < 0.05).

	Undisturbed	Disturbed sites		
	Under P	Under L	Intercanopy	Gap P
C mineralization index (CO ₂ -C/SOM-C)	$0.99b \pm 0.30$	$1.84a\pm0.91$	$1.21b \pm 0.88$	$0.83b \pm 0.22$
Humification index (HA/SOM) (%)	$\textbf{7.60} \pm \textbf{5.11}$	6.90 ± 5.27	$\textbf{13.01} \pm \textbf{17.24}$	9.31 ± 5.77
Humus type (HA/FA) (%)	$\textbf{3.81} \pm \textbf{4.06}$	4.48 ± 7.60	$\textbf{6.92} \pm \textbf{13.29}$	$\textbf{1.87} \pm \textbf{1.81}$
Available N index (NO ₃ -N/total N) (%)	$2.03a\pm1.31$	$0.92b \pm 1.03$	$0.36b \pm 0.29$	$2.34a\pm2.40$

NO₃ content was higher only in Gap P sites. In contrast, total N was significantly lower in Under L and Intercanopy sites in summer, whereas it did not show significant differences in the other sites (Fig. 1).

Abundance of ammonifier and cellulolytic microorganisms was positively and significantly correlated with content of SM (r=0.63; p<0.001 and r=0.92; p<0.001, respectively) and with FA (r=0.29; p=0.04 and r=0.46; p<0.001, respectively). Similarly, most labile C and N fractions (FA and NO₃) were also correlated with SM content (r=0.56; p<0.001 and r=0.39; p=0.01, respectively). The pH values were negatively correlated with all the fractions of organic matter (FA: r=-0.37/p=0.01; HA: r=-0.49/p<0.001; and SOM: r=-0.63/p<0.001) relative to the buffer capacity of humic compounds. Soil respiration was positively correlated with all organic matter fractions (SOM: r=0.68/p<0.001; FA: r=0.39/p=0.03 and HA: r=0.42/p<0.001).

PCA of all chemical and biological analyzed soil properties ordinated the variation of the data on the two most significant components (factors 1 and 2), which together accounted for 94% of the total variance. Factor 1 explaining 88.2% of total variance was primarily weighed by SM and SOM contents, whereas factor 2 was affected by SOM, HA, BOM and cellulolytic microorganisms.

Factor 1 distinguished samples from the wet vs. the dry season (Fig. 2). Instead, along the second axis (factor 2), samples were separated in two main groups corresponding to different sites in the wet season; the first comprised all soil samples from Gap P sites and the second grouped Under L and Intercanopy sites. No visual grouping among Under P samples was found along the second axis.

4. Discussion

Our data indicate that soil properties in Nacuñán Reserve are spatially more homogeneous than expected. PCA clearly shows that the main source of heterogeneity is seasonal, and that in spatial distribution is limited to summer, discriminating among soils in the disturbed sites (Gap P), but not sites in undisturbed soil.

4.1. Spatial heterogeneity

Undisturbed soils show similar pattern with respect to humification index, C and N pool, and abundance of edaphic microorganisms, indicating that these processes are regulated at the ecosystem but not site level (Schlesinger et al., 1996). In contrast, at the site level, variables related to labile and highly mobile soil properties (pH, conductivity, SOM, soil respiration, and nitrate), are heterogeneous responding to microclimatic conditions and to differential plant litter deposition (Anderson et al., 2004; Noe and Abril, 2008; Rossi and Villagra, 2003; Rotundo and Aguiar, 2005).

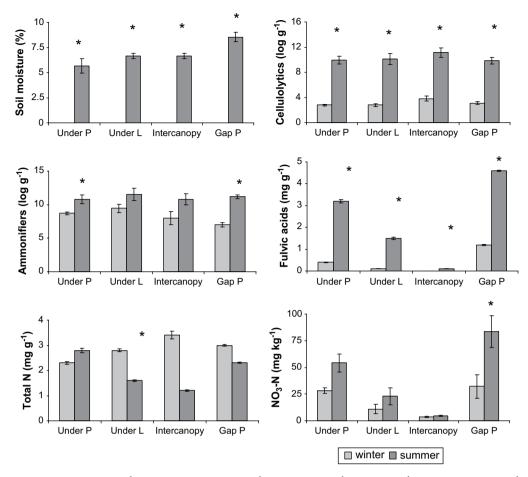


Fig. 1. Soil moisture (%), cellulolytic abundance ($\log g^{-1}$), ammonifier abundance ($\log g^{-1}$), fulvic acids ($mg g^{-1}$), total N ($mg g^{-1}$), and NO₃ content ($mg kg^{-1}$), in winter and summer at the four analyzed sites. Under P: beneath canopy of *Prosopis flexuosa*; Under L: beneath canopy of *Larrea divaricata*; Intercanopy; and Gap P: under *Prosopis flexuosa* canopy removal. Bars indicate SE between sites and * significant differences between seasons in each site (p < 0.05).

Differences in labile fractions of the soil agree with most literature on the presence of "fertility islands" (Anderson et al., 2004; Gutiérrez et al., 1993; Stock et al., 1999). However, Schlesinger et al. (1996) and Schade and Hobbie (2005) mentioned that labile and highly mobile N parameters are very variable in the soil, and therefore, not indication of spatial heterogeneity at landscape level. Thus, Stock et al. (1999) and Farley and Fitter (1999) consider

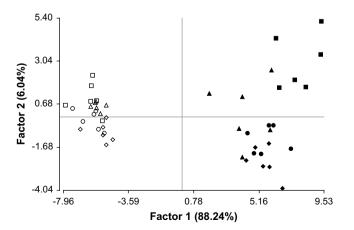


Fig. 2. Principal component analysis (PCA) of the all analyzed chemical and biological properties. Hollow symbols indicate dry season and solid symbols wet season. Squares: Gap P; diamonds: Intercanopy; circles: Under L; and triangles: Under P.

"fertility islands" to be ephemeral because of high soil dynamics in deserts.

Although total SOM content varies among undisturbed sites, our analysis suggests that this is due to bioavailable fractions (BOM and FA). Similar values of HA and humus type indicate a similar degree of maturation of SOM. Moreover, a homogeneous distribution of HA and total N is consistent with N participation in the humus chemical composition (Eichhorn and Hüttermann, 1999).

The significantly higher values of C mineralization index in Under L sites indicate a higher C output than input (Abril and Noe, 2007; Abril et al., 2005), probably because the residue deposition of *Larrea* spp. is low (Noe and Abril, 2008). *Larrea* is an evergreen shrub that sheds leaves opportunistically under dry conditions (Carrera et al., 2000). In the remaining undisturbed sites, C mineralization index values are similar and close to 1, indicating balanced C dynamics, and suggesting a highly homeostatic system (Abril and Noe, 2007; Abril et al., 2005; Eichhorn and Hüttermann, 1999).

The spatial homogeneity of abundance of functional groups and heterogeneity in soil respiration in Nacuñan are consistent with results of the several authors (Bolton et al., 1993; Sponseller and Fisher, 2008). Smith et al. (1994) also detected lower microbial activity (respiration and enzymes) in bare soil areas, but great homogeneity in microbial biomass distribution in ecosystems of semiarid shrub steppes. The observed pattern suggests that microbial populations in deserts are adapted to survive under dry conditions by maintaining low metabolic rates, but become

activated when soil humidity reaches a critical threshold (Abril and Noe, 2007).

The small differences in the stable soil parameters found among sites are probably because in Ñacuñán Reserve the vegetation does not present true patches. Some authors suggest that desert vegetation patches are islands of grasses, trees and shrubs, separated by large areas (between 40 and 60% cover) of completely bare soil throughout the year (Aguiar and Sala, 1999; Mazzarino et al., 1998). The model of Rietkerk et al. (2002) presumes that arid regions are characterized by bare patches 5-20 m in diameter. However, these characteristics do not correspond with Nacuñán Reserve because: a) there are no definite boundaries between sites (instead them a matrix of shrubs with few trees); and b) areas of bare soil are not present normal because grasses beyond the tree canopies when soil humidity increases (Marone et al., 2000). Due to cattle exclusion grasses are not consumed and in the dry season, senescent grass leaves provide important surface cellulosic matter, which is corroborated by abundance of cellulolytic organisms in our results. Whereas the importance of the contribution of grasses to SOM is well known for other communities (Medina and Silva, 1990), it has not been verified in Ñacuñán Reserve.

Moreover, the abundant lignified root system of grasses invades large areas of surface soil, transporting nutrients to the Intercanopy areas; further dead roots supply a highly humifiable material (Ghani et al., 2003). Our results confirm a trend towards a greater humification index and humus type values in Intercanopy sites. The absence of significant differences among sites is consistent with a high variability of humus content in Intercanopy areas (CV between 109 and 239); this in turn may indicate that not all Intercanopy sectors have been covered with the same amount of grasses (Marone et al., 2000).

From this perspective, overgrazing in Intercanopy areas would be the most important cause of fertility losses in areas without woody cover and, consequently, fertility islands in the Central Monte desert may have an anthropogenic origin (Bisigato et al., 2008; Carrera et al., 2003; Mazzarino et al., 1998; Villagra et al., 2009).

4.2. Temporal heterogeneity

PCA results clearly show a marked temporal heterogeneity of soil properties that is related to changes in moisture content. In agreement with other arid zone studies (Austin et al., 2004; Huxman et al., 2004; Xie and Steinberger, 2001), the abundance and activity of some microorganisms and organic matter labile fractions are the most sensitive variables to climatic changes in Nacuñán Reserve.

The seasonal variations detected in this work may be produced by rainfall and warmer temperatures that activate microbial degrading groups of plant residues (cellulolytics and ammonifiers), increasing the amount of FA and NO₃ in the soil. Seasonal dynamics of "fertility islands" has been poorly documented; however, given that sampling in the wet period was performed 4 days after an 18-mm rainfall event, our results may be comparable to those following moisture pulses in deserts. In this context, Austin et al. (2004) mentioned an increase in soil microbial processes after a rainfall event. However, we did not find higher heterotrophic activity in summer, probably because of high summer temperatures. Microbial metabolism does not have a linear relationship with temperature, because it decreases sharply above 40 °C (Abril and Noe, 2007; Conant et al., 2004; Huxman et al., 2004).

The important differences detected in the temporal heterogeneity pattern among sites may be related to chemical composition of leaf litter. It is widely known that *Prosopis* leaves have higher protein content (Noe and Abril, 2008), which supports our findings

that total N does not decrease in Under P sites in summer, unlike in Under L or in Intercanopy sites.

4.3. Effects of tree removal

Cutting isolated individuals of *Prosopis* is a common practice in the region but does not generate very different soil dynamics than presence of the standing trees. PCA only separates Gap P sites from the other two sites (Under L and Intercanopy). Creation of a gap produces an increase in soil respiration and nutrient availability in the short term, which promotes losses due to leaching and runoff (Londo et al., 1999; Prescott, 2002); also greater soil exposure increases desiccation due to evaporation. However, we did not detect differences in nitrate content from standing trees, but we observed an increase in soil moisture content in the area around the trunks. This is probably because logging is recent in our study area (2 years); hence, deposition of lignocellulosic matter still persists. Although gross woody material was removed after the tree was cut, a great amount of leaves and small stems like mulch remained on the soil in the area. This explains the higher soil moisture content as compared with more exposed sites.

Moreover, C dynamics in Gap P indicates a trend towards C (C mineralization index values lower than 1) that may be the result of higher deposition of woody residues. This is clearly reflected in an increase in SOM and BOM. The tendency of higher HA, FA and humification index, and the fact that humus type is slightly lower than Under P would be indicative of an incipient maturation process of humus that is very variable (Eichhorn and Hüttermann, 1999; González et al., 2003).

The high homeostatic capacity detected in Under P sites may conceal short term changes after tree removal. Similarly, Prescott (2002) indicates that canopy gaps larger than single trees are needed to induce changes in N cycling. When plant residues decompose and the area is exposed to harsh climatic conditions, soil will probably start to lose the extra SOM input. However, we could predict that an area with such fertility dynamics will be soon invaded by vegetation, including the resprouting of the cut trunk; thus, the area will not be exposed for long periods and no infertile soil areas would be generated (Luken et al., 1997).

In summary, most of our predictions were not supported by the data. Soil fertility of Ñacuñán Reserve is characterized by: a) a more homogenous spatial pattern than expected from woody plant presence (the entire Ñacuñán Reserve should be seen as a "fertility island" within the Central Monte desert region, due to livestock exclusion; b) a very heterogeneous temporal pattern, showing adaptive mechanisms for highly unpredictable environments; and c) tree removal does not seem to induce infertile soil formation.

Our research provides an important management perspective regarding inappropriate use of forage and forest resources in desert areas. Stimulating grass recovery during wet years through adequate grazing management might be crucial for maintaining productivity in this arid ecosystem.

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