

Relationships between soil chemical parameters and functional plant groups in fertility islands of the Arid Chaco (Argentina)

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SUMMARY

The "fertility islands" are the result of soil particles, water, nutrients, and biomass accumulation under their canopy. The study of soil and plant parameters in fertility islands is important for the redefinition of management strategies. The hypothesis is that *Neltuma flexuosa* and *Larrea divaricata* fertility islands in the Arid Chaco improve soil chemical properties under their canopies affecting the quality and quantity of forage. The objective is to evaluate soil chemical properties on the response of plants in fertility islands. The effect of nurse plants over soil chemical properties and their relation with functional plant groups was studied. Livestock carrying capacity (LCC) significantly increased under the canopy of *N. flexuosa*. Decreasers were positively related to the *N. flexuosa* canopy, and negatively to *L. divaricata* canopy. Soil organic carbon (OC) related positively with decreaseers in *N. flexuosa* islands, but negatively in *L. divaricata* islands where there seems to exist allelopathy effect. Extractable phosphorus correlated positively with decreaseers.

Keywords: canopy, forage, *Larrea divaricata*, *Neltuma flexuosa*, nurse plants

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RESUMEN

Las "islas de fertilidad" son el resultado de la acumulación de partículas de suelo, agua, nutrientes y biomasa bajo su canopia. El estudio de parámetros de suelo y de vegetación en islas de fertilidad es importante para la redefinición de estrategias de manejo. La hipótesis es que las islas de fertilidad de *Neltuma*

flexuosa y *Larrea divaricata* en el Chaco Árido mejoran las propiedades químicas del suelo bajo su canopia afectando la calidad y cantidad de forraje. El objetivo es evaluar las propiedades químicas del suelo sobre la respuesta de las plantas en islas de fertilidad. Se estudió la influencia de plantas nodrizas sobre propiedades químicas del suelo y su relación con grupos funcionales de plantas. La capacidad de carga ganadera (LCC) se incrementó significativamente bajo la canopia de *N. flexuosa*. Las especies decrecientes se relacionaron positivamente bajo canopia de *N. flexuosa*, y negativamente bajo *L. divaricata*. El carbono orgánico del suelo (OC) se relacionó positivamente con las especies decrecientes en islas de *N. flexuosa*, pero negativamente en las islas de *L. divaricata* donde aparentemente ocurre alelopatía. El fósforo extractable se correlacionó positivamente con las especies decrecientes.

Palabras clave: canopia, forraje, *Larrea divaricata*, *Neltuma flexuosa*, plantas nodrizas

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INTRODUCTION

The United Nations Convention to Combat Desertification (UNCCD, 2015) defined land degradation neutrality as “a state whereby the amount and quality of land resources necessary to support ecosystem functions and services and enhance food security remain stable or increase within specified temporal and spatial scales and ecosystems”.

In contrast, an ecosystem is subjected to livestock and forestry overuse when plant biomass is consumed by livestock or it is extracted by human beings during a determinate amount of time, surpassing forage or forestry biomass productivity for that period (Wood and Carvalho, 2000). An ecosystem overloaded with livestock negatively affects the normal growth of plants, seedlings, and sprouts of the most palatable species (Teich et al., 2005), reducing their abundance and indirectly increasing the abundance of less palatable species. Livestock and forestry exploitation may also affect soil, directly through soil compaction, reducing soil hydraulic conductivity, or indirectly by altering the vegetation responsible for cycling nutrients and soil mulching (Kremers and Boosten, 2018; Karlin et al., 2019).

In arid and semiarid lands, plants and especially trees, are considered the best regulators in terrestrial natural ecosystems (Karlin, Galán et al., 2013). The reduction of plant cover increases bare soil, affecting the physical, chemical and biological attributes by alteration of erosion controls and mineralization (Naldini et al., 2021).

Ecosystems in arid and semiarid lands show considerable spatial heterogeneity regarding soil, plants, and fauna due to both natural and anthropic causes. Anthropic causes promote ecosystems with a shrubby matrix and bare soil of reduced physicochemical fertility. Trees and shrubs are sparse as a consequence of a sustained extraction within the ecosystems. They usually enhance environmental conditions under canopy compared to intercanopy (Tongway and Ludwig, 2005; Karlin, Coirini et al., 2021; Karlin, Zapata et al., 2021). Such areas are known as “fertility islands” and are the result of an important accumulation of soil particles, water, nutrients and biomass under the canopy (Rossi and Villagra, 2003; Ridolfi et al., 2008).

It has been proved that trees understorey modify the physical, chemical, and biological dynamics in ecosystems, regulating the amount and availability of nutrients, water and the functioning of living

organisms, creating special micro-environments compared to those from the intercanopy (Dohn et al., 2013). Nevertheless, studies about the influence of shrubs over fertility islands are sometimes contradictory; environmental effects seem to depend on the species, shrub size, and environmental context (Thompson et al., 2005; Qu et al., 2018; Ward et al., 2018).

The ecosystems in the Argentinian Arid Chaco are not the exception to the aforementioned degradation processes. In the last century, these have suffered a critical reduction of productivity and management regulation, which has led to the transformation of primary forests into scrubs. The latter are a product of degradation, selective extraction and livestock facilitation, usually defining fertility islands with isolated nurse species such as mesquite (*Neltuma flexuosa* (DC.) C. E. Hughes & G. P. Lewis) or creosotebush (*Larrea divaricata* Cav.) (Karlin, Karlin et al., 2013). The abundance of forage species depends directly on livestock grazing frequency and intensity, and indirectly on soil and micro-environment conditions. These species can be categorized as “decreasers”, “increasers” or “invaders” according to Dyksterhuis’ classification (Díaz, 2007). The abundance of such species defines the productivity in grazing systems.

Currently, due to changes in productive and conservation paradigms, the role of trees and shrubs in the regulation of environmental and socioeconomic conditions is being revisited. The study of the changes in biotic and abiotic variables inside and outside fertility islands is of vital importance in arid and semiarid ecosystems for the redefinition of management, rehabilitation, and conservation strategies (Varela et al., 2017).

The hypothesis is that *N. flexuosa* and *L. divaricata* fertility islands in the Arid Chaco improve soil chemical properties (organic carbon, phosphorus, electrical conductivity, and pH) under their canopies compared to the intercanopy, positively affecting the quality and quantity of forage.

The objective is to evaluate soil chemical properties (organic carbon, extractable phosphorus, electrical conductivity, and pH) on the biomass response and plant frequencies within and outside the canopy of *N. flexuosa* and *L. divaricata* in fertility islands.

MATERIALS AND METHODS

Study sites

Two plots corresponding to livestock closures

on recovery were selected in the locations of La Patria (31° 32' 00" S, 65° 30' 20" W; 288 m a.s.l.) and Los Medanos (31° 36' 00" S, 65° 33' 00" W; 287 m a.s.l.), both located in the geomorphological unit of dune fields and areas of sand blankets or isolated dunes (Carignano et al., 2014). They are located 13 and 23 km southwest of the Chancaní location, respectively, in the Pocho Department at the westernmost part of the Province of Córdoba, Argentina (Figure 1).

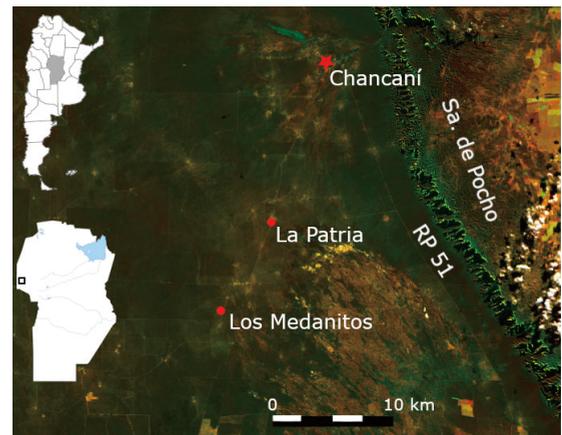


Figure 1. Relative location of the plots under study. Sentinel 2 L2A image, 1/7/2022, false color (R: B12, G: B6, B: B2).

According to Köppen’s climatic classification (Beck et al., 2018), the study area has a warm semiarid climate (BSH). Precipitations range between 350 and 650 mm yearly (Karlin, 2012).

The plot located in La Patria (1.9 ha) is a scrub of *L. divaricata* with a history of intense grazing before its closure in 2015. The plot in Los Medanos (2.1 ha), also closed in 2015, is a woodland of *N. flexuosa* with a history of moderate grazing and wood extraction. Both plots were closed until September 2020 and grazed in low intensities after plant fructification (April-May) between 2017 and 2020.

Experimental design

Soil chemical properties and their relation with functional plant groups were studied within and outside the canopy of *N. flexuosa* and *L. divaricata* nurse plants. In each plot, five individuals of each nurse plant were selected, on the condition that they were isolated forming fertility islands (Figure 2). Transects were extended from the island’s centre towards the intercanopy, all oriented to the north. Transects had a length of two times the canopy

radius (r) of each nurse plant. Each individual had a different canopy radius.

Soil sampling

A superficial layer 10 cm deep was extracted for simple soil samples under the canopy (UC), at the canopy limit (LC) and in the intercanopy (IC) in each fertility island ($n = 60$).

Soil samples were pulverized, sieved and air-dried at 60 °C in a forced-air chamber for three days. Soil organic carbon content (OC) was determined by the Walkley and Black method (Nelson and Sommers, 1996); extractable phosphorus (EP) by the Bray and Kurtz N°1 method (1945); electrical conductivity (EC) by conductometry in the supernatant soil/water=1:1, and pH by potentiometry. Bray and Kurtz N°1 is a common method to determine soil pH near neutrality, below 7.5 (Sims, 2000; Mustapha et al., 2022). It works well for carbonate-lacking soils. However, Ebeling et al. (2008) recommend it for pH 7 to 8,

arguing that such ranges do not affect phosphorus extraction. The 0-10 cm deep soil samples in this study lack significant carbonate content since they did not react to hydrochloric acid. Both EC and pH were measured with a Hanna HI98129 pHmeter-conductimeter.

Plant survey

The modified Point Quadrat method was applied (Passera et al., 1986), measuring plant cover during early winter (June, 2019), late spring (December, 2019) and late summer (March, 2020). Two sectors were identified along the transects; the first (UC) from the central point of the fertility island to the limit of the canopy, and the second (IC) from the limit of the canopy to a point located at a length of two times the canopy radius ($2r$).

The plants found along the transects were identified, obtaining their frequencies by calculating the specific contribution by contact (SCC) using a 1.5 m long by 0.003 m wide needle. SCC (1) is

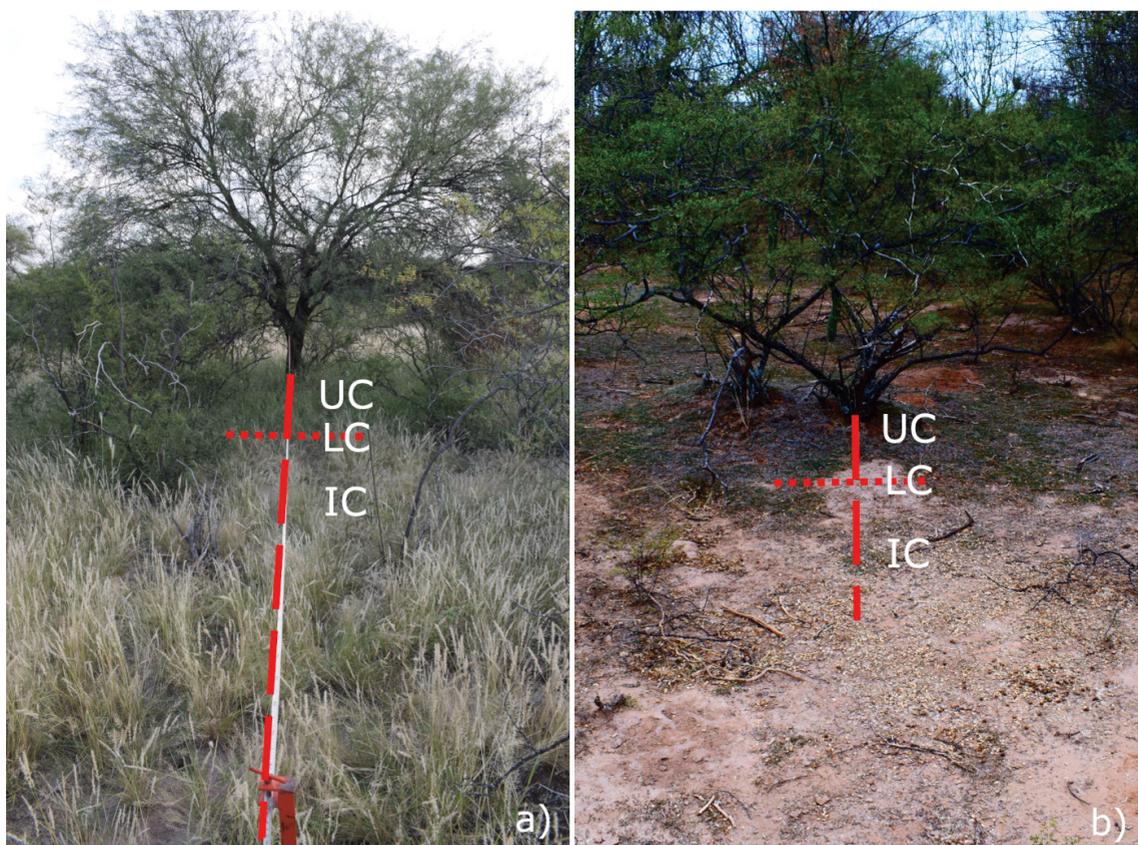


Figure 2. Fertility islands of a) *N. flexuosa* and b) *L. divaricata*. UC: under canopy; LC: canopy limit; IC: intercanopy

the quotient between the number of contacts of each species (C_i) and the sum of contacts of all surveyed species along a transect (bare soil was not accounted). The points along each transect of variable length were taken every 0.20 m.

$$SCC_i = \frac{C_i}{\sum_{i=1}^n C_i} \times 100 \quad (1)$$

The surveyed species were grouped into three categories according to Dyksterhuis (1949): decreaseers, increaseers and invaderes. Decreaseers reduce their frequencies with grazing intensity; increaseers increase their frequencies with a reduction in the decreaseer's competition, but they may decrease if grazing continues after the disappearance of the decreaseers; invaderes are all the ungrazed or unbrowsed species, usually represented by annuals and woody species other than nurse species. The SCC for each species was summed according to the category, obtaining the plant frequencies per category.

Particularly, the frequencies of the lichen *Selaginella sellowii* were discriminated, since it is an important plant indicator for degradation intensity.

Livestock carrying capacity determination

The Specific Quality Indexes (SQI) were considered for each one of the identified species with the Point Quadrat method. The indexes were obtained from Passera and Borsetto (1986) and Karlin (2013). The Pastoral Value (PV) was calculated for each transect and treatment through the following formula (2):

$$PV = 0.1 \times \sum (SCC_i \times SQI_i) \times FC \quad (2)$$

FC is the forage cover calculated through the sum of frequencies of each forage species "i" found at each point along the transects. Considering that 100 unities of pastoral value (UPV) can maintain an animal unit (AU) per hectare, PV was transformed into livestock carrying capacity units (LCC) measured as AU ha⁻¹ (3).

$$LCC = PV / 100 \quad (3)$$

An AU is equivalent to the annual average nutritional requirements of a 400 kg cow gestating and breeding a calf until weaning at 6 months old and 160 kg, including the forage consumed by the calf (Passera et al., 1986).

Statistical analysis

Shapiro-Wilks normality tests were performed. Those parameters that were not significant at a p-value=0.0001 or showed W* values larger than 0.90 were analyzed through ANOVA tests, while those with p<0.0001 or W*<0.90 were analyzed through Kruskal-Wallis tests.

Tests were discriminated by nurse species (*N. flexuosa* y *L. divaricata*), by plot and, in the case of plant frequencies, by season (winter, spring and summer). For plant frequencies, only UC and IC treatments were considered.

Pearson's correlation coefficients between soil and plant parameters were obtained. Only the biological parameters from March were analyzed since they reached their highest expression by the end of the summer. LC treatment was not considered since it had no associated plant data.

All the statistical analyses were performed with the InfoStat statistical software (Di Rienzo et al., 2020).

RESULTS AND DISCUSSION

Normality tests

According to Shapiro-Wilks test results, OC, pH and LCC can be considered with normal distribution. The rest, EP, EC, and the frequencies of the functional plant groups did not show normal distributions; therefore, they were analyzed by Kruskal-Wallis tests.

Soil parameters

The results of the soil chemical parameters (OC, EP, EC and pH) are shown in Figure 3.

Soil organic carbon

In Figure 3a, data show that in UC, in each fertility island category (*N. flexuosa* y *L. divaricata*), OC is significantly higher than in LC and IC. Soil organic carbon declines from the centre of the island towards the intercanopy.

The average contents of soil organic carbon in *N. flexuosa* islands were 1.22 % for UC, 0.86 % for LC and 0.70 % for IC; while in *L. divaricata* islands its values were 1.10 % for UC, 0.79 % for LC and 0.69 % for IC.

No significant differences were found between islands when treatments were compared separately (UC: p - value= 0.2689; LC: p - value = 0.4496; IC: p - value= 0.9059), despite that it is expected

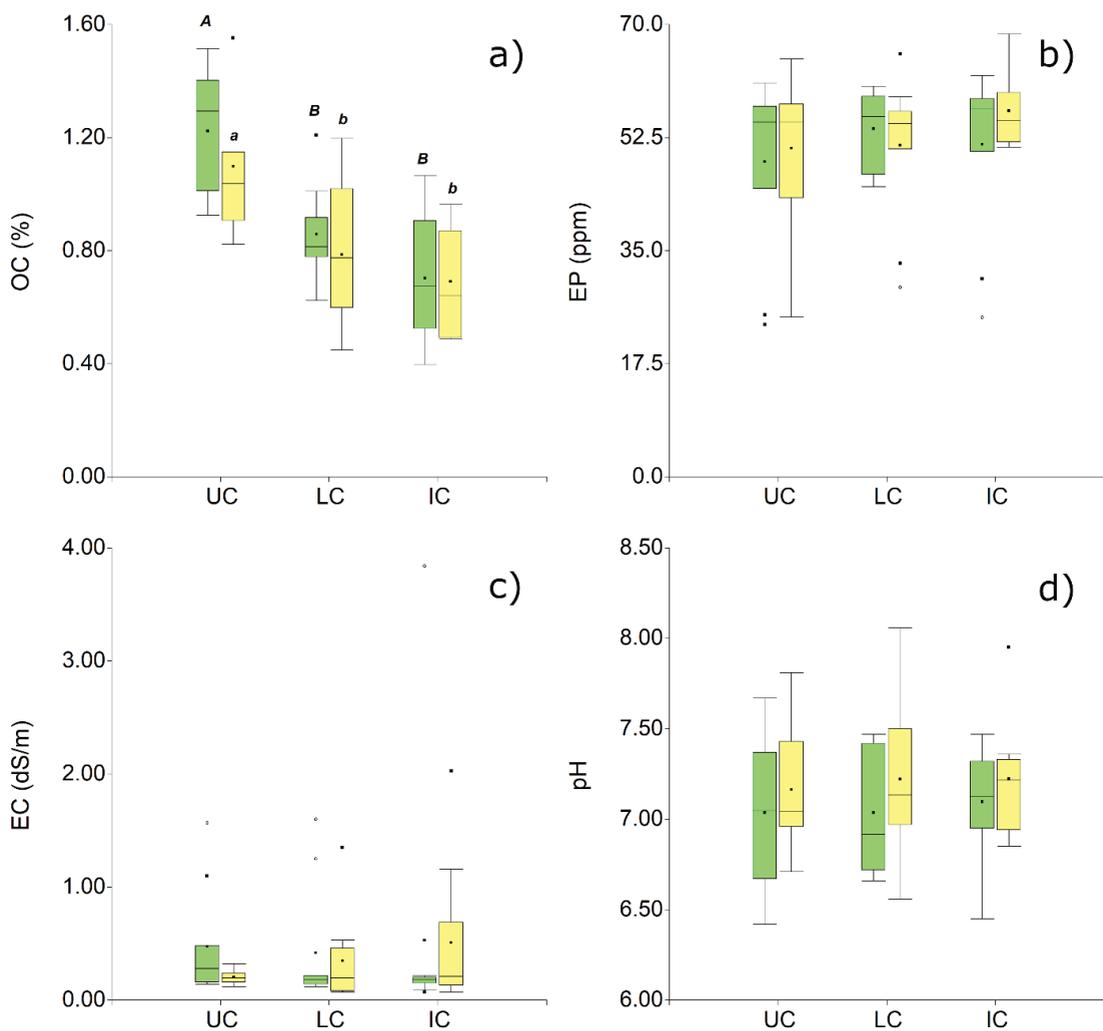


Figure 3. Box-plots of the soil chemical parameters: a) soil organic carbon (OC); b) extractable phosphorus (EP); c) electrical conductivity (EC); d) pH. UC: under canopy; LC: canopy limit; IC: intercanopy. Green bars: *N. flexuosa* islands; yellow bars: *L. divaricata* islands. Different letters indicate statistically significant differences (ANOVA LSD Fisher test, $\alpha=0.05$)

that the litter contribution from mesquite would be higher than that of creosotebush. Similar results were found in woodlands from the Monte region (Argentina) by comparing the influence of the canopy between trees and shrubs (Karlin, Zapata et al., 2021).

Soil organic carbon is concentrated within the fertility islands, basically due to litter falling from the trees or shrubs, especially in *N. flexuosa* islands. On the other hand, trees and shrubs would perform as sediments and litter traps transported by water or wind, enriching the understory soil even more with organic carbon (Aber and Melillo, 2001).

Regarding the use history of the plot, significant

differences were only found in the IC treatment between La Patria (history of intense grazing) and Los Medanitos (history of moderate grazing) (OC: 0.59 % vs. 0.81 %, respectively; ANOVA LSD Fisher, $p=0.0090$), even though both plots were excluded from livestock for three years before the survey. Regarding the other treatments, LC presented only marginal differences (0.74 % vs. 0.90 %, respectively; ANOVA LSD Fisher, $p=0.0846$) while UC did not show significant differences (1.13 % vs. 1.19 %, respectively; ANOVA LSD Fisher, $p=0.6062$). These results can be contrasted with those obtained by Abril et al. (2005), who compared situations of intense grazing with ungrazed sites in the same region (Arid Chaco). They concluded that

carbon content in plots with 52 % of bare soil were significantly poorer (38 % less soil organic carbon) than the control corresponding to a climax *Aspidosperma quebracho-blanco* Schltld. forest. However, the effects of fertility islands were not studied by these authors.

From these results it is evidenced that degradation effects may be buffered by trees and shrubs, differing from the areas lacking their protection and organic matter enrichment.

Extractable phosphorus

No significant differences ($\alpha=0.05$) were observed between treatments for extractable phosphorus, either in *N. flexuosa* islands or in *L. divaricata* (Figure 3b). The p-values obtained were $p=0.6769$ and $p=0.6523$, respectively.

No significant differences were found between plots, despite differences in soil organic contents, and considering that phosphorus can also be added through organic matter (UC, $p=0.5452$; LC, $p=0.2897$; IC, $p=0.2265$).

The lack of statistical differences between treatments shows that phosphorus is controlled by pedogenetic characteristics independently from the influence of nurse plants, *i.e.* the organic source is practically irrelevant. These soils, derived from parental materials enriched in phosphorus, offer high concentrations of this nutrient, compared to other areas or regions (Hang et al., 2015). Thus, while in this study no statistical differences were found, other authors (Gao et al., 2022) discovered evident differences in extractable phosphorus content in fertility islands from hyperarid deserts (Taklimakan desert, China; average precipitations of 43 mm year⁻¹) favouring sites under canopy. However, they also proved that some inorganic fractions showed no concentration differences between treatments in the studied fertility islands (*Alhagi sparsifolia* Shap., *Karelinia caspia* (Pall.) Less., *Tamarix ramosissima* Ledeb.).

Similarly to the present study, Roos and Allsopp (1997) found that when nurse trees (in their study, *Vachellia sieberiana* (DC.) Kyal. & Boatwr. = *Acacia sieberiana*) are dispersed in low densities within a savanna matrix, these do not offer extra phosphorus under the canopy and therefore the organic fractions are negligible compared to inorganic fractions. Ding and Eldrige (2021) suggest that high concentrations of inorganic phosphorus, low nurse plant cover, and sparse fertility islands promote poorer microbial communities which produce the phosphatase enzyme responsible for organic phosphorus mineralization.

Ochoa Hueso et al. (2011) point out that soil

phosphorus concentrations respond to changes in the plant cover, the kind of plant species, the dominant plant species, and the predominant functional plant group.

Possibly net changes in organic phosphorus may be reasonably small related to the total reservoir pool. Consequently, some more observations over several years are needed to detect significant effects under rehabilitation conditions in degraded environments.

Electrical conductivity

No significant differences ($\alpha=0.05$) were found between treatments for electrical conductivity in any of the fertility island categories ($p=0.2386$ and 0.9169 for *N. flexuosa* and *L. divaricata*, respectively) (Figure 3c). These results differ from those obtained by Rossi and Villagra (2003), who found that electrical conductivity was higher under the canopy of *N. flexuosa* islands in the Natural Reserve of Ñacuñán (phytogeographical province of Monte, Mendoza, Argentina), with drier conditions than the Arid Chaco.

By comparing the UC treatment between *N. flexuosa* and *L. divaricata*, differences ($p=0.0959$) were found, with 0.47 dS m^{-1} against 0.20 dS m^{-1} , respectively. This situation might be caused by the pedestal effect in *L. divaricata*, offering higher infiltration rates and reduced bulk densities compared to those of *N. flexuosa* (basic infiltration: *N. flexuosa*= 38.37 mm h^{-1} , *L. divaricata*= 75.57 mm h^{-1} ; soil bulk densities: *N. flexuosa*= 1.26 Mg m^{-3} , *L. divaricata*= 1.20 Mg m^{-3} ; according to Karlin, Coirini et al., 2021), favouring the salt leaching under the canopy.

Significant differences were also found in the IC between plots, with higher electrical conductivities in La Patria, more degraded than Los Medanitos (0.90 vs. 0.15 dS m^{-1} ; Kruskal-Wallis, $p=0.0080$). In contrast, only marginally significant differences were found in LC ($p=0.0959$), while no significant differences were found in UC ($p=0.1208$). Zarekia et al. (2012) found that grazing intensity in Iran grasslands affects soil electrical conductivity. Under continuous and intense grazing, the soil is exposed to solar irradiation, promoting evaporation and the ascent of soluble salts, compared with sites under rotative and light grazing, aiding herbaceous plant cover.

pH

No significant differences were found between treatments for this parameter ($p=0.9024$ and 0.9126 for *N. flexuosa* and *L. divaricata*, respectively; Figure 3d). These results evidence that canopy

has no effect over this parameter. Significant differences were neither found for UC between nurse plants (p -value=0.4486). Perhaps pH is not a reliable indicator for this kind of system.

When comparing plots, these showed significant differences for all three treatments (UC, $p=0.0002$; LC, $p=0.0024$; IC, $p=0.0008$), evidencing more acidic pH values in Los Medanos (moderate grazing history) compared with La Patria (intense grazing history) (6.84 vs. 7.36; 6.89 vs. 7.37; 6.95 vs. 7.37, respectively). With the lack of canopy effect by the nurse plants, differences may be due to two causes: the influence of the intensity use and herbaceous cover, or differences in the soil parental material. Both Zarekia et al. (2012) and Bakhshi et al. (2020) found that in Iranian arid and semiarid grasslands, pH showed no significant differences according to different grazing intensities. Likewise, in the Argentinian Semiarid Chaco district, Abril and Bucher (1999) did not find differences in this parameter by comparing different degradation situations due to overgrazing. Probably, soil pH differences between plots could be caused by

differences in parental materials, although other causes should not be discarded. The parental material in Los Medanos is formed by fluvial sands and silts with interspersed silty sediments, while silty loessic sediments, with calcium carbonate, can be found in La Patria (Martino et al., 2020). Therefore, despite not reacting with hydrochloric acid in the topsoil of either soil sample, carbonates may have some influence on soil pH differences.

Biological parameters

Livestock carrying capacity

Livestock carrying capacity data were analysed for all three seasons, comparing treatments (UC and IC) and fertility islands (*N. flexuosa* and *L. divaricata*). There were only significant differences ($p=0.0858$) between UC and IC in *N. flexuosa* islands during March, when biomass is fully developed (Figure 4).

By comparing among seasons, LCC during

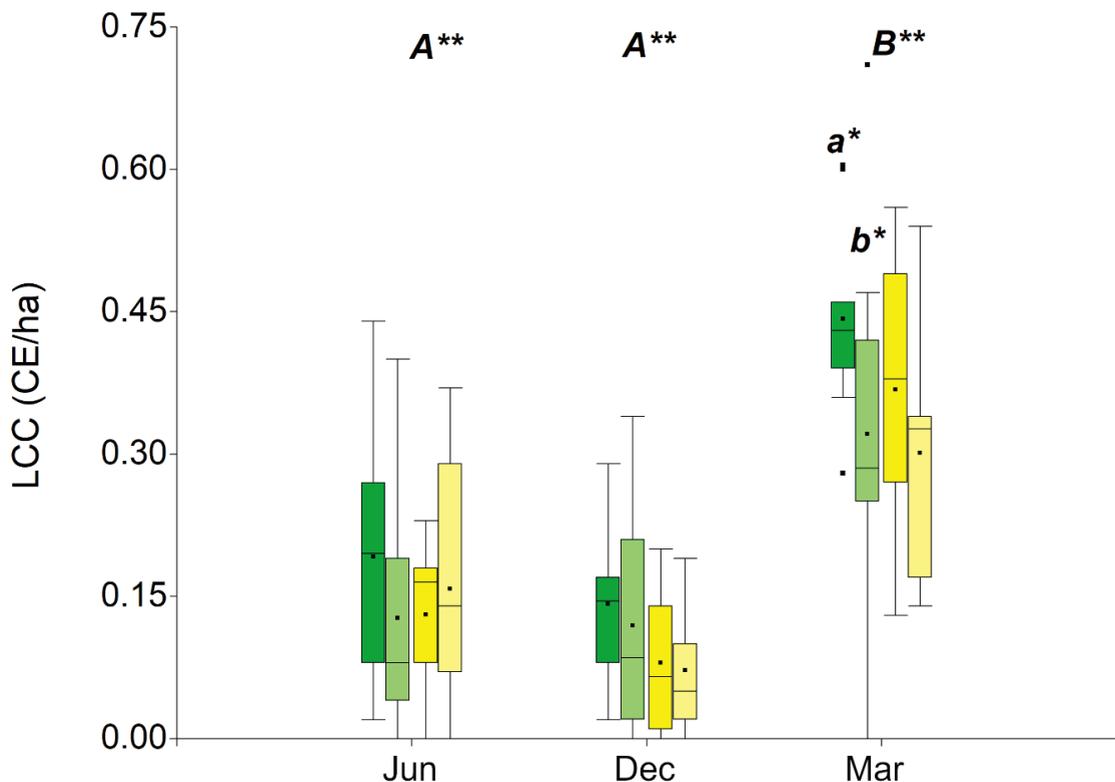


Figure 4. Box-plots of the livestock carrying capacity (LCC). Green bars: *N. flexuosa* islands; yellow bars: *L. divaricata* islands. Dark colours: UC; light colours: IC. Different letters indicate statistically significant differences. Lowercase: between treatments; uppercase: between seasons (ANOVA LSD Fisher test, ** $\alpha=0.05$; * $\alpha=0.1$)

March is higher and more statistically significant than the rest of the seasons ($p < 0.0001$) (Figure 4). The canopy of nurse plants influences the development of grasses after the rainfall season, with higher temperatures and radiation, and in moments in which soil is recharged with water, producing maximum biomass accumulation. However, outside canopy influence grasses are also more developed during March compared to June and December.

Functional plant groups: decreaseers, increaseers and invaderes

The distribution of species according to functional groups (decreaseers, increaseers and invaderes) is shown in Figure 5.

The species classified as decreaseers according to field dynamics were *Setaria* spp., *Leptochloa crinita* (Lag.) P.M. Peterson & N.W. Snow, *Digitaria* spp., *Pappophorum caespitosum* R.E. Fr. These are characterized to reduce their frequencies under growing grazing intensities by ruminants like sheep or goats.

Increaseers, defined by the species *Chloris castilloana* Lillo & Parodi, *Neobouteloua lophostachya* (Griseb.) Gould, *Aristida mendocina* Phil., *Sporobolus pyramidatus* (Lam.) Hitchc., increase their frequencies according to the reduction of decreaseers, but at higher grazing intensities, they also reduce their frequencies.

Invaderes are represented by annual species such as *Aristida adscensionis* L., straws such as *Jarava* spp. and *Nassella* spp., broadleaf species such as *Pseudabutilon virginianum* (Cav.) Fryxell, *Alternanthera pungens* Kuntz and *Talinum*

spp., and shrubby species such as *Lycium tenuispinosum* Miers, *Senna aphylla* (Cav.) H.S. Irwin & Barneby, *Atamisquea emarginata* Miers ex Hook. & Arn., *Senna acanthoclada* (Griseb.) H.S. Irwin & Barneby, and *Condalia microphylla* Cav. These increase their frequencies according to the reduction of decreaseers and increaseers. Eventually, these species may disappear under extreme degradation conditions, evidencing pedestals covered with *Selaginella sellowii* Hieron. within a matrix of bare soil (Karlin, Karlin et al., 2013; Figure 2b). Invaderes are not preferred by the animals due to their high toxicity, low palatability or prickliness. Such species appear in situations under high grazing pressure or erosion signs, indicating ecological disturbances.

According to Kruskal-Wallis tests, the only functional groups that offer significative differences between treatments (UC and IC) at $\alpha = 0.05$ are the decreaseers in *N. flexuosa* islands in each season (June: 0.0394; December: 0.0364; March: 0.0492).

Under the canopy of *N. flexuosa*, the recovery processes seemed to be accelerated. Decreaseers have been favoured by the nurse plants (Figure 5a), and possibly the seed bank suffered fewer losses of decreaseers compared to spaces in the intercanopy. In the intercanopy, the frequency of decreaseers is lower maybe due to adverse biophysical conditions, such as reduced soil moisture content, higher air temperature, higher radiation (Karlin, Coirini et al., 2021) or reduced nutrient contents.

Under reduced grazing pressure, decreaseers might reduce the frequency of straws (*Jarava* spp. and *Nassella* spp., representing invaderes) through

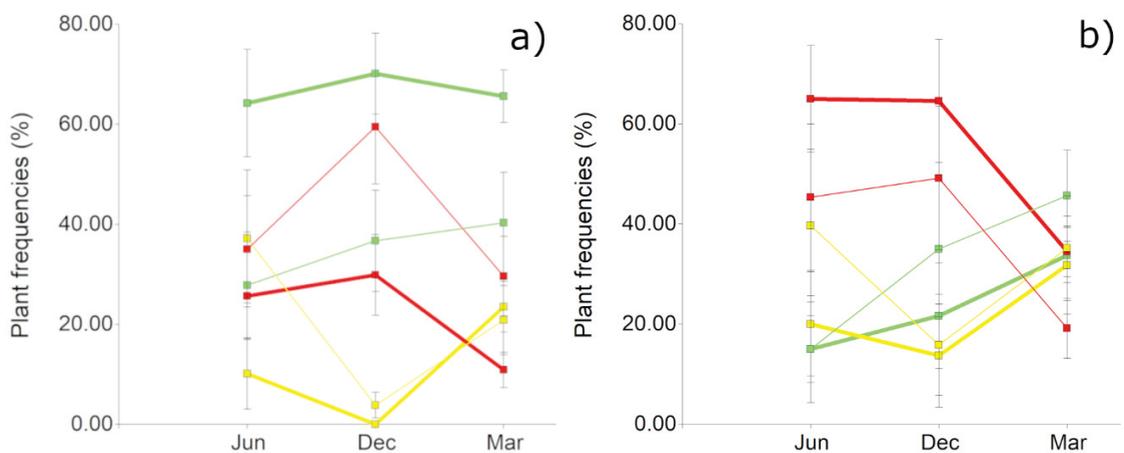


Figure 5. Frequency (%) of the plant functional groups in *N. flexuosa* (a) and *L. divaricata* (b) fertility islands. Green lines: decreaseers; yellow lines: increaseers; red lines: invaderes. Thick lines: UC; thin lines: IC. Bars indicate the standard error

interspecific competence (Crawley, 1990).

L. divaricata nurse plants did not show suitable conditions for decrease under their canopy compared to the intercanopy (Figure 5b). On the contrary, IC has a frequency of decrease 35.8 % higher than UC, although no significant differences were found ($p=0.5810$). Allelopathic effects of the creosotebush may affect the growth of the species under their influence (Mahall and Callaway, 1991). However, the lack of significance requires more detailed studies. Similarly, studying *L. tridentata* as nurse species, Schafer et al. (2012) found that annual species increased their abundance along a gradient from sites under canopy towards the interspaces, without their influence. Soil water during the rainy season could dilute or leach allelopathic substances, improving the frequency of decrease (Lei, 2010), as seen in Figure 5b.

According to the results, *N. flexuosa* might act as a facilitator, while *L. divaricata* could be an inhibitor (Dohn et al., 2013). Nevertheless, it is evident in both cases that precipitations and temperature favour the growth and frequency of decrease and increase, compared to invaders. While frequencies of decrease + increase rise, frequencies of invaders fall, and vice versa. Such relation is evidenced in the following linear regression (4):

$InvF = 96.69 - 0.96 \times (DecF + IncF)$ ($R^2 = 0.93$;
CpMallows = 1620.30; p -value < 0.0001) (4)

Selaginella sellowii is a "cicatrizing" species from arid lands accompanied by other biological organisms such as cyanobacteria, algae, lichens, mosses and microfungi, forming biocrusts (Figure

2b). Its cover changes depending on the nurse species, season or treatment, as shown in Figure 6.

Although no significant differences were found between islands, partitioned by season and treatment ($\alpha=0.05$), frequencies of *Selaginella* under the influence of *L. divaricata* canopy during June and December are far more important than under *N. flexuosa*. Nevertheless, standard deviations are quite important during both seasons.

On the other hand, frequencies of *Selaginella* crusts drastically drop during March, when the cover of other species rises markedly and the vegetative structures of this pteridophyte cease to be visible. This species has an important role in soil regulation. It creates a protective living crust in highly degraded sites. It can retain up to three times its weight (Potsch and Arens, 1949) and reduce soil evaporation, controlling erosion and nutrient losses (Castillo-Monroy et al., 2016), stabilizing pedestals formed by overgrazing and sedimentation.

Soil-plant relationships

Pearson's correlation coefficients are shown in Table 1, discriminated by fertility island.

It is difficult to predict the behaviour of the plant under the canopy in either nurse plant by using soil chemical variables independently as proxies. However, some significant relations between parameters can be identified. For instance, it is expected for soil organic carbon to be closely correlated with mineralized nitrogen available for

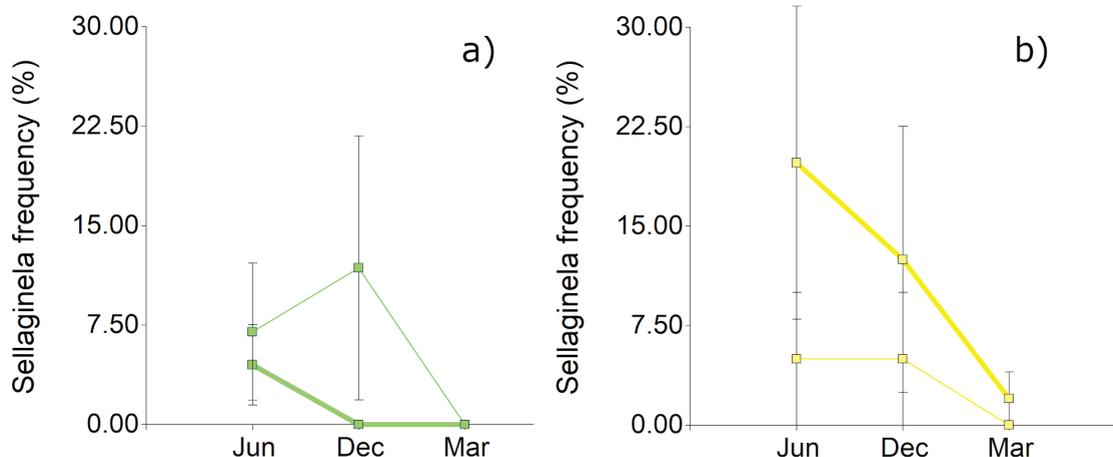


Figure 6. Frequencies of *Selaginella sellowii*; in a) *N. flexuosa* fertility islands (green lines) and b) *L. divaricata* fertility islands (yellow lines); UC (thick lines) and IC (thin lines). Bars indicate the standard error

Table 1. Pearson's correlation coefficients between soil and plant parameters (the latter, only for late summer season) for each category of fertility islands. OC: soil organic carbon; EP: soil extractable phosphorus; EC: electrical conductivity; LCC: livestock carrying capacity; DecF: frequencies of decreaseers; IncF: frequencies of increaseers; InvF: frequencies of invaderes; Self: frequencies of *Selaginella*; (mar): March. In bold, significant correlations: *** $p < 0.001$; ** $0.001 < p < 0.05$; * $0.05 < p < 0.1$

<i>N. flexuosa</i> fertility islands									
	OC	EP	EC	pH	LCC (mar)	DecF (mar)	IncF (mar)	InvF (mar)	Self (mar)
OC									
EP	0.23								
EC	-0.15	-0.1							
pH	-0.20	-0.32	$-2.70 \cdot 10^{-3}$						
LCC (mar)	0.07	-0.34	$-3.70 \cdot 10^{-3}$	0.25					
DecF (mar)	0.59**	0.49**	0.09	-0.24	0.09				
IncF (mar)	0.04	-0.23	-0.16	-0.12	-0.22	-0.38			
InvF (mar)	-0.52**	0.06	0.10	0.14	-0.46**	-0.51**	-0.09		
Self (mar)	0	0	0	0	0	0	0	0	
<i>L. divaricata</i> fertility islands									
	OC	EP	EC	pH	LCC (mar)	DecF (mar)	IncF (mar)	InvF (mar)	Self (mar)
OC									
EP	-0.41*								
EC	-0.50**	0.16							
pH	-0.17	0.44*	0.32						
LCC (mar)	0.26	-0.42*	-0.14	0.14					
DecF (mar)	-0.47**	0.41*	0.40*	0.34	-0.02				
IncF (mar)	0.24	-0.19	-0.16	-0.26	-0.12	-0.80***			
InvF (mar)	0.20	-0.20	-0.25	0.01	0.23	0.06	-0.64**		
Self (mar)	0.01	0.16	-0.12	-0.07	-0.36	0.10	-0.25	0.29	

plant growth (Carranza et al., 2012). Nevertheless, soil organic carbon does not correlate significantly with LCC (as a proxy for plant biomass) during March in either of the fertility islands (Table 1).

As seen before, soil organic carbon is higher in the UC treatment in both island categories (Figure 3a). Nevertheless, it is positively related to decreaseers in *N. flexuosa* islands, but negatively in *L. divaricata* islands (Table 1). It means that within *L. divaricata* islands, decreaseers are inhibited by the influence of this nurse species, instead of being promoted by the higher carbon contents under their canopy, compared to the intercanopy. This reinforces the idea that creosotebush may produce allelopathic effects (Mahall and Callaway, 1991). This effect does not occur under the influence of *N. flexuosa*.

The Bray and Kurtz N°1 method to estimate extractable phosphorus (Sims, 2000) is a measure of the potential availability of phosphates in non-clayey, non-calcareous, neutral or slightly acidic soils by the plants ($pH < 7.5$, as occurs in the study sites, Figure 3d). For this study, extractable phosphorus had positive and significant correlations with the frequencies of decreaseers; however, it had negative and significant correlations with LCC ($p=0.07$ in *L. divaricata* islands; $p=0.01$ when both

islands are combined). Therefore, extractable phosphorus is inversely related to grass biomass (proxied by LCC, significantly higher under the canopy of *N. flexuosa*; Figure 4) as also found by Chidumayo (1997) and Riginos et al. (2009) for dry savannas. Riginos et al. (2009) suggest that maybe phosphorus is more intensely extracted by nurse trees or shrubs, under their canopies; therefore, this may reduce available phosphorus. This effect might be possible for *L. divaricata* because it has superficial roots and may compete with herbaceous plants, but improbable for *N. flexuosa*, with deeper and extended rooting (Villagra et al., 2011). The other possible explanation is that phosphorus content could be affected by the understory plants. However, no significance was found for EP between treatments in favour of the UC (Figure 3b), and possibly the correlation between EP and LCC is independent of nurse plant influence. Besides, phosphorus content show relatively high concentrations (always superior to 23 ppm and averaging 52 ppm), above the critical threshold for the normal development of plants. This threshold for plants ranges between 15 and 25 ppm, depending on soil characteristics, plants and environmental conditions (Beegle, 2005).

Regarding electrical conductivity, this parameter only correlates positively and marginally with

decreasers in *L. divaricata* islands, since both parameters increase their values with the distance from the centre of the island. This effect is probably unimportant since EC do not show significant differences between treatments, and such values should not affect plant performance (Figure 3c). pH correlates with neither plant parameter.

Functional plant groups have predominantly negative relations among them. Decreasers compete with both increasers (highly significant in *L. divaricata* islands) and invaders (moderately significant in *N. flexuosa* islands). Increasers and invaders compete significantly only in *L. divaricata* islands (Table 1).

It is frequently addressed that decreaser species usually produce more forageable biomass than other categories, especially compared with increasers (Díaz, 2007). However, in this study higher decreaser frequencies do not necessarily mean an increase in the carrying capacity. LCC correlates negatively with invaders in *N. flexuosa* islands. As seen in Figure 5, invaders have higher frequencies under the *L. divaricata* canopy compared with *N. flexuosa*. Invaders seem to be facilitated by creosotebush and inhibited by mesquite, possibly due to light intensity, which is reduced in the latter, according to Karlin, Coirini et al. (2021). Nevertheless, these authors found that the correlation between invaders and light intensity under canopy was not significant.

The frequencies of *Selaginella* are null under the canopy of *N. flexuosa*, while it develops better under the *L. divaricata* canopy. This may be due to differences in plant and litter cover since it is considered that the development of this pteridophyte is reduced under closed canopy (by the nurse plant and/or understory plants) or due to high litter concentration conditions (Castillo-Monroy et al., 2016). Both plant cover and litter content were higher under the canopy of *N. flexuosa* compared with *L. divaricata* (Karlin, Coirini et al., 2021).

CONCLUSIONS

N. flexuosa canopy has significant effects on livestock carrying capacity during March, when plants show their maximum expression. On the contrary, the canopy of *L. divaricata* has no significant effect on this variable. The frequency of decreasers improves under *N. flexuosa* canopy, compared to *L. divaricata* canopy. There is no clear relationship between functional plant groups and biomass productivity.

Soil chemical variables relate differently to

biological variables. Even though both OC and LCC parameters were higher under the canopy of both fertility islands, these parameters did not relate significantly. LCC and EP correlated negatively, but only significantly in *L. divaricata* islands, perhaps due to the fact that phosphorus tended to increase towards IC and LCC tended to decrease. LCC showed no significant relationships with either EC or pH.

Soil chemical variables relate better with the frequencies of functional plant groups; however, relations depended on the island. OC related positively with decreasers in *N. flexuosa* islands, but negatively in *L. divaricata* islands. In the latter, there seemed to exist some sort of allelopathy effect that inhibited potential positive effects of OC over this functional plant group. EP correlated positively with decreasers and there seemed to be some sort of control over this kind of functional plant group.

The behaviour of the other functional plant groups seemed to depend on competing effects among them, except for *Selaginella* which seemed to depend on other factors different than those evidenced in this paper, such as plant cover or litter cover. Further studies should be done in the future to get some more detailed relations.

The characteristics of the islands promote different effects on the vegetation under their influence. LCC and the frequency of decreasers are enhanced by the canopy of *N. flexuosa* offering higher digestible biomass for livestock. Such nurse species cover should be promoted to improve productivity and environmental quality, altogether with management practices that tend to recover grasslands through closures and rotative grazing.

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