Journal of Arid Environments 227 (2025) 105314

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Biophysical and environmental changes in livestock disturbed areas in a South-American desert woodland. Potential implications for natural or assisted re-vegetation

Lucía Nadia Biruk [a,b,*], María Elena Fernández [c], Julieta Nelida Aranibar [d], Carla Valeria Giordano [b]

[a] Dipartimento di Scienze della Vita (DSV), Università degli Studi di Trieste, Via L. Giorgieri 10, Trieste, 34127, Trieste, Italy
[b] Instituto Argentino de Investigaciones en Zonas Áridas (IADIZA), CONICET-UNCUYO-Gobierno de Mendoza, Av. Ruiz Leal S/N, Ciudad de Mendoza, 5500, Mendoza, Argentina
[c] Instituto de Innovación para la Producción Agropecuaria y el Desarrollo Sostenible (IPADS), INTA-CONICET, Oficina Tandil, General Rodríguez 370, Tandil, 7000, Buenos Aires, Argentina
[d] Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CONICET-UNCUYO-Gobierno de Mendoza, Av. Ruiz Leal S/N, Ciudad de Mendoza, 5500, Mendoza, Argentina

ARTICLE INFO

Keywords:
Abiotic stress
Drylands
Nutrients
UV-B
Vegetation cover

ABSTRACT

Livestock breeding is among the main productive activities in drylands, often reducing vegetation cover, impacting the surrounding environment and plant regeneration. However, the magnitude of the change in environmental variables in response to vegetation changes has rarely been assessed in arid ecosystems. Our objective was to quantify changes in vegetation cover and floristic composition, as well as the associated microclimatic and edaphic variables that can challenge the ecosystem's restorative capacity in the Monte desert woodland of Argentina. We surveyed sites at 600 (disturbed) and 2000 m (relatively undisturbed) from five rural livestock posts. We found that disturbed sites had lower vegetation cover, altered floristic composition and more stressful environmental conditions for plants. The widest difference was a 50 % decrease in soil NO_3^--N concentration, coupled with a 30 % increase in solar radiation (mainly UV-B), a 4 °C increase in air temperature, and coarser soil texture. Potential constraints to plant regeneration would be therefore not only related to low water availability, but also to lower fertility, higher radiation and temperature. Decisions on species selection to restore these ecosystems must therefore consider plant traits related to nutrient use and uptake capacity, and resistance to photo-oxidative stress, in addition to drought resistance.

1. Introduction

Drylands cover about 41 % of the Earth's land surface and are home to 38 % of the world's human population (MEA, 2005). They include ecosystems with aridity indices (ratio of precipitation to potential evapotranspiration) lower than 0.65, including hyper-arid, arid, semi-arid and sub-humid ecosystems, constituting the most extensive biome on the planet (Kimura and Moriyama, 2019). They are characterised by low, highly variable, and unpredictable rainfall, low vegetation cover, low soil nutrient content (Whitford and Duval, 2019), high solar radiation, low humidity, and in hot deserts, high temperature, resulting in high evapotranspiration. These extreme climatic conditions for plants, and the strong dependence of these ecosystems on rainfall regime, make them prone to degradation when disturbed (Reynolds et al., 2007).

One of the most common economic activities in drylands is livestock breeding (Thornton, 2010). Grazing is one of the key drivers of dryland degradation that results in alterations in vegetation and soil, which can affect ecosystem functioning in the short and long terms (Eldridge et al., 2017). Studies in several arid and semi-arid ecosystems with livestock report lower vegetation cover, species richness (e.g. Gaitán et al., 2018), and functional biocrust diversity (Mallen-Cooper et al., 2018) than similar ecosystems without livestock activity. Livestock also favours soil degradation, both directly through trampling and indirectly through vegetation cover and biocrust reduction, which decreases nutrient concentration, organic matter content and soil stability, and also alters

* Corresponding author. Dipartimento di Scienze della Vita (DSV), Università degli Studi di Trieste, Via L. Giorgieri 10, Trieste, 34127, Trieste, Italy.
E-mail address: luciabiruk@gmail.com (L.N. Biruk).

https://doi.org/10.1016/j.jaridenv.2024.105314
Received 22 March 2024; Received in revised form 3 December 2024; Accepted 25 December 2024

water infiltration (Eldridge et al., 2017; Gaitán et al., 2018). In addition, vegetation cover reduction increases photosynthetically active radiation (PAR) and ultraviolet- B (UV-B) solar radiation reaching the soil surface due to reduced shading and increased bare soil albedo (Dedkov et al., 2020), altering energy balance and near-surface micro-environment (Jankju, 2013). Reduced vegetation cover also modifies water availability on the topsoil and deeper soil layers by decreasing effects of plants canopies on soil water evaporation on the topsoil but increasing water use in deeper layers (e.g. Jankju, 2013). These alterations in vegetation, soil, nutrients, water, and micro-environment can affect natural plants regeneration, through impacting germination, seedling establishment and further plant growth (Príncipe et al., 2019).

The way in which the disturbed environment affects plant regeneration will depend on the magnitude of the environmental changes compared to the undisturbed habitat in which plants evolved, and on the regeneration niche of the different species (Roque Marca et al., 2021). Different conceptual approaches (e.g. King and Hobbs, 2006; Scheffer et al., 2012) propose that there are structural or functional thresholds that when are surpassed during a natural or anthropogenic disturbance the system is no longer able to self-recovery to the original condition (or stable state). In those cases, the sole removing of the disturbance agent (in this case, livestock grazing) is not enough for the ecosystem recovery, and active restoration actions are needed, at least to accelerate the plants regeneration process (e.g. Villagra et al., 2009). In this context, understanding the biophysical conditions of a disturbed habitat is essential to make decisions on restoration actions. Re-vegetation is the most commonly used restoration practice in arid and semi-arid ecosystems (Piñeiro et al., 2013), but deserts are often difficult to restore due to the high rate of post-transplant mortality associated with extreme environmental conditions (Vallejo et al., 2012). Knowing the abiotic environment of the disturbed habitat may enable accurate choices on species selection, nursery breeding practices, and post-transplant amendments (Piñeiro et al., 2013).

In this study, we aimed to quantify changes in the biophysical environment of areas disturbed mainly (but not only) by extensive livestock grazing in an arid ecosystem, the Central Monte desert dominated by *Neltuma flexuosa* in South America. Despite its fragility and heavy history of anthropogenic disturbance (Villagra et al., 2009; Goirán et al., 2012), this is the Argentine ecoregion least represented in ecological restoration studies (Rovere, 2015). To quantify the changes in the biophysical environment due to human-induced disturbances, we measured vegetation cover and floristic composition, together with plant growth resources and abiotic environmental stressors for plant development. We discuss our results in relation to background knowledge on the ecophysiology of plant species from the Monte desert. Measuring the magnitude of environmental change can improve our understanding of livestock grazing effects on biophysical properties that might challenge the natural regeneration capacity of the system.

2. Materials and methods

2.1. Study area and sites selection

The Central Monte Desert is a South-American hot desert, with a mean annual rainfall of 160 mm (average of the period 1972–2014) mostly occurring in late spring and summer. Mean annual temperature is 18.5 °C, with absolute maximal and minimal of 48 °C in summer and −10 °C in winter, respectively (Meglioli et al., 2017). The region comprises a NW-SE oriented valley-dune system, with a 6–15 m deep subterranean watershed that supports woodlands dominated by the phreatophyte species *Neltuma flexuosa*. The study area has different landscape units (valleys, depressions, sand dunes), with associated plant communities. Woody plants (trees, shrubs) dominate vegetation, with a minority presence of grasses and herbaceous species. *Neltuma flexuosa* woodlands were intensively logged in the last century during the expansion of the railway and agricultural oasis (Villagra et al., 2009). This ecosystem is home to a rural population descendant of the Huarpe indigenous people, who are organised in single-family livestock settlements, scattered in low density over the territory (Goirán et al., 2012). Livestock is mainly goats-based and, to a lesser extent, cattle, which are raised mainly for self-consumption. Livestock activity produces a clear decrease in vegetation cover, mainly near livestock posts, where animals concentrate each day to drink water from groundwater wells. Livestock effects on vegetation are attenuated in areas distant from watering points, as observed in other arid areas worldwide (e.g. Goirán et al., 2012).

Within this ecosystem, our study area was located within the Bosques Telteca Nature and Cultural Reserve (32° 20′S; 68° 00′W) and in surrounding areas. The reserve is open (i.e. not surrounded by any kind of fence), with livestock posts both inside and outside it, showing a continuity at landscape level in vegetation and land use. We selected 5 family livestock breeding posts: La Primavera, Las Delicias, El Diamante, Santa Lucía, and La Esperanza (Fig. 1). We followed Goirán et al. (2012), who found that there is a gradient of vegetation cover, i.e. an increase in vegetation cover from the stalls towards the undisturbed woodland, assessed with the soil adjusted total vegetation index (SATVI). At each livestock breeding post, we drew a direction line and selected a disturbed site (D) ∼ 600 m away from the post, and a relatively undisturbed site, considered as a control (C) ∼ 2000 m away from it (Figs. 1 and 2). All study sites were located in inter-dune valleys. Field measurements and sampling were carried out between August 27th and 31st, 2018. Measurements were done in winter because it is the most stable season for nutrient, chloride and soil water determinations, as rainfall is almost null and most of the vegetation is not actively growing. This allowed us to reduce the heterogeneity within and between sites, getting a conservative value of the variation in the measured conditions.

2.2. Vegetation, signs of livestock presence and human activity

We determined the floristic composition and vegetation cover at disturbed and control sites using the modified point-quadrat method (Passera et al., 1983). At each of the sites, we plotted three transects (50 m long, 6 m apart) parallel to each other. We registered the presence of vegetation (to species level), leaf litter or bare soil every 0.5 m, adding up a total of 100 observations per transect. We expressed the cover data as an average of the three transects. In addition, we walked along a strip transect (6 m wide and 50 m long, covering an area of ∼300 m^2 per site), recording domestic animal faeces as signs of livestock presence (goats, cows and horses). We also recorded any presence of pruning scars or stumps as indicators of human extraction of wood as fuel source or other rural uses.

2.3. Environmental variables

2.3.1. Solar radiation

We measured photosynthetically active radiation (PAR) photon irradiance and ultraviolet-B (UV-B) irradiance. We measured PAR with a 1 m long integrating bar connected to a LI-190SB quantum sensor (Li-Cor, Lincoln, USA), and we measured UV-B with a Skye SKU 430 hemispherical sensor (280–315 nm) connected to a SpectroSense2 (Skye Instruments Ltd, Powys, UK). We recorded radiation along the central transect used to measure vegetation cover, every 2.5 m, for a total of 20 points per transect per site. We placed the PAR integrating bar perpendicular to the transect at each of the measurement points, and recorded PAR photon irradiance. At each PAR recording point, we also took 10 UV-B irradiance measurements along 1 m, every 10 cm, and calculated an average value. We then averaged the data of the 20 PAR and UV-B measurement points along the transect, obtaining an average value per site. We performed the measurements on completely clear days, 3 h around solar noon. Due to time constraints, we surveyed one disturbed and one control site relative to one livestock post each day. We completed measurements at all pairs of disturbed and control sites of the

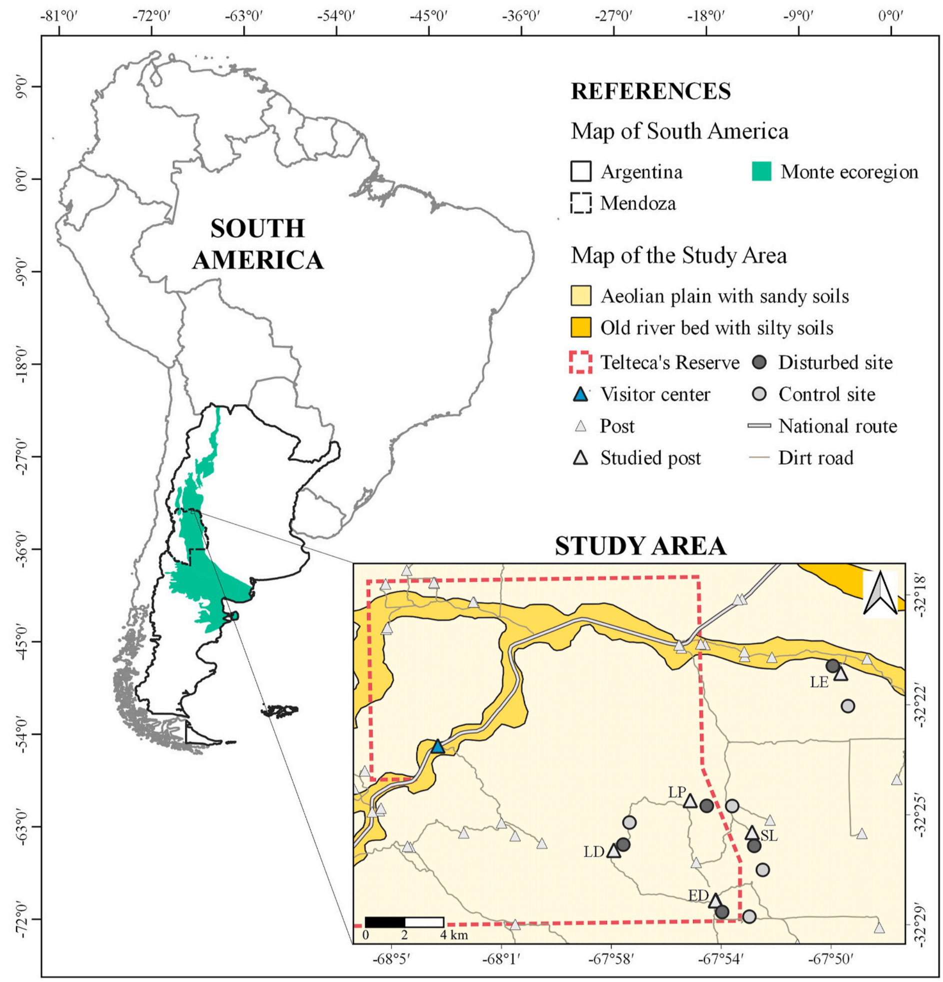

Fig. 1. Map of the study area.
The study was carried out in Bosques Telteca Nature and Cultural Reserve, and its surrounding area, Mendoza province, Argentina. Letters indicate the names of the studied posts, *LP*: La Primavera, *LD*: Las Delicias, *SL*: Santa Lucía, *ED*: El Diamante and *LE*: La Esperanza. Map created using the free and open source QGIS with layers extracted from Arana et al. (2017) and LADYOT - IADIZA – CONICET (Personal communication).

5 livestock posts on 5 consecutive days.

2.3.2. *Air temperature and vapor pressure deficit*

We installed a temperature (T) and relative humidity (RH) sensor (Hygrobutton, iButton DS1923, Maxim Integrated, San Jose, USA) protected from direct solar radiation, 50 cm above the soil surface in the centre of each disturbed and control site, and took measurements at half-hourly intervals during 2 days. We calculated the Vapor Pressure Deficit (VPD) as the vapor pressure difference between the leaf and the air, considering that the air inside the leaf is saturated with water (RH = 100 %) and that the temperature of the leaf is equal to the temperature of the air, following Ewers and Oren (2000). We calculated the average daily VPD (Total mean) and the average of maximum VPD values, i.e. of the values between mid-morning and mid-afternoon (Maximum mean). Regarding T, we considered the maximum, minimum and mean daily values.

2.3.3. *Rainfall*

We installed one rain gauge in the centre of each disturbed and control site. Rain gauges were built up with a polyvinyl chloride pipe of 110 mm internal diameter, 1 m height, with a plastic cap at the bottom and a plastic funnel at the top, and were filled with a 2 cm oil layer to avoid water evaporation. We measured the water level inside rain gauges with a tape meter, during one year (from August 30th, 2018 to August 15th, 2019), every 60 days. Although we did not expect an effect of the disturbance on rainfall level, we recorded this variable in order to determine whether differences in soil water content or vegetation cover might be associated with differences in rainfall among sites, if any. In this regard, rainfall is scarce and often differentially falls in patches across areas a few kilometres apart.

2.3.4. *Soil temperature*

We buried temperature sensors (Thermochron iButton DS1921, Maxim Integrated, San Jose, USA) 15 cm deep in the soil in the centre of each disturbed and control site. We selected that depth to survey a soil zone that is likely to be explored by seedling roots of woody desert species. Sensors took measurements half-hourly during 2-days.

We took soil samples at 15–25 cm depth, every 5 m along the central transect used for the determination of vegetation cover. We took a total of 10 samples per site, in which we measured the variables detailed below. We expressed the results as an average of the 10 samples per site.

2.3.5. *Soil pH and electrical conductivity (EC)*

We placed 25 g of soil in 50 g of distilled water and shook for 30 min. Then we filtered the sample, and on the liquid phase we measured pH and EC with an UP-25 sensor (Denver Instrument, New York, USA) and an LF 91 conductivity meter (WTW, Weilheim, Germany).

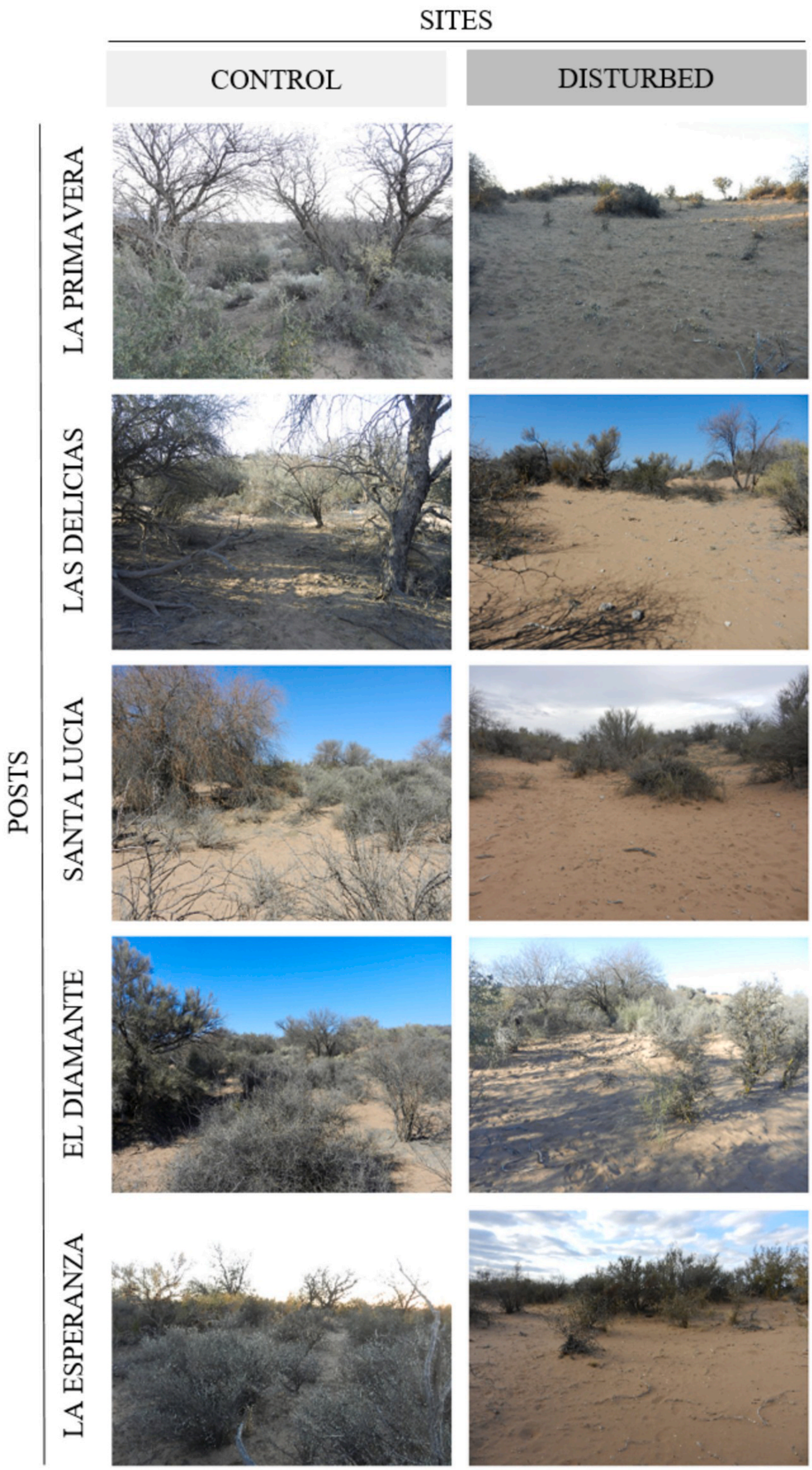

Fig. 2. Sites pictures.
Photographs depicting representative control and disturbed sites associated with each post inside and around the Bosques Telteca Nature and Cultural Reserve, Mendoza, Argentina.

2.3.6. Soil chlorides

We determined the chloride concentration in the sample using the argentometric method. This consisted of the titration of an aqueous solution, obtained by stirring the substrate in distilled water, with a solution of silver nitrate.

2.3.7. Soil moisture

We took around 100 g soil samples, which we placed in hermetically sealed bags and weighed them in the field using a 3-digit portable balance (Scout SPX223, Ohaus Corporation, Parsippany, USA). Then, we dried them at 105 °C for 48 h, and determined the relative water content by the gravimetric method.

2.3.8. Soil organic matter (OM)

We determined the percentage of organic matter using the dry combustion method (Davies, 1974). This consisted of obtaining the dry weight of a soil sample and subsequent ignition of the organic matter in a muffle at 430 °C for 2 h. Then, we calculated the amount of organic matter by the gravimetric method using a high-precision scale (Pioneer™ InCal PA214, Ohaus Corporation, Parsippany, USA).

2.3.9. Soil texture

We obtained a single sample of 100 g for each site, from the mixture of 10 g of each of the samples taken. We removed plant material by sieving the sample with a 2 mm pore mesh. Then, we determined soil particle size distribution by dry mechanical sieving. We sieved the soil sample during 5 min through a battery of 5 sieves of decreasing mesh opening, using a mechanical shaker. Then we weighed on a high precision scale (PioneerTM InCal PA214, Ohaus Corporation, Parsippany, USA) each of the fractions remaining in the sieves.

2.3.10. Soil nutrients

We calculated total nitrogen (N) by means of the Kjeldahl method (Pearcy et al., 1989), consisting of digestion of the sample in an acid medium, subsequent distillation and titration of the resulting solution. Nitrates were estimated by the cadmium reduction method (Jones, 1984) using the HACH NitraVer5 reactive kits, and phosphates were estimated by carbonic extraction using the Arizona technique (Mc George, 1939). We calculated the concentration of nitrates (NO_3^--N) and phosphate (PO_4^-) by spectrophotometry, with a HACH DR 2800 spectrophotometer (HACH Company, Colorado, USA).

2.4. Data analysis

We tested the differences between control and disturbed sites regarded to vegetation, soil, and aboveground environment variables using generalised linear model (GLM) based on *a)* binomial distribution with *logit* link function for plant cover (except herbs), soil moisture content, organic matter and texture (proportion data); *b) Tweedie* distribution for herbs cover (proportion data with excess zeros); *c) Poisson* distribution with natural logarithmic link function for the number of species and signs of livestock presence (count data) and *d) Gaussian* distribution with the identity link function for the rest of the measurements (continuous data). We run one independent GLM (α level = 0.05) for each abovementioned variable (response variable), considering sites (C and D) and posts (LP, LD, SL, ED and LE) as explanatory variables. Although post identity was not our variable of interest, we had to include it as part of our experimental design, i.e., we examined non-independent sites. We incorporated post in our models as a fixed effect – rather than as a random effect- to avoid singular fits (i.e. variances equal zero or close to zero) due to the low levels of this variable and the small sample sizes (Gomes, 2022). We run the models with and without the interaction term (post x site), and selected the most parsimonious model based on AIC and BIC differences between models. In most cases, the selected model was without the interaction. The homoscedasticity and normality of residuals assumptions were visually assessed.

Complementarily, we explored whether the measured variables (sections 2.2 to 2.4) allow us to characterize sites with different degrees of disturbance (C and D) by means of principal component analysis (PCA). To characterize the sites according to *a) the vegetation cover* (section 2.2) we considered the cover of each species relative to the total vegetation cover of each site and computed a PCA with a Hellinger pre-transformation. We removed the species which its contribution to the PCA was null/insignificant (e.g. rare species). We determined the correlation (*Pearson* coefficient) between species relative cover (Fig. S1) and excluded the highly correlated ones ($r \geq 0.72$) in order to avoid highly redundancy in the data. Then, we discriminated the sites based on *b) the environmental variables* measured (sections 2.2 to 2.4). We first imputed the missing data for rainfall and VPD (0.83 % of the total data). We determined the *Pearson* linear correlation between the measured variables (Fig. S2) and excluded the highly correlated ones ($r \geq 0.85$) in the same way as we did with the previously described PCA. In both cases, we evaluated the species/variable contribution to each principal component (PC1 and PC2) through correlation analysis (*Pearson*'s coefficient – Table S2).

We used the statistical software R (version 4.3.2 software, R Core Team, Vienna, Austria).

3. Results

3.1. Vegetation and signs of livestock presence

In spite of the differences between posts that arise as part of landscape-level heterogeneity (Table S1), disturbed (D) sites showed ~ 20 % less vegetation cover than control (C) sites, consistent with a greater livestock presence, as suggested by the proximity of these sites to the posts, and the highest amount of domestic animal faeces (Table 1). These differences in vegetation cover were mainly due to a lower cover of woody species on disturbed sites. Despite differences in vegetation cover, most of disturbed and control sites did not differ in litter cover.

We detected a difference in the floristic composition, but not in the number of species surveyed. Although both disturbed and control sites shared a high proportion of species, *Larrea divaricata*, *Mulguraea aspera* and *Panicum urvilleanum* were only observed in disturbed sites, and *Atriplex lampa*, *Senna aphylla*, *Leptochloa crinita* and *Setaria leucopila* were only recorded in control sites (Table 1).

As expected, we found a higher number of domestic livestock faeces, including goats, cattle and horses, in the disturbed sites than in the control ones (Table 1). At the same time, we did not distinguish the presence of pruning scars or stumps in any of the sampled sites, which confirms that the main anthropogenic agent of disturbance at present is livestock.

3.2. Environmental variables

We found mostly higher UV-B radiation at the disturbed sites, although differences in PAR between disturbed and control sites were only recorded at two of the five posts studied. Where differences in solar radiation were recorded, this was ~30 % higher in disturbed sites than in control sites (Table 2). PAR and UV-B midday values registered in control sites were around 863 ± 92 μmol m^{-2} s^{-1} and 1 ± 0.1 W m^{-2} respectively. The daily maximum air temperature 50 cm above the topsoil was ~4 °C higher in disturbed than in control sites. Likewise, maximum daily evaporative demand was ~20 % higher in disturbed sites (Table 2). Rainfall was similar in both types of sites.

We found that disturbed sites had ~2 °C higher average daily soil temperature and daily minimum soil temperature than control sites, but we did not detect differences in daily maximum soil temperature, contrary to air temperature records (Table 2). Our results show that disturbed sites had lower (~14 % less) chloride concentration than control sites. In addition, most of disturbed sites showed lower OM than control sites, although OM values were low in all cases, ranging from

Table 1

Vegetation and sings of human activity.

Vegetal cover, floristic composition and signs of livestock presence for each site type associated to 5 different posts inside and around the Bosque Telteca Nature and Cultural Reserve. The cover values are indicated as the mean ± SE (n = 3), while the total species and animal faeces are indicated as absolute values (n = 1).

Post	La Primavera		Las Delicias		Santa Lucía		El Diamante		La Esperanza		*Data*
Site	**C**	**D**	**C**	**D**	**C**	**D**	**C**	**D**	**C**	**D**	*comparison**
Cover (%)											
Bare soil	**42.57 ± 6.74**	**66.01 ± 4.44 •**	**19.80 ± 5.51**	**59.74 ± 7.15 •**	**21.78 ± 4.12**	**47.52 ± 3.02 •**	**40.92 ± 7.19**	**54.13 ± 7.24**	**40.26 ± 5.12**	**51.49 ± 9.20**	*Int*
Leaf litter	**8.58 ± 0.66**	**7.92 ± 0.57**	**13.53 ± 3.89**	**5.61 ± 0.33**	**8.91 ± 2.49**	**5.61 ± 1.32**	**9.24 ± 2.16**	**5.61 ± 1.65**	**8.25 ± 1.75**	**14.19 ± 3.63 •**	*Int*
Vegetation	**48.84 ± 7.37**	**26.07 ± 4.33**	**66.67 ± 8.03**	**34.65 ± 6.95**	**69.31 ± 4.00**	**46.86 ± 3.68**	**49.83 ± 9.29**	**40.26 ± 6.89**	**51.49 ± 3.48**	**34.32 ± 6.06**	*C > D*
Woody plants	**48.51 ± 7.14**	**21.45 ± 4.93**	**66.67 ± 8.03**	**29.04 ± 8.27**	**69.31 ± 4.00**	**46.86 ± 3.68**	**49.83 ± 9.29**	**40.26 ± 6.89**	**50.83 ± 3.63**	**33.97 ± 5.75**	*C > D*
Trees	**25.41 ± 9.74**	**14.19 ± 2.38**	**61.06 ± 8.86**	**12.54 ± 3.68 •**	**24.09 ± 10.9**	**34.65 ± 3.18**	**33.33 ± 2.58**	**22.77 ± 7.30**	**23.76 ± 6.02**	**21.78 ± 1.51**	*Int*
Bulnesia retama	*2.31 ± 2.31*	*3.30 ± 1.75*	*11.22 ± 9.31*	*7.92 ± 4.68*	*7.92 ± 4.00*	*7.26 ± 3.89*	*9.90 ± 0.99*	*11.55 ± 5.64*	*8.91 ± 0.57*	*6.93 ± 2.62*	
Geoffrea decorticans	*12.54 ± 2.38*	*7.26 ± 1.19*				*8.25 ± 0.87*	*0.33 ± 0.33*		*3.96 ± 2.06*	*7.26 ± 2.58*	
Neltuma flexuosa	*10.56 ± 8.66*	*3.63 ± 2.31*	*44.55 ± 5.14*	*4.62 ± 1.19*	*16.17 ± 7.44*	*19.14 ± 1.84*	*23.10 ± 2.16*	*11.22 ± 2.16*	*10.89 ± 3.75*	*7.59 ± 2.16*	
Shrubs	**32.67 ± 2.62**	**8.91 ± 2.97**	**31.35 ± 12.5**	**20.79 ± 8.93**	**53.47 ± 7.92**	**17.82 ± 0.57**	**26.73 ± 11.03**	**24.75 ± 8.30**	**29.04 ± 1.19**	**12.87 ± 4.68**	*C > D*
Atamisquea emarginata	*2.31 ± 1.32*		*17.16 ± 4.06*		*2.97 ± 0.99*	*0.66 ± 0.66*	*6.27 ± 4.44*	*0.99 ± 0.99*	*0.33 ± 0.33*	*3.30 ± 3.30*	
Atriplex lampa	*4.95 ± 0.99*				*5.28 ± 2.70*				*0.66 ± 0.66*		
Boungainvillea spinosa	*1.65 ± 0.87*	*0.33 ± 0.33*		*3.63 ± 2.01*	*2.64 ± 1.44*	*2.31 ± 1.44*	*4.29 ± 2.31*	*6.93 ± 2.49*	*4.62 ± 1.32*		
Larrea divaricata		*2.97 ± 2.97*		*1.35 ± 1.30*				*3.96 ± 2.49*		*9.24 ± 2.88*	
Lycium tenuispinosum	*12.21 ± 4.93*	*2.31 ± 2.31*	*14.19 ± 8.43*	*1.65 ± 1.65*	*13.53 ± 0.87*	*8.58 ± 1.65*	*4.62 ± 1.65*	*6.27 ± 2.31*	*4.62 ± 3.15*	*0.30 ± 0.30*	
Mulguraea aspera		*1.32 ± 0.87*		*3.63 ± 3.15*				*2.64 ± 1.32*			
Senna aphylla	*0.99 ± 0.57*								*1.65 ± 1.65*		
Suaeda divaricata	*1.65 ± 0.66*				*6.93 ± 1.71*	*0.99 ± 0.57*			*2.31 ± 1.44*		
Trichomaria usillo	*8.91 ± 1.51*	*1.98 ± 1.51*		*10.23 ± 3.81*	*22.11 ± 5.43*	*4.30 ± 2.30*	*11.55 ± 3.45*	*3.96 ± 3.96*	*14.85 ± 2.62*		
Herbs	**0.33 ± 0.33**	**4.62 ± 1.19 •**		**5.61 ± 1.75 •**	**0.33 ± 0.33**			**0.66 ± 0.66**	**2.97 ± 1.14**	**2.31 ± 1.84**	*Int*
Aristida mendocina								*0.66 ± 0.66*	*2.31 ± 0.66*	*2.31 ± 1.84*	
Leptochloa crinita					*0.33 ± 0.33*				*0.66 ± 0.66*		
Panicum urvilleanum		*4.62 ± 1.19*		*5.61 ± 1.75*							
Setaria leucopila	*0.33 ± 0.33*										
Total species	**11**	**9**	**4**	**8**	**9**	**8**	**7**	**9**	**12**	**7**	*C = D*
Animal faeces	**7**	**21**	**9**	**17**	**6**	**17**	**6**	**13**	**13**	**15**	*C < D*
Goat	1	5	0	2	0	5	0	2	3	2	
Cow	4	11	0	10	3	4	4	3	5	4	
Horse	2	5	9	5	3	8	2	8	5	9	

C: Control, *D*: Disturbed. When the interaction between post and site (*Int*) is statistically significant • denotes differences between sites within the same post. *According to GLMs (α level = 0.05 - Table S1)

Table 2

Environmental variables.

Environmental variables for each site type associated to 5 different posts inside and around the Bosque Telteca Nature and Cultural Reserve. The values are indicated as the mean ± SE, with the exception of maximum and minimum temperatures, rainfall and soil texture which are indicated as absolute values.

Post	**La Primavera**		**Las Delicias**		**Santa Lucía**		**El Diamante**		**La Esperanza**		*n*	*Data*
Site	**C**	**D**	**C**	**D**	**C**	**D**	**C**	**D**	**C**	**D**		*comparison**
Solar radiation												
PAR (μmol $m^{-2} s^{-1}$)	969 ± 64	1298 ± 35 •	496 ± 76	1246 ± 43 •	962 ± 68	1099 ± 81	931 ± 91	1052 ± 89	955 ± 90	974 ± 76	*10*	*Int*
UV-B (watts m^{-2})	1.19 ± 0.06	1.68 ± 0.05 •	0.55 ± 0.06	1.28 ± 0.04 •	0.91 ± 0.05	0.98 ± 0.07	1.15 ± 0.11	1.29 ± 0.07	1.06 ± 0.08	1.37 ± 0.06 •	*10*	*Int*
Air temperature (°C)												
Mean	15.8 ± 0.8	16.0 ± 0.9	14.9 ± 0.6	15.1 ± 0.9	15.5 ± 0.7	15.5 ± 0.8	15.3 ± 0.8	16.9 ± 0.9	14.9 ± 0.7	15.8 ± 0.8	*96*	*C = D*
Maximum	32.3	33.6	27.1	34.0	30.1	31.7	31.2	34.7	29.3	34.2	*1*	*C < D*
Minimum	4.3	4.4	5.6	3.2	5.2	5.0	4.6	5.0	4.4	4.4	*1*	*C = D*
VPD (kPa)												
Total mean	1.4 ± 0.1	1.4 ± 0.1	1.2 ± 0.1	-	1.3 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	1.5 ± 0.1	1.2 ± 0.1	1.4 ± 0.1	*96*	*C = D*
Maximum mean	2.7 ± 0.3	3.0 ± 0.3	2.0 ± 0.2	-	2.5 ± 0.2	2.6 ± 0.3	2.5 ± 0.3	3.2 ± 0.2	2.2 ± 0.2	2.8 ± 0.3	*26*	*C < D*
Rainfall (mm $year^{-1}$)	228	227	180	238	159	-	158	116	308	282	*1*	*C = D*
Soil temperature (°C)												
Mean	15.4 ± 0.3	17.6 ± 0.3	14.1 ± 0.3	16.1 ± 0.5	14.9 ± 0.4	17.1 ± 0.5	17.2 ± 0.6	19.0 ± 0.4	15.3 ± 0.4	16.6 ± 0.3	*96*	*C < D*
Maximum	20.7	22.2	19.7	24.8	21.7	25.0	27.0	26.5	22.4	22.0	*1*	*C = D*
Minimum	10.8	13.6	9.0	9.1	8.7	10.5	9.5	13.1	8.2	11.4	*1*	*C < D*
Soil pH (-)	7.96 ± 0.13	8.07 ± 0.12	8.21 ± 0.08	7.88 ± 0.10	8.05 ± 0.21	8.00 ± 0.11	7.94 ± 0.12	7.63 ± 0.09	7.57 ± 0.09	7.85 ± 0.08	*10*	*C = D*
Soil EC (uS/cm)	226 ± 42	113 ± 10	227 ± 20	125 ± 11	206 ± 26	177 ± 20	232 ± 65	170 ± 19	176 ± 14	112 ± 11	*10*	*C > D*
Soil chlorides (μg g^{-1})	42.8 ± 2.2	39.0 ± 3.4	56.6 ± 6.8	45.6 ± 3.2	45.8 ± 5.6	44.4 ± 4.2	49.0 ± 12.2	37.4 ± 2.2	40.0 ± 1.6	36.4 ± 2.4	*10*	*C > D*
Soil moisture (%)	1.19 ± 0.09	1.62 ± 0.23	1.46 ± 0.15	0.86 ± 0.06 •	1.64 ± 0.16	1.48 ± 0.07	1.65 ± 0.15	1.10 ± 0.09 •	1.27 ± 0.06	1.50 ± 0.18	*10*	*Int*
Soil OM (%)	0.64 ± 0.05	0.47 ± 0.03 •	0.94 ± 0.10	0.59 ± 0.04 •	0.72 ± 0.08	0.73 ± 0.07	0.92 ± 0.08	0.63 ± 0.06 •	0.69 ± 0.05	0.54 ± 0.03	*10*	*Int*
Soil texture (%)												
Fine sand	61.74	71.14	52.65	72.01	48.55	58.47	49.41	61.29	51.88	70.54	*1*	*C < D*
Very fine sand	22.21	12.30	23.44	18.41	30.59	24.23	25.88	14.16	28.45	20.39	*1*	*C > D*
Silt and clay	10.52	2.95	16.60	3.02	14.45	11.84	14.69	6.48	11.26	5.37	*1*	*C > D*
Soil nutrients (μg g^{-1})												
Total Nitrogen	202 ± 21	95 ± 15 •	277 ± 21	129 ± 15 •	182 ± 19	207 ± 46	255 ± 25	174 ± 31 •	174 ± 19	101 ± 10 •	*10*	*Int*
Nitrates-N	1.3 ± 0.3	0.7 ± 0.1	3.9 ± 0.4	1.7 ± 0.5	2.1 ± 0.8	1.8 ± 0.6	3.5 ± 1.4	0.8 ± 0.2	0.9 ± 0.2	1.0 ± 0.2	*10*	*C > D*
Phosphates	7.2 ± 2.1	4.8 ± 1.4	24.1 ± 2.8	3.0 ± 0.7 •	18.4 ± 1.6	12.5 ± 1.6	13.7 ± 2.3	8.0 ± 1.7	8.9 ± 1.6	6.8 ± 1.6	*10*	*Int*

C: Control, *D*: Disturbed. When the interaction between post and site (*Int*) is statistically significant • denotes differences between sites within the same post. *According to GLMs (α level = 0.05 - Table S1)

0.47 ± 0.03 % to 0.94 ± 0.10 % (Table 2).

Disturbed sites had lower values of soil EC than control sites, but in all cases the soil was non-saline. On the other hand, pH was alkaline (~7.9) and similar in both types of sites. Relative soil water content was low and similar between disturbed and control sites in the majority of the cases, although at the two posts where differences were found, relative soil water content was lower at the disturbed sites. In all cases, 90 % of the soil consisted of fine and very fine particles, silt and clay. However, soil texture was coarser in disturbed sites than in control sites. The disturbed sites were also found to be impoverished in total N and nitrates concentration, with differences ~35 % and ~48 % respectively than the control sites (Table 2). Phosphate concentration was mostly similar between the two levels of disturbance.

3.3. Characterization of disturbed and control sites

Control and disturbed sites were characterized by a different floristic composition and relative vegetation cover (Fig. 3), together with different values of aboveground and soil variables (Fig. 4). Likewise, the control sites were more heterogeneous in terms of these variables that the disturbed ones (i.e. disturbed sites presented lower dispersion of the data).

Regarding the vegetation, the first two PCA components (PC1 and PC2) explained 63.0 % of the total variance (39.0 % and 24.0 %, respectively – Fig. 3). The PC1, significantly due to *Bulnesia retama*, *Larrea divaricata*, and *Suaeda divaricata* presence (Fig. S3), segregated the sites into two groups, corresponding to control and disturbed sites. An exception was observed in the disturbed site Santa Lucía, which presented a vegetation array more similar to the control sites. The PC2, instead, was significantly correlated with *Neltuma flexuosa* (Fig. S3) and segregated the control sites in two groups: Santa Lucía, La Primavera and La Esperanza sites differed from Las Delicias and El Diamante sites in that they had a higher cover of shrub species. The latter, on the other hand, were characterized by a high coverage of the tree species *N. flexuosa*.

Considering the environmental variables, the first two PCA components (PC1 and PC2) explained 62.7 % of the total variance of the data. Alike to vegetation PCA, the PC1 (which explained 45.0 % of the total variance) segregated the sites in two groups, corresponding to control and disturbed sites (Fig. 4). The variables that contributed the most to

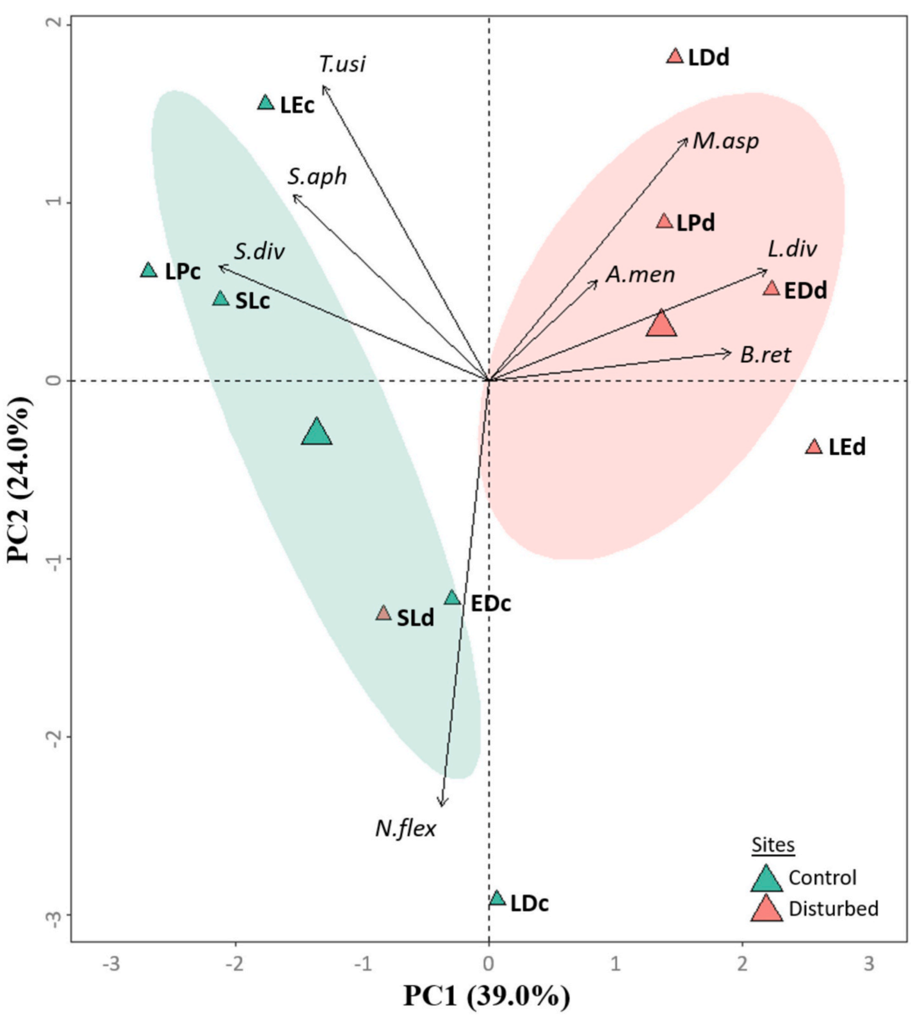

Fig. 3. Vegetation cover – PCA.
Principal component analysis (PC1 and PC2) of the vegetation cover among control and disturbed sites associated to 5 different posts in the area of Bosques Telteca Nature and Cultural Reserve, Mendoza, Argentina. Bold letters indicate the names of the studied posts, **LP:** La Primavera, **LD:** Las Delicias, **SL:** Santa Lucía, **ED:** El Diamante and **LE:** La Esperanza and the sites **c:** control and **d:** disturbed. Italic letters indicate the name of the plant species, *S.div: Suaeda divaricate, S.aph: Senna aphylla, T.usi: Trichomaria usillo, M.asp: Mulguraea aspera, A.men: Aristida mendocina, L.div: Larrea divaricata, B.ret: Bulnesia retama* and *N.flex: Neltuma flexuosa.* Triangles with different color indicate vegetation cover under different site types. Ellipses represent the confidence interval (α level = 0.05) and larger triangles in ellipses indicate the mean values (centroids). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

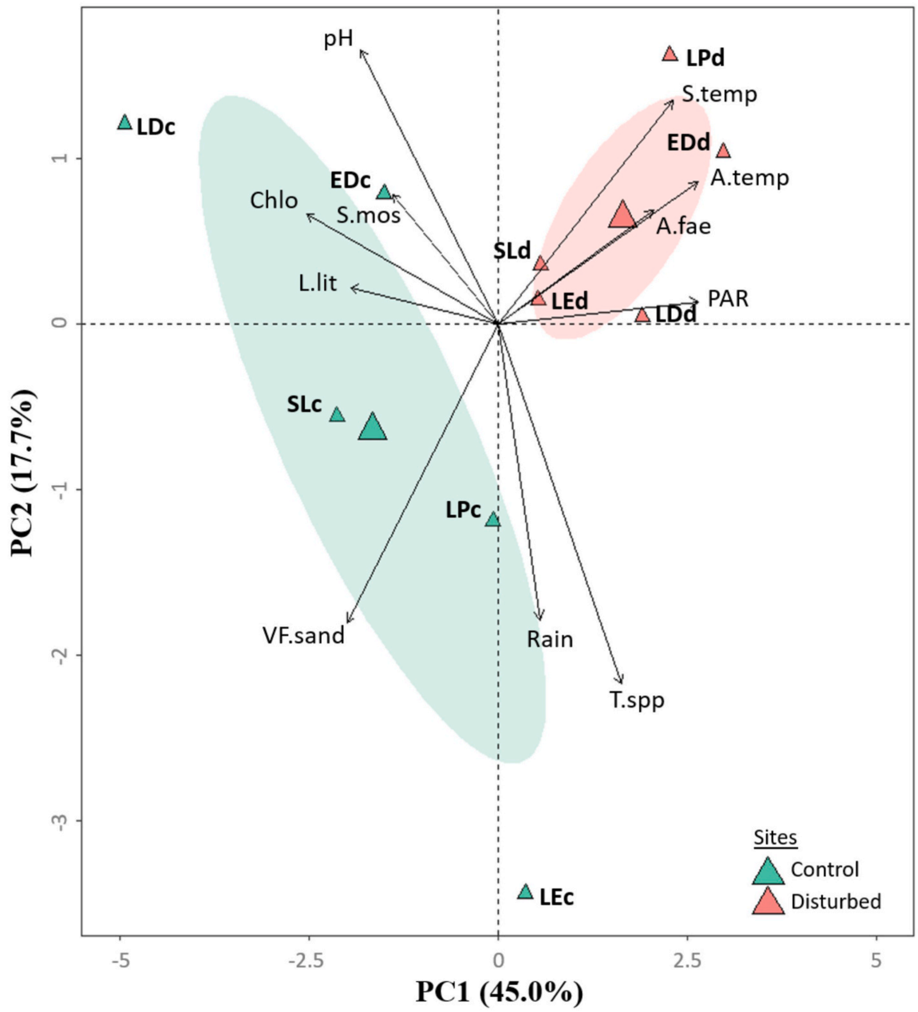

Fig. 4. Environmental variables – PCA.
Principal component analysis (PC1 and PC2) of the environmental variables among control and disturbed sites associated to 5 different posts in the area of Bosques Telteca Nature and Cultural Reserve, Mendoza, Argentina. Bold letters indicate the names of the studied posts, **LP:** La Primavera, **LD:** Las Delicias, **SL:** Santa Lucía, **ED:** El Diamante and **LE:** La Esperanza and the sites **c:** control and **d:** disturbed. Normal letters indicate the variables, Chlo: Chlorides, L.lit: Leaf litter, S.temp: Soil mean temperature, A.temp: Air maximum temperature, A.fae: Animal faeces, T.spp: Total species, Rain: Rainfall and VF.sand: Very fine sand. Triangles with different colors indicate environmental variables under different site types. Ellipses represent the confidence interval (α level = 0.05) and larger triangles in ellipses indicate the mean values (centroids). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

this separation were PAR, soil and aerial temperatures and the number of animal faeces higher in disturbed than in control sites, and litter cover, chlorides concentration and fine soils particles higher in control than in disturbed sites (Fig. 4, Fig. S3). The PC2 was highly correlated with the number of species (Fig. S3) and explained 17.7 % of the total variance of the data. It had a greater effect in the control than in the disturbed sites, as in the PCA of plant cover. In summary, the microenvironmental variables that allowed discriminating the disturbed and control sites were somehow related to changes in vegetation cover and composition. These changes were associated to changes in the above and belowground microenvironment: solar radiation, temperature, soil erosion, chlorides concentration and surface soil moisture.

4. Discussion

Our results show that sites highly disturbed mainly by livestock activity presented lower vegetation cover, somewhat altered floristic composition, and more stressful environmental conditions for plant growth than control sites, with low human disturbance, which is in agreement with expectations. The most dramatic environmental differences were a reduction of about 50 % in nitrate concentration in an ecosystem already highly limited by nutrients, and an increase of about 30 % in solar radiation (mainly reflected by an increase in UV-B). This was accompanied by an increase in evaporative demand of about 20 %, along with higher air temperatures (difference of ~4 °C), and coarser soil texture (with probably lower water retention). In the following subsections we discuss the relationship between variables at the light of antecedents in this and other systems, and the potential implications for vegetation restoration based on ecophysiological information of woody species of the Monte desert ecosystem.

4.1. Livestock grazing reduces vegetation cover and alters floristic composition

Our records of vegetation cover at both types of sites (57 % at control sites and 36 % at disturbed sites) are consistent with values reported by Goirán et al. (2012) using satellite images, and by García et al. (2015) and Magnano et al. (2023) based on field surveys in the same ecosystem. However, unlike the last authors, we did not observe a decrease in the number of species sampled due to the land-use intensity. It is important to note that Magnano et al. (2023) studied as their degraded (highly disturbed) sites plots much closer to the livestock settlement (~50 m away from the rural post) than in our study (600 m). Of the total species sampled, most were reported as forage species for domestic livestock (goats, cattle and horses), except *Larrea divaricata* (Egea et al., 2014). *Atriplex lampa* is one of the species most consumed by goats, especially in winter (Egea et al., 2014). So, it seems that the grazing pressure could have contributed to shape the plant community of the disturbed sites, notably decreasing the abundance of *A. lampa*, as well as *S. aphylla*, *S. leucopila* and *L. crinita*, although their abundances were already very low (or sometimes absent) in the control sites. In the opposite direction, livestock grazing may have favoured *L. divaricata*, because it is a non-palatable species (Guevara and Estevez, 2018). An exception to these vegetation trends was observed in Santa Lucía post, where the disturbed site presented a rather similar vegetation composition than all the control sites. This might be due to the different history of livestock use in this post compared to the other posts (personal communication, gathered from informal interviews with people living in the posts and Telteca's park rangers). In this regard, the posts –except Santa Lucía- were characterized by a long-term (at least 80 years) use dominated by all-year round goat grazing. In Santa Lucía, this year-round goat grazing was introduced in the system six years before the present study. Previously, the post was characterized by cattle raising, which was restricted to shorter temporal grazing windows each year, during the most productive period in terms of forage availability for this type of livestock. More studies are needed relating the history and diversity of management strategies to the vegetation conditions in the region.

4.2. Livestock-disturbed sites show low soil fertility

The livestock-disturbed sites showed a scenario of increased abiotic stress compared to the control sites. The strongest effect of disturbance was on the concentration of nitrogen, one of the most important macronutrients for plants. At the studied ecosystem, the dunes and the inter-dune valleys (the former with 20 % less vegetation cover than the latter) also showed similar differences as those observed in the present study in soil N, according to records taken in summer (Guevara et al., 2010). Therefore, it seems that a difference in vegetation cover in the order of 20 % -both occurring naturally due to differences at the landscape level or due to different anthropogenic pressure- may be a key driver of the differential N levels. In a previous study it was shown that, despite differences in soil fertility, *N. flexuosa* trees growing in both landscape units did not differ in leaf N concentration, suggesting that this species has mechanisms to compensate for nutrient deficiency (Guevara et al., 2018). This compensation in N uptake in poorly fertile soils may be due to symbiosis with N-fixing bacteria in this leguminous species. In this regard, earlier studies of foliar ^{15}N natural abundance indicated that C4 grasses and *N. flexuosa* trees from dune flanks may fix atmospheric N_2 (Aranibar et al., 2014). This large difference in soil fertility between disturbed and undisturbed sites suggests that, either in the process of natural re-colonisation of disturbed areas, or through active restoration programmes, plants that can establish symbiosis with micro-organisms that fix atmospheric N, may be more likely to become established, as recorded in other desert systems (e.g. Carrillo-García et al., 2002). On the other hand, cyanobacteria and cyanolichens in biological soil crusts (BSC) can also fix atmospheric N_2 and favour the release of PO_4^- in alkaline soils such as those of the studied Monte ecosystem or other deserts (Chaves et al., 2020). Thus, in this scenario of disturbance of the Monte, in which the normal low soil water is accompanied by reduced N in the soil, as well as solar radiation is increased, the role of BSC can be fundamental when trying to restore an area with reduced vegetation cover.

Another soil variable reflecting the potential impact of the lower vegetation cover in the disturbed sites was the chloride content. Soil chloride distribution is used as an indicator of water transport, particularly in arid and semi-arid systems (Herczeg and Leaney, 2011). In desert systems, low soil chloride pools –as observed in disturbed sites in our study- indicate low rates of vegetation water uptake and high deep-water drainage (Scanlon et al., 2005).

4.3. Livestock-disturbed sites show high solar radiation

Another feature of the disturbed sites was an increase of about 30 % in solar irradiance, recorded in winter in the present study, with differences mainly associated with UV-B radiation. These differences are likely to become more pronounced in the summer. Excessive UV-B can limit plant growth through its effect on molecular damage (Hideg et al., 2013). However, plants possess mechanisms to protect themselves from excessive solar radiation, either by reflecting or absorbing it. In the former case, trichomes and epicuticular waxes are efficient in reflecting UV-B and PAR (Holmes and Keiller, 2002). In our study ecosystem there are various species from the family *Zygophyllaceae* (i.e. *Larrea divaricata*, *Bulnesia retama*), characterised by the presence of waxes on their leaves and stems that provide protection against excess radiation and desiccation (Ruiz Leal, 1972). Desert plants are naturally adapted to high solar radiation, and the ability to tolerate excess radiation in open sites will depend on the species' traits and their plasticity. In this regard, studies on four representative species of the Central Monte desert, *Bulnesia retama*, *Neltuma argentina*, *N. flexuosa* and *N. alpataco*, demonstrated that these species did not show plasticity in epicuticular waxes or photoprotective compounds against water stress (Biruk et al., 2022). Therefore, although the species are adapted to current deserts conditions, it remains open the question about their adaptability to face even higher radiation stress arising as a consequence of reduced vegetation cover due to livestock pressure.

4.4. Livestock-disturbed sites show increased air temperature

The mean temperature increase of 4 °C recorded in winter at the disturbed sites compared to the control sites is likely to intensify in summer. This temperature difference is the midpoint of the range of temperature increases predicted by the Intergovernmental Panel on Climate Change towards the end of the 21^{s}t century (IPCC, 2023). Considering that this system is a hot desert where we have recorded air temperatures up to 50 °C in the shade in summer (unpublished results), the higher temperatures measured in the disturbed sites, coupled with the aridity of the ecosystem, are likely to contribute to increased environmental stress challenging plant growth and survival at the low vegetation-covered sites. High evaporative demand associated with rising temperature increases atmospheric drought, accentuating the soil water deficit. Although desert plants are adapted to this extreme environment, how much these changes will impact plant growth and survival will depend on the physiological thresholds of the different species in their ability to tolerate or avoid soil and atmospheric drought and high temperatures. There are studies of some of the species of the Monte desert in response to drought conditions, showing a multiplicity of responses (e.g. Biruk, 2021; Biruk et al., 2022). However, there are no specific studies about heat tolerance of any of them. In this regard, high temperatures *per se* can be lethal for plants (Teskey et al., 2015). Moreover, a common mechanism to dissipate high temperature is by means of transpiration cooling, which is highly impaired under conditions of low soil water content –a phenomenon known as hot-drought (Hammond et al., 2022). More studies are needed about the behaviour of native species under multiple environmental stress in order to predict the fate of these systems in response to degradation and climate change as well as to guide the selection of species according to the environmental characteristics of the sites to be actively restored.

5. Conclusion

This study provides a quantitative assessment of the increased environmental stress in livestock-disturbed areas compared to the conditions already stressful for plants' development typical of arid ecosystems. From our results, disturbed sites in inter-dunes valleys approach biophysical conditions of dune flanks in terms of soil chemistry, soil texture, plant cover and temperature. This assessment, although partial and limited, can be a preliminary guide for decision making to revert this degradation path with active restoration strategies, which in addition to livestock exclusion would mean planting of selected species (i.e., those found in dunes) with different transplanting interventions (use of organic amendment, irrigation, shading, BSC inoculation, etc.). In this regard, although some recovery of the vegetation structure may be possible if the system has not surpassed the structural and functional threshold that define its state, it is known that recruitment of grasses and woody species is highly limited in disturbed arid ecosystems due to high abiotic stress (Bosco et al., 2018), and thus active interventions are needed to reverse the degradation process (e.g. Fick et al., 2016). For instance, a grazing exclusion experiment in the Dry Chaco region (a close but less arid ecosystem than ours) has shown that after 7–8 years of livestock removal, only palatable grass species increased their cover, with no changes in woody species, herbs, forbs and vines (Trigo et al., 2020). Our results suggest that the traits to be determined for the selection of species include, not only their drought resistance, but their mechanisms of heat tolerance, photoprotection and nutrient use, either in relation to the efficiency of use or the association with soil microorganisms that allow plants to overcome the strong limitation of water, nutrients and high irradiance and temperature in disturbed sites. Considering that interannual variation in rainfall and temperature is high and not predictable in these ecosystems, this work is a starting point for understanding environmental changes at disturbed sites, but a broader picture would be obtained by including summer measurements in different years as well as ecophysiological studies of different species in the field.

CRediT authorship contribution statement

Lucía Nadia Biruk: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **María Elena Fernández:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Julieta Nelida Aranibar:** Writing – review & editing, Supervision, Methodology. **Carla Valeria Giordano:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank the families of the studied posts, in particular Doña Isabel, Don Carme, Diego, Zeverino and Doña Nelly, for their kindness and hospitality at opening their homes to our surveys. We highly appreciate Diego Zeverini, Clara Stinga and Sergio Alesci for their invaluable collaboration in field work; Alejandra Medero, Marcelo Quiroga and Enrique Mas for laboratory assistance; Pamela Krug and Francesco Petruzzellis for their advice on statistical analysis, and Eugenia Vázquez and Aranzazú Guevara, for their unconditional support during sampling and manuscript production. We also thank the Dirección de Recursos Naturales Renovables of Mendoza province for the permission to work in Telteca's Natural Reserve and park ranger staff for their logistic assistance and hospitality. This study was funded by grants awarded by the "Consejo Nacional de Investigaciones Científicas y Técnicas" (CONICET, PUE IADIZA 2016-0042 to Giordano C. V.), by "Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación" (PICT 2011–2521 to Giordano C. V.), and by the "National Geographic Society" (EC-179C-18 to Biruk L. N.).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2024.105314.

Data availability

Data will be made available on request.

References

Arana, M.D., Martinez, G.A., Oggero, A.J., Natale, E.S., Morrone, J.J., 2017. Map and shapefile of the biogeographic provinces of Argentina. Zootaxa 4341 (3), 420–422. https://doi.org/10.11646/zootaxa.4341.3.6.

Aranibar, J.N., Goirán, S.B., Guevara, A., Villagra, P.E., 2014. Carbon and nitrogen dynamics in a sandy groundwater-coupled ecosystem in the Monte Desert, indicated by plant stable isotopes. J. Arid Environ. 102, 58–67. https://doi.org/10.1016/j.jaridenv.2013.11.005.

Biruk, L.N., 2021. Ecofisiología de especies leñosas del Monte Central: aportes para la selección de especies y métodos de cultivo para la restauración de tierras secas. Tesis Doctoral. Universidad de Buenos Aires. Facultad de Ciencias Exactas y Naturales). See. https://hdl.handle.net/20.500.12110/tesis_n6794_Biruk. (Accessed 18 March 2024).

Biruk, L.N., Fernández, M.E., González, C.V., Guevara, A., Rovida-Kojima, E., Giordano, C.V., 2022. High and diverse plastic responses to water availability in four desert woody species of South America. Trees 36, 1881–1894. https://doi.org/10.1007/s00468-022-02335-8.

Bosco, T., Bertiller, M.B., Carrera, A.L., 2018. Abiotic factors affect the recruitment and biomass of perennial grass and evergreen shrub seedlings in denuded areas of Patagonian Monte rangelands. J. Environ. Manag. 118–128. https://doi.org/10.1016/j.jenvman.2018.04.020, 2018.

Carrillo-García, Á., León De La Luz, J.L., Bashan, Y., Bethlenfalvay, G.J., 2002. Nurse plants, mycorrhizae, and plant establishment in a disturbed area of the Sonoran Desert. Restor. Ecol. 7 (4), 321–335. https://doi.org/10.1046/j.1526-100X.1999.72027.x.

Chaves, J.B., Aranibar, J.N., Gatica, M.G., 2020. Species and functional plant diversity enhance ecosystem functions in the central Monte desert. J. Veg. Sci. https://doi.org/10.1111/jvs.12952.

Davies, B., 1974. Loss-on-ignition as an estimate of soil organic matter. Soil Sci. Soc. Am. Proc. 38, 150–151. https://doi.org/10.2136/sssaj1974.03615995003800010046x.

Dedkov, V.P., Danzhalova, E.V., Tkachenko, S.N., Khadbaatar, S., Ariunbold, E., Gunin, P.D., Bazha, S.N., 2020. The influence of vegetation on reflected solar radiation in arid and extra-arid zone of Mongolian Gobi. Geography, Environ., Sustain. 13 (4), 72–80. https://doi.org/10.24057/2071-9388-2020-91.

Egea, A.V., Allegretti, L., Lama, S.P., Grilli, D., Sartor, C., Fucili, M., Guevara, J.C., Passera, C., 2014. Selective behavior of Creole goats in response to the functional heterogeneity of native forage species in the central Monte desert, Argentina. Small Rumiant Res. 120 (1), 90–99. https://doi.org/10.1016/j.smallrumres.2014.04.005.

Eldridge, D.J., Delgado-Baquerizo, M., Travers, S.K., Val, J., Oliver, I., 2017. Do grazing intensity and herbivore type affect soil health? Insights from a semi-arid productivity gradient. J. Appl. Ecol. 54, 976–985. https://doi.org/10.1111/1365-2664.12834.

Ewers, B.E., Oren, R., 2000. Analyses of assumptions and errors in the calculation of stomatal conductance from sap flux measurements. Tree Physiol. 20, 579–589. https://doi.org/10.1093/treephys/20.9.579.

Fick, S.E., Decker, C., Duniway, M.C., Miller, M.E., 2016. Small-scale barriers mitigate desertification processes and enhance plant recruitment in a degraded semiarid grassland. Ecosphere 7 (6), e01354. https://doi.org/10.1002/ecs2.1354.

Gaitán, J.J., Bran, D.E., Oliva, G.E., Aguiar, M.R., Buono, G.G., Ferrante, D., Nakamatsu, V., Ciari, G., Salomone, J.M., Massara, V., García Martínez, G., Maestre, F.T., 2018. Aridity and overgrazing have convergent effects on ecosystem structure and functioning in Patagonian rangelands. Land Degrad. Dev. 29, 210–218. https://doi.org/10.1002/ldr.2694.

García, V., Aranibar, J.N., Pietrasiak, N., 2015. Multiscale effects on biological soil crusts cover and spatial distribution in the central Monte Desert. Acta Oecol. 69, 23–45. https://doi.org/10.1016/j.actao.2015.08.005.

Goirán, S., Aranibar, J.N., Gomez, M.L., 2012. Heterogeneous spatial distribution of traditional livestock settlements and their effects on vegetation cover in arid groundwater coupled ecosystems in the Monte desert (Argentina). J. Arid Environ. 87, 188–197. https://doi.org/10.1016/j.jaridenv.2012.07.011.

Gomes, D.G.E., 2022. Should I use fixed effects or random effects when I have fewer than five levels of a grouping factor in a mixed-effects model? PeerJ 10, e12794. https://doi.org/10.7717/peerj.12794.

Guevara, A., Giordano, C.V., Aranibar, J.N., Quirga, M., Villagra, P.E., 2010. Phenotypic plasticity of the coarse root system of *Prosopis flexuosa*, a phreatophyte tree, in the Monte Desert (Argentina). Plant Soil 330, 447–464. https://doi.org/10.1007/s11104-009-0218-4.

Guevara, A., Pancotto, V.A., Mastrantonio, L., Giordano, C.V., 2018. Fine roots of *Prosopis flexuosa* trees in the field. Plant and soil variables that control their growth and depth distribution. Plant Ecol. 219, 1399–1412. https://doi.org/10.1007/s11258-018-0889-0.

Guevara, J.C., Estevez, O.R., 2018. Sustainable use of rangelands of the Mendoza plain (Argentina). Revista de la Facultad de Ciencias Agrarias de la UNCuyo 50 (1), 295–307. See: https://ri.conicet.gov.ar/handle/11336/92640.

Hammond, W.M., Williams, A.P., Abatzoglou, J.T., Adams, H.D., Klein, T., López, R., Saénz-Romero, C., Hartmann, H., Breshears, D.D., Allen, C.D., 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. Nat. Commun. 13, 1761. https://doi.org/10.1038/s41467-022-29289-2.

Herczeg, A., Leaney, F.W., 2011. Review: environmental tracers in arid-zone hydrology. Hydrogeol. J. 19 (1), 7. https://doi.org/10.1007/s10040-010-0652-7.

Hideg, E., Marcel, A., Jansen, K., Strid, A., 2013. UV-B exposure, ROS, and stress: inseparable companions or loosely linked associates? Trends Plant Sci. 18 (2). https://doi.org/10.1016/j.tplants.2012.09.003.

Holmes, M.G., Keiller, D.R., 2002. Effects of pubescence and waxes on the reflectance of leaves in the ultraviolet and photosynthetic wavebands: a comparison of a range of species. Plant Cell Environ. 25, 85–93. https://doi.org/10.1046/j.1365-3040.2002.00779.x.

IPCC, 2023. Climate change 2023: synthesis report. In: Lee, H., Romero, J. (Eds.), Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Core Writing Team. IPCC, Geneva, Switzerland, p. 184. https://doi.org/10.59327/IPCC/AR6-9789291691647.

Jankju, M., 2013. Role of nurse shrubs in restoration of an arid rangeland: effects of microclimate on grass establishment. J. Arid Environ. 89, 103–109. https://doi.org/10.1016/j.jaridenv.2012.09.008.

Jones, M.N., 1984. Nitrate reduction by shaking with cadmium: alternative to cadmium columns. Water Res. 18 (5), 643–646. https://doi.org/10.1016/0043-1354(84)90215-X.

Kimura, R., Moriyama, M., 2019. Recent trends of annual aridity indices and classification of arid regions with satellite-based aridity indices. Remote Sensing Earth Sys. Sci. 2, 88–95. https://doi.org/10.1007/s41976-019-00014-w.

King, E.G., Hobbs, R.J., 2006. Identifying linkages among conceptual models of ecosystem degradation and restoration: towards an integrative framework. Restor. Ecol. 14 (3), 369–378. https://doi.org/10.1111/j.1526-100X.2006.00145.x.

Magnano, A.L., Meglioli, P.A., Novoa, E.V., Chillo, V., Alvarez, J.A., Alvarez, L.M., Sartor, C.E., Vázuez, D.P., Vega Riveros, C.C., Villagra, P.E., 2023. Relationships between land-use intensity, woody species diversity, and carbon storage in an arid woodland ecosystem. For. Ecol. Manag. 529, 120747. https://doi.org/10.1016/j.foreco.2022.120747.

Mallen-Cooper, M., Eldridge, E.J., Delgado-Baquerizo, M., 2018. Livestock grazing and aridity reduce the functional diversity of biocrusts. Plant Soil 429, 175–185. https://doi.org/10.1007/s11104-017-3388-5.

Mc George, W.T., 1939. Factors influencing the availability of native soil phosphate fertilizers in Arizona soils. Ariz. Agric. Exp. Stn. Tech. Bull. 40–57. https://repository.arizona.edu/handle/10150/199481. (Accessed 18 March 2024).

Meglioli, P.A., Aranibar, J.N., Villagra, P.E., Vega Riveros, C., 2017. Spatial patterns of soil resources under different land use in *Prosopis* woodlands of the Monte desert. Catena 149, 86–97. https://doi.org/10.1016/j.catena.2016.09.002.

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-Being: Desertification Synthesis. World Resources Institute, Washington, DC.

Passera, C.B., Dalmasso, A.D., Borsetto, O., 1983. Método de point quadrat modificado. Taller de arbustos forrajeros para zonas áridas y semiáridas, pp. 71–79.

Pearcy, R.W., Ehleringer, J.R., Mooney, H.A., Rundel, P.W., Brinkley, D., Vitousek, P., 1989. Soil nutrient availability. In: Plant Physiological Ecology. Springer, Netherlands, pp. 75–96.

Piñeiro, J., Maestre, F.T., Bartolomé, L., Valdecantos, A., 2013. Ecotechnology as a tool for restoring degraded drylands: a meta-analysis of field experiments. Ecol. Eng. 61, 133–144. https://doi.org/10.1016/j.ecoleng.2013.09.066.

Príncipe, A., Matosa, P., Sarris, D., Gaiola, G., do Rosário, L., Correia, O., Branquinho, C., 2019. Mediterranean drylands microclimate affects more tree seedlings than adult trees. Ecol. Indicat. 106, 105476. https://doi.org/10.1016/j.ecolind.2019.105476.

Reynolds, J.F., Smith, D.M.S., Lambin, E.F., Turner, B.L., Mortimore, M., Batterbury, S.P., Downing, T.E., Dowlatabadi, H., Fernández, R.J., Herrick, J.E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M., Walker, B., 2007. Global desertification: building a science for dryland development. Science 316 (5826), 847–851. https://doi.org/10.1126/science.1131634.

Roque Marca, N., López, R.P., Naoki, K., 2021. Effect of shade and precipitation on germination and seedling establishment of dominant plant species in an Andean arid region, the Bolivian Prepuna. PLoS One 16 (3), e0248619. https://doi.org/10.1371/journal.pone.0248619.

Rovere, A.E., 2015. Review of the science and practice of restoration in Argentina: increasing awareness of the discipline. Restor. Ecol. 23 (5), 508–512. https://doi.org/10.1111/rec.12240.

Ruiz Leal, A., 1972. Flora popular mendocina. In: Deserta 3, CONICET, Gobierno de Mendoza. Universidad Nacional de Cuyo.

Scanlon, B.R., Reedy, R.C., Stonestrom, D.A., Prudic, D.E., Dennehy, K.F., 2005. Impact of land use and land cover change on groundwater recharge and quality in the southwestern US. Global Change Biol. 11, 1577–1593. https://doi.org/10.1111/j.1365-2486.2005.01026.x.

Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., van de Koppel, J., van de Leemput, I.A., Levin, S.A., van Nes, E.H., Pascual, M., Vandermeer, J., 2012. Anticipating critical transitions. Science 338 (6105), 344–348. https://doi.org/10.1126/science.1225244.

Teskey, R., Wertin, T., Bauweraerts, I., Ameye, M., McGuire, M.A., Steppe, K., 2015. Responses of tree species to heat waves and extreme heat events. Plant Cell Environ. 38 (9), 1699–1712. https://doi.org/10.1111/pce.12417.

Thornton, P.K., 2010. Livestock production: recent trends, future prospects. Philosophical Trans. Royal Soc. B 365, 2853–2867. https://doi.org/10.1098/rstb.2010.0134.

Trigo, C.B., Villagra, P.E., Coles, P.C., Marás, G.A., Andrade-Díaz, M.S., Núñez-Regueiro, M.M., Derlindati, E.J., Tálamo, A., 2020. Can livestock exclusion affect understory plant community structure? An experimental study in the dry Chaco forest, Argentina. For. Ecol. Manag. 463, 118014. https://doi.org/10.1016/j.foreco.2020.118014.

Vallejo, V.R., Smanis, A., Chirino, E., Fuentes, D., Valdecantos, A., Vilagrosa, A., 2012. Perspectives in dryland restoration: approaches for climate change adaptation. New Forests 43, 561–579. https://doi.org/10.1007/s11056-012-9325-9.

Villagra, P.E., Defossé, G.E., Del Valle, H.F., Tabeni, S., Rostagno, M., Cesca, E., Abraham, E., 2009. Land use and disturbance effects on the dynamics of natural ecosystems of the Monte Desert: implications for their management. J. Arid Environ. 73 (2), 202–211. https://doi.org/10.1016/j.jaridenv.2008.08.002.

Whitford, W.G., Duval, B.D., 2019. Ecology of Desert Systems. Academic Press.