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Consequences of anthropogenic disturbances on soil seed bank diversity and nurse shrub effect in a semiarid rangeland

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Abstract What is the effect of common land use histories on the diversity, richness, spatial distribution and abundance of the soil seed bank (SSB)? Does the effect change between different microsites under shrub canopy? To address these questions we selected seven sites with different grazing and fire histories in the Patagonian Monte desert. We took soil samples in seven microsites at different distances of the trunk along a windward/leeward transect through shrub patches to estimate the SSB of perennial grasses, shrubs and annuals. Shrubs SSB was scarce. The nurse shrub effect on perennial grass SSB was evident at sites with a low disturbance intensity (as sites without continuous grazing), and higher on the leeward side under the shrub canopy. High disturbance intensity (such as permanent grazing) promoted a decrease in perennial grass SSB and an increase in annuals SBB (especially non-native). Land use histories related to fire showed a moderated disturbance response (medium values for both groups). Differences between land use histories varied depending on the windward/leeward microsite from which the SSB was analysed. Our results suggest a nurse effect of the shrub patches on the spatial distribution and abundance of the SSB, but this effect decrease under continuous grazing. Fire seems to have a positive effect on perennial grass SSB. Nevertheless, fire characteristics must be controlled. Moreover, perennial grass SSB was almost depleted under continuous grazing,

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driving the grazed system towards a vulnerable state; and annual non-native species take advantage of this disturbance and dominate the SSB.

Keywords Grazing · Fire · Nurse · Predominant wind · Perennial grasses · Monte

Introduction

In arid and semiarid environments, the vegetation is typically distributed in patches (islands) immersed in a bare soil matrix ("interpatches") (Aguiar and Sala 1999). These patches are dominated by shrubs, with grasses, dwarf shrubs, herbs and biological crusts growing under their canopy (Bisigato and Bertiller 1999; Cecchi et al. 2001). Several mechanisms have been proposed to explain the maintenance of these structures, including a complex balance between competition and facilitation (Caballero et al. 2008). The formation of islands as a product of grazing has recently been highlighted in the semiarid regions (Allington and Valone 2013). Disturbances, such as herbivory, fire and drought, forge the structure and functioning of grassland ecosystems (Oesterheld et al. 1999). Under grazing conditions, key resources, such as water and nitrogen, are more available in the shrub patches (Allington and Valone 2013). Also, shrub patches act as a seed source driven by enhanced local conditions, as protection against desiccation, herbivory and wind erosion (Kinloch and Friedel 2005), which are effects related to facilitation processes (Callaway 2007). The shrubs capability to act as seed trap through the accumulation of seeds transported by animals (Marone et al. 1998a) or wind (Aguiar and Sala 1994; Acosta and Agüero 2001) may also be considered as nurse effect that facilitates soil seed bank formation and maintenance. All these processes combined form a spatial pattern in the soil seed bank and seedling recruitment that reinforces the heterogeneous distribution of the vegetation (Edwards and Crawley 1999; Caballero et al. 2008).

Concentration of defoliation and trampling in the interpatches reduces the cover of perennial grasses and biological crusts that protect the soil, leading to edaphic changes that decrease nutrient concentration and water infiltration, and increase the loss of vegetation cover in these spaces (Fuls 1992; Allington and Valone 2013). These losses of vegetation and soil cover may, eventually, result in a partial reduction of the soil seed bank (Caballero et al. 2008). In addition, cattle may indirectly affect pollination levels through modifications in the assembly between plants and their particular pollinators, and in the plant community overall (Vázquez and Simberloff 2004; Tadey 2008). Once that situation is reached under grazing conditions, the interpatches are seldom revegetated and they become the centres from which the desertification process advances in these systems (Fuls 1992; Chartier and Rostagno 2006; Chartier et al. 2011).

In the semiarid shrublands, fire is considered as an "endogenous" disturbance that models the vegetation structure; and human activities promote changes on fire regime that may divert the natural history of these environments (Haubensak et al. 2009). In the Monte desert, for over a century the hot and dry summer months create an environment prone to wildfires, as in other semi-arid regions of Argentina (Bóo et al. 1996; Cabido and Zak 1999). Although, the loss of fine fuels promoted by livestock grazing and the installation of firebreaks caused the reduction of the frequency of natural fires that controlled the density of woody plants and enhanced grass cover (Bóo et al. 1996; Kröpfl et al. 2007). Therefore, in many arid systems, controlled fires are commonly used as a management tool to promote

changes in the vegetation that leads to a reduction in the shrub layer and an improvement in the cover of desirable perennial grasses (Bran et al. 2007; Peláez et al. 2010). Once fire has occurred, wind redistributes nutrients and propagules accumulated under the shrub canopy (Bóo et al. 1996; Ravi and D'Odorico 2009), homogenizing the distribution of the vegetation (Rostagno et al. 2006). However, Peter et al. (2013) did not found evidence that support the benefits of this practice. On the contrary, it may potentially trigger an erosive process leading to desertification (Ravi et al. 2010).

The regional differences in climate and evolutionary history cause large scale changes, and also changes in soil nutrients, microclimate, and seed and plants distribution at the microsite level (Bisigato et al. 2009). The heterogeneity generated by the patch structure is more complex than the patch-interpatch dichotomy, inducing changes in the soil seed bank density and composition (Caballero et al. 2008). Changes in the shrub canopy promoted by grazing or wind erosion cause an anisotropic development in vegetation patches following the predominant wind direction (Ares et al. 2003; Aerts et al. 2006; Bisigato et al. 2009). In addition to these processes that promote vegetation heterogeneity, wind and rain may cause that the microsites in the patches become heterogeneous as well. Particles such as leaves and small stems can enter in a wind "tunnel" and deposited at the leeward side of the patch (Whitford 2002). These processes might have an impact on the nurse effect of the shrubs along a windward–leeward transect.

In arid and semiarid systems of Argentina, such as the southern Monte desert, several studies analysed the soil seed bank (Bertiller 1992, 1998; Bisigato and Bertiller 1999; Fernández et al. 2002; Mayor et al. 2003; Pazos and Bertiller 2008; Bertiller and Ares 2011; Franzese et al. 2015). The results and generalizations that can be made from previous studies vary because they focused on different species, functional groups, land use histories and/or microsites. The study of the horizontal distribution of the seed bank is extremely important for securing a reliable method to estimate seed bank density from samples that are taken randomly (Thompson 1986). To generate a better understanding of the soil seed bank, we designed a study to analyse the changes in different microsites according to the dominant wind direction and different land use histories at the same time, involving different functional groups and their main species.

According to the previous information and the study objectives, we tested three hypotheses: (1) Grazing by domestic livestock, an "exogenous" disturbance that promotes loss of vegetation and soil cover at interpatches, promotes shrub facilitation over the abundance of the soil seed bank, decreasing in the windward side of the patch and increasing in the leeward side; (2) Post-fire erosion, an "endogenous" disturbance that redistributes propagules from the patches to the interpatches, homogenizes the differences between the windward and leeward sides of the patch and masks the nurse effect of the shrub; (3) Grazing diminishes the reproductive performance of perennial species, with negative effects on the soil seed bank of perennial grasses and positive effects on the soil seed bank of annual plants. On the other hand, the recovery of perennial grasses cover in burnt sites enhances its soil seed bank abundance.

Materials and methods

Study area

The study area is in the department of Adolfo Alsina (40°40′S, 64°10′W), Río Negro province, Argentina, and the vegetation is representative of the Patagonian Monte. The

climate is subtemperate dry, with warm summers (mean temperature 24 °C) and mild winters (mean temperature 7 °C). Mean annual precipitation is around 255 mm, with high variability within and between years. A moderate northwesterly wind occurs throughout the year (Godagnone and Bran 2009). Soils are Aridisols. Vegetation in the area is characterized by shrubland steppe, corresponding to the Monte Phytogeographical Province, South District, North Patagonia Sub-district (Roig et al. 2009); with a herbaceous layer of predominantly winter-growing grasses. This community is dominated by *Larrea divaricata*, *Chuquiraga erinacea* and *Condalia microphylla* in the shrub layer, and *Nassella tenuis* in the herbaceous layer. Other shrubs, e.g. *Prosopis flexuosa* var. *depressa*, *Senna aphylla*, *Lycium chilense*, *Monttea aphylla*, *Schinus johnstonii* and *Ephedra ochreata* can be found in the area. The perennial grasses *Poa ligularis*, *Piptochaetium napostaense*, *Jarava plumosa*, *Pappostipa speciosa*, *Nassella longiglumis* (=*N. clarazii*), and the annual species *Schismus barbatus*, *Erodium cicutarium* and *Daucus pusillus* (Cabrera 1971) are also commonly found in the herbaceous layer. The study area has almost 100 years of livestock grazing history, with an average stocking rate of ≈ 0.18 sheep ha^{-1} (Peter et al. 2013).

Sampling design

The study area was 30×10 km of a vegetation unit which comprised several ranches with different land uses. Seven sites with different land use histories related to grazing and fire were selected using the judgment employed by Peter et al. (2013):

- Heavily-grazed site (HG): grazed by sheep at an average stocking rate, but located ≤600 m from the water point.
- Moderate-grazed site (MG): grazed by sheep at an average stocking rate, but located ≥2500 m from the water point.
- Ungrazed site (UG): located near a railway from which domestic livestock had been excluded for over 50 years.
- Recently burned site (B7): burned in 2007 (6 years before sampling) which remained grazed by sheep at the average stocking rate, but located ≥2500 m from the water point.
- Burned ungrazed site (BU): burned in 2002 (11 years before sampling) excluded to livestock after the fire.
- Burned grazed site (BG): burned in 2002 (11 years before sampling) which remained grazed by sheep at the average stocking rate, and located ≤600 m from the water point.
- Long ungrazed and grazed site (LU): excluded to livestock for more than 40 years, and overgrazed by sheep at a normal stocking rate for 1 year but without sufficient recovery periods in 2008 (5 years before sampling), being severely deteriorated at that time.

Three years after the fire of 2002, a 5 years drought event took place, and mean annual rain ranged from 35 to 75% of the average value (Funk et al. 2012). HG and MG were included in the same paddock, but were 2000 m apart from each other. So, grazing intensities of these sites were selected using piospheres (Bisigato and Bertiller 1997; Washington-Allen et al. 2004; D'Odorico et al. 2013), which are radial grazing gradients created in arid lands from the water point. UG was located at <100 m from MG, and surrounded by a wire fence to exclude it from livestock grazing. The burned sites (BG and BU) were separated by fence.

Previous studies at these sites had provided information about species frequency for the same land use histories, so this information can be taken as a lead towards understanding

the general structure of each community. These studies showed a high frequency of *P. ligularis* in ungrazed sites and a high frequency of *N. tenuis* and *P. lanuginosa* under grazing conditions (Peter et al. 2013). After the occurrence of fire, the frequency of the shrub *L. divaricata* decreased, whereas the preferred grass, *Pappophorum caespitosum,* increased. On the other hand, under grazing conditions (and without fire) shrubs with dense canopies, such as *C. erinacea* tend to be replaced by species with open canopies like *L. divaricata* (Peter et al. 2013). Considering the previous information and general knowledge of the study site, we established a gradient from the highest to lowest disturbance:

$$HG > MG > B7 > BG > BU > LU > UG$$

To study the soil seed bank (SSB), five shrubby patches with a radius greater than 1 m were chosen randomly at each land use history paddock. Seven microsites were located on each patch along an east-to-west (leeward–windward) transect, establishing one microsite at the side of the trunk of the shrub, two on the shrub edges, two at middle distances between the edges and the trunk, and two in interpatch areas at the same distance from the edge as the middle microsites (n = 35) (Fig. 1).

Soil samples were taken at two different seasons to ensure that seeds from the diverse functional groups were released but not germinated. Samples were taken in mid spring (November 2012) for the annual winter species and at the end of summer (April 2013) for perennial grasses. One soil sample was taken from each microsite using a 5 cm deep, 10 cm diameter open-ended soil corer. Samples included litter. Previous studies in similar arid systems suggest that the largest portion of the SSB is located in the first three cm of the soil (Pazos and Bertiller 2008; Caballero et al. 2008). Each sample was washed and sieved with a 0.5 mm sieve (500 μm), dried in a stove at 55 °C on textile bags and store in plastic containers in a dry and dark place. Samples were observed under a stereoscopic microscope and all seeds/fruits were removed manually, identified to the species level (when possible) and counted. Only potentially viable seeds were included in the analysis, that is, firm seeds that resisted the application of light pressure (Bertiller and Aloia 1997; Mayor et al. 2003; Tuesca et al. 2004). As all fruits found on the samples were uniseminate, we will refer to them as seeds from now on.
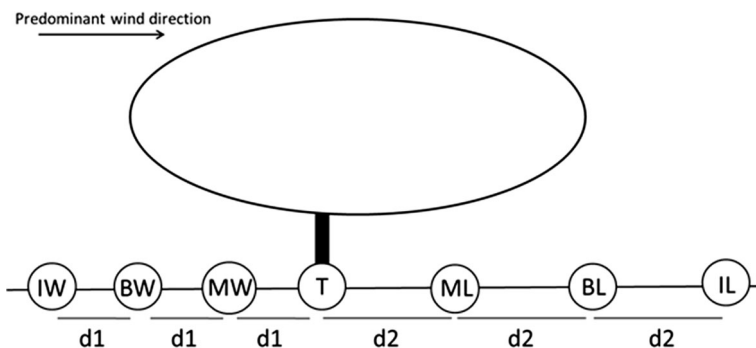
Fig. 1 Selected microsites related to a shrub. *I* interpatch, *B* border, *M* middle, *T* trunk, *W* windward, *L* leeward, *d* distance

Statistical analyses

As few species were consistent in their appearance in the SSB between and within sites, statistical analyses were carried out over species data summed up into two functional groups: perennial grasses and annual herbs + grasses (annuals). The shrubs + dwarf shrubs functional group was not analysed because data were scarce.

We estimated richness and Shannon–Weaver diversity index of the SSB. Their confidence intervals were estimated using the bootstrap method of corrected percentiles ($\alpha = 0.05$, 500 randomizations), and statistical differences were assumed when confidence intervals did not overlap (Pla and Matteucci 2001; Pla 2006). To identify the dominant species of each functional group in the SSB, Student's t tests were performed comparing the media per patch of the two species with the highest number of seeds on each land use history. When data did not met the normality requirement Wilcoxon's test was used.

Differences between sites and microsites were analysed using ANOVA (F). Homoscedasticity was tested using a Levene test and data were transformed when needed in order to meet this requirement. Data which did not comply with ANOVA requirements (whether transformed or untransformed) were analysed using a Kruskal–Wallis nonparametric test (H) to compare mean values. Tukey test was used to determine the significance of the differences between variables ($\alpha = 0.05$) when ANOVA or Kruskall Wallis results were significant.

All the statistical analyses were carried out using InfoStat software (Di Rienzo et al. 2011).

Results

Seeds from 36 species were found in the SSB: eight perennial grasses, 15 shrubs and dwarf shrubs, and 13 annual species (of which, four were non-native) (Table 1). Perennial grasses SSB showed the highest diversity in the ungrazed sites with low or null disturbances, and the lowest in HG and BG (Fig. 2a). Annual species diversity showed an almost inverse response (Fig. 2b). Perennial grasses richness showed the highest values in the sites that were: ungrazed and undisturbed, had a low disturbance or were recently burned (Fig. 2a). Annuals richness showed similar values between the land use histories, except for BG where it was slightly higher than MG, HG and LU (Fig. 2b).

Perennial grasses

The most abundant perennial grass species in the SSB was *Nassella tenuis* in all the grazed sites (being the only perennial grass species in HG) (Table 1). The ungrazed sites with disturbances (BU and LU) showed a co-dominance between *N. tenuis* and *Poa* spp. Meanwhile, in the ungrazed site without disturbances (UG) the most abundant grass species was *Poa* spp. (Table 1). *Poa* spp. includes *Poa ligularis* and *Poa lanuginosa*, both are forage perennial grasses and their seeds cannot be distinguished from each other.

Comparisons between microsites did not showed any significant differences in the SSB of perennial grasses on any land use history. However, comparisons between land use histories showed different results depending on the microsite from which they were made (Table 2). As a general trend (without separating the analysis by microsite), the lowest abundance of perennial grass in the SSB was observed in grazed sites that were not burned

Table 1 Soil seed bank composition in sites with different land use histories: mean values of seeds m^{-2} ± EE for each functional group (italic values) and for all species found in the soil seed bank

	UG	LU	BU	BG	B7	MG	HG
Perennial grasses	*345.71 ± 143.62*	*414.29 ± 88.15*	*415.24 ± 138.95*	*103.81 ± 24.09*	*300.0 ± 62.11*	*9.52 ± 3.76*	*5.71 ± 2.15*
Bromus spp.	4.76 ± 2.78	2.86 ± 2.86	0.95 ± 0.95		0.95 ± 0.95		
Jarava plumosa		0.95 ± 0.95			0.95 ± 0.95		
Melica sp.	1.9 ± 1.9	0.95 ± 0.95			5.71 ± 2.89		
Nassella longiglumis	0.95 ± 0.95	1.9 ± 1.33			2.86 ± 1.6	0.95 ± 0.95	
Nassella tenuis	12.38 ± 4.12	**233.33** ± 6.96	**188.57** ± 26.39	**96.19** ± 23.93	**257.14** ± 55.55	**7.62** ± 3.37	**5.71** ± 2.15
Unidentified perennial grasses		4.76 ± 2.42					
Piptochaetium napostaense			0.95 ± 0.95				
Poa spp.	**325.71** ± 143.57	**169.52** ± 64.33	**224.76** ± 129.46	7.62 ± 3.89	32.38 ± 14.56	0.95 ± 0.95	
p	<0.0001	0.426	0.785	<0.0001	<0.0001	0.0468	0.011
Statistic	W = 1658.5	t = −0.801	t = 0.274	W = 897.5	W = 825.0	W = 1154.5	W = 1137.5
Shrubs + dwarf shrubs	*144.76 ± 29.28*	*36.19 ± 24.69*	*9.52 ± 3.76*	*36.19 ± 20.88*	*20.0 ± 7.51*	*29.52 ± 8.51*	*6.67 ± 2.66*
Unidentified asteraceae		0.95 ± 0.95					
Baccharis spp.	2.86 ± 1.6	0.95 ± 0.95		0.95 ± 0.95	3.81 ± 2.98	8.57 ± 3.95	0.95 ± 0.95
Boopis anthemoides	17.14 ± 9.5		1.9 ± 1.33		3.81 ± 3.81		
Brachyclados lycioides	0.95 ± 0.95						
Chuquiraga erinaceae	1.9 ± 1.33	1.9 ± 1.33	1.9 ± 1.33			1.9 ± 1.33	
Condalia microphylla	1.9 ± 1.33	20.95 ± 14.34			2.86 ± 1.6	3.81 ± 2.27	
Ephedra spp.		1.9 ± 1.9					
Grindelia brachystephana					2.86 ± 2.86		

Table 1 continued

	UG	LU	BU	BG	B7	MG	HG
Gutierrezia gilliesii					0.95 ± 0.95		
Hysterionica jasionoides	19.05 ± 8.67						5.71 ± 2.55
Larrea spp.						13.33 ± 4.96	
Margyricarpus pinnatus	77.14 ± 20.62		2.86 ± 1.6	33.33 ± 20.95	0.95 ± 0.95		
Monttea aphylla	7.62 ± 5.13	1.9 ± 1.9		0.95 ± 0.95	0.95 ± 0.95	0.95 ± 0.95	
Schinus johnstonii	16.19 ± 6.88	7.62 ± 7.62	0.95 ± 0.95		3.81 ± 1.82	0.95 ± 0.95	
Senecio melanopotamicus			1.9 ± 1.9	0.95 ± 0.95			
Annual	845.71 ± 126.0	654.29 ± 166.36	4290.48 ± 1097.32	3553.33 ± 643.23	7680.0 ± 1760.82	15 541.9 ± 1875.18	5563.81 ± 894.93
Dicotyledoneae							
Bowlesia incana	9.52 ± 7.68	12.38 ± 4.55	0.95 ± 0.95	6.67 ± 4.69	0.95 ± 0.95	739.05 ± 434.44	1985.71 ± 690.41
Daucus pusillus	**581.91** ± 91.06	12.38 ± 4.55	72.38 ± 30.63	29.52 ± 7.94	28.57 ± 10.77	87.62 ± 29.34	
Erodium cicutarium[a]	9.52 ± 2.92	74.29 ± 24.64	15.24 ± 7.01	14.29 ± 5.84		30.48 ± 12.99	27.62 ± 7.67
Galium richardianum	0.95 ± 0.95	21.9 ± 11.43	32.38 ± 14.49	41.9 ± 24.19	0.95 ± 0.95	6.67 ± 3.82	
Gamochaeta spp.	6.67 ± 2.99	1.9 ± 1.33	24.76 ± 10.96	40.95 ± 12.15	152.38 ± 57.93	1111.43 ± 481.62	530.48 ± 161.13
Hemiaria cinerea[a]	42.86 ± 19.55		144.76 ± 43.1	**1553.33** ± 326.65	7.62 ± 5.13	**13** 253.33 ± 1785.01	560 ± 227.92
Medicago minima[a]		0.95 ± 0.95					
Micropsis australis							0.95 ± 0.95
Pelletiera verna	5.71 ± 2.15	**447.62** ± 137.19	**3981.9** ± 1099.06	**1798.1** ± 395.79	**5546.67** ± 1581.31	1.9 ± 1.9	3.81 ± 2.27
Plantago patagonica	141.9 ± 37.26	22.86 ± 9.93	5.71 ± 2.15	21.9 ± 6.55	34.29 ± 16.02		0.95 ± 0.95
Spergula ramosa	0.95 ± 0.95	72.38 ± 48.32	2.86 ± 2.1	35.24 ± 15.34	2.86 ± 1.6		
Monocotyledoneae							

Table 1 continued

	UG	LU	BU	BG	B7	MG	HG
Hordeum sp.				0.95 ± 0.95	5.71 ± 4.83	34.29 ± 16.71	2.86 ± 1.6
Schismus barbatus[a]	45.71 ± 43.77		9.52 ± 5.39	10.48 ± 4.05	**1900** ± 925.34	277.14 ± 54.07	**2451.43** ± 328.67
p	<0.0001	0.0014	0.0069	0.635	<0.0001	<0.0001	0.0013
Statistic	W = 1617.0	W = 983.5	W = 1017.0	t = −0.477	W = 1641.0	W = 710.5	W = 969.5

Land use histories are arranged from the lowest to the highest disturbed sites. The statistic value for the comparison between the two more abundant species in the perennial grasses and annual species is below each group (p < 0.05, t = Student's t test, W = Wilcoxon test), bold numbers indicate the dominant species of each group

UG ungrazed site, *LU* ungrazed for a long period then grazed site, *BU* burned ungrazed site, *BG* burned grazed site, *B7* burned in 2007 and grazed site, *MG* moderate grazed site, *HG* heavily grazed site

[a] Non-native species
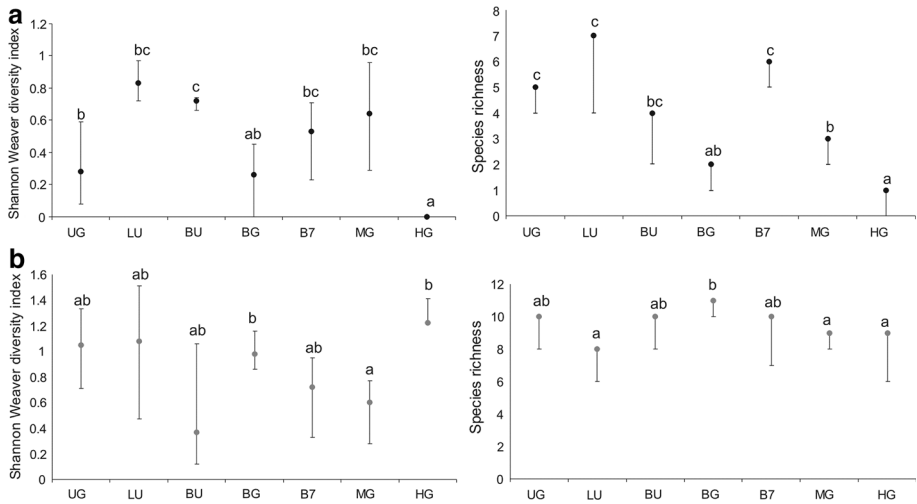
Fig. 2 Shannon Weaver diversity index and species richness of the soil seed bank of perennial grasses (**a**) and annual species (**b**) for each land use history. Land use histories are arranged from the lowest to the highest disturbed sites. *UG* ungrazed site, *LU* ungrazed for a long period then grazed site, *BU* burned ungrazed site, *BG* burned grazed site, *B7* burned in 2007 and grazed site, *MG* moderate grazed site, *HG* heavily grazed site

(MG and HG). Meanwhile, the more abundant perennial grass SSB was found in all the ungrazed sites and in the recently burned grazed site (UG, LU, BU and B7).

Perennial grass SSB differences between land use histories showed the same trend on windward microsites, agreeing with the general trend in the land use histories previously described (Table 2). The only exception was the ungrazed undisturbed site (UG), which showed an abundant perennial grass SSB at the windward border that differed from all grazed sites except the recently burned one (B7). At the trunk microsite, ungrazed sites with disturbance (BU and LU) showed a more abundant perennial grass SSB than the highly grazed site (HG). The leeward microsites showed the same differences as the windward microsites, except for the interpatch where the ungrazed undisturbed site showed an intermediate SSB but larger than in the medium grazed unburned site (MG) (Table 2).

By excluding the land use histories with a mean perennial grass SSB with less than 50 seeds m^{-2} from the analysis, significant differences between microsites were observed. The middle microsite on leeward side had a larger perennial grass SSB than both borders and interpatches microsites (p = 0.0238, H = 14.46) (Fig. 3a).

Annuals

The annual plants SSB was dominated by native species in the ungrazed and in the recently burned site and by non-native in the grazed unburned sites, with a co-dominance of native and non-native species in those with an medium disturbance (Table 1).

The annual plant SSB only showed significant differences between microsites in UG (Table 3), where the highest abundance in the SSB was found in the trunk and ML, and the lowest in IW and MW (p < 0.0001, F = 6.055, data transformed to square root) (Fig. 3b).

Table 2 Mean values of seeds of perennial grasses in the soil seed bank in general and on each microsite (seeds m^{-2} ± EE) in sites with different land use histories

Land use histories	General	Microsites							Microsites comparisons		
		IW	BW	MW	T	ML	BL	IL	p	Statistic	Transf
UG	345.66 ± 144.66 B	153.33 ± 107.81 AB	173.33 ± 26.67 C	200 ± 94.87 B	400 ± 163.64 ABC	1286.67 ± 949.65 B	80 ± 24.94 AB	126.67 ± 55.18 BCD	0.4176	H = 5.97	
LU	414.33 ± 165 B	273.33 ± 153.26 B	313.33 ± 154.78 C	340 ± 90.92 B	886.67 ± 431.61 BC	620 ± 250.91 B	393.33 ± 222.71 B	73.33 ± 58.12 ABC	0.264	F = 1.362	sq rt
BU	415.33 ± 176.66 B	166.67 ± 52.7 B	153.33 ± 62 BC	313.33 ± 121.38 B	1360 ± 853.32 C	593.33 ± 305.58 B	180 ± 73.48 B	140 ± 38.59 CD	0.054	F = 2.393	sq rt
BG	103.6 ± 43 AB	100 ± 60.55 AB	6.67 ± 6.67 AB	133.33 ± 48.3 AB	166.67 ± 134.58 ABC	126.67 ± 46.43 AB	100 ± 43.46 AB	93.33 ± 50.99 ABCD	0.431	F = 1.023	
B7	300 ± 89.33 B	213.33 ± 134.41 B	255.33 ± 136.87 ABC	493.33 ± 274.55 B	106.67 ± 33.99 ABC	406.67 ± 237.21 B	173.33 ± 61.82 B	453.33 ± 149.29 D	0.573	F = 0.807	
MG	9.66 ± 3.33 A	6.67 ± 6.67 A	0 ± 0 A	0 ± 0 A	26.67 ± 12.47 AB	26.67 ± 19.44 A	6.67 ± 6.67 A	0 ± 0 A	0.1284	H = 4.81	
HG	5.66 ± 2.66 A	0 ± 0 A	6.67 ± 6.67 AB	0 ± 0 A	6.67 ± 6.67 A	13.33 ± 8.16 A	6.67 ± 6.67 A	6.67 ± 6.67 AB	0.6891	H = 1.67	
p		0.0215	0.0064	0.004	0.003	0.0032	0.0225	0.0125			
Statistic	H = 24.07	H = 13.81	H = 15.85	H = 18.11	F = 4.524	H = 19.36	H = 14.06	H = 14.67			
Transf					sq rt						

Land use histories are arranged from the lowest to the highest disturbed sites. Different letters indicate significant differences in soil seed bank abundance between sites ($p < 0.05$, F = ANOVA, H = Kruskal–Wallis), cells are colored with different shades of grey as a visual key

Transf data transformation (*Sq rt* square root), *I* interpatch, *B* border, *M* middle, *T* trunk, *W* windward, *L* leeward, *UG* ungrazed site, *LU* ungrazed for a long period then grazed site, *BU* burned ungrazed site, *BG* burned grazed site, *B7* burned in 2007 and grazed site, *MG* moderate grazed site, *HG* heavily grazed site

Comparing the different land use histories, the largest annuals SSB was observed in the more disturbed sites (B7, MG and HG) and the smallest in the less disturbed ones (Table 3).

Comparing land use histories in each microsite, MG showed a higher annual SSB than ungrazed sites in all microsites except in the trunk microsite which did not show any significant differences between sites (Table 3). The differences between land use histories observed in the leeward microsites were more marked than in the windward microsites, especially in the leeward interpatch, where sites that showed an intermediate SSB in other microsites were significantly different.

Discussion

The perennial grass SSB diversity and richness were enhanced by the exclosures but were higher when the site had some disturbance, this may show that under undisturbed conditions one species dominates over the others, decreasing grass diversity. Nevertheless, severe grazing conditions reduce grass diversity up to its minimum, which shows that only few species could resist this kind of disturbance in the Monte system.

All land use histories showed similar annuals species richness, but the diversity was different between sites, showing changes in species dominance, as can be observed in Table 1. The differences in species abundance depended of the land use history, and this may imply that all the annual species can develop under different disturbances, but the reproductive success of non-native annuals is greater under higher disturbances.

Studies in similar systems also showed a low abundance of the shrub SSB (Bertiller 1998; Franzese et al. 2015). The SSB formation is a strategy that gives an advantage to short living species that can seek some sort of benefit out of disturbances, which could explain why shrubs may not be well represented in the SSB. Moreover, the large size of their seeds makes them prone to predation and makes their burial more difficult (Bertiller 1998; Fenner and Thompson 2005).

Perennial grass SSB

The results did not support our first hypothesis about the nurse effect of shrubs on the SSB, as we did not find any significant differences between the microsites in the land use histories studied. This might be a result of a high variability among samples, as is common in arid zones (Maestre and Cortina 2005), which hindered the statistical analysis in showing significant differences. When data from land use histories with a mean SSB >50 seed m^{-2} were pooled together (enhancing n), statistical tests were able to find significant differences. The general trend observed among microsites shows a nurse effect of shrubs on SSB formation or maintenance. However, contrarily to our hypothesis, it seems that shrubs might act as nurses over the SSB abundance in ungrazed and/or burned sites. Under unburned continuous grazed sites the identification of facilitation processes is very difficult because the low plant cover in the interpatches promotes a higher seed wind loss (Marone et al. 1998a). The low SSB abundance in the interpatches was observed in other similar systems (Aguiar and Sala 1997; Bertiller 1998; Fernández et al. 2002; Caballero et al. 2008). Differences found in the SSB between microsites were associated with the horizontal seed movement caused by the wind, even if seeds are provided with anchorage mechanisms (Pazos and Bertiller 2008). On the other hand, previous studies in the same
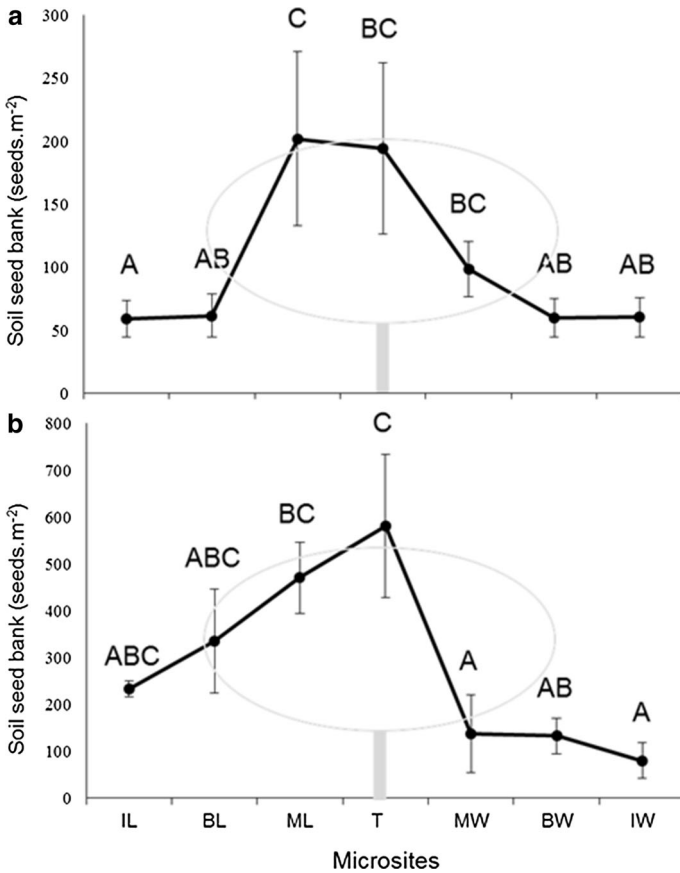
Fig. 3 Mean soil seed bank abundance among different microsites (mean ± EE). **a** Perennial grasses mean soil seed bank excluding sites with less than 50 seeds m^{-2} (MG and HG). **b** Annual plants mean soil seed bank in the ungrazed undisturbed site (UG). *Different letters* indicate significant differences between microsites (p < 0.05). *I* interpatches, *B* border, *M* middle, *T* trunk, *L* leeward, *W* windward

area showed a homogeneous seed rain, without any differences between interpatches and the middle canopy microsite. In that study predominant wind effects were not considered (Leder et al. 2015). So, the nurse effect related to the predominant wind on the differential formation or maintenance of the SSB is evident and depends on the microsite.

These results showed that nurse effects on SSB promote a heterogeneous under-canopy spatial distribution in arid shrublands with moderated disturbances. This heterogeneity must be taken into account when SSB studies are carried out. In many of the previous studies in similar shrublands sampling was random (Aguiar and Sala 1997; Pazos and Bertiller 2008; DeFalco et al. 2009; Moreno-de las Heras et al. 2016) or focused on the patch-interpatch dichotomy (Bertiller 1998; Bisigato and Bertiller 1999; Mayor et al. 2003; Rolhauser et al. 2013; Franzese et al. 2015), without specifications of the under-canopy microsite from which the SSB samples were collected (distance from the trunk and orientation related to the predominant wind direction).

The scarce perennial grass SSB found under grazing conditions agrees with the description of Leder et al. (2015) for the perennial grasses seed rain in the same land use

Table 3 Mean annual plants abundance in the soil seed bank in general and by microsite (seeds m^{-2} ± EE) in sites with different land use histories

Land use histories	General	Microsites							Microsites comparisons		
		IW	BW	MW	T	ML	BL	IL	p	F	Transf
UG	845.71 ± 126 AB	240 ± 114.21 A	400 ± 114.02 A	413.33 ± 246.89 A	1746.67 ± 457.85 A	1413.33 ± 227.69 A	1006.67 ± 331.73 A	700 ± 52.7 AB	<0.001	F=6.055	sq rt
LU	654.29 ± 166.36 A	326.67 ± 182.7 A	366.67 ± 181.66 A	400 ± 224.1 A	1053.33 ± 659.76 A	853.33 ± 407.79 A	1260 ± 823.23 A	320 ± 133.58 A	0.702	F=0.634	sq rt
BU	4290.48 ± 1097.32 BC	3406.67 ± 2221.15 AB	2220 ± 1231.78 AB	6666.67 ± 4264.86 AB	7206.67 ± 4936.64 A	4000 ± 2476.09 AB	4260 ± 2793.69 A	2273.33 ± 1689.88 AB	0.863	F=0.414	
BG	3553.33 ± 643.23 CD	2526.67 ± 847.18 AB	4413.33 ± 2267.81 AB	4053.33 ± 3043.35 AB	3453.33 ± 1555.37 A	3020 ± 1536.68 AB	3880 ± 1264.63 AB	3526.67 ± 1582.45 BC	0.993	F=0.119	
B7	7680.0 ± 1760.82 D	5626.67 ± 3468.74 AB	3773.33 ± 1901.91 AB	3920 ± 1230.52 AB	9286.67 ± 3346.47 A	8220 ± 4889.12 ABC	9846.67 ± 7582.76 AB	086.67 ± 7557.21 BC	0.934	F=0.295	sq rt
MG	15 541.9 ± 1875.18 E	9240 ± 4477.45 B	10 406.67 ± 3585.83 B	18940 ± 5645.68 B	11 480 ± 4630.15 A	26 406.67 ± 5512.01 C	16 853.33 ± 3553.47 B	15 466.67 ± 5149.62 C	0.184	F=1.602	
HG	5563.81 ± 894.93 D	3006.67 ± 1199.79 AB	3133.33 ± 1103.58 AB	5066.67 ± 1563.33 B	11 093.33 ± 3945.38 A	8173.33 ± 2861.34 BC	5613.33 ± 1903.46 AB	2860 ± 909.91 BC	0.098	F=2.010	
p	<0.0001	0.002	0.004	<0.0001	0.0531	0.0055	0.0197	0.0055			
Statistic	H=107.78	H=18.28	H=15.06	H=18.31	H=12.42	F=6.579	F=4.138	F=4.66			
Transf						ln(x+1)	ln(x+1)	ln(x+1)			

Land use histories are arranged from the lowest to the highest disturbed sites. Different letters indicate significant differences in soil seed bank abundance between sites ($p < 0.05$, F = ANOVA, H = Kruskal–Wallis), cells are colored with different shades of grey as a visual key

Transf data transformation (*sq rt* square root), *I* interpatch, *B* border, *M* middle, *T* trunk, *W* windward, *L* leeward, *UG* ungrazed site, *LU* ungrazed for a long period then grazed site, *BU* burned ungrazed site, *BG* burned grazed site, *B7* burned in 2007 and grazed site, *MG* moderate grazed site, *HG* heavily grazed site

histories. Logically, a scarce seed rain will result in a small SSB. So, these results support the idea of the negative effect of cattle on SSB formation and maintenance (Chambers 2000; Caballero et al. 2008). The higher seed availability in ungrazed sites was observed in the seed rain by Leder et al. (2015) and other authors on SSB (Mayor et al. 2003).

Studies with controlled fires showed a higher cover of desirable perennial grasses 5 years after the occurrence of the fire, probably with a higher water, light and/or nutrients use as a result of the reduction of woody plants cover (Peláez et al. 2010). This may be reflected in the seed production and may explain that burned sites showed a SSB similar to the less disturbed sites, especially when fire occurred recently (6 years before sampling).

The perennial grass SSB was dominated by *Poa* spp. in the ungrazed undisturbed site and by *N. tenuis* in the grazed unburned sites. These findings agree with that described by Leder et al. (2015) for the seed rain in the same sites and by Mayor et al. (2003) in the SSB of the Caldenal. Nevertheless, in the burned places with 10 years recovery, the dominant species varies between the seed rain and the SSB. In the ungrazed burned site the seed rain was dominated by *P. speciosa* (Leder et al. 2015), a less preferred grass. The fact that *P. speciosa* was not represented in the SSB agrees with studies in other ecosystems (Ghermandi 1997; Mayor et al. 2003; Pazos and Bertiller 2008) where its domain in the herbaceous stratum was not reflected in the SSB. This could be explained because the species produces large seeds which may be preferred by insects (Fenner and Thompson 2005), birds and rodents (Marone et al. 1998b, 2000), and this may mean that only a small amount remains available for entering the SSB. In the grazed burned site with 10 years recovery (BG) the seed rain was dominated by *Poa* spp. (Leder et al. 2015), although *N. tenuis* was dominant in the SSB. This can be explained by the low dispersal capacity of seeds of *Poa* spp. (Pazos and Bertiller 2008) that may make it difficult for a horizontally homogeneous SSB formation that allows a stronger representation of this species in all samples and, also, by remaining close to the mother plant it can enhance the risk of seed predation (Fenner and Thompson 2005). Also, seeds of *Poa* spp. have trichomes that allow its anchorage to the soil surface, but also to other elements, such as branches and leaf litter, which may make its entrance into the SSB difficult. Nevertheless, if the anchorage secures the *Poa* spp. seeds to the soil surface, they do not have a mechanism to promote burial and, then, its addition to the SSB. We must incorporate the negative effect of cattle over grasses with few and dense floriferous stems with a lot of seeds into the equation (O'Connor and Pickett 1992), as this species, and the negative effects of grazing on the cover, density and frequency of *P. ligularis* in similar systems (Bóo et al. 1993; Mayor et al. 2003; Morici et al. 2006; Funk et al. 2012; Peter et al. 2013; Franzese et al. 2015). *Nassella tenuis* is, however, a naturally abundant species under disturbances (Fernández et al. 2009; Peter et al. 2013) and its seeds have a higher dispersal capacity as the result of a long spiraled and geniculated awn, and an efficient anchorage and burial mechanism composed of a combination between the awn and a sharp tip (O'Connor 1991; Chambers 2000). These characteristics of *N. tenuis* may result in an overall advantage over the *Poa* spp. when it comes to dispersal and entry into the SSB.

The general trend observed among the perennial grass SSB of different land use histories was different according to the microsite from which the sample was taken. Thereby, while the ungrazed undisturbed site showed a high SSB abundance as a general trend, analysis by microsites showed that this abundance occurred in BW, ML and IL. These results are important as they highlight that nurse effects might promote a high SSB horizontal heterogeneity, which could generate results that may not be trustworthy and may not accomplish the objectives of SSB studies in arid ecosystems.

Annual species SSB

As annual species respond to the changes in resources availability and these changes are frequently caused by disturbances (Beever et al. 2006), the differences in the annuals SSB between land use histories reflected the intensity of the disturbance in each site, with an increase in seed abundance that follows the disturbance intensity.

Thus, the annuals SSB abundance supported our third hypothesis and the disturbance gradient that we pointed out: sites with a long land use history involving a continuous disturbance such as grazing or with a severe disturbance like fire and little recovery time under grazing, seem to behave like sites with "strong" disturbances with an abundant SSB of annual species. On the other hand, sites with more years of post-fire recovery seem to show an "intermediate" disturbance when grazed and a "low" disturbance when ungrazed. Meanwhile, sites with many years of cattle exclosure or with long periods of rest before and after the impact of a disturbance like grazing also seem to represent "low" disturbance situations. Moreover, the annuals SSB in sites with high and intermediate disturbances, partially or totally dominated by non-native species, reinforces the disturbance intensity proposal. This could be explained by the characteristics of annual species that turns into invaders on account of their short life cycles with an early maturity, their elevated amount of seeds of a small size, their high dispersal capacity and their seeds with shapes that facilitate their entry into the SSB (Fenner and Thompson 2005; Venable et al. 2008; Franzese et al. 2015).

Several studies described an increase of *S. barbatus* and other non-native annuals (as *Herniaria cinerea*) under grazing conditions (Distel and Bóo 1995; Mayor et al. 2003; Pucheta et al. 2011; Busso et al. 2016), and Cano (1988) proposed the presence of these species as indicators of poor grazing management. The dominance of *Pelletiera verna* in burned sites may be explained since its seeds are less vulnerable to fire damage as they have a small surface/volume ratio (Fenner and Thompson 2005). There is not much previous information about *D. pusillus*, the species that dominates the ungrazed undisturbed site. It is not considered as a forage herb, and Morici et al. (2003) only found this species at a distance of 2000–2500 m from the water point, which may indicate that, although it is not consumed by cattle, it is negatively affected by them. This can explain the high abundance of *D. pusillu*s in the SSB of the ungrazed undisturbed site.

Comparisons between land use histories on each microsite showed that on the windward side, the moderately grazed site had a larger annuals SSB than the sites with low disturbances sites. The site with the highest disturbance did not differ from any land use history at the windward interpatch and border, and this can be explained by the high exposition of these microsites to the predominant winds as the bare soil areas are larger under this disturbance (Fuls 1992; Allington and Valone 2013), allowing a higher wind speed. Under this severe disturbance the SSB formation will be compromised, not because of low seed availability, but due to the complications for seed anchorage to the microsites soil surface and for SSB entry in soils highly compacted by cattle trampling (Fuls 1992). The trunk microsite showed that the microenvironment at the centre of the shrub canopy was similar among land use histories when it comes to annuals SSB maintenance. At the leeward side, the differences among land use histories were similar to the windward side, except for the interpatch, in which the grazed and burned sites also had larger annuals SSB than the disturbed ungrazed site. These results may indicate that after a fire, the leeward interpatch gains some balance between a disturbed and a safe site for annual plant establishment, that later enhance annuals SSB.

Conclusions

In contrary to our assumptions, higher disturbances did not promote a shrub nurse effect on the formation or maintenance of the SSB. The nurse effect is evident at sites under moderate disturbances or undisturbed, and is depleted when disturbances increase. An important challenge for the conservation of desirable species (e.g. palatable perennial grasses) is to understand which microsite characteristics promote an abundant SSB under each land use history. So, we need to promote land use management that improves the replication of these characteristics at microsites in which the SSB formation or maintenance is scarce. As well as the reproductive performance of plants at different microsites, studies are needed that analyse the differences in SSB formation between microsites and land use histories, to find out if the disturbance affects the entry of seeds into the SSB or its maintenance once they are under the soil surface. If there is a high seed availability, low SSB abundance can be a result of a small amount of seed buried, a high seed mortality, a high germination and seedling mortality, or SSB wind loss.

This study concludes in an outlook of concern, as sites with continuous grazing showed a very small amount of perennial grasses in the SSB. Microsite conditions that do not allow SSB formation or maintenance may also make seedling recruitment and establishment difficult, in which case these grazing systems will mainly depend on the re-sprouting capacity of adults and vegetative reproduction. In the study area, vegetative reproduction does not occur naturally in the grass species, except for *Poa lanuginosa*. On the other hand, non-native annuals are greatly favoured by grazing and, as they are species with a winter cycle, their recruitment dynamics must be studied as they may become strong competitors to perennial grass seedlings, which also have winter germination. The nurse effect over the SSB in the leeward side of the patches will, probably, also promote seedlings emergence. In the light of the SSB knowledge, further studies involving seedling recruitment must be made to confirm that the patch structure has a positive effect on both.

Fire seems to have a positive effect on the perennial grass SSB. Nevertheless, as the soil seed bank displays high interannual variability, further studies should be made in order to know if these changes in seed abundance affect the spatial pattern variation from year to year. On the other hand, fire characteristics must be controlled, as was described in several studies, since high temperatures during fire and post-fire drought conditions can promote plant mortality causing the opposite effect.

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