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Does sheep selectivity along grazing paths negatively affect biological crusts and soil seed banks in arid shrublands? A case study in the Patagonian Monte, Argentina

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A B S T R A C T

Domestic animals potentially affect the reproductive output of plants by direct removal of aboveground plant parts but also could alter the structure and fertility of the upper soil and the integrity of biological crusts through trampling. We asked whether sheep selectivity of plant patches along grazing paths could lead to negative changes in biological crusts and soil seed banks. We randomly selected ten floristically homogeneous vegetation stands distributed across an area (1250 ha) grazed by free ranging sheep. Vegetation stands were differently selected by sheep as estimated through sheep-collaring techniques combined with remote imagery mapping. At each stand, we extracted 15 paired cylindrical soil cores from biological crusts and from neighboring soil without crusts. We evaluated the crust cover enclosed in each core and incubated the soil samples at field capacity at alternating 10–18 °C during 24 months. We counted the emerged seedlings and identified them by species. Sheep selectivity along grazing paths was largest at mid-distances to the watering point of the paddock. Increasing sheep selectivity was associated with the reduction of the cover of biological crusts and the size and species number of the soil seed bank of preferred perennial grasses under biological crusts. The size of the soil seed bank of annual grasses was reduced with increasing sheep selectivity under both crust and no crust soil conditions. We did not detect changes in the soil seed banks of less- and non- preferred species (shrubs and forbs) related to sheep selectivity. Our findings highlight the negative effects of sheep selectivity on biological crusts and the soil seed bank of preferred plant species and the positive relationship between biological crusts and the size of the soil seed bank of perennial grasses. Accordingly, the state of conservation of biological crusts could be useful to assess the state of the soil seed banks of perennial grasses for monitoring, conservation and planning the sustainable management of grazing lands.

1. Introduction

Grazing by domestic animals affects not only the aboveground vegetative tissues of the preferred plants but also their reproductive output through the removal of reproductive tissues and the reduction of seed production (Bertiller, 1992, 1996; Milchunas and Lauenroth, 1993; Paruelo et al., 2008). Moreover, animal trampling may negatively affect the structure of the upper soil layer by destruction of soil aggregates and fragmentation of biological crusts (Belnap and Eldridge, 2003; Du Toit et al., 2009: Scutari et al., 2004). Biological crusts are important in relation to soil surface roughness and protection from erosion, trapping moisture, fixing carbon and nitrogen, and seed retention and entrapment (Belnap, 2003; Belnap and Eldridge, 2003; Belnap et al., 2003; Caballero et al., 2008; DeFalco et al., 2009; Lalley and Viles, 2008; Pietola et al., 2005; Williams et al., 1995; Warren, 2003). Seeds represent an important component of plant regeneration and the source of variation for genetic differentiation and evolution of plants in desert ecosystems (Kemp, 1989). Therefore, both grazing and trampling could conduce to reductions in the size of the soil seed bank, the quality of microsites for plant re-establishment, and the potential for restoration of preferred plants (Bisigato and Bertiller, 2004; Cousens et al., 2008; Pazos and Bertiller, 2008; Yoshihara et al., 2010).

Studies on the impacts of free ranging grazers on vegetation have usually been based on comparisons along gradients from water sources or those induced by other factors of animal concentration like mineral licks or bedding grounds (Pringle and

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Landsberg, 2004; Washington-Allen et al., 2004). The concept of piosphere predicts that areas neighboring watering points would concentrate more animals and would be more degraded than those far away from them. However, decisions by animals along their grazing paths could be related to factors other than the presence of water sources, such as structural features of vegetation or landscape not directly associated with feeding or nutritional issues (Bertiller, 1996; Bertiller and Ares, 2008; Pringle and Landsberg, 2004). Bertiller and Ares (2008) found that visual impairment and anti-herbivore defenses were primary factors inducing sheep selectivity of vegetation patches within paddocks.

Whether non-piospheric, local selectivity along grazing paths could lead to negative changes in biological crusts and soil seed banks is an issue scarcely explored. This information is relevant to identifying sites of potential land degradation in the context of planning sustainable management for arid shrublands. We hypothesized that free ranging domestic grazers negatively affect the potential for restoration of plants preferred by sheep through their selective impact on patches along their grazing paths, independently of piosphere trends. We predicted that grazing selectivity would be negatively related to the cover of biological crusts (prediction 1) and to the size and species number of the soil seed bank of preferred plants (prediction 2), and that grazing selectivity would not affect the number of species and the size of the soil seed bank of non- or less-preferred plants (prediction 3).

2. Methods and materials

The study area (about 48.000 $km^{2)}$ is representative of the Xeromorphic Tall Shrub community of *Larrea divaricata* Cav. and *Stipa spp*. characteristic of the Patagonian Monte (Ares et al., 1990; León et al., 1998). Vegetation covers from 40 to 60% of the soil and consists of a two-phase mosaic formed by plant patches with high plant cover, dominated by shrubs and perennial grasses, alternating with areas of bare soil or scattered plants (Bisigato and Bertiller, 1997). Annual grasses and herbs are a minor component of the plant cover and grow in small patches distributed underneath the external crown or at the border of shrub-grass patch canopies. Biological crusts containing the lichen *Collema coccophorum* Tuck., among other components, are frequent at the external crown or at the border of shrub-grass patches (Scutari et al., 2004). The area has been grazed by free ranging sheep since the beginning of the 20th century. Annual and perennial grasses account for the most preferred plant life forms by sheep (Baldi et al., 2004).

Within the study area, we selected a 1250 ha paddock at Smit's Ranch (42°38′S, 65°23′W) submitted to the usual stocking rate for the area (approximately 0.10 sheep ha^{-1}). We randomly selected ten floristically homogeneous vegetation stands (*sensu* Mueller-Dombois and Ellenberg, 1974) of about 2-ha each across the paddock. Each vegetation stand corresponded to one of six vegetation units identified and mapped in a previous study at the same paddock. At each stand, we visually estimated the cover of woody species and perennial grasses using cover categories with increments of 1% (Bertiller and Ares, 2008). Since annuals and perennial herbs had very low cover and were patchily distributed, we estimated the cover of these plant groups within their patches and weighed the cover by patch abundance. We visually assessed the internal cover and abundance of patches of annuals and perennial herbs in a sub-sample (c.a 0.1 ha) representative of each stand (Bisigato and Bertiller, 1997). Further, we randomly selected fifteen sampling sites at each vegetation stand for sampling the soil seed banks and biological crust covers. At each sampling site, we selected the nearest shrub-grass patch and the largest biological crust located at the patch border. Biological crusts dominated by the lichen *C. coccophorum* Tuck. (ranging from 5 to 20 cm^2) with well defined borders were present at the patch borders of all shrub-grass patches selected. We extracted two cylindrical soil cores (6.5 cm diameter, 2 cm depth), at the center of the biological crust and at the neighboring soil without biological crust (crust/no crust soil conditions, respectively) and we visually estimated the crust cover within each core. We extracted the samples from patch borders since in previous studies these locations were identified as the main regeneration microsites for perennial grasses (Bisigato and Bertiller, 2004). After extraction, we incubated soil samples at field capacity in a climatic chamber during 24 months (lighting period: 12 h, 18 °C; dark period: 12 h, 10 °C) and we stirred them at monthly intervals.

We counted the emerged seedlings and identified them by species at weekly intervals. We used these counts to assess the size and the species number of the soil seed bank by group of preferred plants (perennial grasses, annual grasses) and plants non- or less-preferred by sheep (tall, medium and dwarf shrubs, perennial forbs, annual forbs) (Baldi et al., 2004; Bisigato and Bertiller, 1997). We calculated ($n = 15$) the number of species (mean number of species) and the size (mean seed number dm^{-2}) of the soil seed bank of each plant group under each soil condition (crust/no crust) by stand.

Values of sheep selectivity obtained by Bertiller and Ares (2008) corresponding to the paddock used in this study were calculated from 40,000 records of positions of six ewes harnessed with standard GPS receivers during April 2005 (two ewes), September 2005 (three ewes), and January 2006 (one ewe). The records were overlaid onto the image files of a classified Landsat-7 image of the paddock (six homogeneous vegetation units: *VU*) verified through ground truth sampling. The relative sheep selectivity (*Si*) at each pixel of the image was defined as the ratio:

$$S_i = fp_i/pa_i$$

where fp_i is the frequency of positions of sheep on the image pixel classified as VU_i relative to all recorded positions in the paddock, and pa_i is the fraction of image pixels classified as VU_i in the paddock (see Bertiller and Ares, 2008 for more details).

From these S_i values, we selected those corresponding to the vegetation stands sampled in this study. We used ANCOVA (factor: crust/no crust soil condition; covariate: sheep selectivity) to test the effects of soil condition × sheep selectivity interactions on the size and species number of the soil seed bank. In those cases in which interactions were not significant, we used regression analyses to relate seed bank traits (size, species number) to sheep selectivity and crust cover. We used Oneway ANOVA or Mann Whitney *U* test (when assumptions of ANOVA were not met) to

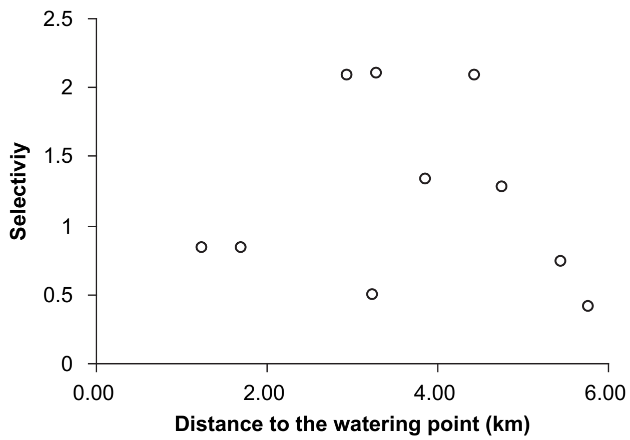

Fig. 1. Values of sheep selectivity of the ten vegetation stands in relation to the distance to the watering point.

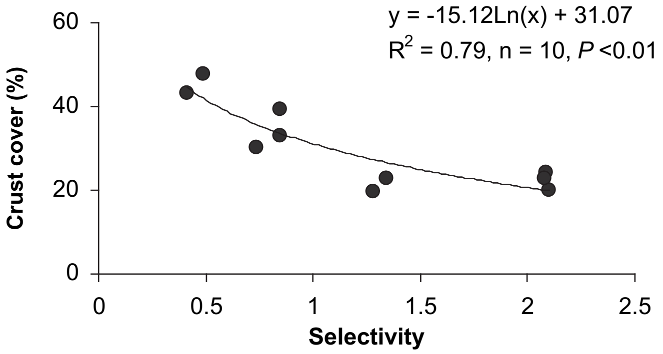

Fig. 2. Cover of biological crusts in relation to sheep selectivity.

perform comparisons crust/no crust and regression analysis to test the relationship between sheep selectivity and plant cover of the different plant groups (Norusis, 1997).

3. Results

3.1. Sheep selectivity in relation to distance to the watering point and plant cover

Values of sheep selectivity were independent of the distance to the watering point (non-piospheric ordering). The highest values of sheep selectivity occurred at mid-distances to the watering point (Fig. 1). Sheep selectivity was positively related to changes in the cover of medium shrubs ($R^2 = 0.23$, $n = 10$, $P = 0.03$). The cover of the other plant groups did not significantly vary with sheep selectivity.

3.2. Prediction 1. Reduction in the cover of biological crusts with increasing grazing selectivity

The cover of biological crusts was negatively correlated to sheep selectivity (Fig. 2).

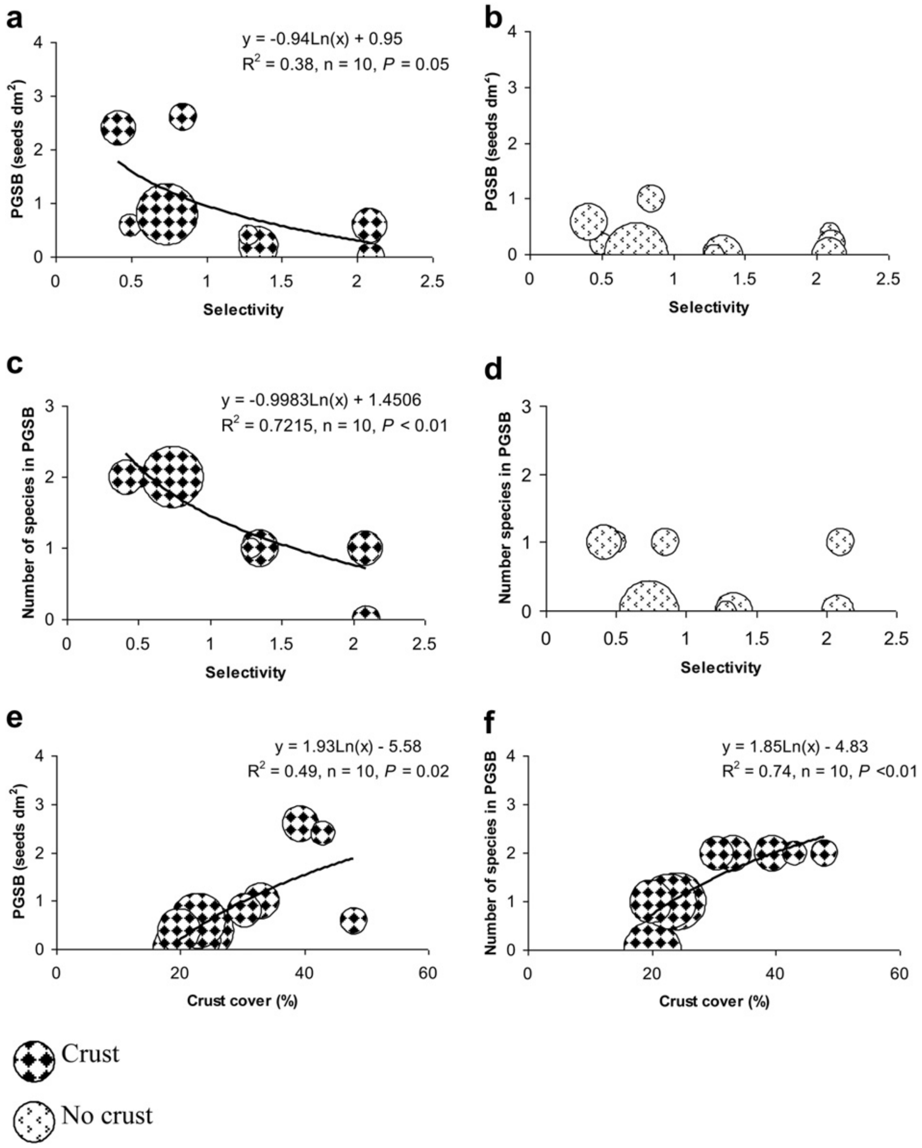

Fig. 3. Size of PGSB (soil seed bank of perennial grasses) (a) crust and (b) no crust soil conditions, in relation to sheep selectivity; number of species in PGSB (c) crust and (d) no crust soil conditions, in relation to sheep selectivity; (e) size of PGSB and (f) number of species in PGSB, in relation to crust cover. The size of the bubbles in (a) to (d) indicates the cover of perennial grasses (%) at each vegetation stand (minimum: 2.0, maximum 17.5), and in (e) to (f) the value of sheep selectivity (minimum: 0.41, maximum 2.09).

3.3. Prediction 2. Reduction in the size and species number of the soil seed bank of preferred plants with increasing grazing selectivity

The size of the soil seed bank of perennial grasses (PGSB) decreased with increasing sheep selectivity under biological crusts (Fig. 3a) and did not vary with sheep selectivity under no crust soil conditions (Fig. 3b). The PGSB was larger ($U = 22.0$, $P = 0.03$) and had higher species number ($F = 8.5$, $P < 0.01$) under biological crusts than under no crust soil conditions ($U = 22.0$, $P = 0.03$). The size (Fig. 3a and b) and species number (Fig. 3c and d) of the PGSB increased with increasing crust cover (Fig. 3e and f, respectively) and were not related to the cover of perennial grasses or to plant cover of other life forms (data not shown). We did not find significant interactions between sheep selectivity and soil condition (crust/no crust) on the size and species number of PGSB.

The size of the soil seed bank of annual grasses (AGSB) decreased with increasing sheep selectivity both under crust and no crust soil conditions (Fig. 4a and b, respectively) while the number of species did not vary with sheep selectivity (data not shown). The variation in the size of the AGSB was not significantly related to annual grass cover (Fig. 4a and b), to plant cover of other life forms (data not shown), or to presence or cover of biological crusts (data not shown). We did not find significant interactions between sheep selectivity and soil condition (crust/no crust) on the size and species number of AGSB.

3.4. Prediction 3. No change in the size and species number of the soil seed bank of non- or less-preferred plants with increasing grazing selectivity

The size and species number of the soil seed banks of tall shrubs (TSSB) and perennial herbs (PHSB) were very small and did not vary with sheep selectivity under both crust and no crust soil conditions. Also, the size and species number of TSSB and PHSB did not change with the cover of biological crusts or cover of these life forms (Table 1a and b). Medium shrubs did not form a detectable soil seed bank. The size and the species number of the soil seed bank of dwarf shrubs (DSSB) did not vary with selectivity, presence/cover of biological crusts but the size of the DSSB increased with increasing cover of this plant group ($R^2 = 0.25$, $n = 20$, $P = 0.02$, logarithmic function). The size and the species number of the soil seed bank of annual herbs (AHSB) did not vary in relation to the cover of annual herbs or the sheep selectivity but the size of the AHSB was significantly higher under biological crusts than under the soil without crusts ($F_{1,\ 20} = 6.29$, $P = 0.02$) (Table 1a and b). We did not find significant interactions between sheep selectivity and soil condition (crust/no crust) on the size and species number of PHSB, DSSB and AHSB.

4. Discussion

Our findings showed that sheep selectivity of plant patches along their grazing paths driven by the avoidance of visual impairment and anti-herbivore physical and chemical plant defenses (Bertiller and Ares, 2008) had negative effects on biological crusts and on the size of the soil seed bank of plants preferred by sheep. In this scenario, the reduction of the cover of biological crusts with increased sheep selectivity could result from mechanical disturbance of crusts caused by sheep trampling and/or from changes in other soil attributes affecting biological crust formation (Belnap and Eldridge, 2003; Langhans et al., 2010; Scutari et al., 2004).

The size of the soil seed bank of perennial grasses (PGSB) was significantly greater under crusts than under no crust soil conditions and both species number and size of the soil seed bank of this plant group increased with increasing cover of biological crusts but were unrelated to perennial grass cover. This finding could be

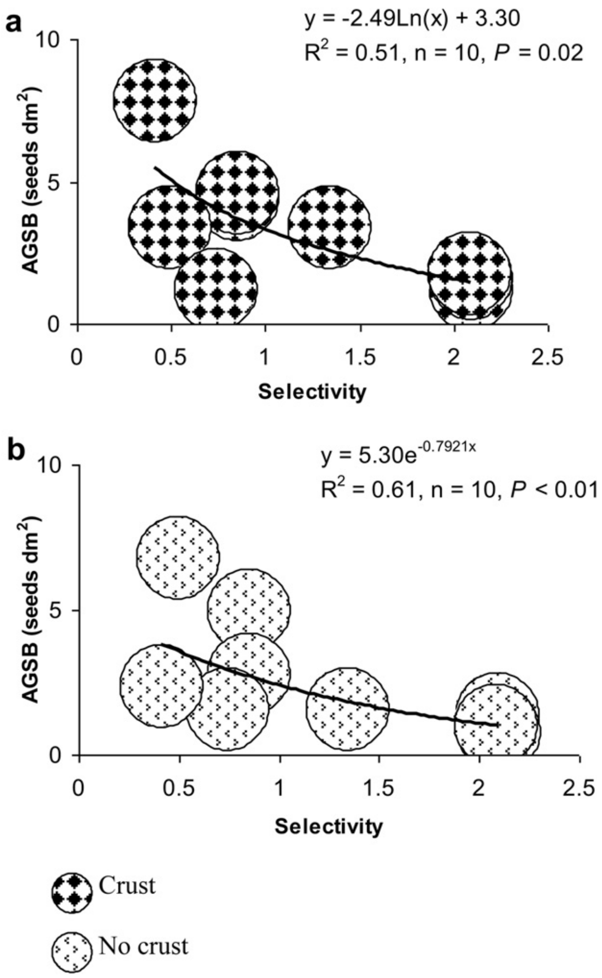

Fig. 4. Size of AGSB (soil seed bank of annual grasses) (a) crust and (b) no crust soil conditions in relation to sheep selectivity. The size of the bubbles indicates the cover of annual grasses (%) at each vegetation stand (minimum: 0, maximum 0.1).

associated with a stronger effect of grazers on reproductive than on vegetative grass tissues but also with high retention of perennial grass seeds in crusts with high cover at sites with low sheep selectivity. In this sense, there is evidence of the importance of biological crusts in relation to surface roughness, seed entrapment, soil stabilization and protection from erosion (Belnap, 2003; Belnap and Eldridge, 2003; Lalley and Viles, 2008; Warren, 2003; Williams et al., 1995). Accordingly, our findings provide circumstantial evidence of the role of biological crusts in seed entrapment since other soil surface attributes not assessed in our study could had also contributed to retention of perennial grass seeds under crusts at sites with low sheep selectivity.

The size of the soil seed bank of annual grasses (AGSB) was reduced with increasing sheep selectivity both in crust and no crust soil conditions. Plants of annual grasses are very small and usually elevate only a few centimeters above the soil surface (Correa, 1971–1999) but they are an important dietary component of sheep during the reproductive period in spring (Baldi et al., 2004; Somlo, 1997). Based on these observations, we speculate that the reduction in the size of the AGSB could be due to sheep trampling acting on small plants and the soil surface, including soil crusts, but also to the removal of reproductive tissues by sheep.

We did not find effects of sheep selectivity on the soil seed bank of non- or less-preferred species. As reported in other studies, the soil seed banks of medium and tall shrubs and that of perennial forbs were very small (Bertiller, 1998; Busso and Bonvissuto, 2009;

Table 1

a. Size (S) (seeds dm^{-2}) and species number (N) of the soil seed bank of tall shrubs (TSSB), medium shrubs (MSSB), dwarf shrubs (DSSB), perennial herbs (PHSB), and annual herbs (AHSB) under no crust (soil without biological crusts) and crust (soil with biological crusts) soil conditions at the ten vegetation stands (VS). Standard errors of means are in parentheses. b. sheep selectivity, as estimated through sheep-collaring techniques (S_i),. CC: Crust Cover, and cover of tall shrubs (TSC), medium shrubs (MSC), dwarf shrubs (DSC), perennial herbs (PHC), and annual herbs (AHC) at the 10 vegetation stands (VS).

a.

	TSSB		MSSB		DSSB		PHSB		AHSB	
VS	S	N	S	N	S	N	S	N	S	N
No crust										
1	0	0	0	0	0	0	0	0	10.1	5
2	0	0	0	0	0	0	0	0	25.5	4
3	0	0	0	0	0.6	2	0.2	2	15.7	3
4	0	0	0	0	0	0	0	0	21.7	7
5	0	0	0	0	0	0	0	0	18.1	4
6	0	0	0	0	0.2	1	0	0	7.4	4
7	0	0	0	0	0.4	1	0	0	15.3	5
8	0	0	0	0	0.4	1	0	0	13.9	5
9	0	0	0	0	0	0	0	0	29.1	7
10	0	0	0	0	0	0	0	0	23.5	4
Mean	0	0	0	0	0.16 (0.07)	0.5 (0.2)	0.02 (0.02)	0.1 (0.1)	18.0 (2.2)	4.8 (0.4)
Crust										
1	0	0	0	0	0	0	0	0	14.9	6
2	0	0	0	0	0	0	0	0	34.9	4
3	0	0	0	0	0.6	1	0	0	10.4	3
4	0	0	0	0	0.2	1	0	0	52.2	7
5	0	0	0	0	0	0	0	0	30.9	4
6	0	0	0	0	0	0	0	0	18.7	5
7	0	0	0	0	0.2	1	0	0	23.5	4
8	0.2	1	0	0	1	1	0	0	30.7	5
9	1	2	0	0	0.4	1	0	0	47.8	5
10	0.2	1	0	0	0	0	0	0	37.2	6
Mean	0.14 (0.1)	0.4 (0.2)	0	0	0.24 (0.11)	0.5 (0.2)	0	0	30.1 (4.3)	4.9 (0.4)

b.

VS	S_i	CC	TSC	MSC	DSC	PHC	AHC
1	0.84	33.0	16	1	19	0.05	0.07
2	0.84	39.4	25	6	7	0.07	0.07
3	0.49	47.9	11	9	16	0.03	0.04
4	0.74	30.3	25	3	9	0.52	0.02
5	0.41	43.0	21	6	6	1.04	0.05
6	2.09	24.1	23	19	11	0.53	0.03
7	2.10	20.0	7	22	9	0.54	0.02
8	1.34	22.9	18	9	16	2.04	0.06
9	2.08	22.8	19	6	12	0.53	0.05
10	1.28	19.8	1	32	8	0.05	0.06

DeFalco et al., 2009). The soil seed bank of dwarf shrubs was not affected by sheep selectivity but it was positively related to the cover of this plant group. Since changes in the cover of dwarf shrubs were not associated with sheep selectivity, our results suggest that factors other than sheep selectivity affecting the cover of this plant group could have effects on their soil seed bank. In this sense, Bisigato and Bertiller (1997) reported piosphere effects influencing the cover of dwarf shrubs in ecosystems of the Patagonian Monte. The soil seed bank of annual herbs (AHSB) was not modified by sheep selectivity probably due to their low preference by sheep. Moreover, AHSB was larger under biological crusts than under no crust soil conditions and it was not related to crust cover. It is possible that very small and rounded seeds of annual herbs without anchorage appendices (Correa, 1971–1999) could easier penetrate into crust cracks or in the soil between crust fragments than other larger, oblong seeds such as those of perennial and annual grasses (Thompson et al., 1993).

5. Conclusions

Sheep selectivity along grazing paths induced by factors other than distance to watering points had negative impacts on biological crusts and on the soil seed bank of preferred plants (perennial and annual grasses). Particularly important is the effect of sheep selectivity on biological crusts and the association between these and the soil seed bank of perennial grasses. According to this, crust condition could be used as an indicator of the state of conservation of perennial grass soil seed banks in the context of monitoring or planning the sustainable management of grazing shrublands. Further studies should conveniently be focused to address the value and mechanisms of retention by biological crusts of seeds with different morphology, the effect of sheep trampling on the cover of biological crusts, and the separated effect of trampling or tissue removal by grazing on the soil seed banks.

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