Original article

# Grazing impact on desert plants and soil seed banks: Implications for seed-eating animals

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A B S T R A C T

We assess whether the knowledge of livestock diet helps to link grazing effects with changes in plant cover and soil seed bank size, aiming at inferring the consequences of grazing on seed-eating animals. Specifically, we test whether continuous and heavy grazing reduce the cover, number of reproductive structures and seed reserves of the same grass species whose seeds are selected and preferred by granivorous animals in the central Monte desert, Argentina. Grass cover and the number of grass spikes usually diminished under grazing conditions in the two localities studied (Telteca and Ñacuñán), and soil seed bank was consistently reduced in all three years evaluated owing to a decline of perennial grass and forb seeds. In particular, the abundance of those seeds selected and preferred by birds and ants (in all cases grass species) declined 70–92% in Ñacuñán, and 52–72% in Telteca. Reduction of perennial grass cover and spike number in grazed sites reinforced the causal link between livestock grazing and the decline of grass soil seed reserves throughout failed plant reproduction. Grass seed bank depletion suggests that grazing may trigger a "cascade" of mechanisms that affect the abundance and persistence of valuable fodder species as well as the availability of seed resources for granivorous animals.

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## 1. Introduction

Grazing by domestic animals is the most globally widespread land use, and a major driver of global vegetation change (Díaz et al., 2007; Steinfeld et al., 2006). The impact of grazing differs among plant communities (Oesterheld and Semmartin, 2011), although some response patterns appear to be reasonably consistent for arid and semiarid vegetation. The most common reaction of woody plants and forbs is a neutral response (Díaz et al., 2007), but intense livestock grazing reduces the cover and abundance of tall perennial grass species with tussock architecture (Bisigato and Bertiller, 1997; Díaz et al., 2007; Dreber and Esler, 2011; Gonnet, 2001; Jones, 2000; Milesi et al., 2002; Tessema et al., 2012). Intense grazing decreases the allocation to reproductive structures by diminishing photosynthetic surfaces and reproductive tillers, or removing rudimentary or well formed inflorescences (Butler and Briske, 1988;

Gutman et al., 2001; Noy-Meir and Briske, 1996). A decline in seed production can lead to reduced soil seed banks (Dreber and Esler, 2011; O'Connor and Pickett, 1992; Sternberg et al., 2003), especially under continuous grazing during flowering and seed-set periods (Sternberg et al., 2003).

Soil seed bank is an essential part of arid and semiarid communities (e.g., Gutiérrez and Meserve, 2003; Marone et al., 2000a), where seeds are the only means of dispersal and access to new regions for many plant species (Kemp, 1989), and the main food for granivorous animals like ants, birds and rodents (Kelt et al., 2004; Marone et al., 2000b). Several bird species in the central Monte desert (*Zonotrichia capensis*, *Diuca diuca*, *Saltatricula multicolor*, *Poospiza torquata*, *Poospiza ornata*, *Phrygilus carbonarius*) consume and select medium-sized to large seeds (0.2–1.0 mg) of several perennial grasses like *Setaria leucopila*, *Pappaphorum* spp., *Trichloris crinita*, *Digitaria californica*, *Diplachne dubia* and *Aristida* spp. all year round but, especially, in autumn and winter (Marone et al., 1998b, 2008). Birds also prefer grass seeds to forb seeds of similar size (Cueto et al., 2001, 2006) and, although they eat a lot of the tiny *Sporobolus cryptandrus* seeds (0.07 mg) in the field, laboratory trials have shown that these seeds are a less-preferred food item (Cueto et al., 2006). The specialized granivorous Monte ants
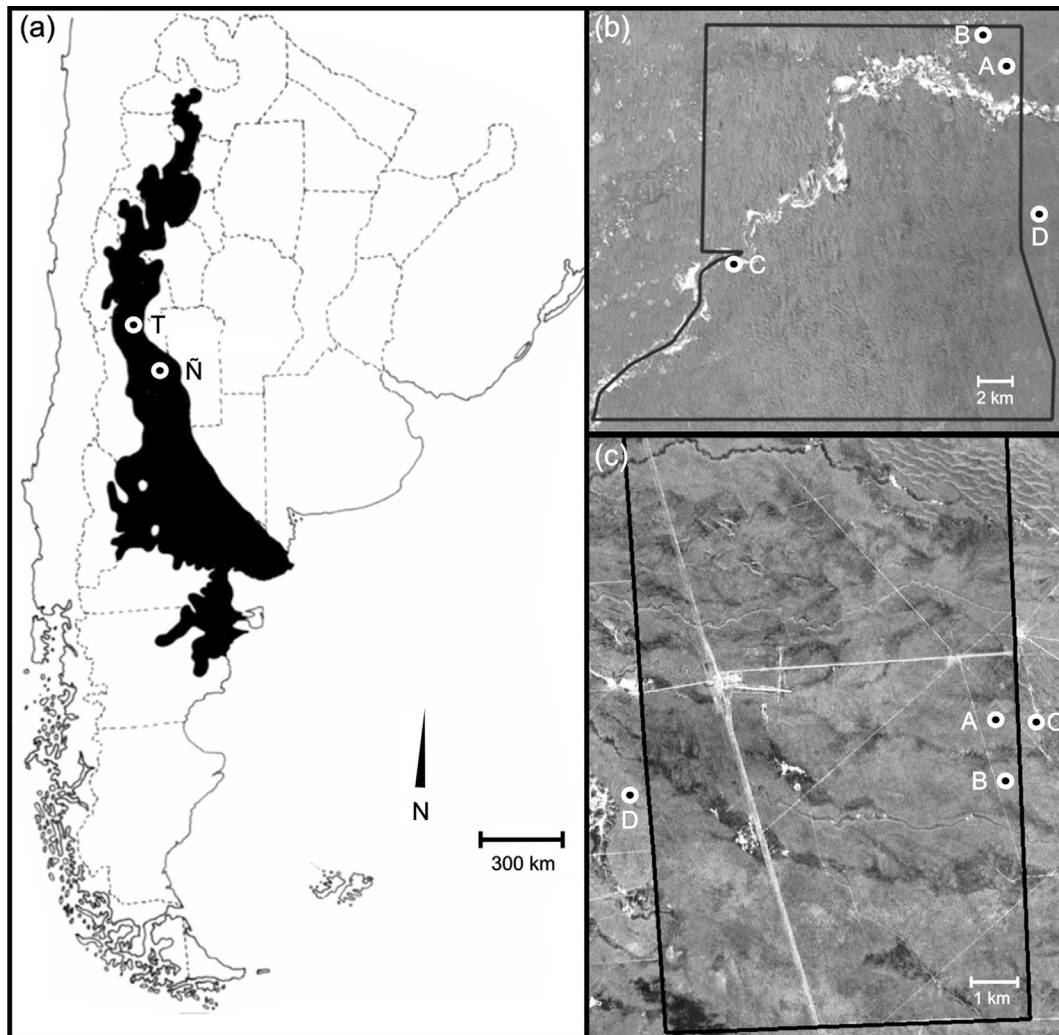
**Fig. 1.** Map showing study localities: Telteca Natural Reserve (T) and Biosphere Reserve of Ñacuñán (Ñ) in the Monte desert of Argentina (black area; a). A detailed view of study localities (Telteca, b; Ñacuñán, c) based on high-resolution Google Earth imagery indicates the location of study sites that have been subjected to nil or low (A and B) and high (C and D) grazing pressure. The boundary of Telteca and Ñacuñán reserves are indicated with black lines.

*Pogonomyrmex rastratus*, *Pogonomyrmex mendozanus* and *Pogonomyrmex inermis* consume >90% of grass seeds in summer and autumn (Pirk et al., 2009b). Most of them are medium-sized to large seeds of *Aristida* spp., *T. crinita*, *Pappaphorum* spp., *D. californica*, and *S. leucopila*, whereas the smaller seeds of *Stipa ichu* and *S. cryptandrus* are infrequent in diets of those ants (Pirk et al., 2009b). Choice experiments confirmed that *P. rastratus*, *P. mendozanus* and *P. inermis* prefer grass seeds (e.g., *Aristida* spp., *Pappaphorum* spp. and *S. leucopila*) to both forb and shrub seeds (Pirk and Lopez de Casenave, 2011), and medium-sized and large grass seeds to smaller seeds (Pirk and Lopez de Casenave, 2010). Other ant species like *Pheidole spininodis* have a very similar diet to that of the three sympatric *Pogonomyrmex* species (Pirk et al., 2009a).

Diet of granivorous animals widely depends on grass species that are heavily consumed by domestic livestock in the central Monte desert, where cattle and goat grazing is the most widespread land use, with an average stocking rate of 28 ha per large stock unit, year-long (Guevara et al., 1997). Cow's diet in the full rainy season in summer (i.e., when most grasses are setting seeds; Pol et al., 2010) includes 10% shrubs, 84% grasses and 6% forbs, while in the dry winter season these proportions average 49%, 45% and 6%, respectively. Perennial grass species in cow's summer diet include

*Panicum urvilleanum*, *S. cryptandrus*, *Chloris castilloniana*, *Pappaphorum philippianum*, *D. californica*, *S. leucopila*, *Aristida* spp., together with the annual short grass *Bouteloua aristidoides* (Guevara et al., 1997). Although Guevara et al. (1997) do not mention the perennial *T. crinita* in cow's diet, this species is one of the most important forage grasses in several arid and semiarid areas of Argentina, including the Monte (Greco and Cavagnaro, 2002; Quiroga et al., 2010). Goats in the central Monte desert and neighboring regions mainly consume shrubs and trees, which together represent >60% of the annual diet (Allegretti et al., 2012; Dayenoff et al., 1997). Goat's diet, notwithstanding, also includes grasses which can constitute >30% of summer diet in some regions (Dayenoff et al., 1997; Gründwaldt et al., 1994). The prevalent grass species in goat's diet are *P. urvilleanum*, *Pappophorum* spp., *T. crinita*, *Setaria* spp. and *Aristida* spp. (Allegretti et al., 2012; Dayenoff et al., 1997; Gründwaldt et al. 1994).

Given the patterns of plant consumption by cows and goats in the central Monte desert, a general effect (e.g., consumption of leaves, tillers, panicles and seeds) of livestock grazing on grass soil seed bank and ultimately their consumers is expected. We test the response of tall perennial grass plants and their seeds to grazing, and assess whether the knowledge of livestock diet helps to link such responses with the plausible mechanisms underpinning them

(i.e., livestock consumption). Specifically, we expect that grazing will reduce grass cover (but have a lesser impact on forb, shrub and tree cover), the number of grass spikes and the soil seed bank of several of the same grass species whose seeds are selected and preferred by granivorous animals.

## 2. Materials and methods

### 2.1. Study locations

The study was carried out in open woodlands of *Prosopis flexuosa* ("algarrobales") of two localities of the central Monte desert of Argentina: Telteca Natural Reserve (32°20′S; 68°00′W), and Biosphere Reserve of Ñacuñán (34°03′S; 67°54′W) together with surrounding grazed areas (Fig. 1b and c). Both protected areas are located on the plains at the eastern foothills of the Andes, in Mendoza province (Fig. 1a).

Telteca Reserve is located on northeast Mendoza, on the alluvial plain of the Mendoza River. The climate is arid and seasonal, with annual rainfall of $155 \pm 104$ mm (mean $\pm$ SD, 1971–1987), widely concentrated in spring and summer (October–March). Mean ($\pm$SD) annual temperature is $18.7 \pm 6.7\ °C$ (González Loyarte et al., 2009). Topography comprises a north-northwest − south-southeast oriented valley dune system. High and intermediate landscape positions are dominated by shrubs of *Larrea divaricata*, *Tricomaria usillo*, *Bulnesia retama*, and *Atriplex lampa* accompanied by small trees (<3 m height) of *P. flexuosa*, and a sparse layer of the stoloniferous grass *P. urvilleanum*. Lowlands are generally covered by taller *P. flexuosa* and *Geoffroea decorticans* trees (5–10 m height) (Alvarez et al., 2006) accompanied by most of the species found in higher topographic positions (González Loyarte et al., 2000). Grass cover in high, intermediate and lowlands is dominated by perennial (*T. crinita*, *Aristida mendocina*, *Pappophorum* spp., *Setaria* spp., *Sporobolus rigens*) and annual species (*Bouteloua barbata*, *B. aristidoides* and *Aristida adsencionis*). Forb cover is very low and highly variable among years and includes annual and biannual species (*Heliotropium mendocinum*, *Chenopodium* spp., *Gomphrena mendocina*, *Tribulus* spp. and *Sphaeralcea* spp.) (González Loyarte et al., 2000). Local settlers live in homesteads or "puestos" located in interdune positions and based around hand-dug wells that reach the water table and supply both people and livestock with water. The area around the "puestos" is most heavily grazed by goats and cattle (Jobbágy et al., 2011).

Biosphere Reserve of Ñacuñán is located on the alluvial plain between Tunuyán and Diamante rivers, in the east-central portion of Mendoza Province. Ñacuñán's climate is dry and seasonal. Mean ($\pm$SD) annual temperature is $15.9 \pm 7.2\ °C$ and mean annual rainfall is $342 \pm 111$ mm (1972–2004). Seventy five percent of the rainfall occurs in spring and summer (October–March). The main habitat of the reserve is an open woodland where *P. flexuosa* and *G. decorticans* trees are scattered within a matrix of tall shrubs (*L. divaricata*, *Condalia microphylla*, *Capparis atamisquea*, and *A. lampa*), low shrubs (*Lycium* spp., *Junellia aspera* and *Acantholippia seriphioides*), and perennial grasses (*T. crinita*, *Pappophorum* spp., *S. cryptandrus*, *Aristida* spp., *D. californica*, *S. leucopila*, *S. ichu*). Forb cover (*Chenopodium papulosum*, *Phacelia artemisioides*, *Parthenium hysterophorus*) is highly variable from year to year (Marone, 1991). The reserve has been effectively excluded from cattle grazing since 1972, when it was fenced. Floristic composition at adjacent cattle ranches is very similar (Gonnet, 2001; Milesi et al., 2002).

### 2.2. Sampling design

Four 3-ha study sites floristically and topographically similar were assessed in every location. Two sites were located in intense year-long grazed areas and the other two in nil-low grazing areas (Fig. 1b and c). In Telteca, sites A and B received low grazing pressure since the creation of the reserve in 1986 (TLG), and sites C and D were subjected to the more intense grazing that is typical of the region (THG). In the same way, sites A and B of the Reserve of Ñacuñán were placed inside the reserve excluded from cattle grazing for 40 years (ÑLG), and sites C and D were located in neighboring cattle ranches, where grazing regime has been usually intense (ÑHG). All study sites were >1.5 km apart from each other.

### 2.3. Grazing pressure

Since there are no records about the actual livestock density in the sampling sites, we used the proportion of livestock dung at each grazing condition as a proxy for grazing pressure (von Müller et al., 2012). Since the presence of dung reflects not only current livestock density but also their abundance in the recent past, it is a confident indicator of overall grazing pressure in the area (Cingolani et al., 2002; Teich et al., 2005). We made estimations separately for small livestock (goats) and large livestock (mostly cows but some horses too). In the two sites representing every contrasting grazing condition in both localities we randomly established eight 300 m long transects. In each transect we registered the presence or absence of dung inside a 50 cm square sampler over 30 sampling points separated by 10 m during July 2013. At each point, the sampler was located randomly at a distance of 1−5 m on the left or right side of the transect. At every square we detected the presence or absence of clearly recognizable dung remains regardless of its degree of decomposition. We estimated mean values and standard deviation (SD) of the proportion of dung within each transect for nil-low and high grazing sites in Telteca and Ñacuñán ($n = 16$).

### 2.4. Plant cover and grass spikes

In order to compare plant cover and number of grass spikes in nil-low and highly grazed conditions of Telteca and Ñacuñán, 17−20 parallel transects (25 m long, >20 m apart) were interspersed in the two sites representing every contrasting grazing condition in both localities. Within each transect, we recorded and identified to the level of genus or species all plants touching a "point quadrat" stick in 25 random sampling points. Additionally, we counted the number of spikes from adult individuals (i.e., plants producing new seeds or that had previously produced seeds) of annual and perennial grasses that contacted the stick on the same 25 random sampling points. Percentage plant cover of grasses, forbs, low (<1 m) and tall shrubs (>1 m), and trees, together with the number of grass spikes was calculated for each transect. We estimated mean values and standard error (SE) for every condition ($n = 39$ and 40 in nil-low grazed sites, and $n = 37$ and 40 in the grazed sites of Telteca and Ñacuñán, respectively). Vegetation samplings were performed at the end of the growing and reproductive season of most perennial grasses (March−May; Pol et al., 2010) in 2009 (Telteca) and 2010 (Ñacuñán).

### 2.5. Soil seed bank

We studied the composition and size of soil seed banks in contrasting grazing conditions in October−November 2009, 2010 and 2011 in Telteca, and in October−November 2010, 2011 and 2012 in Ñacuñán. Sixty soil samples were collected each year in the two sites representing every contrasting grazing condition in both localities ($n = 120$), with the exception of Telteca in 2009, when we sampled one site per grazing condition (sites A and C, both $n = 60$). Soil core samples in every condition were allocated according to the cover of the main microhabitats in the landscape: beneath the

canopy of trees (15%) and tall shrubs (35%), under low shrubs (13%) and grasses (17%), and on bare soil (20%) (Marone and Horno, 1997). For this purpose, 6 parallel transects (100 m long, >20 m apart) were set in an area of about 3 ha in every site representing each grazing condition and locality. In every transect, we established 10 sampling stations 10 m apart, where a soil core belonging to a randomly determined microhabitat was collected. We used a cylindrical sampler, 3.2 cm diameter and 2 cm deep (ca. 80% of seeds are found in the upper 2 cm of soil; Marone et al., 1998a) to collect soil samples. Soil samples were air-dried and sifted through a 0.27 mm mesh sieve at the laboratory. The finer fraction was discarded (the smallest seeds recorded in the habitats, genera *Sporobolus* and *Descurainia*, did not pass the sieve), and the coarser fraction was washed in the same sieve under water pressure. The residue on the mesh was dried and searched for seeds under a stereoscopic microscope. We identified seeds to species or genus using a reference collection and recorded the number of seeds that did not crumble when probed with forceps (Marone and Horno, 1997; Marone et al., 1998a). Seeds recorded were ascribed to one of four functional plant groups: annual grasses, perennial grasses, forbs, and shrubs.

### 2.6. Statistical analyses

One-way ANOVAs were conducted to test differences in dung proportion between grazing conditions. Similar analyses were carried out to assess grazing effect on the cover of plant functional groups, the number of grass spikes and soil seed bank size in Telteca and Ñacuñán. Checks for assumptions of ANOVA were done visually according to Quinn and Keough (2002). Raw data were transformed using square root (cover of grasses and trees), and logarithm (cover of forbs, tall and low shrubs, annual and perennial spikes, soil seed bank) (Zar, 1996). Results displayed are untransformed values.

## 3. Results

### 3.1. Grazing pressure

At Telteca, dung proportion of large livestock was higher in THG ($0.46 \pm 0.02$, mean $\pm$ SD) than in TLG ($0.17 \pm 0.02$, $F_{1,31} = 99.42$, $P < 0.001$). In contrast, dung proportion of goats showed no differences between conditions (THG $= 0.30 \pm 0.04$, TLG $= 0.25 \pm 0.02$, $F_{1,31} = 1.14$, $P = 0.29$). At Ñacuñán, where we did not record dung of goats, dung proportion of large livestock was $0.39 \pm 0.03$ in ÑHG. Within the reserve (ÑLG) we did not register dung of livestock at all.

### 3.2. Plant cover and grass spike

High grazing pressure resulted in a significant reduction of grass cover in Telteca ($F = 4.00$, $df = 2, 74$, $P = 0.04$) and Ñacuñán ($F = 15.75$, $df = 2, 78$, $P < 0.01$; Fig. 2). Conversely, forb and tree cover did not differ between grazing conditions in Telteca (forbs: $F = 0.19$, $df = 2, 74$, $P = 0.66$; trees: $F = 0.54$, $df = 2, 74$, $P = 0.47$), and Ñacuñán (forbs: $F = 0.8$, $df = 2, 78$, $P = 0.37$; trees: $F = 0.83$, $df = 2$, 78, $P = 0.36$). Shrubs showed an inconsistent response to grazing. Low shrub cover was similar in low and highly grazed conditions in Telteca ($F = 1.19$, $df = 2, 74$, $P = 0.28$), whereas it declined under grazing pressure at Ñacuñán ($F = 9.45$, $df = 2, 78$, $P = 0.03$; Fig. 2). Tall shrub cover was higher in more intense grazed areas of Telteca ($F = 7.1$, $df = 2, 74$, $P = 0.01$), but it did not differ between conditions in Ñacuñán ($F = 0.99$, $df = 2, 78$, $P = 0.32$; Fig. 2).

Grazing regimes also affected the number of spikes produced by perennial grasses (Table 1). This effect was more pronounced in Ñacuñán (a reduction of 92%) than in Telteca (56%), where the
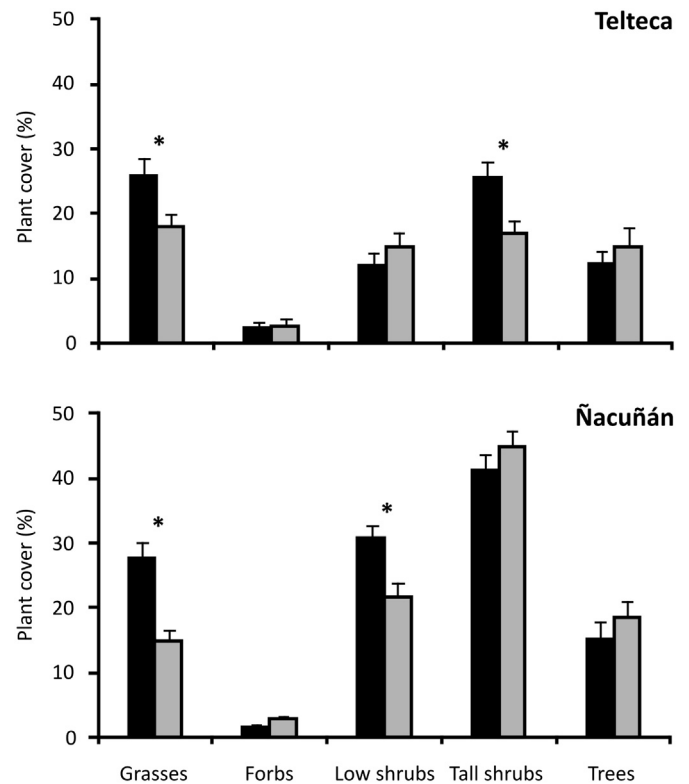


**Fig. 2.** Plant cover (mean + SE) by functional group under nil-low (black bars) and high (gray bars) grazing pressure in *Prosopis* open woodlands of Telteca (2009) and Ñacuñán (2010), central Monte desert, Argentina. Asterisks indicate significant differences between grazing regimes (one-way ANOVA, $P < 0.05$).

difference was not significant. We did not record annual grass individuals with spikes in Ñacuñán, where the cover of annual grasses is very low. In Telteca, the number of annual grass spikes was on average more abundant in slightly than in highly grazed areas, but again differences were not significant (Table 1).

### 3.3. Soil seed bank

High grazing resulted in a significantly smaller total soil seed bank in Telteca as well as Ñacuñán (Table 2). On average, seed banks were 2–3 times more abundant in nil-low grazing conditions in Telteca (range: 1.9–4.7) and Ñacuñán (1.6–3.9; Table 2). In both localities and grazing regimes, the seed bank was mostly composed of grass and forb species (Fig. 3). Seed abundance of tall and low shrubs was very low and did not differ between high and low grazing regimes (Fig. 3). Conversely, the seed bank of perennial grasses did vary between grazing regimes, a pattern that was consistent between years and localities. Perennial grasses were, on average, 2–4 (Telteca) and 3–6 (Ñacuñán) times more abundant in the soil bank of nil-low grazing conditions. Forb seeds followed the same pattern than perennial grasses in Telteca, where on average there were 4–9 times more seeds in less disturbed areas (Fig. 3). At Ñacuñán, forb seeds were also more abundant in less disturbed sites in 2010 and 2011, but did not differ in 2012 (Fig. 3).

Among grass seeds, those selected and/or preferred by birds as well ants (i.e., *Aristida* spp., *D. californica*, *Pappophorum* spp., *S. leucopila*, *S. cryptandrus* and *T. crinita*) were consistently reduced by grazing in all localities and years (Table 3). As a whole, these seeds were 70–92% more abundant in nil-low grazed condition at Ñacuñán, and 52–72% at Telteca (Table 3). When every species is considered separately, in 90% (27 out of 30) of paired comparisons

**Table 1**
Mean (±SE) number of spikes of perennial and annual grasses by transect in *Prosopis* open woodlands that have been subjected to nil-low and high grazing pressure in Telteca (TLG and THG) and Ñacuñán (ÑLG and ÑHG), central Monte desert, Argentina. Results from one-way ANOVA are shown.

| | Telteca | | | | | Ñacuñán | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | TLG | THG | *df* | *F* | *P* | ÑLG | ÑHG | *df* | *F* | *P* |
| Perennial grasses | 38.77 ± 15.27 | 17.16 ± 3.05 | 74 | 1.12 | 0.29 | 94.53 ± 20.07 | 7.60 ± 1.72 | 78 | 50.57 | <0.0001 |
| Annual grasses | 28.67 ± 9.02 | 14.19 ± 2.80 | 74 | 0.85 | 0.36 | 0.00 | 0.00 | – | – | – |

**Table 2**
Mean (±SE) total soil seed bank density (seeds/m$^2$) in *Prosopis* open woodlands that have been subjected to nil-low and high grazing pressure in Telteca (TLG and THG) and Ñacuñán (ÑLG and ÑHG), central Monte desert, Argentina.

| Year | Telteca | | Ñacuñán | |
|---|---|---|---|---|
| | TLG | THG | ÑLG | ÑHG |
| 2009 | 6883 ± 1225 | 3297 ± 1030 | – | – |
| 2010 | 4064 ± 446 | 2073 ± 339 | 2623 ± 364 | 1617 ± 292 |
| 2011 | 11352 ± 2198 | 2397 ± 414 | 3683 ± 583 | 954 ± 136 |
| 2012 | – | – | 5007 ± 1288 | 2167 ± 345 |
| Overall Mean | 7433 ± 2122 | 2589 ± 366 | 3711 ± 690 | 1579 ± 351 |

(i.e., 6 species × 2 localities × 3 years = 36, but because *D. californica* and *S. cryptandrus* were almost absent in Telteca, there were only 30 contrasts) grass seeds were more abundant in less or nil grazed conditions (Table 3). On the other hand, annual grass seeds were very scant in all study conditions at Ñacuñán, but some of these seeds (*B. aristidoides* and *B. barbata*) where abundant in Telteca, where they suffered numerical reductions by grazing only during one year (2011; Fig. 3).

## 4. Discussion

A challenge for disturbance ecology and ecosystem management is predicting which plant species will be promoted or diminished by grazing, and ecologists have developed several conceptual models to make these predictions (e.g., Cingolani et al., 2005; Milchunas et al., 1988; Oesterheld and Semmartin, 2011). Similar efforts are needed to predict grazing effects on different consumer species all along the food web that starts on the grazed plant. Some difficulties to build these "cascade models" are similar to the obstacles of classical models intended to predict grazing effects on plant composition (e.g., models should include causal relationships if they want to progress from merely describing patterns to a mechanistic understanding of species response to grazing) (Graff et al., 2007; Oesterheld and Semmartin, 2011). A plausible basis for any conceptual "cascade model" is offered by the chain of causal relationships: livestock diet ↔ plant composition ↔ seed reserves ↔ granivorous animals' diet (and ecological flexibility). The establishment of the first three components of the chain should serve to predict the cascade effects of grazing in arid and semiarid grassy areas (Marone et al., 2000b).
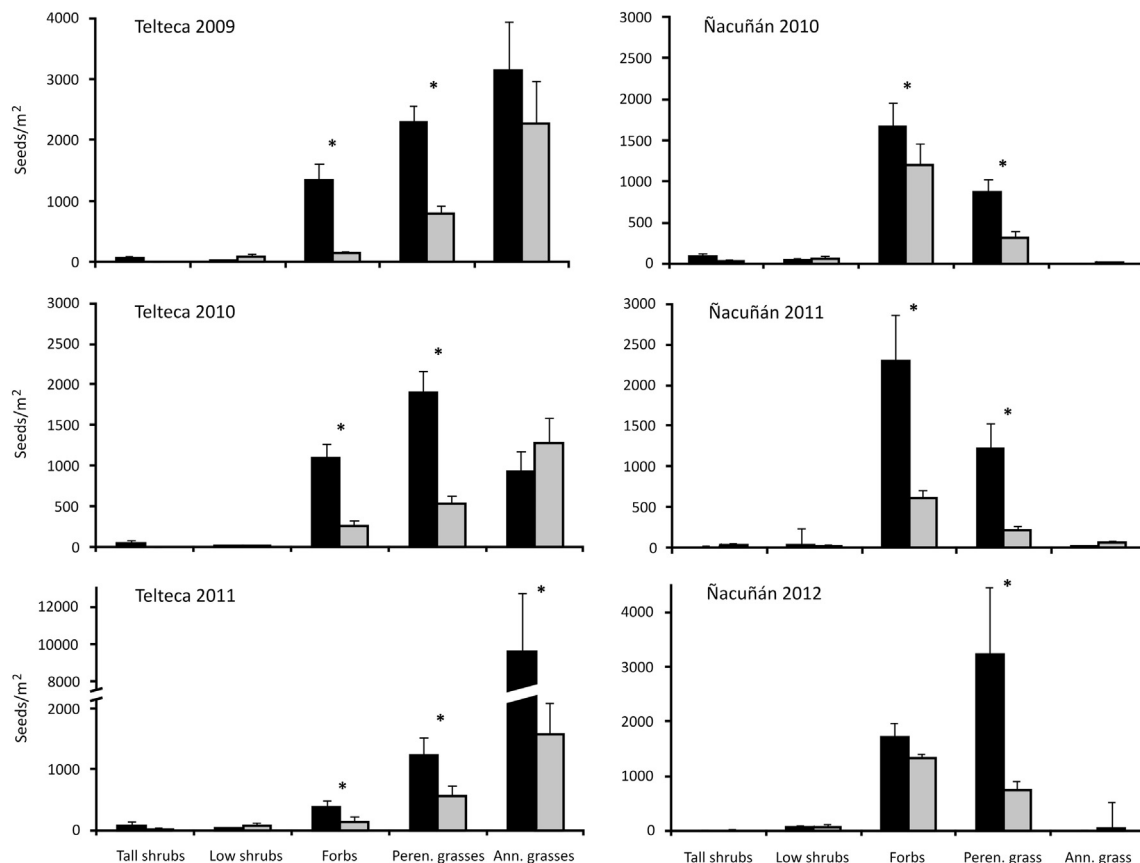


**Fig. 3.** Soil seed bank density (mean + SE) by plant functional group in *Prosopis* open woodlands under nil-low (black bars) and high (gray bars) grazing pressure in Telteca (2009, 2010 and 2011) and Ñacuñán (2010, 2011 and 2012), central Monte desert, Argentina. Asterisks indicate significant differences between grazing regimes (one-way ANOVA, *P* < 0.05).

**Table 3**

Mean soil seed bank density (seeds/m²) of the most abundant seed species in *Prosopis* open woodlands subjected to nil-low and high grazing pressure in Telteca (TLG and THG) and Ñacuñán (ÑLG and ÑHG), central Monte desert, Argentina. Available information of seed vulnerability to seed-eating birds and ants is also shown: seeds may be no (x), low (lc) or highly consumed (hc); selected (s) or not selected (ns); and preferred (p) or not preferred (np). The hyphen indicates no information available.

| | Seed vulnerability[a] | | Telteca | | | | | | Ñacuñán | | | | | |
| | Birds | Ants | TLG | | | THG | | | ÑLG | | | ÑHG | | |
| Shurbs | | | 2009 | 2010 | 2011 | 2009 | 2010 | 2011 | 2010 | 2011 | 2012 | 2010 | 2011 | 2012 |
| *Acantholippia seriphioides* | x | x | 0 | 0 | 0 | 0 | 0 | 0 | 31 | 31 | 62 | 52 | 21 | 31 |
| *Larrea* spp. | x | lc ns | 0 | 0 | 0 | 0 | 0 | 0 | 83 | 0 | 0 | 31 | 41 | 0 |
| *Lycium* spp. | x | lc ns | 21 | 10 | 31 | 83 | 10 | 73 | 10 | 10 | 0 | 10 | 0 | 31 |
| *Suaeda divaricata* | x | lc ns | 41 | 135 | 73 | 0 | 0 | 21 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total shrubs | | | 62 | 145 | 104 | 83 | 10 | 93 | 124 | 41 | 62 | 93 | 62 | 62 |
| Perennial grasses | | | | | | | | | | | | | | |
| *Aristida* spp. | lc s p | hc s p | 311 | 62 | 467 | 581 | 21 | 41 | 52 | 73 | 41 | 10 | 31 | 31 |
| *Chloris castilloana* | x | lc ns | 83 | 104 | 10 | 41 | 21 | 0 | 0 | 21 | 31 | 0 | 0 | 0 |
| *Cottea pappophoroides* | x | lc | 21 | 0 | 0 | 62 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| *Digitaria californica* | lc s p | hc s | 0 | 0 | 0 | 0 | 0 | 10 | 10 | 73 | 342 | 41 | 0 | 21 |
| *Diplachne dubia* | lc s | lc | 0 | 0 | 10 | 21 | 0 | 0 | 10 | 10 | 0 | 0 | 0 | 0 |
| *Neobouteloua lophostachya* | lc ns | lc | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 21 | 0 | 0 | 31 | 467 |
| *Pappophorum* spp. | hc s p | hc s p | 207 | 31 | 41 | 0 | 0 | 10 | 52 | 62 | 104 | 31 | 31 | 10 |
| *Setaria leucopila* | hc s p | lc s p | 726 | 467 | 197 | 21 | 145 | 52 | 166 | 301 | 498 | 73 | 83 | 145 |
| *Sporobolus phleoides* | – | lc ns | 104 | 197 | 62 | 0 | 0 | 21 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sporobolus cryptandrus* | hc s np | lc | 0 | 0 | 0 | 62 | 0 | 0 | 270 | 477 | 2146 | 73 | 10 | 41 |
| *Stipa ichu* | x | lc s | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 10 | 0 | 62 | 10 | 10 |
| *Trichloris crinita* | hc s p | hc s | 726 | 995 | 425 | 0 | 270 | 425 | 290 | 197 | 62 | 21 | 10 | 10 |
| Total perennial grasses | | | 2198 | 1856 | 1213 | 788 | 456 | 560 | 860 | 1244 | 3224 | 311 | 218 | 736 |
| Annual grasses | | | | | | | | | | | | | | |
| *Bouteloua aristidoides* | np | hc ns | 2301 | 321 | 7505 | 2281 | 902 | 850 | 0 | 0 | 0 | 0 | 0 | 21 |
| *Bouteloua barbata* | – | hc ns | 850 | 404 | 2136 | 0 | 373 | 736 | 0 | 10 | 0 | 10 | 41 | 0 |
| *Eragrostis* spp. | lc np | x | 104 | 41 | 21 | 0 | 73 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total annual grasses | | | 3255 | 767 | 9662 | 2281 | 1348 | 1586 | 0 | 10 | 0 | 10 | 41 | 21 |
| Forbs | | | | | | | | | | | | | | |
| *Chenopodium* spp. | lc ns np | lc ns np | 352 | 218 | 52 | 0 | 73 | 41 | 570 | 560 | 746 | 684 | 352 | 995 |
| *Conyza* spp. | lc ns | lc | 0 | 0 | 0 | 0 | 0 | 0 | 31 | 31 | 10 | 10 | 21 | 21 |
| *Descurainia* spp. | lc ns np | x | 0 | 0 | 0 | 0 | 0 | 0 | 591 | 31 | 21 | 52 | 0 | 0 |
| *Glandularia mendocina* | lc s np | lc | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 156 | 52 | 41 | 31 | 52 |
| *Heliotropium mendocinum* | lc ns | lc ns np | 767 | 643 | 259 | 0 | 145 | 52 | 10 | 10 | 21 | 83 | 21 | 10 |
| *Lappula redowskii* | lc s p | lc | 0 | 0 | 0 | 0 | 0 | 0 | 73 | 301 | 176 | 10 | 10 | 21 |
| *Parthenium hysterophorus* | lc s np | lc | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 73 | 52 | 0 | 21 | 21 |
| *Phacelia artemisoides* | x ns np | x | 0 | 0 | 0 | 0 | 0 | 0 | 145 | 715 | 435 | 31 | 21 | 41 |
| *Plantago patagónica* | x ns np | x | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 21 | 41 | 0 | 0 | 0 |
| *Sphaeralcea miniata* | lc ns np | lc | 0 | 0 | 0 | 0 | 0 | 10 | 41 | 249 | 41 | 156 | 83 | 31 |
| Total forbs | | | 1120 | 860 | 311 | 0 | 218 | 104 | 1472 | 2146 | 1596 | 1068 | 560 | 1192 |
| N | | | 60 | 120 | 120 | 60 | 120 | 120 | 120 | 120 | 120 | 120 | 120 | 120 |

[a] Low/highly consumed seeds (lc/hc) represent less/more than 10% of the diet of at least three out of six seed-eating bird species (Marone et al., 2008), and one out of three harvester ant species (Pirk and Lopez de Casenave, 2006; Pirk et al., 2009b; Pol et al., unpublished). Selected/not selected seeds (s/ns) were more/less consumed than expected by seed availability in the field by six bird species as a whole (guild selection; Marone et al., 2008) or by *Pogonomyrmex* harvester ants (Pirk et al., 2009b; Pol et al., unpublished). Seeds preferred/not preferred (p/np) were/were not systematically consumed (>50% of seeds offered) at least by two out of four bird species tested in choice experiments (Cueto et al., 2001, 2006; Marone and Camín, unpublished), or were/were not removed first by ants in paired choice experiments (Pirk and Lopez de Casenave, 2011).

Diet composition of cows and goats suggests a generalized negative effect of grazing on perennial grasses in Telteca and Ñacuñán, and the cover of these grasses was consistently smaller in grazed sites, whereas other vegetation variables did not change or changed inconsistently. Tree and forb cover remained unchanged. Low shrub cover declined under intense grazing only in Ñacuñán, and tall shrub cover was reduced only in Telteca. The reduction of some shrub species might be a result of consumption since cows and goats browse on several shrub species, but we did not record reductions of the most consumed shrub species (e.g., *T. usillo*, *A. lampa*, *Lycium* spp.) in the grazed condition. Although the pattern of plant cover changes might have been affected by habitat heterogeneity not related to grazing and requires more study, it mostly reinforced the idea that – as was expected by livestock diet composition – the main and more general impact of grazing on vegetation occurred on perennial grasses. This pattern coincided with previous results attained in similar *Prosopis* woodlands (Kerley and Whitford, 2000) and desert grassy shrublands (Brotherson et al., 1983).

Mean number of grass spikes seems to be lower under grazing conditions. At Ñacuñán, where only perennial grasses were present, grass spikes diminished significantly under disturbed conditions, and the same tendency occurred at Telteca. A reduction of perennial grass cover, summed up to a plausible decline in the number of reproductive structures, supports the idea of a causal link between livestock grazing and the reduction of grass soil seed reserves mainly due to failed reproduction (Gutman et al., 2001). Given that the transient soil seed bank of perennial grasses heavily depend on continued seed production for its replenishment (Marone et al., 1998b; Noy-Meir and Briske, 1996), the average reduction of perennial grass seeds, in particular those species selected and/or preferred by seed-eating animals (Table 3), we found in grazed areas of Ñacuñán as well as Telteca confirmed the "cascade model" expectations.

Forb cover did not vary between grazing conditions, but the size of the forb seed bank was usually low in the grazed sites of Telteca and Ñacuñán. We did not expect this result under the general hypothesis since forbs are scarcely and only occasionally consumed by

cows and goats, making a direct effect of livestock on these plants and their seeds unlikely. Forb species, most of which are annual dicots, form mostly persistent soil seed banks in the central Monte desert, and germinate only occasionally (Marone et al., 2000a; Sartor and Marone, 2010), making the link between plant cover and soil seed bank size weaker and difficult to establish. More studies are needed therefore to assess the causes of the plausible reduction of forb seed banks under grazing conditions. Some of them should test indirect effects of livestock on forb growth and seed production, like trampling effects on soil physical features (e.g., soil compaction), and the increment of soil sun irradiation in grazed areas (Castellano and Valone, 2007; Milchunas and Lauenroth, 1993; Yates et al., 2000) since both mechanisms can reduce forb seed germination and recruitment (Bertiller, 1992; Kobayashi et al., 1999; Sternberg et al., 2004; Striker et al., 2011).

Notable reductions of perennial grass seed reserves under grazing conditions have been already reported in the Monte desert (Blendinger and Ojeda, 2001; Gonnet, 2001; Milesi et al., 2002). We can then expect major implications of grazing for seed-eating animals and granivory as an ecosystem process. Seed-eating animals could show behavioral (e.g., diet shift) and/or numerical responses to grazing, depending on their ecological flexibility. Previous field experimental studies have shown that birds consume greater amount of tiny-grass seeds and of several forb seeds when the availability of the more attractive medium-sized and large grass seeds diminish in the habitat (Marone et al., 2008), and lab experiments confirmed that the former seeds are less preferred or suboptimal items for the birds: *S. cryptandrus* seeds are less preferred for *Z. capensis* and *P. ornata*, and *C. papulosum* seeds are less preferred for *Z. capensis*, *D. diuca* and *P. ornata* (Cueto et al., 2006). Similar studies with *Pogonomyrmex* ants also suggest that some shrub and forb seeds are suboptimal or alternative food items for these insects, which consume a greater fraction of them in spring, when the preferred grass seeds are scarce in the habitat (Pirk and Lopez de Casenave, 2006; Pirk et al., 2009a,b). Thus, even though Monte's birds and ants show certain degree of behavioral flexibility, they may not be able to circumvent heavy and continuous grazing effects since livestock can reduce preferred grass seeds as well as the less preferred or alternative grass and forb seeds. Numerical reductions of granivorous populations (Martin and McIntyre, 2007; Nicolai, 2005; Seymour and Dean, 2010) might then be expected as a consequence of livestock in the Monte.

Since selected or preferred grass seeds are usually also the bigger ones, changes on grass seed reserves provoked by grazing might also have an implication for granivory if the hypothesis of a more negative effect of grazing on large seeded plant species than on plants with small or tiny seeds (Dreber et al. 2011; McIntyre and Lavorel, 2001; Westoby et al., 1992) was correct. In our study, notwithstanding, neither the absolute nor the relative number of small grass seeds increased as a consequence of grazing. Ungrazed areas of Ñacuñán had an average of 978 small seeds/m$^2$, and grazed areas a mean of 235 seeds/m$^2$. In Telteca, the slightly grazed fields had 62 seeds/m$^2$ whereas the intensively grazed ones had 45 seeds/m$^2$. Moreover, the relative abundance of small grass seeds in grazed sites of Ñacuñán – the only locality where small grass seeds were relatively abundant – was 55% (978 small seeds/1776 total seeds per m$^2$) whereas it represented 56% (235/418 seeds/m$^2$) within the reserve. An effect of grazing on the average size of seeds in the soil appears not plausible and then should not be included in the "cascade model" for granivory in the Monte desert.

Livestock is by far the single largest anthropogenic use of land. About 73% of the word's pastures and rangelands are located in dry areas, and have been degraded to some extent (Steinfeld et al., 2006). The magnitude of the grazing effect on wildlife species is always a matter of dispute, but contenders usually coincide on one point: better science is needed to inform management and policy (e.g., Brown and MacDonald, 1995; Fleischner, 1996; Noss and Cooperrider, 1994). The development of conceptual "cascade models" based on key natural history features that link causes with plausible effects is a way to complement descriptive studies aiming at improving predictive perturbation ecology.

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