EFFECT OF GRAZING AND DROUGHT ON SEED BANK IN SEMIARID PATCHY RANGELANDS OF NORTHERN PATAGONIA, ARGENTINA

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Premise of research. The soil seed bank (SSB) plays a critical role in vegetation regeneration after stress and/or disturbance events. Here, we analyzed how drought and grazing influence the SSB of shrub patches and interpatches in a rangeland from northern Patagonia.

Methodology. Soil samples were collected from shrub patches and interpatches on heavily grazed, moderately grazed, and ungrazed sites at the end of a multiyear drought and 2 yr after the end of the drought. Sampling was done immediately before seed dispersion of the dominant species in order to study the persistent seed bank. Seeds were separated from the mineral soil by elutriation and grouped into four life-forms: annual grasses, perennial grasses, forbs, and shrubs.

Pivotal results. In all sampling conditions, the SSB was markedly dominated by forbs. Total seed density and seed density of every life-form were higher in shrub patches than in interpatches. Seed density of grasses and shrubs was not influenced by drought and grazing in both shrub patches and interpatches. In contrast, seed density of forbs was negatively influenced by drought in interpatches and positively influenced by grazing in shrub patches.

Conclusions. The results suggest that in patchy rangelands of northern Patagonia the SSB of shrub patches is less severely depleted than that of interpatches during multiyear droughts, particularly for forbs under high grazing intensity. However, the growth of the SSB after drought is a slow process in both shrub patches and interpatches. Our results highlight the importance of grazing pressure alleviation during drought conditions to safeguard the SSB, which is the only source of seedling recruitment for most species in northern Patagonia rangelands.

Keywords: dry grasslands, grazing intensity, shrub steppes, vegetation distribution.

Online enhancements: supplemental tables.

Introduction

In arid and semiarid lands, where vegetation is commonly arranged in shrub patches with high plant cover alternating with interpatch areas with low plant cover or bare soil (Aguiar and Sala 1999), the spatial pattern of the SSB commonly mirrors the spatial heterogeneity of established vegetation (Bertiller 1998; Caballero et al. 2008; Moreno-de las Heras et al. 2016). Since dense shrub patches can ameliorate physical stress (Aguiar and Sala 1994) and herbivore pressure (Mikchunas and Noy-Meir 2002) on herbaceous vegetation that grows beneath their canopy, they may play a critical role as a source of seeds for vegetation recovery under grazing and/or drought conditions.

Grazing by large herbivores can induce changes in SSB density, composition, richness, and diversity (Bertiller 1992; Milberg 1995; Pecó et al. 1998). Livestock grazing can affect the SSB directly through depressing seed production of preferred species (Pehrsson 1988; O’Connor and Pickett 1992) or indirectly by inducing modifications in species composition (Loucougaray et al. 2004; Moreno García et al. 2014; Pol et al. 2014). The intensity and direction of grazing-induced modifications in the SSB may vary according to the historical grazing regimes, herbivory level, and resource availability of the site (Mikchunas et al. 1988). In environments with low availability of resources and short evolutionary history of grazing, increasing grazing intensities is expected to change the composition and reduce the density, richness, and diversity of the SSB (Mikchunas et al. 1988). Modifications in bo-
tanical composition (Kinukan and Smeins 1992; O’Connor and Pickett 1992) and reductions in richness and diversity (Sternberg et al. 2003) of the SSB have been documented in heavy grazed rangelands of arid regions.

Drought can differentially affect seed production of the species in a community, leading to modifications in composition, density, richness, and diversity of the SSB (Fenner and Thompson 2005; Pakeman 2011; del Cacho and Lloret 2012). Particularly, the seed production of perennial grasses is highly sensitive to drought stress (Schwinning and Sala 2004). Consequently, after a prolonged drought period, seeds of perennial grasses are commonly poorly represented in the SSB compared with annual grasses and forbs (O’Connor 1991; Gutiérrez et al. 2000).

The interaction of grazing and drought can synergistically affect the SSB in grassland communities, since rainfall and herbivory are primary drivers of vegetation dynamics (O’Connor 1995; Fuhlendorf et al. 2001; van Coller et al. 2018). For instance, the combination of drought and sustained heavy grazing, particularly for a successive number of years, is capable of causing the local extinction of perennial grass populations (O’Connor 1991), while it can increase the establishment and cover of annual forbs (Riginos et al. 2018).

In the steppes of northern Patagonia, Argentina, the vegetation is organized in shrub-dominated patches alternating with interpatches of either bare soil or low herbaceous cover (Bisigato and Bertiller 1997; Kropfl et al. 2013). This spatial distribution of the vegetation may result primarily from water limitations in the ecosystems (Aguir and Sala 1999; Ludwig et al. 1999), and patchiness may be reinforced by livestock grazing (Augustine 2003; Rietkerk et al. 2004; Ren et al. 2015). The shrub patches act as a trap for seeds transported by wind and water (Bertiller 1998; Pazos and Bertiller 2008). Moreover, the shrub patches provide a favorable environment for understory plant growth compared with interpatch areas (Pazos and Bertiller 2008). The canopy of woody plants mitigates abiotic stress and can give protection from grazing (Soliveres et al. 2012). Both seed entrapment and improved growth environment determine a marked seed concentration in shrub patches (Bertiller 1998). However, there is still scarcity of information on the effects of multiyear drought and sustained heavy grazing on the SSB.

We hypothesize that in the shrub steppes of northern Patagonia the SSB (1) is less severely depleted in shrub patches than in interpatches during multiyear droughts, particularly in combination with sustained heavy grazing, and (2) increases faster after multiyear drought in shrub patches compared with interpatches, especially under high grazing intensity. From these hypotheses we expected (1) higher seed density in shrub patches than in interpatches at the end of a multiyear drought and (2) a faster increase in seed density in shrub patches than in interpatches after a multiyear drought, particularly under sustained heavy grazing. Complementarily, since perennial grasses commonly have a transient SSB (Thompson et al. 1997), and drought combined with grazing can markedly decreases seed production (O’Connor and Pickett 1992), we expected that seed density of perennial grasses in the SSB will be the most negatively affected by grazing and drought. To test these hypotheses, we analyzed the SSB in shrub patches and interpatches under different grazing intensities at the end of a multiyear drought and 2 yr after the end of the drought event.

**Methods**

**Study Area**

The study was conducted in temperate and semiarid shrub steppes of northeastern Patagonia, Argentina (lat. 40°41′–40°46′S, long. 64°06′–64°30′W), which belong to the Monte Phytogeographical Province (Cabrera 1971). Overall characteristics of climate, soil, and vegetation of the study area have been described by Godagnone and Bran (2009). Mean monthly air temperatures range from 7°C in July to 24°C in January, with an annual mean of 14°C. Mean annual rainfall is 255 mm (CV 40%), with peaks in autumn and spring, and the mean annual potential evapotranspiration is 800 mm. During the 2 yr preceding the study period (2007–2008) and the first year of the study period (2009), the annual mean precipitation was marked below (multiyear drought conditions) the long-term historical average precipitation. In the next two years of the study period (2010–2011), the annual mean precipitation was close to or reached the long-term historical average precipitation (fig. 1).

The vegetation is dominated by shrubs such as Cerquiraga erinacea and Condalia microphylla. Perennial grasses are mainly represented by Nassella tenuis and, to a lesser extent, Poa ligularis, Nassella longiglumis, Piptochaetium napoanense, Pappostipa speciosa, and Jarava plumosa. The most abundant annual grasses are Bromus secalinus and Schismus barbatus, and the most abundant forb is Erodium cicutarium. All dominant herbaceous plants are cool-season species. There is also a biological soil crust composed of cyanobacteria, bryophytes, lichens, bacteria, and algae. Scientific names are according to the Flora Argentina (Zuloaga and Morrone 2007).

Sheep and cattle were introduced into the study area at the beginning of the last century, causing the displacement of the guanaco (Lamas guanacoides), which is the main large native herbivore in Patagonia Region (Godagnone and Bran 2009). Since then, the vegetation has been heavily grazed because the density of domestic livestock surpassed the carrying capacity of the system (Oesterheld et al. 1992; Cecchi and Kropfl 2002). Sustained heavy grazing may have accentuated the spatial pattern of vegetation in shrub patches with high plant cover within a matrix of bare soil or low herbaceous cover (Funk et al. 2018).

**Sampling Design**

We analyzed the SSB in grazed and ungrazed areas in September 2009 (last year of the multiyear drought period) and September 2011 (second year with near-long-term average precipitation after the multiyear drought). Soil samples were taken immediately before seed dispersion of the dominant species in order to study the persistent seed bank (Thompson and Grime 1979). They were taken in three sampling sites, each in a different commercial ranch. Sites were separated from one another by no more than 30 km. They had a similar grazing history (ca. 0.36 sheep equivalent per hectare, year-round grazing), soil type, and plant community type. Each sampling site comprised a square paddock of 625 ha, with a water source located at one corner. Within each paddock we sampled at two distances from the water source: 600 and 2500 m, within an area of ca. 1 ha.
We assume these distances to represent different grazing intensities, based on the creation of piosphere effects, which determine a decreasing intensity of grazing radiating out from the water source (Bisigato and Bertiller 1997). We also sampled grazing exclosures adjacent to each paddock, which were 1 ha in size and had not been grazed for 10 or more years. In this way, we arbitrarily defined three grazing intensities: heavy grazing (HG) at 600 m from the water source, moderate grazing (MG) at 2500 m from the water source, and ungrazed (UG) at exclosures. We used the UG condition as a control since it represented the less disturbed vegetation state in the study site.

At all sampling sites and levels of grazing intensity, we randomly collected soil samples for seed bank analysis in two different microsites: shrub patches and interpatches. For the purpose of this study, we defined a shrub patch as a discrete unit of the spatial pattern of vegetation with an upper shrub layer and a lower layer composed of perennial grasses, annual species, and/or biological soil crusts associated with soil mounding. Interpatches are characterized by scarce vegetation and soil degradation. At each sampling date we took 90 samples, or 10 samples per grazing intensity and per site. Of these 10 samples, five corresponded to shrub patches and five to interpatches. Each soil sample consisted of a soil core (10 cm in diameter and 5 cm deep) and the litter above it. Samples were stored in sealed bags and taken to the laboratory, where they were air-dried for 20 d before processing. Dried samples were elutriated with tap water as many times as necessary for them to pass through a set of graduated stacked sieves (15-cm diameter) with mesh sizes of 1, 0.71, 0.5, and 0.25 mm. After elutriation, samples were allowed to air-dry for 72 h. All material retained in each of these sieves was observed under a dissecting microscope to extract and count all viable seeds, which were determined to the genus or species level (for details, see Loydi et al. 2012). Seeds were considered to be viable when they resisted light hand pressure with a tweezer (Busso and Bonvissuto 2009). Seeds were grouped into the dominant plant life-form in the area: annual grasses, perennial grasses, forbs, and shrubs. Only viable seeds were considered for analysis.

**Statistical Analyses**

Data were analyzed according a randomized complete block split-plot analysis of variance (ANOVA) design, where each site was considered a block, the year (2009 vs. 2011) was the main factor, and the grazing intensity was the split factor. Analyses were performed for each microsite (shrub patches and interpatches) separately since this factor proved to have a significant interaction ($P < 0.05$) with grazing intensity and year. Analyses were done for total seed density and for seed density of each life-form. Data were $(x + 1)^{1/2}$ transformed prior to analyses to meet ANOVA assumptions. In “Results,” we present data before transformation. Tukey honest significant difference was used as a post hoc test ($P < 0.05$) for mean comparisons between the grazing intensity and between years within each microsite. Seed density between shrub patches and interpatches was compared using a paired Wilcoxon test, since data were not normally distributed and homoscedasticity was not possible to achieve. We also calculated species richness of the SSB under the different experimental conditions and made comparisons between grazing intensity using corrected confidence intervals obtained by bootstrap method (500 iterations; Pla and Matteucci 2001). Non-overlapping confidence intervals were considered as significant differences between means. All analyses were made using InfoStat software (Di Rienzo et al. 2009).

**Results**

In both shrub patches and interpatches the SSB was markedly dominated by forbs (~70%), equally in 2009 and 2011 (fig. 2). In the shrub patches, species richness increased or decreased at increasing grazing intensity in 2009 and 2011, respectively (fig. 3). In contrast, in the interpatches species richness was similar among the grazing intensities in 2009, whereas it was higher in UG and MG compared with HG in 2011.

Regarding grazing intensities, in the shrub patches the total seed density was significantly highest at HG and similar between MG and UG. This response was mainly due to enhanced
seed density of forbs at increasing grazing intensity, since for the other plant life-forms no significant differences were observed among grazing intensities. In contrast, total seed density and seed density of every plant life-form were similar at all grazing intensities in the interpatches (table 1).

Total seed density increased or tended to increase after the drought in the interpatches and the shrub patches, respectively. Seed density of forbs in 2011 almost doubled from 2009 in both microsites, although the difference was significant for interpatches only. For the rest of the plant life-form, seed density was similar between sampled years in both interpatches and shrub patches (table 1).

For total seed density and for seed density of each plant life-form (annual grasses, perennial grasses, forbs, shrubs), the interaction term between grazing intensity (HG, MG, UG) and year (2009: drought conditions; 2011: near-normal precipitation conditions) was not significant ($P > 0.05$) at the level of both shrub patches and interpatches.

Total seed density was higher ($P < 0.01$) in the shrub patches than in the interpatches at all grazing intensities during both sampled years. At the end of the multiyear drought (2009), total seed density in the shrub patches was three, five, or nine times higher than in the interpatches for the UG, MG, and HG, respectively. Two years after the multiyear drought (2011), total seed density was three times (UG and MG) or 11 times (HG) higher in the shrub patches than in the interpatches. In 2009, seed density of all plant life-forms was higher ($P < 0.05$) in the shrub patches than in the interpatches at all levels of the grazing intensity, except for perennial grasses in the UG condition. In 2011, the same response was observed in the HG condition; that is, seed density of all plant life-forms was higher ($P < 0.05$) in the shrub patches than in the interpatches, while there were no differences between microsites for either annual or perennial grasses in MG or forbs in UG (table A2; tables A1, A2 are available online).

**Discussion**

Our results supported the hypothesis of the shrub patches as the major reservoir of seeds in the soil bank during a multiyear drought, particularly for forbs under sustained heavy grazing. On the other hand, we did not find support for the hypothesis of a faster growth of the SSB in the shrub patches than in the interpatches 2 yr after a multiyear drought event at all grazing intensities.

The enhanced seed density in the shrub patches compared with the interpatches, accentuated under sustained heavy grazing, can be attributed to reduced abiotic stress (more nutrient and water availability, less eolic erosion of soil; Bertness and Callaway 1994) and protection against herbivory (less defoliation and trampling; Milchunas and Noy-Meir 2002; Callaway et al. 2005) on the understory vegetation. According the stress-gradient hypothesis (Bertness and Callaway 1994), the beneficial effects of shrubs on the understory herbaceous vegetation are expected to be magnified in multiyear drought events, since as stress increases, the improved environmental condition in the shrub patches depart further from those in the interpatches. The combined effects of mitigating stress and disturbance forces benefit understory plant growth and seed production, potentially increasing SSB density. However, under sustained heavy grazing and prolonged drought, animals are forced to graze understory vegetation in shrub patches (Bisigato and Bertiller 1997), which
relaxes plant completion and may explain enhanced seed density, particularly of some plant functional groups like forbs in this study. Moreover, the seed redistribution caused by the wind and water from the interpatches with low vegetation produces the accumulation of seeds in the shrub patches (Aguiar and Sala 1997; Kinloch and Friedel 2005; Pazos and Bertiller 2008).

Contrary to expectation, we did not observe a faster increase of the SSB from the different plant life-form in the shrub patches as compared with the interpatches 2 yr after the multiyear drought event. Moreover, the growth in the SSB of forbs was higher in the interpatches than in the shrub patches. A possible explanation is that the structural and functional attributes of vegetation such as seed production can be strongly reduced after multiyear droughts and may constrain the ability of ecosystems to respond to a subsequent increase in precipitation (Oesterheld et al. 2001). This argument is consistent with the fact that SSB density responded in the same way to the different grazing intensity at the end of the multiyear drought (2009) and after 2 yr with precipitations close to the long-term average precipitation (2011). Also, better environmental conditions in the shrub patches than in the interpatches after the drought event may have resulted in a higher transference to the seedling bank in the former than in the latter microsite (Marone et al. 2000).

Forb seeds were the most abundant in the SSB at all levels of the studied factors (i.e., grazing intensity, year, and microsite), a phenomenon that has also been observed in rangeland communities in different parts of the world (e.g., Bertiller 1992; Gutiérrez and Meserve 2003; Solomon et al. 2006). Frequently, forbs have small isodiametric seeds with hard cover that facilitate seed penetration into and persistence in the soil (Sternberg et al. 2003; Fenner and Thompson 2005; Burmeier et al. 2010), which may explain their widespread dominance. We also observed that grazing can markedly increase the abundance of forbs in the SSB, which coincides with results from previous studies (e.g., Kinukan and Smeins 1992; O’Connor and Pickett 1992; Russi et al. 1992; Loydi et al. 2012). Grazing reduces the competitive ability of native perennial grasses and favors invasion of other native and exotic species, including forbs (Briske 1991; Corbin and D’Antonio 2004). In contrast, shrub seeds were the second most abundant in the SSB. Even though shrub seeds were much more plentiful in the shrub patches than in the interpatches, the latter microsites would gather the best environmental conditions for shrub seedling establishment under grazed conditions (Bisigato and Bertiller 1999). This would boost shrub encroachment, a common phenomenon over much of the arid and semi-arid regions of the world (Eldridge et al. 2011).

Perennial grasses were comparatively less represented in the SSB than the previous life-forms (forbs and shrubs). Normally, the persistence of perennial grasses depends to a great extent on vegetative reproduction and a relatively long life span of established individuals, which makes them less dependent on the SSB compared with annual species (Milberg 1995; Caballero et al. 2008). Also, seeds of perennial grasses have relatively limited longevity, leading to the development of short-term persistent seed banks (<5 yr; Bertiller and Aloia 1997; Peco et al. 1998; Sternberg et al. 2003). Moreover, seeds of perennial grasses can suffer high depredation by insects (particularly ants), rodents, and birds (Mayor et al. 2003; Pazos and Bertiller 2008). Nonetheless, perennial grasses were still fairly represented in the SSB—to a greater extent in the shrub patches than in the interpatches under heavy and moderate grazing conditions—at the end of the drought event. Because multiyear droughts can induce the death of established individuals of perennial grasses in semiarid ecosystems (Breshears et al. 2016; Munson et al. 2016), the SSB is important for the postdrought recovery of their populations. In contrast, overall seed density of annual grasses was rather similar to the seed density of perennial grasses, departing from the expected superiority of the former over the latter plant.
### Table 1

Results of ANOVA and LSmeans Seed Density (Seed m⁻²) in Shrub Patches and Interpatches

| Site, type         | Year | Grazing intensity | F₁,₂ | P  | F₂,₈ | P  | F₂,₈ | P  |
|--------------------|------|-------------------|------|----|------|----|------|----|
| Shrub patch:       |      |                   |      |    |      |    |      |    |
| Total              | 2009 | 10,366            | 5839 | 16,184 | 10.18 | 0.08 | 10,417 | 7481 | 13,838 | 12,185 | 8990 | 15,865 | 28,079 | 23,104 | 33,540 | 18.59 | <0.001 | 0.33 | 0.72 |
|                   | 2011 | 22,957            | 15,905 | 31,300 | 14.26 | 0.06 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
| Shrubs             | 2009 | 1862              | 1377 | 2420 | 14.26 | 0.06 | 2420 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
|                   | 2011 | 3285              | 2629 | 4014 | 5.69 | 0.14 | 4014 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
| Forbs              | 2009 | 8929              | 4,923 | 14,119 | 14.26 | 0.06 | 14,119 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
|                   | 2011 | 16,925            | 11,186 | 23,847 | 5.69 | 0.14 | 23,847 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
| Annual grasses     | 2009 | 529               | 331 | 774 | 1.92 | 0.30 | 774 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
|                   | 2011 | 357               | 198 | 363 | 1.92 | 0.30 | 363 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
| Perennial grasses  | 2009 | 459               | 355 | 577 | 4.71 | 0.16 | 577 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
|                   | 2011 | 619               | 497 | 755 | 4.71 | 0.16 | 755 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
| Interpatch:        |      |                   |      |    |      |    |      |    |
| Total              | 2009 | 10,366            | 1462 | 30,03 | 20.09 | <0.05 | 1462 | 129 | 4384 | 4,923 | 14,119 | 11,186 | 23,847 | 22,957 | 11,186 | 23,847 | 20.09 | <0.05 | 0.97 | 0.15 | 0.86 |
|                   | 2011 | 10,366            | 1462 | 30,03 | 20.09 | <0.05 | 1462 | 129 | 4384 | 4,923 | 14,119 | 11,186 | 23,847 | 22,957 | 11,186 | 23,847 | 20.09 | <0.05 | 0.97 | 0.15 | 0.86 |
| Shrubs             | 2009 | 1862              | 1377 | 2420 | 14.26 | 0.06 | 2420 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
|                   | 2011 | 3285              | 2629 | 4014 | 5.69 | 0.14 | 4014 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
| Forbs              | 2009 | 8929              | 4,923 | 14,119 | 14.26 | 0.06 | 14,119 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
|                   | 2011 | 16,925            | 11,186 | 23,847 | 5.69 | 0.14 | 23,847 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
| Annual grasses     | 2009 | 529               | 331 | 774 | 1.92 | 0.30 | 774 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
|                   | 2011 | 357               | 198 | 363 | 1.92 | 0.30 | 363 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
| Perennial grasses  | 2009 | 459               | 355 | 577 | 4.71 | 0.16 | 577 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |
|                   | 2011 | 619               | 497 | 755 | 4.71 | 0.16 | 755 | 198 | 861 | 23,067 | 1641 | 30,725 | 23,067 | 1641 | 30,725 | 18.59 | <0.001 | 0.33 | 0.72 |

Note. LSmeans seed density (back-transformed) of different floristic groups. Values in brackets indicate the confidence intervals. Different superscript uppercase letters in the same row indicate significant differences among means (P ≤ 0.05); 2009 = last year of the multiyear drought period; 2011 = second year with near-long-term average precipitation after the multiyear drought; UG = ungrazed; MG = moderate grazed; HG = heavy grazed.
life-form (Grime 2001). It is possible that the methodology employed here for quantifying SSB has led to an underestimation of annual grasses, since its main contributing species, Schismus barbatus, has very small seeds (seed mass = ca. 0.08 mg; Pake and Venable 1996). Gross (1990) argued that smaller seeds may be underestimated when using the elutriation method to recover seeds from soil samples.

In the shrub patches, species richness was increased by precipitation in the UG and depressed in the HG condition. A more stressful competitive environment in the shrub patches of the enclosure (UG condition) may explain the lowest species richness in this type of microsite at the end of the drought event (2009). Variations in species richness in UG and HG conditions were mainly due to increases or decreases in forbs and grasses, respectively (table A1), which is consistent with findings in other arid and semiarid ecosystems (Kinukan and Smeins 1992; Tessema et al. 2016).

In conclusion, in shrubby steppe of northern Patagonia the SSB was less severely depleted in shrub patches than in interpatches for the different plant life-forms at the end of a multiyear drought, particularly for forbs under sustained heavy grazing. Although at relatively low density, perennial grasses were still fairly represented in the SSB at the end of the multiyear drought. With the exception of forbs in the interpatches, 2 yr after the end of the drought there was not a significant growth of the SSB of all plant life-forms. Our results highlight the importance of grazing pressure alleviation during drought conditions for safeguarding the SSB, which is the only source of seedling recruitment for most species in northern Patagonian rangelands.

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