Applied Vegetation Science 19 (2016) 454–461

Impact of stocking rate on species diversity and composition of a subtropical grassland in Argentina

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Keywords
Controlled livestock density; Evenness; Grazed vs ungrazed; Grazing intensity; Life forms; Species richness

Nomenclature
Carnevali (1994)

Received 24 September 2014
Accepted 23 December 2015
Co-ordinating Editor: Alicia Acosta

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Abstract

Questions: What is the effect of a range of controlled stocking rates on plant species richness and diversity?

Location: Subtropical grasslands of Corrientes, Argentina, South America.

Methods: We studied the effect of three controlled stocking rates (0.6, 0.8 and 1.0 cow equivalents·ha^{-1}) on species diversity and composition during 8 yr. We calculated species diversity using the antilog of the Shannon-Wiener index, and considered its two components, richness and evenness. We also assessed the proportion of prostrate and erect species. Species abundance was based on biomass estimations.

Results: Species diversity under high stocking rates gradually decreased throughout the experiment and became nearly 50% lower than under low stocking rate. This decline was largely accounted for by changes of evenness because species richness was not affected by stocking rates. Species composition clearly diverged among the three treatments over time. Low stocking rate maintained a fairly constant relative cover of erect and prostrate grasses throughout the experiment, whereas intermediate and high stocking rate treatments were gradually and consistently enriched in prostrate grasses and forbs. These effects occurred simultaneously with drastic inter-annual changes likely driven by annual precipitation.

Conclusions: The range of stocking rates had no effect on species richness, but reduced diversity through the effect on evenness. High stocking rate progressively increased the proportion of prostrate species in the biomass.

Introduction

Grazing is a major control of grassland species composition and diversity (McNaughton 1983). In the last decades, several models aimed at explaining the effects of grazing on grasslands species richness and diversity have been proposed (Oesterheld & Semmartin 2011). Milchunas et al. (1988) proposed that species diversity peaks at intermediate grazing intensity and this response varies with primary productivity and evolutionary history of grasslands. Cingolani et al. (2005) added the multiple equilibrium model (Westoby et al. 1989), suggesting that reversibility of changes is directly related to evolutionary history of grasslands. However, these models have most often been tested on grazed vs ungrazed plant communities instead of a gradient of controlled stocking rates (Milchunas & Lauenroth 1993).

Thus, our knowledge of the effects of intermediate stocking rates, which are the range of variation most frequently found in nature or in managed grasslands, is comparatively poor. Most studies that did evaluate a gradient of stocking rates lacked control of that variable and inferred it instead from county records, interviews with local people (De Bello et al. 2007; Haynes et al. 2013), distance to drinking water (Dorrough et al. 2007; Han et al. 2008; Tarhouni et al. 2010; Peter et al. 2012), distance to herder huts (Haynes et al. 2013), density of faeces (Gonnet et al. 2003), proportion of bare ground (Thornber et al. 2008; Jones et al. 2011) or species composition (Taylor & Ralphs 1992; Li et al. 2008). Grazing gradients so measured can be only correlatively assigned to stocking rates (Adler & Hall 2005) and in some cases imply redundancy or circularity in the cause–effects relationships (i.e. abundance of vegetation adapted to grazing implying higher

Applied Vegetation Science
Doi: 10.1111/avsc.12229

stocking rates). Much less evidence on the effect of grazing comes from field trials that experimentally controlled stocking rate, were truly replicated (Hurlbert 1984) and lasted long enough to evaluate changes in species composition and structure. As a consequence, the range of variation among actual stocking rates is less understood than the effects of exclusion.

The few studies that experimentally controlled stocking rate for more than 5 yr and evaluated the effects on species diversity and composition showed various results: species diversity was maximized under intermediate stocking rates in *Stipa purpurea* alpine grasslands of Tibet (Duan et al. 2010) and upland grasslands of France (Dumont et al. 2009), while it was highest in less heavily grazed and abandoned treatments in upland grasslands of Scotland (Marriott et al. 2009). It increased with grazing intensity in mesophilous communities of the French Atlantic coast (Marion et al. 2010), while it sharply decreased under high stocking rates in semi-arid grasslands of China (Zhang et al. 2004) and did not significantly change under different stocking rates in heathlands of northern Spain (Jáuregui et al. 2008), riparian grasslands of New Mexico (Lucas et al. 2004), alpine meadows of China (Zhou et al. 2006; Zhu et al. 2008) and semi-arid grasslands of China (Ren et al. 2012). Similarly, species richness responded contrastingly to different stocking rates, increasing (Del Pozo et al. 2006; Pavlů et al. 2007), decreasing (Škornik et al. 2010; O'Connor et al. 2011) or remaining the same (Dumont et al. 2011; Liu et al. 2011; Campbell et al. 2013) with grazing intensity. This diversity of responses probably relates to the different grassland types studied, which range from sub-humid to semi-arid, tropical to temperate and lowland to upland (Milchunas et al. 1988). Subtropical grasslands of the neotropics are clearly underrepresented by this kind of study. Thus, in spite of all the evidence accumulated on the interaction grassland–grazer, there is still a large gap in knowledge on the structure and function of these ecosystems. This understanding is needed to develop ecologically based recommendations for range management and assess the appropriate stock density needed to maintain species diversity.

The subtropical grasslands in south-central Corrientes, northern Argentina, are composed of herbaceous species, mainly graminoids with fast summer growth (genera *Andropogon*, *Paspalum*, *Botriochloa*, *Schizachyrium* and *Sporobolus*; Benítez & Fernández 1977; Pizzio et al. 1986). The effect of controlled stocking rates on the structure of these grasslands dominated by *Andropogon lateralis* has not yet been evaluated. This paper aims to analyse the impact of different controlled livestock densities on the species composition and diversity of this neotropical grassland, using a mid-term experiment that encompassed climatic variations.

Methods

Study site

The experiment was carried out at the Mercedes Experimental Station (INTA, Corrientes, Argentina; 29°11′ S, 58°02′ W). According to USDA soil taxonomy, soils are vertic argiudolls, a loess type soil, from sandstone under humid conditions with a horizon mostly composed of expanding clay. Mean annual precipitation is 1478 mm, with a high inter-annual variability that has ranged from 758 to 2263 mm in the last 60 decades (Bianchi & Cravero 2010). Mean monthly temperature ranges between 13.8 °C in Jul and 25.4 °C in Jan. Vegetation is classified as a mosaic of open herbaceous savanna and prairies. The former is dominated by tall grasses (e.g. *Andropogon lateralis*) and the latter by short grasses (*Paspalum notatum*). Other species are: *Sporobolus indicus, Schizachyrium paniculatum, Paspalum plicatulum, Bothriochloa laguroides, Setaria parviflora* and *Rhynchospora praecinta*. This landscape, characterized by the presence of mosaics of patches dominated by tall and short species, covers an area of 50 000 km^2 including northern Argentina, Uruguay and southern Brazil (Purnell & Hein 1969; Carnevali 1994; Pallarés et al. 2005). Although the entire region has been subjected to grazing for several centuries, these grasslands are not considered anthropogenic. They have not been cropped and the balance between woody and herbaceous species is explained not only by grazing, but also by drainage and soil depth, since most probably there were no trees before the introduction of domestic livestock (Carnevali 1994; Pallarés et al. 2005).

Experimental design and data collection

An experimental area of 35.2 ha was divided into nine paddocks. Three livestock densities were established (0.6, 0.8 and 1.0 cow equivalents·ha^{-1}, namely low, medium and high stocking rates, respectively) by varying the size of the paddock, with three replicates per treatment. The experimental area was previously grazed under a pressure equivalent to the medium stocking rate. Low and medium stocking rates correspond to a moderate range of grazing intensities observed in the region, whereas high stocking rates would correspond to a situation of overgrazing. In Feb 1980, the treatments were applied by assigning four animals per paddock: two 8-mo-old calves and two 20-mo-old steers. Every year the steers were replaced by 8-mo calves. In this way, each animal remained for 2 yr in the paddock before being replaced. The experiment ended in Dec 1987. Throughout the experiment, grazing was continuous. Although data were collected almost 30 yr ago, the range of experimental stocking rates is the same as those currently observed in this region (Kurtz et al. 2015).

Relative biomass of each species was recorded every 2 mo on each paddock through the Botanal method (Hargreaves & Kerr 1978). For each paddock and sampling date, the proportion of all species in the biomass was visually estimated (Appendix S1). A permanent grid of imaginary lines 25-m apart was superimposed over each paddock. At each crossing point, relative biomass for each species was estimated in a 0.5 × 0.5 m plot. Since paddocks varied in size, the number of plots per paddock ranged between 44 and 82. In total, there were 557 plots per sampling date. Sampling dates were in the first half of Feb, Apr, Jun, Aug, Oct and Dec 1980–1987. The data from August were not considered in this analysis because species identification was uncertain due to the prevalence of dead biomass (end of winter). We considered the data sampled in February 1980 as the base line (Year 0).

Data analyses

For each sampling date, we averaged all plots per paddock in order to analyse the data at the paddock level, which was our truly replicated experimental unit. For each paddock and date, we calculated the Shannon-Wiener (H′) diversity index, $H' = -\sum p_i \cdot \ln(p_i)$, where pi is the relative abundance of species i in the biomass. To facilitate the interpretation of H′, we took its antilog (eH′), which is the number of species that would, if each were equally common, produce the same H′ as the sample. We also considered the two components of H′ (richness and evenness). Richness (S) was the number of species counted on each sampling date. Evenness was estimated with the Shannon index (J), where $J = H'/\ln(S)$.

To analyse changes in floristic composition, a detrended correspondence analyses (DCA; Hill & Gauch 1980) was performed for 72 units (3 treatments × 3 replicates × 8 yr) using only the data sampled in Oct (the month with the highest species richness) and downweighting for rare species. Mean relative biomass of each species in the paddock was used to carry out the DCA (Appendix S1). Each species was assigned an erect or prostrate growth form.

We analysed the effects of stocking rates by means of a linear mixed-effects model with a nested design for repeated measures (Crawley 2007). We considered six response variables: the first four were the difference between each year and the baseline (year 0) for species diversity (eH′), richness (S), evenness (J) and the proportion of erect and prostrate species (for each paddock, we calculated the difference between a given sampling date and the baseline and then averaged those differences on an annual basis). The other two response variables were the scores of the first two DCA axes. The explanatory variables for all models were stocking rate and year in the fixed term. Year nested in paddock was the random term. Hence, we tested whether the grazing treatments were responsible for the time trajectories of paddocks. As in the previous analysis, there were 72 data points per response variable (3 treatments × 3 replicates × 8 yr). The level of significance for all analyses was $P < 0.05$.

Statistical analyses were performed with R 3.1.0 (R Foundation for Statistical Computing, Vienna, AT), using packages nlme, vegan and lattice (Sarkar 2008).

Results

Throughout the experiment, species diversity decreased (time effect: $t = -3.87$, $P = 0.0003$), but the decrease was steeper in high than in low stocking rates (Fig. 1a; $t = -2.87$, $P = 0.028$). Paddocks under high stocking rate showed a consistent steep decrease, whereas paddocks under low and medium stocking rates showed more fluctuations and a shallower negative trend (Fig. 1a). Evenness also significantly decreased with time (time effect: $t = -6.76$, $P = 0.001$; Fig. 1b). In this case, both the medium and high stocking rates decreased faster than the low stocking rate ($t = 2.07$, $P = 0.083$). Species richness significantly increased with time after an initial decrease ($t = 5.23$, $P = 0.0001$) and was not affected by stocking rate ($P > 0.05$).

The DCA on species composition showed a clear gradient among growing seasons and stocking rates in the background of strong differences among paddocks (Fig. 2a). Figure 2b-d show subsets of Fig. 2a, with details of the time trajectory of each paddock. Together, these figures show that species composition of all paddocks was fairly similar at the beginning of the experiment, with most data points located in the centre left of Fig. 2a. As the experiment progressed, species composition of medium and high stocking rates differentiated from low stocking rate, with data points radiating to the right along Axis 1 and up and down along Axis 2. In most paddocks this trend was directional until year 7, and reversed by year 8. Consequently, species composition in year 7 differed most from the initial situation. Data points of both DCA axes significantly increased throughout the experiment (Axis 1: $t = 8.57$, $P = 0.001$; Axis 2: $t = 5.34$, $P = 0.0001$), thus confirming the strong species composition changes since the establishment of stocking rate treatments. The subsets show that each paddock followed a particular trajectory across years, but trajectories were wider in paddocks with medium and high stocking rates (i.e. they expanded across a broader area of the graph; notice that Axis 1 scale differs between treatments).

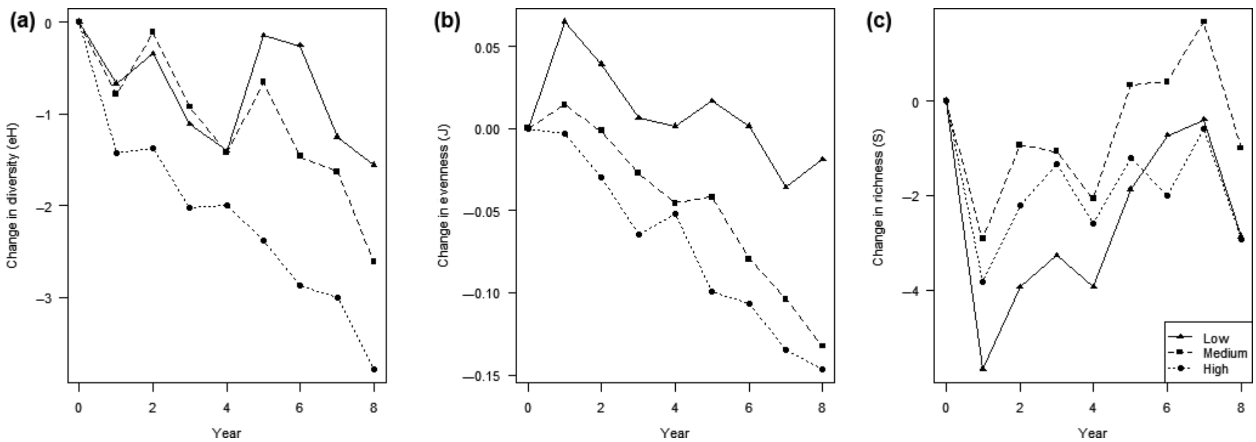

Fig. 1. Change of diversity, evenness and richness with respect to the beginning of the experiment throughout 8 yr under different stocking rates: (**a**) Species diversity, (**b**) evenness, (**c**) richness. Each point is the average of the five seasonal measurements per year ($N = 3$). At time 0, absolute numbers ranged from 6.8 to 9.7 for species diversity, 0.66 to 0.80 for evenness and 17–20 for richness.

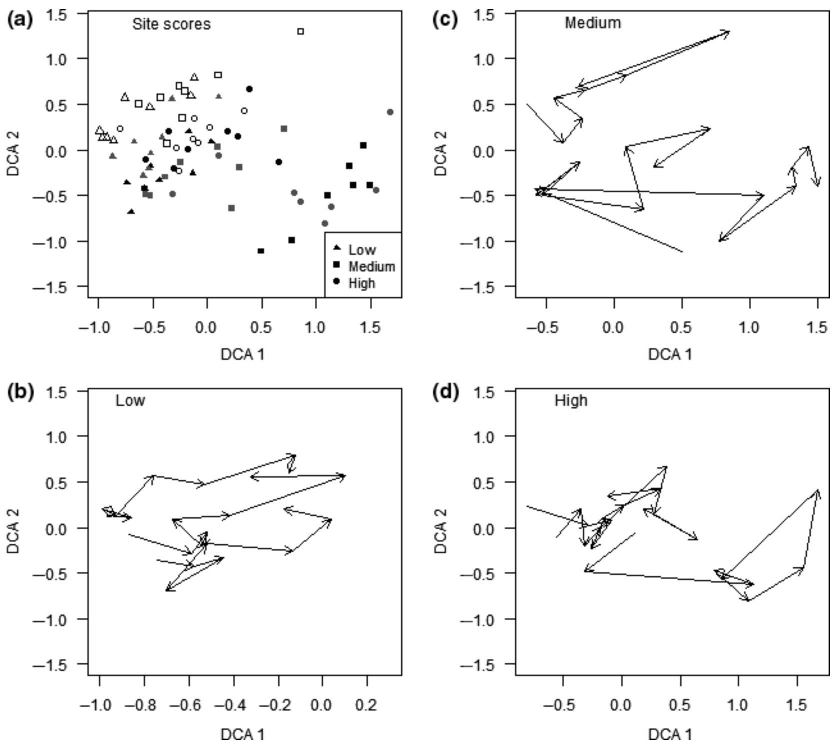

Fig. 2. Detrended correspondence analysis (DCA) of the 72 data points (3 paddocks × 3 treatments × 8 yr) based on species relative biomass: (**a**) Scores of data points in DCA Axes 1 and 2, with different symbols for different stocking rate treatments. Black, grey and open symbols refer to different paddocks within treatments; (**b–d**) subsets of data points representing low, medium and high stocking rates, showing the time trajectory of each paddock.

Composition of growth forms differed significantly among treatments and years (Fig. 3). In paddocks under low stocking rate, erect species accounted for 71% of total biomass, with little change throughout the experiment (Fig. 3a; $t = 0.331$, $P = 0.7514$). In contrast, in paddocks under high stocking rate, the relative biomass of erect species decreased from 61% at the start of the experiment to 26% at the end ($t = 3.13$, $P = 0.0026$). Medium stocking rates did not produce a significant effect on the relative biomass of erect species ($t = -0.34$, $P = 0.744$). Changes in the relative biomass of erect species necessarily reflect opposite trends in the biomass of prostrate species. In all

Doi: 10.1111/avsc.12229

treatments, the species whose relative biomass significantly decreased ($P < 0.05$) along DCA Axis 1 had an erect growth form and were mostly grasses (Appendix S1, Fig. 3b). In contrast, the species whose relative biomass significantly increased had prostrate growth form and were mostly forbs (Appendix S1, Fig. 3b). No clear pattern of growth forms emerged on Axis 2 (Appendix S1, Fig. 3b).

Discussion

We showed that the range of stocking rates likely encountered by these grasslands had no effect on species richness. In contrast, high stocking rate decreased evenness and, as a result, the species diversity values. Species composition changed throughout the experiment in response to stocking rate: under medium and high stocking rates, the relative abundance of grasses decreased and forbs increased. Time was a dominant factor, and the responses were affected by idiosyncratic differences among paddocks.

The lack of effect of stocking rates on species richness contrasts with the wide differences observed in grazed–ungrazed comparisons in grasslands with similar precipitation. For the Flooding Pampa grasslands, Rusch & Oesterheld (1997) found 70% more species under grazing than in exclosures. In the Campos grasslands of Uruguay, Altesor et al. (2005) found 45% more species in grazed than in ungrazed plots. Across a transect from Pampean to Campos grasslands, Lezama et al. (2014) observed up to 106% increases of species richness in grazed vs ungrazed situations. Most frequently, grazed communities show higher richness than ungrazed ones (Cingolani et al. 2005). The potential mechanisms by which grazers may increase species richness are diverse (Milchunas et al. 1988; Milchunas & Lauenroth 1993; Olff & Ritchie 1998): grazers may increase resource availability (light and N) and its spatial heterogeneity, and may alter the competitive balance between species. In summary, grazing precludes the establishment of competitive hierarchies and so promotes co-existence. We speculate that low stocking rate in our study was a disturbance regime strong enough to keep competitive exclusion from progressing to the point of reducing richness. In the current study, species richness was much more responsive to inter-annual variations, presumably precipitation-driven, than to grazing pressure. Coincidently, Ren et al. (2012) found that temporal variability in precipitation and temperature was more important than grazing in determining vegetation dynamics in Mongolia.

In contrast to the lack of effect on richness, high stocking rate decreased diversity through its effect on evenness. This result also contrasts with studies that compared grazed vs ungrazed situations, where grazing frequently increased the species diversity index (Rusch & Oesterheld 1997; Altesor et al. 2005; Cingolani et al. 2005). When field experiments controlled different levels of stocking rates, the responses have been diverse, as shown in the introduction (e.g. Del Pozo et al. 2006; Dumont et al. 2009; Marriott et al. 2009; Marion et al. 2010; Campbell et al. 2013). Some of these differences among studies may stem from environmental conditions of each study site. Indeed, models of the effects of grazing on plant community structure and diversity (Milchunas et al. 1988; Huston 1979) predict larger responses of species richness and diversity to stocking rates along a moisture gradient. In addition, the duration of the experiments and the delayed response of each system may account for the different responses found in the literature. For example, Zhang et al. (2004) reported an increase of species diversity indices under the high stocking rate treatments for the first 2 yr of the experiment and the opposite response after the third. Similarly, Del Pozo et al. (2006) found that species richness was maximized at intermediate stocking rates in the first 2 yr of the experiment and at high stocking rates some years later. Stocking rate experiments are logistically complex and

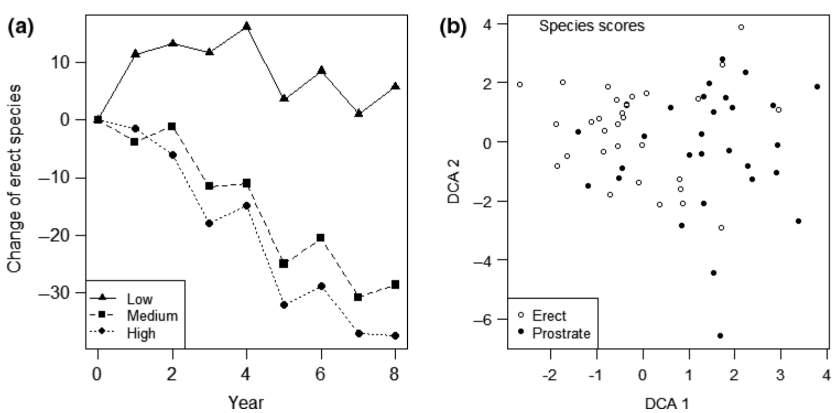

Fig. 3. (**a**) Changes of relative biomass of erect species with respect to the beginning of the experiment and throughout 8 yr under different stocking rates; (**b**) DCA species scores differentiating erect and prostrate growth forms (Appendix S1).

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Doi: 10.1111/avsc.12229 © 2016 International Association for Vegetation Science

economically expensive. As a consequence, very few last long enough to observe definite patterns. In fact, in our study, the decrease of species diversity and evenness did not reach a new steady state after 8 yr.

Community composition changed throughout the experiment, as revealed by the DCA, with prostrate species becoming more abundant under medium and high stocking rate treatments. However, idiosyncratic differences between paddocks of the same treatment and inter-annual variations also drove important changes in community composition. Erect species invest more energy in above-ground production and successfully compete for light (Milchunas & Lauenroth 1993), but are more vulnerable to grazing (Milchunas et al. 1988). Therefore, they are dominant in ungrazed or lightly grazed grasslands and are replaced by prostrate species under higher grazing intensities (Diaz et al. 2006). Prostrate species fully or partially avoid grazing and become more competitive under high grazing intensity (McNaughton 1984; Milchunas & Laurenoth 1993).

Our results show that stocking rates induced a strong species turnover (Figs 2 and 3, Appendix S1), but species losses were balanced by gains and resulted in no change of richness (Fig. 1). Erect and prostrate species had a similar proportion in the biomass under low stocking rates, but increasing stocking rates resulted in a higher dominance of prostrate species, thus reducing evenness and species diversity (Fig. 1). Although other plant functional traits can be responsible for the effect on evenness, plant height is considered one of the best predictors of species response to grassland management, and is coupled with other more relevant functional traits (Diaz et al. 2006; Klimešová et al. 2008). In general, evenness responds more rapidly to disturbance than richness, and precedes species local extinction (Hillebrand et al. 2008).

The suite of changes described above is relevant to the long-term stability of these grasslands. The increase of crop area in the Pampa and Chaco regions in Argentina during the last five decades (Viglizzo et al. 2011) increased grazing pressure on the subtropical natural grasslands that we studied (Irisarri 2012). Our results indicate that increasing grazing pressure will lead to strong changes in species composition that will most likely reduce forage quality because of the loss of palatable grasses and the increase of forbs. In addition, a reduction in species diversity through a reduction in evenness will compromise the stability of ecosystem function (Hillebrand et al. 2008).

Conclusion

Most knowledge of grazing effects on grassland community structure comes from comparisons between exclosures and grazed plots. This knowledge cannot be extrapolated to the differences in grazing intensity found within the range of stocking rates actually applied to grasslands. Changing from low to high stocking rate had no effect on species richness, but reduced diversity through the effect on evenness. Species composition changed markedly as a result of time and stocking rate. In the event of increasing stocking rates, grazing management should include careful monitoring of plant community structure and explore strategies to mitigate the adverse effects on species composition and diversity.

Acknowledgements

We thank Olegario Royo, Carlos Benitez and Juan Gregorio Fernandez, from INTA Mercedes Experimental Station. Three anonymous reviewers significantly improved the first version of this manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of all species found in the experiment, their growth habit, relative biomass at the beginning (1980) and at the end (1987) of the experiment in each treatment (%) and species scores in both DCA axes (only of those species present in Oct of any year).