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Stable states in relation to grazing in Patagonia: a 10-year experimental trial

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A 10-year sheep grazing experiment was conducted in southern Patagonia to test the hypothesis that high stocking rates would promote transitions from open grasslands to dwarf shrublands. Treatments included three stocking rates and an exclosure. Total aerial vegetation cover grew in all treatments, but especially under low stocking rates and exclosure. Short grasses and herbaceous dicots increased significantly in these last treatments. Bunchgrasses increased under low stocking rates, but decreased in the exclosure. Cover of dwarf shrubs did not change in any treatment. Diversity of the community, measured in Shannon-Wiener and species richness index, increased in the exclosure, and species richness was reduced under high stocking rates. Transitions were explored by means of PCA. While all treatments moved along the axes of the multivariate space, we detected no thresholds and found no indications of having induced transitions to alternate states with the grazing treatments imposed.

The open grasslands at our experimental site could be considered stable states induced by a century of domestic grazing, and they withstood 10 years of grazing at 0·60 sheep ha^{-1} without unfavourable transitions. Even though, loss of palatable species and diversity could indicate that moderate, variable stocking rates (average 0·40 sheep ha^{-1}) would be closer to 'sustainable' in the long-term. Vegetation seems to retain the ability to build up cover and diversity after a stocking rate reduction.

Keywords: sheep grazing; rangelands; state and transition; diversity; trend; thresholds; Patagonia

Introduction

The Magellanic Steppe covers about 3 million ha in southern Patagonia and Tierra del Fuego (Sistema Regional de Soporte de Decisiones, 1997). These grasslands are dominated by *Festuca gracillima*, a cool-season tussock bunchgrass, with a diverse associated community of up to 35 species of short grasses, herbaceous dicots and dwarf shrubs. Total vegetation aerial cover can reach 80% (Faggi, 1983; Anchorena, 1985; Roig & Faggi, 1985).

Sheep were introduced into the area around 1886 (Barbería, 1995). Forty-seven family-owned farms were established in the 1·2 million ha of the xeric variant (Boelcke *et al*., 1985) of the Magellanic Steppe, and sheep stocks increased rapidly, reaching a stable number by the turn of the twentieth century (Barbería, 1995). Continuous grazing of unherded flocks was the usual practice on these first farms and this traditional management practice has remained mostly unchanged up to the present (Barbería, 1995). The mean size of the paddocks is 5000 ha, and stocking rates range from 0·35 to 0·50 ewe equivalents ha^{-1} $year^{-1}$ (Oliva & Borrelli, 1993).

Patagonian grasslands are considered to be sensitive to grazing because of their short evolutionary history of grazing (Mack & Thompson, 1982; Markgraf, 1985). Milchunas *et al*. (1988) presented a general model that takes into account this evolutionary background but also considers that, as Coughenour *et al*. (1985) pointed out, adaptations to enhance survival in semi-arid environments may promote tolerance or avoidance of grazing. A moderate change in community physiognomy and composition is expected for Patagonian grazed grasslands in this model. Diversity (measured as species richness or other diversity indicators) is predicted to increase under light stocking rates, declining slowly from the peak as grazing increases (Milchunas *et al*., 1988).

A number of examples of grazing-induced floristic changes have been described in Patagonia. The most common tendency is an increase in shrub cover with a decrease of

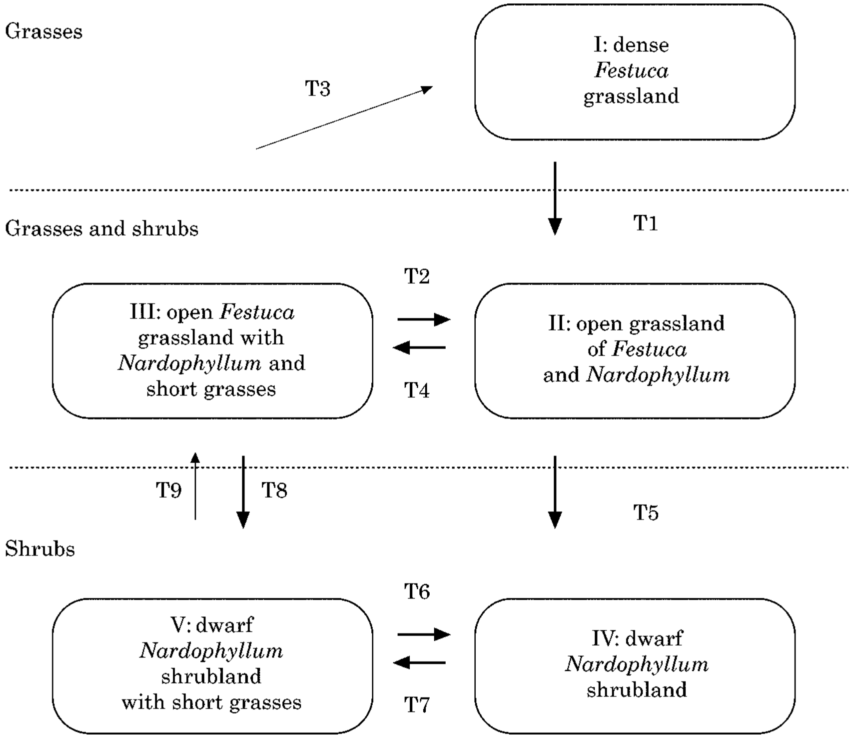

Figure 1. State and Transition model for xeric Magellanic Steppe (redrawn and simplified from Oliva & Borrelli, 1993). Dashed lines indicate thresholds between grassland and open grassland domains on one side, and open grassland and shrubland domains on the other.

grasses (Movia *et al.*, 1987; Baetti *et al.*, 1993; Bertiller, 1993; Bonvissuto *et al.*, 1993; Fernandez & Paruelo, 1993; Nakamatsu *et al.*, 1993*a,b*; Rostagno, 1993). In the Magellanic Steppe, Borrelli *et al.* (1984, 1988) studied fence line contrasts and found that overgrazed areas were dominated by dwarf shrubs, either *Nardophyllum brioides* or *Nassauvia ulicina*, and considered that 70% of the area was in fair or poor range condition. Similar trends were described by Faggi (1983), Roig & Faggi (1985) and Anchorena (1985). A State and Transition model (Westoby *et al.*, 1989) for the Magellanic Steppe was developed by Oliva & Borrelli (1993) (Fig. 1). In this model, grazing promotes transitions T1 and T5, from dense grasslands (I) to dwarf shrublands (IV). Rest allows short grasses to build up, leading to states V and III, but restoration of the initial plant community follows an alternate path and involves two additional transitions (T9 and T3) that are considered of low probability (Oliva & Borrelli, 1993).

Festuca gracillima bunchgrasses protect the soil in these wind-beaten steppes. In contrast, shrub-dominated states show low vegetation cover (Anchorena, 1985), low diversity (Faggi, 1983) and wind erosion signs (Borrelli *et al.*, 1988). Although *F. gracillima* is not a preferred species, it accounts for one-third of the sheep's intake (Borrelli, 1994; Posse *et al.*, 1996; Manero & Alegre, pers. comm.) and constitutes the only forage available in winter when ground is covered by snow.

The objective of this study was to test experimentally hypotheses about the response of the Magellanic grassland to different intensities of grazing. Our initial hypothesis at the population scale was that: (1) bunchgrasses, short grasses and herbaceous dicots would decrease, and dwarf shrubs would increase under high stocking rates. At the community scale, and based on the State and Transition model of Fig. 1, additional hypothesis were that, beginning with open grasslands of State II: (2) continuous heavy grazing would promote transition 5, leading to a dwarf shrubland of State IV; (3) moderate grazing would maintain dominance of *Festuca gracillima* and stabilize the grassland in State II; and (4) light grazing would allow short grasses to increase promoting the transition T4 into State III. In relation to diversity of the community, and according to the Milchunas *et al.* (1988), we also expected that (5) diversity (species richness and Shannon-Wiener indices) would decrease under the high stocking rate treatment.

Material and methods

Study area

A grazing trial was set up in 1986 on Estancia Moy Aike Chico, 60 km NNW from Río Gallegos (51°47′ S, 68°47′ W), on the 'Santacrucense' site (Wijnhoud & Sourrouile, 1972), within the xeric variant of the Magellanic Steppe (Boelcke *et al.*, 1985). Mean annual rainfall is 182 mm, and mean temperature is 12·7°C (De Fina *et al.*, 1968). Climate is oceanic, with low thermal amplitude and evenly distributed rainfall, with a maximum in summer (January or February) and minimum in early spring (September or November) (Burgos, 1985). Strong winds are a distinct feature, with a mean intensity of 27 km h^{-1}. These flat plateaux range from 100 to 150 m a.s.l. They present a high number of scattered depressions that collect water in the winter and early spring and dry out in summer (Anchorena, 1985).

Soils were originated from Pliocene and Pleistocene fluvioglacial sediments (Patagonian pebbles) that covered continental Miocene deposits (Scalabrini *et al.*, 1985) and could have been enriched by loess layers in the Pleistocene (Frederiksen, 1988). They are sandy and rich in organic matter in the first 10 cm. An argilic horizon with abundant pebbles lies beneath. Soils have been classified as Borolic haplargids (Salazar Lea Plaza & Godagnone, 1990).

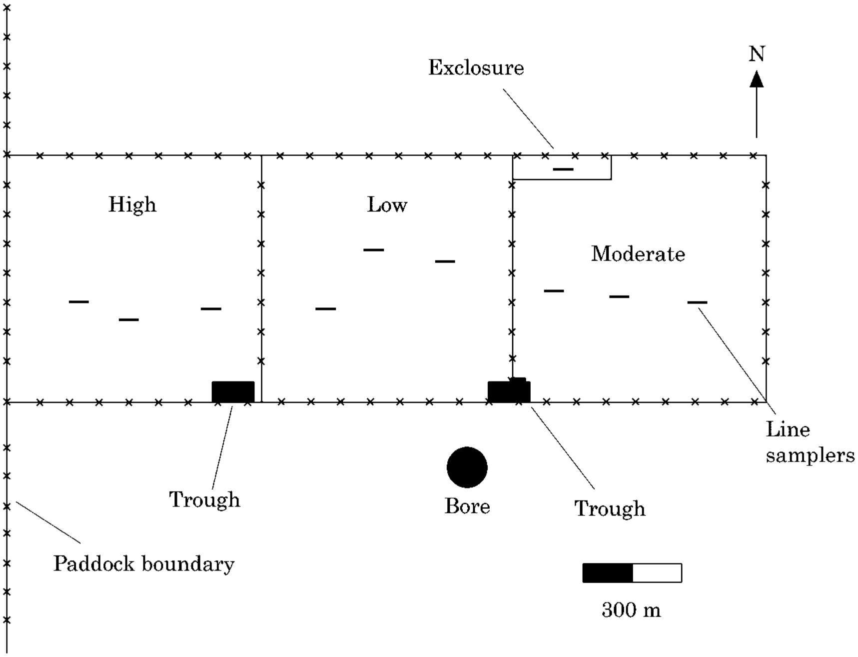

Figure 2. Diagram showing the setting of the experimental paddocks.

Treatments and design

The experimental site was within a 5000 ha paddock that had been stocked historically at a continuous rate of 0·50 ewe equivalents ha^{-1} year^{-1} (EE ha^{-1} year^{-1}) (Borrelli, pers. obs.) and was dominated by an open *Festuca* grassland (State II in Fig. 1), with patches of dwarf *Nardophyllum* shrubland (State IV). Three adjacent 40 ha paddocks were established in 1986 to begin an experimental grazing trial. Water was supplied from a pre-existing well 150 m away from the grazing trial boundary (Fig. 2). Corriedale wethers were introduced in 1987, starting three grazing intensity treatments. In 1988 a 1·5 ha exclosure was built within the moderate stocking rate experimental unit. The wethers were replaced by adult ewes of the same breed in 1990. A common high stocking rate in the area, 0·65 EE ha^{-1} year^{-1} (Oliva & Borrelli, 1993) was applied in the initial high stocking rate treatment. In 1993, it was increased to 0·75 EE ha^{-1} year^{-1}, the upper bound of real stocking rates used in a paddock scale in the drier portion of the Magellanic Steppe. Moderate stocking rate ranged between 0·34 and 0·48 EE ha^{-1} year^{-1} (mean 0·40 EE ha^{-1} year^{-1}) and was adjusted in order to leave 20 to 25 mm of *Poa dusenii* stubble height, following the methodology of Borrelli (1990) and Cibils (1993). Light stocking rate was adjusted to leave more than 25 mm of *Poa dusenii* stubble height, and ranged between 0·15 and 0·26 EE ha^{-1} year^{-1} (mean 0·21 EE ha^{-1} year^{-1}).

Sampling

Three point-quadrat lines (Levy & Madden, 1933) were installed within a central course in an eastern, central and western location of each paddock to sample the grazing gradient imposed by the sheep's tendency to graze facing the dominant westerly winds. The lines were oriented in E–W direction, with the starting point of each one randomly selected within this general location. The 50 m lines were sampled with needles every 10 cm, totaling 500 points per line and 1500 points per treatment. Needle touchs were classified as: bare ground and erosion pavement, litter, dead standing material, lichens, mosses, and living material of a particular species. The percentage of points registered on each category is an estimator of its absolute aerial cover (Levy & Madden, 1933). Observations began in April 1987 and were undertaken in autumn every 2 years until 1997. The first observation in the exclosure was made in 1989. Species were determined following Nicora (1978) and Correa (1969, 1971, 1984, 1988*a*,*b*).

Data analysis

The evolution of cover within paddocks was analysed by means of a linear regression using time as independent variable and arc-sine transformed cover as dependent variable. The population in this case was the paddock, and the experimental unit was the point quadrat line sample. The model:

$$Y_i = \beta_0 + \beta_1 X_i + e_i$$

is assumed for the line samples of each paddock, and the statistical hypothesis:

$$H_0: \beta_1 = 0.$$

tests the existence of a linear relationship between time and cover of each species or group of species. Standard tests of regression assumptions were performed. No inferential statistic tests between treatments were done because no replicates were available for the paddocks (Hurlbert, 1984). Conclusions are drawn for each paddock individually and cannot be extrapolated to all the grasslands in the area. Attributing the observed differences between paddocks to the grazing effect is done from the ecological perspective (Wester, 1992), and is a matter of discussion.

Floristic changes in point-quadrat line samples and the existence of thresholds were examined using the multivariate methodology suggested by Friedel (1991). A standardized matrix of species cover was calculated. Fourteen species that accounted for 3% cover or more were included in the analysis, together with estimates of litter, bare soil and total vegetation cover. Principal Components Analysis was performed using the line samples as individuals. Eigenvalues and Eigenvectors were calculated using the PRINCOMP program included in the SAS package (SAS/STAT Institute Inc., 1988).

Diversity was assessed using the species richness index (total number of species recorded in each 500 point line sample) and the Shannon-Wiener index:

$$H' = -\sum pi \ln pi$$

where pi = relative cover of species i (Magurran, 1989).

Results

Rainfall during the experiment was variable. The first 3 years constituted a dry period that finished in 1990. From 1990 to 1992 precipitation was above the mean (Fig. 3), while in subsequent years it was alternatively below and above average.

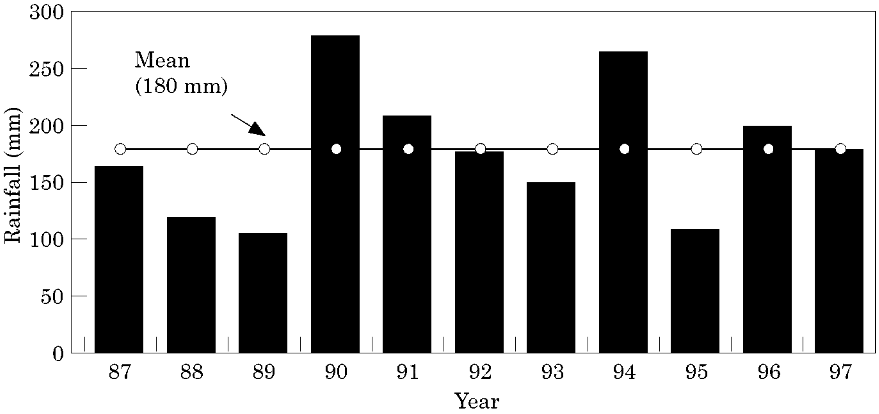

Figure 3. Annual rainfall during the grazing trial.

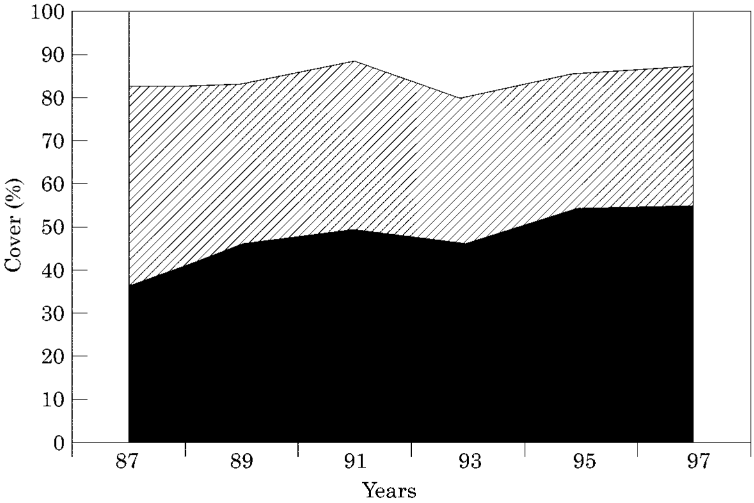

Figure 4. Vegetation cover (■), bare soil (▨) and litter (□) in all the treatments between 1987 and 1997. The slopes of the regressions of increase in vegetation cover and decrease in bare soil over time are significant at $p < 0{\cdot}001$ ($R^2 = 0{\cdot}338$ and $R^2 = 0{\cdot}167$, respectively). Regression for litter is non-significant.

Total vegetation cover

Initial mean vegetation cover was 36%, but it increased to 55 % by 1997 (Fig. 4). The increasing trend of cover and the reduction of bare ground were significant for the grazing trial as a whole (Fig. 4). Thirty-five long-lived perennial species and one biennial species were recorded. A few annual species such as *Erophila verna* or *Thlaspi* sp. were observed in springtime and were not present at the sampling dates, but they do not constitute an important forage resource.

The absolute initial cover of the paddock subjected to moderate grazing was 10% higher than the ones that were grazed with low and high stocking rates (Fig. 5). The

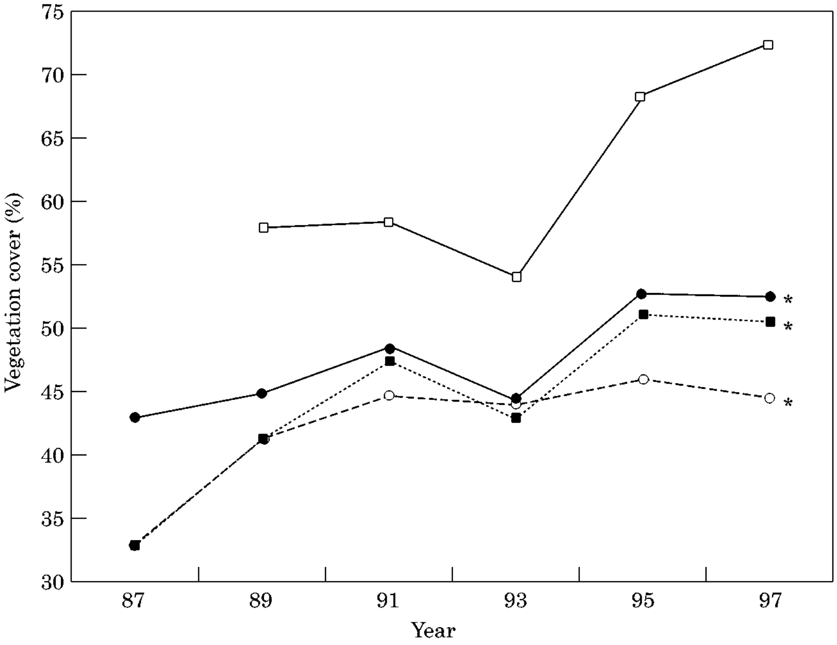

Figure 5. Evolution of cover in paddocks subjected to high (○), moderate (●) and light (■) grazing intensities and exclosure (□) (means). Asterisks indicate that the slope of the linear regression time × cover of the strata is significant in that paddock.

initial cover values for the exclosure were not recorded, but were probably close to those of the moderate grazing paddock because it was built within its boundaries.

Vegetation cover increased significantly within our paddocks (Table 1), except in the exclosure where the increase was noticeable ($R^2 = 0{\cdot}640$) and cover reached 70% total in 1997 but the regression was not significant due to the reduced degrees of freedom (Fig. 5; Table 1). In the paddocks under low and moderate stocking rates, about half of the ground was covered by vegetation in 1997. The paddock under high stocking rate followed this general trend in the first 4 years, but after 1990 its cover fluctuated around 45%.

Cover by strata

Bunchgrass cover was not reduced in the high stocking rate paddock (Fig. 6(a); Table 1). It only increased significantly in the low stocking rate treatment. Initial cover of bunchgrasses in the exclosure was 25%, and was reduced significantly to 15% by 1997, probably due to increased competition from short grasses and herbaceous dicots. Cover of dwarf shrubs did not change in any treatment during the experiment (Fig. 6(b)). Short grasses and herbaceous dicots showed a very marked increase in the exclosure, where they accounted for over 50% of the absolute cover by 1997. In the low stocking rate paddock (Fig. 6(c); Table 1) they also increased significantly, and their cover approached 25%, the value of the moderate stocking paddock. Under high stocking rates, cover of this palatable stratum built up in the first 4 years, but then fluctuated around 14% (Fig 6(c)).

Table 1. R^2 *coefficients for the regression time × cover of categories sampled by the point-quadrat lines, within paddocks subjected to different treatments. Shaded areas denote significant changes and asterisks indicate the significance under the hypothesis that the slope is null. The sign of the slope is indicated in parentheses*

	Grazing intensity			
	High	Medium	Low	Exclosure
Total vegetation cover	(+) 0·432**	(+) 0·440**	(+) 0·641**	(+) 0·640 NS
Bare ground	(−) 0·132 NS	(−) 0·203 NS	(−) 0·665**	(−) 0·845*
Bunchgrasses	(+) 0·108 NS	(+) 0·129 NS	(+) 0·465*	(−) 0·743*
Short grasses and herbs	(+) 0·211 NS	(+) 0·080 NS	(+) 0·401**	(+) 0·862*
Dwarf shrubs	(+) 0·001 NS	(−) 0·007 NS	(−) 0·006 NS	(−) 0·604 NS
Species richness	(−) 0·285*	(+) 0·024 NS	(−) 0·123 NS	(+) 0·899*
Shanon-Wiener index	(−) 0·026 NS	(+) 0·016 NS	(−) 0·057 NS	(+) 0·919**

*$p < 0{\cdot}05$; **$p < 0{\cdot}01$; NS = not significant.

Cover by species

Three species are dominant in the community: *Festuca gracillima* (11·28% absolute cover), *Nardophyllum brioides* (9·53% abs. cover) and *Poa dusenii* (11·21% abs. cover) dominate the bunchgrass, dwarf shrub and short grass strata, respectively. The changes in cover of these species in our experimental paddocks follow closely the trend described in Table 1 and Fig. 6 for their respective vegetation stratum.

Within each stratum, some less dominant species show a contrasting response to our treatments (Table 2). The palatable short grass *Rytidosperma virescens* (0·83% abs. cover) decreased in the moderate and high stocking rate paddocks. *Bromus setifolius* (0·65% abs. cover) behaved in a similar manner, although its changes were not significant. The juncaceae *Luzula chilensis* (0·13% abs. cover) decreased significantly, and disappeared altogether in the 1997 readings of the high stocking rate paddock. The palatable sedge *Carex andina* (1·13% abs. cover) increased significantly in all the treatments except under high stocking rates. In contrast, the unpalatable short grass *Festuca pyrogea* (1·80% abs. cover) increased significantly in the high and moderately grazed paddocks. Within the dwarf shrub strata, a similar increase under high stocking rates was observed in *Colobanthus lycopodioides* (0·30% abs. cover).

Diversity of vascular plants

Diversity, as measured by the Shannon-Wiener index, increased significantly in the exclosure (Table 1) and decreased (although non-significantly) in the high stocking treatment. By 1997 the latter was clearly separated from the rest (Fig. 7(a)). Moderate

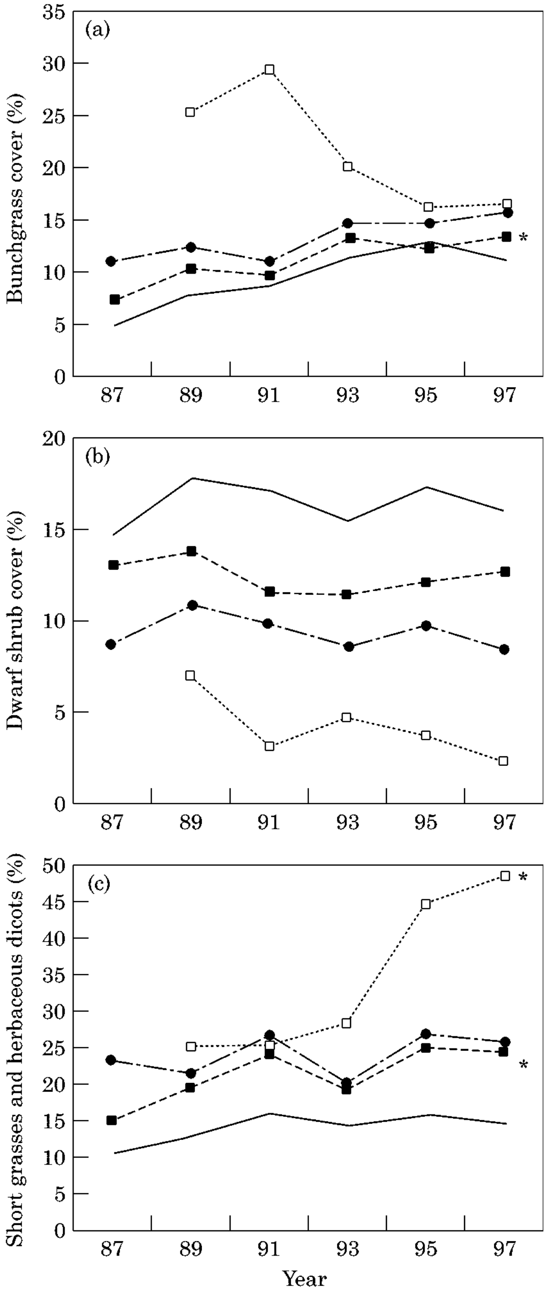

Figure 6. Evolution of cover of (a) bunchgrasses, (b) dwarf shrubs and (c) short grasses and herbaceous dicots in paddocks subjected to high (—), moderate (●) and light (■) grazing intensities and exclosure (□) (means). Asterisks indicate that the slope of the linear regression time × cover of the strata is significant in that paddock.

and low stocking rate treatments maintained, with fluctuations, their values for this index throughout the experiment (Fig 7(a); Table 1).

Species richness followed a similar trend. It increased significantly in the exclosure,

Table 2. R^2 *coefficients for the regression time × cover of species sampled by the point-quadrat lines, within paddocks subjected to different treatments. Shaded areas denote significant changes and asterisks indicate the probability under the hypothesis that the slope is null. The sign of the slope is indicated in parentheses*

		Grazing intensity			
		High	Moderate	Low	Exclosure
Bunch-grasses	*Festuca gracillima*	(+) 0·108 NS	(+) 0·133 NS	(+) 0·461**	(−) 0·743 NS
Dwarf shrubs	*Nardophyllum brioides*	(+) 0·004 NS	(−) 0·004 NS	(+) 0·001 NS	(−) 0·018 NS
	Colobanthus lycopodiodes	(+) 0·238*	(+) 0·341*	(+) 0·104 NS	(−) 0·286 NS
Short grasses	*Poa dusenii*	(+) 0·202 NS	(+) 0·005 NS	(+) 0·604**	(+) 0·625 NS
	Rytidosperma virescens	(−) 0·361*	(−) 0·274*	(−) 0·019 NS	(+) 0·574 NS
	Bromus setifolius	(−) 0·065 NS	(−) 0·024 NS	(+) 0·191 NS	(+) 0·536 NS
	Festuca pyrogea	(+) 0·543*	(+) 0·490**	(+) 0·042 NS	(+) 0·093 NS
Grami-noids	*Luzula chilensis*	(−) 0·222*	(−) 0·169 NS	(−) 0·201 NS	(+) 0·460 NS
	Carex andina	(+) 0·177 NS	(+) 0·252*	(+) 0·559**	(+) 0·849*
Dicots	*Cerastium arvensis*	(+) 0·163 NS	(+) 0·018 NS	(−) 0·003	(−) 0·448 NS

*$p < 0{\cdot}05$; **$p < 0{\cdot}01$; NS = not significant.

and by 1997 it reached the highest value, with 21 species. The high stocking rate paddock, on the contrary, lost species significantly and only 13 species were recorded in the 1997 reading (Fig. 7(b); 1).

Principal Components Analysis

Component I (PC I) accounted for 33% of the variation and Component II 12%. The first PC was strongly and positively related to total vegetation cover and species including the main bunchgrass *F. gracillima*, the dominant short grass *Poa dusenii*, and the small palatable sedge *Carex andina* (Table 3). Bare soil and the dwarf shrub *Nardophyllum brioides* were correlated negatively to this axis.

The second Principal Component was related negatively to a dwarf shrub *Nassauvia darwinii* and the short grass *Hordeum comosum*. It related positively to the cover of *Festuca pyrogea* and *Colobanthus lycopodioides* (Table 3).

The movement of the trend line samples in the space created by PC I and II is shown in Fig. 8. For the sake of clarity, we present trajectories of the different treatments separately, even though they were grouped in the analysis. The exclosure was set up in 1988, so the starting point corresponds to the 1989 assessment, after a

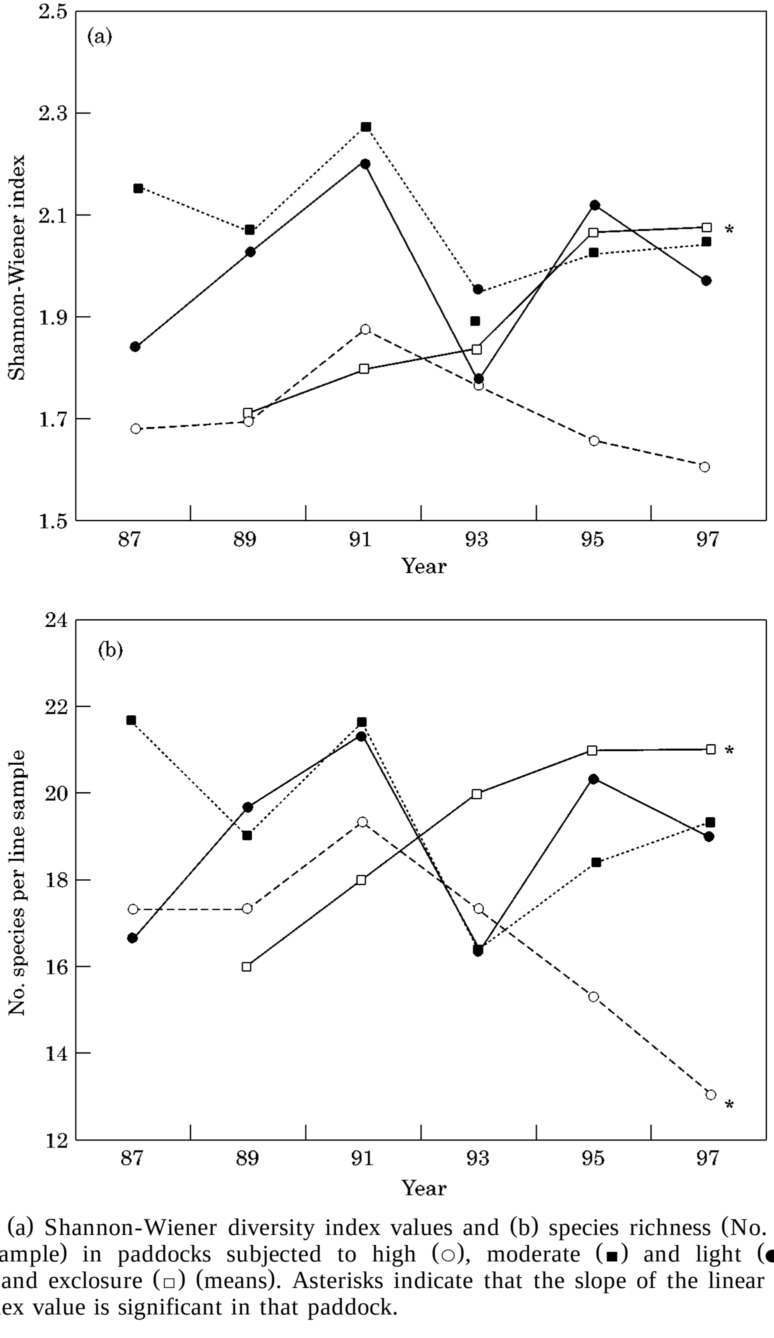

Figure 7. (a) Shannon-Wiener diversity index values and (b) species richness (No. of species per line sample) in paddocks subjected to high (○), moderate (■) and light (●) grazing intensities and exclosure (□) (means). Asterisks indicate that the slope of the linear regression time × index value is significant in that paddock.

year of grazing exclosure. The starting point of the line samples of the moderate and exclosure treatment line samples had a higher value for PC I, due to the fact that these paddocks had a higher initial cover than the ones that were used for high and low stocking rate treatments.

The exclosure line sample moved towards the positive side of PCI and II (Fig. 8). This movement can be explained by the increase of total species cover. Low and

Table 3. *The ten characters with the greater contribution to the Eigenvectors of Principal Components I and II. An estimation of forage value of the species (Manero & Alegre, pers. comm.) is included*

PCI

Species/character	Species description	Forage value	Contribution to PCI
Total vegetation cover	–	–	(+) 0·366
Carex andina	Sedge	High	(+) 0·313
Festuca gracillima	Bunchgrass	Intermediate	(+) 0·311
Poa dusenii	Short grass	High	(+) 0·307
Acaena sp.	Herb	High	(+) 0·292
Bromus setifolius	Short grass	High	(+) 0·274
Cerastium arvensis	Herb	High	(+) 0·265
Rytidosperma virescens	Short grass	High	(+) 0·259
Nardophyllum brioides	Dwarf shrub	Low	(−) 0·310
Bare soil	–	–	(−) 0·340

PCII

Species/character	Species description	Forage value	Contribution to PCII
Festuca pyrogea	Bunchgrass	Intermediate	(+) 0·394
Colobanthus licopodiodes	Dwarf shrub	Low	(+) 0·333
Total vegetation cover	–	–	(+) 0·288
Nardophyllum brioides	Dwarf shrub	Low	(+) 0·245
Carex andina	Sedge	High	(+) 0·219
Cerastium arvensis	Herb	High	(−) 0·182
Rytidosperma virescens	Short grass	High	(−) 0·193
Litter	–	–	(−) 0·280
Hordeum comosum	Short grass	High	(−) 0·385
Nassauvia darwinii	Dwarf shrub	Low	(−) 0·454

moderate stocking rate line samples followed the same trend, although in this case there was a tendency to move to higher values of PCII. High stocking rate line samples remained on the negative side of PCI, and showed a moderate tendency to increase PCII values, due to a buildup of *Festuca pyrogea* and *Colobanthus lycopodioides* that behaved like increasers (Table 2).

Thresholds were not evident, as the movement of the line samples in the ordination space was linear, and did not stabilize to indicate that an alternative state had been reached (Fig. 8).

Discussion

Vegetation cover behaviour in relation to stocking rates

A regional or landscape-scale process could be driving the general increase in vegetation cover in all of our treatments (Fig. 4; Table 1). Plant establishment and growth processes of perennial bunchgrasses, short grasses, graminoids and herbaceous dicots (Fig. 6(a–c); Table 2) are involved in these cover shifts, and they could have long-lasting effects in the vegetation structure.

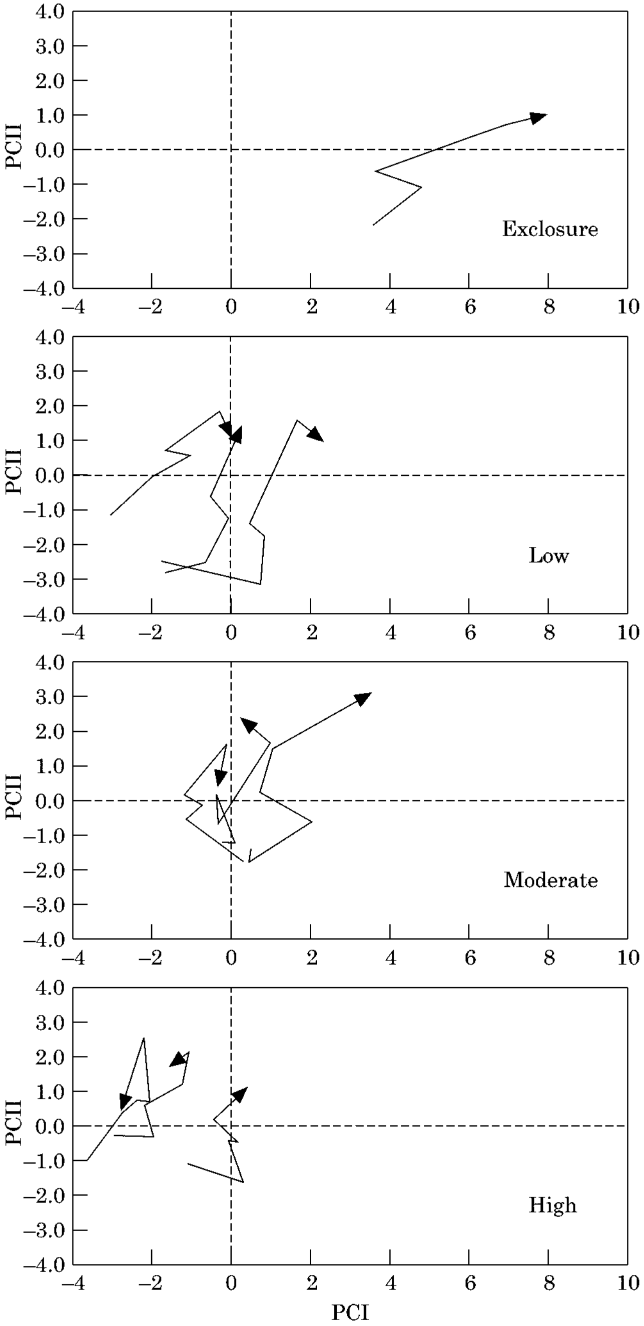

Figure 8. Trace of the time trend of each line sample in the space defined by the first two Principal Components. Traces start in 1987 position, and the arrows point to the last observation in 1997. The exclosure line sample starts in 1989. Main characters contributing to the Eigenvectors of the Principal Components are shown in Table 1.

A long-term climatic fluctuation could be an explanation for the cover modification, but no increase in rainfall was apparent. De Fina *et al.* (1968) analysed the 1950–60 meteorological data and estimated by interpolation that the mean rainfall in Moy Aike had been 182 mm, a figure that matches our 1987–1997 average (Fig. 3).

Alternatively, our results could be explained by the fact that historic distribution of grazing in the area was uneven. Our grazing trial was built close to a watering point (Fig. 2) not far from the western side fence of a typical 5000 ha paddock that had historically been stocked at a mean rate of 0·50 EE ha^{-1} $year^{-1}$ (Borrelli, pers. obs.). Western areas of paddocks are usually overgrazed due to the fact that sheep tend to face the dominant WSW winds while grazing. The communities in our experiment could have actually experienced a rest effect, as the real historic grazing pressure at this site was surely higher than the paddock mean, and possibly higher than 0·62 EE ha^{-1} $year^{-1}$, our high stocking rate treatment. A historical gradient of use could also explain the initial differences between the experimental units. Cover in 1986 in the moderate stocking rate paddock was 10% higher than the other two grazing treatments (Fig. 4). This could presumably be explained by the relative position of this paddock as it was the most distant from the watering point and from the western boundary fence (Fig. 2).

This likely history of high animal concentrations in the experimental area may have predisposed the response of the grasslands in our 10-year grazing trial. In particular, the cover of short grasses and herbaceous dicots, a vegetation stratum that constitutes up to 50% of the forage intake (Posse *et al.*, 1996), was not reduced in the high stocking rate paddock (Table 1). The bunchgrass cover did not follow the expected reduction, and the dwarf shrubs did not increase in this treatment either. On the other hand, the vigorous increase in the short grasses and herbaceous dicots in the paddocks under low stocking rate and exclosure (Fig. 6(c)) probably indicates that these species were under pressure in the grazed community and were able to increase in cover when utilization rates were reduced.

Grazing-induced transitions

The communities of the high stocking rate paddock fluctuated least in the multivariate space of the PCA (Fig. 8). The light, moderate and exclosure treatments showed larger shifts in PCI, a trend that is related to the increase in short grasses and herbaceous dicots (Table 3). It is noteworthy that other studies using the same methodology in Australia found that the floristic composition on highly grazed areas fluctuated much more in relation to moderately stocked ones (Foran *et al.*, 1986; Friedel, 1991). These differences could be related to the previous conditioning by a long history of grazing of the sites, and to the fact that Patagonian grasslands are dominated by perennial grasses. The long-lived populations integrate disturbances over a long period of time, as opposed to the annual-dominated communities of central Australia that respond promptly to rainfall and grazing in pulse-decay functions (Westoby, 1980).

The changes under exclosure and low grazing intensities could be interpreted in relation to the State and Transition model for the Magellanic Steppe (Fig. 1) as T4 transitions from open grasslands with *Festuca* and *Nardophyllum* (State II) to communities with increased dominance of short grasses (State III). No increase in shrub cover, as required for T5, was observed. The model suggested that the initial transition (T1) between the supposed pristine community (the dense *Festuca* grassland, State I) and the open grassland of *Festuca* and *Nardophyllum* (State II) was not reversible. Our results conform to this model because the increase in cover of bunchgrasses after 10 years of low stocking rates is moderate (Fig. 6(a)) and the process is not likely to restore bunchgrass cover to the 40% of the State I (Oliva & Borrelli, 1993). On the other hand, it is interesting that in the exclosure the bunchgrass cover actually decreased significantly (Fig. 6). Total withdrawal of grazing would not restore the 'original' grassland, but establish a secondary community with shared dominance of bunchgrasses, short grasses and herbaceous dicots.

Although physiognomy of the highly grazed areas did not change, a closer analysis reveals contrasting strategies of species in relation to grazing (Table 2). Most short grasses declined in the high stocking rate paddock, although not all of the changes were significant (*Luzula chilensis*, *Rytidosperma virescens* and *Bromus setifolius* are examples), but *Festuca pyrogea* significantly increased cover in the high and moderate stocking rate paddocks. The dwarf shrub *Colobanthus lycopodioides* also increased (Table 2). These species have low palatability (Manero & Alegre, pers. comm.) and seem to be capable of colonizing bare patches of soil (Oliva, pers. obs.), so they can take advantage of the disturbance caused by grazing.

Vascular plant diversity in relation to stocking rates

The most noticeable effects of the high stocking rate treatment was a species richness reduction (Table 1), as palatable species such as *Luzula chilensis* or *Rytidosperma virescens*, present in the initial line quadrat readings, became very rare or disappeared altogether in the late observations (Table 2). The exclosure, on the contrary, showed increased species richness due to the palatable short grasses, such as *Agropyron patagonicum*, *Agrostis inconspicua*, *Trisetum cumingii* or *Deschampsia flexuosa*, that were not recorded initially but were detected in the late point-quadrat readings. In addition, the equitability of cover distribution within the community increased as the bunchgrasses cover decreased and short grasses and herbs built up (Tables 1 and 2). Both effects are manifest in the increased values of Shannon-Wiener diversity index (Table 1; Fig. 7).

The observed decline in diversity of the community under higher stocking rates conforms to the Milchunas *et al.* (1988) model for semi-arid rangelands with a short history of grazing and to the observations of Schlichter *et al.* (1978) who also found that grazing induced a decrease in species richness, diversity and equitability when they compared 20-year exclosures and areas with light and heavy grazing in Chubut, Patagonia. The importance of this diversity loss under real management situations is nevertheless controversial due to the fact that grazing in real paddocks is not evenly distributed (Senft *et al.*, 1984; Ash & Stafford-Smith, 1996). The observed reduction of diversity at the community scale could be balanced with the increased heterogeneity generated by grazing at the landscape scale (West, 1993) that provides refuges for rare palatable plant populations, as well as disturbed habitats suitable for species such as *Festuca pyrogea* or *Colobanthus lycopodioides* that increase in highly grazed treatments (Table 2).

Sustainable management

The grasslands analysed could have reached a stable state after more than a century of continuous grazing at intensities of 0·50 EE ha^{-1} year^{-1} or more. Walker & Noy-Meir (1982, p. 556) defined a stable system as 'one that changes very little over time, and that responds slowly to outside pressure'. On the other hand, they defined a resilient system as 'one that can change quite markedly as a result of a disturbance, but that then returns towards its original equilibrium condition'. The open grasslands in our paddocks could be regarded as stable states, and within their domain of attraction they could prevent the grassland system from moving to the shrubland domain, at least under the range of grazing pressures that we applied.

This stability was not expected because clearly the thresholds into shrublands have been reached in the recent grazing history in the Magellanic Steppe. The area exhibits a patchwork of degraded dwarf shrublands that are supposed to be originated from high grazing pressures (Borrelli *et al.*, 1984, 1988; Anchorena, 1985; Oliva & Borrelli, 1993). Similar shrub increases have also been described elsewhere in Patagonia by Leon & Aguiar (1985), Bertiller & Deffossé (1993), Bonvisutto *et al.* (1993), Paruelo & Golluscio (1993), Fernandez & Paruelo (1993), Nakamatsu *et al.* (1993*a*,*b*) and Rostagno (1993). These states could have been reached by accumulation of small changes over long periods, such as the reduction in the size structure that interferes with the vegetative growth of dominant bunchgrass populations (Oliva, 1996). They could also result from occasional periods of high stress, such as combinations of drought and grazing, or from unusually high grazing intensities generated by stock concentration in certain areas of the landscape, such as waterholes, northern-faced slopes or the eastern side of N−S oriented fences. All these possibilities need further research as our grazing trial does not provide evidence about the nature of the shrubland−grassland transition.

The stability of the open grasslands suggests that a ‘sustainable’ (WCED, 1987) use for continuous grazing could be feasible under the entire range of stocking rates we applied, but animal production issues have to be taken into account to establish management practices that are also sustainable from the social and economic points of view (Goodland, 1993). High stocking rates would be economically rewarding, since wool production in the 0·60 sheep ha^{-1} paddock was higher on a per ha basis (Borrelli *et al.*, unpublished) and wool is the main source of income of the farms in southern Patagonia (Barbería, 1994). There is however a risk of using wool production as a guideline for management in discontinuously stable systems. As Noy-Meir (1975) pointed out, in these cases animal productivity is only reduced after the unfavourable transitions take place, and is not therefore a sensitive indicator of the state of the system. A reduction in the diversity and in the cover of palatable species such as *Luzula chilensis* could be regarded as unavoidable under grazing at commercial stocking rates, but could also be an early warning of degradation processes in the community (Soriano, 1956). On the other hand, the variable stocking rates of our moderate stocking treatment, that were adjusted annually in relation to forage availability and averaged 0·40 sheep ha^{-1}, obtained highest meat and wool production per animal and also higher meat production per ha (Borrelli *et al.*, unpublished). The increased potential for diversification, and the fact that communities did not lose diversity or highly palatable species, suggest that they are most likely to be sustainable rates in the long-term.

The exclosure and low stocking rate treatments do not provide information from a productive point of view, but they are relevant for future conservation plans. Even these small communities showed a tendency to build up cover of grasses and herbaceous dicots and to incorporate rare, palatable species that are not usually found in grazed areas. The ability to respond to lowered grazing pressures is an important characteristic, taking into account that the Magellanic grasslands are not included in the network of protected areas of Argentina.

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