Research article

Can livestock grazing maintain landscape diversity and stability in an ecosystem that evolved with wild herbivores?

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A B S T R A C T

The livestock industry is converting mountain ecosystems in central Argentina into rocky deserts. However, it helps to conserve plant biodiversity, presumably because the ecosystem has evolved under wild herbivores now locally extinct. We hypothesized that low or moderate livestock stocking rates, instead of the high stocking rates currently used for commercial production, might mimic pre-hispanic herbivore pressures. Thus, the mosaic of physiognomies necessary to maintain landscape diversity and soil integrity could be preserved. To test this hypothesis we tracked physiognomic changes in 200 plots (16 m² each) under different stocking rates, including livestock exclusion, for five years. Contrary to our expectations, we found that both low and moderate stocking rates failed to maintain landscape diversity. As observed for livestock exclusion, low to moderate stocking rates promote retraction and, finally, elimination of short grazing lawns and their replacement by tall tussock grasslands, or possibly by woody vegetation. In turn, heavy grazing pressure maintains the desired short lawn patches in the landscape, but also promotes a concomitant loss and eventual elimination of woodlands, together with an expansion of bare rock as a consequence of soil erosion. These results indicate that the present mosaic of physiognomic types is difficult to maintain and raise questions about the past stability of the ecosystem. We suggest that during the last 400 years of livestock production in the ecosystem, short lawns have been maintained by means of heavy stocking rates and anthropogenic fires ignited to eliminate tussocks. However, this relative stability of lawns has been attained concomitantly with a progressive loss of soils and woodland area. We also discuss some possible explanations for the maintenance of short lawns before the introduction of livestock, based on main climatic and floristic shifts during the late Holocene.

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Introduction

Livestock grazing may be necessary to maintain rangeland ecosystem structure and function when native wild herbivore populations are decimated or extinct, or if livestock presence is ancient in the ecosystem (Perevolotsky and Seligman, 1998; Cingolani et al., 2005a, 2008a). In productive grasslands, the absence of grazing disturbance can lead to the dominance of a few large and competitive plant species, reducing alpha diversity (Milchunas et al., 1988; Osem et al., 2002; Cingolani et al., 2005a, 2008a; Altesor et al., 2006). Additionally, the accumulation of standing and dead biomass may alter fire regimes in undesired ways (Hobbs et al., 1991). Conversely, intense trampling by livestock, uneven animal distribution and excessive plant consumption can produce irreversible ecosystem degradation, even in productive ecosystems (Mwendera et al., 1997; Cingolani et al., 2005a, 2008a). If not evolved under heavy grazing of large herbivores, productive ecosystems may collapse under livestock maintained at commercially optimal stocking rates (Diamond, 2005; Cingolani et al., 2005a, 2008a; Lunt et al., 2007). In such cases, native plant diversity might only benefit from light livestock grazing, i.e. with densities well below the commercial optimum (Milchunas et al., 1988; Cingolani et al., 2005a).

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The upper belt of Córdoba Mountains (Argentina), in southern South America, is a productive ecosystem composed of a mosaic of tall grasslands, short lawns, woodland patches and rocky areas (Cingolani et al., 2003, 2004). Contrasting evidence complicate the classification of this ecosystem as having "long" or "short" evolutionary history of grazing (*sensu* Milchunas et al., 1988). On the one hand, this area was continuously occupied by large herbivores since geological times (Díaz et al., 1994). After the extinction of Pleistocene mega-herbivores about 10 000 years ago, the ecosystem sustained populations of wild middle-sized herbivores, such as camelids (*Lama guanicoe*) and deer (*Ozotoceros bezoarticus*), until their local extinction at the beginning of the 20th century (Medina, 2006; Medina and Rivero, 2007). Additionally, it was suggested that local inhabitants raised domestic camelids (*Lama glama*) in the area before the European settlement; and finally, domestic European livestock were introduced in these mountains, about 400 years ago (Díaz et al., 1994). In line with this background, the rapid loss of alpha diversity in grassland communities when livestock are excluded supports the idea that vegetation is adapted to herbivory (Díaz et al., 1994; Pucheta et al., 1998a; Cingolani et al., 2003, 2010). The tolerant response of most grazed plants, including the dominant tree *Polylepis australis* Bitter, provided further support for this hypothesis (Díaz et al., 2001; Cingolani et al., 2007; Giorgis et al., 2010). On the other hand, alternative evidence challenges the idea of a long evolutionary history of heavy grazing. Archaeological studies indicate that populations of wild camelids declined progressively in the area during the Holocene, as human populations grew and hunting pressure increased (Medina and Rivero, 2007). Additionally, Medina et al. (2007, cited in Pastor et al., 2012) analyzed bone remains and did not find convincing evidence of pre-hispanic rise of domestic camelids. These records suggest that the introduction of European domestic livestock represented a rapid increase in grazing pressure, generating a novel impact on the system. In agreement with the latter view, we have observed that livestock introduction has triggered soil erosion processes, still active, which are driving the system into a rocky desert (Cingolani et al., 2008b; Cáceres, 2009; Cingolani et al., 2013). Moreover, heavy consumption of *P. australis* by livestock seems to have contributed to woodland retraction, despite tolerant response of this species to moderate browsing levels (Teich et al., 2005; Renison et al., 2006; Cingolani et al., 2008b; Giorgis et al., 2010).

Since these findings reveal negative effects on ecosystem properties driven either by livestock exclusion or by high stocking rates, we surmised that the system is adapted to low or moderate grazing pressure, but not to the high grazing pressures exerted by livestock in large portions of the area (Cingolani et al., 2008b). Therefore, we hypothesized that low or moderate livestock grazing pressures can mimic the pre-hispanic herbivore grazing, preserving the mosaic of physiognomic types necessary to sustain landscape plant diversity and wildlife (Cingolani et al., 2008a, 2010). We tested this hypothesis by tracking physiognomic changes under different livestock grazing pressures for five years. This was facilitated by the creation of a National Park, where livestock were maintained or re-introduced in some areas, with different management schemes, while excluded in others (APN, 2007). In the present contribution we aim to analyze how livestock stocking rate and timing of grazing influence changes in plant physiognomy. We predict that (1) grazing exclusion will produce an expansion of woody plants and tussock grasses, and a retraction of bare rock and short lawn-forming plants; (2) low or moderate stocking rates will prevent directional physiognomical changes, i.e. will maintain a stable mosaic; and (3) high stocking rates will produce an expansion of lawn-forming short plants and bare rock, along with a retraction of woody plants and tussock grasses. In our analysis, we also considered the influence of site and landscape physical properties on physiognomic changes.

Methods

Study area

The study was conducted in the upper belt of Córdoba mountains (1700–2800 m a.s.l.), in part of the Quebrada del Condorito National Park and surrounding private properties (Córdoba Province, Argentina, Fig. 1). At 2200 m a.s.l. mean temperatures of the coldest and warmest months are 5.0 and 11.4 °C, respectively, with no frost-free period. Mean annual precipitation is 900 mm, mostly concentrated in the warmest months, from October to April (Cabido, 1985; Colladon et al., 2010). During the study period (2004–2009), hydrologic year rainfall (September to August) was similar to or lower than the long term average (908, 901, 771, 834 and 868 mm, from the first to the last study year, respectively, Colladon et al., 2010). The landscape is a mosaic of woodlands, grasslands, rocky outcrops and erosion stone-lands. Woodlands are generally small patches dominated by *P. australis*. Grasslands can be dominated by tall tussock grasses, such as *Poa stuckertii* (Hack.) Parodi, *Deyeuxia hieronymi* (Hack.) Türpe and *Festuca* spp., or by forbs and short graminoids (i.e., short grasses, sedges and rushes) in which case they are called "grazing lawns" (*sensu* McNaughton, 1984). Rocky outcrops have variable levels of plant cover, including all life-forms, whereas erosion stone-lands are always scarcely vegetated (Cingolani et al., 2004). Most species within the local flora are characteristic of this upper mountain belt and a good number of them are endemics (Cabido et al., 1998). In some portions of the National Park, livestock were maintained or re-introduced in an attempt to prevent loss of plant diversity and excessive biomass accumulation, which can trigger wildfires (APN, 2007). Different livestock management schemes have been implemented, involving variable stocking rates and timing of grazing (Table 1, Fig. 1). In the surrounding, privately owned areas stocking rates are generally higher than inside the National Park, and fire is often used to reduce tussock cover and stimulate regrowth. These private properties are part of National and Provincial Reserves, which were created as buffer areas for the National Park, but few effective conservation actions have been taken in these areas.

Sampling design and field measures

In September 2004 we established 142 permanent plots (4 m × 4 m). In September 2005 and 2006 we added 40 and 18 plots, respectively, totalling 200. We distributed the plots in fenced paddocks or areas limited by natural boundaries (hereafter named "paddocks" for simplicity), with variable stocking rates and timing of grazing (Fig. 1, Table 1). Plots were representative of paddocks' vegetation and topography, except that we did not select tall closed woodlands or sites completely dominated by rock or in very steep slopes. At the initial date some plots contained two or more physiognomies (e.g. short lawn and tussock grassland). The land-use history up to the start of our study was not homogeneous across paddocks. Within the National Park, most paddocks under livestock grazing were the result of approximately five years of the same management practice. The age of exclosures at the initial date, both within and outside the National Park, varied between two and five years. In turn, plots under livestock grazing located outside the National Park had a longer and uninterrupted history of livestock grazing, which is more difficult to track.

At plot set up, we measured slope aspect (degrees from the North), slope inclination (%) and soil depth (cm). We also
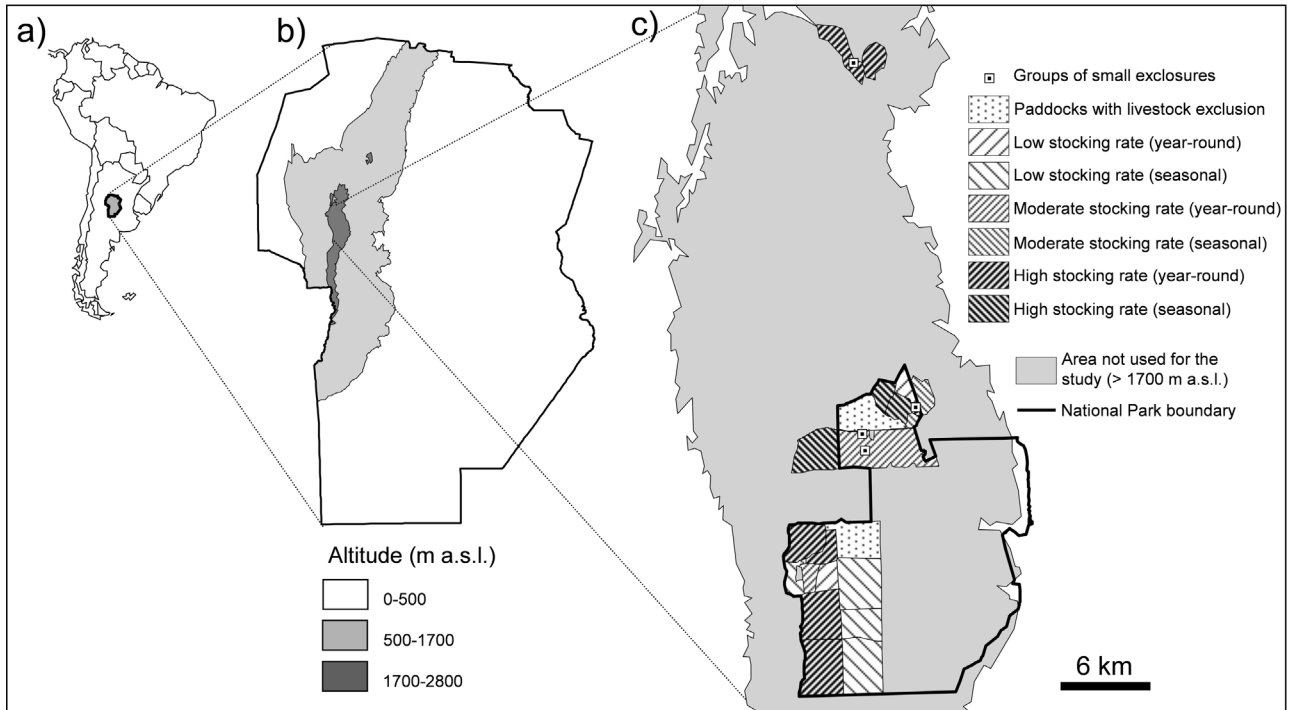
Fig. 1. Location of Córdoba province in Argentina, South-America (a), location of Córdoba mountains in Córdoba province (b), and study area location, with central point at 31° 30′ S, 64° 49′ W, within Córdoba mountains (c). In the last map, study paddocks with different ranges of stocking rates and timing of grazing are indicated.

measured location and altitude (m a.s.l.) with a Global Positioning System. To characterize the surrounding landscape of each plot in an area of 900 m² or larger, we obtained different landscape variables from a Geographic Information System (GIS): slope inclination (%) and indices of insolation, roughness and topographic position (Cingolani et al., 2008b).

From the initial date (2004, 2005 or 2006) and every year thereafter until 2009, we visited each plot in September to standardize the estimations at the driest and most inactive period of the year. We qualitatively categorized soil moisture from 1 (very dry) to 5 (wet), following Cingolani et al. (2003). We then averaged data of all years to have a relative estimation of the soil moisture content of each plot. At the same dates, we estimated the cover percentage of the following 10 vascular plant growth forms: trees (*P. australis* and *Maytenus boaria* Molina); shrubs (*Berberis hieronymi* C.K. Schneid., *Satureja* spp., *Gaultheria poeppigii* DC. and others); tall forbs (mainly suffruticose species,

such as *Stevia* spp., *Achyrochline* spp. and one vine); cacti (*Gymnocalycium* spp.); ferns (*Blechnum* spp. and others); thick-leaved tussock grasses (mainly *P. stuckertii*, which has broader and thicker leaves than other tussock grasses, hereafter "thick tussocks", see Table 5); thin-leaved tussock grasses (mainly *D. hieronymi* and *Festuca* spp.; hereafter "thin tussocks"); perennial graminoids (*Carex* spp., *Bromus* spp., *Chascolytrum subaristatum* (Lam.) Desv. and others); annual graminoids (mainly *Muhlenbergia peruviana* (P. Beauv.) Steud.); and short forbs (*Lachemilla pinnata* (Ruiz & Pav.) Rothm., *Eryngium nudicaule* Lam. and others). We also estimated the cover of lichens (not considering those on rocks), mosses, litter, bare soil and bare rock. In all cases cover was estimated to the nearest 5% (10%, 15%, 20%, etc.), except for low cover values (<10%), which were estimated to the nearest 1%. When cover was far less than 1%, we recorded 0.1%. The total sum of cover values may exceed 100% because the canopies of the different plant growth forms can overlap.

Table 1

Distribution of the 200 study plots according to annual stocking rate (categorized arbitrarily only for descriptive purposes) and timing of grazing. The number of paddocks included in each category and the conservation areas to which they belong are included in the last two columns.

No. of plots	Annual stocking rate (CU ha⁻¹)[a]	Timing of grazing[b]	No. of paddocks	Conservation area[c]
36	Exclusion (0.00–0.02)	–	6[d]	NP–PP
13	Low (0.08–0.18)	Year-round	2	NP
31	Low (0.08–0.18)	Seasonal	4	NP
49	Moderate (0.18–0.23)	Year-round	2	NP
8	Moderate (0.18–0.23)	Seasonal	2	NP–PP
45	High (0.23–0.35)	Year-round	7	NP–PP
18	High (0.23–0.35)	Seasonal	3	NP–PP

[a] CU ha⁻¹: cattle units per ha of non-rocky surface during the study.
[b] Timing was different in all paddocks with seasonal livestock grazing, varying from only one to nine months with livestock in different periods of the year.
[c] NP: National Park; PP: private properties within National and Provincial Reserves.
[d] Sites with livestock exclusion were distributed in two large livestock-free paddocks, and in four groups of different (but closely associated) small exclosures, within the grazed paddocks.

Data processing and analyses

Physiognomic changes

To track physiognomic changes, we first reduced all the cover variables estimated in the field into five physiognomic categories: (1) "woody plants", which resulted from summing up trees, shrubs, cacti, tall forbs and ferns, (2) "thick tussocks", (3) "thin tussocks", (4) "short herbaceous plants" (hereafter "short plants"), which resulted from summing up short forbs, short perennial graminoids and short annual graminoids, and (5) bare rock. We excluded bare soil, lichens and mosses from the analyses because they cover very small proportions of the plots. We included ferns with woody plants because they were absent in most plots but when present, they had low cover and were strongly associated with woody species (data not shown). In all the other cases, the merged growth forms were structurally similar but also showed a strong co-variation among them (data not shown), so the reduction into five categories produced almost no information loss.

For each of the 200 plots, we calculated the cover change rate of each physiognomic category as the slope of a linear regression between time and cover (%year^{-1}). We discarded September 2009 data for 22 plots that were burned during a wildfire in July of that year. Therefore, and because the initial date also was variable among plots, for 121 plots slopes were calculated from six dates (i.e. a five-year period from 2004 to 2009), for 58 plots slopes were calculated for a four-year period (2005–2009, or 2004–2008) and for the remaining 21 plots slopes were calculated for a three-year period (2005–2008 or 2006–2009). Positive values of slopes indicate a cover increase during the period, negative values a cover reduction, and close to zero values indicate that the physiognomic category under analysis remained relatively constant.

Stocking rate and seasonality index

For each paddock, we calculated monthly stocking rate (Cattle Units per ha of non-rocky surface, hereafter CU ha^{-1}) from September 2004 to August 2009, based on detailed data provided by National Park administration and land owners. From this monthly data we calculated the annual stocking rate for each plot, according to the paddock where the plot was located. We also calculated the winter stocking rate (from July to September, the driest period of the year) and the summer stocking rate (from January to March, the wettest period of the year). To obtain stocking rate averages, we considered the actual monitoring period of each plot. For example, for plots monitored from 2005 to 2009 we averaged stocking rates from September 2005 to August 2009, whereas for plots monitored from 2004 to 2008 we averaged stocking rates from September 2004 to August 2008. Thus, even in the same paddock, some plots had slightly different stocking rates than others. From data on winter and summer stocking rates we calculated a "seasonality index" (SI) for each plot as:

$$SI = \frac{WSR - SSR}{WSR + SSR + 0.01}$$

where WSR was the winter stocking rate, and SSR was the summer stocking rate. Thus, plots in paddocks used only in winter had positive values close to 1, plots in paddocks with continuous stocking rate or permanent exclusion had values of zero or close to zero, and those used only in summer had negative values close to −1.

Statistical analyses

To aid in the interpretation of results, we performed descriptive statistics of the initial cover values for the five physiognomic categories, across the set of 200 plots. We also analyzed the co-variation among the initial values of the five categories through pair-wise Pearson correlations.

Using mixed models (Maxwell and Delaney, 2004; Seltman, 2013) we analyzed the effects of annual stocking rate, seasonality, and initial physiognomy on physiognomic change. Cover change rates of the five physiognomic categories (woody plants, thick tussock grasses, thin tussock grasses, short plants, and bare rock) were the dependent variables, and paddock was the subject variable. Independent variables/terms were (1) initial cover of the category under analysis, (2) squared initial cover, (3) annual stocking rate, (4) interaction between annual stocking rate and initial cover, (5) interaction between annual stocking rate and squared initial cover, (6) seasonality index and (7) interaction term between seasonality index and annual stocking rate. The inclusion of the initial cover values, their squared terms and the interaction terms was based on an exploratory visual analysis of scatter-plots. We selected a combination of terms to explain the cover change rate of each category using a manual backward stepwise procedure, discarding non-significant variables/terms ($p > 0.05$), and redundant random-effects. Once the variables/terms were selected, we explored if site and landscape variables explained additional variability in cover changes. Therefore, we added to the models, in a forward stepwise procedure, the following physical site and landscape variables, retaining only the significant ones ($p \leq 0.05$): local slope (%); soil depth (cm); soil moisture index (dimensionless); altitude (m a.s.l.); landscape slope (%); landscape insolation index (dimensionless); landscape roughness (dimensionless) and landscape topographic position (%) (Cingolani et al., 2008b). After selecting final models, we explored the normality of residuals and their Euclidean spatial autocorrelation using Moran index (Diniz-Filho et al., 2003). We interpreted the results of the models using sensitivity plots.

Finally, we performed correlation analysis between change rates, to interpret the change of each category relative to the changes of the others. For each physiognomic category, we excluded plots with initial cover less than 10% because they showed little or no changes in response to stocking rate (see *Results* section).

Results

Initial cover of physiognomic categories

Initial cover varied from 0% to 70% and 75% for woody plants and bare rock, respectively, and from 0% to ca. 100% for the other three physiognomic categories (Table 2). Thin tussocks and short plants were present in most plots and had the highest average cover, whereas woody plants were absent or with low abundance in most plots. Woody plants and bare rock were loosely but positively correlated, indicating that both physiognomic categories tended to co-occur at the initial date. Most of all the other pair-wise correlations among initial cover values were negative and significant. Generally, up to four physiognomic categories were present in a plot (i.e. mean value was 3.5 categories per plot), and those plots with the highest number of categories included bare rock and woody species. Conversely, plots that tended to be dominated by short plants had the lowest number of categories (Table 2).

Mixed models

The change rates of all physiognomic categories except thin tussock grasses were explained by a combination of initial cover and annual stocking rate (Table 3). In the four cases (woody plants, thick tussocks, short plants and bare rock) annual stocking rate explained change rates only if interacting with the initial cover value and/or its squared term. Thus, when these categories were absent at the initial date (i.e. no cover), annual stocking rate produced no effect on change rates. Additionally, seasonality index, soil moisture and

Table 2
Descriptive statistics for the initial cover values of each physiognomic category, and for the total number of categories per plot (last column). For the five physiognomic categories, the first row indicates the proportion of plots in which the category was present. Their pair-wise Pearson correlations (r-values) with each other, and with the number of categories per plots, are also included in the last five rows.

| | Cover (%) | | | | | |
	Woody plants	Thick tussocks	Thin tussocks	Short plants	Bare rock	No. categories per plot
Presence (%)	41	61	96	98	49	–
Mean	4.4	16.5	32.9	34.1	10.1	3.5
Median	0	1	21	23	0	4
Range	0–69	0–100	0–102	0–101	0–75	1–5
Correlations	r					
Woody plants	–	−0.18*	−0.08	−0.26*	0.31*	0.25*
Thick tussocks	–	–	−0.26*	−0.43*	−0.28*	−0.12
Thin tussocks	–	–	–	−0.43*	−0.28*	−0.00
Short plants	–	–	–	–	−0.16*	−0.28*
Bare rock	–	–	–	–	–	0.43*

* $P \leq 0.05$.

landscape slope helped to explain some of the changes. For the four significant models, the explained variance varied from 14% to 37% if only the fixed effects were considered, and from 20% to 45% when both fixed and random effects were considered (Table 3). For all models, residuals had a slightly higher Kurtosis than expected for a normal distribution, because of the high number of cases with initial cover values close to zero. Since repetitions of all analyses eliminating data with zero initial values attained a normal distribution of residuals and gave very similar results (data not shown), we decided to maintain the original analyses using all data, for the sake of better comparability among results. Residuals were not positively autocorrelated, according to the Moran Index based on the inverse of the Euclidean distance, indicating that results are not flawed due to spatial dependence (Diniz-Filho et al., 2003).

Responses to stocking rate

Woody plants, when present at the initial date, increased under livestock exclusion and low stocking rates (<0.12 CU ha^{-1}), which was evidenced in the positive values of their cover change rates (Fig. 2a). With higher stocking rates, woody plants retracted, as shown by the negative values of their cover change rates. Either the increase or the decrease was faster with higher initial woody cover (see the different slopes of the lines in Fig. 2a). Additionally, the advance of woody plants was facilitated on steep slopes, whereas

their retraction was facilitated on gentle slopes (Table 3). The difference in the variance explained considering fixed effects only, or fixed plus random effects (8%) indicates that, besides the above-mentioned variables, unmeasured characteristics of the paddock have some influence on cover changes (hereafter "idiosyncratic paddock effects"). The change rate of woody plants was significant and negatively correlated with change rates of most of the other physiognomic categories (Table 4). These correlations indicate that when woody plants advanced in response to livestock exclusion or reduction, they replaced bare rock, thin tussocks and short plants; and conversely, when woody plants retracted in response to moderate or high stocking rates, they were replaced by these cover categories.

Thick tussocks advanced or remained stable in most of the plots (Fig. 2b). The models indicated that this category, when initially present in the plots, advanced faster with livestock exclusion, particularly when the initial cover was close to 50%. As stocking rate increased, the advance of thick tussocks was slower. With the highest stocking rates considered in this study, thick tussocks tended to remain stable or even slightly decrease if initial cover was close to 100% (Fig. 2b). The potential of a high stocking rate to stabilize thick tussocks was strengthened when animals were concentrated in winter months, and was weakened when animals were concentrated in summer months (Fig. 2b). Additionally, soils with high moisture facilitated the advance of thick tussocks (Table 3). The

Table 3
Mixed models for the cover change rate of the five physiognomic categories. All the coefficients included in the models represent the fixed effects (i.e. average slopes) of each variable/term, and were significantly different from zero ($P \leq 0.05$). Intercepts did not differ from zero ($P > 0.05$) for any cover change rate, except for short plants.

| | Cover change rate of physiognomic categories | | | | |
	Woody plants	Thick tussocks	Thin tussocks	Short plants	Bare rock
Intercept (fixed effect)	−0.01	−1.21	−0.16	2.10	−0.06
[Initial cover]	0.07	0.42	ns	−0.05	−0.06
[Initial cover]^2	ns	4.3×10^{-3}	ns	ns	ns
[Annual stocking rate]	ns	ns	ns	ns	ns
[Seasonality index]	ns	ns	ns	ns	ns
[Initial cover] × [annual stocking rate]	−0.64	−1.03	ns	ns	0.21
[Initial cover]^2 × [annual stocking rate]	ns	0.01	ns	1.2×10^{-3}	ns
[Seasonality] × [annual stocking rate]	ns	−5.21	ns	ns	ns
[Soil moisture]	ns	0.60	ns	−0.65	ns
[Landscape slope]	0.06	ns	–	–	–
Random effects[a]	I	S(ic)	–	I	S(ic)
r^2 (fixed effects only)	0.37	0.37	–	0.14	0.16
r^2 (fixed + random effects)	0.45	0.38	–	0.20	0.36

ns: not significant terms ($P > 0.05$), discarded from the models.

[a] Non-redundant random effects included in the models: I: intercept; S(ic): slope for the initial cover. Random effects represent the idiosyncratic between-paddock variability in intercepts and/or slopes.
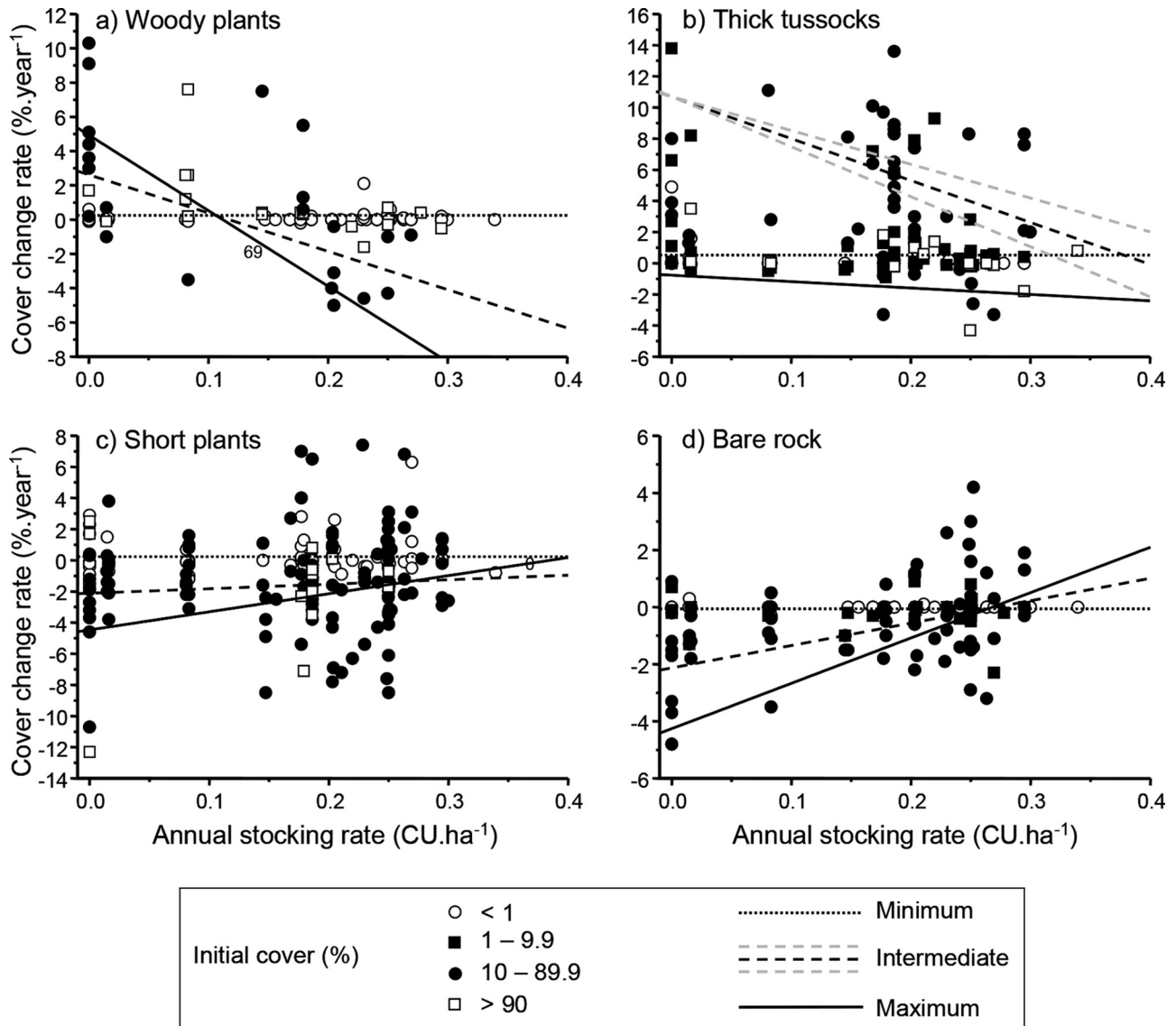
Fig. 2. Change in cover of (a) woody plants, (b) thick tussocks, (c) short plants and (d) bare rock against annual stocking rate for the 200 plots. In all figures, each sampling plot was represented with a different symbol according to its initial cover (%) of the four respective physiognomic categories. Initial cover was arbitrarily subdivided into four classes for illustrative purposes only. In the four figures, lines were drawn based on the mixed models considering minimum, intermediate and maximum initial cover values of the respective physiognomic categories. In all cases, the minimum value was equal to zero, the maximum value was variable depending on the category considered (see Table 2), and the intermediate value represented half of the maximum. In (b) the black lines were drawn assuming a year-round grazing (i.e. seasonality index = 0), and lower and upper grey lines were drawn assuming that animals were concentrated in winter (seasonality index = 1) or in summer (seasonality index = −1) respectively. For thick tussocks and short plants, soil moisture index was considered constant, with the average value across the 200 plots (2.8), and the same was done with landscape slope for woody plants (average across all 200 plots: 5.4%).

Table 4

Pearson correlations (r-values) of the cover change rates of the four physiognomic categories that responded to stocking rate (thin tussocks excluded) with the change rates of the other four categories (thin tussocks included). For each of the four categories, the analysis was performed excluding plots with initial cover < 10%. When correlations were performed with all 200 plots, the trends were similar but weaker.

	Woody plants change	Thick tussocks change	Short plants change	Bare rock change
N[a]	23	58	138	67
Woody plants	–	0.06	−0.09	−0.51[*]
Thick tussocks	0.13	–	−0.39[*]	−0.25[*]
Thin tussocks	−0.45[*]	−0.71[*]	−0.49[*]	0.05
Short plants	−0.53[*]	−0.37[*]	–	0.10
Bare rock	−0.68[*]	−0.16	−0.01	–

[a] Number of plots considered in the analysis (i.e. initial cover ≥ 10%).

[*] $P \leq 0.05$.

difference in variance explained considering only fixed effect or fixed plus random effects is almost null (1%), indicating the absence of idiosyncratic paddock effects on changes in thick tussocks. Correlations with the change rates of the other categories indicated that when thick tussocks advanced, they mainly replaced thin tussocks and secondarily short plants (Table 4).

Short plants showed both negative and positive change rates in the individual plots (Fig. 2c). However, on average, this physiognomic category tended to decrease (i.e. negative average change rates were observed in the regression lines), even at the highest stocking rates considered in this study. The strongest reduction was observed when initial cover was high and soils were moist (Fig. 2c, Table 3). The differences between variance explained with and without random effects (6%) indicated some idiosyncratic paddock effects on changes in short plants. Correlations showed that when short plants retracted, they were replaced mainly by thin tussocks, and secondarily by thick tussocks (Table 4).

Rock cover increased in response to stocking rates >0.25 CU ha^{-1} and decreased with lower stocking rates (Fig. 2d). The strongest response was detected with high initial rock cover, whereas little response was observed with low initial cover, even at high stocking rates. Site and landscape variables did not contribute to explain changes, but paddock idiosyncratic effects were important (20%) to explain the expansion or retraction of bare rock. Correlations with other cover change rates indicated that when bare rock expanded, it mainly replaced woody plants. Likewise, when bare rock retracted, it was mainly replaced by woody plant canopy.

Discussion

Were our predictions confirmed by our results?

This study is the first attempt to measure vegetation change in the area over time under different management scenarios, and provides much more detailed information than previous studies about mechanisms that explain vegetation dynamics. As expected, we found that plant physiognomy is consistently modified in response to stocking rate. However, our predictions were only partially supported by our results. We confirmed that livestock exclusion produces an advance of woody plants and tall tussock grasses, and a retraction of bare rock area and short lawn-forming plants. We also confirmed that high stocking rates promoted a retraction of woody plants and an expansion of bare rock. However, we did not find the expected stabilization of short plants and tussock cover at low to moderate stocking rates, but rather an advance of tussocks at the expense of short plants at all stocking rates except the highest ones (>0.3 CU ha^{-1}), when some stabilization occurred.

Response to grazing exclusion

An advance of woody vegetation and/or tall grasses with grazing exclusion or very low stocking rates is not surprising and has been reported for a wide variety of ecosystems (e.g. Hansson and Fogelfors, 2000; Fuhlendorf et al., 2001; Altesor et al., 2006; Bakker and Moore, 2007; Collantes et al., 2013; but see Walker et al., 2003). This result is consistent with the global grazing synthesis reported by Díaz et al. (2007), showing that a release from grazing pressure favours tall plants. In our study area, woody vegetation replaced thin tussocks and short plants, but also advanced over bare rock surfaces due to the lateral expansion of individual plant canopy (A.M. Cingolani, personal observation). These results are in agreement with previous studies. When released from livestock, net growth (in terms of biomass, volume, or plant height) and seed production of small and medium-sized *P. australis* trees strongly

increase, as well as survival of saplings (Teich et al., 2005; Giorgis et al., 2010; Pollice et al., 2013). Likewise, the increase of tall grasses replacing short plants in response to grazing release has been widely reported for sub-humid or semi-arid ecosystems, including our study area, particularly if tall woody plants are absent or in low abundance and therefore cannot colonize the site (McNaughton, 1983; Pucheta et al., 1998a; Fuhlendorf et al., 2001; Díaz et al., 2001; Cingolani et al., 2003, 2007; Osem et al., 2004; Pavlů et al., 2006; Kohyani et al., 2011).

The increase in standing biomass after grazing release intensifies competition for light; this fact has been proposed as the ultimate cause of the replacement of short plants for taller plants, either grasses or woody species (Westoby, 1998; Weiher et al., 1999). In our study area tall grasses have low specific leaf area (SLA) and high leaf toughness compared with most short herbaceous species (Díaz et al., 2001; Cingolani et al., 2007; Table 5). These attributes suggest that tall grasses are more shade- and litter-tolerant than short plants (Fynn et al., 2011). Since accumulated litter is one order of magnitude higher, and light availability at the soil level one order of magnitude lower in closed tussock grasslands than in short lawns (Vaieretti et al., 2013, and unpublished data), we can speculate that besides occupying space, tussocks create an exponentially more hostile environment for short plants as they advance. Considering plant height at maturity, it would be expected that woody plants outcompete tussocks after a prolonged time of grazing exclusion. We did find an advance of woody plants over thin tussocks in this situation, but not over thick tussocks. The immediate reason for this is that woody plants and thick tussocks seldom co-occurred in the plots at the initial date (only in 18% of the plots, and in most cases with very low cover values of one of them or both). Both growth forms are segregated in the landscape; while thick tussocks tend to occur on flat and smooth plateaus, woody plants are generally clumped near rock outcrops, steep slopes or deep ravines where they find protection from livestock browsing and fires (Renison et al., 2002, 2006; Cingolani et al., 2008b). This lack of co-occurrence makes it difficult to evaluate any hypothesis about a possible advance of woody plants over thick tussocks, particularly considering the short seed dispersal of *P. australis* trees (up to 10 m from the seeder tree; Torres et al., 2008; Zimmermann et al., 2009). Yet, some previous reports suggest that under a low-disturbance regime, in the long term *P. australis* woodlands would replace thick tussock grasslands on well drained soils (Renison et al., 2005; Torres et al., 2008; Cingolani et al., 2008b; Zimmermann et al., 2009; Landi and Renison, 2010).

In our study area, only woody plants and thick tussock grasses advanced with grazing exclusion, whereas thin tussocks did not show any consistent response to grazing intensity. In fact, the response of thin tussocks seems to be dependent on the presence and response of the other physiognomic categories. Under grazing exclusion they can replace lawns (Pucheta et al., 1998a; Cingolani et al., 2003), but they can also be replaced by thick tussocks or woody plants, as shown by the correlations between change rates (see Table 4). Early studies about plant communities in the area had interpreted the widespread *D. hieronymi* thin tussock grassland as the climax community, whereas the *P. stuckertii* thick tussock grassland was interpreted as an edaphic community associated with poorly drained soils (Cabido, 1985; Cabido et al., 1987). Later studies, as well as the present findings, challenge this assumption. *P. stuckertii* is indeed favoured under high soil moisture conditions, as shown by our results, but it can also dominate in well drained soils, advancing at the expense of thin tussocks or short plants after some years of livestock exclusion (Cingolani et al., 2003). Hence, in the absence of grazing by large herbivores, thick tussocks can dominate large portions of the landscape, a fact that is currently evident in the National Park (Flores et al., 2012). Thin tussocks of *D.*

Table 5
Plant attributes of the most abundant species of tall tussocks and short plants in the study area (data from Cingolani et al., 2007).

	Plant	Leaf attributes				
	Height (cm)	Area (mm^2)	SLA (mm^2 mg^{-1})	Width (mm)	Toughness (N mm^{-1})	Thickness (mm)
Tall tussocks						
Poa stuckertii	85	2099	5.8	6.3	7.4	0.37
Festuca lilloi	76	178	4.6	0.9	17.9	0.20
Deyeuxia hieronymi	66	108	9.0	1.3	15.6	0.29
Short plants						
Muhlembergia peruviana	4	5	13.4	1.0	2.0	0.15
Alchemilla pinnata	3	253	13.6	2.7	0.6	0.24
Carex fuscula	5	498	16.5	5.8	2.7	0.22

SLA: specific leaf area.

hieronymi and *Festuca lilloi* Hack. are tall plants at maturity. However, *P. stuckertii* is even taller and has larger leaves (Table 5). Thus, dominance of thick over thin tussocks in the absence of disturbance may be due to competition for light. *P. stuckertii* also has lower SLA and higher leaf toughness than *D. hieronymi*, the dominant thin tussock (Table 5); these traits might confer *P. stuckertii* with greater tolerance to litter accumulation and shade (Fynn et al., 2011). Our findings on vegetation change are consistent with this interpretation, but we cannot rule out other complementary explanations for the dominance of thick over thin tussocks, which could be related to different incidence of natural enemies, allelopatic effects of *P. stuckertii* litter, and higher intrinsic seed production or seed viability of *P. stuckertii* tussocks (Pickett et al., 1987; Facelli and Pickett, 1991; Bosy and Reader, 1995). Competition for soil resources also has been proposed as a mechanism influencing relative grass abundance (Fynn et al., 2005, 2011). These authors have found that in productive environments grasses with high SLA have competitive advantages over similar-sized neighbours with lower SLA (Fynn et al., 2005, 2011). However, our results did not agree with these findings, since thick tussocks outcompeted the dominant thin tussock *D. hieronymi*, despite the higher SLA of the latter. Moreover, our results suggest that the competitive advantages of *P. stuckertii* are even greater in the most humid soils with highest nutrient content (see also Cingolani et al., 2003).

In summary, after monitoring physiognomic changes under a lustrum of grazing exclusion or very low stocking rates, we detected a consistent advance of woody plants and thick tussock grasses, whereas the response of thin tussocks depended on the presence and response of other cover types. Thus, we suggest a successional pathway for mesic environments where thin tussocks replace short plants, and woody plants and/or thick tussocks replace thin tussocks. A specific study design addressing dynamics on edge areas between woodlands and grasslands would be necessary to confirm that woodlands ultimately outcompete thick tussock grasses under long-term grazing exclusion.

Response to grazing pressure

Our findings on the dynamics of woody plants under moderate and heavy grazing confirmed our predictions. Low stocking rates maintained woody plants with relatively stable cover, whereas moderate to high stocking rates drove their retraction. Browsing damages tissues and may produce seedling mortality or retard growth and maturation of individuals (Hansson and Fogelfors, 2000; Danell et al., 2003; Vandenberghe et al., 2007; Bakker and Moore, 2007). In our study area, the main tree species, *P. australis*, is highly consumed by livestock. For individuals <2 m high, animals consume a large proportion of current year productivity, and at high stocking rates, even old tissues, producing a reduction in the size of individuals, and sometimes their death (Teich et al., 2005; Giorgis et al., 2010).

Our results on the dynamics of tall and short grasses were different than predicted. A low or moderate grazing level did not stop the retraction of lawn-forming short plants, and a high grazing level did not produce their advance (solid and dashed lines in Fig. 2c). The heaviest stocking rates analyzed here (0.23–0.35 CU ha^{-1}) are representative of the stocking rates attained during the last decades in large privately owned ranches, including those that were later expropriated to create the National Park (Cabido, 1999). However, in unfenced areas used by small-scale producers, average effective stocking rates can reach higher values (e.g. 0.46 CU ha^{-1}, data from Cáceres, 2009, recalculated considering effective area). Extrapolating our regression results, we can speculate that under such conditions, short plants may advance at the expense of taller growth forms, but this remains to be tested.

Our findings contrast with observations in other ecosystems, where the replacement of tall grasses by shorter species under high or even moderate grazing pressure was detected (Tomanek and Albertson, 1953; Stemberg et al., 2000; Fuhlendorf et al., 2001; Walker et al., 2003; Pavlů et al., 2003; Collantes et al., 2005; McIvor et al., 2005; Cromsigt and Olff, 2008). Our results also contrast with a simulation model for African grasslands, which predicts an expansion of grazing lawns in the landscape under increasing grazer densities (Archibald, 2008). The mechanisms generating grazing-lawns are still an issue of debate (Cromsigt and Olff, 2008), but are in general related to two alternative or complementary mechanisms (Cingolani et al., 2005b; Fynn et al., 2005; Díaz et al., 2007; Cromsigt and Kuijper, 2011). On the one hand, when defoliated, tall herbaceous plants lose proportionally more photosynthetic tissue than shorter plants (i.e. shorter plants escape better from herbivory). On the other hand, tall plants recover from tissue damage more slowly than short plants due to structural and physiological trade-offs (i.e. short lawn-forming plants are generally more tolerant to herbivory than taller plants, which in our study area is reflected in the higher SLA of their leaves, Table 5, Cingolani et al., 2007). In any case, repeated defoliation reduces tall grasses height for a period long enough to allow short species to colonize (Cromsigt and Olff, 2008). This means that replacement can occur if tall grasses are consumed, at least moderately or in some periods of the year (McIvor et al., 2005). In our study area, thick tussocks of *P. stuckertii* are rarely detected defoliated in the field (Cingolani et al., unpublished data). Accordingly, habitats dominated by this species are avoided either by livestock or by the recently re-introduced native camelids (von Müller, 2011; Flores et al., 2012). This fact might explain why in our study area, even high stocking rates fail to reduce the abundance of thick tussock grasses, producing their replacement by shorter species.

Although herbivores avoid thick tussocks, the expansion of this growth form was controlled by the highest stocking rates

analyzed here, especially if animals were concentrated in the winter season. This is probably because small individuals (<50 cm) are consumed when growing isolated outside or at the edges of the thick tussock grassland, particularly in winter when other forage resources are scarce (A.M. Cingolani, personal observation; Barri et al., 2014). Indeed, unpalatable species have been found to be well consumed when growing next to more palatable species, a phenomenon known as "associational palatability" (Cromsigt and Kuijper, 2011). Grazing lawns are dominated by palatable and nutritious species, and are strongly selected by herbivores (McNaughton, 1984; Cromsigt and Olff, 2008; Flores et al., 2012; Vaieretti et al., 2013; du Toit and Olff, 2014). Hence, the grazing pressure exerted on the few unpalatable thick tussocks growing in the lawn could be particularly heavy, and the relative fitness would be higher for the more tolerant short species (Fynn et al., 2005; Cromsigt and Kuijper, 2011).

The high selectivity of herbivores for short lawns in our study area (von Müller, 2011; Flores et al., 2012; Vaieretti et al., 2010) results in a much higher localized stocking rate in a given lawn patch than the average stocking rate of the paddock, particularly if lawn patches are scarce in the landscape (von Müller, 2011). These studies suggest that scarce lawn patches in a matrix of tussock grasslands would be easier to conserve than lawns occupying large extensions, where livestock are better distributed (Archibald et al., 2005; von Müller, 2011). However, we found results in the opposite direction, since the advance of thick tussocks was accelerated when they already covered half of the plot. In turn, plots completely dominated by short plants showed no changes, indicating a role of propagule pressure of tussocks driving their expansion, which is consistent with the transient nature of the tussock seed banks (Funes et al., 2001).

Unlike grasslands dominated by thick tussocks, those dominated by thin tussocks are not avoided by herbivores (von Müller, 2011; Flores et al., 2012). In particular, *D. hieronymi* and *Festuca* spp. tussocks are consumed to some extent, especially in scarcity periods (Falczuk, 2002; Barri et al., 2014). These results suggest that the replacement of thin tussock grasses by short plants under heavy grazing pressure would be possible; however we did not find this outcome. Our results failed to show a consistent response of thin tussocks to stocking rate, or a consistent increase in short plants under high stocking rate. As already discussed, the response of thin tussocks seems to be complex and dependent on the presence and response of the other physiognomic categories. A more specific analysis would be needed to unveil thin tussocks dynamics in response to the combined effect of grazing intensity and presence and changes of other growth forms.

Bare rock surface responded somewhat different than expected. We found stabilization at moderate to high stocking rate, unlike our predicted low stocking rate. However, the bare rock changes that we could estimate visually were those caused by an increase or decrease of plant canopy, algae or litter covering already bare rocky surfaces (i.e. without soil profile). In turn, we were not able to detect the much slower, but persistent, advance of bare rock surfaces caused by the loss of the whole soil profile in rock-soil contact areas, even at low and moderate stocking rates (see a more complete analysis of soil erosion processes in Cingolani et al., 2013). We therefore suggest that the stabilization of bare rock surface at the moderate-high stocking rates detected in the present study should be interpreted with caution, since our estimations do not account for changes in soil integrity (Cingolani et al., 2013).

Stability of the system

Our results indicate that the system, with the different grazing management practices considered in this study, is not stable.

None of the stocking rates nor exclusion were able to maintain the five physiognomic categories under stable conditions. Short lawns and tussocks at best may be stabilized at very high stocking rates (>0.30 CU ha^{-1}), but then bare rock increases while woody plants decrease. If woody plants are stabilized with low stocking rates, tussocks advance replacing short plants. Other studies involving long-term monitoring of ecosystems at different stocking rates also showed that stability in physiognomy is rare (Biondini et al., 1998; Hansson and Fogelfors, 2000; Stemberg et al., 2000; Walker et al., 2003; Bakker and Moore, 2007).

If livestock alone are unable to reduce thick tussock cover, at least at the usual stocking rates for the area, how were the large extensions and/or patches of lawns created and maintained until the present? A local belief is that repeated burning of tussocks, combined with livestock grazing, is the only way to eliminate thick tussocks, allowing the creation and maintenance of short lawns. Indeed, the reduced fire ignitions in the area since the creation of the National Park and the government control outside the Park have probably contributed to the general advance of thick tussocks. During the last decade, we have observed small patches of burned tussocks (both thin and thick), and also have studied the effects of a large wildfire. In all cases, the tussock cover was recovered by regrowth after one or two years, even if the burned patches were grazed after the fire (Cingolani et al., unpublished data). These observations agree with local knowledge that only a high fire frequency combined with grazing can permanently eliminate tussocks. Accordingly, in the oak-juniper savannas in North America, fire combined with grazing was found to be much more effective in maintaining landscape heterogeneity than grazing alone (Fuhlendorf and Engle, 2004). However, and in disagreement with those authors' suggestion for their study ecosystem, in our area fires do not seem to contribute to ecosystem integrity. We measured a surface soil loss of about 0.4–0.6 cm (for ungrazed and grazed sites, respectively) during a year following a wildfire, in comparison with almost null surface soil loss in unburned plots (Cingolani et al., 2013).

In summary, our results, together with previous findings, suggest that the creation and maintenance of lawns, which need high stocking rates and presumably frequent fires, have high ecological costs. One of them is the loss of large amounts of soil and vegetated surfaces due to heavy grazing and fire (Renison et al., 2010; Cingolani et al., 2013). Indeed, 20% of the upper belt of Córdoba mountains has already lost its soil in the last 400 years of livestock history, resulting in bare rock at present (Cingolani et al., 2008b, 2013). Another cost of the maintenance of lawns by high stocking rates and fire is woodland retraction, as shown by our results and previous studies (Renison et al., 2002, 2006, 2010; Teich et al., 2005; Giorgis et al., 2010). Since paddocks or grazing areas always bear a portion of woodlands, in particular at early successional stages with small individuals (Cingolani et al., 2004; Giorgis et al., 2010; Renison et al., 2011), it would be difficult to maintain lawns without impairing woodlands or preventing their maturation.

All in all, our results suggest that while woodlands are advancing or retracting, depending on the present stocking rate, the dynamics of herbaceous vegetation tends to a progressive retraction of lawns concomitant with thick tussock advance, particularly within the National Park. The progressive thick tussock advance, which is favoured by soil moisture, could be even faster than observed in this study, since our monitoring was done during a period that was drier than the historical average (Colladon et al., 2010). Then, if current extensions of lawns have been maintained until the present by rancher activities (fire and livestock grazing) the question arises as to what was the system like before the introduction of livestock grazing 400 years ago. Was landscape configuration characterized by large areas of lawns? If so, were lawns maintained by native

wild herbivores such as camelids (*L. guanicoe*) and other herbivores and/or natural fires or fires induced by pre-Columbian native people? Or, alternatively, was the system dominated by *P. stuckertii* tussock grasslands and *P. australis* woodlands? *P. stuckertii* is an endemic species rarely present at altitudes below 1700 m a.s.l., and its abundance increases towards higher altitudes and at colder and damper sites (Cingolani et al., 2003, 2008b). *P. australis* is a high-altitude species that also tends to perform better at sites with higher moisture (Cingolani et al., 2008b; Marcora et al., 2008, 2013; Tecco et al. unpublished data). The literature on vegetation dynamics in central Argentina during the Holocene suggests climatically driven changes in C3:C4 species (Silva et al., 2011) and *Poaceae* subfamilies (López et al., 2010) during the last millennium. Both studies indicate changes towards colder and wetter conditions in our study area (but see Cioccale, 1999). Accordingly, we hypothesize that during most of the Holocene, *Poa* tussocks and *P. australis* woody plants were restricted by a warmer and drier climate, combined with wild herbivore pressure and fires. Climatic changes concomitant with a release of herbivory pressure at the end of the Holocene (Medina and Rivero, 2007) might have triggered an expansion of *P. stuckertii* tussocks and *P. australis* woody plants at the expense of lawns and thin tussocks. This process could have been stopped/reversed with the introduction of livestock 400 years ago, and the associated increase in fire ignitions. Behling and Pillar (2007) suggested a similar interpretation to explain the grasslands/woodlands mosaic dynamics in the southern Brazilian highlands detected through palaeoecological studies. This topic is relevant to understand current vegetation dynamics, and more studies of paleovegetation would be needed in our study area to adequately test these hypotheses.

Acknowledgements

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