



Predicting cover types in a mountain range with long evolutionary grazing history: a GIS approach

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ABSTRACT

Aim To determine how the distribution and cover of different vegetation types are affected by physical factors and livestock in a mountain range with a long evolutionary history of grazing.

Location Upper vegetation belt of the Córdoba mountains (1700–2800 m a.s.l., 31°34' S, 64°50' W) in central Argentina.

Methods Using GIS, we analysed the relationships of plant cover types to physical features (physiography and topography) and indicators of accumulated livestock pressure (distance to human settlements and roads) through multinomial logistic regression. We predicted a present vegetation map which was validated with a real map. We then constructed two maps simulating minimum and maximum values of accumulated livestock pressure for the whole area. Map comparisons allowed evaluation of the possible influence of livestock, both in extension and intensity.

Results Both physical features and livestock pressure influenced the occurrence of vegetation units. The overall accuracy of the predicted map at the pixel level was low (26%) indicating low habitat specificity of the vegetation units. We suggest that some part of the unaccounted for variance was due to livestock pressure patterns that were not fully captured by our indicators. Our models proved adequate for predicting the total percentages of vegetation units at coarser scales. The extrapolations showed that under a history of low livestock pressure, such as in sites far away from human settlements and roads, the area would be dominated by woodlands, tussock grasslands and natural rock outcrops. Under a history of heavy livestock pressure, in turn, rock exposed by erosion, tussock grasslands and natural rock outcrops would dominate.

Main conclusions Vegetation units showed low habitat specificity, and were associated with accumulated livestock pressure, indicating that livestock and its associated activities are important factors structuring the landscape and have important consequences for the integrity of the ecosystem. Results suggest that although this system evolved with large herbivores, it has experienced irreversible degradation processes, and intensification of current domestic livestock pressure is likely to lead to even more land degradation.

Keywords

Argentina, fire, grazing lawns, livestock pressure, mountain ecosystems, physiography, topography, tussock grasslands, woodlands.

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INTRODUCTION

Land-cover change is the most important driver of global change in terms of its total effects on ecosystem structure and functioning and the consequent losses of ecosystem services

(Sala *et al.*, 2000). Compared with agriculture, land-cover changes caused by extensive grazing by domestic livestock seem less important. However, this activity occupies 25% of the world's terrestrial surface and produces a strong environmental footprint (Asner *et al.*, 2004). The effect of livestock on

the integrity of ecosystems is still controversial (Belsky, 1986; Painter & Belsky, 1993; Illius & O'Connor, 1999), partly because domestic grazing has variable effects on ecosystem structure and processes (Milchunas & Lauenroth, 1993; Landsberg *et al.*, 2003; Asner *et al.*, 2004). It has been argued that in systems with long evolutionary histories of grazing, vegetation is adapted to large herbivores, and consequently domestic livestock does not damage ecosystem structure and functioning (Milchunas *et al.*, 1988; Perevolotsky & Seligman, 1998; Adler *et al.*, 2004, 2005) and may even be necessary for conservation purposes (e.g. Dolek & Geyer, 2002; Laiolo *et al.*, 2004; Rook *et al.*, 2004). However, there is also evidence of irreversible land degradation in systems that evolved under high grazing pressure, such as African deserts and savannas (Milton *et al.*, 1994; Illius & O'Connor, 1999; Fynn & O'Connor, 2000; Tobler *et al.*, 2003). According to Cingolani *et al.* (2005), it would not be the length of the evolutionary history of grazing *per se*, but rather any difference between present and evolutionary grazing pressure that determines the susceptibility of the system to domestic livestock.

Unfortunately, analysing the relationship between evolutionary grazing pressure, present grazing pressure and the degree, extension and reversibility of land transformation is still a challenge, due to several methodological constraints. The evolutionary history of grazing is often a matter of controversy and is difficult to assess (Lauenroth, 1998; Adler *et al.*, 2004; Cingolani *et al.*, 2005). In addition, evaluating the impact of domestic grazing on ecosystem integrity is difficult, especially in systems where the original condition is unknown because land transformations are widespread and irreversible. When the system has passed a threshold, reaching an alternative stable state (Westoby *et al.*, 1989), results of experiments using the grazing exclusion method could lead to erroneous interpretations (Cingolani *et al.*, 2005). Long-term grazing trials may be a sound way to evaluate the effects of grazing management on the functioning and structure of an ecosystem (Laycock, 1967; Collins *et al.*, 1998; Oliva *et al.*, 1998; Schuman *et al.*, 1999; Fynn & O'Connor, 2000), but for most systems such data are not available. An alternative approach is to interpret present-day vegetation types as the result of accumulated livestock pressure and associated management practices using indirect indicators, such as the proximity to water (Lange, 1969; Landsberg *et al.*, 2003; Adler *et al.*, 2005), villages (Skarpe, 2000) or night paddocks (Tobler *et al.*, 2003), as well as indicators of soil disturbance (Adler & Morales, 1999), present grazing intensity (Noy-Meir *et al.*, 1989; Adler & Morales, 1999) and even biological indicators such as the abundance of a given growth form or species (Dyksterhuis, 1949; Jauffret & Lavorel, 2003). This is often the only feasible approach, and regardless of some associated limitations it provides sound information for management decisions which cannot wait for the results of long-term grazing trials.

The main limitation of this retrospective approach is that the effects of grazing and related management practices are difficult to distinguish from the effect of abiotic factors, as they are usually associated and often interact to produce complex

land-cover changes (Westoby *et al.*, 1989; Adler & Morales, 1999; Illius & O'Connor, 1999). Such difficulties are present in the upper belt of the Córdoba Mountains (Argentina), where management recommendations are needed but no data on long-term grazing trials are available. It has been argued that this ecosystem evolved under relatively high grazing pressures, due to wild herbivores (*Lama guanicoe* and others) that more recently have been replaced by domestic herbivores (Díaz *et al.*, 1994). The resilience of the herbaceous vegetation, the loss of plant diversity with livestock exclusion and the capacity of the main woody species (*Polylepis australis*) to regrow suggest that the system is well adapted to herbivory (Díaz *et al.*, 1994; Pucheta *et al.*, 1998; Teich *et al.*, 2005). However, some studies suggest that three centuries of domestic grazing with associated fire (used as a management tool to produce grass regrowth) and increased erosion processes have led to the retreat of woodlands, driving the system to alternative states, some of them irreversible and less productive (Pucheta *et al.*, 1997; Cingolani *et al.*, 2003, 2004, 2005; Teich *et al.*, 2005; Renison *et al.*, 2006). These studies challenge traditional thought, which suggests that soil erosion and woodland cover in the high Córdoba mountains respond mainly to natural abiotic factors (Cabido *et al.*, 1987; Enrico *et al.*, 2004). To date, studies in this region have independently investigated different aspects of the relationship between land use or physical environment and vegetation (Cabido *et al.*, 1987; Pucheta *et al.*, 1998; Renison *et al.*, 2002; Cingolani *et al.*, 2003; Teich *et al.*, 2005; Renison *et al.*, 2006), but no integrated study has been carried out involving simultaneously all vegetation types and all kinds of multiple structuring factors.

Here we attempt to fill that gap and overcome the inherent difficulties of retrospective studies using a Geographic Information System (GIS) to perform a landscape-integrated study which incorporates anthropogenic and abiotic factors. More specifically, we aim to determine how the different plant cover units are related to physical factors and indicators of accumulated livestock pressure in a mountain range with a long evolutionary history of grazing, thus contributing to the understanding of the type, degree and spatial extension of the influences of livestock on this type of ecosystem. Our hypothesis is that in the upper belt of the Córdoba Mountains the change from natural to domestic grazing and associated fires has had an important impact on ecosystem structure, despite the long evolutionary grazing history of the area. We therefore predict that this effect will be reflected in significant relationships between the occurrence of each vegetation unit and at least one of the accumulated livestock pressure indicators used in this study.

METHODS

Study area

The study was performed in the upper vegetation belt of the Córdoba Mountains (1700–2800 m a.s.l., 31°34' S, 64°50' W,

see Fig. 3) in central Argentina. Vegetation consists of a mosaic of tussock grasslands, grazing lawns, outcrop communities, *Polylepis australis* woodlands and eroded areas with exposed rock surfaces (Cingolani *et al.*, 2004). The 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 840 mm, with most rainfall concentrated in the warmer months from October to April (Cabido, 1985). The main economic activity in the area is livestock rearing, which began early in the 17th century and completely replaced large native herbivores by the beginning of the 20th century (Díaz *et al.*, 1994). Large fenced properties coexist with unfenced areas occupied by small stakeholders. Generally, unfenced areas have high densities of family households, and animal stocking rates are usually higher than in fenced properties. In both fenced and unfenced properties, most livestock rearing activities are concentrated around rancher houses where sheep and goats (which were more abundant a few decades ago) are kept overnight. In addition, when no fencing is present, owners tend to maintain cattle close to houses. Burning is concentrated near roads, where livestock ranchers burn opportunistically when in transit. Additionally, livestock is often reduced in paddocks far away from roads and houses because it is more difficult to manage and to control predation. Because of this, we considered distances to houses and roads as indicators of accumulated livestock pressure and associated activities (see below). Effective stocking rates (considering only vegetated non-rocky land when calculating the paddock area) can vary from 0.1 to *c.* 2 cow equivalent ha⁻¹, depending on

management, animal habitat preferences and physical barriers limiting distributions (Teich *et al.*, 2005).

In 1997 the national park 'Quebrada del Condorito' was created in part of the study area and 26,000 ha were expropriated. The lands surrounding the park were declared National and Provincial Water Reserves (12,000 and 117,000 ha, respectively), but continued under private ownership and traditional livestock management. Although domestic grazing pressure and fire are now restricted in the national park, this restriction is very recent and the satellite image used to map vegetation (January 2001) was prior to any changes in land use due to conservation policies. Natural fires are not very frequent or extensive, because electrical storms are generally accompanied by rain.

Vegetation map and other GIS layers

We used a vegetation map of 30 × 30 m resolution and 87% accuracy obtained from a TM satellite image of January 2001 (Cingolani *et al.*, 2004) to determine the association of vegetation units with physical factors (topography and physiography) and accumulated livestock pressure indicators. The vegetation map shows eight units that were defined as mosaics of different community types and rock patches (Cingolani *et al.*, 2004; Table 1). Our study included 1246 km² above 1700 m a.s.l., now belonging to the national park and the surrounding Provincial Water Reserve (see Fig. 3).

Roads, tracks, horse and trekking trails (hereafter 'roads') were recorded in the field with GPS, as were human

Table 1 Vegetation units (v1–v8), brief description, area (ha), proportion of the study area (%) and number of sampling points used to analyse their relation with grazing pressure indicators and physical factors in the Córdoba Mountains. For a more detailed description of vegetation units see Cingolani *et al.* (2004).

Vegetation unit	Description	ha	%	Sampling points
v1 Closed woodland	Dominated by <i>Polylepis australis</i> woodlands. Frequent rock outcrops below the canopy. Small patches of visible rock outcrops, and of tussock grasslands	3157	2.5	50
v2 Open woodland	Mosaic of <i>P. australis</i> woodlands, shrubby grasslands and rock outcrops	11,674	9.4	189
v3 Thick tussock grassland	<i>Poa stuckertii</i> (a grass with thick leaves) grasslands often mixed with hydromorphic <i>Eleocharis</i> – <i>Alchemilla</i> lawns. Small patches of <i>Alchemilla</i> – <i>Carex</i> lawns or <i>Deyeuxia hieronymi</i> tussock grasslands	5053	4.1	80
v4 Thin tussock grassland	<i>Deyeuxia</i> and/or <i>Festuca</i> spp. (grasses with thin leaves) grasslands with small patches of other communities	24,922	20.0	402
v5 Lawn	Dominated by <i>Alchemilla</i> – <i>Carex</i> lawn, with some patches of other community types. Flat rock pavements are generally found at the bottom of concavities which get flooded in the rainy season	4810	3.9	79
v6 Tussocks and outcrops	Mosaic of tussock grasslands and rocky outcrops with small patches of eroded stony grasslands and erosion pavements. Very sparse <i>Polylepis</i> individuals are sometimes present	37,969	30.5	608
v7 Erosion and outcrops	Mosaic of rocky outcrops and eroded stony grasslands and rock pavements, with small fully vegetated patches	30,572	24.5	488
v8 Erosion pavements	Dominated by flat, massive bare rock erosion pavements covering more than 80% of the surface	6426	5.2	104
Total		124,583	100	2000

settlements (settler houses, abandoned houses, tourism lodges and a small village). Rivers, permanent and temporary streams and elevation contours with an interval of 25 m were digitized from topographic maps. Physiographic units were obtained from Cabido *et al.* (1987). The original nine units were reduced to four clearly differing in terms of topography, substrate rock and degree of dissection: (1) unit A, very steep escarpments (on granite or metamorphic rocks), covering 3.5% of the total area, (2) unit B, rocky hills, slopes and deep ravines on granite, occupying 66.5% of the total area, (3) unit C, rocky hills and slopes on metamorphic rocks, occupying 8.1% of the total area, and (4) unit D, plateaus, which include flat areas on granite, with low to moderate degree of dissection, and valley bottoms, occupying 21.9% of the total area.

From the elevation contours we constructed a digital elevation model with 30 × 30 m resolution, and obtained slope percentage, three insolation indices, a roughness index and a topographic position index (ERDAS, 1995). Insolation indices were constructed by integrating slope and aspect in a unique measure: the sine of the angle of the sun's rays reaching the surface at the azimuth on three different dates (the winter solstice, the summer solstice and either equinox). These indices do not take into account the projected shadows, and vary on a scale from 0 (no direct insolation) to 1 (maximum insolation, i.e. the sun's rays at 90°). The index of roughness was calculated as the standard deviation of the winter insolation (the most contrasting) using a circular kernel of radius 315 m. The topographic position was also calculated using a circular kernel of radius 315 m, as (height of the centre – minimum value in the circle)/(difference between the maximum and minimum height in the circle) (Ackerly *et al.*, 2002). The value of topographic position varies between 0 (the lowest topographic position in relation to the surrounding landscape) and 1 (the highest position).

For water courses, roads and human settlements we created distance layers. In the first case, we created two alternative distance layers, one considering the distance to all rivers and

streams (including temporary ones) and the other considering only permanent rivers and streams. We also created two alternative layers for roads, one for the distance to both moderately and intensively used roads, and the other layer for the distance to only intensively used roads. For human settlements we created one distance layer. Both distances to roads and the distance to human settlements were considered as indicators of accumulated livestock pressure and associated activities including burning (for simplicity, hereafter 'livestock pressure indicators'), although in more recent years these indicators have also been partially related to touristic activities. Although these could be only approximate indicators they are easy to measure objectively, and more precise information related to long-term livestock management is not available for the whole area. Other indicators, such as dung counts (related to present livestock densities) or evidence of fires are imperfect for our criteria as they do not necessarily reflect long-term processes.

Data gathering and construction of a multinomial logistic model

We selected 2000 pixels through stratified random sampling, with the number of points per vegetation unit proportional to its percentage cover in the study area (Table 1) and the additional restriction that each selected pixel should be at least 350 m away from any other to minimize spatial autocorrelation. For each selected pixel we obtained data from 13 layers. One layer was categorical (physiographic unit) and the remaining layers were continuous (Table 2).

We used multinomial logistic regression (Tutz, 1998) to obtain a model (i.e. a set of related logistic equations) that predicts the probabilities of occurrence of all vegetation units as functions of the physical characteristics and livestock pressure indicators obtained from the GIS. For each continuous variable, besides the one-order term, we also considered the positive square root term and the quadratic term. We imposed on the desired model the following restrictions. First,

Table 2 Independent continuous variables used to predict vegetation units, the units in which they are expressed, range, mean and 25th, 50th (median) and 75th percentiles.

Variable	Units	Range	Mean	Percentiles		
				25th	50th	75th
Slope inclination	%	0–100	15	6	11	19
Fall–spring (equinox) insolation	Index	0.36–1	0.84	0.82	0.85	0.88
Winter (solstice) insolation	Index	0–1	0.58	0.54	0.59	0.63
Summer (solstice) insolation	Index	0.7–1	0.972	0.968	0.984	0.991
Topographic position	Index	0–1	0.52	0.37	0.52	0.67
Roughness	Index	0–0.364	0.060	0.033	0.049	0.072
Altitude above sea level	km	1.7–2.7	2.017	1.872	2.034	2.150
Distance to permanent water courses	km	0–4.26	0.560	0.20	0.44	0.79
Distance to all water courses	km	0–4.26	0.259	0.09	0.18	0.30
Distance to human settlements	km	0–6.06	1.55	0.75	1.29	2.07
Distance to highly used roads	km	0–10.08	3.24	1.29	2.89	4.89
Distance to moderate–highly used roads	km	0–6.72	1.68	0.54	1.26	2.46

it should not include simultaneously both measures of distance to rivers or both measures of distance to roads, because these were pairs of alternative variables which had many identical values. Second, it should not include simultaneously two highly correlated pairs of variables (winter insolation and autumn–spring insolation, $r = 0.97$; summer insolation and slope percentage, $r = -0.87$; roughness index and slope percentage, $r = 0.70$), to avoid instability in the models. All other pairs of variables had absolute correlation coefficients (Pearson) below 0.55 and were allowed simultaneously (Afifi & Clark, 1984). Finally, the model should not include all three terms of the same variable (order one, square root and quadratic) nor produce one or more U-shaped relationships (formed by two terms of the same variable), because according to our criteria these models are biologically meaningless. In this way, only monotonic or unimodal relationships were allowed. To obtain a model that fulfilled these restrictions, we selected the relevant variables/terms with a manual forward stepwise procedure adding at each step the significant ($P < 0.05$) variable/term which most improved the deviance (chi-square statistic) if the addition did not violate the restrictions imposed. In a second step, we tested for two-way interactions between selected terms/variables and included them in the models, in a similar forward stepwise procedure.

To visualize the shape and sign of the relationships between each variable and the probability of occurrence of each unit, we performed sensitivity plots fixing all other variables as constants (at low, medium and high values for variables showing significant interactions with the explored variable). This was necessary because the shape and sign of the relationships was not easily deducible from the set of related equations in the multinomial model.

Validation of the models: comparing the true map and the predicted map

We generated a predicted map from the multinomial logistic model. First we created eight probability layers (one for each vegetation unit) at the same resolution as the vegetation map (30×30 m) using the related logistic equations of the model. Once the eight probability maps were obtained, we constructed a probabilistic predicted vegetation map, randomly assigning pixels to classes, with randomizations restricted by the distribution of probabilities. Since the final map was probabilistic, different runs gave different results at the pixel level. However, in terms of percentages for the whole area, percentages at different sectors of interest and percentages at each cell of the confusion matrix (see below), maps resulting from different runs were almost equal, so we arbitrarily chose one of them. We preferred this probabilistic method rather than deterministically assigning to each pixel the class with higher probability because in the latter way we would fail to reproduce correctly the proportion of each unit in the whole area, underestimating units with low cover and overestimating units with high cover (van de Rijt *et al.*, 1996).

Once the predicted map was obtained, we calculated a confusion matrix for the whole area, where the predicted map was compared with the real map pixel by pixel. This confusion matrix gave information about the degree of habitat specificity and the strength of the associations between vegetation units and livestock pressure indicators, considering all pixels of the map and not only those pixels used for constructing the model.

Due to our special interest in livestock pressure indicators, we validated our set of models for their ability to correctly predict proportions of vegetation units at different distances from sources of livestock disturbance (human settlements and roads). To do this, we divided the study area into 10 distance classes (combining the distance variables selected in the models) with approximately similar numbers of pixels. For each distance class we calculated the percentage of each unit from the predicted and from the real map. We then performed regressions, one for each unit, with the predicted percentage as an independent variable and the real percentage as a dependent variable. Significant positive regressions (i.e. slopes greater than zero) indicate that models correctly predict trends in relation to livestock pressure indicators. For a given vegetation unit, an intercept and a slope not different from zero and one, respectively, indicates that the models are unbiased to predict its proportion in relation to accumulated livestock pressure indicators. A slope of more or less than one indicates some bias of the models to predict vegetation in relation to these indicators. These results were considered when interpreting the simulations explained in the next section.

Interpretation of livestock impact

To interpret the overall effect of livestock we created probability layers for each vegetation unit, but simulating maximum and minimum livestock pressure. For each pixel, probabilities were calculated considering the true values of each predictor layer, except for distance to roads and human settlements, which were considered constant, with low and high values, respectively (almost the minimum and maximum values used to construct the models). From these probability layers we created a 'high livestock pressure map' and a 'low livestock pressure map' and compared them. These maps extrapolate, for the whole area, the situations near and far from the human settlements and roads. They represent how the whole area may have looked if livestock pressure history had been similar to the history at the sites close and far, respectively, from roads/houses.

RESULTS

Multinomial logistic model

The presence of the vegetation units was partially explained by physical characteristics and livestock pressure indicators (Table 3). Physical variables selected in the multinomial

Table 3 Variables/terms included in the final multinomial logistic model. For each vegetation unit (v1–v8, see description in Table 1) the general trend of the relationship (other factors being constant) is indicated. When the sign/shape of the relationship changes according to the value of other variables due to a significant interaction term (indicated in the last row), both trends are indicated. For physiography, when significant, the unit with highest probability (other factors being constant) is indicated by a letter.

	v1	v2	v3	v4	v5	v6	v7	v8
Physical characteristics								
1. Altitude/altitude ²	∩	-	+	∩/-	+	=	-/+	=
2. Topographic position	-	-	-	=	=	-	+	+
3. Slope ^{0.5}	+	+	-	-/+	-	+	-/+	-
4. Insolation (autumn–spring)	-	-	-	-	+	=	+	+
5. Physiography	=	A	D	A	D	C	B	B
Livestock pressure indicators								
6. Distance to roads (intensive use) ²	+	+	=	-/+	=	=	-	-
7. Distance to settlements ^{0.5}	+	+	+	+	-	=	-	-
Significant interactions		1 × 3		1 × 3, 3 × 6	1 × 3		1 × 3, 3 × 6	

+, positive; -, negative; ∩, unimodal; =, not significant for the specific unit (i.e. the probability of occurrence did not vary consistently with the variable).

A, very steep escarpments; B, rocky hills, slopes and deep ravines on granite; C, rocky hills and slopes on metamorphic rocks; D, plateaus.

logistic model were altitude (both the one-order and the quadratic term, although for some units only one term was significant), topographic position (only the one-order term), autumn–spring insolation (only the one-order term) and slope percentage (only the square root term). Livestock pressure indicators selected were distance to intensively used roads (quadratic term only) and distance to human settlements (square root only). Selected interaction terms were slope × altitude and slope × distance to intensively used roads (Table 3). The maximum rescaled pseudo R^2 of the model was 0.373 (Nagelkerke, 1991).

Closed woodlands

Closed woodlands (vegetation unit v1) had greater probability of occurrence at intermediate altitudes above sea level (maximum at 1930 m a.s.l.) and low topographic positions, in sites with low insolation and steep slopes. In turn, physiography did not influence this unit. Both livestock disturbance indicators showed a significant positive relationship, indicating that closed woodlands increase their frequency far from sources of disturbance.

Open woodlands

Open woodlands (v2), like closed woodlands, increased their probability of occurrence at low topographic positions, in sites with low insolation and steep slopes. Unlike closed woodlands, the maximum occurrence of this unit was at the lowest altitudes and in the 'very steep escarpments' physiographic unit (unit A). The interaction between slope and altitude did not modify substantially the general trends of relationships between both variables and the occurrence of open woodlands. Like closed woodlands, open woodlands increase their probability of occurrence at large distances from human settlements and intensively used roads.

Thick tussock grasslands

Thick tussock grasslands (v3) increased their occurrence at high altitudes and low topographic positions, in relatively flat sites with low insolation. They were preferentially found in plateaus (unit D) and were almost absent in very steep escarpments (unit A). The probability of occurrence of these grasslands increased far from houses, but was not modified by distance to roads.

Thin tussock grasslands

Thin tussock grasslands (v4) were very widespread and showed complex relationships with the selected variables. They were more frequent in sites with low insolation and in steep escarpments (unit A), followed by plateaus (unit D). The lowest frequency was attained in rocky hills on granite (unit B). For sites with moderate and gentle slopes (less than 10%) they were more frequent at intermediate altitudes (maximum varying from 2000–2300 m a.s.l. as slope decreased from 10 to 0) but at steeper slopes this unit decreased its probability of occurrence with altitude. The relationship with slope was negative in most cases except at low altitudes and/or far away from sources of disturbance, where the probability of occurrence was constant or increased with slope. The relationship with distance to roads was negative at sites with a slope of less than 30%, and positive for steeper slopes, while the relationship with distance to human settlements was always positive.

Lawns

Lawns (v5), like thick tussock grasslands, tended to increase with altitude, except at steep slopes (higher than 20%) where lawns were almost absent and did not vary appreciably with altitude. Lawns also increased at flat sites or with gentle slopes, except at low altitudes (less than 1900 m a.s.l.), where they

were almost absent and did not vary with slope. This unit was more frequent in plateaus (unit D), with very low occurrence in other physiographic units. Lawns increased with proximity to human settlements, while distance to roads was not significant.

Tussocks and outcrops

Tussocks and outcrops (v6) showed significant associations with few variables. They increased their probability of occurrence at low topographic positions and steep slopes. Additionally, this unit had a higher probability of occurrence at metamorphic hills (unit C), but did not show any relationship with livestock pressure indicators.

Erosion and outcrops

Erosion and outcrops (v7) occurred preferentially at upper topographic positions in sites with high insolation. They increased with altitude except at flat sites (slopes lower than 5%), where this unit decreased slightly with altitude. The relationship with slope was positive at high altitudes and negative at low altitudes, with shapes slightly variable according to distance to roads. This unit was very frequent in rocky hills on granite (unit B) and relatively scarce in other physiographic units. The probability of occurrence decreased sharply with distance from intensively used roads, except at sites with gentle slopes (less than 5%), where the relationship was almost constant. This unit was always more frequent close to human settlements than far from human settlements.

Erosion pavements

Erosion pavements (v8), like erosion and outcrops, were more frequent in sites with high insolation at upper topographic positions, and in hills on granite (unit B). Unlike erosion and outcrops, erosion pavements were more frequent in flat sites or with gentle slopes. Both distance to human settlements and distance to intensively used roads were significant and negative, indicating that erosion pavements had more probability of occurrence in more intensively disturbed sites.

Validation of the models

Predicted percentages of each unit for the whole area were very close to the real percentages indicated in Table 1 (a difference of less than 0.15%), indicating that in general terms our models were not biased when predicting probabilities for sites not used in the construction of the models. Overall accuracy at the pixel level between the real and the predicted map was 26.3%. This relatively low overall accuracy, also reflected in the confusion percentages of the producer (Table 4) and user (not shown), indicates that, at present, there is no strong topographic specificity of the vegetation units nor a tight association with livestock pressure indicators, at least considering the variables used in this study. For example, closed woodlands

Table 4 Producer confusion matrix at the pixel level. For each unit in the real map, the correctly predicted percentage is indicated in bold, while the percentages predicted as other units are indicated with non-bold values. Vegetation units (v1–v8) as in Table 1.

Predicted	Units in the real map							
	v1	v2	v3	v4	v5	v6	v7	v8
v1	8	4	2	2	1	3	2	1
v2	17	15	8	9	6	9	7	6
v3	3	4	12	6	13	3	2	2
v4	19	21	30	25	29	19	16	16
v5	2	2	10	6	17	2	2	2
v6	31	31	21	28	17	34	32	31
v7	17	19	14	20	14	25	32	34
v8	3	4	3	4	3	5	7	8

were correctly predicted in only 8% of the pixels, and most of the remaining closed woodlands were predicted as open woodlands (17%), tussocks and outcrops (31%), erosion and outcrops (17%) and thin tussock grasslands (19%) (Table 4). This suggests that under situations (of topography and distance to sources of disturbance) similar to those where we find woodlands today, it is more probable to find outcrops with tussock grasslands or units other than closed woodlands. Conversely, we found closed woodlands in only 9% of the cases that were predicted to be closed woodlands. This means that under the best combination of conditions for closed woodlands (low topographic positions, intermediate altitudes, far away from intensively used roads, etc.), woodlands occupy only 9% of the pixels (user confusion matrix, not shown).

Distance to intensively used roads and distance to human settlements were used to validate the model in relation to livestock pressure indicators. We constructed a map combining both variables, which resulted in 10 distance classes with a similar number of pixels each. Regressions analysing real percentages as a function of predicted percentages across the 10 classes were significant for all eight vegetation units (Fig. 1) indicating that the general trends of model predictions along livestock pressure gradients were correct. Slopes and intercepts in all cases except one did not differ significantly from one and zero, respectively, indicating that the models produce almost unbiased predictions. The only case for which we detected a bias was for erosion and outcrops (v7), where slope was greater than one and intercept lower than zero, showing that models underestimated the proportion of this unit in classes where it has low cover (large distance classes), and overestimated it in classes where it has high cover (short distance classes). In other words, the model underestimated the cumulative negative effects of livestock pressure on soil erosion.

Interpretation of the impact of livestock

When simulating high and low livestock pressure for the whole area, we found important differences in total percentages

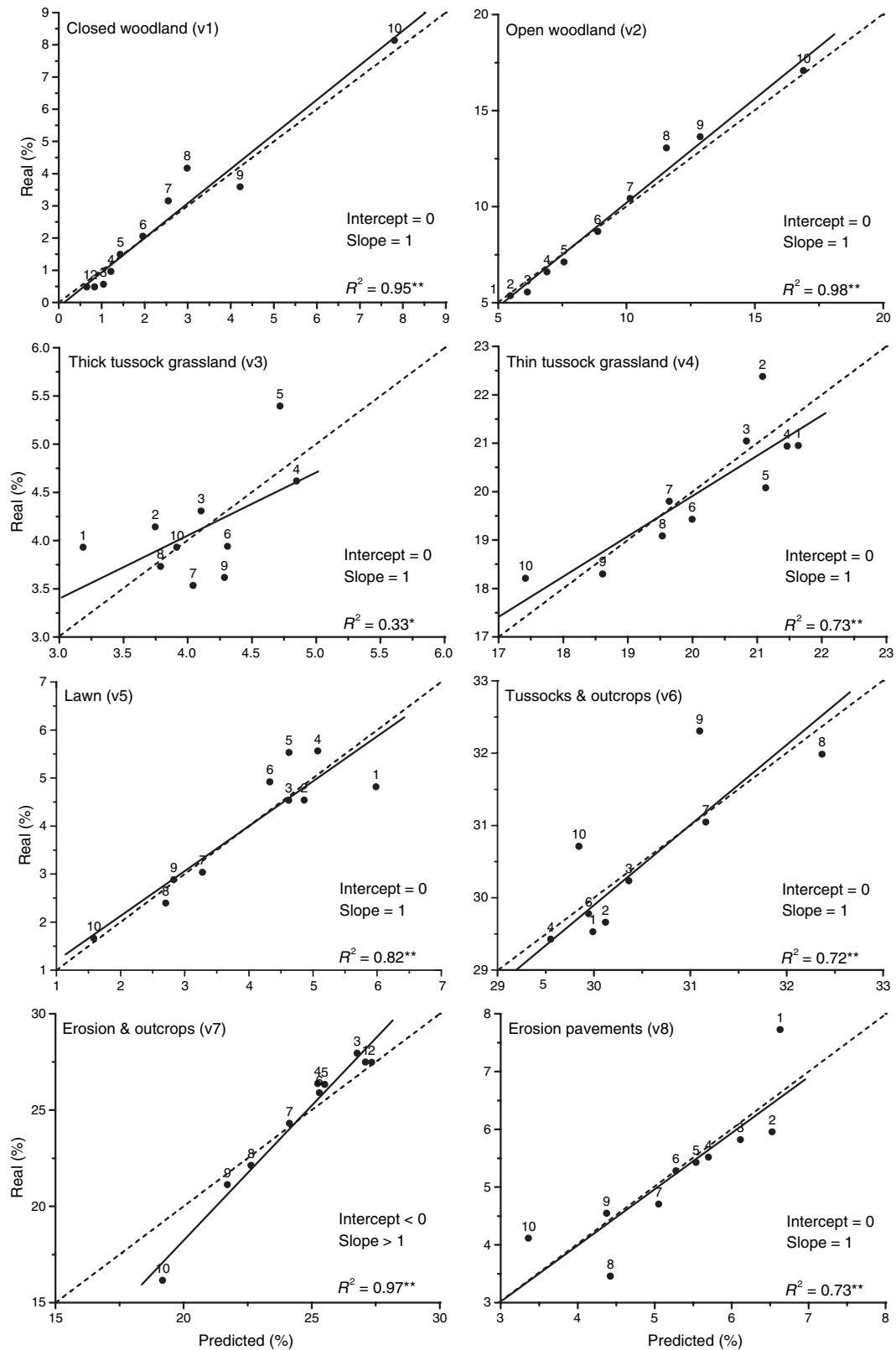


Figure 1 Validation of logistic models with a distance map from sources of livestock-related disturbance. Real proportions (%) of the eight vegetation units (v1–v8) as functions of their predicted values according to the models for 10 distance classes from sources of livestock-related disturbance (1–10, from close to far distance classes). The fit of the regressions is indicated by their R^2 (lower right corner of each plot), and the significance of the model (i.e. slope significantly different from 0) with an associated asterisk. It is also indicated if the intercept is not different (=) or different (< or >) from zero, and if the slope is not different (=) or different (< or >) from one.

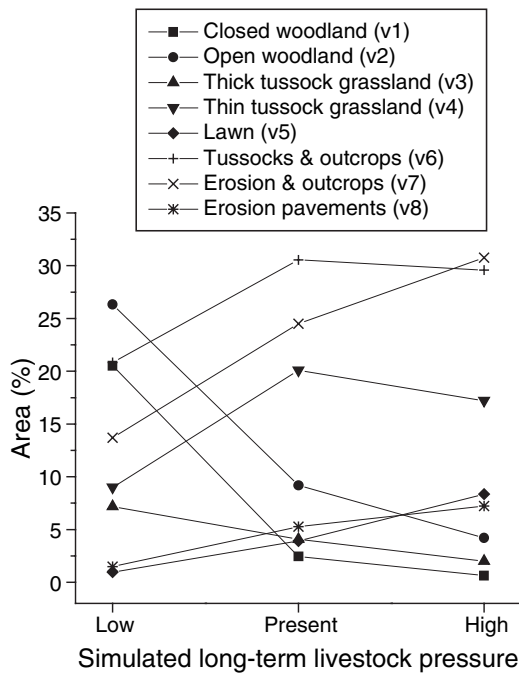


Figure 2 Interpretation of long-term livestock impact: area occupied by the different vegetation units according to the simulated models for a history of low livestock pressure (far away from roads and human settlements), present (the true values of distance to roads and human settlements) and high livestock pressure (close to roads and human settlements).

occupied by each vegetation unit (Figs 2 & 3). On the one hand, the simulated history of low livestock pressure showed a landscape dominated by open and closed woodlands (v1 and v2) and tussocks and outcrops (v6). Both types of tussock grasslands (v3 and v4) and erosion and outcrops (v7) occupy less surface, while erosion pavements (v7) and lawns (v5) were almost absent. When simulating a history of high grazing pressure we found a very different situation. The landscape appeared to be dominated by erosion and outcrops (v7) in the first place, and by tussocks and outcrops (v6) in second place. Thin tussock grasslands (v4), lawns (v5) and erosion pavements (v8) followed, while woodlands (v1 and v2) and thick tussock grasslands (v3) were very scarce. The increase of eroded surfaces with livestock pressure should probably be higher than detected by our model because, as shown before, the model underestimated the effect of livestock pressure on the occurrence of the erosion and outcrop unit (v7; Fig. 1).

DISCUSSION

Grazing evolutionary history, long-term domestic grazing and land-cover changes

Our main results indicate that domestic grazing and associated activities may produce important land-cover changes even in a rangeland with a long evolutionary grazing history. Our

simulations suggest that under a history of relatively low livestock pressure the landscape would be dominated by woodlands, tussock grasslands and natural outcrops, with a relatively low proportion of eroded surfaces; and the opposite would have happened under a history of heavy livestock pressure.

Many of the detected changes are irreversible, or very slowly reversible, such as the notorious increase in eroded surfaces. The retreat of woodlands is reversible only if seed sources are not completely eliminated or strong erosion does not take place (Renison *et al.*, 2004), and even then, the recovery of woodlands may be difficult in the presence of livestock (Teich *et al.*, 2005). In line with these results, important changes in vegetation structure associated with long-term livestock pressure were found in African ecosystems (Skarpe, 2000; Tobler *et al.*, 2003), and irreversible soil erosion associated with livestock activities was documented, despite the long evolutionary grazing history of this continent (Milton & Hoffman, 1994; Hary *et al.*, 1996; Illius & O'Connor, 1999; Fynn & O'Connor, 2000; Zeidler *et al.*, 2002; Jauffret & Lavorel, 2003).

Given that our study area has a long evolutionary history of grazing (Diaz *et al.*, 1994), the reasons for these irreversible transformations could be that: (1) a threshold has been passed between intensity of present and evolutionary grazing pressure, (2) sheep, cattle and goats have different effects on ecosystem from native South American camelids, and/or (3) the practice of burning vegetation makes the difference.

The first explanation implies that although the area experienced high densities of wild herbivores during its evolutionary history, the present domestic livestock pressure is much higher, at least in the most stocked areas, and the system has broken its limits of resilience. This explanation has been suggested by Cingolani *et al.* (2005) for areas irreversibly degraded by livestock, regardless of whether vegetation is adapted to herbivory. Oesterheld *et al.* (1992) found that systems with wild herbivores have a herbivore biomass one order of magnitude lower than systems with similar primary productivity managed extensively with livestock. They attribute this difference to practices such as the control of predators and parasites, veterinary care, organization of the herds and fencing, among others. As no data on past densities of wild large herbivores are available for our study area, we may assume that livestock biomass is probably one order of magnitude greater than biomass of past wild herbivores. Further supporting this assumption, using a relationship between animal biomass density and precipitation obtained by Coe *et al.* (1976) for African ecosystems, in our system we obtained a value of 68 kg ha⁻¹, which implies a stocking rate of 0.17 cattle equivalent ha⁻¹. This value represents densities one order of magnitude lower than present livestock stocking rates in heavily grazed sites of our study area (Teich *et al.*, 2005).

The second possible explanation is that even if grazing pressure is no different from the evolutionary past, the kinds of animals can make the difference. It is well accepted that

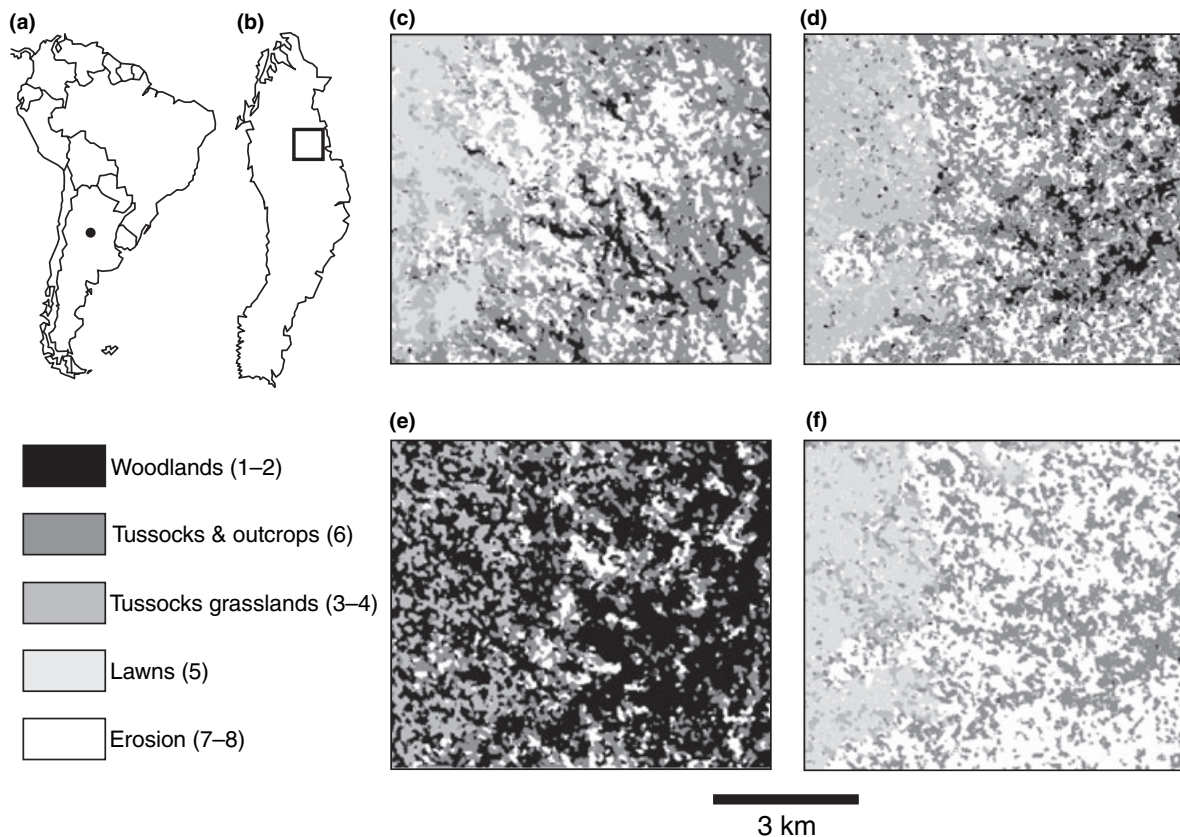


Figure 3 (a) Location of the study area in South America. (b) The whole study area indicating the representative portion selected to be shown in detail. Details of (c) the real vegetation map (Cingolani *et al.*, 2004), and the simulated maps under (d) present conditions, (e) low livestock pressure and (f) high livestock pressure. For the sake of clarity in the presentation, in parts (c)–(f) some vegetation units were merged (the number of the units indicated between brackets in the legend) and a 3×3 filter was applied to the original maps.

livestock produces important amounts of soil erosion in various ecosystems of South America (Molinillo, 1993; Fjelds  & Kessler, 1996). Native camelids, having hooves with a ‘cushion’, exert less pressure on soils than European livestock (Coates & Ayerza, 2004). The soils of our study area are fragile, and erosion is triggered easily (Cabido *et al.*, 1987; Cingolani *et al.*, 2003). It is thus very likely that the higher pressure exerted on soils by sheep and cattle in comparison with wild herbivores may be a cause of such widespread soil erosion, even under a simulated history of low disturbance.

The third explanation relates to fire use. In the study area, natural fires are uncommon because electrical storms occur in the rainy season. At present, fires are lit by livestock owners at the end of the dry season, to eliminate accumulated dry biomass of tussock grasses, and produce green regrowth in the period of greater shortage, as reported for other mountain grasslands in Argentina (Molinillo, 1993). Fires temporarily expose the soil surface triggering soil erosion, especially when combined with livestock trampling (Johansen *et al.*, 2001; Wondzell & King, 2003; Asner *et al.*, 2004). Fire also burns *Polylepis* trees, especially when not protected by rocks, and surviving trees resprout from their bases, leaving tissues within the reach of livestock (Renison *et al.*, 2002). Fire is used to produce forest conversion to grasslands in many humid and

subhumid ecosystems of the world (Asner *et al.*, 2004), and a global scale simulation indicated that without fire (both natural and anthropogenic), closed forests in the world would double from 27% to 56% of land surface area (Bond *et al.*, 2005).

We consider that in our study area a combination of these three factors is the most likely origin of the reported landscape-scale vegetation changes and land degradation, despite the long grazing history and the adaptation of plants to herbivory. We suggest that current animal densities are higher than past wild animal densities, the types of animals are more damaging to soils, and fires have probably increased considerably after the introduction of domestic livestock. However, further studies will be necessary to determine the relative importance of these different factors and revert ongoing degradation.

Structuring factors of vegetation

Vegetation units responded to a combination of physical features and accumulated livestock pressure, although a great proportion of the variance at the pixel level remains unexplained. Our interpretation is that because some vegetation units are related in a successional sequence, the unit actually present in a given pixel depends to a great extent on the history

of disturbance (Hunter, 1990). Although this history was considered in our model, the predictors used (distance to houses and roads) have some limitations. Using these predictors, we have missed information at two spatial scales. At broad scales, we did not take into account differences in management associated with sharp limits between properties or areas used by different stakeholders. Additionally, we have missed the small-scale heterogeneity related to physical barriers or other factors affecting animal habitat utilization and fire occurrence, or stochastic elements related to the recent history of disturbance. In summary, we attribute the relatively poor predictive power of our model to unaccounted for variability in the disturbance history, although we cannot rule out that we have also missed some relevant physical variable.

Despite the low habitat specificity, our results indicate a clear difference between the habitats occupied by pure grasslands, especially lawns and thick tussock grasslands (v5 and v3), and the habitats occupied by all other units. Lawns and thick tussock grasslands share very similar habitats, both occurring in plateaus (physiographic unit D) at high altitudes. Lawns tend to be close to houses, while thick tussock grasslands tend to be far away from them. This agrees with previous studies showing the strong influence of grazing and fire in the transformations between lawns and tussock grasslands (Díaz *et al.*, 1994; Pucheta *et al.*, 1997, 1998; Cingolani *et al.*, 2003). The other pure grassland unit (thin tussock grasslands, v4) is also abundant in plateaus at high altitudes, but shows less habitat specificity since it also occupies large areas in other habitats, in part because it pooled communities with different dominant tussock species (Table 1). Thin tussock grasslands are successional communities which replace some lawns when excluded from livestock and fire (Pucheta *et al.*, 1998), but if exclusion is prolonged they can be replaced by thick tussock grassland or woodland, depending on the abiotic conditions and the availability of *Polylepis* propagules (Cingolani *et al.*, 2003; Torres *et al.*, in press). This was reflected in our simulations, which showed that under a history of low disturbance, thin tussock grasslands would occupy a relatively low surface compared with present distribution.

According to previous works, open woodlands tend to be at higher topographic positions than closed woodlands (Cabido & Acosta, 1985; Enrico *et al.*, 2004; Renison *et al.*, 2006). Enrico *et al.* (2004) attributed these differences to higher water stress at upper topographic positions, while Cabido & Acosta (1985) suggested that both communities could be related in a successional sequence. Renison *et al.* (2006) failed to find a relationship between topography *per se* and *Polylepis* density and suggested, with strong evidence, that closed woodlands are found in lower topographic positions due to a lower incidence of browsing and fires. In the present study, comprising the whole landscape, we found practically no differences between the behaviour of closed and open woodlands in relation to either physical or livestock-related predictor variables. Both units were more frequent far away from sources of livestock-related disturbance, at low topographic positions and altitudes,

and in steep sites with low insolation. However, the differences in the shape of the relationships between livestock pressure indicators and the probability of occurrence of each unit (more pronounced for closed woodlands far away from sources of disturbance, plot not shown) together with evidences from previous studies (Renison *et al.*, 2002, 2006; Teich *et al.*, 2005) indicate that both units are probably related in a successional sequence, being open woodlands maintained as such by browsing and/or more frequent fires.

Tussocks and outcrops (v6) also occupy very similar habitats to woodlands (v1 and v2), suggesting that they are in areas where fire and browsing produced an almost complete elimination of *Polylepis*. This interpretation is supported by previous results (Renison *et al.*, 2002, 2006; Teich *et al.*, 2005) and by the difference between both units in their relationships with livestock pressure indicators. Under a simulated history of low livestock pressure, tussocks and outcrops (v6) occupy a smaller area than at present, while woodlands occupy a larger area. The relationship with altitude was different for woodlands than for tussocks and outcrops. While woodlands decrease at high altitudes, tussocks and outcrops do not vary, suggesting that besides the effect of disturbance, temperature limits the growth of *Polylepis* (Renison *et al.*, 2006). Low temperature could be particularly detrimental for this species after a fire or a browsing event, because recovery is retarded.

Erosion and outcrops (v7) was previously interpreted as the consequence of strong erosion operating during long periods on the original unit of tussocks and outcrops (v6) (Cingolani *et al.*, 2004). Our results support this interpretation, since the eroded unit (v7) increased with increasing livestock disturbance, and occupied larger areas than at present under a simulated history of heavy livestock disturbance. Additionally, unit v7 tended to occur at higher topographic positions than unit v6, which is in line with previous results suggesting that upper topographic positions are more susceptible to erosion (Cingolani *et al.*, 2003).

Management implications

The simulated situations far away from sources of livestock disturbance showed a landscape with high proportions of woodlands and tussock grasslands. This vegetation is efficient in retaining rain water, a highly valuable attribute for the Córdoba Mountains, which provide water to over 2 million people. Additionally, *Polylepis* woodlands harbour a high proportion of endemic species (Robledo *et al.*, 2006). When simulating a situation close to sources of livestock disturbance, the proportion of tussock grasslands and woodlands experienced an important decrease, while bare rock increased. This scenario is clearly undesirable for the conservation of water resources and *Polylepis*-associated endemic species. Conversely, lawns (v5), which are associated with heavy livestock pressure, would be a desirable unit to conserve due to their high alpha plant diversity (Pucheta *et al.*, 1998; Cingolani *et al.*, 2003). When simulating a history of light disturbance, desirable for the conservation of water resources, this unit was almost

completely eliminated, a result in line with field studies (Pucheta *et al.*, 1998; Cingolani *et al.*, 2003). Under a history of heavy disturbance, this unit occupies large surfaces but only in the plateaus (physiographic unit D), since it is the habitat most prone to be lawn-dominated. In other physiographic units, a higher livestock stocking rates converts tussock grasslands into lawns, but simultaneously lawns are converted to eroded surfaces (Cingolani *et al.*, 2003). Thus, for lawn conservation, heavy grazing would not be recommendable in most situations. Due to the strong preference of animals for grazing lawns (Cingolani *et al.*, 2004) it is possible that, even with low herbivore densities, patches of this community can be preserved within the matrix of thin and thick tussock grasslands (personal observation). Thus, we conclude that a situation 'far from roads and houses' is desirable for the conservation of the Córdoba Mountains, and livestock-associated disturbance should be maintained at these relatively low levels, provided that patches of lawns are preserved within the thin and thick tussock grassland units.

An additional implication of our results is that they challenge the largely established idea of our study area as a climatically determined grassland with woodlands restricted only to special habitats in deep ravines (Cabido, 1985; Cabido & Acosta, 1985; Díaz *et al.*, 1994; Pucheta *et al.*, 1998; Cingolani *et al.*, 2003). Our study showed that a great number of grasslands can share similar habitats with woodlands, and that livestock and associated fires have an important influence on the occurrence of these units. This suggests that the system is at present strongly 'consumer controlled' (Bond, 2005), and indicates that it should be managed as an integrated landscape, and not be considered as having 'woodland' and 'grassland' habitats as two separate and clear-cut environments.

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BIOSKETCH

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