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The interplay among grazing history, plant-plant spatial interactions and species traits affects vegetation recovery processes in Patagonian steppe

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Abstract: Since the early 20th century Patagonian arid steppes have been subjected to overgrazing that led to the degradation of plant communities. We hypothesized that the interplay among grazing history, plant-plant spatial interactions and species traits affects recovery and assemblage of shrub community after short-term abandonment in north-eastern Patagonian arid steppe (Peninsula Valdés, Argentina). We compared six sites (two in grazed pastures, and four in short-term ungrazed pastures, two of which intensively grazed, while the other two low intensity grazed in the past) with regard to: shrub cover percentage (10 m × 10 m plots); shrub patch dimension, species richness, and spatial interactions among shrub species depending on patch dimension (patches sampled along transects); species richness and composition, vertical relations among species, and traits related to avoidance strategies and disturbance (1 m × 1 m plots sampled along transects). Our results indicated that recovery processes in abandoned pastures act through the increase in shrub patch size, formation of new patches, change in patch composition and richness, and in within-patch relations among shrub species. No significant differences were found between sites subjected to different past grazing intensities. The increase in shrub cover was due to a significant expansion of the dominant shrub *Chuquiraga avellanedae*. The mechanism of new patch formation and spread was mainly based on facilitative processes acting between the dwarf shrubs, poorly palatable and disliked by wild herbivores, and young individuals of the dominant species emerging from their canopy. As patch size increased, dwarf shrubs were covered by taller ones or grew at the edge of the patch, indicating a phase of competitive exclusion. Plant-plant spatial interactions involved changes in the composition of plant traits linked to avoidance strategies, which were indicators of grazed conditions and of plots with shrub cover lower than 50%, while less need for defence against animal browsing was highlighted in ungrazed pastures and shrub-dominated plots. As the density of herbivores is recognized as the key factor in biodiversity conservation and ecosystem recovery, management plans devoted to conservation of biodiversity and forage resources should work to recreate grazing conditions close to the wild ones or to impose a short-term period of ecosystem rest that allows the plant community to recover.

Abbreviations: HG–high intensity grazing before sheep exclusion; ISA–Indicator Species Analysis; LG–low intensity grazing before sheep exclusion; SPT–Species position type.

Species nomenclature: Flora Argentina (http://www.floraargentina.edu.ar)

Introduction

For centuries, Patagonia's vast expanses of arid grasslands supported large herds of wild herbivores grazing on native grasses and scrubs. In the early 20th century, pioneers established a system of land use that could not succeed given the region's ecology, because stocking rates were above the carrying capacity of the pasture (Rostagno and del Valle 1988). Long-term effects of overgrazing include decrease of the dimension of shrub patches, reduction of species richness, reduction of cover of palatable plants, and increase of unpalatable woody plants (e.g., Bisigato and Bertiller 1997, Milchunas and Lauenroth 1993, Perelman et al. 1997).

In the Patagonian steppe, the vegetation shows the typical patchy distribution of water-limited ecosystems (Soriano et al. 1994) in which patches dominated by shrubs alternate with bare soil areas, hosting few annual species (Aguiar and Sala 1999, Ludwig et al. 2004). This ecosystem is composed of different patch types, marked by phases of building and degeneration (Aguiar and Sala 1999). The building phase starts with the establishment of woody plants. As they grow, the microenvironment changes because of higher water infiltration, reduction in radiation reaching the soil, and accumulation of seeds, fine soil particles and plant debris (Rostagno et al. 1991, Evans and Ehleringer 1994, Halvorson et al. 1995, Mazzarino et al. 1996). These environmental ameliorations promote the establishment of beneficiary species (*sensu* Valiente-Banuet et al. 1991). Positive plant-plant spatial interaction is a well known process acting in harsh environments and promoting species richness and diversity (Pugnaire and Luque 2001, Callaway et al. 2002, Flores and

Jurado 2003, Kikvidze et al. 2011, Catorci et al. 2011b). It is also a key factor in grazed systems where non palatable plants provide refuge for the more palatable ones (Callaway et al. 2005, Patty et al. 2010, Li et al. 2011). The nurse canopy dimension plays an important role, because large canopies provide a greater range of surface microsites and have a greater capacity to ameliorate harsh environmental conditions (e.g., Pugnaire and Luque 2001, Maestre et al. 2005, Catorci et al 2011b, Howard et al. 2012). The degenerative phase starts with the death of dominant individuals. This leads to wind and water induced loss of soil fine particles (Aguiar and Sala 1999). Moreover, palatable plants lose the protection against the herbivore bite, and thus species richness decreases (Callaway et al. 2005).

The processes related to patch and community dynamism undergo selective pressure due to the number of herbivores, their foraging ecology, and the livestock composition (Kausrud et al. 2006, Zheng et al. 2010, Catorci et al. 2012b, Allred et al. 2012). Tadey (2006) demonstrated that arid environments are not less sensitive to grazing than more humid ones. Indeed, not all plants growing in poorly productive environments are resistant to grazing (Cingolani et al. 2005), and changes in species cover may be traced back to the herbivores selection on the basis of relative palatability (Hunt 2001, Bertiller and Ares 2008, Onatibia et al. 2010). Several authors found close relations between herbivory and some plant traits that can be regarded as functional responses to herbivory, such as plant chemical and mechanical defences, life history, growth form, clonality, plant height, and leaf morphology (e.g., Lavorel et al. 1997, 2007, Díaz et al. 2007a, Peco et al. 2012). Palatability of flowers and fruits may affect the sexual reproduction and persistence of plants as well (Pelliza et al. 1993).

While processes related to the effects of overgrazing on Patagonian steppe are well known (e.g., Perelman et al. 1997, Cipriotti and Aguiar 2005, Cesa and Paruelo 2011), little is known about the mechanisms that lead to vegetation recovery after abandonment, and more investigations should address this issue.

Our general hypothesis was that the interplay among plant-plant spatial interactions, grazing history, and species functional traits plays a role in plant community recovery and assemblage after abandonment. More specifically, since overgrazing was proposed as a control factor of patch size in Patagonian steppe, decreasing shrub cover and species richness, and changing the spatial interactions among species (Aguiar and Sala 1998, Bertiller and Bisigato 1998), we hypothesized that (1) short-term sheep grazing cessation triggers recovery processes leading to the increase in shrub cover, patch size and structural complexity, and species richness. If so, we expect that (2) different grazing intensities in the past could have affected differently shrub encroachment, species richness and composition. Based on the above mentioned considerations about plant traits and species palatability, we hypothesized (3) an increase in abundance of traits not involved in avoidance strategies and in species palatability after grazing cessation and along a gradient of increasing patch structural heterogeneity.

Materials and methods

Study area

The study area is located in Península Valdés (included in the Unesco World Heritage List), in the north-eastern portion of the Chubut province (Patagonia). Part of the study area is included in the San Pablo de Valdés Reserve (coordinates range 42°36’ - 42°43’S, and 64°10’ - 64°15’W) which extends over 7,360 hectares. Inside the reserve, sheep rearing (about 2,800 individuals) was forbidden in 2005, and starting that year the guanaco (*Lama guanicoe* P.L.S. Müller, 1776) population began its increase from 200 to the current number of 1,100-1,200 individuals. Outside the protected area, sheep rearing follows traditional livestock management methods, with a high stocking rate.

The study area is almost flat, ranging from 10 to 80 m a.s.l. Mean annual precipitation is about 240 mm, with high inter-annual variation; the rainfall is homogeneously distributed during the year, with slight peaks in autumn (April-May). According to Rivas-Martínez (2010), the study area is included in the Mediterranean macrobioclimatic region, with xeric oceanic bioclimate, upper mesomediterranean thermotype, and semiarid ombrotype.

Soils are moderately deep, not much permeable, and have a sandy-textured surface horizon on a sandy clay loam-textured subsurface horizon.

The plant landscape is mostly characterized by *Chuquiraga avellanedae*-dominated shrub communities.

Sampling design

We selected six sites, two of which were outside the protected area (grazed pastures), and four inside the reserve (short-term ungrazed pastures) using a space-for-time substitution approach (Pickett 1989). This approach has proven its validity to infer many aspects of vegetation dynamics, providing significant insights into the patterns and mechanisms of regeneration and succession (Foster and Tilman 2000, Garnier et al. 2004). Distance between sites was greater than 5 km.

The sites inside the reserve differ in past grazing intensity: two of them were intensively grazed, while the others were low intensity grazed areas, based on the assumption that the distance from watering points can be a proxy for stocking rate (Landsberg et al. 2003, Riginos and Hoffman 2003).

To reach our goals we chose two scales, the community level and patch level. To study the first level, we randomly laid out ten 10 m × 10 m plots in each of the six sites, and a total of 60 plots were selected. Regarding the patch scale, one linear transect 200 m long was randomly laid out in each of the six sites, as there was no strong environmental gradient structuring the vegetation. Along each transect, 20 points (one every 10 m) were located and shrub patches matching the points were selected (106 in all out of 120, while 14 falled on bare soil).

Moreover, 240 plots of 1 m^2 (1 m × 1 m) were placed along other six linear transects 200 m long (one for each site). The distance between consecutive plots was 5 m. Plots falling in areas covered by faeces and crossed by vehicle and animal tracks were not considered (20 in all). Thus, 74 plots were established in currently grazed pastures, 74 in ungrazed sites formerly subjected to high grazing intensity, and 72 in ungrazed areas formerly subjected to low grazing intensity. Finally, plots were clustered according to the type of vegetation structure. Four vegetation cover types were considered: shrub cover greater than 90%; ranging from 51 to 90%; ranging from 11 to 50%; lower than 10%.

Data collection

In 10 m × 10 m plots, the total cover percentages of shrubs were visually estimated by four observers at each corner of the plot; values were then averaged.

As regards the 200 m long linear transect, in each considered patch, maximum height, length (measured along the direction of maximum spread), and width (measured orthogonally to the direction of maximum length) were measured, and the shrub species were listed. Linear measurements were taken using a graduated rod. The surface area of patches was estimated by the Bézout method, that consists in approximating the perimeter of the patch with a broken line and then calculating the area as sum of areas of rectangle trapezia whose oblique sides correspond to the segments of the broken line, and whose heights were measured along the line of maximum patch length. The spatial interactions of shrubs (hereafter called SPTs, namely Species position types) were categorized as follows: shrub forming patches without other species (SPTI); dominant shrub structuring the patch (SPTII); shrub co-occurring with shrubs structuring the patch, but with a subordinate (lower cover value) role (SPTIII); shrub under the canopy of dominant or subordinate shrubs (SPTIV); shrub at the edge of the patch (SPTV); tall shrub emerging with its canopy from the dominant shrub layer (SPTVIa); shrub emerging with thin shoots from the dominant shrub layer (SPTVIb); juvenile shrub emerging from the dominant layer, composed of dwarf shrubs (SPTVII).

In each 1 m × 1 m plot, the total shrub cover and the species cover percentages were visually evaluated. To detect the vertical plant-plant relations among species, the recorded individuals of each species were assigned to one of the following categories: projecting their canopy over individuals of other species; growing below the canopy of other species; emerging with isolated shoots or stems over the dominant patch canopy; not covered by other plants.

As it is known that pasture management determines different types of functional responses (e.g., Sternberg et al. 2000, Bullock et al. 2001, de Bello et al. 2006, Rusch et al. 2009), the following plant traits related to disturbance and defence strategies were chosen: plant form (tall shrub > 2.0 m; low shrub 0.3-2.0 m; dwarf shrub < 0.3 m; liana; succulent; perennial graminoid herb; perennial non-graminoid herb; annual graminoid; annual non-graminoid); leaf morphology (broad, i.e. length less than two times the width; narrow, i.e. length more than two times the width; imbricate; prickly; transformed, e.g. scale-like leaves on photosynthetic stem); leaf/flower position (leaves/flowers or flowering shoots distributed at the ground level, in prostrate plants; leaves/flowers or flowering shoots distributed along the stem, in upright plants, never in prostrate shoots); clonal growth organs (present/absent); defence type (chemical defence, e.g. resins, toxic substances; mechanical defence, i.e. spiny/prickly leaves, spines on the stem, stem/branches/twigs transformed into spines; leaf toughness; no defence); leaf hairiness (present/absent). As a general indicator of the interaction between plants and herbivores, plant palatability features (high - plant eaten by grazers; poor - plant eaten only when it has young and soft leaves or buds, at the beginning of the growing season; absent - plant not eaten by grazers) were considered as well. Data on traits were collected in the field; data on chemical defences and palatability were gathered from field observations and bibliographic data (Puig et al. 1996, 1997, Baldi et al. 2004) and from the observations of the San Pablo de Valdés Reserve staff. Field work was performed in November and December 2011.

Data analysis

In the 10 m × 10 m plots, Mann-Whitney U-tests (for not normally distributed data) were performed to identify differences in shrub cover between grazed and ungrazed treatments, and within the latter ones, between conditions subjected to high and to low past grazing intensity. We accounted for spatial autocorrelation in the statistical tests by adjusting the Type I error rate to a more conservative value. For this purpose, using the approach indicated by Dale and Fortin (2002), we set the significance threshold at 0.001.

The same tests were performed to identify differences in shrub patch dimensions and in shrub richness between grazed and ungrazed conditions, and between high and low intensity of grazing before sheep exclusion. Correlations between patch dimensions (height, length, width, and surface area) in the different treatments were examined using Spearman rank correlation coefficients. As surface area was strictly positively correlated to the three maximum patch dimensions, only surface area was used for further analyses. To verify whether the number of shrub species was correlated with patch dimensions, correlation coefficients between shrub species richness and patch size were calculated. The range of patch dimension was divided into classes. The optimal number of classes was evaluated using Sturges' (1926) formula. The frequency distribution of classes in the grazed and abandoned treatments was then calculated.

To assess the role of shrub species in structuring the patches and their spatial interactions in relation to patch di-

Table 1. Mean maximum length, width, height (m), and surface area (m^2) of shrub patches (± standard error), compared in grazed and ungrazed conditions, and in ungrazed sites subjected to high intensity (HG) and to low intensity (LG) grazing before sheep exclusion. Significance of differences was assessed using Mann-Whitney U-test ($^{**}P < 0.01$; $^{*}P < 0.05$; n.s.: not significant).

	Grazed	Ungrazed	*P*	Ungrazed HG	Ungrazed LG	*P*
Length	1.31 ± 0.13	2.13 ± 0.20	**	2.36 ± 0.25	1.89 ± 0.32	n.s.
Width	1.06 ± 0.11	1.53 ± 0.15	*	1.76 ± 0.20	1.20 ± 0.22	n.s.
Height	0.55 ± 0.05	0.84 ± 0.08	**	0.94 ± 0.10	0.71 ± 0.13	n.s.
Surface area	1.00 ± 0.16	2.43 ± 0.33	*	2.82 ± 0.42	1.90 ± 0.52	n.s.

mension change, Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997, McCune and Grace 2002) was run on the response variables matrix "plots-by-SPT occurrences of each shrub species" using patch surface area classes as grouping variable, in grazed and ungrazed treatments.

Species richness in plots of 1 m^2 was calculated separately for plots belonging to each management condition and vegetation structure as the average species number per plot. Paired sample t-tests (for normally distributed data) or Mann-Whitney U-tests (for not normally distributed data) were performed to identify differences in species richness values between grazed and ungrazed plots and between ungrazed sites subjected to high intensity and to low intensity grazing before sheep exclusion.

To detect indicator species of each treatment (currently grazed and ungrazed) and of each past grazing intensity, ISA was performed as well. ISAs, computed using plots of 1 m^2, were run on the response variable matrix "plots-by-species cover", using management type (grazing, abandonment) and past grazing intensity as grouping variables. Statistical elaborations were performed separately for the four types of vegetation structures.

Trait binary data (presence/absence) were transformed into quantitative data. For this purpose, the matrix "plots-by-species cover" was multiplied by the matrix "species-by-traits" to provide a matrix "plots-by-trait cover", which formed the basis for the following analyses (Pakeman et al. 2009, Catorci et al. 2012a). To identify how abandonment affects trait composition, ISA was performed on the matrix "plots-by-trait cover", using management type (grazing, abandonment) as grouping variable. We used plots of 1 m^2 where shrub cover was higher than 10%. Within grazed and ungrazed pastures, indicator traits of each shrub cover type were detected by ISA, performed on the matrix "plots-by-trait cover", using type of vegetation structure as grouping variable.

Data on shrub cover, patch dimensions and species richness were expressed as mean ± standard error.

Normality distribution and variance homogeneity of shrub cover, patch dimensions, and species richness, were assessed using the Kolmogorov-Smirnov test and the Levene test, respectively. As regards ISAs performed on different data sets, the statistical significance ($P < 0.05$) of the observed maximum indicator values was tested using the Monte Carlo test, based on 4,999 permutations; indicator values greater than 20 were considered of interest.

Table 2. Correlation (Spearman ρ) between shrub species number and patch surface area for the different treatments (HG: high intensity grazing before sheep exclusion; LG: low intensity grazing before sheep exclusion; $^{**}P < 0.01$; $^{*}P < 0.05$).

Treatment	Surface area
Grazed	0.330*
Ungrazed	0.816**
Ungrazed HG	0.782**
Ungrazed LG	0.858**

The Kolmogorov-Smirnov test, the Levene test, paired sample t-test, Mann-Whitney U-test, and Spearman rank correlation analysis were performed using SPSS 8.0 software (SPSS Inc. 1997); ISAs were run using PCORD 5.0 software (McCune and Mefford 2006).

Results

The comparison between grazed and ungrazed 10 m × 10 m plots showed that shrub cover percent value was significantly greater ($P < 0.001$) in the ungrazed (52.97 ± 1.77) than in the grazed condition (25.44 ± 1.85), while no significant difference ($P = 0.180$) was found between plots subjected to high grazing pressure (50.70 ± 2.19) and those subjected to low grazing intensity before sheep exclusion (55.24 ± 2.74).

Shrub patch size increased significantly in ungrazed plots in comparison to grazed ones (Table 1). Differences in size between plots in sites subjected to past low and high grazing intensity were not statistically significant (Table 1). Patch dimensions and surface area were highly positively correlated (Spearman $\rho > 0.80$; $P < 0.01$), considering each treatment singly.

In grazed pastures, most patches were concentrated in the low dimension classes, while in ungrazed areas, patches were more heterogeneous in size (Figure 1). The number of shrub species per patch was significantly higher ($P < 0.001$) in ungrazed (2.66 ± 0.15) than in grazed (1.32 ± 0.09) treatment, while no significant difference was found between past low and high grazing intensity. Shrub species number was more highly positively correlated with patch surface area in ungrazed than in grazed conditions (Table 2).

With regard to SPTs, ISA showed that in the grazed treatment, the lower dimension classes had no indicator SPTs (Table 3). In ungrazed conditions, *Chuquiraga avellanedae* (forming patches without other species or emerging as juvenile individuals from the dominant dwarf shrub layer) and

Table 3. Shrub species with different locations (SPTs) in the patches, indicator of surface area classes in grazed and ungrazed conditions, as performed by Indicator Species Analysis. Only locations with statistically significant indicator values greater than 20 are indicated (I: shrub forming patches without other species; II: dominant shrub structuring the patch; III: shrub co-occurring with shrubs structuring the patch, but with a subordinate role; IV: shrub placed below the dominant or subordinate shrubs; V: shrub placed at patch edge; VIa: shrub, more than 1 m tall, emerging from the dominant shrub layer; VIb: shrub emerging with thin shoots from the dominant shrub layer; VII: juvenile shrub emerging from the dominant layer, composed of dwarf shrubs; $^{**}P < 0.01$; $^{*}P < 0.05$; n.s.: not significant). (1) Surface area classes as in Figure 1.

		Surface area class[1]							
	Species	1	2	3	4	5	6	7	8
Grazed	*Chuquiraga avellanedae*	n.s.	n.s.	n.s.	II*				
	Prosopidastrum globosum	-	n.s.	n.s.	III*				
	Lycium chilense	-	n.s.	n.s.	IV*				
Ungrazed	*Chuquiraga avellanedae*	I**, VII**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Nassauvia ulicina	II**	n.s.	-	-	-	-	n.s.	-
	Schinus johnstonii	-	n.s.	VIa*	VIa*	-	IV*	-	-
	Acantholippia seriphioides	n.s.	n.s.	V**	n.s.	V*	n.s.	n.s.	n.s.
	Chuquiraga erinacea subsp. *hystrix*	n.s.	n.s.	VIa*	n.s.	n.s.	n.s.	n.s.	n.s.
	Lycium chilense	-	VIb*	n.s.	IV*	n.s.	n.s.	n.s.	IV*

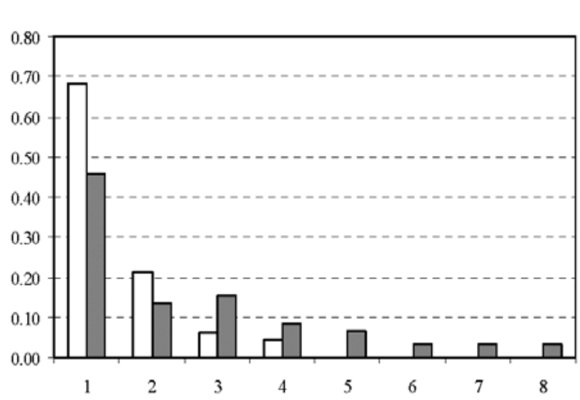

Figure 1. Frequency distribution of shrub patch surface area classes in grazed pastures (white bars) and ungrazed pastures (grey bars). Surface area classes (m^2): 1 - 0.0-1.2; 2 - 1.3-2.4; 3 - 2.5-3.6; 4 - 3.7-4.8; 5 - 4.9-6.0; 6 - 6.1-7.2; 7 - 7.3-8.4; 8 - 8.5-9.6

Nassauvia ulicina (occurring as dominant shrub) were indicators of small patches. Even if not highlighted by ISA, *C. avellanedae* (with II, III or IV SPTs) was the most frequent shrub in all the dimension classes, except the smaller ones, in both grazed and ungrazed treatments (Appendices 1 and 2).

Emerging shrubs (*Lycium chilense*, *Schinus johnstonii*, and *Chuquiraga erinacea* subsp. *hystrix*) and dwarf shrubs growing at the patch edge (particularly *Acantholippia seriphioides*) were indicators of patches falling in the intermediate-upper dimension classes (Table 3).

Abandoned pastures had significantly higher ($P < 0.001$) species richness per 1 m^2 plot (5.54 ± 0.13) than grazed ones (4.69 ± 0.17). In all the shrub cover classes species richness followed the same trend: 5.00 ± 0.27 vs. 3.17 ± 0.40 (P = 0.004) for shrub cover higher than 90%; 5.59 ± 0.18 vs. 4.93 ± 0.20 (P = 0.047) for shrub cover ranging from 50 to 90%; 5.74 ± 0.26 vs. 5.13 ± 0.52 for shrub cover ranging from 10 to 50% (P = 0.234); 5.70 ± 0.38 vs. 4.29 ± 0.34 for shrub cover lower than 10% (P = 0.025). Pastures subjected to past high grazing intensity did not differ significantly in species richness from those subjected to past low grazing intensity in all the structure types.

Table 4. Observed indicator values of species in 1 m x 1 m plots, as performed by Indicator Species Analysis. Statistical elaborations were run in plots placed in patches with shrub cover > 90%, ranging from 51 to 90%, ranging from 11 to 50%, and ≤ 10%, to compare grazed and ungrazed conditions. Only statistically significant indicator values greater than 20 are indicated ($^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$).

Vegetation structure	Treatment	Species	Indicator value
Shrub cover > 90%	Grazed	*Chuquiraga avellanedae*	69.6**
		Piptochaetium napostatense	28.6*
	Ungrazed	*Chuquiraga erinacea* subsp. *hystrix*	73.9**
Shrub cover 51-90%	Grazed	*Chuquiraga avellanedae*	54.5*
		Schismus barbatus	52.9***
		Hoffmannseggia trifoliata	21.9*
	Ungrazed	*Acantholippia seriphioides*	60.9***
		Pappostipa speciosa	50.3***
		Chuquiraga erinacea subsp. *hystrix*	34.8***
		Poa ligularis	45.8***
		Jarava neaei	38.6**
		Senecio subulatus	27.5**
Shrub cover 11-50%	Ungrazed	*Schismus barbatus*	78.7**
		Chuquiraga avellanedae	75.2**
		Hordeum murinum	37.5**
		Piptochaetium napostaense	37.5**
Shrub cover ≤ 10%	Grazed	*Arenaria serpens*	46.8**
		Hordeum murinum	42.6**
		Pappostipa humilis	21.4*
	Ungrazed	*Senecio subulatus*	47.8**
		Hoffmannseggia trifoliata	41.0*
		Poa lanuginosa	33.3*

The indicator species of each treatment in the different vegetation structures are shown in Table 4. In shrub-dominated plots, *C. avellanedae* was indicator of grazed condition, while the shrubs *C. erinacea* subsp. *hystrix*, *Senecio subulatus*, *A. seriphioides*, and the herbs *Poa ligularis*, *Pap-*

Table 5. Observed indicator values of species in 1 m × 1 m plots, as performed by Indicator Species Analysis. Statistical elaborations were run in plots placed in patches with shrub cover > 90%, ranging from 51 to 90%, ranging from 11 to 50%, and ≤ 10%, to compare past high and low intensity grazed conditions in currently ungrazed pastures. Only statistically significant indicator values greater than 20 are indicated (HG: high intensity grazing before sheep exclusion; LG: low intensity grazing before sheep exclusion; $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$).

Vegetation structure	Treatment	Species	Indicator value
Shrub cover > 90%	Ungrazed HG	*Chuquiraga erinacea* subsp. *hystrix*	100***
	Ungrazed LG	*Prosopidastrum globosum*	66.7**
Shrub cover 51-90%	Ungrazed HG	*Chuquiraga erinacea* subsp. *hystrix*	64.9***
		Pappostipa speciosa	50.0**
		Poa lanuginosa	25.2*
	Ungrazed LG	*Poa ligularis*	53.6***
		Senecio subulatus	40.1**
		Prosopidastrum globosum	25.0**
Shrub cover 11-50%	Ungrazed HG	*Acantholippia seriphioides*	82.2***
	Ungrazed LG	*Poa ligularis*	79.4***
		Senecio subulatus	62.5***
		Chuquiraga avellanedae	61.9*
		Hoffmannseggia trifoliata	50.0**
		Nassauvia fuegiana	31.2*
Shrub cover ≤ 10%	Ungrazed HG	*Acantholippia seriphioides*	76.0**
	Ungrazed LG	*Nassella tenuis*	77.9**

Table 6. Observed indicator values of traits related to disturbance and defence strategies in grazed and ungrazed conditions, as performed by Indicator Species Analysis in 1 m × 1 m plots. The data set composed of relevés carried out in plots with shrub cover > 10% was used for statistical elaboration. Only statistically significant indicator values greater than 20 are indicated ($^{***}P < 0.001$; $^{**}P < 0.01$).

Treatment	Trait	Indicator value
Grazed	Spiny leaf	55.7**
	Spiny tough leaf	55.1**
	Annual graminoid	53.7***
	Flowering shoots at the ground level	22.7**
Ungrazed	Perennial graminoid	81.4***
	Narrow leaf	78.1***
	Leaf toughness	77.5***
	High palatability	68.6***
	No defence strategies	67.8***
	Leaves on upright stem	55.8***
	Flowering shoots on upright stem	55.8***
	Non-hairy leaf	55.6***
	Absence of clonal growth organs	55.6***
	Clonal growth organs	48.4**
	Chemical defences	28.4**

postipa speciosa, and *Jarava neaei* were indicators of ungrazed pastures. In plots with shrub cover ranging from 11 to 50%, *C. avellanedae* was indicator of ungrazed treatment. The indicator species of each past grazing intensity in the four vegetation structures are shown in Table 5.

Table 7. Observed indicator values of traits in different vegetation structures (shrub cover > 90%, 51-90%, 11-50%, ≤ 10%) as performed by Indicator Species Analysis. Relevés carried out in 1 m x 1 m plots were used for statistical elaboration. Only statistically significant indicator values greater than 20 are indicated ($^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$; n.s.: not significant).

Vegetation structure	Trait	Indicator value	
		Grazed	Ungrazed
Shrub cover > 90%	Low shrub	70.3***	70.9***
	Spiny leaf	69.0**	65.9***
	Non-hairy leaf	68.6**	63.5*
	Leaves on upright stem	68.8**	63.5***
	Flowering shoots on upright stem	68.8**	63.5***
	Poor palatability	68.9*	61.1*
	Tough leaf	-	20.1*
	No clonal growth organs	68.5**	63.3***
	Spiny tough leaf	69.0**	65.2***
Shrub cover 51-90%	Low shrub	65.6***	65.5***
	Spiny leaf	65.9***	66.3***
	Spiny tough leaf	65.9***	63.5***
	Poor palatability	65.5***	77.6***
	Non-hairy leaf	63.4***	62.9***
	Leaves on upright stem	63.2***	62.8***
	Flowering shoots on upright stem	63.2***	62.7***
	Absence of clonal growth organs	63.2***	62.6***
	Perennial graminoid	-	62.5***
	Narrow leaf	n.s.	56.6*
	Clonal growth organs	n.s.	55.0**
	Transformed leaf	n.s.	21.0**
Shrub cover 11-50%	Annual graminoid	74.4***	35.0**
	No palatability	-	47.6*
	Annual non-graminoid	n.s.	38.1***
	Leaves on prostrate stems	-	40.1**
	Hairy leaf	-	39.2**
	Imbricate spiny leaf	-	23.3***
Shrub cover ≤ 10%	Hairy leaf	59.3***	71.5***
	Annual non-graminoid	41.7**	47.9**
	Perennial graminoid	72.4**	-
	Perennial non-graminoid	35.1*	n.s.
	Leaves on prostrate stems	n.s.	66.1***
	Annual graminoid	n.s.	53.1***
	Dwarf shrub	-	38.6*
	Flowering shoots at the ground level	n.s.	37.5***

C. avellanedae was the most common shrub that composed the canopy of patches (about the 80% and 63% of plots in grazed and ungrazed treatments, respectively). Appendix 3 reports the relative frequencies of species for each type of vertical relation, divided into the four considered shrub cover classes. Appendix 4 shows the relative frequency values of vertical relations for each recorded species in each treatment. Some species changed their relative frequency with regard to the type of spatial relation. *Hoffmannseggia trifoliata*, *Jarava ambigua*, *Pappostipa speciosa*, *Plantago patagonica*, *Poa ligularis*, *P. lanuginosa*, and *Senecio subulatus* had greater frequency values as isolated individuals in ungrazed treatment than in grazed one.

As regards plant functional traits, annual graminoid, spiny or spiny tough leaf, and flowering shoots at the ground level were indicator traits of grazed pastures; perennial graminoid, non-hairy leaf, narrow leaf, high palatability, absence of defence strategies, leaves and flowering shoots on upright stems, both presence and absence of clonal growth organs, leaf toughness, and chemical defences were indicators of ungrazed pastures (Table 6). In grazed conditions, annual and perennial herb species, and hairy leaves were indicators of plots with shrub cover lower than 10% or ranging from 11 to 50%; perennial species, spiny leaf, spiny tough leaf, non-hairy leaf, flowering shoots and/or leaves on upright stems, poor palatability, absence of clonal growth organs, characterized shrub-dominated patches (Table 7). In abandoned grasslands, dwarf shrubs and annual species, imbricate spiny leaf, hairy leaf, leaves and flowering shoots on prostrate stems, and no palatability were indicators of plots with shrub cover lower than 50%; the same indicator traits of grazed conditions, as well as perennial graminoids, tough leaf, narrow leaf, transformed leaf, and presence of clonal growth organs, characterized shrub-dominated patches (Table 7).

Discussion

In line with Cipriotti and Aguiar (2012), an increase in average dimensions and cover percentage of shrub patches, was recorded in the ungrazed treatment. Sheep grazing maintains small and equally sized patches, in which SPTs remained substantially unchanged. Instead, abandonment determines the occurrence of heterometric patches (Figure 1) characterized by different SPTs for each patch dimension class (Table 3). This suggests that vegetation recovery processes may act through the change in within-patch relations among shrub species. Abandonment leads to the increase in woody species richness as well. Instead, the lower correlation coefficients between shrub species richness and patch dimensions in grazed sites indicate an overall negative impact of sheep grazing on the shrub species richness. These results contradict the hypothesis that grazing triggers woody species encroachment in arid and semi-arid ecosystems (Archer 1994, Perelman et al. 1997, Walker et al. 1981, Weber et al. 1998), but corroborate other observations showing the opposite trend (e.g., Adler et al. 2005, Manier and Hobbs 2006, Watson et al. 2007, Cipriotti and Aguiar 2012). It was demonstrated that herbivore browsing can have a negative effect on woody species depending on their palatability and defence traits (Riginos and Hoffman 2003, Augustine and McNaughton 2004). Our results showed that difference in grazing history does not affect species richness and the recovery capacity of shrub vegetation but may play a key role in short term recovery processes as regards the encroachment of palatable species. Indeed, most indicator species of low past grazing intensity were highly palatable plants (*Prosopidastrum globosum, Poa ligularis, Hoffmannseggia trifoliata, Nassella tenuis*), while indicators of intense past grazing (*C. erinacea* subsp. *hystrix*, *Acantholippia seriphioides*, *Pappostipa speciosa*) were poorly palatable species.

The increase in shrub cover percentage in the abandoned condition is due to a significant three-dimensional expansion of shrubs (Table 1) and to new patch formation (Table 3). The increase in patch dimensions is mainly due to the spread of *C. avellanedae* individuals, dominant in grazed and in ungrazed sites. The growth of individuals sometimes leads to the fusion of patches, that in ungrazed conditions were composed of two or three individuals of *C. avellanedae* (Catorci, pers. obs.).

The mechanism of new patch formation and spread emerged as mainly based on facilitative processes acting between the dwarf shrubs *Nassauvia ulicina* and *A. seriphioides* and young individuals of *C. avellanedae* emerging from their canopy. Indeed, as shown in Appendix 2, the structure of the smallest patches in ungrazed sites was mainly composed of these dwarf shrubs, from which only young individuals of *C. avellanedae* emerged. Moreover Valiente-Banuet and Verdú (2007) and Catorci et al. (2011b) argued that high level of positive plant-plant spatial interaction indicate the occurrence of facilitative interaction. Dwarf shrubs likely play a key role in the recovery processes because they are poorly palatable and are disliked by guanaco (Puig et al. 1996). We observed the bite marks of guanacos on isolated young individuals of both *C. avellanedae* and *C. erinacea* subsp. *hystrix* (Catorci, pers. obs.). Thus it could be argued that the presence of a quite large number of wild camelids may affect the recovery processes.

In the ungrazed sites, as the dynamic processes go on and patch size increases, *C. avellanedae* tends to become the dominant species structuring the patches. Dwarf shrubs were covered by taller ones or grew at the edge of the patch, indicating a phase of competitive exclusion. This change in the equilibrium between facilitative and competitive processes, previously observed in other dry ecosystems (Callaway and Walker 1997), may be considered a vital driving force of patch dynamic processes.

The tallest shrubs (*Lycium chilense*, *Schinus johnstonii*, and *C. erinacea* subsp. *hystrix*) occur in the middle of patches of the mid-upper dimension classes. All of these tall shrubs have palatable leaves (at least when leaves are young) and/or fruits, thus they need to be far from the patch edges (where herbivores may reach them). Thus the encroachment of *C. avellanedae* confirms the hypothesis that dominant species play a key role in the organization of the plant community (Grime 1998, Howard et al. 2012). Indeed, multi-species assemblage depends on how dominant species interact with the main disturbance regime and resources (Carrick 2003, Midoko-Iponga et al. 2005, Kraaij and Ward 2006, Riginos and Young 2007).

As indicated by ISA (Table 4), palatable perennial graminoids (e.g., *Jarava neaei*, *Piptochaetium napostaense*, and *Poa ligularis*) were found more frequently below or with stems emerging from the shrub canopy than outside the shrub-dominated patches (Appendix 3, Appendix 4). Thus it can be argued that palatable plants need facilitative interactions to establish themselves, also after sheep grazing cessation. The herbaceous seedling establishment may be related to amelioration of harsh conditions determined by shrubs enchroachment and to the presence of a large number of guanacos. Indeed, Baldi et al. (2004) indicated that guanaco showed a preference for perennial grasses, and only when resources are scarce do they select palatable shrubs. However, as shown in Appendix 4, some highly palatable herbs (i.e., *H. trifoliata*, *P. ligularis*, *P. lanuginosa*) in ungrazed condition are more frequently isolated than in grazed condition. This might indicate that the observed positive plant-plant interactions among shrubs and herbs are mostly related to disturbance intensity rather than to a generic amelioration of environmental conditions.

Some unpalatable herbs (e.g., *Pappostipa humilis*, *Arenaria serpens*, and *Hordeum murinum*) and the annual grass *Schismus barbatus* are indicators of grazed pastures and usually occur outside the shrub-dominated patches (Appendix 3). Following Valiente-Banuet and Verdú (2007), we can argue that these plants do not need facilitative interaction.

In accordance with Díaz et al. (2007b), the indicator traits of grazed conditions are few and mainly devoted to strong avoidance strategies (spiny leaf, spiny tough leaf, annual life history, flowering shoots and leaves at the ground level). Instead, the indicator traits of ungrazed treatment are more numerous and indicate less need for defence against animal browsing (Table 6).

The assessment of the indicator traits set along the shrub cover gradient (Table 7) highlighted a trend quite similar to that between grazed and abandoned plots. Plots with shrub cover lower than 50% are characterized by traits devoted to avoidance strategies (e.g., no palatability, hairy leaf, leaves and flowering shoots on prostrate stems) or linked to disturbance (e.g., annual species). Instead, shrub-dominated plots have indicator traits related both to avoidance mechanisms and traits that do not imply defence strategies and are not linked to disturbance. This trait composition is typical of semi-arid systems subjected to low disturbance intensity, in which nurse species have avoidance strategies, while beneficiary ones are not endowed with morphological or chemical defences against herbivore bite (Callaway et al. 2000, Milchunas and Noy-Meir 2002, Rebollo et al. 2002, Catorci et al. 2011b). Absence of clonal ability is an indicator trait of shrub-dominated plots (shrub cover greater than 50%), both in grazed and in ungrazed conditions (Table 7). Eckert (2002) demonstrated that clonal strategies are favoured in harsh environmental conditions. In addition, intense grazing could provide further advantage to clonal species (Catorci et al. 2012a). In the study case, the absence of clonal ability could be explained as the combined effect of environmental amelioration and the decrease of disturbance intensity. In plots sampled in abandoned sites not entirely covered by shrubs (51-90%), clonal ability and “perennial graminoids” are indicator traits. Both these traits were not highlighted in grazed plots with the same shrub cover range. The affirmation of clonal ability in such condition may be linked to the advantages in resource capture and exploitation given by the fast occupation of new locations (de Kroon et al. 2005, Catorci et al. 2011a), thus actively contributing to the patch dynamism.

Conclusions

Recovery processes are underway in the studied system after short term grazing cessation; we observed patch dynamism mechanisms marked by facilitative and competitive processes involving the interplay between plant functional traits and plant-plant spatial interaction. The effectiveness of these ecological processes is filtered in different ways by past and current disturbance intensity and type. Indeed, patch composition changed according to the interplay among the species traits devoted to the herbivory defence strategy and clonal ability, plant-plant spatial interaction (both positive and negative), dominant shrub cover value and herbivory intensity. The density of herbivores, including that of wild camelids, emerged as the key factor in biodiversity conservation and ecosystem recovery. Thus management plans devoted to biodiversity and conservation of forage resources should work to recreate grazing conditions close to the wild ones (as regards herbivory density) or to impose a short-term period of ecosystem rest that allows the plant community to recover.

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Appendices

Appendix 1. Relative frequencies (%) of shrub species in patches sampled using 200 m transects.

Appendix 2. Relative frequencies of shrub species position types within the patches sampled using 200 m transects.

Appendix 3. Relative frequencies of each species in 1 m x 1 m plots, indicated for each type of vertical relation with the other species in each vegetation structure of each treatment.

Appendix 4. Relative frequency (%) of species in 1 m x 1 m plots, indicated for each type of vertical relation with the other species in each treatment (a: projecting its canopy on individuals of other species; b: growing below the dominant shrub layer; c: emerging over the dominant shrub layer; d: not covered by shrubs and isolated).

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