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Direct and indirect effects of grazing constrain shrub encroachment in semi-arid Patagonian steppes

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Arid ecosystems; Biotic interactions; Browsing; Demography; Desertification; Population dynamics; Matrix models; Neighborhood analysis; Sheep grazing; Woody encroachment

Nomenclature
Correa (1971–1984) and Ulibarri (1986)

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Abstract

Question: What are the long-term effects of grazing exclusion on the population structure and dynamics of, and interactions among, three dominant shrub species?

Location: Grass-shrub Patagonian steppe, Chubut, Argentina.

Methods: Permanent plots were established in grazed paddocks and paddocks excluded from grazing in representative Patagonian rangelands. Shrub abundance, population size-structure, short-term (two 3-yr periods) and long-term (matrix models) population dynamics, and neighborhood interactions of three native and codominant shrub species (*Mulinum spinosum*, *Senecio filaginoides* and *Adesmia volckmanni*) were measured and analysed using different statistical approaches.

Results: The total density of shrubs was 74% higher in paddocks excluded from grazing, owing mainly to increases in *Mulinum* (80%) and *Senecio* (68%) species. However, differences in size structure between ungrazed and grazed paddocks were only detected in *Mulinum*. Demographic rates differed between shrub species, time-periods and grazing conditions. In particular, recruitment in the short term (especially in wet years) and population growth rate in the long term (λ) were higher in paddocks excluded from grazing only in *Mulinum* populations. *Senecio* populations showed a marginal increase in recruitment and mortality independent of the grazing condition in the wet and dry period. Grazing exclusion modified the balance of neighborhood interactions among the three shrub species. In grazing-exclusion paddocks, there was a balance between positive and negative interspecific interactions, while in grazed paddocks there were more negative intraspecific and interspecific interactions, resulting in a net negative balance of neighborhood interactions.

Conclusions: Our understanding of woody encroachment in arid rangelands can be informed through evaluation of direct and indirect effects of grazing exclusion on the abundance and demography of dominant woody species. In Patagonian arid steppes, the occurrence of woody encroachment in rangelands excluded from grazing can be explained by altered responses in plant-animal and plant-plant interactions among shrub species.

Introduction

Woody plant encroachment is a global phenomenon that is commonly associated with altered disturbance regimes (Scholes & Archer 1997; van Auken 2000). In arid and semiarid rangelands, woody encroachment is typically linked with overgrazing (Reynolds et al. 2007) and can hinder sustainable land use by impoverishing rangeland condition (Fensham et al. 2005). Many studies describe the phenomenon of encroachment and its impact on floristic composition, diversity, cover and productivity (Perelman et al. 1997; Nano & Clarke 2008), mostly reporting short-term responses at the level of growth-form, or inferring processes from snap-shot studies. However, encroachment is dependent on population-level processes

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of woody species, involving recruitment, survival, growth, reproduction and dispersal. A comparatively small number of studies examine the effects of grazing on these processes, permitting inference of long-term population dynamics (Eldridge et al. 1990; Watson et al. 1997; Manier & Hobbs 2006). In view of the global and regional trends towards increasing dominance of woody species, understanding the population mechanisms and dynamics behind woody encroachment is a pressing issue for ecology and related applied sciences (Sankaran et al. 2004, 2005).

Originally, shrub encroachment was considered an indirect grazing effect resulting from changes in grass abundance and the vertical distribution of water in the soil. Walter (1971) proposed that shrubs and grasses coexisted because of niche separation, with deeper-rooted shrubs accessing different soil water resources from shallower-rooted grasses. As grazing reduces grass biomass, more water flows to lower soil layers, thus promoting shrub encroachment (Walker et al. 1981; van Langevelde et al. 2003). Although several studies have corroborated Walter's (1971) hypothesis (Knoop & Walker 1985; Sala et al. 1989), the shortcomings of the niche separation explanation for the co-existence of growth forms have also been recognized by a number of authors (Higgins et al. 2000; Jeltsch et al. 2000; Wiegand et al. 2005, 2006). Other studies have proposed that grazing also promotes changes in shrub demography through indirect effects that alter the fire regime. In temperate savannas and grasslands, grazing reduces grass and flammable biomass, diminishes fire frequency and grass competition, and increases recruitment and survival of woody plants (Roques et al. 2001).

However, grazing does not always trigger woody encroachment in arid ecosystems (Adler et al. 2005; Ward 2005; Lunt et al. 2010; Nano & Clarke 2010) because browsing can have a direct negative effect on woody species according to their palatability and defense traits (Riginos & Hoffman 2003; Augustine & McNaughton 2004). In addition, the introduction of domestic livestock can either reduce or increase recruitment of certain palatable woody species, depending on the organs (leaves, flowers, fruits) affected by browsing and its effects on dispersal (Milton 1995; Hunt 2001; Tews et al. 2004). Hence, the net effect (direct and indirect) of livestock grazing on population demography and subsequent multi-species assemblage organization is dependent on how dominant plant species interact with the main disturbance regime (e.g. drought, grazing and fire) and resources (Carrick 2003; Midoko-Iponga et al. 2005; Kraaij & Ward 2006; Riginos & Young 2007).

Because woody encroachment is a demographic process, quantifying the population dynamics of dominant shrub species in grazed and ungrazed fields offers an important avenue for evaluating the role of grazing in woody encroachment. Dominant species play a key role in the organization of the plant community (Grime 1998) and, by contrast with 'plant-type' or 'growth-form' approaches, understanding their population dynamics (as proposed by Hadar et al. 1999) increases the robustness of the inferences regarding the processes behind woody encroachment. We therefore compared the abundance, size-structure, population dynamics and neighborhood interactions of three native and dominant shrub species across two different grazing regimes from the semi-arid Patagonian grass-shrub steppes to understand the controls exerted by grazing on vital population rates (e.g. recruitment, growth and mortality rates). An earlier regional-scale study in this ecosystem suggested that overgrazing increases the cover of particular shrub species (Perelman et al. 1997), although the study used a correlative approach. We addressed two main questions: (1) what are the main long-term effects of grazing exclusion on shrub population structure and vital population rates of the three dominant species? and, (2) What are the effects of grazing exclusion on the interactions among the dominant shrub species?

Methods

Study site

The study site was ca. 100 km^2 and was located at the Rio Mayo INTA Experimental Station and on privately owned, neighboring rangelands in South Central Patagonia, Chubut Province, Argentina (45°41′ S, 70°16′ W; 500 m asl). Mean annual precipitation is 153 mm (1960 to present) and ranges between 47 mm and 230 mm. More than 70% of the precipitation falls during the cold season, from Mar to Aug (Jobbágy et al. 1995). Mean annual temperature is 8.1 °C and mean monthly temperature ranges from 2 °C in Jul to 14 °C in Jan. Soils are coarse textured (sandy), with cobbles and pebbles making up 50% of soil mass. There is a cement-like layer at 0.45–0.6 m depth that constrains root penetration only in some shrub species (Paruelo et al. 1988). The vegetation corresponds to the dominant community of the Occidental District of the Patagonian steppe (León et al. 1998). This community is co-dominated by grasses and shrubs, which cover 28% and 12%, respectively, and constitute more than 96% of the total plant cover and biomass (Fernández-Alduncin et al. 1991). The dominant grass species are *Stipa speciosa* Trin. Et Rupr., *Stipa humilis* Vahl., and *Poa ligularis* Nees ap. Steud., and the dominant shrub species are *Mulinum spinosum* (Cav.) Pers., *Senecio filaginoides* AD and *Adesmia volckmanni* Philippi. Sheep husbandry has been the main economic activity in this area for more than 100 yr and stocking rates usually range between 0.2 and 0.4 sheep ha^{-1} (Golluscio et al. 1998).

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Nomenclature follows Correa (1971–1984) and Ulibarri (1986). Hereafter, we refer to the shrub species as *Mulinum*, *Senecio* and *Adesmia*.

Co-dominant shrub species have marked differences in their root systems (Fernández-Alduncin & Paruelo 1988; Golluscio et al. 2006), hydraulic architecture (Bucci et al. 2009) and grazing preference by sheep. Sheep prefer the inflorescences of *Mulinum* (Jan-Feb) to other tissues because of the sharp-spiny leaves and high concentration of secondary metabolites (Bonvissuto et al. 1983; Cavagnaro et al. 2003). Sheep also browse *Adesmia* twigs and leaves at the start of the growing season when tissues are soft and not lignified. *Senecio* is not browsed because of high concentrations of secondary metabolites (Cavagnaro et al. 2003).

Population structure

One to three permanent plots (10 m × 10 m) were established randomly within representative mixed-shrub vegetation in four different paddocks (1–3 ha) where grazing has been excluded since 1954, 1972, 1983 and 1994, and in four different neighboring grazed paddocks near to water points (300–600 m) (each of these paddocks is treated as a replicate, therefore we averaged data in paddocks with two or three permanent plots). The number and identity of shrubs in each plot were recorded. We counted established individuals and seedlings larger than 5 cm. We used *t*-tests to elucidate differences in the density of each shrub species between rangelands excluded from grazing and rangelands with continued grazing. Data did not show significant departure from normality and variances between both groups (i.e. grazing exclusion paddocks and grazed paddocks) were homogeneous.

A second data set (i.e. intensive survey) was used for neighborhood analyses and to detect differences in population size structure (see below) for each species with and without grazing. In Jan 1997, we established three widely spaced 10 m × 10 m plots in representative vegetation within the largest grazing-exclusion paddock (ungrazed since 1983) and three in an adjacent grazed paddock. Despite the reduced statistical power in comparison with the previous data set, this intensive survey eliminated variation associated with different times since grazing exclusion. The identity and spatial location of all established shrubs were recorded. Each plant was measured (height and two perpendicular diameters) and the percentage dead of crown cover was visually estimated as an index of plant vitality. Reproductive status was scored as the presence or absence of flowers during the flowering season (Dec-Feb).

To study the differences in size structure using the second data set, we calculated the sum of height and average diameter. This size index accounts for the differences in crown architecture for each shrub species (i.e. hemisphere and inverted cone forms). We built empirical accumulated probability distributions of size for each shrub species and used the Kolmogorov–Smirnov non-parametric *D*-statistic as a test of significance of the differences among the size distributions. Differences in the percentage of flowering individuals for each shrub species between grazing regimes were tested by χ^2 tests from a 2 × 2 contingency table. The relationships between shrub size and reproductive status were examined using logistic regressions in each grazing regime.

Short-term responses of population dynamics

In Jan 2000 and 2003, the permanent plots established in Jan 1997 were revisited to quantify recruitment, growth and mortality of shrub individuals and estimate the respective vital rates for each species and grazing regime. All live shrubs were counted and measured again as in the original census; new and dead plants were also recorded. Statistical differences in recruitment and mortality for each shrub species were determined by two-way ANOVA, where the first factor was 'grazing,' and the second factor was 'period' ('1997–2000' and '2000–2003'). *Post hoc* comparisons were made using Tukey's tests.

Long-term responses of population dynamics

Changes in population structure during the entire period (1997–2003) for each shrub species and grazing condition were used to build projection matrices to study long-term population dynamics. Six different projection matrices were built to represent each shrub species in each grazing regime. Each projection matrix had three stages: 'young' (size index ≤ 40 cm), 'sapling' (size index 41–80 cm) and 'adult' (size index > 80 cm). We estimated the transition rates (Table 1) between sampling dates from a database with more than 1000 shrubs classified by species, size, and grazing regime made with the data collected in this study.

Using a deterministic and density-independent approach, population growth was projected by multiplying the transition matrix (**A**; Table 1) by a column vector (**n**), incorporating the number of individuals in each of the three stages. Hence, the population size for any time ($\mathbf{n}_t$) was calculated as $\mathbf{n}_t = \mathbf{A}^{\mathbf{t}} \times \mathbf{n}_0$, assuming that matrix **A** remains constant during the projection period, and where $\mathbf{n}_0$ is the initial population size structure (Caswell 2001). We used a deterministic approach because we had only one sampling interval and therefore we could not estimate alternatives to matrix **A** associated with rainfall variation (i.e. the main stochastic factor). The properties and facilities of these kinds of models are detailed in Caswell (2001). The dominant eigenvalue of the matrix

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Table 1. Matrix population models for each dominant shrub species and grazing condition: (*a*) *Mulinum* excluded, (*b*) *Mulinum* grazed, (*c*) *Senecio* excluded, (*d*) *Senecio* grazed, (*e*) *Adesmia* excluded and (*f*) *Adesmia* grazed. Matrix elements indicated in Roman fonts represent the transition probabilities (from columns to rows) among life stages (**Y**: Young; **S**: Sapling and **A**: Adult), while fecundities are indicated in italics.

	Y	**S**	**A**
(*a*)			
Y	0.33	0	*2.56*
S	0.61	0.12	0
A	0.03	0.88	0.99
(*b*)			
Y	0.11	0	*0.74*
S	0.78	0.25	0.03
A	0	0.5	0.94
(*c*)			
Y	0.05	0	*0.96*
S	0.68	0.15	0
A	0.09	0.7	0.73
(*d*)			
Y	0.13	0	*0.73*
S	0.44	0.27	0
A	0.19	0.63	0.73
(*e*)			
Y	0.2	0	*0.29*
S	0.6	0.25	0
A	0.2	0.75	0.96
(*f*)			
Y	0.05	0	*0.85*
S	0.5	0.04	0
A	0.25	0.95	0.99

and the right and left eigenvectors associated with the first eigenvalue allow the estimation of the asymptotic population growth rate (λ), the stable size structure ($\mathbf{w}$), and the reproductive value ($\mathbf{v}$), respectively, both at equilibrium and under the ergodic hypothesis (the ergodic hypothesis states that results of matrix projection are independent of the initial conditions; Caswell 2001).

We also performed elasticity analyses of λ to evaluate the effect of small changes in three major and aggregated demographic processes (i.e. stasis, growth and fecundity) on the growth rate of shrub populations. Matrix elements were classified and clumped as follows: elements from the main diagonal represent stasis (i.e. the permanence in the same plant stage), elements from the lower diagonals represent growth (i.e. the advance across plant stages) and elements from the first row in the last column (adults) represent fecundity or recruitment (i.e. the input of new young plants). We needed to include a retrogression transition from adult to sapling in one case (*Mulinum* in grazed paddocks) because of a possible extreme browsing event (Bonvissuto et al. 1983).

We used bootstrapping techniques to detect statistical differences in the population growth rates (λ) between the two grazing regimes for each shrub species (Efron & Tibshirani 1993). Three global populations were built, one for each species, collapsing the two different grazing regimes. A total of 1000 randomizations were then performed from these global populations to define the new matrices and calculate the dominant eigenvalues with the aim of generating a distribution relative to the null model of no difference between grazing conditions; these were then compared with the observed values. In addition, we estimated the confidence interval ($\alpha = 5\%$) for the population growth rate (λ) for each shrub species and grazing condition with the aim of detecting differences in respect to the equilibrium condition ($\lambda = 1$).

Spatial neighborhood analyses

Six maps of the spatial distribution of shrub individuals were drawn with the polar coordinates obtained from fieldwork. The maps were used to obtain the distances to the nearest neighbors and the sum of sizes for each pair of individuals (target+neighbor) (Welden & Slauson 1986). With these data, we built the linear regressions between the separation distance between nearest neighbors and their sizes for each grazing condition and pair of species (e.g. *Mulinum-Mulinum, Mulinum-Adesmia*, *Mulinum-Senecio*, etc.) by pooling the data for all respective plots within each grazing regime. From the analysis of regression between size and distance we estimated the interaction importance (R^2, coefficient of determination) and the interaction intensity (β_1, slope) (Briones et al. 1996; Shackleton 2002). Positive slopes indicated a biologically negative net effect of interaction (e.g. competition), whereas negative slopes indicated a biologically positive net effect of interaction (e.g. facilitation). The main stresses in semi-arid Patagonian steppes that might be ameliorated by plant facilitation are water deficit and grazing (Aguiar et al. 1992; Graff et al. 2007; Armas et al. 2008; Golluscio et al. 2009).

Results

Population structure

In 1997 (baseline for demographic analysis), total shrub density in grazing exclusion paddocks was, on average, 74% higher than in grazed paddocks ($t_6 = 4.18$, $P = 0.006$). *Mulinum* and *Senecio* were the most responsive species. The density of *Mulinum* species in grazing exclusion paddocks was, on average, 80% higher than in grazed paddocks ($t_6 = 4.59$, $P = 0.004$; Fig. 1). Small individuals contributed particularly to this effect, with small individuals of *Mulinum* being almost twice more frequent in grazing exclusion paddocks than grazed paddocks ($D = 0.313$, $P = 0.01$; Fig. 2a). The percentage of reproductive individuals of *Mulinum* was 48% lower in grazing exclusion paddocks than grazed paddocks ($\chi^2_1 = 12.62$;

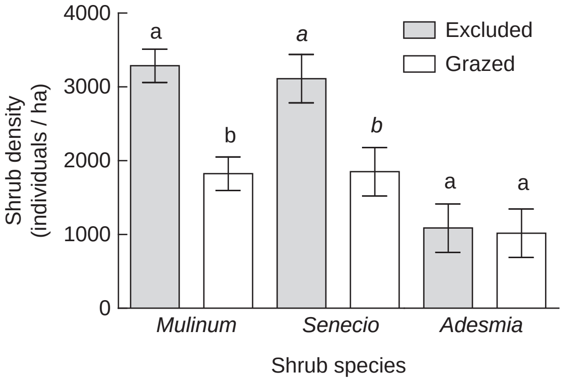

Fig. 1. Mean density of dominant shrub species in grazing exclusion and grazed paddocks. The vertical bars indicate means ±1 SE. Roman and italic letters indicate significant differences between grazing conditions within each shrub species at 1% and 5% significance level, respectively.

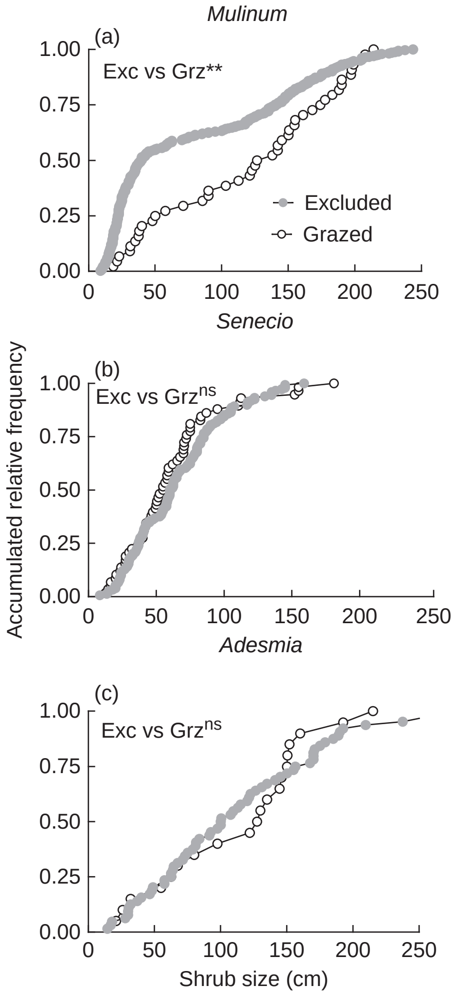

Fig. 2. Distribution of accumulated relative frequency of shrub size for the dominant shrub species in grazing exclusion and grazed paddocks. (**a**) *Mulinum spinosum*, (**b**) *Senecio filaginoides* and (**c**) *Adesmia volckmanni*.

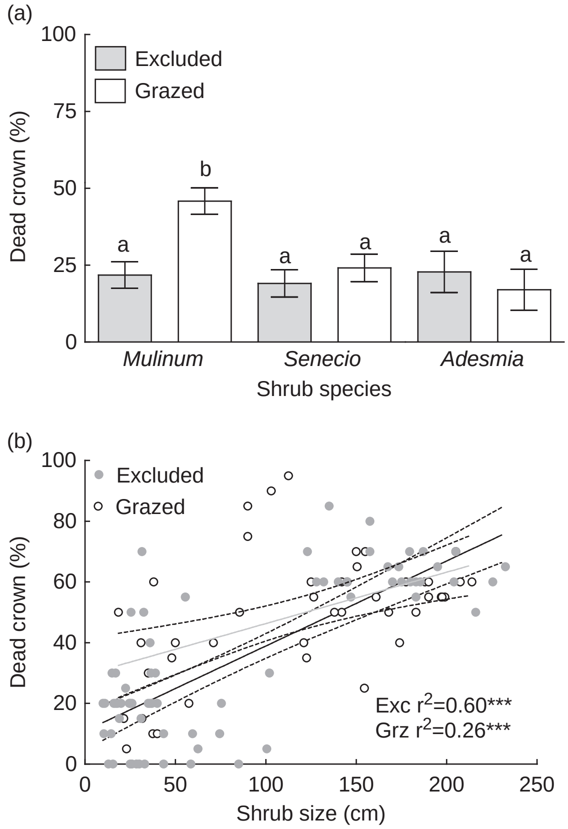

Fig. 3. (**a**) Per cent dead crown cover for the dominant shrub species in grazing exclusion and grazed paddocks. The vertical bars indicate means ±1 SE and different Roman letters indicate significant differences between grazing conditions within each shrub species ($P < 0.05$). (**b**) Linear regression between the shrub size (cm) and the dead crown cover (%) for *Mulinum spinosum* in grazing excluded (tinted circles and black solid line) and grazed (empty circles and tinted solid line) paddocks. Dashed lines indicate the upper and lower limits of 95% confidence intervals.

$P < 0.001$), consistent with the high proportion of small plants. Further, *Mulinum* plants in grazing exclusion paddocks had a lower percentage of dead crown cover than individuals in grazed paddocks ($F_{1,6} = 18.32$, $P = 0.005$; Fig. 3a), mostly owing to small individuals (Fig. 3b).

Senecio was also more abundant in grazing exclusion paddocks, with a mean difference of 68% between grazing regimes ($t_6 = 2.68$, $P = 0.036$; Fig. 1). By contrast with *Mulinum*, the percentage of reproductive individuals of *Senecio* in grazing exclusion paddocks was 52% higher than in grazed paddocks ($\chi^2_1 = 4.62$; $P = 0.03$). The size structure and per cent dead crown cover of neither *Senecio* nor *Adesmia* differed between grazing regimes (Fig. 2b and c), and *Adesmia* density did not differ between grazing regimes ($t_6 = 0.15$, $P = 0.88$; Fig. 1).

Mulinum was the only species to show a significant relationship between reproductive status and shrub size

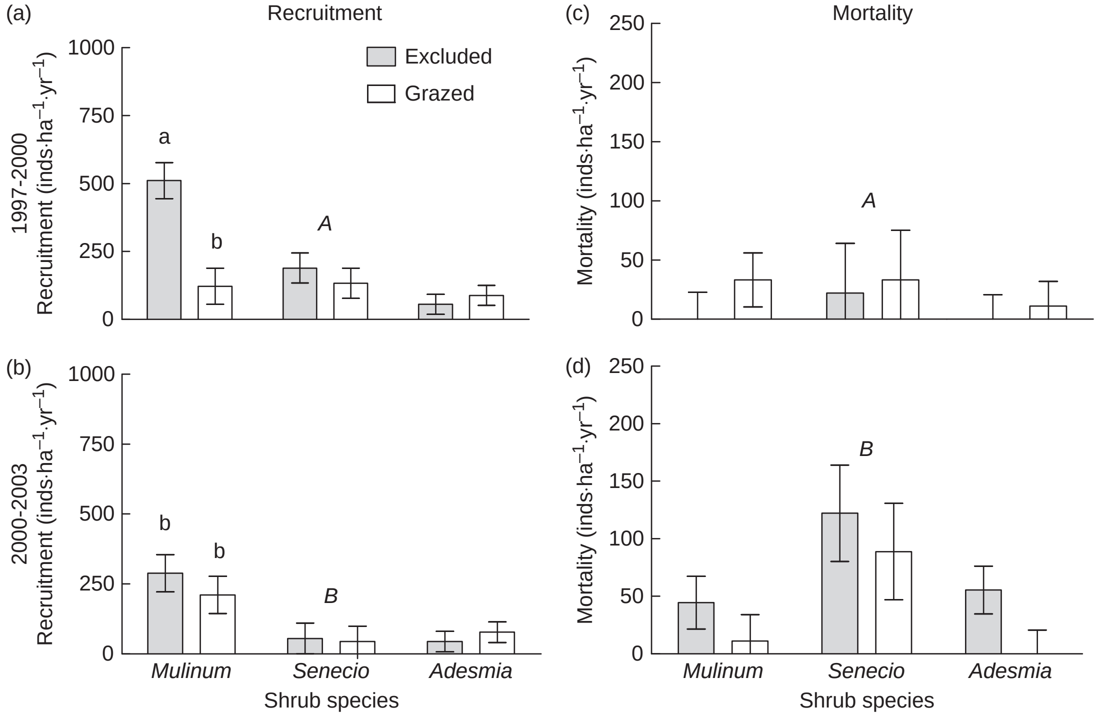

Fig. 4. Recruitment (**a**, **b**) and mortality (**c**, **d**) rates during the periods 1997–2000 (**a**, **c**) and 2000-2003 (**b**, **d**) for the dominant shrub species in grazing exclusion and grazed paddocks. The vertical bars indicate means ± 1 SE. Different lower-case Roman letters indicate significant differences ($P < 0.05$) in recruitment rates between grazing conditions and periods only for *Mulinum* species. Different uppercase italic letters indicate marginal differences ($0.07 < P < 0.09$) between periods in recruitment and mortality only for *Senecio* species. The absence of letters indicates no detection of significant differences within each shrub species.

($y = \frac{e^{(-6.4+0.12x)}}{1+e^{(-6.4+0.12x)}}$ $r^2 = 0.79$, $P < 0.001$ and $y = \frac{e^{(-3.2+0.05x)}}{1+e^{(-3.2+0.05x)}}$ $r^2 = 0.68$, $P < 0.01$ in excluded and grazed conditions, respectively), and showed large differences in shrub size at reproductive maturity between grazing regimes. Reproductive plants in grazing exclusion paddocks were, on average, 63% smaller than in grazed paddocks (0.3 versus 0.8 m).

Population dynamics

Short-term responses

Shrub recruitment and mortality differed between species, periods and grazing regimes. *Mulinum* populations in the 1983 grazing exclusion paddock had a higher recruitment rate (511 individuals $\cdot$ ha^{-1} $\cdot$ yr^{-1}) than in nearby grazed paddocks only in the 1997–2000 period ($F_{1,8} = 5.41$, $P = 0.04$; Fig. 4a,b). *Senecio* populations had marginally higher recruitment rates ($F_{1,8} = 4.04$, $P = 0.079$; Fig. 4a,b) and marginally lower mortality rates ($F_{1,8} = 3.54$, $P = 0.09$; Fig. 4c,d) in the first period than in the second period, but there were no differences between grazing regimes. No significant differences were detected in the mortality rates of *Mulinum* and *Adesmia* between periods or grazing regimes.

Long-term responses

Long-term analyses partially mirrored the populations' short-term responses. *Mulinum* populations showed a larger difference between grazing regimes than those of *Senecio* and *Adesmia*. Sheep grazing clearly constrained the population growth of *Mulinum* species in the long term, diminishing the asymptotic growth rate by 25% ($P < 0.05$; Fig. 5a). *Mulinum* populations in grazing exclusion paddocks had asymptotic growth rates higher than at the equilibrium condition ($\lambda = 1$), but in grazed paddocks had asymptotic growth rates that were not statistically different from those at the equilibrium condition (Fig. 5a). By contrast, *Senecio* and *Adesmia* populations in grazing exclusion and grazed rangelands reached the equilibrium condition ($\lambda = 1$) as a marginal situation (i.e. $\lambda = 1$ was the lower limit for the 95% confidence intervals for λ) and showed 97.5% of confidence for $\lambda > 1$ (Fig. 5a).

Elasticity analyses indicated that paddocks with sheep grazing had more homogeneous shrub responses in terms of the relative contribution of each demographic process to the growth rate. In grazed paddocks, stasis and growth were the dominant demographic process affecting population growth rate for all three species (ca. 0.45–0.6;

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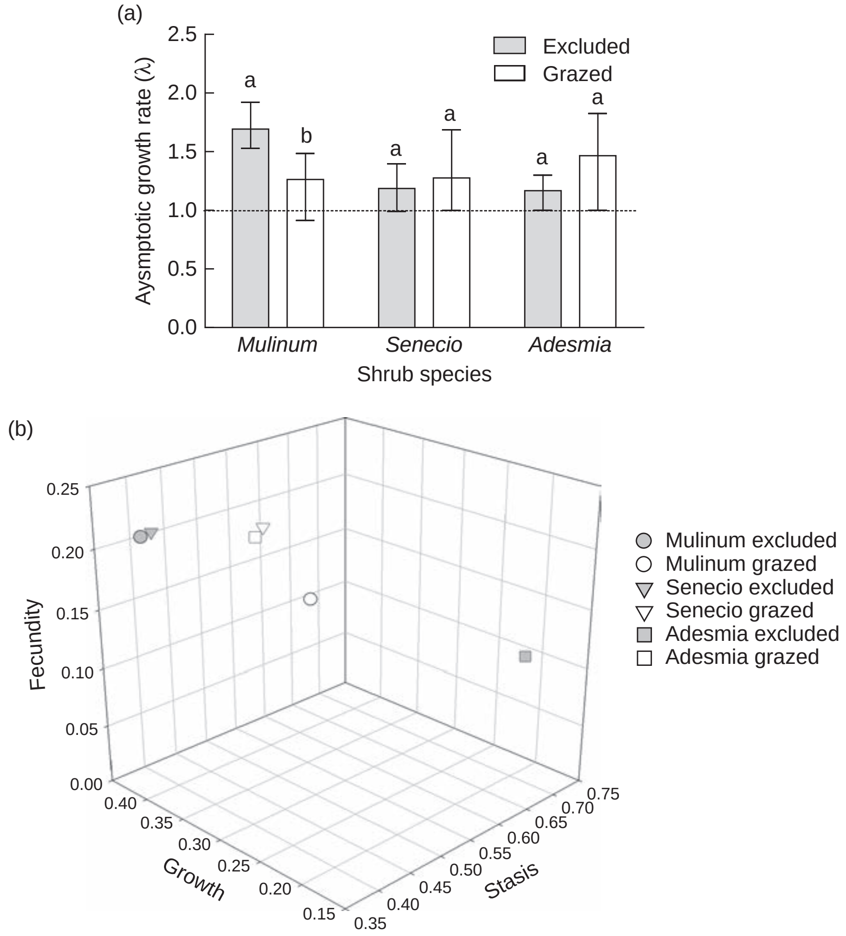

Fig. 5. Results derived from the matrix model projections for the dominant shrub species (*Mulinum*, *Senecio* and *Adesmia*) in grazing exclusion and grazed paddocks based on the surveyed period (1997–2003). (**a**) Asymptotic population growth rates (λ). The horizontal dashed line indicates the equilibrium condition ($\lambda = 1$) and vertical lines indicate the limits of confidence intervals ($\alpha = 0.05$) by bootstrapping techniques. Different Roman letters indicate significant differences between grazing conditions within each shrub species ($P < 0.05$). (**b**) Elasticities with the relative contribution from stasis, growth and fecundity to the asymptotic population growth rate (λ) for each dominant shrub species and grazing condition.

Fig. 5b). However, in grazing-exclusion paddocks, there were large differences between shrub species. *Mulinum* and *Senecio* had lower relative contribution by stasis to the growth rate, while *Adesmia* had higher relative contribution (< 0.45 and > 0.7 respectively; Fig. 5b).

Spatial neighborhood analyses

In the grazing exclusion paddocks there was no evidence for intra-specific interactions, while in grazed paddocks *Mulinum*-*Mulinum* and *Senecio*-*Senecio* pairs showed negative interactions (*Mulinum*: $F_{1,7} = 12.43$, $P = 0.009$; Fig. 6d. *Senecio*: $F_{1,16} = 17.59$, $P < 0.001$; Fig. 6e). Because of the low density of *Adesmia*, there were not enough intra-specific pairs in grazed rangelands to perform a regression analysis for this species. The inter-specific interactions in the grazing exclusion paddocks was positive for *Mulinum*-*Adesmia* pairs ($F_{1,16} = 5.47$, $P = 0.032$; Fig. 7a) and negative for *Mulinum*-*Senecio* pairs ($F_{1,41} = 11.95$, $P = 0.001$; Fig. 7b). By contrast, in grazed paddocks, we detected significant negative interaction only in *Mulinum*-*Adesmia* pairs ($F_{1,8} = 7.56$, $P = 0.025$; Fig. 7d).

Discussion

We found that total shrub density was higher in Patagonian steppes where sheep had been excluded than in grazed steppes. This result contradicts the concept that woody encroachment is triggered by domestic grazing (Perelman et al 1997) (at least during the last 10-40 yr), but is consistent with recent revisions of this issue (Adler et al. 2005; Manier & Hobbs 2006; Watson et al. 2007). For example, many woody encroachments are the result of overgrazing followed by a change in grazing pressure

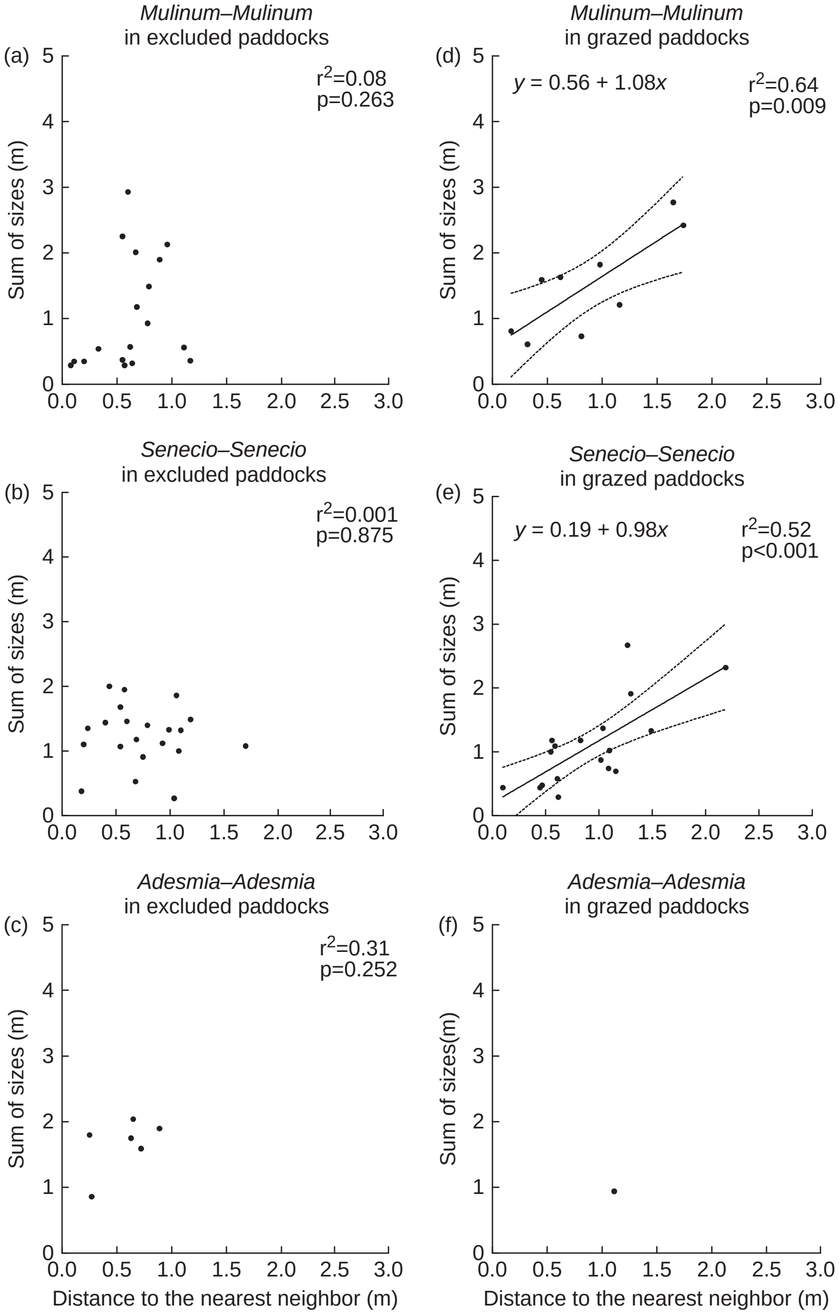

Fig. 6. Scatter plots with intraspecific relationships in the grazing exclusion (**a**–**c**) and grazed (**d**–**f**) paddocks. Linear regression between the nearest-neighbor distance (m) and summed shrub size (m) for the conspecific pairs of shrubs. Dashed lines indicate the upper and lower limits of 95% confidence interval only from the significant linear regression analysis.

(Franco & Morgan 2007; Lunt et al. 2010), offering a possible explanation for the trends we observed.

Importantly, our results challenge the common approach to studies of shrub encroachment that considers shrubs as a single response group, because dominant species showed different demographic responses. *Mulinum* was the species most responsive to grazing exclusion, whereas there was no detectable response from *Adesmia*. Although *Mulinum* and *Senecio* both increase in density in paddocks from which grazing was excluded, other population attributes changed only for *Mulinum*. The number of small individuals was more than 30% higher, and per cent of dead crown cover and shrub size at the reproductive stage were lower in the grazing exclusion paddocks relative to the grazed paddocks.

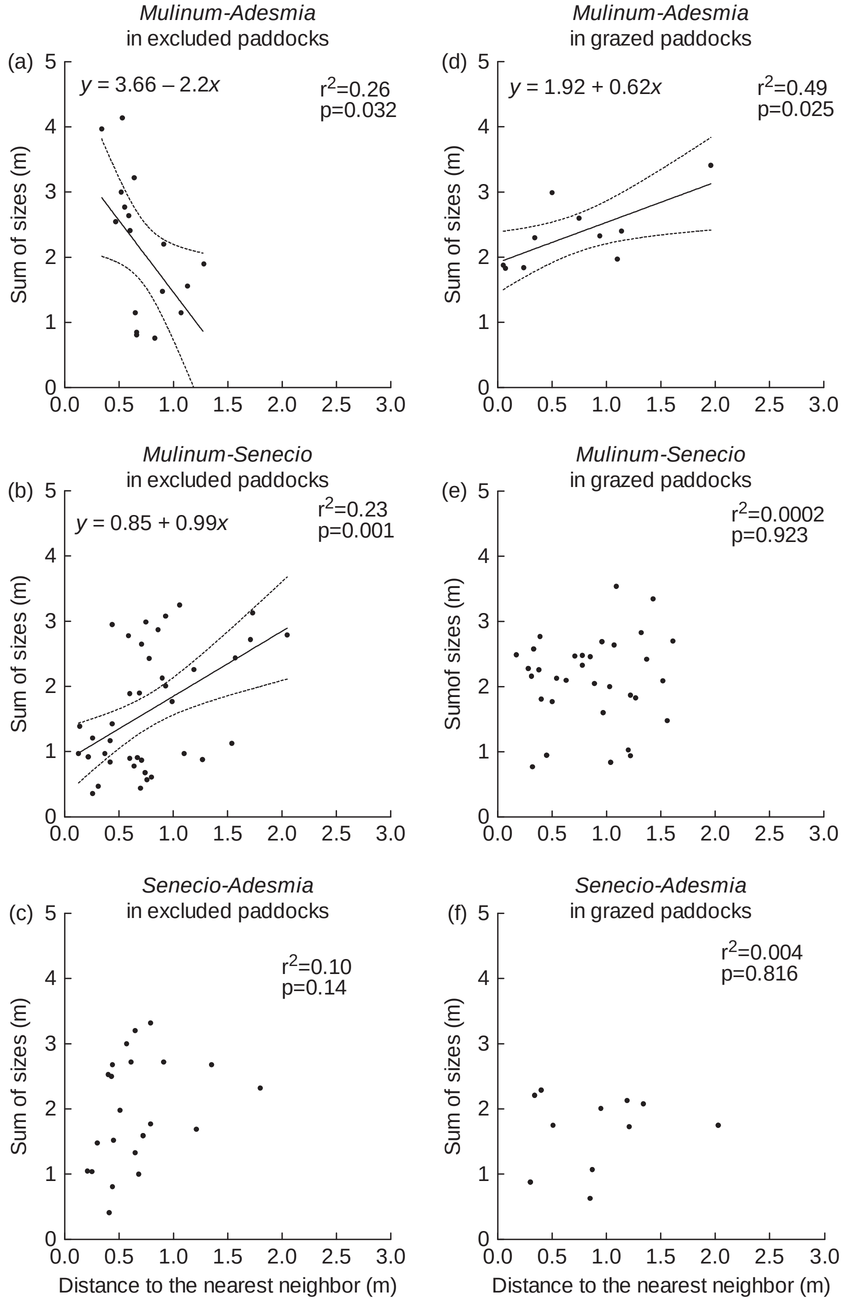

Fig. 7. Scatter plots with interspecific relationships in the grazing exclusion (**a**–**c**) and grazed (**d**–**f**) paddocks. Linear regression between the nearest neighbor-distance (m) and summed shrub size (m) for the heterospecific pairs of shrubs. Dashed lines indicate the upper and lower limits of 95% confidence interval only from the significant linear regression analysis.

Moreover, in the grazing exclusion paddocks, *Mulinum* had a higher recruitment rate during the first 3-yr period (three consecutive summers with rainfall pulses higher than 40 mm) and a higher population growth rate in the long term (λ) than in grazed paddocks.

Grazing can suppress shrub density through direct or indirect negative effects. The direct and indirect effects most commonly studied are browsing and trampling by herbivores and changes in grass or woody canopy and the environment (e.g. microclimate, fire regimes, soil properties), respectively. Sheep browsing of reproductive structures is the best-known direct effect on *Mulinum* shrubs in these steppes. During early summer, sheep browse the flowers of *Mulinum* plants (Bonvissuto et al. 1983). Floral herbivory controls the output of viable seeds and has a direct effect on the number of recruits (Fernández et al. 1992), consistent with demographic data in our study that showed *Mulinum* recruitment episodes (triggered by summer rainfall events) were enhanced in the absence of grazing. To our knowledge, there have not been any reports regarding vegetative propagation or permanent soil seed banks (Correa 1971–1984) that could buffer this direct effect. This result concurs with other studies of palatable woody species, where limitations on regeneration during early stages such as emergence or recruitment are reported as the processes most affected by browsing (Milton 1995; Watson et al. 1997; Hunt 2001).

Another indirect grazing effect on *Mulinum* populations may occur through the effect of grazers on grasses. In a previous study, experimental grass removal in grazing exclusion paddocks decreased the density of small individuals of *Mulinum* by 50% (Cipriotti & Aguiar 2010). Therefore, reduction in the cover of live biomass, standing dead biomass, and litter biomass of grasses driven by grazing (Cipriotti & Aguiar 2005) may also contribute to the patterns observed in this study. Modifications in the vegetation canopy can affect plant recruitment by altering the microclimate and/or topsoil properties, or diminishing protection against droughts, herbivores, fire or abrasive winds and finally causing greater mortality mainly during the recruitment phase (Vetaas 1992; Breshears et al. 1998). Although most of these environmental changes were originally associated with modifications in the woody canopy (Pugnaire et al. 1996), more recent studies report a similar role of tussock grasses in promoting survival of shrub seedlings in arid lands (Maestre et al. 2001). Thus, positive grass-to-shrub feedbacks during specific plant stages could be a mechanism by which woody encroachment is delayed in grazed rangelands, at least for species with requirements equivalent to those of *Mulinum*.

Other indirect effects of grazing highlighted by our demographic approach were changes in interactions among the dominant shrub species (both intraspecific and interspecific). The change from predominantly negative outcomes in grazed conditions (three negative interactions) to a balance of positive and negative interactions (one positive and one negative interaction) with grazing exclusion points to interactions among shrubs species as a mechanism controlling woody encroachment that has been less frequently studied (but see Barnes & Archer 1999; Meyer et al. 2008). In this Patagonian ecosystem, grazing may decrease nitrogen availability (Golluscio et al. 2009) leading to negative interactions despite decreases in shrub density. Although the spatial distribution and size of individuals may be influenced by factors other than biotic interactions (e.g. disturbances, seed dispersal, environment heterogeneity, allelopathy) (Shackleton 2002), the dominance of negative interactions under grazing plus negative direct browsing effects suggests mechanisms to explain the absence of woody encroachment in grazed sites. However, it should be noted that our study of shrub interactions was limited by low statistical power.

By contrast with our results, previous regional descriptive studies have found positive associations between sites with high cover of *Senecio* and higher grazing pressures (Perelman et al. 1997). Moreover, a number of factors suggest mechanisms through which grazing might favor *Senecio*: it is highly avoided by sheep because of its high concentrations of secondary metabolites (Cavagnaro et al. 2003) and it is the only shrub species with a root distribution similar to that of grasses (< 0.25 m depth), showing a pulse of recruitment when grasses are removed in grazing exclusion paddocks (Fernández et al. 1992; Cipriotti & Aguiar 2010). Hence, the unexpected low abundance of this shrub species in grazed paddocks could be explained by the indirect grazing effects associated with the modifications in the network of interactions with other grass and shrub species. These inferences are supported by the changes observed in the elasticity of the asymptotic growth rate (λ) for *Mulinum* and *Senecio* populations (Fig. 5b). In grazing exclusion paddocks, growth (i.e. the advance across plant stages) was the most sensitive demographic process affecting λ for both species, but in grazed paddocks, stasis (i.e. the permanence in the same plant stage) and growth had similar elasticities, thus indicating poor resource conditions.

Finally, our study has emphasized the value of mechanistic demographic approaches to evaluating and managing worldwide trends of woody species encroachment. Long-term monitoring experiments provide a better understanding of the ecological processes regulating plant and herbivore populations because of the large temporal scale over which demographic processes occur (Bakker et al. 1996), and the need to account for effects of inter-annual climate variability on vital rates. In the Patagonian steppes, regional descriptive studies (Perelman et al. 1997) support the general view of woody encroachment as grazing pressure increases. However, monitoring of permanent plots in our study showed an opposite trend, indicating that grazing can constrain woody expansion at longer temporal scales, particularly in arid regions. Further, our results suggested that explanations other than the often-invoked soil water niche separation hypothesis (Walker et al. 1981; Sala et al. 1989) are needed to explain shrub dynamics in our ecosystem (Jeltsch et al. 2000). This explanation has traditionally underestimated the role of differences in plant traits (effects and responses) between species within each growth form, and the intensity of interactions between coexisting grass, shrub and herbivore species

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across different plant stages. As in other arid ecosystems, we suggest that in the Patagonian steppes, biotic interactions are a fundamental driver of population dynamics and community organization and deserve greater attention (Aguiar et al. 1992; Sankaran et al. 2004; Armas & Pugnaire 2005).

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