

Resource partitioning and interactions enable coexistence in a grass-shrub steppe

P.A. Cipriotti^{a,*}, M.R. Aguiar^b

^a Cátedra de Métodos Cuantitativos Aplicados, Departamento de Métodos Cuantitativos y Sistemas de Información, Facultad de Agronomía, Universidad de Buenos Aires, Avda. San Martín 4453, C1417DSE Buenos Aires, Argentina

^b Cátedra de Ecología – IFEVA, Departamento de Recursos Naturales y Ambiente, Facultad de Agronomía, Universidad de Buenos Aires/CONICET, Avda. San Martín 4453, C1417DSE Buenos Aires, Argentina

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ABSTRACT

We revisited a growth-form removal experiment after 12 years with the aim to compare the long-term population responses of three shrub species. Specifically, we were interested to know if the resource partitioning and plant interactions act as complementary mechanisms of the shrub-grass coexistence. In 1983 different plots from grass-shrub Patagonian steppes were submitted to three treatments: control, grass-, and shrub-removal during three consecutive years. In 1997 we studied nine plots from the original experiment and recorded all shrubs to compare shrub density, population size structure, vitality, spatial patterns and neighbourhood interferences of three native and co-dominant shrub species: *Mulinum spinosum*, *Senecio filaginoides*, and *Adesmia volckmanni*. After 12 years of recovery, shrubs as a growth-form group, fully re-established in plots where they were removed and attained 75% higher density in grass-removal plots than in control plots. However, long-term population responses of *Mulinum*, *Senecio*, and *Adesmia* to removals were distinctive. On the other hand, negative and positive interferences among shrub species and between shrubs and grasses generated a complex network. Morphological and functional differences in shrub and grass species and their interactions at population level and long-term could be a key to achieve a better comprehension of shrub-grass coexistence from semi-arid ecosystems.

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1. Introduction

The coexistence of shrubs and grasses, and lately, the study of the mechanisms regulating shrub encroachments have intrigued ecologists for the past century (Archer, 1995; Jeltsch et al., 2000; Sankaran et al., 2004; Scheiter and Higgins, 2007; van Auken, 2000). Replacement of grasses by woody plants (trees or shrubs) has been reported in many semi-arid and arid lands across different continents around the World (Fensham et al., 2005; Scholes and Archer, 1997; Wiegand et al., 2006) promoting major changes in biodiversity and ecosystem functioning (e.g. productivity, decomposition and carbon storage, nitrogen and water dynamics) (Aguiar et al., 1996; Jackson et al., 2000; Maestre et al., 2009; Paruelo et al., 1998; Schlesinger et al., 1990) and jeopardizing the sustainability of economic activities (e.g. animal husbandry) due to reduction in

biomass and quality of forage resources (Gutman et al., 2000; House et al., 2003; Sharp and Whittaker, 2003; Walker et al., 1981). In view of the global trends towards the increasing dominance of woody species, understanding the controls of woody populations is a pressing issue for ecology and related applied sciences (Sankaran et al., 2004, 2005). Here, we focus on the role of resource partitioning and plant interactions as the main controls of the coexistence between both growth-forms. In particular, we aimed at two different types of interactions: grasses vs. shrubs, and among shrub species.

Coexistence between both growth-forms is one of the three conundrums of mixed woody-herbaceous plant communities and several hypotheses have been proposed to explain it (House et al., 2003). The first and most studied hypothesis is the niche separation, also known as the Walter's hypothesis. Walter's (1971) hypothesis, which is a special case of the niche differentiation theory, assumes that water is the main limiting resource. It states that shrubs have, compared to grasses, deeper roots and therefore, use different soil water resources. Despite the fact that several published studies supported Walter's hypothesis (e.g. Golluscio et al., 1998; Knoop and Walker, 1985; Sala et al., 1989; Walker and Noy-Meir, 1982), other studies highlighted shortcomings of

* Corresponding author. Present address: Department of Ecological Modelling, Helmholtz Centre for Environmental Research – UFZ, Permoserstraße 15, 04318 Leipzig, Germany. Tel.: +49 341 235 1706; fax: +49 341 235 1473.

E-mail addresses: pablo.cipriotti@ufz.de, cipriotti@agro.uba.ar (P.A. Cipriotti), aguiar@agro.uba.ar (M.R. Aguiar).

this hypothesis. On one hand, in the current theoretical background on community ecology it is still debated if the niche differentiation hypothesis is enough to explain species coexistence (Jeltsch et al., 1998, 2000; Wiegand et al., 2006; Zobel and Pärtel, 2008). On the other hand, there are field evidences that support the importance of intra growth-form differences in the root systems (i.e. at the species level; Montaña et al., 1995; Gibbens and Lenz, 2001; Rodriguez et al., 2007; Leva et al., 2009) and challenge the hypothesis about root niche separation between both growth-forms as the only one driver of coexistence. In consequence, several works point to the role of different disturbances like grazing, fire or drought, and the stochastic dynamics of plant demography as the main controls on shrub-grass coexistence (Carrick, 2003; Morgan et al., 2007; Riginos and Young, 2007; Roques et al., 2001; Tews et al., 2004). An alternative hypothesis, the balanced competition, proposes that shrubs and grasses, instead of partition, compete for resources. The balanced competition hypothesis states that intra growth-form competition (shrub on shrub or grass on grass) is more intense than inter growth-form competition (shrub on grass). Intensity of intra growth-form competition determines that either shrubs or grasses never achieve enough biomass to outcompete the other growth-form. This hypothesis has been less explored than the niche separation hypothesis (see the few or the lack of studies cited in reviews by House et al., 2003; Sankaran et al., 2005; Scholes and Archer, 1997. But see Meyer et al., 2008; Scheiter and Higgins, 2007). In our view both hypotheses are complementary since some shrub species may partition resources with grasses whereas other species compete according to their morphological and functional traits (Jeltsch et al., 2000).

Manipulation of grass and shrub abundance was the main experimental protocol used to study the niche separation hypothesis (e.g. Golluscio et al., 1998; Knoop and Walker, 1985; Sala et al., 1989). However, these studies in general reported the first years after manipulations and only response variables at the growth-form level. We propose that in order to explore the balanced competition hypothesis and the complementarities with the niche separation hypothesis it is necessary to study the response at the intra growth-form differences, especially in multi-species assemblages. In this way, we can explore in detail the role of the different species to sustain the shrub-grass coexistence, contrary to the original functional group view based just on the growth-form attribute. Furthermore, we believe that it is necessary to study the coexistence of species with long-term studies because of the inherent demographic type of issue studied and the life-span of the species involved (e.g. Roques et al., 2001). To achieve this goal, we revisit a removal experiment performed from 1983 through 1985 in a large grazing excluded area (ca. 4 ha) to test the soil water partition between shrubs and grasses in the grass-shrub steppe from Western Patagonia, a semi-arid ecosystem co-dominated by native grasses and shrubs (ca. 150 000 km² in area).

The selective experimental removal of grasses and shrubs from Patagonian steppes led to the conclusion that the two growth-forms, in general, used different soil water resources (Golluscio et al., 1998; Sala et al., 1989). In shrub-removal plots, response variables (i.e. leaf water potential of one species, soil water potential and total above ground production of grasses) indicated that grasses did not respond to shrub-removal supporting the notion that they used mostly water from the top soil layer. In grass-removal plots, water percolation to deep soil layers (>0.3 m) increased, and so did total above ground production of shrubs. However, shrub growth did not fully compensate the grass production in control plots, supporting the idea that population level responses (plant recruitment and growth of new individuals) occur in a time frame larger than the three evaluated years. After the first three years (1983–1985) the experimental plots were

abandoned and plant succession proceed without further intervention. The main goal of our work was to revisit those plots after 12 years and compare the long-term population responses of three native shrub species that account for >90% of shrub production and differ in ecologically relevant traits.

The dominant shrub species are: *Mulinum spinosum* (Cav.) Pers. (Apiaceae), *Senecio filaginoides* AD. (Asteraceae), and *Adesmia volckmanni* Philippi (Fabaceae) (Soriano, 1956). These shrub species have marked differences in their root systems and hydraulic architecture (Bucci et al., 2009; Fernández-Alduncin and Paruelo, 1988; Golluscio et al., 2006). Root biomass of *S. filaginoides* shrubs is concentrated at 0.25 m soil depth, similar to grass species but with long lateral spread (>2 m) (Fernández-Alduncin and Paruelo, 1988; Leva et al., 2009). Roots of *M. spinosum* shrubs have similar lateral spread but most root biomass is concentrated between 0.4 and 0.6 m (Fernández-Alduncin and Paruelo, 1988). Finally, root biomass of *A. volckmanni* shrubs is concentrated between 0.6 and 0.9 m (Golluscio et al., 2006). In addition, there are marked differences among these shrub species in the hydraulic conductivity, specific leaf area, wood density and leaf water potentials (Bucci et al., 2009).

From our approach we try to determine if different functional responses at population level occurs among shrub species according to the water partition or balanced competition mechanisms. Based on the classic niche partition hypothesis we expected that in the long-term, selective grass-removal will not benefit any shrub species. However, according to the balanced competition hypothesis we expected that shrub-removal will benefit shrub species much more than grass-removal because the release of high intense plant competition within the same growth-form; while grass-removal would benefit only those shrub species with shallow roots similar to grasses. Our predictions state that shrub species with roots located in the top soil layer (*Senecio*) will encroach in plots where grasses were removed because the similar root depth, while deep-rooted shrubs (*Mulinum* and *Adesmia*) will respond much more to the shrub-removals.

2. Material and methods

2.1. Study site

The study site is located at the INTA Experimental Field in Rio Mayo, province of Chubut, Argentina in South Central Patagonia (45° 41' S, 70° 16' W, 500 m a.s.l.). The mean annual precipitation is 152 mm ($n = 37$ years; 1961–1998) and ranges between 47 and 230 mm (driest and wettest year in the record, respectively). More than 70% of total precipitation falls during autumn and winter (Jobbágy et al., 1995). The mean annual temperature is 8.1 °C; mean monthly temperature ranges from 2 °C in July to 14 °C in January. The soil is coarse textured (sandy), with 50% of cobbles and pebbles in the soil profile. There is a cemented layer (i.e. CO₃Ca) at 0.6 m depth (Paruelo et al., 1988). Vegetation corresponds to the dominant community in the Occidental District of the Patagonian steppe (Soriano, 1956). Almost 50% is bare ground, the rest is mostly covered by grasses (28%), shrubs (<12%), and litter 10% (Fernández-Alduncin et al., 1991; Golluscio et al., 1982). Forbs contribute less than 1% to total plant cover (Golluscio and Sala, 1993). The dominant grass species, estimated as biomass or cover are: *Stipa speciosa* Trin. Et Rupr., *Poa ligularis* Nees ap. Steud., and *Stipa humilis* Vahl. The dominant shrub species are: *M. spinosum* (Cav.) Pers., *S. filaginoides* AD., and *A. volckmanni* Philippi. Nomenclature follows Correa (1971–1984) and Ulbarri (1986). Hereafter, we refer to the shrub species as *Mulinum*, *Senecio*, and *Adesmia*.

2.2. Experimental setup

We sampled nine of the original twelve plots (400 m² in area) established in 1983 inside a large herbivore enclosure (ca. 4 has.) because problems to identify correctly all plots under the same treatment. From the original experiment, the twelve plots under natural water inputs (i.e. only rain or snowfall. We excluded all watered plots from the current study) were managed during three consecutive years (1983, 1984 and 1985) as follow: control (vegetation untouched), total grass-removal, and total shrub-removal. In treated plots above and belowground biomass was removed with hand tools (see Golluscio et al., 1998; Sala et al., 1989 for details). After 1985 no further removals were practiced. In 1997, we defined one 100-m² area at the center of each plot (three plots per treatment) to avoid edge effects, where all shrub plants were identified, located in a map and measured, and also measured the total shrub and grass cover.

2.3. Shrub population sampling

For each individual shrub we registered: species, height, two perpendicular crown diameters (aerial canopy) and individual vitality. We visually estimated the proportion of dead crown as an index of plant vitality. We also recorded plant location (i.e. main stem rooting point) inside the plot with polar coordinates. Additionally, we measured the shrub and perennial grass cover in the plots with the line interception method. In each plot we randomly located one 10 m-transect along which we recorded the canopy interception. Here we present data for overall grass cover expressed as percentage.

2.4. Statistical analyses

Differences in shrub density (total) were determined using one-way analyses of variance with removal treatment as main factor with three levels: “control”, “grass-removal”, and “shrubs-removal”. In addition, differences in shrub species density and percentage of dead crown were determined using multivariate one-way analyses of variance (Wilks’ lambda statistic). The main factor was “removal treatment” with three levels: “control”, “grass-removal”, and “shrubs-removal”, and the multiple responses were associated to each shrub species: “*Mulinum*”, “*Senecio*”, and “*Adesmia*”. Percentage of dead crown was transformed by arcsine function before perform the statistical analysis to meet the Normal distribution assumption. We used the *F*-statistic from the one-way analyses of variance for post-hoc comparisons of treatment means for each shrub species across the removal treatments. Because we have only three replicates we assumed the normality and homogeneity of variances for our analyses. To study the differences in plant size we calculated the sum of height and mean diameter. This size index represents properly the different crown architecture for each shrub species (i.e. hemisphere or inverted cone), and it is also a good estimator of demographic stage and age (Crisp and Lange, 1976). We built the accumulated probability distributions of plant size for each shrub species and treatment by pooling all data from the respective three plots. Then, we used the Kolmogorov–Smirnov non-parametric statistic (*D*) as a test of significance of the differences among size distributions from different treatments (Steel and Torrie, 1980).

2.5. Analysis of spatial vegetation patterns

We used the spatial coordinates of each shrub to study the univariate (intra-specific) spatial patterns and the size-distance relationships among nearest neighbours (intra- and inter-specific). In both analyses we pooled the data for each species or pair-species and treatment from the respective three plots. To characterize the spatial

distribution of shrub species we used the *O*-ring statistic (Wiegand and Moloney, 2004; Wiegand et al., 1999), which is closely related to Ripley’s *K*-function and the pair-correlation function *g*(*r*) (Haase, 1995; Ripley, 1981). The *K*-function counts the number of points within concentric circles of radius *r* around all points of the target pattern. Instead the ring statistic (*O*) replaces the circles used for calculation of Ripley’s *K* by open rings. Unlike the *K*-function, which characterizes the spatial patterns in a cumulative way, the *O*-statistic characterizes the pattern for each distance and therefore spatial pattern at small scales does not directly influence the pattern at higher scales (because these points are not contained in the ring). To calculate the *O*-statistic a ring of radius *r* and 1 cell width ($\delta r = 0.1 \times 0.1$ m) was centered on each plant and the number of neighbours within that ring was recorded. For *n* plants distributed in an area *A*, the density ($d = n/A$) is the average number of plants per unit area. The function *O*(*r*) is the expected number of points within a ring with radius *r* from an arbitrary point. If points are randomly distributed in space (Poisson distribution), the expected result of *O*(*r*) equals the overall density of points ($O(r) = n/A$).

We studied the spatial patterns for shrubs as group and for each shrub species in the three treatments using Monte Carlo simulations under the uni-variate complete spatial randomness (CSR) null model to estimate the 99% confidence envelopes ($n = 99$, $\alpha = 0.01$). Under the Monte Carlo simulations, plant density and plot size were preserved but the plant spatial distribution was randomized according to the null model (Haase, 1995). We compared our observed pattern with a simulated pattern where shrubs were randomly distributed (null model). Further details about the *O*-ring statistic and the program to calculate are provided in Wiegand et al. (1999), and Wiegand and Moloney (2004).

Finally, we studied the effect of spatial relationships between neighbours. We calculated the distances to the nearest neighbours for each plant and the sum of sizes for each pair of individuals (target + neighbour) (Shackleton, 2002; Welden and Slauson, 1986; Welden et al., 1988). For each treatment we built linear regressions between the separation distance among nearest neighbours and their sum of sizes for all possible species combination (6). From the analysis of regressions we estimated the interaction importance (R^2 , coefficient of determination) and the interaction intensity (β_1 , slope) (Briones et al., 1996; Goldberg et al., 1999; Welden et al., 1988; Wilson, 1991). Positive slopes indicate a negative net effect of interference (e.g. competition); while negative slopes indicate a positive net effect of interference (e.g. facilitation).

3. Results

3.1. Population structure

3.1.1. Plant density

Total shrub density in control plots was 6167 ± 328 plants·ha⁻¹ (mean $\pm$ 1 SE). Removal of grasses increased the total shrub density to 1.75 times the density in the control plots ($F_{2,6} = 10.32$, $P = 0.01$; Fig. 1a), and shrubs were able to fully recover after removal (Fig. 1a). On the other hand, the total grass cover did not differ among treatments (Fig. 1a, inset). Different shrub species were responsible for these responses to treatments (Wilks’ $\lambda = 0.0153$, $P = 0.028$; Fig. 1b). Plant density of *Mulinum* in shrub-removal plots was 65% higher than in control plots ($F_{2,6} = 30.69$, $P < 0.001$; Fig. 1b), whereas plant density of *Senecio* in grass-removal plots was three times higher than in control plots ($F_{2,6} = 23.21$, $P = 0.001$; Fig. 1b). Plant density of *Adesmia* did not differ among treatments.

3.1.2. Plant size

Population size structure of *Mulinum* differed among treatments. Main difference occurred in the percentage of small

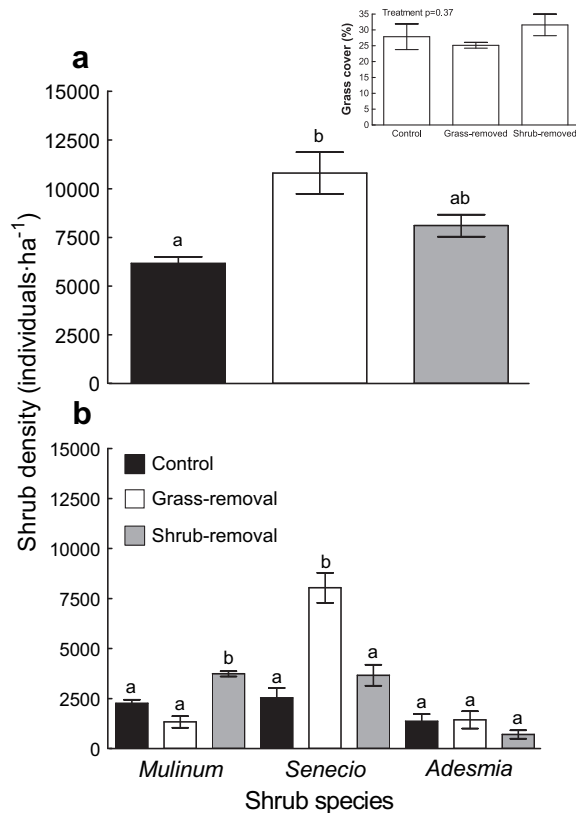


Fig. 1. Shrub density in the three treatments: control, grass-, and shrub-removal. Selective removal was applied from 1983 to 1985, and then the treated plots were abandoned for 12 years. a) Total density of shrubs (individuals/ha). Inset: Total grass cover (%) in the same treatments. b) Species-specific density (individuals/ha). *Mulinum*: *Mulinum spinosum*; *Senecio*: *Senecio filaginoides*; *Adesmia*: *Adesmia volckmanni*. Vertical bars indicate means $\pm$ SE ($n = 3$). Different letters indicate significant differences among treatments within each shrub species (P -value < 0.05).

individuals (< 50 cm size), 50%, 25% and 75% in control, grass-removal and shrub-removal, respectively (Fig. 2a; Table 1 in Electronic supplemental material). *Senecio*'s population size structure differed in the grass-removal treatment for the intermediate size class (20% more in grasses removal than control) (Fig. 2b; Table 1 in Electronic supplemental material). *Adesmia*'s size structure did not differ between the removal treatments and control (Fig. 2c; Table 1 in Electronic supplemental material).

3.1.3. Dead crown

Mulinum ($F_{2,6} = 33.12$, $P < 0.001$) and *Senecio* ($F_{2,6} = 6.94$, $P = 0.03$) had higher mean percentage of dead crown in grass-removal plots than in control plots (Fig. 3). However, the largest effect occurs on *Mulinum* populations. Correlations between dead crown and individual plant size for each species showed that *Mulinum* had a greater percentage of dead crown particularly in small individuals growing in grass-removal plots compared to control plots (Fig. 1a in Electronic supplemental material), whereas *Senecio* increments were in all size classes (Fig. 1b in Electronic supplemental material) in the grass-removal plots.

3.2. Spatial pattern analysis and neighbourhood relationships among shrubs

3.2.1. Spatial patterns

As a growth-form group, shrubs showed a light aggregation at short distances (0.5–1.2 m) in grass- and shrub-removal treatments

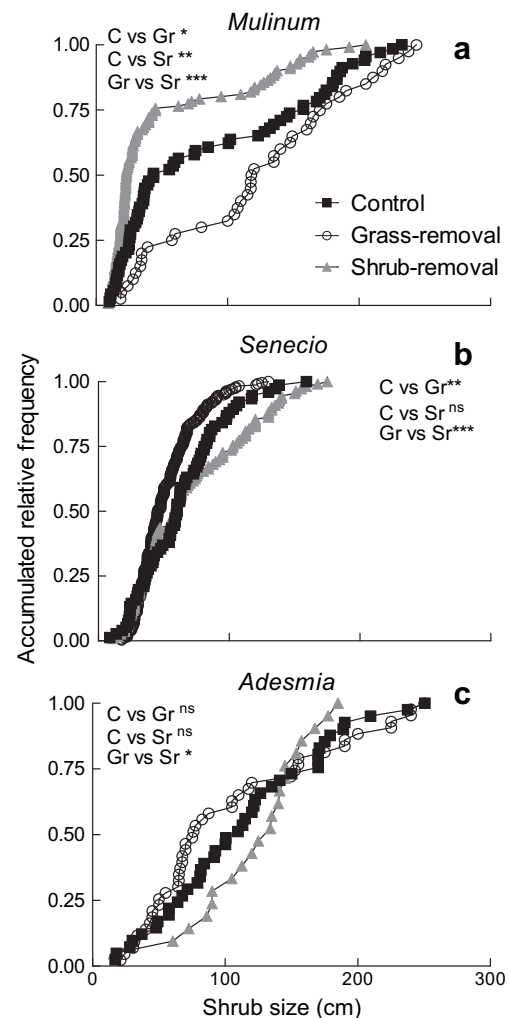


Fig. 2. Accumulated relative frequency of shrub size for: a) *Mulinum spinosum*, b) *Senecio filaginoides* and c) *Adesmia volckmanni* in the three treatments (C: control, Gr: grass-removal, and Sr: shrub-removal). Shrub size was calculated as the sum of height and mean diameter.

(Fig. 4a–c). At species level, only *Mulinum* and *Senecio* had enough plants to study the spatial patterns, but solely the latter presented non-random patterns in treated plots. In the grass- and shrub-

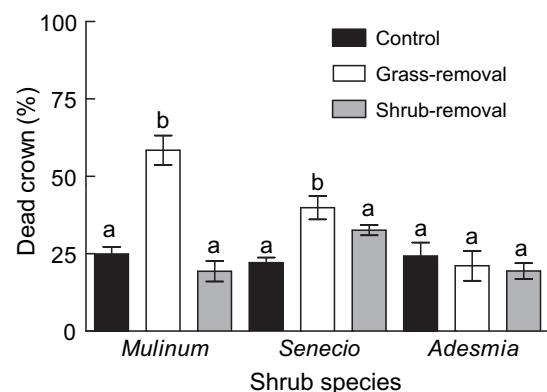


Fig. 3. Dead crown percentage for the dominant shrub species (*Mulinum spinosum*, *Senecio filaginoides* and *Adesmia volckmanni*) in the control, grass-, and shrub-removal treatments. Vertical bars indicate means $\pm$ SE ($n = 3$). Different letters indicate significant differences among treatments within each shrub species (P -value < 0.05).

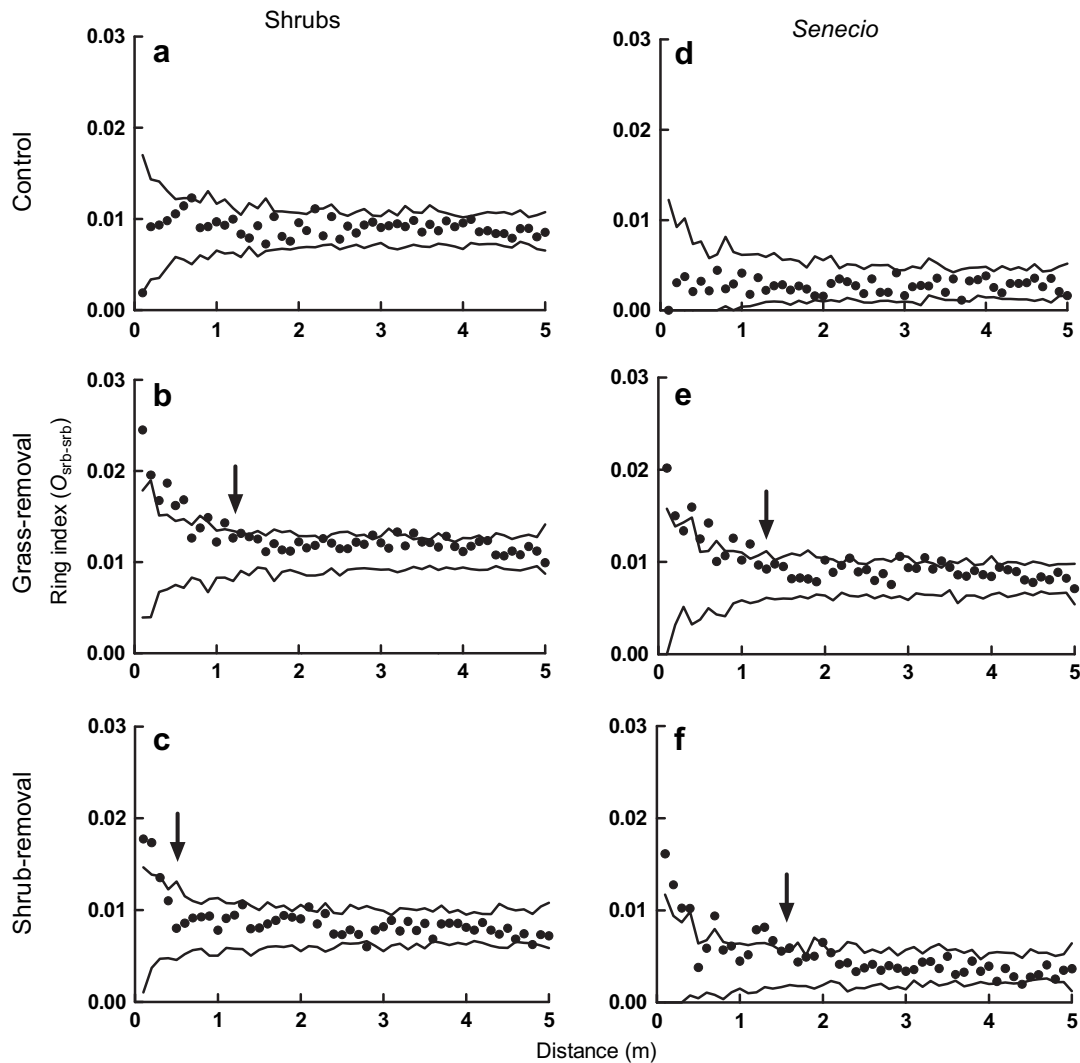


Fig. 4. Uni-variate spatial patterns in shrubs (a–c), and *Senecio filaginoides* plants (d–f) in the control, grass-, and shrub-removal treatments. Circles indicate the O-ring statistic calculated from the three respective plots and lines indicate the upper and lower limits of 99% confidence interval for a random spatial distribution (null model CSR). Black arrows indicate the maximum spatial scale of significant aggregation.

removal plots *Senecio* individuals presented a clumped pattern at distances 1–1.5 m (Fig. 4e and f).

3.2.2. Neighbourhood relationships

Intra-specific relationships were only present in shrub-removal plots, especially *Mulinum*–*Mulinum* and *Senecio*–*Senecio* pairs showed positive relationships, but with different slopes in each species (Fig. 5h and i). Significant inter-specific relationships occur in control (Fig. 6a and c) and shrub-removal plots (Fig. 6g and i). Regressions were negative for *Adesmia*–*Mulinum* pairs (Fig. 6a and g) and positive for *Mulinum*–*Senecio* pairs (Fig. 6c and i). Despite the last relationship was statistically significant in shrub-removal plots, it had a very low R^2 .

4. Discussion

Shrub population's structure differed across the three treatments studied. Compared to control plots total shrub density was 75% higher in the grass-removal and not different in the shrub-removal plots. *Mulinum* and *Senecio* explained most of the total shrub response to shrub and grass-removal, respectively. We confirmed our predictions since *Mulinum* (one deep-rooted

species) increased in the shrub-removal plots, while *Senecio* (the shrub species with a root distribution similar to grasses) increased in the grass-removal plots. In addition, the species level analyses from grass removal indicate a striking array of responses of the three dominant species that underline: first, the individual species' role in the shrub-grass coexistence and second, the importance of negative and positive interactions at different levels (i.e. intra-specific, among shrub species, and between grasses and shrubs). The complex network of interactions focused on the woody component may result in shrub-grass coexistence and bring support to both the niche separation and the balanced competition hypotheses (House et al., 2003; Peltzer and Köchy, 2001). Although it is usual to invoke these interactions as determinants of the shrub/grass balance or system buffering mechanisms, the empirical evidence at population and long-term level is meager (cf. Jeltsch et al., 2000; Maestre et al., 2003; Sankaran et al., 2004; Scholes and Archer, 1997).

Our long-term study brings a different perspective compared to what was measure and infer in the first years. During the early phase of this experiment (first three years) indicates that grasses and shrubs, considered as functional groups, in general utilize different soil water resources. Grasses did not respond to shrub-

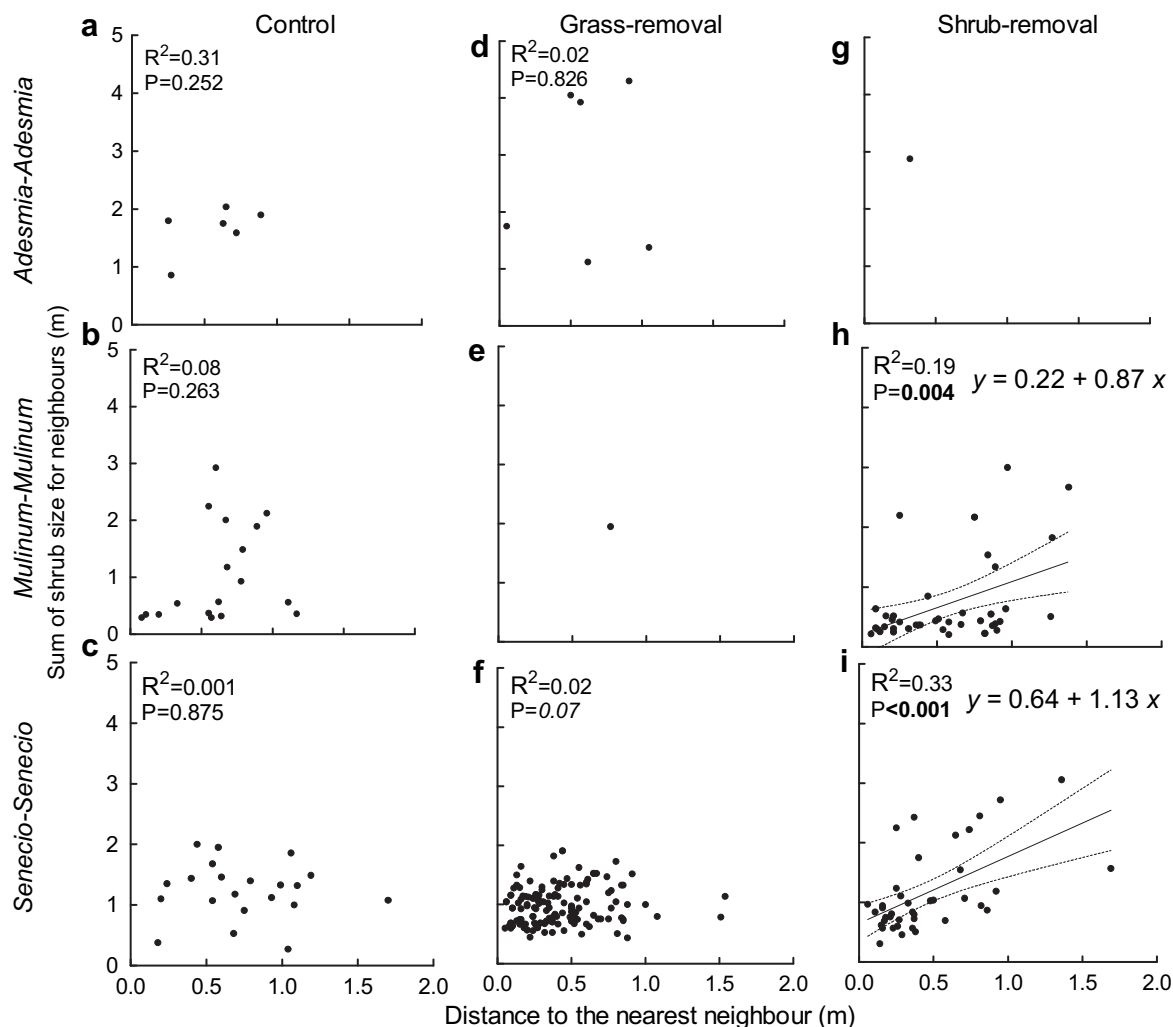


Fig. 5. Scatter plots with intra-specific relationships in the control (a–c), grass-removal (d–f), and shrub-removal (g–i) treatments. Linear regression between the nearest neighbour distance (m) and summed shrub size (m) for the conspecific pairs of shrubs. Dashed lines indicate the upper and lower limits of 95% confidence interval only from the significant linear regression analysis.

removal since utilize mostly water from the top soil layer, whereas shrubs utilize water mostly from the bottom soil layer (Sala et al., 1989). Removal of grasses, increased shrub production but did not fully compensate grass production in control plots. Our study indicates that population long-term responses (12 years) contradict the early results, because the *Senecio* encroachment triggered by grass-removal indicates plant competition rather than resource partitioning. In addition, our results are more coherent with a big pulse of emergence of *Senecio* seedlings recorded during the first years after the grass-removal that may not be detected as changes in shrub production (Fernández et al., 1992). On the other hand, remaining grass species in the shrub-removed plots were unable to impede the re-colonization by *Mulinum*. Therefore, cumulative effects from the population biology of different species result in a different perspective (than the initial response), and therefore matters for the understanding of shrub-grass coexistence. In the following we discussed the different responses for each shrub species.

Mulinum showed a remarkable capacity to establish and grow after the removal of shrubs, reaching higher densities than in control plots. In grass-removal plots, *Mulinum*'s density was not different than in control. We infer that *Mulinum* density is controlled by shrub–shrubs competition rather than by grass

competition. Supporting this interpretation we found that association between distance and size of neighbours was negative and significant for *Mulinum–Mulinum* and *Mulinum–Senecio* pairs (i.e. intra- and inter-specific competition). Contrary to our expectations, instead of competing, grasses may play some positive role in the recruitment of *Mulinum* (i.e. facilitation on shrub seedling emergence and survival). We found a significant decrease in the percentage of small individuals in grass-removal plots. Moreover, small individuals in the same plots showed a higher percentage of dead canopy (i.e. a reduced vitality). *Mulinum* seedlings can avoid water competition with grasses if roots grow fast and reach deep soil layers (high water content) during the first growing season (Sala et al., 1989). Fernández (1993) reported that seedling recruitment of *Mulinum* occurs predominantly in grass micro-sites. In addition, our field survey confirmed that small individuals of this species mostly grow near to tussock grasses (data not shown). We interpret that this is indicative of facilitation of grasses on shrubs recruitment, at least during the first years. In Patagonia, strong dry winds promote plant water stress therefore grasses can compete with shrub seedlings but also protect them against desiccation (Aguiar et al., 1992; Graff et al., 2007). Facilitation of herbaceous species on woody plants, especially at early shrub regeneration stages, was previously inferred from eco-physiological variables

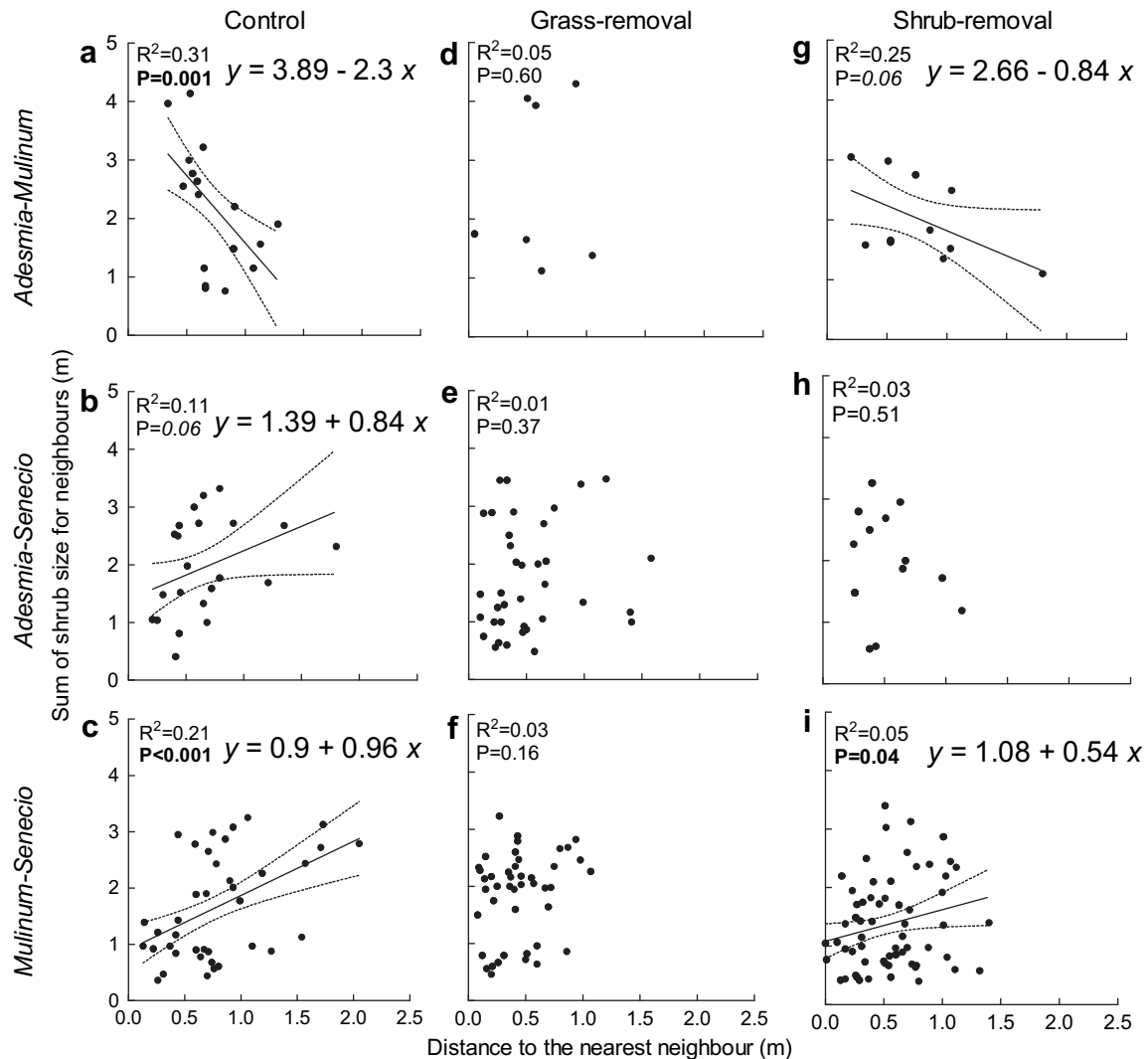


Fig. 6. Scatter plots with inter-specific relationships in the control (a–c), grass-removal (d–f), and shrub-removal (g–i) treatments. Linear regression between the nearest neighbour distance (m) and summed shrub size (m) for the heterospecific pairs of shrubs. Dashed lines indicate the upper and lower limits of 95% confidence interval only from the significant linear regression analysis.

(Espigares et al., 2004; Garcia-Fayos and Gasque, 2002; Maestre et al., 2001;). Our results confirmed this notion and add evidence of facilitation controlling population dynamics and shrub-grass coexistence.

Senecio's response to grass-removal was explosive, achieving a 3-fold increase of density (compared to control). This population showed an increase in the proportion of small- and medium-sized plants, which may be indicative of both, a recruitment outburst soon after grass-removal, and then a rapid growth of established individuals. Competition with grasses must be intense because they share the same water resource (0–0.25 m soil layer) (Fernández-Alduncin and Paruelo, 1988). Also, in the grass-removal plots the intra-specific competition must be intense due to the high density. During the first years after the experimental treatments, Fernández et al. (1992) reported a 10-fold increase – compared to control plots – in *Senecio* seedling density six years after grass-removal. High density may have triggered an intense intra-specific resource competition that reduced density to the value we measured (i.e. self-thinning). Supporting this interpretation we observed that dead canopy percentage in grass-removal is significantly higher than in control or shrub-removal plots. After 1986 grass slowly

recovered in grass-removal plots and competition with *Senecio* must have increased. In shrub-removal plots *Senecio* density was not different from control plots indicating that although grasses were present *Senecio* managed to reestablish and grow. In both removal treatments we detected that *Senecio* showed a similar clumped distribution pattern. Clumping occurred at short distance, even in the grass-removal plots, where *Senecio* density was maximum. This may be indicative of environmental heterogeneity or simply seed dispersal constraints (Cousens et al., 2008; Eriksson and Ehrlén, 1992).

Adesmia's density – and the other population response variables – showed no differences among the three treatments studied. Lack of response to grass-removal might be indicative that this population has neutral or no interaction with grasses. On the other hand, the lack of response to shrub-removal might be indicative that population dynamics is also not constrained by intra- or inter-specific interactions. However, the neighbourhood analyses indicate a positive interference among plants of *Adesmia* and *Mulinum* (i.e. probably facilitation) perhaps because higher nitrogen soil content in the neighbourhood of the legume species (Armas et al., 2008; Golluscio et al., 2006; Pugnaire et al., 1996). *Adesmia* is the

shrub species with the deepest root system (0.6–0.9 m) (Golluscio et al., 2006); hence our results are more coherent with the niche partition hypothesis proposed by Walter (1971).

Future developments in the shrub-grass coexistence question will derive from a conceptual model that includes main biotic controls between stages of woody species (Barot and Gignoux, 2004; Sankaran et al., 2004). Our data support that in this Patagonian community, the network of interactions (negative and positive) at the growth-form and species level could be able to buffer the dominance of each growth-form, and hence maintains the shrub-grass ratio (Fig. 7). For example, adult grasses can constraint *Senecio* recruitment but foster *Mulinum* recruitment (i.e. net effect between competition and facilitation). On the other hand, adult shrub of the three species facilitates the recruitment of grasses around shrubs (Aguiar and Sala, 1994; Cipriotti and Aguiar, 2005). Under high shrub density, intra-specific competition is an intense control of *Mulinum* and *Senecio* population dynamics, probably affecting growth of seedlings and/or saplings. This negative feedback at high woody plant density has been proposed as a buffer mechanism that impedes woody encroachment (*sensu* Jeltsch et al., 2000), yet, in our knowledge, data supporting it are rare (but see Shackleton, 2002). In this sense, *Mulinum* appears as a key shrub species in this network, because it interacts with the other two shrub species and grasses with positive and negative outcomes. However, it is necessary to make a note of caution regarding the interpretation of size-distance relationships as indicative of biotic interactions. The spatial distribution and plant sizes may be also influenced by disturbances, seed dispersal, environment heterogeneity, allelopathy, herbivory, seed predation, competition, facilitation, and possibly other factors (Briones et al., 1996; Carrick, 2003; Shackleton, 2002; Welden and Slauson, 1986; Welden et al., 1988; Wilson, 1991). Some of these factors can be rule out from our study (e.g. herbivory, disturbances), however other remains unknown (e.g. allelopathy, seed predation). Certainly, more studies are needed in order to confirm our inferences about the plant interactions based on the detected interferences.

As in other ecosystems around the globe, shrub-grass coexistence in Patagonia was studied under the assumption that

differences in root systems between growth-forms were larger and more significant than differences in the same growth-form (Sala et al., 1989). This assumption in Patagonian grass-shrub steppes is challenged by differences in root morphologies of shrub and grass species (Bucci et al., 2009; Fernández-Alduncin and Paruelo, 1988; Golluscio et al., 2006; Leva et al., 2009; Rodriguez et al., 2007), and the intensity and importance of intra- and inter-specific biotic interactions (Aguiar and Sala, 1994; Aguiar et al., 1992; Armas et al., 2008; Graff et al., 2007). Similarly, recent works from other arid ecosystems have reported morphological and eco-physiological differences in woody species, most of them related to differences in the root systems, but also in the canopy architecture (Gibbens and Lenz, 2001; Hierro et al., 2000). In this sense, our study indicates two main results relevant to increase our comprehension of shrub and grass coexistence and our ability to designate appropriated managements. First, the long-term population responses are quite different among shrub species, and second, shrub species interact with grasses and among them in different ways. These results support our ideas that shrub-grass interaction is not as simple as described in the Walter's two-layer hypothesis at least at the woody side, and that both niche separation and balanced competition (House et al., 2003; Sankaran et al., 2004) are complementary mechanisms controlling the shrub-grass coexistence in this community. Therefore, the original functional group view based just on the two growth-forms according to the resource partitioning hypothesis could hide important information for a full understanding of coexistence. Being plant coexistence a result of demographic processes it is necessary to study population level responses for at least a decade in order to detect the long-term trends in "the cumulative effects of interactions" (*sensu* Peltzer and Köchy, 2001) and use a network perspective to grasp the full extent of interactions among dominant species.

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Appendix. Supplementary material

Supplementary material associated with this article can be found in the online version, at doi:10.1016/j.jaridenv.2010.05.006.

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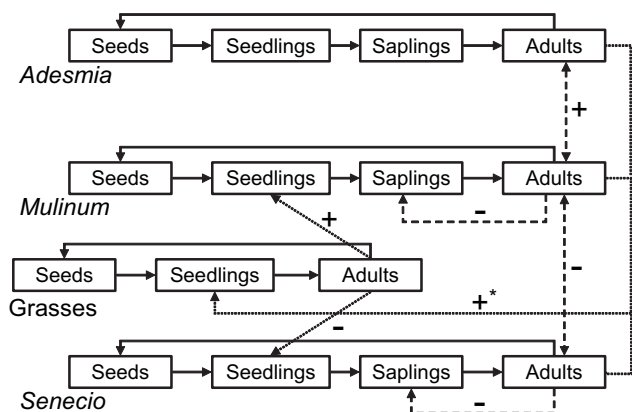


Fig. 7. Conceptual model representing the network of interactions among the dominant shrub species and perennial tussock grasses. Boxes indicate the demographic stages; solid arrows indicate the demographic transitions (individuals) among stages. Broken lines indicate plant–plant interactions. Dashed arrows indicate the main interactions between shrub species; dotted arrows indicate interactions between shrub species and grasses. Signs indicate the net balance between competition and facilitation. * Information for positive interactions from shrubs to grasses is based on Aguiar et al., 1992 and Aguiar and Sala 1998.

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