# Is the balance between competition and facilitation a driver of the patch dynamics in arid vegetation mosaics?

## Pablo A. Cipriotti and Martín R. Aguiar

*P. A. Cipriotti (cipriott@agro.uba.ar), Depto de Métodos Cuantitativos y Sistemas de Información, Facultad de Agronomía – IFEVA, Univ. de Buenos Aires / CONICET. Av. San Martín 4453 (C1417DSE), Ciudad de Buenos Aires, Rep. Argentina. – M. R. Aguiar, Cátedra de Ecología, Depto de Recursos Naturales y Ambiente, Facultad de Agronomía – IFEVA, Univ. de Buenos Aires, Argentina.*

In most arid ecosystems, the vegetation is organized into two-phase mosaics, where high-cover vegetation patches are interspersed in a matrix of low plant cover. We studied the role of the biotic interaction balance (competition/facilitation) between shrubs and grasses as a driver of patch dynamics and maintenance of two-phase vegetation mosaics. Following Watt's seminal model, we conducted two field experiments in which we manipulated different vegetation patches to obtain the different stages along the building and degradation dynamics of high-cover patches. In addition we applied two possible belowground competition treatments (natural and experimentally reduced). We measured plant variables (emergence, survival, height, flower culms) on grass seedlings and transplants. We integrated all plant measurements into a single positive and negative component, to calculate the net balance along three stages of the patch dynamics proposed. The net biotic interaction balance was negative during the early and mature stages of high-cover patches because the average standardized effect from the negative component was below −0.44, while the positive component was not different from zero. However, the net biotic interaction balance was positive during the degraded stages of high-cover patches because the negative average component was −0.37, while the positive component reached 0.58. The negative net effects during early and mature stages of high-cover patches can be explained by the occurrence of wet years, because high rainfalls hide the aboveground facilitation. Our findings point out the importance of complementary mechanisms to the interaction balance in the mosaic maintenance (e.g. trapping of seeds by shrubs) according to the inter-annual rainfall variability.

Biotic interactions are major drivers of the spatial structure and dynamics of plant communities, and understanding their role in a variable spatio-temporal domain is a central issue in community ecology (Callaway and Walker 1997, Holmgren et al. 1997, Armas and Pugnaire 2005). The net balance of biotic interactions among plants (competition and facilitation) has been posited as a main driver of the vegetation patch dynamics in arid ecosystems (Aguiar and Sala 1999, Olff et al. 1999). Several studies have quantified this balance across climatic, resource, and disturbance gradients (Holzapfel and Mahall 1999, Olofsson et al. 1999, Pugnaire and Luque 2001, Graff et al. 2007, Dohn et al. 2013), with a specific focus on stressful environments (Callaway et al. 2002, Maestre et al. 2003, Maestre and Cortina 2004). However, there are fewer empirical studies that have linked plant interactions, patch dynamics, and the maintenance of the spatial organisation of vegetation communities (but see Schenk and Mahall 2002, Barbier et al. 2008).

Watt (1947) proposed that plant communities are organised as an array of different vegetation patches linked by a common working dynamic. Several plant community types (e.g. grasslands, woodlands, forests, savannas) include internal cyclical dynamics, in which the colonization of bare ground patches 'upgrade' to a fully vegetated patch. In time, vegetated patches can 'downgrade' to bare ground, closing the loop of the gap-phase dynamics (Remmert 1991, Soriano et al. 1994, Herben et al. 2000, Meyer et al. 2009). In most arid and semi-arid ecosystems, the vegetation is organized into two-phase mosaics with high-cover vegetation patches interspersed in a matrix of low or null plant cover (Noy Meir 1981, Fuentes et al. 1984, Couteron and Kokou 1997). High-cover patches take the form of bands or spots of different sizes, and they are usually formed by woody and herbaceous plants (Aguiar and Sala 1999). The two-phase vegetation mosaics have been identified as a key attribute of the structure and functioning of arid ecosystems because they can affect diversity, productivity, water dynamics, carbon and nutrient cycling (Cornet et al. 1988, Ludwig and Tongway 1995, Segoli et al. 2008). In addition, population processes, such as seed dispersal and seedling recruitment are conditioned by the particular spatial arrangement of local plant populations or individuals (Montaña 1992, Riginos et al. 2005, Segoli et al. 2012).

In mixed woody–grass communities, woody plants play a central role in the building phase of high-cover patches, because they change the hydrological properties (e.g. increasing

infiltration), trap seeds, ameliorate microclimate conditions, and promote nutrient enrichments (Pugnaire et al. 1996, Dunkerley 1997, Facelli and Brock 2000, Giladi et al. 2013), thus facilitating the recruitment of new individuals in their neighbourhood. Nevertheless, these effects may change as time passes, due to woody plant growth, as well as the increase of total plant density in the patches. Consequently, the competition–facilitation balance promoted by woody plants may change along their different life-stages.

During the building phase of high-cover patches, the net balance between competition and facilitation is expected to be positive due to the fact that woody plant facilitation increases and the low density of herbaceous plants results in low intensity of competition. However, during the degradation phase of high-cover patches, this situation is reversed because the woody nucleus may begin its senescence (i.e. facilitation disappears) and plant density reaches a maximum. In turn, the net balance of plant–plant interactions becomes negative. Currently, these processes have been mostly tested by modelling approaches (Lefever and Lejeune 1997, Couteron and Lejeune 2001, Dickie et al. 2005, Boonkorkuea et al. 2010, Kealy and Wollkind 2012). Few field experiments have been able to manipulate and separate both components of the biotic interaction balance (i.e. competition and facilitation) in order to set a clear link between this balance and the spatial patterns of vegetation communities (but see Schenk and Mahall 2002, Alados et al. 2006, Barbier et al. 2008). To investigate the role of the biotic interaction balance (i.e. competition/facilitation) as a specific mechanism driving patch dynamics and the maintenance of two-phase vegetation mosaics from arid ecosystems, we conducted two manipulative field experiments addressing the building and degradation phases in a two-phase vegetation mosaic from the Patagonian grass–shrub steppe. We expected, in line with our hypothesis, that net interaction balance would result positive in early stages of high-cover patches, thereby promoting the building phase, but would become negative in mature high-cover patches promoting the degradation phase.

## Material and methods

### Study site

The study site is located at the Rio Mayo INTA Experimental Station in South Central Patagonia, Chubut Province, Argentina (45°41′S, 70°16′W; 500 m a.s.l). Mean annual precipitation is 153 mm (1960–present) and ranges between 47 and 245 mm. More than 70% of the precipitation falls during the autumn and winter season, from March to August (Jobbágy et al. 1995). The mean annual temperature is 8.1°C and the mean monthly temperature ranges from 2°C in July to 14°C in January. The landscape is typically flat and soils are coarse textured (sandy), with cobbles and pebbles making up 50% of the soil mass. The vegetation is co-dominated by tussock perennial grasses and shrubs, which cover 28% and 12% of the area, respectively (Fernández-Alduncin et al. 1991). The dominant tussock grass species are *Pappostipa speciosa*, *P. humilis* and *Poa ligularis*, whereas *Bromus pictus* is a subdominant bunch grass species. The dominant shrub species are *Mulinum spinosum*, *Senecio filaginoides* and *Adesmia volckmanni*. The vegetation is spatially organised as a two-phase spotted mosaic comprising mostly by individual shrubs that are surrounded by a dense ring of grasses as high-cover patches and scattered grass tussocks in a matrix of bare soil as low-cover patches (Soriano et al. 1994, Cipriotti and Aguiar 2005, Golluscio et al. 2005). The grass species composition in the high- and low-cover patches is quite similar, but it strongly depends on the context situation related to sheep domestic grazing. In ungrazed sites dominate palatable and less palatable grass species (e.g. *Poa ligularis, Hordeum comosum, Bromus pictus* and *Pappostipa* spp.) in both patch types, while in grazed sites grass palatable species were replaced by less palatable species (*Pappostipa* spp.) (Cipriotti and Aguiar 2005).

### Building phase experiment

The building experiment followed a split-plot design to test the effects of belowground competition and the stage of vegetation patches (as a surrogate of facilitation intensity effect due to the aerial protection of shrubs of increasing size and biomass; Aguiar and Sala 1998, Armas et al. 2008) during the building phase. In split-plot designs, there are two different plot sizes associated with the two variation sources. In this experiment, the whole plot was considered as the 'patch stage' (four levels), and the sub-plot was considered as 'competition' (two levels). The building phase was represented by a four-staged gradient from bare soil to mature high-cover patches. We delimited a ¼-ha experimental area in an excluded grazing paddock (ca 5 ha) including approximately 1000 vegetation patches formed around shrubs of different stages (juvenile, young and adult shrubs, but no seedlings) and a similar quantity of bare soil patches. We randomly selected ten patches of bare soil; ten patches formed by a small juvenile shrub (0.1–0.3 m in diameter) without a grass ring or with an incipient grass ring (< 25% grass cover of shrub canopy circumference, hereinafter referred to as 'completeness' sensu Soriano et al. 1994); ten patches formed by a large young shrub (0.3–0.6 m in diameter) with a moderate cover of grass ring (30–50% completeness); and ten patches formed by an adult shrub (0.6–1 m in diameter) with a high cover of grass ring (> 60% completeness). To avoid shrub species-specific effects, all shrub patches selected for both experiments were represented by a single plant of *Mulinum spinosum*, a dominant and key shrub species in this vegetation community (Cipriotti and Aguiar 2012). This experiment was settled in the field for 12 months (May 2003 to May 2004).

### Degradation phase experiment

The degradation experiment also followed a split-plot design to test the effects of belowground competition and the stage of vegetation patches, where the degradation phase of high-cover patches was represented by a reversal five-staged gradient from mature high-cover to bare soil patches. As in the building phase experiment, the whole plot from the split-plot design was considered as the 'patch stage' (five levels), and the sub-plot was considered as 'competition' (two levels). In the same excluded grazing paddock, we delimited a

new ½-ha experimental area, enclosing approximately 700 mature vegetation patches formed only by adult shrubs. Therein, we randomly selected ten patches of bare soil (BS) and forty mature high-cover patches formed by a living adult shrub (0.6–1 m in diameter) with a dense grass ring (>60% completeness) with the same criteria, used to define the mature stage of high-cover patches in the previous experiment. Each patch was treated in order to represent the experimental gradient of natural degradation of high-cover patches according to the random assignation of treatment. Ten patches remained intact (LS: mature and living shrub); ten with a killed shrub set in place with wires and spikes and an untouched complete grass ring (DS: dead shrub – start of degradation phase, shrub protection by a not functionally canopy); ten without shrub (killed and removed) and an untouched complete grass ring (PD: partially degraded, disappearance of shrub protection and high competition); and ten without shrub (killed and removed) and a manually thinned grass ring (FD: fully degraded, disappearance of shrub protection and mortality of grasses due to high competition) to resemble grass density of bare soil patches (30–50% of plants removed with minimum soil disturbance). The experimental degradation gradient of high-cover patches was thinking to separate a priori aboveground facilitative effects (i.e. by detecting canopy protection through LS or DS vs PD or FD contrasts), belowground facilitative effects for nutrients (i.e. by detecting fertility islands through LS or DS vs BS contrasts), and belowground facilitative effects for water (i.e. by preliminary detection of hydraulic lift through LS vs DS contrasts). This experiment was conducted from June 2002 to May 2003.

## Common manipulation for both experiments to estimate belowground competition

We sowed grass seeds and transplanted grasses in order to estimate key vital rates (emergence, survival, growth and flowering) in all patch types for both experiments under two belowground competition treatments: reduced and natural. Reduced competition was generated, in both experiments (building and degradation), by burying PVC tubes (0.2 m tall × 0.3 m wide) in the upper soil layer. We dug a pit and covered the pit wall with a PVC tube before refilling with sieved soil. To generate the natural competition treatment, in another position in the same patch, we only dug a pit and refilled it with sieved soil. This experimental protocol has been verified as effective in controlling belowground competition in the upper soil layers (0–0.3 m; Fowler 1986, Casper and Jackson 1997, Cipriotti and Aguiar 2005). Despite the belowground competition can be initially reduced in the natural treatment by the soil removing and sieving, roots growth during the early spring is able to colonize quickly these soil volumes (Soriano et al. 1987).

In both experiments, we manually added ten seeds into each pits (at a sowing depth of 1.5 cm) and transplanted a young individual (five tillers) of a native grass species (*Bromus pictus*) during late autumn (May–June). We used the grass *B. pictus* as a plant phytometer because of its sensitive responses to micro-environmental conditions generated aboveground by the shrub canopy and below-

ground by root competition (Cipriotti and Aguiar 2005, Cipriotti et al. 2008). Seeds had been harvested in the study site in the previous growing season. The germination rate, as previously measured in growth chambers, was $94 \pm 2.23\%$ (mean $\pm$ 1 SE; Rotundo and Aguiar 2004). The individuals selected to transplant were obtained from adult plants (five tillers per transplant) in the same study site and harvested two days prior to field transplanting.

## Plant measurements and statistical analysis

The response variables evaluated were: emergence (Aug–Sep), survival, and size of seedlings (Jan–Mar); and survival, growth and number of flower culms of transplants (Jan–Mar) for each patch-stage and competition treatment. Data were analysed using linear models with a split-plot design, each experiment separately. The main factor or whole plot was the 'patch stage' (four or five levels according to the experiment), and the sub-plot was 'competition' (two levels), both fixed factors, while replicate (patch) was considered a random factor. According to the response variable, we used general or generalized linear models. Percentage variables from the grass seedling measurements (i.e. emergence and survival) were analyzed after applying the logit transformation. We used ANOVAs to determine the statistical significance of model terms, and we performed post hoc comparisons with Tukey-HSD tests with a significance level of 5%. To evaluate the survival of the transplanted grasses, we used a logistic analysis and $\chi^2$-tests using a binary response variable (alive or dead).

To answer our specific question regarding the interaction balance, we summarized the single results from the different phase experiments and response variables by calculating a synthetic measure of the negative ($\Omega-$) and positive ($\Omega +$) component (a priori) of the biotic interaction balance. Following a meta-analysis approach we calculated the standardized size effect or mean difference (Cohen's $d$; Hedges and Olkin 1985) of each $i$th biotic response variable for negative $\left(\bar{X}_{i,c+} - \bar{X}_{i,c-}\right)$ or positive component $\left(\bar{X}_{i,f+} - \bar{X}_{i,f-}\right)$ of the balance, standardized by the common standard deviation ($S_i$) for each component (i.e. numerators in Eq. 1 and 2). Then, we averaged the standardized effect sizes and pooled them (Eq. 1, 2) according to the total plant variables measured ($n = 6$) for three stages of high-cover patches along the cyclic succession (i.e. early high-cover patches (juveniles and young), mature high-cover patches (adults and living shrubs), and degraded high-cover patches (partially and fully degraded high-cover patches)). To estimate the negative component a priori, we calculated the mean difference between the belowground natural ($c+$) and reduced competition ($c–$) treatments, for each patch stage (Eq. 1). To estimate the positive component a priori, we calculated the mean difference between the early, mature or degraded patch stages ($f+$) and the bare soil patches ($f–$) under the reduced belowground competition treatment (Eq. 2). See Supplementary material Appendix 1 Table A1 for more details about raw data for the calculus of mean differences.

$$\Omega- = \frac{\sum_{i=1}^{i=n}\left[\left(\bar{X}_{i,c+} - \bar{X}_{i,c-}\right)/S_i\right]}{n} \quad (1)$$

$$\Omega+ = \frac{\sum_{i=1}^{i=n}\left[\left(\bar{X}_{i,f+} - \bar{X}_{i,f-}\right)/S_i\right]}{n} \quad (2)$$

We then calculated the approximate confidence intervals based on the estimation of the average of the standardized size effect and its deviation for each balance component and patch stage (Kelley 2007, Viechtbauer 2007). All statistical analyses were performed with the software Statistica ver. 9.1, except for the meta-analysis that was done with the package *metafor* from R environment (Viechtbauer 2010).

## Results

### Building phase experiment

Belowground competition did not affect seedling emergence, but it did reduce the survival and the height of seedlings, regardless of the stage of high-cover patches (Fig. 1, Supplementary material Appendix 1 Table A2). Global mean emergence was $78.7 \pm 1.71\%$ (mean $\pm 1$ SE; Fig. 1a), while at the end of the experiment, survival and height means decreased due to competition by 22.8% (Fig. 1b) and 25% (Fig. 1c), respectively. The shortest and tallest seedlings were found in bare soil patches and mature stage of high-cover patches, respectively (Fig. 1c). Belowground competition reduced the survival of grass transplants (Supplementary material Appendix 1 Table A3), and their number of tillers and floral culms (Supplementary material Appendix 1 Table A4), regardless of the stage of high-cover patches (Fig. 2). Belowground competition reduced the survival of grass transplants by 10% (Fig. 2a), but the number of tillers and floral culms decreased by 18.9% (Fig. 2b) and 46.2% (Fig. 2c) from reduced to natural competition treatments, respectively.

### Degradation phase experiment

Belowground competition reduced the emergence, survival, and height of seedlings, regardless of the stage of high-cover patches (Fig. 3, Supplementary material Appendix 1 Table A5). Survival was the most sensitive vital rate, with a mean reduction of 47% (Fig. 3b), while emergence and height means decreased by 9.9% (Fig. 3a) and 11.7% (Fig. 3c) from reduced to natural competition treatments, respectively. Degradation stage reduced seedling height, with the shortest seedlings found in bare soil patches (Fig. 3c, Supplementary material Appendix 1 Table A5). Belowground competition reduced the survival of grass transplants by 21.1%, regardless of the stage of high-cover patches (Fig. 4a, Supplementary material Appendix 1 Table A6). There was a significant effect of the patch stage on the number of tillers and floral culms (Supplementary material Appendix 1 Table A7). Grass transplants located in the grass ring of high-cover patches where shrub had been removed (partially and fully degraded stages) had a 137.8% more tillers (Fig. 4b) and 261.5% more floral culms (Fig. 4c) than other patch stages.
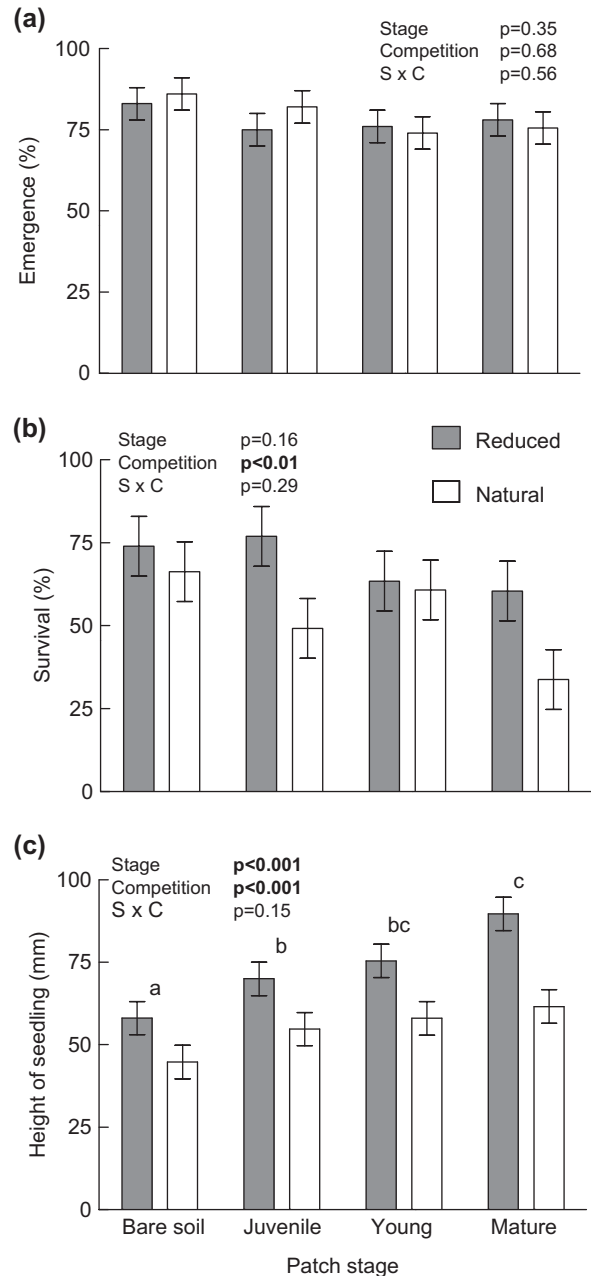


Figure 1. Building phase experiment. Emergence (a), survival (b) and height (c) of grass seedlings across four patch stages (bare soil, juvenile, young, and mature shrubs) and two levels of belowground competition (reduced and natural). The vertical bars indicate means $\pm$ SE. Different letters in (c) indicate significant differences ($p < 0.05$) across patch stages.

### Net biotic interaction balance

The net biotic interaction balance during early stages of high-cover patches was negative because the average standardized negative component was –0.44, while the positive component was not different from zero (Fig. 5, Supplementary material Appendix 1 Fig. A1). In the mature stages of high-cover patches, the net biotic interaction balance still remains negative, as the average standardized negative
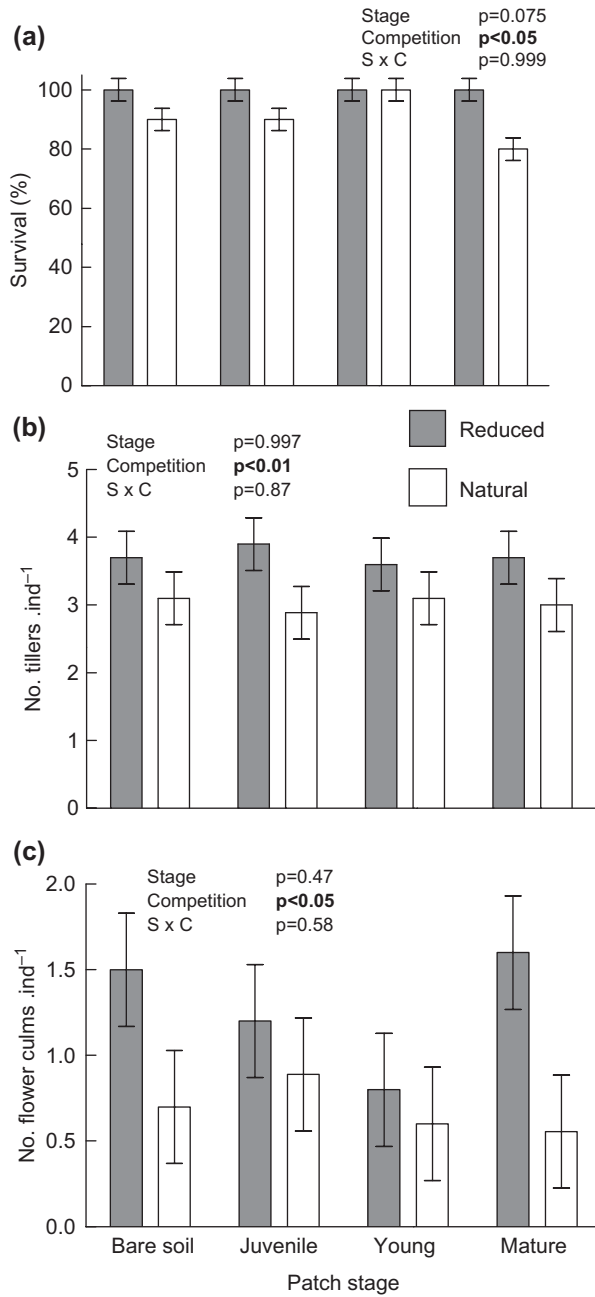
Figure 2. Building phase experiment. Survival (a), number of tillers (b) and floral culms (c) of transplanted grasses across four patch stages (bare soil, juvenile, young, and mature shrubs) and two levels of belowground competition (reduced and natural). The vertical bars indicate means ± SE.
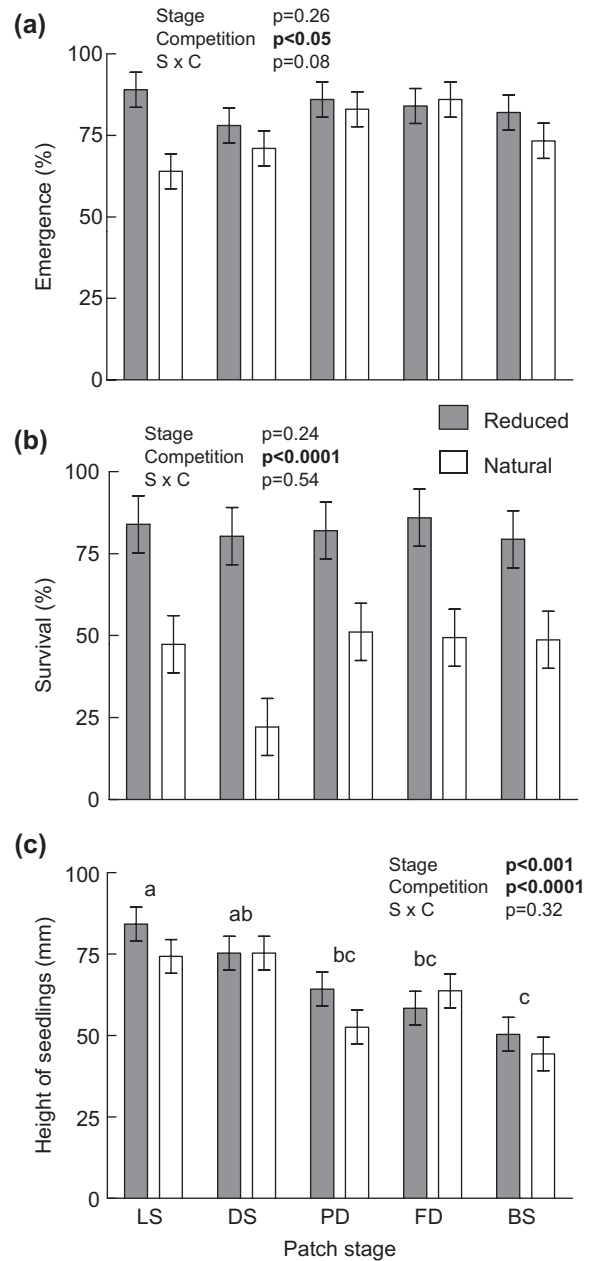


Figure 3. Degradation phase experiment. Emergence (a), survival (b) and height (c) of grass seedlings across five patch stages (LS: living shrub, DS: dead shrub, PD: partially degraded, FD: fully degraded, and BS: bare soil) and two levels of belowground competition (reduced and natural). The vertical bars indicate means ± SE. Different letters in (c) indicate significant differences ($p < 0.05$) across patch stages.

component was −0.66, while the positive component reached 0.18 (but was still not statistically different from zero) (Fig. 5, Supplementary material Appendix 1 Fig. A1). However, from degraded stages of high-cover patches, the net biotic interaction balance becomes positive because, even though the average standardized negative component remains negative, as −0.37, the positive component was 0.58 (Fig. 5, Supplementary material Appendix 1 Fig. A1). In the last case, both components were statistically different from zero ($p < 0.05$).

## Discussion

Our results contradict the hypothesis that biotic interaction balance regulates the patch dynamics and the mosaic maintenance in the Patagonian steppes (Soriano et al. 1994, Aguiar and Sala 1999). According to this hypothesis, we would have expected positive net balances to be significant at the early stages of the building phase of high-cover patches (i.e. specifically by promoting recruitment and grass growth), while negative net balances would have become significant during
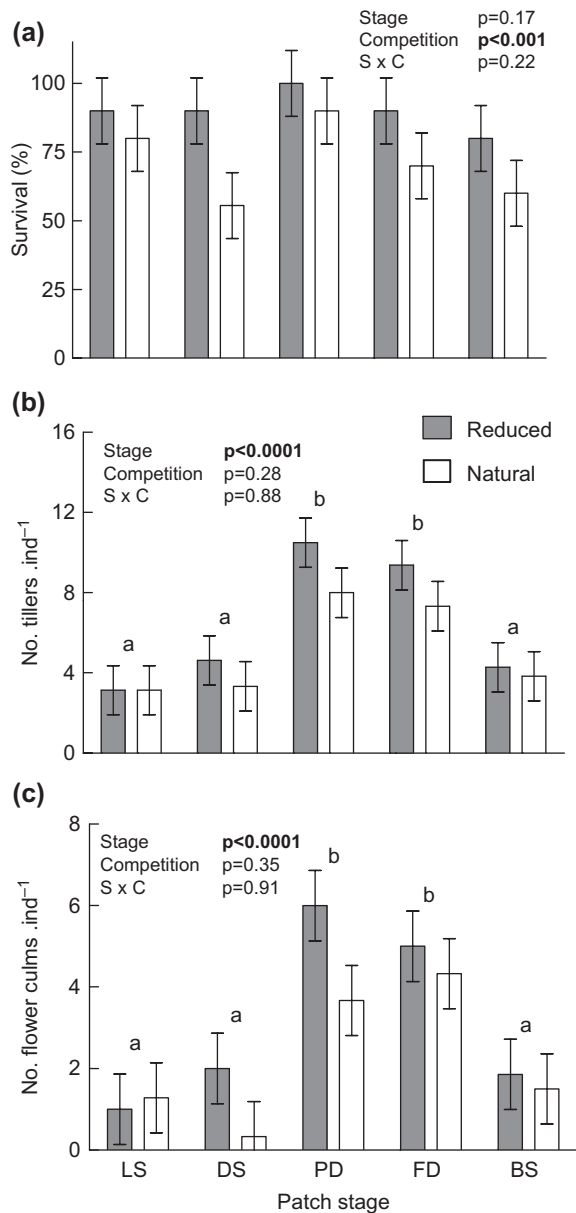
Figure 4. Degradation phase experiment. Survival (a), number of tillers (b) and floral culms (c) of transplanted grasses across five patch stages (LS: living shrub, DS: dead shrub, PD: partially degraded, FD: fully degraded, and BS: bare soil) and two levels of belowground competition (reduced and natural). The vertical bars indicate means ± SE. Different letters in (b) and (c) indicate significant differences (p < 0.05) across patch stages.

mature and degraded stages of high-cover patches (i.e. by promoting poor performance and grass mortality). In other words, we would have expected a significant interaction effect from the statistical analysis for both field experiments. In contrast, our results (based on main vital variables such as emergence, survival, growing, and flowering) suggest more complex mechanisms involved in the patch dynamics and maintenance of two-phase spatial mosaics, mainly due to the fact that the belowground competition was present throughout all different stages of high-cover patches and dominated the balance in early and mature patch stages,

while facilitation became significant only in degraded stages of high-cover patches (Fig. 5, Supplementary material Appendix 1 Fig. A1). This asseveration is strengthened given the high statistical power (0.71–0.77) of our experiments to detect medium size effects (f = 0.25) for the interaction effect under split-plot designs (Faul et al. 2007). In addition, since we have conducted two independent field experiments running in different growing seasons, the probability of detecting a significant interacting effect in at least one of them is higher than 0.93.

The significance and persistence of competition effects (–0.66 – –0.37) on the interaction balance across all patch stages suggests that belowground competition is very intense, even in bare soil or early stages of high-cover patches. The intense natural competition occurs even under a possible lowering of it associated to the soil disturbance applied to equalize the initial conditions for both competition treatments. While previous findings for Patagonian steppes support the role of aerial facilitation and nutrient enrichment promoted by shrubs on grass seedlings (Soriano and Sala 1986, Aguiar and Sala 1994, Armas et al. 2008), there is limited knowledge regarding the role of belowground competition and the net balance of biotic interactions across all patch types of this mosaic. Intense belowground competition across vegetation patches with large differences in aboveground plant biomass (Cipriotti and Aguiar 2005, Golluscio et al. 2005) can be explained by high roots biomass, at least at the upper 30 cm (Aguiar et al. 1992, Leva et al. 2009). This can be a distinctive aspect of the spotted mosaics compare to banded mosaics. In the former, roots are able to colonize and intensively explore high-cover patches as well as bare ground, integrating both mosaic phases.

The positive effects during the degradation of high-cover patches described in our study differ from the often reported woody facilitation on grass recruitment (i.e. emergence, survival and growth of seedlings) previously observed in this study site (Aguiar et al. 1992, Aguiar and Sala 1994) and in many other arid ecosystems (Pugnaire et al. 1996, Maestre et al. 2003). The facilitative effects on the number of tillers and flower culms in transplants located in degraded stages of high-cover patches are possibly related to a high nitrogen pulse associated with the shrub removal and a consequent mineralization pulse of the high organic matter pool in the soil underneath (Armas et al. 2008). We think that the experimental effect of killing shrub may be different to the natural senesce and death of shrubs, and then a slower rate of nutrient liberation through decomposition controlled by the inter-annual variation of rainfall is expected to occur (Yahdjian and Sala 2010). However, the soil nitrogen content measured in the high-cover patches formed by mature living shrubs, dead shrubs and shrub debris did not show differences among them (Cipriotti 2006), supporting our previous inferences about the role of facilitation during degradation. On the other hand, our results show that despite the well documented changes in environmental variables from microsites associated with woody plants (i.e. shade, evaporation rate, water content, fertility islands, etc. Vetaas 1992, Breshears et al. 1998), grass seedling survival was constrained by belowground competition in the different experimental mosaic phases tested (Fig. 1b, 3b). Moreover, we were unable to detect any net positive effect from shrubs
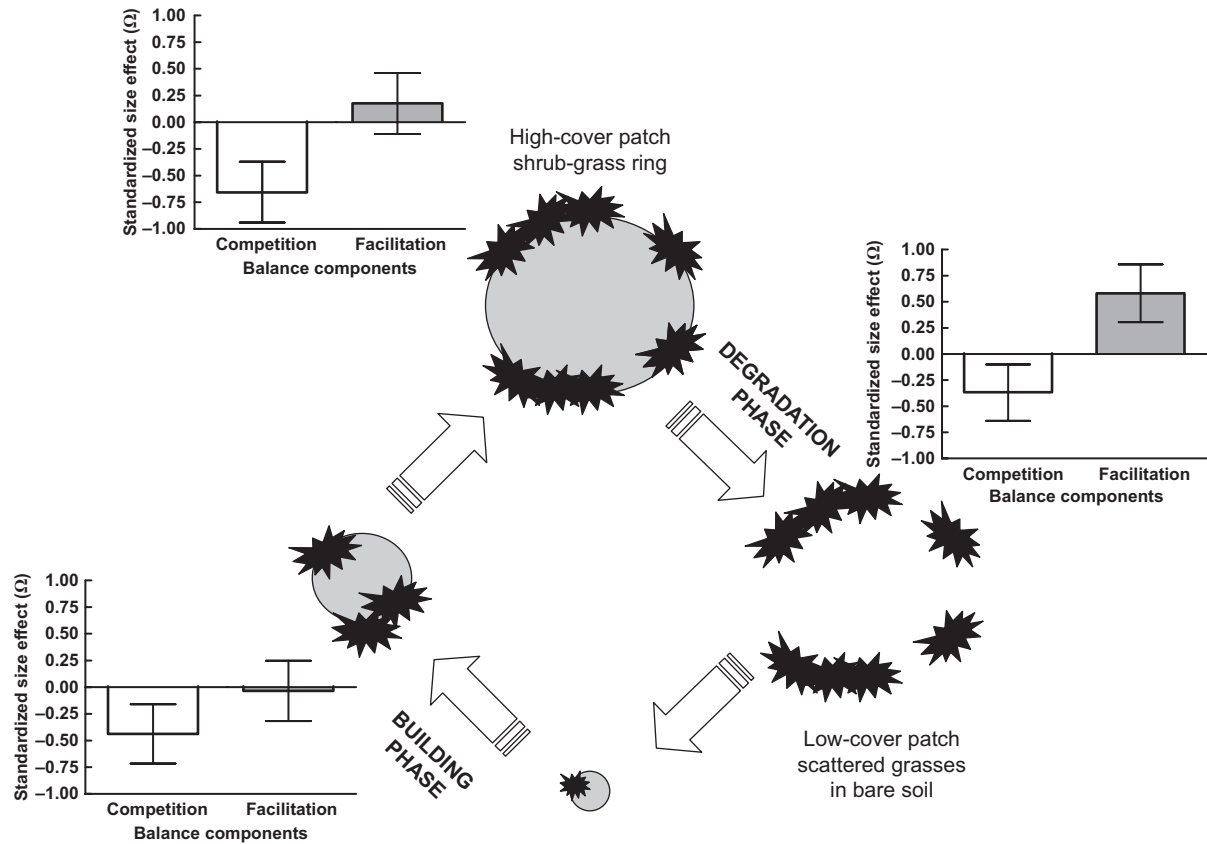
Figure 5. Scheme of the cyclic succession linking the different phases of the spotted vegetation mosaic proposed by Soriano et al. (1994) for the occidental grass–shrub Patagonian steppes. Stages and phases are represented from above. Gray circles represent shrubs, while black shapes represent tussock grasses. Inset graphs showed both components ($\Omega-$ and $\Omega+$) of estimated biotic net interactions balance for three different stages of high-cover patches along the cyclic succession (i.e. early, mature and degraded). Wide bars indicate the average of standardized mean differences and narrowed hated vertical bars indicate the upper and lower approximated limits of confidence interval (95%).

on grass recruitment during the building phase, as was previously suggested (Soriano and Sala 1986, Aguiar et al. 1992). But, there was a marginal increase of grass survival in young shrubs and under the natural competition treatment (Fig. 2a). This subtle positive effect could be explained by the occurrence of hydraulic lift promoted by young shrubs with roots in top and bottom soil layers (Muñoz et al. 2008, Armas et al. 2010, Prieto et al. 2011). These results indicate the importance of calculating the net interaction effects, in order to fully capture the consequences of the single processes studied. We suggest that net interaction balance estimation is a critical aspect which allows for the integration of interactions in a community context.

In the context of the evaluation of biotic interactions in arid ecosystems, the role of climatic variability should be addressed. The current absence of positive effects from adult shrubs to grass seedling survival in both experiments (building and degradation) may be explained by the high annual rainfall which occurred in both years ($> 240$ mm year$^{-1}$ versus annual mean $= 153$ mm year$^{-1}$), as wet years in arid ecosystems can mask potentially facilitative effects (Kitzberger et al. 2000, Tielbörger and Kadmon 2000, Riginos et al. 2005, Valiente-Banuet and Verdú 2008). Similarly, differences found in the significance of the negative effects between

both experiments on seedling emergence would be explained by rainfall variability during the cold season between growing seasons (2002/2003 and 2003/2004). However, previous studies conducted in the Patagonian steppes suggest that it is not common to find significant effects of belowground competition on the emergence of grass seedlings, since seedling emergence occurs predominantly during autumn and winter, when the main environmental driver is low temperature and soil water content is at its highest (Rotundo and Aguiar 2005, Cipriotti et al. 2008). Results from both field experiments reinforced the hypothesis that plant survival was the most sensitive demographic bottleneck affected by belowground competition, at least when no extreme water deficits occur, which are likely in dry years in the Patagonian steppes (annual rainfall $< 130$ mm).

In studies of plant–plant interactions, the observed responses can be species specific. Our study case is not the exception and we have abundant eco-physiological information to support main differences among co-dominant shrub and grass species within each life form. The three dominant shrub species in Patagonian steppes differ in shrub canopy structure, root architecture, phenology, leaf traits, physical and chemical defenses against herbivory, N-fixation capacity (Fernández-Alduncin and Paruelo 1988, Cavagnaro et al.

2003, Golluscio et al. 2006, Bucci et al. 2009). Similarly occurs among grass species (Adler et al. 2005, Oyarzábal et al. 2008, Rotundo and Aguiar 2008, Verón et al. 2011, Leva et al. 2013). In addition, our chosen phytometer (*Bromus pictus*) is the most drought tolerant species at the seedling stage from Patagonian steppes (Rotundo et al. 2006). Hence, belowground competition effects here reported, may be higher for other grass species and in consequence the facilitative effects would result more important for them. Summarizing, we cannot assure that net interaction balance here estimated across different stages of high-cover patches based on *B. pictus* responses in patches conformed by the shrub species *Mulinum spinosum* does not vary for other co-dominant shrub or grass species.

Based on the findings of our study we suggest that in spotted mosaics the maintenance results from more complex interactions of mechanisms than originally proposed. In addition to competition and facilitation, a new model needs to include seeds load that compensates the negative outcome of the interactions balance, and the inter-annual rainfall variability that may switch the balance. Because the differential seed distribution among vegetation patches in windy environments (Puigdefábregas et al. 1999, Pueyo et al. 2008, Giladi et al. 2013), the effect of the net outcome of the biotic interaction balance on grass recruitment is probably secondary and controlled by the inter–annual climate variability. Therefore, we propose that shrubs are involved in two different pathways during the building phase of high-cover patches, according to climate conditions. Firstly and most important, shrubs trap and retain grass seeds during dispersal, promoting higher recruitment near them, even under a negative interaction balance. This pathway is independent of climate conditions. Density of grass seeds near the shrubs (i.e. periphery of shrub circumference) can be four times higher than seed density in low-cover and bare soil patches (Aguiar and Sala 1994, 1997, Fernández-Alduncin et al. 2002). Secondly, in dry years (not covered in this two-year study) shrubs can facilitate the recruitment of grass seedlings under its canopy by reducing the atmospheric demand for water (Soriano and Sala 1986, Aguiar et al. 1992), but this effect can be hindered during wet years (our results). Finally, during the degradation phase of high-cover patches we cannot discard belowground facilitative effects associated to nutrients enrichments, especially in wet years (Armas et al. 2008, Austin 2011).

Alternatively to the balance of biotic interactions, the most frequent mechanism proposed to explain the maintenance of two-phase mosaics is a positive feedback between vegetation and resources, basically through the lateral water redistribution (run-off and run-on) (Thiéry et al. 1995, Galle et al. 1999, Ludwig et al. 1999, Dunkerley 2002). This occurs especially in banded mosaics, areas of low or null plant cover located on gentle slopes, with sealed or crusted soils, and with intense rainfall events, which promote water run-off to areas of high plant cover with high infiltration rates that act as barriers to the lateral water redistribution (Dunkerley and Brown 1999, Valentin et al. 1999, Wu et al. 2000, Imeson and Prinsen 2005, Puigdefábregas 2005). On the contrary, in the grass-shrub Patagonian steppes the vegetation is spatially organised as a two-phase spotted mosaic located on a flat terrain with coarse sandy soils, and where most rainfall pulses are lower than 10 mm (Golluscio et al. 1998). In this case, water run-off is insignificant and therefore there is no resource redistribution between mosaic phases. Two-phase spotted mosaics have also been described in African, Mediterranean and other American ecosystems (Couteron and Kokou 1997, Fuentes et al. 1984, García-Fayos and Gasque 2002, Pazos et al. 2010). We suggest that in spotted mosaics, there is significant seeds redistribution among vegetation patches that can be more important than plant interactions and/or resource distribution to explain the mosaic maintenance.

During past decades, the role of plant facilitation has been proposed as a structuring force in stressed vegetation communities (Callaway 1995, Holmgren et al. 1997, Maestre and Cortina 2004, Brooker et al. 2008). However, the role of facilitation in arid ecosystems is still a subject of debate (Maestre et al. 2005, Lortie and Callaway 2006). In addition, hypotheses regarding the balance between plant competition and facilitation as a driver of gap succession dynamics and the maintenance of two-phase vegetation mosaics were the working mechanism in many modelling approaches (Klausmeier 1999, Couteron and Lejeune 2001, HilleRisLambers et al. 2001, van de Koppel et al. 2002, Kéfi et al. 2007). However, field experiments able to disentangle negative and positive components of the interaction balance to test their effects on the maintenance of complex spatial organisations of vegetation are rare (but see Schenk and Mahall 2002, Alados et al. 2006, Barbier et al. 2008). Our findings support the notion that interaction balance is rather variable in space and time (Rousset and Lepart 2000, Tielbörger and Kadmon 2000, Tewksbury and Lloyd 2001, Miriti 2006, Schiffers and Tielbörger 2006, Dohn et al. 2013). We suggest that patch dynamics results from a more complex array of processes, in which other mechanisms besides biotic interaction balance allow for the maintenance of vegetation mosaics (e.g. seed trapping) and where the inter-annual climate variability can tip the net outcome of the interaction balance.

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Supplementary material (available online as Appendix oik.01758 at ＜www.oikosoffice.org/readers/appendix＞). Appendix 1.