

# A complex network of interactions controls coexistence and relative abundances in Patagonian grass-shrub steppes

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## Summary

**1.** The coexistence of shrubs and grasses has intrigued ecologists for the past century, and the conundrum of shrub–grass coexistence is at the core of debates on the functioning of semi-arid ecosystems. Here, we explored how the interplay of root competition and facilitation between life-forms at different life stages and demographic bottlenecks controls the long-term coexistence of multiple shrub and grass species in semi-arid Patagonian steppes.

**2.** We used the spatially explicit and individual-based simulation model DINVEG that integrates the abundant information on the semi-arid Patagonian grass–shrub steppes to test six competing hypotheses on the mechanisms that govern the coexistence and relative abundances of several grass and shrub species. The structurally realistic model allows for a direct comparison of model outputs with a wide range of previously collected field data.

**3.** We formulate three competing hypotheses on vertical root overlap between grasses and shrubs (no overlap, partial overlap, full overlap) that were crossed with two hypotheses on asymmetric shrub–grass facilitation (with and without). Each of the six variants of DINVEG were tested in their ability to generate dynamics in accordance with detailed field data, and we performed global sensitivity analyses to reveal demographic bottlenecks and controls.

**4.** The hypothesis combining partial vertical root overlap with no facilitation was the most likely hypothesis given the data. It created demographic bottlenecks in recruitment and emergence that controlled grass and shrub abundances, respectively, and only this hypothesis generated a situation where grasses controlled shrub abundances (by limiting shrub recruitment), but where grass abundance was only weakly controlled by shrubs. Internal water dynamics generated reduced competition of shrubs to neighbored grasses that was sufficient to produce the observed ring of grasses around shrubs, and most of the parameterizations that approximated the observed species-specific abundances were able to reproduce the observed equilibrated spatial patterns of the mature community.

**5. Synthesis.** We found a complex network of mechanisms that controlled growth-form coexistence and relative abundances in the Patagonian grass-shrub steppe where both, demographic bottlenecks and species interactions across life-forms, species and life stages were important. Our study points to alternative mechanisms of shrub–grass coexistence that may play an important role in dry grasslands and steppes where fire and herbivory are not key drivers and provide an avenue to detect them.

**Key-words:** arid ecosystems, biotic interactions, competition, determinants of plant community diversity and structure, facilitation, individual-based models, niche separation, plant demography, plant–plant interactions

## Introduction

The shrub–grass balance is at the core of debates on the functioning of semi-arid ecosystems (House *et al.* 2003; Sankaran, Ratnam & Hanan 2004; Higgins, Scheiter & Sankaran 2010;

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Baudena, D'Andrea & Provenzale 2010). Understanding this issue is important for predicting how semi-arid systems respond to climate change and human impact (Reynolds *et al.* 2007; Tietjen & Jeltsch 2007). Coexistence between growth forms is one of the conundrums of mixed woody–herbaceous plant communities, and several hypotheses have been put forward to explain it (House *et al.* 2003; Sankaran, Ratnam & Hanan 2004). Briefly, there are two contrasting sorts of controls evoked to explain shrub/tree–grass coexistence, bottom-up controls (resources: water, nitrogen, etc.) and top-down controls (e.g. fire, herbivory, etc.). The first and most studied bottom-up hypothesis is that of niche separation. Walter's hypothesis (1971), which is a special case of the niche differentiation theory, assumes that water is the main limiting resource and states that shrubs have, compared with grasses, deeper roots and therefore use different soil water resources. While several field studies supported Walter's hypothesis (e.g. Sala *et al.* 1989; Golluscio, Sala & Lauenroth 1998; Ward, Wiegand & Getzin 2013), there is also substantial evidence against this hypothesis (Higgins, Bond & Trollope 2000; House *et al.* 2003; Sankaran, Ratnam & Hanan 2004; Bond 2008).

Alternative hypotheses on controls of shrub/tree–grass coexistence focus on demographic bottlenecks caused by disturbances due to top-down controls such as grazing, fire or stochastic extreme drought events that limit growth and/or recruitment (Nano & Clarke 2010), or balance between negative and positive plant interactions (Aguiar, Soriano & Sala 1992; Maestre, Bautista & Cortina 2003). These mechanisms safeguard against one life-form gaining complete dominance over the other (e.g. Higgins, Bond & Trollope 2000; Jeltsch, Weber & Grimm 2000). For example, grazing or fire has been identified as an important top-down control that suppresses the woody component in humid savannas (Bond 2008). Alternatively, a storage effect in combination with climatic variability may stabilize coexistence between life-forms by varying competitive dominance over time (Chesson 2000; Adler *et al.* 2006).

Modelling studies on tree–grass coexistence suggest that simple single-mechanism explanations based on only one type of control may not be sufficient to explain the patterns observed in real systems and that such simple explanations failed to build a comprehensive and general understanding of growth-form coexistence (e.g. Wiegand, Saltz & Ward 2006; Scheiter & Higgins 2007; Bond 2008; Meyer, Wiegand & Ward 2009; Baudena, D'Andrea & Provenzale 2010; Higgins, Scheiter & Sankaran 2010). For example, Baudena, D'Andrea & Provenzale (2010) included life stage structure in a deterministic tree–grass model and assumed that a tree could be out-competed by grasses only as seedling. Stable tree–grass coexistence was possible, even in the absence of explicit niche separation and disturbances. Other studies have emphasized the role of patch dynamics in a heterogeneous space as a key to explain the coexistence of both life-forms (Meyer, Wiegand & Ward 2009). Sankaran, Ratnam & Hanan (2004) provided a comprehensive review on the different assumptions and processes hypothesized to explain coexistence and the relative productivity and cover of the woody and grass components in savannas. They suggested a more detailed approach that explicitly considers demographic and competitive

effects at different life stages of grasses and woody vegetation to capture the potentially complex competitive balance in real systems. Such an integrative framework on plant demography is a promising avenue to reach a better understanding about the coexistence of grass and woody vegetation (Sankaran, Ratnam & Hanan 2004; Bond 2008).

While most modelling studies on coexistence of grass and woody plants focused on two functional groups (trees or shrubs vs. grasses) and often in the context of disturbances (top-down controls such as fire or herbivory), a more challenging task is to explain the simultaneous coexistence and relative abundances of multiple grass and shrub species that interact (positively and/or negatively) in a spatial context and at different life stages. In addition, multispecies arid steppes are in general characterized by a remarkable spatial structure which includes strong clumping or banding of vegetation (e.g. Aguiar & Sala 1999). For example, the Patagonian steppe is characterized by a ring of grasses in the immediate neighbourhood of shrubs that is not altered by grazing (Soriano, Sala & Perelman 1994; Cipriotti & Aguiar 2005), whereas adult shrubs showed a surprising lack of spatial structures (Golluscio *et al.* 2005; Wiegand *et al.* 2006).

In this study, we used the spatially explicit and individual-based simulation model DINVEG that integrates the abundant information on the semi-arid Patagonian grass–shrub steppes (Cipriotti *et al.* 2012) to test six competing hypotheses on the mechanisms that govern the coexistence and relative abundances of several grass and shrub species. DINVEG assumes that most species interactions in this water-limited system are mediated by soil water dynamics and consider different life stages of shrubs and grasses to elucidate the role of interactions during the seedlings stage (Sankaran, Ratnam & Hanan 2004). In its current version, DINVEG did not include fire and grazing effects, because there is not sufficient scientific support for the role of both top-down controls on the natural plant community dynamics in the Patagonian steppes previous to livestock expansion (see *Materials and methods*). The structural realism of DINVEG allows for direct comparison of model outputs with a wide range of previously collected field data measured at different levels of organization (Cipriotti *et al.* 2012). Use of diverse field data ('patterns') is the key for hypothesis testing based on recent methods of inverse model parameterization and model selection (Wiegand *et al.* 2003; Wiegand, Revilla & Knauer 2004; Grimm *et al.* 2005; Hartig *et al.* 2011; Martínez *et al.* 2011; Cipriotti *et al.* 2012). This allows us to rank competing hypotheses and understand how the interplay of root competition between life-forms at different life stage, facilitation and demographic bottlenecks controls the long-term coexistence of multiple grass and shrub species in the Patagonian steppes.

We formulate three competing hypotheses on vertical root overlap between grasses and shrubs (no overlap, partial overlap and full overlap) that were crossed with two hypotheses on above-ground shrub–grass interactions (with and without asymmetric aerial facilitation). For each of these six hypotheses, we searched the ecologically feasible 'demographic' parameter space (i.e. parameters governing emergence, recruitment, growth, reproduction and mortality) to find the combination of model parameters that yield simultaneous agreement with the

observed patterns. A hypothesis that failed in one or more patterns was not in agreement with the observations and rejected.

## Materials and methods

### STUDY AREA

The model was developed and parameterized for the semi-arid grass–shrub steppes from the Occidental District of the Patagonian Phytogeographic Province (León *et al.* 1998). This vegetation district expands ca. 150,000 km<sup>2</sup> between the Sub-Andean and the Central District of Patagonia. Most of the information included in our model was obtained in the INTA Rio Mayo Experimental Field Station and neighbouring ranches, Chubut, in South Western Patagonia (45°41'S, 70°16'W, 500 m a.s.l.), Argentina. The mean annual rainfall at this site is 153 mm ( $n = 37$ ), it ranges between 47 and 230 mm (driest and wettest year in the record, respectively), and ca. 73% falls during the autumn and winter (March to September; Jobbágy, Paruelo & León 1995). Mean annual temperature is 8.4 °C, with mean monthly temperature ranging between 2 °C and 14 °C, in July and January, respectively (Paruelo *et al.* 1998). Strong winds blow predominantly from west to east. Soils have an upper sandy layer with 50% of cobbles and pebbles, and a cement-like stony layer (i.e. CO<sub>3</sub>Ca) at 0.45–0.6 m deep (Paruelo, Aguiar & Golluscio 1988).

In these steppes, almost 50% of soil cover is bare ground and the rest is mostly covered by tussock grasses (26 ± 5% SE), shrubs (12 ± 4%) and litter 5% (Golluscio, León & Perelman 1982; Fernández-Alduncin, Sala & Golluscio 1991). The dominant tussock grass species are *Pappostipa speciosa* Trin. et Rupr., *P. humilis* Vahl. and *Poa ligularis* Nees. ap Steud., whereas *Bromus pictus* Hook. is a sub-dominant bunch grass species. The dominant shrub species are *Mulinum spinosum* Cav. (Pers.), *Senecio filaginoides* AD. and *Adesmia volckmanni* Philippi. Above-ground primary production ranges between 10 and 120 g<sup>-2</sup>·year<sup>-1</sup> (mean 56 g<sup>-2</sup>·year<sup>-1</sup>; Jobbágy & Sala 2000). Grasses and shrubs account for 53% and 43% of total ANPP, respectively, while a heterogeneous group of forbs account for the rest. Unlike in other shrub–grass systems, fire is basically absent (due to low biomass and the specific climate conditions), and the density of native herbivores was very lower in comparison with the current (last 120 years) domestic sheep livestock (Oesterheld, Sala & McNaughton 1992). Thus, fire and grazing are not key processes that control natural plant community dynamics in the Patagonian steppes.

Soriano, Sala and Perelman (1994) postulated a community dynamics driven by facilitation (e.g. due to reduced evaporation close to shrubs; Soriano & Sala 1986), underground competition for soil moisture and seed distribution (Aguiar, Soriano & Sala 1992; Aguiar & Sala 1994, 1997). The hypothesis stated that the strong winds accumulate seeds around shrubs and that asymmetric facilitation of grass seedlings at microsites close to shrubs produces the 'rings' of grasses around shrubs (Soriano & Sala 1986; Aguiar, Soriano & Sala 1992). However, for mature grass tufts, competition for water becomes intense, outweighs facilitation and prevents recruitment of new individuals in the ring. After age (or drought) driven mortality of the shrub, the grass ring finally disintegrates.

### MODEL OVERVIEW

To fulfil our objectives and to take advantage of the existing field observations, the DINVEG model integrates the following elements: (i) it considers the most important functional types in steppe (represented by the dominant shrub and grass species), (ii) it describes

different life stages and includes the main demographic processes (i.e. seed dispersal, emergence, recruitment, growth, reproduction and mortality), (iii) it is able to accommodate different scenarios of vertical root overlap between shrubs and grasses, and (iv) it is spatially explicit to test whether asymmetric aerial facilitation is driving the community dynamics and spatial organization as postulated by Soriano, Sala and Perelman (1994). Cipriotti *et al.* (2012) provides a detailed description of the model and the method of inverse parameterization (based on the version with partial root overlap and aerial facilitation). A model description following the standard ODD protocol (Overview, Design concepts, Details) for individual-based models (Grimm *et al.* 2010) is provided in Appendix S1 in Supporting Information.

### MODEL STRUCTURE AND RESOLUTION

DINVEG simulates the spatial and temporal dynamics of three grass species (*P. speciosa*, *Poa ligularis* and *B. pictus*) and the three shrub species (*M. spinosum*, *S. filaginoides* and *A. volckmanni*). To completely describe the life cycle of grasses and shrubs, the model contains empirical rules on seed dispersal and seed bank (rule 1), emergence (rule 2), seedling recruitment (rule 3), facilitation (rule 4), growth (rule 5), competition for water (rule 6), competition for space (rule 7), mortality (rule 8) and seed production (rule 9) (Appendix S1; Fig. S1). Most of these processes are conditioned by soil water content at different layers and plant transpiration which is described by the soil water balance simulation model DINAQUA (Paruelo & Sala 1995).

The model has four types of objects: grass tufts, shrubs, soil seed bank and soil water. Soil water content is simulated for six layers (the thickness of each soil layer is 0.1 m) to allow for different levels of vertical root overlap and to describe the water dynamics in the soil. Space is represented with a 50 × 50 m grid of homogeneous environmental conditions, simulating an area of 2500 m<sup>2</sup>. The cell size is 0.2 × 0.2 m (spatial resolution), which is the approximate size of one grass tuft, but shrubs may occupy several cells (max 21 cells).

### MODEL VARIABLES

Grass tufts were characterized by species, location ( $x$ ,  $y$  coordinates), age, stage (seedling, adult, dead), above-ground plant biomass (g) and a growth memory (a record of the individual growth during the last 3 years). For adult plants, there are fixed values of root biomass in each soil layer according to the plant biomass of adults (Paruelo & Sala 1995). Shrubs were additionally characterized by their size (number of cells) and neighbourhood (the area immediately adjacent to the shrub in which shrubs may exert facilitation to grass seedlings; i.e. the grass ring). The soil seed-bank records for each cell and species the number of viable seeds (and its decay) and seedlings. Soil water is estimated by DINAQUA for each cell at six different layers as the volumetric soil water content. These output variables allow for a direct comparison with the following field observations: plant cover, plant density, ANPP (measured for all plants, only shrub, only grass, and for individual species), and uni- and bi-variate spatial patterns (i.e. spatial pattern of shrubs and spatial grass–shrub association) to test for the observed spatial organization of the vegetation (for details see Appendix S2; Table S2).

### WATER DYNAMICS, DEMOGRAPHY AND COMPETITION

Each hypothesis was implemented as a version of DINVEG. Each model version was run for a given model parameterizations in monthly time steps (to accommodate seasonal dynamics of tempera-

ture and rainfall) during 200 years. All simulations were conducted under a typical climate series (i.e. MAP = 153 mm year<sup>-1</sup>; CV = 33%; Appendix S1). Based on the rainfall and temperature data and the root overlap hypothesis, DINAQUA calculates for each cell the monthly transpiration of grasses, shrubs and the soil water content of six soil layers in dependence on the biomass of grasses and shrubs in the focal cell and its immediately 3 × 3 cell neighbourhood. This neighbourhood considers the observed lateral root distribution (Aguilar & Sala 1994; Leva, Aguilar & Oesterheld 2009). Interactions between plants occurred through soil water as an intermediary (cf. Goldberg *et al.* 1999). If more plant biomass is concentrated in a particular cell or individual, more water will be transpired and less water remains in soil layers. This indirectly controls seedling emergence, recruitment, growth and mortality.

Each life-history event occurred during particular months according to the schedule observed in the field. Emergence and recruitment depended on the water content in specific soil layers, and growth and seed production on plant transpiration, both calculated by DINAQUA. Plant mortality was modelled with a species-specific annual mortality rate which increased under water stress. Seed dispersal followed simple dispersal kernels parameterized from field data that considered the dominant wind direction.

## MODEL EVALUATION

### Alternative models

The three alternative hypotheses (R1, R2 and R3) about vertical root overlap of shrubs and grasses were implemented directly in DINAQUA. The 'root segregation hypothesis' (R1) assumes that grass and shrub roots do not overlap. Grass roots occupied the upper soil layers (0–0.3 m), while shrub roots occupied the lower soil layers (0.3–0.6 m). The 'partial root overlap hypothesis' (R2) assumes vertical root overlap at an intermediate soil layer (0.2–0.4 m), but grasses have exclusive access to the upper soil layer (0–0.2 m) and shrubs to the lower soil layer (0.4–0.6 m). The 'root overlap hypothesis' (R3) assumes that grass and shrub roots overlap at the intermediate and upper soil layer (0–0.4 m).

To model asymmetric aerial facilitation from shrubs to grasses (due to reduced evaporation through shrub shade and wind protection; hypothesis F+), we assumed that grass seedlings located in the neighbourhood of large shrubs (i.e. biomass >500 g) had recruitment probabilities that were elevated with factor  $fac = 0.5 + \text{ShrubBiomass}/1000$  (Cipriotti *et al.* 2012). For the range of observed shrub biomasses, this factor ranged usually between 1 and 2, as observed in the field (Aguilar & Sala 1994). The alternative hypothesis of no asymmetric aerial facilitation (F0) assumes  $fac = 1$  for all shrubs.

### Model parameterization

Each version of the DINVEG model contained for each species 17 model parameters (Table S1; Appendix S1). Because the model was structurally realistic, we could directly or indirectly estimate the values of 12 parameters from published data or field measurements (Cipriotti *et al.* 2012). However, five parameters that governed emergence ( $t_c$ ), recruitment ( $t_r$ ), growth ( $t_g$ ), reproduction ( $t_s$ ) and mortality ( $p_{mk}$ ) were uncertain. We assumed a sigmoid relationship between the probability of a demographic event and soil water contents or plant transpiration (see Fig. S2; Appendix S1). This was carried out in a way that the event occurred more frequently if the parameter value was lower. We varied these parameters over their ecologically feasible

range and searched for each model version the combination of model parameters that produced agreement between observed and simulated patterns (Wiegand *et al.* 2003; Wiegand, Revilla & Knauer 2004; Grimm *et al.* 2005; Martínez *et al.* 2011; Cipriotti *et al.* 2012). This allowed us to model aspects of the system that are known, but allow the empirical patterns to 'speak for themselves' with regard to aspects that are unknown (Nelson, McCauley & Wimbert 2004).

We systematically sampled the parameter space (five demographic parameters per species) using a Latin hypercube design (McKay, Beckman & Conover 1979). This stratified sampling method results in equal probabilities for each parameter (i.e. uninformative priors in a Bayesian framework). In total, we tested for each model version 10 000 different model parameterizations. All simulations were initialized with the same vegetation plot that was representative for Patagonian grass-shrub steppes in good condition (i.e. not degraded by overgrazing) under a typical climate series (for details on generation of initial condition, see Appendix S1). DINVEG was then run for 200 years to approach a stochastic equilibrium (see Cipriotti *et al.* 2012, their fig. 5), and the data from year 200 were used for comparison with field data.

We used multiple rejection filters (Wiegand, Revilla & Knauer 2004; Hartig *et al.* 2011) to divide the 10 000 parameterizations into two classes – likely and unlikely. The data on plant cover, plant density and ANPP that characterized the vegetation state in a non-spatial way (called in the following 'main patterns') were used as filters. To this end, we tested whether the value of a simulated variable was within conservatively wide envelopes of the corresponding field data (i.e. mean ± 2 SD). This resulted in a total of 14 independent filters (Table S2; Appendix S2). We accepted only parameterizations for which the simulated values of all 14 filters were located inside the observed ranges. Note that, a given filter rejects only parameterizations that yield a clearly unlikely model output and that the power of the multiple filters is grounded in the fact that each filter disregards unlikely behaviour in a different aspect of the community dynamics (Wiegand, Revilla & Knauer 2004).

### Model selection

A hypothesis was rejected if not a single parameterization was accepted. In this case, the model produced at least in one variable a clearly unlikely model output which points to a structural deficiency. A hypothesis was more likely if the number of accepted parameterizations was larger. This is because the acceptance ranges for individual filters were conservatively wide and a model that incorporates the 'correct' internal mechanisms should be robust against small changes in the parameters and yield many accepted parameterizations. On the other hand, if all hypotheses yield many accepted parameterizations, our data are not sufficient to distinguish among competing hypotheses. In analogy to Bayesian analyses, the accepted parameterizations represent the posterior sample and can be used to assess parameter uncertainty, correlations between parameters and marginal posterior densities (i.e. the probability assigned to the different possible values for the respective parameter).

### Model analysis

Because most demographic events in the model were triggered by soil water, we suspect the existence of demographic bottlenecks (Cipriotti *et al.* 2012). To identify such bottlenecks, we first estimated, based on the 10 000 parameterizations of the selected model, the rank correlation between the species (and grass and shrub) abundances and all 30 model parameters (Cipriotti *et al.* 2012). This global sensitivity

analysis allowed us to assess which parameters had the strongest effects on each species and life-form (i.e. grasses and shrubs). In a second step, we assessed which of the parameters had large correlation coefficients and strongly restricted (marginal) posterior range. A restricted acceptance range combined with high sensitivity points to a bottleneck. We also checked for correlations among parameters on accepted parameterizations to detect possible compensatory effects (e.g. good match can be achieved by high emergence and low survivorship or low emergence and higher survivorship).

### Model validation

We verified and validated the model in three ways. First, we tested whether the posterior densities of the demographic parameters yield biologically reasonable values. Secondly, we used the independent data on the spatial distribution of the six species (i.e. the univariate spatial pattern of shrubs and the spatial associations of grasses around shrubs; Table S2; Appendix S2) to test the accepted parameterizations that passed the filters related with the (non-spatial) observed vegetation state (see Appendix S3). Finally, we mimicked with DINAQUA the conditions of field measurements to directly compare simulated and field data based on daily volumetric soil water content (SWC) (see Appendix S3).

### Results

The likelihood that a single pattern (e.g. total shrub or grass abundance) was matched for a given model parameterization was relatively high; however, the likelihood that multiple patterns were matched for grasses and shrubs together was substantially lower (Table 1 and Fig. 1). In general, we observed a strong inverse relationship between shrub and grass cover (Fig. 1), and among the densities of the different grass and shrub species (Figs S3 and S4; Appendix S3). This was expected because the 10 000 parameterizations cover the ecologically feasible parameter space and include also parameterizations producing unrealistic dominance of species or life-forms. However, the observed balance between life-forms

(Fig. 1) or species (Figs S3 and S4; Appendix S3) was difficult to attain, and the different hypotheses were not equally successful in this.

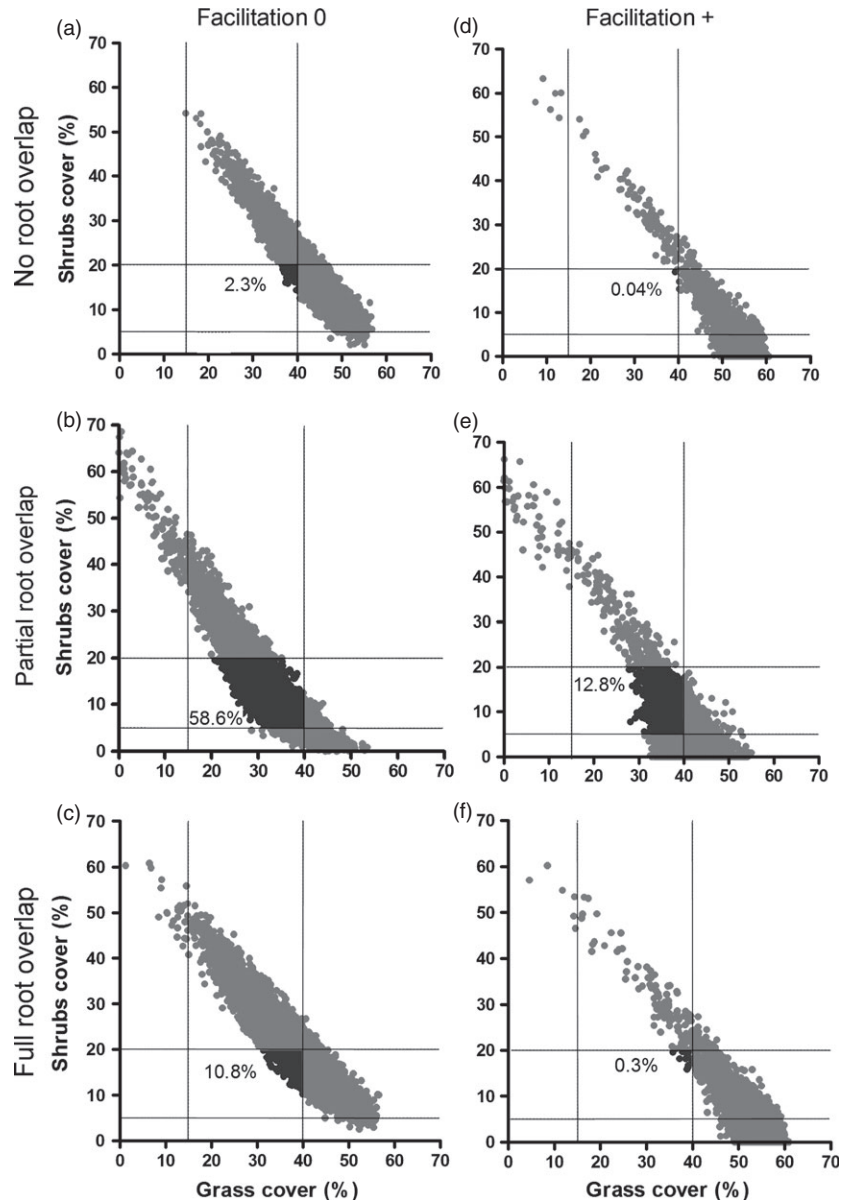
### EVALUATION OF HYPOTHESES ON SHRUB-GRASS ROOTS OVERLAP AND FACILITATION

The six competing hypotheses differed substantially in their capability to describe the multiple characteristics of the Patagonian grass-shrub steppe (Table 1). Partial vertical root overlap between grasses and shrubs without facilitation (hypothesis R2\_F0) generally received more support from the field data (Table 1); in almost all cases, it yielded the highest proportion of accepted parameterizations. Somewhat unexpectedly, the model variant with aerial facilitation (R2\_F+) performed poorer, especially in matching grass and shrub cover and grass and shrub ANPP (Table 1). Similarly, full vertical root overlap without facilitation (hypothesis R3\_F0) yielded one parameterization that produced outputs in agreement with the field observations (Table 1). We can therefore not fully reject these hypotheses, but hypothesis R2\_F0 received clearly the highest support from the data. In contrast, we could reject the 'no overlap' hypotheses (R1\_F0 and R1\_F+) and the hypothesis with full root overlap and facilitation (R3\_F+), because none of the 10 000 parameterizations produced model outputs in accordance with the observed data (Table 1).

Figure 1 illustrates one reason for success or failure of the different hypotheses. The best hypothesis R2\_F0 did well in matching the observed grass and shrub cover simultaneously, and 58% of all parameterizations were able to do so compared with 12.8 and 10.8% for model R2\_F+ and R3\_F0, respectively (Fig. 1b and Table 1). Hypothesis R2\_F0 yielded also a good match for the other patterns; this becomes evident when looking at the ratio of parameterizations that matched a given grass and shrub pattern relative to that which matched

**Table 1.** Summary of the inverse parameter estimation and evaluation of the six alternative variants of DINVEG model based on the main patterns. Numbers indicate the percentage of the 10 000 parameterizations for which the simulated output variables was within the observed field range. The six alternative model versions are related to hypotheses on underground competition (explicit vertical root structure: R1, R2 and R3) and facilitation (F0 and F+, without and with facilitation effect). Bold font indicates lumped patterns for grasses and/or shrubs

Main patterns	No overlap (R1)		Partial overlap (R2)		Full overlap (R3)	
	F0	F+	F0	F+	F0	F+
Grass cover	50.9	2.1	86.9	34.3	49.5	2.4
Shrub cover	38.4	9.8	59.8	13.5	50	14.8
<b>Grass and shrub cover</b>	<b>2.3</b>	<b>0.04</b>	<b>58.6</b>	<b>12.8</b>	<b>10.8</b>	<b>0.3</b>
Grass abundance	49.7	64.4	23.3	43.2	51.9	68.7
Shrub abundance	11.4	16.4	42.7	41.1	17.7	22.1
<b>Grass or shrub abundance</b>	<b>49.8</b>	<b>40.3</b>	<b>50.4</b>	<b>73.5</b>	<b>17.7</b>	<b>46.5</b>
<b>Grass and shrub abundance</b>	<b>6.1</b>	<b>4.9</b>	<b>15.6</b>	<b>12.8</b>	<b>13.8</b>	<b>9.7</b>
Grass-specific abundance	22.1	0.7	7.8	9.9	11.2	1.1
Shrub-specific abundance	1.5	0.2	3.9	2.1	2.3	0.3
<b>Grass- or shrub-specific abundance</b>	<b>14.4</b>	<b>1</b>	<b>11.8</b>	<b>11.9</b>	<b>13.9</b>	<b>1.5</b>
<b>Grass- and shrub-specific abundance</b>	<b>0.04</b>	<b>0.02</b>	<b>0.51</b>	<b>0.22</b>	<b>0.07</b>	<b>0</b>
<b>Grass and shrub ANPP</b>	<b>64.8</b>	<b>30.2</b>	<b>50.6</b>	<b>24.4</b>	<b>78.2</b>	<b>29.6</b>
<b>ALL MAIN PATTERNS</b>	<b>0</b>	<b>0</b>	<b>0.19</b>	<b>0.03</b>	<b>0.01</b>	<b>0</b>



**Fig. 1.** Relationships between shrub and grass cover for the six hypotheses: a, d) no vertical root overlap (Walter hypothesis), b, e) partial vertical overlap, and c, f) full vertical overlap. a, b, c) no facilitation and d, e, f) facilitation. Dotted lines indicate the acceptance range for the two growth forms ( $\text{mean} \pm 2 \cdot \text{SD}$ ), and the shaded areas indicate the parameterizations with match in both patterns. Percentages indicate the relative number of simulations that were within the field range.

a grass or shrub pattern (Table 1). However, all other hypotheses tended to produce too high shrub cover for a given grass cover. As expected, facilitation enhances this effect (cf. corresponding F0 and F+ hypotheses in Fig. 1). Thus, grass does not control shrub abundances in all R1 and R3 hypotheses.

#### MODEL ANALYSIS

When analysing the results of the best hypothesis (i.e. partial vertical root overlap without facilitation, R2\_F0) in more detail, we found that the shrub emergence thresholds showed the strongest rank correlations with the species-specific shrub abundances ( $r_{\text{Sp}} \approx -0.68$ ; Table 2) and total shrub abundance ( $-0.35 \leq r_{\text{Sp}} \leq -0.28$ ). Negative correlations indicate that more emergence yields higher abundance. This hypothesis yielded also strongly reduced posterior parameter ranges

(Figs 2 and S5; Appendix S3). The shrub recruitment thresholds were also important in determining shrub abundances ( $-0.5 \leq r_{\text{Sp}} \leq -0.47$ ; Table 2) and showed strongly reduced posterior parameter range (Figs 2 and S5; Appendix S3). Negative correlations ( $r_{\text{Sp}} \approx -0.47$ ) between the emergence and recruitment parameters in all three shrub species point to moderate compensatory behaviour. Thus, shrub recruitment parameters are somewhat more important than indicated by their rank correlations.

For grasses, the recruitment threshold showed overwhelmingly the largest correlations with species-specific abundance ( $r_{\text{Sp}} \approx -0.84$ ; Table 2) and total grass abundance ( $r_{\text{Sp}} \approx -0.4$ ) and strongly reduced posterior parameter range (Fig. 2). The emergence threshold, which showed also narrow posterior parameter range (Fig. 2), was of secondary importance for grasses ( $r_{\text{Sp}} \approx -0.31$  Table 2). Again, we find negative correlations ( $-0.37 \leq r_{\text{Sp}} \leq -0.59$ ) between the

**Table 2.** Rank correlations between model parameters and abundances of shrubs, grasses and individual species, taken over the 10 000 parameterizations of the best hypothesis R2\_F0. A high correlation coefficient indicates that this parameter strongly determines the respective abundances. Correlations larger than 0.2 and statistically significant ( $P < 0.001$ ) are shown in bold. Note that a negative correlation indicates (except for mortality rates) that more frequent occurrence of the demographic event positively influences abundance (the lower the threshold is lower, the higher frequency of the event)

Parameter	Grasses	<i>Bromus</i>	<i>Poa</i>	<i>Pappostipa</i>	Shrubs	<i>Mulinum</i>	<i>Adesmia</i>	<i>Senecio</i>
Emergence threshold <i>Bromus</i>	-0.14	<b>-0.31</b>	0.06	0.06	0.14	0.08	0.11	0.10
Emergence threshold <i>Poa</i>	-0.15	0.07	<b>-0.32</b>	0.05	0.15	0.11	0.11	0.10
Emergence threshold <i>Pappostipa</i>	-0.18	0.05	0.06	<b>-0.33</b>	0.17	0.12	0.12	0.12
Growth threshold <i>Bromus</i>	0.03	-0.02	0.02	0.02	0.03	0.02	0.02	0.03
Growth threshold <i>Poa</i>	0.00	0.01	-0.01	-0.01	0.05	0.03	0.05	0.02
Growth threshold <i>Pappostipa</i>	0.01	0.02	-0.01	0.00	0.05	0.03	0.04	0.04
Recruitment threshold <i>Bromus</i>	<b>-0.39</b>	<b>-0.84</b>	0.11	0.13	<b>0.28</b>	0.18	<b>0.22</b>	0.19
Recruitment threshold <i>Poa</i>	<b>-0.44</b>	0.10	<b>-0.85</b>	0.09	<b>0.33</b>	<b>0.23</b>	<b>0.25</b>	<b>0.22</b>
Recruitment threshold <i>Pappostipa</i>	<b>-0.44</b>	0.14	0.11	<b>-0.85</b>	<b>0.34</b>	<b>0.21</b>	<b>0.27</b>	<b>0.22</b>
Mortality rate <i>Bromus</i>	-0.15	<b>-0.25</b>	0.03	0.02	0.14	0.09	0.10	0.10
Mortality rate <i>Poa</i>	-0.10	0.03	-0.19	0.04	0.08	0.06	0.06	0.04
Mortality rate <i>Pappostipa</i>	-0.11	0.03	0.02	-0.19	0.10	0.06	0.08	0.06
Emergence threshold <i>Mulinum</i>	0.19	0.07	0.10	0.09	<b>-0.30</b>	<b>-0.68</b>	-0.01	-0.01
Emergence threshold <i>Adesmia</i>	<b>0.25</b>	0.10	0.11	0.12	<b>-0.35</b>	0.01	<b>-0.67</b>	0.00
Emergence threshold <i>Senecio</i>	0.16	0.07	0.06	0.09	<b>-0.28</b>	0.00	0.00	<b>-0.70</b>
Growth threshold <i>Mulinum</i>	0.08	0.05	0.05	0.03	-0.04	-0.03	-0.04	-0.02
Growth threshold <i>Adesmia</i>	0.07	0.03	0.03	0.03	-0.03	-0.01	-0.05	0.00
Growth threshold <i>Senecio</i>	0.07	0.03	0.04	0.04	-0.04	-0.02	-0.05	-0.02
Recruitment threshold <i>Mulinum</i>	0.14	0.06	0.07	0.07	<b>-0.24</b>	<b>-0.47</b>	-0.03	-0.03
Recruitment threshold <i>Adesmia</i>	0.15	0.08	0.06	0.08	<b>-0.22</b>	-0.01	<b>-0.40</b>	0.00
Recruitment threshold <i>Senecio</i>	0.12	0.06	0.07	0.06	<b>-0.23</b>	-0.03	-0.02	<b>-0.50</b>
Mortality rate <i>Mulinum</i>	0.11	0.05	0.07	0.05	-0.12	-0.21	-0.02	-0.02
Mortality rate <i>Adesmia</i>	0.14	0.07	0.05	0.08	-0.13	0.02	-0.25	0.01
Mortality rate <i>Senecio</i>	0.04	0.01	0.03	0.01	-0.05	0.00	-0.01	-0.12

emergence and recruitment parameters in all three grass species which indicates that grass emergence parameters are somewhat more important than indicated by their rank correlations. Thus, grass recruitment and shrub emergence were strong demographic bottlenecks, controlled primarily by the abundance of species within the same plant functional type.

Interestingly, total (and species-specific) shrub abundances were correlated with grass recruitment parameters (mean  $r_{sp} \approx 0.32$ ; Table 2), indicating competitive effects from grasses to shrubs. In other words, shrubs were additionally controlled by grasses (positive correlation means that more grass recruitment yields lower shrub abundance). However, the shrub emergence parameters were only weakly correlated with grass abundances ( $0.24 \geq r_{sp} \geq 0.16$ ; Table 2), indicating a weaker control of grasses by shrubs.

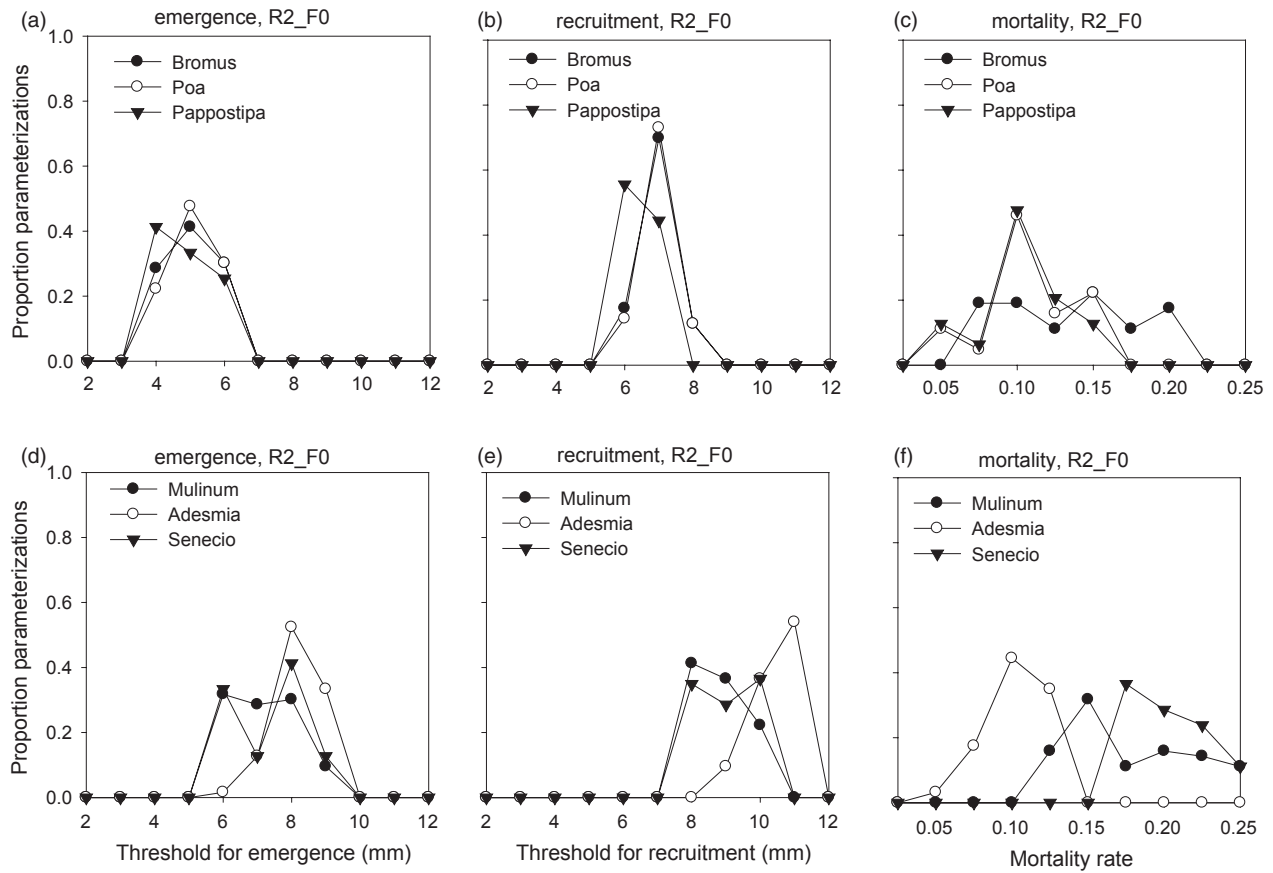
We repeated the global sensitivity analysis also for the other hypotheses (Appendix S3; Tables S3–S8) and found several differences in their correlation structure compared with the best hypothesis (i.e. R2\_F0). Interestingly, only the partial vertical root overlap hypotheses yielded at the same time a control of total shrub abundance by grasses and a weak control of total grass abundance by shrubs (Table 2). As expected, R1\_F0 did not show cross-correlations between grasses and shrubs (Table S3), and R3\_F0 and R3\_F+ showed too weak control of shrub abundance by grasses, but too strong control of grass abundance by shrubs (Tables S7 and S8). Thus, the rejected hypotheses did not yield the subtle balance of controls

that allowed R2\_F0 (and to a lesser extent R2\_F+) to yield simultaneous agreement in all observed patterns.

#### MODEL VALIDATION

We found strongly reduced ranges of the emergence and recruitment parameters, (Fig. 2) and the excluded values were located at the lower prior range (i.e. the demographic event occurred too often) and the higher prior range (i.e. the demographic event occurred only rarely). The intermediate posterior ranges of the emergence and recruitment parameters were in agreement with expectations of a semi-arid ecosystem. Additionally, grass thresholds were approximately 2 mm lower than that of shrubs which indicated that the emergence and recruitment events were more frequent for grasses than shrubs. According to the long-term climate series used, the recruitment events for grass species occurred in approximately 50% of all years, while shrubs only recruited in 23% of all years. Annual mortality rates ranged between 5% and 20% for grasses (Fig. 2c) and 5–25% for shrubs (Fig. 2f).

Almost all parameterizations of the model version with partial vertical root overlap and no facilitation (R2\_F0) that matched the main patterns matched also the more detailed spatial patterns (17 of 19 parameterizations). This is a surprising result, because this hypothesis does not assume a direct facilitation mechanism between grasses and shrubs. However, it was able to generate the observed grass ring around shrubs



**Fig. 2.** Marginal posterior parameter distribution for the 51 parameterizations of the R2\_F0 hypothesis that matched all grass- and shrub-specific abundances for three parameters: emergence threshold (a, d), recruitment threshold (b, e) and mortality rates (c, f) in grasses (a, b, c) and shrubs (d, e, f). The x-axes show the full prior parameter ranges.

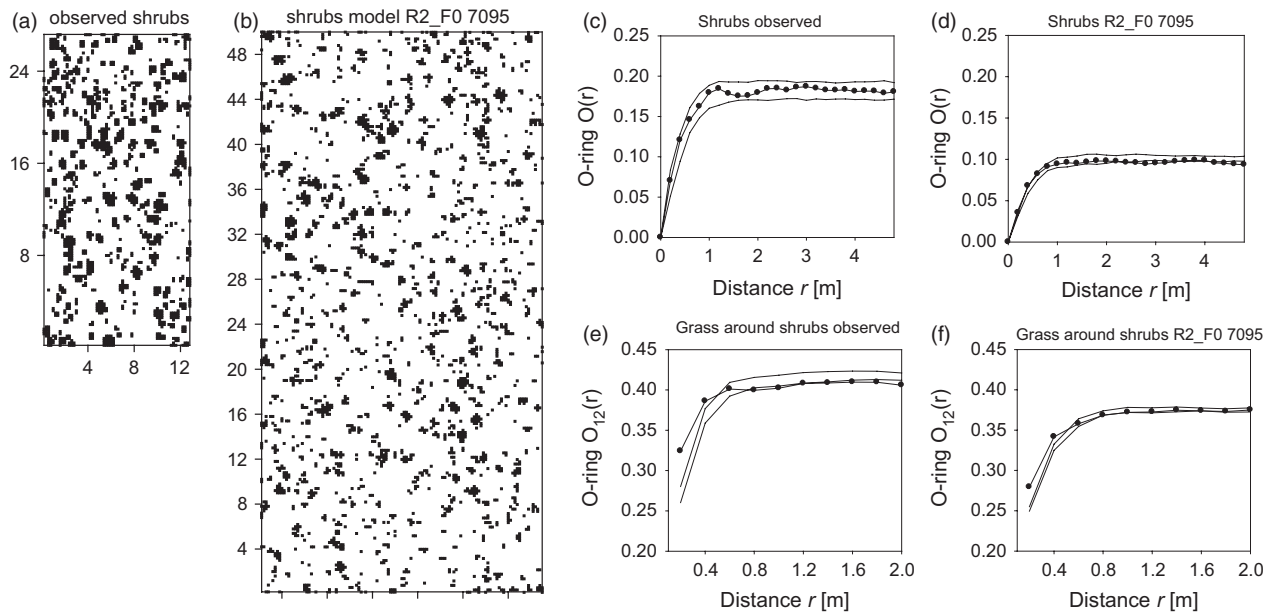
as indicated by small-scale attraction in the spatial pattern analysis (Fig. 3e, f). The rejected hypotheses with facilitation (R1\_F+ and R3\_F+) yielded aggregation of shrubs (not observed in the field) and a weak attraction of grasses around shrubs (Figs S6, S10; Appendix S3). The hypothesis with root segregation and no facilitation (R1\_F0) yielded a weak tendency to shrub aggregation and an only weak attraction of grasses around shrubs (Fig. S7; Appendix S3). The three hypotheses that showed at least one accepted parameterization (i.e. R2\_F0, R2\_F+ and R3\_F0) showed randomly distributed shrubs; however, the observed grass attraction (i.e. Fig. 3e) was best matched by hypothesis R2\_F0 (Fig. 3f); hypotheses R2\_F+ with facilitation yield a somewhat too strong grass attraction (Fig. S8f; Appendix S3), and as expected, hypothesis R3\_F0 with root overlap and no facilitation did not show the observed grass attraction (Fig. S11f; Appendix S3).

Soil water dynamics simulated at the cell level in a spatial domain was related to the plant cover and the dominance of each growth-form across different microsites. Shrub cells were still wet during the season of increasing water deficit which is critical for seedling survival (i.e. the end of the growing season December-February), but grass cells were much drier (Fig. 4). The difference between shrub and grass microsites was largest for the no vertical root overlap

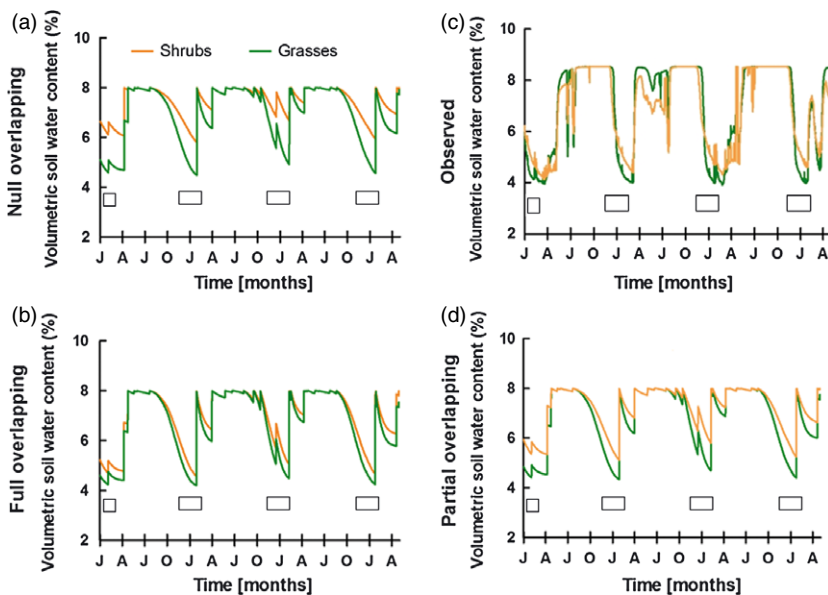
hypothesis (Fig. 4a), and almost disappeared for the full vertical overlap hypothesis (Fig. 4b). For the selected model with partial vertical root overlap between grasses and shrubs, these differences were intermediate (Fig. 4d) and in best agreement with the independent field data (Fig. 4c).

## Discussion

In this study, we used a model of intermediate complexity to test several competing hypotheses on the factors that determine the coexistence of several shrub and grass species. This allowed us to explore big questions of arid land research such as: Are root-determined niches relevant? How important is plant facilitation? How are the competitive interactions between major life-forms modified by the life stages of neighbours? and How does this contribute to coexistence? We found a complex network of mechanisms that controlled growth-form coexistence and relative abundances where demographic bottlenecks, species interactions among life stages and storage effects were important. Because multiple field data measured at different levels of organization were used to constrain the model behaviour and to test our alternative hypotheses (Wiegand *et al.* 2003; Wiegand, Revilla & Knauer 2004; Grimm *et al.* 2005), we are confident that our



**Fig. 3.** Point pattern analysis of observed and simulated vegetation maps. (a) Observed spatial pattern of shrubs, (b) part of the  $50 \times 50$  m plot simulated by DINVEG showing all shrubs. The observed pattern was represented in the  $20 \times 20$  cm resolution as the simulated data. (c) Observed pattern of shrubs is represented by the  $O(r)$  (closed discs) that gives the probability that a cell covered by a shrub has a cell covered by a different shrub at distance  $r$ , together with the simulation envelopes being the 5th lowest and highest values of the  $O(r)$  derived from simulations of a null model where the shrub objects were randomized without overlap (Wiegand *et al.* 2006). (d) Same as c), but for an accepted parameterization of hypothesis R2\_F0 generated with DINVEG at simulation year 200. (e) Analysis of observed association of grasses around shrubs measured with the bivariate  $O_{12}(r)$  that yields the probability that a grass tuft is located at distance  $r$  from a cell covered by a shrub. The simulation envelopes were based here on a null model that displaced the grass cells to random locations not covered by a shrub. (f) Same as e), but for DINVEG output.



**Fig. 4.** Daily volumetric soil water content (SWC) during four growing seasons 1999–2002 for two different microsites (i.e. shrubs and grasses) in the top soil layer (0–15 cm). (a) Simulated by DINAQUA model (Paruelo & Sala 1995) for no vertical root overlap (R1), (b) simulated for full vertical root overlap (R3), (c) observed data by soil water sensors placed at 15-cm soil depth, (d) simulated for the selected model with partial vertical root overlap. The boxes indicate the period December–February which is critical for seedling survival (months in x-axis are: January, April, July and October).

model analysis identified the main drivers of shrub–grass coexistence and the maintenance of the spatial patterns in the Patagonian steppe.

#### VERTICAL ROOT OVERLAP BETWEEN SHRUBS AND GRASSES

Model selection showed that not all hypotheses were able to generate the balance between life-forms and/or species

observed in the field. The model version that incorporated partial vertical root overlap of shrubs and grasses without additional aerial facilitation received most support from the data and yielded for the largest set of parameters with simultaneous matches in all main patterns. Previous physiological studies on adult plants supported the niche separation hypothesis between growth forms in the Patagonian steppe (Sala *et al.* 1989; Golluscio, Sala & Lauenroth 1998; Golluscio, Sigal Escalada & Pérez 2009). However, more recent studies

of root architecture and soil water use reported that different grass and shrub species in Patagonian steppes can overlap at intermediate soil layers (Bucci *et al.* 2009; Leva, Aguiar & Oesterheld 2009). This is particularly relevant if we account for differences across life stages. Model selection therefore favoured the 'most subtle' hypothesis of partial vertical root overlap that allowed adult grasses exclusive access to soil water in the upper layer (0–0.2 m), only shared with grass and shrub seedlings, and adult shrubs exclusive access to the lower soil layer (0.4–0.6 m). However, adult grasses and shrubs competed for soil water at the intermediate layer (0.2–0.4 m) which added one element of 'reciprocate' control.

Shallow soil water, which is mostly related to frequent small rainfall events (events <10 mm represent 58% of total annual precipitation; Golluscio, Sala & Lauenroth 1998), is only used by adult grasses and grass and shrub seedlings (Cipriotti *et al.* 2008). Competition for this resource allows grasses to control shrubs (i.e. grasses are the species with a higher drought tolerance; Golluscio, Oesterheld & Aguiar 2005; Golluscio & Oesterheld 2007). This was another important element of control in the favoured hypothesis. The ability of grasses to out-compete tree seedlings is well known in savannas (e.g. Scholes & Archer 1997) and stabilized a deterministic savanna model even without disturbance (Baudena, D'Andrea & Provenzale 2010).

Deep soil water which is more related to larger rainfall events is preferentially consumed by established shrubs. Deep percolation is frequent in Patagonia because most precipitation occurs during winter when plant growth is low due to low temperature (Paruelo & Sala 1995). However, a critical element of the favoured hypothesis was that grasses and shrubs competed for soil water of the 0.2 and 0.4 m layer. Thus, grasses may affect deeper soil water through root uptake and interception of water that would otherwise reach the bottom layers.

#### DEMOGRAPHIC BOTTLENECKS IN SHRUBS AND GRASSES

Detailed analysis of the favoured model (R2\_F0) showed that the Patagonian grass–shrub steppe is likely to show demographic bottlenecks related with stochastic precipitation. Interestingly, the demographic bottlenecks were different for shrubs and grasses. Shrub abundance was mostly controlled by emergence which occurs during April–September, whereas grass abundance was mostly controlled by the survival of grass seedlings at the end of growing season (i.e. December–February, when grass recruitment is defined). The different demographic bottlenecks between life-forms may relate to the rapid deepening of shrub roots into the lower soil layers. This desynchronized the environmental conditions that control short-term establishment of shrubs and grasses and point to operation of a storage effect (Chesson 2000; Adler *et al.* 2006). Indeed, looking in detail into a simulation with an accepted parameterization of the R2\_F0 model showed that the grass and shrub population dynamics satisfy the three conditions for a storage effect outlined by Adler *et al.* (2006).

First, both life-forms have long life spans to buffer their populations against unfavourable years, because droughts in Patagonian steppes occur usually every 4–6 years (Fig. S13; Appendix S3). Secondly, shrubs and grasses differed in their response to climatic variation, and, in consequence, there are no relationships between grass and shrub population growth rates (Fig. S14; Appendix S3). Thirdly, growth rates of grasses during favourable years (i.e. high rainfall during the grass bottleneck period December–February) were highest when the grass population had low abundance (Fig. S15; Appendix S3). The third point is the most important to assure a spatial storage effect with a subadditive behaviour (*sensu* Chesson 2000), because the effect of competition on growth rate is more important during favourable (wet) years (Fig. S15; Appendix S3). In addition to the storage effect which buffered grasses against competitive exclusion, we found that only the hypothesis with partial vertical root overlap yielded a situation where grasses controlled shrub abundances but where grass abundance was only weakly controlled by shrubs.

The posterior distribution of the demographic parameters showed also some differences among species and which point to different strategies. For example, *A. volckmanii* showed higher emergence and recruitment thresholds and lower mortality (Fig. 2d, e) which agree with the known longevity of this species (Nuñez unpubl. data; Fernández *et al.* 1992; Oñatibia *et al.* 2010), while *S. filaginoides* and *M. spinosum* showed higher mortality rates (12–25%) and lower recruitment thresholds. Note that, other interspecies differences were, based on field data, already incorporated into the model parameterization. Thus, coexistence within life-forms with the observed abundances was most likely a result of small differences in life history and demography with respect to variability in precipitation that created temporal niches, combined with limited seed dispersal that allowed different species at different locations/time to win stochastic competition.

The strong dependency of the demographic bottlenecks (i.e. grass recruitment and shrub emergence) on small rainfall events during particular periods of the year suggests that the dynamics of the steppe may be especially sensitive to climate change (Tietjen & Jeltsch 2007). Subtle shifts in the precipitation regime can change the grass–shrub balance and the fragile network of interactions and controls that governs the dynamics of the steppe. Due to lack of long-term data, we could not use here temporal patterns for model assessment, but such data collection is in progress and may allow future studies to explore the temporal dynamics in more detail.

#### BALANCE BETWEEN POSITIVE AND NEGATIVE INTERACTIONS

Our results call for a revision of earlier hypotheses about the role of positive effects of woody species on grass recruitment reported from short-term field studies in these Patagonian steppes (Aguiar, Soriano & Sala 1992; Aguiar & Sala 1994) and also from other arid ecosystems (Callaway 1995; Maestre, Bautista & Cortina 2003; Brooker *et al.* 2008). In most cases,

woody plant facilitation of grasses has been conceptualized as a plant interaction with a positive outcome for grasses and null effects on shrubs or trees (e.g. Pugnaire *et al.* 1996; Maestre, Bautista & Cortina 2003). In contrast, our analysis suggests that adult shrubs did not compete with grass seedlings (or even facilitate them), but adult grass tufts control shrub abundance by competing with shrub seedlings. A similar result was found by Riginos (2009) where trees facilitate grass on the individual level, but grass controls tree abundance at the landscape level. Changes in the net interaction balance with life stage are difficult to study in the field because of logistic constraints in long-term surveys at plant level. Modelling is therefore an alternative way to test these changes and their effects in long-term dynamics (Donzelli, De Michele & Scholes 2013).

Somewhat surprisingly we found that the internal soil water dynamics of model versions R1\_F0 and R2\_F0 created a reduced competition between shrubs and grass seedlings that was already sufficient to generate the observed ring of grasses around shrubs (Fig. S7f, S9f; Appendix S3). The mechanism of ring formation in these model versions is as follows: large shrubs did not access water from the upper soil layer, and neighbouring grass seedlings and grasses (i.e. in the ring) gained access to otherwise unused water. Grass seedlings outside the shrub-ring patches are for geometric reasons more likely to suffer competition from adult grasses than grass seedlings in the ring. However, this does not mean that facilitation does not occur in the field (we did not test the full range of aerial facilitation strengths). It only means that the conspicuous spatial pattern of grasses clustering around shrubs does not necessarily require positive interactions, but can also be produced by spatial modulation of competitive effects.

#### THE SPATIAL AND TEMPORAL HETEROGENEITY

The hypotheses about growth-form coexistence addressed here were tested through model simulations in a realistic spatially explicit way considering temporally variable limiting resource (i.e. soil water availability). Interestingly, we found that almost all accepted parameterizations generated the observed two-phase vegetation mosaic, but the best parameterizations of the R1 and R3 hypothesis (which did not match all main patterns) did mostly not reproduce the observed spatial patterns (Figs S6, S7, S10, S11; Appendix S3). This indicates that spatial patterns and mechanisms of coexistence are intimately linked and that a misrepresentation in the internal model relationships yields also a misbalance in the spatial patterns.

Interestingly, most of the accepted parameterizations produced the observed equilibrated spatial pattern of the mature community (i.e. random patterns of shrubs and the ring of grasses in the immediate neighbourhood of shrubs; Figs S8 and S9; Appendix S3), but it is not observed by the other hypotheses (Figs S6, S7, S10; Appendix S3). To find out why shrubs showed a random pattern, we explored whether dead shrubs were randomly distributed with respect to surviving shrubs (the null model moved dead shrubs to random

locations not occupied by surviving shrubs; Wiegand *et al.* 2006). We found that dead shrubs were both in the field (Fig. S12a; Appendix S3), as well in the model outputs (Fig. S12b; Appendix S3), not randomly distributed around surviving shrubs but more likely to be located in the immediate neighbourhood of surviving shrubs. This result points to a spatial self-regulation effect of shrubs caused by competition for water which counteracts tendencies to aggregation. A clustered distribution of shrubs would not allow for the development of the ring of grasses around shrubs. Thus, we found that grass–shrub community dynamics are driven by a complex network of plant interactions that change between and within life-forms, and across plant stages. It is noteworthy that the partial vertical root overlap is necessary to produce this diversity of interactions and that neither stronger (total overlap) nor weaker competition (no overlap) between functional types was capable of producing the observed patterns. However, the net outcome of this complex network of interactions yields a remarkably equilibrated spatial pattern of the mature community which is not a consequence of lack of interactions within and between life-forms.

#### Conclusions

Results of our model analyses suggest that an integrative perspective based on plant demography in a spatially explicit context is necessary to reveal the potential control mechanisms working in semi-arid grass–shrub steppes (Sankaran, Ratnam & Hanan 2004). We found that even in absence of strong top-down controls, a complex interplay of demographic bottlenecks, biotic interactions across plant species and stages, and storage effects was necessary to generate in the model the observed shrub and grass abundances. Only a model with explicit consideration of different life stages and an explicit vertical root structure with partial overlap between grasses and shrubs yielded internal control mechanisms required to match the multiple field observations. This outlines the importance to complement simple models in search of general mechanisms (e.g. Baudena, D'Andrea & Provenzale 2010; Higgins, Scheiter & Sankaran 2010) with structurally realistic models of intermediate complexity that can be tested for particular sites against a variety of field observations (Evans *et al.* 2013). Our approach allowed the identification of subtle effects that can be easily overlooked if the model is not rich enough in structure to be tested against multiple observations (i.e. avoids the problem of non-uniqueness). The inverse approach of model parameterization and model selection was very effective in this and opens new avenues for the use of realistic models of intermediate complexity to follow a more integrative perspective in solving the woody–grass coexistence question.

An interesting aspect of our results is that the coexistence mechanism is based on differences in bottom-up controls across different plant species and life stages, but that top-down controls were relatively unimportant in our study site. This is in contrast to C4 tropical or subtropical humid grassland and savanna ecosystems where the top-down controls

fire and grazing are key processes (Bond 2008; Accatino *et al.* 2010). Thus, our study points to alternative mechanisms of shrub–grass coexistence that may play an important role in dry grasslands and steppes from America, Asia and Oceania where fire does naturally not occur and where grazing pressure was relatively low previous to the human expansion. As proposed by Bond (2008), it is necessary to conduct intercontinental comparisons as most of the theoretical concepts on shrub/tree–grass coexistence were developed for African ecosystems where density and diversity of large herbivores are greater than in several mixed woody–grass communities from other continents. Certainly, we cannot expect that exactly the same complex network of interactions as found here would control coexistence and relative abundances in other systems, but similar mechanisms involving demographic bottlenecks and species interactions among life stages may operate, and our study provides avenues to detect them.

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## References

- Accatino, F., De Michele, C., Vezzoli, R., Donzelli, D. & Scholes, R.J. (2010) Tree–grass co-existence in savanna: interactions of rain and fire. *Journal of Theoretical Biology*, **267**, 235–242.
- Adler, P.B., HilleRisLambers, J., Kyriakidis, P.C., Guan, Q. & Levine, J.M. (2006) Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proceedings of the National Academy of Sciences*, **103**, 12793–12798.
- Aguiar, M.R. & Sala, O.E. (1994) Competition, facilitation, seed distribution, and the origin of patches in a Patagonian steppe. *Oikos*, **70**, 26–34.
- Aguiar, M.R. & Sala, O.E. (1997) Seed distribution constrains the dynamics of the Patagonian steppe. *Ecology*, **78**, 93–100.
- Aguiar, M.R. & Sala, O.E. (1999) Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology and Evolution*, **14**, 273–277.
- Aguiar, M.R., Soriano, A. & Sala, O.E. (1992) Competition and facilitation in the recruitment of seedlings in the Patagonian steppe. *Functional Ecology*, **6**, 66–70.
- Baudena, M., D'Andrea, F. & Provenzale, A. (2010) An idealized model for tree–grass coexistence in savannas: the role of life stage structure and fire disturbances. *Journal of Ecology*, **98**, 74–80.
- Bond, W.J. (2008) What limits trees in C-4 grasslands and savannas? *Annual Review of Ecology Evolution and Systematics*, **39**, 641–659.
- Brooker, R.W., Maestre, F.E., Callaway, R.M., Lortie, C.L., Cavieres, L.K., Kunstler, G. *et al.* (2008) Facilitation in plant communities: past, the present, and the future. *Journal of Ecology*, **96**, 18–34.
- Bucci, S.J., Scholz, F.G., Goldstein, G., Meinzer, F.C. & Arce, M.E. (2009) Soil water availability and rooting depth as determinants of hydraulic architecture of Patagonian woody species. *Oecologia*, **160**, 631–641.
- Callaway, R.M. (1995) Positive interactions among plants. *Botanical Review*, **61**, 306–349.
- Chesson, P.L. (2000) General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology*, **58**, 211–237.
- Cipriotti, P.A. & Aguiar, M.R. (2005) Effects of grazing on patch structure in a semi-arid two-phase vegetation mosaic. *Journal of Vegetation Science*, **16**, 57–66.
- Cipriotti, P.A., Flombaum, P., Sala, O.E. & Aguiar, M.R. (2008) Does drought control emergence and survival of grass seedlings in semi-arid rangelands? An example with a Patagonian species. *Journal of Arid Environments*, **72**, 162–174.
- Cipriotti, P.A., Aguiar, M.R., Wiegand, T. & Paruelo, J.M. (2012) Understanding the long term spatial dynamics of semiarid grass shrub steppes through inverse parameter selection for simulation models. *Oikos*, **121**, 848–861.
- Donzelli, D., De Michele, C. & Scholes, R.J. (2013) Competition between trees and grasses for both soil water and mineral nitrogen in dry savannas. *Journal of Theoretical Biology*, **332**, 181–190.
- Evans, M.R., Grimm, V., Johst, K., Knuutila, T., de Langhe, R., Lessells, C.M. *et al.* (2013) Do simple models lead to generality in ecology? *Trends in Ecology and Evolution*, **28**, 578–583.
- Fernández, R.J., Nuñez, A.H. & Soriano, A. (1992) Contrasting demography of two Patagonian shrubs under different conditions of sheep grazing and resource supply. *Oecologia*, **91**, 39–46.
- Fernández-Alduncin, R.J., Sala, O.E. & Golluscio, R.A. (1991) Woody and herbaceous aboveground production of a Patagonian steppe. *Journal of Range Management*, **44**, 434–437.
- Goldberg, D.E., Rajaniemi, T., Gurevitch, J. & Stewart-Oaten, A. (1999) Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, **80**, 1118–1131.
- Golluscio, R.A., León, R.J.C. & Perelman, S.B. (1982) Caracterización fitosociológica de la estepa del oeste de Chubut, su relación con el gradiente ambiental. *Boletín de la Sociedad Argentina de Botánica*, **21**, 299–324.
- Golluscio, R.A. & Oesterheld, M. (2007) Water use efficiency of twenty-five co-existing Patagonian species growing under different soil water availability. *Oecologia*, **154**, 207–217.
- Golluscio, R.A., Oesterheld, M. & Aguiar, M.R. (2005) Phenology of twenty-five Patagonian species related to their life form. *Ecography*, **28**, 273–282.
- Golluscio, R.A., Sala, O.E. & Lauenroth, W.K. (1998) Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. *Oecologia*, **115**, 17–25.
- Golluscio, R.A., Sigal Escalada, V. & Pérez, J. (2009) Minimal plant responsiveness to summer water pulses: ecophysiological constraints of three species of semiarid Patagonia. *Rangeland Ecology Management*, **62**, 171–178.
- Golluscio, R.A., Pérez, J.A., Paruelo, J.M. & Ghersa, C.M. (2005) Spatial heterogeneity at different grain sizes in grazed versus ungrazed sites of the Patagonian steppe. *Ecoscience*, **12**, 103–109.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W., Railsback, S.F., Thulke, H., Weiner, J., Wiegand, T. & DeAngelis, D.L. (2005) Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science*, **311**, 987–991.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J. & Railsback, S.F. (2010) The ODD protocol: a review and first update. *Ecological Modelling*, **221**, 2760–2768.
- Hartig, F., Calabrese, J., Reineking, B., Wiegand, T. & Huth, A. (2011) Statistical inference for stochastic simulations models - theory and application. *Ecology Letters*, **14**, 816–827.
- Higgins, S.I., Bond, W.J. & Trollope, W.S.W. (2000) Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology*, **88**, 213–229.
- Higgins, S.I., Scheiter, S. & Sankaran, M. (2010) The stability of African savannas: insights from the indirect estimation of the parameters of a dynamic model. *Ecology*, **91**, 1682–1692.
- House, J., Archer, S., Breshears, D.D. & Scholes, R.J. & NCEAS Tree-Grass Interaction Participants (2003) Conundrums in mixed woody–herbaceous plant systems. *Journal of Biogeography*, **30**, 1763–1777.
- Jeltsch, F., Weber, G. & Grimm, V. (2000) Ecological buffering mechanisms in savannas: a unifying theory of long-term tree–grass coexistence. *Plant Ecology*, **161**, 161–171.
- Jobbágy, E.G., Paruelo, J.M. & León, R.J.C. (1995) Estimación del régimen de precipitación a partir de la distancia a la cordillera en el noroeste de la Patagonia. *Ecología Austral*, **5**, 47–53.
- Jobbágy, E. & Sala, O.E. (2000) Controls of grass and shrub aboveground production in the Patagonian steppe. *Ecological Applications*, **10**, 541–549.
- León, R.J.C., Bran, D., Collantes, M., Paruelo, J.M. & Soriano, A. (1998) Grandes unidades de vegetación de la Patagonia extra andina. *Ecología Austral*, **8**, 125–144.

- Leva, P.E., Aguiar, M.R. & Oesterheld, M. (2009) Underground ecology in a Patagonian steppe: root traits permit identification of graminoid species and classification into functional types. *Journal of Arid Environments*, **73**, 428–434.
- Maestre, F.T., Bautista, S. & Cortina, J. (2003) Positive, negative, and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. *Ecology*, **84**, 3186–3197.
- Martínez, I., Wiegand, T., Camarero, J.J., Batllori, E. & Gutiérrez, E. (2011) Elucidating demographic processes underlying tree line patterns: a novel approach to model selection for individual-based models using Bayesian methods and MCMC. *American Naturalist*, **177**, E136–E152.
- McKay, M.D., Beckman, R.J. & Conover, W.J. (1979) Comparison of three methods for selecting values of input variables in the analysis of output from a computer code. *Technometrics*, **21**, 239–245.
- Meyer, K.M., Wiegand, K. & Ward, D. (2009) Patch dynamics integrate mechanisms for savanna tree-grass coexistence. *Basic and Applied Ecology*, **10**, 491–499.
- Nano, C.E.M. & Clarke, P.J. (2010) Woody-grass ratios in a grassy arid system are limited by multi-causal interactions of abiotic constraint, competition and fire. *Oecologia*, **162**, 719–732.
- Nelson, W.A., McCauley, E. & Wimbert, J. (2004) Capturing dynamics with the correct rates: inverse problems using semiparametric approaches. *Ecology*, **85**, 889–903.
- Oesterheld, M., Sala, O.E. & McNaughton, S.J. (1992) Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature*, **356**, 234–236.
- Oñatibia, G.R., Aguiar, M.R., Cipriotti, P.A. & Troiano, F. (2010) Individual plant and population biomass of dominant shrubs in Patagonian grazed fields. *Ecología Austral*, **20**, 269–279.
- Paruelo, J.M., Aguiar, M.R. & Golluscio, R.A. (1988) Soil water availability in the Patagonian arid steppe: gravel content effect. *Arid Soil Research Rehabilitation*, **2**, 67–74.
- Paruelo, J.M. & Sala, O.E. (1995) Water losses in the Patagonian steppe: a modelling approach. *Ecology*, **76**, 510–520.
- Paruelo, J.M., Beltrán, A., Jobbágy, E.G., Sala, O.E. & Golluscio, R.A. (1998) The climate of Patagonia: general patterns and controls on biotic processes. *Ecología Austral*, **8**, 85–101.
- Pugnaire, F.I., Haase, P., Puigdefabregas, J., Cueto, M., Incoll, L.D. & Clark, S.C. (1996) Facilitation and succession under the canopy of the leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos*, **76**, 455–464.
- Reynolds, J.F., Stafford Smith, D.M., Lambin, E.F., Turner II, B.L., Mortimore, M., Batterbury, S.P.J. et al. (2007) Global desertification: building a science for dryland development. *Science*, **316**, 847–851.
- Riginos, C. (2009) Grass competition suppresses savanna tree growth across multiple demographic stages. *Ecology*, **90**, 335–340.
- Sala, O.E., Golluscio, R.A., Lauenroth, W.K. & Soriano, A. (1989) Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia*, **81**, 501–505.
- Sankaran, M., Ratnam, J. & Hanan, N.P. (2004) Tree-grass coexistence in savannas revisited - insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, **7**, 480–490.
- Scheiter, S. & Higgins, S.I. (2007) Partitioning of root and shoot competition and the stability of savannas. *The American Naturalist*, **170**, 587–601.
- Scholes, R.J. & Archer, S.R. (1997) Tree-grass interactions in Savannas. *Annual Review of Ecology and Systematics*, **28**, 517–544.
- Soriano, A. & Sala, O.E. (1986) Emergence and survival of *Bromus setifolius* seedlings in different microsites of Patagonian arid steppe. *Israel Journal of Botany*, **35**, 91–100.
- Soriano, A., Sala, O.E. & Perelman, S.B. (1994) Patch structure and dynamics in a Patagonian arid steppe. *Vegetatio*, **111**, 127–135.
- Tietjen, B. & Jeltsch, F. (2007) Semi-arid grazing systems and climate change: a survey of present modelling potential and future needs. *Journal of Applied Ecology*, **44**, 425–434.
- Walter, H. (1971) *Ecology of Tropical and Subtropical Vegetation*. Oliver & Boyd, Edinburgh, UK.
- Ward, D., Wiegand, K. & Getzin, S. (2013) Walter's two-layer hypothesis revisited: back to the roots!. *Oecologia*, **172**, 617–630.
- Wiegand, T., Revilla, E. & Knauer, F. (2004) Reducing uncertainty in spatially explicit population models. *Biodiversity and Conservation*, **13**, 53–78.
- Wiegand, K., Saltz, D. & Ward, D. (2006) A patch-dynamics approach to savanna dynamics and woody plant encroachment - Insights from an arid savanna. *Perspectives in Plant Ecology, Evolution and Systematics*, **7**, 229–242.
- Wiegand, T., Jeltsch, F., Hanski, I. & Grimm, V. (2003) Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. *Oikos*, **100**, 209–222.
- Wiegand, T., Kissling, W.D., Cipriotti, P.A. & Aguiar, M.R. (2006) Extending point pattern analysis to objects of finite size and irregular shape. *Journal of Ecology*, **94**, 825–837.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Model description following the ODD protocol (adapted from appendix of Cipriotti et al. 2012).

**Appendix S2.** Details on observed patterns (adapted from appendix of Cipriotti et al. 2012).

**Appendix S3.** Additional model results.