Appendix A1

Model details

In the following we present the different rules and equations that govern the model dynamics of vegetation, in Table A1 we summarized the main equations for each rule, and in Table A2 we presented all model’s parameters. In addition, we presented reference that justify the values for seven structural parameters that we estimated directly from published data or measured in the field (i.e. seed dispersal distances \( d_{\text{max}} \), life span \( \text{age}_{\text{max}} \), max biomass \( b_{\text{max}} \), maximal shrub size per cells, seed viability \( v \), and minimum biomass \( b_{\text{min}} \) to reproduce), and five parameters determined indirectly from published or unpublished data (i.e. soil-seed bank decay rate \( p_{\text{ext}} \), potential plant growth \( g_{\text{max}} \), overgrowth ability \( p_{\text{over}} \), max seed output \( s_{\text{max}} \), and annual mortality rates \( p_{\text{mk}} \)).

**Rule 1. Seed dispersal**

Seed dispersal occurred in January if conditions during the previous months allowed for seed production (rule 9). Seeds were distributed in the neighborhood of individual mother plants according to a seed kernel estimated from field studies (Aguiar and Sala 1997, Fernández et al. 2002, Perea 2005) and from very well known functions in the specialized literature (Nathan and Muller-Landau 2000) which considers seed traits (i.e. wing-loading of different
seed morphologies), plant height and wind speed and dominant direction. Generally, shrubs have larger seed shadows than grasses. Because wind blows predominantly from the west we assumed that seed shadows were approximately two or three times larger to the east than to the west, north, and south.

We used a simple exponential dispersal kernel from each mother plant:

\[
p_{i,j}(d_{\text{max}}, d_{*,ij}) = \frac{\exp\left[-\frac{d_{*,ij}}{d_{\text{max}}}\right]}{\sum_{i=1}^{N} \sum_{j=1}^{N} \exp\left[-\frac{d_{*,ij}}{d_{\text{max}}}\right]}
\]

(A1)

where \(p_{ij}\) is the probability of a cell \((i, j)\) to receive a seed, \(d_{\text{max}}\) the species specific maximal dispersal distance (main text Table 1), \(d_{*,ij}\) the “effective” distance of cell \((i, j)\) to the centre of a grass cell (or centroid of a shrub group of cells), and the double sum integrate all cells within the dispersal area from each mother plant. To consider the east-asymmetry in the kernel we decomposed the real distance \(d_{ij}\) into a east–west component \((= dx_{ij})\) and a north–south component \((= dy_{ij})\) and calculated the effective distance as \(d_{*,ij} = [(0.5dx_{ij})^2 - (dy_{ij})^2]^{0.5}\) if \(dx_{ij} > 0\) and \(d_{*,ij} = d_{ij}\) otherwise.

All seeds produced by a plant \(k\) (\(= \text{Seeds}_k\)) were distributed according to their kernel and the resulting soil seed bank (\(= \text{Seeds}_{i,j}\)) in a given cell \((i, j)\) is the superposition of all seed shadows \(\text{Seeds}_{i,j,k}\) from plants \(k\):

\[
\text{Seeds}_{i,j,k} = p_{i,j,k} \times \text{Seeds}_k
\]

\[
\text{Seeds}_{i,j} = \sum_k \text{Seeds}_{i,j,k}
\]

(A2)

All seeds which were dispersed outside the grid were lost. Seeds that enter the soil seed bank of an occupied cell could not germinate until the plant died. Not germinated seeds remained in the soil seed bank. Soil seed bank decay was represented by a negative exponential equation:

\[
\text{Seeds}_{i,j}(t + 1) = \text{Seeds}_{i,j}(t) \times \left(1 - p_{\text{ext}} \right)
\]

(A3)

with an annual decay rate \(p_{\text{ext}}\) evaluated in March, after the end of the growing season.
(Chambers and MacMahon 1994). Differences between species in the annual extinction rate \( p_{ext} \) were educated guesses based on Bertiller and Aloia (1997), Bertiller (1998), Rotundo and Aguiar (2004, 2005), and unpublished data from Rotundo (2005) (Table A1).

**Rule 2. Emergence**

Emergence of grass and shrub seedlings occurred between April and September in non-occupied cells that contained a non-empty seed bank. The probability of emergence:

\[
 p_e (swc_{10}, t_e) = \frac{1}{1 + \exp[-(swc_{10} - t_e)]}
\]

 depended on the soil water content in the first 0.1 m layer \( = swc_{10} \) calculated by DINAQUA, and a specific soil water thresholds \( (t_e, \text{ Table A1; Soriano 1960, Soriano and Sala 1983, Aguiar et al. 1992, Bisigato and Bertiller 1999, Pazos and Bertiller 2008).} \)

In an empty cell, a competitive lottery determines which of the species present in the soil seed bank will emerge if the soil water conditions are adequate. The lottery was applied among species present in the seed bank and did not depend on seed abundance. The month of emergence was registered because early emergence increases the recruitment probability at the end of the first growing season (rule 3). Note that the soil water content of a focal cell depends on precipitation, evaporation and consumption (i.e. transpiration) by adult plants in the 8 neighboring cells; therefore emergence is controlled by water competition of neighboring plants.

**Rule 3. Seedling recruitment**

Recruitment occurred in early summer (October to December). This is the critical period for plant recruitment in the Patagonia steppe because top soil layers start to desiccate as growing season proceeds due to decreases of precipitation and increasing temperatures, radiation and wind speed (atmospheric demand).
Grasses recruit one year after emergence if conditions are favorable, whereas shrubs recruit after two years (Aguiar et al. 1992, Fernández et al. 1992). The probability of plant recruitment \( p_r \) for a particular month between October and December is calculated as

\[
p_r(swc_i, t_r, fac) = \frac{fac}{1 + \exp[-(swc_i - t_r)]}
\]

where \( swc_i \) is the soil water content for the \( i \) soil layer explored by plant roots estimated by DINAQUA, \( t_r \) a specific threshold, and \( fac \) a parameter that controls the shrub facilitation effect for grasses (rule 4).

Because seedlings are very sensitive to water shortage we monitored the water content of the seedlings' cell during the entire one or two year period up to recruitment. If soil water content for a particular month was below the threshold \( t_r \) the seedling died: during the first three months after emergence of both life-forms we demanded \( swc_{i=1} > t_r \) for the 0–0.1 m layer. In the following months and before the first year, the threshold is controlled in the 0–0.2 m soil layer \( (i = 2) \). For shrubs, the threshold is controlled in 0–0.3 m soil layer \( (i = 3) \) during October to December in the second year.

**Rule 4. Shrub facilitation**

Grass seedlings located in the immediate neighborhood of a shrub cell (zone of influence) had higher probability of recruitment than seedlings not neighbored by shrubs. Depending on biomass of the shrub neighbor \( (0.5 – 3.5 \text{ kg shrub}^{-1}) \), the recruitment probability \( (p_r; \text{ Eq. A5}) \) is multiplied by the factor

\[
fac = \begin{cases} 
1 & \text{if shrub biomass} \leq 500\text{g} \\
\frac{0.5 + \text{Shrub Biomass}}{1000} & \text{if shrub biomass} > 500\text{g}
\end{cases}
\]

which ranges between 1 and 3. This rule is derived from analyses by Aguiar et al. (1992) and Aguiar and Sala (1994) that found that grass seedling recruitment increased between two and
three times if seedlings were located close to adult shrubs. Unpublished data support the increasing effect of facilitation with shrub biomass (Cipriotti 2006), especially young shrubs with low biomass and low height did not facilitate grass seedlings against wind and desiccation to the same extent as adult shrubs.

**Rule 5. Plant growth**

Growth of shrubs and grasses could occur at any month if the climate and soil water conditions were adequate. The growing season expands generally from September to January when temperature and soil water are propitious to plant growth (Golluscio and Sala 1993, Paruelo and Sala 1995, Golluscio et al. 2005). Plant growth is species-specific and modeled as the product of potential growth ($G_{pot}$; Eq. 7a) and a probability to grow ($p_g$; Eq. 7b). For shrubs and grasses we assumed that maximum plant biomass was reached close to the maximum plant age and used the first derivative of a logistic function that relates plant biomass to age to describe potential growth:

$$G_{pot}(age, g_{max}, age_{max}) = g_{max} \exp\left[ -0.5 \left( \frac{age - 0.5 \cdot age_{max}}{0.375 \cdot age_{max}} \right)^2 \right]$$  \hspace{1cm} (A7a)

which depended on the species-specific maximum plant growth ($g_{max}$), plant age ($age$) and longevity ($age_{max}$).

The probability to grow

$$p_g(transp, t_r) = \frac{1}{1 + \exp\left[-\frac{(transp - t_r)}{t_{th}}\right]}$$  \hspace{1cm} (A7b)

depended on the water condition of the year based on plant transpiration ($transp$) (estimated by DINAQUA) and specific growth threshold ($t_{th}$).

We estimated the plant growth parameters from field measurements of annual aboveground productivity for each growth-form, species density, plant biomass, plant phenology, and transpiration data for shrubs and grasses (Fernández et al. 1991, Golluscio and
Maximum plant growth parameters (i.e. $g_{\text{max}}$, $c_1$ and $c_2$) were estimated from field data and the mesic or xeric characteristics of species based on response of species to water availability (Soriano and Sala 1983, 1986, Bucci et al. 2009) and compared with field and greenhouse assays (Cipriotti et al. 2008).

There were no data of maximum age for Patagonian grasses. Based on data from other semiarid ecosystems (Fair et al. 1999) and tussock size-structure we assumed a maximum age of 20–25 years for the three grass species. Maximum age for shrubs derived from unpublished relationships between size and wood rings for *Adesmia* and *Senecio* (Núñez unpubl.). Because *Mulinum* does not have true wood rings; we estimated the same maximum age as *Senecio* (30 years) based on removal field experiments and size-structure (Cipriotti and Aguiar 2010).

Biomass data were obtained directly from field measurements (Oñatibia 2009).

**Rule 6. Plant competition for water**

The model assumes that competition between grasses and shrubs occurred through soil water as an intermediary (sensu Goldberg et al. 1999). Water acquisition depends on the root distribution and the biomass of each growth-form (effect sensu Goldberg et al. 1999). The rate of biomass accumulation depends on different relationship between water availability and growth rate (response sensu Goldberg et al. 1999).

DINAQUA calculated the soil water content for six soil layers and water transpiration by shrubs and grasses for $10 \times 10$ combinations of shrub and grass biomass and under certain climate and soil conditions (section ‘Links between the vegetation dynamic and water balance models’ in main text for details). Because the cell size used in DINVEG is small in comparison to the area explored by roots, we considered an area of $3 \times 3$ cells (i.e. the kernel of a moving window) around the focal cell to estimate the water inputs to the vegetation model. This area was selected according to previous competition studies and lateral root
distribution (Aguiar et al. 1992, Aguiar and Sala 1994, Leva et al. 2009). For shrubs occupying more than one cell the estimated biomass results to integrate the different moving windows for each shrub-cell. DINVEG calculates the biomass of grasses and shrubs in the moving window around a focal cell and DINAQUA calculates the proportion of water transpired by grasses and shrubs and the water remaining in each soil layer. Also, DINVEG calculated the proportion of water transpired by the focal plant and neighbours in accordance with the plant biomass distribution. In this way, DINVEG and DINAQUA determined the competition effects between plants. 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 controls seedling emergence and recruitment. Ultimately, competition among adult grasses or shrubs depended on plant biomass and specific requirements for growth (rule 5) or seed production (rule 9).

*Rule 7. Plant competition for space*

In addition to plant water competition that affects all demographic processes, field observations of dead tufts under shrubs suggested a simple spatial competition effect. In order to implement this effect we included a probability $p_{\text{over}}$ of a shrub growing into a neighboring cell occupied by a grass. This probability is equal to 0 for grasses and is greater than 0 for specific shrubs ($Mulinum > Senecio > Adesmia$). Overtopped grasses died at the end of the following growing season.

*Rule 8. Mortality*

The annual mortality $p_m$ was the sum of a species-specific annual mortality rate $p_{mk}$ and a factor $p_{\text{hist}}$ that considered stress of plants determined by their growth history:

$$p_m = p_{mk} + p_{\text{hist}}$$  \hspace{1cm} (A8a)
The factor $p_{\text{hist}}$ subsumes the influence of plant age, spatial plant competition, and the impact of drought and/or water competition in limiting plant growth. The rationale behind is that plants that had slow growth during the past three years ($g_r$ is the average growth during the last three years and $t_{gr}$ the species-specific growth threshold) are stressed and should have a higher annual mortality probability (Hawkes 2000, Wiegand et al. 2004). We also assumed that older plants (i.e. $age > 0.75 \cdot age_{\text{max}}$) have a higher mortality rate $p_{mk}$. Note that overgrowing by shrubs may additionally increase the mortality rate of grasses (rule 7).

\begin{equation}
    p_{\text{hist}} = \begin{cases} 
    0 & g_r \geq t_{gr} \\
    1 - \frac{g_r}{t_{gr}} & g_r < t_{gr}
\end{cases}
\end{equation}

(A8b)

\begin{equation}
    g_r = \frac{grw_{-1} + grw_{-2} + grw_{-3}}{3}
\end{equation}

(A8c)

Rule 9. Seed production

The model assumes that seed production occurred for all species in December if water transpiration requirements were met and plant biomass exceeded a species-specific minimum value. Seed production

\[ Seeds(s_{\text{max}}, v, P_s) = s_{\text{max}} \times v \times p_s \]

(A9a)

depends on a species-specific maximum number of seeds ($s_{\text{max}}$), seed viability ($v$), and on annual water condition via a factor

\[ p_s(transp, t_s) = \frac{1}{1 + \exp\left[-(transp-t_s)\right]} \]

(A9b)

which was based on annual transpiration ($transp$) and a species specific threshold $t_s$. The minimum plant biomass for seed production and maximum number of viable seeds were estimated through field measurements of size, plant biomass, and number of seeds (Rotundo 2005, Cipriotti 2006, Cipriotti and Aguiar 2010), and published data on viability and weight.
of seeds for dominant grass and shrub species (Soriano 1960, Soriano and Sala 1986, Fernández et al. 2002).
Table A1. Summary of equations, parameters and bibliographic sources included in DINVEG to simulate the vegetation dynamics.

<table>
<thead>
<tr>
<th>Processes</th>
<th>Equations</th>
<th>Parameters</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seed dispersal</td>
<td>$p_{ij}(d_{ij},d_{max}) = \exp\left(\frac{-d_{ij}}{d_{max}}\right)$</td>
<td>$d_{max}$, Max species-specific seed dispersal distance (depends on direction EW or NS) [cells].</td>
<td>Aguiar and Sala 1997, Fernández et al. 2002</td>
</tr>
<tr>
<td></td>
<td>$\sum d_{ij} \exp\left(\frac{-d_{ij}}{d_{max}}\right)$</td>
<td>$d_{ij}$, Distance between the individual center and any cell (i,j) from its dispersal kernel [cells].</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$p_{2ij}$, Probability for any spatial cell to contain seeds.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil seed bank</td>
<td>$\text{Seeds}<em>{ij} = p</em>{2ij} \times \text{Seeds}_{i}$</td>
<td>$p_{2ij}$, Probability to contain seeds of cell (i,j) from the dispersal kernel of $k^b$ plant.</td>
<td>Bertiller and Aloia 1997, Bertiller 1998, Rotundo and Aguiar 2004, Rotundo and Aguiar 2005,</td>
</tr>
<tr>
<td></td>
<td>$\text{Seeds}<em>{ij} = \sum</em>{k=1}^{n} \text{Seeds}_{ij,k}$</td>
<td>$\text{Seeds}_{ij,k}$, Number of seeds produced by $k^b$ plant [n].</td>
<td>Rotundo 2005.</td>
</tr>
<tr>
<td></td>
<td>$\text{Seeds}<em>{ij} = \text{Seeds}</em>{ij}(t+1) = \text{Seeds}<em>{ij}(t) \times (1 - p</em>{out})$</td>
<td>$\text{Seeds}_{ij,k}$, Number of seeds in cell (i,j) from the dispersal kernel of the $k^b$ plant [n].</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$p_{out}$, Annual specific extinction rate from the soil seed bank.</td>
<td></td>
</tr>
<tr>
<td>Seedling Emergence</td>
<td>$p_{s}(\text{swc}<em>i, t</em>{swc}) = \frac{1}{1 + \exp\left[\frac{t_{swc} - t_s}{\text{swc}_i}\right]}$</td>
<td>$\text{swc}_i$, Soil water content in the top soil layer (0-10 cm) [mm].</td>
<td>Soriano 1960, Soriano and Sala 1983, 1986, Aguiar et al. 1992, Fernández et al. 1992,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$t_s$, Soil water content threshold affecting seedling emergence [mm].</td>
<td>Bisigato and Bertiller 1999, Cipriotti and Aguiar 2005, Cipriotti et al. 2008, Pazos and</td>
</tr>
<tr>
<td>Seedling Recruitment</td>
<td>$p_r(\text{swc}<em>i, t</em>{fac}) = \frac{\text{fac}}{1 + \exp\left[\frac{t_{fac} - t_s}{\text{swc}_i}\right]}$</td>
<td>$\text{swc}_i$, Soil water content for the $i^b$ soil layer [mm].</td>
<td>Aguiar et al. 1992, Fernández et al. 1992, Aguiar and Sala 1994, Bisigato and Bertiller 2004,</td>
</tr>
<tr>
<td></td>
<td>$\text{fac} = \begin{cases} 1 &amp; \text{if } \text{sh} \leq 500\text{g} \ \frac{0.5 + \text{sh}}{1000} &amp; \text{if } \text{sh} &gt; 500\text{g} \end{cases}$</td>
<td>$t_r$, Soil water content threshold affecting plant recruitment [mm].</td>
<td>Cipriotti and Aguiar 2005, Cipriotti et al. 2008.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$p_r$, Aerial facilitation effect from shrubs to plant recruitment [mm].</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$\text{sh}$, Shrub biomass [g].</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$p_{pi}$, Probability of plant recruitment.</td>
<td></td>
</tr>
<tr>
<td>Plant Growth</td>
<td>$G_p(age, g_{max}, g_{age_{max}}) = g_{max} \exp\left[-0.1 \frac{age-0.33 \text{age}<em>{max}}{0.375 \text{age}</em>{max}}\right]$</td>
<td>$g_{max}$, Species specific max growth under no resource constraints [g-month$^{-1}$].</td>
<td>Soriano and Sala 1983, Fernández et al. 1991, Golluscio and Sala 1993, Parsuelo and</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$g_{age_{max}}$, Species specific life-span [years].</td>
<td>2009, Ohatibia et al. 2010, Nuñez unpub.</td>
</tr>
<tr>
<td></td>
<td>$p_g(\text{transp}, t_{transp}) = \frac{1}{1 + \exp\left[\frac{-t_{transp} - t_{g}}{\text{transp}}\right]}$</td>
<td>$\text{transp}$, Plant transpiration rate [mm-day$^{-1}$].</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$g = P_g \times G_p$</td>
<td>$t_g$, Transpiration threshold affecting plant growth [mm-day$^{-1}$].</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$p_{pg}$, Probability of plant growth.</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$g$, Effective plant growth [g-plant$^{-1}$-month$^{-1}$].</td>
<td></td>
</tr>
<tr>
<td>Plant Mortality</td>
<td>$P_{m} = P_{mak} + P_{init}$</td>
<td>$p_{m}$, Species specific mortality annual rate [%].</td>
<td>Hawkes 2000, Wiegand et al. 2004, Cipriotti 2006, Nuñez unpub.</td>
</tr>
<tr>
<td></td>
<td>$P_{init} = \begin{cases} 0 &amp; \frac{\text{gr}}{t_{e}} \geq \frac{\text{g}<em>{e}}{t</em>{e}} \ 1 - \frac{\text{gr}}{\text{g}<em>{e}} &amp; \frac{\text{gr}}{t</em>{e}} &lt; \frac{\text{g}<em>{e}}{t</em>{e}} \end{cases}$</td>
<td>$p_{init}$, Annual plant mortality rate [%].</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\text{gr} = \text{gr}<em>{w1} + \text{gr}</em>{w2} + \text{gr}_{w3}$</td>
<td>$gr_e$, Average plant growth in the last three previous growing seasons [g].</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$t_{e}$, Annual plant growth threshold affecting plant mortality [g-plant$^{-1}$-year$^{-1}$].</td>
<td></td>
</tr>
<tr>
<td>Plant Seed output</td>
<td>$\text{Seeds}(s_{max}, v, P_s) = s_{max} \times v \times P_s$</td>
<td>$s_{max}$, Species specific max seed output [n].</td>
<td>Soriano and Sala 1986, Fernández et al. 2002, Rotundo 2005.</td>
</tr>
<tr>
<td></td>
<td>$p_{transp}(t_{transp}) = \frac{1}{1 + \exp\left[\frac{-t_{transp}}{\text{transp}}\right]}$</td>
<td>$v$, Species specific seed viability [%].</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$p_s$, Probability of seed output.</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$\text{transp}$, Plant transpiration rate [mm-day$^{-1}$].</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$t_{transp}$, Transpiration threshold affecting plant seed output [mm-day$^{-1}$].</td>
<td></td>
</tr>
</tbody>
</table>
Table A2. Model parameters for the five species simulated in the DINVEG model. Parameter ranges were derived for ungrazed Patagonian Occidental grass-shrub steppes under the current climatic conditions.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Equation**</th>
<th>Mulinum</th>
<th>Adesmia</th>
<th>Senecio</th>
<th>Poa</th>
<th>Bromus</th>
<th>Stipa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seed dispersal</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximal dispersal distance E-W (m)</td>
<td>(d_e^{\text{max}})</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Maximal dispersal distance N-S (m)</td>
<td>(d_n^{\text{max}})</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>Soil seed bank</td>
<td></td>
<td>2–3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual decay rate (%)</td>
<td>(p_{\text{ext}})</td>
<td>20</td>
<td>30</td>
<td>20</td>
<td>60</td>
<td>40</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>Seedling emergence</td>
<td></td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Emergence soil water threshold* (mm)</td>
<td>(t_e)</td>
<td>6</td>
<td>7.5</td>
<td>6.5</td>
<td>4.5</td>
<td>5</td>
<td>3.7</td>
<td></td>
</tr>
<tr>
<td>Plant recruitment</td>
<td></td>
<td>5–6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Recruitment soil water threshold* (mm)</td>
<td>(t_r)</td>
<td>8</td>
<td>9.5</td>
<td>8.5</td>
<td>6.2</td>
<td>6.5</td>
<td>5.5</td>
<td></td>
</tr>
<tr>
<td>Plant growth</td>
<td></td>
<td>7a–b</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum plant size (cells)</td>
<td>-</td>
<td>21</td>
<td>21</td>
<td>21</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Life span (years)</td>
<td>(a_{e}^{\text{max}})</td>
<td>30</td>
<td>60</td>
<td>30</td>
<td>20</td>
<td>20</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>Maximum biomass (kg ind(^{-1}))</td>
<td>-</td>
<td>4</td>
<td>5</td>
<td>3</td>
<td>0.2</td>
<td>0.15</td>
<td>0.25</td>
<td></td>
</tr>
<tr>
<td>Potential plant growth (g ind(^{-1}) year(^{-1}))</td>
<td>(g_{\text{max}})</td>
<td>200</td>
<td>100</td>
<td>150</td>
<td>16</td>
<td>10</td>
<td>20</td>
<td></td>
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<tr>
<td>Growth transpiration threshold* (mm ind(^{-1}) year(^{-1}))</td>
<td>(t_{tr})</td>
<td>12</td>
<td>17</td>
<td>12</td>
<td>7</td>
<td>10</td>
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<tr>
<td>Overgrowth probability (%)</td>
<td>(p_{\text{over}})</td>
<td>40</td>
<td>10</td>
<td>20</td>
<td>na</td>
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Table A2 continued

<table>
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<tr>
<th>Symbol</th>
<th>Equation**</th>
<th>Mulinum</th>
<th>Adesmia</th>
<th>Senecio</th>
<th>Poa</th>
<th>Bromus</th>
<th>Stipa</th>
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<tr>
<td>Plant mortality</td>
<td>8a–c</td>
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<tr>
<td><strong>Annual mortality rate</strong></td>
<td>$P_{mk}$</td>
<td>15</td>
<td>8</td>
<td>20</td>
<td>10</td>
<td>15</td>
<td>10</td>
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<tr>
<td><strong>Mortality growth threshold (g ind$^{-1}$ year$^{-1}$)</strong>†</td>
<td>$t_{gr}$</td>
<td>10</td>
<td>5</td>
<td>15</td>
<td>5</td>
<td>5</td>
<td>4</td>
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<tr>
<td>Plant seed output</td>
<td>9a–b</td>
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<td></td>
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<tr>
<td><strong>Maximum seed output</strong></td>
<td>$s_{max}$</td>
<td>8000</td>
<td>4000</td>
<td>12000</td>
<td>1500</td>
<td>200</td>
<td>1000</td>
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<tr>
<td><strong>Seed viability (%)</strong></td>
<td>$\nu$</td>
<td>50</td>
<td>50</td>
<td>40</td>
<td>30</td>
<td>80</td>
<td>50</td>
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<tr>
<td><strong>Minimum biomass for reproduction (kg ind$^{-1}$)</strong></td>
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<td>0.75</td>
<td>1</td>
<td>0.75</td>
<td>0.07</td>
<td>0.05</td>
<td>0.11</td>
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<tr>
<td><strong>Seed transpiration threshold</strong> (mm ind$^{-1}$ year$^{-1}$)</td>
<td>$t_{s}$</td>
<td>26</td>
<td>28</td>
<td>24</td>
<td>23</td>
<td>22</td>
<td>28</td>
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</tbody>
</table>

* parameters included in the inverse calibration
** see details of rules and equations in Appendix A1
na: not applicable (see rule 7 in Appendix A1)
† if the plant has grown during the last three years less than the threshold it dies
Appendix A2
Details on summary statistics and their observed ranges

We evaluated the performance of the different model parameterizations by comparing the output of the model against a set of summary statistics derived from independent field data and/or published data. We used basic summary statistics that characterized the observed vegetation at our study site in a non-spatial way and detailed summary statistics that quantified additionally spatial aspects and size distributions of individual plants.

Most of our summary statistics are given by one value (e.g. shrub cover, density or biomass). Because these data are subject to observation error and stochastic variability within the study site we defined match of the basic summary statistics (i.e. cover, densities and ANPP) based on conservatively wide ranges derived from field observations. Note that we aim to exclude with each individual summary statistics only model parameterizations that produce model behavior that can be clearly excluded. This is also necessary to avoid a bias model fitting. However, because each summary statistic excludes different model parameterizations all summary statistics taken together will considerably constrain the model behaviour to allow for model parameterization (see Wiegand et al. 2004 for a detailed discussion of this issue).

Grass and shrub cover

The proportion of bare soil and the proportion of area covered by the two dominant life forms are basic features of the Patagonian steppes that are related with grazing and degradation (Aguiar et al. 2005, Cipriotti and Aguiar 2005). We accepted a range in total cover between 30% and 65% to represent the range of conditions that typically occur in the Patagonian Occidental grass-shrub (Golluscio et al. 1982). We accepted ranges in grass and shrub cover between 15–40% and 5–20%, respectively (Golluscio et al. 1982).
Grass and shrub densities

The individual-based model allows us to use the density of shrubs and grasses as summary statistics. We accepted densities ranging between 9–13 and 0.4–1 plants·m$^{-2}$ for grasses and shrubs, respectively, as reported by Aguiar et al. (2005), Cipriotti and Aguiar (2005, 2010).

Species-specific densities

Shifts in species composition may occur in response to grazing and are therefore important indicators of degradation. For the six dominant grass and shrub species we determined acceptance ranges based on different field studies (Oesterheld and Oyarzábal 2004, Aguiar et al. 2005, Cipriotti and Aguiar 2005). For palatable grasses (*Bromus* and *Poa*) we accepted densities between 2 and 8 plants·m$^{-2}$, and for less palatable species (*Stipa* spp.) we accepted densities ranging between 5–7 plants·m$^{-2}$. For shrubs, we accepted densities between 0.2–0.5, 0.1–0.4 and 0.05–0.3 m$^{-2}$ for *Mulinum*, *Senecio* and *Adesmia*, respectively.

Annual productivity of grasses and shrubs

Annual net primary productivity (ANPP) is an important part of ecosystem functioning that can be used to characterize vegetation additionally to cover and species densities. We used the average grass and shrub ANPP and the range of ANPP for grass and shrub individuals as summary statistics. The model should simulate annual net primary productivity values (ANPP) of grasses and shrubs that agree with field measures in the study site during the last 20 years (Fernández et al. 1991, Jobbágy and Sala 2000). We accepted average ANPP values for grasses and shrubs if they ranged between 26.5 g·m$^{-2}$·year$^{-1}$ and 85.8 g·m$^{-2}$·year$^{-1}$. Data on the range of fresh biomass measured on adult shrub and grass individuals (Oñatibia et al. 2010) ranged between 50 to 250 g·plant$^{-1}$, for grass tussocks and 500 to 5 000 g·plant$^{-1}$ for shrub individuals, depending on plant species and age.
Cover of high-cover patches

Grasses and shrubs in the Patagonian steppes are spatially organized as a two-phase mosaic comprising shrubs surrounded by a ring of grasses and scattered grass tussocks in a matrix of bare soil (Soriano et al. 1994, Cipriotti and Aguiar 2005). We used the cover of high-cover patches as summary statistic to evaluate detailed aspects of interactions among shrub and grass individuals. According to Cipriotti and Aguiar (2005) the cover of high-cover patches ranged in areas excluded from grazing between 18% and 38%.

Size-structure of shrubs

The size distribution of shrubs provides more detailed information on the functioning of the steppe. To determine the size structure of the three dominant shrub species we used data from different permanent field plots (Cipriotti and Aguiar 2010, Oñatibia et al. 2010). To this end we first fitted an empirical relationship between the diameter and the biomass of 30 shrubs harvested at the field (Oñatibia et al. 2010), and used it to estimate the biomass for all shrubs measured at field plots. These data were use to estimate a cumulative frequency distribution to then compare the simulated data against the field pattern (Oñatibia et al. 2010).

Spatial shrub-shrub and shrub-grass aggregation

Additional very detailed characteristics of spatial structure of the shrub grass community are the significant spatial aggregations of adult shrubs (of all species joined) at short distances (0.5–1 m) and the attraction of grass (of all species joined) around shrubs at short distances (0.1–0.7 m) reported from these steppes (Aguiar et al. 2005, Wiegand et al. 2006, Cipriotti and Aguiar 2010). To test for occurrence of these spatial patterns in the simulated data we calculate the uni-variate and bi-variate O-ring statistics (Wiegand and Moloney 2004). As
null model for univariate analysis of shrubs we used random distribution of shrubs (CSR null model, Appendix A3) and as null model for the bivariate analysis we kept the location of the shrubs but distributed the grass tussocks randomly over the space not occupied by shrubs (for details see Appendix A3). Then, we standardized the *O-ring* statistics relative to the maximum (i.e. a pair correlation function) for each spatial point pattern analysis with the aim to make valid the comparisons across simulated and field data and avoid differences according to the extent and grain from field and simulation spatial surveys.
Appendix A3

Spatial pattern analysis

To characterize the spatial distribution of shrubs or the spatial associations between grasses and shrubs, we used techniques of spatial point pattern analysis and the $O$-ring statistics (Wiegand and Moloney 2004) as summary statistic. To characterize the spatial pattern of shrubs we represented a shrub by its central cell and used the univariate O-ring statistic $O(r)$ which is the proportion of the shrubs at distance $r$ away from an average shrub of the pattern (i.e. a neighborhood density function). To estimate the $O$-statistic, a ring of radius $r$ and 1 cell width ($\Delta r = 0.2 \times 0.2$ m) was centered on shrub and the number of shrub neighbors within that ring is recorded. For $n_1$ shrubs distributed in an area $A$, the density ($d = n_1 / A$) is the expected proportion of shrubs per unit cell. If the shrubs are aggregated at a given spatial scale $r$ the neighborhood density is larger than the density (i.e. $O(r) > n_1 / A$).

To characterize the spatial association of grasses around shrubs we used a slightly more complex approach because studying facilitation in the ring requires maintenance of the explicit shapes of the shrubs. For this purpose we used techniques for spatial analysis of objects of real shape and finite size presented in Wiegand et al. (2006). To represent shrubs we used all cells they occupy and calculated the bivariate O-ring statistic $O_{12}(r)$. This summary statistic is the proportion of grass cells at distance $r$ away from an average cell covered by a shrub. If the grasses are at a given spatial scale $r$ positively associated to shrubs, the neighborhood density $O_{12}(r)$ of grasses around shrub cells will larger than the overall density of grass cells (i.e. $O_{12}(r) > n_2 / A$).

To test if the observed summary statistics departed from the null model of randomly distributed shrubs or grasses, we conducted Monte Carlo simulations under the null model of complete spatial randomness (CSR) and generated simulator envelopes ($n = 19$, alpha = 0.05). For the univariate analysis we randomized the pattern of the central cell of the shrubs and in
the bivariate case we kept the full shrub pattern fixed, but randomize the grass individuals over all cells not occupied by shrubs.
References


Perea, R. 2005. Dispersión secundaria de diásporas de gramíneas patagónicas amenazadas por


