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Understanding the long-term spatial dynamics of a semiarid grass-shrub steppe through inverse parameterization for simulation models

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Desertification threatens 70% of all dry lands worldwide by diminishing the provision of economic and ecosystem services. However, since long-term vegetation dynamics of semiarid ecosystems are difficult to study, the opportunities to evaluate desertification and degradation properly are limited. In this study, we tailored, calibrated and tested a spatially-explicit simulation model (DINVEG) to describe the long-term dynamics of dominant grass and shrub species in the semiarid Patagonian steppe. We used inverse techniques to identify parameterizations that yield model outputs in agreement with detailed field data, and we performed sensitivity analyses to reveal the main drivers of long-term vegetation dynamics. Whereas many parameterizations (10–45%) matched single field observations (e.g. grass and shrub cover, species-specific density, aboveground net primary production [ANPP]), only a few parameterizations (0.05%) yielded simultaneous match of all field observations. Sensitivity analysis pointed to demographic constraints for shrubs and grasses in the emergence and recruitment phase, respectively, which contributed to balanced shrub-grass abundances in the long run. Vegetation dynamics of simulations that matched all field observations were characterized by a stochastic equilibrium. The soil water content in the top layer (0–10 cm) during the emergence period was the strongest predictor of shrub densities and population growth rates and of growth rates of grasses. Grasses controlled the shrub demography because of the resource overlap of grasses with juvenile shrubs (i.e. water content in the top layer). In agreement with field observations, ecosystem function buffered the strong variability in precipitation (a simulated CV in ANPP of 16% vs CV in precipitation of 33%). Our results show that seedling emergence and recruitment are critical processes for long-term vegetation dynamics in this steppe. The methods presented here could be widely applied when data for direct parameterization of individual-based models are lacking, but data corresponding to model outputs are available. Our modeling methodology can reduce the need for long-term data sets when answering questions regarding community dynamics.

According to the United Nations (UNEP, Agenda 21), approximately 70% of all dry lands (representing a total area of 3.6 billion hectares, a quarter of the total land surface of the earth) is endangered by desertification. The principal causes are human land use activities and climatic variability in combination with complex ecosystem dynamics (Reynolds and Stafford Smith 2002, Reynolds et al. 2007). Replacement of grasses by woody plants (trees or shrubs) and changes in the spatial organization of arid rangelands have promoted major changes in biodiversity and ecosystem functioning (e.g. productivity, decomposition and carbon storage, nitrogen and water dynamics) (Schlesinger et al. 1990, Scholes and Archer 1997, Jackson et al. 2000), jeopardizing the sustainability of animal husbandry (Sharp and Whittaker 2003). Therefore, understanding the processes governing coexistence of different life forms and emergence of spatial patterns is important for predicting how semiarid plant communities respond to land use (e.g. grazing) and climate change (Sankaran et al. 2004, Tietjen and Jeltsch 2007).

However, understanding patterns and processes of vegetation dynamics in semiarid rangelands is an inherently difficult task due to several factors such as the mismatch in time scales between observation and vegetation change, the occurrence of complex event-driven dynamics, spatial heterogeneities, and non-equilibrium ecosystem dynamics (Wiegand et al. 1995, Jeltsch et al. 2000, Briske et al. 2003, Peters and Havstad 2006). As a consequence, a purely observational or experimental approach is often not feasible. One possibility to overcoming these limitations is the use of individual-based and spatially-explicit computer simulation models (Wiegand et al. 1995). This approach provides understanding of arid rangeland dynamics by focusing on the processes and mechanisms that drive vegetation dynamics at the level of individual plants. Although there is little availability of long-term field data on full vegetation dynamics, short-term studies often provide data on seedling recruitment, plant growth, reproduction, seed dispersal, and plant–plant interactions. The basic approach is to incorporate the data on individual plant behavior in the form of simple rules into an individual-based model (IBM; Grimm and Railsback 2005) that simulates the fate and the interactions of individual plants in a spatially-explicit context (within the community), the sum of which represents community dynamics (Wiegand et al. 1995). This approach addresses one of the major challenges in ecology; understanding how processes at small scales determine patterns at large scales (Levin 1992).

However, data for direct parameterization of individual-based models are usually not available for all parameters and there is often uncertainty in the formulation of mechanisms and processes (Wiegand et al. 2003, 2004a, Grimm and Railsback 2005, Hartig et al. 2011). One promising approach for model parameterization is to take advantage of the ability of individual-based models to generate outputs at larger scales such as community composition or average plant cover (called 'patterns'; Wiegand et al. 2003, Grimm et al. 2005). The task then is to find model structures and parameterizations that generate (larger-scale) outputs consistent with the corresponding field data (Wiegand et al. 2004a, Hartig et al. 2011). However, model fitting is quite challenging in the case of computationally-demanding models like IBMs (Wiegand et al. 2003, DeAngelis and Mooij 2003, Grimm et al. 2005, Martínez et al. 2011). Additionally, there is no established approach that would parallel model selection for statistical models (Burnham and Anderson 2002; but see Wood 2010, Hartig et al. 2011, Martínez et al. 2011).

To overcome these difficulties, we used inverse techniques of pattern-oriented modeling (Wiegand et al. 2003, 2004a, Grimm et al. 2005, Kramer-Schadt et al. 2007, Hartig et al. 2011) to fit a model to larger scale data. This approach required model simulations over the entire parameter space. Suitable parameterizations were detected by a multiple filtering mechanism that accepts parameterizations only if they yield simultaneous agreement with observed data in several outputs of the model and a model with severe structural errors will fail to yield agreement in some of the model outputs (Martínez et al. 2011). If the observed data provide sufficient information on system dynamics and the model shows no severe structural errors, the observed data constrain not only the model outputs but also the internal model functioning to produce reasonable behavior (Wiegand et al. 2004a). Under this assumption, we can study the internal model behavior to better understand the main processes governing the ecological system under study and use the model to make large-scale predictions.

In this study, we integrated the abundant field data on the population dynamics and spatial organization of the semiarid Patagonian grass-shrub steppe collected during the last 50 years into a spatially explicit and individual-based model. The vegetation model explicitly separates belowground and aboveground processes by including a previously developed soil water balance model (DINAQUA; Paruelo and Sala 1995). Soil water dynamics are the main limiting factor for the steppes. The ultimate goals of our model were to understand the role of different plant processes on the long-term dynamics and spatial organization of vegetation in Patagonian grass–shrub steppes and to identify the most sensitive processes at the plant level that would allow us to detect degradation at early stages. However, before this could be accomplished we needed to parameterize and test the model against multiple field data. Therefore, we focused on three specific tasks. In the first step, we evaluated the ability of our model to generate dynamics in accordance with detailed field data and determined the values of unknown parameters using inverse parameterization techniques. In the second step, we performed a global sensitivity analyses to identify the main controls of vegetation with special emphasis on the shrub-grass balance. Finally, we characterized the emerging long-term dynamics for simulations that agreed with the available field data.

Methods

Study area

The model was based on the semiarid grass-shrub steppe of the Occidental District of the Patagonian Phytogeographic Province (León et al. 1998). This vegetation district covers approximately 150 000 km^2 between the SubAndean and the Central District of Patagonia. Most of the information included in our model was obtained from the INTA Rio Mayo Experimental Field Station and neighboring ranches in Chubut, southwestern Patagonia (45°41′S, 70°16′W, 500 m a.s.l.), Argentina. The mean annual rainfall (MAP) at this site is 153 mm (n = 37, 1961–1998), ranging between 47 and 230 mm (driest and wettest year on record, respectively), and mostly (ca 73%) falling during the autumn and winter (March to September; Jobbágy et al. 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 with high intensities. Soils have an upper sandy layer with 50% cobbles and pebbles, and a cement-like stony layer (i.e. CO_3Ca) at 0.45–0.6 m depth (Calciorthids, Paruelo et al. 1988).

Almost 50% of soil cover is bare ground and the rest is covered by tussock grasses (26 ± 5% SE), shrubs (12 ± 4%), and litter (5%) (Golluscio et al. 1982, Fernández-Alduncin et al. 1991). The dominant tussock grass species are *Stipa speciosa*, *S. humilis* and *Poa ligularis*, whereas *Bromus pictus* is a sub-dominant bunch grass species. The *Stipa* spp. species are generally less palatable and have higher C:N ratios than *P. ligularis* and *B. pictus* (Semmartin et al. 2004). The dominant shrub species are *Mulinum spinosum*, *Senecio filaginoides* and *Adesmia volckmanni*. Aboveground primary production ranges between 10 and 120 g m^{-2} year^{-1}

(annual mean 56 g m^{-2} $year^{-1}$; Jobbágy and Sala 2000). Grasses and shrubs account for 53% and 43% of total aboveground net primary production [ANPP], respectively, while a heterogeneous group of forbs account for the rest.

Model overview

We tailored an individual-based, spatially-explicit model (DINVEG) to simulate the vegetation dynamics of the grass-shrub steppe. DINVEG simulates the spatial and temporal dynamics of the dominant grasses *Stipa* spp., *P. ligularis*, *B. pictus* and the dominant shrubs *M. spinosum*, *S. filaginoides* and *A. volckmanni*. These species cover the main functional roles present in the steppe and can be thought of as plant functional types. In the simulation of vegetation dynamics, most processes were conditioned by soil water, the main limiting resource in this plant community. To describe the soil water dynamics, we integrated a previously developed soil water balance model (DINAQUA; Paruelo and Sala 1995) into DINVEG. To present DINVEG, we followed the standard ODD protocol for individual-based models suggested by Grimm et al. (2006). This protocol comprises three major blocks: overview, design concepts and details. In the following sections, we present the overview and design concepts. The details, rules and formulas used in the model are presented in the Supplementary material Appendix A1.

Purpose

The purpose of the modeling study was to understand the role of different plant processes on the long-term dynamics and spatial organization of vegetation in arid ecosystems.

Scales

We simulated a 50×50 m steppe plot with a spatial resolution of 0.2×0.2 m (cell size). One cell corresponded to the approximate size of one grass tuft, but shrubs could occupy several cells. We selected this resolution to adequately represent the ecologically relevant processes (e.g. facilitation, competition, seed dispersal). In addition, the model simulated seven vertical layers and the seed soil bank. The first layer represented the aboveground occupation by shrubs or grasses, and six 0.1 m thick belowground layers contained the root occupation and water dynamics in the soil layers (i.e. 0–0.1 m, 0.1–0.2 m, 0.2–0.3 m, 0.3–0.4 m, 0.4–0.5 m, 0.5–0.6 m). This is the relevant scale for the soil characteristics, water dynamics, and root systems for the Occidental Patagonian steppes (Paruelo et al. 1988, Paruelo and Sala 1995). DINVEG uses a monthly time step, whereas DINAQUA uses a daily time step (Paruelo and Sala 1995). Therefore, we integrated the daily information from DINAQUA to a monthly time step.

State variables

DINVEG comprises four types of objects: grass tufts, shrubs, the soil seed bank, and soil water. It simulates the spatial and temporal dynamics of the first three objects, whereas soil water dynamics were modeled by DINAQUA (see section 'Links between the vegetation dynamic and water balance models').

Grass tufts were characterized by an identity number, species (*Stipa* spp., *P. ligularis* or *B. pictus*), location (*x*, *y* coordinates), age, stage (i.e. seedling, adult, dead), aboveground plant biomass (g), and growth history (a record of individual growth during the last three years). According to sizes observed in the field, grass tufts occupy only one cell in the model. Shrubs were additionally characterized by size (number of cells), and the area immediately adjacent to the shrub in which shrubs may exert influence on grass seedlings (i.e. the grass ring or zone of influence) (Aguiar and Sala 1994). Based on observed shrub sizes, we allowed shrub size to vary between one and a maximum of 21 cells.

The soil seed bank records the number of viable seeds and seedlings per species for each cell. Soil water is estimated by DINAQUA for each cell at six different depths as the volumetric soil water content. DINAQUA considers the grass and shrub biomass within the nine cell quadrat around the focal cell, as well as monthly radiation, daily precipitation and daily temperature data (see 'Links between the vegetation dynamic and water balance models').

Process overview and scheduling

For each individual, we simulated the main life history events of seed production, seed dispersal, plant growth, and mortality (Fig. 1). For non-occupied cells, we considered seedling emergence and recruitment, and for all cells in the grid we simulated the soil seed bank dynamics (Fig. 1). Each life history event occurred during particular months according to the schedule observed in the field. Because the Patagonian steppe is a water-limited ecosystem we assumed that the occurrence of the emergence and recruitment events depended on water content in specific soil layers, and growth and seed production on plant transpiration (Fig. 1), both calculated by DINAQUA. Plant mortality was modeled with a species-specific annual mortality rate, which increased under water stress. Seed dispersal followed dispersal kernels parameterized from field data that considered the dominant wind direction. In the Supplementary material Appendix A1 (Model details), we provide a detailed description of the different rules and equations that govern the model dynamics in DINVEG.

Design concepts

Population and community dynamics emerge from the behavior of individual plants, and the life history of the different species is represented by the empirical rules set. DINVEG describes three types of interactions between individuals: belowground water competition, aerial facilitation in the ring (i.e. shrub neighboring cells), and mortality of grass tufts in the ring if the shrub increases in size and overgrows grasses. The majority of model parameters were directly estimated from the literature or unpublished data (Supplementary material Appendix A1 Table A1). However, for uncertain parameters we used an inverse parameterization approach (Wiegand et al. 2003, 2004a, Hartig et al. 2011) based on data from several vegetation studies in the

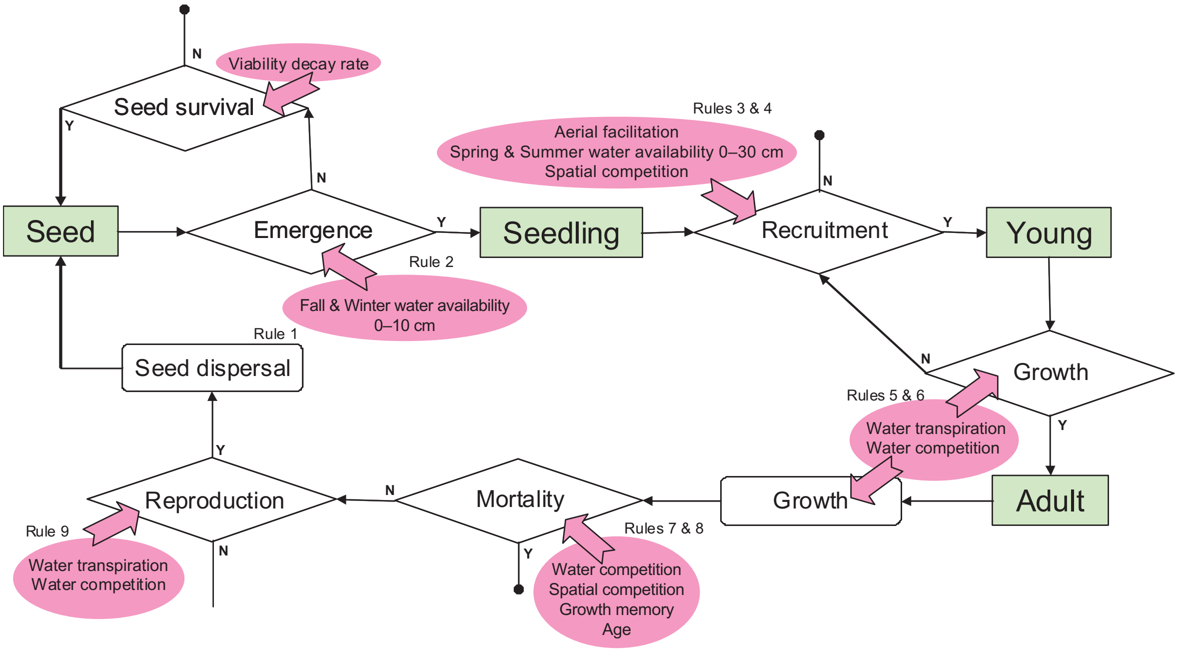

Figure 1. Flow chart of the DINVEG model. The green boxes indicate the different individual stages. Diamonds represent decision processes and rectangles are alternatives processes. Black thin solid arrows represent demographic transitions, whereas pink thick arrows represent the main controls for each process. Soil water content and transpiration control population process such emergence, recruitment, plant growth, mortality and reproduction.

study area (see section 'Model parameterization'). We also conducted a local sensitivity analysis of main output variables with respect to the model parameters.

Initialization

We constructed a 200-year rainfall and temperature time series by randomizing a record of 31 years of daily precipitation and temperature from the study area. A randomization procedure was used to simulate climatic series that considered the observed autocorrelation between years as autoregressive models and conserved mean values and inter-annual variability (i.e. MAP = 153 mm year^{-1} and a coefficient of variation $\left[CV = \frac{SD}{\bar{X}}100\right]$ of 33%).

The DINVEG rules rely heavily on inputs from the soil water balance model DINAQUA such as soil water content of the *i*th soil layer (swc_i) or plant transpiration (*transp*) (Supplementary material Appendix A1 Table A1). However, direct coupling of DINAQUA and DINVEG by calling DINAQUA whenever a DINVEG rules requires an input would be computationally ineffective. We therefore used an alternative approach and generated a data bank that contained the monthly values of soil water content swc_i and plant transpiration *transp* for all DINAQUA input parameters (such as ANPP) that may occur for the selected climatic series in this steppe. Whenever a DINVEG rules required an input DINAQUA it looked it up from the data bank. The data bank was created for a given climate time series for an array of 10 × 10 classes of grass and shrub ANPP ranging between 0–90 g m^{-2} year^{-1} (with a width of 10 g m^{-2} year^{-1}). These ANPP ranges are likely to occur in the Patagonian steppe (Jobbágy and Sala 2000). The transformation of the continuous ANPP values into the 10 discrete classes caused a small approximation error. For example, under representative conditions the approximation error yielded approximately 7% for the output variable transpiration. The approximation error was calculated as the mean of the absolute differences between the estimated transpiration based on exact ANPP values and that based on the corresponding discrete ANPP values, taken over a biomass range representative for the Patagonian steppes. Then, this mean was expressed as percentage of the output model calculated with the exact inputs.

Input

The main input variables for DINVEG are provided by the soil water balance model DINAQUA that was developed and calibrated for the Patagonian steppe (Paruelo and Sala 1995). The DINAQUA input used to simulate the soil water dynamics were organized in three blocks: climate, vegetation and soil. Climate input variables refer to monthly radiation, daily precipitation and daily temperature data which are provided by the climatic series. Vegetation input variables refer to ANPP of grasses and shrubs (simulated by DINVEG), root distribution in soil layers and transpiration parameters for each growth form (estimated for the steppe by Paruelo and Sala 1995). Soil input variables refer to the number of soil layers, their thickness, water content at field capacity and water content at wilting point for each soil layer.

Links between the vegetation dynamic and water balance models

The vegetation model simulates the demographic processes in a cell using as input the soil water content and transpiration that corresponds to the ANPP of grasses and shrubs in an area of 3 × 3 cells [i.e. the kernel of a moving window (0.6 × 0.6 m)] around the focal cell. We used the 3 × 3 cell neighborhood because the cell size used in DINVEG is small in comparison to the area explored by roots. If the cell was vacant or occupied by a seedling, the processes simulated by DINVEG were emergence and recruitment and the DINAQUA-generated inputs were soil water content of the different layers. If the cell contained an established plant, the processes were growth, seed production and mortality and the DINAQUA-generated inputs were transpiration of each growth form.

Model evaluation

Our approach is an inverse modeling technique that identifies (from a large systematic sample of the parameter space) those parameterizations that yield agreement between model outputs and corresponding field data (e.g. plant cover, species composition, spatial pattern) that are quantified by summary statistics. This approach requires the following general steps: 1) the raw data is condensed into summary statistics to capture different characteristic features of the steppe (Grimm et al. 2005, Komuro et al. 2006, Csilléry et al. 2010, Hartig et al. 2011), 2) the match between the summary statistics calculated from simulated and observed data for a given parameterization and model are then quantified, 3) a given model must then be parameterized, and 4) if alternative models are formulated, the candidate model(s) most likely given the data is selected (Wiegand et al. 2003, 2004a).

Summary statistics and their observed ranges

We used ‘basic’ summary statistics (i.e. plant cover and plant density at life-form and species level, and ANPP at life-form level) that characterized the observed vegetation state at our study site in a non-spatial way and a set of ‘detailed’ summary statistics (i.e. cover of high-cover patches, shrub size structure, shrub aggregation, and grass-shrub associations) that quantified detailed spatial patterns and size distributions of individual plants from the spatial organization of vegetation as two-phase mosaics (Table 1).

The basic summary statistics are given by average values (e.g. shrub cover, density or ANPP; Table 1). Because these data are subject to observation error and stochastic variability within the study site, we defined the match of the basic summary statistics based on conservatively wide ranges given by the observed mean ± 2 SD (Table 1). The data were derived from field observations at ungrazed sites that represent the Occidental Patagonian steppes. This criterion works well if we assume that the system is near a stochastic equilibrium. This assumption is reasonable for these Patagonian steppes (Aguiar et al. 2005), but the presence of strong temporal trends (e.g. those induced by climate change) would complicate the inverse approach. For details on the acceptance ranges and field studies see Table 1. Details on the criteria for matching basic and detailed summary statistics are provided in the Supplementary material Appendix A2, while the spatial pattern analyses are explained in Supplementary material Appendix A3.

Model parameterization

The DINVEG model contained a total of 17 parameters for each species group (Supplementary material Appendix A1 Table A2). The values of seven structural parameters for grasses (three species) and shrubs (three species) were estimated directly from published data or measured in the field (Supplementary material Appendix A1), five parameters have been indirectly determined from published or unpublished data, and five parameters that governed the life history events of emergence (t_e), recruitment (t_r), growth (t_{tr}), reproduction (t_s), and mortality (p_{mk}) were unknown and therefore varied over their entire range.

Table 1. Criteria and acceptance range for field patterns fulfillment against model outputs.

Summary statistic	Acceptance range	Bibliographic sources
Basic summary statistics		
Total cover	30–65%	Aguiar et al. 2005, Fernández-Alduncin et al. 1991, Golluscio et al. 1982
Grass cover	15–40%	
Shrub cover	5–20%	
Grass density	7–13 plants m^{-2}	Aguiar et al. 2005, Rotundo and Aguiar 2005, Oesterheld and Oyarzábal 2004
Density of *Bromus*	2–6 plants m^{-2}	
Density of *Poa*	2–4 plants m^{-2}	
Density of *Stipa* spp.	4–6 plants m^{-2}	
Shrub density	0.3–1 plants m^{-2}	Cipriotti and Aguiar 2005, Cipriotti and Aguiar 2010
Density of *Mulinum*	0.2–0.5 plants m^{-2}	
Density of *Senecio*	0.1–0.4 plants m^{-2}	
Density of *Adesmia*	0.05–0.3 plants m^{-2}	
Grass ANPP	10–49 g m^{-2} $year^{-1}$	Fernández-Alduncin et al. 1991, Jobbágy and Sala 2000
Shrub ANPP	11.3–47.3 g m^{-2} $year^{-1}$	
Total ANPP	26.5–85.8 g m^{-2} $year^{-1}$	
Detailed summary statistics		
Cover of high-cover patches	18–38%	Cipriotti and Aguiar 2005, Soriano et al. 1994
Size-structure of shrubs	no differences in the cumulative frequency distributions	Cipriotti and Aguiar 2010, Oñatibia et al. 2010
Shrub aggregation	significant at 0.5–1 m	Cipriotti and Aguiar 2010, Wiegand et al. 2006
Grass–shrub association	significant at 0.1–0.7 m	Cipriotti and Aguiar 2005, Wiegand et al. 2006

We used a hierarchical approach for estimation of the 30 parameters that were unknown and demanded first that the set of basic summary statistics describing plant cover, density and ANPP (Table 1) were met. In a second step, we compared the model outputs generated by the parameterizations that passed the criteria of the first step with the set of detailed summary statistics that were related with spatial structure. We can regard the first step as model fitting and the second step as validation because it uses independent data.

To estimate the values of the unknown parameters, we used an inverse approach similar to that described in Wiegand et al. (2004a). We systematically sampled the entire parameter space using a Latin hypercube design (Stein 1987), a stratified sampling method without replacement. The Latin hypercube results in equal probabilities for each parameter corresponding to uninformative priors in a Bayesian framework. For each unknown parameter, we selected an interval within which the parameter was varied (i.e. lower and upper limits) and divided it into 10 equidistant subintervals. We generated a total of 10 000 model parameterizations. Note that this approach estimates the unknown parameters conditionally on the current knowledge of the other parameters (and the assumed model structure), assuming no uncertainty in their values. To test this assumption we also conducted model parameterizations where all parameters were varied within their observed ranges and following their probability density function (when this information was available from bibliography or field data), instead of being fixed to their most likely value.

For each parameterization a DINVEG simulation was run for 200 years. All simulations were initialized with the same vegetation plot that represented Patagonian grass-shrub steppes in good condition (i.e. not degraded) under a typical climate series (i.e. MAP = 153 mm year^{-1}; CV = 33%). We then compared the mean of the summary statistics (i.e. calculated from the last 100 years and the whole plot) with the ranges calculated from the field observations and determined whether or not it was matched (Table 1). Only parameterizations for which the simulated data produced simultaneous match in all summary statistics were accepted.

Sensitivity analyses

We evaluated the sensitivity of the model at two levels of biological organization (growth-form and species) by calculating multiple backward stepwise regression analyses and Spearman rank correlation coefficients between a model output variable and a parameter. We studied the response in the average ANPP of grasses and shrubs, and grass, shrub and species-specific densities to changes in the four soil water content or transpiration thresholds t_e, t_r, t_{tr} and t_s, and the mortality rate p_{mk}. We conducted a global sensitivity analysis (Wiegand et al. 2004a) by using all 10 000 model parameterizations for the multiple regressions and correlation analyses.

The sensitivity analyses allowed us to explore potential demographic constraints in emergence, recruitment, growth, and seed production because each threshold parameter triggered the occurrence of one key demographic event. Consequently, we can identify the more influential processes on long-term vegetation dynamics. We assumed that the most sensitive threshold parameter with respect to species density will point to a demographic constraint. This is because in this case a slightly lower threshold value will allow for more frequent occurrence of the associated demographic process and if this process was indeed limiting then the density of the respective species should greatly increase if the parameter value decreases. This will be noted by a steeper slope (and correlation) in the relationship between the threshold parameter and species abundance.

Results

Inverse model parameterization

The probability that total shrub or grass cover (or total shrub and grass density) matched individually for a given model parameterization was relatively high (Table 2). For example, total grass or shrub cover matched in 34.4% and 13.5% of all parameterizations, respectively. Total grass (or shrub) density matched in more than 40% of all parameterizations, whereas grass and shrub ANPP matched in 24% of all parameterizations. These results demonstrate that it was relatively easy for DINVEG to reproduce field data of single variables (but note that we used conservatively wide acceptance ranges).

Results show, in general, a strong inverse relationship between shrub and grass cover (and density) because high shrub density was associated with low grass density and vice versa (Fig. 2). While the two basic density summary statistics individually matched in more than 40% of all parameterizations, we found that only 12.8% of all parameterizations simultaneously matched shrub and grass density (Fig. 2, Table 2). Finally, simultaneous match in all species specific densities was only reached by 0.22% of all parameterizations, and when requiring an additional match in ANPP, this figure was further reduced to 0.05% (i.e. 5 parameterizations; Table 2).

Table 2. Summary of the inverse parameter estimation for DINVEG model based on the basic patterns. Numbers indicate the percentage of parameterizations for which the simulated output variables was within the observed field range.

Basic pattern	Acceptance (%)
Total grass cover	34.3
Total shrub cover	13.5
Total grass and total shrub cover	12.8
Total grass density	43.2
Total shrub density	41.1
Total grass and total shrub density	12.8
Species specific grass densities	9.9
Species specific shrub densities	2.1
Species specific grass and shrub densities	0.22
ANPP	24.4
All basic patterns	0.05

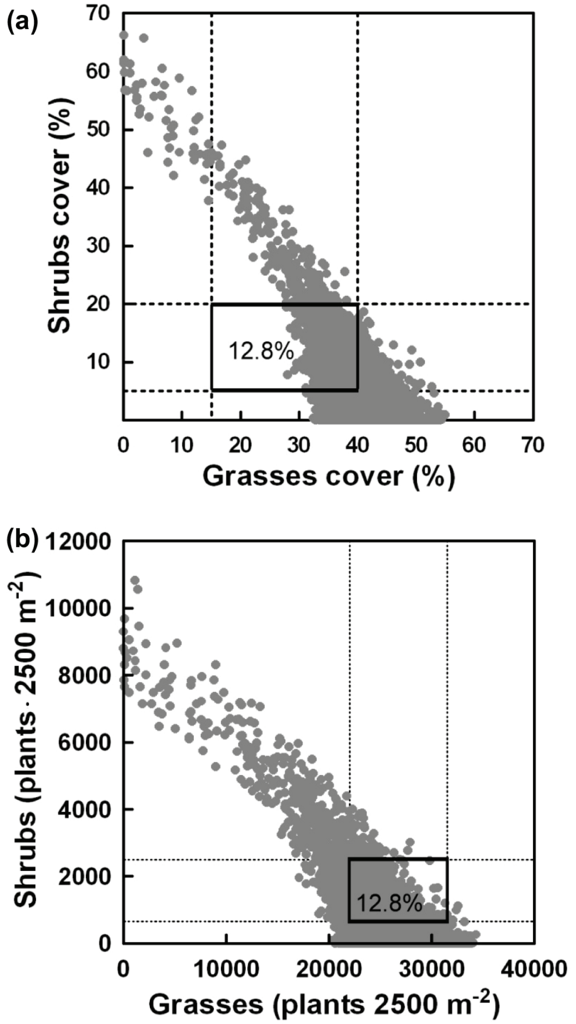

Figure 2. Relationships between (a) shrub and grass cover and (b) shrub and grass density simulated by DINVEG during 200 years for the whole set of parameters used during the calibration. Dotted lines indicate the field abundance range for both growth-forms (mean ± 2SD) and the box the parameterizations with match in both patterns. Percentages indicate the relative number of simulations fallen within the field range.

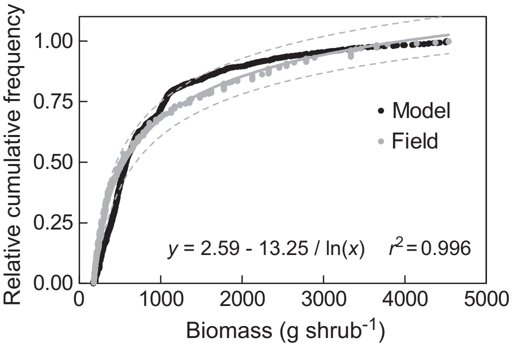

Figure 3. Relative cumulative frequency of biomass distribution of shrubs from field (gray circles) and simulated data. Gray dashed lines indicate the prediction envelope (95%) from the logarithmic function fitted to the field data.

Model validation with detailed summary statistics

All five parameterizations of the model that matched the basic summary statistics also matched the detailed summary statistics. The mean aerial cover of high cover patches of the mosaic (i.e. shrubs surrounded by a dense grass ring) simulated by DINVEG (23%) was well within the 95% prediction envelope (18–38%) reported for ungrazed conditions (Cipriotti and Aguiar 2005). In addition, the size structure based on shrub biomass simulated by DINVEG agreed well with the variation observed in the field (Fig. 3; Cipriotti and Aguiar 2010, Oñatibia et al. 2010).

The spatial patterns of the simulated vegetation at year 200 (Fig. 4a, c) were also in good agreement with that observed on the steppe. Figure 4 shows an example for one simulation with a parameterization that matched all field data simultaneously. Shrubs showed an aggregation at short distances (< 1 m; Fig. 4b) similar to that observed in the field (Cipriotti and Aguiar 2010). We also found that positive spatial associations between simulated grasses and shrubs occurred at short distances (< 0.7 m; Fig. 4d), as has been commonly reported for these grass-shrub steppes (Cipriotti and Aguiar 2005).

Although we had no long-term data on life form or species-specific densities to contrast against the model outputs, the inter-annual variability of the time series of plant species density and net productivity simulated by DINVEG was well within the envelopes (mean ± 2 SD) from field data of grazing-excluded plots (Fig. 5). Equilibrium conditions were reached after approximately 25 years for all plant species in density and net productivity dynamics (Fig. 5).

Sensitivity analysis

Grass density was strongly correlated with the recruitment thresholds of the three grass species and weakly correlated with the emergence thresholds of *Adesmia* and *Bromus* (Table 3A). The correlation of grass density with grass recruitment thresholds was negative because a high recruitment threshold means fewer opportunities for recruitment and hence less recruitment of grass seedlings. However, the correlation with emergence thresholds of shrubs were positive because higher thresholds mean lower shrub density and therefore higher grass density. Shrub density showed overall weaker correlations, but with more parameters, indicating more complex interactions. Total shrub density was negatively correlated with shrub emergence and recruitment thresholds, and positively with the recruitment thresholds of all three grasses (Table 3F). Total grass and shrub ANPP were correlated with recruitment and emergence threshold parameters, but additionally with maximum plant growth and growth threshold parameters (Table 3B, G). Regression analyses showed that shrub ANPP was poorly explained by model parameters ($R^2 = 0.39$, $p < 0.001$), whereas grass density, grass ANPP and shrub density were better explained ($R^2 = 0.87 - 0.88$, $p < 0.001$). Finally, the slope values of the multiple regression analysis agreed well with the respective correlation coefficients. This indicates that a strong correlation between an output variable and a parameter translated in our case into a large sensitivity of the output variables to the demographic parameters (Table 3).

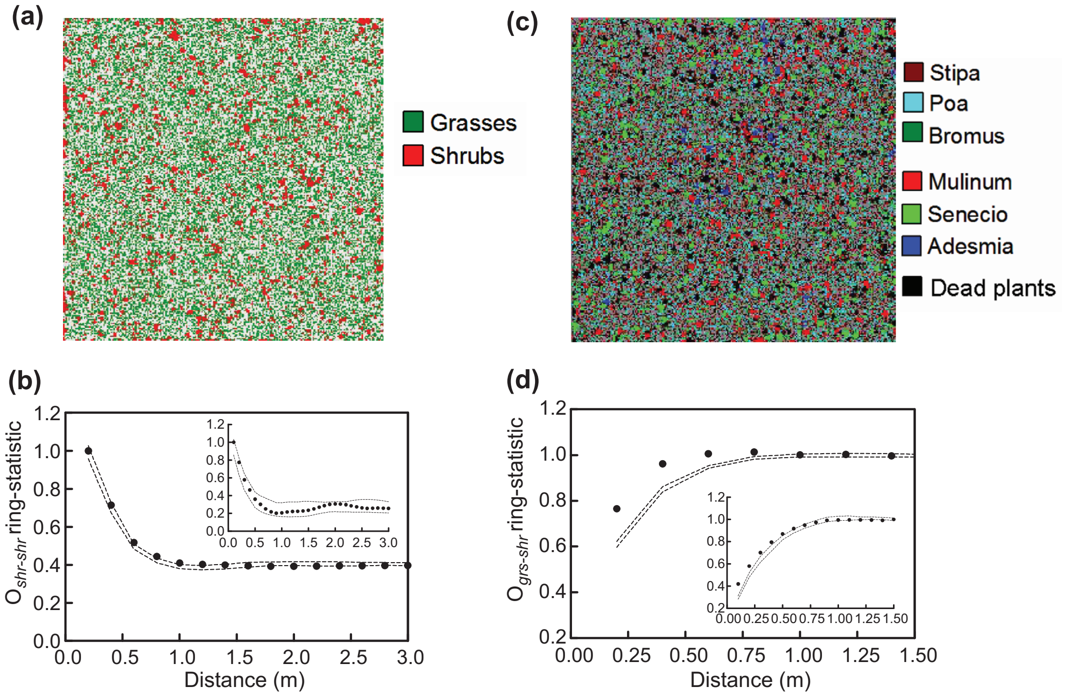

Figure 4. Summary of the spatial structure of the two-phase mosaic simulated by DINVEG after 200 years for the calibrated parameters and a typical climate series and a representative vegetation origin from the grass-shrub Patagonian steppe. Vegetation maps (50 × 50 m) for: (a) the two main life forms, and (c) the six dominant plant species. (b) Relative univariate *O*-ring statistic for the spatial aggregation of shrubs. (d) Relative bivariate *O*-ring statistic for the grass-shrub associations. Dashed lines indicate the simulation envelopes (95%) for CSR of shrubs (b) or the null model with CSR for grass tufts and fixed shrubs (d). Insets in panels 'b' and 'd' quantify the respective spatial patterns from field surveys.

As expected, threshold parameters of individual species were the strongest determinants of its own density (Table 3C–E, H–J). Again, density of a given grass species correlated most strongly with its own recruitment threshold (Table 3C–E), whereas the density of a given shrub species correlated strongly with its emergence threshold (Table 3H–J). Thus, the most important demographic constraint for grasses is the recruitment phase (Fig. 6a), whereas the most important demographic constraint for shrubs is emergence (Fig. 6b). However, for individual shrub species we found interspecific interactions with grass recruitment thresholds (Table 3H–J), whereas grass density was not strongly correlated with shrub parameters (Table 3C–E). For example, the abundances for all shrub species showed positive correlations with grass recruitment thresholds of *Poa* and *Stipa* species ($0.21 < r_{SP} < 0.27$; $p < 0.001$), indicating that grass density controlled shrub density. Interestingly, the other parameters governing mortality, growth and reproduction showed a generally low sensitivity to the model output variables analyzed (Table 3).

We assumed that uncertainty in the five parameters (per species) estimated from published or unpublished data can be neglected in a first approximation. To test this assumption we conducted model simulation where we allowed these parameters to change within their observed ranges. We found that model predictions were generally in agreement with that of our main parameterization. The results of the sensitivity analysis identified emergence and recruitment parameters as the most influential parameters on response variables such as plant cover, density and ANPP (results not shown).

Dynamics of the Patagonian grass-shrub steppe

We used the data generated by the model simulations of the five parameterizations that produced a match of all summary statistics to explore the dynamics shown by the model. The dynamics can be characterized as a stochastic equilibrium with considerable inter-annual variability. While the coefficient of variation of the input rainfall data was 33%, the variability of total shrub density was lower (CV = 19%), and that of grass density was considerably lower (CV = 9%). Variability in ANPP was somewhat between that of grasses and shrubs (CV = 16%). Thus, ecosystem function buffered environmental fluctuations.

The simulated ANPP was moderately explained by a second order polynomial regression (Fig. 7) with the precipitation in the warm period of the current year and the total precipitation in the previous year as the main predictors ($r^2 = 0.27$, $p < 0.001$). All second order terms in the regression analysis were significant, but the estimated effects differed in the sign of the coefficients. While the quadratic coefficient of the annual previous precipitation was negative, the quadratic coefficient of precipitation in the warm period was positive and one order of magnitude higher, pointing to differences in the slope changes.

Total grass and shrub densities for each simulation were highly correlated along years ($r = 0.69$, $p < 0.001$), pointing to a common driver. We explored the underlying reason for this high correlation by regressing the density (N_t) and population growth rates (i.e. $N_{t_0} - N_{t_{-1}} / t_0 - t_{-1}$) for each focal species against the main environmental input variables

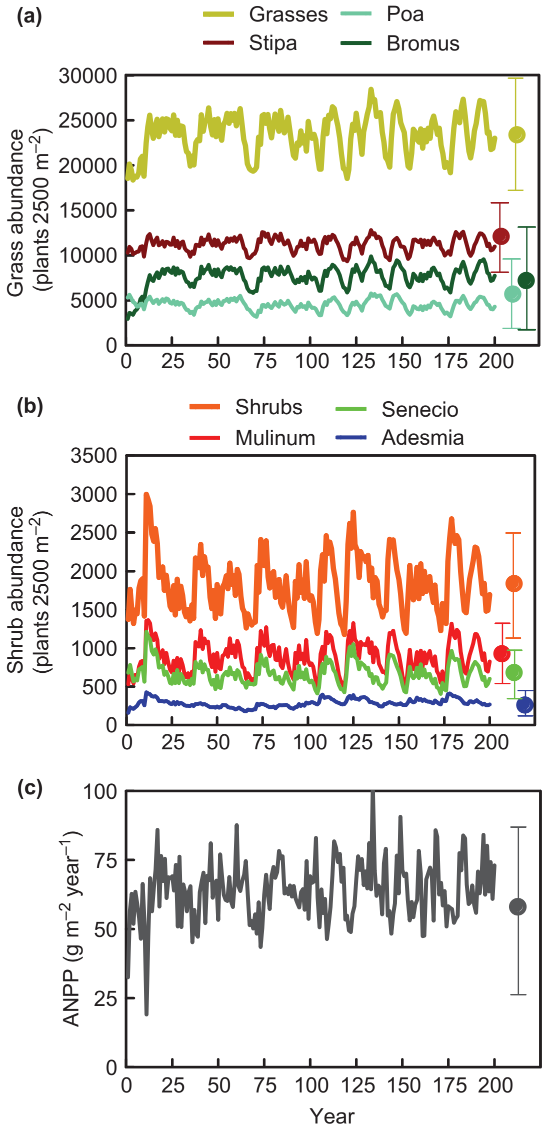

Figure 5. Time series of (a) grass species density, (b) shrub species density, and (c) total annual net primary productivity (ANPP) simulated by DINVEG during 200 years for calibrated parameters in a plot of 1/4 ha. Thin vertical bars indicate envelopes (mean ± 2 SD) for field species density data and ANPP of grazing excluded paddocks from Patagonia. Deviation from field data represents spatio-temporal variability.

(i.e. precipitation and the water content for different soil layers) for the current and previous years (t_0, $t-1$ or $t-2$), considering two main seasons (i.e. cold [emergence] or warm [recruitment] season). Generally, the environmental variables that were significantly related to plant density (or population growth rate) were different among grass and shrub species.

For the shrub species *Mulinum* and *Senecio*, the strongest control of plant density and population growth rate was the current soil water content in the top layer (0–10 cm) during the emergence period ($r^2 = 0.3$–0.42, $\beta = 0.47$–0.5, $p < 0.001$). This also explained the synchronous short-term fluctuations between both species ($r = 0.89$, $p < 0.001$; Fig. 5b). However, the density and population growth rate of *Adesmia* showed weaker correlations with environmental variables than *Mulinum* and *Senecio* ($0.43 < r < 0.53$, $p < 0.01$) and the environmental controls were weaker and less significant in explaining plant density or population growth rate ($r^2 = 0.1$–0.17, $\beta = 0.3$, $p = 0.03$).

For the three grass species, we found that the environmental variables explained the population growth rate better ($0.58 < r^2 < 0.68$, $p < 0.01$) than plant density ($0.2 < r^2 < 0.35$, $p < 0.01$). Two strong environmental drivers were common to the three grass species: the current soil water content in the top layer (0–10 cm) during the emergence period ($\beta = 0.57$–0.62, $p < 0.001$) and the current soil water content in the intermediate layers (10–30 cm) during the recruitment period ($\beta = 0.2$–0.36, $p < 0.001$).

Discussion

In this study, we tackled a persistent problem in model parameterization in spatially-explicit and individual-based simulation modeling, which has hindered wider application of these types of models (Wiegand et al. 2004a, Grimm and Railsback 2005). Analysis of mechanistically-rich simulation models requires considerable effort (DeAngelis and Mooij 2003, Wiegand et al. 2003, Grimm and Railsback 2005). This is because the different mechanisms are often governed by many model parameters (our six species model had a total of $17 \times 6 = 102$ parameters), and even in systems that are well studied (as for example the Patagonian steppes), not all model parameters can be directly determined from field data ($12 \times 6 = 72$ parameters were based on field data). Uncertainty in model parameters, error propagation, and lack of rigorous methods of model selection have been the major points of criticism against mechanistically-rich, individual-based and spatially-explicit simulation models (DeAngelis and Mooij 2003, Wiegand et al. 2004a, Grimm and Railsback 2005, Martínez et al. 2011).

Our approach took advantage of the ability of individual-based models to generate outputs at larger scales that can be compared with field observations (Grimm et al. 2005). In many applied problems, such as degradation in semiarid rangelands, there are usually not the time and resources available to conduct detailed field studies that would allow for direct parameterization of the model. However, larger scale data such as community composition and abundances are routinely collected. We demonstrated in this study that such data are a valuable source of information that can be used for inverse parameterization (see also Wiegand et al. 2004a) and assessment of long-term community dynamics.

The inverse pattern oriented approach presented here parallels recent developments in Approximate Bayesian computation (ABC) used especially in evolutionary genetics (Csilléry et al. 2010, Hartig et al. 2011). Similar to our approach, ABC bypasses exact likelihood calculations by using summary statistics and simulations. Our approach of model fitting is analogous to the rejection filter approach, which is one of three major ABC algorithms for model fitting (Beaumont et al. 2002, Hartig et al. 2011). Model parameterizations are generated from a probability distribution. The data generated by model simulation are then reduced to summary statistics, and the sampled parameters

Table 3. Spearman rank correlation (r_{SP}) and slope (β_1) coefficients between model parameters and growth-form or species density and ANPP calculated for all 10 000 parameterizations of the DINVEG model. Shown are the largest slopes and correlations for each species and growth form ($p < 0.001$) in descending order.

Prediction	Parameters	r_{SP}	β_1
(A) Total grass density	*Stipa* recruitment threshold	−0.44	−0.43
	Poa recruitment threshold	−0.44	−0.42
	Bromus recruitment threshold	−0.39	−0.4
	Adesmia emergence threshold	0.25	0.23
	Mulinum emergence threshold	0.19	0.21
(B) Total grass ANPP	*Poa* recruitment threshold	−0.36	−0.35
	Stipa recruitment threshold	−0.36	−0.36
	Bromus recruitment threshold	−0.34	−0.33
	Mulinum emergence threshold	0.27	0.28
	Poa max plant growth	0.21	0.19
	Stipa max plant growth	0.19	0.19
(C) Mean *Bromus* density	*Bromus* recruitment threshold	−0.84	−0.81
	Bromus emergence threshold	−0.31	−0.33
	Bromus mortality rate	−0.25	−0.26
(D) Mean *Poa* density	*Poa* recruitment threshold	−0.85	−0.82
	Poa emergence threshold	−0.32	−0.34
	Poa mortality rate	−0.19	−0.2
(E) Mean *Stipa* density	*Stipa* recruitment threshold	−0.85	−0.81
	Stipa emergence threshold	−0.33	−0.33
	Stipa mortality rate	−0.19	−0.19
(F) Total shrub density	*Adesmia* emergence threshold	−0.35	−0.32
	Stipa recruitment threshold	0.34	0.32
	Mulinum emergence threshold	−0.3	−0.31
	Poa recruitment threshold	0.33	0.3
	Bromus recruitment threshold	0.28	0.29
	Senecio emergence threshold	−0.28	−0.28
	Mulinum recruitment threshold	−0.24	−0.25
	Senecio recruitment threshold	−0.23	−0.23
	Adesmia recruitment threshold	−0.22	−0.22
(G) Total shrub ANPP	*Mulinum* emergence threshold	−0.25	−0.28
	Mulinum growth threshold	−0.21	−0.25
	Mulinum recruitment threshold	−0.19	−0.22
	Senecio growth threshold	−0.16	−0.17
	Senecio emergence threshold	−0.17	−0.16
	Stipa recruitment threshold	0.17	0.16
	Poa recruitment threshold	0.15	0.16
	Mulinum mortality rate	−0.12	−0.14
(H) Mean *Mulinum* density	*Mulinum* emergence threshold	−0.68	−0.66
	Mulinum recruitment threshold	−0.47	−0.5
	Mulinum mortality rate	−0.21	−0.22
	Stipa recruitment threshold	0.21	0.21
	Poa recruitment threshold	0.23	0.2
(I) Mean *Adesmia* density	*Adesmia* emergence threshold	−0.67	−0.64
	Adesmia recruitment threshold	−0.4	−0.41
	Adesmia mortality rate	−0.25	−0.26
	Stipa recruitment threshold	0.27	0.25
	Poa recruitment threshold	0.25	0.23
	Bromus recruitment threshold	0.22	0.21
(J) Mean *Senecio* density	*Senecio* emergence threshold	−0.7	−0.66
	Senecio recruitment threshold	−0.5	−0.5
	Stipa recruitment threshold	0.22	0.22
	Poa recruitment threshold	0.22	0.21
	Bromus recruitment threshold	0.18	0.2

are accepted or rejected on the basis of the distance between the simulated and the observed summary statistics. The subsample of accepted values contains the fitted parameter values, and allows evaluation of the uncertainty in parameters given the observed statistics (Csilléry et al. 2010) and prior field data included in the model structure and parameterization.

However, in contrast to the rejection approach in ABC, we converted the distance between the simulated and the observed summary statistics into a binary measure of model fit for each summary statistic. Binary measures of model fit have also been advocated by others (Reynolds and Ford 1999, Komuro et al. 2006). The reason for using binary measures is that observations are subject to errors

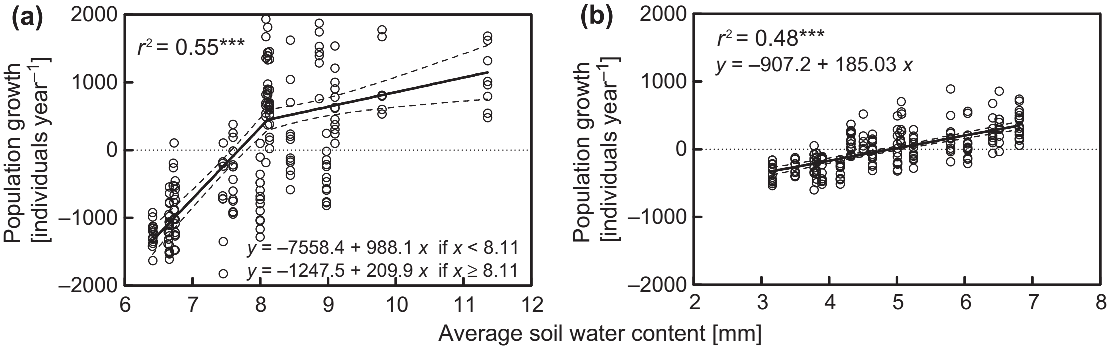

Figure 6. Annual population growth of grasses (a) and shrubs (b) related to the average soil water content during the recruitment phase (October–December) in the first two soil layers (0–20 cm) and the emergence phase (July–September) in the top soil layer (0–10 cm), respectively. Both data were built from a 200 year simulation with calibrated parameters. Dashed lines indicate the lower and upper limits of 95% confidence envelopes from the respective fits.

and inherent stochasticity that needs to be considered. Our approach would be able, in theory, to minimize the distance between the simulated and the observed summary statistics, but differentiating parameterizations with distances below the level of uncertainty does not seem necessary. Doing so may cause bias or overfitting (Wiegand et al. 2003, 2004a, Latombe et al. 2011). In our study we used conservative, wide acceptance ranges for the summary statistics. With this, we aimed to exclude, based on each individual summary statistics, only model parameterizations that produced model outputs that were clearly unrealistic. However, all summary statistics taken together considerably constrained the parameter space and model behavior (see also Wiegand et al. 2004a for a detailed discussion of this issue).

Clearly, a valid parameterization had to balance the different demographic processes correctly to yield the observed ANPP, species-specific cover and densities. Only few parameterizations were able to do so. However, the fact that our model was able to match multiple field observations

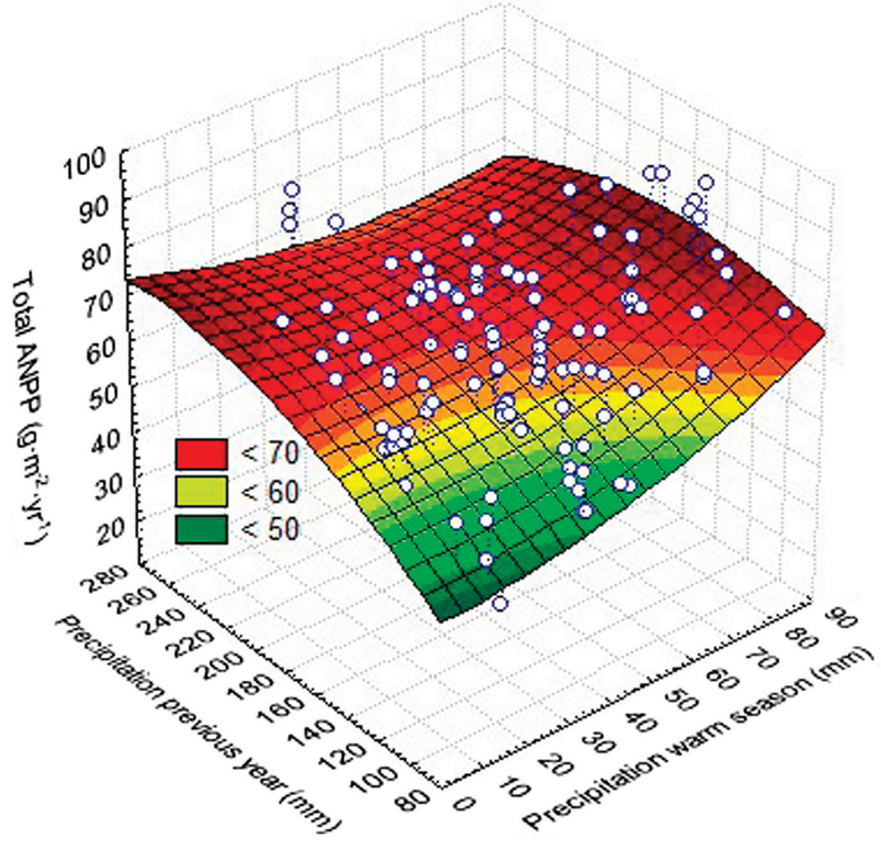

Figure 7. Polynomial relationship between the total ANPP simulated by DINVEG with the calibrated parameters and the current precipitation during the warm period (P_w) and the immediate previous annual precipitation (P_{t-1}) for a representative initial vegetation condition and a typical climate series. The 2nd order polynomial function is $ANPP = 17.24 + 0.42\ P_{t-1} + 0.16\ P_w - 0.0008\ P_{t-1}^2 + 0.0025\ P_w^2 - 0.0017\ P_{t-1}\ P_w$ ($r^2 = 0.27$, $p < 0.001$). Circles are the simulated data by DINVEG.

is important because it shows that the model structure is consistent with the current data on the Patagonian steppe. In contrast, a model with missing or incorrectly specified mechanisms would fail to match some of the observed data (Martínez et al. 2011) and subsequent modeling cycles are required to identify the missing or incorrectly specified mechanisms (Wiegand et al. 2003). The weak impact of the variability of 'fixed' parameters on model results can be explained by the narrow ranges of the 'fixed' parameters compared to the unknown parameters that were varied over their entire range. In addition, this type of inverse parameterization is not prone to error propagation (Wiegand et al. 2003). This could also contribute to the reduced impact of 'fixed' parameters on model results.

The detailed summary statistics evaluate aspects of spatial structure that are substantially different from the compositional features tested by the basic summary statistics. We asked if the basic summary statistics were already able to constrain the model behavior sufficiently to generate spatial structures that match the corresponding field observations. Interestingly, we found that model parameterizations that matched the basic summary statistics (Table 1) generated the observed two-phase mosaic pattern where high-cover patches (co-dominated by shrubs surrounded by a dense grass ring) are interspersed in a low cover and grass-dominated matrix (Cipriotti and Aguiar 2005). This confrontation of the fitted model with detailed data on spatial structure can be regarded as model validation. Thus, given that the overall model structure does not contain severe structural errors, routinely collected compositional data can provided sufficient information to constrain the internal model behavior in a way that even subtle spatial patterns were correctly predicted.

Dynamics of the Patagonian grass-shrub steppe

Our sensitivity analyses considered 'fast' variables such as plant density as well as a 'slow' variables (e.g. cover). The results for grass and shrub ANPP and density agreed with previous long-term field studies on woody or perennial grass species from semi-arid ecosystems (Milton 1995, Watson et al. 1997, Fair et al. 1999) where regeneration (i.e. emergence and recruitment) was the most important demographic process for the maintenance of plant populations. Interestingly, recruitment and emergence parameters were significantly correlated with slow and fast variables (Table 3). Thus, the shrub-grass balance and long-term vegetation dynamics can be strongly modified by environmental variables that affect recruitment and emergence. We found that the soil water content in the upper (0–10 cm) and intermediate soil layers (10–30 cm) at the end of the growing season was especially important for this, given that seed availability is not constrained (Aguiar et al. 1992, Rotundo and Aguiar 2005, Cipriotti et al. 2008).

Our finding that recruitment and emergence parameters were the most sensitive parameters with respect to long-term population growth rates contrasts with results typically derived from matrix models for woody species where the stasis (i.e. survival) is generally the most sensitive demographic parameter (Silvertown et al. 1993, Franco and Silvertown 2004). The reason for this difference may be grounded in different modeling philosophies and assumptions. The matrix is usually deterministic (i.e. no changes of transitions or fecundities with time) and density-independent (i.e. the transitions or fecundities do not depend on plant density). However, our model allowed transitions among plant stages to change in response to annual rainfall (which introduced a considerable stochasticity typical for event-driven semiarid systems) and intra- and inter-specific interactions (e.g. water competition, aerial facilitation or space competition) were density-dependent.

Interestingly, grasses controlled the shrub demography. This result is probably caused by water competition in the upper soil layers exerted by grasses (especially adults) on the early life stages of shrubs (e.g. seedlings or recruiters). The first two years after their emergence, the roots of shrubs are constrained to the upper soil layers (0–10, 10–20 or 20–30 cm depending on time since emergence) and share water resources with grasses (i.e. rules no. 2, 3 and 6 from Supplementary material Appendix A1). This temporal resource overlap between shrubs and grasses generates an effective control for shrubs. Because the soil water content during emergence and recruitment is the key demographic process for grasses, they are mostly self-controlled (i.e. the higher water efficient species) and spatial competition with shrubs can be neglected, except for *M. spinosum* where it plays only a minor role (see rule no. 7 from Supplementary material Appendix A1).

The dynamic aspects of ecosystem functioning simulated by DINVEG were in good agreement with field observations from these Patagonian steppes. For example, the inter-annual variability of total ANPP simulated by DINVEG (CV = 16%) was within the range estimated for our study site (15–27%). This result confirms results from a field study by Paruelo et al. (2000) that suggested that biotic constrains in ecosystem functioning buffer the high environmental variability in rainfall (i.e. CV = 33%). The moderate predictive power of the relationships between simulated ANPP and annual or seasonal rainfall ($r^2 = 0.2$–0.4, $p < 0.01$) were also in agreement with field studies and point to biotic constrains on ANPP that contribute to differences between the spatial and temporal models of ANPP (Lauenroth and Sala 1992, Yahdjian and Sala 2006). In addition, the time lags of ANPP responses agree with memory effects reported in semiarid grasslands (Oesterheld et al. 2001, Wiegand et al. 2004b, Bartelt-Ryser et al. 2005) and/or the slow dynamics of water drainage and the shrub responses related to this water source (Golluscio et al. 1998, Jobbágy and Sala 2000, Paruelo et al. 2000).

Conclusions

We showed that inverse parameterization of individual-based and spatially-explicit simulation models allows for an integration of short-term data on individual plant behavior with larger scale patterns that are routinely collected. Our approach allowed us to identify the key ecological processes that control long-term vegetation dynamics and to 'reconstruct' important characteristics of long-term community dynamics. For the Patagonian steppes, seedling emergence and recruitment are critical processes for long-term vegetation dynamics. While sheep grazing is known to influence these processes, our study shows that the predicted increase of dry years (Gian-Reto et al. 2002) is likely to play an increasing role in controlling emergence and recruitment of both grass and shrub species (Cipriotti and Aguiar 2010).

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Supplementary material (available online as Appendix O20317 at <www.oikosoffice.lu.se/appendix>). Appendix A1–A3.