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Community ecology

Plant species richness and shrub cover attenuate drought effects on ecosystem functioning across Patagonian rangelands

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Drought is an increasingly common phenomenon in drylands as a consequence of climate change. We used 311 sites across a broad range of environmental conditions in Patagonian rangelands to evaluate how drought severity and temperature (abiotic factors) and vegetation structure (biotic factors) modulate the impact of a drought event on the annual integral of normalized difference vegetation index (NDVI-I), our surrogate of ecosystem functioning. We found that NDVI-I decreases were larger with both increasing drought severity and temperature. Plant species richness (SR) and shrub cover (SC) attenuated the effects of drought on NDVI-I. Grass cover did not affect the impacts of drought on NDVI-I. Our results suggest that warming and species loss, two important imprints of global environmental change, could increase the vulnerability of Patagonian ecosystems to drought. Therefore, maintaining SR through appropriate grazing management can attenuate the adverse effects of climate change on ecosystem functioning.

1. Introduction

Rangelands cover about 25% of the Earth's land surface, making it the most extensive land cover on the Earth [1]. About 78% of rangelands are located in drylands (hyper-arid, arid, semi-arid and dry-subhumid ecosystems), which are grazed by managed livestock [1]. Aboveground net primary productivity (ANPP) is a key ecosystem attribute because it determines forage availability, and thus the herbivore carrying capacity [2]; moreover, it is closely linked to energy flow and nutrient and carbon cycles, and therefore has been proposed as an integrative estimate of ecosystem functioning [3].

Drylands are characterized by high interannual climate variability, and drought is a frequent phenomenon in these environments [4]. The extent, severity, duration and frequency of droughts will increase as a consequence of climate change [5], negatively affecting the sustainability of rangelands and the livelihood of more than 200 million households [6]. Thus, understanding the responses of ecosystem functioning to drought is of paramount importance for developing effective resource management and climate change mitigation strategies.

Mean annual precipitation (MAP) has been found to control ecosystem functioning at regional scales [7]. There is also increasing evidence that biotic attributes, such as cover and species richness (SR), also influence ecosystem

functioning [8]. The diversity–ANPP relationship in response to drought has been assessed in experimental grasslands [9], but it is largely unknown how biotic attributes modulate this relationship at regional scales [10]. Here, we evaluated to what extent the relative impact of a drought event on ecosystem functioning was affected by abiotic (drought severity, temperature) and biotic (vegetation structural attributes) drivers in Patagonian rangelands. We used the annual integral of the normalized difference vegetation index (NDVI-I) as a surrogate of ecosystem functioning. This index has been shown to be a good estimator of ANPP because it is directly related to the photosynthetically active radiation absorbed by plant canopies [11]. We tested the following hypotheses: (i) a decline in NDVI-I is positively related to drought severity; (ii) this decline is higher in warmer sites because of increased water evaporation with higher temperature; (iii) shrubs are more resistant to drought than grasses, so the decline in NDVI-I is lower in sites with greater relative shrub cover (SC); and (iv) higher plant SR attenuates the effects of drought on NDVI-I.

2. Material and methods

(a) Study area and field sampling

The study area is an 800 000 km² territory located in Patagonia (southern Argentina). Vegetation is dominated by grasslands, shrub-grass steppes and shrublands, with plant cover ranging between 15% and 60%. Soils are mainly sandy and loam-sandy textured. MAP and mean annual temperature (MAT) range from 100 to 750 mm, and from 4.5°C to 16°C, respectively. Grazing by domestic herbivores is the most widespread land use in the region. We studied 311 sites (electronic supplementary material, S1), which are part of a long-term monitoring system [12]. Within each site, we conducted vegetation surveys using the point-intercept method in two 50 m-long transects [13]. In each transect, we recorded the type of interception (plant species, bare soil or litter) every 20 cm (500 records per site). From these data, we calculated grass and shrub cover. We found that the mean cover of annual species was less than 1%, thus we used the number of perennial plant species as a surrogate of SR. Field sampling was conducted between 2008 and 2012, and each site was surveyed once during September to February.

(b) Climatic data

We obtained monthly rainfall data for the January 2000–December 2011 period interpolating data from 185 weather stations by Ordinary Kriging [8]. From these estimations, we calculated the growing season precipitation (July to June of the following year, PPT) and its 11-year average (MAP) for each site. We calculated a drought severity index (DSI) for each growing season and each site as

$$DSI = \frac{100 \times PPT}{MAP}.$$

Growing seasons with DSI values between 40 and 55 are considered severely dry, 55 and 80 moderately dry and 80 and 110 not dry [14]. We identified only a moderate drought in 2007–2008, when the mean DSI across the 311 sites studied was 67 (electronic supplementary material, S2). Therefore, we analysed the changes in NDVI-I during that growing season.

We estimated MAT from the MODIS satellite (MOD11A2 product), which provides temperature estimates with a 1 km spatial resolution every 8 days [15].

(c) Annual integral of normalized difference vegetation index

We obtained NDVI-I data using the MOD13Q1 product from MODIS, which provides data every 16 days with a resolution of 250 m. For every site and year, we calculated NDVI-I as the area under the curve resulting from adding the 23 images from July until June of next year. From the 11 annual NDVI-I, we obtained the mean (NDVI-I_{mean}). We calculated the relative change in NDVI-I induced by drought in 2007–2008 (Δ NDVI-I) as

$$\Delta NDVI-I = 1 - \frac{NDVI-I_{2007-2008}}{NDVI-I_{mean}}.$$

(d) Data analysis

To test our hypotheses, we used an *a priori* model showing hypothesized relationships between Δ NDVI-I (dependent variable) and both biotic and abiotic factors (independent variables) in a path-relation network (electronic supplementary material, S3) and analysed it using structural equation modelling (SEM; [16]). This enabled us to evaluate the relative importance and direct/indirect effects of abiotic and biotic factors as drivers of Δ NDVI-I. Data used for this analysis can be found in the electronic supplementary material, S4.

3. Results

The SEM model satisfactorily fitted our data, and explained approximately 40% of the variation in Δ NDVI-I (figure 1). MAT showed the strongest (and positive) relationship with Δ NDVI-I and 98.8% of its effect was direct (figures 1 and 2). DSI showed a negative relationship with Δ NDVI-I, but its direct path size was about 60% of that of MAT (figure 2). SR and shrub cover had a significant negative relationship with Δ NDVI-I. The size of these paths was about 30% of that of MAT (figure 2). Grass cover had no significant relationship with Δ NDVI-I (figure 1).

4. Discussion

Our observations across a broad range of environmental conditions and their multivariate treatment provided new insights about how climate and vegetation control the effects of drought on NDVI-I. In a previous study, we found that NDVI-I was positively related to vegetation cover [12]. In sparsely vegetated ecosystems, like those we studied, vegetation cover is closely related to ecosystem functional attributes such as ANPP [17], soil nutrient cycling and storage [18] and soil water infiltration and run-off [19]. As predicted by our hypotheses, we found that declines in NDVI-I increased with drought severity and MAT, and that these effects were attenuated by shrub cover and SR. These results suggest that two important imprints of global environmental change, climate warming and species loss, could increase the vulnerability of Patagonian ecosystems to drought, which will likely become more recurrent and intense in the future [5].

Strong positive MAP–ANPP relationships have been found in drylands at the regional scale [7]. Thus, it was not surprising to find a positive relationship between the magnitude of the decrease in precipitation and the decline in NDVI-I during a dry year (negative path DSI– Δ NDVI-I in figure 1). Evaporative water loss increases with temperature [20], likely enhancing the effects of drought severity on

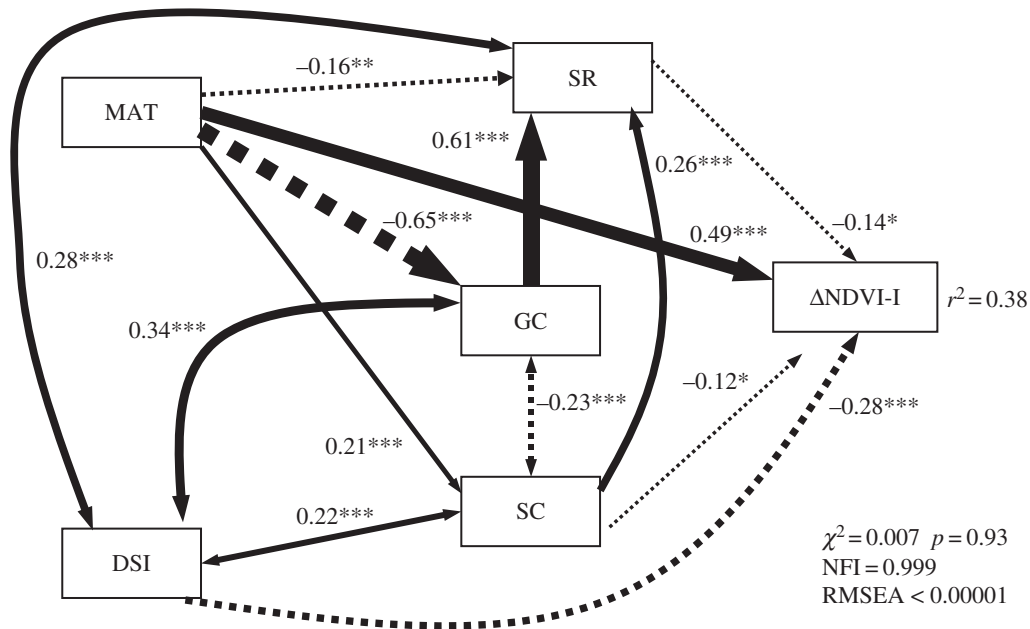


Figure 1. Structural equation model characterizing the influence of mean annual temperature (MAT), drought severity index (DSI), shrub cover (SC), grass cover (GC) and species richness (SR) on changes in the annual integral of NDVI induced by a drought event (Δ NDVI-I). The numbers adjacent to the arrows are path coefficients indicating the strengths of the effect. The width of the arrows is proportional to the magnitude of the path coefficients. Full arrows indicate positive relationships, dotted arrows negative relationships. Non-significant ($p > 0.05$) paths were eliminated. Single-headed arrows indicate a hypothesized causal influence of one variable upon another. Double-headed arrows indicate correlation without causal relationship. Goodness-of-fit statistics: chi-squared test (χ^2), normed fit index (NFI) and root mean square error of approximation (RMSEA). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

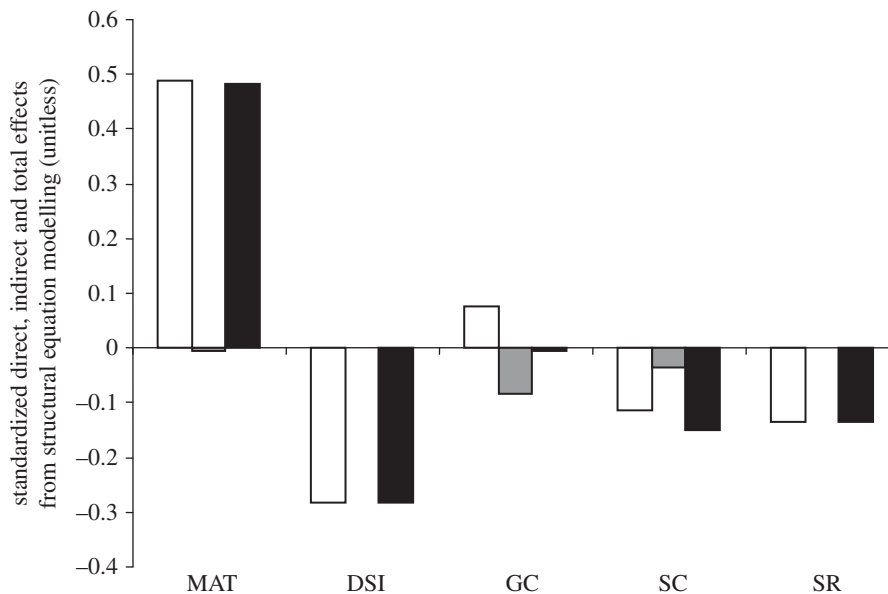


Figure 2. Standardized direct (white), indirect (grey) and total effects (black) of mean annual temperature (MAT), drought severity index (DSI), shrub cover (SC), grass cover (GC) and species richness (SR) upon changes in the annual integral of NDVI.

productivity, as shown by the dominant positive relationship between MAT and Δ NDVI-I.

As we expected, the decline in NDVI-I was lower in sites with greater relative shrub cover. Shrubs have deeper root systems than grasses, which allow them to use water stored in deeper layers of soil [21], and a lower relative growth rate and foliar dynamic than grasses, which makes them less vulnerable to water shortages [22]. Our results agree with findings from manipulative experiments conducted in the Patagonian steppe, where a reduction in precipitation decreased the

ANPP of grasses, but not of shrubs [23]. Plant SR attenuated the negative effects of drought on NDVI-I. More diverse ecosystems have a higher probability of containing drought-tolerant species, and a more complete use of available resources because of niche complementarity and synergistic interactions among species [24]. Regardless of the mechanism involved, our results agree with experimental studies showing that higher SR is associated with lower sensitivity of ANPP to drought [9]. Our findings indicate that SR and shrub cover can contribute to buffer the negative effects of drought on ecosystem functioning,

and should be maintained by range management interventions. Such practices would increase the resistance of rangelands to drought, a major component of ongoing climate change, and would positively impact the provision of fundamental ecosystem services upon which millions of people depend worldwide.

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