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SPECIAL FEATURE

GRASS–WOODLAND TRANSITIONS

Vegetation structure is as important as climate for explaining ecosystem function across Patagonian rangelands

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Summary

1. Drylands cover about 41% of Earth's land surface, and 65% of their area supports domestic livestock that depends on the above-ground net primary productivity (ANPP) of natural vegetation. Thus, understanding how biotic and abiotic factors control ANPP and related ecosystem functions can largely help to create more sustainable land-use practices in rangelands, particularly in the context of ongoing global environmental change.

2. We used 311 sites across a broad natural gradient in Patagonian rangelands to evaluate the relative importance of climate (temperature and precipitation) and vegetation structure (grass and shrub cover, species richness) as drivers of ANPP, precipitation-use efficiency (PUE) and precipitation marginal response (PMR).

3. Climatic variables explained 60%, 52% and 12% of the variation in grass cover, shrub cover and species richness, respectively. Shrub cover increased in areas with warmer, drier and winter rainfall climates, while the response observed for both grass cover and species richness was the opposite. Climate and vegetation structure explained 70%, 60% and 29% of the variation in ANPP, PUE and PMR, respectively. These three variables increased with increasing vegetation cover, particularly grass cover. Species richness also increased with ANPP, PUE and PMR. ANPP increased, and PUE decreased with increasing mean annual precipitation, whereas PMR increased with the proportion of precipitation falling in spring–summer. Temperature had a strong negative effect on ANPP and PUE, and a positive direct effect on PMR. Standardized total effects from structural equation modelling showed that vegetation structure and climate had similar strengths as drivers of ecosystem functioning. Grass cover had the highest total effect on ANPP (0.58), PUE (0.55) and PMR (0.41). Among the climatic variables, mean annual precipitation had the strongest total effect on ANPP (0.51) and PUE (−0.41), and the proportion of the precipitation falling in spring–summer was the most influential on PMR (0.36).

4. *Synthesis.* Vegetation structure is as important as climate in shaping ecosystem functioning Patagonian rangelands. Maintaining and enhancing vegetation cover and species richness, particularly in grasses, could reduce the adverse effects of climate change on ecosystem functioning in these ecosystems.

Key-words: above-ground net primary productivity, drylands, ecosystem services, grass–shrub balance, mean annual precipitation, precipitation marginal response, precipitation-use efficiency, species richness

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Introduction

Arid, semi-arid and dry subhumid ecosystems (drylands hereafter) cover about 41% of the Earth's land surface and provide habitat and other ecological services to one-third of the global population (Millennium Ecosystem Assessment 2005). Globally, drylands are primarily used as rangelands, in which natural vegetation is grazed by managed livestock (Asner *et al.* 2004). Above-ground net primary productivity (ANPP) is a key attribute of rangelands because it is closely linked to energy flow and nutrient and carbon cycles (Chase *et al.* 2000), and therefore has been proposed as an integrative estimate of ecosystem functioning (McNaughton *et al.* 1989). Understanding what controls ANPP can provide fundamental insights into the structure and function of ecosystems (Huxman *et al.* 2004), particularly in rangelands. In these ecosystems, the magnitude and seasonality of ANPP determines forage availability and constrains the carrying capacity of herbivores (Oesterheld, Sala & McNaughton 1992). Therefore, understanding what drives spatiotemporal patterns in ANPP may greatly help land managers and policy makers to promote more efficient and sustainable use of rangelands (Graetz 1991). Furthermore, clarifying how climate affects ANPP is critical for predicting the impact of climate change on the functioning of drylands, and their provision of key ecosystem services (Knapp *et al.* 2002).

There has been significant progress in understanding controls on ANPP of drylands at the regional to continental scale, derived mostly from correlative analyses (e.g. Sala *et al.* 1988; Paruelo *et al.* 1999; Bai *et al.* 2008). These studies have revealed that a large proportion of the variation in ANPP can be accounted for by its positive relationship with mean annual precipitation. Two other ecosystem attributes linking ANPP and precipitation have been proposed: precipitation-use efficiency (PUE, ratio of annual ANPP to annual precipitation; Le Houérou 1984) and precipitation marginal response (PMR, the slope of the annual precipitation–ANPP relationship; Verón, Oesterheld & Paruelo 2005). Le Houérou (1984) proposed PUE as an effective integral measure for evaluating the response of ANPP to spatiotemporal changes in precipitation. This author suggested that PUE has a stable value in drylands world-wide. Consequently, spatiotemporal departures from the average PUE could be used as an indicator of desertification (Justice *et al.* 1991; Prince, Brown de Colstoun & Kravitz 1998). However, several studies have shown that PUE varies with changes in precipitation, temperature, nutrient contents and vegetation characteristics (Paruelo *et al.* 1999; Huxman *et al.* 2004; Bai *et al.* 2008). Verón, Oesterheld & Paruelo (2005) showed that PUE is a measure of efficiency, since it expresses the amount of ANPP derived from all precipitation inputs, whereas PMR provides information about vegetation sensitivity to interannual changes in precipitation.

Most of our knowledge about controls of ANPP in drylands comes from research conducted across natural environmental gradients (e.g. Sala *et al.* 1988; Paruelo *et al.* 1999; Ma *et al.* 2010). While these gradients provide an invaluable tool for understanding the mechanisms controlling ecosystem processes such as ANPP (Sagarin & Pauchard 2010), multiple biotic and abiotic factors covary along natural gradients, and it is often difficult to disentangle their independent effects. This can lead to an error in the interpretation of some results; for example, a number of studies have shown that ecosystem PUE decreases (Huxman *et al.* 2004) or increases (Bai *et al.* 2008) with increasing mean annual precipitation. These contrasting results come in part from other controlling factors that may confound the effects of precipitation on ANPP and PUE across spatial scales. Some of these factors are structural characteristics such as plant species richness and the grass–shrub balance, which have been found to play important roles as drivers of ecosystem functioning in drylands (Aguiar *et al.* 1996; Eldridge *et al.* 2011; Maestre *et al.* 2012). Indeed, attributes such as species richness are often proposed as critical for maintaining and enhancing ANPP and related ecosystem functions in grasslands world-wide (e.g. Flombaum & Sala 2008; Zavaleta *et al.* 2010). Similarly, plant density has been found to be a significant driver of ANPP responses in semi-arid grasslands after drought events (Yahdjian & Sala 2006). Despite the recognized importance of vegetation structure as a major driver of ecosystem functioning, there is currently a lack of research evaluating how plant richness and cover modulate controls on ANPP, PUE and RMP by climate at the regional scale. Such studies are certainly needed to improve the accuracy of models that aim to predict changes in ANPP in response to climatic attributes (e.g. Lee *et al.* 2010), particularly in the context of rapid climate and vegetation changes (Grimm *et al.* 2013).

We evaluated the relative importance of abiotic (climate) and biotic (vegetation structure) as drivers of regional variations in ANPP, PUE and PMR. In doing this, we took advantage of the heterogeneous vegetation structure and comprehensive climatic variation found in Patagonia (southern

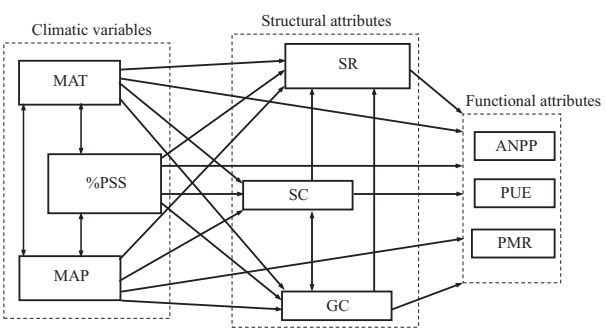

Fig. 1. *A priori* conceptual model depicting pathways by which climatic variables may impact directly or indirectly (through its influence on vegetation structure) upon surrogates of ecosystem functioning. Single-headed arrows indicate a hypothesized causal influence of one variable upon another. Double-headed arrows indicate correlation without causal relationship. MAT, mean annual temperature; MAP, mean annual precipitation; %PSS, proportion of precipitation falling in spring–summer; GC, grass cover; SC, shrub cover; SR, species richness; ANPP, above-ground net primary productivity; PUE, precipitation-use efficiency; PMR, precipitation marginal response.

South America), one of the world's largest rangelands. Specifically, we assessed how temperature and both the amount and seasonal distribution of precipitation can interact with the cover of grasses and shrubs and plant species richness to influence ANPP, PUE and PMR using an *a priori* causal model (Fig. 1) and structural equation modelling (SEM; Grace 2006). Our *a priori* model is based on what previous studies, both experimental and observational, have observed in multiple terrestrial ecosystems (e.g. Sala *et al.* 1988; Paruelo *et al.* 1999; Bai *et al.* 2008; Flombaum & Sala 2008; Zavaleta *et al.* 2010). In relatively undisturbed ecosystems, climate exerts the primary control on ecosystem structure and functioning at broad geographical scales (Chapin, Matson & Vitousek 2011). However, over 100 years of grazing have induced strong changes in the structure of Patagonian ecosystems (e.g. León & Aguiar 1985; Bisigato & Bertiller 1997), which could weaken the climate–structure relationship and therefore increase the role of structural characteristics as controlling factors on ecosystem functioning. Our hypothesis therefore is that vegetation structure is as important as climate as a driver of variations in ANPP, PUE and PMR across Patagonian rangelands.

Materials and methods

STUDY AREA

The study area of 800 000 km^2 represents approximately 90% of Patagonia, in southern Argentina (Fig. 2, Table 1). The vegetation is dominated by grasslands, shrub–grass steppes, shrublands and semi-deserts (Soriano 1956). Dominant soils have loam-sandy and sandy textures and belong mainly to the Aridisols and Entisols orders

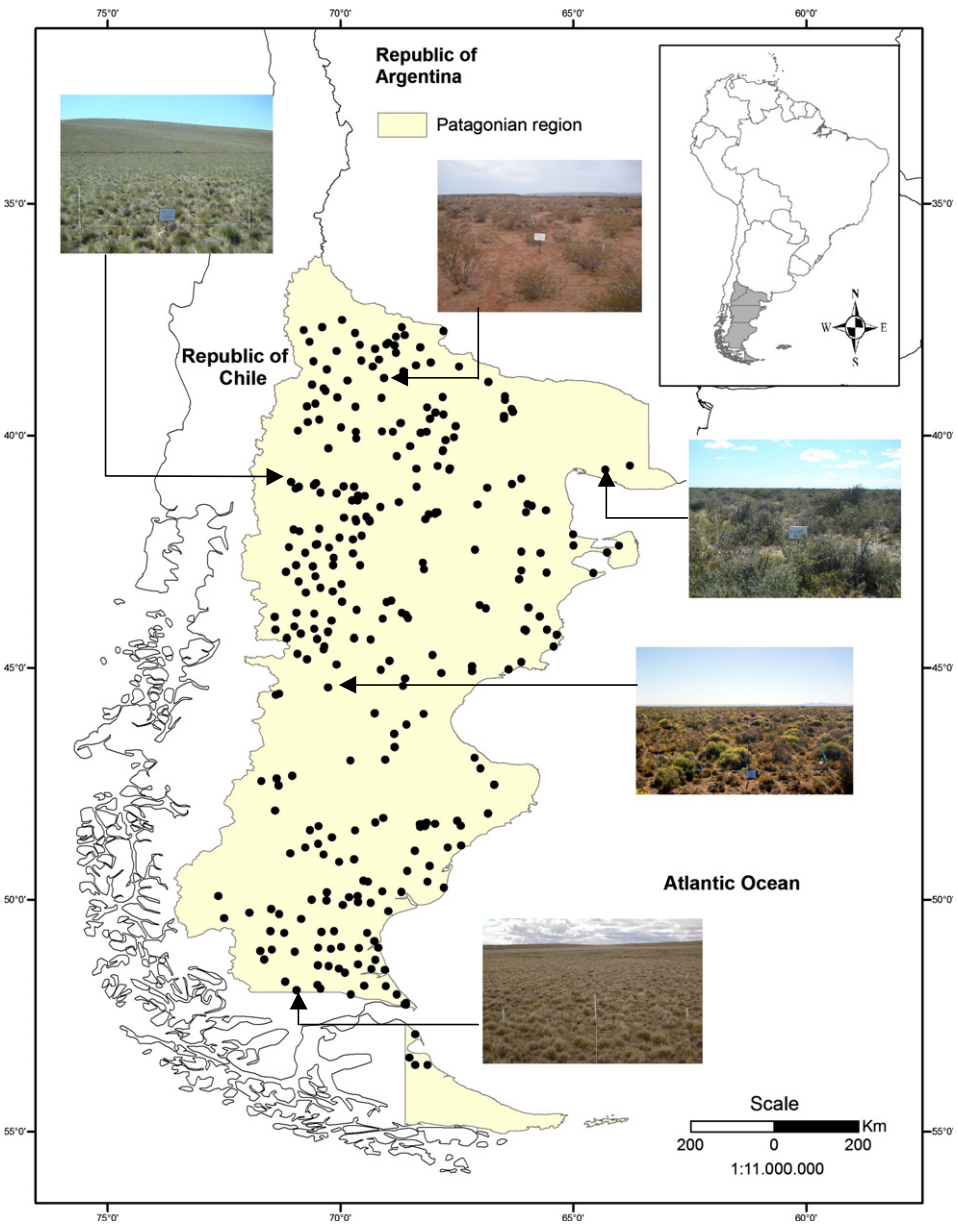

Fig. 2. Location of sampling sites (black dots), with some examples of the vegetation types studied.

Table 1. Main structural and functional attributes of the studied sites (n = 311). Abbreviations as in Fig. 1

Variable	Mean	Standard deviation	Minimum	Maximum
MAP (mm year^{-1})	261.8	107.5	110	742
%PSS	40.8	6.9	24.2	55.0
MAT (°C)	9.6	2.4	4.7	15.5
GC (%)	17.9	16.6	0	93.4
SC (%)	21.5	11.2	0	65.6
SR (number of species)	15	6.8	2	40
ANPP (unitless)	5.2	1.8	2.3	12.9
PUE $\times$ 10^3 (unitless)	21.0	6.7	7.1	52.4
PMR $\times$ 10^3 (unitless)	4.0	2.2	0.057	13.6

(del Valle 1998). Mean annual precipitation and temperature range from 100 to 750 mm and from 4.5 to 16 °C, respectively. Grazing by domestic herbivores is the most widespread human use in the area.

VEGETATION DATA

We studied 311 sites, which are part of the MARAS (Spanish acronym for 'Environmental Monitoring for Arid and Semi-Arid Regions') network (Fig. 2; Oliva *et al.* 2011). The sites are located in flat areas (slope <10%) within ranches displaying the typical diversity of livestock and rangeland management conditions of the area. Since the area sampled on the ground is smaller than the pixel size of the MODIS (Moderate Resolution Imaging Spectroradiometer) sensor that was used to estimate ANPP, we located the sites in homogeneous areas to ensure that the sampled area described the surrounding MODIS pixels (Gaitán *et al.* 2013). Within each site, we placed two 50-m-long transects on which we conducted vegetation surveys using the point intercept method (Müller-Dombois & Ellenberg 1974). Along each transect, we recorded the type of ground surface (plant species, bare soil or litter) every 20 cm (500 records per site). The number of perennial plant species recorded in these transects was used as our surrogate of species richness. The percentage cover of a given species was calculated as the total number of records for that species in relation to the 500 records registered at each site. Species-specific cover values were grouped into grass cover and shrub cover, which represented 94.4 $\pm$ 7.6% (mean $\pm$ standard deviation) of total vegetation cover across all study sites.

CLIMATIC DATA

Precipitation

We obtained monthly precipitation maps throughout the study area from January 2000 until December 2011 by interpolating monthly precipitation data from 185 weather stations using ordinary kriging (Goovaerts 1997, see Appendix S1 in Supporting Information). From these maps, we extracted estimated monthly precipitation data for each site and calculated mean annual precipitation and the proportion of annual precipitation falling during spring and summer (October–March).

Temperature

Temperature for each site was estimated using the MODIS Land Surface Temperature (LST) and Emissivity Product (MOD11A2), which provides estimates of day and night LST with a 1-km spatial resolution every 8 days (Wan & Li 1997). Temperature estimates derived from MOD11A2 are a very good predictor of the mean 8-day temperature recorded in weather stations in the study area (r^2 = 0.93; Gaitán, Raffo & Umaña 2011). Hence, we used MOD11A2 data to obtain mean annual temperature for the 2000–2011 period.

ESTIMATING ANPP, PUE AND PMR

We used the Normalized Difference Vegetation Index (NDVI) to estimate ANPP at our study sites. Several studies have shown that the annual integral of NDVI (I-NDVI) is a good estimator of ANPP (Tucker *et al.* 1983; Prince 1991). In the Patagonian steppe, Paruelo *et al.* (2004) found a highly significant relationship (r^2 = 0.84, P < 0.001) between NDVI and ANPP estimated from biomass harvests. NDVI data for each site were acquired using the MOD13Q1 product from MODIS, which provides 23 data captures per year (every 16 days) with a pixel size of 250 $\times$ 250 m. These data are geometrically and atmospherically corrected and include a reliability index of data quality based on the environmental conditions in which the data were recorded and ranging from 0 (good quality data) to 4 (raw or absent data) (Justice *et al.* 2002). As a surrogate of ANPP for 11 growing seasons (from 2000–2001 to 2010–2011), we calculated I-NDVI as the sum of 23 data from July until June of next year. When pixel reliability was higher than 1 and to avoid using poor quality data, NDVI data were replaced by the mean of closest dates with pixel reliability 0 or 1. This was necessary for <5% of the data used.

We calculated PUE for each site as the ratio of the mean ANPP of the 11 growing seasons to the corresponding mean annual precipitation. To calculate PMR, we first analysed the annual precipitation–ANPP relationship using simple linear regression. To do this, 70 different accumulated precipitation periods, ranging from 6 to 12 months, were considered (Fig. S1). Twelve-month-accumulated precipitation between March and February ($AP_{Mar–Feb}$) was the time that best explained interannual variations in ANPP (mean r^2 = 0.41, P < 0.05 in 72% of the studied sites; Fig. S1). Therefore, the PMR for each site was calculated as the slope of the linear regression between $AP_{Mar–Feb}$ and ANPP.

DATA ANALYSIS

We used SEM to evaluate the relative importance and direct/indirect effects of climate and vegetation structure (species richness, grass cover and shrub cover) as drivers of variations in ANPP, PUE and PMR (Fig. 1). We did not include in our *a priori* model structural variables such as the ratio between C_3 and C_4 species and the cover and diversity of annual species because only three C_4 grasses species were found in our study sites (corresponding to <4% of the number of grass species recorded) and the mean cover of annual species was <1%. We constructed separate models for ANPP, PUE and PMR. We used the χ^2 statistic, the normed fit index and the root mean square error of approximation index as measures of model fit to our data (Grace 2006). Path coefficient estimates were obtained using the maximum-likelihood estimation technique; they are the equivalent of standardized partial regression coefficients and are interpreted as relative effects of one variable upon another (Grace 2006).

To account for potential effects caused by the spatial structure of the data, we first analysed the spatial autocorrelation of the residuals of the SEM models conducted. Since we found spatial autocorrelation at small spatial scales in these residuals (Fig. S2), we conducted additional SEM models with those sites separated by a distance >40 km, which is the distance at which spatial autocorrelation in ANPP, PUE and PMR was strongest (as revealed by correlograms, data not shown). The residuals

of this reduced SEM model, conducted with 192 sites, did not show spatial autocorrelation (Fig. S2). The path coefficients of this model were very similar to those of the model using all the sites (Fig. S3). Therefore, we concluded that the observed spatial autocorrelation at small spatial scales did not significantly affect our results, and hence, we only present results from models containing all sites in our manuscript.

Ordinary kriging analyses were performed with ARCGIS 10.0 (ESRI 2011), SEM analyses were performed with AMOS 18.0.0 (SPSS 2009), and autocorrelation analyses were performed with GS$^+$ version 9 (Gamma Design Software 2008).

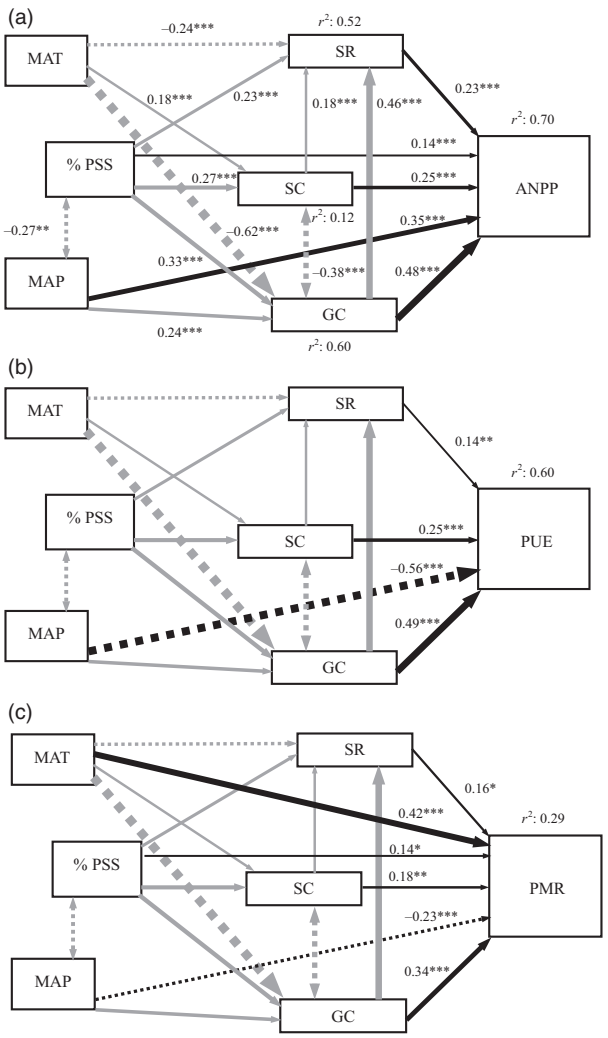

Fig. 3. Structural equation models for (a) above-ground net primary productivity (ANPP), (b) precipitation-use efficiency (PUE) and (c) precipitation marginal response (PMR). Single-headed arrows indicate a hypothesized causal influence of one variable upon another. Double-headed arrows indicate correlation without causal relationship. The numbers adjacent to arrows are path coefficients; they show the strengths of the effect. The widths of the arrows are proportional to the path coefficients. Full (dotted) arrows indicate positive (negative) relationships. Non-significant ($P > 0.05$) paths were eliminated. The grey arrows indicate the common paths in the three models; these path coefficients are the same in all three models and thus are only shown in (a). The r^2 next to response variables indicates the proportion of variance explained. Goodness-of-fit statistics: $\chi^2 = 0.18$ ($P = 0.67$, d.f. = 1), NFI (Normed Fit Index) = 0.99 and RMSEA (Root Mean Square Error of Approximation Index) <0.0001. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. Abbreviations are as in Fig. 1.

Results

Our *a priori* SEM models explained between 50% and 60% of the variation in grass cover and species richness, although they were only able to explain <15% of the variation in shrub cover. Additionally, our SEM models explained more than 60% of the variation found in ANPP and PUE, yet they only explained approximately 30% of the variation in PMR.

RELATIONSHIPS BETWEEN CLIMATE AND VEGETATION STRUCTURE

Temperature had strong and moderate direct positive effects on grass and shrub cover, respectively (Fig. 3). Temperature

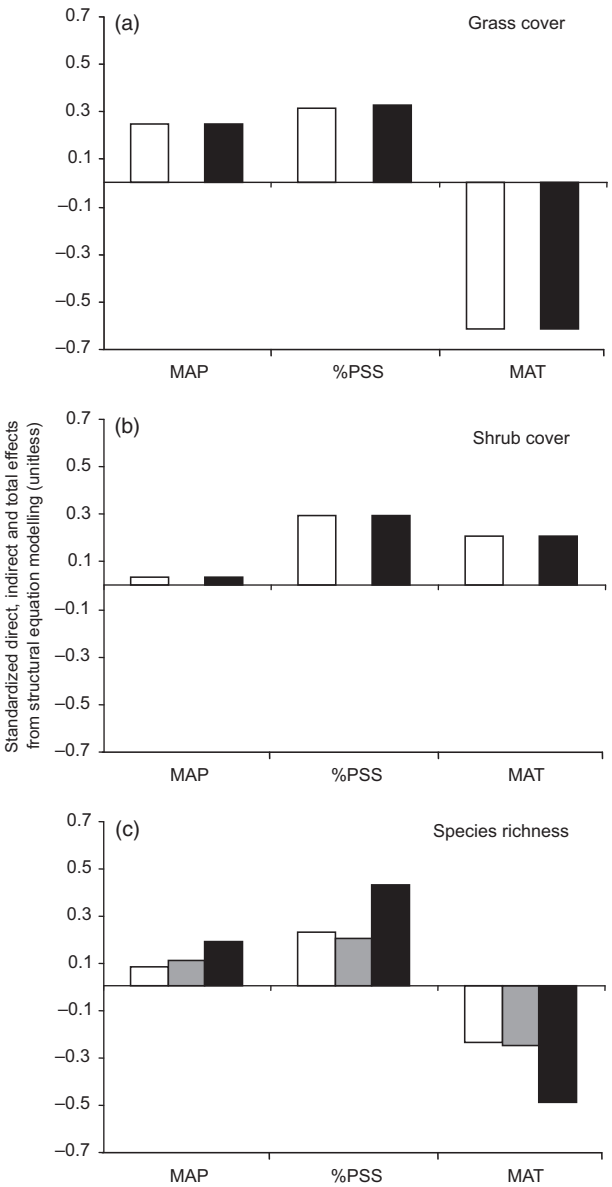

Fig. 4. Standardized direct (white), indirect (grey) and total effects (black) of mean annual precipitation (MAP), proportion of precipitation falling in spring–summer precipitation (%PSS) and mean annual temperature (MAT) upon grass cover (a), shrub cover (b) and species richness (c).

also had a strong negative effect on species richness; about half of this effect was direct, and the other half was mediated by its relationship with grass and shrub cover, which are also related to species richness (see below; Figs 3 and 4). The seasonal distribution of precipitation was more related to vegetation structure than mean annual precipitation. The proportion of precipitation falling in spring–summer was positively related to grass cover, shrub cover and species richness, while mean annual precipitation only had a positive effect on grass cover (Fig. 3). The direct positive effect of the proportion of precipitation falling in spring–summer on grass cover was slightly higher than that on shrub cover. The proportion of precipitation falling in spring–summer was also positively related to species richness; about half of this relationship was direct and half indirect (Fig. 4c). Both grass and shrub cover had positive effects on species richness, but the path coefficient of grass cover on this variable was more than double that of shrub cover (Fig. 3). Shrub cover and grass cover were negatively correlated (Fig. 3).

DIRECT AND INDIRECT EFFECTS OF CLIMATE AND VEGETATION STRUCTURE ON ANPP, PUE AND PMR

Standardized total effects from SEM showed that vegetation structural characteristics and climatic variables had similar strengths as drivers of variation in ecosystem functional attributes. Grass cover had the highest total effect on ANPP (0.58), PUE (0.55) and PMR (0.41). Among the climatic variables, mean annual precipitation had the strongest total effect on ANPP (0.51) and PUE (−0.41), while the proportion of precipitation falling in spring–summer was the most influential climatic variable on PMR (0.36; Fig. 5). About 85% of the effects that grass cover had on functional attributes were direct; the remainder were indirectly mediated by its relationship with species richness. Shrub cover and species richness also had direct positive effects on ANPP, PUE and PMR, but their direct path sizes were about 30% and 50% of those of grass cover (Fig. 5). Most of the effect of precipitation on ANPP was direct (approximately 66%), and the remainder was mediated by the positive effects that precipitation had on grass cover (Figs 3 and 5a). The relationship between precipitation and grass cover partially offset about 25% and 50%, respectively, of the negative direct effect that precipitation had upon PUE and PMR (Fig. 5b,c). Mean annual temperature had a strong negative indirect effect on ANPP and PUE, which was mediated by the negative effect that temperature had on grass cover and species richness and the positive effect that temperature had on shrub cover (Fig. 5a,b). Temperature also had a positive direct effect on PMR, which was partially offset (approximately 60%) by its negative effect on grass cover and species richness (Fig. 5c). The proportion of precipitation falling in spring–summer showed strong positive effects on ANPP, PUE and PMR. Most of these effects were indirect, as they were mediated mainly by the positive effect on grass cover and, to a lesser extent, shrub cover and species richness (Fig. 5a–c). The proportion of precipitation falling in spring–summer also had a direct positive effect on ANPP and PMR (Fig. 5a,c).

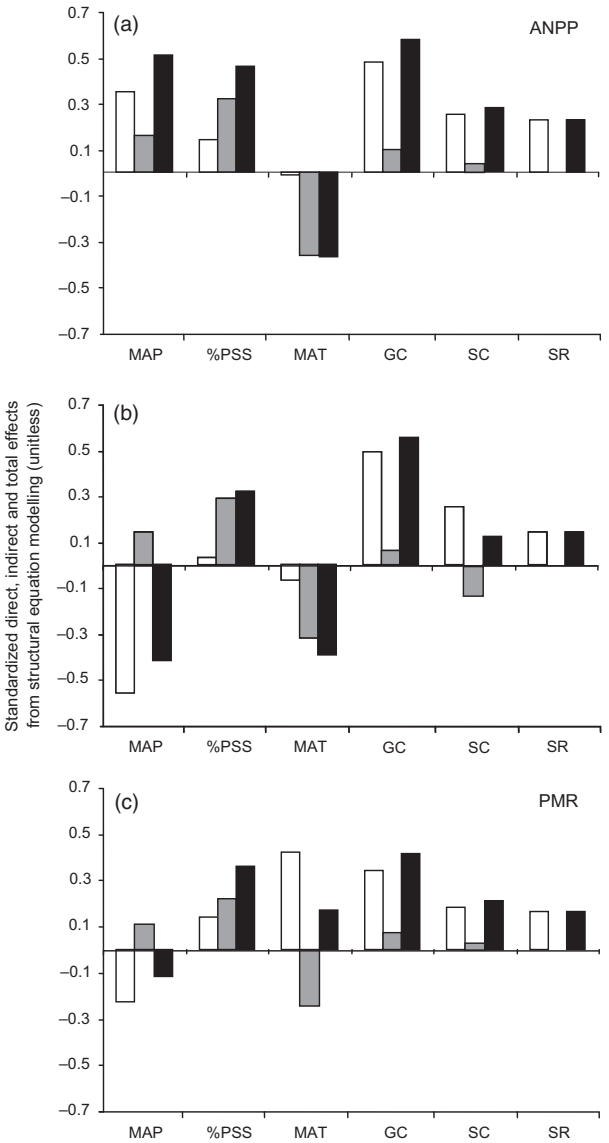

Fig. 5. Standardized direct (white), indirect (grey) and total effects (black) of mean annual precipitation (MAP), proportion of precipitation falling in spring–summer precipitation (%PSS), mean annual temperature (MAT), grass cover (GC), shrub cover (SC) and species richness (SR) upon surrogates of (a) above-ground net primary productivity (ANPP), (b) precipitation-use efficiency (PUE) and (c) precipitation marginal response (PMR).

Discussion

Our results provide important insights into the relationships between climate and ecosystem structure and function, which would be extremely difficult to obtain using small-scale factorial experiments or empirical bivariate studies. According to our hypothesis, we found that vegetation structural attributes explained a significant and unique portion (i.e. independent of that explained by climate) of the variability found in ecosystem functional characteristics at the regional scale, which is

as important as that explained by climate. These results highlight the importance of accounting for both climatic features and vegetation structure when modelling ANPP and related functions at the regional scale and suggest that human impacts can strongly shape ANPP dynamics through their imprint on vegetation structure.

EFFECTS OF CLIMATE ON VEGETATION STRUCTURE

We found that temperature and the amount and seasonal distribution of precipitation were important controls of vegetation structure in Patagonian rangelands. However, climate explained <60% of the variation in grass cover and species richness, and <15% of the variation in shrub cover. These results suggest that other factors, such as human use, and geomorphological and soil characteristics (Jobbágy, Paruelo & León 1996), exert a significant control on vegetation structure. The introduction of livestock to Patagonia over 100 years ago has induced changes in vegetation structure in this area (e.g. León & Aguiar 1985; Bisigato & Bertiller 1997). These changes could explain, at least partially, those variations in vegetation structural attributes not explained by climate.

Across the study area, shrub cover increased, and grass cover and species richness decreased, towards warmer, drier and more winter-dominant rainfall regimes. Other studies have shown how vegetation has shifted from grasslands to shrublands along gradients of decreasing precipitation in Patagonia (Bertiller *et al.* 1995; Jobbágy, Paruelo & León 1996). This could be due to the extensive root system of shrubs, which allows them to use water stored in deeper soil layers (Fernández & Paruelo 1988). Our results support the conceptual model proposed by Sala, Lauenroth & Golluscio (1997) to describe the grass–shrub balance in drylands. According to this model, summer precipitation will favour species such as grasses that have shallow roots. Winter precipitation will be more likely to percolate into the soil and to be stored in deep layers, favouring deep-rooted species such as shrubs.

Both biotic (grass and shrub cover) and abiotic (climatic variables) factors influenced species richness and accounted for 52% of its variation. Species richness increased with vegetation cover, although the impact of grass cover was higher than that of shrub cover. Mean annual temperature was the climatic variable with the highest negative effects on species richness, while the proportion of precipitation falling in spring–summer and mean annual precipitation had positive effects. Direct and indirect effects of temperature on species richness were similar. Evapotranspiration and drought stress increase as temperature increases in water-limited ecosystems, which could explain the negative relationship between temperature and species richness that we found. The proportion of precipitation falling in spring–summer positively affected species richness; about half of this effect was indirect (via their positive impact on grass cover), and the other half was a direct effect. The intraannual distribution of precipitation has been recognized as a factor controlling species richness, as plants have diversified their use of seasonal precipitation (Dodd, Lauenroth & Welker 1998). In our study sites, precipitation patterns varied between being markedly concentrated in autumn–winter (when 75.8% of precipitation fell) to having an even distribution of rain events throughout the year (45.0% of precipitation falling in autumn–winter). A more even rainfall pattern could favour the coexistence of species exploiting soil water resources with different spatiotemporal strategies, while highly concentrated precipitation in winter could constrain it.

DIRECT AND INDIRECT EFFECTS OF CLIMATE AND VEGETATION STRUCTURE ON ANPP, PUE AND PMR

Vegetation cover was a primary driver of variations in ecosystem functioning and had a positive effect on ANPP, PUE and PMR. In sparsely vegetated ecosystems (total plant cover <100%), such as those we studied, plant cover may be a good surrogate for leaf area index (LAI). Previous studies have found positive relationships between cover and the fraction of absorbed photosynthetically active radiation by areas of plant canopy with cover values below 100% (Chen *et al.* 2009). Carlson & Ripley (1997) also suggested that vegetation cover, not LAI, is the key variable in determining surface energy fluxes in these areas. Moreover, as vegetation cover increases, water losses (evaporation, deep drainage and runoff) decrease and uptake by plants increases (Aguiar & Sala 1999). It is also noteworthy that the total effect of grass cover on ANPP, PUE and PMR was twice that of shrub cover, suggesting that shrub encroachment could cause a reduction in ANPP, PUE and PMR (Verón & Paruelo 2010). Aguiar *et al.* (1996) calculated that the replacement of grasses by shrubs in the Patagonia steppe resulted in a 43% reduction in ANPP, which was caused by the inability of shrubs to use water made available by the removal of grasses. Grasses have shallow roots and higher relative growth rates, while shrubs have deep roots and lower relative growth rates (Verón & Paruelo 2010). This makes shrubs more drought tolerant than grasses, while grasses are more sensitive to drought than shrubs, but can quickly make use of available resources.

Species richness had a positive effect on ANPP, PUE and PMR. A large number of manipulative studies conducted under controlled conditions have found positive relationships between species richness and ANPP (see Cardinale *et al.* 2011 for a recent review). Observational studies in naturally occurring ecosystems have produced mixed results ranging from positive to negative and unimodal relationships (Mittelbach *et al.* 2001). Part of these conflicting results may stem from the fact that this relationship is influenced by the interplay of multiple factors that covary across natural gradients. For example, Bai *et al.* (2007) found a positive species richness–ANPP relationship across a broad natural gradient in Inner Mongolia. However, Ma *et al.* (2010) found, in the same area, that both variables covary in parallel with mean annual precipitation and that once this effect was removed, species richness and ANPP were no longer correlated. After accounting for the effects of other factors, we found that species richness explained a significant and unique portion of the variability (15–25%) found in ANPP, PUE and PMR (Fig. 3). Our

findings highlight the importance of species richness for maintaining ecosystem functioning in rangelands and provide further empirical evidence of its important role of providing key ecosystem services linked to ANPP in these areas (Cardinale *et al.* 2012).

Precipitation was the climatic variable with the greatest positive effect on ANPP. This result accords with several studies conducted in drylands at regional and global scales (e.g. Sala *et al.* 1988; Paruelo *et al.* 1999; Yang *et al.* 2008). A novel finding of our study is the quantification of the direct and indirect effects of mean annual precipitation on ANPP. We found that over two-thirds of the total effect of precipitation on ANPP was direct, and the other third was indirect (via the effects of precipitation on vegetation structure). On the other hand, precipitation had a negative effect on PUE and PMR, although these effects were partially offset by its positive effects on grass cover. Previous studies have found negative (Huxman *et al.* 2004), positive (Bai *et al.* 2008) or unimodal (Paruelo *et al.* 1999) relationships between precipitation and RUE. Two alternative reasons could explain our results: (i) as water stress is reduced, the availability of other resources (e.g. nutrients or light) may constrain ANPP (Huxman *et al.* 2004) and (ii) Paruelo, Sala & Beltrán (2000) showed that the proportion of water drainage losses increased with precipitation in Patagonia. This could constrain the conversion of precipitation to biomass and consequently reduce PUE as precipitation increases. The proportion of precipitation falling in spring–summer had a positive total effect on ANPP, PUE and PMR, which was mainly indirect (mediated by its impact on vegetation structure), although the direct effect was also significant. These results indicate that productivity increases as warm and wet seasons overlap, allowing an efficient use of precipitation by reducing drainage losses. Temperature had a strong negative indirect effect on ANPP and PUE through its impact on structural characteristics (negative effect on grass cover and species richness and positive effect on shrub cover). Epstein *et al.* (1996) also found a negative relationship between temperature and productivity, which was attributed to the enhancement of soil evaporation promoted by increases in temperature, which reduce ANPP. In our study, this effect is probably mediated by the effect that temperature has on species richness and the grass–shrub balance. Temperature exerted a positive direct effect on PMR, which was partially offset by its negative indirect effect via structural attributes. Higher temperature could increase PMR due to increasing plant developmental processes, which may be constrained in cold ecosystems such as Patagonian drylands (Ma *et al.* 2010).

ON CAUSE AND EFFECT RELATIONSHIPS USING OBSERVATIONAL DATA

We acknowledge the difficulty of separating climatic and non-climatic influences in ecosystem functioning at regional scales when the controlling factors of the variables of interest (ANPP, RUE and RMP in our case) covary. This difficulty can be resolved with controlled manipulative experiments. In Patagonia, several studies with manipulative experiments have analysed the interplay between climate and structural attributes as drivers of ecosystem functioning (e.g. Sala *et al.* 1989; Golluscio, Sala & Lauenroth 1998; Yahdjian & Sala 2006). However, these studies have been carried out only locally due to the difficulty of replicating expensive and time-consuming experiments at the regional scale. To account for the potential effects of covarying drivers of ecosystem functioning in our study, we utilized SEM. This methodology is being increasingly used in ecology to separate direct and indirect effects of controlling factors on the variable of interest (e.g. Grace 2006; Grace *et al.* 2010; Jonsson & Wardle 2010), particularly when dealing with regional and global geographical gradients where climate influence both structural and functional ecosystem variables (e.g. Bowker, Maestre & Mau 2013; Delgado-Baquerizo *et al.* 2013; Carnicer *et al.* 2014; Cavieres *et al.* 2014). SEM also offers advantages over conventional univariate relationships, as they can lead to misleading impressions when the independent variables are not fully independent (see, for example, Bai *et al.* 2007 and Ma *et al.* 2010). The problems of univariate analysis under these circumstances include: (i) the unanalyzed and unresolved covariances among interacting explanatory variables and (ii) the inability to assign unique explanatory capacity to individual factors (Grace & Bollen 2005). To avoid these problems, SEM can analyse multivariate hypotheses to understand responses controlled by multiple factors (Grace 2006). While we acknowledge that SEM cannot replace experiments and that establishing cause–effect relationships using observational data like ours is always difficult (Grace 2006), using this technique and an *a priori* model based on sound theory and previous findings, we could separate direct and indirect effects of climate and vegetation structure on ANPP, RMP and RUE in the studied ecosystems.

Concluding remarks

A main novelty of this study lies on its regional scale and the large number of field sites sampled scattered over a large area comprising a wide variation in environmental conditions. Our results have important implications for the management and conservation of rangelands in the context of ongoing climate change. Regional models of climate change over southern South America (including Patagonia) for the next century predict an increase in arid conditions due to lower precipitation and higher temperatures (Nuñez, Solman & Cabré 2009). Consistent with our results, these climatic changes are likely to have a negative impact on the sustainability of Patagonian rangelands due to their strong impact on vegetation structure and functioning. The effects of climate change on ecosystem functionality would be both direct and indirect, as climate change will probably increase the proportion of shrubs (generally less palatable than grasses) and decrease the proportion and richness of grasses. Consequently, Patagonian rangelands are likely to be less productive and less efficient at converting precipitation into plant biomass. Grazing has strong effects on vegetation structure and can produce changes in the grass–

shrub balance and species richness (Milchunas & Lauenroth 1993; Sankaran, Augustine & Ratnam 2013). Therefore, overgrazing may accentuate the effects of climate change and promote desertification. Appropriate management of livestock carrying capacity and the use of rotational grazing can offset or mitigate these negative effects of climate change. Maintaining and enhancing species richness, particularly that of grasses, can also be used as a management tool to offset some of these effects. Apart from its role in the ecosystem functional aspects evaluated in this study, it is important to conserve species richness because of its effects or association with several other functional characteristics in drylands (e.g. Cardinale *et al.* 2012; Maestre *et al.* 2012). Finally, the use of long-term monitoring systems such as MARAS, which integrate field-based surveys, remote sensing, climatic data and a multivariate interpretative framework could be a useful tool to detect and provide range managers and government agencies with 'early warning' signals for the onset of desertification processes due to human use and/or climate change.

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Supporting Information

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

Appendix S1. Precipitation estimates.

Figure S1. Relationship between periods of cumulative precipitation and a *proxy* of ANPP.

Figure S2. Correlograms of residuals of structural equation models.

Figure S3. Structural equation models for 192 sites separated by a distance higher than 40 km.