

Original Articles

Functional syndromes as indicators of ecosystem change in temperate grasslands



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ABSTRACT

The lack of an organizing conceptual framework to address ecosystem changes reduces our capacity to distinguish biophysical from direct human impacts on grassland dynamics. This is particularly important for subhumid temperate grasslands, one of the world's most threatened biomes. We identified and mapped 4 functional syndromes of grassland change at the wettest end of its worldwide distribution, the Campos in Uruguay. Syndromes were defined by differences in precipitation use efficiency (PUE, ANPP/precipitation), and in precipitation marginal response (PMR, slope of the linear regression between ANPP and precipitation) between two periods (1981–1995 and 2001–2011). Temporal trends in aboveground net primary production (ANPP, obtained by splicing two sources of NDVI, LTDR and MOD13Q1) were also characterized. To rule out the effect of precipitation we analyzed temporal trends of the residuals from the relationship between ANPP and annual precipitation (RESTRENDS). Functional syndromes associated with increases in seasonality or in the abundance of annual vegetation ($\Delta\text{PMR} > 0$, $\Delta\text{PUE} < 0$, $\sim 14,000 \text{ km}^2$) and vegetation cover loss ($\Delta\text{PUE} < 0$ and $\Delta\text{PMR} < 0$, $> 5000 \text{ km}^2$) were the most abundant. ANPP trends were significantly negative in 3.7% of the area (2475 km^2) and only positive in 0.3%. However, RESTRENDS were significant in 11% of the area ($> 7700 \text{ km}^2$), and mostly negative (in $\sim 7200 \text{ km}^2$). Most of these negative trends and residual trends were associated to seasonality increase and vegetation loss syndromes. These patterns were consistent with observed changes in the region. We highlight that this conceptual framework is suitable for describing patterns of change and potential causes. Moreover, it provides policymakers with a novel tool to guide management and conservation policies, pointing to sites where intervention (i.e. conservation, restoration) is needed.

1. Introduction

Grasslands occupy between 30% and 40% of Earth land surface (White et al., 2000) and harbor a diverse assembly of species and large amounts of carbon. Grass and graminoid dominated habitats (e.g. savannas, steppes, open and close shrublands) occur in areas where mean annual precipitation ranges from 250 to 1000 mm/y and mean annual temperature varies from 0 to 26 °C (Blair et al., 2014). Since the beginning of civilization, grasslands have been a major focus of land use

change given its gentle topography, rich soils and the increasing demand of food, fiber and shelter (Klein Goldewijk and Ramankutti, 2004). Additionally, climate change is expected to modify biophysical conditions -such as water availability or temperature- to which grasslands' dynamics are particularly sensitive (Ponce Campos et al., 2013) and thus may significantly alter its structure and functioning.

Structural features include vegetation cover, biomass, species richness, plant functional type composition, and element stocks. Frequent impacts of grazing upon grasslands structure include increased bare soil

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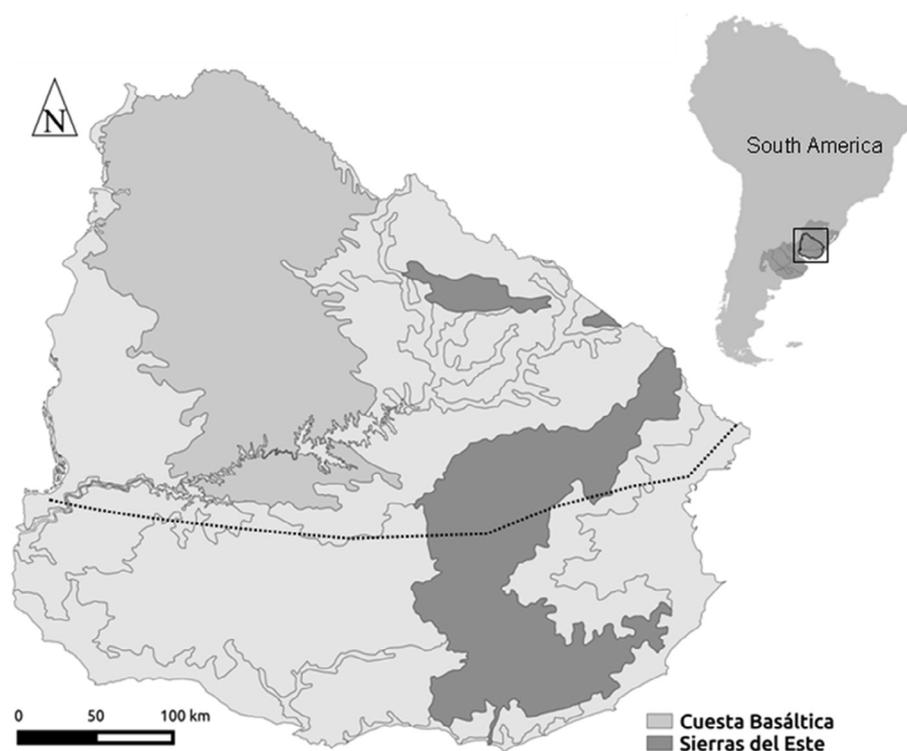


Fig. 1. Study region, the two geomorphological units from the Campos of Uruguay dominated by natural grasslands. The limits of all the geomorphological units are shown and the focal units are highlighted in tones of dark gray. The thick dotted line represents the limit between the Northern Campos and the Southern Campos. The limits of the Rio de la Plata grasslands and Uruguay are shown in the South America map in the upper right.

surface area, decreased herbaceous cover and increased cover of woody shrubs or shrub clusters (Asner et al., 2004). However these findings are not generalizable. Studies from Patagonian steppes showed that at more xeric sites, grazing altered the relative abundance of palatable and not palatable grasses without significant increases in bare soil, shrub cover or species richness (Perelman et al., 1997). In the Pampas grasslands, grazing has been associated to an increase in exotic species and thus in species richness (Rusch and Oesterheld, 1997). In the Uruguayan, Campos shrub encroachment results from grazing exclusion (Altesor et al., 2006), not from overgrazing as in many other areas. Similarly, grazing effects upon soil C and N stocks depend on several site specific characteristics such as soil depth and soil texture (Jobbágy and Jackson, 2000). Functional features describe the exchange of energy and matter among ecosystems components. Most studies have focused on carbon, nitrogen and water flows to assess the impacts of grazing upon grassland functioning (Sala et al., 1996). Again, results do not show a uniform pattern. Oesterheld et al. (1999) analyzed more than 100 paired grazed-ungrazed situations from grasslands and savannas around the world and found that grazing increased aboveground net primary productivity–ANPP, the net increase in vegetative biomass over time, a major component of the carbon cycle- in 28% and decreased it in 72% of the cases irrespectively of the site mean annual precipitation. Other studies have shown that grazing alters the N cycle through increased volatilization and leaching from dung patches (Frank and Evans, 1997; Piñeiro et al., 2006). However N recycling may be accelerated in nutrient rich systems and decelerated in nutrient poor systems (McNaughton et al., 1997).

Generalizations of grassland change are further hampered by the multidimensionality of its causes and by the interactions between structural and functional consequences of grazing and other drivers. For example, when overgrazing leads to woody encroachment, ANPP does not decrease but increase (Huenneke et al., 2002; Maestre et al., 2009). Similarly, if legume shrubs increase their abundance, N stock may increase with grazing (Asner et al., 2004). In turn, climate change, nitrogen deposition, CO₂ fertilization, altered disturbance regimes and vegetation removal or introduction, add considerable complexity to grassland dynamics (Archer et al., 1995; van Auken 2000; Blair et al.,

2014).

Despite its importance, we still lack an organizing framework to rule out direct human impacts from both climate variability and climate change on grasslands over large spatial and temporal extents. What is needed is a synoptic perspective that, by addressing its most salient features, allows the identification of consistent patterns of ecosystem change.

The syndrome concept (Schellhuber et al., 1997; Petschel-Held and Reusswig, 1999; Lüdeke et al., 2004) allows the representation of bundles of consistent patterns resulting from interacting processes. In temperate grasslands, some of these patterns include:

- changes in ecosystem structure, in terms of modifications in the relative abundance of plant functional types (i.e. grasses and shrubs, Paruelo et al., 2008; C₃ and C₄ grasses, Irisarri et al., 2016) or changes in overall vegetation abundance (Asner et al., 2004; Eldridge et al., 2011) and
- alteration of ecosystem functioning either through changes in resource use or in the ability to respond to inter-annual variation in resource availability (i.e. Verón and Paruelo, 2010). Precipitation use efficiency (PUE, mean annual ANPP divided by mean annual precipitation, Le Houerou, 1984) and precipitation marginal response (PMR, the slope of the ANPP-precipitation relationship on an annual scale, Verón et al., 2005) provide robust indicators of changes in ecosystem functioning (Verón et al., 2005, 2006). By tracking grasslands' PUE and PMR (and changes therein) over time, one may identify recurring patterns, i.e. syndromes of grassland change, as they may serve as identifiers of functional and structural changes (Verón and Paruelo, 2010; Kaptué et al., 2015, Verón et al., in press).

Large portions of South American temperate grasslands, particularly, the Rio de la Plata Grasslands (Fig. 1, Soriano, 1991) have been converted to agriculture (Baldi and Paruelo, 2008), tree plantations (Jobbágy and Jackson 2003, 2004), urban areas, or are subjected to grazing by domestic herbivores (Overbeck et al., 2007). Changes in overall plant abundance or plant functional type composition are

apparent when native grasslands are replaced by annual crops, forests plantations or urban areas. However, how grazing affects plant functional types and its consequences on ecosystem functioning remains poorly understood. Lezama and Paruelo (2016) showed that the effect of grazing depends on the relative weight of different factors such as plant grazing selectivity, biomass consumption, trampling and nutrient deposition through urine and feces. Grazing, fire regime or drought may lead to similar changes in vegetation structure: increased bare soil, decreased herbaceous cover or increased cover of woody vegetation (Overbeck et al., 2007; Quiroga et al., 2010). In other cases, vegetation cover may not change, but plant functional types may drastically change, affecting ecosystem functioning (Irisarri et al., 2016) and stability (Ruppert et al., 2015). How these structural changes affect ecosystem functioning properties (i.e. ANPP or ANPP response to precipitation among others) remains poorly understood.

Verón and Paruelo (2010) showed for semiarid grasslands of Patagonia, that PUE is sensitive to changes in total plant cover, whereas PMR rather responds to changes in plant functional type composition. The integration of vegetation response to precipitation allows characterizing functional syndromes through its main abiotic regional control. PUE (Le Houerou, 1984), provides information on the ability of a system to convert precipitation into vegetation growth. PUE is an indicator of overall, rainfall corrected productivity. Naturally PUE will only change slowly over time, as functional composition changes (e.g. shrub encroachment) or abruptly, in cases such as catastrophic disturbances that alter vegetation structure (e.g. fire, plowing). On the contrary, PMR (Verón et al., 2005), describes the sensitivity of vegetation to interannual changes in precipitation. Verón and Paruelo (2010) and Williamson et al. (2012) showed that PMR was lower in shrub- than in grass- dominated ecosystems. Changes in both PUE and PMR within a site were recently put together in a typology of vegetation change syndromes (Kaptué et al., 2015; Verón et al., in press).

Even though the combination of changes in PUE and PMR may be useful to characterize structural changes in vegetation, by itself it does not allow identifying its plausible causes. To sort out this problem, the residual trend method (the temporal slope of the residuals from the relationship between ANPP and precipitation, Evans and Geerken, 2004) was proposed and added to the typology of vegetation change syndromes (Kaptué et al., 2015; Verón et al., in press).

While initially not considered, we contend that including the (potential) causes of change in the definition of syndromes will significantly assist decision making, as could guide in avoiding some (undesirable) changes or promote other (desirable) ones. Remote sensing is particularly well suited to assess land surface properties that may be useful to diagnose vegetation status and change (Verón et al., 2006; Kaptué et al., 2015) and to discriminate between its human and biophysical controls (Evans and Geerken, 2004; Wessels et al., 2007).

The concept of syndrome was originally developed to infer mainly structural aspects of vegetation change in arid and semiarid systems (i.e. Kaptué et al., 2015). In this article we generalize the idea of syndrome typology and propose it as an integrative indicator of functional ecosystem changes. Abrupt changes can be easily characterized from sharp changes in the C gains assessed from remotely sensed data. We

state that syndrome typology would also help to describe and map more subtle changes, i.e. those associated to grazing or climate change. We sought to identify and map functional syndromes of vegetation change, defined by ANPP dynamics (estimated by long term remote sensing data and experimental work) and its response to precipitation (PUE, PMR and residual trends) at the wettest end grasslands' distribution and one of the largest relicts of natural temperate grasslands, the Campos of Uruguay.

2. Methods

2.1. Study area & data

This study comprises two geomorphological units of the Campos of Uruguay dominated by natural grasslands (Fig. 1). The Cuesta Basáltica region is in the mid N Uruguay (between 31° 35' and 32° 12' S and 56° 12' and 27° 20' W), and covers an area of 4.39 million ha. Soil characteristics have prevented the development of agriculture and forestry, shrub and natural forests are scarce, natural grasslands are the dominant vegetation type (Lezama et al., in press) and grazing by cattle and sheep is the main land use. The Sierras del Este region, is located in E Uruguay (between 32° 04' and 34° 54' S and between 53° 43' and 55° 36' W) and covers an area of 2.52 million ha. As in the Cuesta Basáltica, natural grasslands are dominant, although shrublands and native forests are also present. Mean annual precipitation (MAP) in these regions is between 1200 and 1600 mm, being higher in the NE, whereas mean annual temperature is around 19 °C (Castaño et al., 2011). We overlaid a land cover classification (Baeza et al., 2014; Teixeira et al., 2015) to a geomorphological map of Uruguay (Panario, 1988) and gridded the country in cells of 0.05° to match the pixel size of the satellite images (see below), then we selected those cells from the Cuesta Basáltica or Sierras del Este with at least 75% of the area covered by natural grasslands.

2.2. ANPP from the Monteith model

To obtain continuous monthly time series of ANPP estimates for the period 1981–2015, we applied the Monteith model (Monteith, 1972, Fig. 2). This ecophysiological model states that ANPP (or NPP) is positively and linearly related to the total amount of photosynthetic active radiation (PAR; in MJ) absorbed by green vegetation (APAR) during the growing season:

$$\text{ANPP} = \int \text{APAR} \times \varepsilon$$

The constant ε is the radiation use efficiency (RUE; C or DM in $\text{g} \cdot \text{MJ}^{-1}$), and states the amount of radiation “converted” into biomass. APAR results from the product of the incoming radiation (PAR) and the fraction of PAR absorbed by green tissues (fAPAR). fAPAR is positively related to spectral indices such as the Normalized Difference Vegetation Index (NDVI, Rouse et al., 1973). NDVI, PAR and RUE were obtained from different sources.

Monthly NDVI series at a spatial resolution of approximately 0.05° or 2500 ha for the period 1981–2015 were obtained splicing spectral

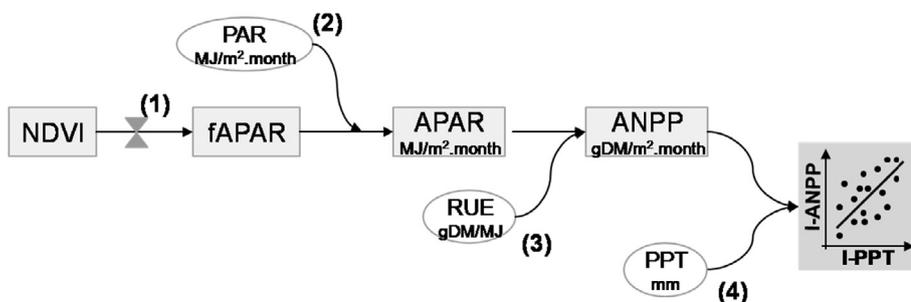


Fig. 2. The algorithm applied to obtain aboveground net primary production (ANPP), and the temporal relation between annual ANPP (I-ANPP) and annual precipitation (I-PPT) from which we derive functional syndromes of ecosystem change. PAR stands for photosynthetic active radiation; fAPAR for the fraction of the PAR absorbed by vegetation; APAR stands for the absorbed PAR and RUE for radiation use efficiency. Data sources: (1) Teixeira et al. (2015), (2) Ceballos and de Oliveira Macedo (2014), (3) Oyarzábal et al. (2011), (4) Chen et al. (2002).

information from two satellite products with different characteristics. The LTDR product (Long Term Data Record) was generated from data collected by the AVHRR sensor on board of different NOAA satellites (Pedelty et al., 2007) and covers the period 1981–1999. This product combines a daily temporal resolution with a spatial resolution of 0.05° (2500 ha at the equator). LTDR NDVI is derived from channels 1 (visible 580–680 nm) and 2 (near infrared 725–1100 nm) of the AVHRR sensor and provides associated quality information that allows estimating the usefulness of the index. The NDVI MOD13Q1 product is derived from bands 4 (red, 620–670 nm) and 5 (infrared, 841–876 nm) of the Terra sensor on board of the NASA earth observing system (EOS-NASA) MODIS (“Moderate Resolution Imaging Spectroradiometer”). This sensor combines a high spatial resolution (250 m) with a moderate temporal resolution (fortnightly, from 2000 onwards), and provides additional quality information. The complete splicing process and the (highly satisfactory) consistency checks on the homogeneous NDVI series obtained from the two platforms are described in Teixeira et al. (2015). fAPAR was estimated from NDVI applying an empirical non-linear relationship between MODIS-NDVI and fAPAR (Los et al., 2000; Piñeiro et al., 2006; Caride et al., 2012) that accounts for the widely described saturation of NDVI at high Leaf Area Index (LAI > 3) and implies a linear relation between the simple ratio index (SR = R/IR = (1 + NDVI)/(1 - NDVI)) and fAPAR. We parameterized this relationship with data from Rio de la Plata grasslands assigning no absorption (fAPAR = 0) to NDVI values corresponding to pixels that had no green vegetation (bare soil) and maximum absorption (fAPAR = 0.95) to NDVI values corresponding to pixels with high amount of green biomass (sown pastures with LAI > 3 and high yielding wheat crops during anthesis, Grigera et al., 2007). The resultant equation was $fAPAR = \min((SR - SR_{\min}) / (SR_{\max} - SR_{\min}), 0.95)$. The extreme values of SR were extracted from Grigera et al. (2007): $SR_{\min} = 1.55$ (NDVI_{min} = 0.215) and $SR_{\max} = 11.62$ (NDVI_{max} = 0.842).

Incidant photosynthetic active radiation (PAR) for South America on a monthly basis for the period 2000–2016 and at a spatial resolution of 0.04° was obtained from INPE's satellite division and environmental systems (DSA, <http://satellite.cptec.inpe.br/radiacao/>, Ceballos and de Oliveira Macedo, 2014). As PAR time series derived from this product did not show trends, mean monthly profiles for the period 2000–2015 were used as representative of the whole 1981–2015 period. Absorbed photosynthetic active radiation (APAR) was obtained as the product of PAR and fAPAR in each centroid of the 0.05° NDVI-fAPAR pixel.

Radiation use efficiency (RUE, in g DM/MJ) for grasslands from Cuesta Basáltica and Sierras del Este was obtained from Oyarzábal et al. (2011). As in the PAR case, mean monthly profiles of RUE (obtained experimentally for the period 2006–2009 in four research sites within the study region) were considered representative of the whole period. Finally ANPP (in gDM/m².month) was obtained as the product between APAR and RUE.

To estimate ANPP we used the Monteith model, instead of some of its partial components (i.e. NDVI or fAPAR) for two reasons. First, using NDVI as estimator of ANPP assumes that PAR, APAR or RUE are constant or strongly covary with NDVI. Several studies in the region demonstrated that this is not the case (Piñeiro et al., 2006; Oyarzábal et al., 2011; Guido et al., 2014). Second, and given the increasing availability of remote sensing data, Monteith Model seems to be the best, if not the only, alternative for estimating ANPP across large spatial scales and long time periods (Field et al., 1995).

2.3. Precipitation data

Precipitation was obtained from the NOAA's precipitation reconstruction over land (PREC/L, <http://www.esrl.noaa.gov/psd/data/gridded/data.precl.html>, Chen et al., 2002). This product provides monthly precipitation estimates (generated by a combination of gauges, remote sensing and modeling) from January 1948 to March 2012 at a

0.5° spatial scale. To evaluate PREC/L precipitation estimates we obtained monthly total ground precipitation from 16 meteorological stations from Uruguay that cover the period from 1948 to 2011 (Dirección Nacional de Meteorología and Instituto Nacional de Investigación Agropecuaria-INIA) not used in the development of PREC/L precipitation estimates. These ground precipitation records were significantly correlated with the corresponding PREC/L estimates ($r_{\text{median}} = 0.822$, $r_{\text{min}} = 0.508$, $r_{\text{max}} = 0.926$).

2.4. Statistical analyses

2.4.1. Trends in ANPP

Trends in the annual integral of ANPP (I-ANPP, the production during the growing season, i.e. the sum of monthly ANPP values from July to June) from 1981 to 2015 were estimated in each pixel by means of linear regression against time. In order to consider temporal autocorrelation we fitted different residual error structures (Zuur et al., 2009), and the best was selected by means of second order Akaike information criterion (AICc, Burnham and Anderson, 2002).

2.4.2. Temporal I-ANPP models and residual trend analyses (RESTRENDS)

To discriminate between trends in I-ANPP driven by precipitation from trends driven by other causes (i.e. to rule out the effect of annual precipitation upon I-ANPP) we applied residual trend analyses (Evans and Geerken, 2004). This method consists in estimating the temporal trends in residuals from the regression of I-ANPP against annual precipitation (I-PPT). We considered only a linear relation between I-ANPP and I-PPT, as the inter-annual precipitation variability is relatively low.

2.4.3. Functional syndromes

The identification of vegetation functional syndromes, as proposed by Verón et al. (2006), was based on the difference between the PUE and PMR from a given pixel to those of a reference situation, a temporal one in our case. For this, we split the whole period in two sub-periods of approximately the same duration (~10 years), from 1981 to 1995 (previous period) and from 2001 to 2011 (recent period). Within each period and pixel, and only if at least 5 years of data were available, PUE was estimated as the quotient between mean integral annual above-ground net primary production (mean I-ANPP) and mean integrated annual precipitation (mean I-PPT). With the same criteria (at least 5 years of data in each period), PMR was estimated as the slope of the linear relationship between I-ANPP and I-PPT per pixel and period (Lauenroth and Sala 1992; Verón et al., 2005, 2006). When regression was not significant, PMR was considered zero. Finally we calculated ΔPUE as $PUE_{\text{recent period}} - PUE_{\text{previous period}}$ and ΔPMR as $PMR_{\text{recent period}} - PMR_{\text{previous period}}$.

The four quadrants of the biplot between ΔPMR and ΔPUE , define functional syndromes associated with different vegetation responses to rainfall, and with characteristic time scales (Fig. 3). ΔPUE , can be interpreted as reflecting changes in the average efficiency of precipitation use by vegetation, i.e., the mean (precipitation corrected) productivity. ΔPMR represents changes in the vegetation responsiveness to inter-annual precipitation variability. These indicators are representative of processes in different time domains, particularly in sites in which sudden changes have not occurred. We summarize these domains through the terms “slow” and “fast” to refer to changes in ΔPUE and ΔPMR respectively, but not to say that sudden events (fires, abrupt land use changes) cannot change them.

The combination of positive or negative ΔPMR and ΔPUE reduces the syndromes to four possible combinations. Each one of them characterizes a specific type of vegetation change (Fig. 3). The lower left quadrant (in which $\Delta PMR < 0$ and $\Delta PUE < 0$, “F⁻S⁻”, Fig. 3) is associated with vegetation loss and a general reduction in vegetation responsiveness to precipitation, either fast or slow, as more precipitation would be lost to evaporation and runoff. In turn, the upper left quadrant ($\Delta PMR > 0$ and, $\Delta PUE < 0$ “F⁺S⁻”, Fig. 3) represents

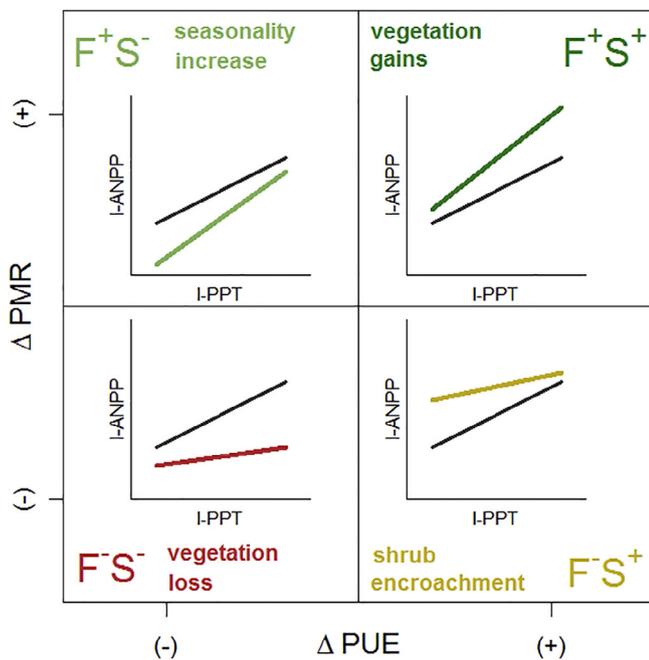


Fig. 3. Functional syndromes defined by the joint distribution of temporal dynamics of precipitation marginal response (ΔPMR) and precipitation use efficiency (ΔPUE). The gray line in each inset, depict the reference situation (i.e. the reference temporal relation between I-ANPP and I-PPT) and is the same in the four quadrants. The color lines represent the expected changes in the temporal relation between I-ANPP and I-PPT in the corresponding quadrant. The letters on the corners refer to increases (+) or decreases (-) in fast (F) or slow (S) vegetation responsiveness to precipitation.

increases in seasonality (“annualization” or “herb encroachment”, Kaptué et al., 2015), a pattern associated with an increase in the abundance of ephemerals and annual plants, or herbaceous C_4 vegetation versus shrubs. This syndrome reflects the fact that forbs and grasses tend to respond faster to precipitation as the relative growth rate (growth rate per mass unit) is usually higher for grasses than for shrubs and trees (Lambers et al., 1999).

The lower right quadrant ($\Delta PMR < 0$ and, $\Delta PUE > 0$ “F⁻S⁺”, Fig. 3), is associated with reductions in fast responsiveness of vegetation to precipitation and concomitant increases in slow responsiveness. This feature is characteristic of sites with significant reductions in seasonality, reductions in vegetation with rapid response to precipitation and increases in woody vegetation (“shrub” or “woody encroachment”, Kaptué et al., 2015), i.e. grazed sites where fire is absent or suppressed. Finally, the upper right ($\Delta PMR > 0$ and, $\Delta PUE > 0$ “F⁺S⁺”, Fig. 3) has been related to increases in fast and slow vegetation responsiveness to precipitation and represents overall vegetation gains, as the fraction of precipitation lost to drainage, runoff or bare soil evaporation should decrease. Increased vegetation cover, on the other hand, would allow for larger responses to wet years as more water can be transpired with higher leaf areas.

3. Results

3.1. I-ANPP patterns

Mean I-ANPP for the period 1981–2015 was 673.9 g/m².yr (S.E. = 1.126 g/m².yr, n = 1855, Fig. S1, Table 1). Minimum mean I-ANPP was 516.9 g/m².yr and occurred in a pixel from Cuesta Basáltica whereas maximum mean I-ANPP occurred in a pixel from Sierras del Este and was 842.1 g/m².yr.

Mean I-ANPP in Sierras del Este (704.6 g/m².yr, S.E = 1.996 g/m².yr, n = 615) was 7% (*t* statistic = -20, p-value < 0.001, Fig. S1c)

Table 1

Mean values, percentiles 5%, 95% and number of pixels (n) considered in the calculation of mean I-ANPP, ΔPUE , ΔPMR , I-ANPP trends and residual trends, for all grassland dominated sites (General) and broken down by geomorphological unit (Cuesta Basáltica, CB, and Sierra del Este, SE).

	Mean I-ANPP (g/m ² .year)	ΔPUE (g/m ² .year.mm)	ΔPMR (g/m ² .year.mm)	I-ANPP trend (g/m ² .year ²)	Residual trend (g/m ² .year ²)
General	637.9 (600.7, 761.4)	-0.062 (-0.121, 0.016)	-0.056 (-0.397, 0.266)	-10.160 (-16.846, 7.998)	-5.408 (-7.992, 3.723)
CB	658.6 (593.9, 723.3)	-0.074 (-0.124, -0.019)	0.124 (-0.248, 0.272)	-11.716 (-16.474, -7.112)	-6.059 (-7.996, -4.436)
SE	704.6 (623.4, 783.9)	-0.016 (-0.089, 0.038)	-0.205 (-0.469, 0.101)	-5.313 (-16.810, 12.190)	-1.018 (-7.018, 5.439)
	n = 1855	n = 840	n = 840	n = 99	n = 310
	n = 1240	n = 667	n = 667	n = 75	n = 270
	n = 615	n = 173	n = 173	n = 24	n = 40

higher than that from Cuesta Basáltica (658,6 g/m².yr, S.E = 1.138 g/m².yr, n = 1240). ANPP values were comparable to those reported for other grasslands from Rio de la Plata, derived from satellite imagery (Piñeiro et al., 2006; Paruelo et al., 2010; Baeza et al., 2010) or biomass harvesting (Rusch and Oesterheld, 1997; Perez and Frangi, 2000; Altesor et al., 2006). Our remote sensing estimation is more accurate as compared to those proposed by MODIS product MODIS17A3H (GPP/NPP) because MODIS bases its estimation of radiation use efficiency on land cover maps (Zhao et al., 2005). For grasslands in Uruguay, the MODIS land cover map has a misleading classification that assumes it is an area dominated by crops, a land use/cover class with highest RUE value in MODIS database. This would represent an overestimation of NPP and ANPP.

3.2. Trends in I-ANPP

I-ANPP trends were significant in only 4% of the analyzed area (99 pixels, or 2475 km², Fig. 4, Table 1) and mainly negative ($b_1 = -10.16$ g/m².yr², S.E. = 0.663 g/m².yr²). The areas with significant negative trends were spread out in Cuesta Basáltica, and more concentrated in Sierras del Este (Fig. 4).

Positive trends were present towards the SE border of Sierras del Este unit and represented only 0.3% of the whole grassland area (8 pixels, Fig. 4). All best fitting models included temporal autocorrelation (i.e. carryover effects) on production dynamics (90% of the models lag 1 residual correlation, and 10% of the models lag 2 residual correlation).

Difference in mean trends between both regions was highly significant (*t* statistic = -2.7, p-value < 0.01), being more than 120% steeper in the Cuesta Basáltica ($b_1 = -11.72$ g/m².yr², S.E. = 0.325 g/m².yr²) than in Sierras del Este ($b_1 = -5.313$ g/m².yr², S.E = 2.306 g/m².yr²).

3.3. Residual trend analyses

Residual trends from the linear relation between I-ANPP and I-PPT were significant in 11% of the area (> 7700 km², or 310 pixels, Fig. 5, Table 1) with a mean value of -5.41 g/m².yr² (S.E. = 0.157 g/m².yr²). Of these trends, 6% were positive and 94% negative. Differences in residual trends between geomorphological units were highly significant (Fig. 5c, *t* statistic = -6.121, p-value < 0.001). Significant residual trends represented 15% of Cuesta Basáltica, were mainly negative (-6.059 g/m².yr², S.E. = 0.078 g/m².yr², 269 negative, 1 positive) and concentrated in the central East part of the area (Fig. 5).

Almost 4% of Sierras del Este exhibited significant residual trends

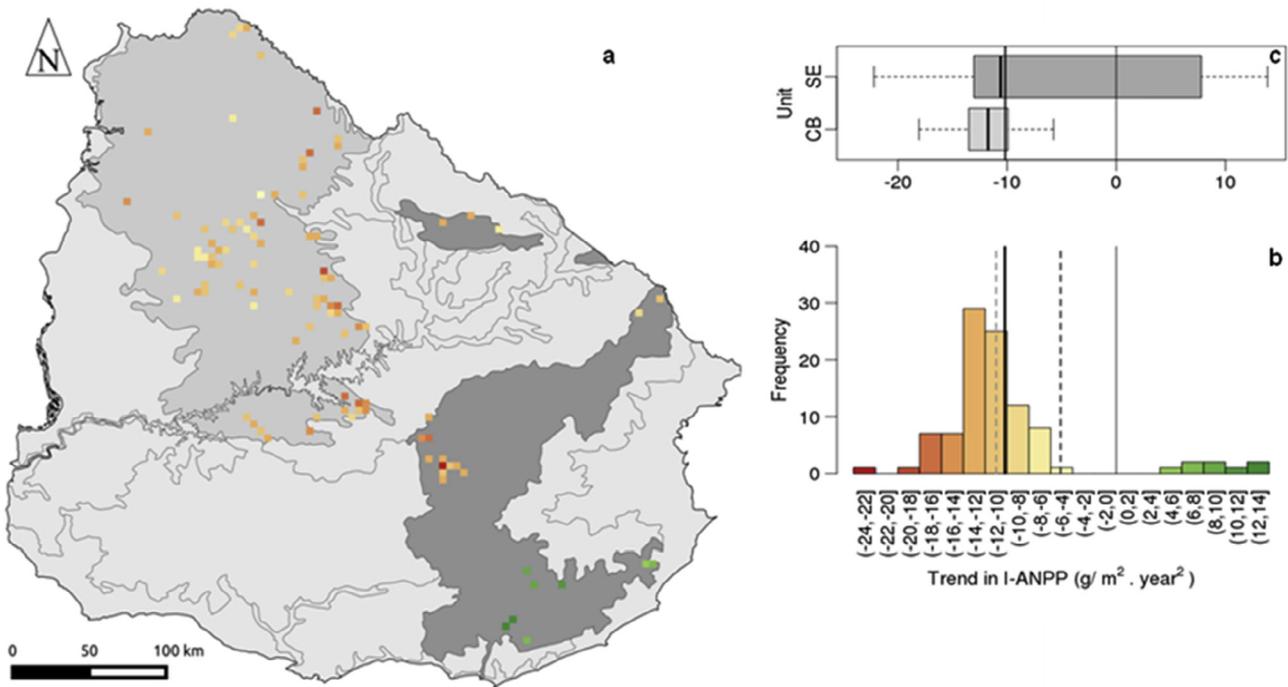


Fig. 4. Map (a) and frequency distribution (b) of significant trends in I-ANPP (grams/m².year²) between 1981 and 2015. The boxplots (c) over the histogram show the distribution of trends for each geomorphological unit, Cuesta Basáltica (CB) and Sierras del Este (SE). Thick vertical black line represents the mean of the distribution of trends in both histogram and boxplots. The vertical dark gray broken line in the histogram represents the mean of trends distribution for Sierras del Este whereas the light gray broken line the mean for the Cuesta Basáltica. The box limits in the boxplots represents the interquartile range.

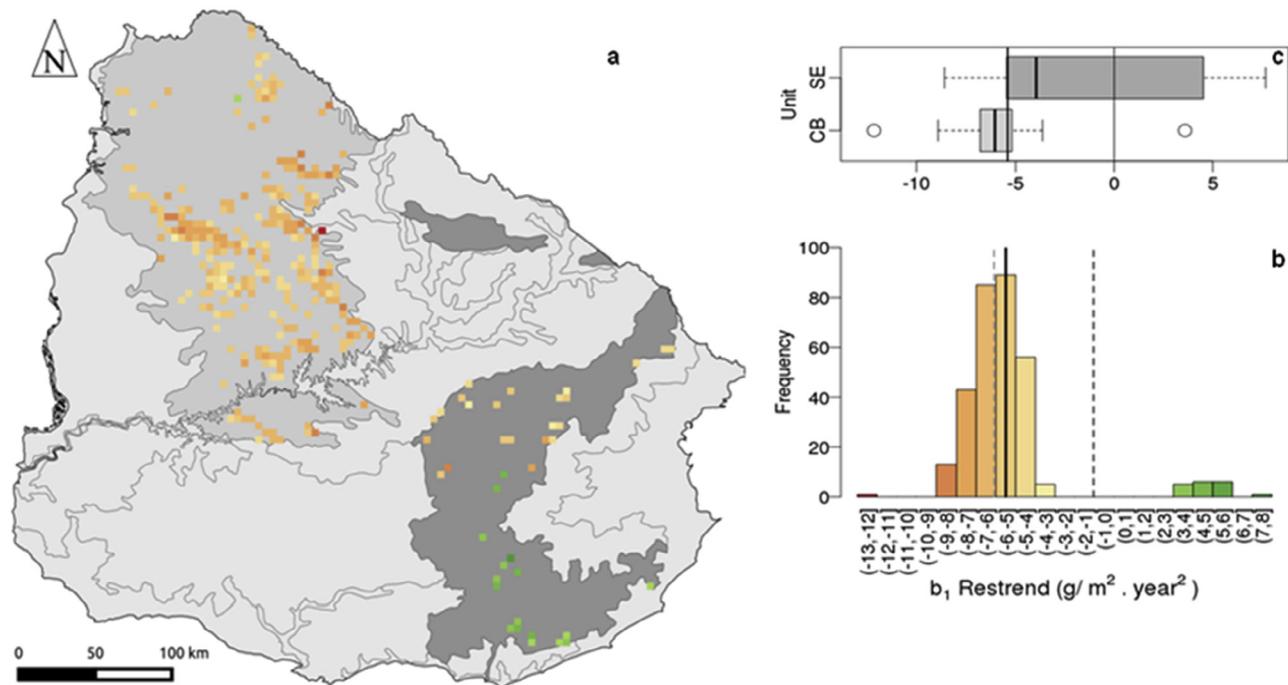


Fig. 5. Map (a) and frequency distribution (b) of significant residual trends of the ANPP-PPT relation (grams/m².year²) between 1981 and 2015. The boxplots (c) over the histogram show the distribution of residual trends for each geomorphological unit, Cuesta Basáltica (CB) and Sierras del Este (SE). Thick vertical black line represents the mean of the distribution of residual trends in both histogram and boxplots. The vertical dark gray broken line in the histogram represents the mean of residual trends distribution for Sierras del Este whereas the light gray broken line the mean for the Cuesta Basáltica. The box limits in the boxplots represents the interquartile range.

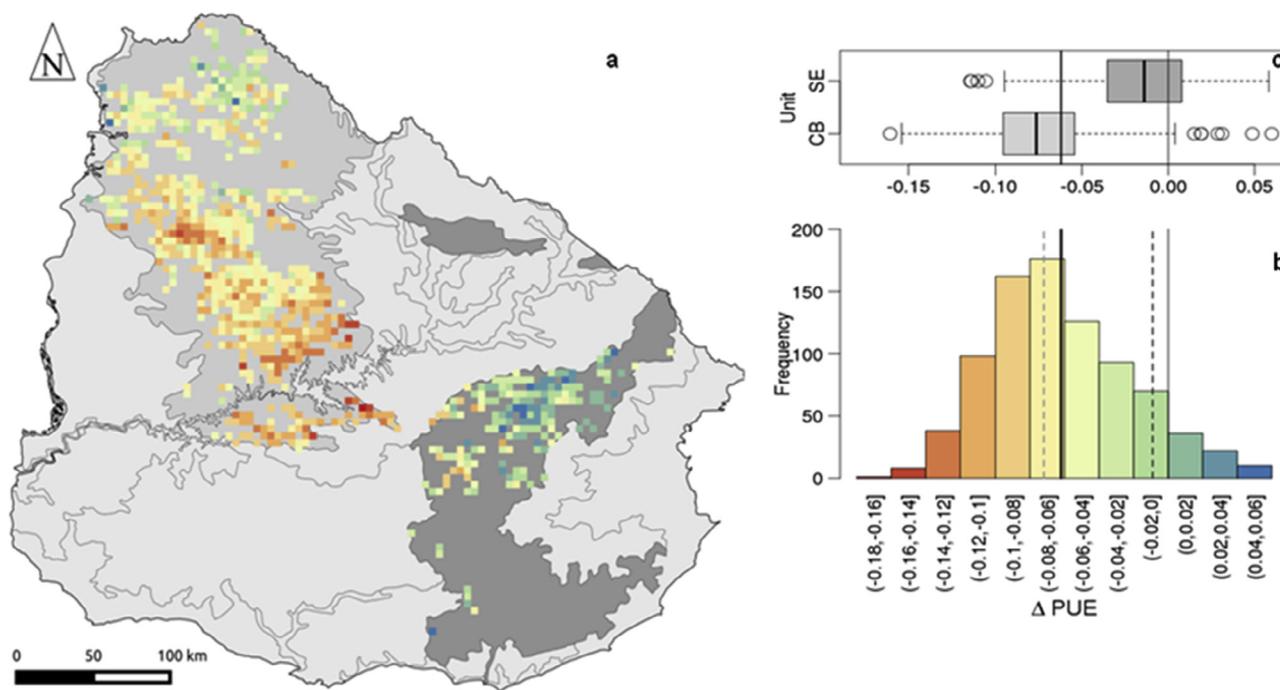


Fig. 6. Map (a) and frequency distribution (b) of Δ PUE (precipitation use efficiency during 2001–2011 vs precipitation use efficiency during 1981–1995). The boxplots (c) over the histogram show the distribution of Δ PUE for each geomorphological unit, Cuesta Basáltica (CB) and Sierras del Este (SE). Thick vertical black line represents the mean of the distribution of Δ PUE in both histogram and boxplots. The vertical dark gray broken line in the histogram represents the mean of Δ PUE distribution for Sierras del Este whereas the light gray broken line the mean for the Cuesta Basáltica. The box limits in the boxplots represent the interquartile range.

($-1018 \text{ g/m}^2\cdot\text{yr}^2$, S.E. = $0.820 \text{ g/m}^2\cdot\text{yr}^2$, $n = 40$) with negative and positive ones equally abundant (23 negative towards the North, 17 positive towards the South of the area).

3.4. Temporal differences in PUE (Δ PUE) and PMR (Δ PMR)

Differences in PUE between the recent (2001–2011) and previous (1981–1995) periods were mostly negative ($-0.062 \text{ g/m}^2\cdot\text{yr}\cdot\text{mm}$, S.E. = $0.0014 \text{ g/m}^2\cdot\text{yr}\cdot\text{mm}$, Fig. 6a, b). This reduction represented 92% of grasslands pixels with both Δ PUE and Δ PMR estimates or $> 19,300 \text{ km}^2$. However this reduction was not spatially uniform, as negative Δ PUE values were more frequent in the Cuesta Basáltica region ($-0.074 \text{ g/m}^2\cdot\text{yr}\cdot\text{mm}$, S.E. = $0.0012 \text{ g/m}^2\cdot\text{yr}\cdot\text{mm}$) and affected an area of $\sim 15,000 \text{ km}^2$ (33% of this unit).

In Sierras del Este the decrease was lower ($-0.016 \text{ g/m}^2\cdot\text{yr}\cdot\text{mm}$, S.E. = $0.0027 \text{ g/m}^2\cdot\text{yr}\cdot\text{mm}$) and affected an area of $\sim 3000 \text{ km}^2$ (11% of the unit). Differences in Δ PUE between regions were highly significant (Fig. 6c, t statistic = -19.2 , p -value < 0.001). Positive Δ PUE values were more frequent in Sierras del Este ($\sim 1500 \text{ km}^2$ or 6% of the unit) than in Cuesta Basáltica ($> 200 \text{ km}^2$ or 0.5% of the unit).

Contrary to Δ PUE, Δ PMR values were mainly positive ($\sim 70\%$ of pixels with estimates of Δ PUE and Δ PMR, or $> 14,000 \text{ km}^2$) concentrated in Cuesta Basáltica (mean = $0.124 \text{ g/m}^2\cdot\text{yr}\cdot\text{mm}$, S.E. = $0.0067 \text{ g/m}^2\cdot\text{yr}\cdot\text{mm}$), while negative ones were concentrated in Sierras del Este (mean = $-0.204 \text{ g/m}^2\cdot\text{yr}\cdot\text{mm}$, S.E. = $0.0149 \text{ g/m}^2\cdot\text{yr}\cdot\text{mm}$, Fig. 7a,b).

Positive Δ PMR represented more than $13,000 \text{ km}^2$ in Cuesta Basáltica (31% of the area) whereas more than $> 800 \text{ km}^2$ in Sierras del Este (3% of the area). In turn, negative Δ PMR affected more than 3000 km^2 (7% of the unit) in Cuesta Basáltica and 3500 km^2 in Sierras del Este (almost 14% of the unit). The difference in Δ PMR between geomorphological units was highly significant (Fig. 7c, $t = 20.089$, p -value < 0.001).

3.5. Synthesis and integration of functional syndromes

The most frequent syndrome was associated with increases in seasonality (Δ PMR > 0 and Δ PUE < 0 , “F⁺S⁻”, Fig. 9) and represented almost $14,000 \text{ km}^2$ ($> 60\%$ of the area with detectable changes or 20% of the whole study area) mostly in the Cuesta Basáltica (43% of the area vs. 4% of Sierras del Este). The next frequent syndrome was associated with vegetation loss (Δ PMR < 0 and Δ PUE < 0 , “F⁻S⁻”, Fig. 9) and affected $> 5300 \text{ km}^2$ ($\sim 25\%$ of the area with detectable changes or $\sim 8\%$ of the whole study area). The incidence of this syndrome was similar between units ($> 10\%$ in the Cuesta Basáltica and $\sim 14\%$ in Sierras del Este). The syndrome associated with decreases in fast responsiveness and increases in slow responsiveness (“shrub encroachment”, Δ PMR < 0 and Δ PUE > 0 , “F⁻S⁺”, Fig. 9) represented 1300 km^2 (6.2% of the area with detectable changes or $< 2\%$ of the whole study area) and was concentrated in Sierras del Este ($\sim 8.5\%$ of the units area).

Finally, the syndrome associated with vegetation gains (Δ PMR > 0 and Δ PUE > 0 , “F⁺S⁺”, Fig. 9) represented more than 400 km^2 ($\sim 1.8\%$ of the area with detectable changes or 0.6% of the whole study area) and was slightly more visible in Sierras del Este (~ 1.1 of the unit) than in Cuesta Basáltica ($\sim 0.7\%$ of the unit).

Altogether significant negative ANPP trends were exclusively related to negative Δ PUE values, but to positive and negative values of Δ PMR (Fig. 8a). The same holds for the joint analysis of Δ PUE, Δ PMR and RESTRENDS (Fig. 8b), although the frequency of significant cases was higher.

Most of the (significant negative) trends in I-ANPP (39 of 75 from Cuesta Basáltica and 6 of 16 from Sierras del Este) and residuals (118 of 222 from Cuesta Basáltica and 1 of 22 from Sierras del Este) were associated with the syndrome described as “seasonality increase” (“F⁺S⁻”). The syndrome “Vegetation loss” (“F⁻S⁻”) was also associated with negative trends in I-ANPP (9 of 75 from Cuesta Basáltica) and residuals (54 of 222 from Cuesta Basáltica and 11 of 22 from Sierras del Este). The remaining syndromes were not associated with

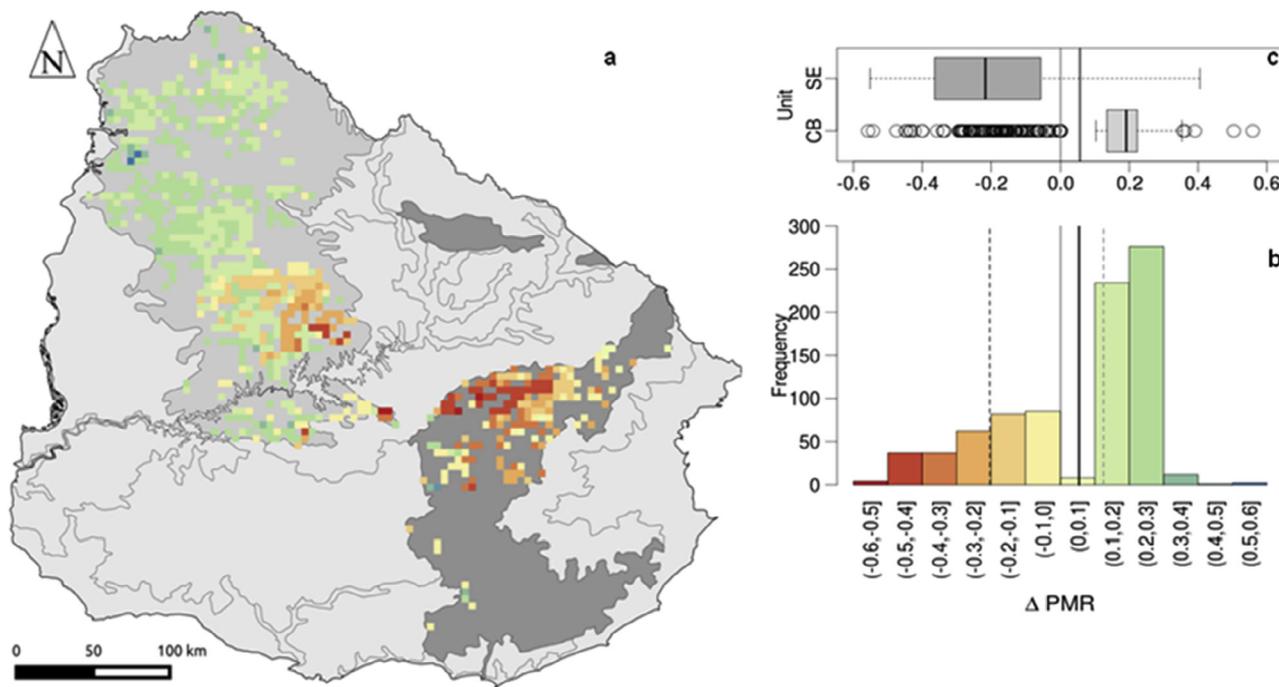


Fig. 7. Map (a) and frequency distribution (b) of ΔPMR (precipitation marginal response during 2001–2011 vs precipitation marginal response during 1981–1995). The boxplots (c) over the histogram show the distribution of ΔPMR for each geomorphological unit, Cuesta Basáltica (CB) and Sierras del Este (SE). Thick vertical black line represents the mean of the distribution of ΔPMR in both histogram and boxplots. The vertical dark gray broken line in the histogram represents the mean of ΔPMR distribution for Sierras del Este whereas the light gray broken line the mean for the Cuesta Basáltica. The box limits in the boxplots represent the interquartile range.

neither significant I-ANPP nor with residual trends, except for a single significant positive one in Cuesta Basáltica, belonging to the “vegetation gains” syndrome (“F+S+”).

4. Discussion

4.1. Anpp

ANPP varied in space across a clear Northwest to Southeast regional

gradient. Average C gains were 7% higher in Sierras del Este than in Cuesta Basáltica (Fig. S1). This pattern reflects the observed gradient in precipitation, as evidenced by spatial patterns in mean integral annual precipitation (mean I-PPT) and correlation between mean I-PPT and I-ANPP (Fig. S2 and Fig. S3). This spatial difference confirms previous descriptions of ANPP and controls regarding edaphic water holding capacity (Baeza et al., 2010; Guido et al., 2014). Shallower soils in the Cuesta Basáltica unit, towards the NW of the regional gradient, retain less water than those from the Sierras del Este towards the SE (Panario,

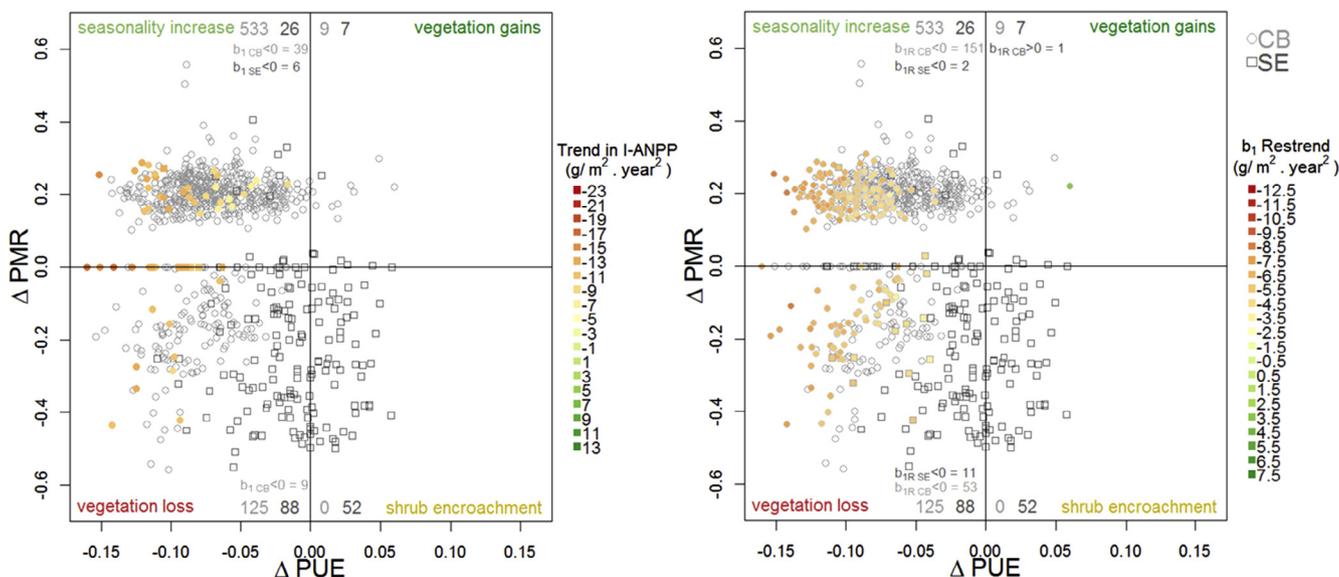


Fig. 8. Scatter among ΔPMR , ΔPUE and significant trends in I-ANPP (a) and among ΔPMR , ΔPUE and significant residual trends (b). Big numbers in each quadrant, represent the total number of pixels from each geomorphological unit that falls in it (light gray, Cuesta Basáltica, dark gray, Sierras del Este). The number of significant trends (in a) and residual trends (in b) are highlighted.

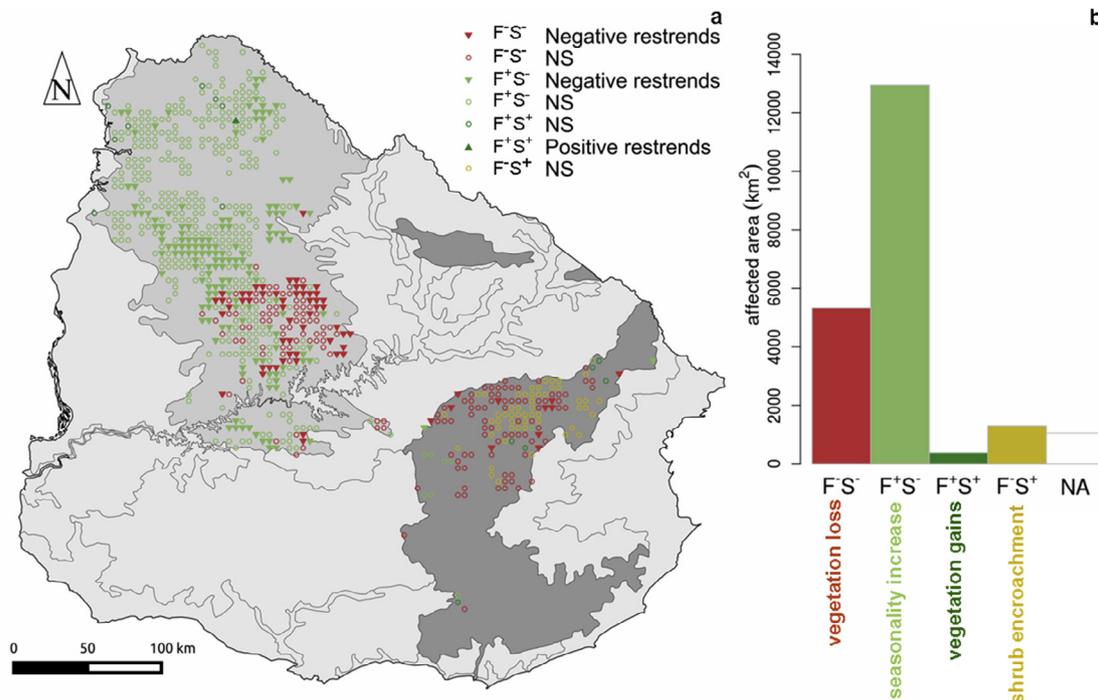


Fig. 9. Spatial distribution of functional syndromes and significant residual trends (a) and frequency distribution of functional syndromes (b). Map legend and classes in the frequency distribution refer to increases (+) or decreases (−) in fast (F) or slow (S) term vegetation responsiveness to precipitation.

1988). Additionally, differences in mean I-ANPP could also be related to contrasting species richness between geomorphological units, with the more diverse Sierras del Este being more productive. Positive effects of plant species and plant functional type richness and diversity on grassland primary production and the mechanisms behind this pattern have been extensively studied at finer spatial scales (i.e., local communities, Tilman et al., 1997; Fridley 2001; Craven et al., 2016). Lezama et al. (2006, in press) found that Sierras del Este is the most diverse and heterogeneous geomorphological unit, comprising 350 species grouped in eight community types. In turn, the Cuesta Basáltica, comprise 274 species along six community types. A higher species pool diversity in Sierras del Este provides a larger array of species and traits that the environment and communities may “select” from, potentially ensuring higher productivity and stability (Naeem and Li, 1997). These are more likely to contain species with higher growth rates than smaller species pools as those from Cuesta Basáltica, and are more likely to contain species better adapted to a wider array of local environmental conditions. This “sampling effect” is an important modulating mechanism of the relationship between plant species diversity and primary production (Fridley, 2001). Moreover in sites with higher richness and species pools, complementarity and facilitation effects promoting species coexistence and overyield (greater biomass production in species mixtures respect to isolated ones) are more likely to occur (de Mazancourt et al., 2013; Craven et al., 2016). An alternative explanation, more compatible with our scale of analysis rests in the fact that Sierras del Este exhibit a greater physiographic and landscape heterogeneity than Cuesta Basáltica. This greater heterogeneity is associated with patches of shrubs and woody vegetation embedded in a grassland matrix, a fact that could increase vegetation production. For semiarid Mediterranean grasslands, Maestre et al. (2009) found that shrubs were associated with greater vascular plant richness, microorganism biomass, soil fertility, N mineralization rates and ANPP.

4.2. Trends in ANPP, residual trends and functional syndromes

ANPP temporal trends, residual trends, and temporal changes in precipitation use efficiency and in precipitation marginal response, all

exhibited a strong NW to SE gradient. Towards the NW, trends in ANPP and in the residuals from the I-ANPP vs I-PPT relationship were steeper, mainly negative and more frequent in Cuesta Basáltica unit. Negative trends in annual C gains estimates were not so common as suggested by a previous study focusing on fAPAR (Teixeira et al., 2015). This difference should represent a warning signal to studies using partial components of Monteith model (i.e. fAPAR or APAR, Fig. 2), and could emerge when PAR seasonal peak occurs at a different moment than fAPAR maximum (Piñeiro et al., 2006).

All significant trends in I-ANPP in the Cuesta Basáltica were negative, whereas in Sierras del Este both positive and negative trends were observed. The same holds for significant residual trends, but the frequency of significant results was much higher. Decoupling the signal of ANPP from that of precipitation allowed us to identify changes in ANPP not associated with changes in precipitation. Differences in area affected by significant trends in ANPP (~2500 km² or ~4% of the grasslands area) vs. residuals (> 7700 km² or ~11% of the grasslands area), point out that probable human induced changes on ANPP (i.e. those not associated with precipitation) were much more important. Between 2000 and 2011 both study areas have experienced a generalized reduction in the area devoted to perennial forage resources (natural grasslands, improved natural grasslands and implanted pastures). Around 68% of censal units from Cuesta Basáltica and 57% from Sierras del Este exhibited reductions in forage area during this period (DIEA, 2011). These transformations (Paruelo et al., 2006), reduced the area available for livestock, and thus, could have increased the grazing pressure on remaining rangelands, probably changing ANPP seasonal dynamics.

Precipitation use efficiency has shown a marked decrease during the past 35 years affecting mostly the Cuesta Basáltica, suggesting reduced ANPP per unit precipitation. In turn, positive ΔPMR values occurred mostly in Cuesta Basáltica, although negative ones were equally frequent in both units.

Most pixels exhibited an increased responsiveness to interannual variation in precipitation and an overall decreased rainfall-corrected productivity; signs for the annualization syndrome (“F⁺S⁻”), a typical response to overgrazing of formerly perennial grasslands (Altesor et al.,

2006). Moreover > 95% of pixels belonging to this syndrome are from Cuesta Basáltica.

The syndrome associated with decreases in both fast and slow vegetation responsiveness (“F⁻S⁻”, Fig. 9), interpreted as vegetation loss was present in sites with negative restraints, i.e. reductions in ANPP greater than those expected given the observed precipitation. Between 2000 and 2011 the area of natural grasslands converted to (summer and double cycle) crops in Uruguay increased by 265% (Volante et al., 2015). The increment in cultivated area was greater in Western Uruguay, particularly in areas adjacent to the Cuesta Basáltica. This could have resulted in degradation process consequence of indirect land use changes (Overmars et al., 2011): the conversion of natural grasslands into crops induced an intensification of grazing in the remaining grasslands. These sites (red triangles downwards in Fig. 9) deserve special attention respect to conservation or restoration actions.

All pixels associated to the “shrub encroachment” syndrome (“F⁻S⁺”) belong to Sierras del Este (Fig. 9) and did not exhibit trends in ANPP or residual trends. This syndrome could be associated with grasslands that exhibit signs of shrub encroachment. Shrub encroachment in Uruguayan rangelands, particularly in Sierras del Este, have been associated with closures to grazing or decreased stocking rates (Altesor et al., 2006). On the other hand, Lezama et al. (2006) showed that the incidence of shrub species in Sierras del Este was higher than in Cuesta Basáltica. If enhanced ΔPUE and decreased ΔPMR could be effectively associated with increased shrub abundance, would explain the higher mean ANPP and the greater incidence of positive trends and residual trends during the period in Sierras del Este.

Finally, the syndrome interpreted as vegetation gains, i.e. increases in both fast and slow vegetation responsiveness (“F⁺S⁺”, Fig. 9) or grasslands vegetation improvement, was equally distributed among both geomorphological units and only one site from the Cuesta Basáltica exhibited significant (positive) restraints.

5. Conclusions

The use of functional syndromes provides a novel framework where structural and functional attributes may be put together. For example, increases in seasonality or annualization, represents a negative effect on long-term use efficiency of precipitation, but a positive one in precipitation marginal response, a consequence of the transformation of grasslands into crops or increased grazing pressure. The conceptual frameworks originally developed to study degradation processes in arid lands (Veron et al., 2005, 2006, Kaptué et al., 2015) and the restrend methodology (Evans and Geerken, 2004; Wessels et al., 2007) also provide the opportunity to unmask more subtle degradation or restoration features, beyond those associated to land use and land cover changes. Our work provides policymakers with comprehensive indicators to guide the design and the implementation of conservation and management policies on a spatially explicit and quantitative base.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2018.09.046>.

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