



Sensitivity of subtropical forest and savanna productivity to climate variability in South America, Uruguay

Christine Lucas, Mauricio Ceroni, Santiago Baeza, Ariel A. Muñoz & Alejandro Brazeiro

Keywords

Climate variability; Fraction of photosynthetically active radiation; Normalized difference vegetation index; Primary productivity; Rio de la Plata Basin; Riparian forests; Savanna; SPOT; Subtropical forests

Received 4 July 2015

Accepted 19 September 2016

Co-ordinating Editor: Duccio Rocchini

Lucas, C. (corresponding author, lucas.christine2@gmail.com)¹,

Ceroni, M. (ceroni.mauricio@gmail.com)²,

Baeza, S. (santiago.baeza@gmail.com)³,

Muñoz, A.A. (arimunoz82@gmail.com)⁴,

Brazeiro, A. (ecologiaap@gmail.com)⁵

¹Polo Ecología Fluvial, CENUR Litoral Norte, Universidad de la República, km. 363 Rt. 3, Paysandú, 60000, Uruguay;

²Centro Interdisciplinario de Respuesta al Cambio y Variabilidad Climática, Espacio Interdisciplinario, Rodó 18431, Montevideo, 11300, Uruguay;

³Departamento de Sistemas Ambientales, Facultad de Agronomía, Universidad de la República, Garzón 780, Montevideo, 12900, Uruguay;

⁴Instituto de Geografía, Pontificia Universidad Católica de Valparaíso, Av. Brasil 2241, Valparaíso, 2362807, Chile;

⁵Instituto de Ecología y Ciencias Ambientales, Facultad de Ciencias, Universidad de la República, Iguá 4225 Montevideo, 11400, Uruguay

Introduction

The sensitivity of forest ecosystems to climate variability varies at different time scales (Barnes et al. 2016; Seddon et al. 2016). Forest productivity and precipitation at annual

Abstract

Questions: Increasing climate variability has major effects on forest productivity, as well as transitions between forest and savanna ecosystems. While drought-induced declines in tropical forest productivity and forest loss is a global concern, forest expansion in subtropical South America predicted by climate models has received little attention. In the forest–grassland transition zone encompassing Uruguay, we ask: (1) how does climate variability affect woodland productivity and at what time scales; and (2) how do different woodland types (riparian, hillside and wooded savanna) differ in their sensitivity to climate variability?

Location: Forests and wooded savanna in Uruguay, subtropical southeast South America.

Methods: Primary productivity was measured as the fraction of photosynthetically active radiation (fPAR) based on monthly normalized difference vegetation index (NDVI) from multitemporal (1998–2012) SPOT imagery at a 1 km × 1 km resolution, covering 19% of Uruguayan woodlands. The effects of accumulated rainfall and mean temperature on the productivity of riparian and hillside forests and wooded savanna were evaluated using correlations and time series analysis over multiple time windows ranging from 1–24 mo.

Results: Inter-annual rainfall variability and seasonal temperatures affected forest productivity even though average conditions were largely non-limiting. Periods of exceptionally high rainfall and warm winters had positive effects on forest productivity, but hot summers had a negative effect on all woodland productivity. Riparian and hillside forest productivity was equally susceptible to drought, showing similar relationships to accumulated rainfall over multiple time periods, as well as similar susceptibility to high summer temperatures. Wooded savanna – a composite cover of trees and a grass/forb understorey – productivity was linked to seasonal rainfall over 3–6 mo, and in general showed the lowest correlation with inter-annual variability in rainfall.

Conclusions: Results suggest functional convergence in the response of riparian and hillside forests to water deficit and hot summers. The increases in forest productivity with increasing rainfall and declining drought risk – as predicted by the IPCC for this region – are a potential mechanism for increased growth and future expansion of forests in this biogeographic transition zone.

time scales are most tightly related in arid and semi-arid ecosystems (Schuur 2003). Meanwhile, recent evidence of the effects of long-term and severe drought on tropical tree growth (Wagner et al. 2014), primary productivity (Asner et al. 2004) and diversity (Engelbrecht et al. 2007)

emphasize the critical role that inter-annual variability in precipitation plays in the functioning of forests in humid climates. Although annual net primary productivity (ANPP) is poorly predicted by mean annual precipitation (MAP) in humid tropical and subtropical climates (Chamaille-Jammes & Fritz 2009; Paruelo et al. 2010), precipitation anomalies over increasing temporal scales affect woody growth, leaf phenology and ANPP. In general, forests respond to precipitation anomalies over long-term periods (up to several years) due to groundwater access by deep roots and the time lag between changes in water availability and bud formation, leaf flushing and cambial growth (Breda et al. 2006; Brando et al. 2010). Nonetheless, severe droughts can have immediate effects on leaf area index and greenness via canopy thinning as a response to soil water deficit (Breda et al. 2006). The effects of long-term climate change on ANPP is a major driver of forest degradation in the neotropics (Hilker et al. 2014) and a precursor to transitions between forests, savanna and grassland biomes worldwide (Scheffer et al. 2012). Despite the focus on forest-to-savanna transitions in the Amazon Basin (Silvério et al. 2013), there are scant data on the relationship between forest productivity and climate in regions of forest expansion under future climate scenarios, including the grassland-dominated humid subtropics of southeastern South America (Anadon et al. 2014).

The impacts of extreme precipitation events differ within a single watershed (Brooks et al. 2011), such that riparian forests may be drought-resistant. Dry periods can provide opportunities for cambial growth in tropical floodplain forests (Schongart et al. 2004). Given their proximity to the water table, riparian forests may be able to maintain higher productivity than upland forests during dry spells, thus playing a critical role as a refuge during drought (Meave & Kellman 1994). The response of upland forest productivity to dry periods is variable – while, in general, decreases in precipitation limit water availability to trees, the increase in sunny days during mild dry periods can have a positive effect on forest productivity (Boisvenue & Running 2006). Although differences in forest susceptibility to drought could be attributed to differences in species tolerance to desiccation, a global analysis shows similar species vulnerability to hydraulic failure during drought in different forest biomes (Choat et al. 2012).

Forest expansion is predicted from climate projections for southeastern South America (SESA) as a result of increasing rainfall and decreasing drought (IPCC 2014). The advance of trees in this highly productive region for agriculture and ranching in natural grasslands has major ecological and economic implications. To date, the response of vegetation to rainfall variability has largely focused on grasslands, agricultural systems and steppe

vegetation, which dominate the landscape and characterize the Pampa biome (Fabricante et al. 2009; Paruelo et al. 2010; Guido et al. 2014; Ceroni et al. 2015). ANPP of South American grasslands is highly correlated with MAP at broad regional scales (Paruelo et al. 1998, 2010), but at finer spatial scales in humid regions the relationship between MAP and vegetation productivity is less strong (Fabricante et al. 2009; Guido et al. 2014). Both NDVI and NDVI-derived fraction of photosynthetically active radiation (fPAR) are used to understand how rainfall variability and land-use change influence grassland productivity (Paruelo et al. 2010; Vassallo et al. 2013; Guido et al. 2014). While NDVI can saturate in forests with dense canopies and high biomass (Huete 2012), it is widely used for monitoring change in forests, savannas and grasslands of southern South America (van Leeuwen et al. 2013; Lezama et al. 2014) and African savannas (Chamaille-Jammes & Fritz 2009; Fabricante et al. 2009). Given their limited extent, the response of subtropical forests to climate variability in the Pampa is poorly understood (Texeira et al. 2015). We expect, given the differences in elevation, water availability and soil drainage rates of riparian forests, hillside forests and wooded savannas in the region (Oliveira-Filho et al. 2013), that forest types will display variable sensitivities to climate variability at different temporal scales.

We aimed to test mechanisms through which forests in humid subtropical climates responded to precipitation and temperature variability at multiple temporal resolutions. Using historical climate data and vegetation indices, we examined how increasing precipitation and temperature will affect the three principal woodland cover classes in Uruguay at temporal resolutions ranging from 1 mo to 2 yr. Previous remote sensing of grasslands, the dominant land cover in the Pampa biome, has examined spatial variability in NDVI (Baeza et al. 2006) and fPAR in Uruguay (Baeza et al. 2010; Guido et al. 2014) and the greater Pampean province (Paruelo et al. 1998, 2010), but with minimal focus on native forest cover classes or combining native forests with other land-cover types such as non-native forest plantations (Texeira et al. 2015). Global analyses indicate moderate–high sensitivity of Uruguayan vegetation to rainfall variability, (Seddon et al. 2016). We used multitemporal remotely sensed NDVI data from SPOT imagery at a 1 km × 1 km spatial scale and NDVI-based fPAR to address: (1) how does climate variability affect woodland productivity and at what time scales; and (2) how do different woodland types (riparian, hillside and wooded savanna) differ in their sensitivity to climate variability? We use these questions as a basis to explore how climate variability affects the productivity of forests expected to advance under IPCC climate predictions (Anadon et al. 2014).

Methods

Study region

Forests in the *Pampa* biome of southeastern South America occur in patches within a landscape dominated by natural grassland and agriculture, or as gallery forests along rivers and streams in Uruguay and south Brazil (Soriano 1992; Brazeiro 2015). Within the Pampa, the transition zone between forest and grassland is known as the Northern *Campos*, which largely covers Uruguay (Paruelo et al. 2010). In Uruguay, native forests cover approximately 5700 km², or ~3.4% of the land area (MGAP/DIEA 2000), and comprise 315 woody species (Haretche et al. 2012), forming a system of corridors and patches that support avian and mammalian biodiversity (Nores et al. 2005) and protect stream integrity. Three major forest cover types are recognized in Uruguay: riparian or gallery forests (*monte ribereño o de galería*) are the most extensive, followed by hillside and ravine forests (*monte serrano y de quebrada*) and wooded savanna (*monte*

parque; Brussa & Grela 2007), distributed unevenly in seven ecoregions (Fig. 1a; Brazeiro 2015). Riparian forests occur throughout Uruguay on fluvial soils with relatively high water-holding capacity; meanwhile, hillside forests largely occur in the eastern Sierras, where soils are fairly superficial, with rocky outcroppings and moderate to poor water-holding capacity (CONEAT 2012). Wooded savannas are restricted to the littoral west along the River Uruguay, sometimes in association with alkaline soils known as *blanqueales* (Brussa & Grela 2007). Mean annual precipitation in Uruguay increases along a south–north gradient from 1000–1500 mm·yr⁻¹. Rainfall is relatively evenly distributed throughout the year (Fig. 2), but is more variable inland than along the coast. Inter-annual variability in precipitation is influenced by a suite of climate phenomena, including the South American Monsoon System, ENSO, and the AAO (Krepper & Zucarelli 2010). The climate is subtropical, with cool winters and hot summers (Fig. 2). Mean annual temperature increases from south to north from 16 to 19 °C.

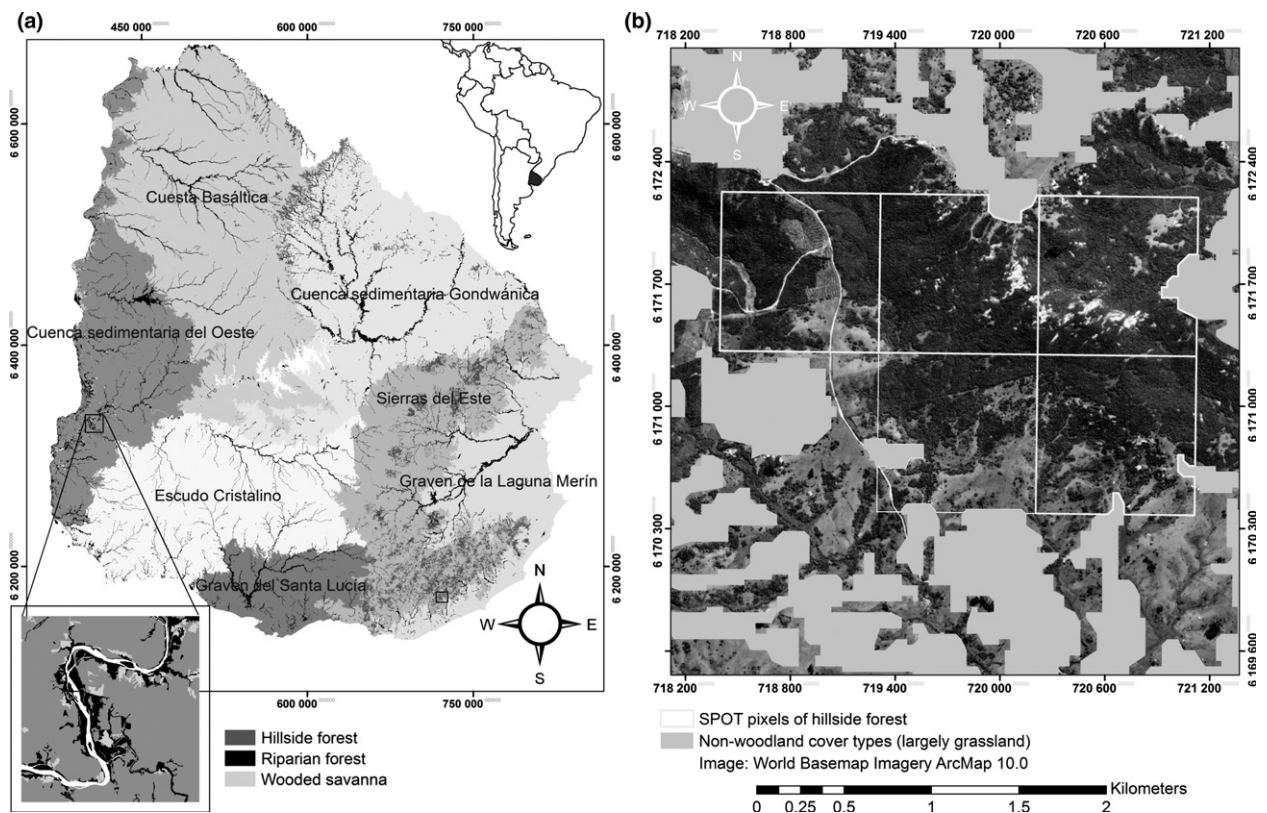


Fig. 1. Map of forest cover in Uruguay and sampling of SPOT pixels within forest and savanna cover classes. **(a)** Land cover of native forest and wooded savanna (both in black) in Uruguay according to the Ministry of Agriculture and Livestock DINOT/FAO 2013 within the eight ecoregions of Uruguay (Brazeiro 2015). Black square in the southeast shows area zoomed in **(b)**. **(b)** Example SPOT satellite pixels of 1 km × 1 km with >90% overlaid with the ‘hillside forest’ land-cover class (*bosque serrano y de quebrada*). Background image obtained from ESRI Basemap Layers in ArcMap 10.0 (incl. composite IKONOS images for South America).

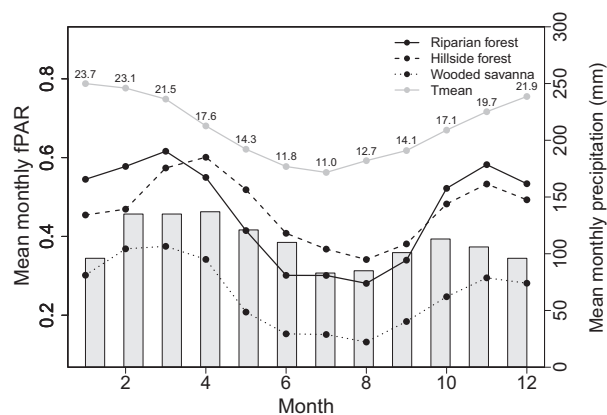


Fig. 2. Climodiagram of mean monthly temperature (values shown above grey points in Celsius) and precipitation (mm, grey bars), with monthly mean fPAR for riparian forest (solid black line) and hillside forest (dashed line) and wooded savanna (dotted line) over the study period (1998–2012).

Phenology of semi-deciduous forests in Uruguay

Forests in Uruguay are classified as semi-deciduous seasonal forests, characterized by the senescence of 30–60% of foliar biomass during winter (Oliveira-Filho et al. 2013). The loss of foliar biomass during austral winter, peaking in Jul–Sept, was shown for canopy species of lowland riparian semi-deciduous seasonal forests in southern Brazil, 215 km from the Uruguayan border (Athayde et al. 2009). Leaf-out is most intense following leaf senescence in Nov (spring), coinciding with increasing photoperiod and temperature. Nonetheless, only 34% of the 24 tree species of the riparian forests studied are deciduous, while 40% are semi-deciduous and 26% are evergreen, resulting in asynchronous leaf phenology among species (Athayde et al. 2009). Although phenological studies of forests in Uruguay are scant, riparian forests tend to be more deciduous than upland hillside forests (Brussa & Grela 2007), potentially because of differences in species composition, as well as different phenological responses to climate and/or hydrology. Given continuous rainfall year-round, it has been suggested that leaf phenology in this region responds largely to temperature and photoperiod, but variation in rainfall could play a role in the unexpected peaks in leaf-out observed throughout the year (Brussa & Grela 2007).

Extraction of NDVI data from SPOT-VGT imagery

NDVI is widely used to evaluate temporal change in phenology and distribution of savannas and woodlands (Mitchard & Flintrop 2013; Higginbottom & Symeonakis 2014). NDVI at a spatial resolution of 1 km × 1 km for the period 1 Apr 1998 to 31 Mar 2012 for all of Uruguay

was previously obtained and processed by Ceroni et al. (2015) from the SPOT-4 and SPOT-5 VEGETATION (VGT-S10) product. NDVI was calculated as: $NDVI = (R_{NIR} - R_{RED}) / (R_{NIR} + R_{RED})$, where R_{NIR} is near-infrared (NIR) reflectance and R_{RED} is the red reflectance. The series ended in 2012, 1 yr following the 2011 land-cover classification data. VGT-S10 products provided 10-d composite NDVI images, applying the maximum-value-composite (MVC) technique to select the ‘best’ ground reflectance values from daily NDVI. Composite data are then post-processed, which includes the incorporation of flags for bad data, clouds and a land mask to reduce the influence of atmospheric conditions; flag data were obtained from the Status Map layer in the S10 product catalogue (<http://www.vgt.vito.be/pages/Vegetation-System/products.html>; <http://www.vgt.vito.be/userguide/userguide.html>). Details regarding the processing of NDVI data are in Ceroni et al. (2015). To reduce additional errors in the NDVI data, we calculated mean monthly NDVI from 10-d increment values. We also calculated the change in monthly NDVI values for each pixel, as abrupt changes in NDVI ($\Delta NDVI > 0.4$) can be an indicator of atmospheric influence (Bojanowski et al. 2009). Among the 168 monthly values for the original data set of $N = 1179$ woodland pixels, $\Delta NDVI > 0.4$ in only 43 of 175 727 instances, and thus no interpolation of NDVI values was used. We used K-means cluster analysis to identify anomalous groups of pixels, which identified a group then removed from the sample with continuously low NDVI values (< 0 in some months) likely influenced by background reflectance from water during flooding events.

Calculation of fPAR

We estimated fPAR from SPOT NDVI using an empirical approximation that assumes a non-linear relationship between SPOT-NDVI and fPAR (Los et al. 2000; Pineiro et al. 2006; Teixeira et al. 2015). This accounts for the commonly noted saturation of NDVI values among many forests with LAI > 3 and implies a linear relation between the simple ratio index ($SR = IR/NIR = (1 + NDVI) / (1 - NDVI)$) and fPAR. Given that we build upon previous research monitoring NDVI, and aim to provide comparative data to previous studies on grassland sensitivity to climate in this region, we did not use other FAPAR products (e.g. Diouf et al. 2015). The NDVI-fPAR relationship was regionally parameterized in the Argentinean Pampa, assigning zero absorption (fPAR = 0) to NDVI values to pixels with no green vegetation (bare soil) and maximum fPAR (fPAR = 0.95) to NDVI values from pixels with high green biomass (Grigera et al. 2007). The resultant equation was:

$$fPAR = \min \left[\frac{SR - SR_{\min}}{SR_{\max} - SR_{\min}} 0.95 \right]$$

where the extreme values of SR were $SR_{\min} = 1.55$ (NDVI = 0.215) and $SR_{\max} = 11.62$ (NDVI = 0.842). While this relationship was calibrated for grassland systems, it has been applied to forests (Teixeira et al. 2015) and tree plantations (Vassallo et al. 2013) in the same region. Moreover, SR values were similar to those derived for deciduous broad-leaf forests globally (Peng et al. 2012), where $SR_{\min} = 1.030$ (NDVI = 0.015) and $SR_{\max} = 11.903$ (NDVI = 0.845), for similar purposes of estimating fPAR from NDVI.

Land-cover classes

Woodland cover classes were obtained from the national Land Cover Classification System for Uruguay based on Landsat TM images from 2011 (DINOT/FAO 2013; Fig. 3). Among four forest class covers, we grouped forests into three classes: riverine (*monte nativo de galería y monte nativo*), hillside (*monte nativo serrano y de quebrada*) and wooded savanna (*monte natural de parque*). We overlaid woodland class covers with SPOT imagery to select pixels of $\geq 90\%$ woodland cover ($N = 1046$ pixels of

1 km \times 1 km; Fig. 1b). We checked woodland class covers for errors and reclassified as 'riparian forest' 60 pixels designated as 'savanna' in the protected area, Montes del Queguay, (www.mvotma.gub.uy/areas-protegidas.html). Given the patchiness of woodlands, we visually classified all 1046 pixels into four tree cover classes, 0–24%, 25–49%, 50–74% and 75–100%, using the ESRI built-in Basemap Layer 'World Imagery' in ArcMap 10.0 at a scale of 1:20 000. As this Basemap Layer includes high-resolution imagery GeoEye IKONOS (1-m resolution) for most of Uruguay, individual trees were easily visible to visually classify tree cover. To reduce the effects of other vegetation classes (e.g. grasslands, bare soil, water) on forest NDVI, we excluded pixels $< 50\%$ tree cover in riparian and hillside forests, resulting in $N = 270$ pixels of riparian forest (7.9% total forest cover) and $N = 273$ pixels of hillside forest (7.9% of total forest cover). Given that wooded savanna is characterized by lower tree density ($\leq 75\%$ tree cover), we used all pixels of $\geq 90\%$ wooded savanna class regardless of tree cover ($N = 45$ pixels; 6.4% of total forest cover). Given their limited extent, wooded savanna reflectance patterns are considered as ecosystem-scale responses in which understorey grass cover is inherent. The final sample of 588 pixels was largely dominated by trees.

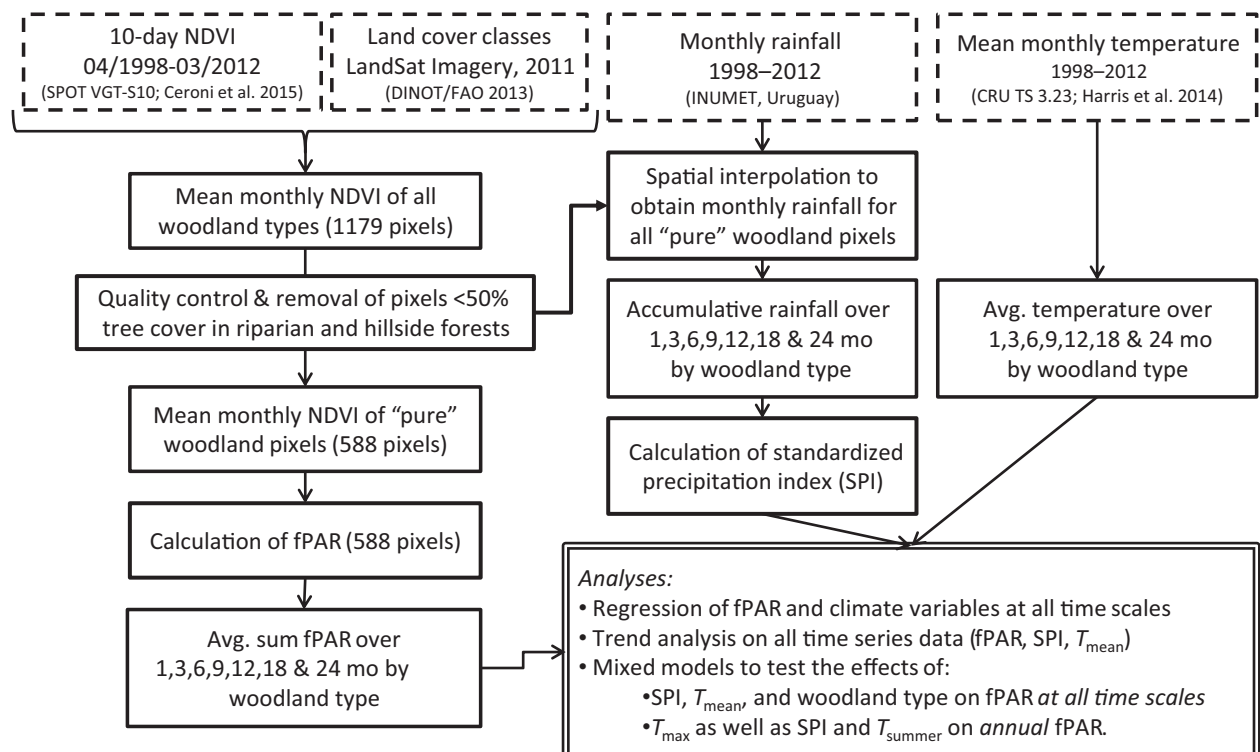


Fig. 3. Flow diagram of methods, data shown in dashed boxes, data processing in solid-lined boxes and the principal statistical analyses in the double-outlined box at the bottom right.

Climate data

Monthly precipitation data for 1998–2012 were obtained from public databases of 18 meteorological stations maintained by the Uruguayan Institute of Meteorology (<http://meteorologia.gub.uy>) and five stations maintained by the National Agricultural Research Institute (INIA, unpubl.). Standard anomalies were used to enhance confidence in these values (Grumm & Hart 2001). To achieve monthly precipitation data for each pixel, precipitation data were interpolated by the Kriging method for each month (Ninyerola et al. 2000), an appropriate method for estimating monthly rainfall in relatively flat regions such as Uruguay. To normalize precipitation data, the standardized precipitation Index (SPI) was calculated as the SD of precipitation fit to a gamma function (McKee et al. 1993). We classified SPI values as severely dry (−2.5 to −1.49), moderately dry (−1.49 to −1.0), mildly dry (−0.99 to −0.01), mildly wet (0–0.99), moderately wet (1.00–1.49) and severely wet (1.50–2.52) (McKee et al. 1993).

We obtained mean monthly temperature (T_{mean}), monthly maximum temperature (T_{max}) and summer temperatures (T_{summer}) from the CRU TS v 3.23 data set (Harris et al. 2014) for 1998–2012. Within Uruguay, the data consisted of 85 0.5° cells. Point data from the centroids of each cell in the 0.5° latitude/longitude grid of cells covering Uruguay were overlaid with forest pixels, such that the temperature time series data were assigned to forest pixels falling within the same 0.5° CRU cell.

Statistical analyses

To compare average (mean \pm SD) woodland fPAR, we used non-parametric Kruskal–Wallis tests (χ^2); to compare variability and averages of fPAR among woodland types we used Tukey HSD tests. We constructed time series for monthly precipitation, SPI, T_{mean} , T_{max} and fPAR values for all 588 pixels of native forest and savanna, as well as separate time series for each of the three woodland types. All time series were checked for autocorrelation function (ACF) and partial autocorrelation (PACF) using R time series packages (R Foundation for Statistical Computing, Vienna, AT; http://www.stat.oek.wiso.uni-goettingen.de/veranstaltungen/zeitreihen/sommer03/ts_r_intro.pdf). To evaluate trends in monthly fPAR, SPI and temperature we used Mann–Kendall trend analysis for the three woodland types (tau; Zhu & Southworth 2013). We tested for spatial autocorrelation of mean annual fPAR among pixels using Anselin Local Moran's I statistic calculated in ArcMap 10.0 to check for spatial grouping. To evaluate the sensitivity of woodlands to precipitation variability at different time scales, we used Pearson correlation coefficient tests (R) to compare the correlation

between fPAR and SPI as well as fPAR and T_{mean} over 1, 3, 6, 9, 12, 18 and 24 mo (Vassallo et al. 2013). To determine at what period of the year seasonal rainfall and temperature were most influential on ANPP we used correlation functions (Blasing et al. 1984) to compare annual fPAR of each woodland class to rainfall and temperature at time intervals of 1–12 mo over 2 yr. A 1-mo lag between fPAR and SPI – normalized rainfall data – was considered for all correlations. To test for the effects of SPI, T_{mean} and vegetation type on fPAR at each time scale (1–24 mo) we used mixed models with an auto-correlation structure (corAR1) to account for temporal auto-correlation of monthly fPAR and SPI values (Zuur et al. 2013). The effects of T_{max} and T_{summer} on mean annual (12-mo) fPAR were tested with similar models (Table 1, Fig. 3). To examine seasonal differences in vegetation response to precipitation, we grouped fPAR data according to season, considering multiple lag times between fPAR and rainfall. We examined the correlation between mean annual rainfall and annual fPAR, as well as mean annual temperature and annual fPAR using values summed over a 'vegetation year', ending with the lowest mean fPAR (Aug) and starting the next month (Sept; Camberlin et al. 2007). Precipitation for vegetative year 1 began in Aug (Camberlin et al. 2007). All analyses were conducted in R 3.0.1.

Results

Hillside forests of the Uruguayan sierra ecoregion had the highest fPAR among woodland types (Figs 2 and 3; Tukey HSD tests $P < 0.05$), and were the least variable over time (0.47 ± 0.08). Riparian forest fPAR on average only surpassed upland forest fPAR in the hottest months of the year (Tukey HSD $P = 0.0006$) and were more variable over time (0.46 ± 0.12 ; Fig. 2). As expected, given the influence of background reflectance from grasses and in many cases alkaline soils (known as *blanqueales* for their white colour), wooded savannas located in the Littoral ecoregion of Uruguay had the lowest fPAR values with the largest range (Tukey HSD tests $P < 0.05$; 0.14 ± 0.14). All woodlands displayed a bimodal annual pattern in productivity, but spring and autumn peaks in fPAR in hillside forests were delayed ~ 2 mo relative to riparian and savanna forests (Fig. 2). NDVI averaged 0.70 ± 0.03 in hillside forests and 0.69 ± 0.06 in riparian forests, but was 0.54 ± 0.12 in wooded savannas. When occurring in the same ecoregion (>10 pixels), hillside and riparian forests had similar monthly mean fPAR values (e.g. 0.42 vs 0.39 in the northern Basaltic ecoregion; Kruskal–Wallis $\chi^2 = 1.9$, $P = 0.18$). Riparian forest fPAR was double that of wooded savanna in the Littoral west (Kruskal–Wallis $\chi^2 = 46.1$, $P < 0.001$).

Table 1. Coefficients (and *P*-values) from mixed models with an autocorrelation structure (corAR1), testing the effects of SPI, mean monthly temperature (T_{mean}), woodland type (riparian, hillside and savanna) and the interaction of SPI and T_{mean} with woodland type across increasing time scales from 1 mo (considering both a 1 and 2 mo time lag between fPAR and rainfall) to 24 mo between 1998 and 2012. 'fPAR – Veg. year' shows coefficients from three models testing the effects of SPI, temperature (T_{mean} , T_{max} or T_{summer}) and woodland type on fPAR in a vegetation year (Sept–Aug). Coefficients for woodland type are expressed as averages.

	SPI	T_{mean}	Woodland type	Woodland \times SPI	Woodland \times T_{mean}
fPAR – 1 mo w/1 mo lag		0.015***	0.21***		
fPAR – 1 mo w/2 mo lag		0.010***	0.21***		
fPAR – 3 mo	0.06***	0.04***	0.46***	0.06*	0.01***
fPAR – 6 mo	0.06***	0.04***	0.86***		0.034***
fPAR – 9 mo	0.16***	0.11***	1.1***		0.031***
fPAR – 12 mo	0.16***				
fPAR – 18 mo	0.19***	0.23***			0.12***
fPAR – 24 mo	0.11***	–0.26***			
fPAR – Veg. Year (T_{mean})	0.14*	–0.84 [†] (T_{mean})	0.85*		
fPAR – Veg. Year (T_{max})	*0.095	**–0.81 (T_{max})			
fPAR – Veg. Year (T_{summer})	*0.038	*–0.58 (T_{summer})	0.84*		

[†] $P < 0.10$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Woodland fPAR response to precipitation variability

Over the 14 yr, two dry periods with marked drops in woodland fPAR occurred, one in 1999/2000 and another in 2008/09, with ten consecutive months of below average rainfall and a total annual rainfall of 923 mm ($70 \pm 2\%$ of MAP; Fig. 4a). Among hillside and riparian forests, the positive correlation between fPAR and accumulated rainfall – expressed as SPI – strengthened over increasing time windows from 3 to 24 mo (Fig. 5). In contrast, fPAR of wooded savanna was most highly correlated with rainfall accumulated over 3 mo, considering a 1-mo lag period (Fig. 5; $R = 0.48$, $P < 0.001$). Mixed models showed that fPAR was explained by variation in rainfall at most time scales >3 mo (Table 1). With respect to the hypothesis that rainfall in certain seasons should be more influential on fPAR, we found that all woodland types were highly correlated with seasonal rainfall in the spring of the current year of growth (Aug–Oct; $R = 0.71$ – 0.76 , $P < 0.05$) and the autumn of the previous year of vegetative growth (Mar–May; $R = 0.77$ – 0.83 , $P < 0.05$). Meanwhile, only riparian forest and hillside forests showed a positive correlation with rainfall in the autumn (May–Jul) 2.5 yr prior ($R = 0.72$ – 0.83 , $P < 0.05$). There was an overall declining trend in fPAR of all three woodland types (Mann–Kendall $\tau = -0.337$, -0.279 and -0.179 for riparian, hillside and savanna woodlands, respectively; $P < 0.0001$ for all tests) and in mean monthly precipitation from 1998–2012 (Mann–Kendall $\tau = -0.109$, $P = 0.035$), most apparent from low rainfall events in 2004–2012 (Fig. 4).

The fPAR and temperature

Temperature was an important driver of seasonality in fPAR for all woodlands, whereby the bi-annual peaks in

productivity occurred during moderate temperatures in spring and autumn, and the decline in fPAR in summer coincides with higher $T_{\text{mean}} > 25$ °C (Fig. 2, Table 1). The effects of T_{mean} on fPAR were confounded by season, such that hot summers had a strong negative effect on fPAR for all woodland types (December–February; $R = -0.64$ to -0.90 , $P < 0.05$), while warm springs had a positive effect only on fPAR of riparian forests (Aug–Oct; $R = 0.64$, $P < 0.05$). Given the contrasting effects of spring and summer temperatures, the overall effect of T_{mean} on 12-mo fPAR was not significant (Table 1). Nonetheless, mixed models showed a negative effect of both maximum temperature (T_{max}) and mean summer temperatures (T_{summer}) on 12-mo fPAR for all woodland types (Table 1). There was no trend in T_{mean} or T_{max} over the time period studied ($\tau = 0.004$ – 0.08 , $P < 0.10$).

Comparisons of fPAR in woodland savannas, riparian forests and hillside forests at the pixel scale

Spatial variability in the correlation between rainfall and fPAR suggest that the response of forests to rainfall variability was most intense in the land-locked interior, while sensitivity to extreme summer temperatures was country-wide (Appendix S1). Among individual forest pixels, there was low variability in fPAR in southern Uruguay, which had lower MAP (1100–1250 mm·yr^{–1}) and lower rainfall variability, and no correlation with MAP in a vegetation year. In contrast, fPAR was lower but more highly correlated with rainfall during a vegetation year in northern and northeastern riparian forests where MAP is high (>1400 mm·yr^{–1}; Appendix S1). A positive correlation between MAP and mean annual fPAR ($N = 14$ yr) in a vegetation year was observed in pixels in north and north-western Uruguay, but not in pixels along the southern

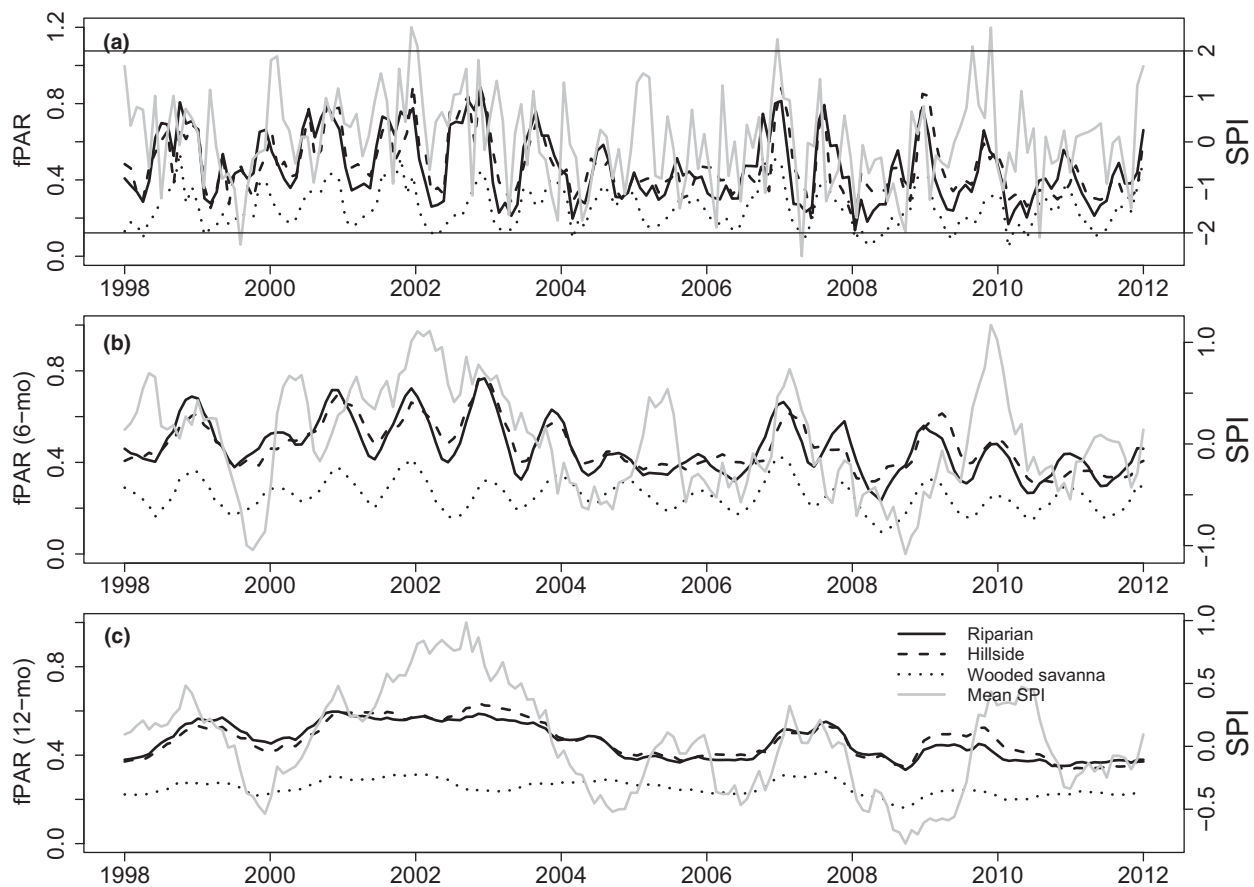


Fig. 4. Time series of the fraction of photosynthetically active radiation – fPAR (left axis) and standardized precipitation index (SPI; right axis), showing original data where horizontal lines indicate extremely dry (–2) and extremely wet (2) months (a); smoothed fPAR and SPI with a 6-mo (b) and 12-mo (c) moving average (MA) filter for three woodland types: riparian forests, hillside forests and wooded savanna.

Atlantic coast. When examining the correlation of fPAR with total accumulated rainfall at multiple time resolutions of 3–24 mo, 98% of all 588 pixels showed a positive correlation between fPAR and accumulated rainfall over 3 mo; and 95% of pixels had a positive correlation between fPAR and accumulated rainfall over 12 mo, excluding some savanna pixels in the littoral zone. The majority (87%) of pixels displayed a negative trend (Mann–Kendall tau tests, $P < 0.05$) in fPAR over the study period, with the exception of some hillside forest pixels along the marine Atlantic coast of southern Uruguay. Minimum fPAR in winter (Jul–Sept) was shown for 87% of pixels, while maximum fPAR in autumn (Mar–May) evident among 62% of pixels. The negative correlation between T_{summer} and fPAR was displayed in the majority of pixels across the country (Appendix S1). High spatial autocorrelation was observed among high fPAR values in the large patch of riparian forest of the Queguay River, coinciding with the largest protected area of native riparian forest, Montes del Queguay, of the National System of Protected Areas (SNAP).

Discussion

We contribute to mounting evidence showing that the productivity of humid tropical and subtropical forests responds to inter-annual variability in precipitation despite the lack of correlation between mean annual rainfall and NAPP (Zhang et al. 2013). This link between water availability and productivity has important implications for forest–grassland transition zones such as Uruguay, which is expected to experience forest expansion under increased rainfall and decreased drought stress under future climate change models (Staver et al. 2011). Second, we demonstrate that although riparian forests green-up sooner than hillside forests following summer, they are neither more productive nor more resilient to precipitation and temperature variability than upland forests. This similarity in the responses of riparian and upland forests to rainfall and temperature supports the convergence of woody species in desiccation tolerance, despite differences in species composition and soil texture (Choat et al. 2012). Finally, we

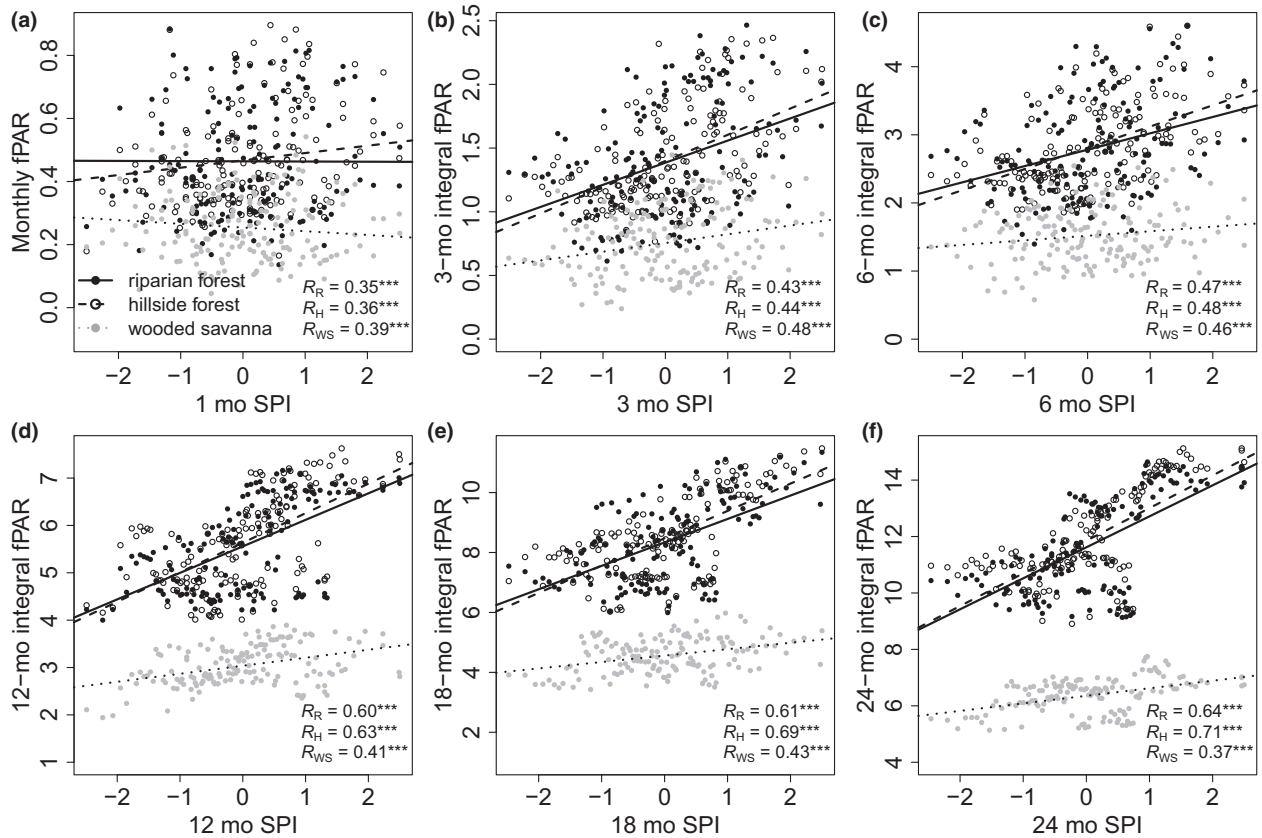


Fig. 5. Correlation between accumulated fPAR and the standardized precipitation index (SPI) at 1, 3, 6, 12, 18 and 24 mo time scales (a–f). Linear fit and correlation coefficient (R) values are shown for the correlation of fPAR and SPI for riparian forests (R), hillside forests (H) and wooded savanna (WS).

emphasize the importance of vegetation cover type in interpreting temporal-scale responses of forest productivity to water availability. Forest fPAR was more sensitive to rainfall variability than wooded savanna fPAR – essentially a composite signal of both trees and a C_3/C_4 grass–forb understorey – reinforcing the broader hypothesis that differences between grassland and forest phenology and productivity in response to climate variability is a potential mechanism or precursor for future changes in carbon pools and biome transitions (Scheffer et al. 2009).

Temporal-scale responses of woodland productivity to climate variability

Pluri-annual trends in precipitation played an important role for forest productivity even when average water conditions are considered non-limiting. The correlation of rainfall with forest productivity in current years and previous years observed here could suggest that the effects of accumulated rainfall operate at multiple scales. Large woody species are generally sensitive to long-term precipitation anomalies, as opposed to short-term monthly

fluctuations in rainfall, due to long-term impacts on groundwater levels as well as lag time between rainfall events and changes in leaf chemistry or canopy structure (Nepstad et al. 1994). Nonetheless, recent studies show that the effects of inter-annual variability in precipitation on the physiological and structural traits that influence fPAR – leaf senescence, LAI and tree canopy cover – manifest from months to years following drought (Brando et al. 2010; Holmgren et al. 2013; Wagner et al. 2014). The importance of accumulated rainfall over supra-annual time scales is related in part to tree physiology and cambial growth, as well as physical properties of the soil. Woody species can accumulate carbohydrate reserves over time, which are later allocated to growth and reproduction (Kozłowski & Pallardy 1997). The physical characteristics of soils and their capacity for long-term water storage also explains the lag time between rainfall events and woody species productivity; for example, water from previous rainfalls can be tightly bound in small pores in the soil profile and stored for later evapotranspiration by trees during dry periods (Brooks et al. 2010). This accumulative and lagged response has been shown among various field-

based measures of ANPP such as leaf production, height growth, radial growth (Wang et al. 2013) and wood density (D'Arrigo et al. 2000). Barring the possibility of correlation among rainfall events, the correlation of woodland fPAR to rainfall in multiple 3-mo periods over 2 yr could indicate both long- and short-term effects of rainfall on the quantity and quality of green foliage in this system.

In the context of climate variability, hot summers were a principal limiting factor for forest productivity at an annual temporal scale, indicating the importance of summer droughts for both riparian and upland woodlands. Contrary to our hypothesis that riparian forests should be less sensitive to drought indicators, riparian and hillside forest productivity displayed minimal differences in sensitivity to rainfall variability, providing little evidence for the resilience of riparian forests to drought or their susceptibility to decreased productivity during extreme rainfall. While we expected riparian forest productivity to be less responsive to hot summers, riparian forest productivity had a negative correlation with temperature, potentially a result of presenting more semi-deciduous and deciduous species (Brussa & Grela 2007). Studies show that regardless of drought tolerance, tree species have similar physiological limitations to soil water deficit (Choat et al. 2012). Similarly, productivity in all ecosystems is limited by rainfall; this convergence among biomes with respect to rainfall use efficiency (ANPP/rainfall; Huxman et al. 2004) could explain the similarity in both seasonality and response to rainfall variability between forest and grassland ecosystems in the Pampa biome (Texeira et al. 2015).

Seasonality of native forests and savanna

Forest sensitivity to extreme precipitation events depended on the timing of rainfall anomalies with respect to growing seasons. The spring and autumn peaks in fPAR in forests and wooded savanna shown here are similar to seasonal patterns of NDVI in surrounding grasslands that dominate the Pampean region of South America (Vassallo et al. 2013; Baeza et al. 2010). Native grasslands in Uruguay have a bimodal annual trend in fPAR, peaking in spring (Nov) and late summer (Feb–Mar; Baeza et al. 2011; Guido et al. 2014). This pattern has been associated with seasonal changes in the relative abundance of C₃ and C₄ grasses in southern Uruguay, whereby C₃ species contribute to the spring peak in ANPP and C₄ grasses contribute to the late summer peak in fPAR (Altesor et al. 2005). For semi-deciduous seasonal forests (Oliveira-Filho et al. 2013), this bimodality may be influenced by differences in photosynthetic activity as well as the timing of leaf flushing and senescence among species. Forests here peaked in greenness at similar times during the year to surrounding grasslands, when temperatures are generally

moderate and PAR is high (Baeza et al. 2010). While grasslands have low greenness in both winter and summer (Baeza et al. 2006), the vast majority of forest pixels displayed minimum greenness in the winter. Seasonal pattern in greenness (NDVI) of native forests differed from tree plantations, which peak annually in summer (Vassallo et al. 2013). Future work should focus on the interacting effects of temperature and precipitation on forest productivity, using evapotranspiration rates or relative humidity as a proximate driver of productivity, as well as the effects of regional climate phenomena, including the Multivariate ENSO Indicator in winter months and the Antarctic Oscillation (AAO) Index (van Leeuwen et al. 2013).

Conclusions

The sensitivity of subtropical forests to climate change is a major concern in the Southern Cone (Pacheco et al. 2010). While increasing annual rainfall and declining drought risk in southeastern South America is assumed to provide favourable climate conditions for forest growth, we provide some of the first evidence to show how different native woodland ecosystems in Uruguay respond to climate variability in terms of leaf phenology and productivity. This link between productivity and climate in subtropical South America implies that with increasing rainfall, the potential for carbon sequestration by native forests increases (Zhang et al. 2010). While native woodland cover is limited relative to the vast grasslands and agriculture that characterize the Rio de la Plata Basin (Eva et al. 2013), forests along riparian corridors are a critical buffer between a terrestrial landscape undergoing rapid agricultural intensification (Achkar et al. 2011; Vassallo et al. 2013) and a hydrological network that serves as the country's principal source of drinking water and energy (Conde & Sommruga 1999). Given that forest productivity increases more rapidly with increasing rainfall in comparison to grasslands in Uruguay (Texeira et al. 2015), increasing rainfall could not only increase productivity, but could be a potential precursor to the predicted encroachment of forests into grasslands (Anadon et al. 2014).

While climate models predict relatively low drought risk for this region, the increasing water demands from an expanding industrial agriculture and forestation places strong demands on groundwater availability (Silveira et al. 2006). Given that native forests generally occur as small patches and corridors within a matrix of grasslands, agriculture and tree plantations, they are potentially susceptible to fluctuations in groundwater levels caused by water consumption in these other land-cover classes. The Rio de la Plata Basin is one of the world's most productive agricultural regions, undergoing rapid land-use conversion and

intensification of agriculture in the past two decades (Baldi & Paruelo 2008). How the functioning of these ecosystems responds to climate variability is an important aspect in sustaining their ecological role for biodiversity and ecosystem health in a changing landscape. While increasing forest productivity with increasing rainfall shown here poses potential benefits for carbon sequestration and wildlife conservation, the potential expansion of forests into native pastures also presents management concerns for maintaining rangeland productivity.

Acknowledgements

We thank the Grupo de Biodiversidad y Ecología de la Conservación (BEC), Instituto de Ecología y Ciencias Ambientales (IECA) of Facultad de Ciencias and the Espacio Interdisciplinario of the University of the Republic of Uruguay for logistical support. Research was funded in part by a post-doctoral fellowship from the Agencia Nacional de Investigación e Innovación (ANII) de Uruguay, the Comisión Sectorial de Investigación Científica (CSIC) and the Center for Climate and Resilience Research (CR)2 (FONDAP 15110009). We thank for advice and comments Federico Haretche, Carolina Toranza, Ludmila Profumo and Madeleine Renom.

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Supporting Information

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

Appendix S1. Colour version of 1b, example SPOT satellite pixels of 1 × 1 km with >90% overlaid with the ‘hillside forest’ land cover class (*bosque serrano y de quebrada*).

Appendix S2. Relationship between accumulated annual fPAR in a vegetation year (Sept–Aug) and mean annual precipitation as well as average temperature in summer for riparian and hillside forests and wooded savanna in Uruguay.

Appendix S3. Time series of fPAR and T_{mean} .

Appendix S4. Correlation (R) between annual fPAR of each woodland class to rainfall and temperature at time intervals of 1-12 mo over 2 years.