

ORIGINAL RESEARCH

Disentangling the signal of climatic fluctuations from land use: changes in ecosystem functioning in South American protected areas (1982-2012)

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Introduction

Global environmental change encompasses different interacting dimensions that alter the structure and function of Earth ecosystems (Vitousek 1994). The evidence about climate change, that is, global increases in temperature and changes in rainfall patterns, is vast and widely accepted (Huntington 2006; IPCC 2007, Mann et al. 2008). Carbon

Abstract

Global environmental change is characterized by changing climate, atmospheric composition and land use. Its impact on ecosystem structure and functioning has been detected throughout the world. While every ecosystem is vulnerable to climate change, the degree of the impact and the magnitude of the ecosystem response are likely to vary. Protected areas of South America provide a 'laboratory' to test expectations of climate change effects on ecosystems at a regional scale. By using protected areas we minimized the effects of land use/land cover changes over ecosystem functioning. We analyzed the temporal trends, that is, directional changes, and spatial heterogeneity of both climatic variables and attributes of the seasonal dynamics of the normalized difference vegetation index, that is, a surrogate of vegetation carbon gains derived from satellite information, on 201 protected areas of South America. Increased productivity and higher seasonality, frequently climate driven, is the most common signal across South American biomes but concentrated on those areas located in the tropics and subtropics. In general, arid and semiarid sites responded positively to increases in precipitation and negatively to increases in temperature, while humid ecosystems responded in the opposite way. Our results provide a preliminary basis for predicting which ecosystems will respond more rapidly and strongly to climate change. We also provide support to the fact that protected areas are not static systems as their functioning is changing with different magnitude and in contrasting directions.

dioxide (CO₂) concentration increase in the atmosphere as a consequence of human activities is the best documented component of Global Change (Vitousek 1994; Cook et al. 2016). Land use/cover change is modifying the Earth's surface at unprecedented rates through afforestation and deforestation, agricultural expansion, intensification of livestock activities and urbanization (DeFries et al. 2004; Foley et al. 2005; Hansen et al. 2013).

The capacity of the biosphere to provide ecosystem services in the long term is threatened by Global Change (Vitousek et al. 1997; Sala et al. 2000). Multiple alterations of ecosystem structure and functioning as a consequence of Global Change were detected in different areas of the planet through remote sensing, dendroecology and other sources of information, such as forest inventories (Spiecker 1999; Paruelo et al. 2004; Boisvenue and Running 2006). Behind those alterations diverse direct factors had been identified. Such factors were generally associated to three dimensions of Global Change: modification in climate, atmospheric composition and land use/cover.

Protected Areas (PAs) are the cornerstone of in-situ global conservation efforts and are directed not only to preserve biodiversity but also to ensure the provision of multiple ecosystem services, including cultural services (Lopoukhine et al. 2012; Dudley et al. 2014; Watson et al. 2014). Protected Areas are not ecological islands or static systems; they are part of a broader socio-ecological context (Cumming et al. 2015) and are, in turn, affected by environmental changes (Alcaraz-Segura et al. 2008; Petorelli et al. 2012). In South America, 20.4% of land surface is under protection, more than in any other continent (UN 2011). Despite the importance of PAs, many South American ecosystems are highly threatened (Myers et al. 2000) and are currently undergoing rapid transformations since some of its biomes present the highest deforestation rates in the world (Hansen et al. 2013). Besides, in South America there is a high disparity between habitat loss and protection (Hoekstra et al. 2005) and even inside protected areas land degradation is extended and increasing (Leisher et al. 2013). Despite this critical situation, our understanding of South American PAs ecosystem functioning is poor. A functional characterization of PAs can be used to derive a baseline or reference situation corresponding to the 'potential' functioning of ecosystems (Garbulsy and Paruelo 2004; Cabello et al. 2012). Having reference situations could also allow to disentangle the relative effects of some of the dimensions of Global Change, for example, land use/cover change and climate/atmospheric changes.

Ecosystem functioning analysis based on remote sensing techniques is recognized as a useful approach for studying Global Change (Kerr and Ostrovsky 2003; Petorelli et al. 2005; Cabello et al. 2012). Many ecosystem functional studies are based on monitoring the temporal dynamics of the normalized difference vegetation index (NDVI), a spectral index associated with the fraction of the photosynthetic active radiation intercepted by green tissues (fPAR; Potter et al. 1993; Sellers et al. 1996; Di Bella et al. 2004), which in turn, is one of the main controls of Carbon (C) gains or net primary productivity

(ANPP; Monteith 1972). Numerous studies have linked satellite derived NDVI with ANPP of different regions and ecosystems of the world, finding a strong correlation between spectral behavior and vegetation functioning (Ruimy et al. 1994; Paruelo et al. 1997; Xiao and Moody 2004; Piñeiro et al. 2006).

Net primary productivity is the main input of C and energy into the ecosystem (Odum 1969) and it was proposed as an integrative variable of ecosystem functioning (McNaughton et al. 1989) and a descriptor of ecosystem health (Costanza 1992; Schlesinger 1997). Given its relationship with NPP, the NDVI magnitude and stability can be used as a surrogate of the provision of regulation ecosystem services (Paruelo et al. 2016). Furthermore, the analysis of NDVI dynamics and its attributes has been widely used to characterize the impact of land-use change impacts on ecosystem functioning, particularly on NPP (Hicke et al. 2002; Guerschman et al. 2003; Paruelo et al. 2004) and recently, on ecosystem services provision as well (Barral and Maceira 2012; Carreño et al. 2012; Volante et al. 2012; Paruelo et al. 2016).

Several studies based on remote sensing techniques partially investigated Global Change effects on South American ecosystems. Garbulsy and Paruelo (2004) derived empirical relationships between ecosystem functional attributes and their variability across environmental gradients analyzing 13 PAs in Argentina. Alcaraz-Segura et al. (2013) explored the environmental and human controls of ecosystem functional diversity in temperate South America. Considering the temporal dimension, Paruelo et al. (2004) analyzed the trends of radiation interception during the period 1981–2000 in South America. Their results showed how land use/cover change controlled those trends in grasslands and dry forests of southern South America. Texeira et al. (2015) analyzed the control exerted by land cover and precipitation over long-term trends in ANPP in South American temperate grasslands and Hilker et al. (2014) in Amazon forests. Leisher et al. (2013) described land degradation across Latin American PAs and their surroundings in the period 2004–2009. Furthermore, land use/cover change impact on functional attributes of ecosystems were explored in southern South America (Guerschman et al. 2003; Volante et al. 2012; Vassallo et al. 2013; Texeira et al. 2015). So far, the climatic controls of C gain trends in South American ecosystems were investigated as part of global studies (Schultz and Halpert 1993; Ichii et al. 2002; Nemani et al. 2003; Seddon et al. 2016). However, the significant climatic changes observed in recent decades (Skansi et al. 2013) and expected for the future (IPCC 2007) highlight the need for a more comprehensive analysis in South American ecosystems disentangling the signal of climatic fluctuations from land use.

Water availability and temperature are the main determinants of NPP spatial variability (Lieth 1973). But whether or not interannual variability in climate account for interannual variability in NPP is both supported (e.g. Lauenroth and Sala 1992; Sala et al. 2012) and challenged (e.g. Goward and Prince 1995; Fernández 2007) in scientific literature. The response of ecosystems to interannual variability in climate is a current and central topic in ecology since it reflects the vulnerability of ecosystem processes, and ultimately human well-being, to climate change (Rustad 2008; Nelson et al. 2013). Virtually every ecosystem may be impacted by climate change, however, the degree of the impact is likely to vary, as well as the magnitude of the ecosystem response. In this context, South American PAs provide a 'laboratory' to test expectations of climate change effects on ecosystem functioning at a landscape scale.

Our analysis sought to answer the following questions: (1) How did the magnitude and seasonality of C gains change over South American ecosystems during the last three decades? (2) Were these changes concurrent with climate changes? (3) Which ecosystems were more sensitive to climatic fluctuations? We analyzed the temporal trends and spatial heterogeneity of both climatic variables and attributes of the seasonal dynamics of the NDVI on PAs of South America as a way to minimize the effects of land use/land cover changes over ecosystem functioning.

Materials and Methods

The analyses were based on NDVI data derived from the Advanced Very High Resolution Radiometer (AVHRR) sensor on board the National Oceanic & Atmospheric Agency (NOAA) satellites. The NDVI is calculated as the difference between the reflectance registered by the AVHRR sensor in the near-infrared (channel 2, 730–1100 nm) and visible (channel 1, 580–680 nm) portion of the electromagnetic spectrum divided by the sum of the reflectance of both channels. The channel 2 is sensitive to atmospheric conditions since it encompasses a broad wavelength interval and thus requires additional data or maximum value compositing for correcting aerosol, haze and clouds effects which can influence observed NDVI (Holben 1986). The GIMMS products (Tucker et al. 2005) are the only freely available for an extensive time period (1981–2015) and currently the most frequently used for evaluating patterns and trends around the world (Pettorelli 2013). While its reliability has been discussed by several authors (e.g. Baldi et al. 2008 and Alcaraz-Segura et al. 2010), good consistency between GIMMS and other NDVI products was also reported (Song et al. 2010; Beck et al. 2011; Zeng et al. 2013). We used a NDVI database spanning the period between July 1981 to December 2012 with

a spatial resolution of c. 64 km², a temporal resolution of 15 days and termed NDVI3g (third generation GIMMS NDVI from AVHRR sensors, downloaded from: ecocast.arc.nasa.gov). The NDVI3g dataset was assembled accounting for various deleterious effects, such as sensor degradation, calibration loss, orbital drift, volcanic eruptions, cloud cover and other effects not related to vegetation change and includes a quality assessment information value generated per pixel (Pinzon and Tucker 2014).

Protected Areas boundaries were obtained from the most comprehensive global dataset on terrestrial protected areas as defined by IUCN: the World Database on Protected Areas (ProtectedPlanet.com, downloaded in February 2015). Protected Areas categorized as I or II by IUCN were selected as representative of natural ecosystems with limited human impact (Table 1). In order to check our assumption that using PAs of categories I and II minimized land use changes, we compared the cumulative human footprint inside and outside the PAs. To do so, we used globally standardized data on infrastructure, land cover and human access which summarize direct and indirect human pressures on the environment (Venter et al. 2016a,b). A map of biomes of South America (Olson et al. 2001) was used to derive vegetation units boundaries.

Mean monthly precipitation and temperature gridded datasets at 0.5° spatial resolution were obtained from the Climatic Research Unit (CRU) of the University of East Anglia (<http://www.cru.uea.ac.uk/data/>). The CRU team

Table 1. International Union for Conservation of Nature and Natural Resources (IUCN) protected area categories I and II (Dudley 2008).

IUCN Category	Description
I a) Strict nature reserve	Category Ia are strictly protected areas set aside to protect biodiversity and also possibly geological/geomorphological features, where human visitation, use and impacts are strictly controlled and limited to ensure protection of the conservation values. Such protected areas can serve as indispensable reference areas for scientific research and monitoring.
I b) Wilderness area	Category Ib protected areas are usually large unmodified or slightly modified areas, retaining their natural character and influence, without permanent or significant human habitation, which are protected and managed so as to preserve their natural condition.
II) National park	Category II protected areas are large natural or near natural areas set aside to protect large-scale ecological processes, along with the complement of species and ecosystems characteristic of the area, which also provide a foundation for environmentally and culturally compatible spiritual, scientific, educational, recreational and visitor opportunities.

constructed and updates this dataset from observations at meteorological stations across the world's land areas. Harris et al. (2014) compared it with other datasets and found a very good agreement for South America. Gridded data matched observations of temperatures much better than those of precipitation, and regional variation in performance indicated that topographically complex regions are the most difficult for these models (Behnke et al. 2016). CRU data were resampled through bilinear interpolation to NDVI3g spatial resolution and aggregated to mean annual temperature (MAT) and total annual precipitation (TAP) over the period 1982–2012.

We developed an NDVI time series based upon a monthly interval across the period 1982–2012 for every NDVI3g pixel located completely within a PA categorized as I or II by IUCN and not intersected by ecoregion limits. First, a filter based on NDVI3g quality flags was applied in order to exclude low quality and unreliable data, meaning that only pixels flagged as 1 or 2 (good value) were considered. Additionally, the bimonthly NDVI values were temporally aggregated to monthly maximum value composites in order to minimize problems not removed previously by the original processing or quality filtering (e.g. cloud contamination) as suggested by Holben (1986). Looking to further minimize noise and spurious values, non-vegetative pixels ($\text{NDVI} \leq 0.1$) were also removed. In order to describe the patterns of ecosystem functioning, we derived for every year and pixel from our 1982–2012 monthly database four attributes that capture in a straightforward way the height and shape of the NDVI annual profile (Fig. 1): NDVI annual mean (NDVI_m), an estimator of total radiation interception and ANPP, the annual maximum (Max)

and minimum (Min) NDVI values, related to the maximum and minimum photosynthetic capacity of the ecosystems and the intra-annual coefficient of variation of NDVI (CV_t), a normalized index of vegetation seasonality (Paruelo and Lauenroth 1998; Pettorelli et al. 2005; Alcaraz et al. 2009; Volante et al. 2012). For each year, only pixels with at least 9 months of good quality values were considered and we excluded from analysis pixels with <7 years per decade of good quality data.

Trends, indexed as the slope of the relationship between the variable and time, were assessed using the Theil-Sen estimator (Wilcox 2003), a method proposed by Theil (1950) and Sen (1968) that estimates the slope of a regression line by computing the slope for all pairs of data having distinct X values (corresponding to years in this study) and then computing the median of these slopes. This is a non-parametric test robust against seasonality, non-normality, heterocedasticity, missing values and inter-annual autocorrelation (Wilcox 2003). The association between trends in NDVI attributes and climatic variables were assessed using the Chi-square test of independence. To quantify the sensitivity of different ecosystems to variation in precipitation and temperature we estimated for each PA the slope of the linear relationship between NDVI_m and TAP (Huxman et al. 2004; Verón et al. 2005) and MAT through linear regression. Collinearity between TAP and MAT was assessed through the Pearson correlation coefficient (threshold > 0.7) and the variance inflation factor (threshold > 5) following Dormann et al. (2013). Slopes with a $P < 0.05$ were considered significant. Statistical analyses were performed in R (www.r-project.org).

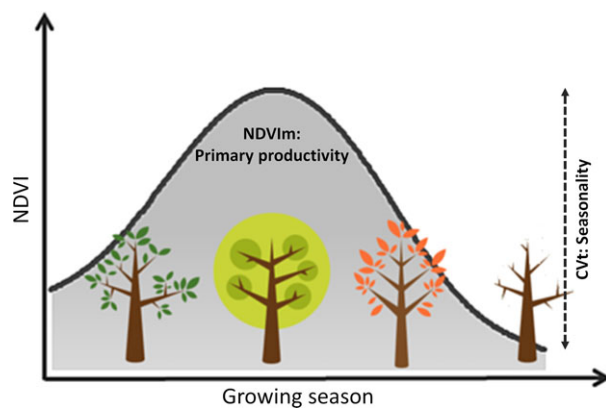


Figure 1. NDVI seasonal profile. NDVI_m is the annual mean of NDVI and a surrogate of annual primary productivity. CV_t is the intra-annual coefficient of variation of NDVI and a normalized index of vegetation seasonality. Max and Min are annual NDVI maximum and minimum values respectively. NDVI, Normalized difference vegetation index.

Results

Two-hundred-thirty-one of the 803 PAs under IUCN category I or II are large enough to contain at least one NDVI3g pixel completely within its boundaries. From this subset, we excluded from the analysis 31 PAs because of lack of good quality data. The remaining 201 PAs encompass 6286 NDVI3g pixels (402304 km²) and contain an average of 31 pixels (1984 km²) each one, ranging from 1 (64 km²) to 353 pixels (22592 km²). The PAs analyzed in this study belong to 61 ecoregions, 9 biomes and 13 countries, 35 (17%) correspond to IUCN category I and 166 (83%) to IUCN category II. They are distributed along a broad environmental gradient and a wide functional space (Fig. 2). Averages over the period 1982–2012 for MAT, TAP, NDVI_m and CV_t spanned from 4°C, 39 mm, 0.12 and 0.04–28°C, 5400 mm, 0.85 and 0.48 respectively. Only the most variable of the lower productivity ecosystems, corresponding to salt flats, the highest Andes and some of the driest deserts are

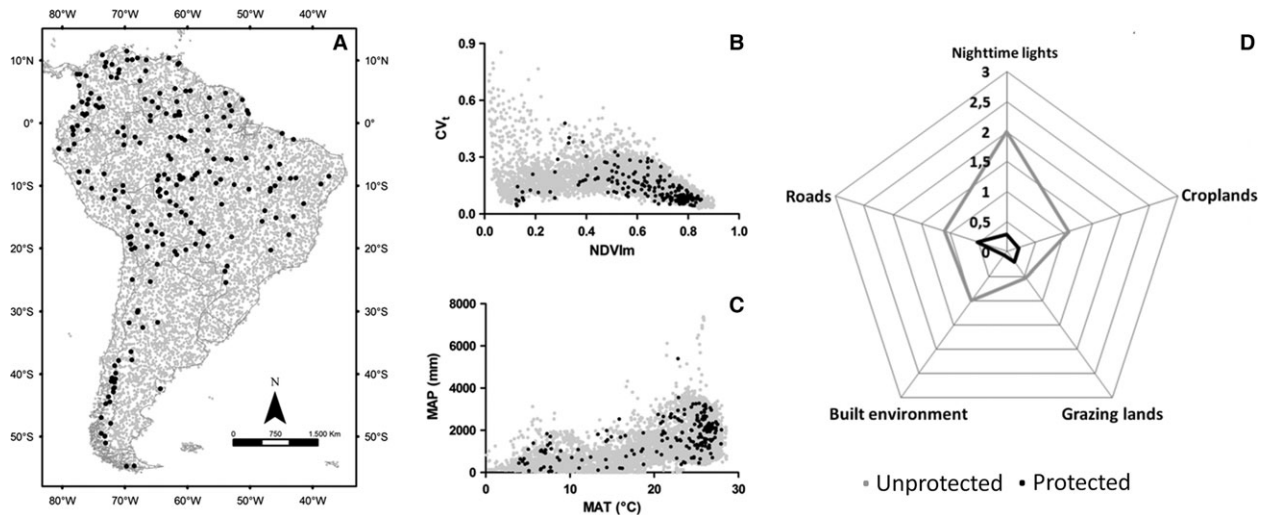


Figure 2. (A) Geographical distribution of the protected areas included in this study (in black), and their distribution in the context of (B) annual mean of NDVI (NDVIm) and intra-annual coefficient of variation of NDVI (CV_t), (C) Mean annual temperature (MAT) and mean annual precipitation (MAP) for the period 1982–2012 and (D) the mean of five variables measuring direct and indirect human pressures on the environment within a 0–10 scale (Venter et al. 2016a,b). In grey are displayed 10,000 points randomly distributed over South America.

underrepresented in our dataset, because we purposely exclude non-vegetation areas and the fact that those systems have low coverage in the PAs network of South America (Juffe-Bignoli et al. 2014). Cumulative human footprint, indexed using land use, infrastructure and human access data, was considerably lower in protected than in unprotected areas (Fig. 2d).

Both NDVIm and CV_t significantly increased over the period 1982–2012 in South American protected ecosystems. When comparing 2008–2012 versus 1982–1986 averages, NDVIm and CV_t increased 2.7% and 11.2%, respectively. Mean annual temperature showed a strong and significant positive trend over the period 1982–2012. The slope of the temporal trend of MAT for the 201 PAs jointly considered was $0.02^{\circ}\text{C}\cdot\text{y}^{-1}$. This value represent an average rise in MAT of 0.65°C during the past three decades. In contrast, TAP did not display a significant trend when considering together all PAs. At the individual PA level (Fig. 3 and Table 2), significant increases in NDVIm and MAT were dominant and the majority of the PAs showed non-significant changes in CV_t and TAP. Upward trends in NDVIm were driven mostly by increases in Max, while increases in Min were less common. Max increases largely exceeded decreases, however, Min increases were scarce and Min decreases widespread. Chi-square test showed that trends in NDVIm were associated with trends in TAP ($P < 0.0001$) and MAT ($P < 0.05$) while CV_t trends were independent of the trends observed in climatic variables.

Biomes differed in the magnitude and direction of the changes (Fig. 4). Significant increases in NDVIm and CV_t

were more common than decreases, however non-significant changes were dominant. The proportion of surface under protection which showed increases in NDVIm ranged between 30% and 41% in tropical and subtropical biomes, in contrast, decreases in NDVIm were found in 17% of its grasslands, savannas and shrublands and in <5% of its forests. A similar pattern was found for CV_t in those biomes. The opposite occurred in flooded grasslands and savannas, where significant decreases in NDVIm exceeded the positives changes (26% vs. 9% of the total protected surface) and CV_t significantly increased in almost 60% of its area. Temperate grasslands, savannas and shrublands exhibited significant changes in NDVIm in only 8%, and in CV_t in 15% of its protected surface. More than 80% of the area located in PAs in mangroves, flooded grasslands and savannas, tropical and subtropical grasslands, savannas, shrublands and moist broadleaf forests showed significant increases in MAT, while in deserts and xeric shrublands and tropical and subtropical dry broadleaf forests the increase was significant in near 40% of the area. In contrast, montane grasslands and shrublands showed a significant decrease of MAT in 42% of its area. Regarding TAP, it significantly increased in 42% of temperate broadleaf and mixed forests and 13% of temperate grasslands, savannas and shrublands and decreased in 50% and 16% of tropical and subtropical dry broadleaf forests and grasslands, savannas and shrublands respectively, while more than 90% of the area located in the other biomes showed non-significant trends.

Interannual fluctuation in NDVIm was significantly related to interannual fluctuations in precipitation, mean

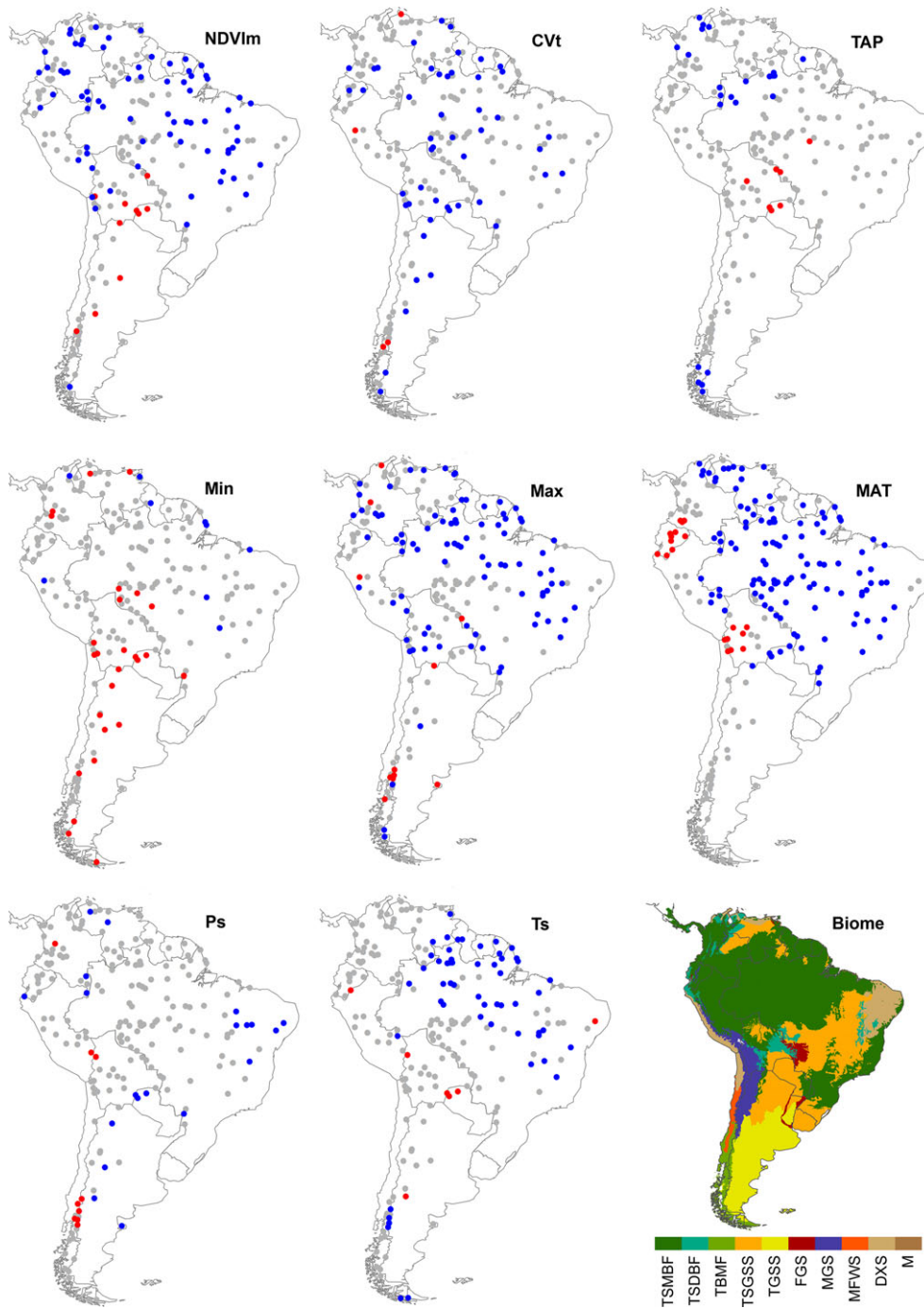


Figure 3. Spatial heterogeneity of temporal trends in NDVI, CVt, Min, Max, TAP and MAT, and sensitivity of NDVI to TAP and MAT fluctuations. Trends were indexed as the slope of the relation of the variable and time during the period 1982–2012. Sensitivities were indexed as the slope of the relationship of NDVI and annual MAT or TAP across years for the period 1982–2012. Dots represent 201 protected areas corresponding to IUCN categories I or II and show significant positive (blue), non-significant (grey) or significant negative (red) values. NDVI, NDVI annual mean; CVt, Intra-annual coefficient of variation of the NDVI; TAP, Total annual precipitation; MAT, Mean annual temperature; Ps, Sensitivity of NDVI to TAP interannual fluctuation; Ts, Sensitivity of NDVI to MAT interannual fluctuation; TSMBF, Tropical & Subtropical Moist Broadleaf Forests; TSDBF, Tropical & Subtropical Dry Broadleaf Forests; TBMF, Temperate Broadleaf & Mixed Forests; TSGSS, Tropical & Subtropical Grasslands, Savannas & Shrublands; TGSS, Temperate Grasslands, Savannas & Shrublands; FGS, Flooded Grasslands & Savannas; MGS, Montane Grasslands & Shrublands; DXS, Deserts & Xeric Shrublands; M, Mangroves.

Table 2. Count of protected areas ($n = 201$) showing significant negative (–), non-significant (ns) and significant positive (+) trends in NDVI mean (NDVIm), Intra-annual coefficient of the variation of the NDVI (CV_t), Total annual precipitation (TAP) and Mean annual temperature (MAT) across the period 1982–2012. Trends, indexed as the slope of the relationship between the variable and time, were assessed using the Theil-Sen estimator. Slopes with a P -value < 0.05 were considered significant.

		NDVIm			CV _t			TAP		
		–	ns	+	–	ns	+	–	ns	+
CV _t	–		4							
	ns	3	97	49						
	+	7	19	22						
TAP	–	4	3			4	3			
	ns	6	105	60	4	128	39			
	+		12	11		17	6			
MAT	–	1	13	5		13	6	1	18	
	ns	4	51	12	4	50	13		60	7
	+	5	56	54		86	29	6	93	16

temperature or both climatic variables in 79 PAs (39%). Collinearity between MAT and TAP was below the recommended threshold in all cases. Significant relationships between NDVIm and precipitation across years were found in 31 PAs, being 22 direct and 9 inverse relationships. Significant relationships between NDVIm and temperature across years were found in 58 PAs, being 56 direct and 2 inverse relationships. Ten PAs showed significant relationships between NDVIm, precipitation and temperature across years. In general, arid and semiarid sites (e.g. PAs located in Argentine Patagonia and Brazilian Caatinga) responded positively to increases in precipitation and negatively to increases in temperature, while humid forests (e.g. temperate forests of Patagonia, and Amazonian tropical and subtropical forests) responded in the opposite way (Fig. 3). Detailed results of individual PAs are provided in the supplementary material.

Discussion

In this article we analyzed c. 402,300 km² of protected ecosystems in South America, an area equivalent to Paraguay, where some of the driest (Salar de Huasco, Chile) and wettest (Utria, Colombia) sites of the world are represented along with deserts, grasslands, savannas, dry forest and tropical rainforests. Our analysis enabled us to characterize changes on ecosystem functioning at a regional scale and provide a preliminary basis for predicting which ecosystems will change its productivity more rapidly and strongly in response to climate change, that is, those with the highest sensitivity and the largest changes in climatic variables. Increased productivity and higher seasonality, frequently climate driven, is the most

common signal across the least modified areas of South American biomes. However, those sites where climate is becoming more arid (upward temperature and downward precipitation trends respectively) showed significant reductions in productivity. Warming and increased variability in precipitation is predicted by climate models (IPCC 2013), but changes in ecosystem functioning depend on the interactions among other factors such as nutrient availability, radiation and changes in plant community composition and structure. These interactions represent one of the largest uncertainties in projections of future ecosystem functioning change.

We found evidences for an increase in C gains (as indexed by NDVIm) during the last three decades over the majority of South American PAs, but concentrated on those located in the tropics and subtropics. An overall increase in C gains during the last decades in South America (assessed using AVHRR-NOAA datasets) was previously reported (Nemani et al. 2003; Paruelo et al. 2004; Baldi et al. 2008; Beck et al. 2011). Long term field monitoring plots also showed a similar pattern (Phillips et al. 1998). Nemani et al. (2003) related C gains increases with the release of climatic constraints, such as declining cloud cover in the Amazon. Mueller et al. (2014) suggested that land use practices could be behind NDVI trends and found that positive trends were associated with intensive land use. In relation with land use, more detailed analysis showed that land clearing for agriculture and overgrazing could be responsive of a reduction in C gains across years while afforestation generated NDVI upward trends (Paruelo et al. 2004; Baldi et al. 2008; Eastman et al. 2013; Vassallo et al. 2013; Teixeira et al. 2015). Carbon gains increases should be considered with caution regarding C balances. Net C balance outcomes are less clear since respiration frequently shows stronger sensitivity to warming (Heimann and Reichstein 2008) and therefore C losses can potentially offset C gains (Crowther et al. 2016). On the other hand, ecosystem services provision and biodiversity can be compromised by the decrease in C gains observed in some arid and semi-arid sites (Paruelo et al. 2016). Other causes may be invoked for changes in C gains (e.g. CO₂ fertilization, biological invasions, increased N deposition) and deserve further investigation (Zhu et al. 2016).

Focusing on protected areas, and hence minimizing land use effects, we found correlative evidence of a positive relationship between C gains trends and temperature and precipitation trends. However, although in different frequency, all possible combination between trends in NDVIm and trends in TAP or MAT were found, supporting the idea that the response to climatic variables varies among ecosystems. While the release of climatic constraints can be true for tropical and subtropical

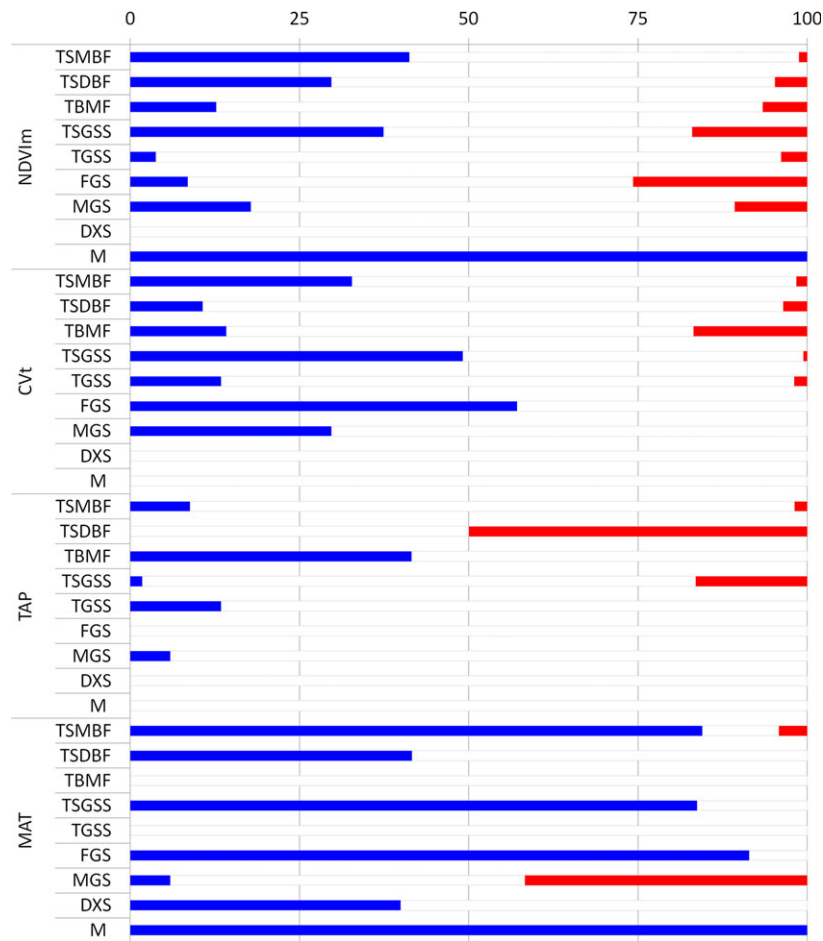


Figure 4. Proportion of area (%) showing significant positive (blue), non-significant (white) and significant negative (red) trends per biome. Trends were indexed as the slope of the relation of the variable and time during the period 1982–2012. Only pixels not intersected by biome boundaries were considered. NDVI_m, NDVI annual mean; CV_t, Intra-annual coefficient of variation of the NDVI. TAP, Total annual precipitation; MAT, Mean annual temperature; TSMBF, Tropical & Subtropical Moist Broadleaf Forests; TSDBF, Tropical & Subtropical Dry Broadleaf Forests; TBMF, Temperate Broadleaf & Mixed Forests; TSGSS, Tropical & Subtropical Grasslands Savannas & Shrublands; TGSS, Temperate Grasslands, Savannas & Shrublands; FGS, Flooded Grasslands & Savannas; MGS, Montane Grasslands & Shrublands; DXS, Deserts & Xeric Shrublands; M, Mangroves.

ecosystems, increases in temperature and decreasing precipitation can be limiting productivity in some temperate and semiarid sites. Upward trends in NDVI intra-annual coefficient of variation, which means a higher variation of the primary productivity through the year, largely exceeded decreases, however non-significant trends were dominant. Seasonality increases when minimum NDVI becomes lower and/or maximum NDVI becomes higher. As for NDVI_m, increases in CV_t were driven mostly by increases in Max, which is related to an increase in productivity during the growing season, with the dormant season not being modified. We were unable to find a climatic association with CV_t shifts, probably because of the coarse temporal scale of our analysis, however we found a significant positive association between Min and TAP changes and Max and MAT

changes. It has been suggested that vegetation seasonality is profoundly impacted by land use change, with significant increases after land clearing for agriculture (Guerchman et al. 2003; Volante et al. 2012), but other drivers not related to land conversion were also identified (Eastman et al. 2013). Our results, gathered on more natural, less modified ecosystems support the idea that other factors than direct human interventions may be operating on generating changes in seasonality. Seasonality changes attributed to land transformation (e.g. Baldi et al. 2008) can be confounded or overestimated if concurrent seasonality changes in natural systems are not taken into account. Furthermore, as regarding C gains decreases, seasonality increases can compromise ecosystem services provision and biodiversity (Paruelo et al. 2016).

Interannual variation in climatic variables significantly accounted for interannual variation in NDVI_m in only 40% of the sites. This can be the outcome of several biogeochemical and vegetation constraints on the response to climatic fluctuations (Fernández 2007). These results are similar to the findings of other analyses based on remote sensing (Schultz and Halpert 1993; Ichii et al. 2002) and field studies performed in the northern hemisphere (e.g. Sala et al. 2012; Mowll et al. 2015). Besides intrinsic differences in sensitivity to changes in climate, other factors related to the temporal scale and not considered in this analysis (e.g. lags that result from legacies of previous years, seasonality, timing and intensity of extreme events) can explain the lack of response of some ecosystems to climatic fluctuation. Furthermore, aspects related to non-linearity or thresholds in the response of productivity to climatic variables may not be captured in our analysis. However, our results regarding C gains sensitivity to climatic fluctuations is coherent with ecosystem-level field experimental evidence and landscape-level observations. Productivity and precipitation changes were found to be positively linked in arid or semiarid lands (Zhao and Running 2010; Wu et al. 2011; Pettorelli et al. 2012) being drier ecosystems more sensitive to increased precipitation (Huxman et al. 2004). The temporal coupling of vegetation activity and water availability was previously reported over the Caatinga region of northeast Brazil by Barbosa et al. (2006) and over Patagonia by Jobbágy et al. (2002). The reduction in C gains related to increased precipitation observed in the forests over the Southern Andes (Fig. 3) can be the result of an extended snow cover during those years with precipitation above the mean. This negative correlation was observed in northern high-latitudes and mountainous regions of the world (Los et al. 2001). Warming increased productivity in cold or not water-limited ecosystems (Rustad et al. 2001; Goetz et al. 2005) as observed in high latitudes and altitudes, and in tropical forests in this study. A reduction in C gains can be expected after heat waves or combined with drought (Ciais et al. 2005; Wu et al. 2011). But despite the significant rise in mean temperature observed during the last decades over the Amazon (Fig. 3), our results showed upward trends in tropical forests C gains. Furthermore, we found a positive response of C gains to increases in temperature which mean that the thermal limit of tropical forests would not be reached yet, as it was suggested for other tropical forests (Clark et al. 2003). We found a large amount of C gains interannual variability not explained by variability in climatic variables (not shown). Other interacting factors such as nutrient availability, radiation (Nemani et al. 2003; Seddon et al. 2016) and changes in plant community composition and structure (Wilcox et al. 2016)

should be taken into account and deserves further investigation.

Conclusion

We found that warming, increased productivity and higher seasonality are the most common signals of environmental change across South American biomes. Furthermore, we provided empirical evidence of a positive relationship between changes in C gains and changes in climate (temperature and precipitation) for the least modified ecosystems in South America. Our results provide a preliminary basis for predicting which ecosystems will change its productivity more rapidly and strongly in response to climate change, that is, those with the highest sensitivity and the largest changes in climatic variables (Fig. 3). Interestingly, we found that functional consequences of climate change can be similar to those expected from land use/cover changes (e.g. land clearing for agriculture). We advocate the use of PAs as a reference situation (Garbulsky and Paruelo 2004) to track the effects of climate change (Pettorelli et al. 2012).

Atmospheric deposition networks, maps of invasive species and a better understanding of the mechanisms which modulate the response of different ecosystems to increased atmospheric CO₂, will help to comprehend the effects of Global Change on ecosystem functioning. Such studies need to be complemented with more detailed analyses, based on experiments and modeling studies. Natural experiments, where some factors are fixed across environmental gradients (e.g. land use in protected areas or vegetation type in widely distributed forest plantations), represent an attractive approach to gain insights into short and long-term effects, and also spatial heterogeneity, of environmental changes on ecosystems. Such natural experiments can be used to disentangle the relative importance of factors such as land use, climatic and biogeochemical changes driving ecosystem functioning to improve forecast of vegetation change, and hence, ecosystem services provision.

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Supporting Information

Additional supporting information may be found online in the supporting information tab for this article.

Figure S1. Location of the 201 protected areas analyzed in this study. Biomes boundaries by Olson (2001).

Table S1. Average values and trends in NDVI_{im}, CV_t, TAP and MAT, and climate sensitivity of NDVI_{im} to TAP and MAT fluctuations for the 201 protected areas analyzed in this study.