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RESEARCH PAPER

The global fire–productivity relationship

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ABSTRACT

Aim It has been suggested that on a global scale, fire activity changes along the productivity/aridity gradient following a humped relationship, i.e. the intermediate fire–productivity hypothesis. This relation should be driven by differing relative roles of the main fire drivers (weather and fuel) along the productivity gradient. However, the full intermediate fire–productivity model across all world ecosystems remains to be validated.

Location The entire globe, excluding Antarctica.

Methods To test the intermediate fire–productivity hypothesis, we use the world ecoregions as a spatial unit and, for each ecoregion, we compiled remotely sensed fire activity, climate, biomass and productivity information. The regression coefficient between monthly MODIS fire activity and monthly maximum temperature in each ecoregion was considered an indicator of the sensitivity of fire to high temperatures in the ecoregion. We used linear and generalized additive models to test for the linear and humped relationships.

Results Fire occurs in most ecoregions. Fire activity peaked in tropical grasslands and savannas, and significantly decreased towards the extremes of the productivity gradient. Both the sensitivity of fire to high temperatures and above-ground biomass increased monotonically with productivity. In other words, fire activity in low-productivity ecosystems is not driven by warm periods and is limited by low biomass; in contrast, in high-productivity ecosystems fire is more sensitive to high temperatures, and in these ecosystems, the available biomass for fires is high.

Main conclusion The results support the intermediate fire–productivity model on a global scale and suggest that climatic warming may affect fire activity differently depending on the productivity of the region. Fire regimes in productive regions are vulnerable to warming (drought-driven fire regime changes), while in low-productivity regions fire activity is more vulnerable to fuel changes (fuel-driven fire regime changes).

Keywords
Fire regime, global change, productivity gradient, pyrogeography.

INTRODUCTION

Fire is a widespread process on the earth that affects most ecosystems (Krawchuk *et al.*, 2009; Pausas & Keeley, 2009). However, fire regimes vary across the globe (Chuvieco *et al.*, 2008), mainly in relation to the spatial variability in climate and in the amount and structure of fuels (Parisien & Moritz, 2009; Pausas & Keeley, 2009). It has been suggested that fire activity may change along a productivity/aridity gradient following a humped (unimodal) relationship (Pausas & Bradstock, 2007; van der Werf *et al.*, 2008). This model suggests that fire activity peaks at intermediate levels of aridity/productivity and decreases towards arid as well as productive ecosystems (the intermediate fire–productivity hypothesis). This model is based on the different relative roles of the main fire drivers (fuel and drought) along the productivity gradient. In moist and

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productive regions, fuel is highly available and fire activity should be driven by the frequency of droughts (e.g. Cochrane, 2003); in contrast, in unproductive arid systems, droughts are the rule but fire regimes are fuel-limited (e.g. Pausas & Bradstock, 2007). This fire–productivity model has important consequences for the global change agenda as it suggests that global climatic changes may have contrasting effects on fire regimes in different ecosystems. For instance, increasing the frequency of droughts would increase fire activity in productive environments but could also reduce fires in dry ecosystems by limiting plant growth and reducing fuel loads. In fact this model is central in pyrogeography research (Krawchuk *et al*., 2009) as it links the global distribution of fire activity to vegetation and climate, and provides a framework for understanding the mechanism of change in fire regimes at a global scale. While there is an extraordinary amount of knowledge regarding fire regimes in some specific areas, notably in North America (see a recent review by Parisien *et al*., 2012), the global picture is still poorly understood (Chuvieco *et al*., 2008; Krawchuk & Moritz 2011). Several regional studies have provided some support for the differential contribution of fire drivers (fuel and weather) to fire activity under different productivity conditions (Spessa *et al*., 2005; Archibald *et al*., 2009; Littell *et al*., 2009; Parisien & Moritz, 2009; Bradstock, 2010; Parisien *et al*., 2012; Pausas & Paula, 2012). The physicochemical model of fire frequency also predicts different fire trends in the USA depending on the climatic conditions (Guyette *et al*., 2002). However, the full intermediate fire–productivity model across all world ecosystems remains to be validated.

With the increasing availability of earth observation products we can now better explicitly test macroecological hypotheses (Pfeifer *et al*., 2012). Specifically, we currently have several years of remotely sensed fire information available for the entire planet (Giglio *et al*., 2006, 2009; van der Werf *et al*., 2008) which enables us to test fire-related hypotheses on a global scale (e.g. Le Page *et al*., 2010). Recent analyses of such data showed a predictable relationship between fire activity and environmental conditions, but a limited support for the intermediate fire–productivity hypothesis (Krawchuk *et al*. 2009; Krawchuk & Moritz 2011). It is possible that the strong influence of humans in current fire regimes (e.g. Guyette *et al*., 2002; Syphard *et al*., 2007; Pausas & Keeley, 2009; Bowman *et al*., 2011; Pausas & Fernández-Muñoz, 2012) may blur the theoretical humped response. Alternatively, the scale considered might not be the most appropriate for depicting such patterns. For instance, Krawchuk & Moritz (2011) use fire and climatic data at a 50 km × 50 km scale (grid system) aggregated by 13 biomes; however, a grid system might not be very appropriate to account for biological variability (grids tend to have a low ratio of between-to-within variability), while the use of 13 biomes might hide considerable within-biome variability (e.g. Schoennagel *et al*., 2004; Parisien *et al*., 2012; Pausas & Paula, 2012).

Van der Werf *et al*. (2008) also used remotely sensed fire data for tropical ecosystems and found a tendency for the intermediate fire–productivity hypothesis; however, the use of a grid system precluded Van der Werf and colleagues from finding any statistical significance. While a grid system is a simple and useful way to compile biological data for macroecological studies, it may not be the most efficient way to account for biological variability because the grids do not necessarily match the regional biophysical heterogeneity. We propose using homogeneous ecological units to better depict fire–climate patterns not only at regional (e.g. Gedalof *et al*., 2005; Littell *et al*., 2009; Parisien & Moritz, 2009; Pausas & Paula, 2012) but also at global scales. Specifically, we propose the use of the world ecoregions (Olson *et al*., 2001) because they are much smaller than biomes and homogeneous from the point of view of climate and vegetation (fuel). Ecoregions therefore have a more biological meaning in relation to fire regimes (e.g. Parisien & Moritz, 2009) than grid cells.

We aim to evaluate the decrease in fire activity at the extremes of the productivity gradient (intermediate fire–productivity hypothesis) by first relating remotely sensed global fire activity with indicators of global productivity using world ecoregions as a sampling unit. We then estimate the effect of climate on fire activity for each ecoregion and relate this estimation with a productivity indicator. We expected to find: (1) the humped relationship between fire activity and productivity; and (2) a stronger effect of warm climate on fire activity at the productive end of the gradient.

METHODS

Geographical unit

Our study units were the terrestrial ecoregions proposed by the World Wildlife Fund (WWF; Olson *et al*., 2001). A terrestrial ecoregion is defined as a relatively large unit of land containing a distinct assemblage of natural communities sharing a large majority of species, dynamics and environmental conditions. These ecoregions represent the original distribution of distinct assemblages of species and communities (Olson *et al*., 2001). The original WWF map included 827 ecoregions distributed in 14 biomes. We first exclude ecoregions that lack burnable vegetation, such as those in Antarctica and those dominated by rocks, ice and lakes. Preliminary analysis showed some inconsistencies between the different environmental maps in very small ecoregions; consequently we excluded the biome Mangroves, and small islands and ecoregions smaller than 200 km^2. The final data set includes 769 ecoregions distributed in 13 biomes, and accounted for the 88% of terrestrial land (Table 1).

Data compilation

Global fire activity information was extracted from FIRMS (Fire Information for Resource Management System, NASA). Specifically we used the monthly gridded summary (0.5° spatial resolution) of fire activity obtained from the MODIS sensor in the satellite Terra for the period January 2001 to December 2009 (the Climate Modeling Grid from FIRMS). We selected the Terra collection over the Aqua satellite because the former had a

Table 1 List of biomes and number of ecoregions considered in each.

Biome	Code	No. of ecoregions
Tropical and subtropical moist broadleaf forests	TrMoist	216
Tropical and subtropical dry broadleaf forests	TrDry	54
Tropical and subtropical coniferous forests	TrConif	16
Temperate broadleaf and mixed forests	TempBroad	83
Temperate coniferous forests	TempConif	53
Boreal forests (taiga)	Taiga	28
Tropical and subtropical grasslands, savannas and shrublands	TrGrass	45
Temperate grasslands, savannas and shrublands	TempGrass	41
Flooded grasslands and savannas	FlGrass	25
Montane grasslands and shrublands	MontGrass	50
Tundra	Tundra	33
Mediterranean forests, woodlands and scrub	Med	39
Deserts and xeric shrublands	Desert	93

longer period of recorded activity (Terra from February 2000; Aqua from June 2002). The Terra and Aqua satellites have different overpass times (e.g. Terra overpasses the equator at approximately 10:30 and 22:30 each day, while Aqua overpasses it at approximately 13:30 and 01:30) and thus they might depict slightly different fire activity. However, the fire activity estimates from the two satellites are very similar (correlation *c.* 0.9 in most areas of the world; Giglio *et al.*, 2006) and the differences are mainly related to seasonality of fire activity which is not considered here. Our preliminary analysis also showed a very high correlation in fire detection between the two satellites (e.g. $r = 0.97$, P-value < 0.0001 for the data set in Fig. S1 in Supporting Information; see below). The traditional fire counts obtained from orbiting satellites are biased at high latitudes owing to non-uniform spatial and temporal sampling. The total number of fire pixels observed in each grid cell is therefore corrected for multiple satellite overpasses and missing observations by normalizing the raw fire pixel counts by the expected equatorial coverage in a complete calendar month containing no missing observations (Giglio *et al.*, 2006). Consequently, as a fire activity indicator, we use the overpass-corrected number of fire incidences in each grid cell obtained from the Terra satellite, which is a robust index of global fire activity (Giglio *et al.*, 2006, 2009).

To ensure that remotely sensed fire activity is a good proxy for fire activity (which is rarely examined) we first related remotely sensed fire activity to official fire statistics from countries with reliable data. We compiled the official statistics on the area burned and the number of fires for 45 different countries for years within the period of the remotely sensed data (January 2001 to December 2009; Table S1). We then aggregated the overpass-corrected number of fire incidences from the MODIS sensor in the Terra satellite (Climate Modeling Grid) for these countries. Finally we tested the relationship between the remotely sensed and official statistics using a standard regression, as well as using a mixed-effect model with the country as a random factor (repeated measures analysis). The results confirmed that remotely sensed fire information correlates with area burned ($r = 0.85$, $P < 0.0001$), and to a lesser extent, with the number of fires ($r = 0.69$, $P < 0.0001$) and thus is a good indicator of fire activity (Fig. S1).

To obtain a fire activity indicator for each ecoregion, we first summed the number of fire incidences from the Terra satellite for each ecoregion and month, and we then averaged the monthly data across the whole period available (2001–09). The fire activity index for each region was then defined as the logarithm (Fig. S1) of the average corrected number of fire incidences in each region divided by the size of the region, rescaled from 0 to 1.

As indicators of the local (ecoregion) productivity we selected two indicators at a global scale obtained from different sources: the net primary production (NPP) and a remotely sensed vegetation index (the normalized differential vegetation index, NDVI). NPP was obtained from the earth's average (17 years) annual NPP compiled by the Socioeconomic Data and Applications Center (of the International Earth Science Information Network, CIESIN; Imhoff *et al.* 2004) at 0.25° spatial resolution. These pixel data were aggregated (summed) by ecoregions and divided by the ecoregion area (units Gg km^{-2}). The NDVI for each ecoregion was computed from the monthly NDVI data (1981–2002) produced by the Global Inventory Modeling and Mapping Studies (Tucker *et al.*, 2005; 0.25° spatial resolution). We first averaged the NDVI pixel data of each month into each ecoregion, and then averaged the monthly ecoregion data across the whole period to obtain an average NDVI value for each ecoregion.

To obtain an indicator of the relative role of fuel and climate on fire activity at the different extremes of the productivity gradient, we compiled for each ecoregion the above-ground biomass and the temporal relationship between fire and climate. Above-ground biomass (Mt ha^{-1}) was obtained from the International Institute for Applied Systems Analyses as compiled by Kindermann *et al.* (2008) and is based on country statistics and downscaled to a 0.5° resolution. We averaged these pixel data at the ecoregion scale. The temporal relationship between fire and climate for each region was obtained by relating monthly climatic and monthly fire activity data. For the latter, we used the same source of information as above (FIRMS, period 2001–09) but at a monthly scale (before averaging across time). The monthly fire activity index for each region was defined as the logarithm of the corrected number of fire incidences in each month and region divided by the size of the region and rescaled from 0 to 1. Climatic information from the same temporal window was obtained from the National Centers for Environmental Prediction (NCEP) Climate Forecast System Reanalysis (CFSR) (Saha *et al.*, 2010). Specifically, we extracted monthly

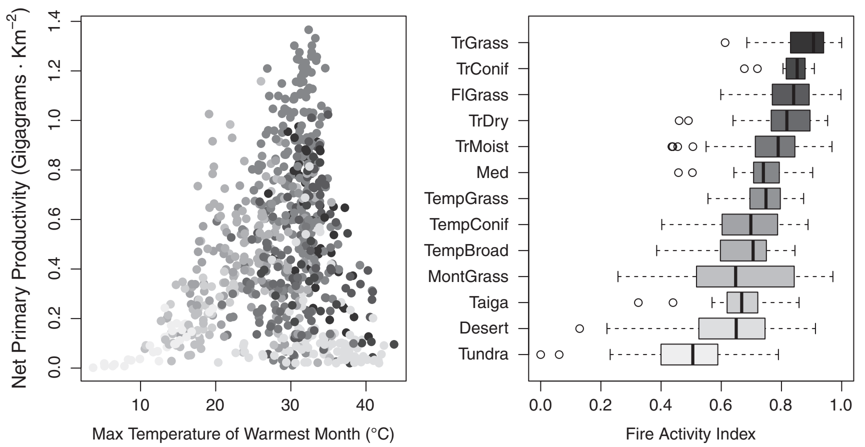

Figure 1 Distribution of the different ecoregions in relation to the maximum temperature of the warmest month and the net primary productivity (left); and boxplot of the fire activity of the different ecoregions by biome (right). The grey scale indicates the fire activity of the biome within each panel; biome codes as in Table 1. More details in the Supporting Information (Figs S2 & S3).

maximum temperature (air temperature 2 m above ground from the ds093.2 dataset) at 0.31° spatial resolution and averaged at the scale of ecoregions.

Analysis

To estimate the proportion of variability in fire activity among biomes and among ecoregions (within biomes), we computed variance component estimates from a mixed-effect model with biome as a random factor. For relating the spatial variability of fire activity with the predictors, we fitted the average fire activity index of each ecoregion against the productivity indicators (NPP, NDVI) using the ecoregions as a sampling unit. Firstly, we used a standard regression. To test for the humped relationship, we then used generalized additive models (GAMs) in which the smoothing parameter is estimated as part of the fitting procedure (Wood, 2006). GAMs are a flexible nonparametric fitting procedure that enables the detection of complex relationships, including humped and skewed trends (Hastie & Tibshirani, 1990). We would find a strong support for the intermediate hypothesis if we found a consistent humped pattern model for the two predictors; and if these models explained greater variance and had lower Akaike information criterion (AIC) values than the linear regression.

The sensitivity of fire to climate was estimated by regressing for each ecoregion the monthly fire activity index against the monthly maximum temperature. The regression coefficient is an indicator of the effect of climate on fire activity; it is similar to the threshold effects described by Pausas & Paula (2012) as fire activity on a log-scale. We then related the regression coefficients of each ecoregion with the indicators of the ecoregion's productivity (NPP, NDVI) using GAMs. If the humped fire–productivity pattern is driven by different drivers at the two ends of the productivity pattern, we would observe a significant and monotonic (i.e. non-humped) relationship. Specifically, it is predicted that most productive ecoregions should be more sensitive to maximum temperatures than dry ecoregions (i.e. positive monotonic functions with productivity). We also related the above-ground ecoregion biomass against NPP to support that most productive regions have higher above-ground biomass.

Geographically distributed data are prone to a high Type I error (Legendre, 1993; Lennon, 2000). To evaluate the magnitude of this bias in our GAM models, we generated spatial autocorrelograms (using the Moran's *I* statistic) of the dependent variable (spatial fire activity index) and of the residual of the models that include the variables related to productivity. Spatial autocorrelograms were computed using NCF software (Bjornstad, 2009). Strong spatial structure in the residuals would suggest that closely located ecoregions do not provide independent data points for testing long-distance effects, while low autocorrelation of the residuals would imply that the regressions are not affected by autocorrelation (Diniz-Filho *et al*., 2003).

RESULTS

Ecoregions are distributed in a wide range of environmental and productivity conditions (Figs 1a, S2 & S3). At the biome scale, fires occurred in all biomes, and the fire activity differs among them ($F_{12,756} = 15.77$, $P < 0.0001$). Tropical grasslands, savannas and dry tropical forest were the biomes with the highest fire activity; while tundra and deserts had the lowest activity (Fig. 1). Despite this, the variability in fire activity was higher within (73.5%) than among biomes (26.5%); suggesting that working at the ecoregional scale should provide a more proximate relationship with fire drivers than working at a biome scale.

There is a large variability in fire activity among ecoregions (Fig. 2, Table S2). Most ecoregions (94%) had some fires during the 9-year period considered; the ones that did not suffer any fire include a variety of vegetation types, mainly tropical moist forest, tundra and deserts. As expected, the two indicators of productivity were significantly and positively correlated ($r = 0.84$, $P < 0.0001$). Fire activity was positively and significantly related to productivity, and the explained variance was *c.* 16–19% (linear models; Table 2). Fire activity also showed a significant humped relationship with productivity, and explained about 29% of the variance (Table 2, Fig. 3). In other words, the humped response increases the explained variance and reduces the AIC in relation to the linear response (Table 2). This hump-shaped relation was not symmetric along the

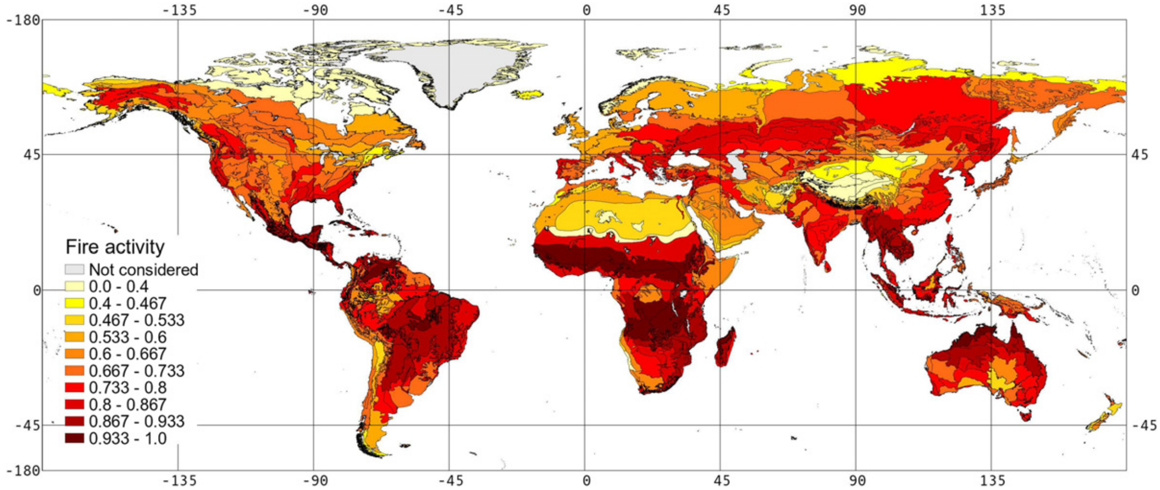

Figure 2 Ecologically based global fire map. The intensity of colour in each ecoregions is related to the fire activity index (from 0 to 1, unitless).

Table 2 Summary of the statistics (*F*-value and explained variance) for the LM and GAM relating the fire activity index with productivity (NPP, NDVI), and model comparison (reduction in the AIC) between LM and GAM for the same dependent and independent variables. Both LM and GAM are significant at $P < 0.0001$. GAMs are represented in Fig. 3.

	LM		GAM		Comparison
Predictors	*F*	Exp Var (%)	*F*	Exp Var (%)	Δ AIC
NPP	168.7	18.6	73.61	28.6	91.2
NDVI	134.7	15.6	45.06	29.1	117.4

LM, linear model; GAM, generalized additive model; NPP, net primary productivity; NDVI, normalized difference vegetation index; AIC, Akaike information criterion.

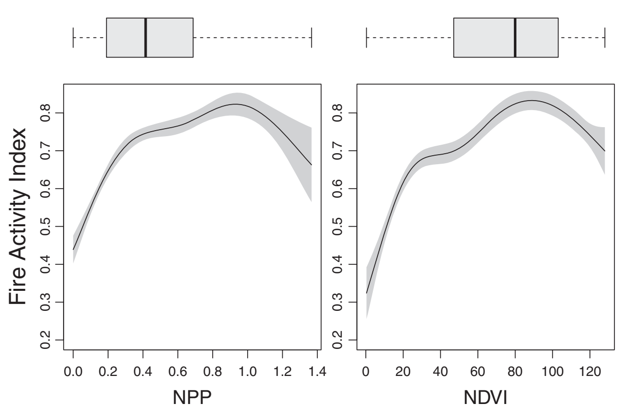

Figure 3 Generalized additive model (GAM) fit of the fire activity index against net primary productivity (NPP) (Gg km^{-2}) and normalized difference vegetation index (NDVI). Tukey's boxplots are shown at the top of each figure summarizing the variability of the *x*-variable among ecoregions; and indicate the median, the first and third quartiles (box), and the range that excludes outliers (whiskers). Shaded regions are the confidence bands for the smoothing (two standard errors above and below the estimate). Summary of the GAM statistics are indicated in Table 2.

environmental gradient; but there was a tendency to be negatively (left) skewed in such a way that the highest fire activity tends to be towards the productive section of the gradient (i.e. towards higher values than the median of the gradient, Fig. 3). Specifically, the median of NPP was located close to the initial hump while the median of NDVI was more towards the drop-off from the hump.

From the 769 ecoregions considered, 539 showed a positive relationship between monthly fire activity and monthly maximum temperature, and in 378 (70%) the relationship was significant (Table S2). Both the regression coefficients of the fire–temperature relationship and the above-ground biomass are linearly related to productivity (linear models in Table 3); the relationship was maintained either considering all the ecoregions or the ecoregions in which the slope was significant ($P < 0.05$). Although the GAM models might slightly increase the explained variance and reduce the AIC, the tendency remained monotonic and positive (Fig. 4). The temperature sensitivity of fire changes along the productivity gradient in such a way that it was very low in low-productivity ecoregions and greatly increased towards the high-productivity section of the global productivity gradient (Fig. 4a). As expected, above-ground biomass was also positively related to productivity – suggesting that biomass is less limiting at the productive end of the gradient (Fig. 4b, Table 3). The same relations were observed for both NPP and NDVI (the latter not shown).

Fire activity across the world showed a spatial structure in such a way that close ecoregions showed a more similar fire activity than expected by chance (Fig. S4). After fitting the models, the autocorrelation was strongly reduced (i.e. in the

Table 3 Summary of the statistics (F-value and explained variance) for the LM GAM relating the regression coefficient of the fire activity–temperature relationship (Coefficient) and the above-ground biomass (Biomass) against productivity variables (NPP, NDVI). All F-values are significant ($P < 0.0001$). AIC comparisons refers to the comparisons between LM and GAM for the same dependent and independent variables. The GAM models against NPP are plotted in Fig. 4.

	LM		GAM		Comparison
Model	*F*	Expl. var (%)	*F*	Expl. var. (%)	Δ AIC
Coefficient–NPP	118.3	14.5	19.7	19.5	29.5
Biomass–NPP	646.8	47.0	165.4	48.3	14.3
Coefficient–NDVI	80.3	10.3	14.0	14.7	22.6
Biomass–NDVI	539.1	42.6	539.1	42.6	0.0

LM, linear model; GAM, generalized additive model; NPP, net primary productivity; NDVI, normalized difference vegetation index; AIC, Akaike information criterion.

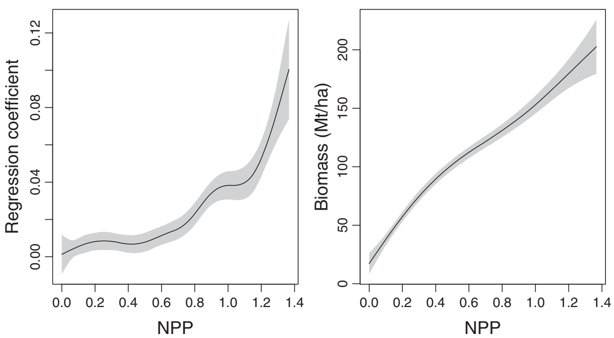

Figure 4 Relationship of the regression coefficients of the monthly fire activity–maximum temperature relationship (left), and of the total biomass (right), against net primary productivity (NPP). Shaded regions are the confidence bands for the smoothing (two standard errors above and below the estimate). See Table 3 for the statistics.

residuals, Fig. S4). The regression coefficients of the relationship between monthly fire activity and monthly maximum temperatures, and the above-ground biomass, were both also highly autocorrelated – but the autocorrelation was drastically reduced after fitting the model against productivity (Fig. S5). Overall, the spatial analysis suggested that the influence of the Type I error on our results is limited.

DISCUSSION

Fires occur in all biomes and in nearly all ecoregions. Different biomes and different ecoregions have different levels of fire activity, and this variability is greater within than between biomes. This differential fire activity is controlled by the productivity, and the relationship is not simple as it decreases towards the extremes of the gradient, supporting the intermediate fire–productivity hypothesis (Pausas & Bradstock, 2007; van der Werf *et al.*, 2008). The results also support the relative role of climate and fuel as drivers of fire activity along the productivity gradient. This is in agreement with regional studies such as those conducted in northern Australia (Spessa *et al.*, 2005), southern Africa (Archibald *et al.*, 2009) or southern Europe (Pausas & Paula, 2012). In moist and productive regions, fuel is not a limiting factor and fire activity is driven by those climatic conditions (e.g. monthly maximum temperatures) that increase drought and flammability (i.e. drought-driven fire regimes). The less productive the system, the less relevant are the high temperatures in driving fire activity; such low-productivity systems being limited by the amount of fuel and thus fire regimes are sensitive to increased fuel levels (fuel-limited fire regimes).

The highest fire activity is not exactly in the middle (i.e. median) of the gradient but closer to the productive end than the arid end. This skewed distribution response may be the consequence of a threshold effect; i.e. increasing productivity increases fire activity up to a level (e.g. high moisture all year round) from which fire activity decreases drastically. In addition, this skewed distribution may also be driven by anthropogenic processes. For instance, deforestation of tropical rain forests in recent decades has increased fire weather and ignitions and thus the level of fire activity in these productive ecosystems that otherwise would rarely burn (e.g. Uhl & Kauffman, 1990; Siegert *et al.*, 2001). This increase is much stronger than the fire changes observed in other ecosystems (Mouillot & Field, 2005). That is, deforestation has probably increased fire activity in the high-productivity section of the gradient. Another factor that may have contributed to the skewed pattern is the strong reduction of fire activity, compared to natural conditions, in some temperate coniferous forests (fire exclusion policy in USA; Covington & Moore, 1994; Mouillot & Field, 2005). However, our results suggest that despite the strong anthropogenic influences on fire regimes in many ecosystems (Pausas & Keeley, 2009; Le Page *et al.*, 2010; Whitlock *et al.*, 2010; Bowman *et al.*, 2011), climate and vegetation still generate a clear underlying pattern of variability in fire regimes (e.g. Archibald *et al.*, 2009; Aldersley *et al.*, 2011). While climate determines the frequency and variability of flammable conditions (e.g. Westerling *et al.*, 2006; Dimitrakopoulos *et al.*, 2011), vegetation type is related to the amount and structure of fuel, which in turn determines the type and intensity of the fire (Pausas & Keeley, 2009) as well as the climatic conditions needed for fires to spread (i.e. the temporal aridity threshold *sensu* Pausas & Paula, 2012).

One of the caveats of the global fire–productivity model is that it does not differentiate between different fire-type regimes such as surface and crown-fire regimes (Keeley *et al.*, 2012). For instance, two ecosystems with similar productivity could have different fire types because of strong differences in fuel structure (Pausas & Keeley, 2009). The use of the different landscape attributes for each ecoregion could form the basis for improving this model. Remotely sensed fire activity data also have some limitations because fire detection may be limited (omission errors) during periods and zones featuring very thick cloud cover. Low-intensity understorey fires and peat fires may also evade detection (Schroeder *et al.*, 2008). Remote sensing data also account for a relatively short temporal window. Despite these limitations, we showed that remotely sensed fire activity is strongly correlated with the area burned and we found a predictable pattern between fire and productivity. These results suggest that despite its limitations, these types of data are appropriate for large-scale studies at least. Some other caveats from previous studies using the same types of global remote sensing data (e.g. van der Werf *et al.*, 2008) were related to the use of arbitrary grid cells and are minimized here by working on homogeneous ecological regions (Littell *et al.*, 2009; Pausas & Paula, 2012). Ecoregions are a promising way to structure the variability of fire activity and environmental information at a global scale because these regions are relatively homogeneous in climate and vegetation, and thus in the main fire regime drivers. The within/between variability ratio and spatial autocorrelation are both minimized by using ecoregions. Thus we encourage macroecological research to use ecologically homogeneous regions instead of grid systems (e.g. Williamson *et al.*, 2011).

In the framework of global change, changes in fire regime are typically associated with warming (e.g. Flannigan *et al.*, 2000; Westerling *et al.*, 2006) and little consideration is given to alternative drivers that may provoke changes in fire regime (e.g. Schwilk & Keeley, 2012). The intermediate fire–productivity hypothesis suggests that changes in both climate and fuel are important factors for predicting alteration in the fire regime, and the relative importance of each factor depends on the productivity of the system. The fact that the sensitivity of fire to high temperatures is much stronger in high-productivity ecosystems implies that small changes in temperature have a much higher effect on fire activity in high-productivity than in low-productivity ecosystems. Consequently, tropical moist forests are the ecosystems most vulnerable to increased fire activity due to global warming (Cochrane, 2003; Scholze *et al.*, 2006; Lewis *et al.*, 2011). In productive ecosystems, small changes in temperature may have much stronger implications through increased fire activity than through the direct effect of increased temperature on plants; in fact, the increased availability of fuels through drought-induced mortality (e.g., Adams *et al.*, 2009; Allen *et al.*, 2010) may even accelerate the increase in fire activity. However, caution is needed to interpret this very high sensitivity of these systems (Fig. 4a) as anthropogenic forcing might influence in this pattern. For instance, most fires in these systems are human-caused, and periods of extensive drought are often taken advantage of to deforest more land; in addition, deforestation also increase air temperature (Nobre *et al.*, 1991). Thus, despite the evidence that in tropical rain forests drought events can significantly increase fire activity even with decreased deforestation rates (e.g. Aragão *et al.*, 2008), the influence of anthropogenic factors in shaping the high fire sensitivity to climate of these systems cannot be discarded. In contrast, fire activity in arid ecosystems should be less sensitive to warming and more sensitive to increased fuel loads and connectivity. These increased fuels may be due to: changes in landscape use and management (Covington & Moore 1994, Pausas, 2004; Pausas & Fernández-Muñoz, 2012), increases in invasive species (Brooks *et al.*, 2004; Keeley *et al.*, 2012) or increases in CO_2 (Bond & Midgley, 2012). In other words, in arid ecosystems, alien invasions not only have implications for biodiversity but also on the fire regime. Given that fire is a spreading process, changes in the fuel structure may generate thresholds of continuity and make fire activity increase exponentially (Pausas & Fernández-Muñoz, 2012). These general predictions on changes in the fire regime changes are at a relatively short scale, as fire changes may create complex feedback process that are difficult to predict. For instance, a short-term increase in fire frequency may finally reduce fuel loads and drive the system towards a fuel-limited dynamics (e.g. Westerling *et al.*, 2011). Thus we advocate the need for a global dynamic model incorporating these possible feedbacks to accurately predict future fire regimes.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Relation of area burnt and number of fires against remotely sensed fire activity.
Figure S2 Summary of the productivity variables by biome.
Figure S3 Distribution of the ecoregions in relation to the maximum temperature of the warmest month and the net primary productivity.
Figure S4 Spatial autocorrelograms for the fire activity and for the residuals of the generalized additive models.
Figure S5 Spatial autocorrelograms for the climatic sensitivity of fire and for the above-ground biomass.
Table S1 Data sources for Fig. S1.
Table S2 Fire activity and climatic sensitivity of fire for each ecoregion.

BIOSKETCHES

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In Figure 3b (right) there is a mistake in the x-axis, where it says NDVI should say Biomass (g_{DM}/m2/Y/ha). Biomass was obtaied from FAO global maps (http://www.fao.org/nr/climpag/climate/index_en.asp). For clarification below we show the same figures for both NDVI and Biomass. The figures are not very different, but the units clearly difer.