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RESEARCH ARTICLE

Climate seasonality, fire and global patterns of tree cover

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Abstract. Vegetation systems with varying levels of tree cover are widely distributed globally, but the determinants of vegetation and tree cover still lack a consistent global framework. How these systems' distribution responds to spatial variability of climate seasonality and associated fire regimes therefore remains unclear. Here, we focus on tree cover distribution at the global level. We develop a model that accounts for the role of seasonality and moisture in the dynamics that link climate, fire and tree cover. We choose predictors that have a clear link to functional processes that control tree physiology and growth, such as freezing tolerance (accounted for in the variable growing season length, GSL) and the balance between water availability and evapotranspiration (accounted for in the variables moisture index and moisture season length). The results show that the relative importance of climate factors and fire frequency as determinants of tree cover hinges on the GSL conditions. For example, significant interactions of tree cover with fire only occur in regions with GSL of 6–7 months or of 12 months. Our data also show a general relationship between maximum tree cover and moisture at the global level that is not visible when examining precipitation. Discontinuities in this relationship occur with frequent fires found under specific levels of seasonal moisture and temperature. A common climatic trait of frequent fires is moisture with a pronounced seasonality and an overall negative balance over the growing season. Frequent fires allow grassland to persist where there could be savanna/woodland as in the case of the North American grasslands. Frequent fires also allow savanna to persist where there could be forest, as found in tropical regions. This quantitative work is useful in improving large-scale land-atmosphere models as well as for identifying conditions of vulnerability for ecosystem diversity.

Keywords. Climate Seasonality, globe, fire, open-canopy ecosystems, tree cover

Introduction

Ecosystems with varying levels of tree cover are widespread from tropical to boreal latitudes. They include tropical and temperate savannas, open woodlands, boreal and high-altitude systems; they support a large diversity of species and provide natural resources for human livelihoods. There is therefore a benefit in building a clear and con-

sistent picture of the environmental determinants of these systems across the globe. Broad-scale studies have often focused on tropical and subtropical savannas (Sankaran et al. 2005, Hirota et al. 2011, Lehmann et al. 2011, Staver et al. 2011, Lehmann et al. 2014) to the exclusion of extra-tropical regions that also support savannas along with other open-canopy systems (Scheffer et al.

2012, Ratajczak et al. 2014). Studying the environmental relationships that characterize these systems globally is particularly relevant because of projected climate change and the likelihood of resultant shifts in ecosystem structure and distribution (Beckage et al. 2006, van der Werf et al. 2008, Bond and Midgley 2012, Moncrieff et al. 2016).

Our study focuses on ecosystems with tree cover ranging from about 10% to 75%, excluding agricultural areas. We interchangeably refer to these systems as “varying tree-cover” or “open-canopy” systems. Our challenge is to unravel the environmental conditions and interactions that give rise to the diverse tree cover of these systems. Complex interactions underlie the effects of biotic and abiotic factors on vegetation (Scholes and Archer 1997, Hill and Hanan 2011, Beckage et al. in press). It has been shown that interrelations of climate and fires play an important role in determining the global distribution of vegetation systems via processes involving water and heat fluxes (Bonan et al. 2003, Hill and Hanan 2011).

The explanatory variables applied here were chosen to be sensitive to the different physiological and ecological responses of trees to environmental conditions across the globe. For example, a focus on mean annual precipitation (MAP) would constrain our understanding of water limitations. In the tropics, MAP alone can explain much of the observed distribution of savannas (Sankaran et al. 2005, Bucini and Hanan 2007, Hirota et al. 2011) due to a relatively narrow temperature range across seasons. However, tree growth is more generally conditional on moisture balance, which is dependent on the joint distribution of precipitation and temperature throughout the year (Stephenson 1990). For instance, drought is determined by the joint interaction of precipitation and temperature; with low temperatures, low rainfall might still be sufficient to maintain a positive moisture balance and support tree growth because of low evapotranspiration. In our study, we use an integrated moisture metric that accounts for both precipitation and potential evapotranspiration to provide a more realistic indication of water availability experienced by plants across the globe.

Some regions are characterized by wide intra-annual temperature and precipitation variation. The seasonal fluctuations of temperature and precipitation also affect tree establishment and growth because the ability of plants to use water and energy is conditional on the seasonal timing of these two resources (Stephenson 1990). For example, seasonality was key to explaining the occurrence of upland grassland in South Africa where there is sufficient water to potentially support savanna (Wakeling et al. 2012). The study showed that the frequency of freezing nights and the short day length during winter, combined with fire cycles, prevented seedlings from reaching maturity, ultimately leading to a treeless grassland. Measures of seasonality have also been included in models of some recent broad-scale studies and resulted important determinants of open-canopy systems’ distribution (Lehmann et al. 2011, Staver et al. 2011, Scheffer et al. 2012, Dantas et al. 2016).

This paper considers factors influencing the degree of canopy openness in ecosystems with varying tree cover by (i) taking a global view and (ii) including seasonality measures of climate variables along with more popular mean-field measures. We apply basic physiological principles to choose the factors that can directly or indirectly (e.g., fire) affect tree growth at broad scales. The work by Wakeling et al. (2012) provides a good example of the importance of both direct and indirect effects of climate on vegetation structure. In their grassland systems, climate seasonality directly limited the growth of savanna tree seedlings by controlling frost and day length. Climate seasonality indirectly impeded seedling survival by favoring fire returns before the seedlings had reached a height above the flame zone.

Methods

We considered the area of grassland, open-canopy and forest ecosystems between 56° S and 80° N. We constructed a set of environmental metrics related to water balance, phenology and fire based on global climatology and remote-sensing products.

Tree cover

The Vegetation Continuous Fields (VCF) product contains proportional estimates for tree cover (Hansen et al. 2003). We used the VCF version V005 (MOD44B) for the year 2001. The VCF tree cover was modelled on spectral data from the Moderate Resolution Imaging Spectroradiometer (MODIS¹) whose observations are at 500 m spatial resolution and generally robustly calibrated, atmospherically corrected and cloud-screened. The VCF tree cover values represent the proportion of each pixel covered by canopies of trees taller than 5 m. In savannas, where tree heights are often below 5 m, VCF might underestimate woody cover.

Fire frequency

The MODIS burned area product (MCD45A1) contains the monthly approximate per-pixel burning date and quality information over the period 2000–2011 at 500 m spatial resolution (Roy et al. 2008). The MCD45A1 algorithm detects the approximate date of burning (accurate to within 8 days) by locating the occurrence of rapid changes in daily surface reflectance time series data. Unmapped areas (missing data) are primarily due to optically thick clouds with an average annual global unmapped area of 43% and up to 68% annual average unmapped in Northern Eurasia. Roy et al. (2008) report that an increasing proportion of burned area might be missed with increasing tree cover.

We derived fire frequency from the MCD45A1 product. For each pixel, the unmapped months were discarded and we defined “equivalent years” as the total number of valid months divided by 12. We then calculated frequency as the number of times the pixel burned over the number of equivalent years. This approach allowed inclusion of all the available observations.

Climate (moisture, growing season length, moist season length)

The WorldClim database² provided rainfall and temperature (Hijmans et al. 2005). The layers were generated through interpolation of average

monthly climate data from weather stations on a 30 arc-second resolution grid, using latitude, longitude, and elevation as independent variables. The CGIAR-CSI database³ provided potential evapotranspiration (Zomer et al. 2008). These data were modeled using the WorldClim Global Climate Data, applying the Hargreaves and Samani (1985) temperature-based method. All our climate data were on a 30 arc-second resolution grid (~1 km resolution at the equator).

We defined ‘growing season length’ (GSL) as the total number of months with mean monthly temperature > 0° C. Freezing temperatures can be considered an ecological threshold because plants can experience tissue damage and dieback from the physical stress of freezing (Pearce 2001). Though a 0° C threshold was used, we do not imply an absolute limit with this value. Frost resistance varies across tree species, depends on the individual history (acclimation) and changes throughout annual environmental variability (Taulavuori et al. 1997, Xin and Browse 2000). Including a thermal threshold is one way to account for temperature constraints on tree physiological activities. We also defined two variables related to moisture (Table 1): ‘moisture index’ (MI) and ‘moist season length’ (MSL). The moisture index was defined as the ratio of annual precipitation to potential evapotranspiration (MAP/PET) averaged over the growing season. Within the growing season period, we calculated the percent of months with $MI \geq 1$ and defined this as moist season length. The moisture index accounts for both water and energy balances and its values directly express the idea of moisture deficit ($MI < 1$), balance ($MI = 1$) or surplus ($MI > 1$). All the climate variables were estimated as monthly averages over the 1950–2000 period. The pixel resolution of the land and climate layers were comparable for the purpose of our analysis and therefore we did not apply any spatial averaging or resampling of pixels.

In summary, our data set included: tree cover percent, moisture index, growing season length, moist season length and fire frequency

1 <http://modis-land.gsfc.nasa.gov/>

2 <http://www.worldclim.org>

3 <http://www.cgiar-csi.org>

(Table 1). We broadly defined ecosystems using the cutoff levels of tree cover percent choosing values comparable to ones found in precedent studies (Hirota et al. 2011, Staver et al. 2011): < 10% grassland, 10–60% savanna, 60–75% woodland and > 75% forest. A drawback of our dataset is the different time periods covered by the original climate and land datasets (Table 1, column ‘Time period’) that can potentially decrease the strength of our results. However, broad-scale patterns of vegetation are more generally a response to long-term climatic patterns. Therefore, the process of averaging over multiple years minimizes the year-to-year variability, providing a more general representation of climate and we assumed that the available 1950–2000 data covered a reasonable period to derive relationships with the 2001 tree cover observations. In the case of fire, we chose to use the MODIS dataset because it is temporally and spatially consistent and

we accepted to work with the limitation of the 12-year period. As a result, our estimates of fire frequency might not represent the actual fire cycles especially in areas where fire recurrence is greater than 6 years. We used the Land Cover Type Yearly Climate Grid (MCD12C1 version V005 for the year 2001; Friedl et al. 2010) with the International Geosphere Biosphere Programme (IGBP) scheme to mask out grid cells classified as cropland, urban and built-up, cropland/natural vegetation mosaics, snow and ice, barren and water bodies. To minimize the edge effects with agriculture areas, we excluded an extra one-pixel buffer zone adjacent to cropland areas.

Analyses

We compiled the data for an initial random sample of 100,000 grid cells, representing a small percentage (0.13%) of the available 500-m cells on land. After subsetting over our latitudinal bounda-

Table 1: Summary of variables and metrics related to climate, fire and land cover type. For the calculation of fire frequency, we used “equivalent years” defined as the total number of months between 2000–2011 with valid observations divided by 12.

Variable	Units	Symbol	Data source	Spatial resolution	Time period	Processing
Tree cover %	%	<i>tc</i>	1	500 m	2001	
Mean monthly precipitation	mm	<i>PPT</i>	2	30 arc-seconds	1950–2000	
Mean monthly temperature	°C	<i>T</i>	2	30 arc-seconds	1950–2000	
Mean monthly potential evapotranspiration	mm	<i>PET</i>	3	30 arc-seconds	1950–2000	
Burned area	date of burning		4	500 m	2000–2011	
Land cover type			5	5600 m		
Growing season length	months	<i>GSL</i>		30 arc-seconds		Total months with mean monthly temperature $\geq 0^\circ\text{C}$
Moist season length	%	<i>MSL</i>		30 arc-seconds		Percent of growing season with $PPT / PET \geq 1$
Moisture index		<i>MI</i>		30 arc-seconds		Average monthly PPT / PET across the growing season
Fire frequency		<i>ff</i>		500 m		Ratio of total number of times a pixel burned to the number of equivalent years.

1 <http://glcf.umd.edu/data/vcf/>; 2 <http://www.worldclim.org>; 3 <http://www.cgiar-csi.org>; 4 <http://modis-fire.umd.edu/index.html>; 5 <http://modis-land.gsfc.nasa.gov/>

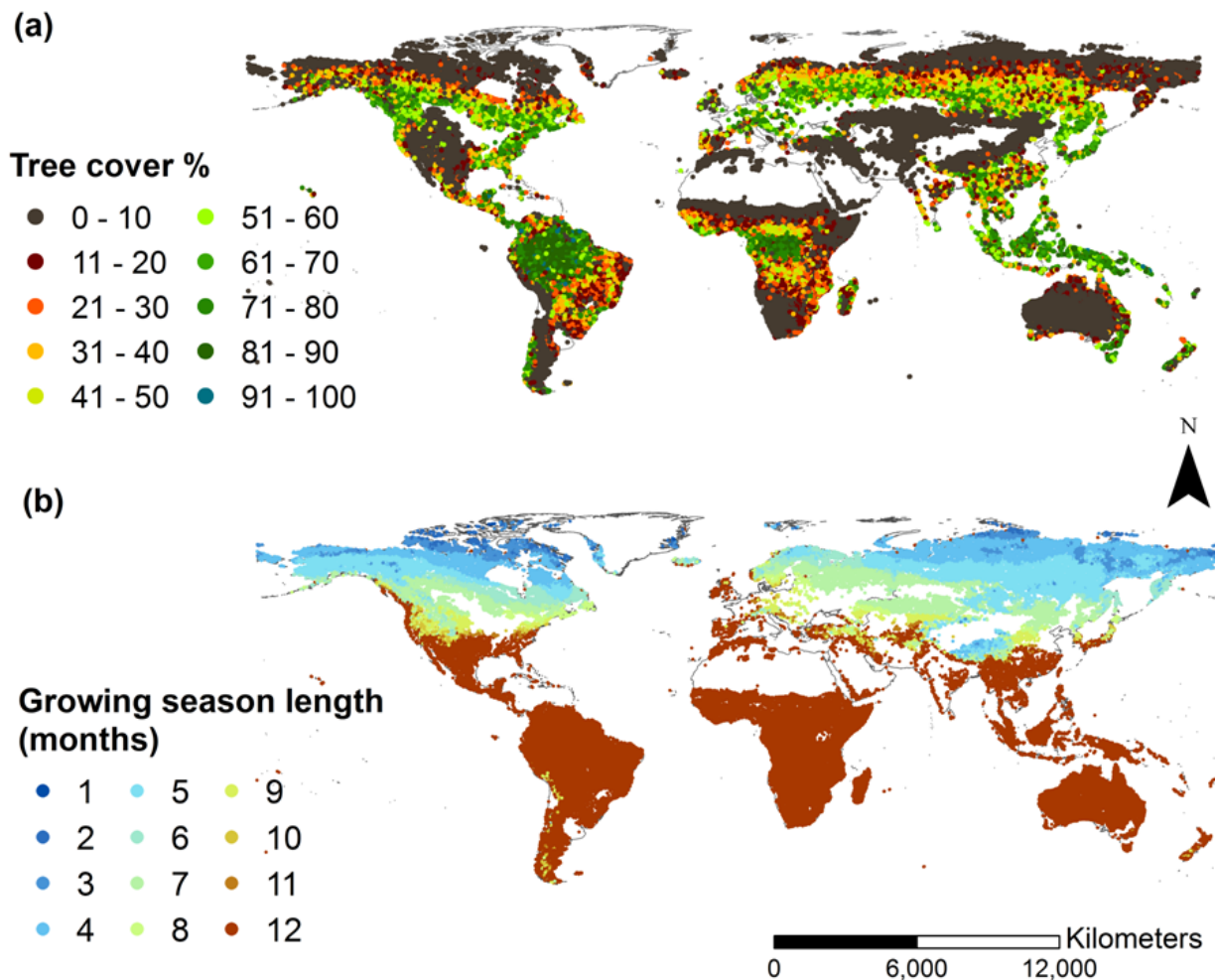


Figure 1. Global distribution of the 64350 sample points. Points are color coded in **(a)** by tree cover percent and in **(b)** by growing season length (GSL). We used the IGBP land cover classification scheme (Land Cover Type Yearly Climate Grid, MCD12C1) to select sites in the following classes: “Evergreen Needleleaf Forest”, “Evergreen Broadleaf Forest”, “Deciduous Needleleaf Forest”, “Deciduous Broadleaf Forest”, “Mixed Forest”, “Closed Shrublands”, “Open Shrublands”, “Woody Savannas”, “Savannas”, and “Grasslands”.

ries and excluding the unwanted land cover classes, we obtained a final sample of 64,350 locations randomly distributed in grassland, open-canopy and forest ecosystems from the equator to sub-polar regions (Fig. 1). In our heuristic approach, we analyzed the sample of tree cover across seasonal ranges and water balance regimes while looking also for fire-mediated effects. Our analysis included both multiple linear regression with model selection using the Bayesian information criterion (BIC; Burnham and Anderson 2002) and quantile regression. We performed our analyses in R (R Core Team 2016). We calculated the upper quantiles of tree cover relative to moisture, applying functions available in the R library “quantreg” (Koenker 2015). We applied a non-parametric piecewise quantile regression by

means of the ‘qss’ function with the default smoothing parameter ($\lambda = 1$) and specified the function as convex increasing. We considered the 95th quantile as a proxy for the limits to woody cover.

Results

The latitudinal changes in the global distribution of tree cover with respect to seasonality and fire are shown in Fig. 2. There is a pronounced association between seasonality and tree cover as well as between seasonality and fire frequency. The two seasonality factors, growing season length (GSL) and moist season length (MSL), exert their influence on tree cover in separate regions (left versus right panels of Fig. 2). The GSL association is stronger at higher latitudes ($> 50^\circ \text{N}$) as is seen

in the shoulder-shaped region (Fig. 2). The mid-latitudes (40–50° N/S) are a transition zone where variability in tree cover is associated with both GSL and MSL. At latitudes < 40°, moisture and its seasonal distribution MSL are the factors mostly associated with variability in both tree cover and fire. Though a geographic view is intuitive and initially useful to observe major trends, ecological patterns do not align simply with latitudes, and other factors such as topography and proximity to water bodies, might be confounding. For example, the Himalayan-Tibetan Plateau and southern Florida are both located around 32° N but are very different ecosystems with the first having growing seasons at least 6 months shorter than the second (Fig. 1b).

The outputs from the regression model of tree cover versus the climate and fire variables (Table 2) provide a robust basis to understand the relationships of tree cover with our predictors. Four classes determined by ranges of growing season length (GSL) have a significant role in describing the tree cover response:

1. Class 1 (GSL ≤ 5 months): maximum tree cover is directly limited by the length of the growing season (Fig. 3). Tree cover stays below 10% for GSL ≤ 3 months. Open-canopy systems occur for GSL values between 3 and 6 months. Forests with up to 80% tree cover only occur if the GSL is ≥ 5 months. Tree cover is positively correlated with the moisture index (MI) but negatively correlated with moist season length (MSL).

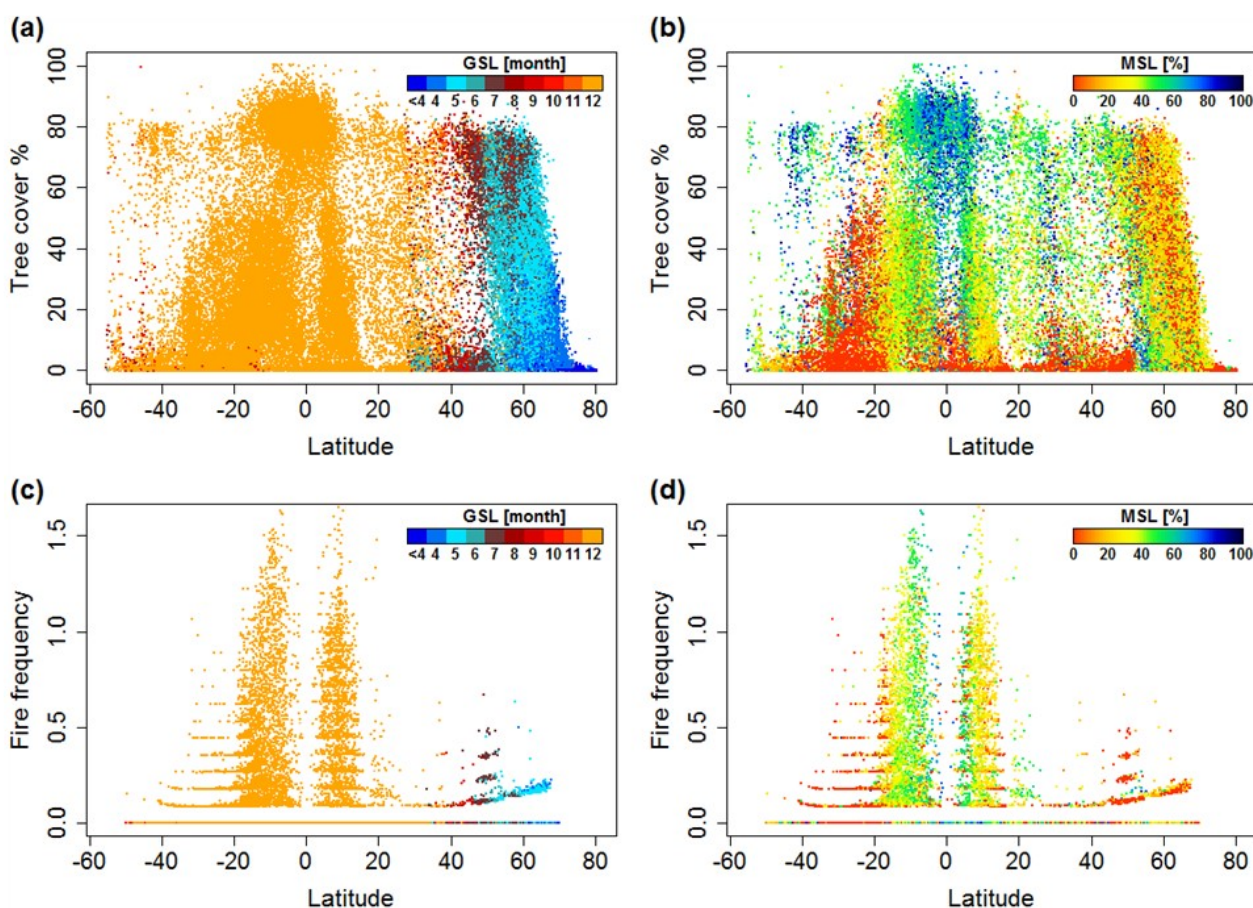


Figure 2. Latitudinal plots with seasonality effects. **(a)** Tree cover versus latitude with points color coded by growing season length (GSL, number of months with average monthly temperature $\geq 0^{\circ}\text{C}$) from blue shading (short growing seasons) to orange shading (longer growing seasons). **(b)** Tree cover versus latitude with points color coded by moist season length (MSL, percent of months with moisture index $\text{MI} \geq 1$ in the growing season) from red to blue shading for increasing MSL. **(c)** Fire frequency versus latitude with points color coded as in **(a)**. **(d)** Fire frequency versus latitude with points color coded as in **(b)**. Each point in these panels represents one or more of the 64350 sample points since points may overlay the same latitudinal coordinate in the graphs. Fire frequencies > 1 are due to pixels that burned more than once a year.

2. Class 2 (GSL = 6–7 months): tree cover has a significant positive relationship with both MSL and MI (Fig. 4a,b). Fire frequency has a significant negative effect on tree cover (Fig. 4c,d).
3. Class 3 ($8 \leq \text{GSL} \leq 11$ months): tree cover is positively associated with all three climate variables: GSL and both moisture variables (MI and MSL). The tree cover distribution in this region shows an abrupt transition between a low (< 10%) and a high range (> 50%) of values with a scarcity of values in the mid-range (10–50%, Fig. 5a). The position of the low-to-high tree cover transition shifts upward in the figure with longer GSL. High tree cover is conditional on either increasing MI or increasing MSL.
4. Class 4 (GSL = 12 months): tree cover is positively related with both climate variables (MI and MSL) and negatively related to fire frequency (Fig. 6). The tree cover distribution shows areas of grassland, savanna and forest, but it is not a continuous distribution. A gap in the range of 55 to 70% tree cover separates savanna from forest states (Fig. 6b).

In general, the BIC-selected model shows a positive association between GSL and tree cover. The MI and MSL variables present a "negative synergy" (negative interaction term) in all the GSL classes (although not significant for class 1). Independently, higher MI and MSL values can be positively associated with tree cover (classes 2, 3 and 4). However, high moisture balance for a long period of time counteracts or inhibits the positive effects of these two variables on tree cover.

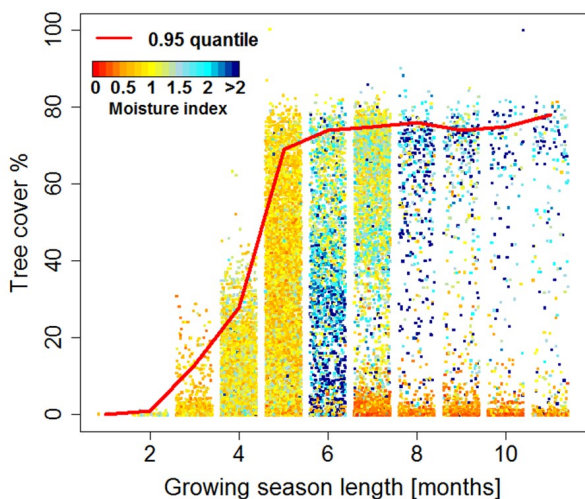


Table 2: Multiple linear regression model with the highest strength of evidence based on the Bayesian Information Criterion (BIC). The model is used for the analysis of tree cover % in relation to the continuous variables growing season length (GSL), moist season length (MSL), moisture index (MI), fire frequency (ff) and to one factor variable ‘class’ with four levels (class = 1 for $\text{GSL} \leq 5$ months; class=2 for $\text{GSL} = 6, 7$ months; class=3 for $8 \leq \text{GSL} \leq 11$ months; class = 4 for $\text{GSL} = 12$ months). All the continuous variables were standardized before modeling. The model’s residual standard error (0.6842) is equivalent to a tree cover of 19.6%.

Variable	Estimate	Std. Error	Pr(> t)
<i>Intercept</i>			
[class = 1]	1.812	0.039	< 0.001
[class = 2]	1.6	0.025	< 0.001
[class = 3]	0.206	0.044	< 0.001
[class = 4]	-0.811	0.054	< 0.001
<i>Slopes</i>			
GSL	1.299	0.023	< 0.001
[class = 1] * MI	0.203	0.036	< 0.001
[class = 1] * MSL	-0.205	0.016	< 0.001
[class = 1] * ff	0.02	0.043	0.646
[class = 1] * MI * MSL	-0.0215	0.019	0.262
[class = 2] * MI	0.181	0.041	< 0.001
[class = 2] * MSL	0.446	0.023	< 0.001
[class = 2] * ff	-0.285	0.056	< 0.001
[class = 2] * MI * MSL	-0.473	0.021	< 0.001
[class = 3] * MI	0.415	0.042	< 0.001
[class = 3] * MSL	0.444	0.025	< 0.001
[class = 3] * ff	-0.004	0.095	0.8045
[class = 3] * MI * MSL	-0.248	0.021	< 0.001
[class = 4] * MI	0.506	0.037	< 0.001
[class = 4] * MSL	0.602	0.017	< 0.001
[class = 4] * ff	-0.088	0.043	0.012
[class = 4] * MI * MSL	-0.168	0.02	< 0.001

Residual standard error: 0.6842 on 60714 degrees of freedom
 Multiple R-squared: 0.532, Adjusted R-squared: 0.5318
 F-statistic: 3450 on 20 and 60714 DF, p-value: < 2.2e-16

Figure 3. Seasonality effect on tree cover: tree cover vs. growing season length (GSL) for sites with $\text{GSL} \leq 11$ months. The 0.95 quantile regression line is superimposed on the scatterplot. Sample points are color coded by moisture to show the limitation of GSL on cover until $\text{GSL} \sim 5$ months.

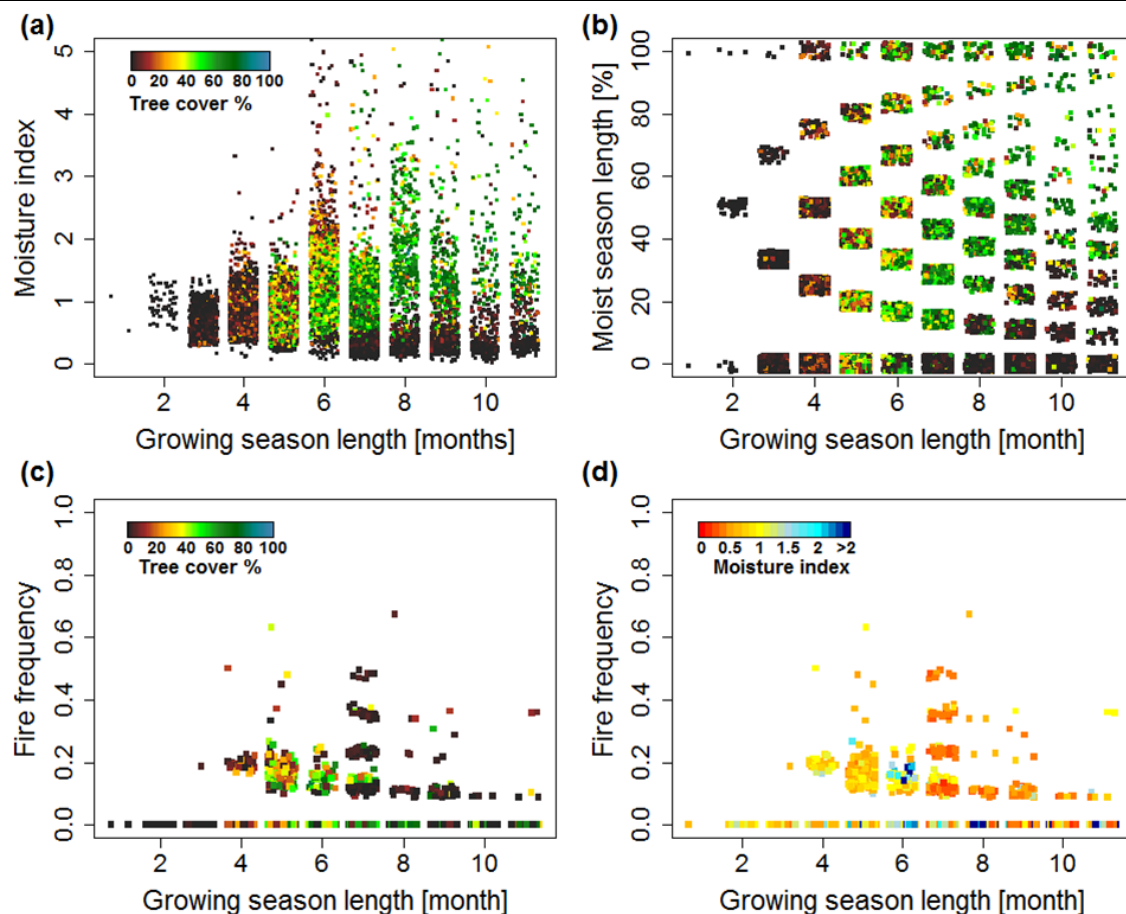


Figure 4. Tree cover, climate and fire frequency relationships for growing season lengths (GSL) of 0–11 months (subpolar and temperate regions). Moist season length (MSL) is the percent of months with moisture index $MI \geq 1$ in the growing season. Around $GSL = 5$, there is a transition from systems where tree cover is mostly limited by GSL to systems where tree cover depends on moisture-fire interactions. **(a)** Tree cover % (z value color-coded as shown in the color bar) in relation to GSL and moisture (MI). **(b)** Tree cover %, z value color-coded as in (a), in relation to GSL and MSL. The boxy structure is due to the discrete monthly values of GSL (MSL is a percent of the monthly values). **(c)** Tree cover %, z value color-coded as in (a), in relation to GSL and fire frequency. **(d)** MI (z value color-coded as shown in the color bar) in relation to GSL and fire frequency.

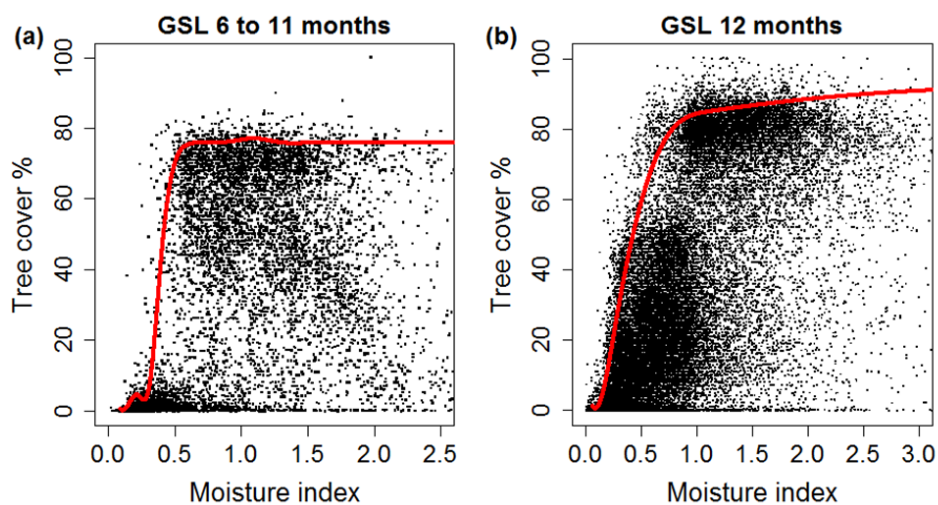


Figure 5. Tree cover vs. moisture index. **(a)** Data for growing season length (GSL) of 6 to 11 months (approximately temperate regions). **(b)** Data for GSL of 12 months (approximately tropical and sub-tropical regions). The 0.95 quantile regression line based on B-spline expansion (function “bs” in R package “splines”) is superimposed in red color in both plots. The clustering in the scatterplots illustrates possible alternative stable states: (a) grassland vs. savanna/woodland, and (b) savanna vs. forest.

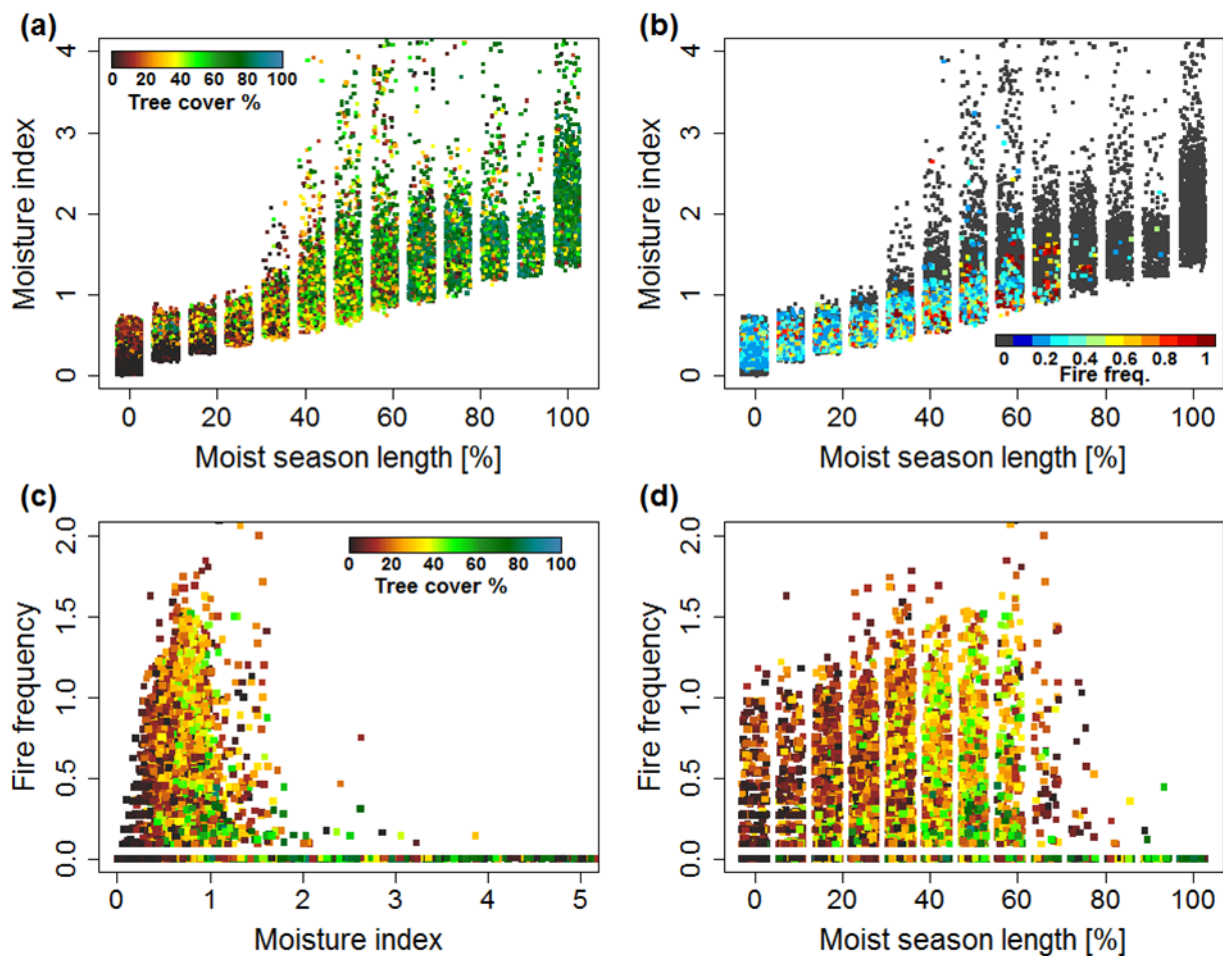


Figure 6. Tree cover, climate and fire frequency relationships for growing season length (GSL) of 12 months (tropical and sub-tropical regions). Moist season length (MSL) is the percent of months with moisture ≥ 1 in the growing season. The MSL controls fire frequency and savanna occurrence. **(a)** Tree cover % (z value color-coded as shown in the color bar) in relation to MSL and moisture index (MI). **(b)** Fire frequency (z value color-coded as shown in color bar) in relation to MSL and MI. **(c)** Tree cover % (z value color-coded as in (a)) in relation to MI and fire frequency. **(d)** Tree cover % (z value color-coded as in (a)) in relation to MSL and fire frequency.

The plots in Figs. 2, 4, and 6 show a pronounced association between seasonality and fire frequency. Generally, fire activity is at its highest in association with marked moisture seasonality: it requires a season of moisture surplus and a season of moisture deficit. There are optimal combinations of GSL, MSL and MI conditions that promote higher fire activity and two prominent fire peaks are visible in the data. One is characterized by GSL of 6–7 months (class 2), $MI \leq 0.5$ and $MSL \leq 20\%$ of the growing season (~ 1 month of water surplus in the growing season; Figs. 4c,d). This fire peak generally overlaps with the temperate grasslands of the northern hemisphere at latitudes of $\sim 50^\circ$ (tree cover $< 20\%$, Fig. 5a) with relative low moisture conditions and a distinct moist seasonality. In contrast, higher moisture conditions ($MI >$

0.5 , $MSL > 20\%$) are associated with a marked decrease in fire activity and an abrupt transition to savanna/woodland (tree cover up to 80%). The second fire peak is characterized by GSL of 12 months (class 4), $MI < 1$ and $MSL < 70\%$ (≤ 6 months of water surplus through the year; Figs. 6b-d). It occurs along the tropical zones in the grassland and savanna regions with a distinct moist season and low moisture conditions (Figs. 5b, 6). The opposite case of moist conditions ($MI > 1$, $MSL > 70\%$) is associated with decreased fire activity and forests.

There are some exceptions to the above behaviors: in class 4, some forests can be found for $MI < 1$ when fire frequencies $ff < 0.2$ (less than once every five years; Figs. 6a,b) and savannas can still be found for $MI > 1$ in combination with rela-

tively high fire frequency (savanna $ff = 0.046$ compared to forest $ff = 0.0005$ for $MI > 1.2$). These wet savannas are characterized by an average MSL = 63% (76% in forest), which keeps them inside the domain of high fire recurrence (Fig. 6d). Other external processes are likely responsible for the existence of these wet savannas including deforestation and/or catastrophic fires in very dry years.

Maximum tree cover increases with moisture across the globe both in tropical and non-tropical regions (99th quantile line in Fig. 7a). This generality would not have been apparent if precipitation was considered instead of moisture (Fig. 7b). In regions with $GSL = 12$ months, the data also support evidence for an important ecological link between MI and occurrence of savannas versus forests (class 4 in the model and black dots in Fig. 7). A value $MI \sim 1$ represents an average balance in monthly moisture. Below this threshold ($MI < 1$, negative moisture balance), moisture is the direct and limiting agent on the maximum tree cover. Above this threshold ($MI > 1$, positive moisture balance), moisture is no longer limiting and maximum tree cover reaches values $> 70\%$. Fig. 7a also shows that the response of tree cover to

moisture for $MI < 0.4$ is weaker in regions with $GSL < 12$ than in regions with $GSL = 12$ and that is due to the suppressing effect of fire (Table 2 fire effect for classes 3 and 4, and Figs. 4, 5a).

Discussion

Ecologists have long been interested in tree distributions along environmental gradients and in the interactions of environmental factors that limit tree establishment and growth. This study provides a coherent global view of the factors associated with tree cover distribution and supports four main findings.

1. Increasing tree cover correlates positively with increasing moisture index (MI) across all levels of GSL.
2. The GSL defines regions of tree cover where relationships among predictors vary in character and strength.
3. Peaks of fire frequency occur as a function of suitable climatic conditions. In general, they require negative average water balances and strong moisture seasonality.
4. In climate conditions conducive to frequent fires, tree cover may have values lower than the potential set by climate (without fire).

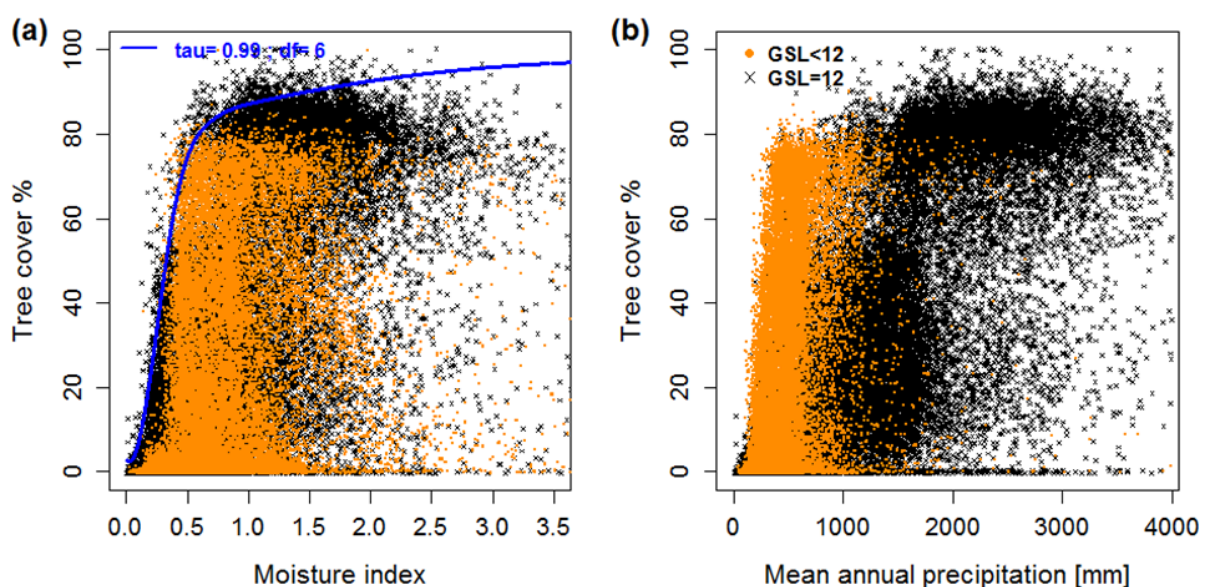


Figure 7. (a) Global tree cover versus moisture index (MI, average growing season moisture); **(b)** Global tree cover versus mean annual precipitation. Black points represent sites with growing season length (GSL) of 12 months (approximately tropical and subtropical regions with latitudes $\leq 40^\circ$ N and S) and orange points represent sites with $GSL < 12$ months. There is a more cohesive pattern of tree cover when MI is used instead of precipitation. (a) shows the non-parametric 0.99 quantile regression line.

This global view is more than an aggregation of the results found separately in tropical, temperate and boreal studies. The use of a global data set and integration of ecological relationships determined from environmental factors suggests a more general framework for broad-scale patterns of tree cover as compared to that obtainable from regional or continental studies. Regions of tree cover-climate-fire dynamics were differentiated by growing season length (GSL), a functional variable that quantifies temperature and energy limitations on vegetation growth. While sometimes aligning with latitudinal gradients, the GSL variable is not confounded by elevation and water body effects. In tropical studies, GSL could be disregarded because it has little variability (GSL = 12) but GSL is a critical factor for the more cohesive effort required in considering data that cross multiple climatic regions and/or include colder climates. Our study also provides insights on how fire itself is related to climate. By capturing the length of alternate periods of moist and dry conditions, the variables MI and MSL allow us to resolve relationships between climate and fire frequency. We find agreement with pyrogeographic studies on the role of seasonality (Dwyer et al. 2000, van der Werf et al. 2008, Krawchuk et al. 2009, Parisien and Moritz 2009, Bowman et al. 2014). Limitations in fire activity change as a function of seasonality: growing season length limits biomass (fire fuel) in cold regions, moist season length limits biomass in regions with intermediate growing seasons but it limits vegetation flammability in moist regions with long growing seasons. Ultimately, our study links both tree cover and fire distributions to climatic determinants. Our results can be compared with previous ecological and pyrogeographic broad-scale studies by approximating GSL regions with latitudinal ranges and by juxtaposing predictors with similar biophysical meaning. We discuss these considerations in more detail below.

Short growing seasons (GSL < 7 months)

Sustained freezing temperatures strongly hamper tree cover but as the growing season lengthens, conditions become more favorable to tree estab-

lishment and growth. The processes which underlie the positive correlation between maximum tree cover and GSL are the likely increased recruitment and survival of trees. The negative relationship between tree cover and moist season length (MSL; Table 2) suggests that relatively long periods of moisture surplus during the growing season are detrimental to trees. This is consistent with Scheffer et al. (2012) who indicated that short growing seasons and water-logging in permafrost soils restrict tree growth. Fires do occur in these regions but the short term of our burned area data was likely insufficient, given the low fire frequencies of these systems, to detect their effect on tree cover.

The step change between open to closed canopy systems (Fig. 3, tree cover up to 30% and up to 80% respectively) at growing season length of 4 months matches the tree line (or ecotone) observed in all the coldest parts of the world where old dwarf shrubs and immature trees give way to forests. Although Scheffer et al. (2012) characterized boreal systems as multimodal based on mean July temperature (their seasonal indicator of temperature constraints), we cannot infer multimodality from the stepwise relationship between tree cover and GSL in Fig. 3. The monthly scale of the GSL variable could be the reason for these abrupt changes. A finer temporal resolution (daily scale) of climate data is necessary to build a smoother gradient of GSL and then examine the relationship of tree cover and GSL for multimodality.

Intermediate growing season (GSL = 7–11 months)

Tree cover becomes more clearly dependent on the interplay of moisture and fires in these regions, which approximately overlap with the temperate regions. Our results are consistent with previous studies of vegetation patterns in the central grasslands of North America (Gleason 1913, Cowles 1928, Changnon et al. 2002, Anderson 2006, Danz et al. 2011). Short mixed grass prairie occurs with more severe droughts, much higher evapotranspiration and existence of major prairie fires (Changnon et al. 2002), which is consistent with our results for MI < 0.5. The range of growing

season moisture from 0.6 to 0.9 marks the transition between the short mixed grass prairie to the west US ($MI < 0.5$) and the tall grass prairie to the east, with tall grasses favored by the higher moisture ratios ($MI > 0.5$). To the north and the south, the tall grass prairie transitions into forest. Grasslands expand to the east even where the average climate could potentially support woodland/forests (Gleason 1913, Cowles 1928). Sauer (1950) identified the following conditions for the existence of tall grass prairies versus woodlands: (1) frequent droughts, (2) a dry season, (3) frequent fires, and (4) a relatively flat terrain. Ecologists recognized that interdependencies between fire and climate lead to difficulty in determining the degree to which climate acts as a surrogate for or acts jointly with fire as the ultimate boundary control. In summary, a complex interplay of seasonal duration and intensity of extremes in both temperature and moisture is required to understand the grassland-woodland transition. Future work can benefit from a larger set of explanatory variables than used here, including metrics of moisture levels, drought and frost frequency within and outside the growing season.

The analysis presented here does not include data on herbivory, soil or topography but we recognize that these factors also play an important role in shaping tree cover and fire patterns (Parisien and Moritz 2009) and should be considered in further analyses beyond those in this paper. Anderson (2006) and Briggs et al. (2005) found the interactions between fire and herbivores (including browsers such as deer and elk and grazers such as bison and cattle) relevant in determining the dominance of grasses or trees. Some studies pointed to topographical influences on fire spatial pattern and frequency and the potential limits of woodland (Geldenhuys 1994, Anderson 2006, Stambaugh and Guyette 2008). Flat or gently rolling landscapes can support more frequent fires necessary for grassland maintenance.

Long growing seasons (GSL = 12)

These regions mainly overlap with tropical and subtropical regions. The relationships between tree cover, moisture and fire found in our study

are similar to the ones found in previous studies (Dwyer et al. 2000, Sankaran et al. 2005, Bucini and Hanan 2007, van der Werf et al. 2008, Hirota et al. 2011, Staver et al. 2011; Fig. 6). Our main scientific contribution for this region is the identification of a general threshold of the moisture index $MI = 0.8$ that marks the release from moisture limitation and separates moisture-limited from disturbance-driven savannas. In precipitation units, this threshold varied from study to study over a range from 650 up to 1600 mm depending on the rainfall data and modeling approaches. This variation in results was not as problematic in our study since moisture better represents water availability and it is independent from absolute rainfall values because it is a ratio. In addition, our results incorporate the seasonal condition that maintains fires (and fire-driven savannas) in mesic regions ($MI > 0.8$): $MSL \leq 70\%$, i.e. at least a 4-month dry season. These seasonal bounds for fire can be related to the fire classes 4 and 5 in Dwyer et al. (2000). The fire-suppression threshold as defined by Hoffmann et al. (2012) can be set around $MI = 0.8$ and $MSL = 70\%$. Levels of $MI > 0.8$ and $MSL > 70\%$ make fires very unlikely and are associated with forests.

Alternative states

The two states of mesic savanna and forest and the two states of mesic grassland and woodland have been considered to represent alternative states maintained by the positive feedback between fire and vegetation (Laycock 1991, Beckage et al. 2009, Warman and Moles 2009, Hirota et al. 2011, Staver et al. 2011, Hoffmann et al. 2012, Ratajczak et al. 2014, Dantas et al. 2016). Although the examination of alternative states was not our objective, we observed tree cover patterns matching cases previously regarded as alternative stable states (Fig. 5). Hanan et al. (2013) warned that alternative state patterns in MODIS tree cover may be artifacts arising from the regression-tree model used to create the product. On the other hand, the partitioning approach of regression trees is apt to capture the abrupt transitions where alternative stable states occur. We advocate for broad-scale analyses using

a composite of independent approaches – mechanistic, experimental and correlative (examples in Bertram and Dewar 2013, De Michele and Accatino 2014, Ratajczak et al. 2014, Laris et al. 2016, Staal et al. 2016) – to determine the source of bimodal tree cover patterns and the degree to which moisture and seasonality, jointly with fire, set thresholds for the emergence of binary states.

Broader significance

Our results quantify important complex relationships that link tree cover and fire to climate. Knowledge of the climatic ranges that support specific ecosystems and fire regimes is especially important for managers and scientists concerned with the effects of climate change on ecosystems (Bowman et al. 2014, Moncrieff et al. 2016). Changes in extrinsic environmental conditions such as climate and fire cycles may remove or add barriers that limit establishment of trees and in particular of invasive tree species (Richardson and Bond 1991, Scholes and Archer 1997). Vegetation structure and total tree cover of a region may change as a consequence of climatic changes (Anadón et al. 2014, Rundel et al. 2014) leading to losses of species habitat, new species assemblages, changes in nutrient and water cycles and cascading implications for ecosystem functioning and biodiversity (Parr et al. 2012). In addition, established tree species, whether native or non-native, sometimes have the capacity to modify the environment in ways that favor their own recruitment (Scholes and Archer 1997) reinforcing the persistence of the new tree cover state. Knowing which factors and relationships are involved in the maintenance of an ecosystem is therefore of fundamental importance for management and conservation.

The results presented here are a snapshot of the nature of interactions of vegetation, fire and climate variables. While contributing to the understanding of current tree cover distributions across landscapes, our results can also increase the efficacy of projections of tree cover change driven by climate change. Modeled climatic projections (and paleoecological records) provide the set of data necessary to build long-term scenarios

of tree cover dynamics that can be used to inform scientists and land managers (Dawson et al. 2016). Given the projected temperature increases and changes in seasonal length in many areas of the globe and the sensitivity of tree cover to moisture and seasonality, we argue that climatic variables accounting for temperature and seasonality should be included as determinants in studies of tree cover under climate change trajectories. In particular, increases in temperature will affect plant available water via evapotranspiration so that tropical studies, which have traditionally based their results on precipitation alone, will also need to include temperature-based metrics in addressing questions related to climate change.

The data used in this study are averaged measures and do not consider individual droughts or extreme events that can be important to fully understand the observed tree cover fraction. By combining decades of data, our methods assumed that there is sufficient temporal stationarity in the interacting ecological and climate processes to take a mean-field approach in assessing tree cover distribution at broad spatial extent. We are aware that trends driven by climate change exist, and believe that temporally varying climate change trends can be considered in similar analyses of tree cover and will potentially lead to an improved understanding of the structure and distribution of open-canopy systems.

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