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Not only trees: Grasses determine African tropical biome distributions via water limitation and fire

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Abstract

Aim: Although much tropical ecology generally focuses on trees, grasses are fundamental for characterizing the extensive tropical grassy biomes (TGBs) and, together with the tree functional types, for determining the contrasting functional patterns of TGBs and tropical forests (TFs). To study the factors that determine African biome distribution and the transitions between them, we performed the first continental analysis to include grass and tree functional types.

Location: Sub-Saharan Africa.

Time period: 2000–2010.

Major taxa studied: Savanna and forest trees and C_4 grasses.

Methods: We combined remote-sensing data with a land cover map, using tree functional types to identify TGBs and TFs. We analysed the relationships of grass and tree cover with fire interval, rainfall annual average and seasonality.

Results: In TGBs experiencing $<$ 630 mm annual rainfall, grass growth was water limited. Grass cover and fire recurrence were strongly and directly related over the entire subcontinent. Some TGBs and TFs with annual rainfall $>$ 1,200 mm had the same rainfall seasonality but displayed strongly different fire regimes.

Main conclusions: Water limitation to grass growth was fundamental in the driest TGBs, acting alongside the well-known limitation to tree growth. Marked differences in fire regimes across all biomes indicated that fire was especially relevant for maintaining mesic and humid TGBs. At high rainfall, our results support the hypothesis of TGBs and TFs being alternative stable states maintained by a vegetation–fire feedback for similar climatic conditions.

KEYWORDS
African vegetation, alternative stable states, fire, mean annual rainfall, rainfall seasonality, savanna, grass cover, tree functional type, tropical forest, tropical grassy biomes

1 | INTRODUCTION

Tropical grassy biomes (TGBs) comprise grasslands and savannas and extend over *c.* 33.5% of terrestrial Africa (Parr, Lehmann, Bond, Hoffmann, & Andersen, 2014). They are characterized by a continuous C_4 grass layer, possibly accompanied by woody overstorey, which can reach up to 80% locally (Parr et al., 2014; Sankaran et al., 2005). Tropical grassy biomes thus comprise areas also referred to as deciduous and dry forests. Their structure and limits are determined by complex and dynamic interactions among biotic and environmental factors such as climate, soil, herbivory and fire, which operate at different spatio-temporal scales (Bond, 2008; Lehmann, Archibald, Hoffmann, & Bond, 2011; Scholes & Archer, 1997). At the wetter end of their distribution range, TGBs transition into tropical rain forests (TFs); a shaded environment with a closed tree layer.

The interplay between biotic and abiotic variables that drives the TGB dynamics and determines their environmental limits and transition to tropical forests is not fully understood and is even controversial in some aspects (e.g., Lehmann & Parr, 2016; Veenendaal et al., 2015).

The most important climatic factor determining the biome distributions is mean annual rainfall (MAR), followed by rainfall seasonality (Lehmann et al., 2011). At the driest end of the gradient, with low and highly seasonal rainfall, grass-dominated ecosystems predominate because trees are water limited (Higgins et al., 2012; Sankaran et al., 2005; Sarmiento, 1984) and suffer from grass competition, especially at their seedling stage (Baudena, D'Andrea, & Provenzale, 2010; D'Onofrio, Baudena, D'Andrea, Rietkerk, & Provenzale, 2015; February, Higgins, Bond, & Swemmer, 2013). The very seasonal rainfall affects the temporal distribution of soil water and probability of fire, thereby helping to maintain open canopies (Lehmann et al., 2011). In areas with high, year-round rainfall, tropical rain forests predominate (Walter, 1973), although there are no definite annual thresholds for precipitation that delimit the biome transitions.

Fire is also extremely important in TGBs (e.g., Bond, Woodward, & Midgley, 2005; Higgins et al., 2007; Scholes & Archer, 1997). As a result of their high productivity during the wet season, followed by rapid drying and high flammability in the dry season (Bond, 2008; Lehmann et al., 2011), C_4 grasses promote fires and maintain open canopies (Beckage, Gross, & Platt, 2011; Lehmann & Parr, 2016; Ratnam et al., 2011, and references therein), which in turn favours them, because they are shade intolerant. This positive feedback is reinforced by savanna trees also being adapted to fire (Bond, 2016; Hoffmann et al., 2012; Ratnam et al., 2011), thanks to a thick protective bark (Gignoux, Clobert, & Menaut, 1997; Hoffmann et al., 2009), and by a preference for open areas, because they too are generally shade intolerant (Bond, 2016; Ratnam et al., 2011). C_4 grasses have been present in Africa for 3–8 Myr, thus for this long time fire has been important in determining the dynamics of the TGBs (Edwards, Smith, & Thresholds, 2010; Lehmann & Parr, 2016). Tropical forests, on the contrary, are characterized mainly by shade-tolerant, fire-intolerant species (Ratnam et al., 2011 and references therein). Closed-canopy forests suppress fires because: (a) reduced light availability hinders C_4 grass growth (Hoffmann et al., 2009); (b) the presence of a humid understorey and lower temperatures limit flammability; and (c) reduced wind speeds limit fire spread (Cochrane, 2003).

Tropical forests and savannas can occur in areas with similar climatic conditions. This is usually interpreted as evidence that the two biomes are alternative stable states maintained by the positive feedback between fire and plant composition that is associated specifically with shade- and fire-related traits of trees and grasses (Dantas, Hirota, Oliveira, & Pausas, 2016; Hirota, Holmgren, Van Nes, & Scheffer, 2011; Staal, Dekker, Xu, & van Nes, 2016; Staal & Flores, 2015; Staver, Archibald, & Levin, 2011b; Yin, Dekker, van den Hurk, & Dijkstra, 2016). Alternative 'bottom-up' explanations (*sensu* Bond, 2008) are also possible, with soil and nutrient content explaining the transitions between TGBs and TFs (Lloyd et al., 2008; Veenendaal et al., 2015; but see also, e.g., Bond, 2010; Staal & Flores, 2015).

The different responses of C_4 grasses and trees, and of savanna and forest trees, to environmental conditions can thus mediate the transition between biomes (Lehmann et al., 2011; Ratnam et al., 2011). Despite their relevance for the structure of TGBs and TFs, grasses and tree functional types have been investigated simultaneously, mostly in small-scale ecological studies (e.g., Dantas, Batalha, & Pausas, 2013; February et al., 2013; Smit & Prins, 2015) or within models (e.g., D'Onofrio et al., 2015; Higgins et al., 2012; van Langevelde et al., 2003; Staver & Levin, 2012). They have not been included in the vast majority of the continental-scale studies, most of which have focused on woody variables, using remote sensing (Hirota et al., 2011; Staal et al., 2016; Staver et al., 2011b; Yin et al., 2016; but see Bertram & Dewar, 2013), or field sites (Dantas et al., 2016; Sankaran et al., 2005; Staal & Flores, 2015; Veenendaal et al., 2015).

Using a recent moderate resolution imaging spectroradiometer (MODIS) product and the European space agency (ESA) Global Land Cover map, we set out to study the factors that determine the distribution of African biomes and the transitions between them, with the aim of conducting the first continental vegetation analysis to include information from grass cover. Furthermore, by using tree functional types to identify savanna and forest trees (generally classifiable in Africa as deciduous and evergreen, respectively; see the Materials and Methods section for details; Bowman & Prior, 2005; Scholes & Archer, 1997; Shorrocks, 2007), we could also avoid the problems associated with identifying the bimodality in MODIS tree cover data recently pointed out by Gerard et al. (2017). We observed, for the first time, that water limitation at the driest end of the TGB distribution (for MAR $\leq$ 630 mm/year) affected not only trees but also grasses, and was the main factor determining the occurrence of dry TGBs. Mesic TGBs, however, were characterized by frequent fires associated with the presence of grass. Some humid TGBs occurred in similar climatic conditions (in terms of MAR and its seasonality) as TFs but had very different fire frequencies, thus supporting the hypothesis of alternative stable states maintained by vegetation–fire feedback.

2 | MATERIALS AND METHODS

2.1 | Satellite data

We analysed data for tree and herbaceous vegetation cover percentages, average fire interval, mean annual rainfall and seasonality, for sub-Saharan Africa from latitudes 35° S to 15° N at 0.5° resolution (*c.* 50 km). A sensitivity analysis performed with these satellite data with grain sizes ranging from 500 m to 100 km has shown that African relationships between climatic, vegetation and fire variables are insensitive to spatial resolution (Staver, Archibald, & Levin, 2011a).

We derived tree cover (*T*) and grass cover (*G*; hereafter also called woody and herbaceous cover, respectively), averaging in space and time the yearly percentage of tree and non-tree vegetation cover products of MODIS vegetation continuous fields (MOD44B VCF) version 051 for the period 2000–2010 (Townshend et al., 2011; Figure 1a,b). We used the ESA global land cover map (ESA CCI-LC, v 1.6.1; 5-year-averaged dataset centred in 2010) to remove pixels with more than one-third of the area affected by anthropogenic activities and covered by water (coastal and inland) and/or with more than one-half of the area occupied by shrubland (MOD44B underestimates tree cover in the presence of shrubs because it does not detect trees shorter than 5 m; Bucini & Hanan, 2007). Cultivations cover most of the area that we discarded in our study (see Supporting Information Appendix S1).

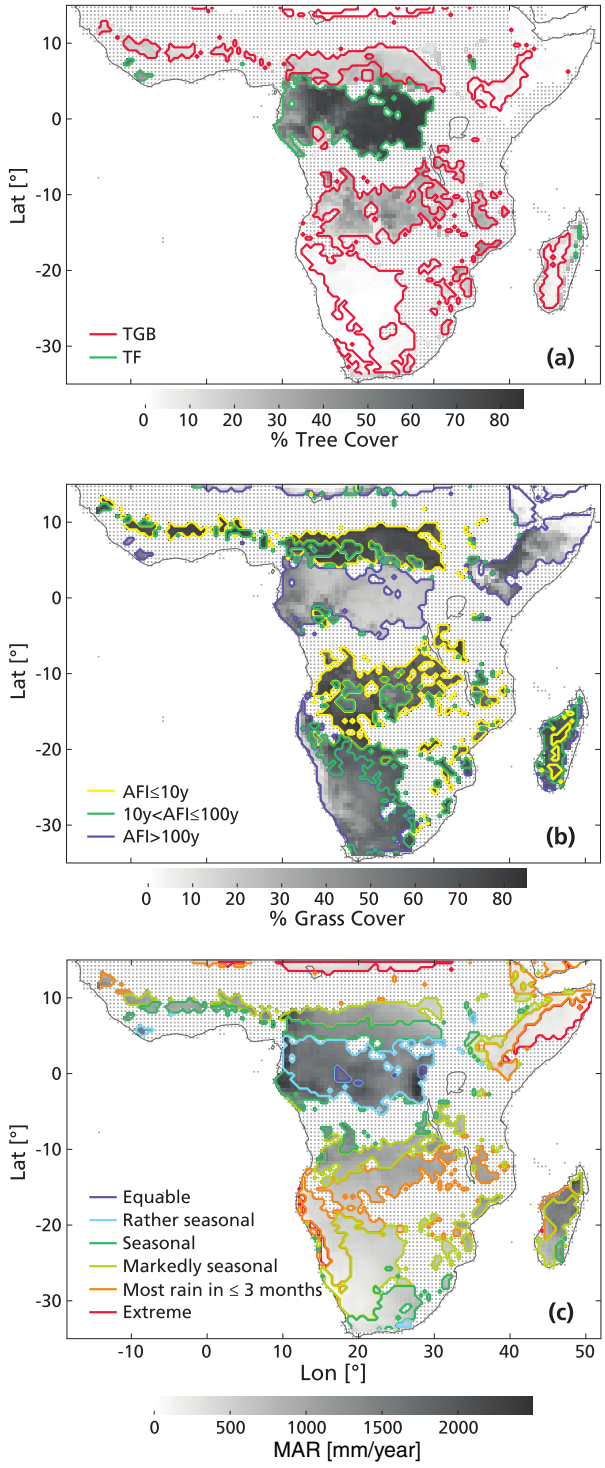

FIGURE 1 (a) Tree cover, (b) grass cover and (c) mean annual rainfall (MAR) for 0.5° cells across Africa (grey colour scale). In (a), red lines delimit TGBs (areas in which cells with ≥ 50% of their area is flagged on the ESA CCI-LC map as deciduous trees and grasslands), and green lines delimit TFs (areas in which cells with ≥ 50% of their area is flagged on the ESA CCI-LC map as evergreen and flooded trees). In (b), lines delimit areas with similar annual average fire intervals (AFI): yellow lines delimit AFI ≤ 10 years, green lines delimit AFI between 10 and 100 years, and violet lines delimit AFI > 100 years. In (c), lines delimit rainfall seasonality classes (Walsh & Lawler, 1981): equable with a definite wetter season [0.20 ≤ rainfall seasonality index (SI) ≤ 0.39; violet line]; rather seasonal with a short drier season (0.40 ≤ SI ≤ 0.59; light blue line); seasonal (0.60 ≤ SI ≤ 0.79; green line); markedly seasonal with a long drier season (0.80 ≤ SI ≤ 0.99; light green line); most rain in ≤ 3 months (1.00 ≤ SI ≤ 1.19; orange line); and extreme, almost all rain in 1–2 months (SI ≤ 1.20; red line). In each panel, dots represent pixels excluded from the analysis (see Materials and methods)

Using the same map, we classified pixels as TGB when they included ≥ 50% of the deciduous trees and grassland classes (ESA CCI-LC codes 60–62, 130) and as TF when they included ≥ 50% of evergreen and flooded tree classes (codes 50, 160, 170; Figure 1a). In Africa, unlike many Neotropical and especially Australian savannas, deciduous trees predominate in TGBs (Bowman & Prior, 2005; Scholes & Archer, 1997; Shorrocks, 2007; see also Supporting Information Table S4.1 for a compact summary of the literature), whereas evergreen trees predominate in TF (Bowman & Prior, 2005; Walter, 1973). Evergreen trees can also occur in African TGBs, but only locally (e.g., Scholes & Walker, 1993; Scholes et al., 2002), and would thus not be detected at the coarse grain of our analysis. Our distinction between TGB and TF based on land cover and tree functional types does not suffer from the drawbacks of previous analyses that separated them on the basis of tree cover (e.g., Hirota et al., 2011; Staver et al., 2011b), a method which could create problems owing to the uncertainties in the MODIS cover data (as recently pointed out by Gerard et al., 2017). We also used the same procedure to identify other land cover types using different ESA CCI-LC codes (see Supporting Information Appendix S1).

We used monthly rainfall measurements from the tropical rainfall measuring mission (TRMM 3B42) precipitation product to derive MAR and a rainfall seasonality index (SI; Walsh & Lawler, 1981), which describes the variability of monthly rainfall within a certain year. The SI is defined as the sum of the absolute deviations of monthly rainfall from the average monthly rainfall of a certain year, divided by the annual rainfall. The MAR and SI were averaged in time over the period 2000–2010 (Figure 1c).

Following Johnson and Wagner (1985), we defined the annual average fire interval (AFI) as the expected return time of fire at any point in the 0.5° cell, calculated as the inverse of the annual average burnt area fraction (BA) in each 0.5° cell (AFI = 1/BA; Figure 1b). The BA was obtained from the monthly MCD45A1 (Collection 5.1) burnt area satellite product in the period April 2000–December 2010 (Roy, Boschetti, Justice, & Ju, 2008; Roy, Jin, Lewis, & Justice, 2005; Roy, Lewis, & Justice, 2002), following Lehsten, Harmand, Palumbo, and Arneth (2010). Given that AFI spans different orders of magnitude, in the analysis we used $\log_{10}$(AFI).

See Supporting Information Appendix S1 for further details.

2.2 | Identifying ranges of mean annual rainfall with different tree–grass dominance

We chose MAR as first independent variable because it has been repeatedly identified as the main explanatory variable for African woody vegetation (Lehmann et al., 2011; Sankaran et al., 2005). We

analysed the cover of trees, grasses, total vegetation [$T + G$; which is connected to the bare soil fraction: 100% − ($T + G$)]. We also analysed the relative dominance of trees and grasses, which we defined by subtracting grass cover from tree cover ($T - G$). To identify the transition points where vegetation showed clearly different dependence on MAR, we used the marked changes in slopes and spread of the four vegetation variables along the MAR axis, because we considered these changes to indicate variations in the underlying ecosystem dynamics. We especially focused on $T - G$, because it expressed the changes in dominance of the two vegetation types along the gradient.

2.3 | Multivariable statistical models

We used generalized linear models (GLMs; McCullagh & Nelder, 1989) to analyse the dependences of the four vegetation cover variables (T, G, $T + G$ and $T - G$) with respect to three predictors: MAR, SI and $\log_{10}$(AFI). We performed the analysis within the different MAR intervals (identified as explained in the previous subsection). To select the models, we used Akaike's information criterion (AIC; Akaike, 1974), and we evaluated the goodness-of-fit with the explained variance, R^2. See Supporting Information Appendix S1 for further details.

Finally, we applied the two-sided Wilcoxon rank sum test to check whether pairs of variables had significantly different statistical distributions at the $p = .05$ level.

3 | RESULTS

3.1 | Overall dependence of tree and grass cover on rainfall and fire

Herbaceous and total vegetation cover were found to increase steeply and with narrow spread as a function of MAR at the driest end of the gradient (Figure 2a,d), whereas tree cover increased more slowly, remaining lower than grass cover (Figure 2b). Consequently, $T - G$ was mostly negative and decreasing, with narrow spread (Figure 2c). At intermediate MAR values, G reached its maximal value, displaying a large spread of values, whereas T continued to increase, although remaining smaller than G (Figure 2a,b). Total vegetation cover

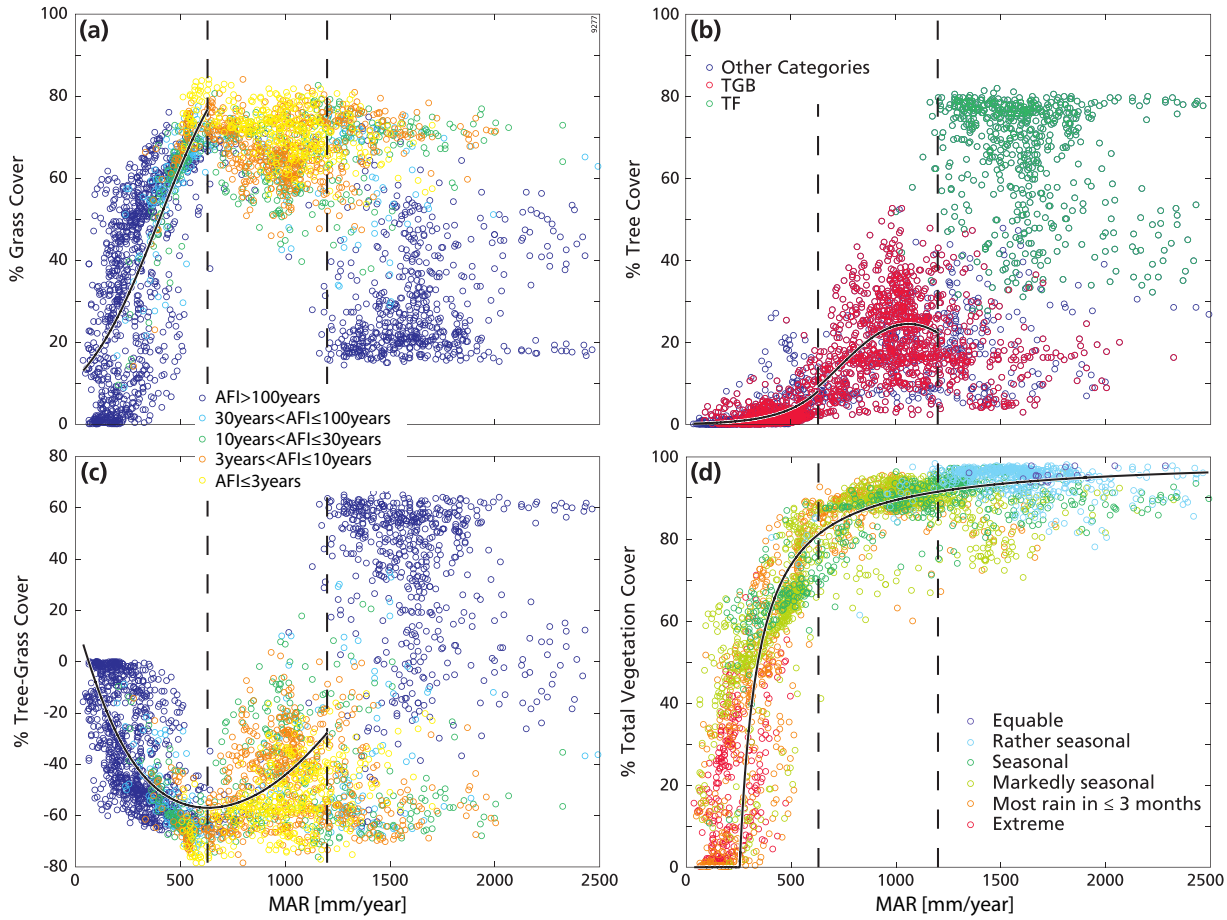

FIGURE 2 Percentage cover of (a) grasses, (b) trees, (c) tree to grass dominance ($T - G$) and (d) total vegetation as a function of mean annual rainfall (MAR). Dashed vertical lines separate the low, intermediate and high MAR ranges (R1, R2 and R3, respectively), in which we analysed the generalized linear models (GLMs) (see Results). Colours indicate additional information: (a) and (c), average fire intervals [AFI, see key in panel (c)]; (b) pixels with predominance of tropical grassy biomes (TGBs; red) or tropical forests (TFs; green); and (d) rainfall seasonality classes corresponding to different rainfall seasonality index (SI) ranges (see panel key and the caption of Figure 1). Continuous black lines represent: (a) and (b), results of best GLM fits in R1 (see Table 1); (c) GLM fit (shown up to 1,200 mm/year), whose minimum marks the threshold between R1 and R2; and (d) the Michaelis–Menten curve fitted to the data

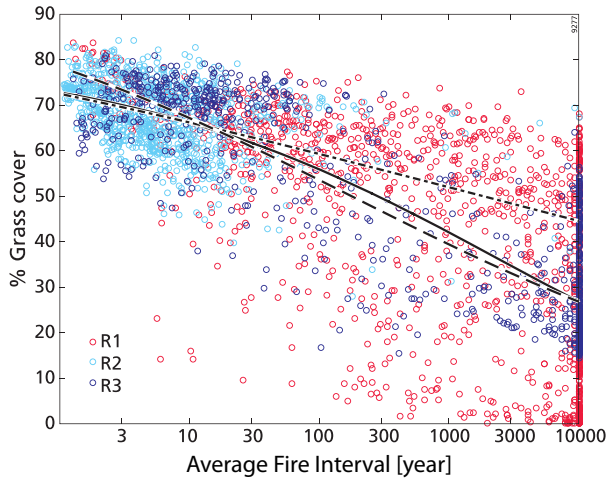

FIGURE 3 Grass cover as a function of average fire intervals (on a logarithmic scale). Red circles = pixels in the low mean annual rainfall (MAR) range (R1); light blue circles = pixels in the intermediate MAR range (R2); blue circles = pixels in the high MAR range (R3). The best GLM fit of grass cover with $\log_{10}$(AFI) is shown by **a** continuous line for the whole dataset, by a dot-dashed line for R2 and by a dashed line for R3

continued to increase with a very narrow spread, but less steeply than at lower MAR. The value of $T - G$ reached a minimum at a MAR of *c*. 630 mm/year and then started to increase with MAR, with very scattered values (Figure 2c). We thus identified that dependence on MAR, especially of G and $T - G$, changed between low and intermediate MAR ranges (which we henceforth refer to as R1 and R2), and we used the minimum in relative dominance to determine the transition point between them.

At even higher MAR, another transition occurred: forests appeared, as the maximal possible tree cover was reached in some of the pixels (Figure 2b). Total vegetation cover plateaued (Figure 2d), and most of the pixels had more tree cover than grass cover (thus $T - G > 0$), although in many pixels grasses still dominated (Figure 2c). We identified the transition at a MAR of 1,200 mm/year, because that was the value at which the 90th quantile of $T - G$ became positive (see Supporting Information Appendix S2 for details about the determination of the MAR ranges). This value is close to the threshold of 1,000 mm/year established by analysing woody cover only, from the same satellite product (Staver et al., 2011b).

Although tree cover strongly depended on MAR but also showed a large spread (see Figure 2b and Hirota et al., 2011; Staver et al., 2011b), total vegetation ($T + G$) varied with a very narrow spread for increasing MAR (Figure 2d). The $T + G$ could easily be captured with a simple implicit-space logistic model for vegetation cover (Levins, 1969), in which the sole assumption is that the colonization rate is linearly dependent on mean annual precipitation. The stable solution of the model is a Michaelis–Menten curve: $b = 1 - [87.5\text{mm/year}/(P - 166.5\text{ mm/year})]$ if $P > 254$ mm/year and $b = 0$ otherwise, where $b = (T + G)/100$ and $P = \text{MAR}$. The specific parameter values were obtained with a linear regression with a high goodness-of-fit ($R^2 = .78$); see Supporting Information Appendix S2 for further details.

Herbaceous cover and $\log_{10}$(AFI) were significantly correlated ($R^2 = .62$; Figure 3). Fires with an average interval of < 10 years occurred only if grass cover was > 45–50%. Fires were most frequent at intermediate MAR (Supporting Information Figure S3.1), where grass was more common. In contrast, T was weakly related to $\log_{10}$(AFI) (Supporting Information Figure S3.2a), with low explained variance ($R^2 = .13$).

3.2 | R1: Low mean annual rainfall (MAR ≤ 630 mm/year)

The R1 range was mainly characterized by long dry seasons and rare fires (Figure 4). Tropical grassy biomes represented 54% of the pixels (mainly grasslands), with the remainder mostly being sparse vegetation or bare soil (see Supporting Information Table S4.2). Mean annual rainfall was the best predictor for grass cover; it increased monotonically with annual rainfall ($R^2 = .55$). Tree cover also increased with MAR, its best predictor, but with a lower explanatory power ($R^2 = .26$; Figure

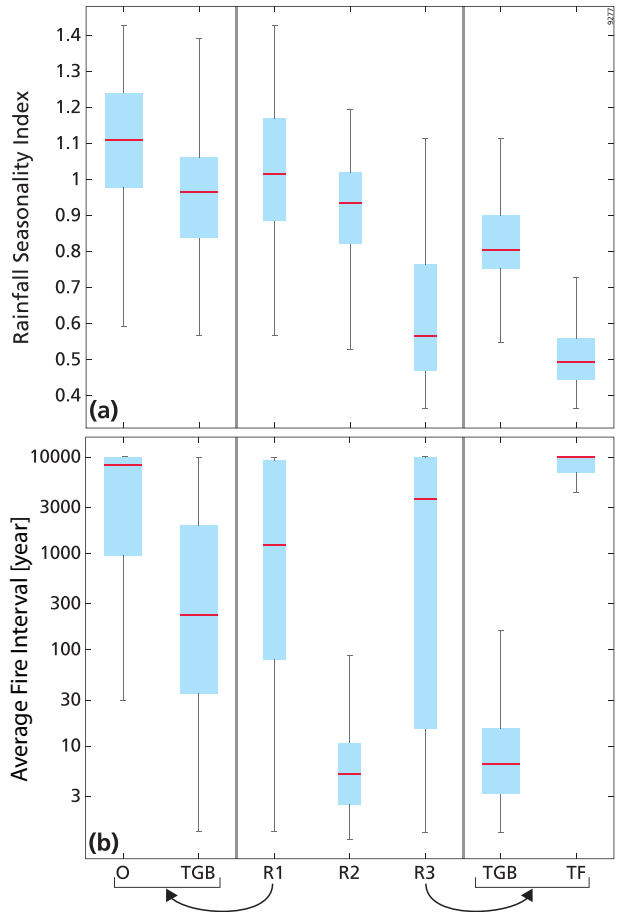

FIGURE 4 Box plots of (a) rainfall seasonality index and (b) average fire intervals [on a logarithmic scale; $\log_{10}$(AFI)]. The low, intermediate and high mean annual rainfall (MAR) ranges (R1–R3) are shown and, on the left of each panel, tropical grassy biomes (TGB) and other categories (O) in R1 (see Supporting Information Table S4.2), and on the right, TGB and tropical forests (TF) in R3. Outliers are not shown. The distribution of rainfall seasonality differed significantly between R1 and R2, whereas the distribution of $\log_{10}$(AFI) in R3 and R1 was indistinguishable

TABLE 1 Results of the generalized linear model analyses in the three mean annual rainfall ranges: low MAR (R1; MAR $\leq$ 630 mm/year), intermediate MAR (R2; 630 mm/year <MAR < 1,200 mm/year) and high MAR (R3; MAR $\geq$ 1,200 mm/year)

MAR range	Vegetation cover (dependent variable) ($y \times 100$)	Abiotic variables (covariates) (x)	Selected model	R^2
R1: Low MAR	$T + G$	MAR	$\text{logit}(y) = -2.17 + 0.0057x$	0.57
	$(T - G)'$	MAR	$\text{logit}(y) = -0.015 - 0.0026x$	0.52
	G	MAR	$\text{logit}(y) = -2.08 + 0.0052x$	0.55
	T	MAR	$\text{logit}(y) = -6.34 + 0.0062x$	0.26
R2: Intermediate MAR	$T + G$	MAR	$\text{logit}(y) = 0.64 + 0.0015x$	0.17
	$(T - G)'$	$\log_{10}$(AFI)	$\text{logit}(y) = -1.21 + 0.24x$	0.10
	G	$\log_{10}$(AFI)	$\text{logit}(y) = 0.97 - 0.30x$	0.23
	T	MAR	$\text{logit}(y) = -8.20 + 0.013x - 6.29 \times 10^{-6}x^2$	0.14
R3: High MAR	$T + G$	SI	$\text{logit}(y) = 4.20 - 2.65x$	0.48
	$(T - G)'$	$\log_{10}$(AFI)	$\text{logit}(y) = -1.61 + 0.62x$	0.74
	G	$\log_{10}$(AFI)	$\text{logit}(y) = 1.29 - 0.57x$	0.76
	T	$\log_{10}$(AFI)	$\text{logit}(y) = -1.99 + 0.69x$	0.71

Note. The dependent variables are as follows: total vegetation ($T + G$), tree–grass relative dominance, rescaled to the range [0:100] [$(T - G)'$], grass cover (G) and tree cover (T). The covariates are as follows: mean annual rainfall (MAR), rainfall seasonality index (SI) and logarithmic average fire interval [$\log_{10}$(AFI)]. Only selected models [i.e. with smaller Akaike information criterion (AIC); see Supporting Information Table S4.4] are reported. The explained variance (R^2) is reported for each case. See Materials and Methods and Supporting Information Appendix S1 for a detailed description of the statistical models and selection procedures. In the models, constant terms are dimensionless, and coefficients of covariate terms with dimension [x^z] ($z = 1$; 3) have dimension [x^{-z}].

2b, Table 1). Trees were also negatively correlated with seasonal variability in precipitation ($R^2 = .19$), and grasses and trees were positively correlated with fire frequency ($R^2 = .37$ and .24, respectively); see Supporting Information Table S4.4. The positive correlation between trees and fire frequency can be understood by considering that in this range both trees and fuel availability and continuity (linked to grasses) increased with MAR (Table 1).

With respect to the other biomes in R1, TGBs experienced more annual rainfall and less seasonal regimes. These TGBs had more grass cover (and slightly more tree cover), with more frequent fires (although still fairly rare; Figure 4; Supporting Information Figure S3.3).

3.3 | R2: Intermediate mean annual rainfall (630 mm/year < MAR < 1,200 mm/year)

In this range, most pixels were TGBs (86%), with markedly seasonal, although not extreme, rainfall and frequent fires (Figure 4). The selected GLMs included only one explanatory variable (Table 1); grasses decreased with $\log_{10}$(AFI) ($R^2 = .23$; Figure 3), whereas trees increased with MAR and stabilized at *c*. 20% cover at the end of the range, but with largely scattered values ($R^2 = .14$; Figure 2b). In general, in R2 the best GLMs explained a smaller fraction of variance of the vegetation variables than in R1 and R3.

3.4 | R3: High mean annual rainfall (MAR $\geq$ 1,200 mm/year)

The wettest areas (R3) had mostly mild rainfall seasonality and rare fires (see Figure 4). Total vegetation cover decreased with increasing rainfall seasonality (Supporting Information Figure S3.2b; Table 1). The other variables were strongly related to fire interval; G decreased with $\log_{10}$(AFI), and T and $T - G$ increased with $\log_{10}$(AFI) (Figure 3, Table 1; Supporting Information Figure S3.2a). Additionally, SI explained a large fraction of variance of these variables, which is not surprising given that SI and $\log_{10}$(AFI) were highly correlated (Supporting Information Table S4.3). In this range, MAR explained the lowest variance of G and T and was not significantly correlated with total vegetation (Figure 2).

In R3, 61% of the pixels were TFs, with a high tree cover on average (66%). Tropical grassy biomes occupied 23% of the pixels, with $T = 17\%$ on average and $G = 70\%$ on average (see Figure 2a,b; Supporting Information Figure S3.3). Forests had a rather seasonal rainfall regime (*sensu* Walsh & Lawler, 1981), with short dry seasons and essentially no fires. Conversely, TGBs had a markedly seasonal rainfall regime, with long dry seasons and frequent fires (Figure 4). The maximal observed tree cover in TGBs (Figure 2b) corresponded to the limit in tree cover, ranging between *c*. 40% (Archibald, Roy, van Wilgen, & Scholes, 2009; Staver et al., 2011b) and 60% (Roy et al., 2008), above which fire has been identified as almost absent.

Most importantly, in 20% of the R3 pixels, the two biomes had overlapping values of seasonality (Figure 4a), showing that both biomes could be observed in the same climatic regime, although displaying statistically distinct fire frequency distributions and plant covers (Supporting Information Figure S3.4). This bimodality occurs in the range SI = 0.55–0.73, where 0.55 is the lower adjacent value of the SI distributions for TGB, and 0.73 is the upper adjacent value of the SI distributions for TF (McGill, Tukey, & Larsen, 1978; see Figure 4a).

Performing the GLM analysis over the two R3 biomes separately, we found that in R3 forests, trees and grasses were significantly correlated with seasonality; trees decreased with SI ($R^2 = .28$; see Supporting Information Figure S3.5), and grasses increased ($R^2 = .25$). In TGBs, however, neither T nor G was found to be significantly correlated with

the explanatory variables. R2 (where TGBs are predominant) and TGB pixels in R3 had very similar distributions of fire intervals, grass cover, tree cover and highly overlapping rainfall seasonalities (although significantly different; Figure 4; Supporting Information Figure S3.3).

4 | DISCUSSION

Across sub-Saharan Africa, we observed marked changes in tree and grass cover and in their relative dominance at different MAR; the changes were generally also associated with different rainfall seasonalities (Figure 4), indicating that the biome succession generally followed clear environmental limits at a broad scale, with transitions that could be marked by clear, at times discontinuous, changes. However, we observed clear differences in fire frequencies across all biomes along the MAR gradient, and also between dry and meso-humid TGBs, and between humid TGBs and forests, indicating that given its feedback with plant type and composition, fire was fundamental in maintaining mesic and humid TGBs. Specifically, we identified three regimes of low, intermediate and high mean annual rainfall, where biome emergence was controlled by different water–fire-driven dynamics (as we summarize and discuss below), and in some humid areas we observed bistability of TGBs and TFs for similar climatic conditions (Figure 5). Despite these different mechanisms and relationships determining the emergence of the various biomes along the MAR gradient, we found that over the entire subcontinent, grass and fire recurrence were strongly related, with low fire frequency corresponding to low grass cover (Figure 3), and that overall the total vegetation cover was controlled mainly and strongly by mean annual rainfall (Figure 2d).

At low precipitation (< 630 mm/year), grasses were dominant though water limited, and fires were rare (Table 1). Within this range, more availability of water, owing to higher MAR and lower seasonality, promoted large increases in grass (similar to what was observed for the Kalahari by Scholes et al., 2002) and, to a much smaller extent, in tree cover. We thus showed here, for the first time at a broad scale, how water limitation acted strongly on the herbaceous component, not only on the woody component (Figure 2). In conditions of low and seasonal precipitation, grasses can prevail over trees, for different reasons (Sankaran, Ratnam, & Hanan, 2004), including higher photosynthetic efficiency in water use (Lloyd et al., 2008), lower costs for plant structure and maintenance (Orians & Solbrig, 1977), better adaptation to (clay) soils (Axelsson & Hanan, 2017; Fensham, Butler, & Foley, 2015; Sankaran et al., 2005), and overlapping rooting depths of grasses and trees (Holdo & Brocato, 2015; Kulmatiski & Beard, 2013) that allow grasses to suppress growth and establishment of tree seedlings (Baudena et al., 2010; D'Onofrio et al., 2015; February et al., 2013). In addition, in dry areas herbivores have a larger impact than fires, although the effects on vegetation structure differ, depending on the type of herbivory (Archibald & Hempson, 2016).

The total dominance of TGBs at intermediate rainfall values (630–1,200 mm/year; R2) was essentially driven by the balance of the different responses of grasses and trees to fire and precipitation. Water availability was limiting to trees because, at the spatial grain of our data, closed canopy was not observed at these precipitation values, and tree dominance increased with MAR within the range (Figure 2, Table 1), in a similar manner to what was reported by Hirota et al. (2011) and Staver et al. (2011b). The highly seasonal regimes in R2 increase the probability of droughts, which negatively affect both juvenile and adult trees by increasing the probability of mortality and reducing their growth rate (Lehmann et al., 2011). In the present study, one key finding was that at intermediate rainfall, grasses were no longer water limited. A second key finding was that overall grass cover increased with fire recurrence, thus providing evidence, for the first time at a continental scale, in favour of the grass–fire feedback hypothesis (Bond, 2008; Dantas et al., 2013; van Langevelde et al., 2003). The marked, albeit not extreme, rainfall seasonality in R2 was also likely to favour fire occurrence by enhancing grass productivity in the wet season and the availability of fuel in the dry season (Lehmann et al., 2011). The relevance of the nonlinear dynamics of a system driven by fine-scale feedbacks between vegetation composition and fires (Pausas & Dantas, 2017) might also explain why only minor parts of the variance of the vegetation variables were explained in R2 (Table 1). Other factors that we did not consider in this research might be responsible for the unexplained variance. Herbivory plays a similar role to fire in shaping the vegetation states and transitions, especially at local scales, although with less effect than fire in terms of consumed biomass (Archibald & Hempson, 2016; Dantas et al., 2016; Hempson, Archibald, & Bond, 2015). Additional variability could be attributable to soil texture influencing the water balance (Staver, Botha, & Hedin, 2017), rainfall partitioning within a season (D'Onofrio et al., 2015; Good & Caylor, 2011; Xu et al., 2015), or human activities, including pastoralism

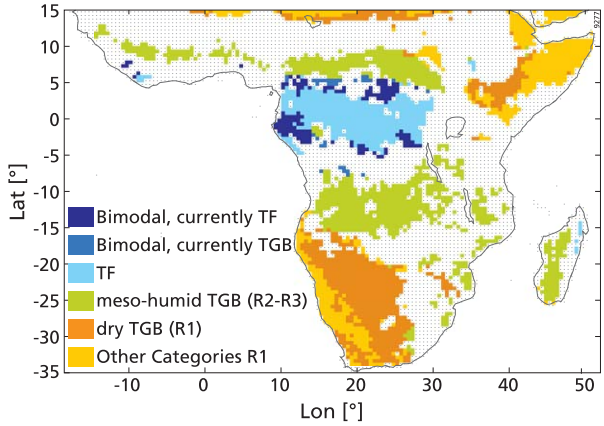

FIGURE 5 Distribution of vegetation states across sub-Saharan Africa. Tropical grassy biomes (TGBs) occurring in dry (R1) or in meso-humid (R2–R3) areas; tropical forests (TFs); other dry biomes (other categories; see also Supporting Information Table S4.2). Some TGBs and TFs were found for similar climatic conditions, as determined by overlapping rainfall seasonality in R3. Biomes are classified based on land cover information from the ESA CCI-LC map, on mean annual rainfall ranges and on bimodality information from our analysis. Dots represents pixels excluded from the analysis (see Materials and Methods) or pixels that were not represented here because they were parts of R2 or R3 but not classified as TGB or TF (< 14% of the pixels analysed)

(Aleman, Blarquez, Gourlet-Fleury, Bremond, & Favier, 2017), which might still be having an impact even though we excluded areas subjected to strong human influence.

Other fine-scale factors and processes not represented at the coarse-grained scale of our analysis (0.5°) include, for example, the occurrence of evergreen trees locally in TGBs (e.g., Scholes & Walker, 1993; Scholes et al., 2002), environmental and demographic stochasticity, and self-organization (e.g., Baudena & Rietkerk, 2013; Staver, 2017).

At high precipitation (MAR > 1,200 mm/year), both savanna and forest states were observed, with very distinct fire frequency distributions (Figure 4). Most of the TGBs and TFs corresponded to distinct rainfall seasonal patterns, with forests growing in areas with the least seasonal regimes, thus revealing that seasonality plays a greater role in savanna–forest transitions than previously reported (Hirota et al., 2011; Staver et al., 2011b). In fact, seasonality and fire return time were highly correlated in this MAR range (Supporting Information Table S4.3), indicating that the biome distributions are possibly also mediated by the connection between seasonality and fire occurrence. The different seasonalities of TGB and TF in humid areas at the continental scale might also be connected to land–atmosphere coupling (e.g., Baudena, D'Andrea, & Provenzale, 2008; Rietkerk et al., 2011; Van Nes, Hirota, Holmgren, & Scheffer, 2014), which is especially strong in tropical Africa (Green et al., 2017; Koster et al., 2004). Savanna and forest biomes with equal annual rainfall have different evapotranspiration and radiative fluxes, which can also affect rainfall seasonality by determining large-scale atmospheric circulation (Yin et al., 2016). Projected changes in seasonal distribution of precipitation, which may occur locally in the tropics (Arnell & Liu, 2001), would trigger transitions between TGB and TF.

Remarkably, however, although 20% of the humid TGBs and forests shared similar climatic constraints, including rainfall seasonality, they maintained different fire frequencies (Supporting Information Figure S3.4). This finding has not been influenced by the uncertainties that seem to have affected previous studies reporting analogous results from remote-sensing analyses, which identified the two biomes by their different typical tree cover values (Hirota et al., 2011; Staver et al., 2011b). That approach has recently been questioned because the algorithm that produces the MODIS cover values includes consistent patterns of under- and overestimation (see also Gerard et al., 2017; Hanan, Tredennick, Prihodko, Bucini, & Dohn, 2014; Staver & Hansen, 2015). Such data uncertainty was much less relevant in our analysis, as we identified TGBs and forests by using different tree functional types, based on their phenology. This finding thus reinforces the view that savanna and forest may be alternative stable states maintained by fires (as proposed by e.g. Dantas et al., 2016; Hirota et al., 2011; Staal & Flores, 2015; Staver et al., 2011b). Thanks to the availability of sufficient water, shade-tolerant forest trees can close their canopies, but the positive vegetation–fire feedback can maintain savannas as an alternative stable state (van Langevelde et al., 2003). A decrease in fire frequency (e.g., as a consequence of management strategies, see Andela et al., 2017), could thus lead to savanna transitioning to forest (see Bond, 2008, and references therein). Differences in soil nutrients are an alternative explanation for forest and savanna occurring in similar climatic conditions, as forest soils display higher nutrient content (Lloyd et al., 2008; Veenendaal et al., 2015). This explanation is still controversial (e.g., Staal & Flores, 2015), because observations suggest that deep savanna soil contains enough nutrients to sustain forests (Bond, 2010), and because of the existence of feedbacks between soil nutrient levels and plant community composition (Veldhuis, Hulshof, Fokkema, Berg, & Olff, 2016) and fires (Pivello et al., 2010). Finally, the distribution of TGBs and TFs (Figure 5) showed that the bimodal areas tended to occur at the boundaries between the two biomes, indicating that spatial structure was also important (see also Pausas & Dantas, 2017; Staal et al., 2016; Wuyts, Champneys, & House, 2017).

The prominent correlation between grass cover and fire intervals across the entire subcontinent (Figure 3) clearly demonstrates the pervasiveness of the connection between grasses and fire at a broad scale. Correspondingly, a hump-shaped relationship of fire intervals with MAR was observed (Supporting Information Figure S3.1). We could generally confirm the intermediate fire–productivity/aridity hypothesis (Krawchuk, Moritz, Parisien, Van Dorn, & Hayhoe, 2009; Pausas & Ribeiro, 2013) for sub-Saharan Africa, given that plant cover grew monotonically with MAR (Figure 2d), and assuming cover as a proxy for productivity (similar to what was observed by, e.g., Dantas et al., 2016; Lehmann et al., 2011). According to the hypothesis, fires are limited by fuel availability and discontinuity in unproductive, dry areas, and by fuel moisture in productive, wet regions. However, the data mostly differed from the hypothetical one-to-one fire–productivity relationship at high rainfall, where TGBs and TFs could both occur as alternatively stable states.

Tree cover increased with MAR in the entire dataset but showed a large spread in values (Figure 2b) influenced by disturbances and climate variability (Good & Caylor, 2011; Hirota et al., 2011; Sankaran et al., 2005; Staver et al., 2011b), and grass cover was clearly water limited at low MAR but very spread out at intermediate values, whereas total plant cover increased with a very narrow spread with MAR up to 1,200 mm/year, where it became approximately constant (Figure 2d). Interestingly, this relationship could be captured very well with a simple implicit-space model for vegetation cover (Levins, 1969), in which plants colonize new space proportionally to the MAR. This shows that water limitation acted most strongly on vegetation as a whole. It is much easier to predict total vegetation than the partitioning between trees and grasses, which involves other types of dynamics and feedbacks (Scholes & Walker, 1993). Such excellent performance by an extremely simple model in predicting large-scale vegetation cover trend seems to support the idea that increasing ecological details at small scales does not assure improved predictions at a larger scale (Levin, 1998).

We found that some areas had low forest-tree cover (< 60%), yet fire was rare or absent. Thanks to the use of tree phenologies, we could identify these as 'degraded forests' that lack the C_4 grasses that permit fire to spread, and we could distinguish them from old-growth savannas (Ratnam et al., 2011; Veldman, 2016; Zaloumis & Bond, 2015). In TFs, the low tree cover was connected to higher seasonality (Supporting Information Figure S3.5), which can be interpreted as evidence of forest retreat during past dry periods, thereby showing that African rain forests are more sensitive to small variations in rainfall seasonality

than in MAR (Malhi, Adu-Bredu, Asare, Lewis, & Mayaux, 2013). However, the absence of fires in these tropical forest sites may be attributable, in part, to inaccurate fire data for humid regions (Favier et al., 2012). Furthermore, in tropical forests, anthropogenic deforestation is known to be very important (Achard et al., 2014; Hansen et al., 2013).

The similarity in structure of TGBs (grass layer with shade-intolerant, fire-tolerant, deciduous trees) has led to assumptions in the literature that they are all regulated by the same processes (Lehmann & Parr, 2016), fostering much debate on their origin. In our study across sub-Saharan Africa and with 0.5° grain size, we have been able to highlight the importance of the overlooked grass layer in characterizing TGBs, alongside the well-known role of woody vegetation. We found that water limitation to grass growth is fundamentally characterizing dry TGBs and acts alongside the well-known water limitation to tree growth. The role of fires was more evident at intermediate and high rainfall values. Tropical grassy biomes where grasses were not water limited were associated with similar tree and grass cover values and frequent fires and experienced a similar marked rainfall seasonality. Despite these similarities, in mesic savannas the trees were still water limited, whereas in humid areas, by distinguishing between forest and savanna trees we found that some TGBs and TFs occurred as alternative states in a similar climate. It is possible that these humid TGBs are maintained by fire and not (as suggested by Bertram & Dewar, 2013; Good, Harper, Meesters, Robertson, & Betts, 2016) determined solely by climatic control. More generally, humid TGBs were the only biome observed in conditions of marked seasonality, and forests the only biome observed in conditions of mild seasonality. This understanding of the nature of the different TGBs is fundamental if we are to protect these biomes threatened by anthropogenic global change (Parr et al., 2014) and to predict their future changes.

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DATA ACCESSIBILITY

The observational datasets used in this study are all freely available. The ESA CCI-LC, v 1.6.1 dataset is available at http://maps.elie.ucl.ac.be/CCI/viewer/download.php. The MODIS datasets (MOD44B and MOD45A1) are available at https://earthdata.nasa.gov. The TRMM 3B42 dataset is available at https://mirador.gsfc.nasa.gov/. Post-processed data are available upon request to the authors.

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REFERENCES

Achard, F., Beuchle, R., Mayaux, P., Stibig, H. J., Bodart, C., Brink, A., ... Simonetti, D. (2014). Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. *Global Change Biology*, *20*, 2540–2554.

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*, 716–723.

Aleman, J. C., Blarquez, O., Gourlet-Fleury, S., Bremond, L., & Favier, C. (2017). Tree cover in Central Africa: Determinants and sensitivity under contrasted scenarios of global change. *Scientific Reports*, *7*, 41393.

Andela, N., Morton, D. C., Giglio, L., Chen, Y., van der Werf, G. R., Kasibhatla, P. S., ... Randerson, J. T. (2017). A human-driven decline in global burned area. *Science*, *356*, 1356–1362.

Archibald, S., & Hempson, G. P. (2016). Competing consumers: Contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150309.

Archibald, S., Roy, D. P., van Wilgen, B. W., & Scholes, R. J. (2009). What limits fire? An examination of drivers of burnt area in Southern Africa. *Global Change Biology*, *15*, 613–630.

Arnell, N., & Liu, C. (2001). Hydrology and water resources. In J. J. McCarthy, O. F. Canziani, N. A. Leary, D. J. Dokken, & K. S. White (Eds.), *Climate change 2001: Impacts, adaptation and vulnerability* (pp. 191–233). Cambridge, UK: Cambridge University Press.

Axelsson, C. R., & Hanan, N. P. (2017). Patterns in woody vegetation structure across African savannas. *Biogeosciences*, *14*, 3239.

Baudena, M., D'Andrea, F., & Provenzale, A. (2008). A model for soil-vegetation-atmosphere interactions in water-limited ecosystems. *Water Resources Research*, *44*, W12429.

Baudena, M., D'Andrea, F., & Provenzale, A. (2010). An idealized model for tree–grass coexistence in savannas: The role of life stage structure and fire disturbances. *Journal of Ecology*, *98*, 74–80.

Baudena, M., & Rietkerk, M. (2013). Complexity and coexistence in a simple spatial model for arid savanna ecosystems. *Theoretical Ecology*, *6*, 131–141.

Beckage, B., Gross, L. J., & Platt, W. J. (2011). Grass feedbacks on fire stabilize savannas. *Ecological Modelling*, *222*, 2227–2233.

Bertram, J., & Dewar, R. C. (2013). Statistical patterns in tropical tree cover explained by the different water demand of individual trees and grasses. *Ecology*, *94*, 2138–2144.

Bond, W. J. (2008). What limits trees in C_4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics*, *39*, 641–659.

Bond, W. J. (2010). Do nutrient-poor soils inhibit development of forests? A nutrient stock analysis. *Plant and Soil*, *334*, 47–60.

Bond, W. J. (2016). Ancient grasslands at risk. *Science*, *351*, 120–122.

Bond, W. J., Woodward, F. I., & Midgley, G. F. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist*, *165*, 525–538.

Bowman, D. M. J. S., & Prior, L. D. (2005). Why do evergreen trees dominate the Australian seasonal tropics? *Australian Journal of Botany*, *53*, 379–399.

Bucini, G., & Hanan, N. P. (2007). A continental-scale analysis of tree cover in African savannas. *Global Ecology and Biogeography*, *16*, 593–605.

Cochrane, M. A. (2003). Fire science for rainforests. *Nature*, *421*, 913–919.

Dantas, V. D. L., Batalha, M. A., & Pausas, J. G. (2013). Fire drives functional thresholds on the savanna–forest transition. *Ecology*, *94*, 2454–2463.

Dantas, V. D. L., Hirota, M., Oliveira, R. S., & Pausas, J. G. (2016). Disturbance maintains alternative biome states. *Ecology Letters*, *19*, 12–19.

D'Onofrio, D., Baudena, M., D'Andrea, F., Rietkerk, M., & Provenzale, A. (2015). Tree-grass competition for soil water in arid and semiarid savannas: The role of rainfall intermittency. *Water Resources Research*, *51*, 169–181.

Edwards, E. J., Smith, S. A., & Thresholds, C. E. (2010). The origins of C_4 grasslands: Integrating evolutionary and ecosystem science. *Science*, *328*, 587–590.

Favier, C., Aleman, J., Bremond, L., Dubois, M. A., Freycon, V., & Yangakola, J. M. (2012). Abrupt shifts in African savanna tree cover along a climatic gradient. *Global Ecology and Biogeography*, *21*, 787–797.

February, E. C., Higgins, S. I., Bond, W. J., & Swemmer, L. (2013). Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology*, *94*, 1155–1164.

Fensham, R. J., Butler, D. W., & Foley, J. (2015). How does clay constrain woody biomass in drylands? *Global Ecology and Biogeography*, *24*, 950–958.

Gerard, F., Hooftman, D., van Langevelde, F., Veenendaal, E., White, S. M., & Lloyd, J. (2017). MODIS VCF should not be used to detect discontinuities in tree cover due to binning bias. A comment on Hanan et al. (2014) and Staver and Hansen (2015). *Global Ecology and Biogeography*, *26*, 854–859.

Gignoux, J., Clobert, J., & Menaut, J. C. (1997). Alternative fire resistance strategies in savanna trees. *Oecologia*, *110*, 576–583.

Good, P., Harper, A., Meesters, A., Robertson, E., & Betts, R. (2016). Are strong fire–vegetation feedbacks needed to explain the spatial distribution of tropical tree cover? *Global Ecology and Biogeography*, *25*, 16–25.

Good, S. P., & Caylor, K. K. (2011). Climatological determinants of woody cover in Africa. *Proceedings of the National Academy of Sciences USA*, *108*, 4902–4907.

Green, J. K., Konings, A. G., Alemohammad, S. H., Berry, J., Entekhabi, D., Kolassa, J., ... Gentine, P. (2017). Regionally strong feedbacks between the atmosphere and terrestrial biosphere. *Nature Geoscience*, *10*, 410–414.

Hanan, N. P., Tredennick, A. T., Prihodko, L., Bucini, G., & Dohn, J. (2014). Analysis of stable states in global savannas: Is the CART pulling the horse? *Global Ecology and Biogeography*, *23*, 259–263.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, *342*, 850–853.

Hempson, G. P., Archibald, S., & Bond, W. J. (2015). A continent-wide assessment of the form and intensity of large mammal herbivory in Africa. *Science*, *350*, 1056–1061.

Higgins, S. I., Bond, W. J., Combrink, H., Craine, J. M., February, E. C., Govender, N., ... Trollope, W. S. W. (2012). Which traits determine shifts in the abundance of tree species in a fire-prone savanna? *Journal of Ecology*, *100*, 1400–1410.

Higgins, S. I., Bond, W. J., February, E. C., Bronn, A., Euston-Brown, D. I. W., Enslin, B., ... Trollope, W. S. W. (2007). Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology*, *88*, 1119–1125.

Hirota, M., Holmgren, M., Van Nes, E. H., & Scheffer, M. (2011). Global resilience of tropical forest and savanna to critical transitions. *Science*, *334*, 232–235.

Hoffmann, W. A., Adasme, R., Haridasan, M., de Carvalho, M.T., Geiger, E. L., Pereira, M. A., ... Franco, A. C. (2009). Tree topkill, not mortality, governs the dynamics of savanna–forest boundaries under frequent fire in central Brazil. *Ecology*, *90*, 1326–1337.

Hoffmann, W. A., Geiger, E. L., Gotsch, S. G., Rossatto, D. R., Silva, L. C. R., Lau, O. L., ... Franco, A. C. (2012). Ecological thresholds at the savanna-forest boundary: How plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters*, *15*, 759–768.

Holdo, R. M., & Brocato, E. R. (2015). Tree–grass competition varies across select savanna tree species: A potential role for rooting depth. *Plant Ecology*, *216*, 577–588.

Johnson, E. A., & Wagner, C. E. V. (1985). The theory and use of two fire history models. *Canadian Journal of Forest Research*, *15*, 214–220.

Koster, R. D., Dirmeyer, P. A., Guo, Z., Bonan, G., Chan, E., Cox, P., ... Yamada, T. (2004). Regions of strong coupling between soil moisture and precipitation. *Science*, *305*, 1138–1140.

Krawchuk, M. A., Moritz, M. A., Parisien, M. A., Van Dorn, J., & Hayhoe, K. (2009). Global pyrogeography: The current and future distribution of wildfire. *PLoS One*, *4*, e5102.

Kulmatiski, A., & Beard, K. H. (2013). Root niche partitioning among grasses, saplings, and trees measured using a tracer technique. *Oecologia*, *171*, 25–37.

van Langevelde, F., Van De Vijver, CaDM., Kumar, L., De Koppel, J. V., De Ridder, N., Andel, J. V., ... Rietkerk, M. (2003). Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, *84*, 337–350.

Lehmann, C. E. R., & Parr, C. L. (2016). Tropical grassy biomes: Linking ecology, human use and conservation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20160329.

Lehmann, C. E. R., Archibald, S. A., Hoffmann, W. A., & Bond, W. J. (2011). Deciphering the distribution of the savanna biome. *New Phytologist*, *191*, 197–209.

Lehsten, V., Harmand, P., Palumbo, I., & Arneth, A. (2010). Modelling burned area in Africa. *Biogeosciences*, *7*, 3199–3214.

Levin, S. A. (1998). Ecosystems and the biosphere as complex adaptive systems. *Ecosystems*, *1*, 431–436.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, *15*, 237–240.

Lloyd, J., Bird, M. I., Vellen, L., Miranda, A. C., Veenendaal, E. M., Djagbletey, G., ... Farquhar, G. D. (2008). Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: A quasi-global estimate. *Tree Physiology*, *28*, 451–468.

Malhi, Y., Adu-Bredu, S., Asare, R. A., Lewis, S. L., & Mayaux, P. (2013). African rainforests: Past, present and future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*, 20120312.

McCullagh, P., & Nelder, J. (1989). *Generalized linear models* (2nd ed., p. 532). London, UK: Chapman & Hall/CRC.

McGill, R., Tukey, J. W., & Larsen, W. A. (1978). Variations of box plots. *The American Statistician*, *32*, 12–16.

Orians, G. H., & Solbrig, O. T. (1977). A cost-income model of leaves and roots with special reference to arid and semiarid areas. *The American Naturalist*, *111*, 677–690.

Parr, C. L., Lehmann, C. E. R., Bond, W. J., Hoffmann, W. A., & Andersen, A. N. (2014). Tropical grassy biomes: Misunderstood, neglected, and under threat. *Trends in Ecology and Evolution*, *29*, 205–213.

Pausas, J. G., & Dantas, VdL. (2017). Scale matters: Fire–vegetation feedbacks are needed to explain tropical tree cover at the local scale. *Global Ecology and Biogeography*, *26*, 395–399.

Pausas, J. G., & Ribeiro, E. (2013). The global fire–productivity relationship. *Global Ecology and Biogeography*, *22*, 728–736.

Pivello, V. R., Oliveras, I., Miranda, H. S., Haridasan, M., Sato, M. N., & Meirelles, S. T. (2010). Effect of fires on soil nutrient availability in an open savanna in Central Brazil. *Plant Soil*, *337*, 111–123.

Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. A., Archibald, S., Lehmann, C. E. R., ... Sankaran, M. (2011). When is a 'forest' a savanna, and why does it matter? *Global Ecology and Biogeography*, *20*, 653–660.

Rietkerk, M., Brovkin, V., van Bodegom, P. M., Claussen, M., Dekker, S. C., Dijkstra, H. A., ... Seneviratne, S. I. (2011). Local ecosystem feedbacks and critical transitions in the climate. *Ecological Complexity*, *8*, 223–228.

Roy, D. P., Boschetti, L., Justice, C. O., & Ju, J. (2008). The collection 5 MODIS burned area product — Global evaluation by comparison with the MODIS active fire product. *Remote Sensing of Environment*, *112*, 3690–3707.

Roy, D., Jin, Y., Lewis, P., & Justice, C. (2005). Prototyping a global algorithm for systematic fire-affected area mapping using MODIS time series data. *Remote Sensing of Environment*, *97*, 137–162.

Roy, D., Lewis, P., & Justice, C. (2002). Burned area mapping using multitemporal moderate spatial resolution data—a bi-directional reflectance model-based expectation approach. *Remote Sensing of Environment*, *83*, 263–286.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., ... Zambatis, N. (2005). Determinants of woody cover in African savannas. *Nature*, *438*, 846–849.

Sankaran, M., Ratnam, J., & Hanan, N. P. (2004). Tree–grass coexistence in savannas revisited –Insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, *7*, 480–490.

Sarmiento, G. (1984). *The ecology of Neotropical savannas* (p. 235). Cambridge, MA: Harvard University Press.

Scholes, R. J., & Archer, S. R. (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, *28*, 517–544.

Scholes, R. J., & Walker, B. H. (1993). *An African savanna: Synthesis of the Nylsvley study* (p. 318). Cambridge, UK: Cambridge University Press.

Scholes, R. J., Dowty, P. R., Caylor, K., Parsons, D. A. B., Frost, P. G. H., & Shugart, H. H. (2002). Trends in savanna structure and composition along an aridity gradient in the Kalahari. *Journal of Vegetation Science*, *13*, 419–428.

Shorrocks, B. (2007). Savannahs. *The biology of African savannahs*. Oxford: OUP Premium.

Smit, I. P. J., & Prins, H. H. T. (2015). Predicting the effects of woody encroachment on mammal communities, grazing biomass and fire frequency in African savannas. *PLoS One*, *10*, e0137857.

Staal, A., & Flores, B. M. (2015). Sharp ecotones spark sharp ideas: Comment on "Structural, physiognomic and above-ground biomass variation in savanna–forest transition zones on three continents – How different are co-occurring savanna and forest formations?" by Veenendaal et al. (2015). *Biogeosciences*, *12*, 5563–5566.

Staal, A., Dekker, S. C., Xu, C., & van Nes, E. H. (2016). Bistability, spatial interaction, and the distribution of tropical forests and savannas. *Ecosystems*, *19*, 1080–1091.

Staver, A. C. (2017). Prediction and scale in savanna ecosystems. *New Phytologist*. http://doi.org/10.1111/nph.14829

Staver, A. C., & Hansen, M. C. (2015). Analysis of stable states in global savannas: Is the CART pulling the horse? – A comment. *Global Ecology and Biogeography*, *24*, 985–987.

Staver, A. C., & Levin, S. A. (2012). Integrating theoretical climate and fire effects on savanna and forest systems. *Ecology*, *180*, 211–224.

Staver, A. C., Archibald, S., & Levin, S. (2011a). Tree cover in sub-Saharan Africa: Rainfall and fire constrain forest and savanna as alternative stable states. *Ecology*, *92*, 1063–1072.

Staver, A. C., Archibald, S., & Levin, S. A. (2011b). The global extent and determinants of savanna and forest as alternative biome states. *Science*, *334*, 230–232.

Staver, A. C., Botha, J., & Hedin, L. (2017). Soils and fire jointly determine vegetation structure in an African savanna. *New Phytologist*, *216*, 1151–1160.

Townshend, J. R., Carroll, M., DiMiceli, C., Sohlberg, R., Hansen, M., & DeFries, R. (2011). *Vegetation continuous fields MOD44B, 2000–2010 percent tree cover, percent non-tree vegetation, Collection 5* (Version 051). College Park, MD: University of Maryland. Retrieved from https://earthdata.nasa.gov/ on 08/12/2016

Van Nes, E. H., Hirota, M., Holmgren, M., & Scheffer, M. (2014). Tipping points in tropical tree cover: Linking theory to data. *Global Change Biology*, *20*, 1016–1021.

Veenendaal, E. M., Torello-Raventos, M., Feldpausch, T. R., Domingues, T. F., Gerard, F., Schrodt, F., ... Lloyd, J. (2015). Structural, physiognomic and above-ground biomass variation in savanna–forest transition zones on three continents – How different are co-occurring savanna and forest formations? *Biogeosciences*, *12*, 2927–2951.

Veldhuis, M. P., Hulshof, A., Fokkema, W., Berg, M. P., & Olff, H. (2016). Understanding nutrient dynamics in an African savanna: Local biotic interactions outweigh a major regional rainfall gradient. *Journal of Ecology*, *104*, 913–923.

Veldman, J. W. (2016). Clarifying the confusion: Old-growth savannahs and tropical ecosystem degradation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150306.

Walsh, R. P. D., & Lawler, D. M. (1981). Rainfall seasonality: Description, spatial patterns and change through time. *Weather*, *36*, 201–208.

Walter, H. (1973). *Vegetation of the earth in relation to climate and the eco-physiological conditions*. New York: Springer-Verlag.

Wuyts, B., Champneys, A. R., & House, J. I. (2017). Amazonian forest–savanna bistability and human impact. *Nature Communications*, *8*, 15519.

Xu, C., Vergnon, R., Cornelissen, J. H. C., Hantson, S., Holmgren, M., van Nes, E. H., & Scheffer, M. (2015). Temperate forest and open landscapes are distinct alternative states as reflected in canopy height and tree cover. *Trends in Ecology and Evolution*, *30*, 501–502.

Yin, Z., Dekker, S. C., van den Hurk, B. J. J. M., & Dijkstra, H. A. (2016). The climatic imprint of bimodal distributions in vegetation cover for Western Africa. *Biogeosciences*, *13*, 3343–3357.

Zaloumis, N. P., & Bond, W. J. (2015). Reforestation of afforestation? The attributes of old growth grasslands in South Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150310.

BIOSKETCH

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SUPPORTING INFORMATION

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

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