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LETTER

Disturbance maintains alternative biome states

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Abstract

Understanding the mechanisms controlling the distribution of biomes remains a challenge. Although tropical biome distribution has traditionally been explained by climate and soil, contrasting vegetation types often occur as mosaics with sharp boundaries under very similar environmental conditions. While evidence suggests that these biomes are alternative states, empirical broad-scale support to this hypothesis is still lacking. Using community-level field data and a novel resource-niche overlap approach, we show that, for a wide range of environmental conditions, fire feedbacks maintain savannas and forests as alternative biome states in both the Neotropics and the Afrotropics. In addition, wooded grasslands and savannas occurred as alternative grassy states in the Afrotropics, depending on the relative importance of fire and herbivory feedbacks. These results are consistent with landscape scale evidence and suggest that disturbance is a general factor driving and maintaining alternative biome states and vegetation mosaics in the tropics.

Keywords

Cerrado, feedbacks, fire, forest, herbivory, mosaic, savanna, savanna–forest transition, thresholds, tropical.

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INTRODUCTION

The global distribution of biomes has been traditionally attributed to climatic constrains on woody plant productivity (Rosenzweig 1968; Polis 1999; Woodward *et al.* 2004). However, under certain climatic conditions, contrasting vegetation types form mosaics separated by sharp boundaries. Outstanding examples of such patterns are the widespread mosaics of humid savanna and forests across the wet tropics (Warman & Moles 2009; Murphy & Bowman 2012) and the mosaics of arid and mesic savanna types in semi-arid Africa (Bell 1982; Huntley 1982; Scholes & Archer 1997; Bond *et al.* 2001). Differences in soil texture and fertility alone do not consistently explain these patterns, and changes in biome boundaries are frequently reported (Bell 1982; Dublin *et al.* 1990; Bond 2008, 2010; Silva *et al.* 2008; Hoffmann *et al.* 2012). Thus, there is an increasing recognition that tropical biome distribution is dynamic and results from complex interactions between resource availability and disturbances, operating at multiple spatial and temporal scales (Bell 1982; Dublin *et al.* 1990; Bond 2008; Warman & Moles 2009; Hoffmann *et al.* 2012).

The Alternative State Theory (AST) provides a suitable framework to explain tropical landscape mosaics (Whittaker & Levin 1977; Scheffer 2009). It postulates that the boundaries between biomes are dynamic rather than static and that two or more biome types can occur under the same environmental conditions as long as they are experiencing different disturbance regimes (Whittaker & Levin 1977; Dublin *et al.* 1990; Scheffer 2009; Warman & Moles 2009; Staver *et al.* 2011). By preventing the course of resource-driven community succession, repeated disturbances modify the competition hierarchy among functional types, providing conditions for the maintenance of certain community configurations in otherwise unsuitable sites (Whittaker & Levin 1977). Thus, disturbance regimes not only affect plant biomass but also select for distinct plant strategies, shaping the functional composition of communities and the relationship between vegetation structure and resource availability (Whittaker & Levin 1977; Scheffer 2009; Warman & Moles 2009; Dantas *et al.* 2013).

Recurrent fires are often suggested as key disturbance drivers maintaining savanna and forest as alternative states (Bond *et al.* 2005; Warman & Moles 2009; Staver *et al.* 2011; Hoffmann *et al.* 2012; Murphy & Bowman 2012). Fire topkills juvenile trees and select for fire-resistant and fire-resilient woody species with open crown architectures, generating well lit communities with a flammable grassy understory (Beckage *et al.* 2009; Warman & Moles 2009; Lehmann *et al.* 2011; Hoffmann *et al.* 2012; Dantas *et al.* 2013). In contrast, most forest species have fire-sensitive trunks (Hoffmann *et al.* 2012; Dantas *et al.* 2013). Thus, a switch to a forest state depends on a sufficiently long fire interval or high resource availability allowing the outcompetition of shade-intolerant savanna trees and grasses (i.e. the inhibition of fires) by means of a closed canopy (Lehmann *et al.* 2011; Hoffmann *et al.* 2012; Dantas *et al.* 2013). Following the disruption of fire feedbacks, fire-driven nutrient losses cease and positive vegetation-resource feedbacks increase canopy closure and reduce forest flammability (Warman & Moles 2009; Lehmann *et al.* 2011; Hoffmann *et al.* 2012; Pellegrini *et al.* 2014, 2015).

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Herbivory also exerts a strong control on woody canopy cover in savannas (Asner *et al.* 2009; Sankaran *et al.* 2013; Staver & Bond 2014). Browsing drives mortality among trees of all size classes and both browsing and grazing impose strong limitations to woody plant regeneration (Bell 1982; Du Toit *et al.* 1990; Moe *et al.* 2009; Sankaran *et al.* 2013). When browsing and grazing are coupled, grazing reduces grass biomass and changes grass composition, dramatically decreasing fire frequencies (Du Toit *et al.* 1990; Scholes & Archer 1997; Moe *et al.* 2009; Staver *et al.* 2012; Hempson *et al.* 2015). Grass removal by grazers increases the frequency of browsing on woody saplings (Riginos & Young 2007), which further stimulates browsing (Du Toit *et al.* 1990). The combination of heavy browsing and low fire frequencies creates a selective pressure that excludes fire-resistant trees while favouring herbivory-resistant shrubs, forming low woody cover grassy communities (Asner *et al.* 2009; Staver *et al.* 2012; Sankaran *et al.* 2013). With decreasing grazing frequency, browsing frequency also decreases (Riginos & Young 2007), while fire frequency increases (Hempson *et al.* 2015) and, as long as fire intensity is not too high, the roles of fire and browsing in plant communities become similar (Dantas & Pausas 2013; Staver & Bond 2014). Because the maintenance of grazing sites is advantageous for grazing species, grazing is often patchy (McNaughton 1984; Hempson *et al.* 2015), resulting in landscape mosaics of contrasting vegetation types and fire regimes in semi-arid Africa (Staver *et al.* 2012). To what extent herbivory and fire interact to shape the distribution of tropical landscape mosaics at the continental scale remains unclear.

The first broad-scale evidence for alternative biome states in the tropics was based on satellite-derived tree-cover data (Hirota *et al.* 2011; Staver *et al.* 2011). However, the suitability of these data is controversial, as the statistical methodology employed with it introduces discontinuities that may compromise interpretations (Hanan *et al.* 2014, 2015; Staver & Hansen 2015). By analysing tree basal area (TBA) data from field studies across tropical America and Africa (Supplementary Information Appendix A Fig. S1) in combination with climate, soil and disturbance regime information, we aimed at disentangling the mechanisms shaping the distribution of tropical savannas and forests. We provide the first empirical (field data-based) evidence that tropical landscape mosaics and biome distribution are better explained by the AST rather than by resource gradients alone, and that disturbance regimes are general factors driving and maintaining biomes as alternative states in the tropics.

MATERIAL AND METHODS

Data compilation

We compiled data on TBA, a plant community metric related to woody canopy cover and community structure, for tropical (including subtropical) savannas and forests of Africa and America (Fig. S1). TBA is a measure of the proportion of the ground area of a plot that is covered by woody plant stems (in m^2 ha^{-1}). Because individual TBA and leaf area are highly correlated (Hoffmann *et al.* 2012), TBA should be a refined and unbiased estimator of the ground area covered by woody species in tropical landscapes. Moreover, because biomes can be broadly characterised in terms of community structure and physiognomy, TBA is a key community-level trait for studying the drivers of tropical biome distribution (Lehmann *et al.* 2014).

We compiled data for 1125 savanna and forest plots distributed across 22 Afrotropical (618 plots) and 14 Neotropical countries (507 plots) (Fig. S1) from a total of 74 published papers (see Supplementary Material Appendix B). For each plot, we also compiled the latitude and longitude in order to link it with climate, soil and fire activity information from global datasets. For the compilation, we defined ‘savanna’ as tropical and subtropical vegetation characterised by the coexistence of woody plants and a continuous grass layer at various tree–grass ratios (Lehmann *et al.* 2014). Pure grasslands (i.e. TBA = 0) and thicket vegetation were not included and are outside the scope of this study. Plots reported as experiencing substantial human disturbance were also discarded and most plots were within protected areas. Further details about TBA data can be found in Appendix B.

Climate, soil and fire data

We compiled mean annual precipitation and mean, minimal and maximal annual temperatures for each plot location from the WorldClim dataset (0.0083° spatial resolution; mostly averages between 1950 and 2000 records) (Hijmans *et al.* 2005). Because only average precipitation was available in the WorldClim dataset, we also compiled precipitation information from the Tropical Rainfall Measuring Mission (TRMM; 0.25° spatial resolution) between 1998 and 2010, to calculate Markham’s rainfall seasonality index (Markham 1970). We obtained soil data for all of the plots from the Soil Grid 1 km Database of the ISRIC World Soil Information System, which is the best global soil dataset currently available (Hengl *et al.* 2014). From this dataset, we extracted data on soil sand percentages (soil texture), soil organic carbon, cation exchange capacity and soil pH. For each plot, we calculated average values for these variables considering the top five layers (i.e. up to 80 cm of depth). More details on the soil data can be found in Appendix B.

Fire activity was based on the Global Fire Location Product (MCD14ML) from MODIS Collection 5 after the quality correction by the University of Maryland (Giglio 2010). Specifically, we used the information from the Terra sensor for the period from 1/2002 to 12/2013 (12 years). This product provides the location of fires (hotspots) as well as the radiative power (in MW), a measure of fire intensity. To estimate the fire activity for each plot location, we defined a cell of 0.125 × 0.125 degrees centred in the geographical coordinates of each plot’s centroid. For these cells, we computed the total number of hotspots and the average radiative power for the period considered. Even though this is the best global fire dataset currently available, its ability to reflect very low-intensity fires, fires below clouds and forest canopies may be limited (see Giglio (2010), for details).

State detection analysis

The number of modes within the frequency distribution of representative tree cover samples may be used as proxies for the temporal dynamics of plant communities (Watt 1947) and provide evidence for multiple vegetation states (Whittaker & Levin 1977; Scheffer 2009; Hirota *et al.* 2011). Positive and negative feedback mechanisms operating in plant communities push these communities towards opposing directions and the resulting outcome is the formation of basins of attraction, representing stable configurations towards which these communities tend to converge. The closer a community is to that stable condition, the more frequent that community state appears in the landscape, reflecting its high resilience to a state shift (Watt 1947; Whittaker & Levin 1977; Scheffer 2009; Hirota *et al.* 2011).

We used hierarchical clustering for parameterised Gaussian mixture models to fit one to five Gaussian mixtures to the frequency distribution of TBA data including both the African and the American continents (together and separated). The selected models were the ones with the lowest integrated completed likelihood criteria, which is the most robust criteria for estimating the number of components in finite mixture modelling (Biernacki *et al.* 2000). We subsequently tested each adjacent bimodality for significance using a likelihood ratio test for bimodality (against unimodality) to avoid equivocal classification of states (Holzmann & Vollmer 2008). Communities were then assigned to groups representing different biome states, and this information was subsequently used to split the regression models described below.

Continuous vs. split multiple regression models

We selected the best subset of environmental variables predicting TBA in the entire dataset and within the Neotropical and Afrotropical subsets. This was carried out using a stepwise procedure in a multiple regression context, in which the models with the lowest AICs were selected. Because minimal and maximum annual temperature were strongly correlated with mean annual temperature ($r > 0.70$) but not with each other ($r < 0.30$), we excluded the later from the analysis to avoid collinearity.

On the basis of the selected subsets, we computed Resource Availability Indices (RAI) for each biogeographic context (i.e. the entire dataset, and the Afrotropical and Neotropical subsets). In all cases, the indices consisted of the first three axes of a principal component analysis (PCA) performed on the selected environmental variables. The three-dimensional RAI were used as explanatory variables in continuous (smooth) multiple regression models with TBA as the response variable. To ensure that we incorporated a range of nonlinear possibilities, we selected the best x-variable transformation (among none, log and reciprocal) using the corrected Akaike Information Criterion (AICc) and the Bayesian Information Criterion (BIC). We subsequently used the Box–Cox method to select the best y-axis power transformation for TBA. This procedure allows the selection of a range of nonlinear models, such as exponential, logarithm, asymptotic, logistic, etc.

We compared these continuous models with split models (i.e. ANCOVA) in which biome state was used as a factor to split the multiple regressions into subsets representing each biome state derived from the state detection analyses. The transformations applied to the continuous models were maintained in the split models. The continuous and the split models were compared using the AICc and BIC; both criteria strongly penalise for each additional parameter estimated. We also tested the differences between continuous and split models using F tests. A higher model fit in the split than in the continuous models would support the AST in which different biomes states respond differently to resource availability.

Quantifying environmental overlap between biome states

We computed three-dimensional environmental hypervolumes for Afrotropical and Neotropical biome states to quantify the proportion of the resource space of a state shared with other vegetation states from the same biogeographic context. These hypervolumes were constructed based on the three resource availability axes (RAI, as already described) obtained after performing a PCA in the selected environmental variables. An overlap between the hypervolumes of two biomes indicates that more than one biome state is possible under certain resource conditions, supporting the AST.

N-dimensional hypervolumes were calculated using the algorithms implemented in the R package 'hypervolume', which thresholds a kernel density estimation of the observations (using 95% quantile thresholds), assuming a hyperbox kernel (Blonder *et al.* 2014). Bandwidths for the hypervolumes were defined using Silverman bandwidth approximations (Blonder *et al.* 2014). To quantify the proportion of the hypervolumes of each biome state that was shared with others, the algorithm uses an inclusion-test approach to define whether a point in the hypervolume of one biome state was within a characteristic distance of at least one point from the hypervolume of the other. The method subsequently identifies points in the first hypervolume that are within or outside the second hypervolume and vice versa. The overlap with each biome state was calculated as the percentage of a biome's total hypervolume that was shared with other biomes from the same biogeographic context. In an alternative states context, the degree of overlap between biome states can provide insights into the extent to which resource space occupation would change if feedbacks were switched off or increased in magnitude.

To search for evidence that disturbance regimes maintained biomes as alternative states, we compared fire frequency and intensity within the zones of hypervolume overlap between each pair of biome state using Wilcoxon rank sum tests. Because disturbance regimes were compared under similar conditions, this approach allowed the detection of differences in fire regime that were not associated with resource differences affecting grass productivity. We also tested for overall differences among biome states in climate, soil and fire variables using ANOVA and Tukey's pair-wise comparisons. In these cases, the variables were log-transformed before the analysis to improve the normality of the residuals. We performed all of the analysis in R v.3.1.2 using the packages 'AICcmodavg', 'bimodalitytest', 'MASS', 'mclust', 'mgcv' and 'stats'.

RESULTS

For the entire dataset and for the Afrotropical subset, TBA followed a tri-modal frequency distribution with the following attractors: wooded grassland, savanna and forest states (Figs 1a,b, S2 and S3; Table 1, and Supplementary Information Appendix C Tables S1 and S2). In contrast, only two biome states were detected in Neotropical communities, savannas and forests; wooded grasslands, although present in the Neotropics, were within the basin of attraction of the savanna state and formed a single grassy state with this vegetation type (Figs 1c, S2 and S3; Tables 1, S1 and S2).

Split regression models based on discrete biome states explained better than continuous models the relationship between TBA and RAI (Figs 1d–f and S4; Tables S3 and S4). The best subset of environmental variables predicting TBA in the continuous models differed between continents. Specifically, temperature was only important when continents were analysed separately and maximal temperature was relevant only in the Afrotropics (Table S3). Moreover, pH was selected in the Tropical and Neotropical sets, but not in the Afrotropical subset (Table S3).

The environmental (RAI) hypervolumes of all biome states overlapped in resource space (Fig. 2; Table 2), suggesting that more than one biome state may exist for certain resource conditions. Nevertheless, all of the biomes states had a fraction of their resource conditions that was not shared with other vegetation states. Within the fraction of the resource space that was shared between savannas and forests, fire frequencies

Table 1 Mean, standard deviation (SD) and thresholds of tree basal area ($m^2\ ha^{-1}$) for each biome state and continent in the fitted models of the state detection analyses (Fig. 1b,c). WG: wooded grassland state; S: savanna state; F: forest state

	Afrotropical			Neotropical	
	WG	S	F	S	F
Mean	1.14	7.58	29.25	6.85	26.96
SD	0.89	3.73	6.94	3.74	10.22
Upper threshold	2.69	15.50	51.66	13.83	67.20
Lower threshold	0.02	2.84	15.63	0.01	13.85

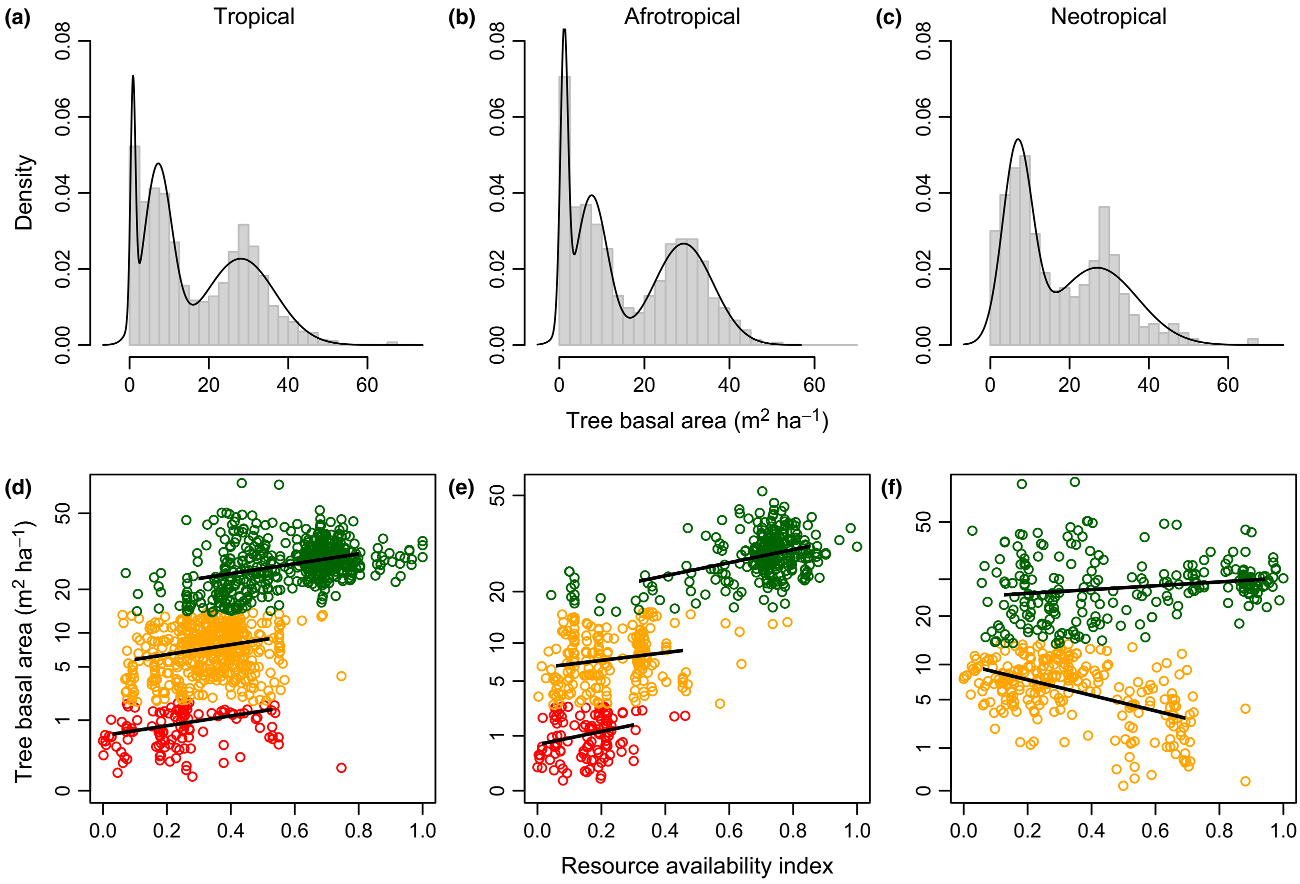

Figure 1 State detection analysis and split regression modelling results. (a–c) State detection results (see Material and Methods section) supporting three states in the Tropical (a) and Afrotropical (b) sets and two in the Neotropical subset of tree basal area data (c; Table S1). Lower panels show the split models (ANCOVA) for TBA against the first axis of the resource availability index for Tropical (d), Afrotropical (e) and Neotropical (f) communities (see Tables S2 and S5 for details). The power transformations of the *y*-axes in d, e and f were selected using the Box–Cox method and were 0.35, 0.43 and 0.47 respectively. Red: wooded grassland state; Orange: savanna state; Green: forest state.

and intensities were much higher in savanna than in forest communities in both continents (Fig. 3 and Tables S5). Within the shared fraction between the wooded grassland and the other two states in Africa, fire frequency was lower in the wooded grassland state than in both the savanna and the forest states, whereas no differences in fire intensity were observed between the wooded grassland and the other biome states sharing similar environmental conditions (Fig. 3 and Table S5; see Fig. S5 for an unrestricted comparison).

DISCUSSION

Savanna and forest communities (as defined in the compiled literature; Fig. S3) were associated with different basins of attraction in both continents (Fig. 1a–c; Table 1), indicating that these vegetation types form multiple biome states subjected to contrasting feedback mechanisms (Watt 1947; Whittaker & Levin 1977; Scheffer 2009). Moreover, in all of the regression analyses, split models better predicted the relationships between TBA and resource availability (Fig. 1d–e), suggesting that those biome states have contrasting patterns of community functioning (Warman & Moles 2009; Dantas *et al.* 2013). Finally, different biome states shared a fraction of their environmental envelopes indicating that, even though these communities are submitted to contrasting feedback mechanisms, some of them may occur under similar resource conditions (Fig. 2; Table 2). Combined, these results are consistent with a dynamic view of biomes and support predictions from the AST.

The frequency distribution of communities with TBA higher than *c.* 7 $m^2\ ha^{-1}$ (see Table 1) was similar across continents (Fig. 1a–c), indicating a universal dynamics for these communities. In contrast, the dynamics of communities with TBA values lower than 7 $m^2\ ha^{-1}$ differed between continents and only in the Afrotropics wooded grasslands formed a third vegetation state. Even though wooded grassland communities occur in the Neotropics, they were nested within the savanna state (Fig. 1c). The idea of two main grassy vegetation states in Africa forming landscape mosaics with sharp dynamic boundaries in the semi-arid transition is not new, although direct broad-scale evidence for this pattern was lacking (Bell 1982; Huntley 1982; Dublin *et al.* 1990; Scholes & Archer 1997; Bond *et al.* 2001; Staver *et al.* 2012). Sharp dynamic boundaries and landscape mosaics are conspicuous features of alternative states characterised by contrasting feedback mechanisms (Watt 1947; Whittaker & Levin 1977; Scheffer 2009; Warman & Moles 2009). While these results must be subjected to further research, this preliminary evidence is consistent with the idea of two main African grassy vegetation states with dynamic properties, as reported in the literature.

Within the shared sections of the RAI gradient (overlap zones in Fig. 2 and Table 2), fire frequencies and intensities were much higher in savanna than in forest communities in both continents (Figs 3 and S5; Tables S5 and S6). These results highlight the role of fire feedbacks in maintaining these biomes as alternative states (Bond *et al.* 2005; Warman & Moles 2009; Staver *et al.* 2011; Hoffmann *et al.* 2012; Dantas *et al.* 2013). The wooded grassland state presented the lowest fire frequencies in Africa when the comparison was restricted to the shared range of resource conditions (Fig. 3; for an unrestricted comparison see Fig. S5), while no significant differences in fire intensity were detected in respect to other states. Because the comparison was restricted to the same range of resource conditions, the low fire frequencies of the wooded grassland state cannot be attributed to lower grass productivities. Although the lack of suitable large-scale her-

Table 2 Percentage of biomes' resource space (rows) shared with other biomes (columns) within biogeographic contexts. WG: wooded grassland state; S: savanna state; F: forest state; Both: both biome states

	Afrotropics				Neotropics	
	WG	S	F	Both	S	F
WG	–	87%	35%	89%	–	–
S	52%	–	41%	74%	–	68%
F	19%	37%	–	37%	45%	–

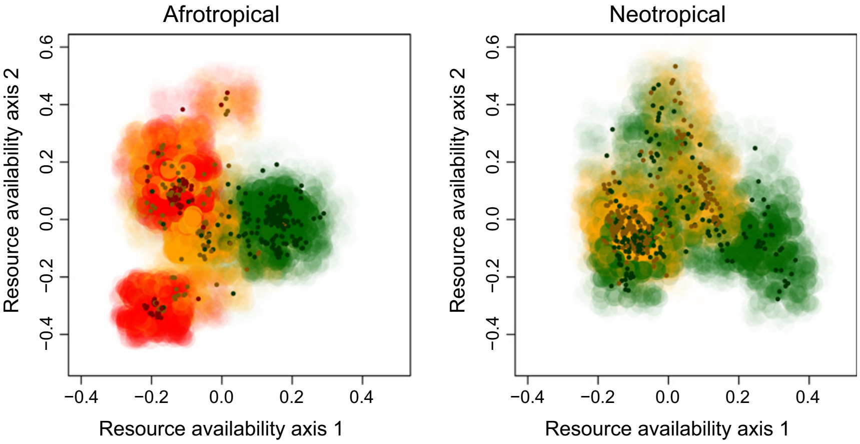

Figure 2 Environmental hypervolumes of Afrotropical and Neotropical biome states. A low cloud transparency indicates a high probability of being in that state. Only the first two (among a total of three) axes of the resource availability indices are shown. Overlap values for each biome state are reported in Table 2. Red: wooded grassland state; Orange: savanna state; Green: forest state.

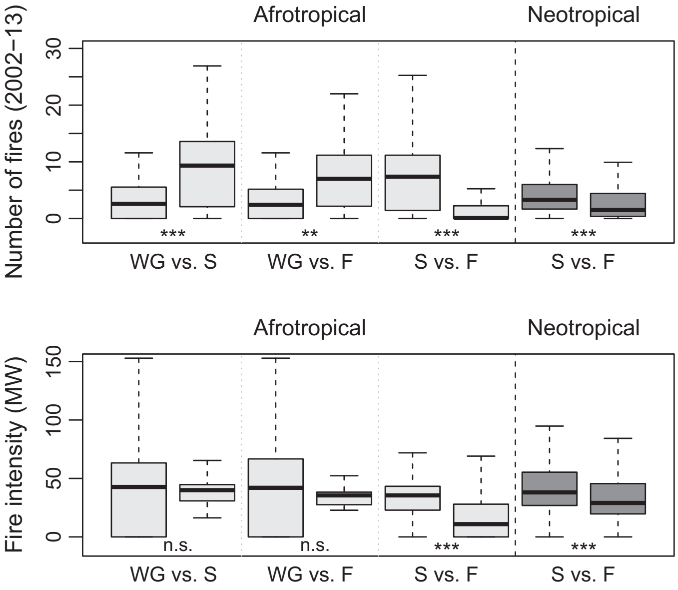

Figure 3 Fire regime differences within zones of resource overlap between pairs of vegetation states in Afrotropical (light grey boxes) and Neotropical (dark grey boxes) communities. Zones of resource-niche overlap are environmental conditions under which the three-dimensional resource availability index hypervolumes of two biome states overlap (see Fig. **2** and Table **2**). See Fig. S5 for a comparison of fire regimes considering the entire range of conditions under which these biome states occur. WG: wooded grassland state; S: savanna state; F: forest state. $***P \leq 0.001$; $**P \leq 0.01$; n.s.: not significant. Outliers are not shown.

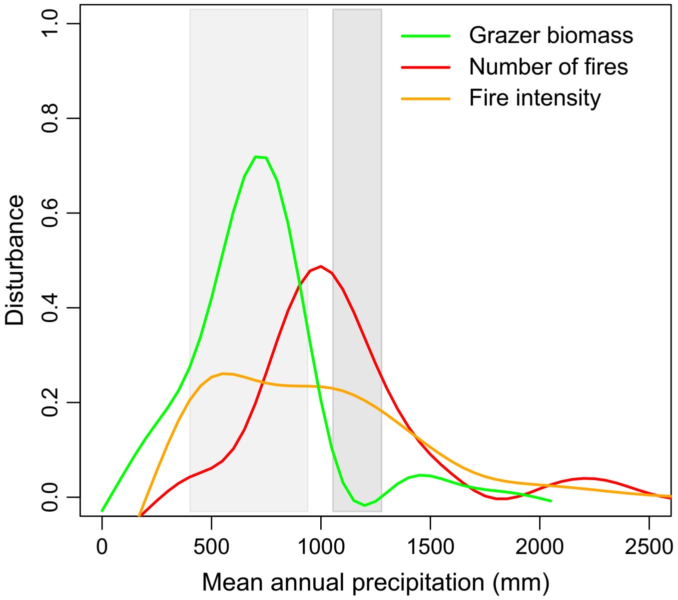

Figure 4 Disturbances (fire and grazing) in relation to precipitation in Africa. Shaded regions represent conditions under which the precipitation quantiles (95%) of two biome states overlap (see Fig. S4b). Light and dark grey bars are rainfall conditions shared by, respectively, the wooded grassland and the savanna states, and the savanna and forest states. Lines were fitted using nonparametric smoothers in general additive models performed on standardised (by range) fire and grazer data. 'Number of Fires' and 'Fire Intensity' refer to the number of active fire records (hotspots) and fire radiative power, respectively, extracted from MODIS data. Grazer biomass data in relation to precipitation were obtained from Hempson *et al.* (2015); for details on these data see Appendix B.

bivory maps precludes a deeper analysis, evidence suggests that the occurrence of the wooded grassland state under conditions prone to savannas and/or forests results from the coupling between grazing and browsing effects, which selects for herbivory-adapted shrubs and grasses (McNaughton 1984; Dublin *et al.* 1990; Bond *et al.* 2001; Asner *et al.* 2009; Moe *et al.* 2009; Staver *et al.* 2012; Sankaran *et al.* 2013; Hempson *et al.* 2015). Five independent arguments support this rationale. First, the low fire frequencies (Fig. 3) found for the wooded grassland state are consistent with reductions in fire frequency mediated by the formation of grazing lawns (McNaughton 1984; Staver *et al.* 2012; Hempson *et al.* 2015). Second, the wooded grassland state was characterised by very low TBA (lower than 2.69 m^2 ha^{-1}; Table 1) suggesting communities dominated by sparse and short woody species similar to those dominated by browsing-adapted shrubs (Bond *et al.* 2001; Staver *et al.* 2012; Sankaran *et al.* 2013). Third, grazing data suggest that the peak of present-day grazer biomass (green line in Fig. 4) coincides with the range of precipitation values in which the wooded grassland and the savanna states are most likely to be found as alternative biome states (light grey shading in Fig. 4). Fourth, a similar bimodality in the structure of African grassy systems resulted from herbivore exclusion in South African arid savannas, suggesting the emergence of tree-dominated communities in certain soil substrates after herbivory was reduced (see Fig. 3A in Asner *et al.* 2009). Finally, the large variability in fire intensity within the wooded grassland state (Figs. 3 and S5) agrees with model predictions of both very low and high fire intensities associated with episodic fluctuation in the grazing–browsing proportions (Van Langevelde *et al.* 2003). This set of independent evidence supports the hypothesis that feedbacks triggered by the coupling of heavy browsing and patchy grazing stabilise shrub-dominated wooded grasslands as an alternative state to tree-dominated savannas and forests in semi-arid Africa. Such a mechanism is consistent with suggestions that herbivory and fire form a single trade-off axis in semi-arid grassy ecosystems, selecting for species with very contrasting strategies (Bond *et al.* 2001; Staver *et al.* 2012). However, because the evidence presented here is indirect, further research is needed to fully elucidate the exact drivers and mechanisms associated with the observed patterns.

The overlaps among the environmental envelopes of tropical biome states can provide insights onto the extent to which disturbance regime changes could affect resource space occupation by these community types. For instance, 68% of the resource space occupied by savannas was shared with forests in the Neotropics, while the same applied to 41% in the Afrotropics (Fig. 2; Table 2). Because forest trees grow faster than savanna trees under the same conditions (Viani *et al.* 2011) and require less nutrients to produce a closed canopy (Silva *et al.* 2013), fire exclusion would probably prevent the occupation of these resource conditions by savanna species due to light competition, particularly in the Neotropics. If the wooded grassland state is considered, fire inhibition could result in a reduction of 74% in the resource space occupied by Afrotropical savannas (Table 2). The wooded grassland state also seems highly influenced by herbivory in Africa and the reduction in grazing below critical levels could reduce resource space occupation by these communities to 11% of their current range (Table 2). The wooded grassland and the savanna states were never present for more than half of the resource space occupied by forests in both biogeographic contexts (Fig. 2; Table 2). Outside the overlapping conditions, resource availability is high (Fig. 2) and forest canopy formation is fast, resulting in the long-term exclusion of savanna and wooded grassland species from the forest seed bank. While the overlaps reported here could potentially decrease if environmental information from finer spatial scales was added, they were sufficiently large to highlight the key role of disturbance in maintaining tropical grassy ecosystems. Moreover, the overlaps would be probably larger if thickets and pure grasslands had been included in the analyses (Bond 2008; Lehmann *et al*. 2011).

The AST provides a suitable framework to understand landscape mosaics. Within this framework, resources have two main roles (1) they contribute to define the range of conditions under which biomes can occur as alternative states; and (2) within this range, resource availability interacts with disturbance regimes and plant traits to influence the probability of a state shift (Whittaker & Levin 1977; Warman & Moles 2009; Lehmann *et al*. 2011; Hoffmann *et al*. 2012). For instance, within the resource range where both savannas and forests can potentially occur, any factor that increases tree growth rates of forest species (e.g. patches of high resource availability) and/or reduces the frequency of fires (e.g. increased fuel moisture, high topographic heterogeneity, grazing) should increase the probability of forest establishment (Warman & Moles 2009; Lehmann *et al*. 2011; Viani *et al*. 2011; Hoffmann *et al*. 2012). Within the range at which only the wooded grassland and the savanna states are possible in Africa, the probability of wooded grasslands should increase with any factor increasing the concentration of grazing activity (e.g. high soil nutrient availability, proximity to water sources or human populations) and decrease with any factor reducing it (e.g. low nutrient availability, high precipitation levels, diseases, high predator density, frequent fires) (Bell 1982; McNaughton 1984; Hempson *et al*. 2015). Finally, within the range of conditions under which the three states are possible in Africa, the probability of forest establishment should increase with decreasing frequency of browsing (e.g. low rainfall) and fire (e.g. both high and low rainfall amounts, overgrazing by livestock), and/or with increasing community productivity (e.g. patches with high level of resources). In the absence of large mammal herbivores (e.g. in South America), low rainfall amounts limiting both fire spread and forest tree growth would favour thickets instead of wooded grasslands (Bond 2008; Lehmann *et al*. 2011) as the lack of browsing control on woody plants would result in the outcompetition of grasses by trees and shrubs (Bond 2008; Lehmann *et al*. 2011; February *et al*. 2013). Such processes can be substantially accelerated by livestock-driven overgrazing (Riginos & Young 2007; Bond 2008).

The distribution of tropical biomes has long been considered to result from overlapping resource gradients imposing limitations to plant productivity. Even when models incorporate disturbances, their effects are generally considered with respect to plant biomass consumption rather than in the assembly of communities in which species have specific growth and resistance strategies. We provide empirical evidence that distinct biome states, characterised by different patterns of community functioning, may share similar environmental conditions as long as these biomes are submitted to different disturbance regimes, supporting the alternative states theory. Moreover, we provide suggestive evidence for alternative grassy states in Africa, depending on the interplay and prevalence of fire and herbivory as disturbance drivers. Overall, our results indicate that disturbance is an important and general factor driving and maintaining alternative biome states and vegetation mosaics in the tropics.

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AUTHORSHIP

All of the authors contributed to the project's final conception; V.L.D. and J.G.P. developed the methodology; V.L.D., M.H. and J.G.P. acquired data; V.L.D performed statistical analyses; V.L.D. wrote the first draft of the manuscript and all authors contributed to the final version.

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