TITLE: Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states

A. Carla Staver[1], *Sally Archibald*[2] *& Simon Levin*[1]

[1] Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544
[2] Natural Resources and Environment, CSIR, Pretoria 0001, South Africa

Running header: Alternative stable states in tree cover in sub-Saharan Africa

ABSTRACT

Savannas are known as ecosystems with tree cover below climate-defined equilibrium values. However, a predictive framework for understanding constraints on tree cover is lacking. We present a) a spatially extensive analysis of tree cover and fire distribution in sub-Saharan Africa, and b) a model, based on empirical results, demonstrating that savanna and forest may be alternative stable states in parts of Africa, with implications for understanding savanna distributions.

Tree cover does not increase continuously with rainfall, but rather is constrained to low (<50%, “savanna”) or high tree cover (>75%, “forest”). Intermediate tree cover rarely occurs. Fire – which prevents trees from establishing – differentiates high and low tree cover especially in areas with rainfall between 1000mm and 2000mm. Fire is less important at low rainfall (<1000mm), where rainfall limits tree cover, and at high rainfall (>2000mm), where fire is rare. This pattern suggests that complex interactions between climate and disturbance produce emergent alternative states in tree cover.

The relationship between tree cover and fire was incorporated into a dynamic model including grass, savanna tree saplings and savanna trees. Only recruitment from sapling to adult tree varied depending on the amount of grass in the system. Based on our empirical analysis and previous work, fires spread only at tree cover of 40% or less, producing a sigmoidal fire probability distribution as a function of grass cover and therefore a sigmoidal sapling to tree recruitment function. This model demonstrates that, given relatively conservative and empirically supported assumptions about the establishment of trees in savannas, alternative stable states for the same set of environmental conditions (i.e. model parameters) are possible via a fire feedback mechanism.

Integrating alternative stable state dynamics into models of biome distributions could improve our ability to predict changes in biome distributions and in carbon storage under climate and global change scenarios.

KEY WORDS: savanna, forest, tree cover, biome distribution, rainfall, fire, multiple stable states

INTRODUCTION

The determinants of the distribution of the savanna biome are a matter of some debate. Traditionally, ecologists have treated savanna and forest distributions, and biome distributions more broadly, as if they are rigidly determined by climate (Whittaker 1974, Breckle 1999, Woodward *et al*. 2004). However, modeling and experimental work have shown that mesic savannas can exist where climate, soils, and topography suggest forest should dominate (Swaine *et al*. 1992, Moreira 2000, Russell-Smith *et al*. 2003, Bond 2008). In Africa, climate constrains maximum tree cover, but tree cover varies substantially below that maximum (Sankaran *et al*. 2005), due to factors including fire and herbivory (Bucini & Hanan 2007, Bond 2008, Sankaran *et al*. 2008).

Biome models that include fire as a major determinant of tree cover perform better in predicting savanna and forest distributions than those based solely on climatic and edaphic inputs (Woodward *et al*. 2004, Bond *et al*. 2005, Scheiter & Higgins 2009). Fire exclusion experiments provide empirical evidence that fire can maintain a savanna where climatic and edaphic conditions could support a closed canopy forest (Swaine *et al*. 1992, Moreira 2000, Russell-Smith *et al*. 2003). However, the effects of fire are strongly context dependent. Sankaran *et al*. (2005) showed that rainfall limits tree cover up to about 650mm mean annual rainfall in Africa, but that fire can reduce tree cover below its potential (see also Bucini & Hanan 2007, Bond 2008, Sankaran *et al*. 2008).

For Africa, existing continental-scale analyses of the tree cover in savanna have focused only on savannas themselves (Sankaran *et al*. 2005, Bucini & Hanan 2007, Sankaran *et al*. 2008) and have been severely restricted in spatial and ecological extent (no data above 1200mm rainfall: Sankaran *et al*. 2005). A more comprehensive analysis of tree cover and of biome distributions in Africa is vital to a more complete understanding of the constraints on savanna distributions and the ecological dynamics that characterize savanna systems. Specifically, an analysis spanning the transition from savanna to forest is necessary for evaluating of the processes that differentiate the two.

We analyzed spatial patterns of tree cover with respect to rainfall and fire frequency using satellite-derived datasets with complete spatial coverage of sub-Saharan Africa. These data allow analyses that were impossible in previous continental-scale analyses of tree cover; in particular, we can explore processes at the transition between forest and savanna.

Additionally, the dataset allows an exploration of scale dependence of determinants of tree cover and biome distributions (Scanlon *et al*. 2007). Climatic determinants of biome distribution are often discussed at regional scales (Williams *et al*. 1996, Sankaran *et al*. 2005), while disturbances that reduce tree cover below its ‘climate potential’ are usually considered as local processes (Sankaran *et al*. 2005). Explicit considerations of scale are included in our analysis of the savanna-forest boundary.

Because these results provide only correlative evidence for the importance of the drivers we identify, we have further evaluated the results of our continental-scale analysis of tree cover with an analytical and mechanistic model of tree-grass dynamics in savannas. This simple model invokes some basic assumptions about the ecology of fire in savannas to produce savanna and forest dynamics similar to those observed in our analysis. Together, the empirical observations and model presented in this paper should add to our theoretical and predictive understanding of the dynamics that constrain savanna and forest distributions.

METHODS

We analyzed patterns of tree cover with respect to rainfall and fire frequency using satellite data. We derived fire frequency and tree cover from MODIS satellite reflectance data at 500m resolution. We derived rainfall from the Tropical Rainfall Measuring Mission best-estimate precipitation product (TRMM 3B43), which has a resolution of 0.25 degrees (approx. 28km x 28km at the equator and 28km x 20km at the southern tip of Africa).

- *Tree cover*: Percentage tree cover was calculated from the MOD44B Collection 3 product (Hansen *et al.* 2003). This product gives percent canopy cover (rather than the projected crown cover) at an appropriate scale and resolution for discriminating regional patterns (Bucini & Hanan 2007, Miles *et al.* 2006). A validation exercise in Zambia yielded root mean square errors (RMSE) of 5.2% (Hansen *et al.* 2002), although the RMSE of the global dataset is estimated at 9.1%. This error decreases substantially when data are averaged over slightly larger scales because geolocation issues account for most error (Hansen *et al.* 2003). The product was only calibrated against trees above 5m tall and may underestimate shrubby species.

- *Fire frequency*: We used the monthly MCD45A1 burnt area product to derive an estimate of fire frequency (Roy *et al.* 2008). MCD445A1 uses change detection procedures based on a bi-directional reflectance distribution function (BRDF) to identify burn scars in the landscape and identifies burnt areas in Africa with high accuracy (R^2=0.75: Roy *et al.* 2008). Improved resolution (500m instead of 1km) and information on data quality make this product more reliable than previous burnt area products. An independent validation by Tsela *et al.* (2010) across biomes demonstrated that accuracy is higher in open systems (R^2=0.86) and lower in pine plantations (R^2=0.38); fires less than 500mx500m in size could be detected but at lower probability. For this analysis, monthly data layers from April 2000 to March 2008 were combined to calculate the number of times a pixel burned in eight years (fire frequency). Pixels with invalid data more than two times a year on average were excluded based on quality flags. This yielded a 500m resolution map of number of burns in eight years (ranging from zero to 13). Savanna fires are grass-fuelled with average return times ranging from two to six years (van Wilgen & Scholes 1997); while an eight year dataset is short, the dataset does span the range of fire frequencies expected in the system.
- *Rainfall*: The TRMM combines satellite-data, rain gauge data, and precipitation models to produce a best-estimate of global precipitation at hourly to annual scales. A validation by Nicholson *et al*. (2003) over West Africa demonstrated a root mean square error of 0.7mm per day and a zero bias, although subsequent validations

indicated that it is less accurate in topographically variable landscapes (Dinku *et al.* 2007). In this analysis, spatially-explicit monthly precipitation rates were summed to produce annual rainfall for each year (1998-2007) and then averaged to estimate mean annual rainfall (MAR).

These data sets, re-projected to an Albers equal area projection, were clipped at 15 degrees north to include only sub-Saharan Africa. Fire and tree data were resampled to align with the larger-scale TRMM data. They were then progressively degraded to produce maps of average tree cover and average fire frequency at 500m, 1km, 2.5km, 5km, 10km, 25km, 50km, and 100km resolution. Rainfall data were not available for fine scales (resolution less than about 25km). However, we have included smaller scales because tree cover does vary at these scales, while rainfall varies over regional to continental scales. To reduce potential pseudo-replication, we have sub-sampled plots at scales smaller than 25km to include only the center plot of each 25km block (i.e. only one tree cover measurement per rainfall measurement).

Rainfall and fire data have been included for the longest available time period, despite the fact that this has resulted in mismatched time periods for the data. This inclusion has allowed us to establish the most rigorous possible estimates for long term mean annual rainfall and fire frequency across sub-Saharan Africa.

The centroid of each TRMM pixel was used to create a regular grid of 22,726 sampling points over sub-Saharan Africa. Rainfall, average percent tree cover, and average fire frequency were extracted at each point for each scale of analysis. At resolutions of 50km and 100km, which are larger than a TRMM pixel, the number of unique data points available was reduced to 6982 and 1751, respectively, but at smaller scales, all of the available sampling points were used.

All analyses were run at all scales. We chose 1km and 50km scales for presentation, but this choice has no qualitative impact on the findings presented herein. Data were extracted in ERDAS 9.3 and ArcGIS 2.8.1 and analyzed in R 2.8.1 (R Development Core Team 2008). Generalized additive model fitting was done with a Gaussian link function using the R package mgcv 1.4-1.1 (Wood 2008).

RESULTS & DISCUSSION

Are savanna and forest distinct states?

Frequency distributions of tree cover across sub-Saharan Africa showed two clear maxima at about 15% and 80% cover with a frequency minimum at about 60%; rainfall did not show a similarly bimodal distribution (Figure 1). The lower of these tree cover peaks represents savanna, the higher peak forest. Sites with intermediate tree cover (50-75%) were rare (density < 5%), although the corresponding range of rainfall occurs frequently. Pixel-scale data were split into savanna and forest subsets based on the mid-point of the minimum interval. This mid-point was consistent across scales, ranging between 60 and 62.5% tree cover, with the savanna peak ending around 40-50% tree cover.

The distribution of savanna and forest tree cover classes along a rainfall gradient indicates that savannas can occur at MAR of up to 2000mm per year and that forests occur frequently at MAR as low as 800mm to 1000mm per year (Figure 2). Precipitation thresholds for each type were defined where the proportion of plots in the class fell below

1% (descending the precipitation gradient for forests, ascending for savanna). Thresholds were constant across scales from 500m to 100km. To further evaluate the range of rainfall at which two alternative states were present, we divided sites into 200mm rainfall classes. Tree cover is distinctly bimodal between MAR 1000mm and 2000mm at all scales (Figure 3 for 1km scale).

Plotting predictions of tree cover versus rainfall (Figure 4 and Table 1) shows that tree cover was strongly related to rainfall only at low rainfall (<1000mm) and at high rainfall (>2000mm). At all intermediate rainfall levels, climate can apparently support forest, but savanna persisted over large areas.

These thresholds for the minimum rainfall that supports forest (1000mm MAR) and the maximum rainfall at which savannas occur (2000mm MAR) differ somewhat from previous estimates calculated from field data, which put the lower limit of forest at 650mm ± 125mm MAR and did not define a maximum rainfall for savannas (Sankaran *et al*. 2005). However, the 1000mm minimum rainfall threshold for canopy closure (forest) is consistent with a continental analysis of fire exclusion experiments by Bond *et al*. (2005). Below 1000mm annual rainfall, fire exclusion resulted in increases in woody cover but not in a transition to closed-tree canopy forest, while above 1000mm annual rainfall, fire exclusion resulted in a transition from savanna to forest (Bond *et al*. 2005). This analysis focuses on tree cover rather than on woody cover; processes that lead to high woody cover at lower rainfall generally do not result in high tree cover and, while important to land managers, can not be explored by this framework. Interestingly, in South American examples, savanna persisted up to 1400mm rainfall in fire exclusion experiments, suggesting that a continental comparison of the processes that differentiate savanna from forest might be fruitful.

Evidence of stabilizing feedbacks

At intermediate rainfall (1000-2000mm MAR), tree cover was strongly reduced when fire was present. Below 1000mm MAR savanna could persist without fire. Fire did not occur frequently above 2000mm MAR (Figure 4). Including the presence/absence of fire as a categorical variable in generalized additive models of mean annual rainfall on tree cover improved model fit significantly across all scales (Table 1). Again, results were scale-invariant; GAMs including both rainfall and fire explained between 54% (at fine scales) and 76% (at coarse scales) of the variation in tree cover. These analyses indicate that, depending on rainfall, fire was probably an important stabilizing feedback operating in savannas.

Fire does not fully explain variation in tree cover response to rainfall. In part, this may be because the available satellite fire record only spans the last 8 years. However, other drivers (e.g. herbivory, nutrient cycling, hydrology, human activity) that are difficult to quantify remotely may also contribute. In addition, this analysis cannot determine whether fire promotes savanna or vice versa. Both are likely. We know from fire exclusion experiments around the world that fire reduces tree cover (Swaine *et al*. 1992, Moreira 2000, Russell-Smith *et al*. 2003). We also know that grass biomass drops off rapidly as tree cover increases (Scholes 2003, Lloyd *et al*. 2008), such that fires can only spread in systems with tree cover of less than about 40% (Hennenberg *et al*. 2006, Archibald *et al*. 2009). These relationships suggest a stabilizing feedback contributing to maintenance of savanna and forest as alternative stable states at intermediate rainfall.

MODEL DESCRIPTION & RESULTS

Our analysis of the distribution of tree cover in sub-Saharan Africa provides correlative evidence a) that rainfall constrains tree cover below 1000mm MAR, b) that savanna and forest are distinct states that are both frequent at intermediate rainfall, and c) that forest dominates strongly above 2000mm MAR. Evaluating the stability of these distinct states is not possible from these short-term data. However, we have incorporated the fire feedback mechanism suggested by our empirical analysis into a simple model to evaluate the potential for savanna and forest to exist as alternative stable states.

The model is non-spatial but we have, in effect, created limited space by holding the total area of grass (*G*), tree saplings (*S*) and adult trees (*T*) constant (see Figure 5). Grass is the default type and occupies all areas not explicitly occupied by saplings or trees. Saplings establish in proportion to the number of trees in the system and can only establish in units occupied by grass (rate constant β). Trees recruit from saplings at a rate $\omega(G)$ in proportion to the number of saplings. The recruitment rate $\omega(G)$ varies with grass as described below. Both saplings and trees die and revert to grass in proportion to their number (rate μ and ν). The model is formally described by the following set of coupled differential equations, which always add to zero (since G+S+T=total area):

$$\frac{dG}{dt} = \mu S + \nu T - \beta G T \qquad (1)$$

$$\frac{dS}{dt} = \beta G T - \omega(G) \cdot S - \mu S \qquad (2)$$

$$\frac{dT}{dt} = \omega(G) \cdot S - \nu T \tag{3}$$

Our model incorporates two fundamental assumptions about savanna ecology. First, based in part on our findings from this study, we assume that fire spread in savannas depends on grass abundance, as reflected in the function $\omega(G)$. Savannas with tree cover below approximately 40% burn frequently, but fire is almost non-existent in systems with tree cover above the 40% threshold (Archibald *et al*. 2009). We can incorporate this nonlinear response of fire frequency to grass abundance via $\omega(G)$, the recruitment of saplings into trees. Fire rarely kills savanna tree saplings, which are able to resprout after fire (Bond & Midgley 2001, Hoffmann *et al*. 2009, Schutz *et al*. 2009) and infrequently affects adult trees (Hoffmann & Solbrig 2003). Fire does impose a major control on the recruitment of tree saplings into adults (Higgins *et al*. 2000, Hoffmann *et al*. 2009). Taken together and averaged over time, these features of savanna systems mean that tree recruitment should be high when grass abundance (and fire frequency) is low, should fall off rapidly near 40% tree cover, and should remain low at high grass abundance (see Figure 5). We make no assumptions about $\omega(G)$ other than smoothness and its general sigmoidal shape.

To solve for equilibria, we set each of equations (1), (2) and (3) equal to zero. One solution is the trivial S=T=0, but there are also internal equilibria defined by the following condition:

$$\omega(\bar{G}) = \frac{\mu\nu}{\beta\bar{G} - \nu} \tag{4}$$

For convenience, define:

$$f(G) = \frac{\mu\nu}{\beta G - \nu} \tag{5}$$

Internal equilibrium points are thus points where:

$$\omega(\overline{G}) = f(\overline{G}) \tag{6}$$

The stability of the equilibria depends on the relative slopes of these two functions, as shown below.

Since S+G+T=0, we can eliminate equation (2) and analyze the stability of equilibria by constructing the Jacobian matrix:

$$J = \begin{bmatrix} -(\nu + \omega(G)) & S\omega'(G) - \omega(G) \\ \nu - \beta G - \mu & -(\mu + \beta T) \end{bmatrix} \tag{9}$$

It can be shown via application of the Routh-Hurwitz stability criteria that the eigenvalues of the Jacobian have negative real parts (i.e. the equilibrium is stable, ignoring the marginal case of zero real parts) if and only if the trace of the matrix is negative and the determinant positive (Edelstein-Keshet 2005).

For this system, the eigenvalues of the Jacobian are always real, and the condition on the trace is trivially satisfied. The condition on the determinant is satisfied when:

$$\omega'(\overline{G}) > \frac{-\beta\mu\nu}{\left(\beta\overline{G} - \nu\right)^2} = f'(\overline{G}) \tag{10}$$

This stability condition makes a graphical analysis of this system of equations intuitive (Figure 5). Where plots of $\omega(G)$ and $f(G)$ intersect, equilibria exist. Those equilibria are stable when the slope of $\omega(G)$ is greater than the slope of $f(G)$. Note that we have made no assumptions about the functional form of $\omega(G)$ in our analysis. However, its functional form will determine the number and stability of equilibria that define the system, and for illustrative purposes we henceforth assume that $\omega(G)$ is sigmoidal. Depending on the values of rate constants, the dynamic system of equations then has between zero and three internal equilibria, with between zero and two stable internal equilibria (Figure 5). Crucially, this sigmoidal form for $\omega(G)$ makes multiple stable equilibria possible. This simple model, based on empirically well-supported assumptions about fire and tree establishment in savannas, suggests that the savanna and forest patterns observed in our empirical analysis of tree cover actually are alternative stable states. In addition, this model suggests that a positive fire feedback within savanna is a sufficient mechanism for promoting alternative stable states. The model also captures situations in which only one stable equilibrium exists, at either low or high grass cover.

CONCLUSIONS

These empirical and modeling results indicate that savanna and forest may reasonably be interpreted as alternative states at intermediate rainfall. At low rainfall, fire does not play a major role in determining tree cover. At intermediate rainfall (between 1000mm and 2000mm), interactions between rainfall and fire produce discontinuities in tree cover with alternative savanna and forest states. At high rainfall, fire is rare and forests dominate. Moreover, savannas appear to have tree cover up to only about 40% to 50%, consistent with studies that have found that grass productivity becomes negligible at tree cover greater than 50% (Lloyd *et al*. 2008).

Ecosystems subject to multiple stable states have distinct configurations under the same set of environmental conditions, as in the model presented here. Multiple stable states are not possible without stabilizing feedbacks that function within a state to maintain it (Scheffer & Carpenter 2003, Sternberg 2001). Transitions among stable states occur when feedbacks break down or when environmental changes exceed thresholds (Carpenter *et al.*1985, Scheffer *et al*. 1993, van de Koppel *et al*. 1997). Those transitions are often rapid and are not reversible on short time scales (Scheffer & Carpenter 2003).

Savanna and forest have sometimes been modeled as alternative stable states (Sternberg 2001, Favier *et al*. 2004b, Beckage *et al*. 2009, Accatino *et al*. 2010, Higgins *et al*. 2010), but empirical evidence has been so far lacking at the continental scale. Paleoecological studies have shown that rapid changes between tree-dominated and grass-dominated systems are common (Gillson 2004), but these span time scales at which climate has varied substantially. The discontinuity in the transition from savanna to forest (Hennenberg *et al*, 2006, Pueyo *et al*. 2010) also suggests alternative stable state dynamics, but existing continental analyses of tree cover have shown only that tree cover in savannas is variable (Sankaran *et al*. 2005, Bucini *et al*. 2007, Sankaran *et al*. 2008).

Within savanna, a number of factors, including fire, might result in stabilizing feedbacks. Fire suppresses tree cover (Swaine *et al*. 1992, Moreira 2000), probably by limiting recruitment of saplings to trees (Hoffmann 1999, Higgins *et al*. 2000). Similarly, there seems to be a threshold above which tree cover (i.e. insufficient grass) suppresses fire (Hennenberg *et al*. 2006, Archibald *et al.* 2009). While other factors influence tree emergence – and the data presented here yield an essentially correlative result – our combination of empirical analysis and modeling supports the sufficiency of rainfall-fire interactions for maintaining savanna and forest as alternative stable states at the continental scale. However, scale-invariance of these results suggests that processes that produce these patterns operate locally (Scanlon *et al*. 2007).

Interpreting savanna and forest as alternative stable states makes understanding the transitions between savanna and forest important. We know, from fire exclusion experiments (Swaine *et al*. 1992, Moreira 2000, Russell-Smith *et al*. 2003) and documentation of forest encroachment from around the world (Loehle *et al*. 1996, Bowman *et al*. 2001, Favier *et al*. 2004a, Goetze *et al*. 2006, Mitchard *et al*. 2009), that changing burning practices and patterns through landscape fragmentation and management policy have resulted in widespread encroachment of forest into savanna.

However, transitions from forest to savanna in the absence of anthropogenic deforestation are less well understood. Paleoecological work suggests that contemporary savannas established in areas that are now wet enough to support forest during a period with drier climatic conditions (Desjardins *et al*. 1996). This hypothesis fits well with the alternative stable state framework presented here, wherein forest could be converted to savanna when rainfall decreased to below 1000mm. Savanna might then be stable even if rainfall increased. In fact, C4 grass evolution and the global expansion of savanna occurred during the Miocene, a period marked not only by aridity but also by increased rainfall seasonality (Keeley & Rundel 2005). A similar rainfall-fire interaction mechanism has been invoked to explain some of the dynamics at the prairie-forest ecotone in the Northern US (Grimm 1983, Grimm 1984).

Global projections indicate that rainfall and fire frequency will change in coming decades due to increasing atmospheric CO_2 and associated climate change. These changes may result in major biome shifts in favor of savanna over forest. Recent work has suggested that the Amazon rainforest may be at risk of severe drying (Phillips *et al*. 2009), putting large areas that are currently forest at risk of a transition to savanna. Our results imply that changes in biome distribution in response to climate change will not result in smooth transitions from savanna to forest or back. We can expect changes to be sudden.

ACKNOWLEDGEMENTS

We gratefully acknowledge William Bond, Ignacio Rodríguez-Iturbe, Lars Hedin and Bob Scholes for their helpful comments. Funding for this work was provided by a grant for the study of ‘The Emergence and Evolution of Ecosystem Functioning’ from the Andrew W. Mellon Foundation and by the South African CSIR Young Researchers Establishment Fund.

WORKS CITED

Accatino, F, *et al*. 2010. Tree-grass co-existence in savanna: interactions of rain and fire. *J. Theor. Biol.* (doi:10.1016/j.jtbi.2010.08.012).

Archibald, S, *et al*. 2009. What limits fire? An examination of drivers of burnt area in Southern Africa. *Global Chang. Biol.* 15, 613-630.

Beckage, B, WJ Platt and LJ Gross. 2009. Vegetation, fire and feedbacks: a disturbance-mediated model of savannas. *Am. Nat.* 174: 805-818.

Bond, WJ and JJ Midgley. Ecology of spouting in woody plants: the persistence niche. *TREE* 16: 45-51.

Bond, WJ, FI Woodward and GF Midgley. 2005. The global distribution of ecosystems in a world without fire. *New Phytol.* 165, 525-537.

Bond, WJ. 2008. What limits trees in C4 grasslands and savannas? *Annual Rev. Ecol. Evol. Syst.* 39, 641-659.

Bowman, D, A Walsh and DJ Milne. 2001. Forest expansion and grassland contraction within a *Eucalyptus* savanna matrix between 1941 and 1994 at Litchfield National Park in the Australian monsoon tropics. *Glob. Ecol. Biogeog.* 10, 535-548.

Breckle, SW 1999. *Walter's Vegetation of the Earth, 4th ed*. Springer: Berlin.

Bucini, G and NP Hanan. 2007. A continental-scale analysis of tree cover in African savannas. *Global Ecol. & Biogeog.* 16, 593-605.

Carpenter, S, JF Kitchell and JR Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35, 634-639.

Desjardins, T, *et al*. 1996. Changes in the forest-savanna boundary in Brazilian Amazonia during the Holocene revealed by stable isotope ratios of soil organic carbon. *Oecologia* 108, 749-756.

Dinku, T, *et al*. 2007. Validation of satellite rainfall products over East Africa's complex topography. *Internat. J. Remote Sens.* 28: 1503-1526.

Edelstein-Keshet, L. 2005. *Mathematical models in biology*. Society for Industrial and Applied Mathematics: Philadelphia. 586 pp.

Favier, C, C de Namur and MA Dubois. 2004a. Forest progression modes in littoral Congo, Central Atlantic Africa. *J. Biogeog.* 31, 1445-1461.

Favier, C. *et al*. 2004b. Modelling forest-savanna mosaic dynamics in man-influenced environments: effects of fire, climate and soil heterogeneity. *Ecol. Model.* 171, 85-102.

Gillson, L. 2004. Testing non-equilibrium theories in savannas: 1400 years of vegetation change in Tsavo National Park, Kenya. *Ecol. Complex.* 1, 281-298.

Goetze, D, B Horsch and S Porembski. 2006. Dynamics of forest-savanna mosaics in north-eastern Ivory Coast from 1954 to 2002. *J. Biogeog.* 33, 653-664.

Grimm, EG. 1983. Chronology and dynamics of vegetation change in the prairie-woodland region of southern Minnesota, USA. *New Phytol*. 93: 311-350.

Grimm, EG. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-19th century. *Ecol Monogr*. 54: 291-311.

Hansen, M, *et al*. 2002. Development of a MODIS tree cover validation data set for Western Province, Zambia. *Remote Sens. Environ.* 83: 320-335.

Hansen, M, *et al*. 2003. Global percent tree cover at a spatial resolution of 500m: first results of the MODIS vegetation continuous fields algorithm. *Earth Interact.* 7, 1-15.

Hennenberg, KJ, *et al*. 2006. Phytomass and fire occurrence along forest-savanna transects in the Comoé National Park, Ivory Coast. *J. Trop. Ecol.* 22: 303-311.

Higgins, S, WJ Bond and WSW Trollope. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *J. Ecol*. 88: 213-229.

Higgins, SI, S Scheiter and M Sankaran. 2010. The stability of African savannas: insights from the indirect estimation of parameters of a dynamic model. *Ecology* 91: 1682-1692.

Hoffmann, WA. 1999. Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology* 80, 1354-1369.

Hoffmann, WA and OT Solbrig. 2003. The role of topkill in the differential response of savanna woody species to fire. *Forest Ecol. Manag.* 180: 273-286.

Hoffmann, WA, *et al*. 2009. Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology* 90: 1326-1337.

Keeley, JE and PW Rundel. 2005. Fire and the Miocene expansion of C4 grasslands. *Ecol. Letters* 8, 683-690.

Lloyd, J, *et al*. 2008. Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: a quasi-global estimate. *Tree Phys* 28: 451-468.

Loehle, C, BL Li and RC Sundell. 1996. Forest spread and phase transitions at forest-prarie ecotones in Kansas, USA. *Landscape Ecol.* 11, 225-235.

Miles, L, *et al*. 2006. A global overview of the conservation status of tropical dry forests. *J. Biogeog.* 33: 491-505.

Mitchard, ETA, *et al*. 2009. Measuring woody encroachment along a forest-savanna boundary in Central Africa. *Earth Interact.* 13: 8.

Moreira, AG. 2000. Effects of fire protection on savanna structure in Central Brazil. *J. Biogeog.* 27, 1021-1029.

Nicholson, SE, *et al*. 2003. Validation of TRMM and other rainfall estimates with a high-density gauge dataset for West Africa. Part I: validation of GPCC rainfall product and pre-TRMM satellite and blended products. *J. Appl. Meteorol.* 42: 1337-1354.

Phillips, OL, *et al*. 2009. Drought sensitivity of the Amazon rainforest. *Science* 323, 1344-1347.

Pueyo, S, *et al*. 2010. Testing for criticality in ecosystem dynamics: the case of Amazonian rainforest and savanna fire. *Ecol Lett* 13: 793-802.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roy, D, *et al*. 2008. The collection of 5 MODIS burned area product – global evaluation by comparison with the MODIS active fire product. *Remote Sens. Env.* 112, 3690-3707.

Russell-Smith, J, *et al*. 2003. Response of *Eucalyptus*-dominated savanna to frequent fires: lessons from Munmarlary, 1973-1996. *Ecol. Monog.* 73, 349-375.

Sankaran, M., *et al*. 2005. Determinants of woody cover in African savannas. *Nature* 438, 846-849.

Sankaran, M, J Ratnam and N Hanan. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecol. & Biogeog.* 17, 236-245.

Scanlon, TM, *et al*. 2007. Positive feedbacks promote power-law clustering of Kalahari vegetation. *Nature* 449, 209-212.

Scheffer, M, *et al*. 1993. Alternative equilibria in shallow lakes. *TREE* 8, 275-279.

Scheffer, M. and SR Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *TREE* 18, 648-656.

Scheiter, S and SI Higgins. 2009. Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modeling approach. *Global Change Biol.* 15: 2224-2246.

Scholes, RJ. 2003. Convex relationships in ecosystems containing mixtures of trees and grass. *Environ. Res. Econ.* 26: 559-574.

Schutz, A, WJ Bond and M Cramer. 2009. Juggling carbon: allocation patterns of a dominant tree in a fire-prone savanna. *Oecologia* 160: 235-246.

Sternberg, LDL 2001. Savanna-forest hysteresis in the tropics. *Global Ecol. & Biogeog.* 10: 369-378.

Swaine, M, W Hawthorne and T Orgle. 1992. The effects of fire exclusion on savanna vegetation at Kpong, Ghana. *BioTropica* 24, 166-172.

Tsela, P, *et al*. 2010. Validation of the MODIS burned-area products across different biomes in South Africa. *Proc. of the 2010 IEEE Internat. Geosc. Remot. Sens. Symp.* 2010: 3652-3655.

van de Koppel, J, M Rietkerk and FJ Weissing. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *TREE* 12, 352-356.

Whittaker, R. 1975. *Communities and ecosystems, 2nd ed*. MacMillan: New York.

Williams, RJ, *et al*. 1996. Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory, Australia. *J. Biogeog.* 23, 747-756.

Woodward, FI, MR Lomas and CK Kelly. 2004. Global climate and the distribution of plant biomes. *Philos. T. Roy. Soc. B* 359, 1465-1476.

Wood, S.N. 2008. Fast stable direct fitting and smoothness selection for generalized additive models. *J. Roy. Stat. Soc. B* 70: 495-518.

Table 1. Results of generalized additive models fitting tree cover to rainfall and fire presence. Results are presented for models fitted without and with fire and for ANOVA/GCV testing whether adding fire improved model fit.

						Terms			Fire improved fit?		
scale	Model	R^2	N	GCV	term	F/t	df	p	F	df	p
500m	tree cover ~ MAR	0.500	22521	232.4	MAR	2434	9.24	<0.001			
	tree cover ~ MAR * fire	0.541		213.6	fire pres/abs	1.566		0.117	225.5	8.88	<0.001
					MAR*fire	221.3	8.74	<0.001			
					MAR*no fire	2473	9.88	<0.001			
1km	tree cover ~ MAR	0.532	22794	211.2	MAR	2790	9.28	<0.001			
	tree cover ~ MAR * fire	0.574		192.3	fire pres/abs	1.414		0.679	292.2	7.73	<0.001
					MAR*fire	284	7.59	<0.001			
					MAR*no	2866	9.9	<0.00			

					fire		2	1			
2.5km	tree cover ~ MAR	0.551	22746	191.3	MAR	2999	9.30	<0.001	322.7	8.65	<0.001
	tree cover ~ MAR * fire	0.600		170.5	fire pres/abs	1.166		0.244			
					MAR*fire	324.5	8.48	<0.001			
					MAR*no fire	3121	9.95	<0.001			
5km	tree cover ~ MAR	0.565	22778	179.2	MAR	3170	9.32	<0.001	342.7	8.29	<0.001
	tree cover ~ MAR * fire	0.613		159.4	fire pres/abs	0.229		0.819			
					MAR*fire	399.6	8.14	<0.001			
					MAR*no fire	3242	9.97	<0.001			
10km	tree cover ~ MAR	0.577	22759	168.9	MAR	3328	9.32	<0.001	353.5	8.36	<0.001
	tree	0.62		149.	fire	0.93		0.348			

	cover ~ MAR * fire	5		6	pres/abs	9					
					MAR*fire	439.6	8.23	<0.001			
					MAR*no fire	3378	9.95	<0.001			
25km	tree cover ~ MAR	0.597	22757	155.4	MAR	3612	9.34	<0.001	420.1	8.62	<0.001
	tree cover ~ MAR * fire	0.652		134.1	fire pres/abs	0.770		0.441			
					MAR*fire	526	8.49	<0.001			
					MAR*no fire	3718	9.97	<0.001			
50km	tree cover ~ MAR	0.615	22703	144.9	MAR	3878	9.35	<0.001	416.6	9.79	<0.001
	tree cover ~ MAR * fire	0.673		123.0	fire pres/abs	3.98		<0.001			
					MAR*fire	550.1	9.66	<0.001			
					MAR*no fire	4014	9.97	<0.001			

100km	tree cover ~ MAR	0.638	22570	131.2	MAR	4249	9.37	<0.001	562.8	10.0	<0.001
	tree cover ~ MAR * fire	0.711		105.0	fire pres/abs	5.96		<0.001			
					MAR*fire	655.9	9.86	<0.001			
					MAR*no fire	4647	10.1	<0.001			
250km	tree cover ~ MAR	0.670	22398	108.0	MAR	4813	9.46	<0.001	877.1	10.0	<0.001
	tree cover ~ MAR * fire	0.763		77.6	fire pres/abs	7.03		<0.001			
					MAR*fire	1173	9.89	<0.001			
					MAR*no fire	5731	10.1	<0.001			

1

FIGURE CAPTIONS

Figure 1. Histograms of percent tree cover (top) and mean annual rainfall (bottom) at 1km (left) and 50km scales (right). For histograms of tree cover, dark grey bars denote categories with proportion of plots of <2.5%; black bars denote the midpoint of the range of grey bars. Lines represent estimated probability density of plots.

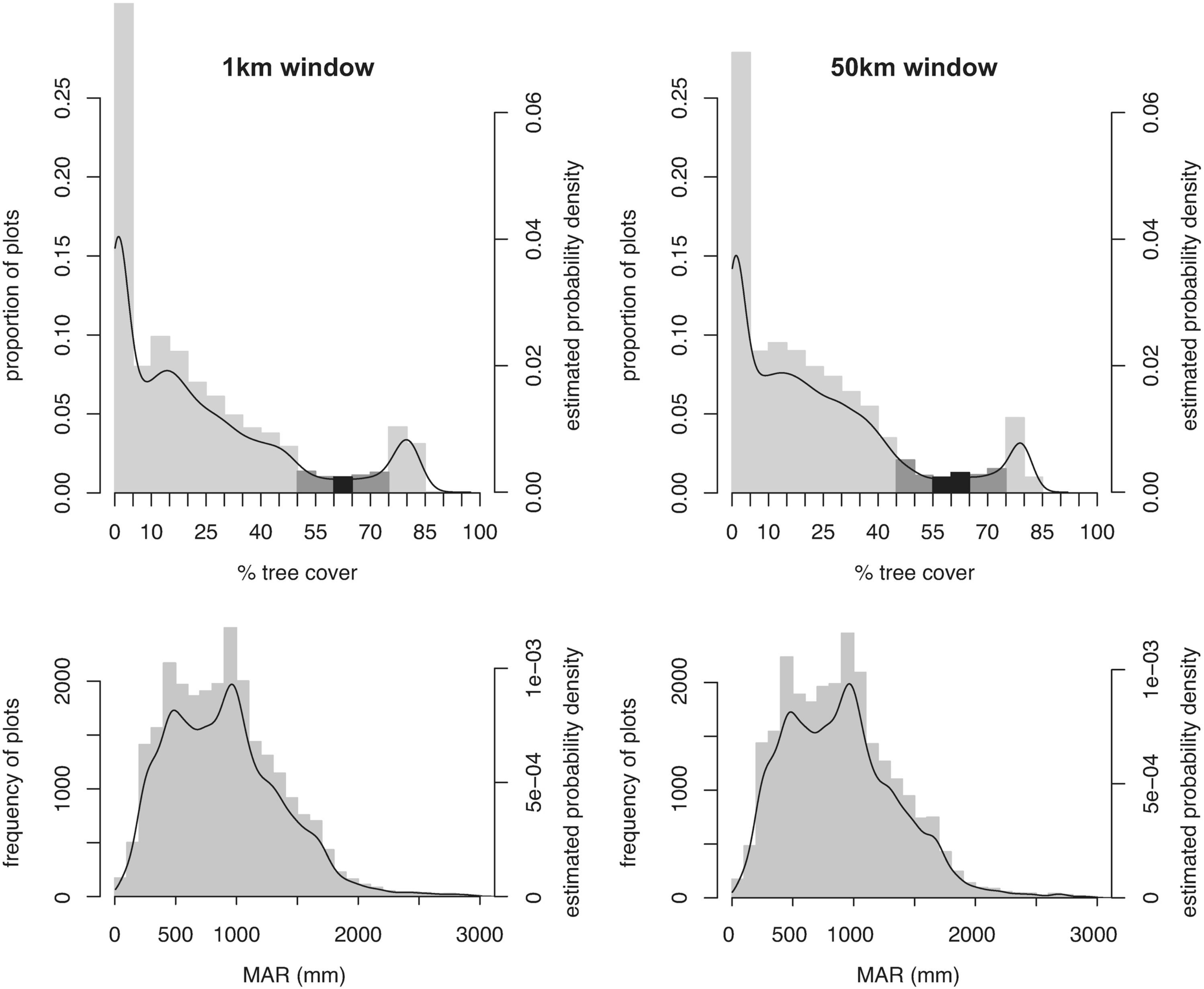
Figure 2. Histograms of savanna (top) and forest (bottom) versus mean annual rainfall at 1km (left) and 50km scales (right). Savanna had <62.5 or <60% and forest had >62.5% or >60% tree cover 1km and 50km scales, respectively. Black bars denote frequency < 1%.

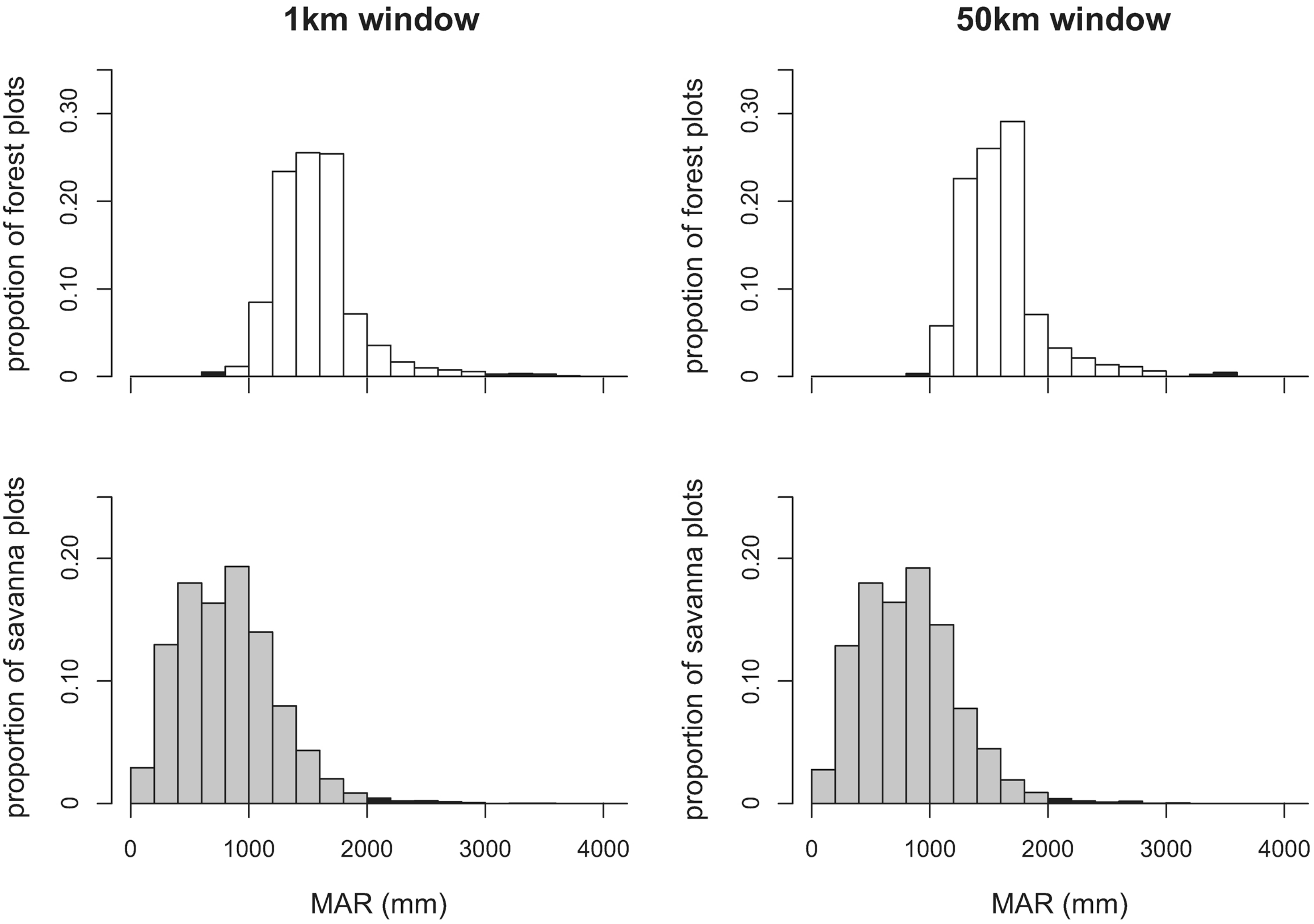
Figure 3. Histograms of percent tree cover categorized by rainfall at the 1km scale. Each plot includes data from a 200mm range in rainfall and is named with the midpoint of that range. Lines represent estimated probability density of plots.

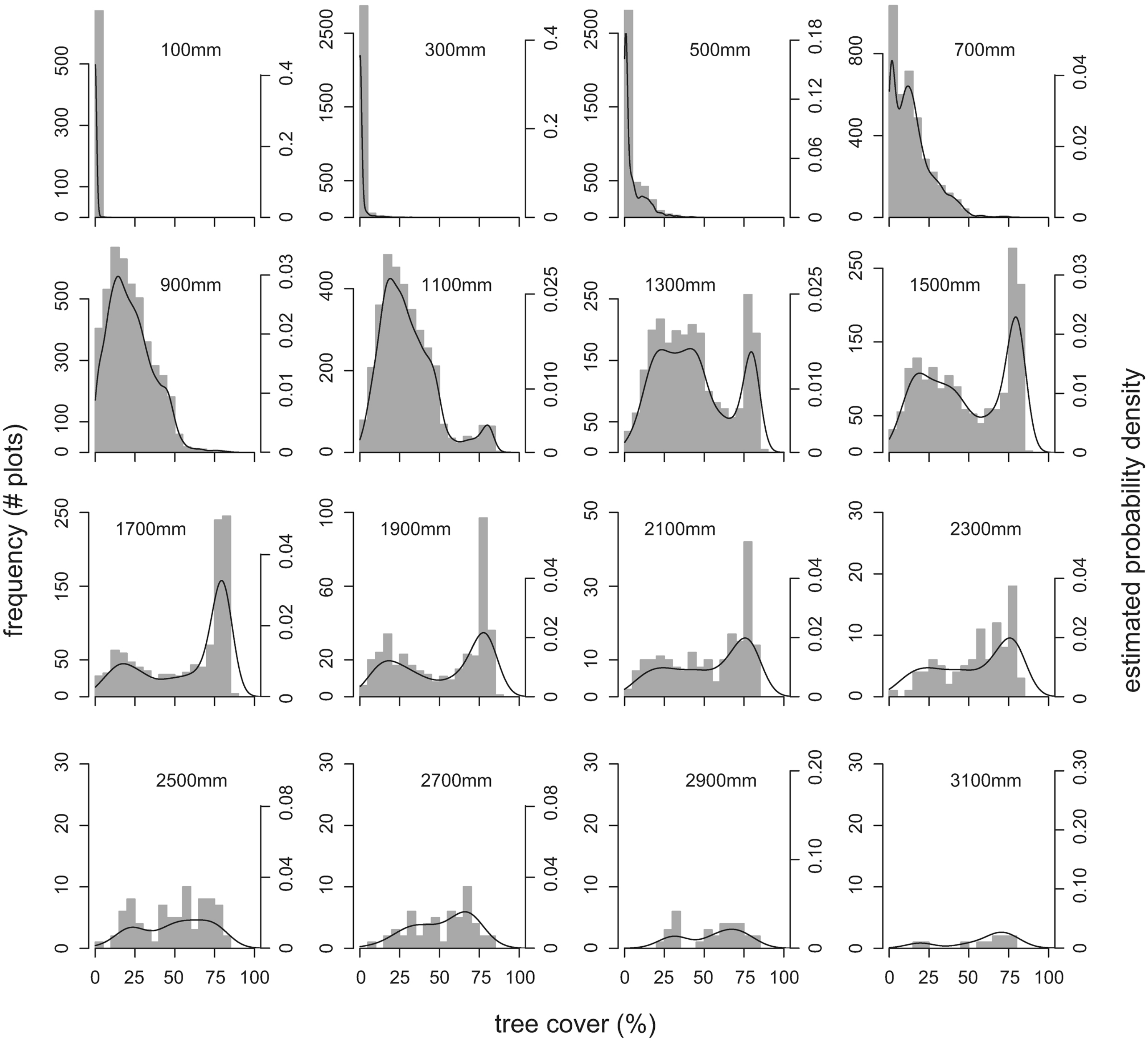
Figure 4. Effects of rainfall and fire on tree cover in sub-Saharan Africa. Top: tree cover v. mean annual rainfall at 1km and 50km scales. Lines represent fits from generalized additive models including rainfall and fire presence as variables (Table 1); fits are significant at both the 1km (R^2=0.574, p<0.001) and the 50km scale (R^2=0.673, p<0.001). Bottom: Mean percent tree cover v. rainfall and fire frequency at 1km and 50km scales.

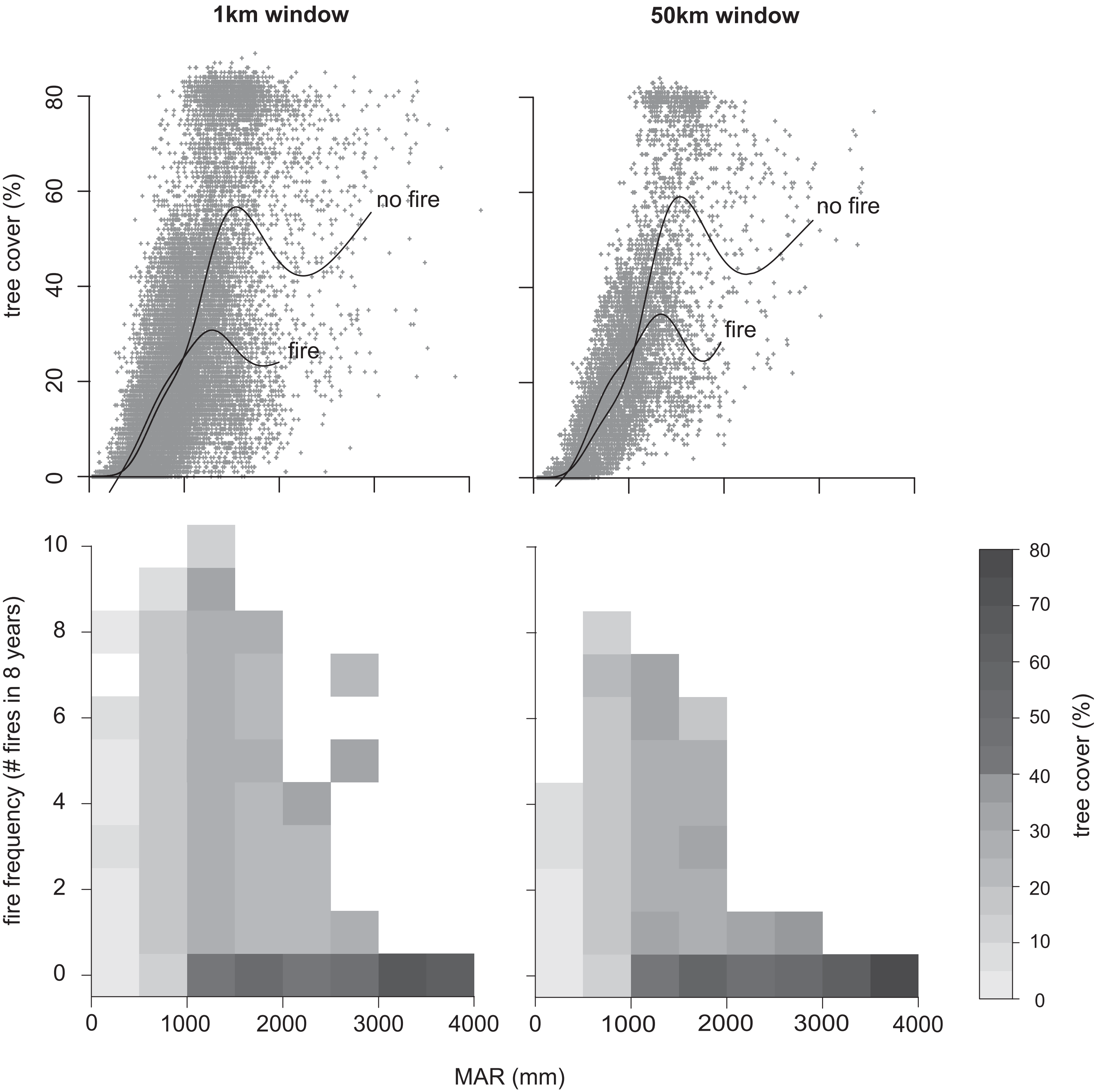
Figure 5. Model outline (a) and graphical analyses of model (b, c & d). Equilibria exist where $\omega(G) = f(G)$ (equation 4). Equilibria are stable where $\omega'(G) > f'(G)$ (equation 16)

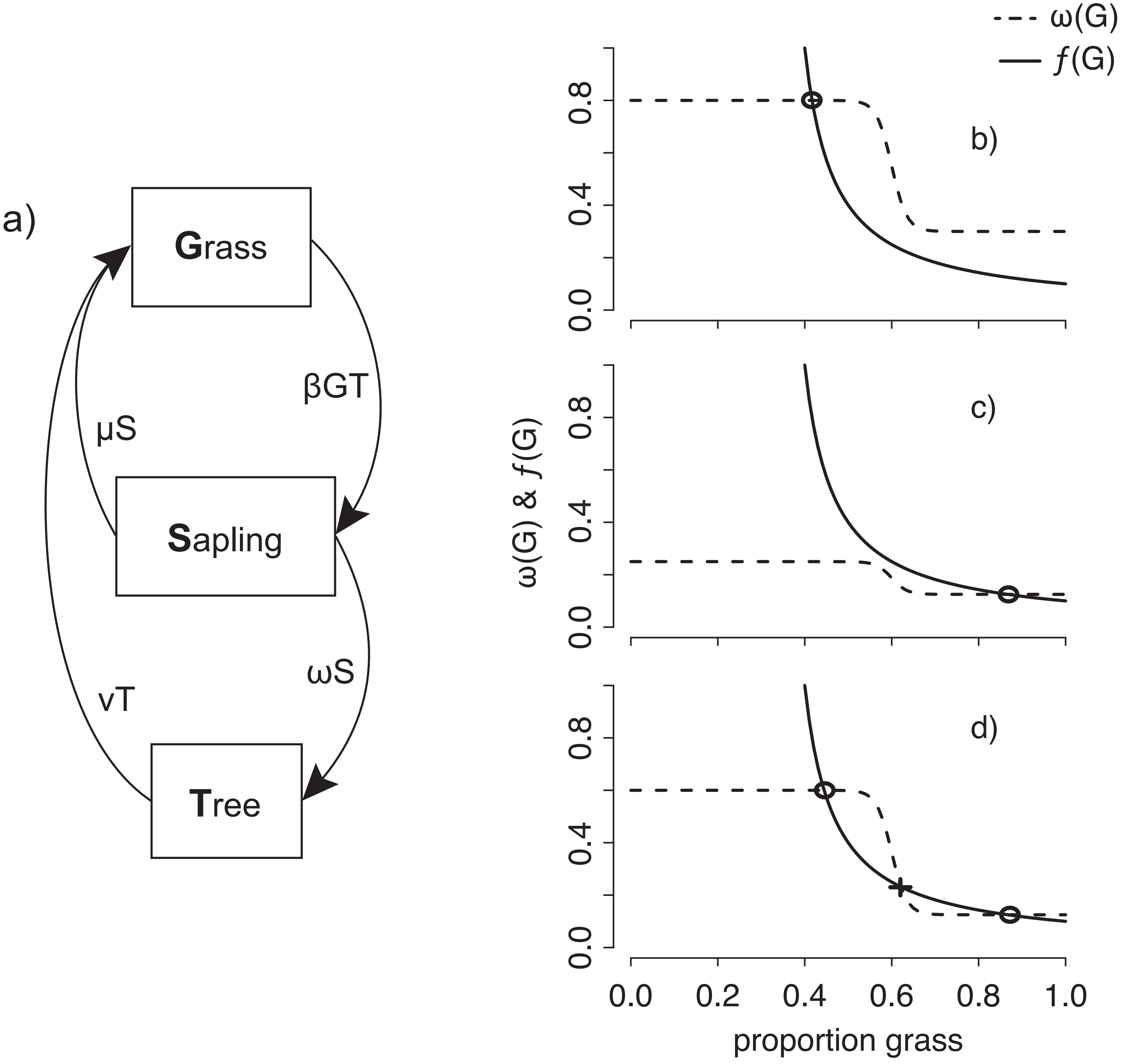
(stable = o, unstable = x). There are between 0 and 3 internal equilibria and between 0 and 2 stable internal equilibria, e.g. b) a stable low grass equilibrium, c) a stable high grass equilibrium, and d) stable high- and low-grass equilibria.


1km window
50km window
proportion of plots
0.00
0.05
0.10
0.15
0.20
0.25
estimated probability density
0.00
0.02
0.04
0.06
% tree cover
0
10
25
40
55
70
85
100
frequency of plots
0
1000
2000
estimated probability density
0
5e−04
1e−03
MAR (mm)
0
500
1000
2000
3000


1km window
50km window
propotion of forest plots
propotion of forest plots
proportion of savanna plots
proportion of savanna plots
0
0.10
0.20
0.30
0
0.10
0.20
0
1000
2000
3000
4000
MAR (mm)
MAR (mm)


100mm
0
100
300
500
0
0.2
0.4
300mm
0
500
1500
2500
0
0.2
0.4
500mm
0
500
1500
2500
0
0.06
0.12
0.18
700mm
0
400
800
0
0.02
0.04
900mm
0
100
300
500
0
0.01
0.02
0.03
1100mm
0
200
400
0
0.010
0.025
1300mm
0
50
150
250
0
0.010
0.025
1500mm
0
50
150
250
0
0.01
0.02
0.03
1700mm
0
50
150
250
0
0.02
0.04
1900mm
0
20
60
100
0
0.02
0.04
2100mm
0
10
30
50
0
0.02
0.04
2300mm
0
10
20
30
0
0.02
0.04
2500mm
0
10
20
30
0
0.04
0.08
2700mm
0
10
20
30
0
0.04
0.08
2900mm
0
10
20
30
0
0.10
0.20
3100mm
0
10
20
30
0
0.10
0.20
0.30
0
25
50
75
100
frequency (# plots)
estimated probability density
tree cover (%)


1km window
50km window
tree cover (%)
0
20
40
60
80
no fire
fire
fire frequency (# fires in 8 years)
0
2
4
6
8
10
0
1000
2000
3000
4000
MAR (mm)
tree cover (%)
0
10
20
30
40
50
60
70
80


a)
Grass
βGT
μS
Sapling
ωS
vT
Tree
ω(G)
f(G)
b)
c)
d)
ω(G) & f(G)
0.0
0.4
0.8
0.0
0.2
0.4
0.6
0.8
1.0
proportion grass