

RESEARCH LETTER

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Key Points:

- This is the first study showing the potential of multiple stable states of vegetation globally based on a process-based vegetation model
- We identify the reason for multiple stable states as the sensitivity of fire to tree cover and illustrate it with a conceptual model
- We identify the potential of multiple stable states in a region in Asia, which has not been in the focus of previous studies

Supporting Information:

- Supporting Information S1

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Multiple stable states of tree cover in a global land surface model due to a fire-vegetation feedback

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Abstract The presence of multiple stable states has far-reaching consequences for a system's susceptibility to disturbances, including the possibility of abrupt transitions between stable states. The occurrence of multiple stable states of vegetation is supported by ecological theory, models, and observations. Here we describe the occurrence of multiple stable states of tree cover in a global dynamic vegetation model and provide the first global picture on multiple stable states of tree cover due to a fire-vegetation feedback. The multiple stable states occur in the transition zones between grasslands and forests, mainly in Africa and Asia. By sensitivity simulations and simplifying the relevant model equations we show that the occurrence of multiple states is caused by the sensitivity of the fire disturbance rate to the presence of woody plant types.

1. Introduction

Forests play an important role within the Earth's climate system [Brovkin *et al.*, 2009] and are highly valuable for human society. They provide energy or building material, store carbon, and regulate climate [Trumbore *et al.*, 2015]. Knowledge on natural vegetation dynamics is therefore of direct relevance for human adaptation to climate change.

Climate exerts an important control on the spatial distribution of vegetation [Woodward, 1987] and fire occurrence [Moritz *et al.*, 2012] on the global scale, but fire and vegetation are also known to interact. Fire plays a crucial role for the geographic distribution of forests, especially in regions where forests transition to grasslands [Bond *et al.*, 2005] and the abundance of trees in an ecosystem feeds back to the fire regime [Archibald *et al.*, 2013]. The feedback between fire and vegetation has been identified as an important process explaining locally observed fire occurrence dynamics [Cochrane, 1999]. This feedback between vegetation and fire can be described as follows (Figure 1): More fire leads to higher grass cover and more grass cover increases the fire frequency due to easily ignitable fine fuels, combined with a dry, hot, and windy microclimate. The frequent fires prohibit the establishment of trees and stabilize the grassland state. On the other hand, an increase in tree cover leads to a decrease in fire due to coarser fuels and a more humid microclimate. The absence of fire allows trees to maintain a closed canopy. Local studies [Trauernicht *et al.*, 2012; Hoffmann *et al.*, 2012] and analysis of satellite-based burned area data sets [Archibald *et al.*, 2009] confirm the suppressive effect of high tree cover fraction on fire.

Feedbacks within a system can lead to the presence of multiple stable states. Systems with multiple stable states typically show an accelerated rate of change when they transition from one stable state to the other [Scheffer *et al.*, 2001]. Moreover, following a strong disturbance they may equilibrate at an alternative stable state and not recover to the initial state. This behavior may require human adaptation and motivates the interest in understanding the dynamics of such systems.

Previous studies provide indications for the presence of alternative stable states of tree cover. A fire exclusion and reintroduction experiment found that after fire exclusion a small proportion of the study site in Australia could not support fire any more due to the absence or patchiness of the grass cover [Scott *et al.*, 2012]. Satellite data show three distinct modes of tree cover in the tropics (forest, savanna, and a treeless state), which are interpreted as multiple stable states [Hirota *et al.*, 2011; Staver *et al.*, 2011a]. The scientific discussion, however, remains controversial. Yin *et al.* [2014] show that the distribution of tree cover can also be explained by one stable state and one slightly drifting state. Moreover, the observed lack of certain tree cover values in satellite

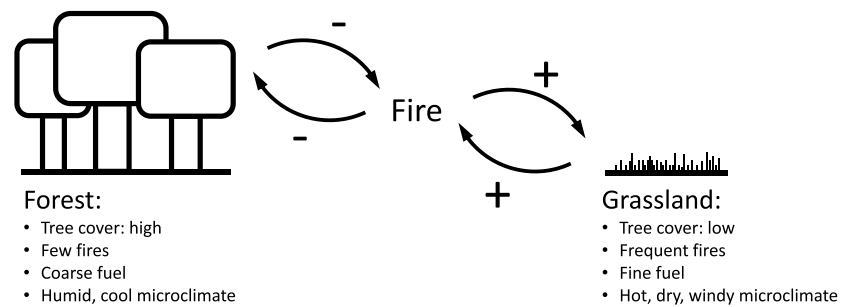


Figure 1. The fire-vegetation feedback: A high tree cover fraction suppresses the occurrence of fires, while an increase of fire decreases tree cover. A high grass cover fraction enhances fire occurrence and higher fire occurrence prohibits the establishment of trees. Fire therefore stabilizes the two stable states, grassland and forest, by regulating tree mortality.

data could be an artifact of the data processing [Hanan *et al.*, 2014]. Staver and Hansen [2015] revise these results in a more realistic analysis showing that artifacts are possible but limited to tree covers less than 20%, while the gap between high and low tree cover is resolved. Recently, considering soil cation differences and including information on shrubs and small trees has led to the conclusion that the transition between low and high tree cover values is smoother than that observed in the MODIS data set [Veenendaal *et al.*, 2015] but is also debated in [Staal and Flores, 2015]. Conceptual models illustrated multiple possible mechanisms for the occurrence of multiple stable states of vegetation, including population dynamics and a sapling state of trees in which they do not survive fires as key characteristic [Staver *et al.*, 2011b; Baudena *et al.*, 2010] or a percolation threshold of fire spread with increasing tree cover due to coarser fuels [Schertzer *et al.*, 2015]. Besides simple conceptual models that can produce multiple stable states due to a vegetation-fire feedback, a complex individual-based regional model (for Africa) showed such a behavior [Higgins and Scheiter, 2012; Moncrieff *et al.*, 2014]. The occurrence of multiple stable states was linked to a higher fire occurrence in the model for low tree cover state [Moncrieff *et al.*, 2014].

Based on the land surface model JSBACH, we investigate the potential for multiple stable states of vegetation by comparing the equilibrium state of simulations with different initializations using two fire algorithms of different complexity. This is the first study of this kind with global coverage. We investigate the interaction between fire and vegetation by adding simulations without fire and performing sensitivity simulations to derive the sensitivity of fire to vegetation and vice versa. We corroborate our results with a conceptual model which is based on the sensitivity simulations of the process-based model.

2. Multiple Stable States in the Process-Based Model JSBACH

2.1. JSBACH: Model Description and Simulation Setup

This study is based on the land surface model JSBACH [Reick *et al.*, 2013], which is the land component of the Earth system model MPI-ESM [Giorgetta *et al.*, 2013]. Two alternative fire algorithms are available within JSBACH: the previous JSBACH fire algorithm [Reick *et al.*, 2013] and the recently implemented process-based SPITFIRE model [Thonicke *et al.*, 2010; Lasslop *et al.*, 2014].

The JSBACH model represents the carbon and hydrological cycle in a process-based way. The representation of vegetation in the model is based on the concept of plant functional types (PFTs). We use only natural vegetation types here, including four tree PFTs, two shrub PFTs, and two grass PFTs (see Table S1 in the supporting information). We are interested in potentially multistable regimes; therefore, no anthropogenic land use or land use change is considered. The fire model interacts with the dynamic vegetation, which computes the spatial distribution of PFTs, directly by providing a burned fraction or fire disturbance rate (F). After burning the cover fractions (part of the grid cells covered with a specific PFT) of the PFTs are reduced and the uncolonized part of the grid cell is increased accordingly. See Reick *et al.* [2013] for further details. We define the tree cover fraction (T) as the sum over the cover fractions of the tree and shrub PFTs.

We perform the following types of simulations:

1. simulations with interactive fire and vegetation, initialized with only grass PFTs or only tree PFTs (type 1);
2. simulations without fire, initialized with only grass PFTs or only tree PFTs (type 2);

3. simulations with a simplified setup and either fire or vegetation prescribed; simulations with prescribed vegetation are repeated for SPITFIRE and the previous JSBACH fire (type 3); and
4. simulations with the simplified setup and interactive fire and vegetation, initialized with only grass PFTs or only tree PFTs (type 4)

All simulations are forced with preindustrial climate (for differences to present-day conditions, see *Giorgetta et al.* [2013]) extracted from the MPI-ESM simulations performed for the Coupled Model Intercomparison Project (CMIP5). The SPITFIRE model furthermore relies on population density (HYDE data set) [Goldewijk, 2001] and lightning rates (a monthly climatology (LIS-OTD), available at <http://ghrc.msfc.nasa.gov>) used for the computation of ignitions. CO₂ concentration was set to 284.725 ppm (corresponds to the year 1850) [Giorgetta et al., 2013]. The initial spatial distribution of the specific PFTs for the grass and tree PFT-only initialization are shown in Figures S1 and S2.

The types 1 and 2 simulations used a 28 year repeated cycle of meteorological forcing, the simulation length was 1200 years. The simplified setup of types 3 and 4 simulations are based on a version of JSBACH where some variables are prescribed from the simulation with the MPI-ESM [Schneck et al., 2013; Lasslop et al., 2014]. Fire disturbance and vegetation dynamics computations are fully included in this setup. However, we exclude wind disturbance and use only 1 year of the preindustrial forcing repeatedly to avoid additional scatter due to interannual variability. Type 3 simulations are performed to characterize the fire-tree cover interaction; more precisely, we derive the overall (or emergent) response of fire to tree cover (for the previous JSBACH fire and SPITFIRE) and the response of JSBACH to fire disturbance. To derive the response of fire to tree cover we perform simulations with prescribed tree cover fractions increasing from 0 to 1 in steps of 0.1. The simulations with prescribed tree cover equilibrate fast (200 simulation years). The response of tree cover to fire is determined from simulations in which the fire disturbance rate is prescribed; these simulations are therefore independent of the fire algorithm. Results presented refer to the state after 1000 years of simulation. Type 4 simulations use the setup of type 3 simulations and a simulation length of 1000 years but fire and vegetation interact.

We identify grid cells with multiple equilibria under the same environmental conditions by performing simulations initialized with only grass PFTs and simulations initialized with only tree PFTs. For the presentation of the results we define grid cells with a tree cover fraction higher than 0.6 as forests and refer to them as grasslands if the tree cover fraction is lower than 0.6. We diagnose multiple equilibria of tree cover for grid cells where the difference in tree cover fraction between the tree-initialized and grass-initialized simulation is larger than 0.1 in an average over the forcing cycle.

2.2. JSBACH: Simulation Results

Previous versions of MPI-ESM using the previous JSBACH fire model did not show multiple stable states of tree cover for different initializations [Brovkin et al., 2009]. With the implementation of SPITFIRE, a process-based fire model, simulations initialized with only tree PFTs converge to a different equilibrium state of vegetation than simulations initialized with only grass PFTs (see Figure 2). Comparing the spatial patterns of this pair of simulations, we find a large part of the global land surface to converge to a similar tree cover fraction (difference less than 0.1) for both initializations; these areas are clearly defined by the grid-cell-specific climate (referred to as “stable forest” or “stable grassland”). For a considerable part of the land surface, however, the equilibrium tree cover fraction depends on the initialization of the vegetation. The difference in global tree-covered area between the two simulations is around 5 Mkm². This corresponds to 8% of the final tree-covered area in the simulation initialized with trees.

The two simulations also show a large difference in burned area. The simulation initialized with grass PFTs has a global burned area of 5.16 Mkm² in equilibrium, the simulation initialized with tree PFTs only 3.12 Mkm². Grid cells that differ in burned area also show a difference in tree cover (Figure S3). The difference between tree- and grass-initialized simulations disappears for simulations without fire (see Figure 2b, dashed lines), the multistability can therefore clearly be attributed to this process. In a climate space, defined by mean annual temperature and mean annual precipitation, most bistable grid cells are characterized by a temperature of 15–25°C and a precipitation between 500 and 1500 mm per year (Figure S4). These mean climate variables are, however, not sufficient to discriminate between grid cells with multistability and those with a single stable state.

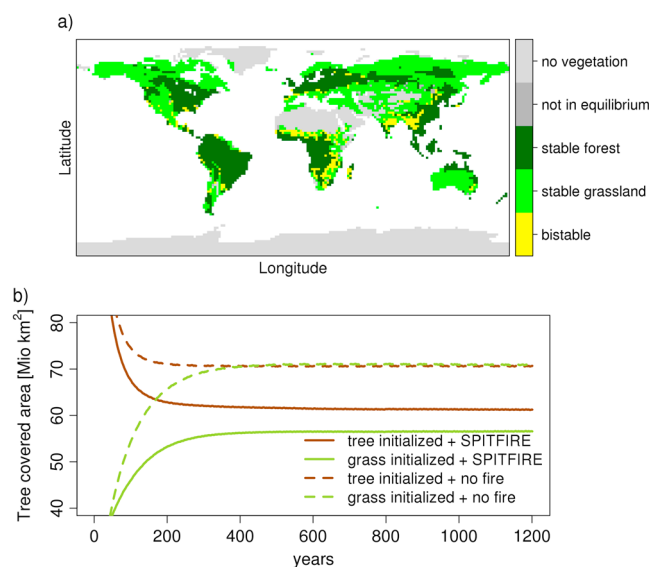


Figure 2. In JSBACH-SPITFIRE the global tree-covered area differs depending on the initialization of the vegetation state. A world initialized with only grass types leads to a lower tree cover than initialization with only tree types. (a) Global distribution of stable forest, stable grassland, and bistable grid cells. (b) Time series of global tree-covered area for simulations initialized with only tree PFTs and only grass PFTs. Points masked as “not in equilibrium” have a change in tree cover of more than 0.005 between the averages over the last two forcing cycles.

The bistable regions are mainly located in Africa and Asia and also at few points on all other continents (Figure 2a). The bistable areas found in Africa are comparable to results of a regional individual-based vegetation model [Higgins and Scheiter, 2012; Moncrieff *et al.*, 2014]. Tropical areas in Africa, South America, and Australia have been the subject of previous studies, which identified a multimodal distribution of tree cover based on remote sensing data as indication of multistability [Hirota *et al.*, 2011; Staver *et al.*, 2011b]. The regions in Asia with multistability in our simulation were not investigated in these studies. According to a reconstruction of the Köppen-Geiger climate classification, the climate of this region is largely described as tropical savanna climate or as temperate with dry winter and hot summer [Peel *et al.*, 2007]. Multistable areas in Africa are found in the same climate zones. In South America we find rather low potential for multistability compared to the studies based on satellite data.

As the previous JSBACH fire model did not show the potential for multistability, the reason for the occurrence in our simulations must lie in the model behavior of SPITFIRE. The recovery of the tree cover after the fire disturbance and the sensitivity of the fire disturbance to tree cover are key to understand the emergence of multistability of a system with interacting fire disturbance and tree cover. We therefore reduce our process-based model to a conceptual tree cover-fire model in the next section, which is based on the model behavior derived from the following sensitivity simulations.

The sensitivity simulations with prescribed tree cover or fire disturbance rate reveal the overall model response of fire to tree cover and vice versa (Figure 3). While the response of tree cover to fire occurrence is similar for all grid cells (Figure 3a), the fire occurrence as a function of tree cover shows distinct differences between stable forest, stable grassland, or bistable grid cells for SPITFIRE (Figure 3b). Stable forest grid cells on average have low burned fractions and a low sensitivity of fire disturbance to tree cover. The stable grass grid cells have rather high burned fractions, e.g., burned fractions higher than 0.1 for a tree cover of 0.4, and increasing further for lower tree cover values. The grid cells showing multiple stable states of vegetation have higher burned fractions than the forest grid cells but lower burned fractions than the grass grid cells (for the same prescribed tree cover). The main difference between stable forest, stable grassland, and bistable grid cells is therefore the strength of the fire regime at the individual grid cell.

The sensitivity of fire to tree cover is related to the principles underlying the SPITFIRE model. The SPITFIRE model distinguishes different fuel classes based on PFT-specific parameters. Fuels of grass PFTs are of smaller size and therefore dry faster. They have a low bulk density supporting high fire spreading rates. The woody litter of trees is represented as coarse fuel, which dries more slowly and has a higher density. These fire-related PFT parameters suppress the spread of fire for a high coverage with tree PFTs and lead to a lower disturbance rate compared to a high coverage of grass PFTs. The strength of the sensitivity of fire to tree cover is modulated by the grid cell-specific climate. The formulation of the fire spread equations is based on laboratory experiments [Rothermel, 1972]. Moreover, a feedback between tree cover and fire occurrence is expected based on site level measurements [Cochrane, 1999; Hoffmann *et al.*, 2012; Trauernicht *et al.*, 2012] and satellite observations [Archibald *et al.*, 2009].

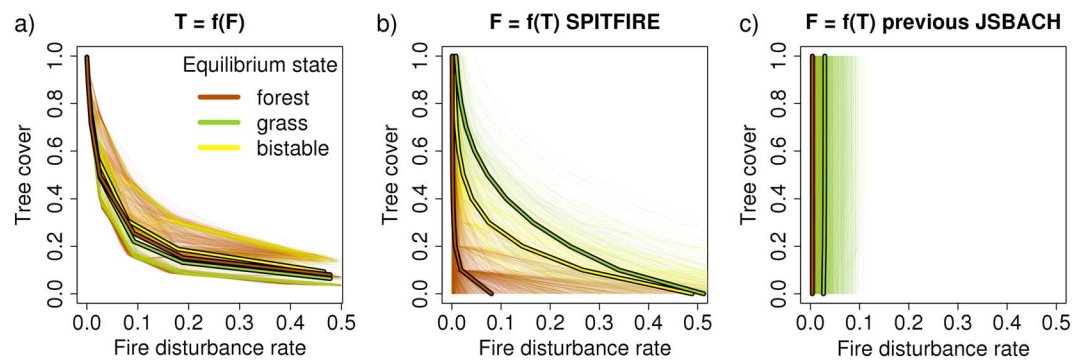


Figure 3. Model states of JSBACH in the fire disturbance rate tree cover phase space without interaction of fire disturbance rate (F) and tree cover (T): i.e., one of them is prescribed. (a) Tree cover (fraction of grid cell) simulated with JSBACH using a prescribed fire disturbance rate (fraction per year), (b) fire disturbance rate as a function of tree cover using the SPITFIRE model, (c) fire disturbance rate as a function of tree cover using the previous JSBACH fire model. Model results are based on a simplified setup with only 1 year of forcing used repeatedly and no wind disturbance. Thin lines each represent one grid cell of the global land surface. Colors indicate whether this grid cell is a stable grassland, forest, or bistable based on the type 4 simulations with interactive vegetation and fire. Thick lines indicate the averages over stable grass, stable forest, and bistable grid cells.

The previous JSBACH fire model shows a clear difference between grid cells with equilibrium forest and equilibrium grass but no dependence of the fire disturbance rate on tree cover (Figure 3c). The missing feedback between fire and tree cover explains the absence of multiple stable states found in *Brovkin et al.* [2009] using the previous JSBACH fire scheme in contrast to the results presented here using JSBACH-SPITFIRE.

3. Conceptual Model of Tree Cover-Fire Interactions

For a better understanding of the differences between grid cells with stable forest, stable grassland, or multiple stable states we develop a conceptual model of fire-tree cover interaction, built on the model behavior of JSBACH-SPITFIRE (Figures 3a and 3b). The model is built on the following assumptions:

1. The area not covered by trees is covered with grasses: grass cover + tree cover (T) = 1. Grass cover is therefore not explicitly included in the model equations
2. Grass has a higher flammability and therefore increases the fire disturbance rate.
3. For a high tree cover fraction fire frequency is a constant minimum disturbance which depends on the local climate.
4. Fire disturbance rate (F) directly translates into tree mortality due to fire.

These assumptions are expressed in the following equations:

$$F = \frac{1}{\phi_{\min}} + \frac{1}{\phi_g} \cdot (1 - T)^2 \quad \text{for } 0 \leq T \leq 1, \tag{1}$$

where ϕ_{\min} (years) is the climate-related minimum fire return interval if only trees are present (the inverse of the fire disturbance rate or the fraction of trees affected by fire), the fire disturbance rate (F) (year^{-1}) increases with an increasing presence of grasses. The disturbance rate of only grasses ($T = 0$) is $1/\phi_g$ (year^{-1}) + $1/\phi_{\min}$ (year^{-1}). The nonlinear increase of disturbance rate with decreasing tree cover (caused by the second term of equation (1)) is chosen to resemble the behavior of JSBACH-SPITFIRE (Figure 3b). Fire reduces the tree cover and trees need a certain establishment time (τ_t (years)) to recover. The sum of the two processes gives the change in tree cover over time:

$$\frac{dT}{dt} = \min\left(\frac{1}{\tau_t} - T \cdot F, 1 - T\right) \quad \text{for } 0 \leq F \leq 1. \tag{2}$$

The conceptual model reproduces the sensitivities found for JSBACH-SPITFIRE: burned fraction as a function of tree cover decreases for high tree cover values (Conceptual model: Figure 4, red lines; JSBACH-SPITFIRE: Figure 3b), tree cover fraction as a function of fire disturbance rate increases for low fire disturbance rates (Conceptual model: Figure 4, black lines; JSBACH: Figure 3a). This conceptual model allows us to explore how changes in fire regime (ϕ_g and ϕ_{\min}) or vegetation regrowth (τ_t) change the potential occurrence of multiple

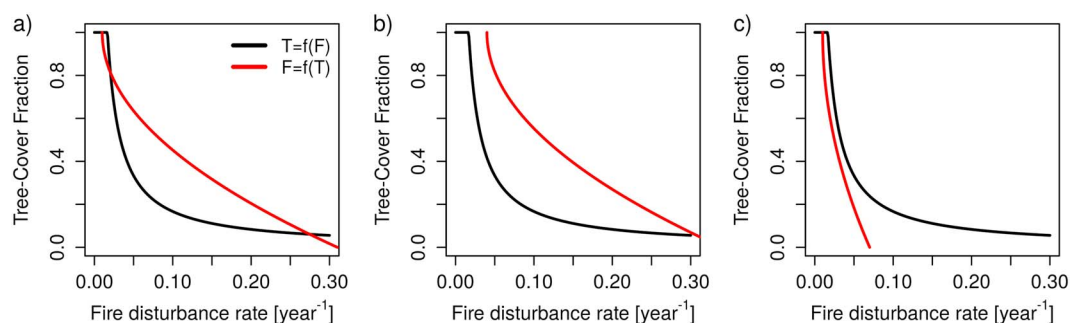


Figure 4. Equilibrium curves of a simple conceptual model (equations (1) and (2)). The red curve is equation (1), while the black curve is obtained from equation (2) for the equilibrium case $\frac{dT}{dt} = 0$. (a) The parameters of equations (1) and (2) are set to $\phi_{\min} = 100$ years (minimum fire disturbance), $\phi_g = 3.33$ years (additional fire due to grasses), $\tau_t = 60$ years (establishment time of trees). (b) Parameters are set to $\phi_{\min} = 25$ years, $\phi_g = 3.33$ years, and $\tau_t = 60$ years. (c) Parameters are set to $\phi_{\min} = 100$ years, $\phi_g = 6.66$ years, and $\tau_t = 60$ years.

stable states. The equilibrium of the system with interacting fire disturbance and tree cover are the points where the tree cover determined by a prescribed fire disturbance rate yields the same fire disturbance rate as if this specific tree cover is prescribed. These are the points where the tree cover as a function of fire disturbance (solution of equation (2) for $\frac{dT}{dt} = 0$) and fire disturbance as a function of tree cover (equation (1)) intersect. Three intersections (equilibrium points) are necessary to obtain grid cells with two stable states (Figure 4a); one of the equilibrium points would be unstable in that case. When shifting the system toward a regime with higher fire occurrence, the curves intersect only for a low tree cover value, which yields a grassland equilibrium state (Figure 4b). Assuming a moister climate with lower fire occurrence, we find only one equilibrium point for a high tree cover value and therefore a forest equilibrium state (Figure 4c).

The relation between fire regime and equilibrium states (grass, forest, or bistable) of JSBACH-SPITFIRE (Figure 3b) agrees with the conceptual model: high fire occurrence leads to stable grasslands and low fire occurrence to stable forests. For intermediate fire occurrence, where the probability for multiple intersections of the curves is highest, we identify the bistable grid cells. Moreover, it is not possible to obtain multiple intersections and therefore equilibria without a sensitivity of fire occurrence to tree cover as observed for the previous fire model of JSBACH (Figure 3c).

The occurrence of intersections for the conceptual model depends on the relation between the model parameters. If $\tau_t/\phi_{\min} \leq 1$ and ϕ_g is sufficiently small, multiple stable states occur (equations are detailed in the supporting information). Changes in fire disturbance rates (ϕ_{\min} and ϕ_g) as well as changes in the recovery time (τ_t) of forests can therefore shift the ecosystems between stable grassland, stable forest, and multiple stable states of vegetation states.

4. Conclusions

In this study we investigate the occurrence of multiple stable states of vegetation under the same meteorological forcing in a global simulation with the vegetation model JSBACH-SPITFIRE. Due to the absence of multiple stable vegetation states in simulations without fire we can attribute the occurrence of the multiple stable states to the presence of fire. Based on a comparison of sensitivity simulations with SPITFIRE and the previous JSBACH fire model (which shows no multiple stable states in vegetation), we identify the sensitivity of fire disturbance to tree cover fraction in SPITFIRE as the key model characteristic responsible for the occurrence of multistability. This is explained by comparing the results of the JSBACH-SPITFIRE model behavior with a conceptual model, which is derived from the overall behavior of the complex model.

Our study, using only natural vegetation types, indicates potentially multistable regions in Asia, a region which was not in the focus of previous studies on multiple stable states of tree cover. The Köppen-Geiger climate classification characterizes these regions as tropical savanna or temperate climate with dry winter and hot summer [Peel *et al.*, 2007], the same climate classes as the multistable regions in Africa.

The occurrence of multiple stable states implies that under climate change with gradual changes in environmental forcing, the vegetation may respond in a nonlinear way. The model shows a distinct difference in the fire occurrence sensitivity to tree cover between grid cells with one and multiple stable states, due to grid

cell-specific climate, while the vegetation recovery is similar. The occurrence of fire on the global scale is to a large extent modulated by humans [Bowman *et al.*, 2011; Hantson *et al.*, 2015; Knorr *et al.*, 2014]. The human control on fire occurrence implies the possibility to actively control and conserve ecosystems in a resilient state. Furthermore, fire occurrence is controlled by climate. It is therefore likely that the occurrence of bistable tree cover states changes with climate change and future social developments. Both factors therefore need to be considered for interpreting past changes and for future projections of vegetation changes.

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References

- Archibald, S., D. P. Roy, B. W. van Wilgen, and R. J. Scholes (2009), What limits fire? An examination of drivers of burnt area in Southern Africa, *Global Change Biol.*, *15*(3), 613–630, doi:10.1111/j.1365-2486.2008.01754.x.
- Archibald, S., C. E. R. Lehmann, J. L. Gomez-Dans, and R. A. Bradstock (2013), Defining pyromes and global syndromes of fire regimes, *Proc. Natl. Acad. Sci. U.S.A.*, *110*(16), 6442–6447, doi:10.1073/pnas.1211466110.
- Baudena, M., F. D'Andrea, and A. Provenzale (2010), An idealized model for tree-grass coexistence in savannas: The role of life stage structure and fire disturbances, *J. Ecol.*, *98*(1), 74–80, doi:10.1111/j.1365-2745.2009.01588.x.
- Bond, W. J., F. I. Woodward, and G. F. Midgley (2005), The global distribution of ecosystems in a world without fire, *New Phytol.*, *165*(2), 525–537, doi:10.1111/j.1469-8137.2004.01252.x.
- Bowman, D. M. J. S., et al. (2011), The human dimension of fire regimes on Earth, *J. Biogeogr.*, *38*(12), 2223–2236, doi:10.1111/j.1365-2699.2011.02595.x.
- Brovkin, V., T. Raddatz, C. H. Reick, M. Claussen, and V. Gayler (2009), Global biogeophysical interactions between forest and climate, *Geophys. Res. Lett.*, *36*, L07405, doi:10.1029/2009GL037543.
- Cochrane, M. A. (1999), Positive feedbacks in the fire dynamic of closed canopy tropical forests, *Science*, *284*(5421), 1832–1835, doi:10.1126/science.284.5421.1832.
- Giorgetta, M. A., et al. (2013), Climate and carbon cycle changes from 1850 to 2100 in MPI-ESM simulations for the Coupled Model Intercomparison Project phase 5, *J. Adv. Model. Earth Syst.*, *5*, 572–597, doi:10.1002/jame.20038.
- Goldewijk, K. K. (2001), Estimating global land use change over the past 300 years: The HYDE database, *Global Biogeochem. Cycles*, *15*(2), 417–433.
- Hanan, N. P., A. T. Tredennick, L. Prihodko, G. Bucini, and J. Dohn (2014), Analysis of stable states in global savannas: Is the CART pulling the horse?, *Global Ecol. Biogeogr.*, *23*(3), 259–263, doi:10.1111/geb.12122.
- Hantson, S., S. Pueyo, and E. Chuvieco (2015), Global fire size distribution is driven by human impact and climate, *Global Ecol. Biogeogr.*, *24*(1), 77–86, doi:10.1111/geb.12246.
- Higgins, S. I., and S. Scheiter (2012), Atmospheric CO₂ forces abrupt vegetation shifts locally, but not globally, *Nature*, *488*(7410), 209–212, doi:10.1038/nature11238.
- Hirota, M., M. Holmgren, E. H. Van Nes, and M. Scheffer (2011), Global resilience of tropical forest and savanna to critical transitions, *Science*, *334*(6053), 232–235, doi:10.1126/science.1210657.
- Hoffmann, W. A., S. Y. Jaconis, K. L. Mckinley, E. L. Geiger, S. G. Gotsch, and A. C. Franco (2012), Fuels or microclimate? Understanding the drivers of fire feedbacks at savanna-forest boundaries, *Austral Ecol.*, *37*, 634–643, doi:10.1111/j.1442-9993.2011.02324.x.
- Knorr, W., T. Kaminski, A. Arneith, and U. Weber (2014), Impact of human population density on fire frequency at the global scale, *Biogeosciences*, *11*, 1085–1102, doi:10.5194/bg-11-1085-2014.
- Lasslop, G., K. Thonicke, and S. Kloster (2014), SPITFIRE within the MPI Earth system model: Model development and evaluation, *J. Adv. Model. Earth Syst.*, *6*, 740–755, doi:10.1002/2013MS000284.
- Moncrieff, G. R., S. Scheiter, W. J. Bond, and S. I. Higgins (2014), Increasing atmospheric CO₂ overrides the historical legacy of multiple stable biome states in Africa, *New Phytol.*, *201*(3), 908–915, doi:10.1111/nph.12551.
- Moritz, M. A., M.-A. Parisien, E. Battlori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe (2012), Climate change and disruptions to global fire activity, *Ecosphere*, *3*(6), 49, doi:10.1890/ES11-00345.1.
- Peel, M. C., B. L. Finlayson, and T. A. McMahon (2007), Updated world map of the Köppen-Geiger climate classification, *Hydrol. Earth Syst. Sci.*, *11*(5), 1633–1644, doi:10.5194/hess-11-1633-2007.
- Reick, C. H., T. Raddatz, V. Brovkin, and V. Gayler (2013), Representation of natural and anthropogenic land cover change in MPI-ESM, *J. Adv. Model. Earth Syst.*, *5*, 459–482, doi:10.1002/jame.20022.
- Rothermel, R. C. (1972), A mathematical model for predicting fire spread in wildland fuels, *Tech. Rep. USDA Forest Serv. Res. Pap. INT-115*, U.S. Dep. of Agric., Intermountain For. and Range Exp. Stat., Ogden, Utah.
- Scheffer, M., S. Carpenter, J. a. Foley, C. Folke, and B. Walker (2001), Catastrophic shifts in ecosystems, *Nature*, *413*(6856), 591–596, doi:10.1038/35098000.
- Schertzer, E., A. C. Staver, and S. A. Levin (2015), Implications of the spatial dynamics of fire spread for the bistability of savanna and forest, *J. Math. Biol.*, *70*(1–2), 329–341, doi:10.1007/s00285-014-0757-z.
- Schneck, R., C. H. Reick, and T. Raddatz (2013), Land contribution to natural CO₂ variability on time scales of centuries, *J. Adv. Model. Earth Syst.*, *5*, 354–365, doi:10.1002/jame.20029.
- Scott, K., S. A. Setterfield, M. M. Douglas, C. L. Parr, J. Schatz, and A. N. Andersen (2012), Does long-term fire exclusion in an Australian tropical savanna result in a biome shift? A test using the reintroduction of fire, *Austral Ecol.*, *37*(6), 693–711, doi:10.1111/j.1442-9993.2012.02379.x.
- Staal, A., and B. M. Flores (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*(18), 5563–5566, doi:10.5194/bg-12-5563-2015.
- Staver, A. C., and M. C. Hansen (2015), Analysis of stable states in global savannas: Is the CART pulling the horse?—A comment, *Global Ecol. Biogeogr.*, *24*(8), 985–987, doi:10.1111/geb.12285.
- Staver, A. C., S. Archibald, and S. A. Levin (2011a), The global extent and determinants of savanna and forest as alternative biome states, *Science*, *334*(6053), 230–232, doi:10.1126/science.1210465.
- Staver, A. C., S. Archibald, and S. Levin (2011b), Tree cover in sub-Saharan Africa: Rainfall and fire constrain forest and savanna as alternative stable states, *Ecology*, *92*(5), 1063–1072, doi:10.1890/10-1684.1.

- Thonicke, K., A. Spessa, I. C. Prentice, S. P. Harrison, L. Dong, and C. Carmona-Moreno (2010), The influence of vegetation, fire spread and fire behaviour on biomass burning and trace gas emissions: Results from a process-based model, *Biogeosciences*, 7(6), 1991–2011, doi:10.5194/bg-7-1991-2010.
- Trauernicht, C., B. P. Murphy, T. E. Portner, and D. M. J. S. Bowman (2012), Tree cover-fire interactions promote the persistence of a fire-sensitive conifer in a highly flammable savanna, *J. Ecol.*, 100(4), 958–968, doi:10.1111/j.1365-2745.2012.01970.x.
- Trumbore, S., P. Brando, and H. Hartmann (2015), Forest health and global change, *Science*, 349(6250), 814–818, doi:10.1126/science.aac6759.
- Veenendaal, E. M., et al. (2015), Structural, physiognomic and above-ground biomass variation in savannaforest transition zones on three continents how different are co-occurring savanna and forest formations?, *Biogeosciences*, 12(10), 2927–2951, doi:10.5194/bg-12-2927-2015.
- Woodward, F. I. (1987), *Climate and Plant Distribution*, 188 pp., Cambridge Univ. Press, Cambridge, U. K.
- Yin, Z., S. C. Dekker, B. J. J. M. van den Hurk, and H. A. Dijkstra (2014), Bimodality of woody cover and biomass across the precipitation gradient in West Africa, *Earth Syst. Dyn.*, 5(2), 257–270, doi:10.5194/esd-5-257-2014.