

1 **Forests, savannas and grasslands: Bridging the**  
2 **knowledge gap between ecology and Dynamic Global**  
3 **Vegetation Models**

4 **M. Baudena<sup>1</sup>, S. C. Dekker<sup>1</sup>; P. M. van Bodegom<sup>2,3</sup>; B. Cuesta<sup>4</sup>; S.I.**  
5 **Higgins<sup>5</sup>; V. Lehsten<sup>6</sup>; C. H. Reick<sup>7</sup>; M. Rietkerk<sup>1</sup>; S. Scheiter<sup>8</sup>; Z. Yin<sup>9</sup>; M.**  
6 **A. Zavala<sup>4</sup>; V. Brovkin<sup>7</sup>**

7 [1]{Copernicus Institute of Sustainable Development, Environmental Sciences Group,  
8 Utrecht University, 3508 TC Utrecht, The Netherlands}

9 [2]{VU University Amsterdam, Department of Ecological Science, de Boelelaan 1081,  
10 1081 HV Amsterdam, NL}

11 [3]{Leiden University, Institute of Environmental Sciences, Einsteinweg 2, 2333 CC  
12 Leiden, the Netherlands}

13 [4] {Forest Ecology and Restoration Group, Department of Life Sciences, Ctra. Madrid-  
14 Barcelona km. 33,6. University of Alcalá, 28805 Alcalá de Henares (Madrid), Spain}

15 [5] {Department of Botany, University of Otago, PO Box 56, Dunedin 9054, New  
16 Zealand}

17 [6] {Department of Physical Geography and Ecosystem Science, Lund University,  
18 Sölvegatan 12, S-223 62, Lund, Sweden}

19 [7] {Max Planck Institute for Meteorology, Bundesstr. 53, 20146 Hamburg, Germany}

20 [8] {Biodiversity and Climate Research Centre (LOEWE BiK-F), Senckenberg  
21 Gesellschaft für Naturforschung, Senckenberganlage 25, 60325 Frankfurt am Main,  
22 Germany}

23 [9] {Institute for Marine and Atmospheric research Utrecht, Utrecht University, Utrecht,  
24 the Netherlands}

25 \* Correspondence to: m.baudena@uu.nl; address: Environmental Sciences, Copernicus  
26 Institute of Sustainable Development, Faculty of Geosciences, Utrecht University, P.O.  
27 Box 80115, 3508 TC Utrecht; phone: + 31 30 253 6483; fax: + 31 30 253 2746

28

1 **Abstract**

2 The forest, savanna, and grassland biomes, and the transitions between them, are  
3 expected to undergo major changes in the future, due to global climate change.  
4 Dynamic Global Vegetation Models (DGVMs) are very useful to understand vegetation  
5 dynamics under present climate, and to predict its changes under future conditions.  
6 However, several DGVMs display high uncertainty in predicting vegetation in tropical  
7 areas. Here we perform a comparative analysis of three different DGVMs (JSBACH,  
8 LPJ-GUESS-SPITFIRE and aDGVM) with regard to their representation of the  
9 ecological mechanisms and feedbacks that determine the forest, savanna and grassland  
10 biomes, in an attempt to bridge the knowledge gap between ecology and global  
11 modelling. Model outcomes, obtained including different mechanisms, are compared to  
12 observed tree cover along a mean annual precipitation gradient in Africa. By drawing  
13 on the large number of recent studies that have delivered new insights into the ecology  
14 of tropical ecosystems in general, and of savannas in particular, we identify two main  
15 mechanisms that need an improved representation in the compared DGVMs. The first  
16 mechanism includes water limitation to tree growth, and tree-grass competition for  
17 water, which are key factors in determining savanna presence in arid and semi-arid  
18 areas. The second is a grass-fire feedback, which maintains both forest and savanna  
19 occurrences in mesic areas. Grasses constitute the majority of the fuel load, and at the  
20 same time benefit from the openness of the landscape after fires, since they recover  
21 faster than trees. Additionally, these two mechanisms are better represented when the  
22 models also include tree life stages (adults and seedlings), and distinguish between fire-  
23 prone and shade-tolerant forest trees, and fire-resistant and shade-intolerant savanna  
24 trees. Including these basic elements could improve the predictive ability of the  
25 DGVMs, not only under current climate conditions but also and especially under future  
26 scenarios.

27

28 **1 Introduction**

29 Savannas cover about a fifth of the Earth land surface, and have wide socioeconomic  
30 importance regarding land use and biodiversity (Scholes, 2003). Savannas are the  
31 central biome in the transition between grasslands and forests, and they are  
32 characterized by the coexistence of two types of vegetation: trees (i.e. woody

1 vegetation), and grasses (i.e. grasses and herbs). In most of the savanna ecosystems, we  
2 observe highly shade intolerant and fire tolerant C<sub>4</sub> grasses and C<sub>3</sub> trees. This savanna  
3 definition is generally valid, with the exception of a few regions (e.g. the Neotropical  
4 cerrado where C<sub>3</sub> grasses dominate, see Lloyd et al., 2008, Ratnam et al. 2011). For a  
5 long time ecologists have been fascinated by savannas, because trees and grasses  
6 coexist, while competing mainly for the same resource, namely water, which is the main  
7 limiting factor (Sankaran et al., 2004; Scholes and Archer, 1997; Walter, 1971).  
8 Classical ecological theory, such as the competitive exclusion principle, predicts that  
9 only one vegetation type can survive in these conditions (Hutchinson, 1961; Tilman,  
10 1982). To solve this conundrum, numerous experimental and modeling studies explored  
11 the nature of tree-grass competition and coexistence (e.g. Higgins et al., 2000; House et  
12 al., 2003; Sankaran et al., 2004; Scholes and Walker, 1993; Walker and Noy-Meir,  
13 1982). Grasses can outcompete trees in the driest environments, where tree growth is  
14 water-limited (Higgins et al., 2012), and they have a particularly strong competitive  
15 effect on tree seedlings, as grasses and tree seedlings compete for water in the same  
16 surface layer (Baudena et al., 2010; Bond, 2008; February et al., 2013; Sankaran et al.,  
17 2004; Wakeling et al., 2011; Yin et al., 2014b). In less arid conditions, however, adult  
18 trees can potentially grow deeper roots and reach deeper water than grasses (Kulmatiski  
19 and Beard, 2013; Walter, 1971; Ward et al., 2013), although overlap between grass and  
20 tree roots can be high in some savannas (e.g. February and Higgins, 2010; Higgins et  
21 al., 2000; House et al., 2003).

22 In addition to water availability, fire is an important driver of tree-grass dynamics. C<sub>4</sub>  
23 grass biomass enhances fire spread in open ecosystems, due to its high flammability. At  
24 the same time, grasses benefit from fire because they recover faster than trees, and  
25 profit of the open spaces after fire, thus originating a positive feedback mechanism that  
26 enhances savanna formation and presence (as shown by e.g. long term fire-exclusion  
27 experiments, Higgins et al., 2007, or model studies, e.g. Higgins et al., 2008; van  
28 Langevelde et al., 2003; see also Hoffmann et al., 2012). Fires may also limit tree  
29 seedling recruitment and growth, thus reducing tree dominance further (e.g. Hanan et  
30 al., 2008; Higgins et al., 2000). This grass-fire feedback is characteristic of tropical  
31 savannas and grasslands, while in most of the other biomes woody species produce  
32 most fuel for fires (e.g. boreal forests, Bonan and Shugart, 1989). Fire is essential to  
33 savanna persistence in wetter areas, which would be forested otherwise. The grass-fire

1 feedback is reinforced by the differences between savanna and forest trees. In contrast  
2 to savanna trees and grasses, forest trees are fire prone and shade tolerant, adapted to  
3 persist in conditions of low light availability and in absence of fire (Ratnam et al., 2011;  
4 Rossatto et al., 2009). Thus, when fires are absent and water supply is sufficient, forest  
5 trees outcompete grasses and savanna trees because of light limitation, while if fires are  
6 active, savanna trees persist but fires and shade intolerance limit their cover, keeping  
7 savannas open (Hoffmann et al., 2012). This feedback, which we define as “vegetation-  
8 fire feedback”, and which is an extended description of the abovementioned grass-fire  
9 feedback, possibly leads to bistability of forest and savanna in mesic regions (e.g. van  
10 Nes et al., 2014; Staver and Levin, 2012).

11 Savannas are expected to undergo major changes in the future due to increasing  
12 temperature and CO<sub>2</sub> concentration, modified rainfall patterns, and subsequently  
13 changed variability in fire regimes (Intergovernmental Panel on Climate Change -  
14 IPCC, 2007). In recent years, an increase in woody cover has been observed in savannas  
15 all over the world (e.g. Bowman et al., 2010; Buitenwerf et al., 2012; Donohue et al.,  
16 2013; Ward, 2009; Wigley et al., 2010). Several studies tried to explain wood expansion  
17 by overgrazing or decreasing fire frequency, which would enhance grass mortality and  
18 thus favor woody vegetation (Scholes and Archer, 1997). However, CO<sub>2</sub> increase is  
19 probably one of the main causes of woody encroachment, leading to savanna  
20 expansions (e.g. at the expense of grasslands). As water use efficiency increases with  
21 CO<sub>2</sub> (e.g. de Boer et al., 2011), thus decreasing the water need for growth, increased CO<sub>2</sub>  
22 concentration leads to a shift in tree-grass competition for water, possibly favoring C<sub>3</sub>  
23 trees over C<sub>4</sub> grasses (Bond and Midgley, 2000; Bowman et al., 2010; Kgope et al.,  
24 2010; Polley et al., 1994; Wigley et al., 2010). In African savannas, paleo-ecological  
25 evidence of the last glacial period, as well as observations of the last 50-100 years,  
26 suggests that increasing CO<sub>2</sub> coincides with an increase in savanna woody plant growth  
27 (Bond et al., 2003; Scheiter and Higgins, 2009). These transformations could have  
28 larger effects on global biogeochemical cycles and precipitation than for any other  
29 biome, due to the large extent and productivity of savannas (IPCC, 2007; Snyder et al.,  
30 2004).

31 Dynamic Global Vegetation Models are an important tool to understand large scale  
32 vegetation dynamics, and they are considered important also to study the forest,

1 savanna, and grassland biomes, and their interactions within past, current and future  
2 climates (Higgins and Scheiter, 2012; Murphy and Bowman, 2012). Some DGVMs are  
3 part of Earth System Models (ESMs), where they describe the interactive role of the  
4 Earth land surface in the climate system. Given their global application, DGVMs  
5 necessarily keep the descriptions of vegetation dynamics simple. For example, they  
6 represent the enormous plant trait diversity of tropical regions through distinguishing  
7 only one or two plant functional types (PFTs). Nevertheless, they realistically reproduce  
8 the distribution of the majority of the world biomes (Fisher et al., 2010; Sitch et al.,  
9 2003). However, projections of vegetation distribution by DGVMs are often uncertain,  
10 especially for the forest, savanna, and grassland biomes (Bonan et al., 2003; Cramer et  
11 al., 2001; Hely et al., 2006; Hickler et al., 2006; Sato et al., 2007; Sitch et al., 2008).  
12 This is probably a consequence of the fact that most DGVMs were not specifically  
13 designed for these tropical systems (House et al., 2003), and thus they do not include  
14 the specific internal feedbacks typical of these biomes (Moncrieff et al., 2013).  
15 Improving the DGVM representation of ecological processes under present climatic  
16 conditions is essential for projecting biome boundary shifts and climate change impacts  
17 into the future (Beerling and Osborne, 2006; Murphy and Bowman, 2012; Sitch et al.,  
18 2008).

19 To evaluate why DGVMs may have difficulties predicting the distribution and  
20 dynamics of savannas, we will analyze three DGVMs, with a particular emphasis on the  
21 representation of what in the following we call the “ecological interactions” between  
22 grasses and trees, i.e. the most important tree-grass competition mechanisms, and the  
23 feedbacks with their environment. While physiological processes are often included in  
24 detail into DGVMs, the ecological interactions are not represented with the same  
25 accuracy in many models, despite their potentially large influence on the DGVM  
26 outcomes (e.g. Fisher et al., 2010; Scheiter et al., 2013). Reflecting on the current  
27 ecological understandings about savannas, we will describe whether and how the key  
28 mechanisms are included in current DGVMs. We chose to analyze three different  
29 DGVMs: JSBACH (Brovkin et al., 2009; Raddatz et al., 2007; Reick et al., 2013), LPJ-  
30 GUESS-SPITFIRE (Smith et al., 2001; Thonicke et al., 2010) and aDGVM (Scheiter  
31 and Higgins, 2009). JSBACH represents a DGVM as typically used in ESMs (and  
32 representative for most models included in the current IPCC coupled model inter-  
33 comparison project, CMIP5). LPJ-GUESS additionally includes the demography of

1 PFTs, which is likely to affect competition dynamics, and it includes SPITFIRE, i.e. a  
2 new specific module to represent fire dynamics. Finally, aDGVM represents a new class  
3 of DGVMs, including functional variation within PFTs (e.g., phenology, allocation and  
4 physiology adapt to changing environmental conditions). The aDGVM was specifically  
5 designed for African vegetation and savannas. In the following, we will focus on the  
6 African continent, where savannas occupy large areas, and where all of the three models  
7 have been applied (Brovkin et al., 2009; Hickler et al., 2009; Higgins and Scheiter,  
8 2012; Lehsten et al., 2009; Scheiter and Higgins, 2009). Focusing on one continent has  
9 also the advantage that the mechanisms driving the dynamics are more likely to be  
10 similar (Lehmann et al., 2014). We will compare the model outputs with observations  
11 from field and remote sensing data (Hirota et al., 2011; Sankaran et al., 2005; Staver et  
12 al., 2011). We attempt to bridge the knowledge gap between our ecological  
13 understanding and the representations of vegetation in global vegetation models. Our  
14 aim is to determine which mechanisms need to be included or improved in the  
15 representation of ecological interactions of existing DGVMs in the forest, savanna, and  
16 grassland biomes, to ameliorate the current vegetation model predictions, as well as  
17 their projections under future (e.g. climate change) scenarios.

18

## 19 **2 Methods**

### 20 **2.1 Model descriptions**

21 DGVMs were developed to quantify transient responses of terrestrial ecosystems to  
22 past, present and future climates, and this required an inclusion of modeling vegetation  
23 dynamics in addition to biogeochemical processes (Cramer et al., 2001; Pitman, 2003;  
24 Prentice et al., 2007). To account for processes at subgrid-scale, DGVMs often assume  
25 fractional vegetation cover within the model grid cell (tiling, or mosaic approach).  
26 Vegetation description is based on PFTs, which aggregate and represent species with  
27 similar functions. Biomes are then represented by a mixture of PFTs, such as evergreen  
28 and deciduous, broadleaved and needleleaved trees, shrubs, C<sub>3</sub> and C<sub>4</sub> grasslands, which  
29 dominate in a particular climate. Savannas are typically simulated as a mixture of  
30 tropical, broadleaved, deciduous trees (“savanna trees” here after), and mostly C<sub>4</sub>

1 grassland, while forests have mostly tropical, broadleaved, evergreen trees (“forest  
2 trees” here after).

3 DGVMs in general have a quite standard set of assumptions to represent plant  
4 physiology, including photosynthesis and biomass production. Most of them calculate  
5 Gross Primary Production (GPP) by a coupled photosynthesis-transpiration scheme and  
6 estimate autotrophic respiration as a function of temperature. Net Primary Production  
7 (NPP) is dependent on the climate and CO<sub>2</sub>, and scaled up to the plant or PFT level by  
8 building up below and above ground carbon and leaf area (e.g., Sitch et al., 2003).  
9 Processes affecting PFT composition, such as competition for resources, mortality, and  
10 demography (i.e. what we call here the ecological interactions) are included into  
11 DGVMs as separate modules that interact with the physiological and phenological  
12 modules.

13 For the purpose of this paper, we will focus on the description of how the ecological  
14 processes relevant for tropical vegetation dynamics are included in the three selected  
15 DGVMs (JSBACH, LPJ-GUESS-SPITFIRE and aDGVM). Only the physiological  
16 aspects relevant for the difference in PFT composition in grasslands, savannas and  
17 forests will be described. JSBACH is part of an ESM, and was designed to represent the  
18 interactive role of vegetation and land surface in the climate system. While LPJ-GUESS  
19 has been included in an ESM in several studies, LPJ-GUESS-SPITFIRE has never been  
20 used in such contest, and the same holds for aDGVM. Both models are so far used only  
21 “offline”, i.e. they are driven by external forcing, such as climate and CO<sub>2</sub> changes,  
22 without being coupled to a general circulation model, and thus without feeding back to  
23 the climate. The models used in this study have their intrinsic limitations, for example  
24 they all neglect nutrient cycling. A summary of the ecological interactions important in  
25 the tropical areas and included into the models is presented in Table 1.

### 26 **2.1.1 JSBACH (DYNVEG)**

27 DYNVEG (Brovkin et al., 2009; Reick et al., 2013) is the submodel for vegetation  
28 dynamics implemented in the land surface component JSBACH (Raddatz et al., 2007)  
29 of the Max Planck Institute - Earth System Model (MPI-ESM, (Giorgetta et al., 2013)).  
30 DYNVEG groups its various PFTs into a grass class (C<sub>3</sub> and C<sub>4</sub> grasses), and a woody  
31 class (trees and shrubs). Within the woody class, DYNVEG distinguishes between two

1 PFTs for tropical trees, with different photosynthetic abilities, which nonetheless do not  
2 have different fire or shade tolerances, so they do not correspond to what we call  
3 savanna and forest tree in this paper. DYNVEG assumes dominance of the woody over  
4 the grass class, i.e., trees have competitive advantage and typically outcompete grasses.  
5 Within a class, the competition among PFTs is indirect via NPP: a PFT with higher NPP  
6 outcompetes PFTs with lower NPP. All PFTs share the same soil water bucket, and  
7 there is no separation of root zones between woody and grass classes. Woody and grass  
8 classes compete for newly available habitable space, with woody types outcompeting  
9 grasses in the absence of disturbances. The space available for colonization can be only  
10 part of the total area, i.e. some parts of the habitat are considered inhospitable. This  
11 fraction constitutes a sort of resource limitation to tree development, since it is  
12 calculated as a function of the average NPP over the last years of simulations, which in  
13 turn depends on water (and other resource) availability (Reick et al., 2013). JSBACH  
14 overestimates GPP and NPP in water-stressed conditions (Dalmonech and Zaehle,  
15 2013), which partly explains an overestimation of tree cover fraction in drylands  
16 (Brovkin et al., 2013). Elevated CO<sub>2</sub> concentration increases water use efficiency of all  
17 PFTs.

18 DYNVEG includes a simple representation of fire disturbance. The fraction of burned  
19 area increases with higher amount of litter (i.e. fuel), mostly produced by woody  
20 vegetation, and decreasing air humidity (a substitute of litter moisture). As a result,  
21 savannas in North Africa with relatively low air humidity and high productivity are  
22 frequently burned. After the fire, the burned area is quickly occupied by grasses, while  
23 woody cover is recovering slowly. Thus, in these transient dynamics, grasses are  
24 indirectly slowing down tree growth. Fire disturbance is the main process that keeps a  
25 mixture of trees and grasses in drylands.

## 26 **2.1.2 LPJ-GUESS-SPITFIRE**

27 LPJ-GUESS (Smith et al., 2001) was developed to incorporate forest age structure into  
28 LPJ (Sitch et al., 2003), thus simulating gap model behavior and including the  
29 competition of different age cohorts for light and water. For each grid cell, LPJ-GUESS  
30 simulates a number of replicate patches. For the tropical regions, LPJ-GUESS results in  
31 one type of (C<sub>4</sub>) grasses, and two types of tree PFTs, savanna and forest trees, where the  
32 former are fire tolerant and shade intolerant, and the latter are fire intolerant and shade

1 tolerant. In LPJ-GUESS, trees and grasses use common water in a superficial soil layer  
2 (0.5 m deep), but trees have part of their roots in a deeper soil layer (1 m). At high water  
3 availability, trees outcompete grasses by limiting light availability.

4 The fire module SPITFIRE (SPread and InTensity of FIRE, Lehsten et al., 2009;  
5 Thonicke et al., 2010) was coupled to LPJ-GUESS to include the role of vegetation  
6 fires. The effect of fire, simulated by SPITFIRE, varies for the different demographic  
7 stages (or height classes). For each fire, fuel load, wind speed and a proxy for fuel  
8 moisture are used to calculate the rate of spread of a potential fire. The fuel load  
9 depends on NPP and decomposition rates, which are both related to climate. Grassy  
10 fuels are more flammable (due to their lower fuel bulk density), but trees can  
11 accumulate more fuel over years without fire, since they decompose more slowly.  
12 Hence if burned at high to medium fire frequency, grasslands provide more fuel than  
13 forests, while if forests are allowed to accumulate fuel over longer time periods, they  
14 result in higher fuel loads than grasslands. All fires remove the above ground biomass  
15 of all grasses. Low intensity fires can cause high mortality of all young trees, while the  
16 effects on tall trees are limited for savanna trees, and more pronounced for forest trees.  
17 In general, damage to trees may be underestimated by SPITFIRE in the current  
18 parameterization. In fact, frequent fires lead to high mortality of young (small) age  
19 cohorts, while the direct effects on old age cohorts are very limited, and only large fires  
20 can cause a high mortality even for highly resistant savanna trees. Further details on the  
21 implementation of fire effects on vegetation can be found in Lehsten et al. (2009).

### 22 **2.1.3 aDGVM**

23 The aDGVM (Scheiter and Higgins 2009) is explicitly designed to study tree-grass  
24 dynamics in savannas. While the original version of the model only simulates savanna  
25 trees and C<sub>4</sub> grasses (Scheiter and Higgins, 2009), an updated version, used for the  
26 current paper, simulates C<sub>4</sub> grasses, C<sub>3</sub> grasses, fire-resistant, shade intolerant, savanna  
27 trees and fire-sensitive, shade tolerant forest trees (Scheiter et al., 2012). The model  
28 uses an individual-based structure to represent trees. Tree recruitment occurs from seed,  
29 and tree seedlings compete with grasses more directly than adult trees.

30 Plants compete mostly for water and light. Light competition is modeled by considering  
31 the light available to grasses below and between canopies. Hence, once a vegetation

1 stand attains a high tree LAI, grass-growth is light-limited. In addition, seedlings and  
2 small trees are shaded by grasses and by adult trees. Savanna trees suffer more from  
3 light limitation than forest trees, which are more shade tolerant. Plants extract water  
4 from different soil layers, depending on their rooting depth, which increases with the  
5 individual root biomass, until reaching maximum value, typically parameterized as  
6 being deeper for trees than for grasses. This allows trees to have exclusive access to  
7 water in deep soil layers. A simple bucket scheme is used to simulate water extraction  
8 and percolation into deeper soil layers. The extent to which soil moisture limits  
9 photosynthesis is calculated as a function of soil moisture in the layers in which the  
10 plant has roots. Hence, rooting depth, the amount of water transpired, and drought  
11 tolerance (i.e. the ability to withstand a low soil water content) determine the outcome  
12 of competition for soil moisture.

13 Fire intensity in the aDGVM is a function of the grass fuel load, its moisture content  
14 and wind-speed (following Higgins et al., 2008). Fire spreads when the fire intensity  
15 exceeds a minimum intensity, when a fire ignition event (for example lightning strike)  
16 occurs, and when ignition probability is exceeded. Days when ignitions occur are  
17 random, the number of ignition events per year is linked to tree cover. Fire is assumed  
18 to consume a large proportion of above ground grass biomass. Aboveground grass  
19 biomass burns as a function of the fire intensity. The aDGVM models the probability of  
20 stem biomass combustion of individual trees (so-called “topkilled” trees, which remain  
21 alive after fire and can resprout from their roots) as being a logistic function of stem  
22 height and fire intensity (following Higgins et al., 2000). This function varies with tree  
23 type. Topkill rates are higher for forest than for savanna trees, and savanna trees have  
24 higher re-sprouting rates than forest trees, which can be killed by a sequence of fires.  
25 Fire affects tree mortality only indirectly, by influencing the carbon balance of topkilled  
26 trees. The fire sub-model and the topkill model together determine whether trees remain  
27 trapped in a cycle of topkill and resprouting, or whether they can attain larger, fire-  
28 resistant sizes. Scheiter and Higgins (2009) illustrated that the aDGVM simulates the  
29 current distribution of African biomes well, and that it can simulate biomass observed in  
30 a longterm fire manipulation experiment in the Kruger National Park, South Africa  
31 (Higgins et al., 2007).

1    **2.2 The model experiment setups**

2    To simulate current conditions, transient simulations were performed where CO<sub>2</sub>  
3    increased to 390 ppm. The JSBACH run used here was a pre-existing CMIP5 historical  
4    simulation under transient forcing from 1850 to 2005, with horizontal resolution of  
5    1.9x1.9° (Giorgetta et al., 2013). LPJ-GUESS-SPITFIRE was driven by a combination  
6    of TRMM (Tropical Rainforest Measuring Mission) data for precipitation and NCEP  
7    data (Kalnay et al., 1996) for temperature and radiation (for details see Weber et al.,  
8    2009). The simulation was run with a spin up of 1000 years, and afterwards the  
9    simulation was performed from 1960 to 2007, with resolution of 1x1°. Fire frequency  
10   was prescribed at each simulated cell using the MODIS MCD45A burned area product  
11   MCD 45 (Roy et al., 2005). LPJ-GUESS-SPITFIRE simulated 100 replicate patches for  
12   each of the 1° cells, and each patch had a probability to burn related to the proportion of  
13   burned area calculated from the MODIS burned area product. If the fire is supposed to  
14   start but the fuel moisture is high, the fire starts instead on the driest day within a 10-  
15   day period. Fires spread only if their potential rate of spread was above a certain  
16   threshold. Since the patch sizes of each of the replicates were below the average fire  
17   size, we simulated the burning of the whole replicate (see Lehsten et al., 2009, for  
18   further details). All 100 replicates of the patch were finally averaged to get a  
19   representative value for the fractional tree cover. The aDGVM used monthly mean  
20   climate data from the CRU database (Climatic Research Unit, New et al., 2000), and  
21   model resolution was 1x1°. A 100 year model spin-up was conducted first, to ensure  
22   that the model was in equilibrium with the environmental conditions, then vegetation  
23   was simulated until 2010. Tree cover was calculated as the sum of the canopy areas of  
24   all trees higher than 0.5 m, without neighbouring trees that shade (and hide) the tree  
25   itself. Tree cover in aDGVM could reach 100% because of the individual canopy  
26   overlaps.

27    **2.3 Observational datasets**

28    For the comparison between data and models, we used two different types of tree cover  
29   observational datasets that have been recently used to study savanna dynamics. One  
30   dataset is a collection of tree cover data from savanna field sites from Africa (Sankaran  
31   et al., 2005), while the other is derived from remote sensing (MODIS, as used e.g. in

1 Hirota et al., 2011; Staver et al., 2011b). In both cases, we selected only the data points  
2 between 35° S and 15° N (following Hirota et al., 2011).

3 The dataset from Sankaran et al. (2005) includes data from 854 field sites across Africa.  
4 They gathered data from several sources, with no recent human influence, not situated  
5 in riparian or seasonally flooded areas, and where vegetation was sampled on a  
6 sufficiently large area (> 0.25 ha for plot measurements and > 100m for transect  
7 sampling). Here, we used projected woody cover and mean annual precipitation. The  
8 latter included estimates from field measurements and regional rainfall maps, and from  
9 fitted climatic grids (see Sankaran et al., 2005 for details). See Fig. 1A for a  
10 visualization of the tree cover as a function of mean annual rainfall.

11 The tree cover dataset, derived from remote sensing data, was the result of two  
12 combined databases. Tree cover data were obtained from the MODIS woody cover  
13 product (MOD44B), developed by Hansen et al. (2003). This product used MODIS  
14 images between Oct 2000 and Dec 2001 to calculate the fraction of tree cover, with a  
15 spatial resolution of 500m. To exclude areas highly influenced by humans, we  
16 combined this data with the global land cover map (GlobCover 2009) with a high  
17 spatial resolution (300m). We excluded land cover types that were classified as “Post-  
18 flooding or irrigated croplands”, “Rainfed croplands”, “Mosaic Cropland (50-70%) /  
19 Vegetation (grassland, shrubland, forest) (20-50%)”, “Mosaic Vegetation (grassland,  
20 shrubland, forest) (50-70%) / Cropland (20-50%)”, “Artificial surfaces and associated  
21 area (urban areas > 50%)”, “Water Bodies” and “Permanent snow and ice”. The mean  
22 annual precipitation was obtained by averaging 42-year (1961-2002) precipitation  
23 record from the CRU project (CRU TS 2.1) with 0.5° resolution. See Fig. 1B for an  
24 illustration of the resulting natural woody cover as a function of mean annual  
25 precipitation. We must note here that despite its wide use, this dataset for tree cover has  
26 received some criticism, since: maximum tree cover never reaches 100%, even for  
27 tropical forests, shrub and small woody plants are under-detected (Bucini and Hanan,  
28 2007), and the observed bimodality between forest and savanna in certain precipitation  
29 ranges (Hirota et al., 2011; Staver et al., 2011) might possibly be induced by the  
30 algorithm used for vegetation classification (Hanan et al., 2014).

1    **2.4 Model comparison to observations**

2    As for the data, for the three models we analyzed the simulated tree cover output (i.e. all  
3    woody vegetation) as a function of the corresponding mean annual rainfall conditions,  
4    and we select only the points in the African continent between 35° S and 15° N. We  
5    masked land use, and we used both vegetation and precipitation averaged over thirty  
6    years. To evaluate the effect of rainfall on the upper limit of tree cover, following e.g.  
7    Sankaran et al. (2005), we used nonlinear quantile regression (Koenker and Park, 1996),  
8    as implemented in the ‘quantreg’ library of the R program. We used 0.90 to 0.99  
9    quantiles and we chose the following nonlinear function:

10    
$$y = a \frac{x^2}{b + x^2}, \quad (1)$$

11    where  $x$  is the mean annual rainfall,  $y$  the estimated quantile regression for percent tree  
12    cover,  $a$  the maximum tree cover (setting  $a=100\%$ , while  $b$  was estimated by the  
13    regression).

14    In the models, the precipitation ranges where grasslands, savannas and forests were  
15    simulated resulted not only from the different representations of vegetation dynamics,  
16    but also from the way climate was included. aDGVM and LPJ-GUESS-SPITFIRE were  
17    forced with (different) climate data, while JSBACH was coupled to an atmospheric  
18    model. Both the rainfall (NCEP, CRU and TRMM) datasets and the simulated climate  
19    have inevitable biases, and are hard to compare with each other. Therefore, precipitation  
20    estimations were not totally comparable, and for this reason, we will compare the  
21    models in the parameter space (i.e., vegetation cover versus mean annual rainfall) and  
22    not in the geographical space. Also, we will not discuss the exact mean annual rainfall  
23    values at which forest, savanna and grassland are observed, but we mostly refer to  
24    ranges of low, medium or high mean annual rainfall. For these ranges, we will perform  
25    a qualitative comparison of the modeled and observed data in the parameter space (i.e.  
26    maximum values, spread, distribution).

27    In addition to mean annual rainfall, other factors such as temperature (Higgins and  
28    Scheiter, 2012), or temporal distribution of rainfall, are known to be important for  
29    tropical grasslands, savannas and forests too. Rainfall heterogeneity, intermittency, and  
30    seasonality affect water availability (D’Onofrio et al., 2014) and fire return times, and

1 are very important predictors of savanna/forest distribution (Lehmann et al., 2011), with  
2 rainfall seasonality reducing growth rates (e.g. limiting water availability, Sarmiento,  
3 1984), influencing root-shoot biomass ratio and local cover (Yin et al., 2014a) and  
4 increasing fire frequency (Archibald et al., 2009). Nevertheless, these factors have not  
5 yet been thoroughly examined in many ecological studies, possibly also because of lack  
6 of accurate rainfall datasets in these areas. Therefore, in the following, we will focus  
7 only on mean annual rainfall, whose importance has extensively been studied. We  
8 separately evaluate arid and semi-arid savannas (Sect. 3.1) and humid savannas and  
9 forests (Sect. 3.2), analyzing also whether and how the ecological interactions are  
10 included in the different models. Finally, we discuss the effect of expected future  
11 climatic changes on the outcome of tree-grass competition in the three models (Sect.  
12 3.3).

13

### 14 **3 Results and Discussion**

#### 15 **3.1 Arid and semi-arid savannas and grasslands: the role of water 16 limitation**

17 In the drier African savanna regions, i.e. with mean annual precipitation lower than a  
18 value estimated between  $650 \text{ mm y}^{-1}$  (Sankaran et al., 2005, see also Fig. 1A) and  $1000 \text{ mm y}^{-1}$   
19 (Staver et al., 2011, see Fig. 1B), observed tree cover displays a maximum value  
20 that is lower than full cover. In this range, for a given annual rainfall, multiple values of  
21 tree cover are observed, representing either grasslands or more or less closed savannas,  
22 but full cover is never reached. The maximum tree cover increases with mean annual  
23 rainfall (see 90<sup>th</sup> quantile regression lines in fig. 1; similar results are obtained with the  
24 99<sup>th</sup> quantile regression lines, not shown), i.e. it depends on water availability. Indeed,  
25 the main mechanisms governing the ecological interactions include: i) water limitation  
26 on tree growth (Higgins et al., 2012); ii) tree competition with grasses, which have an  
27 especially strong competitive impact on tree seedlings (February et al., 2013; Salazar et  
28 al., 2012); iii) fires further reducing woody cover, although savannas are observed  
29 anyway, even if fires were excluded, as shown e.g. with fire exclusion experiments  
30 (Higgins et al., 2007).

1 At a first glance, the relation between tree cover and mean annual rainfall simulated by  
2 the models (Fig. 2) is similar to that observed in the data (Fig. 1). In JSBACH output,  
3 the maximum tree cover increases between zero and 800 mm  $y^{-1}$  approximately, where  
4 it reaches its largest cover (see 90<sup>th</sup> quantile regression curve in Fig. 2A; similar results  
5 are obtained with the 99<sup>th</sup> quantile regression lines, not shown). This increase is mostly  
6 due to the fact that all the PFTs can colonize only a part of the space, which is  
7 calculated dynamically and increased with water availability (although indirectly, via  
8 NPP). In addition, fire related mortality increases with decreasing air humidity, thus  
9 representing another source of water-related limitation in drier areas. At the same time,  
10 the limitation to tree maximum cover is not likely to be the result of competition with  
11 grasses, since trees are assumed to outcompete grasses, and they are affected by some  
12 sort of grass competition at low water availability only temporarily after e.g. a fire (see  
13 also Fig. 3B). JSBACH has a tendency to overestimate maximum tree cover at very low  
14 values of mean annual rainfall (<100 mm  $y^{-1}$ ), as this model is known to overestimate  
15 GPP and NPP (Brovkin et al., 2013).

16 In the LPJ-GUESS-SPITFIRE model output (Fig. 2B), almost no tree cover is observed  
17 until mean annual rainfall is about 300 mm  $y^{-1}$ . In this precipitation range, modeled  
18 trees are water limited and outcompeted by grasses. Compared to the observations, this  
19 model seems to limit tree cover in this precipitation range too strongly. Between about  
20 300 and 900 mm  $y^{-1}$  annual rainfall, the maximum vegetation cover in LPJ-GUESS-  
21 SPITFIRE increases until it reaches a maximum value (about 90% tree cover, see 90<sup>th</sup>  
22 quantile regression line in Fig. 2B), partly due to water limitation that allows tree-grass  
23 coexistence (between about 350 and 650 mm  $y^{-1}$ , Arneth et al., 2010), and partly due to  
24 fires, which further limit tree cover.

25 In the aDGVM output, the tree cover displays a maximum value that grows with  
26 precipitation between zero and about 500 mm  $y^{-1}$  (Fig 2C). In this range, modeled trees  
27 are water limited, while grasses are better competitors in these drier conditions, thus  
28 further reducing the tree cover, which would be higher if the model were run without  
29 grasses (not shown). The aDGVM and LPJ-GUESS-SPITFIRE include differential  
30 rooting depths for individuals, depending on their root biomass, and therefore both  
31 models also represent water competition between grasses and tree seedlings. This  
32 competition is known to be important for tree-grass coexistence (Hanen et al., 2008;

1 Sankaran et al., 2004), while adult trees have deeper roots that make them better  
2 competitors in more humid environments (see Fig 3A and 3C respectively).

3 **3.2 Humid savannas and forests: the role of fire**

4 In more humid conditions, bimodality of vegetation cover below and above 60% is  
5 observed in the MODIS data for precipitation in a range between around 1000 and 2000  
6  $\text{mm y}^{-1}$  (e.g. Hirota et al., 2011; Staver et al., 2011b, see also Fig 1B), i.e. clusters with  
7 low and high tree cover values are observed, corresponding to a bimodality of savanna  
8 and forest cover. Although the validity of this result still needs further investigation  
9 (Hanan et al., 2014), this bimodality has been related to the vegetation-fire feedback,  
10 possibly leading to bistability of savanna and forest in this range, as shown using simple  
11 models (e.g. van Nes et al., 2014; Staver and Levin, 2012). In brief, grass, particularly  
12 abundant in these wet areas, becomes an extremely good fuel in the dry season, which  
13 promotes fire occurrence (i.e. the grass-fire feedback, Higgins et al., 2008; Trollope,  
14 1984). When fire occurs, above ground biomass of all plants is removed. Established  
15 savanna trees and grasses can resprout after fire, but tree seedlings are subject to high  
16 mortality rates and many forest tree species cannot resprout. Together with grasses,  
17 which regrow quickly in the open space after fires, savanna trees benefit from removal  
18 of forest tree competitors, (Ratnam et al., 2011; Hoffmann et al., 2012) leading to a  
19 stable savanna biome at intermediate rainfall values. Yet, environmental conditions  
20 would allow forests in the absence of fire (e.g. Staver and Levin, 2012). Fig. 3A  
21 provides a schematic diagram of this feedback. At the highest end of the rainfall range,  
22 fires are totally suppressed and only forests are observed, since grass growth is inhibited  
23 by tree shade.

24 The role of fire in maintaining savannas in humid environments is included in all of the  
25 models, although in different ways. At high precipitation, JSBACH tree cover output  
26 displays a constant maximum value (above about  $800 \text{ mm y}^{-1}$ ), but the data display  
27 considerable scattering below full tree cover (Fig 2A). In other words, the model  
28 predicts savannas and forests in this range, but the data do not display bimodality of  
29 high and low tree cover values (see Supplementary material, Appendix 1). This is a  
30 consequence of the fact that in this model fire is triggered more by trees than by grasses,  
31 since trees produce larger amounts of litter and thus of fuel. Fire favors grasses because

1 it opens the landscape by reducing the tree cover and generates space for them. Thus,  
2 fire creates a negative feedback because fewer fires occur when tree cover is lower (Fig.  
3 3B), thus preventing hysteresis and bistability in this model.

4 LPJ-GUESS-SPITFIRE simulation results do not show any low tree cover value (e.g.  
5 below 50% cover) for rainfall higher than about 900 mm  $y^{-1}$  (Fig. 2B). Therefore, quite  
6 surprisingly, this model does not predict any savanna in mesic environments. In the  
7 model, though fire frequency is prescribed from the satellite data, fire spread depends  
8 on fuel load (Fig. 3C) and fuel moisture, and thus unfavorable conditions might still  
9 prevent fires. Both grass and tree presence increases fire intensity, opening up space,  
10 and thus favoring grasses. This is not strictly a positive grass-fire feedback, because also  
11 grass-free areas can burn. Thus, as grasses are not fostered by a positive feedback with  
12 fire, they are always outcompeted by trees in LPJ-GUESS-SPITFIRE when water  
13 availability is high, and they do not survive above approximately 900 mm  $y^{-1}$ . At the  
14 same time, this issue is also likely to be connected to fire intensity depending on fuel  
15 moisture. In this model, fire occurrence in a patch is calculated probabilistically from  
16 the proportion of burned area as determined from the remote sensing product. If fire  
17 occurs in a period of high fuel moisture, the intensity will be limited, thus having little  
18 effect on vegetation. This probabilistic approach is necessary because the temporal  
19 extent of the remote sensed data (now only ca. 10 years), used to generate the  
20 probability of burned area for each pixel, is much shorter than the extent of the climate  
21 data for which the model was run (ca. 100 years).

22 In aDGVM, maximum tree cover values can reach full cover above about 500 mm  $y^{-1}$ ,  
23 but the points are still very scattered, and display some clustering at cover around 30-  
24 60% for intermediate rainfall values (Fig. 2C). If we only select points in such rainfall  
25 range (e.g. between 800 mm and 1200 mm  $y^{-1}$ ), we observe that the tree cover  
26 distribution is bimodal (see Appendix 1; note that this conclusion is robust to different  
27 choices for the limits of the rainfall range). aDGVM includes explicitly the grass-fire  
28 feedback, which is reinforced by the difference between fire tolerant savanna trees and  
29 fire sensitive forest trees (Fig 3 A). When the forest trees suppress the savanna trees and  
30 the grasses through light competition, the result is a forest biome with low fire  
31 frequency or even fire suppression, primarily due to scarcity of (grass) fuel. At sites  
32 with regular fire, forest trees cannot persist, resulting in low forest tree cover and

1 intermediate savanna tree cover, with grasses colonizing the open spaces and fostering  
2 fire occurrence. This vegetation state represents a savanna biome. In a certain range of  
3 environmental (e.g. rainfall) conditions, a system initialized as a forest will not shift to a  
4 savanna, unless fire ignition probability is high, while a system initialized as a savanna  
5 will persist in the same state unless fire ignition probability is very low. As a  
6 consequence of including this positive feedback, experiments with the aDGVM show  
7 that fire suppression can lead to transitions and hysteresis between savanna and forest  
8 states (Higgins and Scheiter, 2012; Moncrieff et al., 2013).

9 Finally, we note that at extremely high rainfall values, when water is not limiting and  
10 tree canopies close into a forest, both in LPJ-GUESS-SPITFIRE and in aDGVM trees  
11 exclude grasses through light competition (Fig. 2B-C). This mechanism is included only  
12 implicitly in JSBACH, and it acts along the whole precipitation gradient giving  
13 competitive advantage to trees in general.

### 14 **3.3 Effects of future climatic changes**

15 Hereafter we discuss results from two simple conceptual experiments (namely,  
16 increasing CO<sub>2</sub> concentrations, and decreasing precipitation) to illustrate how the  
17 different representations of the ecological interactions in the three DGVMs could lead  
18 to different predictions of the state of the grassland-savanna-forest transition under  
19 future climatic changes.

20 Expected increase in CO<sub>2</sub> concentration in the future is likely to affect the outcome of  
21 tree-grass competition, mediating both important mechanisms we discussed so far, i.e.  
22 competition for water, and fires. Fire is expected to decrease under increased CO<sub>2</sub> level  
23 because of the decrease in grass fuel load, given that C<sub>3</sub> woody plants are favored over  
24 C<sub>4</sub> grasses under elevated CO<sub>2</sub> levels (Ehleringer et al., 1997). In JSBACH, higher CO<sub>2</sub>  
25 leads to higher productivity of grasses and trees, which in turn increases fire spread and  
26 hence introduces a negative feedback, dampening the increase of tree biomass. In  
27 aDGVM, CO<sub>2</sub> fertilization promotes tree growth, and thus tree establishment in  
28 grasslands, transforming them into savannas or woodlands (with or without fire,  
29 respectively). So in contrast to JSBACH, aDGVM includes a positive feedback, leading  
30 to tree canopy closure in savannas, which, suppressing grass growth, reduces also fire  
31 activity, transforming them into woodlands and forests (Scheiter and Higgins 2009).

1 Due to this positive feedback, CO<sub>2</sub> concentration can induce hysteresis effects on the  
2 vegetation states (Higgins and Scheiter 2012). LPJ-GUESS-SPITFIRE has an  
3 intermediate behavior between the other two models, because grass and woody  
4 vegetation contribute similarly to fuel formation. Also, since in this model fire  
5 frequency is prescribed from remotely sensed data, any effect of changes of CO<sub>2</sub> levels  
6 on fire occurrence would be very limited, though there might be pronounced effects on  
7 resulting vegetation composition.

8 Another consequence of climate change is a possible decrease in precipitation. This  
9 scenario also leads to different model behavior. In JSBACH and LPJ-GUESS-  
10 SPITFIRE, drier conditions would lead to lower (woody) biomass productivity, but the  
11 impact on fire spread differs between these two models. JSBACH predicts no major  
12 effect on fire, as drier conditions would lead to higher fuel flammability, thus  
13 compensating for the impacts of the woody biomass decrease. In LPJ-GUESS-  
14 SPITFIRE the decrease in productivity is dominant, and hence a strong decrease of fire  
15 frequency is expected (Lehsten et al., 2010). In aDGVM the strong positive feedback  
16 would lead to a magnification of the woody vegetation decrease, as lower precipitation  
17 leads to increased grass productivity (because of less competition with woody  
18 vegetation) and lower humidity, increasing the likelihood of fire occurrence.

19 In summary, we expect that in JSBACH, LPJ-GUESS-SPITFIRE and aDGVM, savanna  
20 systems have quite different sensitivities to climate change, and their predictions on the  
21 effect of climate change on fire occurrence diverge substantially. Given the importance  
22 of fires for estimating the global carbon budget (Le Quéré et al., 2013), this is  
23 remarkable, and it illustrates clearly how representing the ecological interactions more  
24 or less accurately can lead in some cases to similar results under present conditions  
25 (where the models have been tuned), but their predictions can diverge substantially  
26 when the models are used for future scenarios.

27 **3.4 Other mechanisms influencing tropical savannas, grasslands and  
28 forests**

29 Up to now we considered water limitation and fires as the main drivers of grassland,  
30 savanna and forest distribution. Several additional factors can be important for  
31 vegetation dynamics, especially at the local scale. The first factor is herbivory.

1 Browsing (particularly by mega-herbivores in Africa) is known to have an important  
2 limiting effect on tree cover, similar to the effect of fire (e.g. Scheiter and Higgins,  
3 2012; Staver et al., 2012), while grazing can favor trees because it limits grass  
4 expansion (e.g. Sankaran et al., 2008). However, large herbivores seem not to be critical  
5 in determining forest and savanna distributions (Murphy and Bowman, 2012).  
6 Secondly, although it has been observed that savannas can be associated with nutrient  
7 poor soils (Lloyd et al., 2008), it is generally accepted that nutrient limitation does not  
8 explain the savanna-forest transition (Bond, 2010; Favier et al., 2012; Murphy and  
9 Bowman, 2012). For these reasons, and to avoid inconsistencies while evaluating  
10 different models, we only used DGVMs that did not include nutrient cycling. Thirdly,  
11 vegetation tends to have local spatial dynamics and to feed back to the environment at  
12 much smaller spatial scales than the DGVMs resolution. These local spatial water-  
13 vegetation interactions are strictly connected to vegetation resilience in arid and  
14 semiarid ecosystems (e.g. Rietkerk et al., 2004), and they can also influence the  
15 coexistence of trees and grasses in the most arid savannas (Baudena and Rietkerk, 2013;  
16 Nathan et al., 2013). Although the local scale is partly taken into account in some  
17 DGVMs by including individual based dynamics or tiling schemes (that represent  
18 different vegetation types and bare soil next to each other within the same cell), these  
19 assume a common use of soil and hydrological resources within the grid cell, thus not  
20 allowing to represent local, sub-grid mechanisms, which are not at all trivial to up-scale  
21 (Rietkerk et al., 2011). Finally, on the African continent the vast majority of fires is  
22 ignited by humans (Archibald et al., 2009; Saarnak, 2001), although their decisions on  
23 when to burn an area, as well as the fire spread and intensity, are still related to fuel  
24 composition (Govender et al., 2006). Humans maintain the grass-fire feedback, since  
25 they aim at keeping the land free from woody vegetation, and also because fire spread is  
26 favored by grass presence (Ratnam et al., 2011). Changes in land use have therefore  
27 strong influences on the current and future outcomes of tree-grass competition. Also,  
28 humans are expected to change their application of fire as a land use tool, as a  
29 consequence of changed environmental conditions. These elements are partly taken into  
30 account in some DGVMs (e.g. in LPJ-GUESS-SPITFIRE), but we do not consider them  
31 here for the purpose of this paper.

32

1    **4 Concluding remarks**

2    Current ecological understanding identifies water limitation and grass-fire feedback as  
3    dominant mechanisms driving the forest-savanna-grassland transition in Africa. In arid  
4    and semiarid savannas, trees are water-limited, and the water competition with grasses  
5    is the key factor determining savanna existence. In these conditions, grasses compete  
6    especially fiercely with tree seedlings. In wetter areas along the climatic gradient,  
7    savannas are maintained by the presence of a grass-fire positive feedback. Fire spread is  
8    increased by grasses, which provide fuel load. Grasses re-grow faster than trees after  
9    fires, while tree recruitment is limited. Thus, trees do not close their canopies, leaving  
10   more free space for grasses. On the other hand, when trees manage to close their  
11   canopies, grasses are outcompeted because of light limitations, and because fire is  
12   suppressed. This grass-fire feedback is reinforced by the higher flammability of forest  
13   trees with respect to savanna trees. Both water limitations and fires act differently on  
14   tree adults and seedlings, which compete more directly with grasses and are the most  
15   sensitive stage in tree life.

16   These mechanisms are to varying extent included in the three DGVMs we analyzed  
17   (JSBACH, LPJ-GUESS-SPITFIRE and aDGVM). Indeed, the three models predict the  
18   main features of the current tree cover along the mean annual rainfall gradient in Africa,  
19   as derived from ground and satellite observations. aDGVM output matches the  
20   observations better than the other two models. This is perhaps to be expected since this  
21   model is specifically designed for African vegetation and it includes more detailed  
22   representations of ecological interactions, especially the vegetation-fire feedback. For  
23   the other two models, the main differences between observations and model outputs are:  
24   i) JSBACH overestimates tree cover in dry areas (see also Brovkin et al., 2013); ii) LPJ-  
25   GUESS-SPITFIRE does not show any savanna at medium to high annual rainfall rates;  
26   iii) both these DGVMs do not show bimodality of savannas and forests in humid areas.  
27   This latter point might feed the debate about whether bimodality between savanna and  
28   forest cover actually exists (see e.g. Hanan et al., 2014). Despite their reasonably good  
29   performances, not all the mechanisms included in JSBACH and LPJ-GUESS-SPITFIRE  
30   are fully appropriate to represent vegetation in the tropics and the subtropics. In  
31   JSBACH, competition between trees and grasses favors the former irrespectively of  
32   water availability, which is one of the reasons behind JSBACH tree cover

1 overestimation. At the same time, in this model, fire is fostered disproportionately by  
2 woody vegetation as compared to grasses, resulting in a negative feedback. This is  
3 responsible for observing savannas in larger parts of the rainfall gradients, and no  
4 savannas would be simulated without them. Although the three models display  
5 comparable outcomes under the current climate, the presence of a negative fire-  
6 vegetation feedback in JSBACH, a positive feedback in aDGVM, and an intermediate  
7 behavior in LPJ-GUESS-SPITFIRE, leads to different predictions of fire frequency and  
8 effects under climate change scenarios between the three models. In JSBACH, the  
9 initial increase in woody vegetation, due to higher CO<sub>2</sub> concentrations, would get  
10 damped by the consequent increase in fire spread. Interesting in this perspective is  
11 that the sensitivity to shifts between forests and savannas is low for JSBACH, as  
12 negative feedbacks are more important, while in aDGVM the positive grass-fire  
13 feedback mechanism results in a large sensitivity to shifts of the different tree-grass  
14 systems. LPJ-GUESS-SPITFIRE has an intermediate behavior between the other two  
15 models, since grass and woody vegetation foster fire in a similar way. Also, in this  
16 model fires seem to be suppressed too easily by high humidity conditions, which cause  
17 savannas to be absent at medium-high annual rainfall values.

18 Tree seedlings are the bottleneck stage of tree life in the forest-savanna-grassland  
19 transition (Salazar et al., 2012; Sankaran et al., 2004), and the two most important  
20 mechanisms we identified here, i.e. water competition and limitation, and fires, tend to  
21 affect tree seedlings particularly strongly. Thus, including tree demography as in LPJ-  
22 GUESS and the aDGVM, improves the representation of ecological interactions in the  
23 models. Also, representing forest and savanna trees with different flammability and  
24 shade tolerances (as in LPJ-GUESS and aDGVM) is beneficial, and they reinforce the  
25 positive grass-fire feedback, if included (as in aDGVM).

26 Having in mind that DGVMs need to be kept as simple as possible, we conclude that the  
27 most important mechanisms to better represent the forest-savanna-grassland transition  
28 are i) how water limits tree growth and regulates tree-grass competition, and ii) the  
29 grass-fire feedback. Distinguishing between tree life stages and representing the  
30 different responses of forest and savanna trees, are less important features for the  
31 models, although they can considerably ameliorate the representation of the two main  
32 mechanisms. As parts of these mechanisms are already included in most DGVMs,

1 extensions should be relatively simple, but they would substantially improve the  
2 predictions of vegetation dynamics and carbon balance under future climate change  
3 scenarios.

4

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13

## 14 **References**

15 Archibald, S., Roy, D., van Wilgen, B. and Scholes, R. J.: What limits fire? An  
16 examination of drivers of burnt area in Southern Africa, *Glob. Chang. Biol.*, 15, 613–  
17 630, 2009.

18 Arneth, A., Lehsten, V., Spessa, A. and Thonicke, K.: Climate-fire interactions and  
19 savanna ecosystems: a dynamic vegetation modelling study for the African continent, in  
20 *Ecosystem Function in Savannas: Measurement and Modeling at Landscape to Global*  
21 *Scales*, edited by M. J. Hill and N. P. Hanan, CRC Press., 2010.

22 Baudena, M., D'Andrea, F. and Provenzale, A.: An idealized model for tree–grass  
23 coexistence in savannas: the role of life stage structure and fire disturbances, *J. Ecol.*,  
24 98(1), 74–80, doi:10.1111/j.1365-2745.2009.01588.x, 2010.

25 Baudena, M. and Rietkerk, M.: Complexity and coexistence in a simple spatial model  
26 for arid savanna ecosystems, *Theor. Ecol.*, 6(2), 131–141, doi:10.1007/s12080-012-  
27 0165-1, 2013.

28 Beerling, D. J. and Osborne, C. P.: The origin of the savanna biome, *Glob. Chang.*  
29 *Biol.*, 12(11), 2023–2031, doi:10.1111/j.1365-2486.2006.01239.x, 2006.

30 De Boer, H. J., Lammertsma, E. I., Wagner-Cremer, F., Wassen, M. J., Dilcher, D. L.  
31 and Dekker, S. C.: Climate forcing due to optimization of maximal leaf conductance in

1 subtropical vegetation, Proc. Natl. Acad. Sci. United States Am., 108(10), 4041–4046,  
2 doi:10.1073/pnas.1100555108, 2011.

3 Bonan, G. B., Levis, S., Sitch, S., Vertenstein, M. and Oleson, K. W.: A dynamic global  
4 vegetation model for use with climate models: concepts and description of simulated  
5 vegetation dynamics, Glob. Chang. Biol., 9(11), 1543–1566, doi:10.1046/j.1365-  
6 2486.2003.00681.x, 2003.

7 Bonan, G. B. and Shugart, H. H.: Environmental factors and ecological processes in  
8 boreal forests, Annu. Rev. Ecol. Syst., 20, 1–28,  
9 doi:10.1146/annurev.es.20.110189.000245, 1989.

10 Bond, W. J.: What Limits Trees in C 4 Grasslands and Savannas?, Annu. Rev. Ecol.  
11 Evol. Syst., 39(1), 641–659, doi:10.1146/annurev.ecolsys.39.110707.173411, 2008.

12 Bond, W. J.: Do nutrient-poor soils inhibit development of forests? A nutrient stock  
13 analysis, Plant Soil, 334(1-2), 47–60, doi:10.1007/s11104-010-0440-0, 2010.

14 Bond, W. J. and Midgley, G. F.: A proposed CO<sub>2</sub>-controlled mechanism of woody plant  
15 invasion in grasslands and savannas, Glob. Chang. Biol., 6, 865–869, 2000.

16 Bond, W. J., Midgley, G. F. and Woodward, F. I.: The importance of low atmospheric  
17 CO<sub>2</sub> and fire in promoting the spread of grasslands and savannas, Glob. Chang. Biol.,  
18 9(7), 973–982, doi:10.1046/j.1365-2486.2003.00577.x, 2003.

19 Bowman, D. M. J. S., Murphy, B. P. and Banfai, D. S.: Has global environmental  
20 change caused monsoon rainforests to expand in the australian monsoon tropics?,  
21 Landsc. Ecol., 25(8), 1247–1260, 2010.

22 Brovkin, V., Boysen, L., Arora, V. K., Boisier, J. P., Cadule, P., Chini, L., Claussen,  
23 M., Friedlingstein, P., Gayler, V., van den Hurk, B. J. J. M., Hurtt, G. C., Jones, C. D.,  
24 Kato, E., de Noblet-Ducoudré, N., Pacifico, F., Pongratz, J. and Weiss, M.: Effect of  
25 Anthropogenic Land-Use and Land-Cover Changes on Climate and Land Carbon  
26 Storage in CMIP5 Projections for the Twenty-First Century, J. Clim., 26(18), 6859–  
27 6881, doi:10.1175/JCLI-D-12-00623.1, 2013.

28 Brovkin, V., Raddatz, T., Reick, C. H., Claussen, M. and Gayler, V.: Global  
29 biogeophysical interactions between forest and climate, Geophys. Res. Lett., 36(7), 1–6,  
30 doi:10.1029/2009GL037543, 2009.

31 Bucini, G. and Hanan, N. P.: A continental-scale analysis of tree cover in African  
32 savannas, Glob. Ecol. Biogeogr., 16(5), 593–605, doi:10.1111/j.1466-  
33 8238.2007.00325.x, 2007.

34 Buitenwerf, R., Bond, W. J., Stevens, N. and Trollope, W. S. W.: Increased tree  
35 densities in South African savannas: >50 years of data suggests CO<sub>2</sub> as a driver, Glob.  
36 Chang. Biol., 18(2), 675–684, doi:10.1111/j.1365-2486.2011.02561.x, 2012.

37 Cramer, W., Bondeau, A., Woodward, F. I., Prentice, I. C., Betts, R. a., Brovkin, V.,  
38 Cox, P. M., Fisher, V., Foley, J. a., Friend, A. D., Kucharik, C., Lomas, M. R.,

1 Ramankutty, N., Sitch, S., Smith, B., White, A. and Young-Molling, C.: Global  
2 response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change:  
3 results from six dynamic global vegetation models, *Glob. Chang. Biol.*, 7(4), 357–373,  
4 doi:10.1046/j.1365-2486.2001.00383.x, 2001.

5 D'Onofrio, D., Baudena, M., D'Andrea, F., Rietkerk, M. and Provenzale, A.: Tree-grass  
6 competition for soil water in arid and semiarid savannas: The role of rainfall  
7 intermittency, *Water Resour. Res.*, n/a–n/a, doi:10.1002/2014WR015515, 2014.

8 Dalmonech, D. and Zaehle, S.: Towards a more objective evaluation of modelled land-  
9 carbon trends using atmospheric CO<sub>2</sub> and satellite-based vegetation activity  
10 observations, *Biogeosciences*, 10(6), 4189–4210, doi:10.5194/bg-10-4189-2013, 2013.

11 Donohue, R. J., Roderick, M. L., McVicar, T. R. and Farquhar, G. D.: Impact of CO<sub>2</sub>  
12 fertilization on maximum foliage cover across the globe's warm, arid environments,  
13 *Geophys. Res. Lett.*, 40(12), 3031–3035, doi:10.1002/grl.50563, 2013.

14 Ehleringer, J. R., Cerling, T. E. and Helliker, B. R.: C<sub>4</sub> photosynthesis, atmospheric  
15 CO<sub>2</sub>, and climate, *Oecologia*, 112(3), 285–299, 1997.

16 Favier, C., Aleman, J., Bremond, L., Dubois, M. a., Freycon, V. and Yangakola, J.-M.:  
17 Abrupt shifts in African savanna tree cover along a climatic gradient, *Glob. Ecol.*  
18 *Biogeogr.*, 21(8), 787–797, doi:10.1111/j.1466-8238.2011.00725.x, 2012.

19 February, E. C. and Higgins, S. I.: The distribution of tree and grass roots in savannas in  
20 relation to soil nitrogen and water, *South African J. Bot.*, 76(3), 517–523,  
21 doi:10.1016/j.sajb.2010.04.001, 2010.

22 February, E. C., Higgins, S. I., Bond, W. J. and Swemmer, L.: Influence of competition  
23 and rainfall manipulation on the growth responses of savanna trees and grasses.,  
24 *Ecology*, 94(5), 1155–64, 2013.

25 Fisher, R., McDowell, N., Purves, D., Moorcroft, P., Sitch, S., Cox, P., Huntingford, C.,  
26 Meir, P. and Ian Woodward, F.: Assessing uncertainties in a second-generation dynamic  
27 vegetation model caused by ecological scale limitations., *New Phytol.*, 187, 666–681,  
28 doi:10.1111/j.1469-8137.2010.03340.x, 2010.

29 Giorgetta, M. A., Jungclaus, J., Reick, C. H., Legutke, S., Bader, J., Boettinger, M.,  
30 Brovkin, V., Crueger, T., Esch, M., Fieg, K., Glushak, K., Gayler, V., Haak, H.,  
31 Hollweg, H.-D., Ilyina, T., Kinne, S., Kornblueh, L., Matei, D., Mauritsen, T.,  
32 Mikolajewicz, U., Mueller, W., Notz, D., Pithan, F., Raddatz, T., Rast, S., Redler, R.,  
33 Roeckner, E., Schmidt, H., Schnur, R., Segschneider, J., Six, K. D., Stockhause, M.,  
34 Timmreck, C., Wegner, J., Widmann, H., Wieners, K.-H., Claussen, M., Marotzke, J.  
35 and Stevens, B.: Climate and carbon cycle changes from 1850 to 2100 in MPI-ESM  
36 simulations for the Coupled Model Intercomparison Project phase 5, *J. Adv. Model.*  
37 *Earth Syst.*, 5(3), 572–597, doi:10.1002/jame.20038, 2013.

38 Govender, N., Trollope, W. S. W. and Van Wilgen, B. W.: The effect of fire season, fire  
39 frequency, rainfall and management on fire intensity in savanna vegetation in South  
40 Africa, *J. Appl. Ecol.*, 43(4), 748–758, doi:10.1111/j.1365-2664.2006.01184.x, 2006.

1 Hanan, N. P., Sea, W. B., Dangelmayr, G. and Govender, N.: Do fires in savannas  
2 consume woody biomass? A comment on approaches to modeling savanna dynamics.,  
3 Am. Nat., 171(6), 851–6, doi:10.1086/587527, 2008.

4 Hanan, N. P., Tredennick, A. T., Prihodko, L., Bucini, G. and Dohn, J.: Analysis of  
5 stable states in global savannas: is the CART pulling the horse?, Glob. Ecol. Biogeogr.,  
6 23(3), 259–263, doi:10.1111/geb.12122, 2014.

7 Hely, C., Bremond, L., Alleaume, S., Smith, B., Sykes, M. T. and Guiot, J.: Sensitivity  
8 of African biomes to changes in the precipitation regime, Glob. Ecol. Biogeogr., 15(3),  
9 258–270, doi:10.1111/j.1466-8238.2006.00235.x, 2006.

10 Hickler, T., Fronzek, S., Araújo, M. B., Schweiger, O., Thuiller, W. and Sykes, M. T.:  
11 An ecosystem model-based estimate of changes in water availability differs from water  
12 proxies that are commonly used in species distribution models, Glob. Ecol. Biogeogr.,  
13 18, 304–313, doi:10.1111/j.1466-8238.2009.00455.x, 2009.

14 Hickler, T., Prentice, I. C., Smith, B., Sykes, M. T. and Zaehle, S.: Implementing plant  
15 hydraulic architecture within the LPJ dynamic global vegetation model, Glob. Ecol.  
16 Biogeogr., 15, 567–577, 2006.

17 Higgins, S. I., Bond, W. J., Combrink, H., Craine, J. M., February, E. C., Govender, N.,  
18 Lannas, K., Moncreiff, G. and Trollope, W. S. W.: Which traits determine shifts in the  
19 abundance of tree species in a fire-prone savanna?, edited by P. Vesk, J. Ecol., 100(6),  
20 1400–1410, doi:10.1111/j.1365-2745.2012.02026.x, 2012.

21 Higgins, S. I., Bond, W. J., February, E. C., Bronn, A., Euston-Brown, D. I. W., Enslin,  
22 B., Govender, N., Rademan, L., O'Regan, S., Potgieter, A. L. F., Scheiter, S., Sowry,  
23 R., Trollope, L. and Trollope, W. S. W.: Effects of four decades of fire manipulation on  
24 woody vegetation structure in savanna, Ecology, 88(5), 1119–1125, 2007.

25 Higgins, S. I., Bond, W. J. and Trollope, W. S. W.: Fire, resprouting and variability: a  
26 recipe for grass–tree coexistence in savanna, J. Ecol., 88(2), 213–229, 2000.

27 Higgins, S. I., Bond, W. J., Trollope, W. S. W. and Williams, R. J.: Physically  
28 motivated empirical models for the spread and intensity of grass fires, Int. J. Wildl. Fire,  
29 17(5), 595–601, doi:10.1071/WF06037, 2008.

30 Higgins, S. I. and Scheiter, S.: Atmospheric CO<sub>2</sub> forces abrupt vegetation shifts locally,  
31 but not globally., Nature, 488(7410), 209–12, doi:10.1038/nature11238, 2012.

32 Hirota, M., Holmgren, M., Van Nes, E. H. and Scheffer, M.: Global resilience of  
33 tropical forest and savanna to critical transitions., Science (80- .), 334(6053), 232–235,  
34 doi:10.1126/science.1210657, 2011.

35 Hoffmann, W. a, Geiger, E. L., Gotsch, S. G., Rossatto, D. R., Silva, L. C. R., Lau, O.  
36 L., Haridasan, M. and Franco, A. C.: Ecological thresholds at the savanna-forest  
37 boundary: how plant traits, resources and fire govern the distribution of tropical  
38 biomes., Ecol. Lett., 15(7), 759–68, doi:10.1111/j.1461-0248.2012.01789.x, 2012.

1 House, J. I., Archer, S., Breshears, D. D. and Scholes, R. J.: Conundrums in mixed  
2 woody-herbaceous plant systems, *J. Biogeogr.*, 30, 1763–1777, 2003.

3 Hutchinson, G. E.: The paradox of the plankton, *Am. Nat.*, 95, 137–145, 1961.

4 Intergovernmental Panel on Climate Change: Climate Change 2007 - The Physical  
5 Science Basis: Working Group I Contribution to the Fourth Assessment Report of the  
6 IPCC (Climate Change 2007), Cambridge University Press., 2007.

7 Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M.,  
8 Saha, S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W.,  
9 Janowiak, J., Mo, K. C., Ropelewski, C., Wang, J., Leetmaa, A., Reynolds, R., Jenne, R.  
10 and Joseph, D.: The NCEP/NCAR 40-year reanalysis project, *Bull. Am. Meteorol. Soc.*,  
11 77(3), 437–471, doi:10.1175/1520-0477(1996)077<0437:TNYRP>2.0.CO;2, 1996.

12 Kgope, B. S., Bond, W. J. and Midgley, G. F.: Growth responses of African savanna  
13 trees implicate atmospheric CO<sub>2</sub> as a driver of past and current changes in savanna tree  
14 cover, *Austral Ecol.*, 35(4), 451–463, 2010.

15 Koenker, R. and Park, B. J.: An interior point algorithm for nonlinear quantile  
16 regression, *J. Econom.*, 71(1-2), 265–283, doi:10.1016/0304-4076(96)84507-6, 1996.

17 Kulmatiski, A. and Beard, K. H.: Root niche partitioning among grasses, saplings, and  
18 trees measured using a tracer technique., *Oecologia*, 171(1), 25–37,  
19 doi:10.1007/s00442-012-2390-0, 2013.

20 Van Langevelde, F., van de Vijver, C. A. D. M., Kumar, L., van de Koppel, J., de  
21 Ridder, N., van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L., Bond, W. J.,  
22 Prins, H. H. T. and Rietkerk, M.: Effects of fire and herbivory on the stability of  
23 savanna ecosystems, *Ecology*, 84(2), 337–350, doi:10.1890/0012-  
24 9658(2003)084[0337:EOFATHO]2.0.CO;2, 2003.

25 Lehmann, C. E. R., Anderson, T. M., Sankaran, M., Higgins, S. I., Archibald, S.,  
26 Hoffmann, W. a., Hanan, N. P., Williams, R. J., Fensham, R. J., Felfili, J., Hustley, L. B.,  
27 Ratnam, J., San Jose, J., Montes, R., Franklin, D., Russell-Smith, J., Ryan, C. M.,  
28 Durigan, G., Hiernaux, P., Haidar, R., Bowman, D. M. J. S. and Bond, W. J.: Savanna  
29 Vegetation-Fire-Climate Relationships Differ Among Continents, *Science* (80- .),  
30 343(6170), 548–552, doi:10.1126/science.1247355, 2014.

31 Lehmann, C. E. R., Archibald, S. a., Hoffmann, W. a and Bond, W. J.: Deciphering the  
32 distribution of the savanna biome., *New Phytol.*, 191(1), 197–209, doi:10.1111/j.1469-  
33 8137.2011.03689.x, 2011.

34 Lehsten, V., Harmand, P., Palumbo, I. and Arneth, a.: Modelling burned area in Africa,  
35 *Biogeosciences*, 7(10), 3199–3214, doi:10.5194/bg-7-3199-2010, 2010.

36 Lehsten, V., Tansey, K., Balzter, H., Thonicke, K., Spessa, a., Weber, U., Smith, B. and  
37 Arneth, a.: Estimating carbon emissions from African wildfires, *Biogeosciences*, 6(3),  
38 349–360, doi:10.5194/bg-6-349-2009, 2009.

1 Lloyd, J., Bird, M. I., Vellen, L., Miranda, A. C., Veenendaal, E. M., Djagbletey, G.,  
2 Miranda, H. S., Cook, G. and Farquhar, G. D.: Contributions of woody and herbaceous  
3 vegetation to tropical savanna ecosystem productivity: a quasi-global estimate., *Tree*  
4 *Physiol.*, 28(3), 451–68, 2008.

5 Moncrieff, G. R., Scheiter, S., Bond, W. J. and Higgins, S. I.: Increasing atmospheric  
6 CO<sub>2</sub> overrides the historical legacy of multiple stable biome states in Africa., *New*  
7 *Phytol.*, 201(3), 908–15, doi:10.1111/nph.12551, 2013.

8 Murphy, B. P. and Bowman, D. M. J. S.: What controls the distribution of tropical  
9 forest and savanna?, *Ecol. Lett.*, 15(7), 748–58, doi:10.1111/j.1461-0248.2012.01771.x,  
10 2012.

11 Nathan, J., von Hardenberg, J. and Meron, E.: Spatial instabilities untie the exclusion-  
12 principle constraint on species coexistence., *J. Theor. Biol.*, 335, 198–204,  
13 doi:10.1016/j.jtbi.2013.06.026, 2013.

14 Van Nes, E. H., Hirota, M., Holmgren, M. and Scheffer, M.: Tipping points in tropical  
15 tree cover: linking theory to data., *Glob. Chang. Biol.*, 20(3), 1016–21,  
16 doi:10.1111/gcb.12398, 2014.

17 New, M., Lister, D., Hulme, M. and Makin, I.: A high-resolution data set of surface  
18 climate over global land areas, *Clim. Res.*, 21, 1–25, 2000.

19 Polley, H. W., Johnson, H. B. and Mayeux, H. S.: Increasing CO<sub>2</sub> - comparative  
20 responses of the c-4 grass *Schizachyrium* and grassland invader *Prosopis*, *Ecology*,  
21 75(4), 976–988, doi:10.2307/1939421, 1994.

22 Le Quéré, C., Andres, R. J., Boden, T., Conway, T., Houghton, R. A., House, J. I.,  
23 Marland, G., Peters, G. P., van der Werf, G. R., Ahlström, A., Andrew, R. M., Bopp, L.,  
24 Canadell, J. G., Ciais, P., Doney, S. C., Enright, C., Friedlingstein, P., Huntingford, C.,  
25 Jain, A. K., Jourdain, C., Kato, E., Keeling, R. F., Klein Goldewijk, K., Levis, S., Levy,  
26 P., Lomas, M., Poulter, B., Raupach, M. R., Schwinger, J., Sitch, S., Stocker, B. D.,  
27 Viovy, N., Zaehle, S. and Zeng, N.: The global carbon budget 1959-2011, *Earth Syst.*  
28 *Sci. Data*, 5(1), 165–185, doi:10.5194/essd-5-165-2013, 2013.

29 Raddatz, T. J., Reick, C. H., Knorr, W., Kattge, J., Roeckner, E., Schnur, R., Schnitzler,  
30 K.-G., Wetzel, P. and Jungclaus, J.: Will the tropical land biosphere dominate the  
31 climate–carbon cycle feedback during the twenty-first century?, *Clim. Dyn.*, 29(6),  
32 565–574, doi:10.1007/s00382-007-0247-8, 2007.

33 Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. a., Archibald, S., Lehmann, C.  
34 E. R., Anderson, M. T., Higgins, S. I. and Sankaran, M.: When is a “forest” a savanna,  
35 and why does it matter?, *Glob. Ecol. Biogeogr.*, 20(5), 653–660, doi:10.1111/j.1466-  
36 8238.2010.00634.x, 2011.

37 Reick, C. H., Raddatz, T., Brovkin, V. and Gayler, V.: Representation of natural and  
38 anthropogenic land cover change in MPI-ESM, *J. Adv. Model. Earth Syst.*, 5(3), 1942–  
39 2466, doi:10.1002/jame.20022, 2013.

1 Rietkerk, M., Brovkin, V., van Bodegom, P. M., Claussen, M., Dekker, S. C., Dijkstra,  
2 H. a., Goryachkin, S. V., Kabat, P., van Nes, E. H., Neutel, A.-M., Nicholson, S. E.,  
3 Nobre, C., Petoukhov, V., Provenzale, A., Scheffer, M. and Seneviratne, S. I.: Local  
4 ecosystem feedbacks and critical transitions in the climate, *Ecol. Complex.*, 8(3), 223–  
5 228, doi:10.1016/j.ecocom.2011.03.001, 2011.

6 Rietkerk, M., Dekker, S. C., de Ruiter, P. C. and van de Koppel, J.: Self-Organized  
7 Patchiness and Catastrophic Shifts in Ecosystems, *Science*, 305, 1926–1929, 2004.

8 Rossatto, D. R., Hoffmann, W. A. and Franco, A. C.: Differences in growth patterns  
9 between co-occurring forest and savanna trees affect the forest-savanna boundary,  
10 *Funct. Ecol.*, 23(4), 689–698, doi:10.1111/j.1365-2435.2009.01568.x, 2009.

11 Saarnak, C. F.: A shift from natural to human-driven fire regime: implications for trace-  
12 gas emissions, *Holocene*, 11, 373–375, 2001.

13 Salazar, A., Goldstein, G., Franco, A. C. and Miralles-wilhelm, F.: Differential seedling  
14 establishment of woody plants along a tree density gradient in Neotropical savannas, *J.*  
15 *Ecol.*, 100, 1411–1421, doi:10.1111/j.1365-2745.2012.02028.x, 2012.

16 Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S.,  
17 Gignoux, J., Higgins, S. I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A.,  
18 Bucini, G., Caylor, K. K., Coughenour, M. B., Diouf, A., Ekaya, W., Feral, C. J.,  
19 February, E. C., Frost, P. G. H., Hiernaux, P., Hrabar, H., Metzger, K. L., Prins, H. H.  
20 T., Ringrose, S., Sea, W., Tews, J., Worden, J. and Zambatis, N.: Determinants of  
21 woody cover in African savannas, *Nature*, 438(7069), 846–849,  
22 doi:10.1038/nature04070, 2005.

23 Sankaran, M., Ratnam, J. and Hanan, N.: Woody cover in African savannas: the role of  
24 resources, fire and herbivory, *Glob. Ecol. Biogeogr.*, 17(2), 236–245,  
25 doi:10.1111/j.1466-8238.2007.00360.x, 2008.

26 Sankaran, M., Ratnam, J. and Hanan, N. P.: Tree-grass coexistence in savannas  
27 revisited - insights from an examination of assumptions and mechanisms invoked in  
28 existing models, *Ecol. Lett.*, 7(6), 480–490, doi:10.1111/j.1461-0248.2004.00596.x,  
29 2004.

30 Sarmiento, G.: *The Ecology of Neotropical Savannas*, Harvard Univ. Press, Cambridge,  
31 Mass., 1984.

32 Sato, H., Itoh, A. and Kohyama, T.: SEIB–DGVM: A new Dynamic Global Vegetation  
33 Model using a spatially explicit individual-based approach, *Ecol. Modell.*, 200(3-4),  
34 279–307, doi:10.1016/j.ecolmodel.2006.09.006, 2007.

35 Scheiter, S. and Higgins, S. I.: Impacts of climate change on the vegetation of Africa: an  
36 adaptive dynamic vegetation modelling approach, *Glob. Chang. Biol.*, 15(9), 2224–  
37 2246, doi:10.1111/j.1365-2486.2008.01838.x, 2009.

38 Scheiter, S. and Higgins, S. I.: How many elephants can you fit into a conservation area,  
39 *Conserv. Lett.*, 5(3), 176–185, doi:10.1111/j.1755-263X.2012.00225.x, 2012.

1 Scheiter, S., Higgins, S. I., Osborne, C. P., Bradshaw, C., Lunt, D., Ripley, B. S.,  
2 Taylor, L. L. and Beerling, D. J.: Fire and fire-adapted vegetation promoted C4  
3 expansion in the late Miocene., *New Phytol.*, 195(3), 653–66, doi:10.1111/j.1469-  
4 8137.2012.04202.x, 2012.

5 Scheiter, S., Langan, L. and Higgins, S. I.: Next-generation dynamic global vegetation  
6 models : learning from community ecology, *New Phytol.*, 198, 957–969,  
7 doi:10.1111/nph.12210, 2013.

8 Scholes, R. J.: Convex Relationships in Ecosystems Containing Mixtures of Trees and  
9 Grass, *Environ. Resour. Econ.*, 26, 559–574, 2003.

10 Scholes, R. J. and Archer, S. R.: Tree-grass interactions in savannas, *Annu. Rev. Ecol.*  
11 *Syst.*, 28, 517–544, 1997.

12 Scholes, R. J. and Walker, B. H.: An African Savanna: Synthesis of the Nylsvley Study,  
13 edited by Cambridge, Cambridge University Press, Cambridge, UK., 1993.

14 Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., Betts, R.,  
15 Ciais, P., Cox, P., Friedlingstein, P., Jones, C. D., Prentice, I. C. and Woodward, F. I.:  
16 Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon  
17 cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs), *Glob.*  
18 *Chang. Biol.*, 14(9), 2015–2039, doi:10.1111/j.1365-2486.2008.01626.x, 2008.

19 Sitch, S., Smith, B. and Prentice, I.: Evaluation of ecosystem dynamics, plant geography  
20 and terrestrial carbon cycling in the LPJ dynamic global vegetation model, *Glob.*  
21 *Chang. ...*, 9, 161–185, 2003.

22 Smith, B., Prentice, I. and Sykes, M.: Representation of vegetation dynamics in the  
23 modelling of terrestrial ecosystems: comparing two contrasting approaches within  
24 European climate space, *Glob. Ecol. ...*, 10, 621– 637, 2001.

25 Snyder, P. K., Delire, C. and Foley, J. a.: Evaluating the influence of different  
26 vegetation biomes on the global climate, *Clim. Dyn.*, 23(3-4), 279–302,  
27 doi:10.1007/s00382-004-0430-0, 2004.

28 Staver, A. C., Archibald, S. and Levin, S. A.: The global extent and determinants of  
29 savanna and forest as alternative biome states., *Science (80-.)*, 334(6053), 230–232,  
30 doi:10.1126/science.1210465, 2011.

31 Staver, A. C., Bond, W. J., Cramer, M. D. and Wakeling, J. L.: Top-down determinants  
32 of niche structure and adaptation among African Acacias., *Ecol. Lett.*, 15(7), 673–9,  
33 doi:10.1111/j.1461-0248.2012.01784.x, 2012.

34 Staver, A. C. and Levin, S. A.: Integrating theoretical climate and fire effects on  
35 savanna and forest systems., *Am. Nat.*, 180(2), 211–24, doi:10.1086/666648, 2012.

36 Thonicke, K., Spessa, A., Prentice, I., Harrison, S., Dong, L. and Carmona-Moreno, C.:  
37 The influence of vegetation, fire spread and fire behaviour on biomass burning and trace

1 gas emissions: results from a process-based model, *Biogeosciences*, 7, 1991–2011,  
2 2010.

3 Tilman, D.: *Resource competition and community structure*, Princeton University Press,  
4 Princeton, New Jersey, USA., 1982.

5 Trollope, W. S. W.: Fire in savannas, in *Ecological effects of fire of southern African*  
6 *ecosystems*, edited by P. D. V Booysen and N. M. Tainton, pp. 199–218, Springer-  
7 Verlag, Berlin, Germany., 1984.

8 Wakeling, J. L., Staver, a. C. and Bond, W. J.: Simply the best: the transition of savanna  
9 saplings to trees, *Oikos*, 120(May), 1448–1451, doi:10.1111/j.1600-0706.2011.19957.x,  
10 2011.

11 Walker, B. H. and Noy-Meir, I.: Aspects of stability and resilience of savanna  
12 *ecosystems*, in *Tropical savannas*, edited by B. J. Huntley and B. H. Walker, pp. 556–  
13 590, Springer-Verlag, Berlin., 1982.

14 Walter, H.: *Natural Savannas*, in *Ecology of Tropical and Subtropical Vegetation*,  
15 Oliver and Boyd, Edinburgh, UK., 1971.

16 Ward, D.: *The Biology of Deserts*, Oxford University Press, Oxford, UK., 2009.

17 Ward, D., Wiegand, K. and Getzin, S.: Walter’s two-layer hypothesis revisited: back to  
18 the roots!, *Oecologia*, 172(3), 617–30, doi:10.1007/s00442-012-2538-y, 2013.

19 Weber, U., Jung, M., Reichstein, M., Beer, C., Braakhekke, M. C., Lehsten, V., Ghent,  
20 D., Kaduk, J. and Viovy, N.: The interannual variability of Africa’s ecosystem  
21 productivity : a multi-model analysis, *Biogeosciences*, 6, 285–295, 2009.

22 Wigley, B. J., Bond, W. J. and Hoffman, M. T.: Thicket expansion in a South African  
23 savanna under divergent land use: local vs. global drivers?, *Glob. Chang. Biol.*, 16(3),  
24 964–976, doi:10.1111/j.1365-2486.2009.02030.x, 2010.

25 Yin, Z., Dekker, S. C., van den Hurk, B. J. J. M. and Dijkstra, H. A.: Bimodality of  
26 woody cover and biomass in semi-arid regime, *Earth Syst. Dyn. Discuss.*, 5(1), 83–120,  
27 doi:10.5194/esdd-5-83-2014, 2014a.

28 Yin, Z., Dekker, S. C., van den Hurk, B. and Dijkstra, H.: Effects of vegetation structure  
29 on biomass accumulation in a Balanced Optimality Structure Vegetation Model  
30 (BOSVM v1.0), *Geosci. Model Dev.*, 7, 821–845, 2014b.

Table 1. Models and their specifics concerning the tree-grass transition

Model	Specific variables for representing tropical vegetation	Variables representing savanna and forest trees	Distinction between savanna structure and tree age	Limiting resources for vegetation	Stable state(s) (in absence of fires)	How is fire represented?	Mechanisms driving savanna	Mechanisms driving forests/grasslands occurrence	Would a CO <sub>2</sub> increase modify the tree-grass transition and how?	Reference
JSBACH/ DYNVEG	No	LAI, PFT fractions, carbon in vegetation pools	No	Uncolonized space, hospitable land (water, indirectly via NPP)	Dominant woody (tree, shrub) PFTs	Fire is a function of air humidity and litter. Fires are mainly fostered by trees, which are also damaged by fire (negative feedback)	Fires	Forests occur in absence of fires (at any climate), while grasslands appear at high frequency of fire occurrence, i.e. at very intense dryness	Only indirectly (by changing litter availability for wildfires)	Brovkin et al 2009, Reick et al. 2013
LPJ-GUESS-SPITFIRE	No	Individual based model. LAI, PFT fractions, carbon in vegetation pools	Yes	Water and light	Depending on climate (mainly precipitation), either forest or grassland is the stable state. Savanna is observed in a relatively small precipitation range.	Fire is prescribed from remote sensing but its effects on vegetation depend on fuel availability and environmental conditions. Fires are fostered by both woody and grass biomass	Fires, water competition	Forests occur given sufficient precipitation, while grasslands appear at high frequency of fire occurrence, or low precipitation.	Higher CO <sub>2</sub> would benefit C <sub>3</sub> vegetation (trees) as compared to C <sub>4</sub> grasses. At the same time though, grasses and trees would produce more litter, which would increase fire intensity and hence might have negative effects on trees.	Smith et al. 2001, Thonicke et al. 2010
aDGVM	Yes	Individual based model. Plant level: LAI, height, basal area, canopy area, biomass in different pools Stand level: LAI, PFT fractions, carbon in vegetation pools of different PFTs, basal area, tree cover	Yes	Water, light, (space, via light competition)	Depending on climate (mostly defined by precipitation): desert, grassland, savanna, forest	Fire intensity is defined by fuel moisture and fuel biomass; fire ignition probability is a constant; fire removes aboveground grass biomass and, depending on height, aboveground tree biomass (topkill); vegetation can re-sprout. Grasses foster fire spread and profit from recurrent fires (positive feedback).	Competition for water, fires	Forests occur at high rainfall levels (where fire is not possible) and at mesic conditions when fire is absent; grasslands occur at more arid conditions when precipitation does not allow tree growth, and at more mesic conditions in the presence of fire.	CO <sub>2</sub> fertilization promotes tree growth and: (1) grasslands are transformed into savannas (2) tree canopy closure in savannas suppresses grass growth and fire activity, such that savannas are transformed into forests	Scheiter and Higgins, 2009, Scheiter et al. 2012

1 **Figure captions**

2 Figure 1

3 Tree cover as a function of mean annual rainfall (mm  $y^{-1}$ ). A) Savanna field data, reprinted  
4 from Sankaran et al. (2005); B) tree cover obtained from MODIS woody cover product (as  
5 e.g. Hirota et al., 2011), where anthropogenic land use is masked as described in the text. For  
6 clarity of representation, we selected only 0.05% of the data. For both databases, we selected  
7 only the data points between 35° S and 15° N in Africa. The dots are data; the continuous  
8 lines are the 90<sup>th</sup> quantile nonlinear regression (99<sup>th</sup> quantile not shown; see values of *b*  
9 coefficients in Tab. B1 in the Supplement). Notice that the field data (A) correspond only to  
10 savanna sites, and thus encompass a smaller rainfall range than the satellite data (B).

11

12 Figure 2

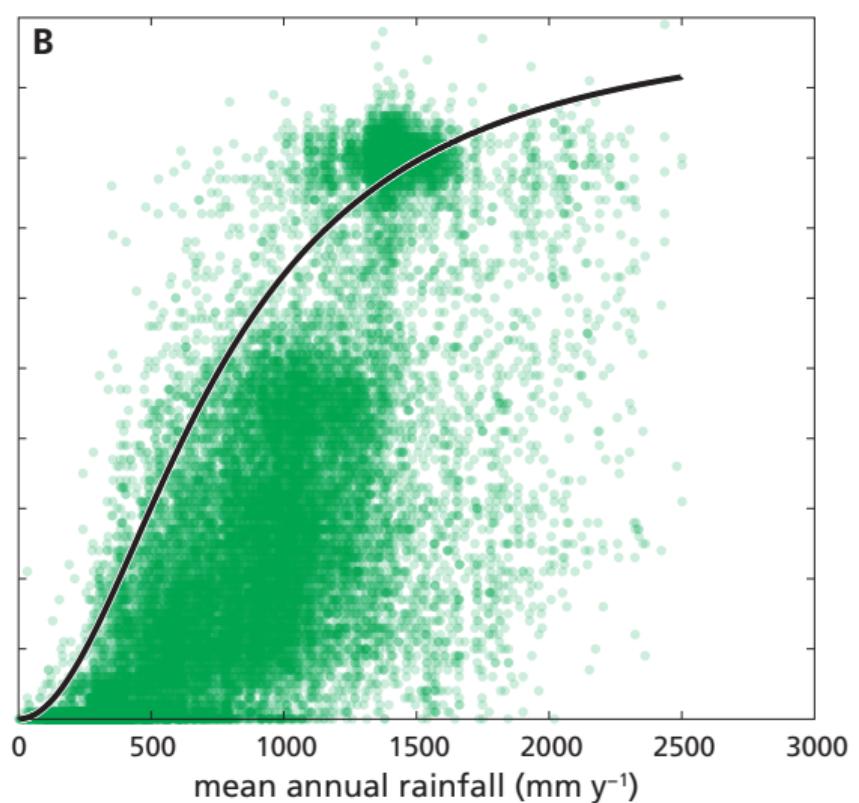
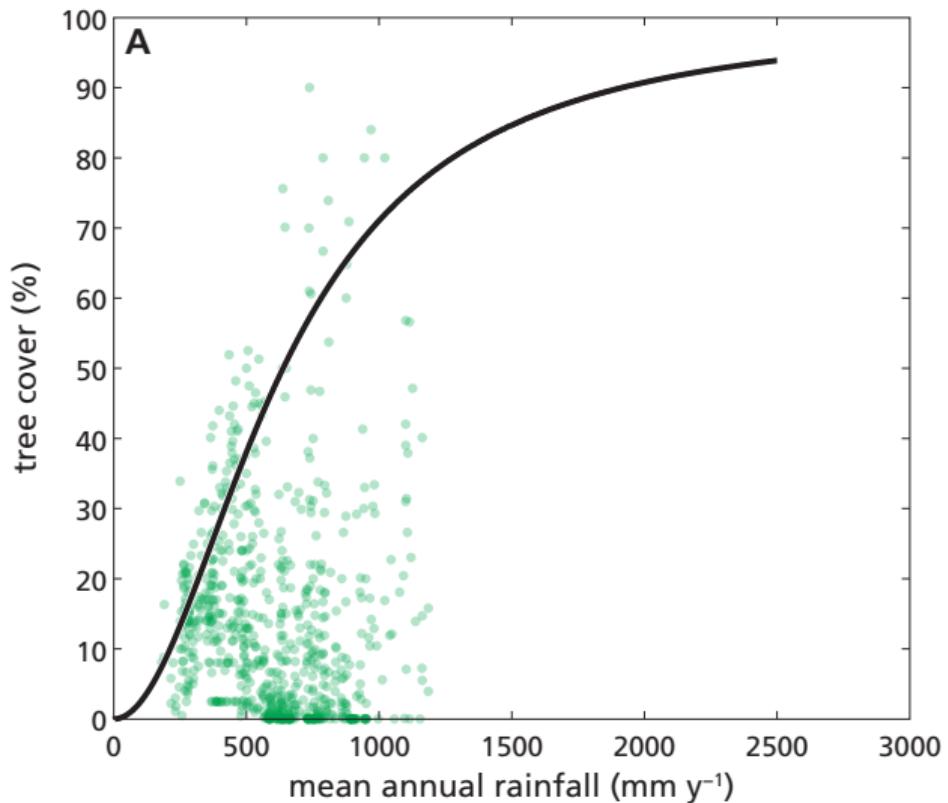
13 Model outputs for tree cover as a function of mean annual rainfall (mm  $y^{-1}$ ) in Africa  
14 between 35° S and 15° N: A) JSBACH; B) LPJ-GUESS-SPITFIRE; C) aDGVM. The dots are  
15 data, the continuous lines are the 90<sup>th</sup> quantile nonlinear regression (99<sup>th</sup> quantile not shown;  
16 see value of *b* coefficients in Table B1 in the Supplement).

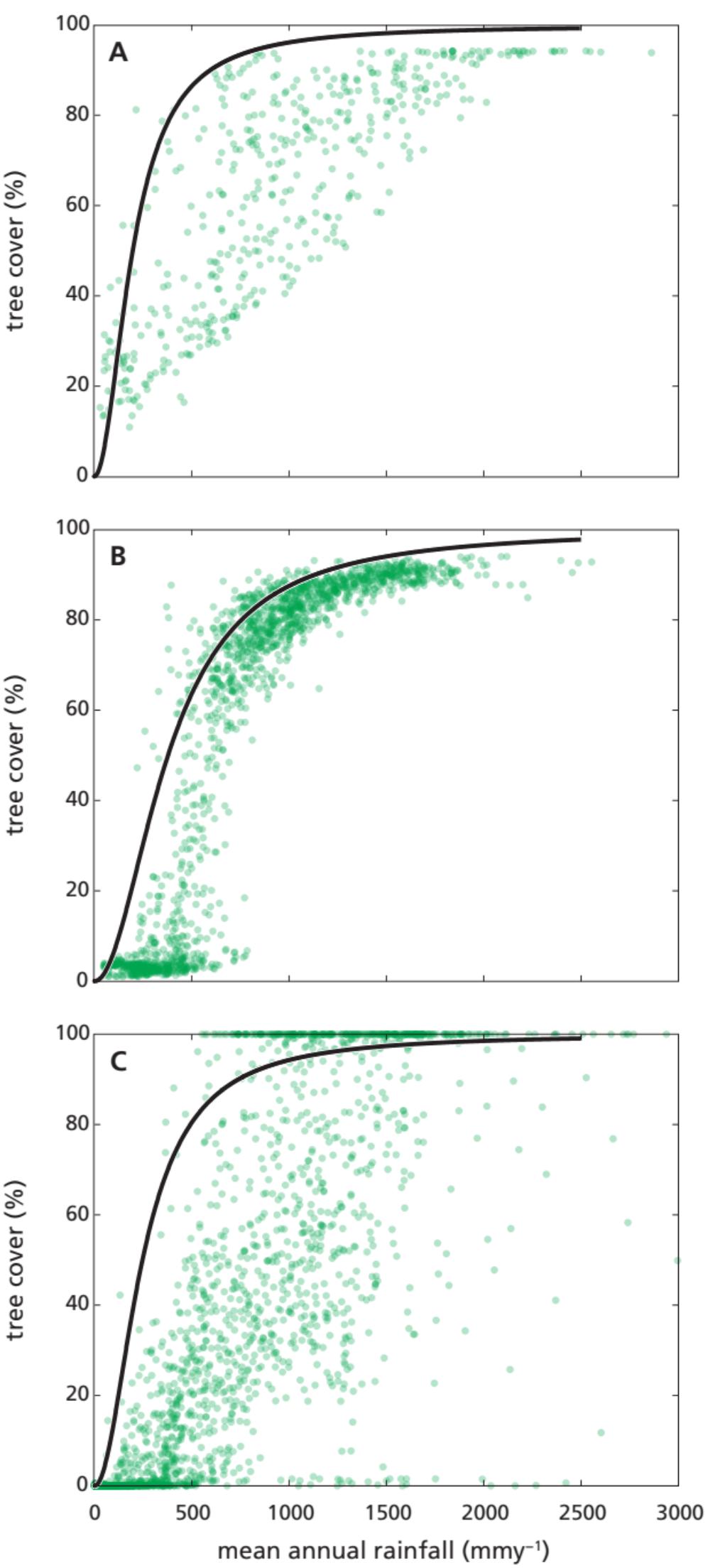
17

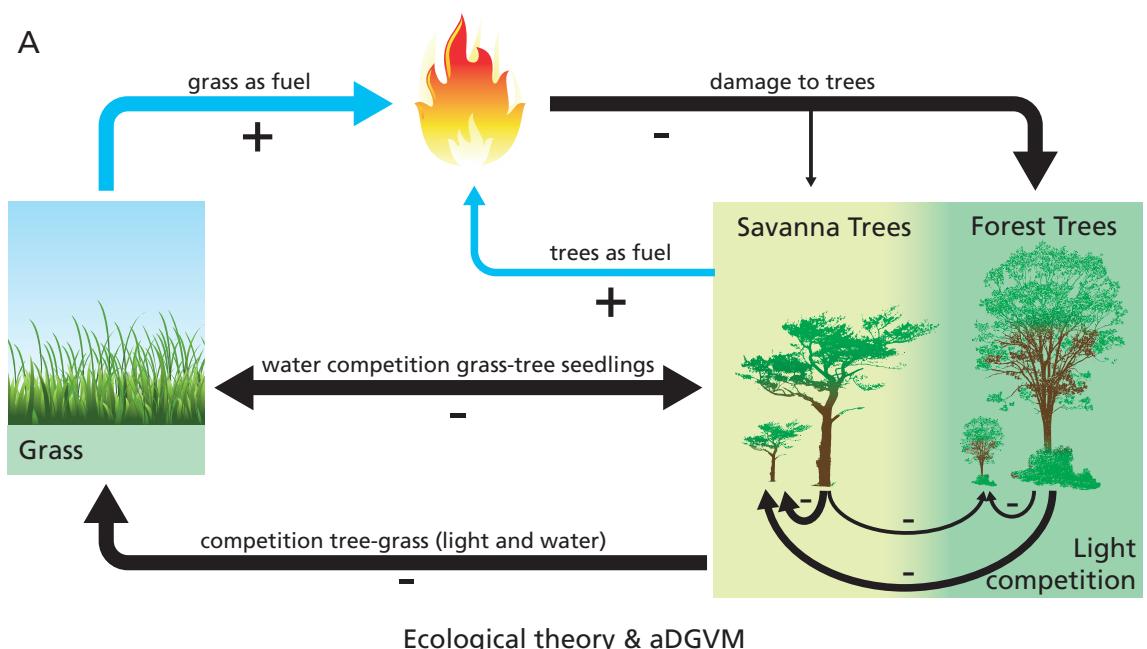
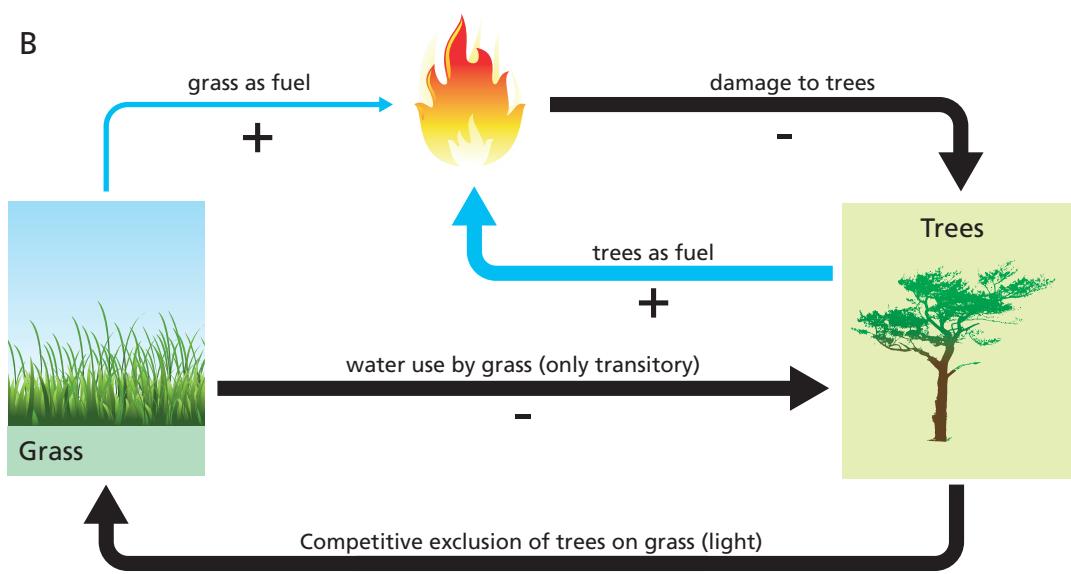
18 Figure 3

19 Schematic diagram of the main ecological interactions that determine the forest-savanna-  
20 grassland transition, according to: A) Ecological theory, and the aDGVM; B) JSBACH; C)  
21 LPJ-GUESS-SPITFIRE. Light blue arrows represent positive effects, dark blue arrows  
22 negative effects. The aDGVM (A) was designed to include the key ecological mechanisms  
23 known from theory, namely: grasses increasing fire spread (positive feedback), distinction  
24 between forest and savanna trees (with fires damaging forest tree mostly, shade intolerant  
25 savanna seedlings and shade tolerant forest seedlings), separate resource competition between  
26 trees and grasses depending on their size (grasses and tree seedlings compete for the same

1 water, while adult trees outcompete grasses for both water and light). JSBACH (B) includes  
2 fires as mainly fostered by tree litter, which are also mainly damaged by fire (negative  
3 feedback). Trees competitively exclude grasses, although temporarily after disturbances  
4 grasses also compete with them for the same water. LPJ-GUESS-SPITFIRE (C) is on one  
5 hand similar to the aDGVM, since it distinguishes tree life stages and it separate between  
6 savanna and forest trees, with analogous representation of water and light tree-grass  
7 competition. On the other hand, it includes a similar effect of tree and grass biomass in  
8 fostering fires.





**A****B****C**