In the following, the comments of the reviewers are reiterated, and our responses (in bold) follow. At the end of the present document a marked-up manuscript version is included.

Response to reviewer #1

The paper addresses the general question of how the feedback mechanisms relevant for tropical vegetation dynamics and described in the ecological literature are represented in Dynamics Global Vegetation Models (DGVMs). Particularly, the authors present a discussion based on the different characteristics of 3 frequently used DGVMs applied for Africa: 1) DYNEVE / JSBACH which is currently coupled to an atmospheric circulation model; 2) LPJ-GUESS which is an offline model and coupled to the SPITFIRE fire module to better represent fire dynamics; 3) aDGVM, an offline process based model designed to represent in detail the main ecological features of forest, savanna and grasslands in Africa.

I identify two major novel aspects: 1) model results are compared to recent field-work and remote-sensed data, and then discussed for both arid/semi-arid and humid regions separately pointing out respective mechanistic processes driving the hypothesis of multi-modality in DGVMs for Africa; 2) surprisingly, even though demography representation has been the subject of major concern in the past few years, the authors show that more basic processes, like tree-grass competition/water limitation and the grass-fire feedback, are still lacking representation in the DGVMs they tested.

Despite many technical differences between the models, the authors found an elegant way of comparing all of model outputs and reach the main core drawbacks they have. Together with the substantial and consistent discussion based on an inter-disciplinary literature, the results presented potentially represent one of the first steps towards identifying forms of improving current vegetation representation in DGVMs to have more reliable predictions for the future.

We thank this reviewer for his/her interesting comments and feedbacks.

Please, find below minor comments and suggestions (p = page number; l = line number).

1. p9473, l22-23 (abstract): “…and distinguish between fire-prone and shade-tolerant savanna trees, and fire-resistant and shade-intolerant forest trees…”. I think it is the opposite. In the rest of the text this information is correctly described, e.g., p9475,110-13 (intro)

Thanks, we now corrected it.

2. p9477, l1: I did not understand why you replaced “feedback mechanisms” by “ecological interactions”. In p9478, l20-22, you mention “Processes affecting PFT composition, such as competition for resources, mortality, and demography (i.e., what we call here the ecological interactions)…” It sounds different than the analogy to feedback mechanisms on p9477. Check to keep the term consistent along the text and with previous studies.

We thank the reviewer for this comment. We now clarify this sentence: “with a particular emphasis on the representation of what in the following we call the ecological interactions” between grasses and trees, i.e. the most important tree-grass competition mechanisms, and the feedbacks with their environment”

3. In which spatial resolution the models were run? If it was different, could it make a difference in the results? I missed this information.

The models were run in the following (horizontal) resolutions: JSBACH: 1.9x1.9°; aDGVM and LPJ-GUESS: 1x1° degree. We now added this information to paragraph § 2.2 (“The model experiment setups”).

So, the model resolutions were indeed different, and for this reason we did not perform a point-by-point model comparison (spin-up time and type of forcing data were different as well). For further details on how we compared models, please see reply #2 to reviewer #2.
4. p9480, l27: “. . . but tree can cumulate . . . ”. Would “accumulate” fit better?

Corrected.

5. p9483, l16: “. . . can potentially shade (and hide) the target tree.”. What are the competitor and target trees? Better described to improve understanding.

We now improved the explanation rephrasing this sentence to:

“Tree cover was calculated as the sum of the canopy areas of all trees higher than 0.5 m, without neighbouring trees that shade (and hide) the tree itself”

6a. p9488, l27-28: “. . . but data do not display bimodality of high and low tree cover (not shown)”. It would be interesting to see a figure of the no-bimodal frequency distribution of JSBACH in the same manner you showed bimodality for aDGVM in the supplements. Moreover, you could try to use latent class analysis to fit the distribution. It seems more convincing than the 2-gaussian approach.

Thanks to this comment of the reviewer we now improved the bimodality test, and we applied it in an intermediate range of precipitation for the three model outputs (thus including JSBACH), as we report now in the new version of the supplementary material. Following previous studies (e.g. Hirota et al., 2011), the test is now performed with the “flexmix” package in R for finite mixture models regression (Grünn and Leisch, 2007; Hirota et al., 2011; Yin et al., 2014), which assumes that each distribution is formed by a mixture of a number of normal distributions. The program implements the finite mixtures of regression models by the expectation–maximization (EM) algorithm (Grünn and Leisch, 2007). To select the best fitting distribution, while being parsimonious at the same time, we use the integrated completed likelihood criterion (ICL), and the Akaike criterion, and we tested one to four potential class models, following Yin et al. (2014). The lowest values of the ICL and AIC identify the best model.

6b. Fig. 2a: even though there is no bimodality for JSBACH outputs, I wonder what are the 3 points (outliers) between 1000 and 1500 mm yr-1. They are completely out of the range. Have you verified that?

We thank the reviewer for pointing this out. In the previous version of the manuscript, this plot represented only tree PFTs, while we intended to include all woody vegetation (as specified in the text). We now corrected this mistake replacing the JSBACH data with woody cover (trees and shrubs). Shrubs are negligible at large scale, but in South-Eastern Africa there are few points where shrubs are dominant (which the reviewer noticed). The overall results were not affected by this minor change.

7. Along the text: I was a bit confused with the terms “high and low tree cover” because they may be ambiguous in the sense that low tree cover may represent low trees (e.g., shrubs) or the abundance of tree cover (which is meaning you use). I suggest a replacement to high and low tree cover values or amounts.

We followed the suggestion and now replaced “tree cover” with “tree cover value” throughout the text.

8. p9488, l19: you use the term vegetation-fire feedback (grasses + savanna trees benefiting from forest tree removal after fires) that leads to a stable savanna biome at intermediate rainfall values. It seems a quite important feedback mechanism (even though without a citation) but it has not been explored along the text and included in the discussion. Does it fit within the secondary improvements related to demography? You could explore it further for the model outputs.

We thank the reviewer for making us aware that the notations “grass-fire feedback” and “vegetation-fire feedbacks” where not clearly explained. We modified the text in several points
(Introduction, §3.2 and Concluding remarks) to clarify that the “vegetation-fire feedback” is an extended description of the grass-fire feedback, including also the effect of the different fire tolerance of forest and savanna trees. The grass-feedback is anyway its main component, because without including the effect on fire of grass biomass the feedback is not active. We also added two citations about the importance of tree differentiation for this vegetation-fire feedback mechanism, beyond grasses (Hoffmann et al., 2012; Ratnam et al., 2011). So the description of the grass-fire feedback, which we recognize as a basic requirement for DGVMs to represent savanna dynamics, can be further extended by additionally distinguishing forest and savanna tree types (in terms of their fire tolerance), thus describing the full vegetation-fire feedback.

9, p9489, l19-20: “... at high precipitation, the fuel does not dry out sufficiently to promote fire spread. This may be caused partly by the average fire probability used in this version of SPITFIRE...”. I do not see the connection of the former sentence (related to drying out to promote fire spread) with the average fire probability, which is related to the representation of fire triggering. Better explanation of what you meant. Besides, has LPJ-GUESS been benchmarked for Africa? The authors mentioned DGVMs are not parameterized for tropical ecosystems, but could not find any commentary on a specific usage of this model for Africa.

To connect the two parts better, we rephrased the sentence in the following way:

"This may be partly due to the fact that this version of SPITFIRE uses a probability of fire spread which depends on average fuel conditions, and thus it is not fully coupled to the drought periods. However, this assumption is necessary because the temporal extent of remotely sensed data for burned area (now ca. 10 years) is well below the temporal extent of the available climate data (50 years)."

About benchmarking, LPJ-GUESS simulations of vegetation distribution have been compared to potential natural vegetation at global scale (including Africa) in Sitch et al. (2003). So, far only aDGVM has been applied specifically to Africa.

10. p9494, l16-17: "... would get dampened by the consequent increase in fire frequency". According to what has been described for JSBACH, wouldn’t it be better “the consequent increase in fire spread”?

We corrected this point.

Response to reviewer #2

This is an interesting study that tackles the ecological reasons behind forest-savanna transitions from the point of view of modeling. The authors opportune use observational data to evaluate model outputs and enrich the paper discussion. The general aim of the paper of identifying gaps in the assumptions or process representation related to the forest-savanna transition issue is laudable.

We thank this reviewer for his/her interesting comments.

Nevertheless I have serious doubts the authors use the right reasoning and technics to reach their conclusions. Four major points called out my attention and I suggest the authors put a bit of thinking over them for a revised version of the paper:

1: On page 9495 authors conclude that water limitation upon tree growth and grass-fire feedbacks are the two most important processes to be considered in model that intend to capture well the forest-savanna transition dynamics. But notice that on page 9474, in the introduction section, authors state the same. It gives the impression authors already had an opinion on what processes were important for models, regardless of the study they conducted.

We thank the reviewer for this comment, which made us realize that we needed to clarify the
fact that the identification of the main ecological mechanisms driving savanna dynamics is not a result of the present paper but it is the outcome of much ecological work in the recent literature. Our aim here is to bridge the gap between ecological knowledge and global modelling, underlying which mechanisms are important to include in DGVMs, and to which extent. Our phrasing on page 9495 was misleading in that respect and we changed it to avoid misinterpretation, together with a sentence in the Abstract.

2: In page 9483 the simulation protocol is described. The fact that the 3 employed DGVMs are run with different input data compromises the intercomparison of their results, since it increases the degrees of freedom in the modeling exercise. We cannot assure for example that model results are a consequence of elevated CO2 or different precipitation patterns. Authors should have a strong argument – rather than that these were the model runs available at hand – to justify such a experimental design in light of the proposed paper objectives.

This paper strictly does not present a model intercomparison project (MIP), nor it includes harmonization. Instead, we focus here on ecological mechanisms that are (or are not) included in different DGVMs, and we qualitatively compare the DGVM outcomes with observations along a rainfall gradient. We agree that the model inputs, including different precipitation (and other forcing) data, spin-up times, and resolutions increase the degree of freedom in this conceptual model comparison. Precisely for this reason, we do not compare at which precipitation values the grassland-savanna-forest transitions take place, but we compare only the precipitation ranges (low, intermediate and high) because we are interested in the way the models catch this transition. We are aware of the limitation of the current approach, but we maintain that at this stage it is more important to identify the most important ecological mechanisms causing discrepancies between model outputs and observations. Given that objective, the current, more qualitative assessment is sufficient, because this already showed that models can predict the right state but for the wrong reasons, which is one of our main conclusions. See also reply to point #4 of this reviewer below.

About the CO2 experiment, we ought to say here that this is not a real model experiment but a conceptual experiment, performed to show what are the consequences of representing the main ecological interactions an inaccurate/incorrect way. So, for this conceptual experiment, the design was consistent. Thanks to this comment of the reviewer, we now included a clearer explanation at the beginning of §3.3:

"Hereafter we discuss results from two simple conceptual experiments (namely, increasing CO2 concentrations, and decreasing precipitation) to illustrate how the different representations of the ecological interactions in the three DGVMs could lead to different predictions of the state of the grassland-savanna-forest transition under future climatic changes."

3: All models seem to be overestimating tree cover in low to moderate precipitation levels (using the regression lines as a basis for comparison). Let’s get the 50% tree cover as a benchmark: observed data places 50% tree cover in roughly 700-800mm of annual rainfall. The 3 considered models reach that benchmark by 200-400 mm. Please comment.

Because of the differences in the precipitation input, we decided not to compare at which precipitation level the models reach a certain cover (e.g. full cover, as the reviewer mentions), to avoid misinterpretation. Instead, by qualitative comparisons, we evaluated whether they catch the effect of water limitation on tree cover as represented by a decreased maximum tree cover at low rainfall (without being more specific on the exact rainfall range). In addition, we expected the models to predict a wide range of tree cover at intermediate rainfall, and possibly even a bimodal distribution of such points, as a consequence of the grass-fire feedback. For these evaluations, qualitative assessments, avoiding interpretation problems due to differences in model set-ups, are valid. Please see also our response to point 2 above.

We now added a sentence in this regard in § 2.4:

"For these ranges, we will perform a qualitative comparison of the modelled and observed data
in the parameter space (i.e. maximum cover value, spread, distribution).”

4: It is interesting to see the evaluation on how elevated CO2 can affect the dynamics of forest-savanna transition zones. But remember nutrient dynamics have shown to play a key role in elevated CO2 responses of forests (e.g. Norby et al. 2010). Many tropical forests and savannas are nutrient limited (especially P-limited). However it seems like the role of nutrient dynamics is poorly explored here. I understand that none of the employed models have nutrient cycling (even though I was curious because JSBACH was one of the first DGVMs to implement N and P cycle, but the authors probably used an earlier model version), but the topic could be further explored. Otherwise the scientific utility of the elevated-CO2 exercise (which in fact is not properly explained in the method section) is reduced.

We agree with the reviewer that nutrient cycles are fundamental for many tropical savannas and forests and it is very important for CO2-enriched experiment. However, within the ecological literature, nutrient limitations are currently not considered as one of the main reason behind savanna existence. Moreover, for the conceptual CO2-experiment, including a nutrient cycling would not have dramatic impacts (as nutrient limitations would mainly reduce, or eventually stop, the CO2-fertilization effect). Because we only discuss the direction of change within our conceptual experiment, this would not change our interpretation.

About the description of the CO2 experiment, please see also above the reply to point #2 of this reviewer.

The JSBACH version used was indeed the CMIP5 version of the model without N and P cycles.

Minor points:

p. 9475, l 3: “enhances open savanna formation presence”

Corrected.

p. 9475, l 26: “leading to woody savanna expansions”

We clarified this line as “leading to savanna expansions (e.g. at the expense of grasslands)”.

p. 9476, line 14: even though DGVM have a considerably limited ability to deal with the enormous plant trait diversity found in tropical regions. Generally tropical forest is represented by only one or two PFTs.

We now added a sentence to underline this point of the reviewer: “For example, they represent the enormous plant trait diversity of tropical regions through distinguishing only one or two plant functional types (PFTs).”

p. 9479, l 12: “Max Planck Institute”

Corrected.

p. 9486,11-8: That is in fact a good argument for investigating these other factors with the use of models. It could have been better explored in the article... 

To explore the effect of factors such as rainfall heterogeneity and seasonality on savanna ecology, in our opinion the best approach is to choose appropriate ecological models that include the relevant ecological interactions. The main point of this article is instead to verify whether the analysed DGVM include a minimal set of mechanisms that are necessary to represent savannas, and to analyse the consequences if they don’t. Therefore, exploring the effect of certain ecological mechanisms, whose importance is not yet fully known, is outside the scope of the present paper.

p. 9486,125: This sentence is not in accordance with the model-data comparison the authors do
We replaced it with: "At a first glance, the relation between tree cover and mean annual rainfall simulated by the models (Fig. 2) is similar to that observed in the data (Fig. 1)."

p. 9489, l25-27: But isn’t this rainfall range selection a little artificial? The study is not convincing in that aDGVM really shows a bimodal tree cover distribution such as evidenced by observational data. Maybe a statistical tool would help here to prove whether the aDGVM modeled distribution – or part of it – is bimodal or not.

We now clarified this point better, and we refined the statistical analysis. The bimodality is observed in an intermediate rainfall range also for the MODIS data (as analyzed in Staver et al., 2011a, 2011b). The bimodality is observed independently of the exact range of mean annual rainfall chosen as we now better specify in the text:

"If we only select points in such rainfall range (e.g. between 800 mm and 1200 mm y⁻¹), we observe that the tree cover distribution is bimodal (see Appendix 1; note that this conclusion is robust to different choices for the limits of the rainfall range)."

Finally, the statistical analysis of the bimodality has been improved (for details please see reply to point #6a of reviewer 1, and Supplementary Information).

p. 9492, l10: And so do many tropical forests (to be associated with nutrient poor soils)

Indeed the conditioning of the nutrient levels on savanna occurrence is not key. We modified the sentence in the following way: “Secondly, although it has been observed that savannas can be associated with nutrient poor soils (Lloyd et al., 2008), this limitation does not seem to explain the savanna-forest transition (Bond, 2010; Favier et al., 2012; Murphy and Bowman, 2012).”

p. 9493: “Indeed, the three models predict reasonably well the current tree cover along the mean annual rainfall gradient in Africa, as derived from ground and satellite observations.” Are the authors sure of this statement? A numerical/qualitative comparison would do very good here.

We perform a qualitative model comparison throughout the paper, please see reply #2 and 3 to this reviewer above. We now better specify this sentence: “...the three models predict the main features of the current tree cover along the mean annual rainfall gradient in Africa, as derived from ground and satellite observations”.

p. 9494: I have the impression the text discussed here would fit better in the discussion section rather than in this “concluding remarks” section.

We understand the point of view of the reviewer. However, we opted for this structure because we do not have the classical “Results” and “Discussion” sections separately but together, and we felt the urge to summarize the discussion points in these final remarks.

References cited


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

M. Baudena¹, S. C. Dekker¹; P. M. van Bodegom²,³, B. Cuesta¹, S.I. Higgins⁵; V. Lehsten⁶; C. H. Reick⁴; M. Rietkerk¹; S. Scheiter⁸; Z. Yin¹; M. A. Zavala⁴; V. Brovkin⁷

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

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

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

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

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

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

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

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

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

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

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

1 Introduction

Savannas cover about a fifth of the Earth land surface, and have wide socioeconomic importance regarding land use and biodiversity (Scholes, 2003). Savannas are the central biome in the transition between grasslands and forests, and they are characterized by the coexistence of two types of vegetation: trees (i.e. woody
vegetation), and grasses (i.e. grasses and herbs). In most of the savanna ecosystems, we observe highly shade intolerant and fire tolerant C_4 grasses and C_3 trees. This savanna definition is generally valid, with the exception of a few regions (e.g. the Neotropical cerrado where C_3 grasses dominate, see Lloyd et al., 2008, Ratnam et al. 2011). For a long time ecologists have been fascinated by savannas, because trees and grasses coexist, while competing mainly for the same resource, namely water, which is the main limiting factor (Sankaran et al., 2004; Scholes and Archer, 1997; Walter, 1971). Classical ecological theory, such as the competitive exclusion principle, predicts that only one vegetation type can survive in these conditions (Hutchinson, 1961; Tilman, 1982). To solve this conundrum, numerous experimental and modeling studies explored the nature of tree-grass competition and coexistence (e.g. Higgins et al., 2000; House et al., 2003; Sankaran et al., 2004; Scholes and Walker, 1993; Walker and Noy-Meir, 1982). Grasses can outcompete trees in the driest environments, where tree growth is water-limited (Higgins et al., 2012), and they have a particularly strong competitive effect on tree seedlings, as grasses and tree seedlings compete for water in the same surface layer (Baudena et al., 2010; Bond, 2008; February et al., 2013; Sankaran et al., 2004; Wakeling et al., 2011; Yin et al., 2014b). In less arid conditions, however, adult trees can potentially grow deeper roots and reach deeper water than grasses (Kulmatiski and Beard, 2013; Walter, 1971; Ward et al., 2013), although overlap between grass and tree roots can be high in some savannas (e.g. February and Higgins, 2010; Higgins et al., 2000; House et al., 2003).

In addition to water availability, fire is an important driver of tree-grass dynamics. C_4 grass biomass enhances fire spread in open ecosystems, due to its high flammability. At the same time, grasses benefit from fire because they recover faster than trees, and profit of the open spaces after fire, thus originating a positive feedback mechanism that enhances savanna formation and presence (as shown by e.g. long term fire-exclusion experiments, Higgins et al., 2007; or model studies, e.g. Higgins et al., 2008; van Langevelde et al., 2003; see also Hoffmann et al., 2012). Fires may also limit tree seedling recruitment and growth, thus reducing tree dominance further (e.g. Hanan et al., 2008; Higgins et al., 2000). This grass-fire feedback is characteristic of tropical savannas and grasslands, while in most of the other biomes woody species produce most fuel for fires (e.g. boreal forests, Bonan and Shugart, 1989). Fire is essential to savanna persistence in wetter areas, which would be forested otherwise. The grass-fire
feedback is reinforced by the differences between savanna and forest trees. In contrast to savanna trees and grasses, forest trees are fire prone and shade tolerant, adapted to persist in conditions of low light availability and in absence of fire (Ratnam et al., 2011; Rossatto et al., 2009). Thus, when fires are absent and water supply is sufficient, forest trees outcompete grasses and savanna trees because of light limitation, while if fires are active, savanna trees persist but fires and shade intolerance limit their cover, keeping savannas open (Hoffmann et al., 2012). This feedback, which we define as “vegetation-fire feedback”, and which is an extended description of the abovementioned grass-fire feedback, possibly leads to bistability of forest and savanna in mesic regions (e.g. van Nes et al., 2014; Staver and Levin, 2012).

Savannas are expected to undergo major changes in the future due to increasing temperature and CO₂ concentration, modified rainfall patterns, and subsequently changed variability in fire regimes (Intergovernmental Panel on Climate Change, 2007). In recent years, an increase in woody cover has been observed in savannas all over the world (e.g. Bowman et al., 2010; Buitenwerf et al., 2012; Donohue et al., 2013; Ward, 2009; Wigley et al., 2010). Several studies tried to explain wood expansion by overgrazing or decreasing fire frequency, which would enhance grass mortality and thus favor woody vegetation (Scholes and Archer, 1997). However, CO₂ increase is probably one of the main causes of woody encroachment, leading to savanna expansions (e.g. at the expense of grasslands). As water use efficiency increases with CO₂ (e.g. de Boer et al., 2011), thus decreasing the water need for grow, increased CO₂ concentration leads to a shift in tree-grass competition for water, possibly favoring C₃ trees over C₄ grasses (Bond and Midgley, 2000; Bowman et al., 2010; Kgope et al., 2010; Polley et al., 1994; Wigley et al., 2010). In African savannas, paleo-ecological evidence of the last glacial period, as well as observations of the last 50-100 years, suggests that increasing CO₂ coincides with an increase in savanna woody plant growth (Bond et al., 2003; Scheiter and Higgins, 2009). These transformations could have larger effects on global biogeochemical cycles and precipitation than for any other biome, due to the large extent and productivity of savannas (IPCC, 2007; Snyder et al., 2004).

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

To evaluate why DGVMs may have difficulties predicting the distribution and dynamics of savannas, we will analyze three DGVMs, with a particular emphasis on the representation of what in the following we call the “ecological interactions” between grasses and trees, i.e. the most important tree-grass competition mechanisms, and the feedbacks with their environment. While physiological processes are often included in detail into DGVMs, the ecological interactions are not represented with the same accuracy in many models, despite their potentially large influence on the DGVM outcomes (e.g. Fisher et al., 2010; Scheiter et al., 2013). Reflecting on the current ecological understandings about savannas, we will describe whether and how the key mechanisms are included in current DGVMs. We chose to analyze three different DGVMs: JSBACH (Brovkin et al., 2009; Raddatz et al., 2007; Reick et al., 2013), LPJ-GUESS-SPITFIRE (Smith et al., 2001; Thonicke et al., 2010) and aDGVM (Scheiter and Higgins, 2009). JSBACH represents a DGVM as typically used in ESMs (and representative for most models included in the current IPCC coupled model inter-comparison project, CMIP5). LPJ-GUESS additionally includes the demography of
PFTs, which is likely to affect competition dynamics, and it includes SPITFIRE, i.e. a new specific module to represent fire dynamics. Finally, aDGVM represents a new class of DGVMs, including functional variation within PFTs (e.g., phenology, allocation and physiology adapt to changing environmental conditions). The aDGVM was specifically designed for African vegetation and savannas. In the following, we will focus on the African continent, where savannas occupy large areas, and where all of the three models have been benchmarked. Focusing on one continent has also the advantage that the mechanisms driving the dynamics are more likely to be similar (Lehmann et al., 2014). We will compare the model outputs with observations from field and remote sensing data (Hirota et al., 2011; Sankaran et al., 2005; Staver et al., 2011). We attempt to bridge the knowledge gap between our ecological understanding and the representations of vegetation in global vegetation models. Our aim is to determine which mechanisms need to be included or improved in the representation of ecological interactions of existing DGVMs in the forest, savanna, and grassland biomes, to ameliorate the current vegetation model predictions, as well as their projections under future (e.g. climate change) scenarios.

2 Methods

2.1 Model descriptions

DGVMs were developed to quantify transient responses of terrestrial ecosystems to past, present and future climates, and this required an inclusion of modeling vegetation dynamics in addition to biogeochemical processes (Cramer et al., 2001; Pitman, 2003; Prentice et al., 2007). To account for processes at subgrid-scale, DGVMs often assume fractional vegetation cover within the model grid cell (tiling, or mosaic approach). Vegetation description is based on PFTs, which aggregate and represent species with similar functions. Biomes are then represented by a mixture of PFTs, such as evergreen and deciduous, broadleaved and needleleaved trees, shrubs, C3 and C4 grasslands, which dominate in a particular climate. Savannas are typically simulated as a mixture of tropical, broadleaved, deciduous trees (“savanna trees” here after), and mostly C4 grassland, while forests have mostly tropical, broadleaved, evergreen trees (“forest trees” here after).
DGVMs in general have a quite standard set of assumptions to represent plant
physiology, including photosynthesis and biomass production. Most of them calculate
Gross Primary Production (GPP) by a coupled photosynthesis-transpiration scheme and
estimate autotrophic respiration as a function of temperature. Net Primary Production
(NPP) is dependent on the climate and CO$_2$, and scaled up to the plant or PFT level by
building up below and above ground carbon and leaf area (e.g., Sitch et al., 2003).
Processes affecting PFT composition, such as competition for resources, mortality, and
demography (i.e. what we call here the ecological interactions) are included into
DGVMs as separate modules that interact with the physiological and phenological
modules.

For the purpose of this paper, we will focus on the description of how the ecological
processes relevant for tropical vegetation dynamics are included in the three selected
DGVMs (JSBACH, LPJ-GUESS-SPITFIRE and aDGVM). Only the physiological
aspects relevant for the difference in PFT composition in grasslands, savannas and
forests will be described. JSBACH is part of an ESM, and was designed to represent the
interactive role of vegetation and land surface in the climate system. While LPJ-GUESS
has been included in an ESM in several studies, LPJ-GUESS-SPITFIRE has never been
used in such contest, and the same holds for aDGVM. Both models are so far used only
“offline”, i.e. they are driven by external forcing, such as climate and CO$_2$ changes,
without being coupled to a general circulation model, and thus without feeding back to
the climate. The models used in this study have their intrinsic limitations, for example
they all neglect nutrient cycling. A summary of the ecological interactions important in
the tropical areas and included into the models is presented in Table 1.

2.1.1 JSBACH (DYNVEG)

DYNVEG (Brovkin et al., 2009; Reick et al., 2013) is the submodel for vegetation
dynamics implemented in the land surface component JSBACH (Raddatz et al., 2007)
of the Max Planck Institute - Earth System Model (MPI-ESM, (Giorgetta et al., 2013).
DYNVEG groups its various PFTs into a grass class (C$_3$ and C$_4$ grasses), and a woody
class (trees and shrubs). Within the woody class, DYNVEG distinguishes between two
PFTs for tropical trees, with different photosynthetic abilities, which nonetheless do not
have different fire or shade tolerances, so they do not correspond to what we call
devanna and forest tree in this paper. DYNVEG assumes dominance of the woody over
the grass class, i.e., trees have competitive advantage and typically outcompete grasses.

Within a class, the competition among PFTs is indirect via NPP: a PFT with higher NPP
outcompetes PFTs with lower NPP. All PFTs share the same soil water bucket, and
there is no separation of root zones between woody and grass classes. Woody and grass
classes compete for newly available habitable space, with woody types outcompeting
grasses in the absence of disturbances. The space available for colonization can be only
part of the total area, i.e. some parts of the habitat are considered inhospitable. This
fraction constitutes a sort of resource limitation to tree development, since it is
calculated as a function of the average NPP over the last years of simulations, which in
turn depends on water (and other resource) availability (Reick et al., 2013). JSBACH
overestimates GPP and NPP in water-stressed conditions (Dalmonech and Zaehle,
2013), which partly explains an overestimation of tree cover fraction in drylands
(Brovkin et al., 2013). Elevated CO₂ concentration increases water use efficiency of all
PFTs.

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

2.1.2 LPJ-GUESS-SPITFIRE

LPJ-GUESS (Smith et al., 2001) was developed to incorporate forest age structure into
LPJ (Sitch et al., 2003), thus simulating gap model behavior and including the
competition of different age cohorts for light and water. For each grid cell, LPJ-GUESS
simulates a number of replicate patches. For the tropical regions, LPJ-GUESS results in
one type of (C₄) grasses, and two types of tree PFTs, savanna and forest trees, where the
former are fire tolerant and shade intolerant, and the latter are fire intolerant and shade
tolerant. In LPJ-GUESS, trees and grasses use common water in a superficial soil layer
(0.5 m deep), but trees have part of their roots in a deeper soil layer (1 m). At high water
availability, trees outcompete grasses by limiting light availability.
The fire module SPITFIRE (SPread and InTensity of FIRE, Lehsten et al., 2009; Thonicke et al., 2010) was coupled to LPJ-GUESS to include the role of vegetation fires. The effect of fire, simulated by SPITFIRE, varies for the different demographic stages (or height classes). For each fire, fuel load, wind speed and a proxy for fuel moisture are used to calculate the rate of spread of a potential fire. The fuel load depends on NPP and decomposition rates, which are both related to climate. Grassy fuels are more flammable (due to their lower fuel bulk density), but trees can accumulate more fuel over years without fire, since they decompose more slowly. Hence if burned at high to medium fire frequency, grasslands provide more fuel than forests, while if forests are allowed to accumulate fuel over longer time periods, they result in higher fuel loads than grasslands. All fires remove the above ground biomass of all grasses. Low intensity fires can cause high mortality of all young trees, while the effects on tall trees are limited for savanna trees, and more pronounced for forest trees. In general, damage to trees may be underestimated by SPITFIRE in the current parameterization. In fact, frequent fires lead to high mortality of young (small) age cohorts, while the direct effects on old age cohorts are very limited, and only large fires can cause a high mortality even for highly resistant savanna trees. Further details on the implementation of fire effects on vegetation can be found in Lehsten et al. (2009).

2.1.3 aDGVM

The aDGVM (Scheiter and Higgins 2009) is explicitly designed to study tree-grass dynamics in savannas. While the original version of the model only simulates savanna trees and C4 grasses (Scheiter and Higgins, 2009), an updated version, used for the current paper, simulates C4 grasses, C3 grasses, fire-resistant, shade intolerant, savanna trees and fire-sensitive, shade tolerant forest trees (Scheiter et al., 2012). The model uses an individual-based structure to represent trees. Tree recruitment occurs from seed, and tree seedlings compete with grasses more directly than adult trees. Plants compete mostly for water and light. Light competition is modeled by considering the light available to grasses below and between canopies. Hence, once a vegetation stand attains a high tree LAI, grass-growth is light-limited. In addition, seedlings and small trees are shaded by grasses and by adult trees. Savanna trees suffer more from light limitation than forest trees, which are more shade tolerant. Plants extract water from different soil layers, depending on their rooting depth, which increases with the
individual root biomass, until reaching maximum value, typically parameterized as being deeper for trees than for grasses. This allows trees to have exclusive access to water in deep soil layers. A simple bucket scheme is used to simulate water extraction and percolation into deeper soil layers. The extent to which soil moisture limits photosynthesis is calculated as a function of soil moisture in the layers in which the plant has roots. Hence, rooting depth, the amount of water transpired, and drought tolerance (i.e. the ability to withstand a low soil water content) determine the outcome of competition for soil moisture.

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

2.2 The model experiment setups

To simulate current conditions, transient simulations were performed where CO₂ increased to 390 ppm. The JSBACH run used here was a pre-existing CMIP5 historical simulation under transient forcing from 1850 to 2005.
LPJ-GUESS-SPITFIRE was driven by a combination of TRMM (Tropical Rainforest Measuring Mission) data for precipitation and NCEP data (Kalnay et al., 1996) for temperature and radiation (for details see Weber et al., 2009). The simulation was run with a spin up of 1000 years, and afterwards the simulation was performed from 1960 to 2007, with resolution of $1\times1^\circ$. Fire frequency was prescribed at each simulated cell using the MODIS MCD45A burned area product (Roy et al., 2005). LPJ-GUESS-SPITFIRE simulated 100 replicate patches for each of the $1^\circ$ cells, and each patch had a probability to burn related to the proportion of burned area calculated from the MODIS burned area product. Fires spread only if their potential rate of spread was above a certain threshold. Since the patch sizes of each of the replicates were below the average fire size, we simulated the burning of the whole replicate (see Lehsten et al., 2009, for further details). All 100 replicates of the patch were finally averaged to get a representative value for the fractional tree cover. The aDGVM used monthly mean climate data from the CRU database (Climatic Research Unit, New et al., 2000), and model resolution was $1\times1^\circ$. A 100 year model spin-up was conducted first, to ensure that the model was in equilibrium with the environmental conditions, then vegetation was simulated until 2010. Tree cover was calculated as the sum of the canopy areas of all trees higher than 0.5 m, without neighbouring trees that shade (and hide) the tree itself. Tree cover in aDGVM could reach 100% because of the individual canopy overlaps.

### 2.3 Observational datasets

For the comparison between data and models, we used two different types of tree cover observational datasets that have been recently used to study savanna dynamics. One dataset is a collection of tree cover data from savanna field sites from Africa (Sankaran et al., 2005), while the other is derived from remote sensing (MODIS, as used e.g. in Hirota et al., 2011; Staver et al., 2011b). In both cases, we selected only the data points between 35° S and 15° N (following Hirota et al., 2011).

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

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

2.4 Model comparison to observations

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

\[ y = \frac{ax^2}{b + x}, \]  

(1)

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

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

In addition to mean annual rainfall, other factors such as temperature (Higgins and Scheiter, 2012), or temporal distribution of rainfall, are known to be important for tropical grasslands, savannas and forests too. Rainfall heterogeneity, intermittency, and seasonality affect water availability (D’Onofrio et al., 2014) and fire return times, and are very important predictors of savanna/forest distribution (Lehmann et al., 2011), with rainfall seasonality reducing growth rates (e.g. limiting water availability, Sarmiento, 1984), influencing root-shoot biomass ratio and local cover (Yin et al., 2014a) and increasing fire frequency (Archibald et al., 2009). Nevertheless, these factors have not yet been thoroughly examined in many ecological studies, possibly also because of lack of accurate rainfall datasets in these areas. Therefore, in the following, we will focus only on mean annual rainfall, whose importance has extensively been studied. We
separately evaluate arid and semi-arid savannas (Sect. 3.1) and humid savannas and
forests (Sect. 3.2), analyzing also whether and how the ecological interactions are
included in the different models. Finally, we discuss the effect of expected future
climatic changes on the outcome of tree-grass competition in the three models (Sect.
3.3).

3 Results and Discussion

3.1 Arid and semi-arid savannas and grasslands: the role of water
limitation

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

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

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

In the aDGVM output, the tree cover displays a maximum value that grows with precipitation between zero and about 500 mm y\(^{-1}\) (Fig 2C). In this range, modeled trees are water limited, while grasses are better competitors in these drier conditions, thus further reducing the tree cover, which would be higher if the model were run without grasses (not shown). The aDGVM and LPJ-GUESS-SPITFIRE include differential rooting depths for individuals, depending on their root biomass, and therefore both models also represent water competition between grasses and tree seedlings. This competition is known to be important for tree-grass coexistence (Hanan et al., 2008; Sankaran et al., 2004), while adult trees have deeper roots that make them better competitors in more humid environments (see Fig 3A and 3C respectively).

### 3.2 Humid savannas and forests: the role of fire

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

The role of fire in maintaining savannas in humid environments is included in all of the models, although in different ways. At high precipitation, JSBACH tree cover output displays a constant maximum value (above about 800 mm y$^{-1}$), but the data display considerable scattering below full tree cover (Fig 2A). In other words, the model predicts savannas and forests in this range, but the data do not display bimodality of high and low tree cover values (see Supplementary material, Appendix 1). This is a consequence of the fact that in this model fire is triggered more by trees than by grasses, since trees produce larger amounts of litter and thus of fuel. Fire favors grasses because it opens the landscape by reducing the tree cover and generates space for them. Thus, fire creates a negative feedback because fewer fires occur when tree cover is lower (Fig. 3B), thus preventing hysteresis and bistability in this model.

LPJ-GUESS-SPITFIRE simulation results do not show any low tree cover value (e.g. below 50% cover) for rainfall higher than about 900 mm y$^{-1}$ (Fig. 2B). Therefore, quite surprisingly, this model does not predict any savanna in mesic environments. In the model, though fire frequency is prescribed from the satellite data, fire spread depends
on fuel load (Fig. 3C) and fuel moisture, and thus unfavorable conditions might still prevent fires. Both grass and tree presence increases fire intensity, opening up space, and thus favoring grasses. This is not strictly a positive grass-fire feedback, because also grass-free areas can burn. Thus, as grasses are not fostered by a positive feedback with fire, they are always outcompeted by trees in LPJ-GUESS-SPITFIRE when water availability is high, and they do not survive above approximately 900 mm y⁻¹. At the same time, this issue is also likely to be connected to the fire spread depending on fuel moisture: In this model, at high precipitation, the fuel does not dry out sufficiently to promote fire spread. This may be partly due to the fact that this version of SPITFIRE uses a probability of fire spread, which depends on average fuel conditions, and thus it is not fully coupled to the drought periods. However, this assumption is necessary because the temporal extent of remotely sensed data for burned area (now ca. 10 years) is well below the temporal extent of the available climate data (50 years).

In aDGVM, maximum tree cover values can reach full cover above about 500 mm y⁻¹, but the points are still very scattered, and display some clustering at cover around 30-60% for intermediate rainfall values (Fig. 2C). If we only select points in such rainfall range (e.g. between 800 mm and 1200 mm y⁻¹), we observe that the tree cover distribution is bimodal (see Appendix 1; note that this conclusion is robust to different choices for the limits of the rainfall range). aDGVM includes explicitly the grass-fire feedback, which is reinforced by the difference between fire tolerant savanna trees and fire sensitive forest trees (Fig 3A). When the forest trees suppress the savanna trees and the grasses through light competition, the result is a forest biome with low fire frequency or even fire suppression, primarily due to scarcity of (grass) fuel. At sites with regular fire, forest trees cannot persist, resulting in low forest tree cover and intermediate savanna tree cover, with grasses colonizing the open spaces and fostering fire occurrence. This vegetation state represents a savanna biome. In a certain range of environmental (e.g. rainfall) conditions, a system initialized as a forest will not shift to a savanna, unless fire ignition probability is high, while a system initialized as a savanna will persist in the same state unless fire ignition probability is very low. As a consequence of including this positive feedback, experiments with the aDGVM show that fire suppression can lead to transitions and hysteresis between savanna and forest states (Higgins and Scheiter, 2012; Moncrieff et al., 2013).
Finally, we note that at extremely high rainfall values, when water is not limiting and tree canopies close into a forest, both in LPJ-GUESS-SPITFIRE and in aDGVM trees exclude grasses through light competition (Fig. 2B-C). This mechanism is included only implicitly in JSBACH, and it acts along the whole precipitation gradient giving competitive advantage to trees in general.

3.3 Effects of future climatic changes

Hereafter we discuss results from two simple conceptual experiments (namely, increasing CO$_2$ concentrations, and decreasing precipitation) to illustrate how the different representations of the ecological interactions in the three DGVMs could lead to different predictions of the state of the grassland-savanna-forest transition under future climatic changes.

Expected increase in CO$_2$ concentration in the future is likely to affect the outcome of tree-grass competition, mediating both important mechanisms we discussed so far, i.e. competition for water, and fires. Fire is expected to decrease under increased CO$_2$ level because of the decrease in grass fuel load, given that C$_3$ woody plants are favored over C$_4$ grasses under elevated CO$_2$ levels (Ehleringer et al., 1997). In JSBACH, higher CO$_2$ leads to higher productivity of grasses and trees, which in turn increases fire spread and hence introduces a negative feedback, dampening the increase of tree biomass. In aDGVM, CO$_2$ fertilization promotes tree growth, and thus tree establishment in grasslands, transforming them into savannas or woodlands (with or without fire, respectively). So in contrast to JSBACH, aDGVM includes a positive feedback, leading to tree canopy closure in savannas, which, suppressing grass growth, reduces also fire activity, transforming them into woodlands and forests (Scheiter and Higgins 2009). Due to this positive feedback, CO$_2$ concentration can induce hysteresis effects on the vegetation states (Higgins and Scheiter 2012). LPJ-GUESS-SPITFIRE has an intermediate behavior between the other two models, because grass and woody vegetation contribute similarly to fuel formation. Also, since in this model fire frequency is prescribed from remotely sensed data, any effect of changes of CO$_2$ levels on fire occurrence would be very limited, though there might be pronounced effects on resulting vegetation composition.
Another consequence of climate change is a possible decrease in precipitation. This scenario also leads to different model behavior. In JSBACH and LPJ-GUESS-SPITFIRE, drier conditions would lead to lower (woody) biomass productivity, but the impact on fire spread differs between these two models. JSBACH predicts no major effect on fire, as drier conditions would lead to higher fuel flammability, thus compensating for the impacts of the woody biomass decrease. In LPJ-GUESS-SPITFIRE the decrease in productivity is dominant, and hence a strong decrease of fire frequency is expected (Lehsten et al., 2010). In aDGVM the strong positive feedback would lead to a magnification of the woody vegetation decrease, as lower precipitation leads to increased grass productivity (because of less competition with woody vegetation) and lower humidity, increasing the likelihood of fire occurrence.

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

3.4 Other mechanisms influencing tropical savannas, grasslands and forests

Up to now we considered water limitation and fires as the main drivers of grassland, savanna and forest distribution. Several additional factors can be important for vegetation dynamics, especially at the local scale. The first factor is herbivory. Browsing (particularly by mega-herbivores in Africa) is known to have an important limiting effect on tree cover, similar to the effect of fire (e.g. Scheiter and Higgins, 2012; Staver et al., 2012), while grazing can favor trees because it limits grass expansion (e.g. Sankaran et al., 2008). However, large herbivores seem not to be critical in determining forest and savanna distributions (Murphy and Bowman, 2012).

Secondly, although it has been observed that savannas can be associated with nutrient poor soils (Lloyd et al., 2008), this limitation does not seem to explain the savanna-
forest transition (Bond, 2010; Favier et al., 2012; Murphy and Bowman, 2012). Thirdly, vegetation tends to have local spatial dynamics and to feed back to the environment at much smaller spatial scales than the DGVMs resolution. These local spatial water-vegetation interactions are strictly connected to vegetation resilience in arid and semiarid ecosystems (e.g. Rietkerk et al., 2004), and they can also influence the coexistence of trees and grasses in the most arid savannas (Baudena and Rietkerk, 2013; Nathan et al., 2013). Although the local scale is partly taken into account in some DGVMs by including individual based dynamics or tiling schemes (that represent different vegetation types and bare soil next to each other within the same cell), these assume a common use of soil and hydrological resources within the grid cell, thus not allowing to represent local, sub-grid mechanisms, which are not at all trivial to up-scale (Rietkerk et al., 2011). Finally, on the African continent the vast majority of fires is ignited by humans (Archibald et al., 2009; Saarnak, 2001), although their decisions on when to burn an area, as well as the fire spread and intensity, are still related to fuel composition (Govender et al., 2006). Humans maintain the grass-fire feedback, since they aim at keeping the land free from woody vegetation, and also because fire spread is favored by grass presence (Ratnam et al., 2011). Changes in land use have therefore strong influences on the current and future outcomes of tree-grass competition. Also, humans are expected to change their application of fire as a land use tool, as a consequence of changed environmental conditions. These elements are partly taken into account in some DGVMs (e.g. in LPJ-GUESS-SPITFIRE), but we do not consider them here for the purpose of this paper.

4 Concluding remarks

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

These mechanisms are to varying extent included in the three DGVMs we analyzed (JSBACH, LPJ-GUESS-SPITFIRE and aDGVM). Indeed, the three models predict the main features of the current tree cover along the mean annual rainfall gradient in Africa, as derived from ground and satellite observations. aDGVM output matches the observations better than the other two models. This is perhaps to be expected since this model is specifically designed for African vegetation and it includes more detailed representations of ecological interactions, especially the vegetation-fire feedback. For the other two models, the main differences between observations and model outputs are: i) JSBACH overestimates tree cover in dry areas (see also Brovkin et al., 2013); ii) LPJ-GUESS-SPITFIRE does not show any savanna at medium to high annual rainfall rates; iii) both these DGVMs do not show bimodality of savannas and forests in humid areas. This latter point might feed the debate about whether bimodality between savanna and forest cover actually exists (see e.g. Hanan et al., 2014). Despite their reasonably good performances, not all the mechanisms included in JSBACH and LPJ-GUESS-SPITFIRE are fully appropriate to represent vegetation in the tropics and the subtropics. In JSBACH, competition between trees and grasses favors the former irrespectively of water availability, which is one of the reasons behind JSBACH tree cover overestimation. At the same time, in this model, fire is fostered disproportionately by woody vegetation as compared to grasses, resulting in a negative feedback. This is responsible for observing savannas in larger parts of the rainfall gradients, and no savannas would be simulated without them. Although the three models display comparable outcomes under the current climate, the presence of a negative fire-vegetation feedback in JSBACH, a positive feedback in aDGVM, and an intermediate behavior in LPJ-GUESS-SPITFIRE, leads to different predictions of fire frequency and effects under climate change scenarios between the three models. In JSBACH, the initial increase in woody vegetation, due to higher CO₂ concentrations, would get dampened by the consequent increase in fire spread. Interesting in this perspective is
that the sensitivity to shifts between forests and savannas is low for JSBACH, as negative feedbacks are more important, while in aDGVM the positive grass-fire feedback mechanism results in a large sensitivity to shifts of the different tree-grass systems. LPJ-GUESS-SPITFIRE has an intermediate behavior between the other two models, since grass and woody vegetation foster fire in a similar way. Also, in this model fires seem to be suppressed too easily by high humidity conditions, which cause savannas to be absent at medium-high annual rainfall values.

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

Having in mind that DGVMs need to be kept as simple as possible, we conclude that the most important mechanisms to better represent the forest-savanna-grassland transition are i) how water limits tree growth and regulates tree-grass competition, and ii) the grass-fire feedback. Distinguishing between tree life stages and representing the different responses of forest and savanna trees, are less important features for the models, although they can considerably ameliorate the representation of the two main mechanisms. As parts of these mechanisms are already included in most DGVMs, extensions should be relatively simple, but they would substantially improve the predictions of vegetation dynamics and carbon balance under future climate change scenarios.

**Acknowledgements**

This study has been initiated during a TERRABITES workshop in 2010 at INIA-UAH, Madrid. We gratefully acknowledge all of the workshop participants for starting an early discussion on the topic, and V. Gayler for kindly preparing the DYNVEG-
JSBACH data. We thankfully acknowledge support of this workshop by TERRABITES COST Action ES0805, which also financed a Short Term Scientific mission to B.C. to get this paper started. S.S. acknowledges financial support by Hesse’s Landesoffensive zur Entwicklung wissenschaftlich-ökonomischer Exzellenz (LOEWE).

References


1 Hickler, T., Prentice, I. C., Smith, B., Sykes, M. T. and Zaehle, S.: Implementing plant
2 hydraulic architecture within the LPJ dynamic global vegetation model, Glob. Ecol.
4
5 Higgins, S. I., Bond, W. J., Combrink, H., Craine, J. M., February, E. C., Govender, N.,
6 Lannas, K., Moncreiff, G. and Trollope, W. S. W.: Which traits determine shifts in the
7 abundance of tree species in a fire-prone savanna?, edited by P. Veski, J. Ecol., 100(6),
9
11 B., Govender, N., Rademan, L., O’Regan, S., Potgieter, A. L. F., Scheiter, S., Sowry,
12 R., Trollope, L. and Trollope, W. S. W.: Effects of four decades of fire manipulation on
14
15 Higgins, S. I., Bond, W. J. and Trollope, W. S. W.: Fire, resprouting and variability: a
17
18 Higgins, S. I., Bond, W. J., Trollope, W. S. W. and Williams, R. J.: Physically
19 motivated empirical models for the spread and intensity of grass fires, Int. J. Wildl. Fire,
21
22 Higgins, S. I. and Scheiter, S.: Atmospheric CO2 forces abrupt vegetation shifts locally,
24
26 tropical forest and savanna to critical transitions., Science (80-. )., 334(6053), 232–235,
28
30 L., Haridasan, M. and Franco, A. C.: Ecological thresholds at the savanna-forest
31 boundary: how plant traits, resources and fire govern the distribution of tropical
33
34 House, J. I., Archer, S., Breshears, D. D. and Scholes, R. J.: Conundrums in mixed
36
38
39 Intergovernmental Panel on Climate Change: Climate Change 2007 - The Physical
40 Science Basis: Working Group I Contribution to the Fourth Assessment Report of the
42
43 Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M.,
44 Saha, S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W.,


<table>
<thead>
<tr>
<th>Model</th>
<th>Specific for tropical vegetation</th>
<th>Variables representing vegetation</th>
<th>Distinction between savanna and forest trees</th>
<th>Free age structure</th>
<th>Limiting resources for vegetation</th>
<th>Stable state(s) (in absence of fires)</th>
<th>How is fire represented?</th>
<th>Mechanisms driving savanna</th>
<th>Mechanisms driving forests/grasslands occurrence</th>
<th>Would a CO₂ increase modify the tree-grass transition and how?</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>JSBACH/ DYNVEG</td>
<td>No</td>
<td>LAI, PFT fractions, carbon in vegetation pools</td>
<td>No</td>
<td>No</td>
<td>Uncolonized space, hospitable land (water, indirectly via NPP)</td>
<td>Dominant woody (tree, shrub) PFTs</td>
<td>Fire is a function of air humidity and litter. Fires are mainly fostered by trees, which are also damaged by fire (negative feedback)</td>
<td>Fires</td>
<td>Forests occur in absence of fires (at any climate), while grasslands appear at high frequency of fire occurrence, i.e. at very intense dryness</td>
<td>Only indirectly (by changing litter availability for wildfires)</td>
<td>Brovkin et al 2009, Reick et al. 2013</td>
</tr>
<tr>
<td>LPJ- GUESS- SPITFIRE</td>
<td>No</td>
<td>Individual based model, LAI, PFT fractions, carbon in vegetation pools</td>
<td>Individual based model</td>
<td>Yes</td>
<td>Water and light</td>
<td>Depending on climate (mainly precipitation), either forest or grassland is the stable state. Savanna is observed in a relatively small precipitation range.</td>
<td>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</td>
<td>Fires, water competition</td>
<td>Forests occur given sufficient precipitation, while grasslands appear at high frequency of fire occurrence, or low precipitation.</td>
<td>Higher CO₂ would benefit C₃ vegetation (trees) as compared to C₄ 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.</td>
<td>Smith et al. 2001, Thonicke et al. 2010</td>
</tr>
<tr>
<td>aDGVM</td>
<td>Yes</td>
<td>Individual based model. Plant level: LAI, height, basal area, canopy area, biomass in different pools</td>
<td>Individual based model</td>
<td>Yes</td>
<td>Water, light</td>
<td>Depending on climate (mostly defined by precipitation): desert, grassland, savanna, forest</td>
<td>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).</td>
<td>Competition for water, fires</td>
<td>Forests occur at high rainfall levels (where fire is not possible) and at mesic conditions when fire is absent; grasslands occur at more and conditions when precipitation does not allow tree growth, and at more mesic conditions in the presence of fire.</td>
<td>CO₂ 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</td>
<td>Scheiter and Higgins, 2009, Scheiter et al. 2012</td>
</tr>
</tbody>
</table>
Figure captions

Figure 1

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

Figure 2

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

Figure 3

Schematic diagram of the main ecological interactions that determine the forest-savanna-grassland transition, according to: A) Ecological theory, and the aDGVM; B) JSBACH; C) LPJ-GUESS-SPITFIRE. Light blue arrows represent positive effects, dark blue arrows negative effects. The aDGVM (A) was designed to include the key ecological mechanisms known from theory, namely: grasses increasing fire spread (positive feedback), distinction between forest and savanna trees (with fires damaging forest tree mostly, shade intolerant savanna seedlings and shade tolerant forest seedlings), separate resource competition between trees and grasses depending on their size (grasses and tree seedlings compete for the same
water, while adult trees outcompete grasses for both water and light). JSBACH (B) includes fires as mainly fostered by tree litter, which are also mainly damaged by fire (negative feedback). Trees competitively exclude grasses, although temporarily after disturbances grasses also compete with them for the same water. LPJ-GUESS-SPITFIRE (C) is on one hand similar to the aDGVM, since it distinguishes tree life stages and it separate between savanna and forest trees, with analogous representation of water and light tree-grass competition. On the other hand, it includes a similar effect of tree and grass biomass in fostering fires.
Figure A: Scatterplot showing the relationship between tree cover (%) and mean annual rainfall (mm y$^{-1}$) for various regions. The data points are scattered along a curve, indicating a positive correlation between the two variables.

Figure B: A more detailed scatterplot with a higher resolution, showing a denser distribution of data points. The curve remains consistent, reinforcing the relationship observed in Figure A.
Appendix A

Bimodality analysis of the three DGVMs in an intermediate rainfall range

Methods

The bimodality test was performed with the “flexmix” package in R for finite mixture models regression (Grünn and Leisch, 2007; Hirota et al., 2011; Yin et al., 2014), which assumes that each distribution is formed by a mixture of a number of normal distributions. The program implements the finite mixtures of regression models by the expectation–maximization (EM) algorithm (Grünn and Leisch, 2007). To select the best fitting distribution, while being parsimonious at the same time, we use the integrated completed likelihood criterion (ICL), and the Akaike information criterion (AIC, Akaike, 1974) and we test one to four potential class models, following Yin et al. (2014). The lowest value of the ICL and AIC identify the best model. If the two indices identified different models, the differences between the resulting distributions are analysed further. In most of the cases the analyses showed that ICL is a better indicator (see also Yin et al. 2014). In some cases the algorithm could not find solutions by adding more normal distributions. In those cases, fewer than four classes are reported.

We performed the bimodality test for the three models output in different mean annual rainfall range. If bimodality was observed in a certain mean annual rainfall range, the sensitivity of this finding to set range boundaries was tested by choosing more narrow rainfall ranges. If in that case no bimodality was observed, the bimodality observed in the wider rainfall range was probably due to a shift of the distribution from a state to another along the gradient. This reduction of the rainfall range was performed only down to at least 100 model points.

Results

According to the bimodality analysis of JSBACH outputs on tree cover, the forest is unimodally distributed for mean annual rainfall between 800 and 1200 mm y⁻¹. According to ICL, three ranges were identified where bimodality occurs (400-800, 500-1000 and 400-900 mm y⁻¹). For those ranges, the AIC identified three or four Gaussians as the best fit for the distribution (see Table A1 and Fig. A1). More detailed analysis, however, showed that the peaks of the bimodal distribution (recognized as the best fit by ICL) were actually not well separated. Thus no bimodality was assessed in JSBACH model output. Please note that the range of mean annual rainfall could not be narrowed down further for this model because too few points would then be selected (JSBACH has 1.9x1.9⁰ spatial resolution, lower than the other two models).
Table A1 ICL and AIC values for JSBACH tree cover output in different mean annual rainfall intermediate ranges. Values in bold represent the minimum value (i.e. the best model according to that index).

<table>
<thead>
<tr>
<th>Range (mm y⁻¹)</th>
<th>ICL</th>
<th>AIC</th>
<th>Comments on differences between ICL and AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>800-1200</td>
<td>-88</td>
<td>-74</td>
<td>-16</td>
</tr>
<tr>
<td>400-800</td>
<td>-24</td>
<td>-34</td>
<td>-4</td>
</tr>
<tr>
<td>500-1000</td>
<td>-55</td>
<td>-60</td>
<td>-35</td>
</tr>
<tr>
<td>400-900</td>
<td>-33</td>
<td>-41</td>
<td>5</td>
</tr>
</tbody>
</table>

Fig. A1 Probability density distribution of tree cover for the JSBACH output, for mean annual precipitation between 400 and 800 mm y⁻¹ mean annual rainfall. Red line represents bimodal distribution (i.e. it is fitted significantly better by a superposition of two normal distributions, according to ICL), denoting not very well separated peaks. Green line represents trimodal distribution (given by a superposition of three gaussians, best fit according to AIC), which captures the non-separateness of the bimodal distribution fitting a third peak in between.

When performing the analysis for LPJ-GUESS-SPITFIRE tree cover data, we observed a bimodality of grassland and forest when considering a quite wide rainfall range (e.g. 400 to 1200 mm y⁻¹, 500-1000 see Table A2). However, when splitting this rainfall range into smaller ranges, the bimodality reduced to unimodality. In one case (600-800 mm y⁻¹), we still observed bimodality of grassland (~15% tree cover) and forest (~70% tree cover). It must be noticed that this bimodality was observed in a very narrow rainfall range only, and it did not represent the bimodality of savanna and forest we are interested in. Thus, we can state that LPJ-GUESS-SPITFIRE does not display bimodality of savanna and forest.
Table A2 ICL and AIC values for LPJ-GUESS-SPITFIRE tree cover output in different mean annual rainfall intermediate ranges. Values in bold represent the minimum value (i.e. the best model according to that index).

<table>
<thead>
<tr>
<th>Range (mm y⁻¹)</th>
<th>ICL</th>
<th>AIC</th>
<th>Comments on differences</th>
</tr>
</thead>
<tbody>
<tr>
<td>500-1000</td>
<td>77</td>
<td>-535</td>
<td>-583 -434 -86 -602 -689 -717 (*) Kind of bimodality between forest and grassland: three peaks, middle peak with very low density, and fourth peak is basically coincident</td>
</tr>
<tr>
<td>800-1200</td>
<td>-1350</td>
<td>-1204</td>
<td>-1196 -1359 -1404 -1424 ($) Unimodal (coincident peaks)</td>
</tr>
<tr>
<td>400-1200</td>
<td>236</td>
<td>-657</td>
<td>-757 -697 -226 -717 -929 -1027 As (*)</td>
</tr>
<tr>
<td>1000-1200</td>
<td>-756</td>
<td>-630</td>
<td>-763 -772 As ($)</td>
</tr>
<tr>
<td>400-700</td>
<td>97</td>
<td>-91</td>
<td>-136 -119 90 -129 -210 -235 Three peaks (fourth peak coincides)</td>
</tr>
<tr>
<td>800-1000</td>
<td>-702</td>
<td>-602</td>
<td>-580 -585 -709 -718 -726 As ($)</td>
</tr>
<tr>
<td>600-800</td>
<td>-62</td>
<td>-234</td>
<td>-234 -69 -254 -283 As (*)</td>
</tr>
</tbody>
</table>

For aDGVM, we performed the analysis for several ranges of rainfall, and we observed bimodality of intermediate (i.e. savanna) and high (i.e. forest) cover values in all of the intermediate rainfall values chosen. See Tab. A3 for indices values. In Figure A2 we depicted the bimodality for data with mean annual rainfall between 800 and 1200 mm y⁻¹.

Fig. A2 Probability density distribution of tree cover for the aDGVM output, for mean annual precipitation between 800 and 1200 mm y⁻¹ mean annual rainfall. The distribution is bimodal between savanna and forest (i.e. it is fitted significantly better by a superposition of two normal distributions).
Table A3 ICL and AIC values for aDGVM tree cover output in different mean annual rainfall intermediate ranges. Values in bold represent the minimum value (i.e. the best model according to that index).

<table>
<thead>
<tr>
<th>Range (mm y⁻¹)</th>
<th>ICL</th>
<th>AIC</th>
<th>Comments on differences between ICL and AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1000-1200</td>
<td>78</td>
<td>71</td>
<td>-1429 -1423 -1423</td>
</tr>
<tr>
<td>800-1200</td>
<td>157</td>
<td>149</td>
<td>-2654 -2648 -2615</td>
</tr>
<tr>
<td>800-1000</td>
<td>83</td>
<td>77</td>
<td>-1230 -1244 -1251</td>
</tr>
<tr>
<td>700-1400</td>
<td>343</td>
<td>334</td>
<td>-4207</td>
</tr>
<tr>
<td>500-1500</td>
<td>616</td>
<td>606</td>
<td>-4931</td>
</tr>
<tr>
<td>1000-1300</td>
<td>139</td>
<td>131</td>
<td>-2121 -2115</td>
</tr>
<tr>
<td>500-800</td>
<td>137</td>
<td>129</td>
<td>-559 -594</td>
</tr>
</tbody>
</table>

References


Table B1

The coefficient $b$ of the quantile nonlinear regression curves for the model and observational data. Values for the 90th and 99th quantile are reported.

<table>
<thead>
<tr>
<th>Data series</th>
<th>Figure panel</th>
<th>$b$, 90th quantile [mm$^2$ y$^{-2}$]</th>
<th>$b$, 99th quantile [mm$^2$ y$^{-2}$]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field observation</td>
<td>Fig. 1A</td>
<td>5.8E+05</td>
<td>3.0E+05</td>
</tr>
<tr>
<td>MODIS observation</td>
<td>Fig. 1B</td>
<td>4.1E+05</td>
<td>1.9E+05</td>
</tr>
<tr>
<td>JSBACH/DYNVEG</td>
<td>Fig. 2A</td>
<td>1.4E+05</td>
<td>6.1E+04</td>
</tr>
<tr>
<td>LPJ-GUESS-SPITFIRE</td>
<td>Fig. 2B</td>
<td>6.1E+04</td>
<td>4.4E+03</td>
</tr>
<tr>
<td>aDGVM</td>
<td>Fig. 2C</td>
<td>3.9E+04</td>
<td>5.4E+03</td>
</tr>
</tbody>
</table>