

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

3 **Response to reviewer #1**

4 The paper addresses the general question of how the feedback mechanisms relevant for tropical
5 vegetation dynamics and described in the ecological literature are represented in Dynamics Global
6 Vegetation Models (DGVMs). Particularly, the authors present a discussion based on the different
7 characteristics of 3 frequently used DGVMs applied for Africa: 1) DYNVEG/ JSBACH which is currently
8 coupled to an atmospheric circulation model; 2) LPJ-GUESS which is an offline model and coupled to
9 the SPITFIRE fire module to better represent fire dynamics; 3) aDGVM, an offline process based model
10 designed to represent in detail the main ecological features of forest, savanna and grasslands in Africa.
11 I identify two major novel aspects: 1) model results are compared to recent field-work and remote-
12 sensed data, and then discussed for both arid/semi-arid and humid regions separately pointing out
13 respective mechanistic processes driving the hypothesis of multi-modality in DGVMs for Africa; 2)
14 surprisingly, even though demography representation has been the subject of major concern in the
15 past few years, the authors show that more basic processes, like tree-grass competition/water
16 limitation and the grass-fire feedback, are still lacking representation in the DGVMs they tested.
17 Despite many technical differences between the models, the authors found an elegant way of
18 comparing all of model outputs and reach the main core drawbacks they have. Together with the
19 substantial and consistent discussion based on an inter-disciplinary literature, the results presented
20 potentially represent one of the first steps towards identifying forms of improving current vegetation
21 representation in DGVMs to have more reliable predictions for the future.
22

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

24
25 Please, find below minor comments and suggestions (p = page number; l = line number).

26 1. p9473, l22-23 (abstract): "... and distinguish between fire-prone and shade-tolerant savanna trees,
27 and fire-resistant and shade-intolerant forest trees. ...". I think it is the opposite. In the rest of the text
28 this information is correctly described, e.g., p9475, l10-13 (intro)
29

30 **Thanks, we now corrected it.**

31
32 2. p9477, l1: I did not understand why you replaced "feedback mechanisms" by "ecological
33 interactions". In p9478, l20-22, you mention "Processes affecting PFT composition, such as
34 competition for resources, mortality, and demography (i.e., what we call here the ecological
35 interactions) ...". It sounds different than the analogy to feedback mechanisms on p9477. Check to
36 keep the term consistent along the text and with previous studies.
37

38 **We thank the reviewer for this comment. We now clarify this sentence:**

39 **"with a particular emphasis on the representation of what in the following we call the**
40 **"ecological interactions" between grasses and trees, i.e. the most important tree-grass**
41 **competition mechanisms, and the feedbacks with their environment"**
42

43 3. In which spatial resolution the models were run? If it was different, could it make a difference in the
44 results? I missed this information.
45

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

49 **So, the model resolutions were indeed different, and for this reason we did not perform a point-**
50 **by-point model comparison (spin-up time and type of forcing data were different as well). For**
51 **further details on how we compared models, please see reply #2 to reviewer #2.**
52
53

1 4. p9480, l27: "... but tree can cumulate...". Would "accumulate" fit better?

2
3 **Corrected.**

4
5 5. p9483, l16: "... can potentially shade (and hide) the target tree.". What are the competitor and
6 target trees? Better described to improve understanding.

7
8 **We now improved the explanation rephrasing this sentence to:**

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

11
12 6a. p9488, l27-28: "... but data do not display bimodality of high and low tree cover (not shown)". It
13 would be interesting to see a figure of the no-bimodal frequency distribution of JSBACH in the same
14 manner you showed bimodality for aDGVM in the supplements. Moreover, you could try to use latent
15 class analysis to fit the distribution. It seems more convincing than the 2-gaussian approach.

16
17 **Thanks to this comment of the reviewer we now improved the bimodality test, and we applied**
18 **it in an intermediate range of precipitation for the three model outputs (thus including**
19 **JSBACH), as we report now in the new version of the supplementary material. Following**
20 **previous studies (e.g. Hirota et al., 2011), the test is now performed with the "flexmix" package**
21 **in R for finite mixture models regression (Grün and Leisch, 2007; Hirota et al., 2011; Yin et al.,**
22 **2014), which assumes that each distribution is formed by a mixture of a number of normal**
23 **distributions. The program implements the finite mixtures of regression models by the**
24 **expectation-maximization (EM) algorithm (Grün and Leisch, 2007). To select the best fitting**
25 **distribution, while being parsimonious at the same time, we use the integrated completed**
26 **likelihood criterion (ICL), and the Akaike criterion, and we tested one to four potential class**
27 **models, following Yin et al. (2014). The lowest values of the ICL and AIC identify the best model.**

28
29 6b. Fig. 2a: even though there is no bimodality for JSBACH outputs, I wonder what are the 3 points
30 (outliers) between 1000 and 1500 mm yr-1. They are completely out of the range. Have you verified
31 that?

32
33 **We thank the reviewer for pointing this out. In the previous version of the manuscript, this plot**
34 **represented only tree PFTs, while we intended to include all woody vegetation (as specified in**
35 **the text). We now corrected this mistake replacing the JSBACH data with woody cover (trees**
36 **and shrubs). Shrubs are negligible at large scale, but in South-Eastern Africa there are few**
37 **points where shrubs are dominant (which the reviewer noticed). The overall results were not**
38 **affected by this minor change.**

39
40 7. Along the text: I was a bit confused with the terms "high and low tree cover" because they may be
41 ambiguous in the sense that low tree cover may represent low trees (e.g., shrubs) or the abundance of
42 tree cover (which is meaning you use). I suggest a replacement to high and low tree cover values or
43 amounts.

44
45 **We followed the suggestion and now replaced "tree cover" with "tree cover value" throughout**
46 **the text.**

47
48 8. p9488, l19: you use the term vegetation-fire feedback (grasses + savanna trees benefiting from
49 forest tree removal after fires) that leads to a stable savanna biome at intermediate rainfall values. It
50 seems a quite important feedback mechanism (even though without a citation) but it has not been
51 explored along the text and included in the discussion. Does it fit within the secondary improvements
52 related to demography? You could explore it further for the model outputs.

53
54 **We thank the reviewer for making us aware that the notations "grass-fire feedback" and**
55 **"vegetation-fire feedbacks" where not clearly explained. We modified the text in several points**

1 (Introduction, §3.2 and Concluding remarks) to clarify that the “vegetation-fire feedback” is an
2 extended description of the grass-fire feedback, including also the effect of the different fire
3 tolerance of forest and savanna trees. The grass-feedback is anyway its main component,
4 because without including the effect on fire of grass biomass the feedback is not active. We also
5 added two citations about the importance of tree differentiation for this vegetation-fire
6 feedback mechanism, beyond grasses (Hoffmann et al., 2012; Ratnam et al., 2011). So the
7 description of the grass-fire feedback, which we recognize as a basic requirement for DGVMs to
8 represent savanna dynamics, can be further extended by additionally distinguishing forest and
9 savanna tree types (in terms of their fire tolerance), thus describing the full vegetation-fire
10 feedback.

11
12 9. p9489, l19-20: “. . . at high precipitation, the fuel does not dry out sufficiently to promote fire spread.
13 This may be caused partly be the average fire probability used in this version of SPITFIRE. . .”. I do not
14 see the connection of the former sentence (related to drying out to promote fire spread) with the
15 average fire probability, which is related to the representation of fire triggering. Better explanation of
16 what you meant. Besides, has LPJ-GUESS been benchmarked for Africa? The authors mentioned
17 DGVMs are not parameterized for tropical ecosystems, but could not find any commentary on a
18 specific usage of this model for Africa.

19
20 **To connect the two parts better, we rephrased the sentence in the following way:**
21 **“This may be partly due to the fact that this version of SPITFIRE uses a probability of fire spread**
22 **which depends on average fuel conditions, and thus it is not fully coupled to the drought**
23 **periods. However, this assumption is necessary because the temporal extent of remotely**
24 **sensed data for burned area (now ca. 10 years) is well below the temporal extent of the**
25 **available climate data (50 years).”**
26 **About benchmarking, LPJ-GUESS simulations of vegetation distribution have been compared to**
27 **potential natural vegetation at global scale (including Africa) in Sitch et al. (2003). So, far only**
28 **aDGVM has been applied specifically to Africa.**

29
30 10. p9494, l16-17: “. . . would get dampened by the consequent increase in fire frequency”. According
31 to what has been described for JSBACH, wouldn't it be better “the consequent increase in fire spread”?

32
33 **We corrected this point.**
34

35 36 **Response to reviewer #2**

37
38 This is an interesting study that tackles the ecological reasons behind forest-savanna transitions from
39 the point of view of modeling. The authors opportunely use observational data to evaluate model
40 outputs and enrich the paper discussion. The general aim of the paper of identifying gaps in the
41 assumptions or process representation related to the forest-savanna transition issue is laudable.
42

43 **We thank this reviewer for his/her interesting comments.**

44
45 Nevertheless I have serious doubts the authors use the right reasoning and technics to reach their
46 conclusions. Four major points called out my attention and I suggest the authors put a bit of thinking
47 over them for a revised version of the paper:

48
49 1: On page 9495 authors conclude that water limitation upon tree growth and grass-fire feedbacks are
50 the two most important processes to be considered in model that intend to capture well the forest-
51 savanna transition dynamics. But notice that on page 9474, in the introduction section, authors state
52 the same. It gives the impression authors already had an opinion on what processes were important
53 for models, regardless of the study they conducted.

54
55 **We thank the reviewer for this comment, which made us realize that we needed to clarify the**

1 **fact that the identification of the main ecological mechanisms driving savanna dynamics is not**
2 **a result of the present paper but it is the outcome of much ecological work in the recent**
3 **literature. Our aim here is to bridge the gap between ecological knowledge and global**
4 **modelling, underlying which mechanisms are important to include in DGVMs, and to which**
5 **extent. Our phrasing on page 9495 was misleading in that respect and we changed it to avoid**
6 **misinterpretation, together with a sentence in the Abstract.**

7
8 2: In page 9483 the simulation protocol is described. The fact that the 3 employed DGVMs are run with
9 different input data compromises the intercomparison of their results, since it increases the degrees of
10 freedom in the modeling exercise. We cannot assure for example that model results are a consequence
11 of elevated CO₂ or different precipitation patterns. Authors should have a strong argument – rather
12 than that these were the model runs available at hand – to justify such a experimental design in light of
13 the proposed paper objectives.

14
15 **This paper strictly does not present a model intercomparison project (MIP), nor it includes**
16 **harmonization. Instead, we focus here on ecological mechanisms that are (or are not) included**
17 **in different DGVMs, and we qualitatively compare the DGVM outcomes with observations along**
18 **a rainfall gradient. We agree that the model inputs, including different precipitation (and other**
19 **forcing) data, spin-up times, and resolutions increase the degree of freedom in this conceptual**
20 **model comparison.**

21 **Precisely for this reason, we do not compare at which precipitation values the grassland-**
22 **savanna-forest transitions take place, but we compare only the precipitation ranges (low,**
23 **intermediate and high) because we are interested in the way the models catch this transition.**
24 **We are aware of the limitation of the current approach, but we maintain that at this stage it is**
25 **more important to identify the most important ecological mechanisms causing discrepancies**
26 **between model outputs and observations. Given that objective, the current, more qualitative**
27 **assessment is sufficient, because this already showed that models can predict the right state**
28 **but for the wrong reasons, which is one of our main conclusions. See also reply to point #4 of**
29 **this reviewer below.**

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

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

39
40 3: All models seem to be overestimating tree cover in low to moderate precipitation levels (using the
41 regression lines as a basis for comparison). Let’s get the 50% tree cover as a benchmark: observed
42 data places 50% tree cover in roughly 700-800mm of annual rainfall. The 3 considered models reach
43 that benchmark by 200-400 mm. Please comment.

44
45 **Because of the differences in the precipitation input, we decided not to compare at which**
46 **precipitation level the models reach a certain cover (e.g. full cover, as the reviewer mentions),**
47 **to avoid misinterpretation. Instead, by qualitative comparisons, we evaluated whether they**
48 **catch the effect of water limitation on tree cover as represented by a decreased maximum tree**
49 **cover at low rainfall (without being more specific on the exact rainfall range). In addition, we**
50 **expected the models to predict a wide range of tree cover at intermediate rainfall, and possibly**
51 **even a bimodal distribution of such points, as a consequence of the grass-fire feedback. For**
52 **these evaluations, qualitative assessments, avoiding interpretation problems due to**
53 **differences in model set-ups, are valid. Please see also our response to point 2 above.**

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

55 **“For these ranges, we will perform a qualitative comparison of the modelled and observed data**

1 **in the parameter space (i.e. maximum cover value, spread, distribution)."**
2

3 4: It is interesting to see the evaluation on how elevated CO₂ can affect the dynamics of forest-savanna
4 transition zones. But remember nutrient dynamics have shown to play a key role in elevated CO₂
5 responses of forests (e.g. Norby et al. 2010). Many tropical forests and savannas are nutrient limited
6 (especially P-limited). However it seems like the role of nutrient dynamics is poorly explored here. I
7 understand that none of the employed models have nutrient cycling (even though I was curious
8 because JSBACH was one of the first DGVMs to implement N and P cycle, but the authors probably used
9 an earlier model version), but the topic could be further explored. Otherwise the scientific utility of the
10 elevated-CO₂ exercise (which in fact is not properly explained in the method section) is reduced.
11

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

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

21 **The JSBACH version used was indeed the CMIP5 version of the model without N and P cycles.**
22

23 Minor points:

24 p. 9475, l 3: "enhances open savanna formation presence"
25

26 **Corrected.**
27

28 p. 9475, l 26: "leading to woody savanna expansions"
29

30 **We clarified this line as "leading to savanna expansions (e.g. at the expense of grasslands)".**
31

32 p. 9476, line 14: even though DGVM have a considerably limited ability to deal with the enormous
33 plant trait diversity found in tropical regions. Generally tropical forest is represented by only one or
34 two PFTs.
35

36 **We now added a sentence to underline this point of the reviewer: "For example, they represent
37 the enormous plant trait diversity of tropical regions through distinguishing only one or two
38 plant functional types (PFTs)."**
39

40 p. 9479, l 12: "Max Planck Institute"
41

42 **Corrected.**
43

44 p. 9486, l1-8: That is in fact a good argument for investigating these other factors with the use of
45 models. It could have been better explored in the article. . .
46

47 **To explore the effect of factors such as rainfall heterogeneity and seasonality on savanna
48 ecology, in our opinion the best approach is to choose appropriate ecological models that
49 include the relevant ecological interactions. The main point of this article is instead to verify
50 whether the analysed DGVM include a minimal set of mechanisms that are necessary to
51 represent savannas, and to analyse the consequences if they don't. Therefore, exploring the
52 effect of certain ecological mechanisms, whose importance is not yet fully known, is outside the
53 scope of the present paper.**
54

55 p. 9486, l25: This sentence is not in accordance with the model-data comparison the authors do

1 subsequently.

2
3 **We replaced it with: “At a first glance, the relation between tree cover and mean annual rainfall**
4 **simulated by the models (Fig. 2) is similar to that observed in the data (Fig. 1)”.**

5
6 p. 9489, l25-27: But isn't this rainfall range selection a little artificial? The study is not convincing in
7 that aDGVM really shows a bimodal tree cover distribution such as evidenced by observational data.
8 Maybe a statistical tool would help here to prove whether the aDGVM modeled distribution – or part of
9 it – is bimodal or not.

10
11 **We now clarified this point better, and we refined the statistical analysis. The bimodality is**
12 **observed in an intermediate rainfall range also for the MODIS data (as analyzed in Staver et al.,**
13 **2011a, 2011b). The bimodality is observed independently of the exact range of mean annual**
14 **rainfall chosen as we now better specify in the text:**

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

18
19 **Finally, the statistical analysis of the bimodality has been improved (for details please see reply**
20 **to point #6a of reviewer 1, and Supplementary Information).**

21
22 p. 9492, l10: And so do many tropical forests (to be associated with nutrient poor soils)

23
24 **Indeed the conditioning of the nutrient levels on savanna occurrence is not key. We modified**
25 **the sentence in the following way: “Secondly, although it has been observed that savannas can**
26 **be associated with nutrient poor soils (Lloyd et al., 2008), this limitation does not seem to**
27 **explain the savanna-forest transition (Bond, 2010; Favier et al., 2012; Murphy and Bowman,**
28 **2012)”.**

29
30 p. 9493: “Indeed, the three models predict reasonably well the current tree cover along the mean
31 annual rainfall gradient in Africa, as derived from ground and satellite observations.” Are the authors
32 sure of this statement? A numerical/qualitative comparison would do very good here.

33
34 **We perform a qualitative model comparison throughout the paper, please see reply #2 and 3 to**
35 **this reviewer above. We now better specify this sentence:**

36 **“...the three models predict the main features of the current tree cover along the mean annual**
37 **rainfall gradient in Africa, as derived from ground and satellite observations”.**

38
39 p. 9494: I have the impression the text discussed here would fit better in the discussion
40 section rather than in this “concluding remarks” section.

41
42 **We understand the point of view of the reviewer. However, we opted for this structure because**
43 **we do not have the classical “Results” and “Discussion” sections separately but together, and we**
44 **felt the urge to summarize the discussion points in these final remarks.**

45
46
47 **References cited**

48 Grün, B. and Leisch, F.: Fitting finite mixtures of generalized linear regressions in R, *Comput. Stat. Data Anal.*,
49 51(11), 5247–5252, doi:10.1016/j.csda.2006.08.014, 2007.

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

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

- 1 Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. a., Archibald, S., Lehmann, C. E. R., Anderson, M. T., Higgins, S.
2 I. and Sankaran, M.: When is a “forest” a savanna, and why does it matter?, *Glob. Ecol. Biogeogr.*, 20(5), 653–
3 660, doi:10.1111/j.1466-8238.2010.00634.x, 2011.
- 4 Sitch, S., Smith, B. and Prentice, I.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon
5 cycling in the LPJ dynamic global vegetation model, *Glob. Chang. ...*, 9, 161–185, 2003.
- 6 Staver, A. C., Archibald, S. and Levin, S.: Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and
7 savanna as alternative stable states., *Ecology*, 92(5), 1063–72, 2011a.
- 8 Staver, A. C., Archibald, S. and Levin, S. A.: The global extent and determinants of savanna and forest as
9 alternative biome states., *Science (80-.)*, 334(6053), 230–232, doi:10.1126/science.1210465, 2011b.
- 10 Yin, Z., Dekker, S. C., van den Hurk, B. J. J. M. and Dijkstra, H. a.: Bimodality of woody cover and biomass across the
11 precipitation gradient in West Africa, *Earth Syst. Dyn.*, 5(2), 257–270, doi:10.5194/esd-5-257-2014, 2014.

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

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1 **Abstract**

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

27

28 **1 Introduction**

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

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1 vegetation), and grasses (i.e. grasses and herbs). In most of the savanna ecosystems, we
2 observe highly shade intolerant and fire tolerant C₄ grasses and C₃ trees. This savanna
3 definition is generally valid, with the exception of a few regions (e.g. the Neotropical
4 cerrado where C₃ grasses dominate, see Lloyd et al., 2008, Ratnam et al. 2011). For a
5 long time ecologists have been fascinated by savannas, because trees and grasses
6 coexist, while competing mainly for the same resource, namely water, which is the main
7 limiting factor (Sankaran et al., 2004; Scholes and Archer, 1997; Walter, 1971).
8 Classical ecological theory, such as the competitive exclusion principle, predicts that
9 only one vegetation type can survive in these conditions (Hutchinson, 1961; Tilman,
10 1982). To solve this conundrum, numerous experimental and modeling studies explored
11 the nature of tree-grass competition and coexistence (e.g. Higgins et al., 2000; House et
12 al., 2003; Sankaran et al., 2004; Scholes and Walker, 1993; Walker and Noy-Meir,
13 1982). Grasses can outcompete trees in the driest environments, where tree growth is
14 water-limited (Higgins et al., 2012), and they have a particularly strong competitive
15 effect on tree seedlings, as grasses and tree seedlings compete for water in the same
16 surface layer (Baudena et al., 2010; Bond, 2008; February et al., 2013; Sankaran et al.,
17 2004; Wakeling et al., 2011; Yin et al., 2014b). In less arid conditions, however, adult
18 trees can potentially grow deeper roots and reach deeper water than grasses (Kulmatiski
19 and Beard, 2013; Walter, 1971; Ward et al., 2013), although overlap between grass and
20 tree roots can be high in some savannas (e.g. February and Higgins, 2010; Higgins et
21 al., 2000; House et al., 2003).

22 In addition to water availability, fire is an important driver of tree-grass dynamics. C₄
23 grass biomass enhances fire spread in open ecosystems, due to its high flammability. At
24 the same time, grasses benefit from fire because they recover faster than trees, and
25 profit of the open spaces after fire, thus originating a positive feedback mechanism that
26 enhances savanna [formation and](#) presence (as shown by e.g. long term fire-exclusion
27 experiments, Higgins et al., 2007, or model studies, e.g. Higgins et al., 2008; van
28 Langevelde et al., 2003; see also Hoffmann et al., 2012). Fires may also limit tree
29 seedling recruitment and growth, thus reducing tree dominance further (e.g. Hanan et
30 al., 2008; Higgins et al., 2000). This grass-fire feedback is characteristic of tropical
31 savannas and grasslands, while in most of the other biomes woody species produce
32 most fuel for fires (e.g. boreal forests, Bonan and Shugart, 1989). Fire is essential to
33 savanna persistence in wetter areas, which would be forested otherwise. [The grass-fire](#)

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

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11 | Savannas are expected to undergo major changes in the future due to increasing
12 | temperature and CO₂ concentration, modified rainfall patterns, and subsequently
13 | changed variability in fire regimes (Intergovernmental Panel on Climate Change -
14 | IPCC, 2007). In recent years, an increase in woody cover has been observed in savannas
15 | all over the world (e.g. Bowman et al., 2010; Buitenwerf et al., 2012; Donohue et al.,
16 | 2013; Ward, 2009; Wigley et al., 2010). Several studies tried to explain wood expansion
17 | by overgrazing or decreasing fire frequency, which would enhance grass mortality and
18 | thus favor woody vegetation (Scholes and Archer, 1997). However, CO₂ increase is
19 | probably one of the main causes of woody encroachment, leading to savanna
20 | expansions (e.g. at the expense of grasslands). As water use efficiency increases with
21 | CO₂ (e.g. de Boer et al., 2011), thus decreasing the water need for grow, increased CO₂
22 | concentration leads to a shift in tree-grass competition for water, possibly favoring C₃
23 | trees over C₄ grasses (Bond and Midgley, 2000; Bowman et al., 2010; Kgope et al.,
24 | 2010; Polley et al., 1994; Wigley et al., 2010). In African savannas, paleo-ecological
25 | evidence of the last glacial period, as well as observations of the last 50-100 years,
26 | suggests that increasing CO₂ coincides with an increase in savanna woody plant growth
27 | (Bond et al., 2003; Scheiter and Higgins, 2009). These transformations could have
28 | larger effects on global biogeochemical cycles and precipitation than for any other
29 | biome, due to the large extent and productivity of savannas (IPCC, 2007; Snyder et al.,
30 | 2004).

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

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Climate Change

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

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

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

17

18 **2 Methods**

19 **2.1 Model descriptions**

20 DGVMs were developed to quantify transient responses of terrestrial ecosystems to
21 past, present and future climates, and this required an inclusion of modeling vegetation
22 dynamics in addition to biogeochemical processes (Cramer et al., 2001; Pitman, 2003;
23 Prentice et al., 2007). To account for processes at subgrid-scale, DGVMs often assume
24 fractional vegetation cover within the model grid cell (tiling, or mosaic approach).
25 Vegetation description is based on PFTs, which aggregate and represent species with
26 similar functions. Biomes are then represented by a mixture of PFTs, such as evergreen
27 and deciduous, broadleaved and needleleaved trees, shrubs, C₃ and C₄ grasslands, which
28 dominate in a particular climate. Savannas are typically simulated as a mixture of
29 tropical, broadleaved, deciduous trees (“savanna trees” here after), and mostly C₄
30 grassland, while forests have mostly tropical, broadleaved, evergreen trees (“forest
31 trees” here after).

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1 DGVMs in general have a quite standard set of assumptions to represent plant
2 physiology, including photosynthesis and biomass production. Most of them calculate
3 Gross Primary Production (GPP) by a coupled photosynthesis-transpiration scheme and
4 estimate autotrophic respiration as a function of temperature. Net Primary Production
5 (NPP) is dependent on the climate and CO₂, and scaled up to the plant or PFT level by
6 building up below and above ground carbon and leaf area (e.g., Sitch et al., 2003).
7 Processes affecting PFT composition, such as competition for resources, mortality, and
8 demography (i.e. what we call here the ecological interactions) are included into
9 DGVMs as separate modules that interact with the physiological and phenological
10 modules.

11 For the purpose of this paper, we will focus on the description of how the ecological
12 processes relevant for tropical vegetation dynamics are included in the three selected
13 DGVMs (JSBACH, LPJ-GUESS-SPITFIRE and aDGVM). Only the physiological
14 aspects relevant for the difference in PFT composition in grasslands, savannas and
15 forests will be described. JSBACH is part of an ESM, and was designed to represent the
16 interactive role of vegetation and land surface in the climate system. While LPJ-GUESS
17 has been included in an ESM in several studies, LPJ-GUESS-SPITFIRE has never been
18 used in such contest, and the same holds for aDGVM. Both models are so far used only
19 “offline”, i.e. they are driven by external forcing, such as climate and CO₂ changes,
20 without being coupled to a general circulation model, and thus without feeding back to
21 the climate. The models used in this study have their intrinsic limitations, for example
22 they all neglect nutrient cycling. A summary of the ecological interactions important in
23 the tropical areas and included into the models is presented in Table 1.

24 2.1.1 JSBACH (DYNVEG)

25 DYNVEG (Brovkin et al., 2009; Reick et al., 2013) is the submodel for vegetation
26 dynamics implemented in the land surface component JSBACH (Raddatz et al., 2007)
27 of the [Max Planck Institute - Earth System Model](#) (MPI-ESM, (Giorgetta et al., 2013).
28 DYNVEG groups its various PFTs into a grass class (C₃ and C₄ grasses), and a woody
29 class (trees and shrubs). Within the woody class, DYNVEG distinguishes between two
30 PFTs for tropical trees, with different photosynthetic abilities, which nonetheless do not
31 have different fire or shade tolerances, so they do not correspond to what we call
32 savanna and forest tree in this paper. DYNVEG assumes dominance of the woody over

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1 the grass class, i.e., trees have competitive advantage and typically outcompete grasses.
2 Within a class, the competition among PFTs is indirect via NPP: a PFT with higher NPP
3 outcompetes PFTs with lower NPP. All PFTs share the same soil water bucket, and
4 there is no separation of root zones between woody and grass classes. Woody and grass
5 classes compete for newly available habitable space, with woody types outcompeting
6 grasses in the absence of disturbances. The space available for colonization can be only
7 part of the total area, i.e. some parts of the habitat are considered inhospitable. This
8 fraction constitutes a sort of resource limitation to tree development, since it is
9 calculated as a function of the average NPP over the last years of simulations, which in
10 turn depends on water (and other resource) availability (Reick et al., 2013). JSBACH
11 overestimates GPP and NPP in water-stressed conditions (Dalmonech and Zaehle,
12 2013), which partly explains an overestimation of tree cover fraction in drylands
13 (Brovkin et al., 2013). Elevated CO₂ concentration increases water use efficiency of all
14 PFTs.

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

23 **2.1.2 LPJ-GUESS-SPITFIRE**

24 LPJ-GUESS (Smith et al., 2001) was developed to incorporate forest age structure into
25 LPJ (Sitch et al., 2003), thus simulating gap model behavior and including the
26 competition of different age cohorts for light and water. For each grid cell, LPJ-GUESS
27 simulates a number of replicate patches. For the tropical regions, LPJ-GUESS results in
28 one type of (C₄) grasses, and two types of tree PFTs, savanna and forest trees, where the
29 former are fire tolerant and shade intolerant, and the latter are fire intolerant and shade
30 tolerant. In LPJ-GUESS, trees and grasses use common water in a superficial soil layer
31 (0.5 m deep), but trees have part of their roots in a deeper soil layer (1 m). At high water
32 availability, trees outcompete grasses by limiting light availability.

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

19 2.1.3 aDGVM

20 The aDGVM (Scheiter and Higgins 2009) is explicitly designed to study tree-grass
21 dynamics in savannas. ~~While the~~ original version of the model only simulates savanna
22 trees and C₄ grasses (Scheiter and Higgins, 2009), ~~an~~ updated version, used for the
23 current paper, simulates C₄ grasses, C₃ grasses, fire-resistant, shade intolerant, savanna
24 trees and fire-sensitive, shade tolerant forest trees (Scheiter et al., 2012). The model
25 uses an individual-based structure to represent trees. Tree recruitment occurs from seed,
26 and tree seedlings compete with grasses more directly than adult trees.

27 Plants compete mostly for water and light. Light competition is modeled by considering
28 the light available to grasses below and between canopies. Hence, once a vegetation
29 stand attains a high tree LAI, grass-growth is light-limited. In addition, seedlings and
30 small trees are shaded by grasses and by adult trees. Savanna trees suffer more from
31 light limitation than forest trees, which are more shade tolerant. Plants extract water
32 from different soil layers, depending on their rooting depth, which increases with the

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1 individual root biomass, until reaching maximum value, typically parameterized as
2 being deeper for trees than for grasses. This allows trees to have exclusive access to
3 water in deep soil layers. A simple bucket scheme is used to simulate water extraction
4 and percolation into deeper soil layers. The extent to which soil moisture limits
5 photosynthesis is calculated as a function of soil moisture in the layers in which the
6 plant has roots. Hence, rooting depth, the amount of water transpired, and drought
7 tolerance (i.e. the ability to withstand a low soil water content) determine the outcome
8 of competition for soil moisture.

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moisture availability

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

28 **2.2 The model experiment setups**

29 To simulate current conditions, transient simulations were performed where CO₂
30 increased to 390 ppm. The JSBACH run used here was a pre-existing CMIP5 historical
31 simulation under transient forcing from 1850 to 2005, with horizontal resolution of

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

21 | 2.3 Observational datasets

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

28 | The dataset from Sankaran et al. (2005) includes data from 854 field sites across Africa.
29 | They gathered data from several sources, with no recent human influence, not situated
30 | in riparian or seasonally flooded areas, and where vegetation was sampled on a
31 | sufficiently large area (> 0.25 ha for plot measurements and > 100m for transect

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1 | sampling). Here, we used projected woody cover and mean annual precipitation. The
2 | latter included estimates from field measurements and regional rainfall maps, and from
3 | fitted climatic grids (see Sankaran et al., 2005 for details). See Fig. 1A for a
4 | visualization of the tree cover as a function of mean annual rainfall.

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

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25 | 2.4 Model comparison to observations

26 | As for the data, for the three models we analyzed the simulated tree cover output (i.e. all
27 | woody vegetation) as a function of the corresponding mean annual rainfall conditions,
28 | and we select only the points in the African continent between 35° S and 15° N. We
29 | masked land use, and we used both vegetation and precipitation averaged over thirty
30 | years. To evaluate the effect of rainfall on the upper limit of tree cover, following e.g.
31 | Sankaran et al. (2005), we used nonlinear quantile regression (Koenker and Park, 1996),

1 as implemented in the ‘quantreg’ library of the R program. We used 0.90 to 0.99
2 quantiles and we chose the following nonlinear function:

$$3 \quad y = a \frac{x^2}{b + x^2}, \quad (1)$$

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

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

20 In addition to mean annual rainfall, other factors such as temperature (Higgins and
21 Scheiter, 2012), or temporal distribution of rainfall, are known to be important for
22 tropical grasslands, savannas and forests too. Rainfall heterogeneity, intermittency, and
23 seasonality affect water availability (D’Onofrio et al., 2014) and fire return times, and
24 are very important predictors of savanna/forest distribution (Lehmann et al., 2011), with
25 rainfall seasonality reducing growth rates (e.g. limiting water availability, Sarmiento,
26 1984), influencing root-shoot biomass ratio and local cover (Yin et al., 2014a) and
27 increasing fire frequency (Archibald et al., 2009). Nevertheless, these factors have not
28 yet been thoroughly examined in many ecological studies, possibly also because of lack
29 of accurate rainfall datasets in these areas. Therefore, in the following, we will focus
30 only on mean annual rainfall, whose importance has extensively been studied. We

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1 separately evaluate arid and semi-arid savannas (Sect. 3.1) and humid savannas and
2 forests (Sect. 3.2), analyzing also whether and how the ecological interactions are
3 included in the different models. Finally, we discuss the effect of expected future
4 climatic changes on the outcome of tree-grass competition in the three models (Sect.
5 3.3).

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7 **3 Results and Discussion**

8 **3.1 Arid and semi-arid savannas and grasslands: the role of water** 9 **limitation**

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

24 At a first glance, the relation between tree cover and mean annual rainfall simulated by
25 the models (Fig. 2) is similar to that observed in the data (Fig. 1). In JSBACH output,
26 the maximum tree cover increases between zero and 800 mm y⁻¹ approximately, where
27 it reaches its largest cover (see 90th quantile regression curve in Fig. 2A; similar results
28 are obtained with the 99th quantile regression lines, not shown). This increase is mostly
29 due to the fact that all the PFTs can colonize only a part of the space, which is
30 calculated dynamically and increased with water availability (although indirectly, via

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1 NPP). In addition, fire related mortality increases with decreasing air humidity, thus
2 representing another source of water-related limitation in drier areas. At the same time,
3 the limitation to tree maximum cover is not likely to be the result of competition with
4 grasses, since trees are assumed to outcompete grasses, and they are affected by some
5 sort of grass competition at low water availability only temporarily after e.g. a fire (see
6 also Fig. 3B). JSBACH has a tendency to overestimate maximum tree cover at very low
7 values of mean annual rainfall ($<100 \text{ mm y}^{-1}$), as this model is known to overestimate
8 GPP and NPP (Brovkin et al., 2013).

9 In the LPJ-GUESS-SPITFIRE model output (Fig. 2B), almost no tree cover is observed
10 until mean annual rainfall is about 300 mm y^{-1} . In this precipitation range, modeled
11 trees are water limited and outcompeted by grasses. Compared to the observations, this
12 model seems to limit tree cover in this precipitation range too strongly. Between about
13 300 and 900 mm y^{-1} annual rainfall, the maximum vegetation cover in LPJ-GUESS-
14 SPITFIRE increases until it reaches a maximum value (about 90% tree cover, see 90th
15 quantile regression line in Fig. 2B), partly due to water limitation that allows tree-grass
16 coexistence (between about 350 and 650 mm y^{-1} , Arneth et al., 2010), and partly due to
17 fires, which further limit tree cover.

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

28 **3.2 Humid savannas and forests: the role of fire**

29 In more humid conditions, bimodality of vegetation cover below and above 60% is
30 observed in the MODIS data for precipitation in a range between around 1000 and 2000
31 mm y^{-1} (e.g. Hirota et al., 2011; Staver et al., 2011b, see also Fig 1B), i.e. clusters with

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

18 | The role of fire in maintaining savannas in humid environments is included in all of the
19 | models, although in different ways. At high precipitation, JSBACH tree cover output
20 | displays a constant maximum value (above about 800 mm y⁻¹), but the data display
21 | considerable scattering below full tree cover (Fig 2A). In other words, the model
22 | predicts savannas and forests in this range, but the data do not display bimodality of
23 | high and low tree cover [values](#) (see [Supplementary material, Appendix 1](#)). This is a
24 | consequence of the fact that in this model fire is triggered more by trees than by grasses,
25 | since trees produce larger amounts of litter and thus of fuel. Fire favors grasses because
26 | it opens the landscape by reducing the tree cover and generates space for them. Thus,
27 | fire creates a negative feedback because fewer fires occur when tree cover is lower (Fig.
28 | 3B), thus preventing hysteresis and bistability in this model.

29 | LPJ-GUESS-SPITFIRE simulation results do not show any low tree cover [value](#) (e.g.
30 | below 50% cover) for rainfall higher than about 900 mm y⁻¹(Fig. 2B). Therefore, quite
31 | surprisingly, this model does not predict any savanna in mesic environments. In the
32 | model, though fire frequency is prescribed from the satellite data, fire spread depends

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1 on fuel load (Fig. 3C) and fuel moisture, and thus unfavorable conditions might still
2 prevent fires. Both grass and tree presence increases fire intensity, opening up space,
3 and thus favoring grasses. This is not strictly a positive grass-fire feedback, because also
4 grass-free areas can burn. Thus, as grasses are not fostered by a positive feedback with
5 fire, they are always outcompeted by trees in LPJ-GUESS-SPITFIRE when water
6 availability is high, and they do not survive above approximately 900 mm y^{-1} . At the
7 same time, this issue is also likely to be connected to the fire spread depending on fuel
8 moisture: In this model, at high precipitation, the fuel does not dry out sufficiently to
9 promote fire spread. This may be partly due to the fact that this version of SPITFIRE
10 uses a probability of fire spread, which depends on average fuel conditions, and thus it
11 is not fully coupled to the drought periods. However, this assumption is necessary
12 because the temporal extent of remotely sensed data for burned area (now ca. 10 years)
13 is well below the temporal extent of the available climate data (50 years).

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14 In aDGVM, maximum tree cover values can reach full cover above about 500 mm y^{-1} ,
15 but the points are still very scattered, and display some clustering at cover around 30-
16 60% for intermediate rainfall values (Fig. 2C). If we only select points in such rainfall
17 range (e.g. between 800 mm and 1200 mm y^{-1}), we observe that the tree cover
18 distribution is bimodal (see Appendix 1; note that this conclusion is robust to different
19 choices for the limits of the rainfall range). aDGVM includes explicitly the grass-fire
20 feedback, which is reinforced by the difference between fire tolerant savanna trees and
21 fire sensitive forest trees (Fig 3 A). When the forest trees suppress the savanna trees and
22 the grasses through light competition, the result is a forest biome with low fire
23 frequency or even fire suppression, primarily due to scarcity of (grass) fuel. At sites
24 with regular fire, forest trees cannot persist, resulting in low forest tree cover and
25 intermediate savanna tree cover, with grasses colonizing the open spaces and fostering
26 fire occurrence. This vegetation state represents a savanna biome. In a certain range of
27 environmental (e.g. rainfall) conditions, a system initialized as a forest will not shift to a
28 savanna, unless fire ignition probability is high, while a system initialized as a savanna
29 will persist in the same state unless fire ignition probability is very low. As a
30 consequence of including this positive feedback, experiments with the aDGVM show
31 that fire suppression can lead to transitions and hysteresis between savanna and forest
32 states (Higgins and Scheiter, 2012; Moncrieff et al., 2013).

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

6 **3.3 Effects of future climatic changes**

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

12 Expected increase in CO₂ concentration in the future is likely to affect the outcome of
13 tree-grass competition, mediating both important mechanisms we discussed so far, i.e.
14 competition for water, and fires. Fire is expected to decrease under increased CO₂ level
15 because of the decrease in grass fuel load, given that C₃ woody plants are favored over
16 C₄ grasses under elevated CO₂ levels (Ehleringer et al., 1997). In JSBACH, higher CO₂
17 leads to higher productivity of grasses and trees, which in turn increases fire spread and
18 hence introduces a negative feedback, dampening the increase of tree biomass. In
19 aDGVM, CO₂ fertilization promotes tree growth, and thus tree establishment in
20 grasslands, transforming them into savannas or woodlands (with or without fire,
21 respectively). So in contrast to JSBACH, aDGVM includes a positive feedback, leading
22 to tree canopy closure in savannas, which, suppressing grass growth, reduces also fire
23 activity, transforming them into woodlands and forests (Scheiter and Higgins 2009).
24 Due to this positive feedback, CO₂ concentration can induce hysteresis effects on the
25 vegetation states (Higgins and Scheiter 2012). LPJ-GUESS-SPITFIRE has an
26 intermediate behavior between the other two models, because grass and woody
27 vegetation contribute similarly to fuel formation. Also, since in this model fire
28 frequency is prescribed from remotely sensed data, any effect of changes of CO₂ levels
29 on fire occurrence would be very limited, though there might be pronounced effects on
30 resulting vegetation composition.

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

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

20 **3.4 Other mechanisms influencing tropical savannas, grasslands and** 21 **forests**

22 Up to now we considered water limitation and fires as the main drivers of grassland,
23 savanna and forest distribution. Several additional factors can be important for
24 vegetation dynamics, especially at the local scale. The first factor is herbivory.
25 Browsing (particularly by mega-herbivores in Africa) is known to have an important
26 limiting effect on tree cover, similar to the effect of fire (e.g. Scheiter and Higgins,
27 2012; Staver et al., 2012), while grazing can favor trees because it limits grass
28 expansion (e.g. Sankaran et al., 2008). However, large herbivores seem not to be critical
29 in determining forest and savanna distributions (Murphy and Bowman, 2012).

30 Secondly, although it has been observed that savannas can be associated with nutrient
31 poor soils (Lloyd et al., 2008), this limitation does not seem to explain the savanna-

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

23

24 | **4 Concluding remarks**

25 | Current ecological understanding identifies water limitation and grass-fire feedback as
26 | dominant mechanisms driving the forest-savanna-grassland transition in Africa. In arid
27 | and semiarid savannas, trees are water-limited, and the water competition with grasses
28 | is the key factor determining savanna existence. In these conditions, grasses compete
29 | especially fiercely with tree seedlings. In wetter areas along the climatic gradient,
30 | savannas are maintained by the presence of a grass-fire positive feedback. Fire spread is
31 | increased by grasses, which provide fuel load. Grasses re-grow faster than trees after
32 | fires, while tree recruitment is limited. Thus, trees do not close their canopies, leaving

1 more free space for grasses. On the other hand, when trees manage to close their
2 canopies, grasses are outcompeted because of light limitations, and because fire is
3 suppressed. This grass-fire feedback is reinforced by the higher flammability of forest
4 trees with respect to savanna trees. Both water limitations and fires act differently on
5 tree adults and seedlings, which compete more directly with grasses and are the most
6 sensitive stage in tree life.

7 These mechanisms are to varying extent included in the three DGVMs we analyzed
8 (JSBACH, LPJ-GUESS-SPITFIRE and aDGVM). Indeed, the three models predict the
9 main features of the current tree cover along the mean annual rainfall gradient in Africa,
10 as derived from ground and satellite observations. aDGVM output matches the
11 observations better than the other two models. This is perhaps to be expected since this
12 model is specifically designed for African vegetation and it includes more detailed
13 representations of ecological interactions, especially the vegetation-fire feedback. For
14 the other two models, the main differences between observations and model outputs are:
15 i) JSBACH overestimates tree cover in dry areas (see also Brovkin et al., 2013); ii) LPJ-
16 GUESS-SPITFIRE does not show any savanna at medium to high annual rainfall rates;
17 iii) both these DGVMs do not show bimodality of savannas and forests in humid areas.
18 This latter point might feed the debate about whether bimodality between savanna and
19 forest cover actually exists (see e.g. Hanan et al., 2014). Despite their reasonably good
20 performances, not all the mechanisms included in JSBACH and LPJ-GUESS-SPITFIRE
21 are fully appropriate to represent vegetation in the tropics and the subtropics. In
22 JSBACH, competition between trees and grasses favors the former irrespectively of
23 water availability, which is one of the reasons behind JSBACH tree cover
24 overestimation. At the same time, in this model, fire is fostered disproportionately by
25 woody vegetation as compared to grasses, resulting in a negative feedback. This is
26 responsible for observing savannas in larger parts of the rainfall gradients, and no
27 savannas would be simulated without them. Although the three models display
28 comparable outcomes under the current climate, the presence of a negative fire-
29 vegetation feedback in JSBACH, a positive feedback in aDGVM, and an intermediate
30 behavior in LPJ-GUESS-SPITFIRE, leads to different predictions of fire frequency and
31 effects under climate change scenarios between the three models. In JSBACH, the
32 initial increase in woody vegetation, due to higher CO₂ concentrations, would get
33 dampened by the consequent increase in fire spread. Interesting in this perspective is

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1 | that the sensitivity to shifts between forests and savannas is low for JSBACH, as
2 negative feedbacks are more important, while in aDGVM the positive grass-fire
3 feedback mechanism results in a large sensitivity to shifts of the different tree-grass
4 systems. LPJ-GUESS-SPITFIRE has an intermediate behavior between the other two
5 models, since grass and woody vegetation foster fire in a similar way. Also, in this
6 model fires seem to be suppressed too easily by high humidity conditions, which cause
7 savannas to be absent at medium-high annual rainfall values.

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

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

26

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5

6 **References**

- 7 Archibald, S., Roy, D., van Wilgen, B. and Scholes, R. J.: What limits fire? An
8 examination of drivers of burnt area in Southern Africa, *Glob. Chang. Biol.*, 15, 613–
9 630, 2009.
- 10 Arneth, A., Lehsten, V., Spessa, A. and Thonicke, K.: Climate–fire interactions and
11 savanna ecosystems: a dynamic vegetation modelling study for the African continent, in
12 *Ecosystem Function in Savannas: Measurement and Modeling at Landscape to Global*
13 *Scales*, edited by M. J. Hill and N. P. Hanan, CRC Press., 2010.
- 14 Baudena, M., D'Andrea, F. and Provenzale, A.: An idealized model for tree–grass
15 coexistence in savannas: the role of life stage structure and fire disturbances, *J. Ecol.*,
16 98(1), 74–80, doi:10.1111/j.1365-2745.2009.01588.x, 2010.
- 17 Baudena, M. and Rietkerk, M.: Complexity and coexistence in a simple spatial model
18 for arid savanna ecosystems, *Theor. Ecol.*, 6(2), 131–141, doi:10.1007/s12080-012-
19 0165-1, 2013.
- 20 Beerling, D. J. and Osborne, C. P.: The origin of the savanna biome, *Glob. Chang.*
21 *Biol.*, 12(11), 2023–2031, doi:10.1111/j.1365-2486.2006.01239.x, 2006.
- 22 De Boer, H. J., Lammertsma, E. I., Wagner-Cremer, F., Wassen, M. J., Dilcher, D. L.
23 and Dekker, S. C.: Climate forcing due to optimization of maximal leaf conductance in
24 subtropical vegetation, *Proc. Natl. Acad. Sci. United States Am.*, 108(10), 4041–4046,
25 doi:10.1073/pnas.1100555108, 2011.
- 26 Bonan, G. B., Levis, S., Sitch, S., Vertenstein, M. and Oleson, K. W.: A dynamic global
27 vegetation model for use with climate models: concepts and description of simulated
28 vegetation dynamics, *Glob. Chang. Biol.*, 9(11), 1543–1566, doi:10.1046/j.1365-
29 2486.2003.00681.x, 2003.
- 30 Bonan, G. B. and Shugart, H. H.: Environmental factors and ecological processes in
31 boreal forests, *Annu. Rev. Ecol. Syst.*, 20, 1–28,
32 doi:10.1146/annurev.es.20.110189.000245, 1989.
- 33 Bond, W. J.: What Limits Trees in C 4 Grasslands and Savannas?, *Annu. Rev. Ecol.*
34 *Evol. Syst.*, 39(1), 641–659, doi:10.1146/annurev.ecolsys.39.110707.173411, 2008.

- 1 Bond, W. J.: Do nutrient-poor soils inhibit development of forests? A nutrient stock
2 analysis, *Plant Soil*, 334(1-2), 47–60, doi:10.1007/s11104-010-0440-0, 2010.
- 3 Bond, W. J. and Midgley, G. F.: A proposed CO₂-controlled mechanism of woody plant
4 invasion in grasslands and savannas, *Glob. Chang. Biol.*, 6, 865–869, 2000.
- 5 Bond, W. J., Midgley, G. F. and Woodward, F. I.: The importance of low atmospheric
6 CO₂ and fire in promoting the spread of grasslands and savannas, *Glob. Chang. Biol.*,
7 9(7), 973–982, doi:10.1046/j.1365-2486.2003.00577.x, 2003.
- 8 Bowman, D. M. J. S., Murphy, B. P. and Banfai, D. S.: Has global environmental
9 change caused monsoon rainforests to expand in the Australian monsoon tropics?,
10 *Landsc. Ecol.*, 25(8), 1247–1260, 2010.
- 11 Brovkin, V., Boysen, L., Arora, V. K., Boisier, J. P., Cadule, P., Chini, L., Claussen,
12 M., Friedlingstein, P., Gayler, V., van den Hurk, B. J. J. M., Hurtt, G. C., Jones, C. D.,
13 Kato, E., de Noblet-Ducoudré, N., Pacifico, F., Pongratz, J. and Weiss, M.: Effect of
14 Anthropogenic Land-Use and Land-Cover Changes on Climate and Land Carbon
15 Storage in CMIP5 Projections for the Twenty-First Century, *J. Clim.*, 26(18), 6859–
16 6881, doi:10.1175/JCLI-D-12-00623.1, 2013.
- 17 Brovkin, V., Raddatz, T., Reick, C. H., Claussen, M. and Gayler, V.: Global
18 biogeophysical interactions between forest and climate, *Geophys. Res. Lett.*, 36(7), 1–6,
19 doi:10.1029/2009GL037543, 2009.
- 20 Bucini, G. and Hanan, N. P.: A continental-scale analysis of tree cover in African
21 savannas, *Glob. Ecol. Biogeogr.*, 16(5), 593–605, doi:10.1111/j.1466-
22 8238.2007.00325.x, 2007.
- 23 Buitenwerf, R., Bond, W. J., Stevens, N. and Trollope, W. S. W.: Increased tree
24 densities in South African savannas: >50 years of data suggests CO₂ as a driver, *Glob.*
25 *Chang. Biol.*, 18(2), 675–684, doi:10.1111/j.1365-2486.2011.02561.x, 2012.
- 26 Cramer, W., Bondeau, A., Woodward, F. I., Prentice, I. C., Betts, R. a., Brovkin, V.,
27 Cox, P. M., Fisher, V., Foley, J. a., Friend, A. D., Kucharik, C., Lomas, M. R.,
28 Ramankutty, N., Sitch, S., Smith, B., White, A. and Young-Molling, C.: Global
29 response of terrestrial ecosystem structure and function to CO₂ and climate change:
30 results from six dynamic global vegetation models, *Glob. Chang. Biol.*, 7(4), 357–373,
31 doi:10.1046/j.1365-2486.2001.00383.x, 2001.
- 32 D’Onofrio, D., Baudena, M., D’Andrea, F., Rietkerk, M. and Provenzale, A.: Tree-grass
33 competition for soil water in arid and semiarid savannas: The role of rainfall
34 intermittency, *Water Resour. Res.*, n/a–n/a, doi:10.1002/2014WR015515, 2014.
- 35 Dalmonech, D. and Zaehle, S.: Towards a more objective evaluation of modelled land-
36 carbon trends using atmospheric CO₂ and satellite-based vegetation activity
37 observations, *Biogeosciences*, 10(6), 4189–4210, doi:10.5194/bg-10-4189-2013, 2013.

- 1 Donohue, R. J., Roderick, M. L., McVicar, T. R. and Farquhar, G. D.: Impact of CO₂
2 fertilization on maximum foliage cover across the globe's warm, arid environments,
3 *Geophys. Res. Lett.*, 40(12), 3031–3035, doi:10.1002/grl.50563, 2013.
- 4 Ehleringer, J. R., Cerling, T. E. and Helliker, B. R.: C₄ photosynthesis, atmospheric
5 CO₂, and climate, *Oecologia*, 112(3), 285–299, 1997.
- 6 Favier, C., Aleman, J., Bremond, L., Dubois, M. a., Freycon, V. and Yangakola, J.-M.:
7 Abrupt shifts in African savanna tree cover along a climatic gradient, *Glob. Ecol.*
8 *Biogeogr.*, 21(8), 787–797, doi:10.1111/j.1466-8238.2011.00725.x, 2012.
- 9 February, E. C. and Higgins, S. I.: The distribution of tree and grass roots in savannas in
10 relation to soil nitrogen and water, *South African J. Bot.*, 76(3), 517–523,
11 doi:10.1016/j.sajb.2010.04.001, 2010.
- 12 February, E. C., Higgins, S. I., Bond, W. J. and Swemmer, L.: Influence of competition
13 and rainfall manipulation on the growth responses of savanna trees and grasses.,
14 *Ecology*, 94(5), 1155–64, 2013.
- 15 Fisher, R., McDowell, N., Purves, D., Moorcroft, P., Sitch, S., Cox, P., Huntingford, C.,
16 Meir, P. and Ian Woodward, F.: Assessing uncertainties in a second-generation dynamic
17 vegetation model caused by ecological scale limitations., *New Phytol.*, 187, 666–681,
18 doi:10.1111/j.1469-8137.2010.03340.x, 2010.
- 19 Giorgetta, M. A., Jungclaus, J., Reick, C. H., Legutke, S., Bader, J., Boettinger, M.,
20 Brovkin, V., Crueger, T., Esch, M., Fieg, K., Glushak, K., Gayler, V., Haak, H.,
21 Hollweg, H.-D., Ilyina, T., Kinne, S., Kornblueh, L., Matei, D., Mauritsen, T.,
22 Mikolajewicz, U., Mueller, W., Notz, D., Pithan, F., Raddatz, T., Rast, S., Redler, R.,
23 Roeckner, E., Schmidt, H., Schnur, R., Segschneider, J., Six, K. D., Stockhause, M.,
24 Timmreck, C., Wegner, J., Widmann, H., Wieners, K.-H., Claussen, M., Marotzke, J.
25 and Stevens, B.: Climate and carbon cycle changes from 1850 to 2100 in MPI-ESM
26 simulations for the Coupled Model Intercomparison Project phase 5, *J. Adv. Model.*
27 *Earth Syst.*, 5(3), 572–597, doi:10.1002/jame.20038, 2013.
- 28 Govender, N., Trollope, W. S. W. and Van Wilgen, B. W.: The effect of fire season, fire
29 frequency, rainfall and management on fire intensity in savanna vegetation in South
30 Africa, *J. Appl. Ecol.*, 43(4), 748–758, doi:10.1111/j.1365-2664.2006.01184.x, 2006.
- 31 Hanan, N. P., Sea, W. B., Dangelmayr, G. and Govender, N.: Do fires in savannas
32 consume woody biomass? A comment on approaches to modeling savanna dynamics.,
33 *Am. Nat.*, 171(6), 851–6, doi:10.1086/587527, 2008.
- 34 Hanan, N. P., Tredennick, A. T., Prihodko, L., Bucini, G. and Dohn, J.: Analysis of
35 stable states in global savannas: is the CART pulling the horse?, *Glob. Ecol. Biogeogr.*,
36 23(3), 259–263, doi:10.1111/geb.12122, 2014.
- 37 Hely, C., Bremond, L., Alleaume, S., Smith, B., Sykes, M. T. and Guiot, J.: Sensitivity
38 of African biomes to changes in the precipitation regime, *Glob. Ecol. Biogeogr.*, 15(3),
39 258–270, doi:10.1111/j.1466-8238.2006.00235.x, 2006.

- 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.*
3 *Biogeogr.*, 15, 567–577, 2006.
- 4 Higgins, S. I., Bond, W. J., Combrink, H., Craine, J. M., February, E. C., Govender, N.,
5 Lannas, K., Moncreiff, G. and Trollope, W. S. W.: Which traits determine shifts in the
6 abundance of tree species in a fire-prone savanna?, edited by P. Vesk, *J. Ecol.*, 100(6),
7 1400–1410, doi:10.1111/j.1365-2745.2012.02026.x, 2012.
- 8 Higgins, S. I., Bond, W. J., February, E. C., Bronn, A., Euston-Brown, D. I. W., Enslin,
9 B., Govender, N., Rademan, L., O'Regan, S., Potgieter, A. L. F., Scheiter, S., Sowry,
10 R., Trollope, L. and Trollope, W. S. W.: Effects of four decades of fire manipulation on
11 woody vegetation structure in savanna, *Ecology*, 88(5), 1119–1125, 2007.
- 12 Higgins, S. I., Bond, W. J. and Trollope, W. S. W.: Fire, resprouting and variability: a
13 recipe for grass–tree coexistence in savanna, *J. Ecol.*, 88(2), 213–229, 2000.
- 14 Higgins, S. I., Bond, W. J., Trollope, W. S. W. and Williams, R. J.: Physically
15 motivated empirical models for the spread and intensity of grass fires, *Int. J. Wildl. Fire*,
16 17(5), 595–601, doi:10.1071/WF06037, 2008.
- 17 Higgins, S. I. and Scheiter, S.: Atmospheric CO₂ forces abrupt vegetation shifts locally,
18 but not globally., *Nature*, 488(7410), 209–12, doi:10.1038/nature11238, 2012.
- 19 Hirota, M., Holmgren, M., Van Nes, E. H. and Scheffer, M.: Global resilience of
20 tropical forest and savanna to critical transitions., *Science* (80-.), 334(6053), 232–235,
21 doi:10.1126/science.1210657, 2011.
- 22 Hoffmann, W. a, Geiger, E. L., Gotsch, S. G., Rossatto, D. R., Silva, L. C. R., Lau, O.
23 L., Haridasan, M. and Franco, A. C.: Ecological thresholds at the savanna-forest
24 boundary: how plant traits, resources and fire govern the distribution of tropical
25 biomes., *Ecol. Lett.*, 15(7), 759–68, doi:10.1111/j.1461-0248.2012.01789.x, 2012.
- 26 House, J. I., Archer, S., Breshears, D. D. and Scholes, R. J.: Conundrums in mixed
27 woody-herbaceous plant systems, *J. Biogeogr.*, 30, 1763–1777, 2003.
- 28 Hutchinson, G. E.: The paradox of the plankton, *Am. Nat.*, 95, 137–145, 1961.
- 29 Intergovernmental Panel on Climate Change: *Climate Change 2007 - The Physical*
30 *Science Basis: Working Group I Contribution to the Fourth Assessment Report of the*
31 *IPCC (Climate Change 2007)*, Cambridge University Press., 2007.
- 32 Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M.,
33 Saha, S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W.,
34 Janowiak, J., Mo, K. C., Ropelewski, C., Wang, J., Leetmaa, A., Reynolds, R., Jenne, R.
35 and Joseph, D.: The NCEP/NCAR 40-year reanalysis project, *Bull. Am. Meteorol. Soc.*,
36 77(3), 437–471, doi:10.1175/1520-0477(1996)077<0437:TNYRP>2.0.CO;2, 1996.

- 1 Kgope, B. S., Bond, W. J. and Midgley, G. F.: Growth responses of African savanna
2 trees implicate atmospheric CO₂ as a driver of past and current changes in savanna tree
3 cover, *Austral Ecol.*, 35(4), 451–463, 2010.
- 4 Koenker, R. and Park, B. J.: An interior point algorithm for nonlinear quantile
5 regression, *J. Econom.*, 71(1-2), 265–283, doi:10.1016/0304-4076(96)84507-6, 1996.
- 6 Kulmatiski, A. and Beard, K. H.: Root niche partitioning among grasses, saplings, and
7 trees measured using a tracer technique., *Oecologia*, 171(1), 25–37,
8 doi:10.1007/s00442-012-2390-0, 2013.
- 9 Van Langevelde, F., van de Vijver, C. A. D. M., Kumar, L., van de Koppel, J., de
10 Ridder, N., van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L., Bond, W. J.,
11 Prins, H. H. T. and Rietkerk, M.: Effects of fire and herbivory on the stability of
12 savanna ecosystems, *Ecology*, 84(2), 337–350, doi:10.1890/0012-
13 9658(2003)084[0337:EOFAHO]2.0.CO;2, 2003.
- 14 Lehmann, C. E. R., Anderson, T. M., Sankaran, M., Higgins, S. I., Archibald, S.,
15 Hoffmann, W. a., Hanan, N. P., Williams, R. J., Fensham, R. J., Felfili, J., Hutley, L. B.,
16 Ratnam, J., San Jose, J., Montes, R., Franklin, D., Russell-Smith, J., Ryan, C. M.,
17 Durigan, G., Hiernaux, P., Haidar, R., Bowman, D. M. J. S. and Bond, W. J.: Savanna
18 Vegetation-Fire-Climate Relationships Differ Among Continents, *Science* (80-.),
19 343(6170), 548–552, doi:10.1126/science.1247355, 2014.
- 20 Lehmann, C. E. R., Archibald, S. a, Hoffmann, W. a and Bond, W. J.: Deciphering the
21 distribution of the savanna biome., *New Phytol.*, 191(1), 197–209, doi:10.1111/j.1469-
22 8137.2011.03689.x, 2011.
- 23 Lehsten, V., Harmand, P., Palumbo, I. and Arneth, a.: Modelling burned area in Africa,
24 *Biogeosciences*, 7(10), 3199–3214, doi:10.5194/bg-7-3199-2010, 2010.
- 25 Lehsten, V., Tansey, K., Balzter, H., Thonicke, K., Spessa, a., Weber, U., Smith, B. and
26 Arneth, a.: Estimating carbon emissions from African wildfires, *Biogeosciences*, 6(3),
27 349–360, doi:10.5194/bg-6-349-2009, 2009.
- 28 Lloyd, J., Bird, M. I., Vellen, L., Miranda, A. C., Veenendaal, E. M., Djagbletey, G.,
29 Miranda, H. S., Cook, G. and Farquhar, G. D.: Contributions of woody and herbaceous
30 vegetation to tropical savanna ecosystem productivity: a quasi-global estimate., *Tree*
31 *Physiol.*, 28(3), 451–68, 2008.
- 32 Moncrieff, G. R., Scheiter, S., Bond, W. J. and Higgins, S. I.: Increasing atmospheric
33 CO₂ overrides the historical legacy of multiple stable biome states in Africa., *New*
34 *Phytol.*, 201(3), 908–15, doi:10.1111/nph.12551, 2013.
- 35 Murphy, B. P. and Bowman, D. M. J. S.: What controls the distribution of tropical
36 forest and savanna?, *Ecol. Lett.*, 15(7), 748–58, doi:10.1111/j.1461-0248.2012.01771.x,
37 2012.

- 1 Nathan, J., von Hardenberg, J. and Meron, E.: Spatial instabilities untie the exclusion-
2 principle constraint on species coexistence., *J. Theor. Biol.*, 335, 198–204,
3 doi:10.1016/j.jtbi.2013.06.026, 2013.
- 4 Van Nes, E. H., Hirota, M., Holmgren, M. and Scheffer, M.: Tipping points in tropical
5 tree cover: linking theory to data., *Glob. Chang. Biol.*, 20(3), 1016–21,
6 doi:10.1111/gcb.12398, 2014.
- 7 New, M., Lister, D., Hulme, M. and Makin, I.: A high-resolution data set of surface
8 climate over global land areas, *Clim. Res.*, 21, 1–25, 2000.
- 9 Polley, H. W., Johnson, H. B. and Mayeux, H. S.: Increasing CO₂ - comparative
10 responses of the c-4 grass *Schizachyrium* and grassland invader *Prosopis*, *Ecology*,
11 75(4), 976–988, doi:10.2307/1939421, 1994.
- 12 Le Quéré, C., Andres, R. J., Boden, T., Conway, T., Houghton, R. A., House, J. I.,
13 Marland, G., Peters, G. P., van der Werf, G. R., Ahlström, A., Andrew, R. M., Bopp, L.,
14 Canadell, J. G., Ciais, P., Doney, S. C., Enright, C., Friedlingstein, P., Huntingford, C.,
15 Jain, A. K., Jourdain, C., Kato, E., Keeling, R. F., Klein Goldewijk, K., Levis, S., Levy,
16 P., Lomas, M., Poulter, B., Raupach, M. R., Schwinger, J., Sitch, S., Stocker, B. D.,
17 Viovy, N., Zaehle, S. and Zeng, N.: The global carbon budget 1959-2011, *Earth Syst.*
18 *Sci. Data*, 5(1), 165–185, doi:10.5194/essd-5-165-2013, 2013.
- 19 Raddatz, T. J., Reick, C. H., Knorr, W., Kattge, J., Roeckner, E., Schnur, R., Schnitzler,
20 K.-G., Wetzel, P. and Jungclaus, J.: Will the tropical land biosphere dominate the
21 climate–carbon cycle feedback during the twenty-first century?, *Clim. Dyn.*, 29(6),
22 565–574, doi:10.1007/s00382-007-0247-8, 2007.
- 23 Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. a., Archibald, S., Lehmann, C.
24 E. R., Anderson, M. T., Higgins, S. I. and Sankaran, M.: When is a “forest” a savanna,
25 and why does it matter?, *Glob. Ecol. Biogeogr.*, 20(5), 653–660, doi:10.1111/j.1466-
26 8238.2010.00634.x, 2011.
- 27 Reick, C. H., Raddatz, T., Brovkin, V. and Gayler, V.: Representation of natural and
28 anthropogenic land cover change in MPI-ESM, *J. Adv. Model. Earth Syst.*, 5(3), 1942–
29 2466, doi:10.1002/jame.20022, 2013.
- 30 Rietkerk, M., Brovkin, V., van Bodegom, P. M., Claussen, M., Dekker, S. C., Dijkstra,
31 H. a., Goryachkin, S. V., Kabat, P., van Nes, E. H., Neutel, A.-M., Nicholson, S. E.,
32 Nobre, C., Petoukhov, V., Provenzale, A., Scheffer, M. and Seneviratne, S. I.: Local
33 ecosystem feedbacks and critical transitions in the climate, *Ecol. Complex.*, 8(3), 223–
34 228, doi:10.1016/j.ecocom.2011.03.001, 2011.
- 35 Rietkerk, M., Dekker, S. C., de Ruiter, P. C. and van de Koppel, J.: Self-Organized
36 Patchiness and Catastrophic Shifts in Ecosystems, *Science*, 305, 1926–1929, 2004.
- 37 Rossatto, D. R., Hoffmann, W. A. and Franco, A. C.: Differences in growth patterns
38 between co-occurring forest and savanna trees affect the forest-savanna boundary,
39 *Funct. Ecol.*, 23(4), 689–698, doi:10.1111/j.1365-2435.2009.01568.x, 2009.

- 1 Saarnak, C. F.: A shift from natural to human-driven fire regime: implications for trace-
2 gas emissions, *Holocene*, 11, 373–375, 2001.
- 3 Salazar, A., Goldstein, G., Franco, A. C. and Miralles-wilhelm, F.: Differential seedling
4 establishment of woody plants along a tree density gradient in Neotropical savannas, *J.*
5 *Ecol.*, 100, 1411–1421, doi:10.1111/j.1365-2745.2012.02028.x, 2012.
- 6 Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S.,
7 Gignoux, J., Higgins, S. I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A.,
8 Bucini, G., Caylor, K. K., Coughenour, M. B., Diouf, A., Ekaya, W., Feral, C. J.,
9 February, E. C., Frost, P. G. H., Hiernaux, P., Hrabar, H., Metzger, K. L., Prins, H. H.
10 T., Ringrose, S., Sea, W., Tews, J., Worden, J. and Zambatis, N.: Determinants of
11 woody cover in African savannas, *Nature*, 438(7069), 846–849,
12 doi:10.1038/nature04070, 2005.
- 13 Sankaran, M., Ratnam, J. and Hanan, N.: Woody cover in African savannas: the role of
14 resources, fire and herbivory, *Glob. Ecol. Biogeogr.*, 17(2), 236–245,
15 doi:10.1111/j.1466-8238.2007.00360.x, 2008.
- 16 Sankaran, M., Ratnam, J. and Hanan, N. P.: Tree-grass coexistence in savannas
17 revisited - insights from an examination of assumptions and mechanisms invoked in
18 existing models, *Ecol. Lett.*, 7(6), 480–490, doi:10.1111/j.1461-0248.2004.00596.x,
19 2004.
- 20 Sarmiento, G.: *The Ecology of Neotropical Savannas*, Harvard Univ. Press, Cambridge,
21 Mass., 1984.
- 22 Sato, H., Itoh, A. and Kohyama, T.: SEIB–DGVM: A new Dynamic Global Vegetation
23 Model using a spatially explicit individual-based approach, *Ecol. Modell.*, 200(3-4),
24 279–307, doi:10.1016/j.ecolmodel.2006.09.006, 2007.
- 25 Scheiter, S. and Higgins, S. I.: Impacts of climate change on the vegetation of Africa: an
26 adaptive dynamic vegetation modelling approach, *Glob. Chang. Biol.*, 15(9), 2224–
27 2246, doi:10.1111/j.1365-2486.2008.01838.x, 2009.
- 28 Scheiter, S. and Higgins, S. I.: How many elephants can you fit into a conservation area,
29 *Conserv. Lett.*, 5(3), 176–185, doi:10.1111/j.1755-263X.2012.00225.x, 2012.
- 30 Scheiter, S., Higgins, S. I., Osborne, C. P., Bradshaw, C., Lunt, D., Ripley, B. S.,
31 Taylor, L. L. and Beerling, D. J.: Fire and fire-adapted vegetation promoted C4
32 expansion in the late Miocene., *New Phytol.*, 195(3), 653–66, doi:10.1111/j.1469-
33 8137.2012.04202.x, 2012.
- 34 Scheiter, S., Langan, L. and Higgins, S. I.: Next-generation dynamic global vegetation
35 models : learning from community ecology, *New Phytol.*, 198, 957–969,
36 doi:10.1111/nph.12210, 2013.
- 37 Scholes, R. J.: Convex Relationships in Ecosystems Containing Mixtures of Trees and
38 Grass, *Environ. Resour. Econ.*, 26, 559–574, 2003.

- 1 Scholes, R. J. and Archer, S. R.: Tree-grass interactions in savannas, *Annu. Rev. Ecol.*
2 *Syst.*, 28, 517–544, 1997.
- 3 Scholes, R. J. and Walker, B. H.: *An African Savanna: Synthesis of the Nylsvley Study*,
4 edited by Cambridge, Cambridge University Press, Cambridge, UK., 1993.
- 5 Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., Betts, R.,
6 Ciais, P., Cox, P., Friedlingstein, P., Jones, C. D., Prentice, I. C. and Woodward, F. I.:
7 Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon
8 cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs), *Glob.*
9 *Chang. Biol.*, 14(9), 2015–2039, doi:10.1111/j.1365-2486.2008.01626.x, 2008.
- 10 Sitch, S., Smith, B. and Prentice, I.: Evaluation of ecosystem dynamics, plant geography
11 and terrestrial carbon cycling in the LPJ dynamic global vegetation model, *Glob.*
12 *Chang.*, 9, 161–185, 2003.
- 13 Smith, B., Prentice, I. and Sykes, M.: Representation of vegetation dynamics in the
14 modelling of terrestrial ecosystems: comparing two contrasting approaches within
15 European climate space, *Glob. Ecol.*, 10, 621– 637, 2001.
- 16 Snyder, P. K., Delire, C. and Foley, J. a.: Evaluating the influence of different
17 vegetation biomes on the global climate, *Clim. Dyn.*, 23(3-4), 279–302,
18 doi:10.1007/s00382-004-0430-0, 2004.
- 19 Staver, A. C., Archibald, S. and Levin, S. A.: The global extent and determinants of
20 savanna and forest as alternative biome states., *Science (80-)*, 334(6053), 230–232,
21 doi:10.1126/science.1210465, 2011.
- 22 Staver, A. C., Bond, W. J., Cramer, M. D. and Wakeling, J. L.: Top-down determinants
23 of niche structure and adaptation among African Acacias., *Ecol. Lett.*, 15(7), 673–9,
24 doi:10.1111/j.1461-0248.2012.01784.x, 2012.
- 25 Staver, A. C. and Levin, S. A.: Integrating theoretical climate and fire effects on
26 savanna and forest systems., *Am. Nat.*, 180(2), 211–24, doi:10.1086/666648, 2012.
- 27 Thonicke, K., Spessa, A., Prentice, I., Harrison, S., Dong, L. and Carmona-Moreno, C.:
28 The influence of vegetation, fire spread and fire behaviour on biomass burning and trace
29 gas emissions: results from a process-based model, *Biogeosciences*, 7, 1991–2011,
30 2010.
- 31 Tilman, D.: *Resource competition and community structure*, Princeton University Press,
32 Princeton, New Jersey, USA., 1982.
- 33 Trollope, W. S. W.: Fire in savannas, in *Ecological effects of fire of southern African*
34 *ecosystems*, edited by P. D. V Booyesen and N. M. Tainton, pp. 199–218, Springer-
35 Verlag, Berlin, Germany., 1984.
- 36 Wakeling, J. L., Staver, a. C. and Bond, W. J.: Simply the best: the transition of savanna
37 saplings to trees, *Oikos*, 120(May), 1448–1451, doi:10.1111/j.1600-0706.2011.19957.x,
38 2011.

- 1 Walker, B. H. and Noy-Meir, I.: Aspects of stability and resilience of savanna
2 ecosystems, in *Tropical savannas*, edited by B. J. Huntley and B. H. Walker, pp. 556–
3 590, Springer-Verlag, Berlin., 1982.
- 4 Walter, H.: *Natural Savannas*, in *Ecology of Tropical and Subtropical Vegetation*,
5 Oliver and Boyd, Edinburgh, UK., 1971.
- 6 Ward, D.: *The Biology of Deserts*, Oxford University Press, Oxford, UK., 2009.
- 7 Ward, D., Wiegand, K. and Getzin, S.: Walter’s two-layer hypothesis revisited: back to
8 the roots!, *Oecologia*, 172(3), 617–30, doi:10.1007/s00442-012-2538-y, 2013.
- 9 Weber, U., Jung, M., Reichstein, M., Beer, C., Braakhekke, M. C., Lehsten, V., Ghent,
10 D., Kaduk, J. and Viovy, N.: The interannual variability of Africa ’ s ecosystem
11 productivity : a multi-model analysis, *Biogeosciences*, 6, 285–295, 2009.
- 12 Wigley, B. J., Bond, W. J. and Hoffman, M. T.: Thicket expansion in a South African
13 savanna under divergent land use: local vs. global drivers?, *Glob. Chang. Biol.*, 16(3),
14 964–976, doi:10.1111/j.1365-2486.2009.02030.x, 2010.
- 15 Yin, Z., Dekker, S. C., van den Hurk, B. J. J. M. and Dijkstra, H. A.: Bimodality of
16 woody cover and biomass in semi-arid regime, *Earth Syst. Dyn. Discuss.*, 5(1), 83–120,
17 doi:10.5194/esdd-5-83-2014, 2014a.
- 18 Yin, Z., Dekker, S. C., van den Hurk, B. and Dijkstra, H.: Effects of vegetation structure
19 on biomass accumulation in a Balanced Optimality Structure Vegetation Model
20 (BOSVM v1.0), *Geosci. Model Dev.*, 7, 821–845, 2014b.
- 21

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

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

1 **Figure captions**

2 Figure 1

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

11

12 Figure 2

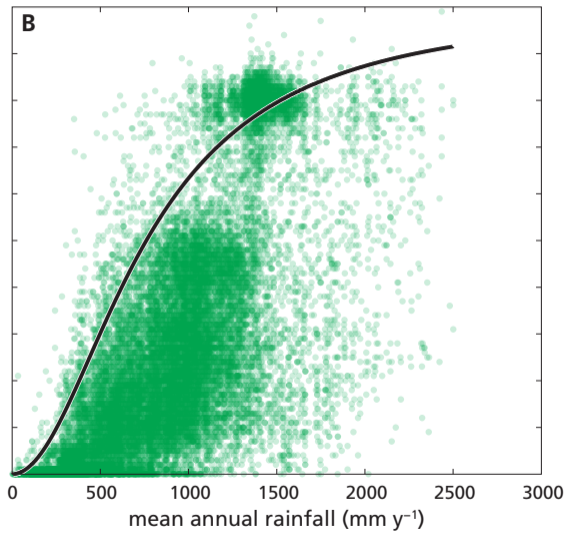
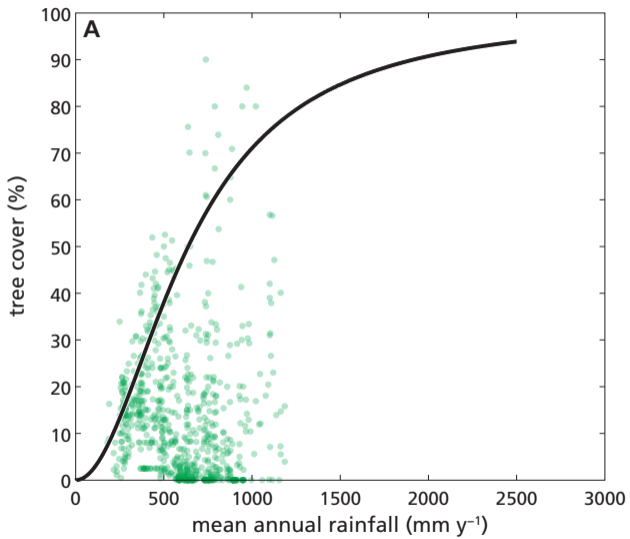
13 Model outputs for tree cover as a function of mean annual rainfall (mm y^{-1}) in Africa
14 between 35° S and 15° N: A) JSBACH; B) LPJ-GUESS-SPITFIRE; C) aDGVM. The dots are
15 data, the continuous lines are the 90th quantile nonlinear regression (99th quantile not shown;
16 see value of *b* coefficients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

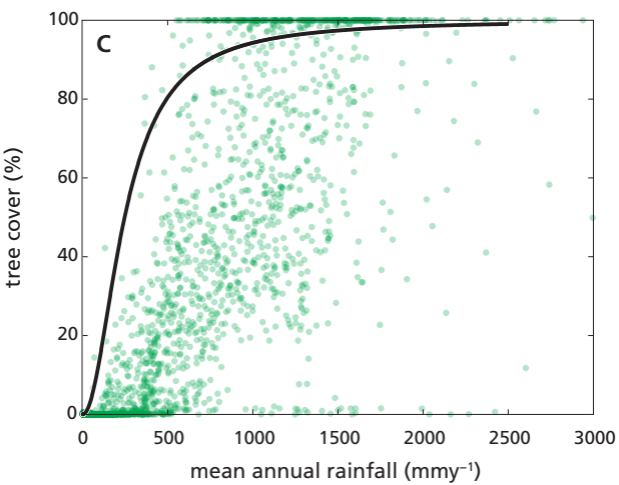
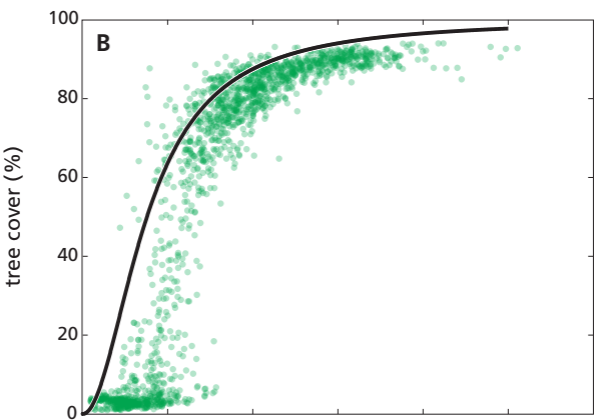
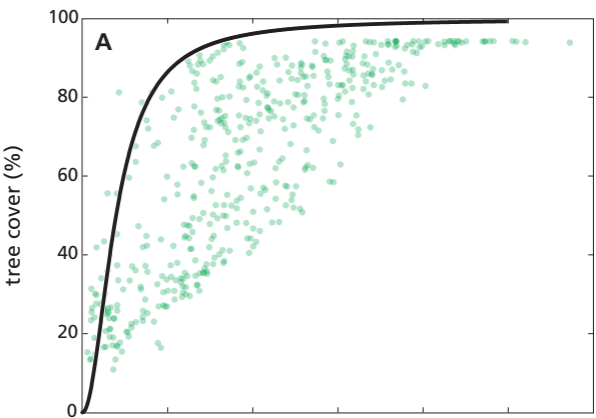
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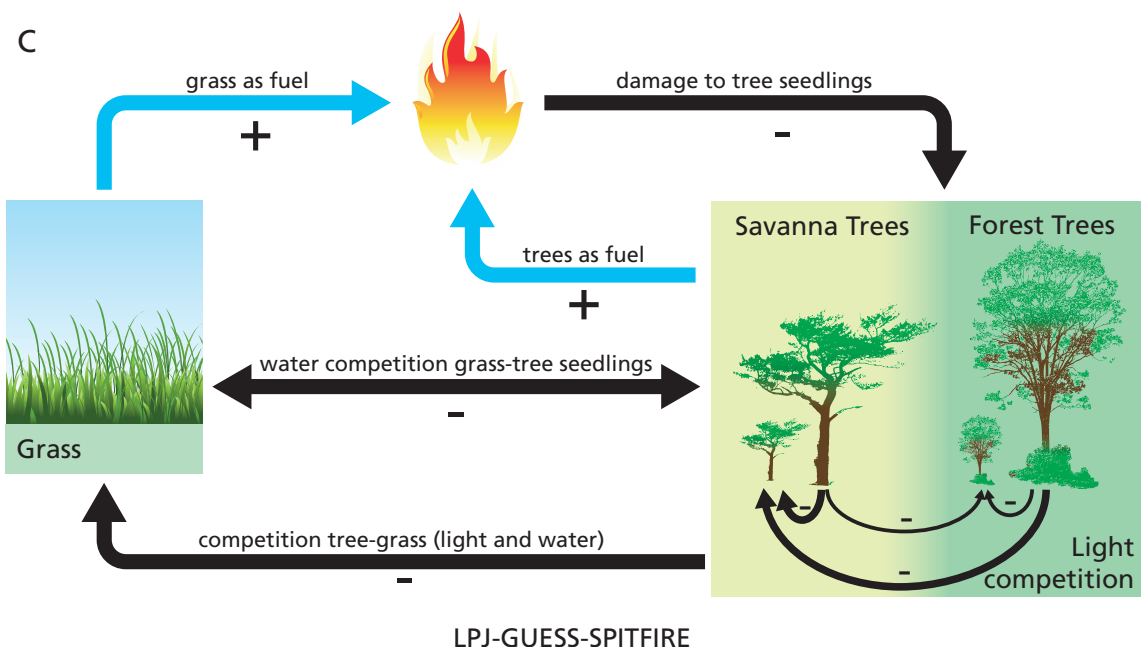
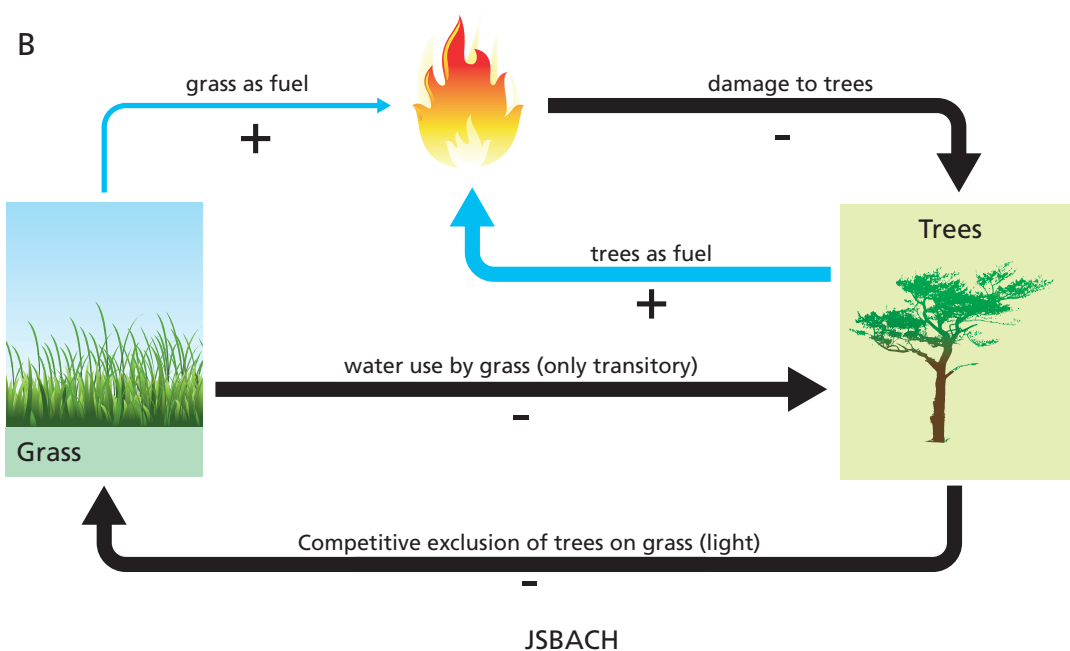
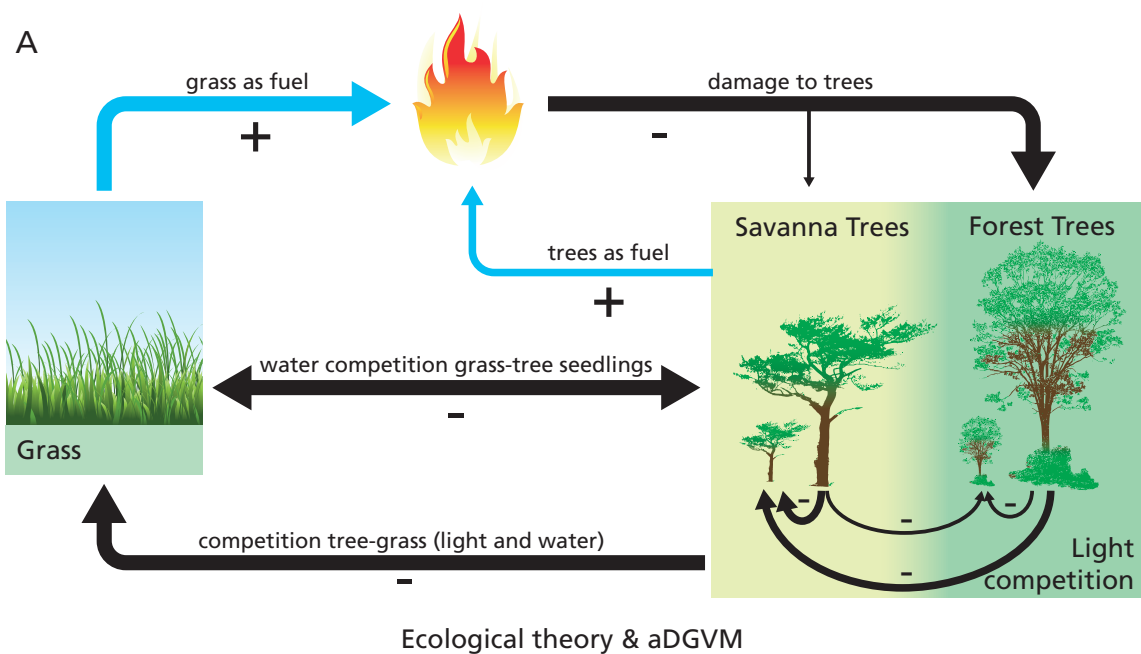
18 Figure 3

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

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







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 (Grün 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 (Grün 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 $1.9 \times 1.9^\circ$ 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).

Range (mm y ⁻¹)	ICL				AIC				Comments on differences between ICL and AIC
	1	2	3	4	1	2	3	4	
800-1200	-88	-74	-16	42	-94	-105	-100	-94	Unimodal (small separation between the peaks)
400-800	-24	-34	-4	46	-30	-60	-68	-63	(%) The two peaks are not well separated, the fit with three (four) Gaussians captures extra peak(s) in between the other two
500-1000	-55	-60	-35	-22	-61	-94	-101	-105	(%)
400-900	-33	-41	5	72	-39	-71	-75	-69	(%)

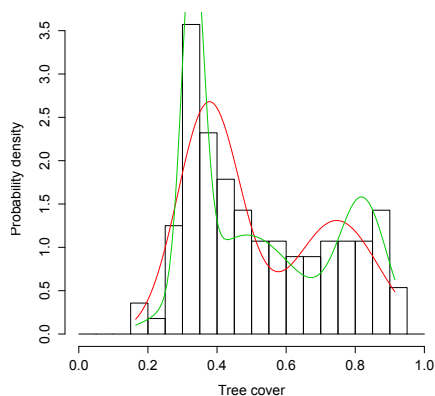


Fig. A1 Probability density distribution of tree cover for the JSBACH output, for mean annual precipitation between 400 and 800 mm y⁻¹ mean annual rainfall. Red line represents bimodal distribution (i.e. it is fitted significantly better by a superposition of two normal distributions, according to ICL), 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).

Range (mm y ⁻¹)	ICL				AIC				Comments on differences
	1	2	3	4	1	2	3	4	
500-1000	77	-535	-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
800-1200	-1350	-1204	-1196		-1359	-1404	-1424		(\$) Unimodal (coincident peaks)
400-1200	236	-657	-757	-697	226	-717	-929	-1027	As (*)
1000-1200	-756	-630			-763	-772			As (\$)
400-700	97	-91	-136	-119	90	-129	-210	-235	Three peaks (fourth peak coincides)
800-1000	-702	-602	-580	-585	-709	-718	-726		As (\$)
600-800	-62	-234	-234		-69	-254	-283		As (*)

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.

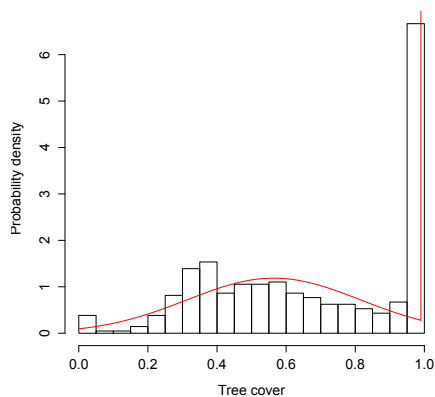


Fig. A2 Probability density distribution of tree cover for the aDGVM output, for mean annual precipitation between 800 and 1200 mm y⁻¹ mean annual rainfall. The distribution is bimodal between savanna and forest (i.e. it is fitted significantly better by a superposition of two normal distributions).

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).

Range (mm y ⁻¹)	ICL				AIC				Comments on differences between ICL and AIC
	1	2	3	4	1	2	3	4	
1000-1200	78	-1412	-1275		71	-1429	-1423		-
800-1200	157	-2634	-2330	-2469	149	-2654	-2648	-2715	(Δ) Four peaks are not well separated (coincide with 2)
800-1000	83	-1213	-1168	-1172	77	-1230	-1244	-1251	As (Δ)
700-1400	343	-4185			334	-4207			-
500-1500	616	-4906			606	-4931			-
1000-1300	139	-2102	-1878		131	-2121	-2115		-
500-800	137	-540	-504		129	-559	-594		As (Δ)

References

- Akaike, H.: A New Look at the Statistical Model Identification, *IEEE Trans. Automat. Contr.*, 19, 716–723, 1974.
- Grün, B. and Leisch, F.: Fitting finite mixtures of generalized linear regressions in R, *Comput. Stat. Data Anal.*, 51(11), 5247–5252, doi:10.1016/j.csda.2006.08.014, 2007.
- Hirota, M., Holmgren, M., Van Nes, E. H. and Scheffer, M.: Global resilience of tropical forest and savanna to critical transitions., *Science (80-.)*, 334(6053), 232–235, doi:10.1126/science.1210657, 2011.
- Yin, Z., Dekker, S. C., van den Hurk, B. J. J. M. and Dijkstra, H. a.: Bimodality of woody cover and biomass across the precipitation gradient in West Africa, *Earth Syst. Dyn.*, 5(2), 257–270, doi:10.5194/esd-5-257-2014, 2014.

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.

Data series	Figure panel	b, 90th quantile [mm² y⁻²]	b, 99th quantile [mm² y⁻²]
Field observation	Fig. 1A	5.8E+05	3.0E+05
MODIS observation	Fig. 1B	4.1E+05	1.9E+05
JSBACH/DYNVEG	Fig. 2A	1.4E+05	6.1E+04
LPJ-GUESS-SPITFIRE	Fig. 2B	6.1E+04	4.4E+03
aDGVM	Fig. 2C	3.9E+04	5.4E+03