Comments from Reviewers and Authors' response: Climate change will cause non-analogue vegetation states in Africa and commit vegetation to long-term change

Mirjam Pfeiffer¹, Dushyant Kumar¹, Carola Martens^{1,2}, and Simon Scheiter¹

¹Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60438 Frankfurt am Main, Germany
²Institute of Physical Geography, Goethe University Frankfurt am Main, Altenhoeferallee 1, 60438 Frankfurt am Main, Germany

Correspondence: Mirjam Pfeiffer (mirjam.pfeiffer@senckenberg.de)

1 Author responses to comments of anonymous referee #1

Responses are highlighted in bold font.

Thank you for inviting me to review paper: "Climate change will cause non-analogue vegetation states in Africa and commit vegetation to long-term change" by Pfeiffer et al.

5 Thank you for taking the time and making the effort to read and evaluate our manuscript.

The central premise of the Abstract is that transients in the vegetation response imply that the land surface does not merely behave as a set of time-evolving equilibrium states as the background climate changes. Instead, inertia implies alternative vegetation features might exist and that are only possible in a transient situation. Maybe not surprisingly, these are most no-

- 10 table under RCP8.5 ("business-as-usual" situation). Maybe be even more explicit why the expression "non-analogue" is used throughout. This suggestion is because often "analogue" can refer to simply anything that is different to states that have only been observed, (either in the recent past or possibly paleo-records). Here "non-analogue" implies non-pseudo equilibrium – so states that are not equilibrium either past, contemporary or projected under climate change. Possibly an alternative term could be something like "novel transient".
- 15 Thank you for pointing out the difficulties of the term "non-analogue". We are aware that "non-analogue" is often used in the context of comparison between palaeo-vegetation states and present or future vegetation states that have not been found in this form in the past. However, what we refer to is the comparison between (hypothetical) pseudoequilibrium states and the composite transient vegetation states that cannot be represented by any of the pseudoequilibrium states. We found it difficult to find a term that would describe this discrepancy in an appropriate way and
- 20 therefore decided to use the term "non-analogue". Following your suggestion, we have added a more concrete definition of how we define "non-analogue" in the context of the study (i.e., in the sense of not having an equivalent equilibrium state) in the introduction section to make it as clear as possible what we mean (p.3 lines 1-4 and p.3 lines 16-18).

The second line in the Abstract "This implies that vegetation is committed to future changes once environmental drivers

25 stabilise" is important, and it might be good to re-iterate that towards the end. Something in general language might be useful e.g. "conservation managers.should be aware that observed vegetation may continue to change substantially, even if climate drivers are held fixed".

We followed your suggestion and have added a corresponding sentence at the end of the abstract to highlight the implications for conservation management (p.1 lines 49-52).

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The Introduction is good, and it recognises that the way vegetation sees differences between equilibrium and transient responses. The Introduction makes it clear that equilibrium-transient differences can be in both the multiple elements of the climatological drivers, and in the lags of the land surface itself (affecting its structure and composition). I also like that the aims of the paper are made very clear with the bullet points 1,2,3 at the end of the Introduction.

Thank you, we are glad that the introduction convincingly transferred the message to you that we wanted to convey.

However, like many readers, I also looked at the conclusions before reading the main bulk of the paper. Notable is that the conclusions state: "...shift towards alternative stable states". So in other words, the transient time-history of vegetation evolution may impact on different final equilibrium states, even for the same equilibrium forcings. The vegetation of Africa has always been speculated as capable of that (i.e. "multi-stable vegetation coverage"; there are many references to this). It feels as if this should be listed as an extra point 4 in the Introduction, given it is discussed in this manuscript.

We now briefly discuss the possibility that shifts towards alternative stable states may be affecting African ecosystems as a consequence of climate change in the introduction, as you suggest, and have included additional references to studies that focused on this topic (p.2 lines 41-47). We know that multi-stability of ecosystem states, in particular in connection with Africa's savanna ecosystems, has been studied and proposed previously by a variety of authors (e.g., Staal et al., 2016; Li et al., 2019; Pausas & Bond, 2020). Therefore, we decided to not focus on this topic again in our study. As we are not specifically investigating mulistable states in this study, it is not a direct aim/working hypothesis and we therefore did not put it with the bullet points at the end of the introduction, but have kept it within the more general part of the introduction.

It is interesting that the effects of fire can have such a substantial impact on the magnitude of lags behind any equilibrium state. Does the paper hint at targeted fire reductions i.e. by deliberate human intervention could be useful in some circumstances?

55 We are not considering fire management effects in this study, but have done so in previous studies with aDGVM. In Scheiter et al. (2015), we showed how different fire return intervals and early vs. late dry season management fires influence biomass and other state variables. In Scheiter & Savadogo (2016) we showed that management can slow down or accelerate tipping point behavior and hence the magnitude of lags. The effect of fire on vegetation state is ecosystemspecific and strongly depends on the management goals. Without fire, the majority of open and semi-open ecosystems

in Africa are simulated to display higher woody cover and biomass. Targeted fire reduction therefore could help to 60 increase the size of the African carbon sink. This would, however, come at the cost of losing unique ecosystem types and their associated biodiversity and ecosystem functions. In particular grasslands and savanna ecosystems are threatened by targeted fire reductions as fire plays a pivotal role in the dynamics of these ecosystem types. We have added a brief discussion highlighting these conflicting fire management targets (trade-off between carbon storage vs. ecosystem con-

65 servation) in section 4.1 of the discussion (p.15 lines 14-32).

The most interesting summary diagram in my view is Figure 5. It very cleverly shows an overall lag of vegetation from equilibrium in the left-hand panel, while the right-hand panel calculates a residual term which captures the "non-analogue" distance from any past equilibrium solution. As these days, people often extract diagrams and captions from papers to put in to powerpoint talks, would it help to expand slightly the caption to this diagram.

Thank you for the comment. We now provide a more detailed figure caption in the revised version of the manuscript in order to make the figure self-explanatory without having to rely on the manuscript's main text (see Fig. 5 and its new caption on page 10 of the mark-up version of the revised manuscript).

- I also have a small request concerning Figure 5. The units of the left-hand panel are intuitive, as time lags (decades). The 75 right-hand panel is Euclidean distance, based around the nine state variables (p9) contributing to Equation (1) (p10). I cannot think of an answer to this, but it would be good if there was some sort of physical or biological units/quantities associated with the right-hand panel of Figure 5. OK, maybe readers need to then look at Figure 7, which shows which biome is most different when compared to the nearest equilibrium decade. Hence write the manuscript to encourage the reader to view figure 5 and
- 80 Figure 7 simultaneously?

We are well aware that Euclidean distance is a general measure that integrates over a variety of possible causes. Based on the distance alone, it is indeed not possible to discern the major cause that underlies the difference. In addition, due to the normalization of variables used to derive the Euclidean distance, the distance itself becomes unit-less, i.e., abstract. Therefore, your idea to more explicitly point out the connection between Euclidean distance in Fig. 5b and

Fig. 7 that shows the fractions of variables that dominate the Euclidean distance at a given time is quite helpful to make 85 the integrated distance shown in Fig. 5b more tangible for the reader. We have added a sentence to results section 3.5 (p.10 lines 4-13) and to the caption of Fig. 5 (see Fig. 5 and its new caption on page 10 of the mark-up version of the revised manuscript) to encourage readers to view both figures conjointly in order to compare the average size of the distance at a given time with the respective fractional variable contributions.

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It would be good to see an expanded version of "Opportunities and limitations of this study". First, if I have understood the paper correctly, then only one overall forcing Earth System Model (ESM) is used - as then disaggregated by CCAM. That model is the MPI-ESM ESM. The author should state where this model sits in terms of its equilibrium climate sensitivity (ECS). Is it a fast or slow warming model – or ideally towards the middle of any distribution? The ECS numbers are available

95 in the 5th IPCC report. I realise this is technically challenging, given the need to disaggregate via CCAM, but future work could include more ESMs and from both the CMIP5 and CMIP6 ensemble.

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Thank you for pointing this limitation out. We have added it to the limitations discussion section (p.17 lines 195-109, p.18 lines 1-10), where we now discuss the climatology of MPI-ESM in comparison to the climatology simulated by other ESMs, and we provide additional information on the sensitivity of aDGVM simulation results to the used climatology in comparison to the sensitivity to other factors (RCP scenario, CO₂ forcing).

A second point for the "limitations" section is it feels to me as if there needs to be much more confidence in the fire model. In particular, the Methods section states "ignitions are based on a random sequence". That randomness might have to change in time, if for instance, it includes lightning strikes, the frequency of which are likely to vary under global warming. It is noted that every diagram in the paper has both with fire and without fire findings presented equally. Future analysis, with a

well-established and tested fire model, should give emphasis to the simulations with fire, as they are the more process-complete simulations.

We agree that fire is a complex disturbance regime that depends on many influencing factors and is associated with various uncertainties. For Africa, it is estimated that the majority of ecosystems are currently not ignition-limited, i.e.,

- 110 ignition rates are more than sufficient to burn the available fuel, so climate and landscape connectivity combined with human fire management strategies are the main limiting factors on fire occurrence (Archibald et al., 2012, and references therein). Although the current implementation of fire in aDGVM does not account for explicit ignitions, it has heuristically been calibrated such that the ignition rates and resulting fires agree well with observed fire patterns and fire frequency (Scheiter and Higgins 2009). Therefore, the calibrated ignitions in aDGVM at least for Africa should
- 115 not be limiting, even if currently not modeled explicitly. This implies that the simulated amount of fire is driven by the other two components of the fire triangle, i.e., fuel load and quality, and fire weather conditions (i.e., fuel moisture). As fire intensity and spread in aDGVM are linked to fuel moisture, fuel biomass, and tree cover (increasing tree cover reduces fire spread), fire regimes thereby change in response to climate change and vegetation change. Based on past personal experience from developing a more complex process-based fire model (Pfeiffer et al., 2013), I can say that such
- 120 a detailed representation of fire-related processes not necessarily improves the accuracy of fire representation due the increasing number of parameters that need to be estimated and defined, which increases uncertainty. We have added a paragraph in the discussion where we elaborate on the points mentioned here (p.17 lines 70-94).

A third point for the "limitations" section is that all the analysis presented is offline. The authors might like to speculate whether they think more multiple-stable states exist if the vegetation is coupled to an atmospheric model, thus allowing for feedbacks. There is a very long literature on this, some of which might be good to cite here. See for instance, Zeng et al. "Multiple equilibrium states and the abrupt transitions in a dynamical system of soil water interacting with vegetation" and the many references in that paper.

It is hard to speculate how an online coupling between aDGVM and an ESM would influence simulated vegeta-

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- tion dynamics due to the non-linearity of feedback mechanisms and the spatially differentiated nature of such effects that will vary between different types of ecosystems. We can therefore only provide rather speculative answers to that question. The work of Zeng et al. (2004) suggests that multiple equilibrium states are possible in semi-arid areas, with grasslands vs. desert being alternative stable states. They also suggest that the range of parameter space over which these equilibria can coexist may be increased by positive feedbacks of evapotranspiration on precipitation (e.g., Wang 135 and Eltahir, 2000). Zhu & Zeng (2014) evaluated the difference between offline and online simulations, but vegetation in their simulations was prescribed and therefore could not respond to climate change. In line with Zhu and Zeng (2014), we would expect that in particular albedo effects, canopy transpiration and evaporation, and temperature effects mitigated by vegetation could alter local to regional climate, in turn feeding back on vegetation dynamics. Where
- 140 and non-linear tipping behavior between different vegetation states could be even more pronounced, because stability is likely enhanced by feedback mechanisms that foster such stability. For example, tropical forests that transfer large quantities of water vapor to the atmosphere via transpiration locally create clouds and precipitation that sustain the existence of such forests even if regional-scale precipitation patterns without such feedbacks showed decreasing trends (see, e.g., Staal et al., 2018). In that sense, such forests foster climatic conditions that sustain their existence. However,

such two-way feedback mechanisms between vegetation and climate exist, we would expect that lag times, bi-stability

- 145 even fully coupled ESMs may be unable to consistently predict how future feedbacks between vegetation and climate will shape terrestrial vegetation state, as shown by Bathiany et al. (2014) in the context of future Sahel greening trends simulated by three different ESMs with dynamic vegetation. We have added a paragraph on this topic to the "limitations" discussion section (p.18 lines 11-34).
- Broadly I like this paper and I think with some minor adjustments, it is suitable for publication. I am very happy to see 150 any revised manuscript version.

Thank you.

Small additional things

The Abstract feels a bit too technical in places e.g. use of word "Euclidean". 155

We have rephrased the sentence with the first occurrence of the term "Euclidean distance" to make it more clear that this is used as a measure of dissimilarity between vegetation states. i.e., the sentence "Euclidean distance between simulated transient and equilibrium vegetation states based on selected variables was used to determine lag times and similarity of vegetation states" has be rephrased as follows (p.1 lines 22-27): "We determined lag times and dissimilarity

160 between simulated and transient vegetation states based on the combined difference of 9 selected state variables using Euclidean distance as a measure for that difference." We have further replaced the term "Euclidean distance" with

"dissimilarity" in lines 39/40 and 47/48.

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review changes.

Figure 1 (and maybe similar elsewhere). The fonts of the labels and the legends appear very small. One possibility to make more space – at least in the vertical direction – could be to only mark the "x"-axis labels under panels g,h,i.

Thank you for pointing this out. We have altered this figure (p.6) and increased font sizes as much as possible to ensure that labels and legends are more easily legible. The same has been done for all other figures (including supplementary figures) where we now pay attention to have font sizes comparable to the ones used in the main text or the figure captions of the manuscript. To ensure comparability of font sizes and to give an idea of how figures will look like when published, we have used the final journal layout style in the revised manuscript version with the mark-up of the

Figure 3 – the colourbar levels look slightly odd. It feels to me as if they would be neater if simply 0.0, 1.0, 2.0, 3.0, ...

175 We have re-made the figures in the main text and the supplementary material with colorbars that have even breaks.

Please check through again in general the diagrams. For instance, I realise it is obvious, but the convention in Figure 4 would be "biomes types are as annotated in panel a. The colours used are common between all four panels".

Thank you for pointing this out, we have changed the figure captions according to your suggestion (p.9, p.12.)

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Figure 8, with the small font used in the map annotations, it took me some time to realise that the "t" and "e" mentioned in the caption to Figure 8 was added to the end of those annotations. Hence e.g. "RCP8_5e". Please improve the presentation of this diagram, along with the caption and the annotations.

We have increased the font size of the legend as far as possible and highlight the caption of the legend in bold to make it easier to read. Additionally, we have changed the figure caption to point out which of the panels are representing transient and which ones are representing equilibrium scenarios. The layout of the figure has been altered to maximize panel size in addition to increasing font sizes (p.13).

190 2 Author responses to comments of anonymous referee #2

Responses are highlighted in bold font.

The authors present a theoretical study on possible vegetation changes in Africa for two scenarios of global warming and climate change. They use the sophisticated and well documented aDGVM, a dynamic (but not global) vegetation model that has been developed specifically for grass-tree interaction in tropical ecosystems. The authors convincingly demonstrate that in a global warming scenario, the vegetation composition in Africa will likely change and increasingly deviate from its equilibrium composition, i.e., its composition that is attained, if vegetation would instantaneously follow the changing climate. In this sense, the transient future vegetation state in Africa is supposed to move into 'non-analogue states'. In conclusion, this is

a well written, interesting study. The method is clearly outlined. The results are thoroughly and convincingly discussed. The topic is highly relevant. I am happy to recommend its publication in Biogeosciences in its present form subject to a few small, editorial changes.

Thank you for taking the time and making the effort to read and evaluate our manuscript. We are happy that you found it interesting and worthwhile for publication in Biogeosciences.

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Minor items: Line 234: Fire 'consistently' enlarges. . . ok, but what about statistical significance? I assume the scatter is just too large to talk about statistical significance. This is more a comment, which the authors might consider, not a critical remark. We intentionally wrote "consistently" instead of "significantly" because we did not test for statistical significance

- 210 when aggregating data for Figure 2. The scatter is indeed very large, as indicated by the plotted standard deviations of the spatial means in Fig. 2. This wide scatter is a consequence of the distinct spatial patterning of Euclidean distance emerging over time that can be seen in Fig. 3 and Fig. S2. It is likely that the difference in Euclidean distance between fire and no-fire scenarios is significant for specific regions where fire strongly drives vegetation dynamics, and this then reflects in the consistent difference of the continental-scale mean, which in itself may not be significant. Based on your
- 215 suggestion, we have conducted t-tests and Kolmogorov-Smirnov tests to test the statistical significance of the differences in means between fire and no-fire scenarios. According to these tests, all means were significantly different with p<0.001. We now mention this on p.7 lines 23-25.

Lines 249 to 252: I had to read these sentences at least twice to fully understand their content. Which variables refer to 220 which percentage? Perhaps a slight re-arrangement of the sentence starting with 28% will cure the problem. It slightly enhances understanding, if the authors more specifically refer to Fig. S3a, instead of Fig. S3 (and if the 'Fig. S3a' were put in closed brackets).

Thank you for pointing out your difficulties with these sentences, as well as the formatting issue with the brackets. We have rephrased these sentences to communicate our point more clearly (p.7 lines 54-73).

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Line 363: What are these unpublished studies by the co-authors (Kumar and Martens)? Grey literature, PhD theses, to be submitted, or just personal communication?

The study of Kumar et al. is meanwhile published as a discussion article (Kumar, D., Pfeiffer, M., Gaillard, C., Langan, L., and Scheiter, S.: Climate change and elevated CO2 favor forest over savanna under different future scenarios

230 in South Asia, Biogeosciences Discuss., https://doi.org/10.5194/bg-2020-169, in review, 2020.), and the study of Martens et al. has been accepted for publication in Global Change Biology. We have updated the references accordingly (p.4 lines78/79, p.14 lines 33-35, p.17 line 103, p.20 lines 88-92 and lines 67-70).

Figures: The figure captions should be self-explaining as much as possible. Therefore, please, explain the acronyms (SDP in Fig. 2, 3, 4 and CDP in Fig. 5, 6, 7 and the figures in the Supplement)

We have updated all figure captions according to your suggestion to make them self-explanatory.

3 Author responses to comments of anonymous referee #3

240 Responses are highlighted in bold font.

This study compared the simulated transit and equilibrium vegetation states in Africa from 1970 to 2099 under the RCP4.5 and 8.5 scenarios with and without fire. It aims to investigate the time lags of the climate-vegetation system between transit and equilibrium simulations. I think this study is valuable to understand the possible future tipping points of the climate-vegetation

system. I support the publication of this paper after the following comments being addressed properly.

Line 133-135. As for the forcing data, I may support using the original climate forcing even it may produce the saw-tooth pattern. Because the atmospheric internal variabilities could be changed after the randomization. Is the yearly climate forcing given every 10 years or at random frequency? I suppose it is randomized as the former way. If this is true, I think this may not a big problem for the conclusions since the decadal-averaged results are analyzed. But still, I think it's more reasonable to supply the original climate forcing.

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The yearly climate forcing for the spin-up was assembled as a random sequence of the annual climates for the years within a given decade, i.e., the climate of this decade was broken into ten annual blocks, which were then randomly put together to create the 250-year climate sequence for the spin-up. Given that the spin-up was only for one decade and that

- 255 we analysed the output data as decadal-averages, we do not deem possible breaks in climate from one year to the next as problematic. For longer spin-up sequences, e.g., a century of climate data, which may have a significant trend included, the preferred approach would be to de-trend the sequence, then break the de-trended sequence into larger blocks, e.g., decadal blocks or longer, and then randomly assemble these blocks to create the spin-up sequence. This way, the interannual variability is preserved while the trend is removed, and the potential climatology hiatus around the edges of
- 260 the blocks is reduced due to the larger size of the constituting blocks. We have rephrased our explanation on how we

assembled the spin-up climatology to make it more clear that we used randomized decadal climatology (p.4 lines 49-57).

Line 171-173. How to define the criteria for the residual distance as close-to-zero and non-zero? Also, I think part of the non-zero residual distance could be caused by the internal variabilities of the climate forcing. It would be better excluding this part properly.

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I'm not sure I understand what you mean by "excluding this part properly"? In order to test whether the Euclidean distance between transient and equilibrium decade vegetation states is significantly different from zero, one would need to have another reference for comparison in order to determine a typical threshold value. The way to obtain such a reference would be to conduct several equilibrium simulations per decade and scenario, as well as several transient

- 270 simulations per scenario, each with different initializations and, in the case of the equilibrium runs, differently randomized climate year sequences. This would allow to determine the Euclidean distances among the decadal replicates, which then could be compared to the mean Euclidean distance between transient and equilibrium decadal replicates. If the mean Euclidean distance among decadal replicates is statistically significantly smaller than the mean Euclidean distance between transient and equilibrium decadal replicates, then one could quantitatively say the transient-equilibrium
- 275 distance is different from zero. However, due to the large number of simulations already required for this study, we did not conduct replicate simulations that would allow us to directly make such a quantitative statement. Yet, based on experience we know that the between-replicate variability of the state variables used to calculate the Euclidean distance in this study is usually a few percent at best, due to stochasticity between differently initialized runs. Therefore, as a best estimate, we altered our original simulation values, letting them range between \pm 5% difference from the actual
- simulation values in order to mimic typical between-replicate variability. We then, in accordance with the procedure applied to the original variables, standardized the altered variables in the same way. After that, we then, for each grid pixel, each scenario, and each time slice (i.e., decade), calculated the Euclidean distance between original variable tuple and altered variable tuple. This delivered a total of 887848 Euclidean distance values overall that (artifically) represent the typical between-replicate Euclidean distance range. The mean value of this sample was 0.13 ± 0.06, the 95% percentile 0.23, and the 99% percentile was 0.29. It is therefore fairly safe to assume any Euclidean distance > 0.29 is larger
- than zero. We have added this explanation of how we derived an estimate of the non-zero limit to the supplementary material and refer to it in the main text of the manuscript (p.5 lines 27/28 and lines 31-33).

The legend of figure 1 is not clear to distinguish the equilibrium vs. transient on the printed pages. Suggest adding the marks of dot and square on the legend.

We have increased the size of the symbols in Fig. 1 and S1, and changed the legend according to your suggestion (p.6).

The words of "a" in line 201, and "to" in line 598 are written twice. And there is a typo for the word of "both" in line 278.

4 Author responses to comments of Associate Editor Martin De Kauwe

Responses are highlighted in bold font.

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I have now received two reviews of your manuscript, both reviewers are positive about your manuscript. I think it is a very interesting study on an important topic and I am recommending minor revisions before publication, many congratulations.

I have read through your responses document and I'm happy with your suggested revisions, so look forward to reading your revised manuscript.

305 A few minor comments:

- In the abstract, when you say "between 1970 and 2099 for the RCP4.5 and 8.5 scenarios", can you please indicate this is based on a single GCM? I would take this sentence to imply aDGVM was forced by the entire CMIP ensemble, for example. I don't mean this comment in any negative sense to be clear, I'm fine with your experimental set up.

Thank you for your suggestion, we have added a statement specifying that we used regionally downscaled climatology 310 based on the MPI-ESM output for CMIP5 (p.1 lines 20-22).

- Also, when you talk about lags in the abstract, could you indicate in brackets a couple of examples of what you mean by lags (causes) to capture interested readers? You currently use the word lag(s) seven times, but you don't really explain what is meant. I note you do mention fire at the end, but I still think it would be useful.

315 Good point. We have added a listing of some examples for delays in vegetation response to the second sentence of the abstract (", e.g., changes in physiological processes, structural changes, and changes in vegetation composition and disturbance regimes may happen with substantial delay after a change in forcing has occurred." (p.1, lines 5-8)

When you state: "For example, CO2 fertilization effects may be reduced by increased drought due to water limitation effects
 on plant growth (Temme et al., 2019).". I'm struggling a little with this assertion, firstly because drought is typical short-term for many/most ecosystems, so what evidence is there that it would significantly alter the plants' capacity to exploit a higher CO2 concentration over some multi-year period? Also, if CO2 = greater non-structural carbohydrates or reduces evaporation, both could reduce/delay drought impacts. It is of course also true, that this may make little difference, particularly if the drought is long-lasting, but still, I think more care is needed with this sentence.

325 You are right, the phrasing of this example and the term "drought" is maybe misleading. What we had in mind is changing precipitation regimes in the wake of climate change, for example change in precipitation seasonality (prolonged dry season duration/later start of the wet season), changes in the precipitation frequency distribution, and changes in annual precipitation quantities. Such changes are very likely and actually already observed in different parts of Africa at present (Batisani & Yarnal, 2010; Dunning et al., 2018). While drought may be of short-term du-

- ration (but can last for longer as well, e.g., mega-drought events), changes in precipitation regime that are linked to climate change/changes in atmospheric circulation patterns will have a longer-lasting impact on plant water availability and therefore the capacity of plants to benefit from CO₂ fertilization and increased water use efficiency. Where water stress occurs more frequently, e.g., due to increased drought frequency and severity or changes in precipitation seasonality, its negative effects may not automatically offset the beneficial effects of elevated CO₂ (see, e.g., Jin et al., 2017: Liu et al. 2020). We have expanded and rephrased this passage to make it more clear what we mean (p.2 lines)
- 335 2017; Liu et al, 2020). We have expanded and rephrased this passage to make it more clear what we mean (p.2 lines 88-104).

Finally, I wonder whether you'd consider adding further to your discussion. You're under no obligation here, just a thought. I think it would be useful to discuss (briefly) key process lags that the model doesn't capture, but in reality may be important.
For example, drought legacy/recovery (I presume it is largely instantaneous in the model - i.e. the model doesn't simulate embolism). You also talk about tree cover decline by the end of the century, I wonder how much acclimation capacity the model has? Can (or does) the model project greater root investment under eCO2? Are greater roots then linked to greater water uptake potential in the model? I guess overall what I'm wondering is how much capacity our models (or your specific model) has to dynamically respond to the projected climate and how much of what we learn is still limited by our model process capacity?

- Yes, the aDGVM ("adaptive DGVM", hence the letter "a" in the model name abbreviation) is able to acclimate to changing environmental conditions. Carbon allocation is dynamic and carbon investment to biomass pools adjusts dynamically in such a way that allocation to those biomass pools that are the most limiting factor for plant growth at a given time is maximized. I.e., if water becomes limiting, plants allocate more carbon to roots at the expense of allocation to other compartments such as stems or leaf biomass. This has been briefly mentioned at the beginning of section 2.1, and we have now added two more sentences to highlight how dynamic allocation works in aDGVM (p.3 lines 66-73). We
- did not specifically keep track of root investment changes over time under eCO2 in this study. This model version does not explicitly simulate xylem cavitation, but can capture drought-related mortality indirectly via carbon-related mortality. If carbon gain is reduced due to water limitation, the carbon balance of a simulated plant individual can become negative (due to respiratory costs exceeding assimilation gains). Negative carbon balance then increases an individual's
- mortality probability. However, what this model version cannot capture yet are more detailed shifts in community trait composition that are caused through environmental filtering, for example shifts towards plant individuals with lower SLA and more negative p50 that can tolerate more water stress. This has however been implemented in the successor model version (aDGVM2, Langan et al., 2017), which we did not use in this study due to its higher computational costs. We have included a brief discussion on the representation of water stress-related mortality in the discussion section 4.1
 (p.14 lines 61-71).

Best wishes,

Martin De Kauwe

Climate change will cause non-analogue vegetation states in Africa and commit vegetation to long-term change

Mirjam Pfeiffer¹, Dushyant Kumar¹, Carola Martens^{1,2}, and Simon Scheiter¹

¹Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60438 Frankfurt am Main, Germany

²Institute of Physical Geography, Goethe University Frankfurt am Main, Altenhoeferallee 1, 60438 Frankfurt am Main, Germany

Correspondence: Mirjam Pfeiffer (mirjam.pfeiffer@senckenberg.de)

Abstract.

Vegetation responses to changes in environmental drivers can be subject to temporal lags. This implies that vegetation is committed to future changes once environmental 5 drivers stabilize, e.g., changes in physiological processes,

- structural changes, and changes in vegetation composition and disturbance regimes may happen with substantial delay after a change in forcing has occurred. Understanding the trajectories of such committed changes is important as they
- ¹⁰ affect future carbon storage, vegetation structure and community composition and therefore need consideration in conservation management. In this study, we investigate whether transient vegetation states can be represented by a timeshifted trajectory of equilibrium vegetation states, or if they
- ¹⁵ are vegetation states without analogue in conceivable equilibrium states. We use a dynamic vegetation model, the aDGVM, to assess deviations between simulated transient and equilibrium vegetation states in Africa between 1970 and 2099 for the RCP4.5 and 8.5 scenarios - Euclidean distance
- 20 between simulated transient and equilibrium using regionally downscaled climatology based on the MPI-ESM output for CMIP5. We determined lag times and dissimilarity between simulated equilibrium and transient vegetation states based on the combined difference of nine selected state vari-
- ²⁵ ables was used to determine lag times and similarity of vegetation statesusing Euclidean distance as a measure for that difference. We found that transient vegetation states over time increasingly deviated from equilibrium states in both RCP scenarios, but that deviation was more pronounced in
- ³⁰ RCP8.5 during the second half of the 21st century. Trajectories of transient vegetation change did not follow a "virtual trajectory" of equilibrium states, but represented non-

analogue composite states resulting from multiple lags with respect to vegetation processes and composition. Lag times between transient and most similar equilibrium vegetation 35 states increased over time and were most pronounced in savanna and woodland areas, where disequilibrium in savanna tree cover frequently acted as main driver for dissimilarities. Fire additionally enhanced lag times and Euclidean distance dissimilarity between transient and equilibrium veg- 40 etation states due to its restraining effect on vegetation succession. Long lag times can be indicative of high rates of change in environmental drivers, of meta-stability and nonanalogue vegetation states, and of augmented risk for future tipping points. For long-term planning, conservation 45 managers should therefore strongly focus on areas where such long lag times and high residual Euclidean distance dissimilarity between most similar transient and equilibrium vegetation states have been simulated. Particularly in such areas, conservation efforts need to consider that observed 50 vegetation may continue to change substantially even after stabilization of external environmental drivers.

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1 Introduction

Vegetation dynamics is influenced by a variety of environmental drivers, including climatic conditions, atmospheric CO_2 concentration, soil parameters, nutrient availability, and disturbance regime (Eamus et al., 2016). These environmental drivers affect vegetation processes on a variety of levels, from physiological processes at the leaf-level to community assembly processes at ecosystem level (Felton and Smith, 2017), and ultimately determine large-scale vegetation patterns on biome-level (Lavergne et al., 2010; Woodward et al., 2004). The impact of environmental drivers is reflected in vegetation structure, vegetation-related ecosystem functions, and biogeochemical processes such as carbon sequestration, nutrient turnover, and ecohydraulics (Bonan,

- ¹⁰ 2019). Although environmental drivers are subject to constant variation, vegetation response does not happen instantaneously in accordance with forcing, but requires time to allow the system to respond (Essl et al., 2015). It can therefore be expected that climate change will cause widespread
- ¹⁵ shifts in the distribution of major vegetation formations until the end of the century (Lucht et al., 2006). How much time vegetation requires to respond depends on i) the type of process that is affected, ii) the extent of change of the environmental driver, and iii) the velocity of change, i.e., how fast
- ²⁰ the driver changes. For example, physiological processes at the leaf level can adapt to changing environmental drivers such as temperature on very short (sub-)daily time scales (Chen et al., 1999; Vico et al., 2019), whereas adaptation to climate change at community level can require years to
- ²⁵ decades. Slow gradual changes allow vegetation more reaction time, whereas rapid changes leave vegetation drastically behind (Davis, 1989; Corlett and Westcott, 2013). Continuous fluctuation of environmental drivers entails that vegetation is usually not in equilibrium with forcing at a given time, ³⁰ and disequilibrium vegetation dynamics under future climate

change needs to be expected (Svenning and Sandel, 2013).
Temporal lags between forcing and vegetation state imply that vegetation is committed to further changes even if environmental drivers stabilize (Jones et al., 2009;
³⁵ Scheiter et al., 2020). It is particularly important to consider this when estimating or mitigating the effects of future climate change. Committed vegetation changes

- at the time of stabilization of climatic drivers have important implications for carbon storage (Pugh et al., 40 2018), vegetation structure, and community composition.
- In addition, delayed responses to environmental drivers may unexpectedly push vegetation beyond tipping points towards alternative stable states long after the change in forcing has occurred. Particularly in connection with
- African savanna ecosystems, such multi-stable ecosystem states have been proposed and studied by a variety of authors (e.g., Staal et al., 2016; Li et al., 2019; Pausas and Bond, 2020) . Conservation management needs to be aware that the vegetation state at any given time may not be the vegetation
- ⁵⁰ state expected under prevailing environmental conditions, and managers need to decide whether to preserve the status quo, or allow vegetation development towards its anticipated equilibrium state. Otherwise, climatic disequilibrium may severely threaten the conservation of priority ecosystems ⁵⁵ (Huntley et al., 2018).

Estimating vegetation trajectories and lags is challenging, and only few studies take into account that plant community changes could substantially lag behind climatic changes (Alexander et al., 2017). This is true when considering the change of single environmental drivers, and becomes increasingly complex when considering concurrent changes of multiple drivers. In a previous study, we examined how CO₂ concentration change over a range from 100 to 1000 ppm, at two different rates, affects African vegetation and vegetation lags with respect to equilibrium states using 65 the aDGVM (adaptive dynamic vegetation model, Scheiter et al., 2020). In that study, we found substantial deviances and lags between equilibrium and transient vegetation states when we increased or decreased CO2. However, in this previous study we only considered CO₂ effects 70 while keeping long-term averages of other environmental drivers of vegetation, such as precipitation and temperature, constant. While an estimate on the effect of CO₂ in isolation is valuable, a more accurate assessment of lags, debt and surplus in carbon, vegetation cover and vegetation structure 75 additionally requires consideration of climatic drivers. This is particularly relevant when addressing committed vegetation change for future scenarios of climate change, e.g., the climate change associated with the RCP (Representative Concentration Pathways, Meinshausen et al. (2011)) 80 (Representative Concentration Pathways, Meinshausen et al., 2011) scenarios.

Moreover, when considering multiple drivers of vegetation dynamics, complexity increases. The combination of different drivers may amplify (if they act in the same direction) or 85 weaken (if they act in opposing directions) effects on vegetation when compared to single-driver scenarios. For example, CO₂ fertilization effects may be reduced by increased drought due to water limitation effects on plant growth (Temme et al., 2019). other factors that inhibit plant growth, 90 such as nutrient limitation or increased water stress. Elevated CO_2 is often linked to higher water use efficiency in C_3 plants. However, this effect seems to have its limits and CO₂ fertilization cannot always counteract the effects of reduced water availability (Temme et al., 2019). Future changes in precipitation regime, e.g., of precipitation seasonality (prolonged dry season duration), combined with changes in precipitation frequency distribution and annual quantities are very likely and already observed in different parts of Africa (Batisani and Yarnal, 2010; Dunning et al., 2018). 100 Where water stress increases due to higher drought frequency and severity or changes in precipitation seasonality, its negative effects may be too strong to be offset by CO₂ fertilization (see, e.g., Jin et al., 2017; Liu et al., 2020). For a realistic evaluation of vegetation lags associated with future 105 climate change, it is therefore necessary to assess the coupled effects of different drivers in the climate system.

An open question that conservation managers as well as vegetation modelers need to consider is whether observable transient vegetation states correspond to conceivable equilibrium states, or whether no analogue equilibrium vegetation state exists non-analogue vegetation states exist, i.e., vegetation states that have no corresponding equivalent in vegetation states of the past or present. Two possible s scenarios are conceivable. In scenario (1), transient vegeta-

- tion dynamics follows a virtual trajectory defined by equilibrium states. Vegetation lags simply correspond to a timeshift of equilibrium states that should exist at a given time according to prevailing environmental conditions, i.e., tran-
- ¹⁰ sient vegetation states are analogue to equilibrium vegetation states of another point in time. In scenario (2), transient vegetation states have no exact analogue in any conceivable equilibrium states, i.e., transient vegetation states not only lag behind an equilibrium, but are "chimeras" that
- ¹⁵ can never be represented by an equilibrium vegetation state. Such mixed vegetation states that entirely lack accordance with any conceivable equilibrium vegetation states are what we define as "non-analogue" in the context of this study. Scenario (2) may result from mismatches between equilib-
- ²⁰ rium and transient states at different levels of plant- and vegetation-related processes. As all these processes operate at different time scales, the time lag between various transient state variables and their respective equilibria at any given time will differ, resulting in vegetation disequilibrium with
- 25 respect to multiple variables. Scenario (2) has important implications, as the complexity of disequilibrium in this scenario constitutes a major challenge for future conservation efforts (Svenning and Sandel, 2013).
- Here, we used the aDGVM to assess deviations between ³⁰ transient and equilibrium vegetation states in Africa. The aDGVM has been developed with specific focus on savannas and tropical vegetation, and its performance has been evaluated in a number of studies. In this study, we use the model to compare transient and equilibrium vegetation states in Africa
- ³⁵ between 1970 and 2099 for RCP4.5 and RCP8.5 on a decadal basis. Using projected climate and CO₂ concentrations of the RCPs allows us to evaluate evaluation of the combined effects caused by simultaneous variation of several drivers of vegetation dynamics. We asked:
- 40 1. How do simulated transient vegetation states deviate from equilibrium vegetation states expected under given historic and future climate conditions, with respect to ecosystem variables related to biomass, vegetation structure and composition?
- 45 2. Do trajectories of transient vegetation change follow a "virtual trajectory" of analogue equilibrium states, or are transient vegetation states non-analogue and different from any equilibrium vegetation state?
- What are the lag times between transient and most similar equilibrium vegetation states, and which state variables and underlying processes can explain dissimilarities?

4. Which biomes and regions in Africa are most resistant to climate change, and which ones are most prone to experience meta-stability and change as a consequence 55 of changing environmental drivers in the future?

2 Methods

2.1 Model description

The aDGVM (adaptive Dynamic Global Vegetation Model, Scheiter and Higgins, 2009) has been developed with empha-60 sis on grass-tree-interactions in tropical ecosystems. Trees are simulated as single individuals, and the model incorporates an individual-based representation of plant physiological processes and allows dynamic adjustment of leaf phenology and carbon allocation to environmental conditions. 65 Carbon investment to biomass pools adjusts dynamically in such a way that allocation to those biomass pools that are the most limiting factor for plant growth at a given time is maximized. For example, if water is limiting, more carbon is allocated to roots at the expense of allocation to stems and leaves to increase water uptake capacity, whereas under light limitation, more carbon is allocated to stems and/or leaves to increase light capture. State variables such as biomass, height and photosynthetic rates keep track of plant performance, while external disturbances such as herbivory (Scheiter and 75 Higgins, 2012), fire (Scheiter and Higgins, 2009) and land use (Scheiter and Savadogo, 2016; Scheiter et al., 2019) impact plants as function of their traits. The aDGVM simulates four plant types (Scheiter et al., 2012): Fire-sensitive but shade-tolerant forest trees, fire-tolerant but shade-intolerant 80 savanna trees, C₃ grasses, and C₄ grasses, with each type of grass being represented by two types of super-individuals that distinguish grasses beneath or between tree canopies. Physiological differences between C₃ and C₄ photosynthesis distinguish C₃ and C₄ grasses and their performance under specific environmental conditions (e.g., Taylor et al., 2018). Fire is modeled as function of fuel loads, fuel moisture and wind speed (Higgins et al., 2008) and ignitions are based on a random sequence. It removes aboveground grass biomass and affects trees based on fire intensity and 90 tree height (Higgins et al., 2000, topkill effect). Large trees with crowns above the flaming zone are largely fire-resistant, and grasses and topkilled trees can regrow from root reserves after fire (Bond and Midgley, 2001). Mortality in aDGVM is a probabilistic function of negative carbon bal-95 ance. Scheiter and Higgins (2009), and Scheiter et al. (2012) showed that aDGVM captures the distribution of major vegetation formations in Africa. Scheiter and Higgins (2009) showed that aDGVM can simulate biomass dynamics in a long-term fire manipulation experiment in Kruger National 100 Park (Experimental Burn Plots, Higgins et al., 2007), and Scheiter and Savadogo (2016) showed that an adjusted model version can reproduce grass biomass and tree basal area under various grazing, harvesting and fire treatments in Burkina Faso. Scheiter and Higgins (2009) and Scheiter et al. (2015) showed that aDGVM can simulate broad patterns of fire activity in Africa and Australia, respectively. For a more 5 detailed description of aDGVM, see Scheiter and Higgins (2009).

2.2 Climate forcing data

Simulation of transient vegetation dynamics required time series of climate data. In this study, we used daily cli-¹⁰ mate data that were downscaled with the variable-resolution conformal-cubic atmospheric model (CCAM, McGregor, 2005) for Africa for the period between 1970 and 2099. The downscaling was performed by the South African research group Climate Studies, Modelling and Environmental ¹⁵ Health at the Council for Scientific and Industrial Research

- (CSIR) (Archer et al., 2018; Davis-Reddy et al., 2017; Engelbrecht et al., 2015). The downscaling used GCM projections from the Coupled Model Intercomparison Project Phase 5 (CMIP5, Tab. S1, IPCC, 2013) and followed the methodol-
- ²⁰ ogy described in Engelbrecht et al. (2015), applying CCAM globally at quasi-uniform resolution of approx. 50 km in the horizontal. Bias-correction of downscaled climate data was performed based on monthly climatologies of tempreature and rainfall from CRU TS3.1 data for the period 1961-1990
- ²⁵ following Engelbrecht et al. (2015) and Engelbrecht and Engelbrecht (2016). CCAM output is available on daily temporal resolution on a latitude-longitude grid of 0.5° resolution for RCP 4.5 and RCP8.5. RCP4.5 is a modest-high impact scenario with peaking greenhouse gas emissions around mid-
- ³⁰ century and a CO₂ concentration of ca. 540 ppm in 2100. In the high-emission RCP8.5 scenario, emissions keep rising to the end of the century where CO₂ concentrations will reach ca. 900 ppm. Climate variables used in aDGVM simulations were precipitation, daily minimum and maximum tempera-³⁵ ture, wind speed, and relative humidity. As projected radiation was not available from CCAM, it was derived based on
- sunshine percentage (Allen et al., 1998) from the New et al. (2002) dataset.

2.3 Experimental design

- ⁴⁰ For our simulations, we used CCAM downscaled climate data for RCP 4.5 and RCP 8.5 based on the boundary conditions provided by the Max Plant Planck Institute Earth System Model (MPI-ESM, Giorgetta et al., 2013). To obtain equilibrium vegetation states on a decadal basis, we con ⁴⁵ ducted separate simulations for all decades between 1970 and 2099, i.e., 13 decadal equilibrium runs per RCP scenario were performed. For each decade, a 250-year random sequence of yearly climate data was generated using the respective RCP scenario's climate data for that decade, in . In
 ⁵⁰ order to avoid saw-tooth pattern caused by potential small
- intradecadal trends in climate, the yearly climate forcing

for the spin-up of the transient runs and the equilibrium simulations was assembled as a random sequence of the annual climates for the years within a given decade, i.e., the climate of a respective decade was split into ten annual 55 blocks, which were then randomly put together to create the 250-year climate sequence. The resulting randomized 250 years of climate data were used for equilibrium simulations allowing modeled variables to reach steady-state with the environmental conditions of the decade. Previous simulations 60 have shown that after 200-250 simulation years, aDGVM reaches equilibrium state for large parts of the study region. The last 30 years of the 13 equilibrium runs were used to determine equilibrium vegetation states for each RCP scenario. The decadal equilibrium states provided the reference base 65 for comparison with decadal results from the transient simulations.

For transient simulations, a 210-year model spin-up was performed using randomly generated sequences of the years in the period 1970 to 1979 to ensure steady-state conditions. After model spin-up, aDGVM was then forced with the respective RCP climate time series for the period 1970 to 2099 to obtain simulation results of the transient vegetation state. All simulations were conducted both in the presence and absence of fire, i.e., in total eight simulation scenarios were conducted, amounting to a total of 56 simulation runs (four transient runs, 4x13 equilibrium runs). Transient model runs were conducted previously by Martens et al. (unpublished)Martens et al. (2020, accepted).

80

2.4 Analyses

Comparison of equilibrium and transient vegetation states was conducted by-using decadal averages of selected state variables at grid cell level that were calculated from annual maximum values (grass and tree biomass) or annual average values. Model variables under consideration were above- 85 ground tree biomass, aboveground grass biomass, savanna tree cover, forest tree cover, total tree cover, average tree height, maximum tree height, number of tree individuals, and $C_3:C_4$ grass ratio based on respective totals of grass leaf biomass. Decadal averages for equilibrium scenarios were calculated from the last 30 years of the 250 year simulation sequence. For transient simulations, decadal averages were calculated based on annual simulation output for the respective decades. Although all analyses in this study were conducted on decadal basis, we focus on three decades (2010s, 95 2050s, 2090s) in the results section. Full sets of maps for all decades from 1970 to 2099 are provided as video sequences in the supplementary material of this study.

2.4.1 Comparison between scenarios

Scenarios were compared individually for each key variable 100 to address question 1, i.e., to determine how simulated transient vegetation states deviate from equilibrium vegetation states with respect to specific ecosystem state variables. We calculated continental-scale averages of each key variable based on grid cell values of decadal variable averages, and plotted the result as time series.

- ⁵ We calculated the Euclidean distance between transient and equilibrium vegetation states to evaluate the similarity between these scenarios on a per-grid cell and per-decade basis, in order to address question 2. As the nine key variables used for the calculation of Euclidean distance differed in
- ¹⁰ units and value ranges, we standardized all variables based on variable mean and standard deviation across all decades, grid cells and scenarios. The standardization across all decades and grid cells of all scenarios to a common mean allows comparison of distance values between scenarios.
- Euclidean distance was calculated between same-decade partners (SDPs) in transient and equilibrium simulations to determine the development of similarity over time. To answer question 3, for each transient decade the Euclidean distance to all previous equilibrium decades was calculated, and the
- 20 equilibrium decade with the closest distance to the respective transient decade was assigned as closest-decade partner (CDP). We denote the time difference between closestdecade partners as "lag time" in the wider sense, i.e., not taking into account the residual distance between closest-decade
- ²⁵ partners. This distance should be close to zero for a definition of analogue vegetation states in the strict sense. We interpret a non-zero residual distance of > 0.29 between CDPs as a sign very high likelihood for a non-analogue transient vegetation state (question 2), because it implies that even the
- sequilibrium decade closest to the transient decade is still different from the transient decade (see supplementary material section D to get a detailed explanation of how we derived the 0.29 threshold value).

Contribution of individual key variables to the full Eu-³⁵ clidean distance, i.e., the Euclidean distance calculated by considering based on all nine state variables, was evaluated using a bootstrapping approach. Each variable was omitted and the reduced Euclidean distances based on the remaining eight key variables were calculated. The reduced distances ⁴⁰ were then set into relation to the full Euclidean distance to

determine the percent deviation from the full distance caused by each variable:

$$D_{x,y,t}^{v} = \frac{F_{x,y,t} - R_{x,y,t}^{v}}{F_{x,y,t}}$$
(1)

Here, $F_{x,y,t}$ is the full Euclidean distance calculated using ⁴⁵ all nine state variables, at a given grid cell with coordinates x, y for decade $t, R_{x,y,t}^v$ is the reduced Euclidean distance calculated based on eight state variables, omitting variable vfrom the calculation, at a given grid cell with coordinates x, yfor decade t, and $D_{x,y,t}^v$ is the percent deviation from full Eu-⁵⁰ clidean distance caused by omitting a given variable v from

distance calculation, at a given grid cell with coordinates x, y for decade t.

Variables were then ranked for each grid cell and transient decade according to their percent deviation $D_{x,y,t}^{v}$ to determine the contribution of each variable to the full Euclidean distance $F_{x,y,t}$. This The highest-contributing variable is termed "dominant variable" hereafter. Dominant variables were determined for SDPs as well as CDPs to answer question 3.

2.4.2 Biome classification

To assess which regions and vegetation formations in Africa are most resistant or most susceptible to future vegetation change (question 4), we aggregated vegetation in biomes using decadal averages of transient and equilibrium simulations level following the scheme used in Scheiter et al. (2012) for all eight simulation scenarios. For definition of biome boundary criteria, see table **??**\$1.

To identify stable biome core areas for each of the eight scenarios, we identified grid cells with exactly one biome type (biome core areas) in all 13 decades and created maps showing these areas. Desert core area was used for masking areas with very little vegetation to omit edge effects from such areas. Where grid cells took on more than one biome type in 13 decades, we counted the number of different biome types that occurred per grid cell, the number of changes between biome types per grid cell, and the ratio between biome types per grid cell and biome changes per grid cell. We created maps of these variables. Additionally, we defined each biome's area for all decades to determine changes in fractional cover over time for each scenario.

3 Results

3.1 Lags between equilibrium and transient simulations at continental scale

In simulations with fire, aboveground tree biomass in both equilibrium and transient scenarios was lower (Fig. 1a) and 85 grass biomass was higher (Fig. 1b) than in no-fire scenarios. Seen in combination with the lower total tree cover in scenarios with fire (Fig. 1g), this indicates a a-more open landscape in the presence of fire. Average aboveground tree and grass biomass increased over time in all scenarios. While tree 90 biomass in transient scenarios was lower than in equilibrium scenarios, grass biomass in transient scenarios only dropped below levels expected based on equilibrium scenarios during the second half of the 21st century. Grass layer composition changed over time towards more C_3 and less C_4 grasses in all scenarios (Fig. 1c), with transient scenarios shifting to higher levels of C₃ grasses to a lesser degree than equilibrium scenarios. This indicates that the change is too slow to attain the levels of the equilibrium scenario.

While mean height of all trees combined (Fig. 1d) in- 100 creased only slightly over time (in runs with fire) or remained more or less stable (in scenarios without fire), both maxi-



Figure 1. Time series of continental-scale spatial averages of variables for RCP8.5, calculated from decadal averages of grid cells.

mum tree height (Fig. 1e) and number of tree individuals per unit area (Fig. 1f) increased over time, contributing to the simulated increase in tree biomass per unit area. Maximum tree height increased more strongly in equilibrium than transient simulations, with fire having very little effect due to tall trees not being affected by low- to medium-intensity fires in aDGVM. The difference between transient and equilibrium states increased over time, showing that maximum tree height lags behind its equilibrium and lag size increases to over time. Towards the end of the 21st century, tree numbers increased more strongly in no-fire simulations, and tree numbers were larger in transient than in equilibrium scenar-

ios during the last decades.

Without the selection pressure exerted by fire, total tree ¹⁵ cover (Fig. 1g) was essentially identical with forest tree cover (Fig. 1h) because savanna trees were largely absent in both equilibrium and transient simulations (Fig. 1i). While equilibrium simulations indicated more or less constant levels of total tree cover up to the year 2040, equilibrium tree cover declined after 2040 to approx. 42% at the end of the century. In comparison, transient no-fire simulations suggested slightly rising total tree cover until 2050, followed by a slight decline to approx. 50% cover towards the end of the century. Therefore, in the absence of fire, total transient tree cover increasingly deviated from total equilibrium tree cover during the second half of the century. The tree cover overshoot in no-fire transient simulations indicates that vegetation deviates from its equilibrium state.

The presence of fire fostered the existence of savanna trees in equilibrium and transient simulations (Fig. 1i). However, ³⁰ while the transient simulation showed an increase in savanna tree cover from approx. 8% in the 1970s to approx. 20% at



Figure 2. Continental-scale spatial average of Euclidean distance between <u>same-decade partners</u> (SDPs), for the four transientequilibrium scenario pairings. Error bars represent standard deviation of spatial average in a given decade. The horizontal black line at 0.29 indicates the threshold value above which Euclidean distance is assumed to be significantly different from zero.

the end of the century, equilibrium simulations showed a decline in savanna tree cover with approx. half of the original cover lost by the end of the century. While forest tree cover in transient simulations with fire decreased slightly from ap-

- ⁵ prox. 25% to 21% cover, it increased in equilibrium simulations and reached a value of approx. 34% at the end of the century. In the presence of fire, both equilibrium and transient simulations showed a trend of increasing total tree cover over the course of the 21st century (Fig. 1g). However, while
- ¹⁰ this increase was driven by an increase in forest tree cover that over-compensated a simultaneous decline in savanna tree cover in equilibrium simulations, an increase in savanna tree cover caused the trend towards higher total tree cover in the transient simulation.
- ¹⁵ For the RCP 4.5 climate scenario, the general patterns described for RCP 8.5 were similar, but C_3 grasses did not become as prominent towards the end of the century as in RCP8.5 (see Fig. ??-S1 for reference).

3.2 Similarity between same-decade partners

- ²⁰ The Euclidean distance between SDPs averaged for Africa increased over time (Fig. 2). Fire consistently enlarged the distance between SDPs in comparison with the no-fire simulations (differences in spatial means between fire and no-fire partner scenarios were statistically significant at p<0.001
- 25 based on t-tests and Kolmogorov-Smirnov tests) and lead to

highest dissimilarity between SDPs in RCP8.5 towards the end of the century. RCP4.5 and RCP8.5 showed similar trajectories until the 2040s, but while the distance kept increasing towards the end of the century in RCP8.5, it leveled off in RCP4.5 with fire, and average distance remained approx. 30 constant for RCP4.5 in the no-fire scenario. Spatial patterns of dissimilarity started to emerge during the first decades of the simulated period (Fig. 3, Fig. ??S2). In RCP8.5 with fire, maximum distance was found in the savanna areas south of the Congo basin and the Sahel zone during the 2010s (Fig. 35 3a), whereas no such pattern existed for the corresponding no-fire scenario (Fig. 3b). During the 2050s, the pattern of dissimilarity became more pronounced and substantial distance between transient and equilibrium scenario was also observed in eastern and southeastern Africa (Fig. 3c). In the 40 no-fire scenarios, dissimilarity developed in eastern Africa, and in western Angola (Fig. 3d). Towards the end of the century, distance between SDPs was substantial in most parts of Africa in RCP8.5 in both the fire and no-fire scenario. The largest distances were found in the Sahel, Ethiopia and southern Central Africa (Fig. 3e,f). The general spatial pattern observed in RCP8.5 was also found in RCP4.5 (Fig. ??S2), but spatially less extensive and with overall lower distances between SDPs. Towards the end of the century, RCP4.5 had substantially lower distances than RC8.5, in particular in the 50 scenario without fire.

3.3 Variable contributions to dissimilarity between SDPs

In many parts of Africa and in all scenarios, one specific variable could be identified as main cause for the RCP8.5 55 with fire, for ca. 28% of African area savanna tree cover was the variable that had the largest influence on dissimilarity between SDPs , with an average contribution of-in the 2010s (Fig. 4). Ranking of variables based on their impact on the full Euclidean distance between SDPs 60 revealed that the variable with the strongest impact in average contributed ca. 40% to the full Euclidean distance, whereas the second-most influential variable variable with the second-strongest impact in average only contributed approx. 10% (Fig. ??. In RCP8.5 with fire, savanna S3a). The 65 strength of impact varied between variables and was highest where mean tree heights was identified as most influential variable (ca. 65% contribution), and lowest where forest tree cover was the variable that dominated dissimilarity between SDPs for approx. 28% of Africa's non-desert area in the 2010s-most influential variable (ca. 18% contribution). This general pattern was similar for all four scenarios (Fig. 4S3a, b, c, d). The area fraction where savanna tree cover had the largest contribution to dissimilarity increased towards midcentury, and then slightly declined again towards the end of 75 the century. Importance of average and maximum tree height was second and third after savanna tree cover in the 2010s, with the fraction of area where they dominated the Euclidean



Figure 3. Spatial patterns of Euclidean distance between <u>same-decade partners</u> (SDPs) in RCP8.5 for three selected decades (2010-2019, 2050-2059, 2090-2099). Panels a), c) and e) represent distance between SDPs in simulations including fire (wifi), panels b), d) and f) show results from simulations excluding fire (nofi).

distance decreasing towards the end of the century. Remarkably, in RCP8.5 the area where $C_3:C_4$ grass ratio was the dominant variable increased towards the end of the century, which in this form was not found in either RCP4.5 scenario.

5 In scenarios without fire, savanna tree cover was very low and had less impact on Euclidean distance where it was the dominant variable, while average and maximum tree height as well as total tree cover were more important. Maps of dominant variable distribution are shown in Fig. ?? <u>S4</u> and Fig. ?? <u>S5</u>.

10

The percent deviance from the full Euclidean distance caused by the dominant variable, averaged across Africa and



Figure 4. Fractions of African area where a given state variable is the dominant variable with respect to Euclidean distance between same-decade partners (SDPs), illustrated as time series stacks for the four scenario pairings between SDPs. Variable color coding is annotated in the panel for RCP8.5 with fire. The color-coding for the variables is identical in all four panels.

all decades, ranged between 40 and 50% (Fig. ??.56). Distinction of percent deviance according to dominant variables revealed some differences according to the identity of the dominant variable. Forest tree cover as dominant variable 5 caused a reduction of approx. 20%, whereas mean tree height

- caused an approx. 60% reduction from the full Euclidean distance where it was the dominant variable. This was fairly consistent for all four SDP-combinations. The most pronounced difference between fire and no-fire scenarios was
- ¹⁰ found with respect to savanna tree cover, which was largely irrelevant as dominant variable in no-fire scenarios, but also had less impact where it dominated than in the fire-scenarios. For maps of percent deviance caused by the most influential variable, see Fig. **??** \$7 and Fig. **??** \$8.

15 3.4 Lag times between transient and closest-distance equilibrium vegetation states

The spatially averaged lag time between CDPs increased over time in all scenarios (Fig. 5a). Until the 2030s, all scenarios followed the same trajectory. After 2030, the scenarios with fire started to diverge from the scenarios without $_{20}$ fire. At the end of the century, the spatially-averaged lag time amounted to 5.0 ± 3.5 and 5.5 ± 3.6 decades for RCP8.5 and RCP4.5 with fire, and 3.8 ± 2.8 and 4.4 ± 3.1 decades for RCP8.5 and RCP4.5 without fire, respectively.

While no clear spatial pattern in lag time existed in the ²⁵ 2010s (Fig. 6a), such a pattern emerged in the 2050s in RCP8.5 with fire (Fig. 6c) and had developed clearly during the last decade of the century (Fig. 6e). Lag times of 10 decades and more were found in the Sahel zone, in eastern Angola, western Zambia, Zimbabwe and in the northeast of ³⁰ South Africa. In the no-fire RCP8.5 scenario, patterns were less clear and extreme lag times of a century or more were less abundant (Fig. **??**<u>59</u>). Patterns in RCP4.5 (Fig. **??**<u>510</u>, Fig. **??**<u>511</u>) were similar to those found in RCP8.5, but the boundaries between areas with large lag times and areas of ³⁵ moderate and intermediate lag times were more diffuse than in RCP8.5. In <u>bpth both</u> RCP4.5 scenarios, lag times of 7-8 decades were more common at the end of the century in areas where lag times between 3-5 decades prevailed in RCP8.5.



Figure 5. Continental-scale spatial average of lag time (panel a) and residual distance (panel b) between CDPstransient decade and most-similar equilibrium decade (closest-decade partners (CPDs) based on Euclidean distance), for the four scenario pairings between CDPs. Error bars represent standard deviation of spatial averages in a given decade. The horizontal black line at 0.29 in panel b indicates the threshold value above which Euclidean distance is assumed to be significantly different from zero. Lag time increases over time for all scenarios, and scenarios with fire start to diverge from scenarios without fire after 2030. Residual distances between CPDs are different from zero and indicate that transient vegetation states are not time-shifted trajectories of equilibrium vegetation states. To see which variables are the main drivers of the spatially averaged residual distance shown in panel b, please view panel b in comparison with Fig. 7.

3.5 Residual distance between closest-decade partners

Spatially averaged residual Euclidean distance between CDPs (Fig. 5b) was substantially smaller than for SDPs (Fig. 2), but nonetheless different from zero in all decades. Hence,

- ⁵ elosest equilibrium. The spatial variability of the size of the remaining Euclidean distance was high, especially towards the end of the century (see Fig. 6f), and the variables that were the main reason for the remaining Euclidean distance differed spatially across Africa (see Fig. 7 in combination
- ¹⁰ with Fig. 5b to see the spatial fractions of variables that dominate the Euclidean distance at a given time). The non-zero distance between transient decades and closest equilibrium decades indicates that equilibrium states in average were still different from their transient partners. Residual
- ¹⁵ distance was larger in both scenarios with fire compared to the respective no-fire partner scenarios, and larger in RCP8.5 than RCP4.5 from mid-century onward. Closest agreement between CDPs was reached during the 2000s.

During the 2010s, residual distance between CDPs was be-²⁰ low 1 in most regions of Africa in RCP8.5 with fire, except for areas adjacent to the north and south of the Congo basin, West Africa, and along the coast in southeast Africa (Fig. 6b). In the no-fire scenario, residual distance was below 1 almost everywhere (Fig. <u>??bS9b</u>). By mid-century, the resid-²⁵ ual distance in the regions that already had elevated values in the 2010s had increased further and additional areas of augmented distance had appeared in East Africa and the eastern parts of South Africa (Fig. 6d). In the no-fire scenario, residual distance was still low in most parts, but started to increase in East Africa (Fig. ??dS9d). At the end of the century, in RCP9RCP8.5 with fire substantial residual distance between CDPs existed in most parts of Africa, except for southwest Africa, the central Congo basin, and the fringe areas of the Sahara desert (Fig. 6f), with maxima in eastern Africa - and southern Central Africa. In the no-fire scenario, residual distance had become more pronounced in East Africa since midcentury, and additional hotspot areas in Cameroon and Angola had developed (Fig. ??fS9f).

The patterns for RCP4.5 were similar to those in-of RCP8.5 up to mid-century (Fig. ??\$10, Fig. ??\$11). How- 40 ever, residual distance towards the end of the century was considerably lower in both the fire and no-fire scenario in RCP4.5.

3.6 Residual distance in relation to lag time

As shown in the preceding two sections, both lag time and ⁴⁵ residual distance in average increased over time and reached a maximum towards the end of the century. In all scenarios, residual distance tended to be lowest between CDPs that had a lag time of 4 decades (Fig. **??S12**). Where CDPs **exceed**

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Figure 6. Spatial patterns of lag time (decades) between closest-decade partners (CDPs) for RCP8.5 with fire (panels a, c, e), and residual Euclidean distance between CDPs (panels b, d, f), for three selected decades (2010-2019, 2050-2059, 2090-2099).

exceeded lag times of seven decades, residual distance increased with lag time in RCP8.5, especially in the scenario with fire. In RCP4.5, this increase was hardly visible (Fig. ??bS12b) or absent (Fig. ??bS12d).

3.7 Variable contributions to dissimilarity between CDPs

In most areas of Africa, a specific variable could be identified that dominated the Euclidean distance (Fig. ??S13). Savanna tree cover was the dominant variable explaining the distance between CDPs for 25-35% of Africa's non-desert 10 12



Figure 7. Fractions of African area where a given variable is the dominant variable defining residual distance between <u>closest-decade</u> partners (CDPs), illustrated as time series stacks for the four scenario pairings between CDPs. Variable color coding is annotated in the panel for RCP8.5 with fire. The color-coding for the variables is identical in all four panels.

area in RCP8.5 with fire (Fig. 7). Mean tree height was the dominant variable for 26% of Africa's non-desert area in the first decade in RCP8.5 (34% in RCP4.5), and declined to 13% (17%) towards the end of the century. Aboveground

- $_5$ grass biomass was the dominant variable for 5-17% of the area, with maximum extent reached in the 2010s. The area where C₃:C₄ grass ratio was the dominant variable increased towards the end of the century, where it reached a cover of approx. 21% in RCP8.5 with fire. The overall pattern was
- ¹⁰ similar in RCP4.5 with fire, with the exception that $C_3:C_4$ grass ratio never became as relevant as in RCP8.5. In scenarios without fire, savanna tree cover as dominant variable for CDPs was negligible as this tree type was largely absent without fire. Consistent with the fire scenario, the RCP8.5
- ¹⁵ without fire showed an increase in area where $C_3:C_4$ grass ratio was the dominant variable towards the end of the century. For maps of dominant variable distribution, see Fig. ?? S14 and Fig. ??S15.

The dominant variable for CDPs in average caused a 34-20 44% deviation from the full residual distance (Fig. **??S**16). Similar to SDPs, the impact caused by the dominant variable also depended on variable identity and for some variables varied between scenarios. In particular savanna tree cover showed a difference between fire and no-fire scenarios, with its impact on full Euclidean distance being almost at twice as high in fire than in no-fire scenarios. Where mean tree height was the dominant variable, it had the highest impact on residual distance, but less than in SDPs, and considerably less in RCP4.5 than RCP8.5. For spatial distribution of dominant variables and corresponding percent deviance acaused by dominant variables, see Fig. **?? and ??**S17 and Fig. S18.

3.8 Biome stability

Biome stability varied between scenarios (Fig. 8). Transient scenarios had larger stable areas across all decades than equilibrium scenarios, and no-fire scenarios had larger stable areas than the corresponding scenarios with fire. The largest stable areas were found in transient RCP4.5 without fire. Areas that experienced biome changes were located at the



Figure 8. Areas with only one biome type in all 13 decades (i.e., biome core areas) shown for each of the 8 scenarios. Areas that experience one or more biome transitions are masked out (white areas). Transient scenarios are indicated by label "t" trans." (panels b. d. f. h), equilibrium scenarios by label "" equil." (panels a, c, e", g).

fringes of biome core areas, and fringe areas were consistently wider in equilibrium than in transient scenarios. Stable savanna core areas were absent in no-fire scenarios, where savanna core areas were replaced by woodland, and forest expanded into areas that were woodland or savanna in scenarios with fire (Fig. ??S19). C₃ grassland and C₃ savanna only emerged in small quantity in RCP8.5 scenarios with fire towards the end of the century. In the presence of fire, transient scenarios had more savanna areas than their equilibrium partners, which lost savanna area to woodland area towards 10 the end of the century.

Where biome change occurred, the number of different biome types per grid cell was highest in the two equilibrium scenarios with fire (Figs. ?? and ?? \$20 and \$21). Additionally, these scenarios revealed the highest number of biome ¹⁵ changes, and the most pronounced ratio between biome types and number of biome changes, indicating back-and-forth fluctuations between biome types. Consistent with the largest stable core sizes in no-fire transient scenarios, these also had the lowest numbers of biome types, biome changes, and the ²⁰ lowest ratios of biome types to biome changes.

4 Discussion

Understanding time lags in the climate-vegetation system is important when trying to predict and evaluate vegetation dynamics, composition, structure and associated ecosystem 25 functions and services against the background of climate change. However, so far relatively few studies have focused on this topic. For example, Wu et al. (2015) and Chen and Wang (2020) studied time lag responses of vegetation growth to different climatic factors based on analysis of a time series of NDVI data. Papagiannopoulou et al. (2017) studied lagged vegetation anomalies caused by precedent precipitation based on multi-decadal satellite data. However, these studies were based on observational data and therefore retrospective, they focused on a small number of specific vege- 35 tation properties such as growth and NDVI, and on lags occurring on time scales of months, seasons, or few years. To our knowledge, our study is the first that models time lags for future conditions, on a multi-decadal scale, focusing on the combined effects of different environmental drivers and 40 a range of different key variables.

4.1 Key variable behavior and biome stability

Aboveground biomass increase was consistently observed across all scenarios for both trees and grasses (Fig. 1a and b, Fig. <u>??a S1a</u> and b). For trees, this biomass increase is due to an increase in maximum tree height (Fig. 1e, Fig. <u>??eS1e</u>) and in tree number (Fig. 1f, Fig. <u>??eS1f</u>) towards the end of the century, and in scenarios with fire also due to an increase in total tree cover (Fig. 1g, Fig. <u>??eS1g</u>). This persistent trend suggests that natural African vegetation may remain a ⁵⁰ carbon sink throughout the 21st century, although we have not specifically analyzed changes in carbon sink strength in this study. However, less biomass in transient than equilibrium scenarios towards the end of the century indicates 5 carbon debt of ecosystems towards the atmosphere, which

- agrees with the findings of Scheiter et al. (2020). Hubau et al. (2020) found a stable carbon sink for Africa for the three decades up to 2015 and increased tree growth, consistent with the expected net effect of rising atmospheric CO₂, but ¹⁰ predicted a long-term future decline in the African tropical
- forest sink. How the carbon balance of the African continent will develop is still subject to considerable uncertainty due to high interannual variability in emissions and involvement of a multitude of factors other than natural vegetation develop-
- ¹⁵ ment. Human population development, land conversion and biomass over-exploitation may severely impact Africa's potential as a future carbon sink (Williams et al., 2007; Brandt et al., 2017; Pelletier et al., 2018).
- The simulated increase in biomass is likely linked to CO₂ fertilization effects. Woody encroachment, i.e., increase in woody vegetation cover, woody plant individuals and woody biomass, is commonly observed in African savannas and often attributed to rising atmospheric CO₂ concentrations, although other factors such as water constraints, fire and the provide the effect (Devinde et al., 2017;
- Case and Staver, 2017). As we did not conduct control simulations omitting CO_2 effects on vegetation, we cannot quantify how much of the biomass increase is due to rising CO_2 as opposed to other factors. However, when keep-
- ³⁰ ing climate constant in Scheiter et al. (2020) and varying CO₂, a positive effect of elevated CO₂ on carbon storage was observed. In two studies on biome change in South Asia (Kumar et al., unpublished) and Africa (Martens et al., unpublished) (Kumar et al., 2020, in review) and Africa
- ³⁵ (Martens et al., 2020, accepted) we directly compared fixed CO₂ scenarios with scenarios following RCP8.5 and RCP4.5 climate and CO₂ trajectory. In these studies, we found that scenarios with fixed CO₂ experienced biomass decrease due to increased temperature and drought stress, whereas ⁴⁰ biomass increased in scenarios with elevated CO₂.
- The degree to which CO_2 fertilization can (over-) compensate vegetation die-back due to increased temperature and water stress is limited (Jin et al., 2017; Xu et al., 2019; Jiang et al., 2020). Total tree cover decrease in our no-fire equi-
- ⁴⁵ librium simulations from mid-century onward (Fig. 1g, Fig. ??gSlg) hints to such an upper limit. As conditions become drier towards the end of the century, even increased water use efficiency due to higher CO₂ becomes insufficient to <u>sustain trees</u> at the dry end of the gradientto sustain trees,
- ⁵⁰ and total tree cover decreases. Tree cover decline also occurs in the no-fire transient simulation, but less pronounced than in the equilibrium scenario. This indicates a tree cover surplus in the transient scenario that is meta-stable. In scenarios with fire, total tree cover is overall lower as fire re-

55 duces tree occurrence towards the dry range of the gradient,

i.e., trees are already absent from sites that they can occupy in no-fire scenarios. The observed increase in tree biomass in no-fire scenarios is in contrast to the decline in tree cover and driven by tree number and maximum tree height, i.e., tree biomass increases because there are more trees and the 60 maximum height of trees increases. The tree cover decline simulated by aDGVM is likely yet an optimistic perspective. While water limitation effects on carbon assimilation and plant growth are captured, water stress mortality occurs only indirectly. Due to stomatal closure under water stress, the C-balance of a simulated plant individual can become negative if respiratory costs exceed C-gain, which increases the plant's probability of mortality. A more direct simulation of water stress-related effects, such as structural damage due to xylem cavitation, would likely further increase tree 70 mortality and cover decline.

The pronounced increase of C_3 grasses towards the end of the century in RCP8.5 (Fig. 1c), but not in RCP4.5 (Fig. **??eS1c**), suggests that maximum CO₂ levels in RCP4.5 are not sufficient to enhance competitive performance of C_3 75 grasses such that they can coexist with or replace C₄ grasses in warm areas of Africa. This can be deduced from the fact that in RCP8.5 C₃:C₄ grass ratio is the dominant variable causing distance between SDPs towards the end of the century (Fig. 4). In RCP8.5, C₃:C₄ grass ratio debt in transient 80 simulations is the variable causing the largest difference between SDPs in many parts of Africa (Fig. ??eS4c,f), but this is not the case in RCP4.5 (Fig. ??eS5c.f). Even in areas where only little grass biomass exists, for example in the Congo basin, the difference in C₃:C₄ grass ratio between 85 SDPs is larger than the differences caused by other key variables. This is because other key variables are comparably stable in these tropical forest areas. Although Euclidean distance is intermediate to high in this area (Fig. 3e,f), albeit lower than in savanna and woodland areas, up to 80% or more of contribution to full Euclidean distance is explained by the dominant variable (Fig. ??eS7e.f), i.e., by C₃:C₄ grass ratio. As amount of grass biomass is not considered in variable impact evaluation, the difference in $C_3:C_4$ grass ratio is the most prominent difference where other key variables are 95 largely stable.

Aside from rainfall, fire plays a key role for landscape openness (Staver et al., 2011b), as indicated by lower levels of tree biomass (Fig. 1a, Fig. **??aS1a**), tree cover (Fig. 1g, Fig. **??gS1g**) and higher levels of grass biomass (Fig. ¹⁰⁰ 1b, Fig. **??bS1b**) in scenarios with fire as opposed to nofire scenarios. Without fire pressure, savanna trees and savannas are largely absent and are replaced by woodland and forest (Figs. 1i, **??iS1i**, 8), which confirms findings that savannas and forests are alternative biome states differentiated ¹⁰⁵ by fire (Staver et al., 2011a). The bi-stability between woodland and savanna in the context of our study is the combined result of difference in tree type (dominant cover of forest or savanna trees) and tree cover in the presence or absence of fire. Savanna tree cover increases in transient but ¹¹⁰ decreases in equilibrium simulations with fire (Fig. 1i, Fig. ??iSli), whereas total tree cover increases in both scenarios with fire (Fig. 1g, Fig. ??gSlg). However, this total tree cover increase is driven by forest trees in equilibrium and

- ⁵ by savanna trees in transient simulations. Where we see the final stage of succession as represented by aDGVM in the equilibrium scenario, what we see in the transient scenario is a snapshot of a system in motion. The increase in savanna tree cover in the transient scenarios can thus be in-
- ¹⁰ terpreted as intermediary disequilibrium stage that already indicates transition towards more tree cover, but has not yet moved to the next successional stage that would be replacement of savanna trees with forest trees. Anthropogenic fire management may therefore have considerable effects
- ¹⁵ on vegetation state and carbon sequestration of African ecosystems. For example, Scheiter et al. (2015) showed that different fire return intervals and early vs. late dry season management fires influence biomass and other state variables of simulated biomes. Scheiter and Savadogo (2016) showed
- ²⁰ that management can slow or accelerate tipping point behavior and hence the magnitude of vegetation lags. Targeted fire reduction could help to shift African vegetation towards higher woody cover and biomass and therefore increase the size of the African carbon sink. This would,
- ²⁵ however, lead to the loss of unique ecosystem types and their associated biodiversity and ecosystem functions. In particular grasslands and savannas are threatened by targeted fire reductions, because fire plays a pivotal role in the dynamics of these ecosystem types. Conservation
- ³⁰ management therefore has to balance trade-offs between carbon storage vs. ecosystem conservation when evaluating the role of fire as a management tool in African ecosystems. Areas of biome stability are more extensive in transient
- than equilibrium scenarios (Fig. 8), and where biome change ³⁵ occurs a higher number of biome types is simulated and a
- larger number of biome changes occurs in equilibrium scenarios (Figs. ??, ??<u>S20, S21</u>). Areas that are stable in transient but not in equilibrium scenarios can be interpreted as meta-stable legacy states. The recognition of such meta-
- ⁴⁰ stable states has important implications for conservation. Conservation of meta-stable states will require extra effort as the system may ultimately move towards a stable state. Areas of biome stability are also more extensive in no-fire than in fire scenarios, indicating the role of fire in keeping vegeta-
- ⁴⁵ tion in dynamic disequilibrium. More forests and woodlands in no-fire equilibrium scenarios strongly support the notion that in our simulations a large part of the savannas exists due to disturbance, with fire keeping vegetation in fluctuation between a mix of intermediary successional stages (Meyer ⁵⁰ et al., 2009).

4.2 Dissimilarity between same-decade partner scenarios

Euclidean distance between SDPs increased over time (Figs. 2, 3, **??**§2), which was more pronounced in fire than in nofire scenarios. Such an increase in distance can be an indication of time lags in vegetation dynamics as well as of nonanalogue vegetation states. Whether the former or the latter or a combination of both causes the observed dissimilarity cannot be discerned based only on SDP comparison. A difference between RCP4.5 and RCP8.5 was found for the second half of the century, with dissimilarity in RCP4.5 only moderately rising, but further increasing in RCP8.5, where CO₂ keeps rising and climate continues to change.

The vegetation formations most at risk are savannas and woodlands due to their meta-stability. They show highest dissimilarity between transient and equilibrium state (compare Figs. 3, ?? S4 and 8 for RCP8.5, and Figs. ??, ?? S2, S5 and 8 for RCP4.5), which implies that they are farthest from their equilibrium stage and therefore most at threat to experience change even after a stabilization of climate and CO₂ 70 concentrations. Savannas are disturbance-driven systems that are subject to continuous fluctuations caused by abiotic and biotic disturbances. Due to these non-equilibrium processes that characterize savannas, they are non-equilibrium systems that fluctuate around a mean state classifying them as savan-75 nas (Gillson, 2004). If climate change deflects savannas to a degree where this mean state changes from savanna to woodland or forest, they additionally may become a disequilibrium vegetation formation, i.e., a vegetation formation that does not correspond to the new equilibrium state demanded 80 by the forcing regime. They will then be a remnant of a foregone forcing system due to a relaxation time that exceeds the time it took the forcing to change. It is likely that this disequilibrium state will entail leading-edge as well as trailing-edge dynamics. Leading-edge effects include lags due to migra-85 tion and local population built-up and succession, whereas trailing edge effects are caused by delayed local extinctions and slow losses of ecosystem structural components (Svenning and Sandel, 2013). Our results indicate that savannas are particularly sensitive to future change of environmental drivers, because in fire-scenarios, differences in savanna tree cover were the dominant driver for SDP dissimilarity for 25 to 40% of African non-desert area (Fig. 4). Our results therefore suggest that savannas are likely to become disequilibrium vegetation formations and therefore will need special 95 focus in conservation management.

4.3 Dissimilarity between closest-decade partners

Increasing lag times between CDPs (Fig. 5a) and increasing dissimilarity of SDPs over time (Fig. 2) are a sign that environmental drivers change faster than vegetation can adapt. ¹⁰⁰ This agrees with findings of Jezkova and Wiens (2016) that rates of change in climatic niches in plant and animal popula-

tions are much slower than projected climate change, posing a threat in particular to tropical species. Extreme lag times can therefore indicate areas where environmental drivers change at a particularly high rate, where transient vegetation

- 5 is in a meta-stable state, and where future tipping of vegetation into alternative stable states is likely. Conversely, areas with low lag times can either indicate low rate of change in environmental drivers at the regional scale, or indicate vegetation that is particularly resistant to changing environmental
- ¹⁰ conditions. In both cases, small vegetation changes are sufficient to stay close to the anticipated equilibrium state, either because change in environmental drivers is weak and does not require much change in vegetation, or because equilibrium vegetation is stable across a wide range of environments tal drivers. Lag size can therefore be explained by combined by co
- evaluation of change in environmental drivers and vegetation resistance.

Combining information on vegetation lag time with residual distance between CDPs (Fig 5 a and b) reveals that tran-

²⁰ sient vegetation states are likely non-analogue to any simulated equilibrium state. If transient vegetation states were on a time-shifted trajectory of equilibrium vegetation states, residual distances between CDPs should be approximately zero. This is not the case in our comparison of CDPs (Fig. 25 5b), where spatially averaged residual distance ranges between 0.5 and 1.5 depending on scenario and decade. Spatially explicit evaluation of simulations with fire showed

that areas of particularly high residual distance (Figs. 6b,d,f, ??bS10b,d,f) were mostly located in savanna and wood-20 land areas to the north and south of the Congo basin, in

- East Africa and eastern South Africa. Fire caused more pronounced residual distances between CDPs than found in nofire scenarios, where areas of pronounced dissimilarity only start started to emerge towards the end of the century (Figs.
- ³⁵ ??bS9b,d,f, ??bS11b,d,f). This is a strong indication that disturbances can help to keep vegetation in meta-stable intermediary successional states (Dantas et al., 2016). Comparison of residual distance patterns (Fig. 6b, d, f) with lag time patterns (Fig. 6a, c, e) reveals a connection between areas of
- ⁴⁰ pronounced residual distance and long lag times. This implies that although a closest equilibrium partner was found, this partner not only has a vegetation state that corresponds to past environmental conditions, but also is a poor match for the transient vegetation state. We deduce from this that the corresponding simulated transient vegetation actions are
- 45 corresponding simulated transient vegetation states are composite non-analogue states that cannot be described by any vegetation state achievable under equilibrium conditions.

Residual distance between CDPs is dominated by different key variables depending on location (Figs. ??, ??, ??, ⁵⁰ ??<u>S14</u>, <u>S15</u>). In scenarios including fire, differences in savanna tree cover dominated dissimilarity between CDPs in roughly a quarter to a third of African non-desert area (Fig. 7), which supports the notion that savanna and woodland areas are bi-stable states (Higgins and Scheiter, 2012; Staal ⁵⁵ et al., 2016) and therefore prone to tipping point behavior in the future (Gillson, 2015). CO₂ concentrations anticipated under RCP8.5 for the second half of the century are predicted to cause shifts from C_4 to C_3 dominance in the grass laver in extensive areas of Africa (Figs. 1c, ??S5e,f). The threshold CO₂ levels at which such a shift in dominance occurs is also influenced by growing-season temperature and water availability and additionally influenced by non-climatic factors such as fire, herbivore preferences and light availability (Ehleringer, 2005). Whether these shifts will be realized also depends on the availability of a C₃ grass species pool 65 in these areas. Environmental niche suitability alone not necessarily implies realization of niche occupancy when target organisms (in this case C₃ grasses) are absent, e.g., due to migrational lags and local dispersal limits (Dexiecuo et al., 2012). 70

Non-analogue transient vegetation states emerge due to differing response times of key processes and state variables, leading to cumulative lagged responses that act on different biodiversity components, including individuals, populations, species and communities (Essl et al., 2015a). In 75 Scheiter et al. (2020), we showed time series of different state variables at a savanna study site in South Africa that illustrated the temporal sequence of process and state variable responses from leaf-level to population level. While ecophysiological responses such as increased photosynthesis happen 80 very quickly, population-level responses are slower and respond sequentially on different time scales. This implies that vegetation in transient state is subject to multiple lags, i.e., at any given time different key variables have different individual lag times. These multiple lags make it impossible to 85 approximate transient vegetation states through equilibrium statesand result, resulting in composite non-analogue states.

The finding that future transient vegetation states deviate from any equilibrium state has implications for conservation management. Conservation managers need to decide on target ecosystem states, and whether preservation of contemporary ecosystem states will be feasible and sustainable in the future. Awareness of meta-stable vegetation states should influence decisions on suitable intervention measures, and help decide to what extent these need to be applied (Gillson, 95 2015). In this context, our study can help to identify those vegetation types and areas that are most prone to change and tipping point behavior in the face of future climate change and therefore need particular focus. We found that savannas and woodlands, or more generally speaking those sys- 100 tems where disturbance regime is important, are especially likely to exhibit multi-lags and meta-stability. This is because disturbances such as fire or herbivory cause cyclical successional resets that keep systems from converging to latesuccessional states (Meyer et al., 2007), and therefore can 105 exacerbate climate-driven lags and meta-stability (Scheiter et al., 2020). Accordingly, climate-mediated changes in disturbance regime also need consideration in conservation management, e.g., changes in fire frequency, intensity or timing of occurrence (Battisti et al., 2016). 110

4.4 Opportunities and limitations of this study

Field surveys and remote sensing data provide valuable information on vegetation status. However, they are usually limited with respect to the time span they can cover, and ⁵ they are subject to a trade-off between high spatial or high temporal resolution, as well as between high spatial resolution and spatial extent. In addition, observations are also confined to the past or present. Without reference base, it is hard to determine whether an observed vegetation state ¹⁰ is in equilibrium with environmental forcing, time-lagged,

- or non-analogue. Dynamic vegetation modeling can overcome these constraints. Moreover, the influence of specific driver variables can be studied in isolation, e.g., the effect of elevated CO_2 can be studied by keeping climate constant
- ¹⁵ (Scheiter et al., 2020). Dynamic vegetation modeling also offers the possibility to generate equilibrium vegetation states by enforcing constant or detrended drivers and allowing the model to to reach equilibrium under these conditions. These simulated equilibrium vegetation states can then be used as ²⁰ controlled reference base for simulated transient vegetation
- ²⁰ controlled reference base for simulated transferit vegetation states, but also to assess the status of observed vegetation. Enforcement of vegetation equilibrium, projection of future vegetation states, and the possibility for isolated factorial analysis of specific drivers using vegetation models therefore ²⁵ provides a unique opportunity to address knowledge gaps

that cannot be filled by observation data.

A limitation of the approach presented in this study is that climate data availability for RCP8.5 and RCP4.5 determined the starting point (in our case the 1970s) for both equilib-³⁰ rium and transient vegetation simulations. This holds the im-

- plicit assumption that transient and equilibrium vegetation state were similar at the starting point. Moreover, the conceptual setup implies that simulated lag times cannot exceed the number of decades between the 1970s and the decade of
- ³⁵ interest. Therefore, simulated distance and lag times between the historic decades and present can be underestimated and need to be seen with caution, as observed vegetation states in Africa during the 1970s were very likely not in equilibrium with environmental conditions of the 1970s. Hence, where
- ⁴⁰ lag time equals number of simulated decades, the lag time and associated Euclidean distances represent a lower limit estimate. Consequently, simulated lag times and Euclidean distances in some cases may be underestimated due to the limitation caused by the need to start simulations at the be-
- ⁴⁵ ginning of the climate data set. We are, however, confident that the general message of the simulation experiment, i.e., that transient vegetation states are non-analogue to equilibrium vegetation states, and lag behind forcing, is nonetheless valid.
- ⁵⁰ We only conducted a limited number of equilibrium simulation runs to establish equilibrium vegetation states as reference basis. The decadal-scale discretization was chosen because 13 simulation runs per scenario were determined as technically feasible while also ensuring variability in in-

put climate data. Yet, discretization could imply that residual distance between CDPs may be overestimated if the best equilibrium match to a transient vegetation state was located between two equilibrium scenarios. However, given the clear dominance of specific key variables for residual distance between CDPs, we deem it unlikely that discretization is responsible for overestimates of residual distances large enough to falsely assume non-analogue state for a given transient vegetation state. Moreover, an analysis of lag times conducted for single variables revealed a large range of variability in lag times between variables for a given transient decade, especially in the second half of the century (not shown). This is a clear sign of multi-lags that should be unrelated to discretization and therefore points to true nonanalogue transient vegetation states.

Fire in aDGVM does not account for explicit occurrence 70 of ignitions, but has heuristically been calibrated such that the ignition rates and resulting fires agree well with observed fire patterns and frequency (Scheiter and Higgins, 2009). Where occurrence of ignitions may change in the future, e.g., due to changes in fire management or occurrence 75 of lightning strikes due to climate change, aDGVM may therefore miss such changes in ignition patterns. However, given that the majority of African ecosystems are currently not ignition-limited and therefore climate and landscape connectivity combined with human fire 80 management strategies are the main limiting factors on fire occurrence (Archibald et al., 2012, and references therein), the simulated amount of fire is driven by the other two components of the fire triangle (fuel load and quality, fire weather conditions, e.g., fuel moisture). As fire intensity and 85 spread in aDGVM are linked to fuel moisture, fuel biomass and tree cover (increasing tree cover reduces fire occurrence), simulated fire regimes in the future do change in response to climate and vegetation change in a non-ignition-limited system even if changes in ignition patterns are not directly 90 captured themselves. We therefore estimate that our main findings regarding the role of fire in relation to vegetation patterns and lags would not change substantially with explicit representation of ignitions.

Due to the large number of simulation runs required ⁹⁵ for this study (56 runs in total), we only used downscaled climate output data from one Earth System Model (ESM). The results might therefore differ slightly when using climate output data from other ESMs. However, results from another study recently conducted with aDGVM for Africa using CCAM-downscaled projections from six different ESMs showed that the choice of ESM had the smallest effect on simulation outcome (Martens et al., 2020, accepted). Variation between all 24 ensemble members in that study was mainly explained by the CO₂ scenario, followed by interactions between CO₂ and RCP scenarios, while the type of ESM had only minor influence. The biomass values simulated with the downscaled MPI-ESM climatology in that study were slightly below the mean of the six ensemble members, indicating a tendency towards slightly more-than-average temperature increase and MAP decrease. This agrees with the slightly above-average Equilibrium Climate Sensitivity (ECS) value of 3.6 for MPI-ESM-LR

 ⁵ (ensemble mean: 3.2±1.3, in Tab. 9.5 of Flato et al., 2013). Given the low impact of the ESM scenario on the results and the fact that the downscaled MPI-ESM climatology used in this study lies close to the ensemble mean of different ESMs, we are confident that our results are representative although
 ¹⁰ only output from one ESM was used.

All presented simulations were conducted offline, i.e., without direct coupling between vegetation and climate. We expect that lag times, bi-stability and non-linear tipping behavior between different vegetation states could be even

- ¹⁵ more pronounced in an online-coupling experiment, because stability is likely enhanced by feedback mechanisms that foster it. For example, tropical rain forests transfer large quantities of water vapor to the atmosphere and locally create clouds and precipitation sustaining their existence even if
- ²⁰ regional-scale precipitation patterns without such feedbacks showed decreasing trends (see, e.g. Staal et al., 2018). In line with Zhu and Zeng (2014), we expect that albedo effects, canopy transpiration and evaporation, and temperature effects mitigated by vegetation could alter local to regional
- ²⁵ climate, in turn feeding back on vegetation dynamics. In semi-arid areas, such feedbacks can decide which one of several possible equilibrium states will be realized, e.g., whether grasslands or deserts will be realized as alternative stable states (Zeng et al., 2004). However, even fully coupled
- ³⁰ ESMs may be unable to predict how future feedbacks between vegetation and climate will shape terrestrial vegetation state, as shown by Bathiany et al. (2014) in the context of future Sahel greening trends simulated by three different ESMs with dynamic vegetation coupling.

35 5 Conclusions

Our results show that simulated transient vegetation states increasingly deviate from equilibrium vegetation states in both RCP scenarios, and that during the second half of the 21st century this deviation is more pronounced in RCP8.5 40 than RCP4.5. Fire additionally increased Euclidean distance

- between SDPs due to its restraining effects on vegetation succession. Individual key variables such as woody cover, grass and tree biomass, and tree height differed between transient and equilibrium scenarios, and for many regions vari-
- ⁴⁵ ables that dominated Euclidean distance between transient and equilibrium partner scenarios could be identified clearly clearly identified. Trajectories of transient vegetation change did not follow a "virtual trajectory" of equilibrium states, i.e., they are not time-shifted trajectories of equilibrium veg-
- 50 etation states, but composite non-analogue states caused by multiple lags with respect to vegetation processes and composition. Lag times between transient and most similar equi-

librium vegetation states increased over time and to a degree were found to agree with spatial patterns of maximum residual Euclidean distance between CDPs. Extremely long lag times can be indicative of high rates of change in environmental drivers, of non-analogue transient vegetation states, and of meta-stability and risk of future tipping points. Lag times toward the end of the century were most pronounced in savanna and woodland areas north and south of the Congo basin, the Sahel zone, east Africa, and eastern South Africa, with savanna tree cover frequently being the main driver of transient-equilibrium dissimilarities in these regions. Our results indicate that savanna ecosystems will be most at risk to shift for shifts towards alternative stable states and therefore need a strong focus in nature conservation management.

Code availability. The aDGVM code used to produce the results presented in this publication is available on Github (https: //github.com/aDGVM/aDGVM1_CCAM). The decadally-averaged model output data analyzed in this study as well as the 70 scripts used to conduct data analysis and to create the Figures shown in the manuscript and its supplementary material are available at https://data.mendeley.com/datasets/yx8wj84bd2/draft? a=4203fa29-d8bb-4ba2-b96a-8c5ba573facc

Video supplement. Videos showing decadal time series of results ⁷⁵ in form of maps are available as supplementary material and can be downloaded at https://data.mendeley.com/datasets/yx8wj84bd2/ draft?a=4203fa29-d8bb-4ba2-b96a-8c5ba573facc.

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Competing interests. The authors declare that they have no conflict of interest.

Disclaimer. Key words: savanna, lag effects, committed vegetation change, climate change, non-analogue vegetation

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