

Dear Editor,

please find the revised version of the manuscript. We carefully considered all the comments and suggestions by the referee, revised the manuscript accordingly, and provide point-by-point responses to all comments. Our revisions are highlighted in bold font in the manuscript. In addition, we checked the for typos and reworded the text where necessary.

We are looking forward to your decision,

Best regard,
Simon Scheiter and co-authors

Responses to RC1 by referee #1

This review is identical to review RC2 but referee #1. We therefore only respond to review RC2.

Responses to RC2 by referee #1

Schieter et al. provide a detailed assessment of the predictions of the aDGVM model in Africa focus on the question of timelags between transient and equilibrium climate states. They clearly illustrate the dependance of time lags and so-called carbon and tree cover 'debt' to the rates of change, the absolute values of CO₂ and the presence or absence of fire. They link these findings back to applications in terms of assessing global carbon budgets, and implications for model benchmarking.

In general the paper is well written and the experimental design and results are both comprehensive and clearly depicted. I have few comments on these except for mostly minor grammatical points. On the discussion points I think there is a little room for improvement. The notion of carbon debt needs a little more by way of explanation, specifically of why it is a debt and to whom the debt is owed, etc.

RESPONSE: We clarified the notation of carbon debt, see our response below.

The specific recommendation that the authors make to the land surface modeling community regarding forcing data, initialization strategies etc. are also a little vaguely worded and could do with some expansion.

RESPONSE: We clarified recommendations regarding model forcing and initialization. See also our response below.

Aside from that I think this manuscript provides a very solid illustration of the likely impact of lags on carbon cycle dynamics, and should provide a firm justification for further research into this topic.

RESPONSE: Thank you for the positive feedback.

Specific Comments

Line 12: Lag effects imply. (as opposed to implicate)

RESPONSE: We replaced 'implicate' by 'imply'.

Line 18: During Earth's history. . .

RESPONSE: We modified as suggested and added the 's'.

Line 25: Needs a reference for RCP8.5.

RESPONSE: We added a reference (Meinshausen et al. 2011).

Line 49: Is 'mismatch' the right word? (given there's no real reason they should be matched in the first place. What about 'The substantial differences between the rate of change in environmental forcing and . . . '?

RESPONSE: We agree and we modified the text as suggested.

Line 52: Delete 'in' before 'constant'

RESPONSE: We deleted 'in'.

Line 63: Not sure I'd use 'oscillate' either. I'm not sure what I would use though, because isn't all vegetation to some extent in a transient successional state?

RESPONSE: We reworded the sentence and now state 'Abrupt and repeated disturbances imply that vegetation is regularly forced into early or intermediate successional states'.

Line 65: Influences 'whether', as opposed to 'if'.

RESPONSE: We reworded as suggested and use 'whether'.

Line 90: I don't really understand this sentence. . .

RESPONSE: We reworded the sentence: 'Yet, previous studies often focused on CO2 levels predicted for 2100, assuming that both CO2 and the climate system will have stabilized by then. Studies on lag effects for a CO2 gradient ranging from pre-industrial to future levels are, however, rare.'

Line 100: I'm not sure that I totally buy that temperature increases are too heterogeneous to be interesting here? Maybe say that CO2 can be used as an illustration of the general principle which is likely extensible to shifts in other drivers?

RESPONSE: We agree that consideration of temperature and precipitation is also important and interesting. Therefore, a study considering these variables is in preparation. A further reason why we ignored these variables is that for most of the simulations, we study a CO2 gradient from 100ppm to 1000ppm and it is challenging (or even impossible) to find time series for temperature and precipitation that cover and correspond to such a large range. Hence, studies considering several climatic variables and CO2 are constrained to a much smaller range (gridded products providing continuous time series are often constrained to the period 1950 to 2099). We included this

justification as well as the suggestion of the referee: 'Datasets containing continuous time series of CO₂ between pre-industrial and future levels and associated climate are rare. While precipitation, temperature, and other environmental variables influence ecosystems, in this study we focus on CO₂ effects. We argue that CO₂ is sufficient to illustrate the general principles underlying lags between environmental conditions and vegetation.'

In the Discussion we already mention that simulations considering various climate variables are necessary and in preparation.

Line 103: What does 'typically' mean in this context?

RESPONSE: We reworded this and state 'vegetation is, in all transient scenarios that we consider, not in equilibrium ...'.

Line 112: Splitting hairs, but isn't it a contradiction to have a 'G' in aDGVM and then also say that it's outright only for savannas? 'Optimise for use in savannas' maybe?

RESPONSE: aDGVM was originally developed for savannas, but with the intention to extend it to the global scale. Therefore, the name contains the 'G'. We considered to replace 'developed' by 'optimized' as suggested. However, 'optimized' might suggest that we used numerical optimization methods to tune and calibrate the model to savanna ecosystems, but this was not done (at least for the model version used in this study). We therefore decided to keep 'developed for savannas'.

Line 121: In this era of 'trait-based' modeling, how is the shade tolerance implemented exactly? As an environmental limit on recruitment?

RESPONSE: We assume that forest trees are less affected by light competition than savanna trees, such that forest trees have higher growth rates in dense vegetation stands with intense light competition than savanna trees. In aDGVM we use parameters that describe the strength of light competition between different grass and tree types, and we used different parameters for savanna and forest trees. We added a statement to clarify this: 'Shade tolerance is implemented by different effects of light availability on tree growth rates. Light availability is in turn influenced by competitor plants. Fire tolerance is implemented by different topkill functions and re-sprouting probabilities after fire.'

Line 126: Should that be kJ/m²/s?

RESPONSE: Fireline intensity is usually given in kW per meter flaming front, which is equal to kJ/m/s. The units in the manuscript are therefore correct.

Line 173: I don't quite understand here why you used all these different CO₂ scenarios, or why you'd expect the vegetation to -not- be at equilibrium with constant forcing? Is it about cycling or oscillations in the intrinsic dynamics of the model?

RESPONSE: We expect that in transient runs, vegetation is not in equilibrium with the environment (i.e. CO₂) because exposure to these CO₂ levels is not long enough to allow vegetation to reach equilibrium. We therefore require all the equilibrium simulations for different CO₂ levels that are transgressed during transient simulations, to determine the deviance between vegetation states at transient vs equilibrium runs. In equilibrium runs, we do expect that vegetation is in equilibrium with

constant forcing. This also includes equilibrium states where state variables oscillate regularly, e.g., due to fire impacts. The different CO₂ scenarios with constant CO₂ forcing are required to identify equilibrium vegetation states for a variety of constant environmental (i.e. CO₂) conditions. In addition, we simulated transient scenarios with increasing and decreasing CO₂ and different rates of change. We checked and reworded the text to make clear why we require all these simulations.

L178: Why was a smoothing algorithm needed? To smooth over stochastic outputs?

RESPONSE: Simulations for equilibrium conditions were only conducted for a set of CO₂ concentrations (100ppm, 150ppm, 200ppm, ..., 1000ppm). In contrast, transient simulations provide model results for a much higher resolution of CO₂ levels between 100ppm and 1000ppm (depending on the rate of change of CO₂). To be able to calculate differences between transient and equilibrium vegetation states for the entire CO₂ gradient, we not only need values at 100, 150, 200ppm, ... in equilibrium simulations, but also values in between. Therefore, we applied the smoothing algorithm. In addition, as mentioned by the referee, smoothing also reduces stochasticity in model outputs. We reworded the text to clarify why we apply smoothing.

L218: Were there 200 replicates for all runs, or just for the study site in SA? (and if so, why?)

RESPONSE: The 200 replicates were only done for the study site, but not for continental-scale simulations. We conducted replicate runs because processes such as fire occurrence or demographic processes are stochastic in aDGVM. Averaging across these replicates allows us to reduce stochasticity and to obtain more robust responses of various state variables. For continental-scale simulations, we typically consider responses for different biomes, i.e., we average over space. Replicate simulation runs were therefore not conducted due to limitations on computation time. For the continental scale simulations we added: 'For continental-scale simulations, we only conducted one model run for each scenario, but no replicates. This single run is sufficient, as we aggregate model results per biome in our analyses.'

L250: I really like this figure. . .Can you make it so that the text doesn't overlap the orange lines?

RESPONSE: We modified Fig 4 to avoid overlap between text and lines.

L275: Why does fire slow down the transition? Is it because systems are stuck in stable equilibria one way or another?

RESPONSE: Yes, we argue in the discussion that fire prevents vegetation transitions and keeps vegetation in the fire-driven state. We also included a short explanation in the results section: 'Longer times in the presence of fire can be attributed to hysteresis effects. High fire activity traps vegetation in a fire-driven state and prevents biome transitions into alternative vegetation states.'

L285: The terminology of 'debt' is slightly confusing to me, especially as the quantities of 'debt' are negative. Does that mean there is negative debt? And to whom is the debt owed? The atmosphere or the ecosystem? I guess a negative carbon debt is a promise that the system will take up more CO₂ in the future?

RESPONSE: Debt refers to carbon storage potential of vegetation that has not been realized yet. It indicates that vegetation has the potential to sequester more carbon under given CO₂ levels than

transient simulation suggest. The potential carbon storage for given CO₂ is defined by the equilibrium simulations. In figures, we plotted debt with negative values to clearly distinguish from surplus (Fig A2) and to make clear that vegetation is committed to substantial changes even if the climate system stabilizes. We revised the definition of carbon debt in the revision (in sec. 3.4) and now state: 'We define debt as carbon storage potential that has not been realized yet, and carbon that the atmosphere owes to vegetation'. We prefer to keep the negative sign to make clear that potential carbon and tree cover exceed carbon and tree cover in transient runs.

L315: I'm tripped up again by the use of 'typically'... Do you mean in the transient simulations? By implication in the real world? Also technically I guess this is a prediction, rather than an illustration, so many change 'show' to something less forceful.

RESPONSE: Yes, we mean that vegetation in transient simulations is not in equilibrium. We reworded the sentence to avoid 'typically' and in the revision we state 'Using a dynamic vegetation model, we predict that vegetation exposed to transient environmental forcing is not in equilibrium with environmental conditions ...'. In the discussion, we also provide references reporting lag effects in empirical experiments.

L320: Also change 'previous findings' to 'previous model results' or suchlike.

RESPONSE: We reworded as suggested to 'with our previous model results indicating that ...'.

L325: I feel like this section is missing a statement on what, if any, other studies have had to say on this topic, for Africa or elsewhere. Or indeed, is this type of analysis totally novel?

RESPONSE: The aim of this paragraph is to put the results presented in this study into the context of previous aDGVM studies and highlight the novelty within the 'aDGVM world'. Yet, we discuss the novel results in the context of previous studies in later sections of the discussion. We therefore prefer to keep this section focused on aDGVM. We slightly reword the section by adding references to aDGVM to make clear that it only refers to aDGVM results.

L328: This justification for why the fire runs have greater lags should perhaps come earlier in the manuscript.

RESPONSE: We added an explanation why fire increases lags in the results. See also our response to comments regarding L275.

L358: This needs a little more clarification. I.e. "(the strong CO₂ effect) can compensate for other predicted changes in climate drivers, e.g. reduced rainfall"

RESPONSE: We reworded as suggested: '... that the strong CO₂ effects can compensate for other predicted changes in climate drivers, such as reduced rainfall'.

L357: Maybe expand on what a high CO₂ sensitiviy might mean for the results of this paper?

RESPONSE: We highlighted the implications of CO₂ sensitivity. In particular, we added: 'If aDGVM overestimates the strength of CO₂ fertilization effects and the sensitivity of vegetation to elevated

CO₂, the size of carbon debt due to lag effects may be overestimated, while the lag size may be underestimated. We are however confident that even with reduced CO₂ sensitivity the overall response pattern would remain, although the quantities might change.'

L385: change to :prevents both savanna and forest trees recruitment"

RESPONSE: We reworded this statement (in response to referee 2): 'Fire rarely occurs in simulated forests, and therefore they reach equilibrium faster than other biome types. Fire activity in forests is sufficient to slightly increase times to reach equilibrium when compared to simulations with fire suppressed.'

L398: Need a reference for 'as is currently often the case'.

RESPONSE: We deleted 'as is currently often the case', because this statement is too bold.

L420: Would it make sense to frame the carbon debt here in terms of the overall carbon budgets of the different RCPs? For example, if emissions stabilises at the end of RCPxx, then the ecosystems would continue to keep absorbing carbon to get to their equilibrium ecosystem state and re-absorb xx PgC from the system?

RESPONSE: Good suggestion, we have reworded and reframed the paragraph as suggested: 'If emissions follow the RCP 2.6 scenario and stabilize after 2100, then ecosystems in Africa would continue to absorb 9 PgC or 18 PgC from the atmosphere in the presence or absence of fire to reach an equilibrium state with environmental conditions. In contrast, ecosystems would absorb 47.5 PgC or 60 PgC in the presence or absence of fire in the RCP 8.5 scenario.'

L439: I don't really understand this part. How can modifications to the initial climate conditions have an impact on the successional stage? Also, I think it's fairly standard to do pre-industrial spin-up and then transient simulations to the present day. Are you proposing an alternative approach to climate drivers here?

RESPONSE: We argue that initial vegetation states (rather than climate) in the model should agree with successional states of vegetation at the beginning of the transient simulation run. This can for example be achieved by considering land-use history, or by ensuring that vegetation height or age is in agreement with observation and not only variables such biomass, NPP, GPP. An approach using forest height for initialization has for example been adopted by Rödig et al. (2017) for initialization of the FORMIND model. We revised this paragraph and added the example by Rödig et al. (2017): 'Rödig et al. (2017) used the Simard et al. (2011) vegetation height product to match observed and simulated successional stages in the FORMIND model.'

Rödig, E, Cuntz, M, Heinke, J, Rammig, A, Huth, A. (2017) Spatial heterogeneity of biomass and forest structure of the Amazon rain forest: Linking remote sensing, forest modelling and field inventory. *Global Ecol Biogeogr.* 26: 1292– 1302.

L444: Further, given that we need to run transient simulations with ramping CO₂, that is slightly at odds with initializing with contemporary observations.

RESPONSE: We don't see a contradiction here, because initialization can also consider transient simulations. For example one could use simulated and observed timeseries of LAI or NDVI for model benchmarking. Such benchmarking would require the use of transient climate and CO₂ forcing.

L474: Maybe cite Julia Nabels work with TREEMIG as illustrative of the complexities of the implementation of seed dispersal?

RESPONSE: We cited the Nabel et al. (2013) Ecological Modelling paper: 'Nabel et al. (2013) used the TreeMig model to illustrate the complexity of simulating seed dispersal and migration in heterogeneous and variable environments.'

L500: Again, I'd argue that it 'predicts' or 'projects' or 'indicates', but perhaps not that it 'shows'.

RESPONSE: As suggested, we replaced 'shows' by 'indicates' and 'predicts' in the Conclusions.

Responses to RC3 by referee #2

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General Comments

This paper considers the lag between a transient and committed vegetation state under changing CO₂ and due to the disturbance effect of fire, using the aDGVM. In my view the paper is well written, clearly structured, and presents relevant and interesting results. The study is structured around 4 hypotheses which consider the current vegetation state, the impact of rate of change, the extent of change, and the effects of fire, which are novel and useful. The methods are explained clearly. The definition of equilibrium presented in equation 1 appears logical, although I wonder if there is already a published method for this that has been used in other studies. The results are presented in a logical way, and the text supports the figures throughout. I believe the conclusions are a valid interpretation of the results and that they are substantial and useful. I have some small comments on specific sections as outlined below, but otherwise I think the paper is of very good quality.

RESPONSE: Thank you for the positive feedback. Regarding the equilibrium conditions, please see our response below.

Specific Comments

Line 19 – Include the time period for the Devonian period to give context

RESPONSE: We added the period (419.2-358.9 Ma).

Line 28 - Paleocene-Eocene Thermal Maximum (PETM), a period with high carbon emissions some 56 million years ago – It would be nice to see a little more about this period and explain why the carbon emissions were high

RESPONSE: We modified the text and added "During the PETM, temperature increased by approximately 5-8K due to massive carbon release likely caused by volcanic activity. As temperature

increased by 6K within a 20ky period, the PETM is often considered as best analogue for current and future climate change (Zeebe 2016)”.

Line 50 – is there a reference for this definition of equilibrium? I wonder if there is another method available which has been used in already published studies that can be referred to. I can see the logic of this method but some extra reference to existing methodology, and why it has been altered if necessary, would make this stronger

RESPONSE: We screened the ecological and land surface modeling literature, particularly the papers cited in our manuscript, but we did not find a similar mathematical definition. Essentially, our approach reflects steady state conditions as used in calculus, i.e., the first derivative has to be zero. As simulated variables are stochastic, we relax this condition by requiring that the first derivative (approximated by the difference between values of subsequent years) has to be smaller than a predefined value for a certain period.

Section 2.1 Line 110 – There aren’t many PFTs represented in aDGVM. However it is mentioned in the discussion that this may cause an underestimation in lag time in forests, and as the study is focused on one savanna location I think it is enough for this study

RESPONSE: aDGVM only simulates two tree PFTs, savanna trees and forest trees and as mentioned by the referee and in the discussion, this prevents a detailed representation of successional dynamics and changes in the community composition. Therefore, our simulations may underestimate lag size in forests. However, despite the low number of PFTs, simulated communities and functional diversity may change in terms of population dynamics (i.e., number of trees, height and age structure), and in terms of phenology and carbon allocation patterns. These features are dynamic in aDGVM and allow simulated plants to adjust to changing environmental conditions. Note that most of our analyses were conducted for Africa at the continental scale, only in Fig 10 we used a site that is currently a savanna (but grassland or forest under low or high CO₂, respectively).

Line 136 – the performance of aDGVM has been evaluated in terms of vegetation, but what about fire? It would be good to see some evidence that the fire model is reliable, at least for the location picked

RESPONSE: In Scheiter and Higgins (2009) GCB and Scheiter et al. (2015) New Phytologist, we showed that aDGVM can reproduce broad patterns of fire activity in Africa and Australia. At local level, Governder et al. (2006) states that natural fire return intervals in Kruger National Park, South Africa, are between 4 and 5 years, and previous aDGVM simulations show that simulated return intervals are in the same order of magnitude. We did, however, not compare simulated fire activity with paleo records to assess if aDGVM can simulate fire regimes at pre-industrial or even lower CO₂. We added a statement: “In Scheiter and Higgins (2009) and Scheiter et al. (2015) we showed that aDGVM can simulate broad patterns of fire activity in Africa and Australia, respectively.”

Section 3.6 Line 300 – can you give an explanation as to why the carbon debt continues to increase when the tree cover debt decreases?

RESPONSE: Both in Fig 7 and Fig 9 tree cover debt saturates because tree cover is limited by 100%, i.e., full canopy closure. As CO₂ increases, more and more grid cells reach closed canopy. Tree cover debt is constrained and saturates. In contrast, even if canopy closure occurs in a grid cell, biomass can further increase, for example by higher tree numbers and taller trees. Therefore, tree biomass

debt continues to increase. We added an explanation in the results, sec. 3.4: "Tree cover debt saturates decreases at higher CO₂ mixing ratios because tree cover in a grid cell is constrained by canopy closure. At higher CO₂ mixing ratios large fractions of Africa reach a forest state and canopy closure. Tree cover debt in these areas is zero. In contrast, biomass in a grid cells and hence biomass debt can further increase even if canopy closure occurs."

Fig 3 Bar plot – if fire is suppressed in forests (L384) would you not expect the forest results in figure 3 a and b to be the same, or would there still be some fire?

RESPONSE: Yes, there would still be some fire, especially in forest areas with lower tree cover. However, fire return intervals are low in these regions. We reworded: "Fire rarely occurs in simulated forests, and therefore they reach equilibrium faster than other biome types. Fire activity in forests is, however, sufficient to slightly increase times to reach equilibrium in comparison to simulations with fire suppressed."

Also from figure 3, I think it would be worth quantifying the lag time and noting in the abstract how much longer it takes to reach equilibrium per X increase in CO₂, which is an important result

RESPONSE: Note that Fig 3 shows times required to reach an equilibrium state and not lag size. As suggested we calculated the relation between CO₂ and times required to reach equilibrium, specifically we calculated averages across all biomes for simulations with fire and without fire. We added in the results and the abstract: "When averaged across all biomes and simulations with and without fire, times to reach an equilibrium state increase from approximately 242 years for 200 ppm to 898 years for 1000 ppm."

Line 256 – Lags are larger at low and intermediate CO₂ mixing ratios and decrease at higher CO₂. How does this fit with 'The time until vegetation reaches an equilibrium state. . . Increase[s] with CO₂' (L236)

RESPONSE: We do not see a contradiction in these statements as they describe different results. L236 describes times to reach equilibrium states in different biome types (Fig 3), whereas L256 describes lags between transient and equilibrium simulations (Fig 4).

Line 270 / Figure 5 and 6 – It follows that the time taken for the transient simulations to reach equilibrium is measured, but how is the time taken to reach equilibrium in equilibrium simulations measured? In other words what is the equilibrium simulation initialised from?

RESPONSE: It is initialized with the 'standard' method of initializing aDGVM, i. e., 100 trees with random biomass below 150 kg (uniform random distribution) and grass biomass of 0.01 kg/m². See also section 2.4. We added grass and tree biomasses used for initialization in the Methods section.

Line 289 – I think specifying that the debt is "larger" would be better than "higher" given the values are increasingly negative

RESPONSE: We reworded as suggested and replaced 'higher' by 'larger'.

Technical Comments

Line 18 – Earth's history?

RESPONSE: We added the s.

Line 25 – Define RCP (Representative Concentration Pathway)

RESPONSE: We defined RCP as suggested.

Line 91 – Does the a in aDGVM stand for anything?

RESPONSE: adaptive Dynamic Global Vegetation Model, it is defined in sec 2.1 and we now write it out in l. 91 as well.

Line 116 - "This approach allows to model how herbivores" – allows us to model?

RESPONSE: We corrected as suggested.

Line 228 – "C4 or C3-dominated vegetation if fire is present or absent" respectively.

In most of the figures C4 grassland and savanna is labeled, but woodland and forest is not labeled as C3 despite being referred to in the text as C3

RESPONSE: We use two different notations: the different biome types (e.g. C3 grassland, C4 grassland, forest) and C3/C4 dominated biomes where we aggregate several biomes. We do not label woodland and forest explicitly as C3 woodland or C3 forest, because these biomes are always dominated by C3 trees; a C4 dominated forest state is not possible. We checked the manuscript to ensure that there is no ambiguity and we modified the biome classification section to define C3 and C4 dominated biomes.

African biomes are most sensitive to changes in CO₂ under recent and near-future CO₂ conditions

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Abstract. Current rates of climate and atmospheric change are likely higher than during the last millions of years. Even higher rates of change are projected in CMIP5 climate model ensemble runs for some RCP scenarios. The speed of ecological processes such as leaf physiology, demography or migration, can differ from the speed of changes in environmental conditions. Such mismatches imply lags between the actual vegetation state and the vegetation state expected under prevailing environmental conditions. Here, we used a dynamic vegetation model, the aDGVM, to study lags between actual and expected vegetation in Africa under changing atmospheric CO₂ mixing ratio. We hypothesized that lag size increases with more rapidly changing CO₂ mixing ratio as opposed to slower changes in CO₂, and that disturbance by fire further increases lag size. Our model results confirm these hypotheses, revealing lags between vegetation state and environmental conditions and enhanced lags in fire-driven systems. Biome states, carbon stored in vegetation and tree cover in Africa are most sensitive to changes in CO₂ under recent and near-future levels. **When averaged across all biomes and simulations with and without fire, times to reach an equilibrium vegetation state increase from approximately 242 years for 200 ppm to 898 years for 1000 ppm.** These results have important implications for vegetation modellers and for policy making. Lag effects **imply** that vegetation will undergo substantial changes in distribution patterns, structure and carbon sequestration even if emissions of fossils fuels and other greenhouse gasses are reduced and the climate system stabilizes. We conclude that modelers need to account for lag effects in models and in data used for model testing. Policy makers need to consider lagged responses and committed changes in the biosphere when developing adaptation and mitigation strategies.

Copyright statement.

1 Introduction

Climate and the composition of the atmosphere have been subject to substantial changes during **Earth's** history (Beerling and Royer, 2011). For instance, paleo-records indicate that the expansion of forest vegetation during the Devonian (**419.2-**

358.9 Ma) dramatically reduced the atmospheric CO₂ mixing ratio (Le Hir et al., 2011) and Milankovitch cycles cause periodic changes in the climate system and the atmosphere on millennial time scales (Milankovic, 1941; Hays et al., 1976). In addition to natural variability, anthropogenic emissions of CO₂ and other green house gasses have caused global warming during the last decades. The 5th assessment report of the Intergovernmental Panel of Climate Change (IPCC) indicates further changes 25 of the climate system in the future (IPCC, 2013, 2014a, b). Since the pre-industrial era, CO₂ increased from approximately 280 ppm to a current value of approximately 400 ppm, and the **Representative Concentration Pathway (RCP) 8.5** climate change scenario projects CO₂ increases to approximately 950 ppm by 2100 (Meinshausen et al., 2011). Proxy data suggest that such CO₂ levels have not occurred since the Eocene/early Oligocene, more than 30 Myr ago (Beerling and Royer, 2011). Current carbon emission rates are unprecedented and higher than during the Paleocene-Eocene Thermal Maximum (PETM), a 30 period with high carbon emissions some 56 million years ago (Zeebe et al., 2016). **During the PETM, temperature increased by approximately 5-8K due to massive carbon release likely caused by volcanic activity. As temperature increased by 6K within a 20ky period, the PETM is often considered as best analogue for current and future climate change (Zeebe et al., 2016).**

The CO₂ increase projected in the IPCC RCP 8.5 scenario corresponds to an average increase of more than 6 ppm per year 35 until the end of the century. In comparison, an increase from approximately 190 ppm during the last glacial maximum to a pre-industrial value of 280 ppm during 26,000 years corresponds to an average rate of 3.5×10^{-3} ppm per year (Barnola et al., 1987). Within this period, Monnin et al. (2001) report peak rates of 2.7×10^{-2} ppm per year in a 300 year period at 13.8ky B.P. A decrease from approximately 900 ppm to 300 ppm during the Oligocene took approximately 10 million years (Beerling and Royer, 2011), which translates into an average rate of -6×10^{-5} ppm per year. As the current rates of CO₂ change are likely 40 unprecedented, no proxy analogues exist to deduce vegetation responses to the ongoing atmospheric and climatic changes (Prentice et al., 1993; Foster et al., 2017). Due to the coarse temporal resolution of many paleo-records, it is, however, still challenging to calculate rates at decadal or even finer temporal resolution for a direct comparisons of past, present and future rates of change (but see Zeebe et al., 2016).

Environmental conditions such as CO₂, precipitation, temperature or soil properties influence plant ecophysiological processes 45 that ultimately drive plant growth, demographic rates, competitive hierarchies, community assembly and biogeographic patterns across the Earth's land surface. These processes are sensitive to both the actual values and to variation of environmental drivers. Different ecological processes operate at various temporal and spatial scales (Penuelas et al., 2013) and determine how ecosystems respond to environmental change. On short time scales (days to months), plasticity allows photosynthesis (Gunderson et al., 2010), carbon allocation and other processes to adapt to changes in environmental conditions (Penuelas et al., 50 2013). At intermediate time scales (years to decades), vegetation is influenced by demographic rates, succession, dispersal, migration and community assembly (Penuelas et al., 2013). At long time scales (centuries and longer), evolutionary processes allow plants to adapt to changing environments and speciation and extinction modify the species pool.

The substantial difference between the rate of change in environmental forcing and ecological responses of vegetation implies 55 that vegetation is not in an equilibrium state with the environment, that is a state where averages of key ecosystem functions such as carbon and water fluxes or vegetation structure remain constant if averages of environmental drivers remain

constant. Rather, forcing lags emerge where the transient vegetation state lags behind rates of change of environmental drivers (Bertrand et al., 2016). Quantifying these lags is crucial for our understanding of ecosystem dynamics because they imply that the observed vegetation state does not fully reflect prevailing environmental conditions and that ecosystems are committed to further changes even if environmental conditions stabilize (Jones et al., 2009; Port et al., 2012). We expect that the size of the 60 lag between equilibrium and transient vegetation states will be influenced by actual values of environmental conditions, the rate at which they change, and by the plant community composition and community-specific ecological processes. Vegetation might have been closer to equilibrium with the environment, with smaller lags, in the past when rates of environmental changes were low, while it is committed to large changes under current and future, rapidly changing climate.

Disturbances such as fire, drought, heat waves or herbivory rapidly modify vegetation states and thereby create disturbance 65 lags, i.e., deviations from the committed vegetation state purely defined by environmental conditions in the absence of disturbance. Lag size is related to the intensity of the respective disturbance. Abrupt and repeated disturbances imply that **vegetation is regularly forced into early or intermediate successional states**. In such a situation, vegetation may never reach the final successional stage but it may be in a dynamic equilibrium state. The ecological resilience of an ecosystem (Holling, 1973; Walker et al., 2004) influences **whether** the system can return into a pre-disturbed state or **whether** it tips into an alternative 70 vegetation state (Scheffer et al., 2001; van Nes and Scheffer, 2007; Veraart et al., 2012). Savannas exemplify an ecosystem type that is strongly influenced by and often reliant on disturbances (Scheiter and Higgins, 2007), and subject to both disturbance and forcing lags. In savannas, fire reduces woody biomass to the benefit of grasses. However, once fire disturbance is removed, fire-driven savannas are committed to transition to higher tree cover (Sankaran et al., 2004; Higgins et al., 2007; Higgins and Scheiter, 2012). It has been argued that alternative vegetation states are possible in areas currently covered by savannas, because 75 depending on their history and fire activity, they can adopt an open savanna state or a closed forest state (Higgins and Scheiter, 2012; Moncrieff et al., 2014). We expect that in areas that allow both savanna and forest states, fire amplifies forcing lags. In such systems, environmental forcings need to cross a tipping point such that vegetation shifts from one ecosystem state into an alternative state (Scheffer et al., 2001).

Deciphering and quantifying lags between transient and equilibrium vegetation states is highly relevant for understanding 80 biogeographic patterns and associated biogeochemical fluxes as well as for conservation and management. The importance of transient states and forcing lags was already highlighted in the 1980s, but often in the context of paleo-ecological studies (Davis and Botkin, 1985; Davis, 1986; Webb III, 1986). For instance, Davis and Botkin (1985) found lagged responses of various species in response to cooling using the JABOWA vegetation model. Changes in the dominance of species were only visible 50 years after cooling. Several empirical studies quantified lag effects, for example in forests (Bertrand et al., 2011, 85 2016; Liang et al., 2018), bird and butterfly communities (Devictor et al., 2012; Menendez et al., 2006), or in tropical forests at the global scale (Zeng et al., 2013). Most of these studies investigated lags with respect to recent temperature changes or in mountain areas with steep temperature gradients. Lag effects were also identified in response to drought (Anderegg et al., 2015). More recently, lag effects received more attention in the context of future climate change. It has been argued that lag 90 effects need to be taken into account when we aim at forecasting future changes in the biosphere and at developing management or mitigation strategies (Svenning and Sandel, 2013; Bertrand et al., 2016). Lag effects imply that vegetation features such as

carbon stocks or tree cover are committed to changes that will be ongoing even if anthropogenic emissions of greenhouse gasses level off and the climate system stabilizes (Jones et al., 2009; Port et al., 2012; Huntingford et al., 2013; Pugh et al., 2018). **Yet, previous studies often focused on CO₂ levels predicted for 2100, assuming that both CO₂ and the climate system will have stabilized by then. Studies on lag effects for a CO₂ gradient ranging from pre-industrial to future levels are, however, rare.**

In this study, we use the **adaptive Dynamic Global Vegetation Model (aDGVM)**, a complex dynamic vegetation model developed for tropical grass-tree ecosystems (Scheiter and Higgins, 2009) to investigate how slow and fast changes in atmospheric CO₂ and fire regimes influence transient and equilibrium distributions of grasslands, savannas and forests in Africa, as well as associated biomass and tree cover. aDGVM is an appropriate modeling tool in this context because it explicitly simulates the rate at which vegetation changes based on underlying ecophysiological processes and underlying environmental conditions. It allows us to simulate both the equilibrium vegetation state for given CO₂ mixing ratios, and transient vegetation dynamics, succession and adaptation of photosynthesis, evapotranspiration, carbon allocation and phenology. We focus on atmospheric CO₂ because it is a main driver of plant growth and both empirical and modeling studies have shown substantial impacts on vegetation growth (Scheiter and Higgins, 2009; Buitenhof et al., 2012; Higgins and Scheiter, 2012; Donohue et al., 2013; Hickler et al., 2015). The CO₂ mixing ratio is almost similar at the global scale while other key drivers of plant growth such as rainfall and temperature vary in space (i.e. between different regions of the world), time (i.e. inter- and intra-annual variability) and between different climate models within the CMIP5 ensemble. **Datasets containing continuous time series of CO₂ between pre-industrial and future levels and associated climate are rare. While precipitation, temperature, and other environmental variables influence ecosystems, in this study we focus on CO₂ effects. We argue that CO₂ is sufficient to illustrate the general principles underlying lags between environmental conditions and vegetation.**

We test the following predictions: (1) **vegetation is, in all transient scenarios that we consider, not in equilibrium with the environment (in this study with atmospheric CO₂)**, and forcing lags occur; (2) the size of the forcing lag is influenced by the rate of change of CO₂; (3) disturbance lags due to fire amplify forcing lags caused by CO₂ change such that biomes with high fire activity will lag further behind environmental changes; (4) the sensitivity of vegetation to changes in the atmospheric CO₂ mixing ratio is sensitive to the absolute value of the CO₂ mixing ratio. We explore the consequences of these predictions for projections of climate change impacts on African vegetation under rates of CO₂ change as predicted in RCP 2.6, 4.5, 6.0 and 8.5, examining the difference between transient and equilibrium vegetation states as the CO₂ mixing ratio change.

2 Methods

2.1 Model description

We used the aDGVM (adaptive Dynamic Global Vegetation Model, Scheiter and Higgins, 2009), a dynamic vegetation model developed for tropical grass-tree systems. The aDGVM integrates plant physiological processes generally used in dynamic global vegetation models (DGVMs, Prentice et al., 2007) with processes that allow plants to dynamically adjust leaf phenology and carbon allocation to environmental conditions. The aDGVM is individual-based and simulates state variables such as

biomass, height and photosynthetic rates of individual plants. This approach allows us to model how herbivores (Scheiter and Higgins, 2012), fire (Scheiter and Higgins, 2009) and land use (Scheiter and Savadogo, 2016; Scheiter et al., 2019) impact individual plants as a function of plant traits. Grasses are simulated by two super-individuals, representing grasses beneath or between tree canopies.

The aDGVM simulates four plant types (Scheiter et al., 2012): C₃ grasses, C₄ grasses, fire-sensitive forest trees and fire-tolerant savanna trees. The differences between C₃ and C₄ grasses are mainly based on physiological differences between C₃ and C₄ photosynthesis. Savanna and forest tree types differ in fire and shade tolerance (Bond and Midgley, 2001; Ratnam et al., 2011). **Shade tolerance is implemented by different effects of light availability on tree growth rates. Light availability is in turn influenced by competitor plants. Fire tolerance is implemented by different topkill functions and re-sprouting probabilities after fire (Scheiter et al., 2012).** The forest tree type is implemented to be more shade-tolerant but less fire-tolerant whereas the savanna tree type is less shade-tolerant but more fire-tolerant. Hence, forest trees dominate in closed ecosystems and in the absence of fire, whereas savanna trees dominate in fire-driven and more open ecosystems.

In the aDGVM, fire intensity is modeled as a function of fuel loads, fuel moisture and wind speed (Higgins et al., 2008). Fire spreads when (1) the fire intensity exceeds a threshold value of 300 kJ/m/s, (2) a uniformly distributed random number exceeds the daily fire ignition probability p_{fire} (1%), and (3) an ignition takes place. Ignition sequences, which indicate days when ignitions take place, are randomly generated. This fire model ensures that fire regimes are influenced by fuel biomass and climate. However, fire ignitions and the ignition probability are not linked to anthropogenic ignitions or the occurrence of lightning. Fire consumes aboveground grass biomass, whereas the response of trees to fire is a function of tree height and fire intensity (topkill effect, Higgins et al., 2000). Seedlings and juveniles in the flame zone are damaged by each fire while tall trees with tree crowns above the flame zone are largely fire-resistant and only damaged by intense fires. Grasses and topkilled trees can regrow from root reserves after fire (Bond and Midgley, 2001). Fire influences tree mortality indirectly due to its negative effect on the carbon balance. In the aDGVM, a negative carbon balance increases the probability of mortality.

The performance of the aDGVM was evaluated in previous studies. Scheiter and Higgins (2009) and Scheiter et al. (2012) show that the aDGVM successfully simulates the distribution of major vegetation formations in Africa in good agreement with observations. Scheiter and Higgins (2009) show that the aDGVM can simulate biomass dynamics observed in a long term fire manipulation experiment in the Kruger National Park (Experimental Burn Plots, Higgins et al., 2007). In Scheiter and Savadogo (2016) we showed that a slightly adjusted model version can reproduce grass biomass and tree basal area under different grazing, harvesting and fire treatments in Burkina Faso. **In Scheiter and Higgins (2009) and Scheiter et al. (2015) we showed that aDGVM can simulate broad patterns of fire activity in Africa and Australia, respectively.**

2.2 Biome classification

We classify vegetation into biome types using the classification scheme presented in Scheiter et al. (2012) and used in previous aDGVM studies. When grass biomass in a simulated grid cell is less than 0.5 t/h and total tree cover is less than 10%, vegetation is classified as desert or barren. When tree cover is less than 10% and grass biomass exceeds 0.5 t/ha, vegetation is, depending on the ratio of C₃ to C₄ grasses, classified as C₃ or C₄ grassland. At intermediate tree cover between 10% and 80%, the

ratio of C₃ to C₄ grass biomass and the cover of savanna and forest trees are used for classification. Vegetation is classified as a woodland if forest tree cover exceeds savanna tree cover, whereas vegetation is classified as savanna if savanna tree
160 cover exceeds forest tree cover. We distinguish between C₃ savanna and C₄ savanna (**hereafter simply denoted as savanna**), depending on the ratio of C₃ to C₄ grasses. Vegetation is classified as forest when tree cover exceeds 80%, irrespective of tree type and grass biomass. **For simplicity, we aggregate biomes into C₃-dominated biomes (woodlands and forests) and C₄-dominated biomes (C₄ grasslands and C₄ savannas).**

2.3 Equilibrium conditions for aDGVM

165 We assume that an aDGVM state variable V_i at time i (see next paragraph for state variables used in the analysis) is in equilibrium if

$$\sum_{i=Y-l+1}^Y |V_i - V_{i-1}| < \epsilon, \quad (1)$$

where Y is the current year of the simulation, l is the number of years used for the calculation of equilibrium conditions (we use $l = 30$) and ϵ is a threshold defining the narrowness of the equilibrium (we use $\epsilon = 0.001$). Trial simulations show that
170 these values allow vegetation to reach equilibrium within feasible model simulation runtime. Using different threshold values changed the time required to reach the equilibrium state but did not change our basic results. Choosing ϵ too small will identify model stochasticity as deviation from equilibrium, whereas choosing ϵ too large will fail to correctly identify the onset of equilibrium conditions. Systematic sensitivity analyses for ϵ and l were not conducted.

We used four modeled state variables V to characterize equilibrium states: savanna tree cover, forest tree cover, aboveground
175 tree biomass and C₃:C₄ grass ratio. We assume that the model is in equilibrium when all four variables fulfill eq. (1) simultaneously and we record the first year when the model is in equilibrium, Y_e . It is possible that one or several variables leave the equilibrium state again after year Y_e , and that the condition in eq. (1) is no longer met for these variables. This can be for example due to stochasticity in rainfall or due to fire. However, such situations are not considered in our analysis.

2.4 Simulation experiments

180 All simulations were conducted for Africa at 2° spatial resolution. In all simulation scenarios, we initialized aDGVM with 100 small trees of both types **with random biomass of up to 150 kg** and two super-individuals representing grasses under and between tree crowns. **Initial grass biomass is 10 g/m²**. All simulation scenarios in this study manipulated only CO₂ whereas **long-term averages of** other climate variables such as precipitation or temperature were kept constant with monthly climatology provided by CRU (Climatic Research Unit, New et al., 2002) for the reference period between 1961 and 1990.
185 This model design allows us to study CO₂ effects in isolation and it avoids interactive effects of several forcing variables on the system state. **For continental-scale simulations, we only conducted one model run for each scenario, but no replicates.** This single run is sufficient, as we aggregate model results per biome in most analyses.

To test the first prediction, i.e., that vegetation is not in equilibrium with the environment, we simulated (1) the equilibrium vegetation state for different CO₂ mixing ratios, and (2) transient vegetation dynamics with increasing and decreasing CO₂ mixing ratio. **Deviations between these simulations at a given CO₂ level indicate lags between environmental conditions and transient vegetation states.** For simulations of the equilibrium state, we set CO₂ to 100 ppm, 150 ppm, ..., 1000 ppm, to cover the entire range of CO₂ mixing ratios used in transient simulations. For each CO₂ level we ran the model until an equilibrium vegetation state was reached, and we recorded the year Y_e when the equilibrium was reached (eq. 1). Equilibrium conditions were derived for each simulated 2° grid cell separately. For each grid cell and each CO₂ level, we classified vegetation in year Y_e into biome types to obtain maps of biome distributions under equilibrium conditions. We calculated the fractional area covered by different biome types in equilibrium. As equilibrium vegetation states were only simulated for a discrete number of CO₂ levels, we used the ‘loess’ smoother in R (R Core Team, 2018) to obtain continuous response curves of fractional cover of biomes for the entire CO₂ range. Smoothing also reduces the effects of stochasticity in model outputs on the responses. We further created maps of the spatial patterns of Y_e .

For simulations of the transient vegetation state, aDGVM was initialized at low (100 ppm) or high (1000 ppm) CO₂ mixing ratio. In each grid cell, simulations were conducted until vegetation fulfilled the equilibrium condition defined in eq. (1). We then increased or decreased CO₂ linearly to 1000 ppm or 100 ppm by 3.5 ppm per year or 0.9 ppm per year (see next paragraph for justification of these rates). We used linear CO₂ changes between a minimum and a maximum CO₂ mixing ratio because linear changes in forcing variables allow the identification of non-linear and tipping point behaviour in the vegetation state (Scheffer et al., 2001). Once CO₂ reached 1000 ppm or 100 ppm, respectively, simulations were continued until vegetation re-established the equilibrium state according to eq. (1), and the duration was tracked. For each grid cell and each simulation year, we classified vegetation into biomes and calculated fractional cover of each biome type. The difference between the vegetation state when first reaching a target CO₂ mixing ratio in transient runs and the equilibrium vegetation state at the target CO₂ mixing ratio is an indicator of the lag size between environmental forcing and vegetation. We used the proportion of Africa covered by different biome types, woody biomass and tree cover as proxies of lag size.

To test the second prediction, i.e., that the difference between transient and equilibrium vegetation is influenced by the rate of change of environmental forcings, we conducted transient model runs where CO₂ changed at two different rates. Specifically, CO₂ mixing ratios were changed by 3.5 ppm per year or 0.9 ppm per year to represent current and past rates of change. The higher rate represents the average CO₂ increase in the RCP 6.0 scenario, where CO₂ increases from current values to approximately 700 ppm in 2100. In the simulations, 3.5 ppm per year implies that CO₂ changes from 100 ppm to 1000 ppm (or vice versa) within 230 years. The 0.9 ppm per year rate of CO₂ change implies a change from 100 ppm to 1000 ppm (or vice versa) within approximately 900 years. This rate overestimates rates of CO₂ change at paleo-ecological time scales by a factor of 100. It nonetheless differs substantially from the higher rate representing the RCP 6.0 scenario, but ensures that model run time is still feasible.

To test the third prediction, i.e., that fire amplifies lag effects, we conducted all simulations described in the previous paragraphs with fire switched on or off.

To test the fourth prediction, i.e., that sensitivity of vegetation to changes in CO₂ is influenced by the CO₂ mixing ratio, we calculated the sensitivity of modeled state variables in relation to changes in CO₂,

$$\delta_V(C) = \frac{|V(C) - V(C + \Delta C)|}{\Delta C} \quad (2)$$

225 Here, $V(C)$ is an aDGVM state variable at CO₂ mixing ratio C , and ΔC is the increment of the CO₂ mixing ratio used to calculate sensitivity. Sensitivity was calculated for the entire gradient considered in the study (i.e. 100 ppm to 1000 ppm) and for all scenarios (i.e. equilibrium and transient, with and without fire). To filter out variability of simulated variables due to model stochasticity and to account for different rates of change of the CO₂ mixing ratio in different scenarios, we used the 'loess' function in R (R Core Team, 2018) for smoothing. The smoothed curves were used for calculations of sensitivity.

230 To explore if vegetation is currently in equilibrium with the atmospheric CO₂ mixing ratio or committed to further change until 2100, we conducted simulations with CO₂ from the RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5 scenarios between 1765 and 2100 (Meinshausen et al., 2011). Climate conditions were kept constant with monthly climatology provided by New et al. (2002) to be able to compare simulations for different RCP scenarios to equilibrium simulations described in previous paragraphs. We compare the simulated vegetation state in these transient runs to the equilibrium vegetation state at selected 235 CO₂ mixing ratios to quantify lags in carbon and tree cover.

We conducted simulations at one selected savanna study site in South Africa (26°S, 28°E) to illustrate how different processes and state variables simulated by aDGVM respond to CO₂ increases between 100 ppm and 1000 ppm at a rate of 3.5 ppm per year. To account for stochastic effects in aDGVM we conducted 200 replicate simulation runs. Simulations were conducted with fire. We analyzed leaf level photosynthetic rates, tree numbers, maximum tree height, mean tree height, forest tree cover 240 and savanna tree cover, averaged for all replicate runs. We plotted time series of these variables both in their native units and normalized between 0 and 1 using minimum and maximum values of the variables to be able to track the temporal lags in these variables.

3 Results

3.1 Equilibrium vegetation state

245 Equilibrium simulations for fixed CO₂ mixing ratios show that the cover of C₄-dominated vegetation (C₄ grasslands and savannas) in Africa decreases with increasing CO₂, whereas the area covered by C₃-dominated woody vegetation (woodlands and forests) increases (Fig. 1, 2). This general pattern is simulated both in the presence and the absence of fire. Fire increases the cover of C₄-dominated vegetation states at the expense of C₃ woody vegetation states. This result indicates that large areas in Africa can be covered by C₄- or C₃-dominated vegetation if fire is present or absent. The proportions of the area where either 250 C₄- or C₃-dominated vegetation is possible peaks at low CO₂ (approximately 200 ppm) and decreases at higher CO₂ mixing ratios. The area covered by C₃-dominated woody vegetation is maximized at 1000 ppm and saturates at 69% in the absence of fire and at 61% in the presence of fire. The area covered by C₄-dominated vegetation peaks at 49% at a low CO₂ mixing ratio in the presence of fire and at 16% in the absence of fire. The area covered by deserts decreases from 46% to 24% as CO₂

increases and these areas are replaced by grasslands, savannas and woodlands (Fig. 1, 2). Areas covered by C₃ grasslands and
255 C₃ savannas increase as CO₂ increases, but even at 1000ppm, coverage is less than 10%, irrespective of the presence or absence
of fire (Fig. A1).

The time until vegetation reaches an equilibrium state varies substantially in different biomes and for different CO₂ mixing
ratios. Times are longest in more open ecosystems, that is in grasslands, woodlands and savannas (Fig. 3). In most biomes,
times tend to increase with CO₂. Times are shortest in forests. The duration is generally longer in the presence of fire than in the
260 absence of fire. **When averaged across all biomes and simulations with and without fire, times to reach an equilibrium
state increase from approximately 242 years for 200 ppm to 898 years for 1000 ppm.**

3.2 Transient vegetation state and forcing lags

When vegetation is initialized at a CO₂ mixing ratio of 100 ppm or 1000 ppm and CO₂ increases or decreases progressively
in transient simulations, the area covered by different biome types at a given CO₂ mixing ratio deviates considerably from
265 the cover in equilibrium simulations (Fig. 4). This pattern is consistent both in simulations with and without fire. Deviance
indicates that vegetation is not in equilibrium with the environment and that it lags behind the environmental forcing. At low
and increasing CO₂, the area covered by grasslands and savanna increases steeply and overshoots the initial cover at 100 ppm,
mainly because grasslands invade into deserts. As CO₂ increases, the areas covered by C₃- and C₄-dominated vegetation
approach the equilibrium state. Trees suppress grasses and eventually fire occurrence, such that forests ultimately manage to
270 invade most of the vegetated area. The deviation between equilibrium and transient cover of C₃-dominated vegetation for slow
changes of CO₂ in the presence of fire (Fig. 4d) is due to transitions from C₄ grasslands and savannas to C₃ grasslands and C₃
savannas.

The aDGVM simulates similar lag effects when CO₂ decreases, indicating hysteresis, which is a signature of alternative
ecosystem states. The change of vegetation cover in transient simulation runs is non-linear although the CO₂ forcing changes
275 linearly. In summary, this result confirms our first prediction, i.e. transient vegetation states deviate from the equilibrium state
and forcing lags occur.

The rate at which CO₂ increases or decreases has a strong impact on the size of the forcing lags (Fig. 4). Fast changes in
CO₂ imply larger lags than slow changes in CO₂. Lags are larger at low and intermediate CO₂ mixing ratios and decrease at
higher CO₂, irrespective of the rate of change of CO₂. This result verifies the second prediction.

280 3.3 Fire and disturbance lags

A comparison of simulations with and without fire shows that fire increases the lag between the CO₂ forcing and vegetation
(Fig. 4). In the scenario with rapidly changing CO₂ mixing ratio, the maximum lag size averaged for entire Africa for C₄-
dominated biomes is 20% and 16.3% with and without fire, respectively, the maximum lag size for C₃-dominated biomes is
19.4% and 16% with and without fire, respectively. In scenarios with increasing CO₂, lag size is maximized between approx-
285 imately 200ppm and 300ppm. When integrated along the entire CO₂ gradient, the mean lag size for C₄-dominated biomes is
11.8% and 6.7% with and without fire, respectively, the mean lag size for C₃-dominated biomes is 11.9% and 6.4% with and

without fire, respectively. These patterns are similar in simulations with slowly changing CO₂ mixing ratio, but percentages are systematically lower. The time to reach equilibrium is longer in simulations with fire than in simulation without fire (Fig. 3), in particular in fire-driven biome types. Times are similar in forests with dense tree canopy, where aDGVM does not simulate fire.

When CO₂ is held constant after the transient phase, vegetation converges towards the equilibrium state. In simulations without fire, times to reach equilibrium were similar in equilibrium simulations and in transient simulations with both slow or fast increases or decreases of CO₂ (Figs. 5, 6). In simulations with fire, we generally observed longer times than in simulations without fire, particularly in grassland and savanna areas and for decreasing CO₂ (Fig. 6). **Longer times in the presence 295 of fire can be attributed to hysteresis effects. High fire activity traps vegetation in a fire-driven state and prevents biome transitions into alternative vegetation states.** In simulations with decreasing CO₂ and fire included, times to reach equilibrium in grasslands and savannas were considerably longer in transient simulations than in equilibrium simulations (Fig. 6). These findings support our third prediction that disturbance lags amplify forcing lags and are particularly relevant in fire-driven systems.

300 3.4 Carbon and tree cover debt

Forcing lags and disturbance lags imply carbon and tree cover debt (for increasing CO₂, Fig. 7) or surplus (for decreasing CO₂, Fig. A2). Debt means that at a given CO₂ mixing ratio, tree cover and carbon stocks are lower in transient simulations than in equilibrium simulations at the same CO₂ level. **Hence, we define debt as carbon storage potential that has not been 305 realized yet, and carbon that the atmosphere owes to vegetation.** Accordingly, surplus means that tree cover and carbon are higher in transient simulations than in equilibrium simulations, **and that vegetation owes carbon to the atmosphere.** Where debts and surpluses occur, carbon and tree cover are committed to further changes, even if environmental forcings stabilize, unless tipping point behavior inhibits vegetation change or allows rapid vegetation changes that compensate debt or surplus.

Carbon debt increases over the entire CO₂ gradient. At current CO₂ levels of 400 ppm, carbon debt for Africa is between -6.3 and -13.6 PgC for different scenarios and it increases to values between -24.8 and -39.9 PgC for 1000 ppm. At high CO₂, 310 debt is higher for simulations without fire than for simulations with fire due to the combined effects of forcing and disturbance lags.

Tree cover debt in the presence of fire peaks at values around -15% between 300 ppm and 400 ppm, i.e. at current CO₂ levels. Debt decreases at higher CO₂ mixing ratios to values between -5.8% and -10%, depending on the scenario. Debt is generally 315 **larger** in presence of fire and when CO₂ changes rapidly. The maximum deviance between transient and equilibrium state (maximum debt and surplus) varies spatially with higher deviance in savannas and woodlands surrounding the central African forest and in the presence of fire. **Tree cover debt saturates or decreases at higher CO₂ mixing ratios because tree cover in a grid cell is constrained by canopy closure. At higher CO₂ mixing ratios large fractions of Africa reach a forest state and canopy closure. Tree cover debt in these areas is zero. In contrast, biomass in a grid cell and hence biomass debt can further increase even if canopy closure occurs.**

320 **3.5 Sensitivity of carbon and tree cover change**

The sensitivity of the fractional cover of different biome types to changes in CO₂ is influenced by the actual values of CO₂ (Fig. 8a, b). In equilibrium simulations, the cover of C₃-dominated biomes is most sensitive at low CO₂ mixing ratios and it decreases as CO₂ increases. In simulations with fire, sensitivity of C₄-dominated biomes is hump-shaped with a peak at ca. 380 ppm. In transient simulations, both C₃- and C₄-dominated biomes are most sensitive to changes in CO₂ mixing ratios between 200 and 600 ppm, depending on the specific scenario (Fig. 8c, d). Sensitivity is generally higher in the presence of fire than in the absence of fire. For rapidly changing CO₂, the peak is found at higher CO₂ mixing ratios than for slowly changing CO₂. These results support our fourth prediction.

3.6 Responses to RCP scenarios

Simulations for CO₂ mixing ratios following trajectories of different RCP scenarios indicate carbon debt (Fig. 9a) and tree cover debt (Fig. 9b) as the CO₂ mixing ratio increases, similar to the simulations with linear changes of CO₂ (Fig. 7). At the current CO₂ mixing ratio of approximately 400 ppm, aboveground tree carbon debt is between -8.9 PgC without fire and -16.5 PgC with fire. In the RCP 2.6 and 4.5 scenarios, carbon debt in Africa accumulates to peak values between -9.9 and -18 PgC and between -12.9 and -22 PgC, respectively and then decreases because in these scenarios, CO₂ decreases (RCP 2.6) or saturates (RCP 4.5) at the middle of the century. In RCP 6.0, debt accumulates to values between -21.2 and -31 PgC, in RCP 8.5 it accumulates to values between -47.5 and -60 PgC until 2100. In contrast, tree cover debt peaks between ca. 300 and 350 ppm at values between -3.3 and -17% in the presence or absence of fire, respectively. **As in the simulations with constant changes in CO₂, tree cover debt decreases as the CO₂ mixing ratio increases towards the end of the century, with a rate depending on the specific RCP scenario.** Generally, both carbon and tree cover debt are higher in the presence of fire than under fire suppression.

340 **4 Discussion**

Using a dynamic vegetation model, we predict that vegetation exposed to transient environmental forcing is not in equilibrium with environmental conditions, and that such transient vegetation states deviate from the vegetation state expected for the prevailing environmental conditions. Vegetation development lags behind changing environmental drivers due to forcing lags. The size of the forcing lag depends both on actual environmental conditions and on the rate at which conditions change. Disturbance lags caused by fire can amplify forcing lags in areas where multiple vegetation states are possible such as savanna areas that also support forest. Our results indicate that vegetation in Africa is most sensitive to changes in the atmospheric CO₂ mixing ratio at current conditions. Hence, even if anthropogenic emissions of CO₂ and the accumulation of CO₂ in the atmosphere were to level off in near future, ecosystems will still be committed to considerable changes.

Our model simulations are consistent with **previous aDGVM model results indicating** that biome distributions over large areas of Africa are dependent on fire (Higgins and Scheiter, 2012), and that these distributions are contingent on historic

vegetation states and likely to change under elevated CO₂ (Scheiter and Higgins, 2009; Higgins and Scheiter, 2012; Moncrieff et al., 2014). While we only considered transient vegetation dynamics in previous **aDGVM** studies, we now show that these results also hold true for simulations with equilibrium conditions. In our transient simulations we further show that linear forcing in CO₂ can cause non-linear responses in vegetation states. This result indicates internal feedback loops and tipping 355 point behaviour in the climate-fire-vegetation system (Scheffer et al., 2001) **and supports our previous findings (Higgins and Scheiter, 2012)**. The potential for alternate biomes, dependent on fire, and hysteresis effects occur both in equilibrium simulations with fixed CO₂ and in transient simulations with variable CO₂ mixing ratio. These effects occur over the entire CO₂ gradient between 100 and 1000 ppm.

4.1 Understanding forcing, disturbance and successional lags

360 Lags between environmental conditions and vegetation states occur if environmental conditions change faster than vegetation can respond. In such a situation, transient vegetation states deviate from the vegetation states that one would expect if prevailing environmental conditions remained constant for a sufficiently long duration. The lag size is defined by the integrated effect of interacting processes including delayed responses in ecophysiology, demography, migration and succession, and by the different timescales on which these processes operate (Penuelas et al., 2013). Rates of change in environmental forcing and intensity 365 and frequency of disturbances further influence lag size. In aDGVM simulations we find a sequence of vegetation responses to changes in the CO₂ mixing ratio that operate at different temporal scales. When CO₂ increases, leaf level photosynthesis and respiration increase instantaneously following the ecophysiology models implemented in aDGVM (Farquhar et al., 1980; Collatz et al., 1991, 1992, Fig. 10). These adaptations imply higher carbon gain, water use efficiency and growth of individual trees in the growing season as well as higher reproduction rates, because in aDGVM, the amount of carbon allocated to reproduction 370 is a function of peak carbon gain. Free air carbon enrichment (FACE) experiments and open top chamber experiments for elevated CO₂ indicate similar responses at the leaf level (e.g., Hickler et al., 2015; Kgope et al., 2010, Raubenheimer, Ripley, et al., unpublished).

In aDGVM, higher growth and reproduction rates of individual plants modify plant population dynamics and vegetation structure. The model simulates an increase in mean tree height after CO₂ starts increasing (Fig. 10). After a delay of approximately 375 70 years, trees can establish more successfully and tree number and savanna tree cover increase. Tree cover increases can be attributed to both increases in tree height, which in aDGVM is linked to an increase in a tree's crown area, and in tree number. Increases in maximum tree height lag behind mean tree height and tree numbers (Fig. 10). All population-level responses in the model are slower than leaf-level responses and lag behind ecophysiological adaptations.

Observing population-level responses to elevated CO₂ in reality is challenging. Historic data from field surveys (Stevens 380 et al., 2017; O'Connor et al., 2014) and remote sensing (Donohue et al., 2013; Skowno et al., 2017) indicate woody encroachment in many savanna areas. These changes were often attributed to historic increases in CO₂ (Midgley and Bond, 2015), but also to land use activities such as over-grazing (Roques et al., 2001). Yet, the strength of CO₂ fertilization effects is debated (Körner et al., 2005) and free air carbon enrichment (FACE) experiments indicate complex responses of vegetation to elevated CO₂ at population level (Hickler et al., 2015). Nutrient limitations (Hickler et al., 2015) and effects of mycorrhizal associa-

385 tions on nutrient economy (Terrer et al., 2016) may add to the complexity of these responses. FACE experiments in savannas and sub-tropical ecosystems are rare. An exception is OzFACE in Queensland, Australia (Stokes et al., 2005) which found increased growth rates for *Eucalyptus* and *Acacia* species. Previous studies showed that CO₂ fertilization effects are strong in aDGVM and **that the strong CO₂ effects can compensate for other predicted changes in climate drivers, such as reduced rainfall** (Scheiter et al., 2015). **If aDGVM overestimates the strength of CO₂ fertilization effects and the sensitivity of vegetation to elevated CO₂, the size of carbon debt due to lag effects may be overestimated, while the lag size may be underestimated. We are however confident that even with reduced CO₂ sensitivity the overall response pattern would remain, although the quantities might change.** In Scheiter et al. (2018) we show that simulated woody cover increases in the Limpopo Province, South Africa, under current conditions broadly agree with remote sensing observations from Stevens et al. (2017), indicating that aDGVM simulates plausible responses to climate change for historic and current conditions.

390 395 Disturbance lags in fire-driven savannas are created by a well-known feedback mechanism between fire and vegetation (Higgins and Scheiter, 2012; Hoffmann et al., 2012). Regular fire is a demographic bottleneck for tree establishment and traps trees in a juvenile state (Higgins et al., 2000). At the population scale, fire preserves a characteristic, open savanna vegetation state (Scheiter and Higgins, 2009) and keeps vegetation from reaching an equilibrium vegetation state, typically woodland or forest with higher tree cover, expected under the prevailing environmental conditions. Yet, reduced fire activity (Hoffmann 400 et al., 2012) or increased tree growth rates due to CO₂ fertilization (Bond and Midgley, 2000) allow more trees to escape the fire trap due to increased growth rates. As a consequence, the increasing tree cover starts to exclude grasses and curtails fire frequency due to reduced fine fuel loads. This dynamic feedback between vegetation and fire dynamics implies that rapid transitions between savanna and forest states are possible.

405 Once fire is excluded at high CO₂ mixing ratio, successional lags delay the establishment of an equilibrium state. These lags are a direct consequence of disturbances and they emerge if plant community composition in the equilibrium state deviates from transient, post-disturbance community composition. The aDGVM simulates fire-tolerant but shade-intolerant savanna trees and fire-intolerant but shade-tolerant forest trees (Scheiter et al., 2012). At low CO₂ and intermediate rainfall, aDGVM simulates a fire-driven savanna state with predominantly savanna trees. Reduced fire activity and transitions to woody plant-dominated habitats imply that savanna trees and grasses are out-competed and gradually replaced by forest trees (Fig. 10). Successional 410 dynamics are slow and delay the adaptation of community composition to elevated CO₂. Empirical studies support successional lags in communities (Fauset et al., 2012; Esquivel-Muelbert et al., 2019), although, these studies reported community responses to drought rather than CO₂.

415 We found that fire-driven savanna and grassland ecosystems take longer to reach equilibrium after the CO₂ forcing stabilizes than forests. Forests are faster to stabilize and to balance their carbon and tree cover debt. In our simulations, this behavior is driven by disturbance-related lags caused by fire. Fire generates a dynamic disequilibrium between climate and vegetation, and it prevents both savanna and forest trees to recruit, to transition into the adult state, and to develop a closed canopy. When tree cover exceeds a critical threshold, fire is suppressed and rapid canopy closure is possible. **Fire rarely occurs in simulated forests, and therefore they reach equilibrium faster than other biome types. Fire activity in forests is, however, sufficient to slightly increase times to reach equilibrium when compared to simulations with fire suppressed.** Moreover,

420 forests represent the final stage in succession in ecosystems simulated by aDGVM. Hence, forests do not allow for further succession in contrast to grasslands and savannas, where savanna trees can invade grasslands, and be replaced by forest trees in later successional stages. aDGVM might underestimate lags in forest systems in contrast to alternative DGVMs or forest models that simulate a higher number of PFTs or species (e.g. Hickler et al., 2012), or that allow plant traits and community composition within a forest system to adapt to changing environmental drivers (Scheiter et al., 2013).

425 **4.2 Implications for adaptation, mitigation and policy**

Lags between transient and equilibrium coverage of different vegetation types or biome types imply debt or surplus in tree cover (Jones et al., 2009), carbon storage, biogeochemical fluxes and community composition (Bertrand et al., 2016). These lags commit ecosystems to further changes even if the rate of climate change is reduced and the climate system converges 430 towards an equilibrium state (Jones et al., 2009; Port et al., 2012; Pugh et al., 2018). This finding has important implications for the development of adaptation and mitigation strategies for climate change.

First, it indicates that such strategies cannot be developed purely based on observed contemporary transient states when attempting to mitigate further changing of climatic drivers. There is an urgent need to understand equilibrium vegetation states, committed changes in vegetation states, and to take them into account in management policies (Svenning and Sandel, 2013). Lag effects are also central to understanding resilience of an ecosystem (Holling, 1973; Walker et al., 2004).

435 Second, our findings imply a high priority and potential for managing fire-dependent ecosystems such as savannas. It has been argued that in these ecosystems, elevated CO₂ is the main driver for shrub encroachment and transitions to forest (Higgins and Scheiter, 2012; Midgley and Bond, 2015). Suitable management intervention can oppose CO₂ fertilization effects and delay undesired vegetation changes (Scheiter and Savadogo, 2016). For instance, the introduction of fire can increase lags between transient and equilibrium vegetation states, whereas fire suppression for example by grazing (Pfeiffer et al., 2019) or 440 fire management (Scheiter et al., 2015) can reduce disturbance-related lags. Other disturbances or land use activities such as herbivory or fuelwood harvesting have similar effects (Scheiter and Savadogo, 2016). Hence the potential for these ecosystems to persist in a disequilibrium state relative to climate and CO₂ creates the opportunity to mitigate changes brought about by global change through management interventions. Conversely, allowing these systems to reach their equilibrium state has the potential to increase the global land carbon sink. While such management is relevant for carbon sequestration (Bastin et al., 445 2019), it is likely to lead to loss of biodiversity concomitant with losses of open savanna and grassland ecosystems (Veldman et al., 2015; Bond et al., 2019). Given the increasing lag size between transient and equilibrium vegetation states, management should decide at the local scale if current or desired vegetation states should be maintained as long as possible or if ecosystems should be managed to account for vegetation changes expected in near future. Ignoring committed changes might imply rapid vegetation shifts that inhibit sustainable management actions.

450 Third, we found that the rate at which environmental conditions change determines the size of the lag between transient and equilibrium vegetation. Following the RCP 8.5 trajectory instead of the RCP 2.6 trajectory will therefore increase carbon debt both due to higher CO₂ mixing ratio and the acceleration of CO₂ enrichment in the atmosphere. **If emissions follow the RCP 2.6 scenario and stabilize after 2100, then ecosystems in Africa would continue to absorb 9 PgC or 18 PgC from the**

atmosphere in the presence or absence of fire to reach an equilibrium state with environmental conditions. In contrast, 455 ecosystems would absorb 47.5 PgC or 60 PgC in the presence or absence of fire in the RCP 8.5 scenario.

Finally, climate and greenhouse gas concentrations in the atmosphere are likely to change at an unprecedented rate (Prentice et al., 1993; Foster et al., 2017). Our results indicate that vegetation is most sensitive to changes in atmospheric CO₂ at the currently prevailing levels and values expected in near future (between approximately 350 ppm and 500 ppm, depending on the simulation scenario and response variable investigated). Hence, we are currently in a period where small changes in CO₂ 460 are likely to have large impacts on long-term vegetation change. The results also show that restoring savannas from heavily encroached wood-dominated states is a long process, particularly if fire is lost from these ecosystems. This finding raises the urgent need for society to act and reduce greenhouse gas emissions as the window of opportunity where human intervention can contribute to reverse climate change impacts might close soon.

4.3 Implications for vegetation modeling

465 The lag effects identified in our study have important implications for vegetation modelling and the process of testing and benchmarking models. Lag effects are prevalent both in results from transient model simulations using time series of climate data, and in data used for benchmarking, including remote sensing products (Saatchi et al., 2011; Simard et al., 2011; Avitabile et al., 2016) or data collected in field surveys. Previous studies identified sources of uncertainty in data-model comparisons (Scheiter and Higgins, 2009; Langan et al., 2017) related to model uncertainties or data uncertainties. We argue that the presence 470 of forcing and disturbance lags can add to disagreement between benchmarks and simulation results, such as modeled and satellite-derived productivity (Smith et al., 2016), carbon stocks, vegetation type, or species composition. Although DGVMs typically simulate transient vegetation states based on time series obtained from climate models, we argue that to improve the benchmarking process, we need to ensure that data and models represent similar successional stages. This can be achieved, e.g. by applying appropriate model initialization methods using historical climate data, **land use and fire history**, or by considering 475 effects of historic legacies on vegetation (Moncrieff et al., 2014). **For example, Rödig et al. (2017) used the Simard et al. (2011) vegetation height product to ensure that successional stages simulated with the FORMIND model agree with observed successional stages.** We concede that this is not an easy task as large-scale data on equilibrium vegetation states or lag sizes are typically not available, and as vegetation states have been modified by human land use for millennia. Remote sensing products such as the GEDI mission (gedi.umd.edu) may provide high-resolution data required to initialize models with 480 biomass and vegetation structure.

The emergence of lag effects also highlights the relevance of adequate representation of demography, succession and disturbance regimes in vegetation models and makes a case for cohort- or individual-based approaches. Understanding and quantifying lags necessitates prioritization and further model development with respect to these processes (Fisher et al., 2018) as well as improved knowledge of the rates at which these processes operate. Accurate representation of rates of changes may 485 contribute to improve data-model agreement (Smith et al., 2016). In-depth model testing against available long-term observations of successional changes in response to climate change and disturbance can further reduce model uncertainties. Fire or herbivore manipulation experiments conducted in Kruger National Park (Higgins et al., 2007) or in Burkina Faso (Savadogo

et al., 2009) exemplify such data sets, in particular because they not only provide time series for benchmarking but also include relevant and documented disturbance processes under controlled conditions.

490 In this study, we only considered natural fire regimes as simulated by aDGVM. However, to understand the full complexity of vegetation lags, further disturbances need to be taken into consideration. This includes anthropogenic fire (planned management fires as well as accidental fires), but also herbivory (grazing and browsing), fuelwood harvesting, deforestation or conversion of natural land to agricultural or forestry areas. In this study we only quantified lags in biome shifts, tree cover and aboveground carbon storage, but our framework can be extended to further ecosystem services in follow-up studies. In
495 addition, we only considered changes in CO₂ in this study whereas changes in other key variables influencing vegetation, particularly precipitation and temperature, were ignored. Previous aDGVM studies show that change in CO₂ is the main driver of simulated future vegetation change due to strong CO₂ fertilization effects (Scheiter and Higgins, 2009; Scheiter et al., 2015, 2018, Martens et al., unpublished). We therefore expect that using time series of both CO₂ and climatic drivers following RCP scenarios will not change the fundamental results of our study. This expectation is supported by simulation results using various
500 climatic drivers for RCP 8.5 and 4.5 (Pfeiffer et al., unpublished).

4.4 Further lags in the climate-vegetation system

In this study, we identified three lags between transient and equilibrium vegetation, namely forcing, disturbance and successional lags. Yet, due to the design of aDGVM our study ignores other lag effects in the climate-vegetation system.

505 Migration lags occur due to a limited speed of seed dispersal and migration under variable climate. Dispersal and migration can, particularly in vegetation, typically not keep pace with climate change (Loarie et al., 2009). Migration lags have been investigated, but often using statistical approaches such as species distribution modelling (Thuiller et al., 2005). Extending DGVMs or forest models with dispersal models is, however, possible. For instance, Blanco et al. (2014) used a spatially explicit version of aDGVM to show that forest expansion rates in *Araucaria* forest-grassland mosaics in southern Brazil are sensitive to characteristics of the dispersal traits of *Araucaria* trees. Sato and Ise (2012) showed with SEIB-DGVM that
510 including dispersal in projections of African vegetation until 2100 implies lagged responses in simulated biome boundary shifts. **Nabel et al. (2013) used the TreeMig model to illustrate the complexity of simulating seed dispersal and migration in heterogeneous and variable environments.**

515 Once a species has migrated into another suitable region, establishment lags due to competition between established and invading species can occur and prevent establishment of invading species. To quantify establishment lags in DGVMs, an accurate description of competition, demography and succession is necessary. Scheiter et al. (2013) argued that competition is often not adequately described in DGVMs. More advanced models are required that simulate competitive interactions between individual plants for space, light, nutrients and water, and consider allelopathic interactions. Novel approaches based on trait variation such as aDGVM2 (Scheiter et al., 2013; Langan et al., 2017), JEDI-DGVM (Pavlick et al., 2013) or LPJmL-FIT (Sakschewski et al., 2015) can be applied to identify establishment lags based on their detailed description of individual plants
520 and plant communities that are characterized by variable and dynamic traits instead of relying on a fixed number of static plant functional types.

At longer time scales, evolutionary lags occur due to evolution of species adapted to changing environmental conditions or to disturbance regimes (e.g., Simon et al., 2009; Guerrero et al., 2013). More advanced vegetation models are required to simulate how evolutionary processes such as trait inheritance, mutation and cross-over allow plants to adapt to changing environmental 525 conditions over many generations. While aDGVM2 (Scheiter et al., 2013) includes these mechanisms, the model has so far not been applied in an evolutionary context. Such an application would require a re-parametrization of mutation and cross-over rates using empirical data to account for the temporal component of evolutionary processes.

Finally, atmosphere-biosphere lags can occur where delayed responses of vegetation change to environmental change feed back to delay responses of the environment. For example, increasing forest cover due to CO₂ fertilization and resulting 530 increase in carbon sequestration may reduce CO₂ enrichment in the atmosphere and associated amplification of radiative forcing. Investigation of atmosphere-biosphere lags requires fully coupled models that simulate biogeochemical fluxes between atmosphere and biosphere. Jones et al. (2009) used such a fully coupled model to investigate lags in Amazon forest die-back, but feed-backs to the climate system were not explicitly considered. Port et al. (2012) used the fully coupled MPI ESM to show 535 that lagged responses of vegetation may, in a scenario where CO₂ emissions are zero after 2120, reduce atmospheric CO₂ by approximately 40ppm until 2300. Another well-studied example is the Sahel greening phenomenon where smooth changes in rainfall regimes trigger abrupt and delayed responses in vegetation cover due to vegetation-atmosphere feed-backs (Brockin et al., 1998; Claussen et al., 1999; Foley et al., 2003).

5 Conclusions

To conclude, our study **indicates** that vegetation generally lags behind changing atmospheric CO₂ mixing ratios. We are 540 currently in a phase of high carbon storage and tree cover debt and vegetation cover deviates substantially from the committed vegetation state. Our study **predicts** that vegetation is most sensitive to changes in atmospheric CO₂ at current levels of atmospheric CO₂ and those expected in near future. This finding indicates the need to act and reduce greenhouse gas emissions. Lags are larger in fire-dependent systems such as savannas than in arid grasslands or forests. Lag effects in vegetation status 545 need to be considered for the development of management plans or mitigation strategies because we expect further changes in vegetation even if emissions of CO₂ and other greenhouse gasses are reduced and the climate system stabilizes. There is an urgent need to understand lag effects not only in response to variable CO₂, but also to other key variables of the climate system such as temperature and precipitation, as well as to extreme events such as heat waves or drought.

Code availability. The aDGVM code as well as scripts to conduct the model experiments and analyze the results are available upon request. Please contact any of the authors.

550 *Author contributions.* SS, SH and GM conceived the study, SS conducted simulations and analyzed results, SS and MP created the figures, SS lead the writing with contributions of all co-authors.

Competing interests. We declare that no competing interests are present.

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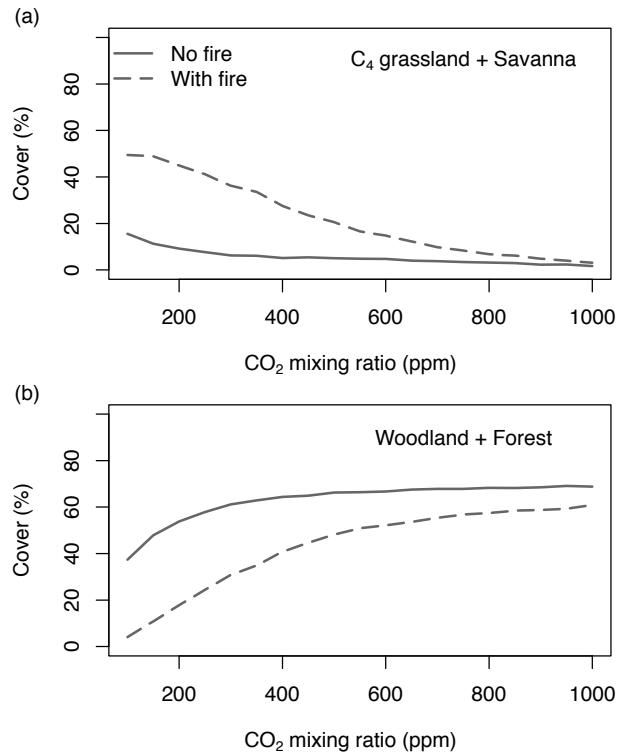


Figure 1. Area of Africa covered by (a) C₄-dominated (C₄ grassland and savanna) and (b) C₃-dominated (woodland and forest) vegetation under equilibrium conditions. Simulations were conducted until vegetation reached an equilibrium state under fixed CO₂. Differences between simulations without fire (solid lines) and with fire (dashed lines) indicate that both C₃- and C₄-dominated vegetation states are possible. Fig. A1 shows cover fractions separated by biome type.

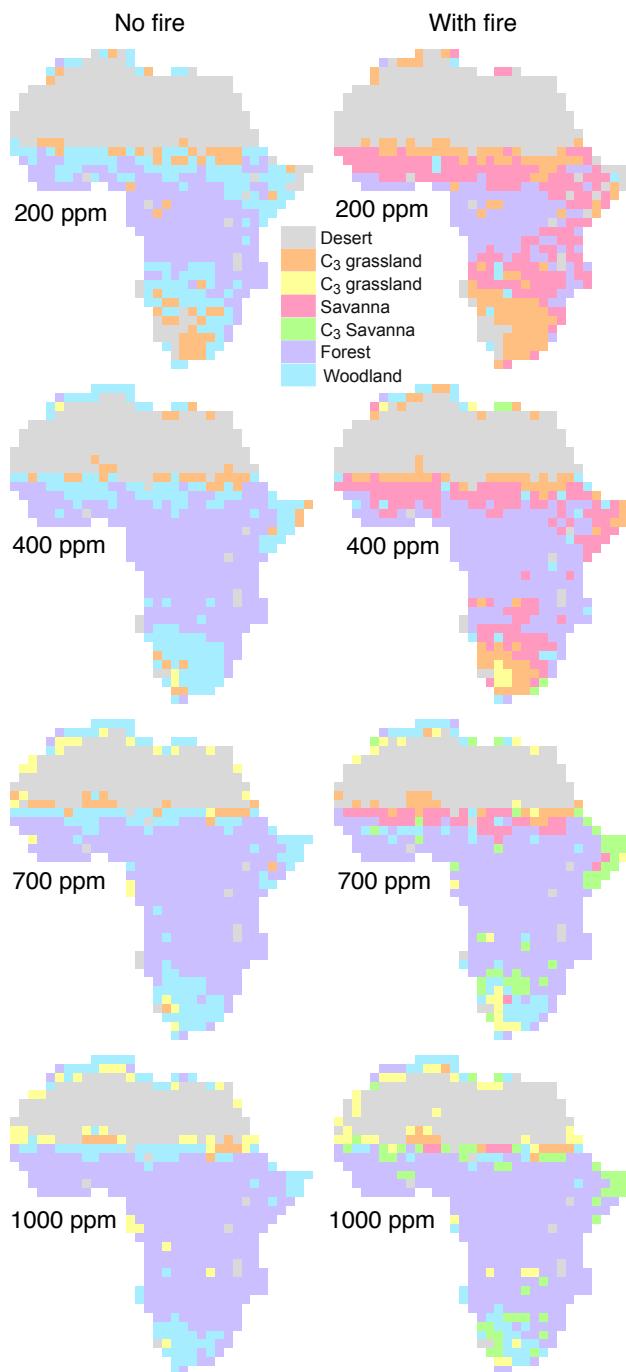


Figure 2. Biome distribution at different CO₂ mixing ratios and in the presence or absence of fire. Simulations were conducted until vegetation reached an equilibrium state under a constant CO₂ mixing ratio.

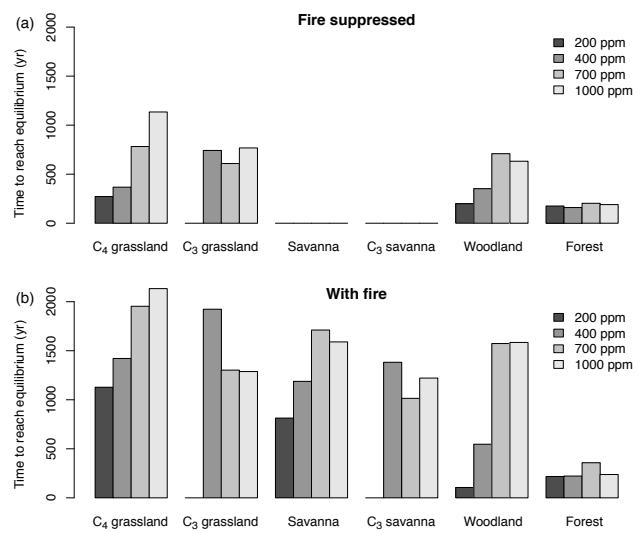


Figure 3. Time required to reach the equilibrium biome state in simulations with fixed CO_2 mixing ratio. Time was averaged for different biome types and different CO_2 mixing ratios. Times to reach equilibrium are shortest in forest, and do not respond strongly to CO_2 . In more open ecosystems (grassland, savanna, woodland) times to reach equilibrium are longer than in forests, and equilibration times increase as CO_2 increases. Times to reach equilibrium are shorter under fire suppression (b) than in the presence of fire (a).

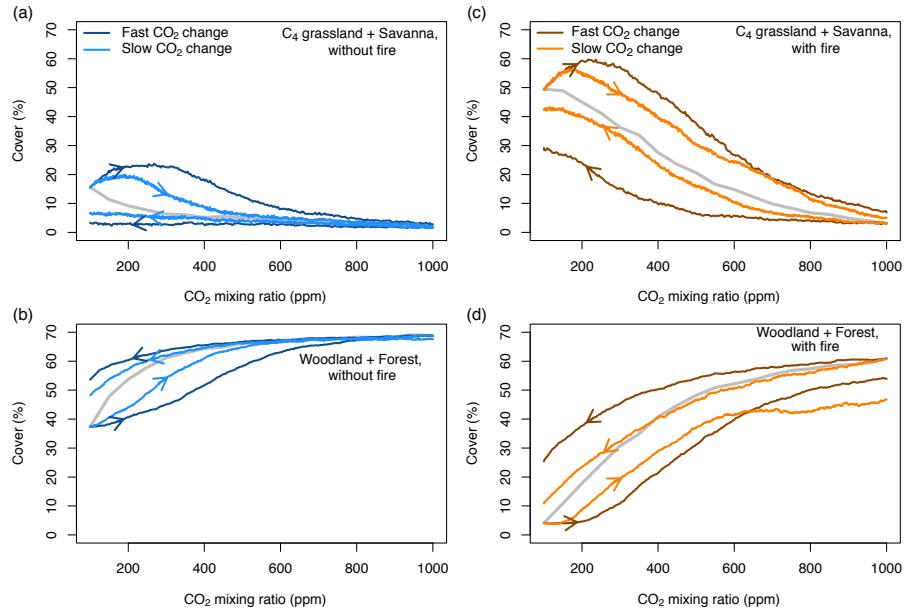


Figure 4. Percentages covered by C₃- and C₄-dominated vegetation in the presence and absence of fire. CO₂ is increased or decreased at two different rates between 100 ppm and 1000 ppm. The gray lines indicate vegetation cover in equilibrium simulations (similar to Fig. 1). Arrows indicate whether CO₂ increases or decreases.

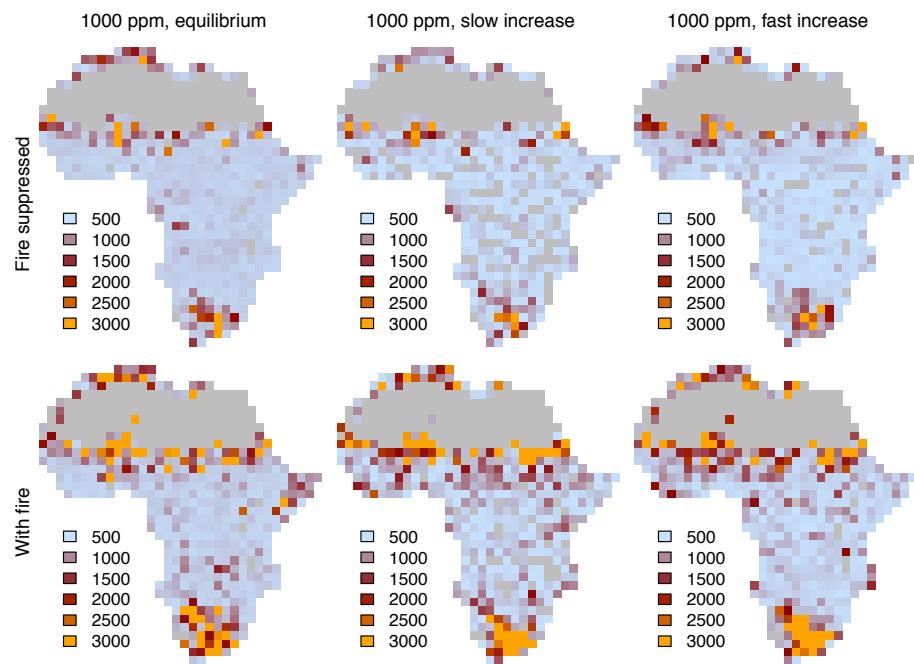


Figure 5. Time required to reach equilibrium in equilibrium simulations and transient simulations with both slow and fast increases of CO₂. Note that 3000 years in the legend means ≥ 3000 years, because simulations were run for a maximum of 3000 years.

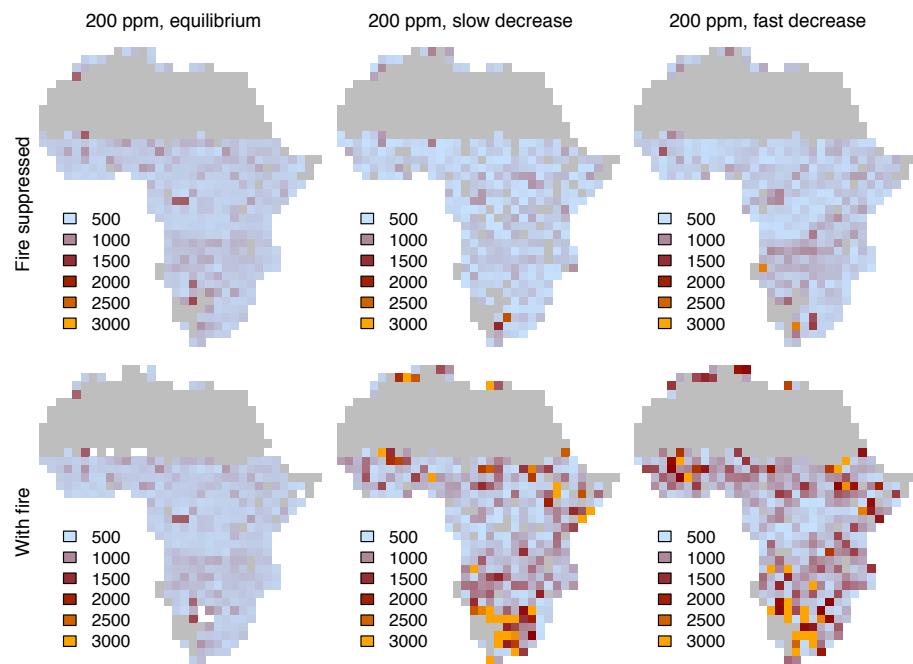


Figure 6. Time required to reach equilibrium in equilibrium simulations and transient simulations with both slow and fast decreases of CO₂. Note that 3000 years in the legend means ≥ 3000 years, because simulations were run for a maximum of 3000 years.

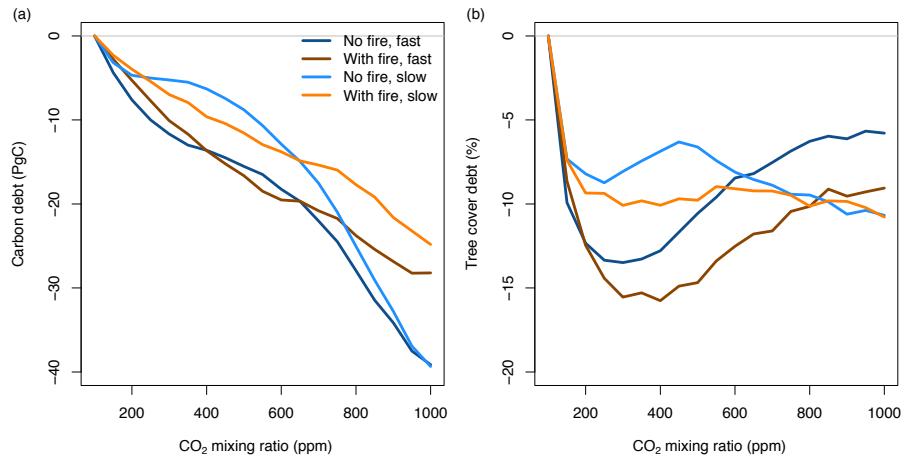


Figure 7. Debt of vegetation carbon and tree cover when the atmospheric CO₂ mixing ratio increases. Lines represent differences between transient and equilibrium simulations averaged for all study sites in Africa (simulated at 2° resolution). See Fig. A2 for decreasing CO₂ and associated tree cover and carbon surplus.

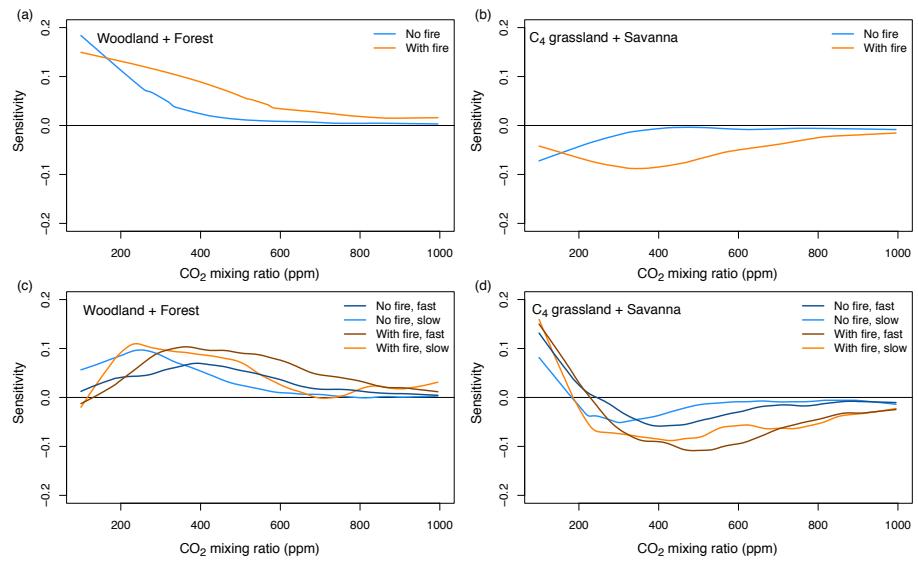


Figure 8. Sensitivity of vegetation cover change to changes in the atmospheric CO₂ mixing ratio (in % change of vegetation cover per ppm increase). Upper panels (a, b) show equilibrium simulations, lower panels (c, d) show transient simulations.

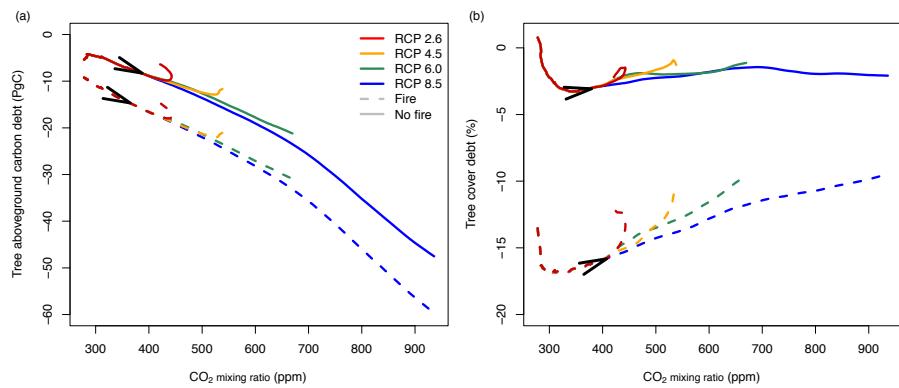


Figure 9. Vegetation carbon and tree cover debt when the atmospheric CO_2 mixing ratio increases according to different RCP scenarios. Lines represent differences between transient and equilibrium simulations averaged for all study sites in Africa (simulated at 2° resolution). Solid lines represent simulations without fire, dashed lines represent simulations with fire. Arrows indicate time between 1950 and 2100.

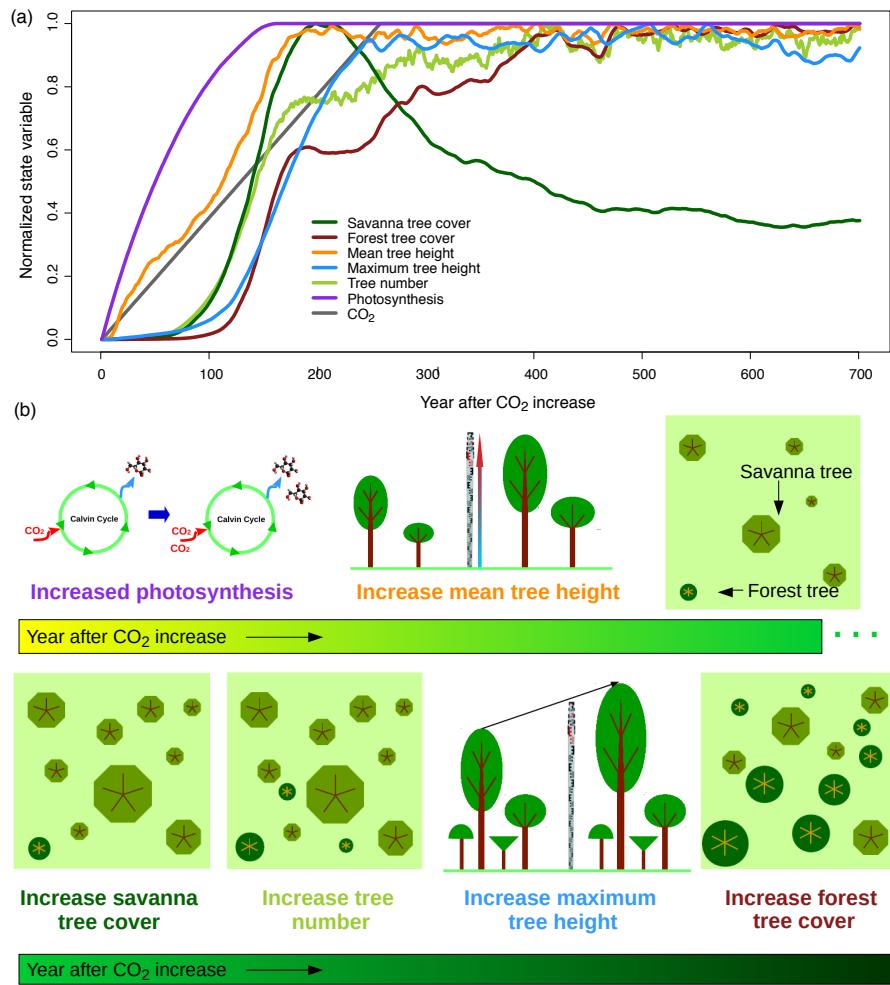


Figure 10. Vegetation responses to increasing CO_2 . Panels show (a) time series of different state variables at a savanna study site in South Africa (26°S , 28°E), and (b) a schematic illustration of processes. State variables represent averages of 200 replicate simulation runs for the site. Normalization of state variables between zero and one based on minimum and maximum values was applied to be able to illustrate temporal lags between variables. Fig. A3 provides the time series without normalization and with units of respective variables.

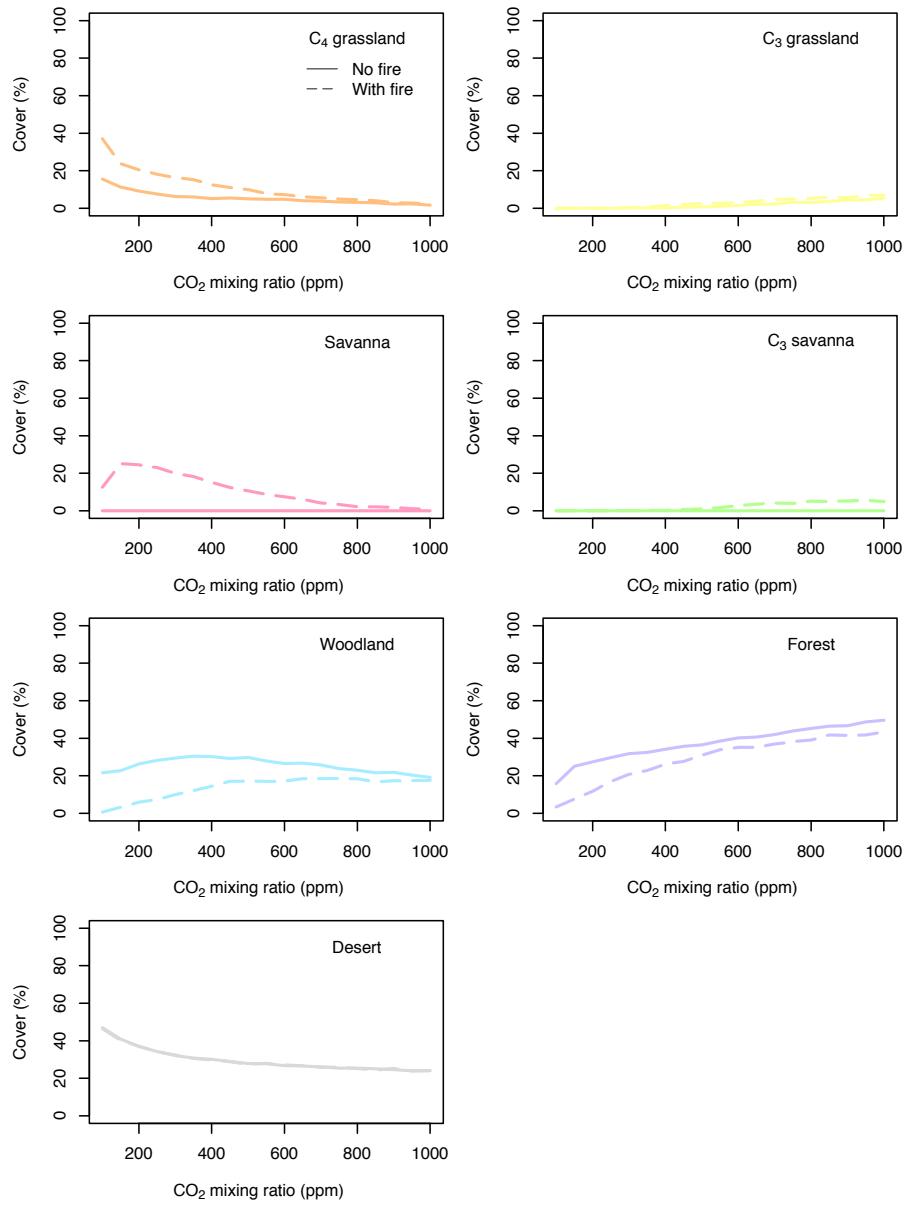


Figure A1. Area of Africa covered by different biome types. Simulations were conducted until vegetation reached an equilibrium state under a given and fixed CO_2 mixing ratio. Differences between simulations without fire (solid lines) and with fire (dashed lines) indicate that fire influences cover fractions of different biome types.

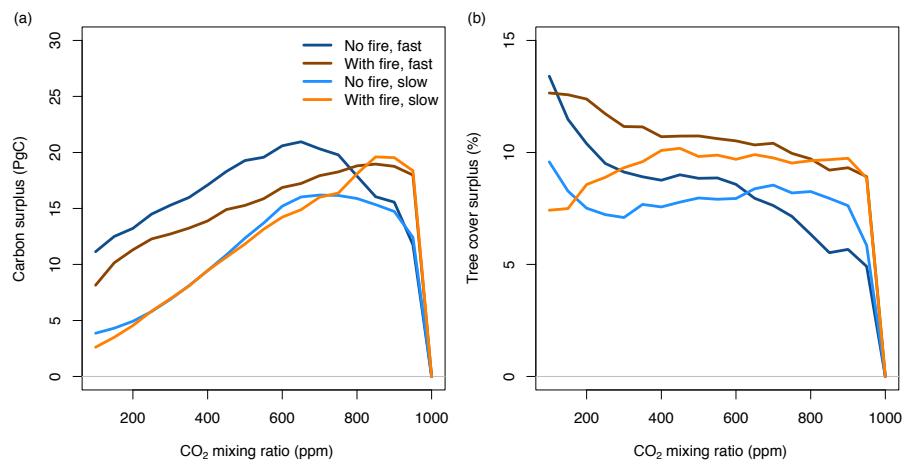


Figure A2. Surplus of tree cover and carbon when the atmospheric CO₂ mixing ratio decreases in transient simulations. Lines represent the differences between transient and equilibrium simulations averaged for all study sites in Africa (simulated at 2° resolution).

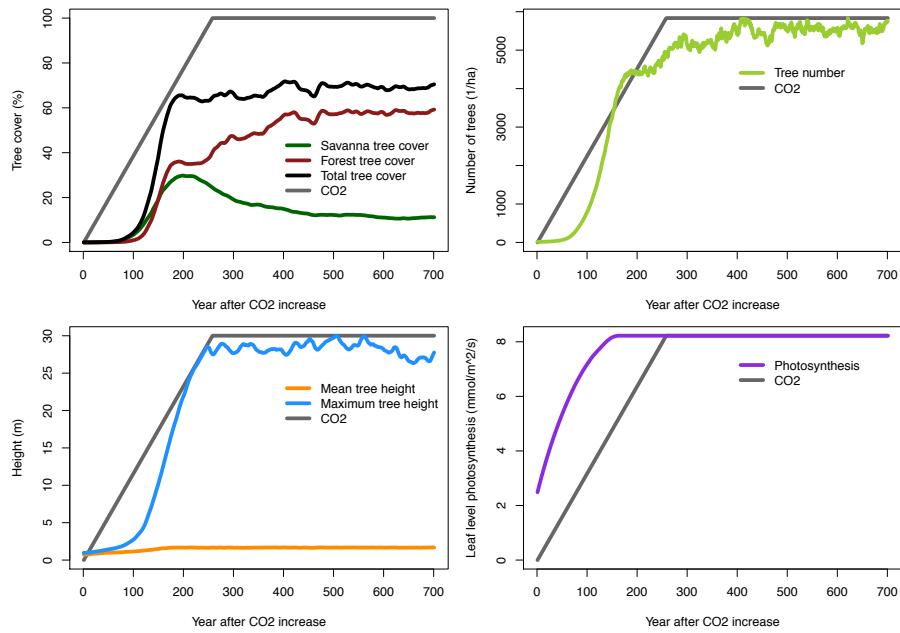


Figure A3. Time series of different state variables at a savanna study site in South Africa (26°S, 28°E). State variables represent averages of 200 replicate simulation runs for the site.