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Interactive comment on "Palaeo plant diversity in subtropical Africa – ecological assessment of a conceptual model of climate–vegetation interaction" *by* V. P. Groner et al.

V. P. Groner et al.

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We thank the referees very much for comments and suggestions, and we address the main issues arising out of the comments in the corresponding responses. Based on the comments by referees and the editor, we made some major changes in the manuscript (among others):

1. Concerning the interest of our approach according to DVM approaches and other approaches taking into account more processes, we explained in the author responses that the purpose of the presented work was the revision of Claussen et al., (2013), including an assessment of the study and an extension of the model by plant types

after pollen reconstructions within the possibilities of the model structure. We did not aim to go towards a new class of models. We are aware of the limited applicability of our conceptual approach. Therefore, we propose not to complicate it any further but to step towards a DGVM for future studies. We extended our final conclusions by a paragraph discussing implications for further studies (DVM, GCM).

2. Regarding the use of the niche concept, we agree that this was not clearly stated in the manuscript. We use the term 'niche' in terms of 'ecological space' regarding moisture requirements, not in terms of 'geographical space'. We adjusted the terminology in the manuscript.

3. We assigned the typical North African physiognomic vegetation types to the four phytogeographic AHP plant types when we introduced the latter in our first manuscript. We understand that it is difficult for the reader to remember this grouping throughout the text and that this might lead to confusions. In the revised manuscript, we introduced a new paragraph after the grouping that describes our usage of terminology. We use the terminology of plant types after Hely et al., (2014) when we consider our work, including the description of the adjusted model and simulations as well as results, discussion and conclusions. Since literature usually refers to the terminology of physiognomic vegetation types, we stick with their terminology in citations and indicate the corresponding phytogeographical plant type after Hely et al., (2014) in brackets to prevent confusions.

4. We extended the discussion towards previous work by Claussen in the context of the assessment of their conclusions in section 2.3 as well as in our final summary and conclusions.

5. We modified the abstract in order to better present our main results.

6. We addressed the suggestion of referee 2 to include sensitivity studies on the sensitivity parameter DB and added a series of plots in the appendix. The effect of different feedback coefficients was already shown by Liu et al., (2006), the work that provides

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the baseline for the model by Claussen et al., (2013) and our model. We therefore prefer not to discuss the effect of DB in great detail in our main manuscript.

Interactive comment on Clim. Past Discuss., 11, 2665, 2015.

Clim. Past Discuss., 11, C1726–C1729, 2015
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We thank the anonymous referee #1 very much for comments and suggestions, and we address here the main issues arising out of the comment.

"I understood that the authors revisited a previous study presenting a conceptual model regarding the potential effect of plant diversity on climate-vegetation feedbacks published by Claussen. However, I found the approach not up to date."

As mentioned, the purpose of the presented work was the revision of Claussen et al., (2013), including an assessment of the study and an extension of the model by plant types after pollen reconstructions within the possibilities of the model structure.

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We did not aim to go towards a new class of models. We are aware of the limited applicability of our conceptual approach, that is why we propose not to complicate it any further but to step towards a DGVM for future studies. However, we think that conceptual niche-based models can still contribute to the understanding of diversity-stability relationships.

“It’s now clearly stated that niche based models are not the adequates tools to answer such questions and dynamic vegetation models should be used. For example, today, dynamic vegetation models are explicitely describing the competition for ressources (light, water, nutrients...) that cannot be described by niche based models [. . .] Generaly when it comes to vegetation function DVM should be prefered to niche based models (just usefulls to describe potential vegetation distribution). “

The niche concept is the underlying principle in the study by Claussen et al., (2013) that we built our work on. We picked up this concept and extended it in the range of possibilities. The focus lies on the relationship between vegetation cover and precipitation, and the distinction between plant types by different precipitation thresholds – niches in terms of moisture requirements – appeared obvious. Other models provide of course many opportunities for more detailed and more accurate simulations of vegetation serving different purposes. However, there are only few model studies considering the effect of diversity on the stability of climate-vegetation systems in a way it was approached by Claussen et al., (2013), and we see the simplicity of conceptual models and the isolated consideration of parameters as an advantage. As mentioned above, we aim to perform future studies with a DGVM in order to consider more processes. The land surface model JSBACH that is part of the Earth System Model we use - MPI-ESM - has compared to other DGVMs a very simple representation of ecosystem processes and a very limited number of interactions implemented. Baudena et al., (2015) showed that JSBACH overestimates tree cover because competition via only NPP favors trees irrespective of water availability, and fire is fostered disproportionally by woody vegetation as compared to grasses, resulting in a negative grass-fire feedback. JSBACH does not account for processes such as root, light, and nutrient competition, fire resistance, shading effects, recruitment, age stages. Conceptual studies in the first place can provide important background information for building in plant-plant interaction and plant-climate feedback in JSBACH.

"Identically, DVM can also give insights when it comes to the impact of an athmospheric CO2 concentration increase, which is important when it comes to water uses efficiency."

The effects of changing atmospheric CO2 concentrations on plant growth and water use efficiency are doubtlessly very important, especially for future projections of vegetation and climate as well as studies of the deep past. However, changes in atmospheric CO2 concentrations were of minor importance during the mid-Holocene compared to changes in precipitation patterns. CO2 changes are therefore not of interest in our study.

"Secondly, the vegetation composition seems to be mainly driven by bioclimatic limits in this study and particularly mean annual amount of prcipitations. Recent studies show that for a identical amount mean annual amount of precipitation the vegetation composition can be drastically different depending of the seasonnality of these precipitations during the year."

It is true that plant growth not only relies on mean annual precipitation but also on seasonality, a parameter that changes over time. We use mean annual precipitation to define our plant types following up on White's classification (1983) where he uses requirements in mean annual precipitation. Even though it would be very interesting to follow changes in seasonality that go in conjunction with insolation changes towards the end of the Holocene, the consideration of seasonality is not provided for in the model formulation and the effort to implement it would be unproportional.

"I would have liked also a figure presenting a temporal comparaison between recorded pollen data and model' simulation to estimate (at least visually) the model accuracy."

Unfortunately, we do not have the pollen data set from Hely et al., (2014), so we cannot present a graphical comparison of pollen and our simulations. We contacted the authors and requested the data, but we did not receive a response. Our comparison is based on the text by Hely et al., (2014) as well as the evolution of “number of taxa” and “number of occurrence” (Fig.3 in Hely et al., (2014)).

Interactive comment on Clim. Past Discuss., 11, 2665, 2015.

Clim. Past Discuss., 11, C1730–C1744, 2015
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Interactive comment on "Palaeo plant diversity in subtropical Africa – ecological assessment of a conceptual model of climate–vegetation interaction" *by* V. P. Groner et al.

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We thank Referee #2 J. Williams very much for thoughtful comments, questions and suggestions. We address here the main issues arising out of the comment. All figures in cluded in the revised manuscript are provided as a pdf in the supplement.

"The scope of the paper seemed a bit narrow to me and overall mainly focusing on confirming the results already reported by Claussen et al. 2013 – i.e. that adding more plant types leads to overall system stability, even though individual plant types might be quite unstable. Given that the model is now attempting to create plant types that are somewhat realistic for North Africa, I think the paper could improve its impact by

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expanding its scope a bit more,"

The purpose of the presented work was actually the revision of Claussen et al., (2013), including an assessment of the study and an extension of the model by plant types after pollen reconstructions within the possibilities of the model structure. With the first part, we intended to set their study, which was based on an ad hoc conceptual model with arbitrarily chosen threshold values, in an ecological context, and we aimed to confirm, or reject, in the second part that their results still hold if the model was adjusted to reconstructions. As mentioned in the conclusions, we propose not to complicate the model any further since other models might be better suited to address the spatial component or more competition related processes.

"a) Adding a qualitative comparison of its results to the pollen time series reported by Hely et al. 2014, "

see specific comment 6.)

"b) Creating a spatially explicit version of the model that simulated shifting vegetation distributions over North Africa for the Holocene and looking for spatial and temporal mosaics in abrupt change, and/or"

see specific comment 5.)

"c) Conducting sensitivity experiments with the overall feedback strength parameter DB. "

see specific comment 3).

SPECIFIC COMMENTS

1. "Niche occupancy. In several places (e.g. P2670L24-25, P2763L27 to P2764L4), the authors state that one species cannot occupy a space left vacant by another species. This statement needs clarification. Are the authors referring to replacement in geographic space (G space) or environmental space (E space)? As written, the text

seems to imply that that a plant type couldn't occupy a piece of ground left vacated by the death of another plant type (no replacement allowed in G space), which would be a poor assumption. But I think that the authors are actually talking about niche stability – i.e. they are assuming that plants have fixed niches in environmental space, and species can't expand their environmental niches even if another plant disappears and removes a competitor from that portion of environmental space."

We use the term 'niche' in terms of 'ecological space' regarding moisture requirements, not in terms of 'geographical space'. We agree that this is not clearly stated in the manuscript. We modified the manuscript in order to be more precise at p.2670 l.20; p.2670 l.26; p.2673 l.28; p.2674 l.4.

"a. So: If text is in fact referring to G-space and model does not allow replacement in geographic space, then authors should defend this assumption. Why couldn't a plant move in to occupy ground left vacant by another dying plant?"

As mentioned above, we refer to the E-space, so the spatial replacement does not play a role in our model. The geographical changes in vegetation cover would require a different definition of plant types and their corresponding niches in the geographical space, hence a different approach.

"b. If instead text is referring to assumption of fixed niches in E-space (a more defensible assumption), then I suggest replacing 'niche occupancy' with 'niche stability' throughout ms. and adding a few supporting references on this topic. There are many papers out there that explore the concept of niche stability and niche conservatism – e.g. Stigall 2012 JBio, Peterson 2011 Jbio."

We agree that the term 'niche occupancy' is not appropriate in all cases. We replaced 'niche occupancy' with 'niche stability' on p.2670 l.24 and added some explanations and supporting literature. Throughout the manuscript, when we speak about plants occupying niches, we see this as the appropriate term since the occupation refers to their presence independent from the stability.

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2.) ”Terminology. The paper goes back and forth between using geographic vs. phytological names for vegetation types: e.g. grasslands, gallery forests, savannas, etc. vs. Saharan type, Sahelian type, Sudanian type, and Guineo-Congolian type. Hard to follow. I suggest using the former terminology throughout the ms., and mentioning the latter terminology only once, to establish equivalency with Hely et al. Papers. ”

We assigned the typical North African physiognomic vegetation types to the four AHP plant types that we used in our paper on p. 2672 l.16-20. We understand that it is difficult for the reader to remember this grouping throughout the text and that this might lead to confusions. In the revised manuscript, we introduced a new paragraph after the grouping that describes our usage of terminology. We use the terminology of plant types after Hely et al.,(2014) when we consider our work, including the description of the adjusted model and simulations as well as results, discussion and conclusions. Since literature usually refers to the terminology of physiognomic vegetation types, we stick with their terminology in citations and indicate the corresponding phytogeographical plant type after Hely et al., (2014) in brackets to prevent confusions.

3.) “Feedback effect. The model assumes a strong feedback effect from the vegetation to the atmosphere (DB set to 1400 mm/yr). I would have been interested to see an analysis in which this was varied from zero to strong and to see the effects of this on the reported hysteresis, for both the simulations with individual and interacting plants.”

The effect of different feedback coefficients was already shown by Liu et al., (2006), the work that provides the baseline for the model by Claussen et al., (2013) and our model. We therefore prefer not to discuss the effect of DB in great detail in our main manuscript. During our working process, we performed sensitivity studies with the parameter DB. In a first attempt, we kept DB homogenous for all plant types but varied the value. This has a strong effect on individual interaction with precipitation, and also an effect on the abruptness of the mean vegetation cover, here mean effective leaf area LS. In the revised manuscript, we added a series of plots to the appendix that show the effect of different DB on plant types interacting individually and together with climate for

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a range of DB values from 0 to 150 mm yr-1 (see Fig. 5-8), and the evolution of LS and precipitation in direct comparison (see Fig. 9). Compared to the difference between individual and combined interaction with precipitation (see Fig. 3 in manuscript), the spread of LS due to variation in specific DB is small between weak (50 mm yr-1) and strong (150 mm yr-1) feedback. We decided for our study to choose the same strong feedback coefficient as Claussen et al., (2013) a) to have a more direct comparison, and b) to see more clearly if there was a stabilizing effect of diversity.

"On p2687L5-6 the authors mention that sensitivity studies with DB show only a minor effect on vegetation cover (LS) – I suggest adding a figure to the main ms. and also showing the effect of DB on modeled precipitation. "

In the manuscript p. 2687 l. 5., we mentioned a second attempt, that was the variation of coefficients between plants, namely DBi, other than the variation of homogenous DB as described above. The choice of specific feedback coefficients DBi had in fact a small impact on the mean cover. Fig. 10 in the appendix shows an ensemble of 30 simulations with different combinations of plant type specific feedback coefficients DBi, ranging from 0 mm yr-1 (no feedback) to 150 mm yr-1 (very strong feedback), and the ensemble mean (black line). The ensemble also includes the homogenous cases DBi = 0 mm yr-1 and DBi = 150 mm yr-1 for all plant types. Similar to the variation in DB, the spread of LS due to variation in specific DBi is rather small, compared to the difference between individual and combined interaction with precipitation. We decided to summarize all feedback effects in the maximum potential effective leaf area Li to minimize the degrees of freedom and to keep the model simple and transparent.

4.) "Li parameterization for plant functional types. The authors appropriately note that Li (effective leaf area) is blending many processes (actual leaf area, leaf albedo, leaf evapotranspiration, etc.). The problem is that it makes it hard to check Li against observational data, and so there is no way to really constrain this parameter. As a result, the parameterization of Li for the various plant types seems plausible but also somewhat arbitrary. "

It is true that it is difficult to check the effective leaf area Li against observational data and that the parametrization is arbitrary to a certain degree. In order to be as accurate as possible, we followed Hely et al., (2009) (p.2679, l. 9 in manuscript) who compared simulated vegetation types with MODIS observations of LAI. The authors followed the classification by Hely et al. (2006), who aggregated White's phytochoria in 10 vegetation classes, which could be derived from model simulations according to their LAI and the ratios of plant functional types. The range of LAI values they use for their classification rules is between 0 and >4.75. We assigned values in that range linearly to our plant types to have at least qualitative estimates of stronger/weaker feedbacks. We added the aspect 'observation-based' in the manuscript.

5.) "Extending to a spatial component. This model is not spatially explicit and is essentially treating all of North Africa as a single location. In the conclusions and elsewhere (e.g. P2687L26-27), the authors state that 'the approach does not allow for a geographically explicit description of vegetation cover evolution'. Why not? Seems like it would be straightforward to extend this model by running it for individual grid cells and then dividing North Africa into many grid cells, each with its own prescribed forcing of insolation and precipitation. This prescribed forcing would be easy for insolation and wouldn't be that hard to come up with reasonable precipitation scenarios for North Africa, based on published paleoclimatic time series. See, for example, Shanahan et al. 2015 Nat Geosci. It would be interesting to see how this model played out spatially. – e.g. does it produce sharp ecotones in vegetation distributions? Do these ecotones shift slowly or quickly over time as precipitation declines? Does it produce a 'temporal mosaic' of abrupt tipping points, as hypothesized by Williams et al. 2011 J. Ecol.? "

During our working process, we performed sensitivity studies with the parameter that determines the slope of background vegetation decline in order to address different regional trends. The main effect of diversity on climate-vegetation system stability did not change in characteristics, we only observed a shift in timing. We therefore decided to stay with our focus on the feedback process rather than on the spatial component

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of vegetation change. For the purpose of spatial simulations, other models might more more appropriate and accurate.

6.) “The paper is right to note that quantitative comparisons can’t be made between the model results and the pollen richness and abundance data presented by Hely et al. 2014 (P2684L26-29). Nonetheless, a qualitative comparison would be informative. Suggest showing a figure making this comparison. (Note, later, on P2689L11-12 the authors assert that the model results compare well to Hely et al., so again a figure would be helpful for the reader to assess this comparison.) ”

Unfortunately, we do not have the pollen data set from Hely et al., (2014), so we cannot present a graphical comparison of pollen and our simulations. We contacted the authors and requested the data, but we did not receive a response. Our comparison is based on the text by Hely et al., (2014) as well as the evolution of “number of taxa” and “number of occurrence” (Fig.3 in Hely et al., (2014)).

7. “Discussion. Almost all of the discussion is placed in the context of Claussen et al. 2013. What about Claussen’s earlier papers, in particular the ones arguing for multiple stable states of North Africa and the prospect for rapid regime shifts between these alternate stable states? Both this paper and Claussen et al. 2013 seems to be backing away from these earlier findings, while showing the interesting effects of increasing plant diversity on system stability. It would be helpful to more explicitly state the implications of these results for the prior work by Claussen. ”

In previous studies that focused on multiple stable states of the climate-vegetation system in North Africa, including those of Claussen (1998), Liu et al., (2006), and Bathiany et al., (2012), it was argued that an abrupt change emerging from the loss of stability of one of the stable climate-vegetation states causes abrupt changes in both the vegetation record and the hydroclimatic record. Our study, however, supports the hypothesis of Claussen et al., (2013) that in an ecosystem with rich plant diversity, multiple stable states can exist, even if the hydroclimate record shows a gradual transition. Hence the latter studies do not invalidate the earlier considerations. Claussen et al., (2013) mentioned the main implications of their study for the ongoing debate on the abruptness of vegetation decline at the end of the AHP: “Our conceptual considerations shed new light on the Lake Yoa record and offer new interpretation of proxy data to reconcile the apparent discrepancy between previous competing interpretations. Our results demonstrate that there is no straightforward link between the strength of the climate-vegetation feedback and the phenomenology of the decline in vegetation cover and precipitation, [...] the gradual drying and asynchronous decline in plant taxa seen in the Lake Yoa record does not refute the assumption of a strong biogeophysical feedback, [...] there is no contradiction between these two aspects. ”

We can support these statements with our results. Since there is no way to determine the cause of weak climate-vegetation feedback – general weak feedback or buffering by high diversity – we cannot prove previous studies wrong that show strong feedback and abrupt vegetation decline. For example, simulations by Claussen (1999) were performed with the lowest possible number of PFTs, one tree and one grass. The low diversity implies a high likelihood for abrupt transitions (Scherer 2005, Claussen et al., 2013). We included this discussion in the manuscript, p. 2676 l.3 and p.2688 l.10.

8. “Abstract – mostly describes model development. Little information about results and findings. “

We agree that the abstract includes too many details of the model development. Please see an overworked abstract in the revised manuscript. From our point of view, the abstract contains the main results and findings of the paper:

1. “In principle, the original model reproduces the main features of different plant types interacting together with climate although vegetation determinants other than precipitation are neglected. However, the model cannot capture the diversity of AHP vegetation”
2. “With the consideration of full environmental envelopes and the prescribed retreat of the tropical gallery forest type we can simulate a diverse mosaic-like environment

as it was reconstructed from pollen." 3."Transient simulations of this diverse environment support the buffering effect of high functional diversity on ecosystem performance and precipitation, concluded by Claussen et al., (2013) from the simple approach." 4. "Sensitivity studies with different combinations of plant types highlight the importance of plant composition on system stability, and the stabilizing or destabilizing potential a single functional type may inherit."

9. "I'm a little unclear about how the precipitation forcing is applied. The model calculates precipitation as the outcome of a feedback between the vegetation and atmosphere. Does the model initiate with an initial decline in precipitation and then the feedbacks take over? Or is a prescribed decline in precipitation applied throughout the Holocene, which is then amplified by the feedbacks. "

The prescribed decline in precipitation is applied throughout the Holocene, and is then amplified by the feedbacks. The background precipitation Pd in absence of vegetation is defined in Equ. 5 in the manuscript, in the section that summarized the model by Claussen. We mentioned this on P2680 l.19, and we added for additional clarity a reference to Equ. 5 in the revised manuscript. We also added the reference to Equ. 1 for the change in Li over time on p.2678 l.21.

10. "PP2673-2674: See Comment 1 above. This paragraph is also is muddling the Eltonian and Grinnellian concepts of niche (see Chapter 1 of Chase & Leibold 2003): The first refers to the functional role of a species in an ecosystem (e.g. an herbivore) and the second refers to the set of environments in which a species can survive. "

We changed the paragraph in order to be more clear, see answer to comment 1.).

11. "P2675L15-16: This overstates the conclusions of Claussen et al. 2013. That paper didn't argue that the distinction between strong and weak feedbacks was no longer relevant, but did argue that they were hard to diagnose and disentangle. "

We agree that the formulation was unclear. We changed the corresponding paragraph on p.2675 l.15 to "One of the main conclusions by Claussen et al., (2013) was that strong or weak climate-vegetation feedback were hard to diagnose and disentangle regarding abrupt climate changes on a regional scale".

12. "P2679L8: I'm confused about DB. I thought it was a prescribed parameter (set to 1400 mm/yr) but here text implies that it is a product of the model. "

This is probably a misunderstanding, caused by an unclear formulation. DB is not a product of the model. The precipitation component induced by feedback (see Equ.11) is the product of DB and Li. It is therefore not practical to vary both parameters since their individual effects on precipitation cannot be disentangled.

13. "Last page, L20-25: This paragraph about expanding the lessons to DVMs and GCMs is interesting and I would have liked to learn more. Many DVMs already incorporate plant diversity at the level of PFTs and roughly at the level of diversity shown here. How would the lessons from this study be applied to improve DVMs? "

We extended the last paragraph in the manuscript by an outlook to explain in more detail what we consider investigating in the future with our land surface model JSBACH, part of MPI-ESM.

TECHNICAL CORRECTIONS

P2666 L17: Which suggested conclusions? Unclear. Void, we deleted that paragraph in revised version.

P2669 L4: Observation based -> Observational implemented

L8: delete 'indeed' implemented

L29: insert comma after literature implemented

P2673L1: insert 'one portion of' before 'its climatic component implemented

L6: in->of implemented

L7: plant’s->plants’ implemented

L12: Suggest inserting citation to recent work by Staver and colleagues, e.g. Staver et al. 2011 Ecology or Science. Implemented

L16-18: awk sentence; hard to follow. We shortened the sentence to “With the niche approach, Claussen et al., (2013) design the effective interaction between vegetation and climate from bottom up”.

P2675L5-6: Do Claussen et al. 2013 assume a positive relationship between diversity and stability, or does this stability emerge as a model outcome? The text here states that this relationship was assumed by Claussen et al; I thought it was touted as a finding by that paper. We changed ’assumption’ to ’finding’.

L8: delete ‘correctly’ implemented

L9: presence-> diversity Misunderstanding of meaning, we actually mean the presence of an individual plant type. We added ’individual’.

L12: ‘appearance’ is misspelled Void, we changed the sentence in revised version.

L12-13: I don’t understand what this sentence is trying to say. Is it saying that resilient plants arrive more quickly, or that their duration of persistence is shortened? Their duration of persistence is shortened, we changed that in the manuscript. L26: delete ‘whole’ implemented

L29: delete ‘ecologically reasonable’ We do not want to repeat Claussen’s findings, but stress that the conclusions are in accordance with literature. Therefore, we did not implement this suggestion.

P2676L1-2: delete the second and third ‘the’s in this sentence implemented

L7: ‘is indeed’ -> ‘offers’ implemented

L11: ‘on’ -> ‘to’ implemented

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L26: What is a ‘ripiculous stripe’? Misspelling of ’ripicolous’, which means ’Inhabiting the banks of rivers and streams’, used similarly to ’riparian’, which means ’Relating to, or located, on the banks of a river or stream’ (http://wordinfo.info). A ripicolous stripe is a stripe of vegetation in a dry environment that can grow because of waterlogging. It is comparable to ’Tiger bush’.

P2677L19: More sophisticated than what? More sophisticated than the model we present. We changed the sentence to “For the geographically explicit simulation of vegetation change, a model more sophisticated than our conceptual approach is required.”

P2678L4: insert ‘differential’ before ‘moisture requirements’. Implemented

P2681L9-10: Show equations 1 and 5 here; don’t make the reader go look for them in Claussen et al. 2013. (In my version of Claussen et al. 2013, only equations 1 and 2 are labeled.) We refer to the Equ.1 and 5 in the manuscript in the section that summarizes the paper by Clausset et al., (2013). We made some changes in the manuscript to make this more clear, see “comment 9.).

L22-23: This opening sentence to this paragraph isn’t very informative; suggest condensing to “In our implementation of the vegetation types described by Hely et al (2014), plant types range from. . .” implemented

L25: set up should be one word. Implemented

P2682L25-26: Insert reference to Fig 3c here implemented

P2683L5: Insert a reference to Fig. 3(d-f) here. Implemented reference to Fig. 3d-e, and we added a sentence concerning precipitation and referred to Fig. 3f on p.2683 l.5.

L11-12: delete clause beginning ‘even though it. . .’ – difficult to follow. Implemented

L12: appearance is misspelled implemented

L16: Therewith->Hence implemented

L19: Insert ‘the’ before ‘combined’ implemented

L20: gradual -> gradually implemented

P2684L1: What is meant by ‘The assumption of a full environmental envelope’? We meant that we include an upward branch like Claussen et al., (2013) as well as a downward branch that accounts for the maximum precipitation as an upper limit for plant growth.

L13-14: Might note here that increased variations is one of the proposed early warning signals for regime shifts. The system has now simplified to just 1-2 plant functional types and those plant functional types are nearing their thresholds, so it makes sense that variance is increasing. We implemented your suggestion and added Scheffer et al., (2001) and Scheffer et al., (2009) as references.

L15: Delete this opening clause and put (Hely et al 2014) reference at end of sentence. We prefer the original version, so we did not change this sentence.

L16 Don’t capitalize North. implemented

P2685L5-7: this statement by ‘even plant communities’ is probably true but isn’t supported by the results shown here – either delete or provide a supporting reference. Deleted

L14: ‘from earlier on’ -> earlier implemented

L17: ‘but the Sudanian type seems to have a large impact in our simulations’. Explain this a bit more – how exactly does the impact manifest? I can see what the authors mean by looking at Fig 4, but the text should explain this a bit more. Should probably also explain why the removal of the Sudanian type is having such a big effect – presumably because it was prescribed to have the highest effective leaf area, and so its removal causes a large drop in Ls. We added “This is mainly because the Sudanian type was prescribed the highest potential effective leaf area, and its removal leaves the interaction with climate to the Saharan and the Sahelian type, which are both sensitive to changes in precipitation and respond abruptly when their minimum thresholds PiC1 are crossed.”

L24: insert ‘that’ inside ‘impact different’ implemented

L27: delete already implemented

P2686L1: plant’s -> plants’ implemented

L2: insert comma before ‘because’ implemented

P2787L8: rephrase opener to ‘In this paper, we extend the conceptual model. . .’ We find the original formulation more appropriate.

L12-15: Long sentence. Break this into two sentences. Implemented

L21-22: Delete this opening sentence. We want to mention the ’niche approach’ at this point, so we changed the sentence to “With the niche approach, the effective feedback between vegetation and climate emerges from the interacting properties of different plant types fulfilling specific ecosystem functions”.

L24-27: I suspect that ‘niche’ is being confused here again with respect to G-space and E-space. See Specific comments #1. We added ’ecological space’

P2788L1-2: I don’t understand what this sentence is trying to say. We want to address that changes in the environment lead to changes in the set of available niches.

L4: What ecological context? Vague, please clarify. Changed to ’ecological state of knowledge’

L3-6: Provide citations to support the statement that ‘diversity can have a stabilizing effect on ecosystems’ and also provide countercitations. Do all ecologists really agree on this point? We discussed the diversity-stability debate already in section 2.3 in

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detail and provided citations that support both sides. We do not see a need to repeat the literature here. We added a reference to section 2.3.

L6: delete 'correctly' implemented

L18: 'set up' should be one word implemented

L22: in the -> into implemented

L26-27: what is meant here by 'mosaic like'? Are the authors referring to temporal mosaics (Williams et al. 2011), spatial heterogeneity, or the combination of both? We refer to a spatial mosaic, using the term from Hely et al., (2014), the work that we based our model vegetation types on.

L2689L5: overturning ->turnover. Implemented

L13-14: I don't really understand what this sentence is trying to communicate. Seems unnecessary. Suggest deleting. With this sentence we want to point to the importance of plant composition for the stability of a climate-vegetation system. We changed the sentence to "The importance of plant composition for the stability of a climate–vegetation system becomes clear comparing different combinations of plant types."

L14-17: Suggest reversing order within this sentence to first state the model result then the caveat. L20: 'that topic' – vague. Which topic? Implemented

L20-25: This paragraph about expanding the lessons to DVMs and GCMs is interesting and I would have liked to learn more. Many DVMs already incorporate plant diversity at the level of PFTs and roughly at the level of diversity shown here. How would the lessons from this study be applied to improve DVMs? See specific comment 13.)

Please also note the supplement to this comment:
http://www.clim-past-discuss.net/11/C1730/2015/cpd-11-C1730-2015-supplement.pdf

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Interactive comment on Clim. Past Discuss., 11, 2665, 2015.

Clim. Past Discuss., 11, C1894–C1898, 2015
www.clim-past-discuss.net/11/C1894/2015/

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Interactive comment on "Palaeo plant diversity in subtropical Africa – ecological assessment of a conceptual model of climate–vegetation interaction" *by* V. P. Groner et al.

V. P. Groner et al.

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We prepared the authors response to the discussion comments under the assumption that we could also provide a revised track change version of the manuscript, as it was demanded by the Editor. Since this was not possible in the framework of the discussion structure, we here provide a supplementary comment to the comment of referee #2 in order to show more clearly the changes in the manuscript. The response to the comment of referee #1 does not include direct changes in the manuscript and is therefore not considered here.

Specific comment #1 – niche definition p.2670 l.20-26: "Claussen et al. (2013) assume

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that each plant type can occupy a share of 1/N of the ecological space. The assumption of niche stability/conservatism - a concept that assumes species maintaining the parameters of their ecological niche following environmental change (Huntley et al., 1989; Peterson et al., 1999; Peterson, 2011; Stigall, 2012) - prohibits the replacement of disappearing plants by remaining plant types. These assumptions are hereinafter referred to as the "niche approach" (Claussen et al., 2013)."

p.2673 l.28 - p.2674 l.4: "The niche approach also implies that once a specific plant type retreats owing to water scarcity, there may not be any other type that is able to occupy its place in the ecological space. From an ecological point of view, existing plants likely benefit from the extinction of others by having less competition and more resources available. It is questionable whether these succeeding species can occupy the niches (ecological space) of disappearing species, including their way of using resources, and overtake their ecosystem functions, or if they just occupy the available barren area (geographical space)."

specific comment #2 - terminology p.2676 l. 20 "Throughout this paper, we use the terminology of phytogeographical plant types after Hely et al. (2014) whenever we refer to our work, including the descriptions of the adjusted model and simulations as well as results, discussions and conclusions. Since literature often refers to the terminology of physiognomic vegetation types, we stick with their terminology in citations and indicate the corresponding phytogeographical plant types after Hely et al. (2014) in brackets to prevent confusions."

specific comment #4 - Li p.2679 l. 8 "Values for Limax are chosen to qualitatively represent the variety of these aggregated properties following observation-based classifications (Hely et al., 2006, 2009)."

specific comment #7 – implications for earlier studies p. 2676 l.3 "These difficulties are not inconsistent with previous studies that proposed strong climate-vegetation feedback, resulting in abrupt shifts from a stable "green" state to a stable "desert" state.

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For example, simulations by Claussen et al. (1999) were performed with the lowest possible number of PFTs, one tree and one grass. The low diversity implies a high likelihood for abrupt transitions (Scherer-Lorenzen, 2005; Claussen et al., 2013)."

p.2688 l.10 "Claussen et al. (2013) argued ecologically reasonable that it is difficult to determine the origin of system stability as the overall feedback strength depends on species composition. These difficulties are not inconsistent with previous studies that proposed strong climate-vegetation feedback, resulting in abrupt shifts from a stable "green" state to a stable "desert" state. Simulations by Claussen et al. (1999) were performed with the lowest possible number of PFTs, one tree and one grass. The low diversity implies a high likelihood for abrupt transitions (Scherer-Lorenzen, 2005; Claussen et al., 2013). In previous studies that focused on multiple stable states of the climate-vegetation system in North Africa, including those of Claussen et al. (1998), Liu et al. (2006a) and Bathiany et al. (2012), it was argued that an abrupt change emerging from the loss of stability of one of the stable climate-vegetation states causes abrupt changes in both the vegetation record and the hydroclimatic record. Our study, however, supports the hypothesis of Claussen et al. (2013) that in an ecosystem with rich plant diversity, multiple stable states can exist, even if the hydroclimate record shows a gradual transition. Hence the latter studies do not invalidate the earlier considerations."

specific comment #8 – abstract "We here critically re-assess a conceptual model dealing with the potential effect of plant diversity on climate-vegetation feedback, and provide an improved version adjusted to plant types that prevailed during the African Humid Period (AHP). Our work contributes to the understanding of the timing and abruptness of vegetation decline at the end of the AHP, investigated by various working groups during the past two decades using a wide range of model and palaeoproxy reconstruction approaches. While some studies indicated an abrupt collapse of vegetation at the end of the AHP, others suggested a gradual decline. Claussen et al. (2013) introduced a new aspect in the discussion, proposing that plant diversity in terms of moisture requirements could affect the strength of climate-vegetation feedback. In a conceptual model study, the authors illustrated that high plant diversity could stabilize an ecosystem, whereas a reduction in plant diversity might allow for an abrupt regime shift under gradually changing environmental conditions. In the light of recently published pollen data and the current state of ecological literature, the conceptual model by Claussen et al. (2013) reproduces the main features of different plant types interacting together with climate, but it does not capture the reconstructed diversity of AHP vegetation. Especially tropical gallery forest taxa, indirectly linked to local precipitation, are not appropriately represented. With a new model version adjusted to AHP vegetation we can simulate a diverse mosaic-like environment as reconstructed from pollen, and we observe a stabilizing effect of high functional diversity on vegetation cover and precipitation. Sensitivity studies with different combinations of plant types highlight the importance of plant composition on system stability, and the stabilizing or destabilizing potential a single plant type may inherit. The model's simplicity limits its application, however it provides a useful tool to study the roles of real plant types in an ecosystem and their combined climate-vegetation feedback under changing precipitation regimes.“

specific comment #13 – last paragraph about DGVMs “For further studies on the effect of plant diversity on the stability of climate-vegetation systems, we propose not to complicate the conceptual model any further by introducing more ad hoc tunable parameters, but to transfer the lessons learned from this study to a comprehensive dynamic vegetation model. Our Earth System Model MPI-ESM did not show abrupt transitions of large scale vegetation cover in previous transient Holocene simulations, and the understanding we gained in this study can help to investigate whether this is an effect emerging from the representation of diversity in our land surface model JSBACH. This process-based model offers the possibility to represent different degrees of plant diversity in various plant properties, and a variety of interactions with the atmosphere to address arising question: Could a more complex model depict AHP plant diversity and reproduce the results from our qualitative conceptual study? Would changes in plant diversity stabilize or destabilize the climate vegetation system in coupled GCM simulations? Could new PFTs designed after pollen reconstructions better represent plant diversity in subtropical Africa? Could the implementation of additional processes in JSBACH, such as root- or light-competition, or additional plant properties, such as fire-resistance, lead to new effects on the climate-vegetation system stability? In summary, a deeper understanding of the role that plant diversity can play in climate-vegetation interaction, and an improved representation of plant diversity based on pollen reconstructions, could in coupled GCM simulations allow for a more realistic consideration of plant-plant interaction and climate-vegetation feedback.“

technical corrections - role of Sudanian type p.2684 l.13 “The system has now simplified to just two plant types and those are nearing their thresholds, which causes the increase in fluctuations. The increase in fluctuations is one of the proposed early warning signals for regime shifts (Scheffer et al., 2001, 2009)”.

p. 2685 l.17 “This is mainly because the Sudanian type was prescribed the highest potential effective leaf area, and its removal leaves the interaction with climate to the Saharan and the Sahelian type, which are both sensitive to changes in precipitation and respond abruptly when their minimum thresholds PiC1 are crossed.”

Interactive comment on Clim. Past Discuss., 11, 2665, 2015.

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Palaeo plant diversity in subtropical Africa – ecological assessment of a conceptual model of climate–vegetation interaction

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Abstract. We here critically re-assess a conceptual model dealing with the potential effect of plant diversity on climate–vegetation feedback, and provide an improved version adjusted to plant types that prevailed during the African Humid Period (AHP). Our work contributes to the understanding of the timing and abruptness of vegetation decline at the end of the AHP, investigated by various working groups during the past two decades using a wide range of model and palaeoproxy reconstruction approaches. While some studies indicated an abrupt collapse of vegetation at the end of the AHP, others suggested a gradual decline. Claussen et al. (2013) introduced a new aspect in the discussion, proposing that plant diversity in terms of moisture requirements could affect the strength of climate–vegetation feedback. In a conceptual model study, the authors illustrated that high plant diversity could stabilize an ecosystem, whereas a reduction in plant diversity might allow for an abrupt regime shift under gradually changing environmental conditions.

~~Based on~~ In the light of recently published pollen data and the current state of ecological literature, ~~we evaluate the representation of climate–vegetation feedback in this conceptual approach, and put the suggested conclusions into an ecological context. In principle, the original model~~ the conceptual model by Claussen et al. (2013) reproduces the main features of different plant types interacting together with climate~~although vegetation determinants other than precipitation are neglected. However, the model cannot capture the~~ , but it does not capture the reconstructed diversity of AHP vegetation. Especially tropical gallery forest taxa, indirectly linked to local precipitation, are not appropriately represented.

~~In order to fill the gaps in the description of plant types regarding AHP diversity, we modify the original model in four main aspects. First, the growth ranges in terms of moisture requirements are~~

~~extended by upper limits to represent full environmental envelopes. Second, data-based AHP plant types replace the hypothetical plant types. Third, the tropical gallery forest type follows the gradual insolation forcing with a linear approximation because it relies more on large scale climate than on regional precipitation amounts. Fourth, we replace the dimensionless vegetation cover fractions with individual effective leaf areas to capture different contributions to climate–vegetation feedback.~~

~~These adjustments allow for the consideration of a broader spectrum of plant types, plant-climate feedbacks, and implicitly for plant-plant interactions. With the consideration of full environmental envelopes and the prescribed retreat of the tropical gallery forest type~~ With a new model version adjusted to AHP vegetation we can simulate a diverse mosaic-like environment as ~~it was~~ reconstructed from pollen~~. Transient simulations of this diverse environment support the buffering~~, and we observe a stabilizing effect of high functional diversity on ~~ecosystem performance and precipitation, concluded by from the simple approach~~vegetation cover and precipitation. Sensitivity studies with different combinations of plant types highlight the importance of plant composition on system stability, and the stabilizing or destabilizing potential a ~~single functional~~ single plant type may inherit. ~~In a broader view, the adjusted modelprovides a~~

The model's simplicity limits its application, however it provides a useful tool to study the roles of real plant types in an ecosystem and their combined ~~climate–vegetation~~ climate-vegetation feedback under changing precipitation regimes.

1 Introduction

Between 9000 and 6000 years BP, a wet phase peaked across North Africa. During this so-called "African Humid Period" (AHP), large areas of the nowadays hyperarid Sahara and arid Sahel region were vegetated (Ritchie and Haynes, 1987; Prentice and Jolly, 2000), a dense fluvial network was developed, and open surface water was widespread (Hoelzmann et al., 1998). Fossil pollen records indicate that the Sahel boundary was shifted northwards by 5 to 7° to at least 23° N (Jolly et al., 1998) and tropical plant taxa might have used river banks as migration paths to enter drier environments (Watrin et al., 2009). Vegetation cover was a diverse mosaic of xeric and tropical species whose ranges do not overlap today (Hély et al., 2014). This "greening" was triggered by changes in the Earth's orbit, resulting in a stronger insolation and higher temperatures in the boreal summer, accompanied by an intensification of the summer monsoon (Kutzbach, 1981; Kutzbach and Guetter, 1986). However, the increase in insolation alone is insufficient to explain the vegetation coverage reconstructed from palaeo records. It has been shown that several feedback mechanisms including ocean (Kutzbach and Liu, 1997; Braconnot et al., 1999), surface water coverage by lakes and wetlands (Coe and Bonan, 1997; Krinner et al., 2012), and vegetation and soil albedo (Claussen and Gayler, 1997; Claussen, 2009; Vamborg et al., 2011) could have amplified the orbital forcing. We here provide a conceptual model adjusted to AHP plant types as a tool to study how plant diversity as an additional parameter might have affected the climate–vegetation interaction under changing precipitation regimes.

Charney (1975) first proposed a positive feedback between vegetation and precipitation in the Sahel to explain the self-stabilization of deserts. This positive feedback provides a mechanism that might allow for the existence of multiple stable equilibria, first shown in coupled model simulations by Claussen (1994) and Claussen et al. (1998). Depending on climate and environmental conditions, the Sahara could exist in a "green" state with high vegetation cover and a "desert" state without vegetation (Brovkin et al., 1998; Bathiany et al., 2012). The potential non-linearity of this feedback might cause an abrupt transition between these states when the system reaches a "tipping point" (Williams et al., 2011). Several climate model studies reproduced such an abrupt transition from "green" to "desert" state at around 5500 years BP for Western Africa (e.g., Claussen et al., 1999; Renssen et al., 2003; Brovkin and Claussen, 2008) and reconstructions of dust flux in the Atlantic supported an abrupt ending of the AHP at least for the Western part of the Sahara (deMenocal et al., 2000).

Later studies highlighted the complexity of desertification history and the variety in timing and rate of regional changes. They challenged the hypothesis of an abrupt vegetation decline and doubted the existence of a strong positive climate–vegetation feedback in subtropical Africa. Pollen and sediment records from Lake Yoa in Eastern Africa indicated a more gradual transition from "green" to "desert" Sahara (Kröpelin et al., 2008; Francus et al., 2013), implying that the vegetation-climate feedback was rather weak. Palaeohydrologically dated records from fluvial, lacustrine and palustrine environments supported a gradual transition from wet to dry conditions (Lézine, 2009; Lézine et al., 2011). Observation based estimates of feedback strength in Northern Africa showed little direct evidence of a strong positive vegetation effect on large-scale precipitation (Liu et al., 2006a). In the framework of the Paleoclimate Modeling Intercomparison Project, Phase II (PMIP2), some models even suggested a negative feedback over Northern Africa for the Mid-Holocene (Braconnot et al., 2007). Liu et al. (2007) demonstrated ~~indeed~~ an abrupt vegetation collapse in coupled transient simulations, but the authors attributed this to a non-linear vegetation response to a precipitation threshold in the presence of strong climate variability, independent of a climate–vegetation feedback. Rachmayani et al. (2015) recently showed a positive effect of vegetation on precipitation caused by evapotranspiration effects rather than albedo effects.

Claussen et al. (2013) introduced a new aspect in the discussion, stating that plant diversity in terms of moisture requirements could affect the strength of climate–vegetation feedback. In a conceptual model study, with hypothetical discrete plant types, they demonstrated that in coupled interaction with precipitation, sensitive plant types tend to sustain longer with decreasing precipitation, while resilient plant types disappear earlier than they would do on their own. The mean vegetation coverage decreased more gradually with strong fluctuations under drying conditions, fairly capturing the decline in pollen influx into Lake Yoa between 6000 and 4000 years BP (Kröpelin et al., 2008).

Plant diversity might therefore increase the stability of the climate–vegetation system in semi-arid regions, buffer the strength of individual plant-precipitation feedback and prevent an abrupt vegetation collapse. The authors suggested that plant composition is of high importance for the rate of transition and a reduction in functional plant diversity may lead to an abrupt regime shift.

We here critically re-assess the conceptual model by Claussen et al. (2013) from an ecological point of view, and provide an improved version that represents the diversity of AHP plant types. Referring to the current state of knowledge in ecological literature we evaluate the representation of plant-plant interaction and plant-climate feedback in the conceptual approach. We further discuss how the suggested conclusions fit in an ecological context. Based on the assessment, we adjust the original model to AHP vegetation by the modification of four fundamental aspects. First, the growth ranges in terms of moisture requirements are extended by upper limits to represent full environmental envelopes. Second, data-based AHP plant types replace the hypothetical plant types. Third, the tropical gallery forest type, indirectly linked to local precipitation, follows mainly the gradual insolation forcing with a linear approximation. Fourth, we replace the dimensionless vegetation cover fraction with individual effective leaf areas to capture different contributions to climate–vegetation feedback. These changes allow for studies on the roles of different real plant types in an ecosystem and their combined climate–vegetation feedback under changing environmental conditions.

2 The conceptual approach by Claussen et al. (2013)

2.1 The model formulation by Claussen et al. (2013)

The approach by Claussen et al. (2013) is based on a conceptual description of climate–vegetation feedback in semi-arid regions (Brovkin et al., 1998; Liu et al., 2006b). The applicability is restricted to a region that experiences a uniform climate, which approximately corresponds to the grid size of a general circulation model (GCM) in the order of $100\,\mathrm{km}^2$. Within this region, the diversity of coexisting plant types $i = 1, \ldots, N$ reflects the heterogeneity of the environment that provides ecological niches for N different plant types. Diversity is here defined in terms of specific moisture requirements and sensitivities to changes in mean annual precipitation P. The model does not explicitly account for direct plant-plant interactions such as competition or facilitation. ~~Each~~ Claussen et al. (2013) assume that each plant type can occupy a share of $1/N$ of the ~~whole area and niche occupation~~ ecological space. The assumption of niche stability/conservatism – a concept that assumes species maintaining the parameters of their ecological niche following environmental change (Huntley et al., 1989; Peterson et al., 1999; Peterson, 2011; Stigall, 2012) – prohibits the replacement of disappearing plants by remaining plant types. ~~This assumption is~~ These assumptions are hereinafter referred to as the “niche approach” (Claussen et al., 2013). The change of relative vegetation cover fraction

V_i (non-dimensional between 0 and 1) under external forcing is determined by

$$\frac{\mathrm{d}V_i}{\mathrm{d}t} = \frac{V_i^{\mathrm{E}}(P) - V_i}{\tau}, \tag{1}$$

with the time step t in years, setting $t = 0$ for present day and negative values for the past, and the vegetation equilibrium timescale $\tau = 5$ years (Liu et al., 2006b). The equilibrium vegetation cover fraction V_i^{E} is a function of mean annual precipitation P and is shaped by lower and upper precipitation thresholds, P_i^{C1} and P_i^{C2} respectively. Their difference $D_i^C = P_i^{C2} - P_i^{C1} > 0$ determines the slope of $V_i^{\mathrm{E}}(P)$ in the intermediate precipitation regime

$$V_i^{\mathrm{E}}(P) = \begin{cases} 1 & P \geq P_i^{C2} \\ \dfrac{(P - P_i^{C1})}{D_i^C} & P_i^{C2} > P > P_i^{C1} \\ 0 & P \leq P_i^{C1} \end{cases}. \tag{2}$$

When all plant types interact together with climate, the mean vegetation cover fraction V_S is calculated as the average of all individual plant types

$$V_S = \frac{1}{N} \sum_{i=1}^{N} V_i \leq 1, \tag{3}$$

assuming that the atmosphere reacts to the average properties of the whole area. The justification for this assumption is that the difference in crucial surface parameters such as albedo and hydrological properties is smaller between considered plant types than the contrast to desert.

Accounting for climate–vegetation feedback, precipitation is a combination of a background precipitation P_d in absence of vegetation that changes with external gradual insolation forcing, and a precipitation component induced by vegetation feedback. The equilibrium precipitation P^{E} is defined as

$$P^{\mathrm{E}}(V_S, t) = P_d(t) + D^B \cdot V_S, \tag{4}$$

with the climate feedback coefficient D^B that determines the feedback strength. For simplicity, Claussen et al. (2013) assumed the same $D^B = 140\,\mathrm{mm\,yr^{-1}}$ for all plant types (Liu et al., 2006b), implying that the feedback is only sensitive to vegetation cover but not to composition. The background precipitation P_d changes linearly with time, mimicking the weakening of the West African monsoon due to continuous change in insolation forcing

$$P_d(t) = P_{d0}\left(1 - (t + 6500)/T\right), \tag{5}$$

where $P_{d0} = 300\,\mathrm{mm\,yr^{-1}}$ is the initial precipitation of the simulation period $T = 6500$ years (Hansen et al., 2007; New and Jones, 1999). The natural variability in precipitation, independent from vegetation, is implemented as additional white noise forcing $P_N(t)$ in the total precipitation

$$P(V_S, t) = \max((P^{\mathrm{E}}(V_S, t) + P_N(t), 0)). \tag{6}$$

The intersections of P and V in a vegetation-precipitation diagram indicate equilibrium coupled states, see Fig. 1. System instability and multiple equilibria exist only for a sufficiently strong positive vegetation feedback with $D^B > D_i^C$ (Liu et al., 2006b).

2.2 Assessment of the model set up by Claussen et al. (2013)

The basic units in the conceptual model by Claussen et al. (2013) are plant types that reflect the heterogeneity of the environment, occupying different n dimensional niches. In the actual realization of plant types in the model fomulation, plant diversity is only expressed in terms of different precipitation thresholds as a proxy for moisture requirements, which reduces the fundamental multi-dimensional niche to one portion of its climatic component. The choice of thresholds implicitly defines ~~plant' s~~ plants' sensitivities to changes in precipitation. Moisture requirement is an established measure to characterize diversity in recent African ecosystems (White, 1983), and the measure is appropriate in the conceptual model because hydrology is the main determinant of plant growth in the subtropics on the considered scale ~~in~~ of the order of $100\,\mathrm{km}^2$ (Coughenour and Ellis, 1993). For a more versatile description of plant's niches and the explanation of actual vegetation composition and spatial distribution within the considered region, further crucial determinants need to be taken into account. The coexistence of trees and grasses in subtropical regions and the maintenance of their ratios is a complex topic, studied for years in the framework of the "savanna question", but still not well understood (Sarmiento, 1984; Scholes and Archer, 1997; Jeltsch et al., 2000; Staver et al., 2011). The complexity arises from the many aspects involved such as mean annual precipitation, seasonality, soil type, soil moisture, surface water availability, community structure, competition, community history, and disturbances (fire, herbivory).

With the niche approach, Claussen et al. (2013) design the effective interaction between vegetation and climate from bottom up~~averaging the cover fractions of all considered plant types~~. Each plant type has specific requirements and responds individually to changes in mean annual precipitation, but the combined interaction of all considered plant types with precipitation determines and smooths the evolution of mean vegetation cover on larger scale. This approach is supported by Williams et al. (2004) who propose that higher order features of ecosystems emerge from plant's individual responses to changing environmental conditions. Ecosystem features such as composition and physiognomy have a large impact on the exchanges of energy, moisture, aerosols, and trace gases between the land surface and atmosphere and finally on precipitation.

The niche approach also implies that once a specific plant type retreats owing to water scarcity, there may not be any other type that is able to occupy its place in the ecological space. From an ecological point of view, existing plants likely benefit from the extinction of others by having less competition and more resources available. It is questionable whether these succeeding species can occupy the niches (ecological space) of disappearing species, including their way of using resources, and overtake their ecosystem functions, or if they just occupy the available barren area (geographical space).

Apart from the diversity in moisture requirements, the variety in feedback strength and climate impact arising from the particular plant properties is not sufficiently reflected in the original model: the dimensionless potential vegetation cover and the homogeneous climate feedback coefficient D^B mainly account for the albedo effect of the total area while inter-plant deviations in colour, reflectance properties, surface roughness, potential leaf area and evapotranspiration capacities are neglected.

2.3 Assessment of the interpretation of results by Claussen et al. (2013)

Based on a number of simulations, Claussen et al. (2013) concluded that diversity can have a buffering effect on ecosystem performance and further on the strength of climate–vegetation feedback. They reasoned that in species-rich ecosystems, the likelihood of some species being pre-adapted to changing environmental conditions is higher than in species poor systems. This relationship between high diversity and ecosystem stability has been debated for several decades, among other things due to the inconsistent definition of stability. We here follow Pimm (1984) who defines stability as a twofold system property: resilience is the speed with which a community returns to a former state having been displaced from it by perturbation, while resistance is the ability to avoid such displacement. Before 1970, ecologists assumed a positive relationship between biodiversity and ecosystem stability based on simplified observations (Elton, 1958; MacArthur, 1955). This intuitive idea was questioned by May (1973), who proposed a destabilizing effect of species richness on ecosystem dynamics based on a statistical model approach with random populations. Long-term field studies on grasslands indicated a positive relation between diversity and ecosystem stability, while functional diversity seemed to be more important than the total number of species (Tilman, 1996; Tilman et al., 1997; Spehn et al., 2005). The overall opinion is nowadays that diversity might on average increase the stability of ecosystems while it serves more as a "passive recipient of important ecological mechanisms that are inherent in ecosystems" than as the driver of this positive relationship (McCann, 2000). On larger scales, extrinsic factors such as disturbance regimes and site history might become the main determinants of community stability (Sankaran and McNaughton, 1999). In the light of this, the ~~assumption~~ finding of a positive diversity–stability relationship by Claussen et al. (2013) is reasonable for a region of the order of $100\,\mathrm{km}^2$. In connection with this relationship, Claussen et al. (2013) concluded ~~correctly~~ that the stability of a climate–vegetation system can determine and arise from individual plant types' presence over longer time scales. In combined interaction with climate, sensitive plants likely grow longer than they would do on their own as they benefit from additional water and facilitation effects in a more live-sustaining environment. The ~~appearence over time~~ duration of persistence of resilient plants is likely shortened as they suffer to a certain degree from additional competition (Brooker, 2006). This effect occurs in the model even though interactions are not explicitly modeled.

One of the main conclusions by Claussen et al. (2013) was that ~~the distinction between strong and~~ strong or weak climate–vegetation feedback ~~is no longer relevant~~ were hard to diagnose and disentangle regarding abrupt climate changes on a regional scale. The feedback between climate and a certain plant type could be strong, but this might be capped in combination with other plant types, resulting in a gradual decline of total vegetation. Indeed, vegetation composition can play a crucial role for the ecosystem and the removal or introduction might change the system stability by changes in the ratio of individual influences (Scherer-Lorenzen, 2005). In order to keep ecosystem function stable, a minimum number of functional types is required that occupy a minimum number of niches. The addition of taxa results in a more and more complex network of interactions. While some taxa are redundant, others are irreplaceable. If these so called "keystone species" disappear, the ~~whole~~ system might collapse. The appearance of new taxa could also interfere networks and change energy and matter fluxes in the system resulting in a destabilization of the ecosystem (McCann, 2000). Hence, Claussen et al. (2013) argued ecologically reasonable that it is difficult to determine the origin of ~~the~~ system stability as the overall feedback strength depends on ~~the~~ species composition. These difficulties are not inconsistent with previous studies that proposed strong climate-vegetation feedback, resulting in abrupt shifts from a stable "green" state to a stable "desert" state. For example, simulations by Claussen et al. (1999) were performed with the lowest possible number of PFTs, one tree and one grass. The low diversity implies a high likelihood for abrupt transitions (Scherer-Lorenzen, 2005; Claussen et al., 2013).

3 Application of the conceptual model by Claussen et al. (2013) to AHP vegetation

3.1 Does the model by Claussen et al. (2013) capture the diversity of AHP vegetation?

The approach by Claussen et al. (2013) ~~is indeed~~ offers a useful tool to deal with the question how diversity might affect climate–vegetation interaction in semi-arid regions. However, the model reaches its limits when it comes to the application to AHP vegetation reconstructed from pollen, here referring to Hély et al. (2014). Hély et al. (2014) applied "White's classification of Africa" (1983) ~~on~~ to palaeobotanical proxy data from several locations in Africa and from the African Pollen Database in order to reconstruct the Holocene vegetation distribution in relation to open surface water, derived from palaeohydrological proxies. Pollen samples were grouped into four phytogeographical types, which are mainly characterized by their precipitation requirements and physiognomic structure: 1. Guineo–Congolian type (tropical humid semi-deciduous or evergreen forest taxa, $> 1500\,\mathrm{mm\,yr^{-1}}$); 2. Sudanian type (tropical dry forest, woodlands, and wooded savanna taxa, 500 to $1500\,\mathrm{mm\,yr^{-1}}$); 3. Sahelian type (grassland or wooded grassland taxa, 150 to $500\,\mathrm{mm\,yr^{-1}}$), and 4. Saharan type (steppe and desert taxa, $< 150\,\mathrm{mm\,yr^{-1}}$).

Throughout this paper, we use the terminology of phytogeographical plant types after Hély et al. (2014) whenever we refer to our work, including the descriptions of the adjusted model and simulations as well as results, discussions and conclusions. Since literature often refers to the terminology of physiognomic vegetation types, we stick with their terminology in citations and indicate the corresponding phytogeographical plant types after Hély et al. (2014) in brackets to prevent confusions.

When defining the precipitation thresholds for each plant type, a direct relation between precipitation and plant available water was assumed by Claussen et al. (2013). This is not appropriate for all AHP plant types. Tropical Guineo–Congolian ~~(GC) taxa~~ taxa (GC type) cannot be captured with this approach using the parameters of Claussen et al. (2013) because the initial precipitation $P(V_S, -6500)$ is too low to reach their minimum threshold P_{GC}^{C1}. These species grow in gallery forest or ~~ripiculous~~ ripicolous stripes where a high water availability is more or less constantly provided, and local precipitation is of minor importance. Xeric species of the Saharan and Sahelian type have special adaptations such as deep trap roots or succulent tissues (e.g., Wickens, 1998) that allow them to grow far below the minimum threshold for a phytogeographic plant type given by literature. Nonetheless, growth ranges of phytogeographic plant types provide a point of reference, and expose that the range of precipitation thresholds assumed by Claussen et al. (2013), between 150 and 370 $\mathrm{mm\,yr^{-1}}$, is far below the variety of thresholds of AHP vegetation reconstructed from pollen (Hély et al., 2014).

Regarding the calculation of mean vegetation with the niche approach, climate–vegetation interaction provides the expected gradual decline in mean vegetation cover towards the end of the AHP. Niches can only be occupied by specialized plant types, for instance gallery forests (GC) cannot grow beyond a certain distance from surface water while steppe plants (Saharan type) do not survive on moist soils along river banks. However, the niche approach does not account for the evolution of vegetation composition in terms of spatial succession. Pollen data from Eastern Africa suggest the decrease in tropical trees and grasses (GC and Sudanian type) starting at around 5500 cal yr BP going hand in hand with the expansion of characteristic desert taxa (Saharan type). The demise of tropical trees (GC and Sudanian type) was temporarily compensated by Sahelian elements (Kröpelin et al., 2008). For the geographically explicit simulation of vegetation change, a ~~more sophisticated model~~ model more sophisticated than our conceptual approach is required.

The large diversity of plant properties besides moisture requirements highlights the importance of plant specific feedback strengths. With a dimensionless vegetation cover fraction, Claussen et al. (2013) mainly account for a homogeneous albedo. Differences in colour and reflectance properties are not implemented. Generally, tropical leaves (GC and Sudanian type) are darker than steppe grasses (Saharan type) (White, 1983) and their albedo-feedback impact should be weighted differently. Structural properties are homogenized assuming the same feedback coefficient for all plant types. The leaf area of tropical taxa (GC and Sudanian type) might be up to three times higher than that of steppe taxa (Saharan type) (Hély et al., 2009), resulting in strong evapotranspiration differences. Evapotranspiration seems to be involved in important feedback mechanisms that influence the strength of the West African monsoon (Rachmayani et al., 2015).

In summary, the original conceptual model by Claussen et al. (2013) seems to capture the stabilizing effect on ecosystem performance by accounting for differential moisture requirements and homogeneous feedback for all plant types. Important determinants of vegetation cover, such as fire or competition, and individual feedback strengths due to albedo and evapotranspiration differences are omitted. The diversity of AHP vegetation reconstructed from pollen data cannot be captured. Especially tropical gallery forest plant types (GC type) are not represented.

3.2 Model adjustment

In order to apply the conceptual model by Claussen et al. (2013) to AHP vegetation, we modify different aspects as described in the present section.

The environmental envelopes in terms of moisture requirements are extended by an upper precipitation threshold. Data-based AHP plant types are implemented, namely the Saharan type, Sahelian type, Sudanian type, and Guineo–Congolian type. Specific tolerance threshold values for these plant types, except for the Guineo–Congolian gallery forest type, are derived from observations on characteristic species (see Table 1), implicitly accounting for competitive interactions and fire that cannot be separated from water constraints. The optimum growth ranges are based on pollen analysis by Hély et al. (2014). The relative vegetation cover fraction (initially $V_{i,\text{max}} = 1$) is replaced by a weighting factor modelled after the leaf area index. This effective leaf area L_i (in m^2 per unit niche area) of each plant type i changes according to V_i in Equ. 1. In equilibrium, L_i^E is specified as a function of total precipitation P

$$L_i^{\mathrm{E}}(P) = \begin{cases} 0 & P \geq P_i^{C4} \\ L_{i,\text{max}} - \dfrac{(P - P_i^{C3}) \cdot L_{i,\text{max}}}{D_i^{C2}} & P_i^{C4} > P \geq P_i^{C3} \\ L_{i,\text{max}} & P_i^{C3} > P \geq P_i^{C2} \\ \dfrac{(P - P_i^{C1}) \cdot L_{i,\text{max}}}{D_i^{C1}} & P_i^{C2} > P \geq P_i^{C1} \\ 0 & P < P_i^{C1} \end{cases}, \tag{7}$$

with a maximum potential extension $L_{i,\text{max}}$. $D_i^{C1} = P_i^{C2} - P_i^{C1} > 0$ for the increasing branch and $D_i^{C2} = P_i^{C4} - P_i^{C3} > 0$ for the decreasing branch of the environmental envelope. For simplicity, we aggregate all surface parameters crucial for climate–vegetation feedback – leaf area, albedo and hydrological properties – in L_i, and keep the climate feedback coefficient D^B constant for all plant types. This is possible because L_S and D^B show up as a product in our model (see Eq. 11). Values for $L_{i,\text{max}}$ are chosen to qualitatively represent the variety of these aggregated properties following observation-based classifications (Hély et al., 2006, 2009). A high L_i also indicates a dark leaf colour, characteristic for tropical taxa (GC and Sudanian type), which is related to a low albedo, a strong climate-feedback, and a potentially abrupt collapse. A lower L_i represents dry bright leaves, characteristic for xeric taxa (Saharan and Sahelian type), and is associated with a low albedo feedback potential. The differences between considered plant types might be smaller than the contrast to desert, but investigating individual roles necessitates disentangling the contributions.

The Guineo–Congolian plant type cannot be captured with this approach as the initial precipitation $P(V_S, -6500)$ is too low to reach its minimum threshold P^{C1}_{GC}. This tropical plant type grows in gallery forest or ripiculous stripes where a high water availability is more or less constantly provided. Local precipitation is less important than the large scale climate which is assumed to be determined by orbital forcing. In order to account for this special relation to water availability, the effective leaf area $L^{\mathrm{E}}_{\mathrm{GC}}$ of this plant type is prescribed with a linear approximation, following the gradual insolation forcing and P

$$L^{\mathrm{E}}_{\mathrm{GC}}(t,P) = -a - \frac{1}{b} \cdot t + c \cdot P. \tag{8}$$

The parameters a, b and c are tuned such that $L^{\mathrm{E}}_{\mathrm{GC}} = 0.5$ for P= 500 mm yr^{-1} because gallery forests potentially cover only a small fraction of semi-arid regions and play therefore only a limited role in climate–vegetation feedback, and $L^{\mathrm{E}}_{\mathrm{GC}} = 0$ for $t = -3000$ because this is the timing of disappearance reconstructed from pollen (Hély et al., 2014).

The effective leaf area L_S of all plant types together is unconstrained and calculated with the niche approach

$$L_S = \frac{1}{N} \sum_{i=1}^{N} L_i. \tag{9}$$

For sensitivity studies on the role of plant composition and the effect of introducing or removing single functional plant types, L_S is calculated with a modified version of the niche approach

$$L_S = \frac{1}{n} \sum_{i=1}^{N} L_i, \qquad N \leq n, \tag{10}$$

where n is the number of existing niches that can be occupied by N different plant types. This calculation implies the lack of relevant ecosystem functions when a niche is not occupied. We use in our simulations $n = N + 1$.

The total precipitation is calculated in an analogous manner to Claussen et al. (2013) (see Equ. 5) as a combination of a background precipitation P_d in absence of vegetation, and a precipitation component induced by vegetation feedback

$$P^{\mathrm{E}}(L_S, t) = P_d(t) + D^B \cdot L_S, \tag{11}$$

with a constant climate feedback coefficient $D^B = 140\,\mathrm{mm\,yr^{-1}}$ (Liu et al., 2006a; Claussen et al., 2013). The initial background precipitation is set to $P_{d0} = 500\,\mathrm{mm\,yr^{-1}}$ which supports based on observational data an average woody fraction of around 80 % (Hansen et al., 2007; New and Jones, 1999), the potential maximum cover in climate driven savannas (Sankaran et al., 2005). The natural variability in precipitation, independent from vegetation, is implemented as additional white noise forcing $P_N(t)$ in the total precipitation

$$P(L_S,t) = \max((P^{\mathrm{E}}(L_S,t) + P_N(t), 0)). \tag{12}$$

~~The model is completed by taking over Eqs. (1) and (5) from the model.~~

3.3 Results from the adjusted model

The environmental envelopes for the four AHP plant types are shown in Fig. 2. Upper and lower precipitation thresholds mark the growth ranges based on moisture requirements, the limiting and therewith determining factor for plant growth in semi-arid regions (Shelford's law of tolerance 1913). Since thresholds are derived from empirical relationships between observed species distributions and environmental variables, the implemented envelopes correspond to the "realized niches" or "climatic niches" that are narrower than the potential "fundamental niches" of plant types, as they implicitly account for further abiotic and biotic constraints (Hutchinson, 1957; Pearman et al., 2008). This constrains the comparison between plants interacting individually or together with climate.

~~The~~ In our implementation of the vegetation types described by Hély et al. (2014)~~provides an insight in the plant diversity during the AHP. Plant~~ , plant types range from xeric desert shrubs and grasses ($< 150\,\mathrm{mm\,yr^{-1}}$) to large tropical trees ($> 1500\,\mathrm{mm\,yr^{-1}}$). Biome sensitivity assessment studies support this ~~set up~~ setup of plant sensitivities, suggesting that the percentage of rainfall decrease necessary to shift from one biome to another seems to be lowest for deciduous forests, followed by semi-deciduous forest, evergreen forest, grasslands, open and finally closed savannas (Hély et al., 2006). It is not clear whether gallery forests are as sensitive to decrease in rainfall as other forest types. Once being established in savannas, positive feedback effects may come into play and stabilize their expansion (Silva et al., 2008). The sensitivities of these plant types to changing environmental conditions are represented by the slopes of the curves in Fig. 2. Saharan and Sahelian plant taxa are mainly drought-adapted species that survive until conditions become very harsh, and they respond quickly if precipitation occurs. The Sudanian type includes herbaceous and woody savanna taxa that grow under a wide range of conditions, so the gradual decline with decreasing precipitation seems reasonable. The prescription of the Guineo–Congolian tropical gallery forest plant type as a linear function of the orbital forcing and local precipitation with relatively low $L_{\mathrm{GC,\,max}}$ accounts for internal stability.

The effective leaf area L_i introduces an additional degree of freedom in the model, acting as a weighting factor for each plant type in the combined interaction with climate. All surface parameters crucial for climate–vegetation feedback – leaf area, hydrological properties, and albedo – merge in L_i. Tropical plants, especially trees, usually achieve higher leaf areas and higher evapotranspiration rates than grasses or other steppe vegetation. Higher evapotranspiration has in turn a larger impact on atmospheric processes and the formation of precipitation than the low leaf area of steppe vegetation.

Simulations of AHP vegetation interacting individually and together with climate, and the corresponding precipitation curves, are shown in Fig. 3. Except for the Guineo–Congolian type, all plant types show an abrupt decline and a pronounced hysteresis effect when they interact individually with climate (Fig. 3a). This low stability ~~reults~~ results from the strong chosen climate feedback coefficient of $140\,\mathrm{mm\,yr^{-1}}$. The corresponding precipitation curves go in conjunction with the abruptness of L_i decline (Fig. 3c). In single interaction with climate, the Guineo–Congolian type declines linearly until it disappears at around year -3000. The Sudanian type starts with $L_{\text{Sudanian,max}} = 3$ and collapses abruptly at around year -3600 due to the strong feedback. It develops a hysteresis of around $500\ \mathrm{years}$. The Sahelian type starts with L_{Sahelian} of around 1.2, reaches $L_{\text{Sahelian,max}} = 2$ at year -4600 and collapses abruptly at around year -2200. It develops a hysteresis of around $1000\ \mathrm{years}$. The Saharan type gradually increases from an initial L_{Saharan} of around 0.1 to $L_{\text{Saharan,max}} = 1$ at around year -3200, before it collapses at around year -2900. It develops a hysteresis of around $300\ \mathrm{years}$.

When all plant types interact together with climate, we observe more gradual responses to the orbital forcing, changes in appearence over time and the almost complete disappearance of hysteresis effects (Fig. 3d–e). This can be interpreted as an enhancement of system stability (Scheffer et al., 2001). The precipitation curve resulting from feedback with L_S shows a smooth decline (Fig. 3f). In combined interaction with the other plant types, the Guineo–Congolian type starts with a higher L_{GC} than alone because this type benefits from local precipitation~~, even though it is only a subordinate water source for the growth of this type. The appearence~~. The appearance over time does not change as orbital forcing surpasses the benefitial effect from local precipitation enhancement. A high potential effective leaf area puts the Sudanian type in a dominant position in the multi-niche system. L_{Sudanian} starts to decline $1500\ \mathrm{years}$ earlier than on its own, but it finally disappears after a more gradual decline around $200\ \mathrm{years}$ later than alone. ~~Therewith~~Hence, its abundance is reduced over time due to the presence of other plant types, while its absolute appearence over time is extended. The hysteresis almost disappears. The decline of the Sahelian type starts $1100\ \mathrm{years}$ earlier in the combined interaction, happens more ~~gradual~~ gradually and ends around $1000\ \mathrm{years}$ earlier than alone. The period of maximum abundance is shifted deeper in the past and the absolute appearence over time is shortened in the considered time frame. The hysteresis almost disappears. The Saharan type starts in combined interaction from $L_{\text{Saharan}} = 0$, increases gradually from year -6000 to its full potential cover at around year -3500 before it disappears again between year -3300 and -3200. The time span of maximum abundance as well as the total appearence over time are reduced due to the presence of the other plant types. The hysteresis almost disappears. The Saharan type is largely outcompeted by other plant types in higher precipitation regimes. It only succeeds in the short period of low precipitation amounts.

Under the assumption of a full environmental envelope, the niche approach gives reasonable results for L_S regarding functional diversity. The evolution of L_S can be divided into three main phases (Fig. 3e). At the beginning of the simulation, L_S is not at its maximum which could be explained in consideration of the physiognomic community structure in reality. Under a high precipitation regime, the Sudanian type has the largest share of vegetation, including many tree species that outcompete undergrowth. With decreasing precipitation in the first phase from year -6500 to -5200, tree cover and therewith ground shading effects are reduced and it becomes easier for undergrowth species to establish. While the composition changes substantially under decreasing precipitation, L_S only increases by 0.2. In the second phase between year -5200 and -3400, L_S slowly decreases by 0.3, slightly below the initial level of 1.1. With the total disappearance of the Sudanian type at around year -3400, the third phase is initiated and therewith a steeper and fluctuating, but still gradual transition to a desert state. The system has now simplified to just two plant types and those are nearing their thresholds, which causes the increase in fluctuations. The increase in fluctuations is one of the proposed early warning signals for regime shifts (Scheffer et al., 2001, 2009). After year -3000, vegetation is completely absent.

Stepping back to the reconstructions by Hély et al. (2014), our simulations show an evolution of plant diversity similar to reconstructions ~~North~~ north of 20° N. Hély et al. (2014) proposed that all these plant types were present around year -6000, diversity was highest in and within plant types, and tropical types (Guineo–Congolian and Sudanian type) reached their maximum extension and abundance. After year -6000, pollen abundance and diversity decreased for all plant types. Tropical types apparently declined in conjunction with latitudinal humid surfaces as they grew mainly in gallery forests. Regarding the abundance of pollen in Hély et al. (2014), vegetation was completely absent after year -3000 North of 20° N. All these observations are also true for our simulations, except for the lack of the Saharan type in the beginning of our simulations in year -6000 due to the assumed low maximum precipitation threshold. Quantitative comparison between Hély et al. (2014) and our simulations is not possible because their reconstructions rely on pollen richness and abundance while we consider the area of growth. High richness and abundance of individual types should not be equated with high plant cover.

So far, we have considered the interaction of AHP plant types interacting individually or all together with climate. We now address the role of plant composition and completeness of required functional types. Claussen et al. (2013) stated that climate–vegetation feedback strength could change if certain plant types were removed or introduced by some external forcing. ~~The relationship between plant composition and system stability is highly complex and diverse within different ecosystems and even plant communities.~~

Our simulations with different combinations of plant types highlight the importance of plant composition on system stability, but we can only make qualitative statements about different scenarios. Figure 4 shows L_S computed from Eq. (10) with different combinations of plant types. In each simulation, one plant type is absent and its niche is not occupied. The removal of tropical plant types tends to enhance the fluctuations and steepness of the transition while the lack of drought-adapted plant types causes a more gradual decline that starts ~~from earlieron~~earlier. It is not possible to determine with the conceptual approach used here if one of the considered plant types actually played a key role for the stability of the climate–vegetation system during the mid-Holocene, but the Sudanian type seems to have a large impact in our simulations. This is mainly because the Sudanian type was prescribed the highest potential effective leaf area, and its removal leaves the interaction with climate to the Saharan and the Sahelian type, which are both sensitive to changes in precipitation and respond abruptly when their minimum thresholds P_i^{C1} are crossed. Nonetheless, we show that there might be large differences in the mean cover over time depending on the involved plant types, the overlap of environmental envelopes and the individual response to changing conditions.

3.4 Limitations of the adjusted model

The adjustment of the model by Claussen et al. (2013) to AHP plant types reconstructed from pollen (Hély et al., 2014) improves the representation of plant diversity during the mid-Holocene and provides a tool to investigate the impact that different plant types might have on the stability of a climate–vegetation system. Nonetheless, the model's simplicity limits its application.

As ~~already ~~mentioned in 2.2, moisture requirement is an established measure to characterize diversity in recent African ecosystems. However the measure is insufficient to describe ~~plant' s ~~plants' niches and to explain actual vegetation composition and spatial distribution within the considered region, because determinants other than precipitation amounts are not taken into account. We do not explicitly implement additional plant growth determining parameters in the adjusted model, but moisture requirements from empirical data implicitly account for such additional factors. Niches in the model describe "realized niches", and contributions of determinants such as fire or competition for nutrients cannot be separated from the difference in water requirements. This complicates the comparison between plant types interacting individually or together with climate because the actual simulation of individual growth is not possible. Nonetheless, water is the limiting factor in subtropical Africa and the effects of additional or reduced precipitation due to the presence of other plant types can be considered with our model.

Another shortcoming is the merging of all surface parameters crucial for climate–vegetation feedback – leaf area, albedo and hydrological properties – in L_i. The individual importance of each of these parameters regarding the effect on atmospheric dynamics and precipitation patterns varies over different latitudes in subtropical Africa (Bathiany et al., 2014): in the Sahara, an increase in plant growth results in a net warming because the surface heating due to albedo decrease surpasses the increase of latent heat flux; the Sahel experiences a net cooling with additional vegetation because evapotranspiration cooling exceeds the albedo warming effect; south of the Sahel, where tree cover and water availability are generally high, the stomatal resistance limits the latent heat flux which results in a net warming. This heterogeneous pattern makes an individual consideration of feedback determinants important, but cannot be performed with our approach as contributions enter the product of L_S and D^B which makes disentangling impossible.

The same applies to the assumption of a homogeneous feedback coefficient D^B for all plant types which does not account for diversity in feedback strength, but anyway it could not be separated from the product with L_S. Another shortcoming of D^B is its arbitrary choice to force strong feedback and abrupt state transition (Liu et al., 2006a). Quantitative estimates of the climate feedback coefficient D_i^B based on remote sensing observations of monthly fraction of photosynthetically active radiation show on average a positive feedback on precipitation in the Saharan region, values range in subtropical Africa from -60 to $120\,\mathrm{mm\,yr^{-1}}$, but little evidence of strong vegetation-precipitation feedback (Liu et al., 2006a). Sensitivity studies with various combinations of D_i^B show only minor changes in the evolution of L_S over time (not shown here).

4 Summary and Conclusions

In the scope of this paper, we critically re-assess the conceptual model by Claussen et al. (2013) in the light of recent ecological literature, and provide an improved version that accounts for plant diversity during the African Humid Period (AHP) as it was reconstructed from pollen by Hély et al. (2014).

Despite its simplicity, the original conceptual model by Claussen et al. (2013) seems to capture the main features of different plant types interacting together with climate, namely the enhancement of climate–vegetation system stability~~, and the~~ . The underlying assumptions are reasonable in an ecological context concluded from literature.

The definition of diversity in terms of moisture requirements is an established and appropriate approach for semi-arid regions because precipitation is there the main determinant of plant growth. Neglecting further crucial factors for vegetation composition and distribution such as fire or competition is therefore reasonable in the simple approach.

~~The focus on functional diversity instead of species diversity becomes clear regarding~~ With the niche approach~~. The~~ , the effective feedback between vegetation and climate emerges from the interacting properties of different plant types fulfilling specific ecosystem functions. Once a plant type disappears as precipitation drops below the requirements, other plant types cannot occupy its niche (ecological space). The prohibition of replacement depicts the fundamental ecological niche in its original sense, but the approach does not allow for a geographically explicit description of vegetation cover evolution. Further, the changes in niches available for occupation that result from substantial changes in the environment over millenia are not implemented.

Regarding the interpretation of transient simulations, the conclusions made by Claussen et al. (2013) fit in the ecological ~~context. Ecologists~~ state of knowledge. After decades of debating, ecologists nowadays agree that biodiversity can have a stabilizing effect on ecosystems, especially under changing environmental conditions (see Section 2.3). Claussen et al. (2013) concluded ~~correctly~~ that the stability of a climate–vegetation system can determine and arise from plant's appearence over time. Sensitive plants likely benefit from additional water and facilitation effects in a more live-sustaining environment, whereas resilient plants might suffer to a certain degree from additional competition. Claussen et al. (2013) argued ecologically reasonable that it is difficult to determine the origin of system stability as the overall feedback strength depends on species composition. These difficulties are not inconsistent with previous studies that proposed strong climate-vegetation feedback, resulting in abrupt shifts from a stable "green" state to a stable "desert" state. Simulations by Claussen et al. (1999) were performed with the lowest possible number of PFTs, one tree and one grass. The low diversity implies a high likelihood for abrupt transitions (Scherer-Lorenzen, 2005; Claussen et al., 2013). In previous studies that focused on multiple stable states of the climate-vegetation system in North Africa, including those of Claussen et al. (1998), Liu et al. (2006a), and Bathiany et al. (2012), it was argued that an abrupt change emerging from the loss of stability of one of the stable climate-vegetation states causes abrupt changes in both the vegetation record and the hydroclimatic record. Our study, however, supports the hypothesis of Claussen et al., (2013) that in an ecosystem with rich plant diversity, multiple stable states can exist, even if the hydroclimate record shows a gradual transition. Hence the latter studies do not invalidate the earlier considerations.

When it comes to the application to AHP vegetation reconstructed from pollen data (Hély et al., 2014), the model by Claussen et al. (2013) reaches its limits. The diversity of AHP vegetation in terms of moisture requirements and climate impact cannot be captured. The direct relation between precipitation and plant cover does not hold for highly specialized xeric plant types or tropical plant types indirectly linked to regional precipitation, and the diversity of feedback strength and climate impact arising from different plant properties is not sufficiently reflected in the original model.

Our modifications refine the model ~~set up~~ setup and account for a more realistic spectrum of plant types, interactions, and feedbacks. The extension of environmental envelopes enables coexistence and superseding of different plant types when conditions and the set of available niches change. The implementation of the vegetation types described by Hély et al. (2014) provides an insight ~~in the~~ into plant diversity during the AHP. Plant types range from xeric desert shrubs and grasses to large tropical trees. Since precipitation thresholds are derived from observational data, abiotic and biotic constraints cannot be completely separated. Together with the full environmental envelopes, the prescribed retreat of tropical gallery forest taxa allows for the representation of a mosaic like spatial environment as it was reconstructed from pollen. The effective leaf area introduces an additional degree of freedom that acts as a weighting factor for each plant type in the combined interaction with climate, accounting for differences in leaf area, albedo and hydrological properties.

Simulations with the adjusted model version support the stabilizing effect of functional diversity on ecosystem performance and precipitation proposed by Claussen et al. (2013), but provide more details on plant ~~overturning~~turnover. When all plant types interact together with climate, we observe rather gradual responses to decreasing precipitation, changes in appearence over time and the almost complete disappearance of hysteresis effects. Over a period of around 3100 years, the mean cover varies little while composition changes completely. The disappearance of tropical types initiates the final steeper and fluctuating, but still gradual transition to a desert state within 400 years. After year −3000, vegetation is completly absent. The temporal evolution of plant types compares well with reconstructions by Hély et al. (2014) North of 20° N.

The importance of ~~composition regarding completeness of essential function types~~ plant composition for the stability of a climate–vegetation system becomes clear comparing different combinations of plant types. ~~With our model,~~ Apparently, the Sudanian type played a leading role for the stability of the climate–vegetation system, but we cannot determine if one of the considered plant types actually played a key role during the mid-Holocene ~~but it seems that the Sudanian type played a leading role for the stability of the climate–vegetation system~~with our model. Nonetheless, we can show that there might be large differences in the mean cover over time depending on the involved plant types, occupied niches and their overlap, and the individual sensitivities to changing conditions.

For further studies on ~~that topic~~the effect of plant diversity on the stability of climate–vegetation systems, we propose not to complicate the conceptual model any further by introducing more ad hoc tunable parameters, but to transfer the lessons learned from this study to a comprehensive dynamic vegetation model. ~~The~~

Our Earth System Model MPI-ESM did not show abrupt transitions of large scale vegetation cover in previous transient Holocene simulations, and the understanding we gained in this study can help to investigate whether this is an effect emerging from the representation of diversity in our land surface model JSBACH. This process-based model offers the possibility to represent different degrees of plant diversity in various plant properties, and a variety of interactions with the atmosphere to address arising question: Could a more complex model depict AHP plant diversity and reproduce the results from our qualitative conceptual study? Would changes in plant diversity stabilize or destabilize the climate vegetation system in coupled GCM simulations? Could new PFTs designed after pollen reconstructions better represent plant diversity in subtropical Africa? Could the implementation of additional processes in JSBACH, such as root- or light-competition, or additional plant properties, such as fire-resistance, lead to new effects on the climate–vegetation system stability?

In summary, a deeper understanding of the role that plant diversity can play in climate-vegetation interaction, and an improved representation of plant diversity based on pollen reconstructions, could in coupled GCM simulations allow for a more realistic consideration of plant-plant interaction and climate–vegetation feedback.

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Table 1. Precipitation thresholds P_i^{C1} to P_i^{C4} (in mm yr^{-1}) and maximum effective leaf area $L_{i,\text{max}}$ (in m^2 per unit niche area) for the African Humid Period (AHP) plant types: Saharan type, Sahelian type, and Sudanian type.

	Saharan type	Sahelian type	Sudanian type
P_i^{C1}	0 absolute minimum	20 *Acacia tortilis* (Baumer et al., 1983)	150 *Celtis integrifolia* (Le Houérou, 2005)
P_i^{C2}	100 Saharan desert boundary 100 mm isohyt (Wickens, 1998)	150 (Hély et al., 2014)	500 (Hély et al., 2014)
P_i^{C3}	150 (Hély et al., 2014)	500 (Hély et al., 2014)	1500 (Hély et al., 2014)
P_i^{C4}	600 *Ziziphus mauretania* (Le Houérou, 2005)	900 *Balanites aegyptica* (Baumer et al., 1983)	1800 *Pterocarpus erinaceus* (Le Houérou, 2005)
$L_{i,\text{max}}$	1	2	3

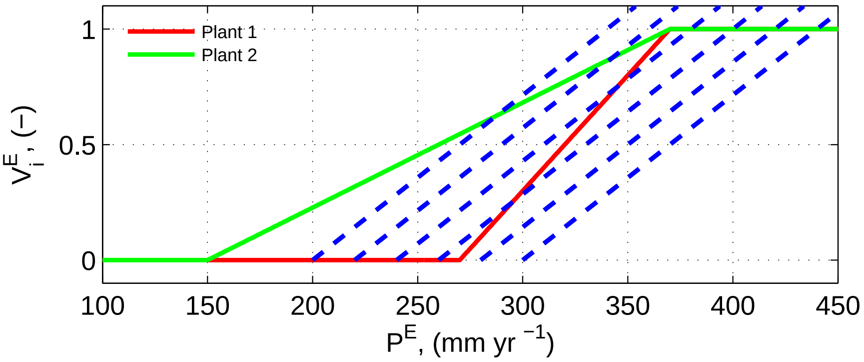

Figure 1. Vegetation–precipitation stability diagram (V_i^{E}, P^{E}) for two hypothetical plant types $i = 1,2$ after Claussen et al. (2013). Full lines depict the equilibrium curves for vegetation cover $V_i^{\mathrm{E}}(P^{\mathrm{E}})$ for plant type 1 which is sensitive (red) and for plant type 2 which is resilient (green) to changes in precipitation. Dashed blue lines show hypothetical equilibrium precipitation curves $P^{\mathrm{E}}(V_i^{\mathrm{E}})$ for different time slices (4500, 4900, 5300, 5700, 6100, and 6500 years BP, from left to right). Intersections between the two types of curvesindicate equilibrium coupled states which can be stable or unstable.

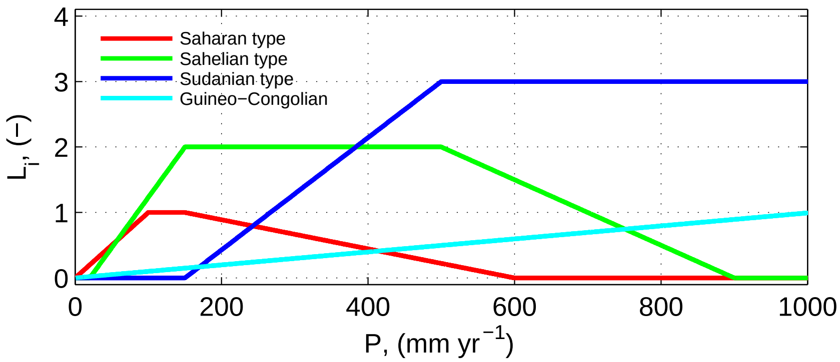

Figure 2. Environmental envelopes in terms of moisture requirements of four African Humid Period (AHP) plant types in the adjusted set up. The effective leaf area L_i is plotted as a function of mean annual precipitation P for the Saharan type (red), Sahelian type (green), Sudanian type (blue) and Guineo–Congolian type (light blue).

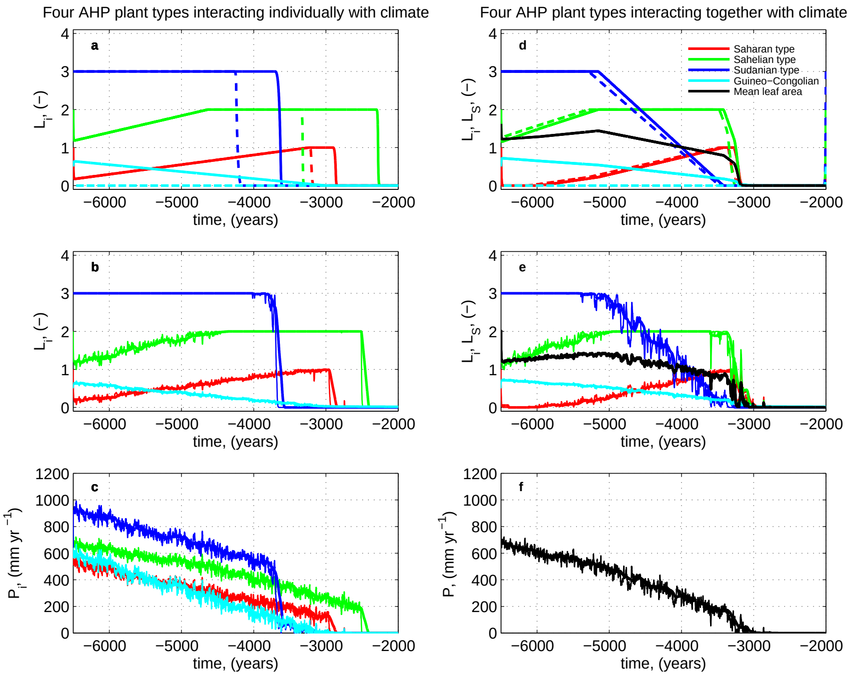

Figure 3. Transient dynamics of four African Humid Period (AHP) plant types interacting individually **(a–c)** and together **(d–f)** with climate. The effective leaf areas L_i and the corresponding precipitation amounts P_i are shown for the Saharan type (red), Sahelian type (green), Sudanian type (blue) and Guineo–Congolian type (light blue). Mean effective leaf area L_S and the corresponding precipitation P are calculated with the niche approach (black) (see Eq. 9). Simulations without background noise **(a, e)** include forward simulations (solid lines) and simulations backward in time (dashed lines). Simulations with background noise are depicted in **(b, e)** for L_i and L_S, and for precipitation P in **(c, f)**. Thin lines show annual mean values and thick lines show a 100 year running mean.

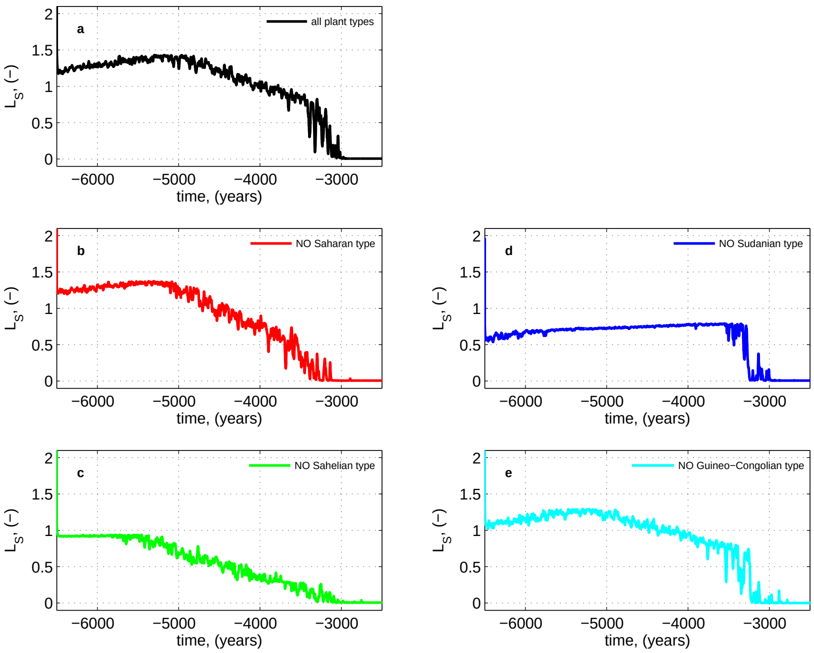

Figure 4. Transient dynamics of mean effective leaf area L_S illustrate the impact of the removal of plant types. Panels **(a–e)** show 100 year running means of different simulation set ups. The mean effective leaf area L_S accounting for all plant types ($N = n = 4$ in Eq. 10) is shown as a reference **(a)**. In each of the other simulations, one niche is not occupied ($N = 3$ and $n = 4$ in Eq. 10): no Saharan type **(b)**, no Sahelian type **(c)**, no Sudanian type **(d)** or no Guineo–Congolian type **(e)**.