Clim. Past Discuss., 11, C1730–C1744, 2015
www.clim-past-discuss.net/11/C1730/2015/

Climate of the Past Discussions

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.

vivienne.groner@mpimet.mpg.de

Received and published: 21 September 2015

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

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.

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

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

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

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

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

---

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