

## ***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.***

**J. Williams (Referee)**

jww@geography.wisc.edu

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This paper develops a vegetation model for North Africa that incorporates precipitation control on plant distributions, a strong vegetation feedback to precipitation, and four plant functional types, each with their own precipitation limits and effective leaf area. Leaf area in turn regulates precipitation feedback to the atmosphere. The model design builds upon a simple conceptual model developed by Claussen et al. (2013 Nat. Geosci.) and extends it here by creating new plant types and parameterizations that more closely represent plant types in tropical and subtropical Africa. The paper relies heavily on Hely et al. 2014 for definition of the plant types and precipitation limits of

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these types.

This is a fairly simple vegetation model that uses precipitation as the only control on vegetation distributions and does not explicitly represent other processes such as fire, grazing, nutrient limits, edaphic controls, etc. But simplicity is often a virtue, not vice, in ecological modeling, and the limitations are appropriately described and acknowledged.

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, e.g. by a) Adding a qualitative comparison of its results to the pollen time series reported by Hely et al. 2014, 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 c) Conducting sensitivity experiments with the overall feedback strength parameter DB.

### **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 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. a. So: If text is in

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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? 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*.

2. Terminology. The paper goes back and forth between using geographic vs. phylogenetic 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.

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. 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.

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.

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

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(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.*?

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.)

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.

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

9. I'm a little unclear about how the precipitation forcing is applied. The model cal-

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culates 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.

10. PP2673-2674: See Comment 1 above. This paragraph is also 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.

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.

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.

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?

#### TECHNICAL CORRECTIONS

P2666 L17: Which suggested conclusions? Unclear.

P2669 L4: Observation based -> Observational

L8: delete 'indeed'

L29: insert comma after literature

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

L6: in->of

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L7: plant's->plants'

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

L16-18: awkward sentence; hard to follow.

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.

L8: delete 'correctly'

L9: presence-> diversity

L12: 'appearance' is misspelled

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?

L26: delete 'whole'

L29: delete 'ecologically reasonable'

P2676L1-2: delete the second and third 'the's in this sentence

L7: 'is indeed' -> 'offers'

L11: 'on' -> 'to'

L26: What is a 'ripiculous stripe'?

P2677L19: More sophisticated than what?

P2678L4: insert 'differential' before 'moisture requirements'.

P2681L9-10: Show equations 1 and 5 here; don't make the reader go look for them in

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Claussen et al. 2013. (In my version of Claussen et al. 2013, only equations 1 and 2 are labeled.)

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. . ."

L25: set up should be one word.

P2682L25-26: Insert reference to Fig 3c here

P2683L5: Insert a reference to Fig. 3(d-f) here.

L11-12: delete clause beginning 'even though it. . .' – difficult to follow.

L12: appearance is misspelled

L16: Therewith->Hence

L19: Insert 'the' before 'combined'

L20: gradual -> gradually

P2684L1: What is meant by 'The assumption of a full environmental envelope'?

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.

L15: Delete this opening clause and put (Hely et al 2014) reference at end of sentence.

L16 Don't capitalize North.

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.

L14: 'from earlier on' -> earlier

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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.

L24: insert 'that' inside 'impact different'

L27: delete already

P2686L1: plant's -> plants'

L2: insert comma before 'because'

P2787L8: rephrase opener to 'In this paper, we extend the conceptual model. . .'

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

L21-22: Delete this opening sentence.

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

P2788L1-2: I don't understand what this sentence is trying to say.

L4: What ecological context? Vague, please clarify.

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?

L6: delete 'correctly'

L18: 'set up' should be one word

L22: in the -> into

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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?

L2689L5: overturning ->turnover.

L13-14: I don't really understand what this sentence is trying to communicate. Seems unnecessary. Suggest deleting.

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

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?

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