

Interactive comment on “Linking plant ecophysiology to the dynamics of diverse communities” by K. Bohn et al.

Anonymous Referee #1

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I read this paper with considerable interest, as I think the JeDi approach is a very promising one. The authors address the issue of whether the plant communities generated by the JeDi model are able to co-exist, given a simple representation of seed establishment, resource competition, mortality and disturbance. This analysis generates some very interesting model hypotheses on the nature of the interactions between the strength of seed competition and the strength of resource competition, and their impact on community structure under differing disturbance regimes. The methods, as I understand them, appear to be sound and the inclusion of the parameters explicitly controlling the strength of different forms of competition is, I think, an important advance.

I found two main problems with the manuscript. The first and largest problem is that

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the writing is, in places, very difficult to follow. In particular, the description of the model requires much attention. (See specific comments for examples of where it is ambiguous). There is also some curious use of language in places, but this is easily corrected.

The second main issue is that the authors somewhat overstretch the novelty of their modeling approach. Reading the discussion section, one might conclude that this is the first time anyone has ever attempted to include competitive interactions in a DVGM. Evidently, this is not the case, and the manuscript suffers from ignoring many recent interesting and relevant developments in the field of dynamic vegetation modeling (listed in the specific comments). It would make for a much more interesting and acceptable paper if a section contrasting the JeDi/DIVE approach to other more sophisticated models was included. There are also repeated references to the models inclusion of ‘ecophysiology’, which in fact is reduced to highly simplistic notions such as relative growth rate, thus doing a disservice to the many models that include much more detailed considerations of physiological processes, and to its inclusion of ‘spatial’ interactions, of which there is no mention in the methods. This over-stretching does a disservice to the authors, as the work is very interesting and useful as it is.

It is important to note that both these points are a question of writing style, rather than scientific content.

Specific Points.

P1: The title references ecophysiology, yet there is little in the way of ecophysiology discussed? How about something along the lines of “The relative importance of disturbance, resource competition and seed competition on community structure”

P2 L5: In the model methods, I don’t see any evidence of a spatially explicit modeling approach. E.g. P6 L5 “Establishment of new individuals is modelled by assuming that all seeds from all PPSs are well mixed over the grid.” Can you clarify what you mean by this?

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P2 L14: "We conclude that linking ecophysiological characteristics of vegetation to competition is a valid approach to determine population dynamics" is a somewhat vague conclusion, arguably has been achieved before by gap models, and does not represent the novel parts of this study, which are, for me, the focus on how explicit parameterisation is required to control the strengths of seed and resource competition.

P3 L15: "Thus it seems necessary to understand how plant species composition changes along with competitive interactions, performance and climate to be able to predict how vegetation responds to environmental change." This sentence is rather awkward and I am not sure what it means. Perhaps you need to delete the 'along'?

P3 L21: "One option . . . to include population dynamics in vegetation models such as the Dynamic Global Vegetation Model (DGVM) LPJ (Sitch et al., 2003) at the cost of increased model complexity." Arguably, some, albeit more abstract, representation of population dynamics is already present, by definition, in all dynamic vegetation models. I think you need to be explicit here about the precise change you are suggesting.

P3 L26: "Can you clarify here what is meant by 'successful'. My understanding is that JeDi selects plant types that are successful in the absence of competition, i.e. those whose physiological traits make it possible for them to successfully reproduce in a given climate. This information is needed to understand what further processes are simulated by DIVE.

P4 L4: "due to its characteristics" needs to be more specific.

P4 L9: "perturbations summarise" should probably be "perturbations include". Also I don't think either disease or herbivory, or arguably fire, should be categorized as abiotic processes as they all depend on biotic drivers.

P4 L10-15: It may be true that the PPS's can be categorized, but is it necessary to categorize them, or to include that statement here?

P4 L20: Can you give a citation for a rule-based model here? Also, not all models are

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rule-based, and DIVE is not the only model that can simulate population dynamics, as this sentence might be interpreted

P5 L4: How is biomass per m2 a constant feature of a plant type? Surely this will vary with environmental conditions? Maybe it changes through time as the output of JeDi, and I have misunderstood, but this needs clarifying.

P5 L4: Should the rate of seed production be linked to the amount of vegetation of a given plant type that is present, rather than just time?

P5 L6: What is 'specific' about 'specific mortality rate'?

P5 L8: Most DGVMs, and indeed all vegetation models, do not use this two-step approach, and combine the estimation of physiological validity in the same model as competitive interactions. How does the two step approach help here?

P6 L6: What are the units of Abare, and indeed, of all the variables introduced in this model description? What is specific about the specific growth rate, and how/why does that relate to seed establishment?

P6 L7: If the growth rate of each PFT is a simple parameter, I think it is stretching it somewhat to claim that the model links 'ecophysiology' to plant dynamics. By reducing the processes of light capture, carbon assimilation, autotrophic respiration and resource allocation into a single parameter, much of our understanding of plant ecophysiology is ignored. It is, of course, a perfectly reasonable simplification, for the purposes of understanding either diversity or competitive interactions, but I think the authors should be less bold in their claims as a result.

P6 L9: Where did fseed come from? What are its units?

P6 L9: Is 'germination fraction' the number of seeds produced by a given PFT that germinate, or the fraction of total germinating seeds that come from each PFT? If this is actually 'seed limitation', can it not just be called that instead? I am having difficulty understanding this section. It is not clear, for example, how the existence of seeds from

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other PPS's affects the rate of colonization of bare ground. This section needs careful re-writing.

P6 L21: Does the phrase 'as they grow toward their adult size' need to be in this sentence?

P6 L22: Change "biomass per occupied m is given with the input" to "biomass per occupied m2 is an output of the JeDi model and an input to DIVE"

P6 L21-24. At the end of this sentence "Establishment includes the increase in fractional coverage of new individuals as they grow towards their adult size, but not the increase in biomass per occupied m2" .I am expecting to learn about how biomass increases. However, we then turn back to consideration of area "This rate of increase in area is captured with a PPS specific growth rate, $\kappa_{grow,i}$ " We then return to consideration of biomass: "The growth rate is determined by the biomass per occupied square meter B_{Mi} and the productivity of a seedling". This results in very high degrees of confusion. Also, if f_{npp} is the growth rate only of the seedling, why does the text then discuss how it controls the development of an adult tree? If K_{grow} is constant with age, is it not just the 'tree' (or plant) growth rate?

P7 L14: Where do the respiration and litter fluxes come from? The JeDi model? I think you need to explain why you think mortality is the ratio of carbon loss to biomass here. Are the conclusions of McGill and Gilgooly applicable to a problem of this scale? Do they match existing observations of tropical tree mortality?

P7 L15: "In order to investigate the effects of perturbations, we incorporate the reaction of perturbations in altered mortality by the factor c_{Mort} , that scales mortality:" This sentence makes no sense to me at all.

P7 L21: Note that mortality rates are calculated _in an analogous manner_ to growth rates

P8 Eqn 8: I don't think you have defined 'k' at any point. Apologies if I missed it.

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P9 L5: What kind of process-based model? What processes would it include?

P9 L23: It is necessary to have both the table and the figure? I would argue in favour of dropping the table, and reducing the length of the discussion of the PPS characteristics.

P10 8-10: If "The PPS i occupies the fractional area A of a grid cell" and $A(t=0)=1$, for all PPS's the sum of the 'A's will be 5. I'm sure this is not the case, but it needs clarification. Also, if "in an initially bare area: $A_{bare} = 1$ " are you suggesting that this simulation is one of these cases? How does that work if all the area is occupied by plants already? This needs re-writing aswell, I think.

P10 L14: "we conduct multiple sensitivity analyses"

P12 L22-28: Figure 5 is very interesting, and could be discussed at greater length.

P13 L8: In the follow_ing

P14 L15: What do you mean by the 'global scale' and 'grid level' comparison here?

P15 L2: "... with DIVE we are able to distinguish resource from seed competition and can show that both processes have different effects, especially when perturbations come into play" This is, in my opinion, the most important point in the study, and should be included in the abstract.

P15 L17: The DIVE approach is potentially (and not necessarily) superior to that contained in area-based DGVMs, but many DGVMs are not area based at the present time and already include the explicit role of competition for resources between plant types. How does this method compare in terms of computational capacity and ecological realism to more sophisticated models (SEIB, LPJ-GUESS, HYBRID, ED, aDGVM etc.) In my opinion, the main advance in this study is to investigate the relative roles of seed and resource competition. Most of the newer models do not pay much attention to seed competition (with some exceptions) and the concept that the strength of competitive exclusion and seed competition are is a complex processes requiring parameterization is not well understood in this literature. To simply state that this approach is better than

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a rule-based approach is a disservice to the intellectual content of this study and to willfully ignore the development of newer vegetation modeling approaches in the last decade.

P16 L2: The same point – not all DGVMs use rule-based approaches.

P16 L16: I would call mortality a 'process' rather than a 'response'

P16 L18: I don't think perturbation rates are uniformly unknown. I would say they are poorly quantified.

P16 L19: 'necessary' rather than 'needed'

P16 L26: There are no data in this paper, so I do not think we are in a position to comment on the likely strength of competitive exclusion. Whether the modeled succession is plausible is not a trivial comparison.

P17 L2: response to what?

P17 L5: estimates of what?

P17 L7: Most models of vegetation do not assume steady states. I don't think the ability to capture transient states is the main strength of this approach.

P17 L12: "The model could be run with a certain setup" is an unnecessary sentence. What kind of observations could help to constrain the values of the competition parameters? I would argue that they are extremely difficult to determine until we have a better understanding of the functional (rather than species) diversity of existing ecosystems. It would be good to have more discussion on this point.

P17 L18: Again, there are very few models that assume a steady state. I don't think you need to include this point.

P17 L18: The model does not simulate spatial dynamics in the sense that I understand. Models of tree migration (e.g. TREEmig – Lischke et al.) simulate how seeds are

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distributed in the landscape with a spatial component. Further, individual based models (SEIB, LPJ Guess, SORTIE) retain spatial information on the location of individual plants. This model does neither, and so I consider that this reference is inaccurate.

P18 L8: Again, DIVE/JeDi are not the only models that can simulate population structure as affected by plant characteristics.

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