

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

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We thank the reviewer for the useful comments. We rewrote many parts of the manuscript and thereby have, we hope, increased the clarity of the manuscript.

Response to general comments:

G2: The writing is not very clear, and presentation of the model needs to be improved. For example, it was not immediately clear to me the links between the output of JeDi and the input for DIVE, and I initially thought the ‘derived’ parameters in Table 1 were derived from DIVE.

> We tried to be more specific about the use of the JeDi model and the development of DIVE. In particular, we tried to make it clear from the beginning in the model description

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that the ‘derived’ parameters in our work originate from the JeDi model. The idea of DIVE is to formulate competitive dynamics and population dynamics in a simple and transparent way, yet to use realistic parameters that can be derived from more detailed process-based models like JeDi.

G3: There are by necessity a number of simplifications and assumptions in the model, but some of these could be quite important, and the comparison with real world situations is a bit lacking. One obvious discrepancy is the fact that although these simulations were done for a tropical environment, the importance of size in competitively excluding smaller PPSs does not agree with the fact that a climax system will contain plants of all sizes (many of the simulations presented contain only 1 or 2 PPSs at climax).

> In our results we show that many sets of the three key model parameters (strength of seed and resource competition and perturbation) lead to high diversity (Figure 6). However, we cannot present all time-series, and rather selected the extremes of possible parameter sets (Figure 5), where diversity in steady state might be low. We might conclude from this that competition is less important in the tropics, since more PPS coexist with less competition. However, we here only used 5 PPS out of 114 that cope with a constant climate without any climatic variability. Because the tropics are not as uniform as we assume in our model, the community might reach much higher diversity under a realistic climate and by using many PPS. Comparisons to real world situations will provide additional insight. Still, estimating the rates of competition and perturbation in real climates will be challenging. In a future study we intend to address this issue. We discussed this issue in a new section in the discussion on the role of competition and perturbations for diversity.

G4: The DIVE inputs are taken from JeDi, which is run in the absence of competition. These are then used as constant inputs in DIVE. Surely plant strategies change in the face of competition, so wouldn’t these values also change? Maybe with the intensity of competition? I think here the relationship between the characteristics of the different

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PPSs is important (i.e. the trade-offs with investment in different traits), are PPSs that are successful in competition-free conditions the same as those in competitive environments?

> This is very good question, indeed one of the questions that motivated this model development. We feel that investigating this aspect is beyond the scope of the current paper, however. It is true that plant strategies change and possibly adapt to competitive interactions, and this is an important aspect of community ecology. We here aim at a more modest initial step. We take the climate as a first filter (Woodward 1987), describing how vegetation would grow and reproduce in the absence of competition (this is what JeDi does). Plant species that are not able to survive under a given set of climatic conditions in isolation, might be able to survive in the presence of biotic interactions because they benefit from parasitism on other plants or from facilitation. We do not consider either. After the climate filter (i.e. JeDi), we describe how competitive interactions lead to community composition through the population dynamics of species that can cope with competition. In DIVE, competition and population dynamics only change the fractional area of plant strategies, therefore only species that can cope with the particular environment could potentially survive competitive interactions. In addition, please see our response to comment of reviewer #1 P5 L4.

Response to specific comments:

Pg 8217 ln 11-12: sentence structure.

> We changed the sentence: "For example a big tree that is smaller in a dryer environment over shades less, allowing small grasses to be more abundant, additionally if due to perturbations many trees die, grasses might exclude trees." into: "For example, water stress resulting in reduced growth may lead to the reduction in shading from trees and so allow the increase in coverage of smaller grasses."

Pg 8217 ln 27: 'understands'? or derives?

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> The sentence "JeDi understands these strategies from trade-offs such as allocation between root and shoot (e.g. Tilman, 1990)" is removed, because we want to concentrate more on the population dynamics here.

Pg 8221 ln 2: fnpp is the productivity of a seedling. Why a seedling, and what happens when the plant is an adult? Note that in table 1 this is defined as seed productivity.

> The variable fnpp described the net primary productivity of a seedling, the description in Table 1 was misleading. We regard only the covered area of the average population and not from different age classes. The growth rate is calculated from the productivity of a seedling, because this describes the time a seedling would need to become an adult. By using this growth rate we can abstract from the area that seedlings would cover to the appropriate gain of area by the population. We rewrote the model description in the methods section and added Figure 2 to better explain how we model establishment.

Eqn 5: specific growth rate is defined as productivity per biomass. This implies that all productivity goes into growth. Shouldn't there be a term accounting for respiration in here?

> We use net primary productivity, we changed the description in Table 1.

Eqn 7: specific mortality is defined from respiration and litter C losses as a fraction of total biomass. Should there not be a term accounting for productivity here i.e. C losses through respiration and litter might be high but if this is balanced by high productivity mortality is low. Or is this implicitly included in the C<sub>mort</sub> parameter? If so, then why is C<sub>mort</sub> an ecosystem parameter and not a PPS parameter? Is there a functionally tangible meaning to the values of C<sub>mort</sub>?

> We have added an explanation in the methods: "In many cases, fast growing plants live shorter, because they have higher metabolic rates, while slow growing plants show the opposite pattern (e.g. Ricklefs 1998, Gilooly 2001, McCoy 2008). An equilibrium GPP (gross primary production) equals the sum of litter fall and respiration. We divide

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by biomass because mortality rates are predicted to be proportional to body size (Gillooly et al. 2001 and Brown et al. 2004). With Eqn. 7 we can distinguish the turnover time of slow versus fast-growing PPS (e.g. a slow and a fast-growing PPS might have the same biomass, but will differ in their GPP resulting in different mortality rates). Therefore Eqn. 7 allows us to abstract from the carbon losses of a PPS into the loss of area. " The values of cMORT express the levels of perturbation from e.g. disease, herbivory, grazing or other disturbances. We discuss it in the section on model limitation and benefits: "These parameters might be specific for each plant strategy and ecosystem. For example different plants might respond differentially to perturbation. But as we express many different types of perturbations in one term (e.g. disease, herbivory, grazing or disturbance), it is a parsimonious assumption that, in sum, its effects might be equal to all species. We chose the parameters to be fixed, because we wanted to include perturbations ... in a simple and transparent way. However, estimating perturbation and competition rates on global scale for many different species remains a challenge."

Pg 8221 ln 18-19: sentence structure.

> The sentence "Under low perturbations, mortality is low, producing ideal conditions where PPSs do only a very low coverage due to mortality." was rewritten: "Low values of cmort correspond to low intensity of perturbations and consequently lower mortality rates."

Pg. 8223 ln 25: described as follows

> The text "They are ordered by dominance from high to low and described in the follow" has been changed: "They are ordered by dominance from high to low and described in the following:"

Pg 8224 ln 7: use a word other than express

> The text "It is not dominant, and might express a high seed producing grass." has

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been changed: "It is not dominant and so might represent a high seed-producing grass."

Pg 8224 ln 8-9: if  $A_{bare} = 1$  shouldn't  $A_i = 0$ ?

>  $A_i(t=0)=0$ , leads to  $g_i(t=1)=0$  for all PPSs, consequently nothing will grow. Therefore we need to start with  $A_i \times f_{seed,i} > 0$  and so we use as initial seed flux  $A_i \times f_{seed,i} = f_{seed,i}$  (Eq. 4). We have changed the text to explain this.

Pg 8224 ln 21: we varied

> The text "Third, we vary the strength of both types of competition..." has been changed: "Third, we varied the strength of both types of competition..."

Pg 8226 ln 25-26: . . .seed competition only partly affects steady state diversity, . . .

> The text has been changed: "Under conditions of high resource competition, seed competition plays only a minor role in affecting species diversity at steady state while under conditions of high seed competition, resource competition can strongly affect species diversity (e.g. Fig. 6a)."

Pg 8227 ln 16: highly abundant?

> The text has been changed: "In early succession in a DIVE simulation, colonisers are highly abundant, competitors are at low abundance and so competition for resources plays a minor role in determining PPS composition."

Pg 8227 ln 24: sentence structure

> The text "As PPSs compete for resources, large PPSs steadily invade the area occupied by smaller PPS, excluding them due that they e.g. capture most of available light (Tilman, 1990)." has been changed: "As PPSs compete for resources, large PPSs steadily invade the area occupied by smaller PPS by capturing more of the available light (Tilman, 1990)."

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Pg 8228 ln 16: remove comma after concluded

> Yes, we removed it.

Pg 8228 ln 23-26: use past tense

> The text has been changed: "Competition may have non-trivial effects on population dynamics. Using DIVE, we evaluated the role of competition and resources and bare soil independently. Different steady states were reached and the progress towards these steady states altered in response to varying strengths of seed and resource competition."

Pg 8228 ln 26: obtained the same

> The text has been changed: "Arora and Boer (2006) obtained similar results by changing one parameter that controlled seed limitation and resource competition."

Pg 8229 ln 7: remove comma after obtained

> The text has been changed: "However, plausible successional patterns were only obtained when both resource and seed competition operated."

Pg 8229 ln 10: under given climatic conditions

> The sentence "DIVE links performance of PPSs under climatic conditions to the resulting competition between PPS." has been removed, because we rewrote and re-structured the discussion.

Pg 8229 ln 22: information

> The text "DIVE does not represent dynamics or competition of individual plants. It rather uses aggregated informations that describes a whole PPS by one set of characteristics." has been changed: "Dive does not represent the dynamics of individual plants. Instead, the aggregated information that represents all the different age classes within a PPS is contained in a single set of PPS characteristics."

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Pg 8230 ln 3: exclude

> The section containing this sentence has been changed.

Pg 8230 ln 28-29: check sentence

> The sentence "Since we showed that considering competition leads to plausible population dynamics, we suggest competition remains strong in DIVE simulations." has been removed. As long as we do not compare our results to data, we are not able to say anything about that. But in the discussion section we write: "Plausible successional patterns, where dominant PPS are abundant, were obtained when at least resource competition operated."

Pg 8231 ln 11-13: The model. . .could be found.

> The text has been changed: "One possible approach to determine realistic parameter values would be to tune the time series DIVE results to empirical data of ecological succession. Alternative climate conditions (e.g. various IPCC scenarios) could be used to produce predictions for vegetation response to climate change. However, care would need to be exercised in that the previous climate's parameters may not necessarily be valid. For example, perturbations such as fire and water stress may increase under different climates."

Pg 8232 ln 2: suggests that

> The text has been changed: "We showed that including competition leads to plausible population dynamics. However in different climates the strength of seed and resource competition might be different and it will be challenging to find them."

Table 2: is this number of decimal places necessary? Table caption is too brief.

> Fewer digits are sufficient and now used. Also we extended the caption.

Table 3: caption: If non of . . . ?

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> The text has been changed: "If neither seed or resource competition operate..."

Fig. 2: Characteristics are normalised. Against what?

> The text has been changed: "We calculate the competitive dominance  $d_i$  of a PPS by normalising its biomass  $B_{Mi}$  with the sum of biomass of all PPSs."

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