

## ***Interactive comment on “Small diversity effects on ocean primary production under environmental change in a diversity-resolving ocean ecosystem model” by A. E. F. Prowe et al.***

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Received and published: 2 February 2014

*We thank the reviewer for his comments and have added our response in italics after the relevant paragraphs.*

I like this – the model is a great synthetic ecological environment for exploring such a wide range of fundamental and practical (model-development) questions as the authors have already demonstrated in a variety of papers over the past few years. I am intrigued by the current approach. But I am not yet entirely convinced that what is being demonstrated in the model comparison experiments is quite what the authors intend. Anyway ...

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*We thank the reviewer for his positive remarks. We agree that some of the limiting aspects of the study were not carefully enough stated and have endeavoured to alter the text to show this. We now also mention additional sensitivity simulations from a different study to argue that our conclusions are indeed valid.*

The importance of marine biodiversity to the future global climate change sensitivity of e.g. primary production is an important assessment to make. One might expect that a highly diverse (emergent) ecosystem model such as the MIT Darwin model might be inherently more stable, or rather: less likely to respond abruptly to environmental change, than the more traditional discrete PFT-based models. Friederike Prowe and co-workers do not quite go this far, but do find in their modelling study that the number of phytoplankton functional types and not necessarily the total represented biological diversity per se appears to be the most important factor in controlling the sensitivity of ocean productivity to climate perturbation. This is a useful result and raises questions (or adds to the debate) about what the ‘best’ future marine ecosystem modelling strategy might be, and whether high diversity / emergent models such as the Darwin model should be the way forward or whether current PFT based models will remain perfectly adequate for assessing the main impacts of future climate change (and ocean acidification) on marine carbon and linked biogeochemical cycling. While I think the overall approach and intention is interesting and valuable, I do have some questions/criticisms about the details of the methodology employed and have some doubts as to whether the methodology is sufficient to support the interpretation (alternatively: there is room for improvement in the methodology and which would lead to a significantly improved paper):

\* If I am reading Figure 4 correctly – my single most serious concern about the methodology arises from the distributions of  $Topt$ . For the full  $n=78$  model, almost all the ‘small’ plankton varieties cluster around the  $KPO4$  for *Prochlorococcus* and there are very few varieties appearing anywhere near the ca.  $0.025 \text{ mmol P m}^{-3}$  value for ‘other small phytoplankton’ (the middle marked vertical line). If the ‘other small phytoplankton’ PFT

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(vertical line) fails to reflect the mean diversity in KPO4 space of the 'other small phytoplankton' varieties in the highly resolved (n=30 or n=78) model, then the comparison between highly resolved and n=4 or n=3 PRT models does not seem valid, i.e. you are creating a PFT in n=4 or n=3 PRT configurations that has no analogue in the highly resolved model. This may not be critical to the interpretation but does rather obfuscate what would otherwise be an extremely conceptually neat and transparent approach. Secondly, the choice of which of the 4 n=4 PFTs to 'remove' (Prochlorococcus) in the n=3 PRT configuration creates an apparent bias in that the PFT with the very lowest KPO4 is been chosen. Surely this is always going to induce a substantially different ecosystem compared to n=4 and n=30 (and 78) particularly as something like ~ 50% of total d n=30 (and 78) variants seem to be clustered at the very lowest KPO4 end? For example, removing the 'other small phytoplankton' PFT might give a rather different result and an n=3 PFT model might look rather more like the higher diversity ones.

*We have conducted another experiment removing the "other small" and now show these results as well. Since there were more Prochlorococcus types in the model initialization, removing them had a larger effect on the PP changes than removing the "other small" in the regions where this PFT dominates (shown now in Fig. 2 and discussed at the end of the results section). We note that the original model was designed to include more Prochlorococcus types for comparison to observations in Follows et al. (2007) - the reason that the ksat is more completely sampled for Prochlorococcus than for "other small". Since one of our main conclusions is that diversity per se has only small effects, we considered the simulation without Prochlorococcus more meaningful as it might indicate an upper constraint on diversity effects. We do not, however, feel that this makes any difference to the final results of the paper, but do agree that the new n=3 experiment is an important addition to this study.*

\* There are potentially important complications about quite what is being compared here. The resolved (n=30 or n=78) has its phytoplankton varieties relatively clustered around the PFTs in KPO4 space (excepting whatever is going on with the 'other small

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phytoplankton'). Certainly, KPO4 space is not by any means evenly populated. The varieties in each PFT cluster are then primarily differing in their value of  $T_{opt}$  (we don't get to see how the varieties are distributed in  $k_{par}$  space – see comment below).

*We now include additional panels in Fig. 4 showing the clustering of  $l_{opt}$  and refer to the relation with light in the text.*

The 'Epply-like' temperature response that is incorporated in traditional PFT-based models and adopted here for n=4 and n=3 configurations is implicit designed to account for a diversity of  $T_{opt}$  values. Hence, for a hypothetical PFT, would one not expect a close similarity between a PFT with an Epply-like response, and a diversity of phytoplankton varieties that differ in their explicit  $T_{opt}$  value but otherwise share similar KPO4 Properties? In other words: are the results and conclusions of the paper really at all that surprising in this respect? Is the methodology used really sufficient to provide a strong test of the hypothesis of 'primary-production [being] largely independent of the number of coexisting phytoplankton types'? Would not having a diversity of sizes (either with a  $T_{opt}$  or Epply-like temperature response) not provide a more appropriate test?

*Yes, we agree with the reviewer and have in fact conducted such simulations for a different study with 6 PFTs with either Epply-like response to temperature or subtypes within the PFTs with individual  $T_{opt}$ . In a simulation with 16 subtypes within each PFT that differ only in their  $T_{opt}$  (an even simpler setup than ours) the geographical range of the PFTs is very similar to a simulation without subtypes within each PFT. Previous studies (e.g., Moisan et al., 2002) had suggested that replacing the Epply curve with a diversity of more realistic specific temperature functions could have an important influence on model behaviour. Our aforementioned study shows, however, that in the current model configurations the individual temperature functions can be approximated by the Epply-curve, and thus supports the notion of the reviewer. However, we would not a priori have expected the two model configurations to respond to environmental changes in the same way, as diversity is also given by nutrient uptake and light use*

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parameters and temperature changes were omitted. This is the main finding of this paper. In a sense, in our 3- and 4-PFT-simulations we are using the fact that the Eppley curve integrates temperature response diversity in order to focus on nutrient uptake diversity. We have now added this discussion to the methods section. As the new title indicates more clearly than before, our study intends to examine the relevance of representing diversity in models rather than real diversity effects (which we believe is currently impossible). However, we agree that some other measure of diversity (such as size) within PFTs might provide a different result, and in fact already point towards this "trait dimensionality" in the discussion. Thus in the revised version of the paper we are very careful to note that the results hold only for the dimensions of diversity within our model, and have added clarifying statements in the discussion and conclusion sections. A study exploring size-based diversity is planned in the near future by the MIT group.

An alternative way of comparing low and high diversity modelling approaches would be to progressively sub-sample the population and have the 4 (or 3) PFTs chosen randomly (but perhaps in an ensemble of sub-sampling) – i.e. much as was done to move from  $n=78$  to  $n=30$  but taken to the extreme. Overall, I am not yet convinced in this study that the comparison is in reality principally between an  $n=4$  model including a parameterization of (Epply) temperature response, vs. a  $n=78$  (or 30) model that is unpicking the underlying diversity in temperature response whilst conforming to the Epply curve and hence in danger of providing only a test of whether the Epply curve 'works'.

*A simulation with 4 PFTs but a Topt temperature response as suggested does not make sense since the limited temperature ranges would prevent niche space to be filled and thus result in much lower PP. This effect can be seen from a simulation with different numbers of subtypes (minimum 15) within 4 PFTs described in Prowe et al. 2012, Ecol. Model. In an experiment where all 78 types have an Eppley-like curve, diversity would then come from the ksat and lopt differences. Here we would expect to find a less*

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*diverse community, but the same or weaker response to PP changes. We can thus still conclude that at least some aspects of diversity within PFTs as represented in our model are not important in order to capture the response to environmental change.*

\* I was surprised that temperature diffusion/mixing were also not simultaneously reduced in the model (alongside nutrients). Why? Surely this rather spoils the attempt at creating an environmental perturbation with some future global change relevance? If, as suggested, it is to 'separate direct effects on the ecosystem from more complex responses driven by physical feedbacks' then why not carry out both possible perturbations (nutrients+phytoplankton only, and nutrients+phytoplankton and temperature) and explicitly separate out the effects. The analysis presented by Dutkiewicz et al. [2013] in GBC earlier this year is extremely relevant in this respect.

*We attempted in this study to examine just one aspect of climate change. We did not use the same physical framework as Dutkiewicz et al. (2013), so were unable to explore both temperature and mixing issues. We believe this is beyond the scope of the study, although we agree that it would be interesting for a follow-on study.*

Other comments / suggestions

\* General: Do prior inter-comparing ecosystem models of different complexity not exist (if only for specific ocean locations rather than global patterns of productivity)? Citing/discussing a little more literature addressing the importance/consequences of different choices in the representation of marine ecosystems would not go amiss.

*We now include text on model intercomparison in the introduction.*

\* General (e.g. Abstract): There is some potential for confusion between 'phytoplankton types' and 'phytoplankton functional types'. Probably 'types' is too ingrained in the Darwin model literature, but making a clearer distinction ('sub-types', 'varieties'?) would be helpful if at all possible.

*Thank you for pointing out the potential for confusion. We have changed the wording*

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to 'PFTs' and 'subtypes' throughout the manuscript.

\* Title: This could be a little simpler and clearer.

*We have now changed the title to "How important is diversity for capturing environmental-change responses in ecosystem models?"*

\* Methods: A table summarizing the different experiments would be useful.

*We have added a table giving details on the simulations with number of PFTs and number of subtypes per PFT.*

\* Page 12576 / Lines 16-27: This is a really interesting and important section and analysis, but I did not find it as easy to follow as I would have liked.

*We have now clarified this paragraph by adding more explanation.*

\* Page 12582 / Lines 15-19: It would be helpful to know a little more about the transient changes induced by the change in vertical mixing coefficient ( $k_e$ ) – would it be possible to have a time-series of e.g. diversity vs. PP (as presented for an annual average and zonally in Figure 2) and for each of the different diversity ( $n$ ) experiments – i.e. the question of whether the rate of response differs between e.g.  $n=78$  and  $n=4$  and whether the degree of represented diversity might affect the time-scales of response (rather than just final magnitude).

*Throughout the different model configurations we find that community composition, and thereby also PFT distribution, adjust very quickly (i.e. mostly within a year) to changes in environmental factors. In figure revision\_fig1.pdf we show the zonal average absolute PP change (as in Figure 2) for the  $n=78$  simulation and the  $n=4$  simulation (i.e. with and without diversity resolved within the PFTs) for the years immediately after the mixing reduction (year 11 and year 12) and the results shown in Figure 2 (10 years after the reduction, i.e. year 20). We do not see any notable difference in the PP response between the simulations with and without diversity resolved. The diversity response is difficult to compare as for the  $n=4$  simulation "diversity" changes really are*

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*PFT changes as opposed to changes of diversity within PFTs. We thus do not feel that this warrants further attention in the ms.*

\* Figure 1: It would be useful to see the corresponding global primary productivity patterns of the 2 default and 2 reduced mixing experiments as well as the anomalies. In addition: could not the corresponding diversity maps also be shown? I appreciate that zonal averages are given in Figure 2, but it is a short paper and I see no reason not to provide a reasonably full set of spatially-explicit results.

*We agree that the absolute PP patterns are of interest, and have added two panels showing the PP prior to the mixing reduction for both the  $n=78$  and the  $n=4$  simulation. We have decided to omit PP patterns 10 years after the mixing reduction, as the broad color scale required does not allow to identify changes, and we feel that these changes are best shown in the difference panels. Regarding diversity, the number of subtypes for the  $n=78$  simulation is published already in Prowe et al., Prog. Oceanogr., 2013, while the  $n=4$  run does not resolve diversity, but only PFT distribution, which is not comparable to the number-of-subtype-diversity for  $n=78$ . We therefore feel that showing spatially resolved diversity changes will not add enough new information to justify several additional panels.*

\* Figure 3: The different lines are not all sufficiently distinct from each other.

*We have adapted the line styles.*

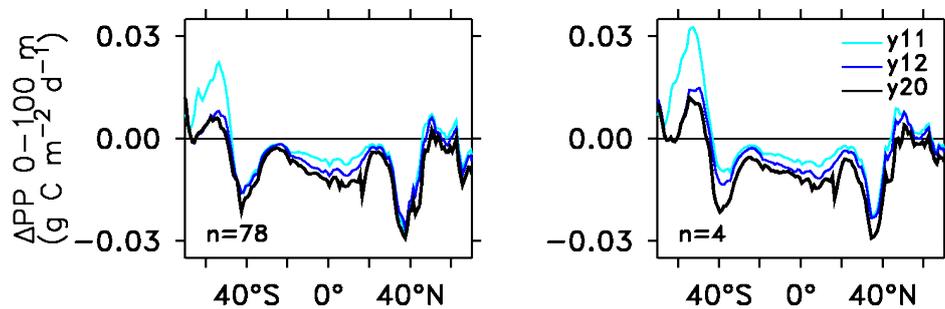
\* Figure 4: Please explicitly label (e.g. with arrows) which vertical line is which PFT. And also make distinct the 2 coincident lines (e.g. one thick/dashed or dashed/colored) for 'diatoms' and 'other large phytoplankton'. Is there a similar diversity in terms of light limitation? If so: it would be helpful for completeness to plot a 2nd set of 4 panels with  $k_{par}$ (?) on the y-axis rather than  $Topt$ . Alternatively, the 4 panels with  $Topt$  on the y-axis could be repeated, but with the colour scale representing  $k_{par}$  rather than biomass fraction.

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We have now labelled the vertical lines to clearly identify the PFTs. We have also added 4 panels showing  $lopt$ , the optimal light intensity for which the light function reaches a maximum, vs.  $kpar$ , since  $lopt$  summarizes diversity in both light half-saturation and light inhibition parameters.

Interactive comment on Biogeosciences Discuss., 10, 12571, 2013.

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**Fig. 1.** time series of PP changes (years 11 and 12; and for comparison year 20 as shown in the ms) after mixing reduction (after year10) for simulations with ( $n=78$ ) and without ( $n=4$ ) diversity within PFTs

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