

# Interactive comment on “Understanding predicted shifts in diazotroph biogeography using resource competition theory” by S. Dutkiewicz et al.

Interactive comment on Biogeosciences Discuss., 11, 7113, 2014.

## Response to Reviewer 2:

We thank Prof Gruber for a thoughtful review. We have considered his points very carefully and have adjusted the text and figures in revised version of the paper to take these into account. Below, Prof Gruber's comments are in black font and our response is in blue. Since the revised version of the text will not be available for the reviewer to examine at this stage, we provide below the excerpts of the new text and the approximate place (page and line number) in the old text where it will be added.

### 1 Summary

Dutkiewicz and her co-authors investigate the possible response of marine diazotrophs to future climate change using a global ocean biogeochemical/ecological model forced with output from an Earth System model of intermediate complexity. The model predicts a biogeographic expansion of the diazotrophs, particularly in response to a presumed increase in the atmospheric deposition of dust, but also in response to warming and the associated increase in vertical stratification and reduction in the vertical supply of macronutrients. Using concepts from classical resource competition theory, Dutkiewicz et al. show that these changes can be successfully predicted by changes in the nutrient supply ratios, which alter the distribution of the niches where diazotrophs can successfully compete against the other phytoplankton.

### 2 Evaluation

Understanding and predicting the future evolution of marine ecosystems is one of the key challenges facing the marine research community. Of particular concern is the response of the lower trophic-level ecosystems, and particularly that of the primary producers, as they provide the basis of (nearly) the entire marine food web. Thus, Dutkiewicz and her co-authors address an issue of high concern, making this study interesting for a broader community. Of particular interest is their use of a theoretical framework to analyze and understand their model-based projections, which makes this paper stand out relative to most other studies that have looked at future changes in lower trophic-level marine ecosystems. The employed model is adequate for the intended task, the results are clearly described, illustrated and discussed, and the conclusions are solidly based upon the presented material. The paper is well written and generally easy to follow. In summary, this is a very good paper, whose publication I am glad to support.

We thank Dr Gruber for his positive remarks.

There are, however, a few of major comments that I would like the authors to consider when preparing the final version of their paper.

- (i) Strengths and limits of resource competition theory: I am convinced by the author's arguments and the presented evidence in this paper as well as those by Ward et al., (2013) and Dutkiewicz et al. (2012). At the same time, I think the authors should also emphasize more the caveats and limits of this approach. Some of this has been discussed by Ward et al. (2013), i.e., strong bottom up control, higher Fe requirements and lower growth rates relative to "normal" phytoplankton, and steady-state assumption, but I think it would be good if some of this was revisited in the light of the 3-D simulations presented here and in light of potential future changes. But I would like to submit that the most important limitation is that the resource competition theory works relatively well for the biogeography of N-fixers, but is of limited use to actually predict the magnitude of N-fixation, which - in the end - is the more important quantity.

In the new text in the discussion we have reiterated some of these caveats and limitations. We note though that although the theoretical framework is almost purely bottom up controlled, the numerical model includes grazers.

In the discussion we will add:

*"However the numerical simulation included additional nutrient constraints, several diazotroph and non-diazotroph species, grazers as well as full three dimensional transport and mixing. The numerical simulations were never in steady state. However, as suggested by our previous studies (e.g. Dutkiewicz et al., 2009), we find that the theoretical framework provided crucial insight into the results of the numerical model in the low latitude regions where diazotrophs typically occur (Luo et al., 2012)."*

With respect to the "higher Fe requirements and lower growth rates relative to "normal" phytoplankton", we suggest that there is a good body of evidence (Berman-Frank et al., 2001; Kustka et al., 2003, among others) to support this assumption. If this is not the case, then our "theory" does not work. We make this more apparent as well:  
Replacing much of the first paragraph of the Discussion (pg 7125):

*"Essential assumptions of the theoretical framework is that the diazotrophs grow slower than other phytoplankton and that they are never nitrogen limited. The former has good empirical support (e.g. Berman-Frank et al., 2001) and the latter is reasonable since they can fix the abundant nitrogen gas. Though we do note that there are likely cases where high oxygen may limit the nitrogen fixation: something we have not taken into account in this paper. A third, though not essential assumption, that we make in the theoretical framework is that diazotrophs require more iron than other phytoplankton (also supported empirically, e.g. Berman-Frank et al., 2001; Kustka et al., 2003)."*

The paper focuses on diazotroph biogeography (presence/absence) so we had not brought up any theoretical ideas on nitrogen fixation rates. But given Dr Gruber and reviewer 1's comments we have decided to include a short section on nitrogen fixation, since the theoretical framework can provide us some insight. Thus, in addition to steady state solutions for the nutrients in Table 4, we now include solutions for the diazotroph biomass  $D^*$ . This is a function of the absolute (not ratio) of net excess supply of the limiting nutrient for diazotrophs. We also provide a new figure which shows that this does provide a measure of  $D^*$ . And with assumption that nitrogen fixation =  $\mu D$ , we can make similar arguments about nitrogen fixation. The results are not as clean as the supply ratio arguments for the biogeography, but does add insight into the changes seen in altered climate experiments.

We have new Section 3.4:

### **"3.4 Nitrogen Fixation**

*Theory: the biomass of the diazotrophs is a function of the net, excess rate of supply of P or Fe (whichever is limiting) over N, relative to the non-diazotroph elemental requirements (Eqs 11 and 12, Table 24). It is also a function of the diazotroph loss rates. In the theory we assume that the diazotrophs fix all the nitrogen that they require (though note that this assumption does not qualitatively change the results, see Dutkiewicz et al., 2009), and that all nitrogen goes to growth, such that  $N_{fix} = \mu DD$ . In steady state this implies that nitrogen fixation is a function of both growth rate and the biomass of diazotrophs, which in turn is a function of the net excess supply of P or Fe. Thus we formally relate the rate of supply of excess P to nitrogen fixation, in accord with Gruber and Sarmiento (1997) and Deutsch et al (2007), but also explicitly incorporate the role of excess iron supply. We note that the theory predicts relationships between fluxes of nutrients and not nutrient concentrations. In particular, it does not suggest clear relationships between nitrogen fixation rate and iron or phosphate concentrations and consistently, they are not observed (Luo et al, 2014).*

*Numerical Model: we find that the diazotroph biomass and nitrogen fixation rates are related to the net excess supply of Fe or P (Fig. 26 e,f): where there is excess supply of both nutrients (top, right quadrant) there is higher biomass and nitrogen fixation, and most grid cells have no (or very low) values in the other quadrants. That some diazotroph are outside their prescribed provinces (discussed above) does lead to some scatter, but about 80% of both diazotroph and nitrogen fixation rates do occur in the anticipated quadrant. However even within the quadrant there is not a strong correlation between biomass/nitrogen fixation and net excess supply of Fe or P. This is because both biomass and nitrogen fixation rates are also modulated by grazing pressure, and, in the case of nitrogen fixation, by diazotroph growth rate which is a function of temperature and light. Thus these scatter plots in terms of absolute excess in supply rates are not as clean as those in supply resource ratio (Fig. 26 a–d) used to describe diazotroph biogeography."*

and additional text in Section 4.3

(pg 7124, lines6-8) *"In HiIron, the increase in biogeographical area and the increase in net excess supply of iron relative to the non-diazotroph needs leads to mostly higher local nitrogen fixation."*

(pg 712421-23) *"Reduction in phosphate supply led to more areas being phosphate limited, and little change in the net excess supply of phosphate relative to the non-diazotroph needs leads to lower nitrogen fixation."*

a paragraph in the Discussion:

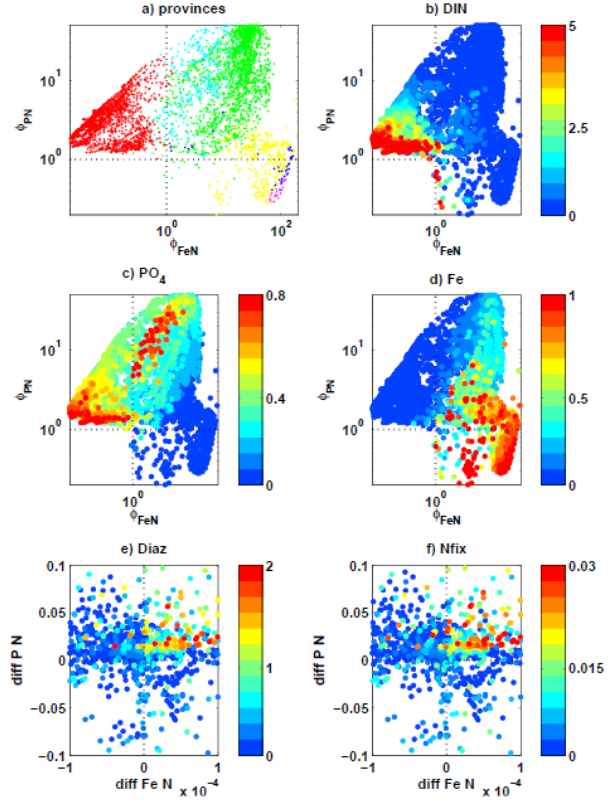
*"The framework also suggests that the change in nitrogen fixation rates will be related to the changes in diazotroph growth rates and to alterations in the net excess supply of phosphate or iron relative to the non-diazotroph needs. The changes in the numerical model are also modulated by how temperature alters growth rates and the intensity of the grazing."*

and extra text in the Conclusion:

*" The theory lays out nicely how the ratio of the nutrient supply dictates the diazotroph biogeography. The absolute changes in the net excess supply of the limiting nutrient and the alteration to the diazotroph maximum growth rate (e.g. through increase temperature) determines the shifts in nitrogen fixation rates."*

**Table 24.** Theoretical framework.

| Equations  | #  |
|--|----|
| $\frac{dB}{dt} = \mu_B \min\left(\frac{N}{N+\kappa_{NB}}, \frac{P}{P+\kappa_{PB}}, \frac{Fe}{Fe+\kappa_{FeB}}\right) B - m_B B$  | 1  |
| $\frac{dD}{dt} = \mu_D \min\left(\frac{P}{P+\kappa_{PD}}, \frac{Fe}{Fe+\kappa_{FeD}}\right) D - m_D D$   | 2  |
| $\frac{dN}{dt} = -\mu_B \min\left(\frac{N}{N+\kappa_{NB}}, \frac{P}{P+\kappa_{PB}}, \frac{Fe}{Fe+\kappa_{FeB}}\right) B + I_N - O_N$   | 3  |
| $\frac{dP}{dt} = -\mu_B \min\left(\frac{N}{N+\kappa_{NB}}, \frac{P}{P+\kappa_{PB}}, \frac{Fe}{Fe+\kappa_{FeB}}\right) R_{NPB} B - \mu_D \min\left(\frac{P}{P+\kappa_{PD}}, \frac{Fe}{Fe+\kappa_{FeD}}\right) R_{NPD} D + I_P - O_P$          | 4  |
| $\frac{dFe}{dt} = -\mu_B \min\left(\frac{N}{N+\kappa_{NB}}, \frac{P}{P+\kappa_{PB}}, \frac{Fe}{Fe+\kappa_{FeB}}\right) R_{NFeB} B - \mu_D \min\left(\frac{P}{P+\kappa_{PD}}, \frac{Fe}{Fe+\kappa_{FeD}}\right) R_{NFeD} D + I_{Fe} - O_{Fe}$ | 5  |
| <b>Equilibrium Solutions</b>   |    |
| $N_B^* = \frac{\kappa_{NB} m_B}{\mu_B - m_B}$ when B is N limited  | 6  |
| $P_B^* = \frac{\kappa_{PB} m_B}{\mu_B - m_B}$ when B is P limited  | 7  |
| $Fe_B^* = \frac{\kappa_{FeB} m_B}{\mu_B - m_B}$ when B is Fe limited   | 8  |
| $P_D^* = \frac{\kappa_{PD} m_D}{\mu_D - m_D}$ when D is P limited  | 9  |
| $Fe_D^* = \frac{\kappa_{FeD} m_D}{\mu_D - m_D}$ when D is Fe limited   | 10 |
| $D^* = \frac{1}{m_D R_{NPD}} ((I_P - O_P) - R_{NPB} (I_N - O_N))$ when D limited by P  | 11 |
| $D^* = \frac{1}{m_D R_{NFeD}} ((I_{Fe} - O_{Fe}) - R_{NFeB} (I_N - O_N))$ when D limited by Fe   | 12 |



**Fig. 26.** Scatter plots for pre-industrial conditions (experiment *Control*). Each model grid cell is plotted as function of its annual averaged (a-d) supply rate ratio  $\phi_{FeN}$  and  $\phi_{PN}$  or (e,f) excess Fe, P supply rate  $((I_{Fe} - O_{Fe}) - R_{NFeB} (I_N - O_N))$  and  $((I_P - O_P) - R_{NPB} (I_N - O_N))$ . (a) Province designation in same colors as in Figure 23 (except for VI which is colored magenta here); (b) Concentration of DIN in the top 100m ( $\mu M$ ); (c) phosphate ( $\mu M$ ); (d) iron (nM); (e) diazotroph biomass ( $\log C m^{-3}$ ); and (f) nitrogen fixation rate ( $\log N m^{-2} yr^{-1}$ ). Dotted lines indicate  $\phi_{FeN} = 1$  and  $\phi_{PN} = 1$  in (a-d) and  $((I_{Fe} - O_{Fe}) - R_{NFeB} (I_N - O_N)) = 0$  and  $((I_P - O_P) - R_{NPB} (I_N - O_N)) = 0$  in (e,f).

- (ii) : Ocean interior changes: The paper leaves the impression that all the changes we see in the surface ocean are solely driven by the response of the lower trophic-level ecosystem to changes in the supply ratio, thereby disregarding the fact that changes in the ecosystem might have important consequences on these supply ratios, i.e., leading to potentially important feedbacks. For example, Sarmiento et al. (2004) and others have shown that e.g. iron fertilization induced changes in upper ocean ecosystem structure (and physiology) in the Southern ocean have worldwide repercussions, as the changes in diatom growth there alter the (preformed) nutrient concentrations of the mode and intermediate waters that are exported toward the lower latitudes and fuel an important part of primary production there. Similar effects can occur elsewhere, e.g., by changes in the remineralization depth of the exported nutrients in response to changes in the nature (and timing) of the exported material. Therefore, I was a bit surprised to see no discussion whatsoever on how nutrients (and their ratios) change in the ocean interior. As written the text implies that all the changes are driven by

changes in the physical transport, but not by changes in the concentrations (or their ratios). I doubt that this is truly the case.

We realize given Prof Gruber's comment and a reread of the paper that we do not make enough of the ecosystem driven changes to nutrient supplies. This was never our intent - in fact we believe that such changes are indeed very important. And though they are a couple of points in the old version where such "feedback" were mentioned (e.g. pg 7121, last bullet point; pg 7122, line 15) we rewritten several sections in the paper to make this more apparent: pg 7121 line 14 ("4.1. Shifts in provinces"):

*"In Phys, we find a marked decrease in the supply of macronutrients (IN and IP). Increased stratification and slower overturning circulation lead to a reduction in the supply from the deep ocean. Moreover, increased primary production in the high latitudes (a response to higher temperatures and higher light with increased stratification, see Dutkiewicz et al., 2013) leads to higher consumption of nutrients at these latitudes and less makes it through mode and intermediate water supply to the lower latitudes (see e.g. Sarmiento et al., 2004)."*

and pg 7122 we change line 7-9 to:

*"In HiIron we also find an increase in regions where  $\phi\text{FeN} > 1$  (Fig. 26b). The increased supply of iron and a small biologically driven decrease in DIN supply (due to higher productivity, especially in higher latitudes) leads to an increased  $\phi\text{FeN}$  and is enough to allow accumulation of Fe to  $\text{Fe}^*D$ ."*

• (iii) Monitoring: The authors suggest that the monitoring of surface nutrient concentrations could be a "clear and easily interpreted indicator of ongoing global change". I have very strong doubts. In fact, even the authors themselves downplay this later on in the paper, given the fact that other processes could completely mask any trend. Perhaps the most important reason for doubt is the potential flexibility of marine phytoplankton with regard to their nutrient stoichiometry (especially with regard to iron). While this does not cause the resource competition theory to fall apart completely, it does cause a substantial shift in the exact location of the transitions between the individual provinces. Furthermore, I have some doubts regarding the transferability of the resource competition theory to other phytoplankton functional groups, i.e., groups where grazing control, seasonal succession, etc, might be more important than for diazotrophs. Therefore, I would remove this aspect from the paper.

We have particularly spend much time thinking on this point. When Prof Gruber states " In fact, even the authors themselves downplay this later on in the paper", we assume he means pg 7125, line 27-39 though pg 7126. These sentence were not supposed to downplay the issue, but to relay when and when not we anticipate a noticeable change. The theory states that the limiting nutrient will be drawn down to low levels, and a non-limiting nutrient will not: this is the real delineation of provinces that we anticipate being able to monitor - flexible stoichiometry will only minorly alter the actual values in the in situ nutrient concentrations, and thus not detract from our hypothesis. Moreover much of the province discussion relates to presence absence of diazotrophs. Even in the model with several non-diazotroph types, the provinces remain strongly delineated. We would agree that the theory will not extend into highly seasonal areas (and thus where there is strong coupling and decoupling of grazing control), and plan to make this point clearer in several point (including discussion and conclusions) of the revised version of the paper.

We are particularly struck by the strong delineation of provinces found in observations in Ward et al (2013) and Schlosser et al (2013), making us believe that this result is important and will be a helpful in future monitoring of the ocean. Thus we have decided to keep this aspect in the paper, and in fact believe it is a major point of the paper. We include additional text though to bolster this perspective:

We change 3rd paragraph of Discussion (pg 7125, lines22-29 and pg 7126 1-10) and add 2 additional paragraphs:

*"Though the theoretical framework specifically uses nutrient **supply** ratios to predict diazotroph biogeography (presence/absence), and the nutrient **supply** differences to suggest nitrogen fixation rates, it does also suggest patterns of nutrient **concentrations** dictated from the province perspective. In particular, the model suggests that in any province, the locally limiting nutrient will be uniformly drawn down to a low, subsistence concentration. Thus we do not anticipate any correlation between nutrient concentrations themselves and diazotroph biomass or nitrogen fixation: Indeed no such correlation was found in the study of Luo et al. (2014) which looked a compilation of observed nitrogen fixation and observed nutrient concentrations. The theory suggest that strong gradients of nutrient concentrations occur between provinces. The theoretical predictions are consistent with the strong transitions in surface phosphate, iron and fixed nitrogen concentrations, we well as the distribution of diazotrophs, observed along the AtlanticMeridional Transect (Moore et al., 2009; Ward et al., 2103).*

*The resource supply ratio framework provides a useful tool for interpreting and synthesizing the shifts in province boundaries, and attendant changes in these sharp nutrient gradients, in the climate change simulations. Local changes from a very low to a high concentration in the surface concentration of a particular nutrient typically reflects a transition away from ecological control (and visa versa). Thus the movement of these sharp transitions in surface nutrient concentrations provides a simple measure of the shifting province boundary. Such a nutrient concentration change will be a much simpler measure of the shifting boundary than the changes in the supply ratio that are actually responsible for the boundary shift. This is true in both models (ours and others) and the real world. Consistently, Schlosser et al. (2013) connected the observed movement of the sharp gradients between high and low surface iron concentrations and the internannual changes in the aeolian iron supply in the Atlantic.*

*We suggest that the very sharp gradients in surface nutrient concentrations associated with the province boundaries provides a relatively simple metric by which to monitor shifts in provinces both in numerical simulations and in nature. Provided it is applied appropriately to sharp gradients associated with actual boundaries (and not indiscriminately to any nutrient gradient) this simple metric reflects complex underlying ecological dynamics. We note that the resource ratio perspective is not likely to be useful in strongly seasonal regimes."*

and add a caveat to in the Conclusions at the end of the fourth paragraph:

*"A good prior mapping of current provinces will be important to ascertain before major changes occur."*

- (iv) Biogeography as an emergent property: Although the authors provide convincing arguments, I have not found a good answer to the question of whether the good agreement between model and theory is simply a consequence of the fact that the model was built according to the concepts of competition theory. Or in other words, that the good agreement between the modeled biogeographic pattern and the nutrient supply ratio is not a truly emergent property of the model, but rather a consequence of the design of the model. There are several elements that point in this direction, e.g., the lack of top-down control for the diazotrophs, the low growth rate and the high Fe demand, etc. This is perhaps more a philosophical comment than one that one can respond to in a straightforward manner. But I encourage the authors to reconsider their conclusions about the real-world

applicability of their results."

This is an interesting point. We are not attempting to say that the biogeography is an surprising "emergent property". If we only looked at the numerical model results - they are complex and reasons for the expansion of diazotroph ranges in future warmer or dustier world is a priori not obvious. Why in particular are the results similar between two very different scenarios? It took using the theoretical framework for us to understand. The fact that such a simple theory can help us understand the much more complex 3-D, non-steady state results from the numerical model is impressive. And yes, there is enough of the same assumptions (lower diazotroph growth rate, similar Michaelis-Menton nutrient parameterization). But I am not sure that I would also a priori believe that transport, non-steady state, additional phytoplankton types etc would still allow there is a be a clear interpretation between the theory and model. We try to include some of this idea in the newer version.

We have altered the second paragraph of the Discussion:

*"The results from our simulations (increase diazotroph geographic range) in both higher iron supply or a warming ocean were not a priori understood without the simpler theoretical framework. The parameterizations in the numerical simulation made the same assumptions as discussed above for diazotrophs growth, iron needs and ability to fix all required nitrogen. However the numerical simulation included additional nutrient constraints, several diazotroph and nondiazotroph species, grazers as well as full three dimensional transport and mixing. The numerical simulations were never in steady state. However, as suggested by our previous studies (e.g. Dutkiewicz et al., 2009; 2012), we find that the theoretical framework provided crucial insight into the results of the numerical model in the low latitude regions where diazotrophs typically occur (Luo et al., 2012)."*

As stated above: the theoretical considerations have already proved useful in the "real world": Ward et al (2013) and Schlosser et al (2013).

### **3 Recommendation**

I recommend acceptance of this manuscript with minor revisions. I do encourage the authors to consider my comments.

Thank you, we found these comments very helpful in re-considering the paper and have helped us add some really important clarifying and caveat paragraphs to the paper.

### **4 Minor comments**

p7120, line 19: "remineralization of organic matter". I don't understand why this has to be included here. It is not really an external input to the upper ocean ecosystem, but an internal one. Please explain.

In our framework "I" (the input of nutrients) includes ALL inputs of nutrients into a grid cell. As written in the theoretical equations (Table 4, Eq 3-5) there is no differentiation between "external" and "internal" sources. So "I" would include nutrients formed as a process of remineralization of organic matter. The numerical model does include DOM and POM explicitly, and thus we include remineralization of DOM/POM as a source/input. In fact we believe that this supply from DOM/POM is becomes quite important in the most oligotrophic regions of the ocean.

p7122, line 10ff: "growth rates of the plankton do not change". I am a bit puzzled here. First, why do the phytoplankton in the Fe limited regions of the Southern Ocean and the Equatorial Pacific not respond to the increased supply of Fe? Second, why aren't we

seeing also changes in the nutrient distribution within the thermocline, driven by the Fe induced changes in production and export in the regions that determine the pre-formed concentrations of these nutrients. See my major comment (ii) above.

This was very poorly worded section of the paper! Thank you for bringing this to our attention. In terms of "growth =  $\mu_j(N/N_K)$ ", we had meant the  $\mu_j$  (which is a function of temperature and light) does not change: growth rate obviously changes as nutrients (particularly iron) change. But this is not apparent from what we wrote in the paper. And in fact this is not an important point to make at this stage in the paper anyway. We reword that paragraph more clearly. Phytoplankton in the Southern Ocean (and any other iron limited region) do indeed respond with increased growth rate. And yes, there is a feedback on the nutrient supply through the thermocline. We do see a reduction in macro-nutrient supply to downstream regions. We had glossed over this in the original text for simplicity. We now include the following text to address these issues: As already stated, pg 7122 lines 7-13 are replaced with

*"In HiIron we also find an increase in regions where  $\phi FeN > 1$  (Fig. 26b). The increased supply of iron and a small biologically driven decrease in DIN supply (due to higher productivity, especially in higher latitudes) leads to an increased  $\phi FeN$  and is enough to allow accumulation of Fe to  $Fe^*D$ ."*

p7128, line 14: "potentially sensitive and powerful indicator". I disagree (see main comment (iii) above).

As replied above - the fact that this has been a powerful indicator in Schlosser et al (2013) in seeing changes in provinces in the real ocean make us believe this is a important point to make in this paper. We do however have the following caveat in the revised version: We change 3rd paragraph of Discussion (pg 7125, lines 22-29 and pg 7126 1-10) with as discussed above.

Figures: The figures have some room for improvement, e.g. better resolution, labeling of axes, choices of colors and relative line widths, etc.

We have included axes labeling in Figure 4 and 7 (an omission before), and increased line widths. We are not sure about the concern on the colours or the resolution. The actual figures have quite high resolution and we wonder whether these are degraded in the type-setting stage and/or the landscape rendition. We will work with the type-editors on a revised version so that the figures look better.

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