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 1:

We thank the Dr Luo for his comments and encouragement. We provide a detailed response to each point below, including an indication where they have led to changes to the manuscript. Below, the reviewers comments are quoted in black font with responses in blue.

We respectfully disagree with two key elements of the review:

- The reviewer cites the fact that a lack of correlation between observed nutrient concentrations and diazotroph biogeography undermines the application of resource supply ratio theory. However, the theory elucidates that the key relationships are between biogeography and *nutrient fluxes*, not *nutrient concentrations*. Indeed the theory suggests that, over broad regions, limiting nutrients will be drawn down to very small, probably uniform subsistence concentrations so we should not expect correlation between nutrient concentrations and diazotroph biomass or nitrogen fixation. We have revised the text in order to more clearly emphasize the distinction between fluxes and concentrations (see below).
- The reviewer largely discusses nitrogen fixation *rates*, whereas the theory we employ largely relates to diazotroph *biogeography* (i.e. the range of diazotrophy). We have also revised the text to clarify this distinction.

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.

General Comments:
The authors use nutrient supply ratios to explain the shift of the modeled nitrogen fixation biogeography. This is an interesting work for improving our understandings of model performance under changing climate. The manuscript is generally concise, well written, and the results are well presented.

Thank you for these positive comments.

Although I agree to use the nutrient supply ratios to interpret the results of this SPE-CIFIC model, I doubt if they can be extended to predict shifts of the diazotroph bio-geography. It depends on how the model is constructed. As in the model of this study the diazotroph growth is determined largely by nutrients, the nutrient supply ratios are certainly important in the model results.

We disagree that these results only valid for this specific model. The success of the resource supply ratio interpretation relies on two key paramterizations: that diazotrophs are never nitrogen limited and that they have slow maximum growth rates relative to non-diazotrophs. Similar parameterizations are used in a number of published models (e.g. Coles et al 2006, and subsequent papers with the same model; Krishnamurphy et al 2009, and subsequent papers with the same model; Le Quere et al, 2005, and subsequent papers with the same model) and we expect the concepts presented here to be relevant to a many of the current generation of such models. We have altered the discussion to reflect this point more clearly:

"The assumptions on growth, iron needs and ability to fix nitrogen have also been made in parameterization of diazotrophs in many other recent marine ecosystem models (e.g. Coles et al., 2006; Krishnamurphy et al., 2009; Le Qu´er´e et al., 2005; including many involved in the Coupled Model Intercomparison Project 5). We suggest, therefore, that our framework could provide a useful tool to interpret inter-model differences in diazotroph distributions and changes in future climate scenarios"

Beyond the world of models, we note that this application of resource supply ratio theory successfully interprets sharp transitions in surface nutrient concentration climatologies, anticipates the pattern of diazotroph *biomass* from Luo et al (2012) and Moore et al (2009) (see Ward et al. 2013) and explains temporal shifts in biogeographic provinces observed by in situ sampling in the Atlantic (Schlosser et al. 2013). We have revised the discussion to emphasize this point, for instance including the following sentences:

"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 Atlantic Meridional Transect (Moore et al., 2009; Ward et al., 2103)."

and

" 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."

However, my and colleagues' recent studies (Luo et al. Earth System Science Data 2012; Luo et al. Biogeosciences 2014) based on field measurements do not support that nutrients are the most important factors controlling N2 fixation.

Luo et al (2014) did not examine nutrient *supply* ratios, which are the most important predictors according to our theory. Any correlation, or lack thereof, between nutrient concentration and diazotroph abundance or nitrogen fixation does not have bearing on the validity of the resource supply ratio theory presented here. We clarify these points by added text to a new section 3.4 (on nitrogen fixation):

"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)."

and the Discussion to clarify these points.

*"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."

As shown in Fig. 1e of this manuscript, measurements show that diazotrophs are most abundant in tropical Atlantic, while very low in subtropical Atlantic. In our papers we also show that N2 fixation rates have same pattern. In addition, we found N2 fixation rates are always high in the Pacific. Even in the South Pacific where the diazotroph abundance seems low, the N2 fixation rates are still high. We believe the N2 fixation activity in tropical Atlantic > Pacific > subtropical Atlantic.

We agree that diazotroph abundance and nitrogen fixation rates may have a more complex relationship than assumed in our simulations; for example symbiotic nitrogen fixers may fix much more than their own requirements. While the Luo et al (2012) database provides an unprecedented overview of global patterns in N-fixation, it does not distinguish between autotrophic and heterotrophic N-fixation. Unfortunately, given that our model relates solely to autotrophic N-fixation, this means our model and the N fixation data cannot be reliably compared in regions like the S. Pacific, where heterotrophic diazotrophy is thought to dominate (Halm et al. 2011).

With further assessment of environmental parameters including physical conditions and nutrient concentrations, we found:

(1) Solar radiation and subsurface oxygen concentration are the best two predictors for the observed spatial distribution of N2 fixation rates. In the model of this manuscript, solar radiation (energy supply) may not be set up as important as nutrients in controlling diazotrophs, although both solar radiation and nutrients are both the fundamental resources for autotrophs. This could be one of the reasons that the model predicts the existence of diazotrophs in cold subarctic regions (Province III&IV in Fig. 3a).

The model does account explicitly for solar radiation as a key factor modulating growth. That PAR is a good predictor could also reflect the fact that high Fe:N supply ratios are found primarily in low-latitude, well-stratified regions, where mixed layer PAR is also high. We have not taken oxygen explicitly into account in this paper but acknowledge its potential physiological importance for diazotrophy. We add the following sentence in the discussion to clarify this:

"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."

(2) Iron is not a good predictor on global scale. Apparently dust deposition in Pacific is the lowest, but N2 fixation rates in Pacific are higher than the subtropical Atlantic where the dust deposition in higher.

We agree: iron alone is not a good indicator of diazotroph biogeography or nitrogen fixation rates. In province VI (portions of the subtropical Atlantic) there is high Fe dust and high Fe, but no diazotrophs because diazotrophs are phosphate limited there. Again, it is the interplay of iron, phosphorus and fixed nitrogen supply rates which is emphasized in our study. Alone they tell us little.

If we just pick out Atlantic, both dust deposition and subsurface oxygen concentration have equal predicting power for N2 fixation rates.

Luo et al. (2014) do not demonstrate predictive power; the algorithms were not tested against independent data. They show correlation, which is not the same as identifying a mechanism. Although this is not the place to do so, we could speculate that high ϕ_{FeN} and ϕ_{NP} are both also correlating with PAR and subsurface oxygen.

As shown in Fig 1f of this manuscript, the model does not reproduce this pattern even in just Atlantic – why dust deposition is highest in the tropical Atlantic while its diazotroph abundance is low?

As stated above, the diazotrophs also need phosphate - and in fact phosphate supply is lowest in some regions where iron supply is highest (including tropical Atlantic, see Figure 5a) - and as such the diazotroph biomass will be lowest there. Note that we do not account for DOP use, so improving the model in this regard might help resolve this anomaly.

(3) We also checked P*, a representative of N:P nutrient supply ratio, it does not show strong correlation to N2 fixation rates.

P* = (N-16P) is not representative of N:P *supply* ratios. It is only representative of ambient N and P concentrations. We too do not expect P* to be a good indicator of N2 fixation rates, and discussed this further in Ward et al 2013. We do not comment on the predictive power of the divergence of P* in the manuscript. It does contribute to the relative supply rates of P and fixed N. However, as we have emphasized, the relative supply rate of iron also needs to be accounted.

I generally support to publish this manuscript. But I'd like to see this inconsistency between the model and the observations to be discussed in this manuscript, to alert the readers that diazotroph biogeography cannot be simply predicted by nutrient supply ratio.

Thank you for encouraging support.

Here we have used resource supply ratio theory to interpret biogeographical shifts, in particular the range of diazotrophy, in climate change simulations. Simplified models and theory provide a framework for interpretation and clarification. At the same time, they *are* simplified and may not account for all variability. We do not claim that nutrient supply ratios are the *only* factor controlling this range but we believe it may be a very significant factor. Correlations, or lack thereof, with iron supply, P* divergence and nutrient concentrations as reported by Luo et al (2014) do not directly test, address or refute the resource supply ratio hypothesis. On the other hand the resource supply ratio hypothesis provides a mechanistic understanding. There is supporting evidence for our hypothesis in the analysis of Ward et al (2013) and the observed short term shifts in the Atlantic (Schlosser et al., 2013).

We agree with the reviewer that it is valuable to discuss the limitations of such models and we do so in the revised discussion. We also include text that highlights the inconsistencies between the modelled nitrogen fixation rates and those of the model, Section 2, line 3 of pg 7117:

"The numerical model is less consistent with rates of nitrogen fixation found by Luo et al. (2012, and further further described in Luo et al., 2014) especially in the South Pacific (where our model suggests

less nitrogen fixation) and South Atlantic (where the model suggests higher). The Luo et al. (2012) compilation does not differentiate between heterotrophic and autotrophic nitrogen fixation, while our model focuses only on autotrophic diazotrophy. Nitrogen fixation in the South Pacific is likely dominated by heterotrophs (Halm et al., 2012). Using hydrogen super-saturation, Moore et al. (2014) suggests higher nitrogen fixation in the South Atlantic than previous observations had found."

Specific Comments:

P7115, ln 11, Luo et al. 2012

Will change, thank you

P7116, ln 15-end, as discussed above, the model does not reproduce the real pattern of diazotrophs and N2 fixation activity.

The data is yet too sparse to clearly reject the predicted patterns. We think that the patterns of model diazotroph biogeography compare to independent observations relatively well, as was also shown in earlier papers with two different compilations of data (Monteiro et al 2010, Ward et al. 2013). We do realize that our nitrogen fixation patterns have more discrepancies to Luo et al (2012, 2014), and we have added text to this point as quoted above.

P7118, ln 13, Eqs. 3-5

Corrected, thank you

Table 3 RNij, please give out parameter values used in this study as they are important in evaluating the model results.

Eqns 3-5 are only the theoretical framework - the actual values of parameters are irrelevant for the theoretical discussion. The values of parameters used in similar (though more complex) equations used for the numerical model are given in Dutkiewicz et al 2012 - where we have directed the reader for these details.

Section 3.1 & Table 5: It seems to me that from Province I to VI, iron is increasing and phosphorus is decreasing. Clarifying this may help readers understand the biogeography.

The provinces are not defined by increasing or decreasing nutrient concentrations: in fact there are more likely fairly uniform values within provinces and steep gradients between provinces (see Fig.4 and 7; as well as those in Ward et al 2013). The provinces are not really even relate to increasing or decreasing nutrient *supply*, but rather on the gradients in supply *ratios*.

P7119 ln 18-25 & Table 4 Equilibrium Solutions: I'd prefer to see the definitions of the symbols right under the table, instead of buried in the main texts.

We will add definitions of ϕNP and ϕFeN to table 3.

P7120, ln 16, ln 23-25: It is not precise to use "slightly above one". What is amount of "slightly"? It also does not have a clear explanation why the threshold will not be exactly one.j

We cannot give an exact number since it will be determined when the excess supply of P and Fe is enough for the ambient P and Fe to reach P^*_D and Fe^*_D. Thus these values depend on the actual I_N, I_{Fe}, I_P as well as the diazotrophs' growth rates and half saturation. By trying to keep the framework general we can only say that it needs to be >1. But this is an important point to clarify and was poorly written in the original version of this paper and thank the reviewer for pointing this out. In the revised version we will explain this further (pg 7129, line 16):

*"Both ϕPN and ϕFeN need to be great enough for excess P and Fe to accumulate to reach P*D and Fe*D respectively for diazotrophs to survive (see Ward et al., 2013). This happens when ϕPN and ϕFeN need are greater than a critical threshold slightly above one. The exact amount though will be dependent on the actual values of the sources IP and IFe as well as diazotroph maximum growth rate and nutrient half saturation constant."*

P7120, ln 22: do not use subscripts for ">1"

Thank you, this was a typo, >1 should not have been in the subscript

P7124, ln 13, remove "an"

Done, thank you.

P7127, ln 13-14, (Luo et al., 2012)

Fig 1. Caption line 5, Luo et al. (2012)

Thanks - will change

Fig 2. Caption "Dashed blue line...Qpn=1 & Qfen=1". That does not make sense to me as Qpn and Qfen cannot be identical. Do you mean that one of them >1 and the other=1? Same for Fig 6.

Apologies, this is confusing. The dashed blue line indicates regions where phi_NP and phi_FeN are both greater than 1 (i.e. regions where diazotrophs are theoretically able to coexist) - the lines are indeed equal to one ϕand greater than one for the other ϕ. We have explained this more carefully in the revised figure caption (and thank the reviewer for pointing this out):

"Dashed blue line bound regions where both ϕPN >1 and ϕFeN >1 (discussed in Sect. 3.3)."

Fig. 4&7: Put legend of the lines instead of explaining the color of the lines in text. Also please label the x-axis (I assume the numbers are in degree North).

Good idea - and yes x-axis is latitude. We have corrected this in the revised version and newer versions of the figures. Thanks

Fig. 7: Mark the new province boundaries as you have done in Fig. 4

There are no new boundaries in the HighDust case - the whole region is in province III. This is indeed confusing though, so we now add the following sentence in the revised figure caption:

"Note that in HiIron the whole transect is Province III (see Fig. 3c)."

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