

Shifts in diazotroph biogeography

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Understanding predicted shifts in diazotroph biogeography using resource competition theory

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Abstract

We examine the sensitivity of the biogeography of nitrogen fixers to a warming climate and increased aeolian iron deposition in the context of a global Earth System Model. We employ concepts from Resource Ratio Theory to provide a simplifying and transparent interpretation of the results. First we demonstrate that a set of clearly defined, easily diagnosed provinces are consistent with the theory. Using the framework we show that the regions most vulnerable to province shifts and changes in diazotroph biogeography are the Equatorial and South Pacific, and central Atlantic. Warmer and dustier climates favor diazotrophs due to an increase in the ratio of supply rate of iron to fixed nitrogen. The analysis suggests that monitoring of real world province boundaries, indicated by transitions in surface nutrient concentrations, would provide a clear and easily interpreted indicator of ongoing global change. We suggest that the emergent provinces could be a standard diagnostic for global change models, allowing for rapid and transparent interpretation and comparison of model predictions and the underlying mechanisms.

1 Introduction

Nitrogen fixation is a major source of exogenous nitrogen to the global ocean and thus plays a critical role in the nitrogen cycle and consequently for marine ecosystems. Potential alterations in the distribution of nitrogen fixing autotrophs (diazotrophs) as the climate changes will therefore have important ramifications.

The observed biogeography of diazotrophs can be understood as a function of nutrient supply ratios (Dutkiewicz et al., 2012, Ward et al., 2013) using concepts from Tilman (1982), with the growth of diazotrophs dependent on an excess supply of both iron and phosphorus over nitrogen, relative to the demands of the non-diazotroph community. The slower growth rates and increased iron requirements associated with nitrogen fixation (Berman-Frank et al., 2001; Kustka et al., 2003) mean that diazotrophs will be

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outcompeted if dissolved inorganic phosphorus (P) or iron (Fe) limits them and their non-diazotroph competitors.

The global ocean can be described by 6 biogeochemical provinces based on resource supply ratios (see Ward et al., 2013; briefly summarized in Sect. 3) with diazotrophs only present in the two provinces where both the Fe : N and P : N supply ratios exceed given criteria. The theory also suggests that the limiting nutrients in the euphotic layer are held at eco-physiologically determined low values, while non-limiting nutrients accumulate according to the excess supply. Ward et al. (2013) showed that these theoretical predictions are consistent with observations along the Atlantic Meridional Transect (Moore et al., 2009), nutrient data from the World Ocean Atlas (Garcia et al., 2006) and in observed diazotroph distribution (Luo et al., 2013). This framework has also been used to understand the shifts in nutrient gradients (interpreted as province boundaries) that occur due to short term changes in iron deposition in the equatorial Atlantic (Schlosser et al., 2013).

Nutrient supplies will change in a warming climate. Model studies have suggested a reduction of macro-nutrient supply to the surface ocean in a warming ocean (Bopp et al., 2001; Steinacher et al., 2010; Dutkiewicz et al., 2013). Likewise, the aeolian iron supply, a major source of bioavailable iron to the ocean, has changed markedly in the past and is likely to change in the future (Mahowald and Luo, 2003; Mahowald et al., 2006; Tegen et al., 2004). Model studies have suggested that such changes will impact phytoplankton. Reduction in macronutrients to the surface is likely to reduce primary production in some regions of a warmer world (e.g. Bopp et al., 2001; Dutkiewicz et al., 2013) and changes in iron supply have been shown to impact nitrogen fixation rates (e.g. Krishnamurthy et al., 2009; Tagliabue et al., 2008). Here we show how the resource supply ratio provides a framework to interpret model predictions.

We focus on how the relative change in nutrient supply will affect the biogeography of diazotrophs and the implication for global nitrogen fixation. We apply the province based theory (Dutkiewicz et al., 2012, Ward et al., 2013) to understand the ecological changes that occur as an earth system model is subject to changes in global tempera-

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ture and atmospheric dust deposition. We first introduce the numerical model (Sect. 2) and results from two hypothetical scenarios of a changing ocean. We use the theoretical framework to map out the provinces and nutrient controls (Sect. 3), and in particular to explain the systems response in climate changes scenarios (Sect. 4). We discuss implications and limitations of our study in Sect. 5.

2 Global numerical model

We use the MIT Integrated Global Systems Model (IGSM) (Dutkiewicz et al., 2005, 2013; Scott et al., 2008; Sokolov et al., 2009), an earth system model of intermediate complexity together with a biogeochemistry and ecosystem model (Dutkiewicz et al., 2009, 2012), as our laboratory for this study. The model resolves the cycling of carbon, phosphorus, nitrogen, silica, iron, and oxygen through inorganic, living, dissolved and particulate organic phases. We resolve several non-diazotroph autotrophs, two diazotrophs and two grazers. See Appendix A for more details and changes relative to our previous studies.

In a control simulation with pre-industrial climate and dust supply (Luo et al., 2008), we find plausible ecological and biogeochemical distributions (similar to Dutkiewicz et al., 2013). In particular the relevant nutrient distributions compare well to observations (Fig. 1a–d). The model underestimates nitrate in the high Northern Hemisphere, but has reasonable values in the sub tropics and equatorial regions. Iron has lowest concentrations in the equatorial Pacific as is observed (though note the paucity of observations), and we appear to overestimate the iron limitation in the Southern Pacific gyres. Otherwise we capture the high iron concentration in the Atlantic and the northern Indian ocean, with lower values elsewhere. We find a distribution of diazotrophs (Fig. 1e and f) which is consistent with the observed distribution of diazotrophs (Luo et al., 2012), though again, note the limitation of the observations. We capture high diazotroph biomass in the tropical Atlantic, though our maximum is slightly south relative to the observations. In particular we also capture the observed lack of diazotrophs in re-

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gions such as the south Pacific gyres and Pacific equatorial region (see Monteiro et al., 2010; Luo et al., 2012) and consistent with the lack of isotopic evidence for nitrogen fixation in the middle of the North Atlantic gyre (Knapp et al., 2005, 2006).

To explore how this distribution shifts in altered climates we conducted a series of sensitivity experiments (Table 1, and see Appendix A). Here we discuss two key integrations which reveal the contributions of changes in ocean circulation and changes in iron deposition independently:

- *Phys*: from pre-industrial conditions the system is perturbed with changes to the physical ocean (e.g. temperature, circulation and mixing) as a result of increasing greenhouse gases in a “business-as-usual” emission scenario (Sokolov et al., 2009; Dutkiewicz et al., 2013; similar to RCP8.5). Dust-borne iron supplies are however maintained at pre-industrial values (Luo et al., 2008). There is a significant increase in the geographical extent of the diazotrophs particularly in the Equatorial and South Pacific by the end of the projected 21st century (Fig. 2b). The area of ocean sustaining diazotrophs increases by 17 % and the total global nitrogen fixation rate also increases by 17 % (Table 2).
- *Hilron*: to explore the response to changes in iron supply, this experiment has iron dust fluxes that are doubled relative to the pre-industrial values, but the physical ocean is held at pre-industrial conditions. In this experiment there is also an increase in the biogeographical distribution of diazotrophs in similar regions to *Phys* (Fig. 2c), with 38 % more area and a 28 % increase in global nitrogen fixation.

Why do both experiments show similar shifts in diazotrophs biogeography given such different alterations to the environment? These results, and the dynamics of the system are most easily interpreted using the province structures associated with resource supply ratios.

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3 Understanding global model results with theory

Before considering the changing distributions of the sensitivity studies (*Hilron, Phys*), we consider the diazotroph biogeography of the *Control* (pre-industrial) simulation. We find that resource ratio theory to be the key to understanding the significantly more complex global numerical model.

Our theoretical framework (Tables 3 and 4) is based on resource competition (Tilman, 1982) and builds directly on our earlier studies Dutkiewicz et al. (2012) and Ward et al. (2013). We consider two groups of phytoplankton (Eqs. 1 and 2, Table 4): non-diazotrophs (P) whose growth can be limited by nitrate, phosphate or iron; and diazotrophs (D) who fix all the nitrogen that they require (relaxing this assumption makes no qualitative difference to our results, Dutkiewicz et al., 2012). We assume here a simple linear loss rate for both phytoplankton. The time rate of change of nutrients ($i = N, P, Fe$, Eqs. 3–6, Table 4) are a combination of phytoplankton uptake, sources I_i (e.g. transport into a location, dust supplies, remineralization of organic matter) and sinks O_i (e.g. transport out of a location, and in the case if iron, scavenging).

When growth and losses are tightly coupled, equilibrium solutions are relevant; as is the case subtropical, oligotrophic regions (Dutkiewicz et al., 2009). In the theoretical framework we solve for equilibrium concentration of phytoplankton and nutrients (Eqs. 6–10, Table 4). For the purpose of this study, we explore the important conclusions of the theoretical framework with the numerical model results, and direct the reader to Ward et al. (2013) and Appendix for further details.

3.1 Provinces, co-existence, nutrient limitation

Theory: because of their lower growth rate, diazotrophs can only co-exist with non-diazotrophs if the non-diazotrophs are nitrogen limited. We define six distinct provinces, related to whether diazotrophs coexist with non-diazotrophs and by whether growth of the different phytoplankton are limited by iron, phosphate, or in the case of non-diazotrophs, by DIN (Table 5).

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Numerical Model: non-diazotrophs are DIN limited in light blue, green, yellow, and dark blue regions (provinces II, III, IV, V, Fig. 3). Diazotrophs and non-diazotrophs coexist in the green and yellow provinces (III and IV), and are limited by iron and phosphate respectively.

In province I (red in Fig. 3), where there is very little iron supply, non-diazotrophs are iron limited (line 3 of Table 5) and diazotrophs are excluded (line 1 of Table 5). In regions with more iron supply, non-diazotrophs will be nitrogen limited but there may still not be enough iron to support diazotrophs (Province II, light blue in Fig. 3). In a region with enough excess iron, diazotrophs can co-exist: they will be iron limited (line 2 of Table 5) while non-diazotrophs are still nitrogen limited (Province III, yellow). With even higher iron supply, diazotrophs are relieved of iron limitation and are instead phosphate limited (Province IV, green). However if phosphate supply is not enough to provide excess, diazotrophs will be excluded (Province V, dark blue). Even lower phosphate supply will lead to non-diazotrophs being phosphate limited (Province VI, orange). Note that these last two provinces only occur in small regions of the Atlantic in this model.

3.2 Ecological control of nutrients

Theory: resource competition theory suggests that the limiting nutrient is controlled ecologically: in equilibrium (denoted by superscript *) the phytoplankton draw the nutrient that limits them down to a specific value that is set by the plankton physiology and mortality (see Table 4, Eqs. 6–10). Where non-diazotrophs (B) are nitrogen limited (Provinces II–V), inorganic nitrogen is drawn down to N_B^* . In province I where non-diazotrophs are iron limited, iron is drawn down to Fe_B^* , and in province III iron-limited diazotrophs (D) draw iron down to Fe_D^* . Similarly, phosphate is drawn down to P_B^* in province IV and P_D^* in province VI.

Numerical Model: in the model nutrients are drawn down low in provinces where they are ecologically controlled and are higher in provinces where they are not. For instance in a transect in the Pacific (Fig. 4c–e), iron is drawn down lowest in province

I (to Fe_B^*) with a increase in concentration into province II and III. In province III iron will be maintained at Fe_D^* which is greater than Fe_B^* . In the numerical model Fe_B^* and Fe_D^* are not uniform values, but are a function of the dominant phytoplankton types (affecting μ_j , κ_{ij} and m_j), temperature and light environment (as these impact μ_j), and grazing pressure. Thus even within province I and III, there are variations in the iron concentrations. DIN is drawn down in in Province III (where non-diazotrophs control it), while phosphate remains high for all three provinces depicted here. Similar patterns occur for a transect between Provinces IV, V and VI (not shown), but instead phosphate and DIN are respectively controlled and iron remains high.

3.3 Nutrient supply ratio controls provinces boundaries

Theory: the boundaries between provinces are controlled by the rates at which iron and phosphate are delivered relative to DIN, normalized by the elemental stoichiometry of the non-diazotrophs (R_{NP_B} , R_{NFe_B}):

$$\phi_{PN} = \frac{I_P^*}{R_{NP_B} I_N^*}$$

$$\phi_{FeN} = \frac{I_{Fe}^*}{R_{NFe_B} I_N^*}$$

Both ϕ_{PN} and ϕ_{FeN} need to be greater than a critical threshold slightly above one for diazotrophs to exist.

Numerical Model: we use model output to compute ϕ_{PN} and ϕ_{FeN} (Fig. 5a and b). Here I_j includes all advection and mixing into a model grid cell, remineralization of organic matter, and in the case of iron, dust and sedimentary sources.

For the most part the pattern of diazotrophy matches the regions where ϕ_{PN} , $\phi_{FeN} > 1$ (Fig. 5c). The threshold is however slightly larger than one (as a consequence of the slightly higher Fe^* and P^* for diazotrophs) and some regions where ϕ_{PN} , ϕ_{FeN} are only slightly greater than one will not support diazotrophs (i.e. Provinces II and IV). In both

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the equatorial Atlantic and Northern Atlantic, ϕ_{PN} is less than 1 (suggesting that no diazotrophs should exist) in regions where model diazotrophs are in fact present. In the Equatorial Atlantic, advection and mixing from surrounding regions with diazotrophs support an immigrant population. The net growth rates of the diazotrophs in these regions, where the theorized ϕ_{PN} is not sufficient, are negative and their population is maintained by transport from upstream (e.g. see Clayton et al., 2013). Similarly, the swift Gulf Stream current carries diazotrophs northward out of the regions that can support positive growth.

4 A changing ocean

We use the province framework to explain the resulting shifting in diazotroph biogeography seen in Fig. 2. The theoretical considerations also provides insight into the shifts in all provinces and the implications for nutrient concentrations.

4.1 Shifts in provinces

In *Phys*, increased stratification and slower overturning circulation lead to a reduction in the supply of macronutrients (I_N and I_P) from the deep ocean to the surface ocean on the timescale presented here. On the other hand I_{Fe} changes less as it is dominated by the atmospheric input (which stays at pre-industrial values in this experiment). As a consequence ϕ_{FeN} is altered, increasing in many locations (Figs. 6a and 4b). We can summarize the subsequent changes to the province boundaries (Fig. 3b) relative to pre-industrial condition (Fig. 3a):

- The $\phi_{FeN} > 1$ area increases (blue line in Figs. 6a and 2b) and therefore province II and III expand at the expense of province I, particularly in the Pacific (Fig. 4b).
- A decrease in phytoplankton biomass in the North Atlantic (a consequence of reduced macronutrient supply, which are limiting here), leads to accumulation of

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unused iron (Dutkiewicz et al., 2012). Consequent higher horizontal gradients of iron lead to an increase in I_{Fe} to downstream areas and consequent large increase in ϕ_{FeN} in this region. Province IV (where $\phi_{FeN} \gg 1$, see Table 5 and Sect. 3.3) therefore increases: diazotrophs become phosphate limited in more regions.

- The large increase in ϕ_{FeN} also leads to a reduction in the area of province V (no diazotrophs) in the North Atlantic.

In *Hilron* we also find an increase in regions where $\phi_{FeN} > 1$ (Fig. 6b). Here though it is almost exclusively the increase in I_{Fe} from higher dust deposition that accounts for the changes. We find very similar (though more severe) changes to the province boundaries: expansion of province II and III at the expense of I in the Pacific (Fig. 7): growth rates of the plankton do not change (as temperatures do not rise), but the increased supply of iron with no concurrent increase in DIN supply is enough to allow accumulation of Fe to Fe_D^* . In the Atlantic, doubling of the highest dust deposition leads to $\phi_{FeN} \gg 1$ and province IV expands and V shrinks (Fig. 3c). Here, though the response is similar to *Phys*, the underlying reason is different: decreased biomass consuming iron in *Phys* vs. increased iron input in *Hilron*. We also find a region in the North Pacific where ϕ_{FeN} become large enough that a region switches from province III to IV (diazotrophs shift from being iron limited to phosphate limited).

4.2 Changes to nutrient concentrations

There are changes to the nutrient concentration in *Phys* after 100 years of warming relative to pre-industrial conditions (*Control*). In general the macro-nutrients (DIN and phosphate) concentrations decrease over the course of the projected 21st century, but iron has a more complex pattern of increase and decrease (Fig. 4c–e).

We can partition the nutrient concentration changes into those that occur because the province boundaries change, and those that occur as a consequence of changes within provinces to the non-limiting, or limiting nutrients:

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- When boundaries shift in the warming scenario, some nutrients change from being ecologically controlled to “free” (or vice versa). This can lead to large changes in concentration (e.g. Fe in Fig. 4e).
- Within provinces non-ecologically controlled nutrients can also have large changes (e.g. DIN in province I, Fig. 4c, and phosphate in provinces I, II, and III (Fig. 4d): changes in supply, or to changes in biomass (and thus consumption of the nutrients) leads to these shifts.
- We also find small decreases in the ecologically controlled nutrients even within provinces (e.g. lower DIN in provinces III, and lower iron in provinces I and III). The growth rate of all the phytoplankton is parameterized to increase as temperatures warm (Eppley, 1972). Higher growth rate, μ_j in *Phys* will lead to lower values to which the limiting nutrient is drawn down (Eqs. 6 to 10) by 2100.

We reinforce this latter result with an additional experiment (*Phys-Temp*, see Appendix A and Table 1) where we allow only the growth rates to change with increasing temperature to 2100 (circulation, and hence macro-nutrient supply, remains as pre-industrial). We found the same decrease in the ecologically controlled nutrients in all province as in *Phys*, but virtually no changes to non-ecologically controlled nutrients. Thus higher growth rates lead to lower Fe^* , P^* , N^* and ambient limiting nutrients are drawn down further in this warmer world.

In *Hilron* we find (Fig. 7) that the nutrient that is ecologically controlled in a given province has virtually no change in concentration relative to the pre-industrial experiment *Control*. For example DIN and Fe do not change in regions which remain in province III. There are changes in the non-limiting, non-ecologically controlled nutrient in the provinces as a response to increased dust (in the case of iron) or phytoplankton biomass changes (in the case of the macronutrients). Lower DIN and PO_4 in the Equatorial Pacific (Fig. 7) is due to the higher biomass. The biggest changes in concentrations occur in the those regions that were within one province in *Control* and

in another in *Hilron*; for instance iron increases most in the regions of the Pacific that were province I in *Control* and province II or III in *Hilron*.

4.3 Global results

The biogeographical distribution of diazotrophs increases in both *Phys* (17 %) and *Hilron* (38 %) (Table 2). In both sensitivity studies there is also an increase in the globally integrated nitrogen fixation rate (17% and 28% respectively). In *Hilron*, the increase in biogeographical area and increase in supply of iron leads to mostly higher local nitrogen fixation, though some areas become phosphate limited and have a reduction instead (e.g. areas which switch from Province III to IV). However, because of increased growth rate of iron limited diazotroph, overall global nitrogen fixation rates increase. However further sensitivity studies (see Table 1 and Appendix A) show that the situation in *Phys* is more complicated. In experiment *Phys-Temp* the growth rates of all the phytoplankton increase as a consequence of higher temperatures (following an Eppley, 1972) over the course of the 21st Century, but the circulation (and hence the supply of nutrients) remained as pre-industrial. Here we find only a small increase in diazotroph biogeography (Table 2), but a large (18 %) increase in nitrogen fixation: as they grew faster in warmer water the diazotrophs fixed more nitrogen. In the converse experiment (*Phys-Circ*), temperatures affecting growth were held at pre-industrial levels, but the circulation (and hence macro-nutrient supply rates) changed as for the warming scenario. Here, though the diazotroph regions increased (14 %), there was no increase in global nitrogen fixation. Reduction in phosphate supply led to more areas being phosphate limited, lower growth rates and lower nitrogen fixation. Thus in the full experiment *Phys* it is primarily the temperature increases, not the regional increases in diazotrophy, that led to the increase in nitrogen fixation. Globally integrated results for the change in the nitrogen fixation rates will therefore be sensitive to the parametrization of phytoplankton growth with changing temperature. The changes to primary production (Table 2) are also dependent on the temperature parameterization (see Dutkiewicz et al., 2013 for further discussion on primary production changes).

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5 Discussion: implications and limitations

We have demonstrated the value of resource ratio framework for interpreting complex simulations of global change scenarios. The framework requires two assumptions: that diazotrophs grow slower than other phytoplankton and that they require more iron (supported empirically, e.g. Berman-Frank et al., 2001; Kustka et al., 2003). These assumption are made in parameterization of diazotrophs in many marine ecosystem models (e.g. Coles et al., 2006; Krishnamurphy et al., 2009; Le Quéré et al., 2005), including ours. We suggest, therefore, that our framework will also be able to explain diazotroph model distributions and changes in future climate scenarios in all such models, including many involved in the Coupled Model Intercomparison Project 5 (CMIP5). We suggest that this province framework would be an excellent way to compare and understand differences between model predictions.

The framework suggests that diazotroph biogeography will change with alterations to the supply rates of Fe and P relative to that of DIN. An increase in ϕ_{FeN} (whether through reduction in DIN supply or a increase in Fe supply) will lead to an increased region supporting diazotrophy. We suggest that calculation of ϕ_{FeN} in other model studies of climate change will be able to help explain changes in diazotroph distribution. However, it should be kept in mind that the globally integrated nitrogen fixation rate changes is related also, and possibly more strongly, to changes to the diazotroph growth rates through the reduction in supply of limiting nutrient or changes to growth rate due to increase in temperature.

The framework also sheds light on the complex alterations to nutrient concentrations in our climate change simulations. We believe that such an approach would also help explain the often confusing nutrient changes seen in other models of global change. The framework could be used to help us understand and anticipate changes that we see (and will begin to see more) in our oceans. Our study suggests that changes in the ecologically controlled (or limiting) nutrient will be small (possibly not detectable), but driven by changes to the physiological characteristics of the phytoplankton as-

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semblages. Large surface nutrient changes may occur to non-limiting nutrient, though such changes will not indicate either ecological or province changes. However, some of the most significant (and observable) changes in the nutrient concentration indicate large scale province shifts. The major regime shifts that such a movement of a province boundary indicates, will thus be most easily observed by the marked nutrient changes. The regime shift suggested by Karl (1999) in the North Pacific subtropical gyre in the 1990's did have an associated large change in phosphate concentrations. And the shorter term shifts in low vs. high surface iron concentrations (interpreted as province boundaries) has been seen as a consequence of interannual shifting dust fluxes (Schlosser et al., 2013).

There are additional process that may affect the changes in nutrient supply that we have not addressed, such as slow temporal shifts in dust supply, changes in aeolian deposition of nitrate and phosphate, and changes in iron chemistry in a more acidic ocean (Shi et al., 2010). It is not, in fact, clear how iron dust supply will change in the future (Mahowald and Luo, 2003; Tegen et al., 2004), so we have discussed here a hypothetical doubling iron dust deposition scenario. We did however also conduct a half iron deposition experiment (*Lolron*, see Tables 1 and 2) with anticipated opposite response. The future ocean is likely to experience a change in supply of both macronutrients and iron dust. We have conducted additional studies that consider changes to both (*Phys+Hilron*, *Phys+Lolron*) which indicate that the two effects can cancel or enhance each other depending on how relative supply rates change.

We have not considered the many other changes that will certainly effect phytoplankton. Increased ocean acidification may change cellular stoichiometry (Riebesell et al., 2007; Finkel et al., 2010) with consequences to nitrogen fixation (Tagliabue et al., 2011). Higher CO₂ appears to increase growth rates of diazotrophs, in particular *Trichodesmium* (Levitan et al., 2007; Hutchins et al., 2013). Such changes are also likely to affect diazotroph biogeography and global nitrogen fixation rates in a future world. We believe that with modifications our theoretical framework will provide insight into

changes that will occur from other alterations to the physical, chemical and grazing controls that may occur due to climate change.

Recent studies have suggested the importance of variable phytoplankton stoichiometry in setting patterns of diazotrophy (Mills and Arrigo, 2010; Weber and Deutsch, 2012). The numerical model used here has fixed stoichiometry. Results with a variable stoichiometry model will certainly change the details of the results. However, given the several orders of magnitude in the changes in ϕ_{FeN} , we suggest that the large scale results from this study will be robust. Ward et al. (2013) conducted a sensitivity study to show that though the boundaries did shift with different assumption of cellular elemental ratios, the broad scale patterns remained robust. Certainly, though, a next step in this province framework is to incorporate variable stoichiometry.

However, even with this simplification, Ward et al. (2013) showed the applicability of resource ratio theory to understand observed diazotroph biogeography (Luo et al., 2013), phosphate and nitrate distributions from World Ocean Atlas (Conkright et al., 2008) as well as the nutrient and diazotroph distributions along the Atlantic Meridional Transect (Moore et al., 2012). And recently Schlosser et al. (2013) have used the theory to interpret the shifts in biogeochemical boundaries (denoted by strong gradients in nutrients) in the (sub)tropical Atlantic due to interannual alterations in the deposition of dust. These studies suggests that the framework is relevant for understanding the real ocean.

6 Conclusions

We have applied a resource ratio framework to an interpretation of the controls on surface ocean nutrients and diazotroph biogeography and, in particular how these may change in a series of experiments representing process that may occur in a future world.

We outlined distinct provinces determined by the biogeography of diazotrophs and the nutrients that limit the community. The province boundaries are dictated by the

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relative supply of Fe and P relative to DIN. Our sensitivity experiments suggest that the most vulnerable regions to province shifts are the Equatorial Pacific and the outer edge of the South Pacific gyre, as well as the the central Atlantic, in particular the central North Atlantic gyre. In these regions we suggest that diazotrophs may have a more favorable environment in a future world with lower macronutrient supply and/or higher iron dust supply.

It is the relative change in nutrient supplies which regulate province shifts. We find similar changes to the distribution of the diazotrophs whether we increased iron supply or decreased nitrate supply: it was the ratio of the two that was important. However, although the ratio of the nutrient supply dictates the diazotroph biogeography, the absolute changes of the limiting nutrient or alteration to the diazotroph maximum growth rate (e.g. through increase temperature) ultimately control the global nitrogen fixation rates.

Our analysis suggests that a potentially sensitive and powerful indicator of global change is the shifting of the transition regions in nutrient concentrations which mark the boundaries of the provinces. Because of this connection, such changes would provide powerful inferences about complex biogeochemical cycles from a relatively simple observed indicator. Resource ratio theory provides the framework to make such interpretations. The position of surface nutrient transitions could, perhaps, be monitored using underway instruments on ships of opportunity.

Without a consistent conceptual framework, models make uncertain and often conflicting predictions. The resource supply ratio framework applied here helps us to understand the results of the more complex numerical model, and provides insight to mechanisms at play in the real ocean. We suggest that the province analysis would be helpful in understanding other numerical models (e.g. those used in the IPCC) and a helpful tool in understanding the differences in responses between models. An understanding of the controls on distinct ecological and biogeographical provinces will help us anticipate changes and understand observed changes in a future warmer world.

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Appendix A

Additional numerical model description

The MIT Integrated Global Systems Model (IGSM) (Dutkiewicz et al., 2005; Scott et al., 2008; Sokolov et al., 2009; Dutkiewicz et al., 2013) has a three dimensional ocean circulation component (MITgcm, Marshall et al., 1997) embedded in it. In this study the ocean has horizontal resolution of $2^\circ \times 2.5^\circ$ and 22 vertical levels ranging from 10 m in the surface to 500 m at depth. Ocean boundary layer physics is parameterized using the KPP formulation (Large et al., 1994) and the effects of mesoscale eddies, not captured at this coarse resolution, is parameterized (Gent and McWilliams, 1990). The carbon cycle in these simulations is parameterized as in Dutkiewicz et al. (2005).

The coupled system is spun up for 2000 years (using 1860 conditions) before simulating 1860 to 2100 changes. Atmospheric greenhouse gas and volcanic observations are specified from 1860 to 2000; for the 21st century we use human emissions for a “business and usual” scenario that is projected by an economics module (Sokolov et al., 2009). This scenario is constructed under the assumption that no climate policies are imposed over the 21st century, and is similar to the Representative Concentration Pathways 8.5 (RCP8.5) used in the Coupled Model Intercomparison Project 5 (CMIP5).

We use the physical ocean fields from the IGSM simulation to drive an ocean biogeochemistry and ecosystem model (see Dutkiewicz et al., 2009, 2012, 2013; Hickman et al., 2010 for full description and parameter values). Different from our earlier studies, this model includes explicit treatment of Chlorophyll such that the Chl:C ratio is dynamic following Geider et al. (1998). Phytoplankton growth rate is a function of the Chl:C, temperature, light and nutrient availability (Geider et al., 1998) as done in Hickman et al. (2010). Iron chemistry includes explicit complexation with an organic ligand, scavenging by particles (Parekh et al., 2005) and representation of aeolian (Luo et al., 2008) and sedimentary (Elrod et al., 2004) sources. Nitrogen fixation is treated as in Monteiro et al. (2010) and Dutkiewicz et al. (2012). However an improvement

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over those studies is inclusion of explicit water column denitrification parameterized such that nitrate is consumed during remineralization of organic matter rather than oxygen when oxygen drops below 4 μM . Stoichiometry of denitrification follows Anderson (1995).

5 We resolve several non-diazotroph types of phytoplankton (analogues of diatoms, coccolithophores, other large eukaryotes, *Prochlorococcus*, and other pico-phytoplankton), as well as two diazotroph types (analogues of *Trichodesmium* and unicellular types, following Monteiro et al., 2010). There are two grazers classes. The biogeochemical and biological tracers are transported and mixed by the climate system model, and interact through the formation, transformation and remineralization of
10 organic matter. Excretion and mortality transfer living organic material into sinking particulate and dissolved organic detritus which are respired back to inorganic form.

The ecosystem model is quasi-spunup (240 years) with pre-industrial (1860) physical conditions and aeolian iron dust supply (Luo et al., 2008). From this initial conditions we
15 conduct a series of experiments (Table 1) (similar to those in Dutkiewicz et al., 2013):

1. *Control*. For another 240 years we use pre-industrial (1860) physical conditions and aeolian iron dust supply (Luo et al., 2008).
2. *Phys*. For 240 years the system is perturbed with changes to the physical ocean (temperature, circulation and mixing) as a result of increasing greenhouse gases in the “business as usual” described above. Iron dust supplies are maintained at
20 pre-industrial values (Luo et al., 2008).
3. *Hilron*. For 240 years the model is run with dust deposition doubled from pre-industrial, but the physical state remains as for pre-industrial conditions (as in *Control*).
- 25 4. *Phys-Temp*. For 240 years the system is perturbed with biological rates that change according to temperatures from the “business as usual” scenario, but circulation, mixing and dust supply remain as for pre-industrial conditions.

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5. *Phys-Circ*. For 240 years the system is perturbed with circulation and mixing changing for the “business as usual” scenario, but the temperatures affecting biological rates remain as for pre-industrial conditions.

6. *Phys+Hilron*. As for *Phys*, but with doubled iron deposition rates.

7. *Lolron*. For 240 year the model is run with dust deposition halved from pre-industrial, but physical state remain for pre-industrial conditions.

8. *Phys+Lolron*. As for *Phys*, but with half iron deposition rates.

The results discussed in this article all come from the last 5 years of these simulations – in the case of *Phys* this would be equivalent to the calendar years 2095–2100.

In the main text we focus on only two of these experiments (*Phys* and *Hilron*) as these illustrate most of the relevant points. The separation of circulation vs. temperature effects (*Phys-Circ* and *Phys-Temp*) are also useful to explain the global implication of the biogeography changes.

Appendix B

More on theoretical framework

Our theoretical framework (Tables 3 and 4) is based on resource competition (Tilman, 1982). It builds directly on our earlier studies Dutkiewicz et al. (2012) and Ward et al. (2013). Dutkiewicz et al. (2012) only considered two nutrients (nitrate and iron). Ward et al. (2013) included phosphate into the theory, but assumed a more simplified representation of nutrient supply (considering only supply from deep water and, in the case of iron, from dust). Here we consider a more detailed treatment of the nutrient supplies.

By manipulating Eqs. (3)–(5) (Table 4) in equilibrium we also obtain Eqs. (11) and (12) (Table 4) for the relative ratio of the supply of nutrients, normalized by the elemental stoichiometry of the non-diazotrophs: $\phi_{\text{PN}} = \frac{I_{\text{P}}^*}{R_{\text{NP}_B} I_{\text{N}}^*}$ and $\phi_{\text{FeN}} = \frac{I_{\text{Fe}}^*}{R_{\text{NFe}_B} I_{\text{N}}^*}$.

$$\phi_{\text{PN}} = 1 + \frac{m_{\text{D}} DR_{\text{NP}_D}}{R_{\text{NP}_B} I_{\text{N}}^*} + \frac{O_{\text{P}} - O_{\text{N}} R_{\text{NP}_B}}{R_{\text{NP}_B} I_{\text{N}}^*}$$

$$\phi_{\text{FeN}} = 1 + \frac{m_{\text{D}} DR_{\text{NFe}_D}}{R_{\text{NFe}_B} I_{\text{N}}^*} + \frac{O_{\text{Fe}} - O_{\text{N}} R_{\text{NFe}_B}}{R_{\text{NFe}_B} I_{\text{N}}^*}$$

Since this representation is different from our earlier studies we discuss it further. (Though we note that the conclusions are similar to those earlier studies.) These expressions are made up of three terms. The second term is only non-zero (and positive) when there are diazotrophs (province III and IV). The third term is dictated by sink terms which will be dominated by transport. However, in the equilibrium assumption if a nutrient is under ecological control, most excess input is taken into biomass and $O_i \approx 0$. Thus $O_{\text{N}} \approx 0$ in provinces II–V, $O_{\text{Fe}} \approx 0$ in I and III, and small in II, $O_{\text{P}} \approx 0$ in IV and VI and small in V. We can therefore determine where the third term in each of Eqs. (11) and (12) are positive or negative and hence whether ϕ_{PN} and ϕ_{FeN} are greater than or less than 1 (see Table 2). For instance in province I, with $O_{\text{Fe}} \approx 0$ and $O_{\text{N}} > 0$, $\phi_{\text{FeN}} < 1$. The boundary between province I and II occurs when $\phi_{\text{FeN}} = 1$ (i.e. when O_{N} also approaches zero as N becomes ecologically controlled). Across province II as ϕ_{FeN} increases, Fe increases until it reaches Fe_D^* at which point diazotrophs can coexist and the province boundary between II and III is reached. Here the second term in Eq. (12) is now positive (this excess iron is utilized by the diazotrophs), but the third term is zero. In province IV, the second term is still positive, iron is no longer ecologically controlled such that the third term is also positive and ϕ_{FeN} is large. Similarly changes in ϕ_{PN} occur moving from VI to V and so on. See the Web Appendix of Ward et al. (2013) for a more detailed theoretical description of these provinces.

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	temperature for growth rate	circulation/mixing	iron dust
<i>Control</i>	pre-industrial	pre-industrial	pre-industrial
<i>Phys</i>	1860–2100	1860–2100	pre-industrial
<i>Hilron</i>	pre-industrial	pre-industrial	double
<i>Phys-Temp</i>	1860–2100	pre-industrial	pre-industrial
<i>Phys-Circ</i>	pre-industrial	1860–2100	pre-industrial
<i>Phys+Hilron</i>	1860–2100	1860–2100	double
<i>Lolron</i>	pre-industrial	pre-industrial	half
<i>Phys+Lolron</i>	1860–2100	1860–2100	half

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	diaz area	N ₂ fixation	primary production
<i>Phys</i>	+17 %	+17 %	−3 %
<i>Hilron</i>	+38 %	+28 %	+3 %
<i>Phys-Temp</i>	+6 %	+19 %	+8 %
<i>Phys-Circ</i>	+14 %	0 %	−11 %
<i>Phys+Hilron</i>	+62 %	+28 %	−2 %
<i>Lolron</i>	−27 %	−9 %	−4 %
<i>Phys+Lolron</i>	−2 %	+4 %	−7 %

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B	non-diazotroph biomass
D	diazotroph biomass
N	dissolved inorganic nitrogen (DIN)
P	phosphate
Fe	dissolved inorganic iron
I_i	supply rate of nutrient $i = \text{N, P, Fe}$
O_i	sink rate of nutrient $i = \text{N, P, Fe}$
μ_j	maximum growth rate of plankton $j = \text{B, D}$
m_j	loss rate of plankton $j = \text{B, D}$
κ_{ij}	half saturation constant of nutrient $i = \text{N, P, Fe}$ for plankton $j = \text{B, D}$
R_{Nij}	elemental ratio of N to $i = \text{P, Fe}$ in plankton $j = \text{B, D}$

Table 4. Theoretical framework.

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

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Table 5. Theoretical Provinces. These descriptions of the provinces come from the framework outlined in Table 4. No entry means there is no theoretical solution.

	I	II	III	IV	V	VI
<i>ecosystem</i>						
diazotrophs	no	no	yes	yes	no	no
limiting diaz	–	–	Fe	PO ₄	–	–
limiting non-diaz	Fe	N	N	N	N	P
<i>nutrient control</i>						
N	–	N _B [*]	N _B [*]	N _B [*]	N _B [*]	–
P	–	–	–	P _D [*]	> P _B [*] , < P _D [*]	P _B [*]
Fe	Fe _B [*]	> Fe _B [*] , < Fe _D [*]	Fe _D [*]	–	–	–
<i>supply ratio</i>						
ϕ_{PN}	–	> 1	≫ 1	> 1	> 1	< 1
ϕ_{FeN}	< 1	> 1	> 1	≫ 1	> 1	–

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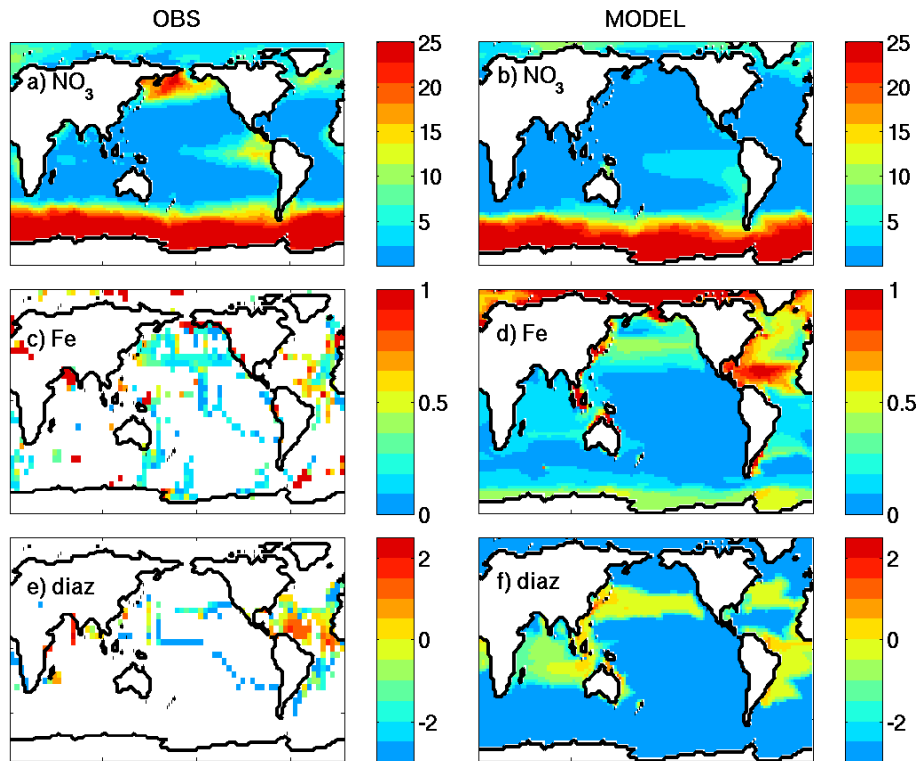


Fig. 1. Observations and Model over top 50 m: **(a)** World Ocean Atlas (Conkright et al., 2008) annual mean nitrate (mmol m^{-3}); **(b)** model pre-industrial annual mean nitrate (mmol m^{-3}); **(c)** composite of all iron measurement in top 50 m (nmol m^{-3}) from compilation of Tagliabue et al. (2012); **(d)** model pre-industrial annual mean iron (mmol m^{-3}); **(e)** composite of all diazotroph biomass measurement (log mg C m^{-3}) from compilation of Luo et al. (2013); **(f)** model pre-industrial annual mean diazotroph biomass (log mg C m^{-3}). Note that composites in **(c)** and **(e)** are made with all available data without regard to date, so do not represent annual mean.

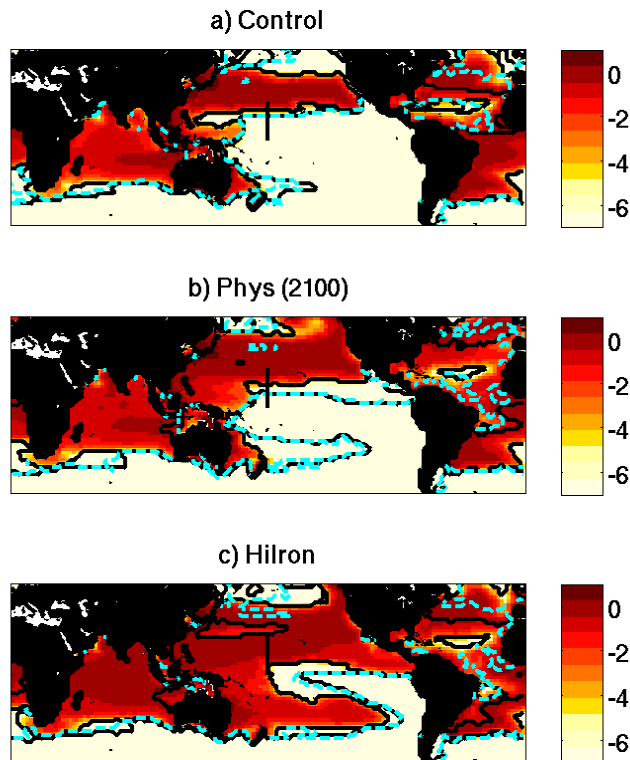


Fig. 2. Nitrogen Fixation rates ($\log gNm^{-2} yr^{-1}$, annual average) for **(a)** pre-industrial conditions (experiment *Control*); **(b)** 2100 conditions if physical fields, including ocean temperatures change in a business as usual emission scenario but with pre-industrial iron dust supply (experiment *Phys*); **(c)** conditions if physical fields remain as if for pre-industrial, but iron dust supply is doubled (experiment *Hilron*). Dashed blue line indicates where $\phi_{PN} = 1$ and $\phi_{FeN} = 1$ (discussed in Sect. 3.3). Black contours indicate the province boundaries in Fig. 3. Black line in Pacific indicates the transect show in Figs. 4 and 7.

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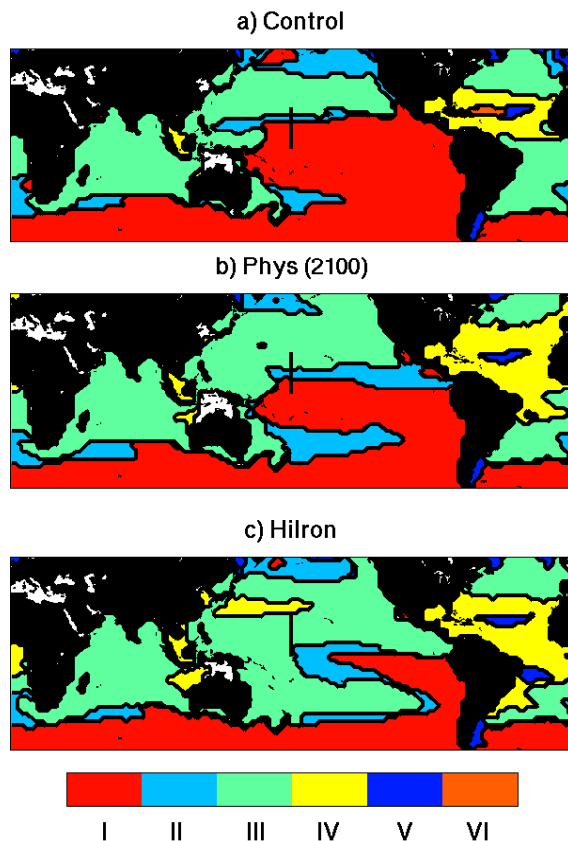


Fig. 3. Subtropical/tropical provinces in the numerical model, defined only by whether diazotrophs and non-diazotrophs co-exist and by which nutrient limits the phytoplankton (first three lines of Table 5) for (a) pre-industrial conditions (experiment *Control*); (b) *Phys* at 2100; (c) *Hi-Iron*. Note unshaded regions (except for Mediterranean which is not resolved in this setup) did not fit into the 6 province categories. Black line in Pacific indicates the transect shown in Figs. 4 and 7.

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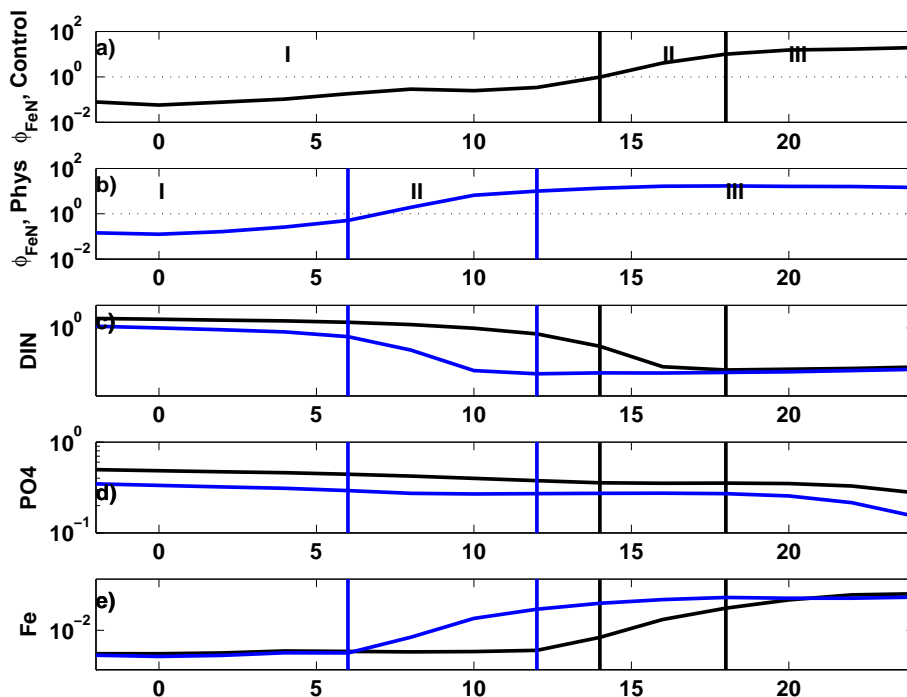


Fig. 4. Model output from Pacific transect shown in Fig. 3. **(a)** ϕ_{FeN} for control simulation; **(b)** ϕ_{FeN} for *Phys* simulation with changes from a warming scenario at 2100; **(c)** DIN (mmol m⁻³); **(d)** PO₄ (mmol m⁻³); **(e)** iron (μmol m⁻³). Vertical lines indicate province boundaries as determined only by presence or absence of diazotrophs, and limiting nutrient(s). Province are labeled (I, II, III). Black line indicate results from *Control*, and blue lines from *Phys*.

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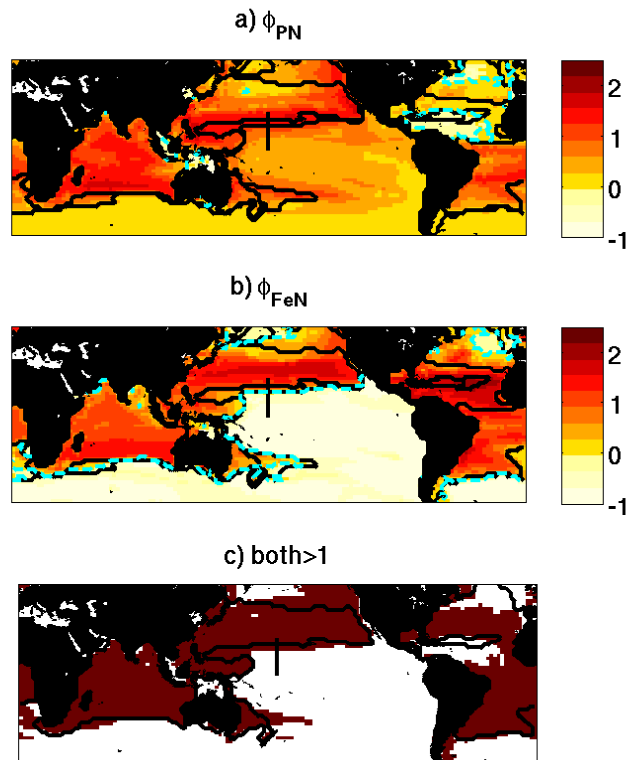


Fig. 5. (a, b) Nutrient supply ratios (log unitless, annual average) into the surface 100 m of the numerical model for pre-industrial conditions (experiment *Control*). **(a)** $\phi_{\text{PN}} = \frac{I_{\text{P}}^*}{R_{\text{NFB}} I_{\text{N}}^*}$ and **(b)** $\phi_{\text{FeN}} = \frac{I_{\text{Fe}}^*}{R_{\text{NFB}} I_{\text{N}}^*}$. Dashed blue line indicates where $\phi_{\text{PN}} = 1$ in **(a)** and $\phi_{\text{FeN}} = 1$ in **(b)**. Black contours indicate the province boundaries in Fig. 3a. Black line in Pacific indicates the transect show in Figs. 4 and 7. **(c)** Brown shaded region indicates where both $\phi_{\text{PN}} > 1$ and $\phi_{\text{FeN}} > 1$, minimum conditions needed to support diazotrophs. Black contour indicates region which do have diazotrophs (compare to Fig. 1f).

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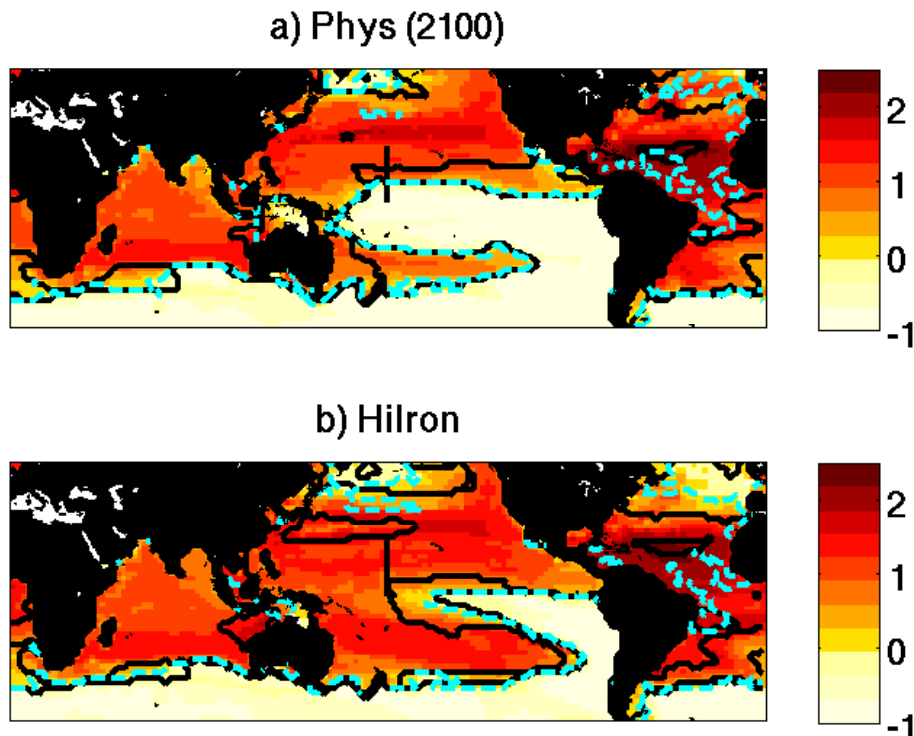


Fig. 6. Iron to nitrogen supply ratio, $\phi_{\text{FeN}} = \frac{I_{\text{Fe}}^*}{R_{\text{NFeB}} I_{\text{N}}^*}$ (log unitless, annual average) **(a)** 2100 conditions if physical fields, including ocean temperatures change in a business as usual emission scenario but with pre-industrial iron dust supply (experiment *Phys*); **(b)** conditions if physical fields remain as for pre-industrial, but iron dust supply is doubled (experiment *Hilron*). Black contours indicate the province boundaries in Fig. 3b and c. Dashed blue line indicates where $\phi_{\text{PN}} = 1$ and $\phi_{\text{FeN}} = 1$ in each experiment.

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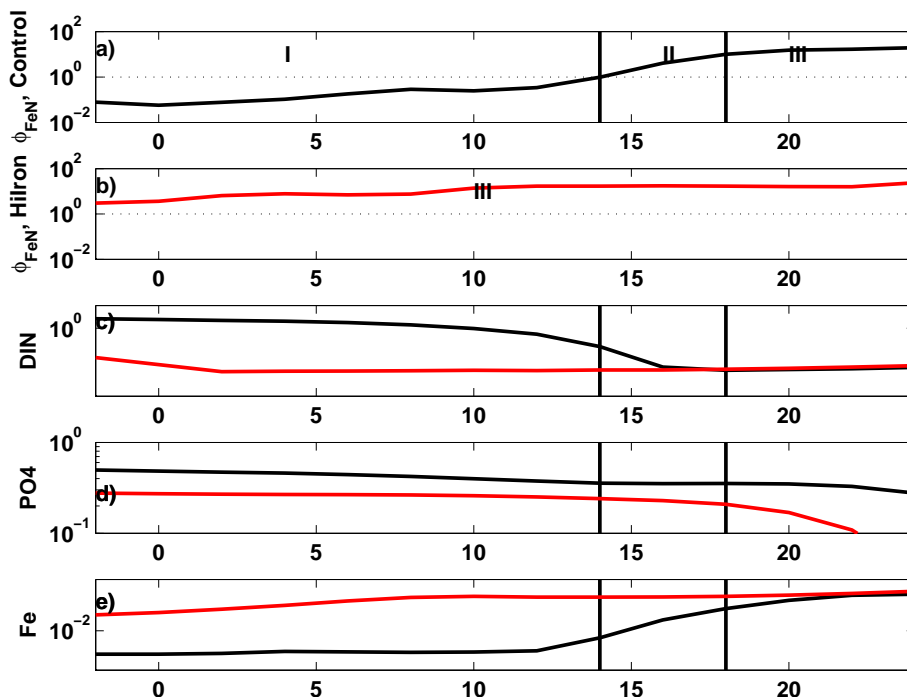


Fig. 7. Model output from Pacific transect indicated in Fig. 3. **(a)** ϕ_{FeN} for control simulation; **(b)** ϕ_{FeN} for *Hilron* simulation with changes from a warming scenario at 2100; **(c)** DIN (mmol m^{-3}); **(d)** PO_4 (mmol m^{-3}); **(e)** iron ($\mu\text{mol m}^{-3}$). Vertical line indicate province boundaries as determined only by presence or absence of diazotrophs, and limiting nutrient(s). Province labeled (I, II, III). Black line indicate results from *Control*, and red lines from *Hilron*.

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