

Review of “Oceanic enrichment of ammonium and its impacts on phytoplankton community composition under a high-emissions scenario” by P. Buchanan et al. for Biogeosciences

The manuscript by Buchanan and coauthors employs a physical biogeochemical model with an improved nitrogen (N) cycle representation to investigate the effect of climate change on the availability of different dissolved inorganic nitrogen (DIN) sources (mainly nitrate, NO₃ and ammonium, NH₄) to phytoplankton, and the consequences for phytoplankton diversity. They find that over most of the surface ocean the availability of NH₄ increases relative to NO₃, with a global mean ratio increasing from ~7% to 12% by the end of the century. The most significant changes are predicted in mid- to low-latitude regions. The model also projects a global decline in diatom biomass of about 3%.

We hasten to note that it is not diatom biomass that declines by 3%, but their relative abundance compared to nanophytoplankton.

By comparing model output with geochemical rate observations and analysis of Tara Oceans’s genomic dataset, the authors suggest that this shift towards higher NH₄/DIN ratio supports (1) an increase in regenerated production, and (2) a decrease in the relative abundance of diatoms, which are more dependent on NO₃, in favor of smaller phytoplankton groups (pico- and nano-phytoplankton) that are more reliant on NH₄.

As climate change reshapes the oceanic ecosystem, it is clear that there will be ecological winners and losers, but the outcomes remain highly uncertain, both in magnitude and patterns. Buchanan and coauthors approach this question from an interesting angle, focusing on shifts in the form of dissolved inorganic nitrogen and how these changes may affect phytoplankton diversity.

We sincerely thank the reviewer for their keen interest in the topic.

This is an interesting study that addresses a globally relevant topic through the use of a state-of-the-art model and a thoughtful analysis of observational data. The model projections and the analysis of the Tara dataset are stimulating and valuable, both on their own and when combined to support a mechanistic interpretation of the changes observed. In fact, the observational constraints presented here could easily become benchmark for future ocean biogeochemical models, particularly for evaluating their representation of DIN dynamics. For these reasons, I believe the study is appropriate for Biogeosciences, and I am ultimately supportive of publication.

We again sincerely thank the reviewer for their support of our work and the results presented herein.

However, the manuscript is dense with information, presenting several complex analyses and interpretations that are not always clearly or convincingly explained.

At times, I found myself wondering whether the results might be more effectively communicated if the study were divided into two separate papers: one focused on the present-day ocean and the role of NH_4/DIN in shaping phytoplankton communities, and another dedicated to future projections and their mechanistic interpretation. The narrative structure of the paper feels somewhat meandering, moving from future model projections and sensitivities to observational analyses, then to model-observation comparisons. This steadily introduces new amounts of information, and a series of new questions are raised halfway through the result section (notably in Section 3.3), increasing the complexity of the narrative. As reflected in my detailed comments below, while I found the study rich with interesting results, I often struggled to follow the logic of the explanations and interpretations— challenges compounded by the paper's structure.

We are thankful for the reviewer's thoughtful comments on how the narrative should be presented. In our revised version, we have added new sections to the methods and results that improve the clarity of the paper and that give more details to the modelling approach. Please see our more detailed responses below.

Furthermore, I am unconvinced by the more assertive interpretation that the modeled diatom decline reflects more intense competition for NH_4 , rather than the more straightforward effect of a general decline in NO_3 supply and concentrations—on which diatoms depend directly, given the model's DIN uptake formulation. To be fair, this interpretation is presented as a suggestion in multiple parts of the paper, and is not necessary for the paper to stand on its own, given the range of interesting results and analyses provided. For example, I find the phrasing of the abstract to be balanced, but many parts of the Results and Discussion present this idea with much less nuance. The authors themselves acknowledge at multiple points that it is difficult to disentangle the effects of an increase in NH_4/DIN from those of a decrease in NO_3 concentrations, and in my view there is no contradiction in proposing that diatom declines reflect both effects. I'm not sure one can simply isolate competition for NH_4 as the main driver of the changes observed — especially given how important circulation driven changes are on a point by point basis. NO_3 and NH_4 uptake occur in parallel and can jointly affect diatom and other phytoplankton.

As the reviewer says, we fully acknowledge the important role that NO_3^- declines have on diatom relative abundance at several places in the manuscript. However, we remain strong in our position that we have indeed isolated the effect of competition specifically for NH_4^+ on diatom relative abundance in our model experiments.

In the revised manuscript we have added a section dedicated to the N limitation formulation and described in more detail the modelling experiments, particularly `modelcompete`. These additions should provide the detail required to convince the reviewer and readers of the paper that we have indeed isolated the effect of

competition for NH_4 on the community composition of phytoplankton in our model experiments.

The new section called “Isolating the effect of competition for NH_4 reads:

Lines 187 – 237:

“2.2.2 Isolating the effect of competition for NH_4^+

A unique aspect of the PISCESv2 biogeochemical model is that it weights uptake of NH_4^+ over NO_3^- when both substrates are low, but as NO_3^- becomes abundant, the community switches towards using NO_3^- as a primary fuel (Fig. 2). This is achieved via

$$l_{\text{PFT}}^{\text{NH}_4^+} = \frac{[\text{NH}_4^+]}{[\text{NH}_4^+] + K_{\text{PFT}}^{\text{N}}} \quad (1)$$

$$l_{\text{PFT}}^{\text{NO}_x^-} = \frac{[\text{NO}_2^-] + [\text{NO}_3^-]}{[\text{NO}_2^-] + [\text{NO}_3^-] + K_{\text{PFT}}^{\text{N}}} \quad (2)$$

$$l_{\text{PFT}}^{\text{DIN}} = \frac{[\text{NH}_4^+] + [\text{NO}_2^-] + [\text{NO}_3^-]}{[\text{NH}_4^+] + [\text{NO}_2^-] + [\text{NO}_3^-] + K_{\text{PFT}}^{\text{N}}} \quad (3)$$

$$L_{\text{PFT}}^{\text{NH}_4^+} = \frac{5 \cdot l_{\text{PFT}}^{\text{DIN}} \cdot l_{\text{PFT}}^{\text{NH}_4^+}}{l_{\text{PFT}}^{\text{NO}_3^-} + 5 \cdot l_{\text{PFT}}^{\text{NH}_4^+}} \quad (4)$$

$$L_{\text{PFT}}^{\text{NO}_x^-} = \frac{l_{\text{PFT}}^{\text{DIN}} \cdot l_{\text{PFT}}^{\text{NO}_x^-}}{l_{\text{PFT}}^{\text{NO}_3^-} + 5 \cdot l_{\text{PFT}}^{\text{NH}_4^+}} \quad (5)$$

Where $K_{\text{PFT}}^{\text{N}}$ is the prescribed half-saturation coefficient for uptake of inorganic nitrogen for a given phytoplankton functional type (PFT); $[\text{NH}_4^+]$, $[\text{NO}_2^-]$, and $[\text{NO}_3^-]$ are the molar concentrations of ammonium, nitrite and nitrate; $l_{\text{PFT}}^{\text{NH}_4^+}$, $l_{\text{PFT}}^{\text{NO}_x^-}$ and $l_{\text{PFT}}^{\text{DIN}}$ are the michaelis-menten uptake terms for NH_4^+ , inorganic oxidised nitrogen (the sum of NO_2^- and NO_3^-), and DIN; and $L_{\text{PFT}}^{\text{NH}_4^+}$ and $L_{\text{PFT}}^{\text{NO}_x^-}$ are the growth limitation factors on NH_4^+ and inorganic oxidised nitrogen. In the above, the resulting $L_{\text{PFT}}^{\text{NH}_4^+}$ and $L_{\text{PFT}}^{\text{NO}_x^-}$ terms (Eqs. 4-5) are influenced by a factor 5 that is applied to $l_{\text{PFT}}^{\text{NH}_4^+}$. This assumes that NH_4^+ uptake is weighted five times more than oxidised inorganic nitrogen, which represents the well-established preference for growth on NH_4^+ (Dortch, 1990). However, as oxidised nitrogen (hereafter NO_3^-) becomes more abundant than NH_4^+ , the $L_{\text{PFT}}^{\text{NO}_x^-}$ term exceeds $L_{\text{PFT}}^{\text{NH}_4^+}$, meaning that phytoplankton switch to new production over regenerated production (see cross over points between solid and dashed lines in Fig. 2).

These dynamics are common to both PFTs: nanophytoplankton and diatoms (Fig. 2). However, a key difference is that the $K_{\text{PFT}}^{\text{N}}$ of diatoms is prescribed as 3-fold greater than that of nanophytoplankton, reflecting their greater average size. As a result, diatoms are always less competitive than nanophytoplankton for NH_4^+ and are less competitive for NO_3^- when NO_3^- is scarce. However, a low $l_{\text{PFT}}^{\text{NH}_4^+}$ for diatoms also results in a higher $L_{\text{PFT}}^{\text{NO}_x^-}$ as NO_3^- concentrations rise. This is evident in Figure 2, where growth by diatoms on NO_3^- (black solid line) overtakes growth by nanophytoplankton on NO_3^- (green solid line) as NO_3^-

becomes abundant. As a result, the model gives diatoms a competitive advantage over nanophytoplankton that accords with theorized growth advantages under high NO_3^- (Glibert et al., 2016a; Lomas and Glibert, 1999; Parker and Armbrust, 2005). Additionally, the switch from regenerated to new primary production occurs at much lower concentrations of NO_3^- for diatoms, aligning with fields studies that identify diatoms as responsible for the majority of NO_3^- uptake in the nitracline (Fawcett et al., 2011).

We sought to isolate the impact of competition for NH_4^+ and thus target the causative relationship between $\text{NH}_4^+:\text{DIN}$ and variations in PFT relative abundance. To do so, we repeated the set of experiments described above (All, Phys, Warm, OA and the preindustrial control) from years 1850 to 2100 but with an alternative parameterization where diatoms were made to have the same growth limitation on NH_4^+ as other phytoplankton, so that there was zero competitive advantage or disadvantage for NH_4^+ between these groups (i.e., making the dashed black and green lines in Figure 2 the same under all conditions). These simulations were completed with “model_{compete}” and were initialised from the same conditions as those done with the default parameterisation, which we call “model_{control}”. All other traits remained unchanged. Importantly, this included the competitive advantage of diatoms at high NO_3^- but also their competitive disadvantage at low NO_3^- (Fig. 2). In other words, when DIN was low, diatoms were equally competitive for NH_4^+ , but still suffered their unique limitations associated with NO_3^- , light, silicate, phosphate, and iron availability, as well as grazing pressure, and this isolated the direct effect of competition for NH_4^+ .

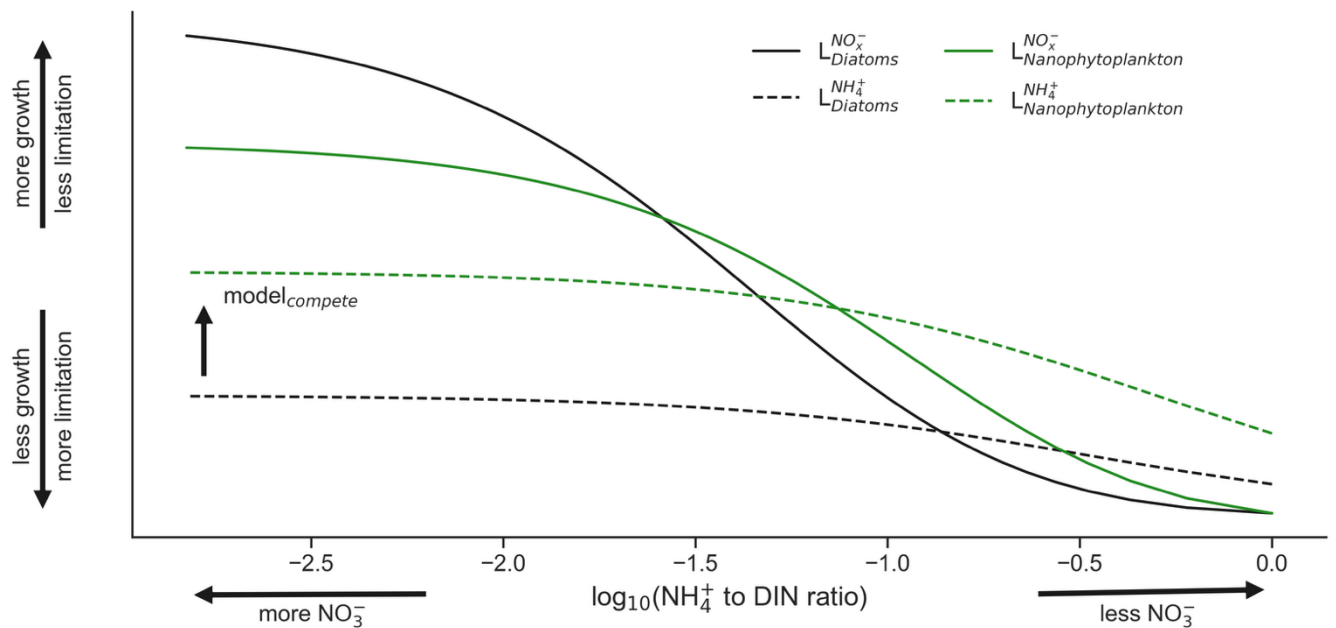


Figure 2. Limitation of the diatom (black) and nanophytoplankton (green) phytoplankton functional types (PFT) in the ocean-biogeochemical model by NO_3^- (solid lines) and NH_4^+ (dashed lines) as a function of the $\text{NH}_4^+:\text{DIN}$ ratio on a \log_{10} scale. Note that the nanophytoplankton PFT is always more competitive for NH_4^+ and is more competitive for NO_3^- when NO_3^- is low, while diatoms become more competitive for NO_3^- when NO_3^- is high.”

We sincerely hope that the review and other readers will be primed by this section to see that our modelling experiments have indeed isolated the effect of NH_4^+ on

phytoplankton community composition changes in our experiments.

Specific comments

Section 2.1: It is somewhat surprising that the model explicitly represents diatoms and nanoplankton, but not picoplankton, given the focus on competition between diatoms and cyanobacteria. The most abundant cyanobacteria in oligotrophic regions, *Prochlorococcus* and *Synechococcus*, fall within the picoplankton size range. But one could argue that the model's nanoplankton functionally encompasses both pico- and nano-plankton. A brief discussion of this issue and the potential limitations it introduces could be included.

We agree with the reviewer. We have included an additional sentence in this section:

Lines 114 – 116:

“While the model does not strictly represent picophytoplankton, implicit variations in the average cell size of the nanophytoplankton type affect nutrient uptake dynamics and may therefore encompass some functionality of picophytoplankton in oligotrophic systems (Aumont et al., 2015).”

The model description in the SI could be expanded for clarity. It would be helpful to include the equations for DIN uptake, as this is central to interpreting the results of decreased NO₃ supply and understanding the distinction between model_control and model_compete experiments. Additionally, including the temperature dependence formulations for phytoplankton and zooplankton growth and grazing would help interpreting the warming-only experiments.

We completely agree and we have included an entirely new section on N limitation parameterisation (see answer above). Regarding temperature-dependent growth, we have also included another sentence in the methods section:

Lines 168 – 172:

“In contrast, experiment “Warm” maintained the preindustrial climatological ocean state and atmospheric CO₂ at 284 ppm, but ensured that the ecosystem component saw increasing temperatures (T in °C) according to the RCP8.5 scenario, which scaled growth of phytoplankton types according to 1.066^T and heterotrophic activity (grazing and remineralisation) according to 1.079^T (Aumont et al., 2015).”

The Tara analysis appears biased by the use of observations from depths shallower than 10 m only (lines 171-172). This likely skews the results towards phytoplankton communities adapted to relatively low NO₃ and high NH₄, in particular in oligotrophic regions, where phytoplankton are commonly found down to 100-200 m depths. This seems like a potentially important limitation, and could benefit from discussion. To my knowledge (but I may be mistaken), Tara Ocean also collected data from deep chlorophyll maxima. Why not including those data in the analysis, or at least consider them in a separate analysis?

We thank the reviewer for raising this important point. We agree that phytoplankton communities in oligotrophic regions often extend well below 10 m, and that samples from the deep chlorophyll maximum (DCM) may provide ecologically distinct information. However, our decision to focus on near-surface samples (<10 m) was guided by several practical and conceptual considerations.

First, the number of Tara Oceans samples from the DCM is substantially smaller than from the near-surface layer, which would considerably reduce statistical power in a global analysis—particularly when stratifying by environmental gradients or when performing region-specific comparisons.

Second, with respect to the $\text{NH}_4^+:\text{DIN}$ ratio, DCM samples do not substantially expand the dynamic range of this ratio. In fact, $\text{NH}_4^+:\text{DIN}$ ratios at the DCM tend to be consistently low, due to the combined effects of lower NH_4^+ concentrations and elevated NO_3^- associated with the nitracline. In contrast, near-surface samples span a much broader and more variable range of $\text{NH}_4^+:\text{DIN}$ values, especially across horizontal gradients in nutrient supply and ocean productivity. This variability is essential for detecting statistically robust relationships between nitrogen substrate ratios and shifts in phytoplankton community composition. By taking the more numerous near-surface samples, we encompass the full range of $\text{NH}_4^+:\text{DIN}$ ratios.

We have added a statement to the revised manuscript clarifying this rationale and acknowledging the limitation explicitly.

Lines 387 – 389:

“We exclusively used the data sets corresponding to surface samples (5-9 m depth) because of greater sampling coverage in the Tara Oceans dataset, which accesses a broad range of $\text{NH}_4^+:\text{DIN}$ ratios spanning many ocean biomes/provinces.”

Section 2.5: the use of model-based fields in the analysis of observations makes me a bit uncomfortable, as it could introduce new, hard to control biases.

We completely share this sentiment because model fields are themselves highly uncertain, and as the reviewer states introduces new biases. Unfortunately, for the $\text{NH}_4:\text{DIN}$ ratio, NH_4 is incredibly scarce as it is a very difficult measurement to make. We must therefore rely on the model to produce fields that can then be used to test our hypotheses.

While we cannot fully address this comment because there is not an observational product with full global coverage of NH_4 , we do provide a new section at the beginning of the results that is a model-data assessment of NH_4 and $\text{NH}_4:\text{DIN}$ ratios in the ocean using the global dataset of NH_4 that was compiled for this study.

Lines 337 – 365:

“3.1 Assessment of modelled NH_4^+ and $\text{NH}_4^+:\text{DIN}$

Concentrations of $0.1 \mu\text{M}$ NH_4^+ or greater exist over continental shelves and in regions of strong mixing with high rates of primary production and subsequent heterotrophy. This accumulation of NH_4^+ in productive regions is reproduced by our model (Fig. 3a). In these eutrophic systems, high NH_4^+ co-occurs with high NO_3^- concentrations, so NH_4^+ makes a small contribution to total DIN (Fig. 3b). These regions include the eastern tropical Pacific, eastern boundary upwelling systems, the northwest Indian Ocean, the subpolar gyres and the Southern Ocean (although we note that the model underestimates NH_4^+ concentrations in the Southern Ocean). In contrast, low NH_4^+ concentrations of less than $0.05 \mu\text{M}$ pervade the oligotrophic gyres of the lower latitudes. As these regions also display very low NO_3^- concentrations, NH_4^+ makes up a much higher fraction of total DIN in both the observations and our model, with the NH_4^+ peak occurring deeper in the water column (Fig. S1).

Eutrophic upwelling systems and oligotrophic waters differed in the major sinks of NH_4^+ (Fig. 3c), consistent with available observations and constraints from theory. In eutrophic waters (here defined by surface nitrate $> 1 \mu\text{M}$), ammonia oxidation represented $49 \pm 29 \%$ (mean \pm standard deviation) of NH_4^+ sinks, but this dropped to $32 \pm 9 \%$ in oligotrophic systems. Measured rates of ammonia oxidation showed a positive relationship with surface NO_3^- concentrations and this was reproduced by the model (Fig. S2), indicating that ammonia oxidation was indeed a greater proportion of the overall NH_4^+ budget in eutrophic regions. In agreement, isotopic methods have shown that the bulk of nitrogen assimilated by phytoplankton in oligotrophic waters is recycled (Eppley and Peterson, 1979; Fawcett et al., 2011; Klawonn et al., 2019; Van Oostende et al., 2017; Wan et al., 2021), implying that most nitrogen cycling occurs without ammonia oxidation. Our model reproduces this feature of oligotrophic systems (Fig. 3c). Overall, the model shows good fidelity to the available observations of NH_4^+ concentrations, $\text{NH}_4^+:\text{DIN}$ ratios, and rates of NH_4^+ cycling that we compiled for this study (Fig. 3; Fig. S1-S2).

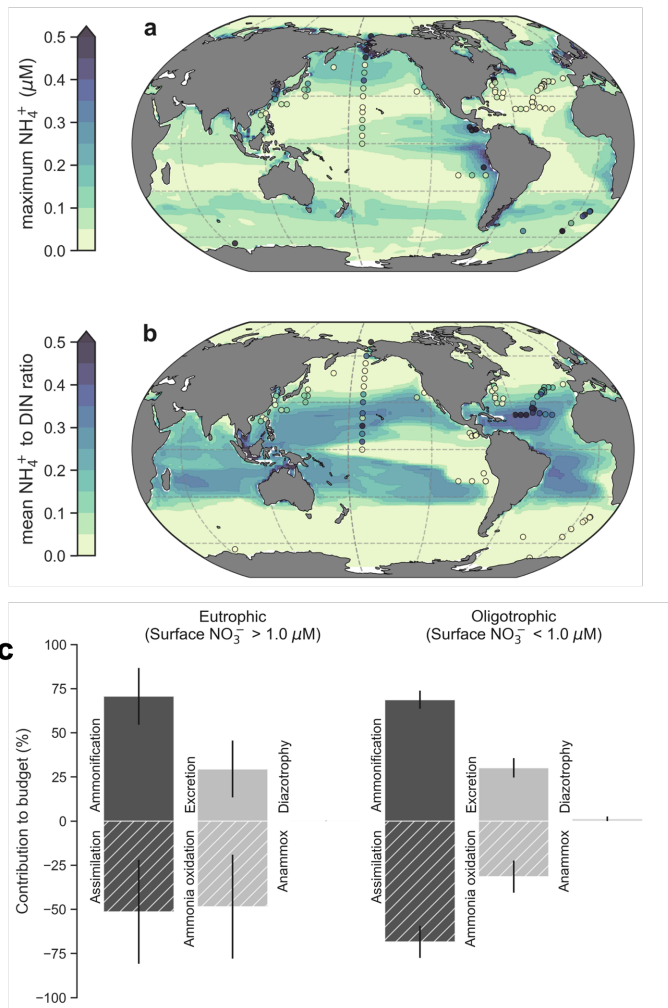


Figure 3. Global patterns of NH_4^+ concentrations, its contribution to DIN in the euphotic zone, and NH_4^+ budgets. (a) The simulated maximum NH_4^+ concentration within the euphotic zone. The maximum was chosen to emphasise basin-scale variations. (b) Average values of the $\text{NH}_4^+:\text{DIN}$ ratio. Modelled values are annual averages of the preindustrial control simulation between years 2081-2100. Observed values following linear interpolation between the surface and 200 metres depth are overlaid as coloured markers. Only those profiles with at least 3 data points within the upper 200 metres are shown. (c) Global mean \pm standard deviations of NH_4^+ fluxes separated into eutrophic and oligotrophic regions. Sources of NH_4^+ are represented by positive values and sinks by negative values.”

This additional section helps build confidence in the model, at the very least in the broad spatial patterns seen across the open ocean.

Figure 2: I suggest including panel S1b, showing present-day NH_4/DIN ratios with observations, in Fig. 2. This would reassure the reader that the model captures the basic N distribution patterns, and would help contextualize the changes shown in panel 2a (e.g., is a change by 10% large or small?) The text too could be more explicit, e.g., line 218, increase by 6%, could specify “from X% to Y%”.

Please see answer above, as we have brought Fig. S1 into the main paper (now Fig.

3). We also added more explicit values of NH_4 :DIN changes.

Lines 368 – 371:

“By the end of the 21st century (2081-2100), NH_4^+ :DIN is projected to increase in over 98% of the upper ocean euphotic layer (Fig. 4a). On average (\pm standard deviation), the fraction of DIN present as NH_4^+ increased by 6 ± 6 % from a preindustrial average of 11.5 ± 11.0 % to 17.5 ± 14 %, with enrichment exceeding 20% in regions with pronounced DIN gradients, such as at the boundary between eutrophic and oligotrophic regimes.”

Lines 219-220: it would be interesting to report the % regenerated primary production and its change.

Great idea. We have included this in our revised manuscript.

Lines 371 – 374:

“The enrichment of NH_4^+ caused an expansion of regenerated production across the ocean, such that NH_4^+ overtook NO_3^- as the main nitrogen substrate for phytoplankton growth in an additional 10% (73% to 83%) of the ocean’s area. Regenerated production also increased as a proportion of net primary production from 60% to 63%.”

The parameterizations for the pH dependence of ammonia oxidation are not well explained. What is the rationale behind including this pH dependence, and how were the specific functional forms shown in Fig. S5 and S7 chosen? Is it as simple as making the rate inversely proportional to the H^+ concentration? (This seems the implication of the formulation invoking the pKa of NH_4 dissociation.) What about the alternative formulation? The SI provides too little detail on these points, and more thorough explanation would help readers understanding the models sensitivities.

We agree with the reviewer that this was not communicated well in the previous version. In our revised manuscript, we have made efforts to communicate the pH effect on ammonia oxidation more explicitly, explaining that this relationship is data constrained.

Lines 172 – 175:

“Experiment “OA” held the circulation and temperature effects on metabolism constant but involved the historical and future projected increase in atmospheric CO_2 . This decreased pH and negatively affected rates of ammonia oxidation at a rate consistent with field measurements (Beman et al., 2011; Huesemann et al., 2002; Kitidis et al., 2011), specifically a loss of ~20% per 0.1 unit decrease in pH below 8.0 (Fig. S1).”

Lines 387 – 389:

“To accommodate some of this uncertainty, we performed an idealized experiment with a weaker relationship between pH and ammonia oxidation that still fit the measurements well but that enforced a 10% decline in ammonia oxidation per 0.1 pH decline rather than 20% (Fig. S6).”

Line 238-240, “in eutrophic regions, where coincidentally, shifts from low to higher $\text{NH}_4\text{:DIN}$ would have the greatest ecological impact”: This could be clarified. The phrasing is a bit confusing, as eutrophic regions are typically characterized by high NO_3 concentrations. If NH_4 becomes more dominant in these areas, does that imply they are no longer eutrophic? Or is the point that even in nutrient-rich waters, a shift in the form of available DIN from NO_3 to NH_4 could significantly affect community structure?

It is indeed the latter point you raise. We have clarified the sentence and logic. Thank you.

Lines 391 – 394:

“Thus, whether pH declines have a strong or weak effect on ammonia oxidation did little to change $\text{NH}_4^+\text{:DIN}$ ratios in eutrophic regions where NO_3^- is abundant and where diatoms represent a larger proportion of the phytoplankton community, and where coincidentally, shifts from low to higher $\text{NH}_4^+\text{:DIN}$ would have the greatest impact on community composition.”

Section 3.2, lines 258-270. The authors make the point that loss of diatoms was “driven by a combination of stimulated microbial metabolism (60%) and physical changes (40%), while ocean acidification had negligible effects”. While this may be accurate at a global mean level, it risks giving the misleading impression that increased microbial metabolism is the dominant driver of diatom loss across the ocean, as compared to decreased NO_3 supply. But it is not true almost anywhere in the ocean, where on a local basis (Fig. S8) changes due to NO_3 supply (or light availability at high latitudes) greatly exceed the low, but consistently negative effects of warming on metabolism. But because physical effects on nutrient supply and light availability are both positive and negative, they tend to cancel out when averaged globally. This distinction between local drivers and global mean effects is not clearly conveyed in the current discussion and should be more explicitly emphasized.

The reviewer is right to point out that the declines in diatoms on a regional sense are driven largely by declines in NO_3^- caused by physical changes (Fig. S7). We have rewritten this paragraph to pay homage to this important effect:

Lines 467 – 483:

“Our climate change simulations projected a future decline in the relative abundance of diatoms globally by an average of 3%, while local declines in the subantarctic, tropical, North Atlantic, North Pacific and Arctic Oceans sometimes exceeded 20% (Fig. 5a,b; Fig. S7). Our sensitivity experiments enabled an attribution of the major drivers, at least in a coarse-grained sense. At a global scale, the loss of diatom representation within marine communities in our model was driven by a combination of stimulated microbial metabolism (60% of full response in experiment “All”) and physical changes (40% of full response in experiment “All”), while ocean acidification had negligible effects (Figure 5c; Fig. S7). Ocean acidification had negligible effects because it largely raised $\text{NH}_4^+\text{:DIN}$ ratios in oligotrophic subtropical gyres where diatoms were already of low proportion (Fig. 4c; Fig. S5). Averaged across the low latitude ocean (40°S – 40°N), diatoms also declined by an

average of 3% driven by the same factors (60% microbial metabolism and 40% physical changes), while more dramatic but very regional declines of diatoms near or exceeding 20% were due primarily to physical changes (Fig. S7). These global and regional declines have been predicted previously and are widely accepted to be due to a decline in bulk nutrient availability in the upper ocean (Bopp et al., 2005), although the large effect of stimulated metabolism here suggests that top-down grazing pressure, which is accelerated by warming, may also play a role (Chen et al., 2012; Rohr et al., 2023). That said, stimulating metabolism also increases phytoplankton nutrient demand, which eventually leads to greater DIN limitation (Cherabier and Ferrière, 2022). We indeed appreciate that the reduction of diatoms from phytoplankton communities as simulated by models is due to nutrient losses, in particular declines in NO_3^- (Kwiatkowski et al., 2020), and our simulations here, at least indirectly, are no different, since both nanophytoplankton and diatom biomass declined.”

Lines 272-282. I find this paragraph unconvincing in its current framing. Since diatoms preferentially take up NO_3^- (given the DIN uptake formulation), it seems straightforward that a decline in NO_3^- supply and concentrations would reduce diatom production and abundance, without the need to shift the emphasis to increased competition for NH_4^+ , which would be a consequence of the change. The reduction in NO_3^- and the resulting increased reliance on (and potential competition for) NH_4^+ seem more like two sides of the same coin, rather than distinct mechanisms. I'm not sure that NH_4^+ competition is the most correct or useful framework for interesting the model changes. The authors end the paragraph by stating: “when NO_3^- concentrations decline, competition for NH_4^+ increases, and declines in diatom relative abundance follow”. But is the middle step, “competition for NH_4^+ increases”, strictly necessary to explain the decline in diatoms? It might be more parsimonious to attribute the decline directly to reduced NO_3^- availability. We hope that the new section (2.2.2 “Isolating the effect of competition for NH_4^+ ”) already shown in our answer above clarifies why our experiments isolate the effect of competition for NH_4^+ . We do not argue against the reviewer that NO_3^- is important, but we do state that the declines in NO_3^- are important indirectly in that it preconditions intense competition for NH_4^+ , which is the direct cause of 70% of the diatom declines in relative abundance. Our experiments with `modelcompete` isolate this effect of NH_4^+ competition.

The analogy (lines 277-278) should help understanding, here I found it confusing. If nutrients represent the volume in the bathtub, why is productivity described as the inflow? Productivity removes nutrients, it doesn't add them. And why is recycling represented as the outflow? Conceptually, recycling returns nutrients to the system. Also, at steady state, one would expect inflow and outflow to be in balance. This needs some rethinking or clarification.

We agree that the previous sentence was confusing, and we have rewritten this sentence.

Lines 490 – 491:

“This is akin to the bathtub analogy, where different volumes (i.e, nutrient concentrations)

can result by varying the inflow (i.e., recycling) even when the outflow is constant (productivity)."

Lines 291-294, "It is therefore possible that reductions in NO₃ and resulting competition for NO₃ was a major contributor to the losses of diatoms from the phytoplankton community in our simulations". This seems like a straightforward explanation for diatom decline, given diatom's functional dependence on DIN forms and the NO₃ declines. But its placement here appears to undercut the argument made a few paragraphs earlier that emphasized competition from NH₄.

This sentence has been removed.

Lines 294-304, the model_compete experiment is interesting, but I see it more as highlighting another side of the same coin, rather than challenging the idea that declining NO₃ is the primary driver of diatom decline. Of course if diatoms had a stronger affinity for NH₄, they would fare better under reduced NO₃. But this doesn't change the underlying cause of their decline, which still originates from the reduction in NO₃.

We agree completely with the reviewer. The loss in NO₃⁻ preconditions the community to compete for NH₄⁺. Thus NO₃⁻ losses are a cause of diatom losses, but are in part an indirect cause, since our experiments show that if diatoms were competitive for NH₄⁺ they would fare much better. We hope that the new detail, in particular section 2.2.2, has clarified this point.

Also, please see our responses below with regard to this issue.

Line 311, "Physical changes no longer exerted a global negative effect on their total nor relative abundance". The global mean masks large regional variability, where large positive and negative changes partially compensate each other. As shown in Fig. S8, physical changes are the main local driver, especially in the Southern Ocean, and in fact, across much of the ocean on a point-by-point basis. This nuance should be acknowledged more clearly.

We agree with the reviewer and have added a clause to this sentence to add nuance to the sentence.

Lines 561 – 563:

"Physical changes, while important regionally, no longer exerted a global negative effect on their total nor relative abundance (blue line in Fig. 5f), while the negative effect of elevated microbial metabolism on relative abundance was ameliorated by 25% (Fig. 5f; Fig. S7-S8)."

Lines 238-240, "determined that a large fraction of the projected declines in diatom relative abundance are due to their competitive exclusion by other phytoplankton in regions where NH₄ becomes more important as a nitrogen source": I am unconvinced that the authors have "determined" that the diatom decline is caused by competitive exclusion, and not by the overall decline in NO₃.

We can attribute this decline in the modelled diatom relative abundance to

competition for NH_4^+ and their competitive disadvantage in this respect, at least in the model, due to our sensitivity experiments with `modelcompete`.

Section 3.3.1 and Fig. 4: this section provides a stimulating and valuable set of analyses and diagnostics that could serve as a useful benchmark for models. More ocean biogeochemical models should adopt this type of diagnostic approach as a standard practice for evaluating nutrient dynamics and phytoplankton competition. We are pleased that the reviewer also values this analysis highly.

Lines 369-371: does it matter than in PISCES the half saturation constants for DIN uptake are not constant but a function of the phytoplankton biomass P ? What are “typical conditions”? To help the reader, the DIN uptake functional forms used by the model should be presented in the SI.

The reviewer is right that the half-saturation coefficients for diatoms and nanophytoplankton are not static but change as a function of phytoplankton biomass as a way to capture changes in the community mean cell size. However, since diatoms half-saturation coefficients are prescribed as being 3-time greater than nano-phytoplankton, they are always greater, meaning that the unique N limitation parameterisation now shown in Fig. 2 will always be the case. We have presented the N limitation functional forms now in section 2.2.2.

Section 3.3.2: this is a stimulating analysis—though at times it felt substantial enough to warrant its own standalone paper. Figures S10-S16 are rich with interesting information, but also dense. I wonder if “goodness of fit” metrics (some of which may be reported in Table S1?) could be included directly on the figures, so that the reader can quickly evaluate the skill of different models.

We agree with the reviewer and thank them for their positive and constructive comments about this analysis, which we also see as highly valuable. All goodness of fit information is indeed presented in Table S1, which the reader will be able to reference. An easy way to understand if a relationship is significant is whether the confidence intervals do not include zero. For example, in Fig. S9, Silicic acid has no significant predictive power for diatom relative abundance for both the 18S rRNA and *psbO* gene counts, but $\text{NH}_4^+:\text{DIN}$ does. We refer the interested reader to Table S1 for the actual degree of significance and the amount of deviance explained by the predictor in question.

Fig. 5: I got a bit lost in the interpretation of the figure. Not being familiar with GAMs, I am confused by the y-axis, “GAM residuals”, which could be clarified. Also, related to the threshold of 4%; in Fig. 5 nothing specifically makes the 4% threshold stand out. The text points to “rapid losses of diatoms as $\text{NH}_4^+:\text{DIN}$ became greater than 4%”, but I struggle to see anything special in this threshold, and overall it seems an arbitrary choice.

We added two new sentences to the legend in Figure 7 explaining what the GAM residuals mean and also why a 4% threshold was chosen.

Lines 819 – 820:

“When GAM residuals are positive this suggests that diatoms do better than predicted by a GAM without the $\text{NH}_4^+:\text{DIN}$ ratio as a predictor, and vice versa.”

Lines 823 – 824:

“The vertical dotted line delineates when NH_4^+ is 4% of DIN, which aligns with the point at which community primary production switches from predominantly NO_3^- -fuelled to NH_4^+ -fuelled (Fig. 6).”

We also point the reviewer to this sentence *“This threshold, where NH_4^+ becomes 4% of total nitrogen stocks, aligned with the point at which primary production becomes dominated by regenerated production (Fig. 6).”* Starting on line 841.

Lines 449-453: points (1) and (3) are general knowledge; point (2) could be as well phrased as “how diatoms are outcompeted as less primary production is fueled by external NO_3 inputs”, which would actually be closer to the mechanistic changes at play.

We agree and have changed this sentence in line with the reviewer’s suggestion.

Section 3.3.4, “The confounding effect of NO_3^- ”: framing the role of NO_3 as a confounding factor underplays its central role in controlling diatom growth, and seems an example of reverse causation and post hoc reasoning. Given the well-established importance of physical changes on NO_3 supply across the ocean, reductions in NO_3 should be taken as the default or “null” mechanisms to explain the diatom declines, rather than a confounding effect. The fact that the whole statistical analysis could be based on NO_3 instead of $\text{NH}_4:\text{DIN}$ as a covariate seem to undermine the entire argument made here.

We agree with the reviewer that NO_3^- is indeed important in that its loss from the environment forces the phytoplankton species to compete for NH_4^+ . We also agree that the loss of NO_3^- and increased competition for NH_4^+ are “two sides of the same coin”, so to speak. And we do hope that this is made clear in our revised manuscript.

We do, however, remain loyal to what the $\text{model}_{\text{compete}}$ results tell us, which is that competition for NH_4^+ is the more direct cause of much of the diatom declines. This detail should be clearer in our revised manuscript due to the addition of section 2.2.2.

In this section and the revised results sections we show that NO_3^- concentrations can (and do!) decline in the experiments conducted with both $\text{model}_{\text{control}}$ and $\text{model}_{\text{compete}}$, but the only difference is that competition for NH_4^+ disadvantages diatoms ($\text{model}_{\text{control}}$) or it doesn’t ($\text{model}_{\text{compete}}$). The model output from our

experiments is therefore clear in this regard. We note here for clarity that we do not discount at any stage the importance of other processes, nutrients, etc., which is evident in our discussion of the changes in diatom relative abundance in the Southern Ocean (Lines 570-575), and we fully acknowledge the importance of these other drivers in our discussion of the results.

We have renamed this section “The indirect effect of NO_3^- ” and we have edited it in the revised manuscript to more clearly communicate the points above.

Lines 862 – 881:

“We fully acknowledge that $\text{NH}_4^+:\text{DIN}$ ratios covary strongly with NO_3^- concentrations. Most of the projected increases in $\text{NH}_4^+:\text{DIN}$ we report here are due to circulation changes that limit NO_3^- injection from subsurface waters into surface waters (Fig. S5). Also, our GAM analysis of the Tara Oceans data could easily be replicated by replacing the $\text{NH}_4^+:\text{DIN}$ ratio with NO_3^- concentration as a key predictor. Indeed, this analysis showed similar results, with NO_3^- being an equally strong predictor of diatom relative abundance as $\text{NH}_4^+:\text{DIN}$. We therefore cannot discount a direct effect of NO_3^- on diatom relative abundance in the Tara Oceans observations.

*In our biogeochemical model, however, we can diagnose whether diatom relative abundance changes are directly due to competition for NO_3^- or NH_4^+ . This allows us to assess whether NO_3^- concentration or the $\text{NH}_4^+:\text{DIN}$ ratio are more appropriate as a predictor of diatom relative abundance. The importance of NH_4^+ is exemplified by the fact that the negative relationship between $\text{NH}_4^+:\text{DIN}$ and diatom relative abundance was reversed in *model_{compete}* (black dotted line in Fig. 7a). Now positive rather than negative, this relationship differs statistically from that predicted from Tara Oceans data (Figure 7b-e).*

*This suggests that competition for NH_4^+ directly controls diatom relative abundance in our model. We fully acknowledge that a scarcity of NO_3^- is a major cause of NH_4^+ enrichment in our experiments because it drives competition for NH_4^+ . However, we wish to emphasize that a potentially important mechanism of diatom decline in the community is due to their poor competitive ability for growth on NH_4^+ , not directly because of decreases in NO_3^- . Decreases in NO_3^- certainly affect diatom growth, but, in our model, they mostly do so indirectly by shifting the regime towards intense competition for NH_4^+ . Given the statistical similarity between the in situ (Tara Oceans) and in silico (*model_{control}*) relationships (Fig. 7) and the dissimilarity in *model_{compete}*, this points to $\text{NH}_4^+:\text{DIN}$ as a key underlying driver of diatom relative abundance in the world ocean.*”

Line 473, “We therefore suggest that competition for NH_4 directly controls diatom relative abundance”: this feels like a forced interpretation and a leap that is not fully supported by the evidence presented.

Please see above response.

Line 477-478, “Decreases in NO_3 certainly affect diatom growth, but we propose that they mostly do so indirectly by shifting the regime towards intense competition for NH_4 .” Another sentence that seems to overstate the authors’ interpretation

without enough supporting evidence, given the direct role of NO_3 in diatom growth, which is explicitly built into the model's functional formulation.

Please see above response.

Line 486-487, "but we recast the attribution of change in terms of competitive exclusion for NH_4 , rather than bulk nutrient declines": see above.

Please see above response.

Technical comments:

Line 66, "become a self-sustaining regime": I would rephrase, partly because the message is a bit unclear, partly because it is hard to imagine a case where primary production in the euphotic zone does not involve an external supply of NO_3 , even in the most oligotrophic regions (where export still occurs and must be ultimately balanced by external nutrient supply).

Line 68 :

"Due to the intense competition for NH_4^+ and resulting shifts towards smaller phytoplankton taxa that are more rapidly recycled in the upper water column, the relative enrichment in NH_4^+ may become a self-sustaining regime unless new inputs of NO_3^- are sufficient to reverse it."

Line 45, "which would work to use up ..." this sentence is a bit obscure, please clarify.

Line 46 – 49:

"One theory posits that their ecological success in turbulent, high NO_3^- environments (Margalef, 1978) may be due to a capacity to store NO_3^- in their vacuoles and then rapidly reduce it when they experience sudden increases in light, which would position diatoms to rapidly consume any excess reductant that would otherwise retard growth (Glibert et al., 2016a; Lomas and Glibert, 1999; Parker and Armbrust, 2005)."

Line 65, "there are numerous localized studies that showcase how phytoplankton taxa shift in response to changes in the composition of DIN": it would be useful to add some references for these studies.

Added.

Line 74: remove repeated "enrichment".

Removed.

Line 129, "defined as those depths where total phytoplankton biomass was greater than 0.1 mmol C m⁻³." This is a bit of an unorthodox definition of euphotic zone, perhaps clarify the rationale and reassure it is generally in line with other common light-based definitions (typically, 1% light levels)

We have changed this from euphotic zone to "upper ocean where primary production is active".

Lines 181 – 183:

"We calculated changes at each grid cell by averaging over the upper ocean where primary

production was active, which was defined as those depths where total phytoplankton biomass was greater than $0.1 \text{ mmol C m}^{-3}$.

Lines 146-149: here a relevant reference could be Tang, et al., 2023, Earth System Science Data, which presents a compilation of nitrification rates. (Presumably data used there and compiled in Tang et al. overlap.)

We agree. We, however, didn't use the Tang dataset because our study predates this dataset.

Line 151, I appreciate the authors reporting the units for primary production; for consistency, they could be added for the other major variables discussed (e.g., ammonia oxidation rates).

Rectified.

Line 194: maybe provide some more detail on the spline approach. What is k , in $k=3$? What is "spline complexity"? Etc.

We have provided a greater description regarding these choices:

Lines 296 – 326:

"Where Y is the predicted response, α is the intercept, $s_n(x_n)$ represents a smooth function (specifically the n^{th} thin-plate spline) fitted to the n^{th} predictor variable x_n , and ε is the model error. Thin-plate splines are flexible and widely used as a smoothing method within GAMs that allow for non-linear relationships between predictors and response variables and do not require specificity around a functional form. They are well suited to handling ecological data where relationships are often non-linear and non-parametric. Predictor variables were mixed-layer depth (m), phosphate (μM), silicate (μM), dissolved iron (μM), and the $\text{NH}_4^+:\text{DIN}$ ratio. Mixed layer depth, phosphate and silicate was measured in situ at the sample locations of Tara Oceans, while dissolved iron and $\text{NH}_4^+:\text{DIN}$ ratios were provided by the model at the same location and month of sampling, since measurements of these properties are scarce. In addition, phosphate and silicate concentrations were available as interpolated products from the World Ocean Atlas (Garcia et al., 2019). An alternative estimate of $\text{NH}_4^+:\text{DIN}$ ratios was provided by the Darwin model (Follows et al., 2007). Predictor variables from models and World Ocean Atlas were extracted at the locations and months of sampling and different combinations of in situ and modelled variables were used to build GAMs. Mixed-layer depth, nutrients (phosphate, silicate and $\text{NH}_4^+:\text{DIN}$) and the relative abundance of phytoplankton taxa were \log_{10} -transformed prior to model building to ensure homogeneity of variance.

Before model testing, we calculated the variance inflation factors (VIFs) of independent variables to avoid multi-collinearity. All covariate VIFs were < 3 , which indicates minimal multicollinearity. GAMs were computed using a low spline complexity ($k = 3$) that prevented overfitting and constrained the smooth functions represent only broad-scale trends in the data."

Line 289: "thid" → "this".

Corrected.

Line 307: should the reference be to Fig. 3e?

Yes. Now it is referenced to Fig. 5d-f.

Line 322, "by the in the", remove "in the".

Corrected.

Line 356: since the exponent is fractional, I would call the function a "fractional-order" Monod function, not a quadratic (where the implied exponent is 2).

Corrected.

Lines 358-359: add the units for the half saturation constants.

Added.

Line 493: "albiet" → "albeit".

Corrected

- Line 496: "ellaboratiung" → "elaborating".

Corrected

Fig. S1 could also show total DIN, so that one has a complete view of the controls on the NH₄/DIN ratio distribution.

This is now Fig. 3 in the main text. We thank the reviewer for the suggestion, but maintain our presentation of NH₄ and the NH₄:DIN ratio, since with these two pieces of information it is possible to understand DIN.

Fig. S8, right column: I'm confused by the units, the values go up to 0.2, but the units say %. Shouldn't Fig. S8c be the same as S3a, where value go up to 20%? The figures also look a bit different, but perhaps it's the contouring that make them look different.

Corrected the units. The reviewer is right and this was a typo.