

# ***Author's response to Anonymous Referee #1 for*** **Variable C/P composition of organic production and its effect on** **ocean carbon storage in glacial model simulations**

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## **1 Introduction**

In this document, referee comments are shown in ***bold and black italics***, and author's discussion response directly below in plain black. For each author's response, the corresponding changes in the manuscript are shown in **blue**.

## **2 General comments**

- 5 – ***Introduction: It might be good to add a sentence detailing the evidence for lower terrestrial carbon storage during glacial times (p2, L.1).***

We agree and will add to the introduction: *Studies of paleoproxy records indicate that carbon storage in the glacial terrestrial biosphere was smaller compared to in interglacial climate* (Shackleton, 1977; Duplessy et al., 1988; Curry et al., 1988; Crowley, 1995; Adams and Faure, 1998; Ciais et al., 2012; Peterson et al., 2014).

- 10 *Added to p. 2, L. 2-5: In addition, studies of paleoproxy records indicate that carbon storage in the glacial terrestrial biosphere was smaller compared to in interglacial climate* (Shackleton, 1977; Duplessy et al., 1988; Curry et al., 1988; Crowley, 1995; Adams and Faure, 1998; Ciais et al., 2012; Peterson et al., 2014).

- ***Section 2.3.1: It would be good to precise whether the wind changes impact the air–sea gas exchange of CO<sub>2</sub>.***

Yes. In cGENIE, gas transfer velocities are calculated as a function of wind speed (described in Ridgwell et al. (2007), and following Wanninkhof (1992)). We will add this information to Section 2.3.1.

- 15 *Added to p. 6, L. 24-26: In cGENIE, gas transfer velocities are calculated as a function of wind speed (described in Ridgwell et al. (2007)), and following Wanninkhof (1992). Consequently, weaker winds also lead to reduced gas exchange with the atmosphere.*

- **Methods and section 3.2.1: If I understand correctly global salinity is not increased during glacial times. If correct, it might be good to clearly state it as well as its impact on solubility changes.**

This is correct. We do not aspire to simulate a full glacial state, but rather to explore the effect of flexible C/P for biological carbon capture in response to a few common glacial forcings. As we do not change salinity, we are likely to overestimate the increase in solubility between *Ctrl* and *GL<sub>comb</sub>*, by  $\sim 6$  ppm (Kohfeld and Ridgwell, 2009). This effect is consistent for any choice of C/P parametrisation, and is therefore not explored further. We will add this information to Section 3.2.1.

Added to p. 11, L. 16-18: *As we do not change salinity, we are simultaneously likely to overestimate the increase in solubility between Ctrl and a glacial-like state, by  $\sim 6$  ppm (Kohfeld and Ridgwell, 2009). This effect is consistent for any choice of C/P parametrisation, and is therefore not explored further.*

- **Section 3.2.3: p. 10, L. 29: Please quantify magnitude and direction of “small”.**

We will clarify the sentence by changing it to: *Increases in RLS cause very small, but global, decreases in surface  $PO_4$  concentrations (global average anomaly =  $-0.016 \mu M$ ) [...]*

Sentence, now on p. 12, L. 8-9, has been changed to: *Our changes in RLS cause very small, but global, changes in  $PO_4$  concentrations (global average anomaly =  $-0.016 \mu M$ ,  $RLS \times 1.25$  in Fig. 7 c), [...].*

- **Section 3.2.3: p. 11, L. 3–4: This is an interesting result that should be emphasized.**

We add here: *The potential implications of this result for warm climate scenarios is further discussed in Section 4.1.*

The suggested change was added to Section 3.2.3, now on p. 12, L. 14-15.

In Section 4.1, we add: *Our sensitivity experiments  $RLS \times 0.75$  and  $RLS \times 1.25$ , reveal that the response in  $pCO_2^{atm}$  to the perturbation is enhanced in GAM compared to RED for both increased and decreased RLS. While increased RLS would be an effect of ocean cooling, and thus of interest for glacial studies, reduced RLS would be a consequence of ocean warming (Matsumoto, 2007). Matsumoto (2007) describes how decreased RLS would have a positive feedback on  $pCO_2^{atm}$  in future warming climate. Our results imply that flexible C/P could have a further re-inforcing effect on this feedback. It would therefore be of interest to apply a parametrisation of flexible C/P in models used for simulations of future climate feedbacks. The suggested text was added to Section 4.1, p. 16, L. 4-9.*

We also add the following sentence to Conclusions: *Flexible C/P also has the potential to be an additional positive feedback of ocean warming on  $pCO_2^{atm}$  in future climate. The suggested text was added on p. 21, L. 5.*

- **Section 3.2.3: p. 10, L. 31–32: This sentence is unclear.**

We suggest clarifying this sentence by changing it to: *Experiments with deeper RLS in 121 ( $RLS \times 1.25_{121}$  and  $RLS \times 1.75_{121}$ ), suggest that about 40 % of the observed differences in  $pCO_2^{atm}$  between GAM and RED can again be attributed to the difference in export flux average C/P.*

As suggested by both referees, all information about experiments with the model version 121 has been moved to Section 4.4 (p. 18). Here, the suggested sentence proved to be redundant, and the information is instead conveyed in the sentence

*[...] the simulations with 121 indicate that, depending on the change in forcing, between 1/3 and 2/3 of the difference in drawdown between RED and GAM is due to the difference in average C/P between the control states (Fig. 6, Table S.2).’, found on p. 18, L. 31-33.*

– **Section 3.2.4: p. 11, L. 11: Shouldn’t iron fertilization lead to an increase in  $P_{rem}$  (instead of  $P^*$ )?**

5 As  $\overline{P^*} = \overline{P_{rem}}/\overline{P_{tot}}$ , and  $P_{tot}$  is constant, an increase in  $P_{rem}$  is equal to an increase in  $P^*$ . We will clarify the sentence by changing it to: *[...] the iron added by the dust forcing allows more efficient usage of P in the HNLC-regions, which increases the ocean storage of biologically sourced carbon  $P_{rem}$  (thus,  $P^*$  increases).*

The suggested change has been made, and is now found on p. 12, L. 22-23.

– **Section 3.2.4: p. 11, L. 16: It is unclear what you mean here with “radionuclide proxy data”**

10 We will clarify the sentence by changing it to: *This subantarctic increase in biological efficiency is consistent with radionuclide proxy data ( $^{10}\text{Be}$ ,  $^{230}\text{Th}$ ,  $^{231}\text{Pa}$ ) from the LGM [...].*

The suggested change has been made, and is now found on p. 12, L. 27-28.

– **Section 4.2: - Please consider amending the title of that section - I would suggest to add all the results of experiment 121 here and thus all the finishing sentences of the diverse paragraph (ex: p. 10, L. 31–32).**

15 We agree that grouping all the results of experiment 121 and the associated discussion in Section 4.2 is a good idea, and will follow this recommendation. We will thereby also change the title of the subsection to *Effect of modified but fixed C/P*.

As suggested, all results from experiments with model version 121 have been grouped into Section 4.4, titled *Effect of modified but fixed C/P*.

20 – **Figure 5: I’m confused as to what is shown here. I think mistakes have been made in the plots or legends as it does not make any sense. How can both HOL and LGM can be shown for CTR? How can both HOL and LGM can be shown for GLcomb? It is really not obvious LGM Pacific is HOL Pac -0.32 permil (h compared to f). Similarly, how do you go from Hol Pac to LGM Pac in CTR (g compared to e)? g looks much more like an Atlantic section than a Pacific one. How can d be LGM Atl and f) Hol Pac? d) might be Pacific.**

25 In this figure, the sub-panels have by mistake been shifted to the wrong positions, which naturally causes unnecessary confusion. We apologise for the mistake and show in Fig. 1 the corrected version of the figure, which will replace Fig. 5 in the revised manuscript. The referee is also confused by how both time slices HOL and LGM can be shown for the *Ctrl*-simulation. This is simply because we have chosen to compare each of the simulations (*Ctrl* and *GLcomb*) with both time slices (HOL and LGM) of the proxy data. Even though we expect, of course, that *Ctrl* should to a higher extent reproduce the patterns we see in the HOL data than in the LGM data, we do not want to assume that the model is successful in this respect. For transparency in the process, we therefore show both comparisons. In order to present this figure in a more accessible way, we will clarify that the columns represent the two model simulations, and that the rows represent the proxy records to which we compare the simulations (see caption of Fig. 1). Note that the update of

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the caption will also apply to Fig. S3. Also, it seems the referee may have misunderstood our subtraction of -0.32‰, though the confusion may be a result of the panels being organised in the wrong order. The contours in panel f shows the Pacific Ocean of the *GLcomb* simulation compared to HOL Pacific proxy records (circles). The contours in panel h also shows the Pacific Ocean of the *GLcomb* simulation, but here, 0.32 ‰ has been subtracted from the simulation data. In panel h, the circles show LGM Pacific proxy records. We describe in Section 2.4 that proxy records of  $\delta^{13}C$  indicate that the LGM ocean was more depleted in  $\delta^{13}C$  than the Holocene ocean. We will clarify that this is also true for the dataset we use here (see Peterson et al., 2014). Gebbie et al. (2015) estimated this difference in whole-ocean  $\delta^{13}C$  to  $-0.32 \pm 0.20\%$ . The low LGM whole-ocean value is attributed to glacial contraction of the terrestrial biosphere, and an associated addition of  $\delta^{13}C$ -depleted carbon of terrestrial origin to the ocean. As we do not simulate this terrestrial contribution of  $\delta^{13}C$ -depleted carbon, we do not expect our *GLcomb*-simulations to reproduce this change in whole-ocean  $\delta^{13}C$ . We therefore subtract 0.32‰ from each point of the *GLcomb* simulation output, before we compare to the LGM proxy records.

The figure and caption have been corrected and updated in accordance with the author's response, and have been added to the manuscript. Note that the clarifications also apply to Fig. S.3.

– **Figure 9: With a fixed Redfield ratio  $AC_{rem}$  should increase with  $P_{rem}$ . I am confused as to why  $AC_{rem}$  increases with  $P^*$  here.**

As stated above,  $\overline{P^*} = \overline{P_{rem}} / \overline{P_{tot}}$ , thus an increase in  $P_{rem}$  is analogous to an increase in  $P^*$ .

As an increase in  $\overline{P^*}$  is analogous to an increase in  $P_{rem}$ , no changes have been made to the manuscript in response to this comment.

– **Table 2: I find the format of this table not ideal and wonder if it would make sense to split the RED and GAM results. Also, it might not be necessary to show the AMOC strength for both experiments. The AABW transport in the Atlantic is extremely low (where did you take it?).**

We agree, and will re-organise the table to show the GAM results below RED results, rather than showing them side by side. However, if the results are presented on different rows, the table would look incomplete if we leave out the AMOC strength for one of the model versions. We would therefore prefer to keep those results in the table.  $\psi_{min}$  in this table is simply the minimum of the Atlantic overturning streamfunction below 556m depth and north of 30°N. As seen in Fig. 2 c–d, the AABW circulation is weak in the Atlantic north of -30°N, while its peak strength is located in the Southern and Pacific Oceans. Due to the lack of a boundary between the Atlantic and the Pacific south of -30°N, it is not possible to compute the basin-specific streamfunction further south, though the Atlantic AABW circulation is likely to be stronger there.

Table 2 has been updated according to the suggestions in the author's response. Note that a clarification has been made in the caption, to specify that the maximum and minimum Atlantic streamfunction was taken north of -30°N. In the published author's response, there was a typo which suggested that this latitude was +30°N, but naturally, the cutoff latitude is that corresponding to the southernmost tip of Africa. We apologise for this typo.



### 3 Minor points and typos

- **Section 2.3.3, p. 6, L. 17: Missing table number**

Here, *Table ??* should be corrected to *Table 2*.

Missing table number corrected to Table 2, see p. 7, L. 28.

- 5
- **Section 2.4, p. 6, L. 22:**

Typo, *retrived* should be corrected to *retrieved*.

Typo corrected, see p. 7, L. 32.

- **Section 2.5, p. 7, L. 13:**

Missing reference marked by (?) should be (Ödalen et al., 2018).

- 10
- **Missing reference corrected to (Ödalen et al., 2018), see p. 8, L. 23.**

- **Section 3.1.1, p. 8: Sverdrup is usually noted “Sv”.**

*SV* will be changed to *Sv* throughout the paper.

Correction has been made throughout the paper.

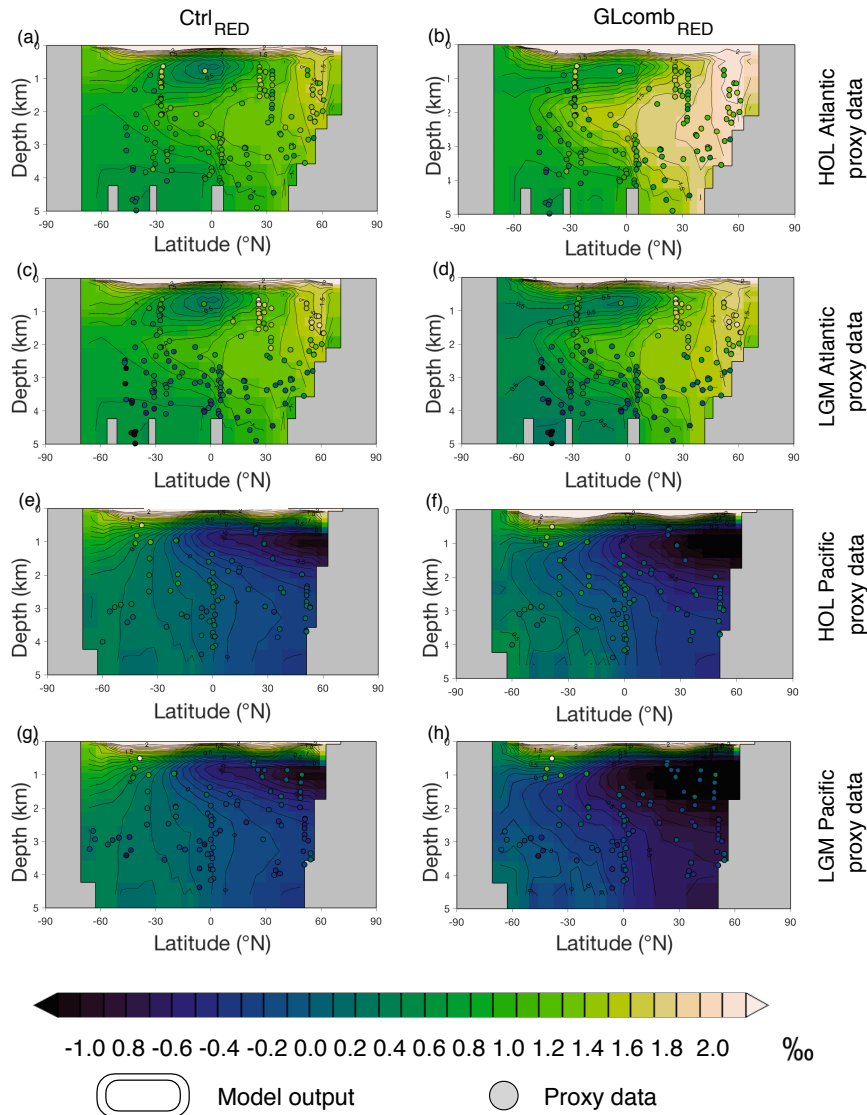
- **Section 3.2.4, p. 11, L. 10: remove one “the”.**

- 15
- Typo, will be corrected.

Sentence removed when information was moved to Section 4.4.

## References

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**Figure 1.** Model ocean  $\delta^{13}C$  (contours) compared to the two proxy record time slices (HOL and LGM) of benthic  $\delta^{13}C$  (circles) of Peterson et al. (2014). The upper half of the figure shows the Atlantic Ocean (panels a–d), while the lower half shows the Pacific Ocean (panels e–h). The columns represent the model simulations ( $Ctrl_{RED}$  or  $Ctrl_{GAM}$ ), while each row represents one of the proxy record time slices (HOL or LGM). The left hand column shows  $Ctrl_{RED}$  (panels a, c, e, g), and the right hand column shows  $GLcomb_{RED}$  (panels b, d, f, h). The rows show, from top to bottom, a–b) HOL Atlantic, c–d) LGM Atlantic, e–f) HOL Pacific, g–h) LGM Pacific. Note that, before we compare  $GLcomb_{RED}$  to LGM observations (panels d and h), a constant of  $0.32\text{‰}$  is subtracted from the simulated  $\delta^{13}C$ , to account for terrestrial release of  $\delta^{13}C$ -depleted terrestrial carbon which is not modelled. The corresponding comparison for model version  $GAM$  is shown in Fig. S.3.

# *Changes in manuscript based on author's response to Referee #2, Pearse James Buchanan*

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## 1 Introduction

In this document, referee comments are shown in ***bold and black italics***, and author's discussion response directly below in plain black. For each author's response, the corresponding changes in the manuscript are shown in [blue](#).

## 2 General comments

5 *The manuscript is well organised in how it presents the methods and results. In this sense, it is very easy as a reader to understand what the authors have done. However, the writing itself requires a lot of polishing. The common usage of “e.g.”, as an example (pun not intended), in mid-sentence makes things simultaneously difficult to read and also leaves me thinking that the authors are purposely choosing to not discuss all the evidence/processes/knowledge on a subject. I strongly suggest that the authors take some time to improve the writing.*

10 As suggested by PJB, we will work to make the writing clearer. Specifically, PJB points out the common usage of e.g. mid-sentence, and questions whether this is intentionally used “to not discuss all the evidence/processes/knowledge on a subject”. This was not our intention, but rather an attempt to avoid the text getting too long. This is why we decided in some cases to only bring up the most relevant examples. We will go through these parts of the text in detail, and add more information.

We have worked through the manuscript to improve the writing, especially in the Introduction and Discussion sections. We have re-written sentences where e.g. was used mid-sentence.

15 *One particularly important part of the manuscript that is not conveyed clearly is their diagnosis of CO<sub>2</sub> capture via variable C:P ratios, as opposed to a simple whole ocean increase in C:P. For instance, in the conclusion the authors state that “About half of the increased drawdown of CO<sub>2</sub> results from different global average C/P in the export production. In addition, flexible stoichiometry allows increased carbon capture through the biological pump, while maintaining or even decreasing the fraction of remineralised to total nutrients in the deep ocean.”. The reader is therefore left confused about*

*what C:P ratios are actually doing. Aren't they contributing to the whole of the increased drawdown? I think what the authors are trying to say is that the spatial and temporal variations in C:P are important for strengthening the biological pump, because they react dynamically to changes in nutrient supply to reinforce further CO<sub>2</sub> drawdown over a simple prescribed whole ocean increase. I would therefore advocate for the authors to make this more clear.*

5 Both Referee #1 and PJB find the discussion of Section 4.2 (Implications of changed average C/P) unclear, and both give useful suggestions on how to clarify this section. The section will thus be re-written based on these suggestions.

In the updated manuscript, Sections 4.2 (now 4.4), and 4.3 (now 4.2) have been re-written, and we have worked to clarify the contributions by CO<sub>2</sub> capture via variable C:P ratios, as opposed to a simple whole ocean increase in C:P. For a reader who has read the updated manuscript, the quoted sentence from the Discussion should now be easier to understand, and it was therefore

10 left unchanged.

*I also think that many of the concepts discussed in this paper with relevance for the sensitivity experiments could be introduced better in the Introduction. This includes previous glacial modelling studies, palaeoproxy evidence and the theories that have been consequently generated for increased oceanic carbon storage due to these prior studies. Temp-dependent remin rates, changes in wind stresses, overturning circulation, polar stratification, solubility (salt and heat), Si-leakage,*

15 *CaCO<sub>3</sub> compensation and production rates, Fe fertilisation, increased N<sub>2</sub> fixation, sea ice expansion, even volcanism. All of these, except volcanism, are feedbacks that were somehow kick-started by changes in solar insolation. While you obviously do not need to discuss all of these in detail, laying out the current “pieces of the puzzle” would help to ground your work in the current stream of consciousness in the paleoclimate community*

PJB details how the Introduction could be extended with a more extensive discussion of concepts, in order to help the reader.

20 We agree that this could be helpful, and we will make additions according to PJB's suggestions.

The Introduction has been extended with more detailed information about evidence of contributors to glacial oceanic carbon storage from previous studies (page 2, lines 7-30), and more detailed information about the background of the concepts behind the sensitivity experiments (page 3, lines 11-20).

### 3 Specific comments

#### 25 3.1 Abstract

– *Page 1, line 8: surely you mean increases rather than decreases? And also you mean Phosphate. Because an increase in Fe deposition, which is a nutrient, has been linked to an increase in C:P ratios. Garcia et al (2018): Nutrient supply controls particulate elemental concentrations in the low latitude eastern Indian Ocean. Nature Communications.*

Yes, “decreases” should be corrected to “increases”, and “nutrients” to “phosphorus” (as we are discussing elemental ratios).

30

Page 1, line 8-9: After re-reading the sentence and PJB's comment, we agree with PJB, and the sentence has been changed to *'If the C/P ratio increases when phosphate availability is scarce, [...]*, in accordance with his comment.

## 3.2 Introduction

- **Page 2, line 2 : Also because of the rapid release of carbon to the atmosphere over the deglaciation, implying its storage somewhere during the glacial.**

We agree and will add this information, along with relevant references.

5 On page 2, lines 5-6, we have added: *‘During deglaciation, radiocarbon evidence indicate that CO<sub>2</sub> was rapidly released from the ocean back to the atmosphere (Marchitto et al., 2007; Skinner et al., 2010).’*

- **Page 2, line 5 : What is the e.g. here referring to?**

This is a formatting issue. The *e.g.*, should be placed before the reference (Broecker, 1982a), which was intended to be given as an example of a key study for the role of ocean sedimentary processes for increased glacial oceanic storage of carbon.

10

The Introduction has been re-written, and this citation is now located on page 2, line 20, together with other relevant references. The formatting issue is thus no longer present.

## 3.3 Methods

- **Page 4, line 20 : suggest citing the more recent estimate of 2.6°C by Bereiter et al (2018): Mean global ocean temperatures during the last glacial transition. Nature.**

15

We thank PJB for the suggestion and will add this reference.

The sentence has been changed to: *‘By applying the above perturbations, we aim to approach, but not fully resolve, some of the characteristics of the Last Glacial Maximum (LGM) ocean, which appears to have had a global average ocean temperature ( $\overline{T_{oce}}$ ) 2.57 ± 0.24 °C colder than the Holocene (Bereiter et al., 2018), [...]’*, see page 5, lines 19-21. See also page 2, line 10; page 7, line 34; and page 13, line 4.

20

- **Page 6, line 1 : suggest citing Moore et al (2013) Processes and patterns of oceanic nutrient limitation. Nature Geoscience. Another paper of note that would be useful for your work is the recent article by Garcia et al (2018) Nutrient supply controls particulate elemental concentrations in the low latitude eastern Indian Ocean. Nature Communications.**

25

We thank PJB for the suggestions and add the reference to Moore et al. (2013) here. The paper by Garcia et al. (2018) is certainly relevant to our work, and this reference will be added already in Section 2.2 (Page 3).

References added in text, see Page 7, line 13 (Moore et al., 2013), and Page 4, line 16 (Garcia et al., 2018a).

- **Page 6, line 17 : “see Table ??”... Please make sure your document is properly formatted before submitting.**

We apologise for the formatting error. *Table ??* should be corrected to *Table 2*.

30

Missing table number corrected to *Table 2*, see page 7, line 28.

– **Page 6, line 22 : Why not use more recent WOA 2018 product?**

When the paper was submitted, WOA18 was only available as a pre-release. We therefore chose to stay with the most up-to-date official release for the initial submission. The official release is now available, and we will therefore use WOA18 for the updated manuscript.

5 In the updated manuscript, we have replaced WOA13 for WOA18 throughout the manuscript, in text, figures and tables. See e.g., page 7, line 32: ‘*Modern data of ocean temperature, oxygen and nutrients are retrieved from the World Ocean Atlas 2018 (Locarnini et al., 2018; Garcia et al., 2018c, b)*’.

– **Page 7, line 13 : Again a question mark is present. Please format properly before submitting.**

10 We are very sorry for having overlooked the formatting errors in our final check before submission. The missing reference marked by (?) should be (Ödalen et al., 2018).

Missing reference corrected to (Ödalen et al., 2018), see page 8, line 23.

### 3.4 Results

– **Page 8, line 29 : The oxygen content of the ocean should be lower in  $Ctrl_{121}$  than for  $Ctrl_{RED}$ . This is because a higher C:P ratio of organic matter should also require more  $O_2$  to remineralise that organic matter. I would like an explanation of why  $O_2$  is higher in  $Ctrl_{121}$  than for  $Ctrl_{RED}$ . See Paulmier, Kriest & Oschlies (2009): Stoichiometries of remineralisation and denitrification in global biogeochemical ocean models. Biogeosciences.**

15 We thank PJB for having identified this inconsistency in our results, which we had failed to notice. This was caused by an issue in the code, which caused an unintentional change in  $O_2:C$  when the fixed C:P stoichiometry was changed. This issue was not present in the runs with flexible stoichiometry, and thus only affected the  $O_2$  in the 121-ensemble. We have re-run  $Ctrl_{121}$  after having corrected the model code. The new resulting average  $O_2$ -concentration is  $152 \mu mol kg^{-1}$ , which is lower than  $Ctrl_{RED}$  ( $166 \mu mol kg^{-1}$ ), but higher than  $Ctrl_{GAM}$  ( $144 \mu mol kg^{-1}$ ).

20 The  $O_2$ -concentrations of the 121-experiments have been corrected throughout the manuscript, and we have added to Methods Section 2.2, Stoichiometry, page 4, lines 25-26: ‘*Note that, while we change the ratio C/P, the ratio C/ $O_2$  remains the same in all experiments. As a result, the P/ $O_2$  ratio changes between experiments.*’.

25 – **Page 11, line 1 : Please explain why a shallow RLS is shallower in a warmer climate. Alternatively, you could provide a more thorough explanation of the effect of temperature on remineralisation rates in the Introduction.**

In line with PJBs suggestion in the General comments, this will be described in more detail in the Introduction, based on the results of Matsumoto (2007).

30 The detailed description of temperature dependent remineralisation rates was too long for the Introduction, and in the updated manuscript it is found in Section 2.3.2, where the sensitivity experiments are described.

Added to Introduction, page 3, lines 15-16: ‘*Ocean cooling reduces the degradation rate of sinking particulate organic carbon, which increases the average depth of remineralisation of organic carbon (Matsumoto, 2007).*’

Added to Section 2.3.2, first paragraph: ‘*In the ocean, phytoplankton growth rates and remineralisation of particulate*



organic carbon are processes that both work more slowly at colder temperatures (Eppley, 1972; Laws et al., 2000). Cooling of the ocean would thus lead to decreased production of particulate organic matter (POC), and simultaneously to a slower degradation of POC, with competing effects on export production (i.e. the amount of C captured by primary production that leaves the surface ocean without being remineralised) (Matsumoto, 2007). However, Matsumoto (2007) shows that the effect of slower remineralisation dominates the effect on export production. It has therefore been hypothesised that the cooling of the glacial ocean led to a deepening of the remineralisation length scale (henceforth denoted RLS) in the ocean, and thereby more efficient retention of organic carbon in the deep ocean (Matsumoto, 2007; Chikamoto et al., 2012), which in turn caused a lowering of  $p\text{CO}_2^{\text{atm}}$ .

- 5
- **Page 11, line 9 : This sentence needs to be clearer with what it's trying to say. Roughly 10% of what? Change in the average composition of what? Of course I can guess what you mean when I stop to think about it, but please make it easier for the reader by saying what you mean.**

We agree with PJB and in order to clarify the sentence, we will change it to: *About a third (~ 10 % of 30 %) of the increase in drawdown can be explained by a change in average C/P composition of the organic material that is exported out of the surface ocean.* This will then be discussed in more detail in Section 4.2, where we will gather all the results and discussion that concerns the 121-ensemble (as suggested by Referee #1).

10

Sentence re-written as suggested in author's response, see page 12, lines 19-21. Results from experiments with changed fixes C/P described in more detail in Section 4.4. (former Section 4.2).

- 15
- **Page 11, lines 22–25 : But not cool enough to align with the more recent estimate of Bereiter et al (2018): Mean global ocean temperatures during the last glacial transition. Nature.**

20

We will add a note on this, and clarify that we are not applying all forcings that are expected to be needed to reproduce a full glacial state.

Added on page 13, lines 7-9: *'Compared to the Bereiter et al. (2018) estimate, our combined experiments  $GL_{\text{comb}}$  and  $A_{\text{comb}}$  achieve 64 and 82 % of the glacial-interglacial difference in  $\overline{T_{\text{oce}}}$ , respectively. As anticipated, our combined forcings do not induce a full glacial maximum state, but a state with glacial-like climate conditions.'*

- 25
- **Page 12, lines 21–25 : Again, I am unsure how you are treating P:O<sub>2</sub> remineralisation requirements in your variable stoichiometry experiments. I think this should be explained. It is also strange once again that your  $GL_{\text{comb}121}$  experiment is better oxygenated than your  $GL_{\text{comb}RED}$  experiment.**

30

In remineralisation, there was an issue in the code which affected the C:O<sub>2</sub> ratio in the 121-experiments. This made the P:O<sub>2</sub> requirements appear strange, which PJB noticed. This has been corrected, and the 121-experiments re-run. After correction, C:O<sub>2</sub> remains the same in all experiments, while the P:O<sub>2</sub> ratio, as a result, changes between experiments. We will clarify this in the Methods section. After the correction described above,  $GL_{\text{comb}121}$  has a lower global average O<sub>2</sub> concentration than  $GL_{\text{comb}RED}$  (96 compared to 122  $\mu\text{molkg}^{-1}$ ), but higher than  $GL_{\text{comb}GAM}$  (74  $\mu\text{molkg}^{-1}$ ). The O<sub>2</sub>-concentrations of the 121-experiments have been corrected throughout the manuscript, and we have added to

Methods Section 2.2, Stoichiometry, page 4, lines 25-26: 'Note that, while we change the ratio C/P, the ratio C/O<sub>2</sub> remains the same in all experiments. As a result, the P/O<sub>2</sub> ratio changes between experiments.'

– **Figure 5 : The panels in this figure do not seem to be arranged correctly.**

We are grateful to both referees for having identified this error. We here provide the updated figure (see Fig. 1), where the sub-panels have been re-arranged in the correct order. Per request of Referee #1, we will also clarify the caption of this figure.

The figure and caption have been corrected and updated in accordance with the author's responses to both referees, and have been added to the manuscript. Note that the clarifications also apply to Fig. S.3.

– **Page 13, lines 1–8 : What conditions affect the fractionation strength of biological carbon assimilation? Is it constant or variable?**

The fractionation strength is variable and will be detailed in an appendix (see below, in author's response to the final bullet point of Discussion).

Added Appendix B:  $\delta^{13}C$  in cGENIE, page 22.

– **Page 13, line 12 : Why not add a figure of sea ice cover in the supplement? Also, can you separate the effects of sea ice cover expansion from the other physical changes in terms of CO<sub>2</sub>? A few studies since the Stephens & Keeling (2000) paper have found that an increase in sea ice cover under glacial conditions actually reduces ocean carbon storage because it prevents organic carbon production. It would be worthwhile to separate this effect from temperature and circulation and note if it is positive or negative on atmospheric CO<sub>2</sub>. Stephens & Keeling (2000) The influence of Antarctic sea ice on glacial–interglacial CO<sub>2</sub> variations. *Nature*. Kurahashi–Nakamura et al. (2007) Compound effects of Antarctic sea ice on atmospheric pCO<sub>2</sub> change during glacial–interglacial cycle. *Geophysical Research Letters*. Sun & Matsumoto (2010) Effects of sea ice on atmospheric pCO<sub>2</sub>: A revised view and implications for glacial and future climates. *Journal of Geophysical Research*. Buchanan et al (2016) The simulated climate of the Last Glacial Maximum and insights into the global marine carbon cycle. *Climate of the Past*.**

We will add a figure of the sea ice anomaly (*GLcomb-Ctrl*) to the supplement. The separation of the effects of sea ice cover expansion from the other physical changes would be highly interesting to isolate. However, we find them to be beyond the scope of this paper, and we wish to keep this paper focused on the effects of flexible C/P on pCO<sub>2</sub>. If PJB is interested in the separation of physical effects in cGENIE, this is explored in (Ödalen et al., 2018). There, we want to point specifically to the simulation *AD/2* in Figure 2, where panel e) details the contributions from the changes in each of the different carbon capture processes to the net change in pCO<sub>2</sub>. The simulation *AD/2* has a reduced biological pump compared to the pre-industrial control, but an enhanced carbon capture due to increased disequilibrium and saturation carbon. This is attributed mainly to ocean cooling and a resulting expansion of sea ice. However, no further separation of the effect of sea ice was made.

Added Figure S.4, see reference on page 14, line 24, and Supplementary Material.

- Page 13, lines 10–23 : *This paragraph would benefit from being clearer in its findings of CO<sub>2</sub> sequestration regarding C:P ratio changes. I have to read this multiple times to understand what the authors are trying to say when comparing Redfield, variable C:P and C:P=121.*

This paragraph will be clarified by concentrating all the results and discussion concerning C/P = 121 to Section 4.2, as suggested by Referee #1. We are confident that this paragraph will become clearer when it is rewritten to focus only on the difference in CO<sub>2</sub> sequestration between Redfield (*RED*) and flexible C/P (*GAM*).

Section 3.3.5, referred to here by PJB, has been re-phrased, shortened and information regarding experiments using model version 121 has been moved to Section 4.4

### 3.5 Discussion

- Page 13, line 28 : *your reference to “model” should be an “empirical model” to avoid confusion with the Earth System Model, GCM, etc.*

Agreed. We will add “empirical”.

Added ‘*empirical*’, page 15, line 7.

- Page 14, lines 1–5 : *The advantages of using empirical/statistical models within biogeochemical ocean GCMs, including the Galbraith & Martiny (2015) parameterisation, was explored rigorously in my 2018 paper in Global Biogeochemical Cycles. It not only improved that model’s biogeochemistry significantly, but also altered the long-term behaviour of the carbon cycle as you have also found. It may be interesting, but I of course leave it up to you whether it’s useful. Buchanan et al (2018) The importance of dynamic biological functioning for simulating and stabilizing ocean biogeochemistry. Global Biogeochemical Cycles.*

We thank PJB for pointing us to this paper, and find the conclusions very interesting. They are well aligned with the study we perform in this paper, and by citing this paper, we will strengthen our arguments. We will thus include the suggested paper in our discussion.

Added to Introduction, page 3, lines 7-10: *In addition, Buchanan et al. (2018) explored the importance of dynamic response of ocean biology, such as flexible stoichiometry, for modelled ocean biogeochemistry in pre-industrial simulations. They found that the dynamic response was fundamental for stabilising the response of ocean DIC to changes in the physical circulation state.*

Added to Section 4.1, page 15, lines 10-16: *‘Previous model ensemble studies have shown that this type of dynamical response of the biology to changes in the modelled ocean state can improve the model’s ability to realistically simulate ocean biogeochemistry (Buchanan et al., 2018). In pre-industrial and future simulations, respectively, Buchanan et al. (2018) and Tanioka and Matsumoto (2017) find that the flexible stoichiometry acts to stabilise the response of ocean DIC to changes in the physical (circulation) state. In our glacial-like simulations, we find that the response of ocean DIC, and thus pCO<sub>2</sub><sup>atm</sup>, to the combined perturbations is greater in the simulations with flexible stoichiometry. Nonetheless, our study confirms the potential importance of dynamical biological response for the outcome of model studies.’*

– **Page 14, line 32 : the conclusions of Odalen et al (2018)... which were? What did Odalen et al (2018) do?**

Here, lines 30–33 should read: *Note that  $Ctrl_{GAM}$  has a larger inventory of DIC, as well as  $C_{soft}$ , compared to  $Ctrl_{RED}$ . Ödalen et al. (2018) found that drawdown of  $CO_2$  in response to a perturbation is larger when the control state has a smaller inventory of DIC and  $C_{soft}$ . Yet, the effect of applying the same perturbation results in a larger drawdown of  $CO_2$  in GAM than in RED. This is thus opposite of the conclusions of Ödalen et al. (2018). The reason is that the flexible stoichiometry in effect increases the drawdown potential, which more than compensates for the increased carbon inventory in the control state.* As stated above, Section 4.2 will be re-written, and clarified. In this way, we will assure that the conclusions of Ödalen et al. (2018) are clearly stated.

Added sentence ‘*Ödalen et al. (2018) found that drawdown of  $CO_2$  in response to a perturbation is larger when the control state has a smaller inventory of DIC and  $C_{soft}$ .*’ (see p. 17, lines 14-16), as suggested in author’s response.

– **Page 15, lines 19–24 : So the proportion of remineralised to preformed phosphorus effectively doesn’t change in the simulations? And yet, you find a large increase in respired C? This must mean that the remineralised phosphorus that is exported into the ocean interior in your  $GLcomb$  simulation is being quickly circulated into the lower overturning cell and returned to the Antarctic Zone, where sea ice prevents gas exchange and biological production, at which point this P is recirculated and becomes preformed, while respired C remains respired and is also recirculated. If this is the case, it merits more discussion in comparison with previous literature on the subject of a more efficient biological pump that invokes more regenerated nutrients as a must for a more efficient biological pump. I suggest Hain, Sigman & Haug (2014) *The biological pump in the past. Treatise on Geochemistry, 2nd Ed.***

The referee has correctly identified that, despite the fact there is no change in remineralised P ( $P_{rem}$ ) in  $GLcomb_{GAM}$  compared to  $Ctrl_{GAM}$ , there is an increase in remineralised C. However, the process described by the referee focuses on what happens after remineralisation, while we suggest that this decoupling happens before the organic material is exported to the deep ocean (see lines 25–31). The forcing components applied to  $GLcomb_{GAM}$  have competing effects on the amount of organic matter that remineralises in the deep ocean. The net effect is that this amount does not change globally (reflected by a constant  $P_{rem}$  compared to  $Ctrl_{GAM}$ ). Meanwhile, changes in ocean circulation, remineralisation depth and dust deposition still cause the local nutrient availability in the surface waters to change. This affects the elemental composition of the exported organic material. In  $Ctrl_{GAM}$ , the average elemental C/P composition is 121/1. In  $GLcomb_{GAM}$ , this average is 134/1. This means that even though the same amount of P is exported to the deep ocean, the organic molecules carry more carbon, which is released in the deep ocean during remineralisation. In  $Ctrl_{GAM}$ , the global average concentration of  $P_{rem}$  is  $1.16 \mu mol kg^{-1}$  (c.f.  $1.17 \mu mol kg^{-1}$  in  $GLcomb_{GAM}$ ). By increasing the average C/P composition of  $1.16 \mu mol kg^{-1}$  organic molecules from 121 to 134 (i.e. by 13 units), this causes an increase in  $C_{rem}$  by  $\sim 15 \mu mol kg^{-1}$ , which corresponds to the observed increase in  $C_{rem}$ . In summary, we suggest this is a result of changes in surface P fields (see Fig. 7), rather than a change in the partitioning between  $C_{rem}$  and  $P_{pre}$  in the recirculation area in the Antarctic Zone. We will clarify this part of the discussion, which comprises lines 19–31 on page 15.

Section 4.2 (i.e. Section 4.3 in the original manuscript) has been re-written to include the discussion outlined in the author's response, see page 16, line 17 through page 17, line 13.

– **Page 16, lines 1–14 :**

Here, each of the questions will be treated separately.

5       – ***I would like to see how variations in P:O<sub>2</sub> requirements were treated in this model.***

C:O<sub>2</sub> requirements were meant to be held constant throughout the simulations, consequently causing changes in P:O<sub>2</sub>. However, an inconsistency in the code caused C:O<sub>2</sub> requirements to change in the simulations of the 121-ensemble, causing an inconsistent behaviour of P:O<sub>2</sub>. This has been corrected, as outlined above.

10       The O<sub>2</sub>-concentrations of the 121-experiments have been corrected throughout the manuscript, and we have added to Methods Section 2.2, Stoichiometry, page 4, lines 25-26: *'Note that, while we change the ratio C/P, the ratio C/O<sub>2</sub> remains the same in all experiments. As a result, the P/O<sub>2</sub> ratio changes between experiments.'*

– ***Also, can you please explain why the deep water formation characteristics of a model affects O<sub>2</sub>?***

15       Deep water formation characteristics of a model affects the amount of time available for remineralisation and, consequently, the oxygen consumption. In addition, due to a lack of resolution deep water formation in climate models generally happens as open water convection, rather than as dense plumes along slopes. This causes too much oxygen to be entrained into the deep ocean. We will add this explanation in the updated manuscript.

20       Page 18, lines 1-12, paragraph extended by lines 6-12: *'Among other factors, model ocean oxygen conditions are also dependent on deep water formation characteristics of the model (Galbraith and de Lavergne, 2018). The deep water formation characteristics of a model affects the amount of time available for remineralisation and, consequently, the oxygen consumption. In addition, due to a lack of resolution deep water formation in climate models generally happens as open water convection, rather than as dense plumes along slopes (Heuzé et al., 2013). This may cause too much oxygen to be entrained into the deep ocean Galbraith and de Lavergne (2018). In cGENIE, this effect is small enough not to cancel the increased O<sub>2</sub> consumption caused by the higher average C/P in Ctrl<sub>GAM</sub> compared to Ctrl<sub>RED</sub>.'*

25       – ***Overall, I find this section a bit sparse and I'm not entirely sure what the point of it is.***

30       The section aims to discuss 1) to what extent our *GLcomb* simulations reproduce proxy observations, in this case for O<sub>2</sub>, and 2) to discuss one of the problems that arose from applying the flexible C/P in GENIE, i.e. that O<sub>2</sub> concentrations in *Ctrl<sub>GAM</sub>* are too low, and its implications for the glacial-like simulation. We agree that the section could be expanded, and we will add the information requested by PJB to make the discussion more comprehensive.

Discussion has been expanded according to suggestions and questions by PJB in the above and below bullet points.

– ***Can you comment on the size of the OMZs? New evidence shows that the OMZs in the Pacific expanded vertically during the glacial. Hoogakker et al (2018) Glacial expansion of oxygen-depleted seawater in the eastern tropical Pacific. Nature***

In the Atlantic,  $Ctrl_{GAM}$  (Fig. 4 e) reproduces the observed extent of the OMZ (Fig. 4 a) better than  $Ctrl_{RED}$  (Fig. 4 c) does. In the Pacific Ocean, the  $O_2$  gradient in the observations (Fig. 4 b) is more gradual compared to that of the control states (Fig. d, f), but the core of the OMZ is well reproduced by the model. The forcings applied to  $GLcomb$  are not sufficient to reproduce a full glacial state (see also author's response to the next main point, regarding Page 16, line 22). Still, we do get a vertical expansion of the OMZ in  $GLcomb_{RED}$  (Fig. 4 h) compared to  $Ctrl_{RED}$  (Fig. 4 c), in agreement with the findings of Hoogakker et al (2018). In  $GLcomb_{GAM}$ , oxygen depletion is too extensive, but the tendency of vertical expansion compared to the control state is present here as well.

Added discussion of glacial vertical expansion of the OMZ in line with author's response (see page 17, lines 25-30).

– **Page 16, line 22 : And yet others achieve relatively good correlations in the Pacific basin using the same data? Menviel et al (2017) Poorly ventilated deep ocean at the Last Glacial Maximum inferred from carbon isotopes: A data–model comparison study. Paleoceanography. Muglia et al (2018) Weak overturning circulation and high Southern Ocean nutrient utilization maximized glacial ocean carbon. Earth and Planetary Science Letters. I think you cannot say that your model doesn't provide good fits to the LGM proxy data because of poor data coverage, and it would be more useful to discuss why the model doesn't fit with the data. It seems like your glacial circulation in the Pacific basin is therefore not accurate?**

The forcings applied to  $GLcomb$  are factors that are likely to be important for the glacial ocean circulation and biogeochemistry. However, these forcings are not sufficient to reproduce a full glacial state (i.e. the use of the term “glacial-like simulations”, rather than “LGM simulation”). Other forcings that have shown to be important for modelling of glacial  $\delta^{13}C$  are, for example, brine rejection (Bouttes et al., 2010, 2011), and freshwater forcing (e.g., Schmittner et al., 2002; Hewitt et al., 2006; Bouttes et al., 2012). The fact that some important forcings are missing (mentioned on lines 27–28) is likely the main cause for the model–data discrepancy, and the reason for why we do not achieve an accurate glacial Pacific Ocean circulation. This will be clarified in the section. We will also clarify, throughout the paper, the fact that we do not aim to produce a full LGM state. This may also call for adjusting the title of the paper.

The discussion in this section (Section 4.5) has been re-phrased and extended to give more detailed explanations of the reasons for model–data discrepancies. For this referee comment, see specifically page 19, lines 25-31: *'The forcings applied to  $GL_{comb}$  are factors that are likely to be important for the glacial ocean circulation and biogeochemistry. However, these forcings are not sufficient to reproduce a full glacial state (i.e. the use of the term glacial-like simulations, rather than LGM simulation). Other forcings that have shown to be important for modelling of glacial  $\delta^{13}C$  are, for example, brine rejection (Bouttes et al., 2010, 2011), and freshwater forcing (Schmittner et al., 2002; Hewitt et al., 2006; Bouttes et al., 2012). The fact that some important forcings are missing is likely the main cause for the model–data discrepancy, and the reason for why we do not achieve a glacial Pacific Ocean circulation consistent with observed  $\delta^{13}C$  patterns.'*

In addition, the title of the paper has been adjusted to: ‘*Variable C/P composition of organic production and its effect on ocean carbon storage in glacial-like model simulations*’

- *Page 16, line 26 : Temperature is not chemical. I also do not understand how you could alter the temperature and salinity of the ocean without altering water mass distributions, and if this is indeed the case, it requires further description as to why earlier in the paper. Also a good spot to talk about why the data in the Pacific are not well reproduced by the model.*

We agree that temperature in itself is not chemical. Here, we were referring to the changes in solubility of CO<sub>2</sub>, which is a chemical response to changes in temperature. This will be clarified in the revised version of the paper. The water mass distribution in cGENIE is strongly constrained by the resolution of the model, especially in the vertical. Changes in temperature and salinity that should cause changes in water mass volume may not be sufficient to allow a water mass to extend to the next vertical level of the model. As a consequence, while the gradient between water masses may become more or less pronounced, the interface of water masses may still remain at the same depth. The section will be clarified, including the above description of why Pacific glacial circulation is not fully reproduced.

The discussion in this section (Section 4.5) has been re-phrased and extended to give more detailed explanations of the reasons for model-data discrepancies. For this referee comment, see specifically page 19, lines 32-34, and page 20, lines 1-10. (Due to the length of the added paragraph, we do not cite it here.)

- *Page 16, lines 24–31 : I don’t follow this paragraph. You state that “Each of the two observational datasets (HOL and LGM) display similar correlations across the two model simulations. This implies that our changes in forcings do not achieve any obvious changes in water mass distribution.” But doesn’t the distribution of  $\delta^{13}C$  change across the glaciation and into the Holocene?  $\delta^{13}C$  in the Atlantic, for instance, is often used to show that the Atlantic meridional overturning was shallower during the glacial, and that this change occurred during Marine Isotope Stage 4 (Oliver et al (2010) A synthesis of marine sediment core  $\delta^{13}C$  data over the last 150000 years. Climate of the Past.)? Moreover,  $\delta^{13}C$  is used as a way to show that the water mass distribution between the Atlantic and Pacific was considerably different during the glacial as compared to the Holocene (Sikes et al (2017) Enhanced  $\delta^{13}C$  and  $\delta^{18}O$  Differences Between the South Atlantic and South Pacific During the Last Glaciation: The Deep Gateway Hypothesis. Paleoceanography.) These studies conflict with what you are saying.*

The proxy data do imply a change in  $\delta^{13}C$  across the deglaciation (whole ocean change  $0.34 \pm 0.19$  ‰, Peterson et al., 2014). What we are trying to say is that our model simulations do not fully reproduce this change. Here we are referring to the fact that the correlation of the HOL proxy records with  $Ctrl_{RED}$ ,  $Ctrl_{GAM}$ ,  $GLcomb_{RED}$ , and  $GLcomb_{GAM}$ , is in all cases between 0.76–0.78. On the other hand, the correlation of LGM proxy records with the same four simulations is in all cases between 0.55–0.58. As our  $GLcomb$ -simulations still correlate so well with the HOL dataset, this suggests the applied forcings have not caused these simulations to be clearly different from  $Ctrl$  in terms of water mass distribution. For the same reason, the correlation with LGM proxy data does not significantly improve from  $Ctrl$  to  $GLcomb$ . Thus, the deglacial change in  $\delta^{13}C$  reflected in the proxy data is not fully captured by the model. This will be clarified in the



updated version of the manuscript.

The discussion in this section (Section 4.5) has been re-phrased and extended to give more detailed explanations of the reasons for model-data discrepancies. For this referee comment, see specifically page 19, lines 12-17; page 19, lines 32-34; and page 20, lines 1-10. (Due to the combined length of the added paragraphs, we do not cite them here.)

- 5 – (Section 4.5 ?): *The ability for simulated  $\delta^{13}C$  to reproduce the proxy data at the LGM will depend strongly on water mass distribution (which apparently doesn't change appreciably) and how biological fractionation is parameterised. If it is constant, the 10% loss in C fixation will cause the ocean to be more positive overall by some constant factor. However, if the parameterisation contains a dependence on aqueous  $CO_2$  and growth rate, both of which are lower, then the fractionation will vary. It would be worthwhile telling the reader what parameterisation is used and, if it does*
- 10 *involve growth rate and aqueous  $CO_2$ , what effect this has.*

The fractionation is dependent on both aqueous  $CO_2$  and growth rate (represented in  $K_Q$ , see appendix). This dependence and its consequences will be detailed by adding the following text in an Appendix:

[... Appendix text given in Author's response removed, as it is now included in the updated manuscript.]

Added sentence on page 20, line 11: 'How  $\delta^{13}C$  is represented in cGENIE is detailed in Appendix B.'

- 15 Added also Appendix B:  $\delta^{13}C$  in cGENIE (page 22).

#### 4 Technical corrections

- *Page 1, line 13 : remove repeated “with”*

We will correct this typo. Page 1, line 13: Removed repeated “with”.

- *Page 5, line 16 : replace “reduced half” with “halved”*

20 The sentence will be changed according to the suggestion.

Page 6, line 16: Replaced “reduced half” with “halved”.

- *Table 1 : “witg” to “with”*

We will correct this typo in the caption of Table 1.

Table 1, caption: Changed “witg” to “with”.

- 25 – *Page 11, line 8 : Inadvisable to begin a sentence with “~”*

The sentence has been rewritten (see above comment for Page 11, line 9).

Page 12, lines 19-21: Sentence re-written.

- *Page 11, line 29 : “SV” to “Sv”*

We will change “SV” to “Sv” throughout the manuscript.

- 30 “SV” replaced by “Sv” throughout the manuscript.

– *Page 13, line 26 : “GCMs” this acronym has not been defined previously.*

We will define the acronym here.

Page 15, line 5: Acronym “GCMs” defined as General Circulation Models.

– *Page 15, line 23 : I assume you mean “0.003” rather than “0003”?*

5

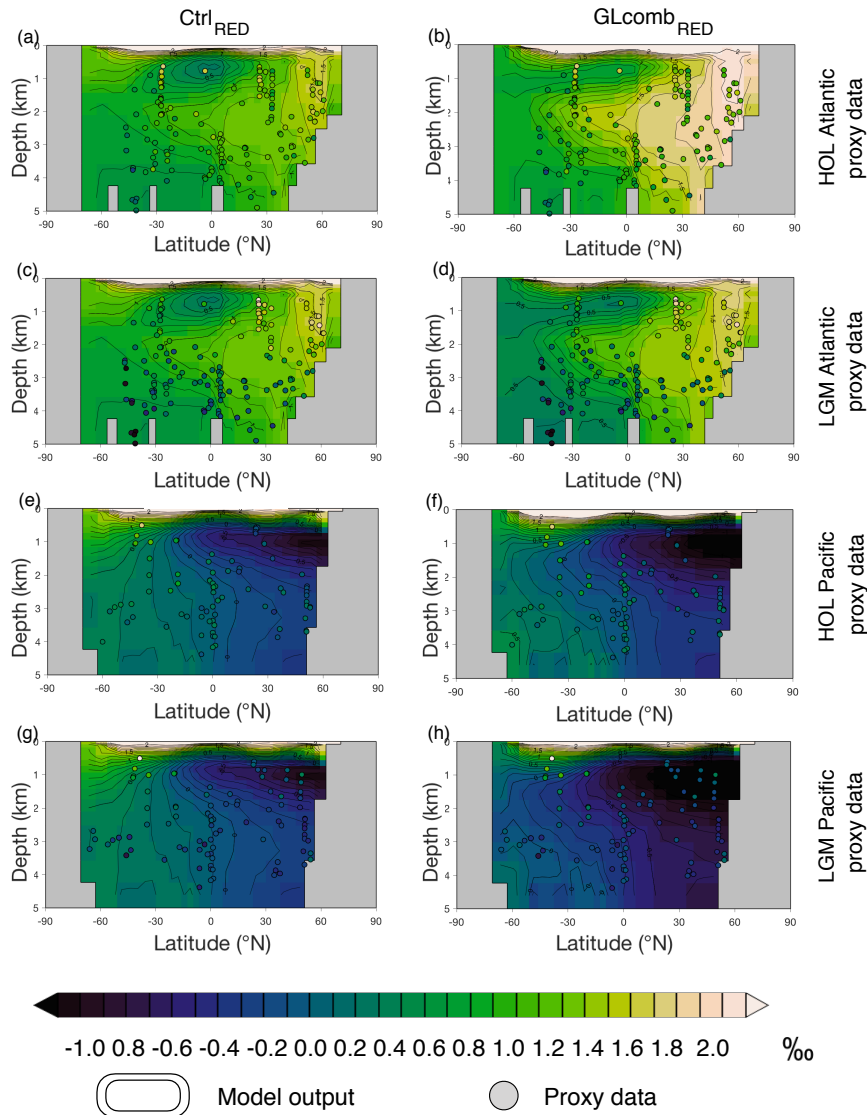
Yes, we will correct this to 0.003.

Page 16, line 32: “0003” corrected to “0.003”

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**Figure 1.** Model ocean  $\delta^{13}C$  (contours) compared to the two proxy record time slices (HOL and LGM) of benthic  $\delta^{13}C$  (circles) of Peterson et al. (2014). The upper half of the figure shows the Atlantic Ocean (panels a–d), while the lower half shows the Pacific Ocean (panels e–h). The columns represent the model simulations ( $Ctrl_{RED}$  or  $Ctrl_{GAM}$ ), while each row represents one of the proxy record time slices (HOL or LGM). The left hand column shows  $Ctrl_{RED}$  (panels a, c, e, g), and the right hand column shows  $GLcomb_{RED}$  (panels b, d, f, h). The rows show, from top to bottom, a–b) HOL Atlantic, c–d) LGM Atlantic, e–f) HOL Pacific, g–h) LGM Pacific. Note that, before we compare  $GLcomb_{RED}$  to LGM observations (panels d and h), a constant of  $0.32\text{‰}$  is subtracted from the simulated  $\delta^{13}C$ , to account for terrestrial release of  $\delta^{13}C$ -depleted terrestrial carbon which is not modelled. The corresponding comparison for model version  $GAM$  is shown in Fig. S.3.

## List of relevant changes

- Abstract
  - Minor changes as suggested by referee #2
- Introduction
  - The introduction has been expanded to give more background to the ocean's role in the glacial-interglacial CO<sub>2</sub> problem, as suggested by referee #2.
- Methods
  - 2.1-2.2, only minor changes
  - 2.3 Replaced estimate of glacial-interglacial global ocean average temperature difference by Headly & Severinghaus (2007) for the more recent estimate by Bereiter et al. (2018).
    - 2.3.1 Clarified descriptions and added references, described air-sea gas exchange dependence on wind speed as suggested by referee #1
    - 2.3.2 Expanded description of temperature dependent remineralisation, and added references.
  - 2.4 Replaced WOA13 for WOA18
  - 2.5 Added missing reference to Ödalen et al. (2018)
- Results
  - 3.1 Minor changes
  - 3.2
    - 3.2.1 Added explanation of why salinity changes are not explored
    - 3.2.2-3.2.4 Moved information about 121-simulations to Section 4.4, as suggested by both referees.
  - 3.3
    - 3.3.1 Replaced estimate of glacial-interglacial global ocean average temperature difference by Headly & Severinghaus (2007) for the more recent estimate by Bereiter et al. (2018).
    - 3.3.2-3.3.4 Minor changes
    - 3.3.5 Text has been clarified and information about 121-simulations has been moved to Section 4.4
- Discussion
  - 4.1 Text has been clarified and expanded by discussing Buchanan et al. (2018). We have expanded the discussion on the implications for warm climate scenarios.
  - 4.2 The former Section 4.2 is now Section 4.4. The section now includes all the information about the 121-simulations, which has been moved here from the results section.
  - 4.3 The former Section 4.3 is now Section 4.2. This section has been clarified and expanded in response to referee comments.
  - 4.4 The former Section 4.4 is now Section 4.3. This section has been expanded to align with suggestions from referee #2.
  - 4.5 The section has been expanded in response to comments of referee #2.
- Conclusions
  - Added sentence about potential implications for warm climate scenarios.
- Figures
  - Fig. 3 Updated to WOA18
  - Fig. 4 Updated to WOA18

- Fig. 5 Both referees pointed out the original version of this figure was incorrect, and found it difficult to interpret. The order of figure panels has been corrected. The description of the figure in the legend and the figure caption has been improved.
- Tables
  - Table 2 Format of table changed as suggested by referee #1.
- Supplementary material
  - Fig. S.3 Improved for clarity (c.f. Fig. 5)
  - Fig. S.4 New figure added (sea-ice anomaly)



## Variable C/P composition of organic production and its effect on ocean carbon storage in glacial model simulations

Malin Ödalen<sup>1</sup>, Jonas Nycander<sup>1</sup>, Andy Ridgwell<sup>2,3</sup>, Kevin I. C. Oliver<sup>4</sup>, Carlye D. Peterson<sup>2</sup>, and Johan Nilsson<sup>1</sup>

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**Abstract.** During the four most recent glacial maxima, atmospheric CO<sub>2</sub> has been lowered by about 90–100 ppm with respect to interglacial concentrations. It is likely that most of the atmospheric CO<sub>2</sub> deficit was stored in the ocean. Changes of the biological pump, which are related to the efficiency of the biological carbon uptake in the surface ocean and/or of the export of organic carbon to the deep ocean, have been proposed as a key mechanism for the increased glacial oceanic CO<sub>2</sub> storage.

5 The biological pump is strongly constrained by the amount of available surface nutrients. In models, it is generally assumed that the ratio between elemental nutrients, e.g. phosphorus, and carbon (C/P ratio) in organic material is fixed according to the classical Redfield ratio. The constant Redfield ratio appears to hold approximately when averaged over basin scales, but observations document highly variable C/P ratios on regional scales and between species. If the C/P ratio decreases when nutrient availability is scarce, as observations suggest, this has the potential to further increase glacial oceanic CO<sub>2</sub> storage in response to changes in surface nutrient distributions. In the present study, we perform a sensitivity study to test how a phosphate-concentration dependent C/P ratio influences the oceanic CO<sub>2</sub> storage in an Earth system model of intermediate complexity (cGENIE). We carry out simulations of glacial-like changes in albedo, radiative forcing, wind-forced circulation, remineralisation depth of organic matter, and mineral dust deposition. Specifically, we compare model versions with the classical constant Redfield ratio and an observationally-motivated variable C/P ratio, in which the carbon uptake increases with decreasing phosphate concentration. While a flexible C/P ratio does not impact the model's ability to simulate benthic  $\delta^{13}C$  patterns seen in observational data, our results indicate that, in production of organic matter, a flexible C/P can further increase the oceanic storage of CO<sub>2</sub> in glacial model simulations. Past and future changes in the C/P ratio thus have implications for correctly projecting changes in oceanic carbon storage in glacial-to-interglacial transitions as well as in the present context of increasing atmospheric CO<sub>2</sub> concentrations.

### 20 1 Introduction

During the last four glacial maxima, atmospheric CO<sub>2</sub> (henceforth  $pCO_2^{glm}$ ) was lowered by  $\sim 90$ –100 ppm compared to the interglacials (e.g., Petit et al., 1999). Due to the difference in size between the oceanic, terrestrial and atmospheric carbon

## Variable C/P composition of organic production and its effect on ocean carbon storage in glacial-like model simulations

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### 20 1 Introduction

During the last four glacial maxima, atmospheric CO<sub>2</sub> (henceforth  $pCO_2^{glm}$ ) was lowered by  $\sim 90$ –100 ppm compared to the interglacials (Petit et al., 1999; Lüthi et al., 2008). Due to the difference in size between the oceanic, terrestrial and atmospheric

reservoirs, where the oceanic reservoir is by far the largest with >90% of their summed carbon contents (e.g., Ciais et al., 2013), it is likely that most of the CO<sub>2</sub> that was removed from the atmosphere was stored in the glacial ocean.

Numerous processes have been identified as possible contributors to increased glacial oceanic storage, for example changes in the strength of the biological pump (e.g., Sarmiento and Toggweiler, 1984; Martin, 1990; Archer et al., 2000; Sigman and Boyle, 2000), sedimentary processes (Broecker, 1982a, e.g.), changes in ocean circulation and sea ice cover (e.g., Boyle and Keigwin, 1987; Duplessy et al., 1988; Stephens and Keeling, 2000; Menviel et al., 2017). Extensive summaries of these processes, and examples of their interactions, are given by e.g. Brovkin et al. (2007); Kohfeld and Ridgwell (2009); Hain et al. (2010); Sigman et al. (2010). Despite the efforts of identifying the responsible processes, models have been struggling to achieve the full lowering of  $pCO_2^{glac}$  expected for a glacial.

10 In this paper, we focus on the biological pump and how it responds to glacial-like changes in climate. Our aim is to investigate how the level of simplification of the biological carbon uptake in an Earth system model may affect the glacial drawdown of  $pCO_2^{glac}$ . Most biogeochemical models used in glacial climate studies have a simple representation of biological production, which assumes that carbon, C, and inorganic nutrients such as phosphorus, P, are taken up in fixed proportion to each other. This is modelled using the average ratio of C/P of the ocean organic matter originally observed by Redfield (1963)

15 (C/P = 106/1), or adjustments to these suggested by e.g. Takahashi et al. (1985) and Anderson and Sarmiento (1994).

We investigate whether allowing for a flexible C/P stoichiometric ratio increases model ocean CO<sub>2</sub> storage in a glacial-like climate. This possibility was suggested by e.g. Broecker (1982b), Archer et al. (2000) and Galbraith and Martiny (2015), but the implications of Redfield versus flexible C/P for glacial ocean carbon storage has not previously been tested in an Earth system model. This type of non-Redfieldian dynamics were applied in the model used in Eggleston and Galbraith (2018) and Galbraith and de Lavergne (2018), but their results were not analysed in terms of difference from a Redfield model version.

20 We conduct a sensitivity study, where we make glacial-like changes in radiative forcing, albedo, wind-forced circulation, remineralisation depth and dust, separately and in combination. We apply these perturbations in two different versions of the Earth system model cGENIE; an original version using fixed Redfield stoichiometry of C/P (Ridgwell et al., 2007) plus a co-limitation by iron (Tagliabue et al., 2016) for biological production, and a modified version using the non-Redfieldian, nutrient concentration dependent, C/P stoichiometry suggested by Galbraith and Martiny (2015) and iron co-limitation.

25 We show that flexible C/P stoichiometry allows a larger glacial ocean CO<sub>2</sub> storage, as predicted by the box-model study of Galbraith and Martiny (2015), and that flexible stoichiometry has the largest impact for perturbations in remineralisation depth and dust forcing. Additionally, we show that flexible stoichiometry allows for increased ocean carbon storage without decreasing the storage of preformed nutrients in the deep ocean.

## 30 2 Methods

### 2.1 Model description

cGENIE is an Earth system model of intermediate complexity, with a 3D frictional-geostrophic ocean (36 × 36 equal area horizontal grid, 16 depth levels), 2D energy-moisture balance atmosphere with prescribed wind fields, interactive atmospheric

carbon reservoirs, where the oceanic reservoir is by far the largest with >90% of their summed carbon contents (reviewed by, Ciais et al., 2013), it is likely that most of the CO<sub>2</sub> that was removed from the atmosphere was stored in the glacial ocean. In addition, studies of paleoproxy records indicate that carbon storage in the glacial terrestrial biosphere was smaller compared to in interglacial climate (Shackleton, 1977; Duplessy et al., 1988; Curry et al., 1988; Crowley, 1995; Adams and Faure, 1998; Ciais et al., 2012; Peterson et al., 2014). During deglaciation, radiocarbon evidence indicate that CO<sub>2</sub> was rapidly released from the ocean back to the atmosphere (Marchitto et al., 2007; Skinner et al., 2010).

5 Numerous processes, both physical and biological, have been identified as possible contributors to increased glacial oceanic storage. As glacial climate was substantially colder than interglacial climate; the global averages of surface, and ocean temperature at the LGM are estimated to have been 3–8 °C and 2.0–3.2 °C colder, respectively, than the pre-industrial (Stocker, 2014; Healy and Severinghaus, 2007; Bereiter et al., 2018). Due to the temperature effect on solubility, a colder ocean can hold more carbon. However, glacial changes in salinity partly offset the temperature effect on solubility (reviewed by, Kohfeld and Ridgwell, 2009). A colder climate is also drier, and the dry conditions led to increased glacial dust deposition compared to interglacial climate (Mahowald et al., 2006). It has been hypothesised that the addition of dust contributed to increased iron availability in the surface ocean, and that this contributed to a strengthening of the biological sequestration of carbon in the glacial ocean compared to interglacials (Martin, 1990). The addition of iron would allow for more complete usage of other nutrients in regions where iron is limiting for biological production. Such strengthening of the retention of biologically-sourced carbon in the deep ocean (or the so-called biological pump), through changes in nutrient availability, light conditions, and/or ocean circulation, has long been considered an important player in the glacial increase in ocean CO<sub>2</sub> storage (Broecker, 1982a; Sarmiento and Toggweiler, 1984; Archer et al., 2000; Sigman and Boyle, 2000). Other studies have pointed to changes in carbonate preservation in coral reefs and deep-sea marine sediments (Berger, 1982; Broecker, 1982a; Archer and Maier-Reimer, 1994). It is likely that reduced ventilation of the deep water, through changes in ocean circulation and expanded sea ice cover acting as a barrier for air-sea gas exchange, contributed to increasing the glacial ocean carbon retention (e.g., Boyle and Keigwin, 1987; Duplessy et al., 1988; Stephens and Keeling, 2000; Marchitto and Broecker, 2006; Adkins, 2013; Menviel et al., 2017; Skinner et al., 2017). Model studies by (Menviel et al., 2017) show that reduced Southern Hemisphere westerly winds produce reduced ventilation of Antarctic Bottom Water (AABW) in line with evidence from proxy records of  $\delta^{13}C$ . In addition, it has been shown that strengthening of the winds over the Southern Ocean was a likely contributor to deglacial outgassing of CO<sub>2</sub> from the ocean to the atmosphere (Mayr et al., 2013). Extensive summaries of the processes responsible for high glacial ocean carbon storage, and examples of their interactions, are given by Brovkin et al. (2007); Kohfeld and Ridgwell (2009); Hain et al. (2010); Sigman et al. (2010). Despite the efforts of identifying the responsible processes, models have been struggling to achieve the full lowering of  $pCO_2^{glac}$  expected for a glacial.

30 In this paper, we focus on the biological pump and how it responds to glacial-like changes in climate. Our aim is to investigate how the level of simplification of the biological carbon uptake in an Earth system model may affect the glacial drawdown of  $pCO_2^{glac}$ . Most biogeochemical models used in glacial climate studies have a simple representation of biological production, which assumes that carbon, C, and inorganic nutrients such as phosphorus, P, are taken up in fixed proportion to

each other. This is modelled using the average ratio of  $C/P$  of the ocean organic matter originally observed by Redfield (1963) ( $C/P = 106/1$ ), or adjustments to these suggested in follow-up studies (Takahashi et al., 1985; Anderson and Sarmiento, 1994).

We investigate whether allowing for a flexible  $C/P$  stoichiometric ratio increases model ocean  $\text{CO}_2$  storage in a glacial-like climate. This possibility was suggested in studies by Broecker (1982b), Archer et al. (2000) and Galbraith and Martiny (2015), but the implications of Redfield versus flexible  $C/P$  for glacial ocean carbon storage has not previously been tested in an Earth system model. This type of non-Redfieldian dynamics were applied in the model used in Eggleston and Galbraith (2018) and Galbraith and de Lavergne (2018), but their results were not analysed in terms of difference from a Redfield model version. In addition, Buchanan et al. (2018) explored the importance of dynamic response of ocean biology, such as flexible stoichiometry, for modelled ocean biogeochemistry in pre-industrial simulations. They found that the dynamic response was fundamental for stabilising the response of ocean DIC to changes in the physical circulation state.

We conduct a sensitivity study, where we apply glacial-like changes in radiative forcing, albedo, wind-forced circulation, remineralisation depth and dust, separately and in combination, to an interglacial control state. Here, changes in radiative forcing and albedo serve to cool the climate, to mimic glacial temperature and ice conditions. The surface wind stress is reduced in the polar regions, in order to pursue reduced AABW ventilation as suggested by paleoproxy evidence (Menviel et al., 2017; Skinner et al., 2017). Ocean cooling reduces the degradation rate of sinking particulate organic carbon, which increases the average depth of remineralisation of organic carbon (Matsumoto, 2007). Drier glacial climate resulted in increased dust deposition, and thereby iron flux, to the ocean (Martin, 1990). All these changes act to increase ocean carbon storage and thereby reduce  $p\text{CO}_2^{\text{atm}}$ . The applied changes are not expected to induce a full glacial maximum model state, but they allow us to explore several important effects on the biological and solubility carbon pumps, and produce a state with glacial-like climate conditions.

We apply the perturbations in two different versions of the Earth system model cGENIE; an original version using fixed Redfield stoichiometry of  $C/P$  (Ridgwell et al., 2007) plus a co-limitation by iron (Tagliabue et al., 2016) for biological production, and a modified version using the non-Redfieldian, nutrient concentration dependent,  $C/P$  stoichiometry suggested by Galbraith and Martiny (2015) and iron co-limitation.

We show that flexible  $C/P$  stoichiometry allows a larger glacial ocean  $\text{CO}_2$  storage, as predicted by the box-model study of Galbraith and Martiny (2015), and that flexible stoichiometry has the largest impact for perturbations in remineralisation depth and dust forcing. Additionally, we show that flexible stoichiometry allows for increased ocean carbon storage without decreasing the storage of preformed nutrients in the deep ocean.

## 2 Methods

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chemistry and ocean biogeochemistry. Model code and user handbook can be found in the cGENIE GitHub repository (cGENIE GitHub repository, 2019). We run a version of cGENIE with the same phosphorus plus iron (Fe) co-limitation scheme as used in the iron cycle model inter-comparison study of Tagliabue et al. (2016). The model branch enabled for use with flexible C:P ratios (see 2.2) is tagged as release v0.9.5, and the model configurations used in this paper are included in this release (cGENIE release v0.9.5, 2019, see Code availability for details).

## 2.2 Stoichiometry

In the original version of the cGENIE Earth system model (Ridgwell et al., 2007), as well as in the version of Tagliabue et al. (2016), the stoichiometric ratios are based on Redfield (1963). Thus, there is a fixed relationship between the number of moles of the elements that are taken up (positive) or released (negative) during production of organic matter in the ocean. This relationship is  $P : C : O_2 = 1 : 106 : -138$ , where  $O_2$  is dissolved oxygen (nitrogen is assumed only implicitly for the purpose of accounting for organic matter creation and remineralisation related alkalinity transformations in the ocean (Ridgwell et al., 2007)). An exception is iron, where Fe:C varies as a function of iron availability as described in Watson et al. (2000).

Although the average elemental composition of organic matter in the ocean is close to the Redfield ratios, the stoichiometry of production of new organic material has shown high in-situ variability. Variability occurs between species, but also within the same species, and has been shown to depend on environmental factors such as nutrient availability, water temperature and light (e.g., Le Quéré et al., 2005b; Galbraith and Martiny, 2015; Yvon-Durocher et al., 2015; Tanioka and Matsumoto, 2017; Moreno et al., 2018). We test the importance of this variability for glacial ocean  $CO_2$  storage by running the same experiments with the fixed Redfield stoichiometry version of cGENIE and with a model version where we have implemented the linear regression model presented by Galbraith and Martiny (2015) (Eq. 1). These two model versions are henceforth denoted *RED* and *GAM*, respectively.

The flexible stoichiometry in *GAM* depends on the ambient concentration of dissolved phosphate ( $[PO_4]$ ) in the water:

$$P : C = 1 : \left( \frac{[PO_4]}{144.9 \mu mol L^{-1}} + 0.0060 \right)^{-1} \quad (1)$$

This relation shows that, when  $[PO_4]$  is low, organisms bind more C per atom of P than they do under high  $[PO_4]$  conditions (Fig. 1). Eq. 1 is applied in cGENIE in the calculations of biological C uptake at the surface ocean based on the surface concentration of  $PO_4$ . In Section 3.1.2, Eq. 1 is also used to translate model surface  $PO_4$  fields to the corresponding surface C/P ratios for the organic matter produced in each grid cell.

## 2.3 Experiments

We start all experiments from an interglacial/modern control state, which has been run for 10,000 years to steady state, using either Redfield ( $Ctrl_{RED}$ ) or variable ( $Ctrl_{GAM}$ ) stoichiometry. The control states have a prescribed  $pCO_2^{atm}$  of 278 ppm and the same climate (Table 1), but due to the differences in C/P, they have different ocean carbon inventories (Table S.1.). In  $Ctrl_{GAM}$ , the export flux of organic matter (see Ridgwell et al., 2007) has a global average C/P composition of 121/1 and

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## 2.3 Experiments

We start all experiments from an interglacial/modern control state, which has been run for 10,000 years to steady state, using either Redfield ( $Ctrl_{RED}$ ) or variable ( $Ctrl_{GAM}$ ) stoichiometry. The control states have a prescribed  $pCO_2^{atm}$  of 278 ppm and the same climate (Table 1), but due to the differences in C/P, they have different ocean carbon inventories (Table S.1.). In  $Ctrl_{GAM}$ , the export flux of organic matter (see Ridgwell et al., 2007) has a global average C/P composition of 121/1 and

thus the global ocean carbon storage is larger than in  $Ctrl_{RED}$ . This also suggest that a perturbation, which increases ocean storage of P through the biological pump, could cause storage of 15 (i.e. 121-106) more carbon atoms in simulations using GAM compared to RED, simply because the average composition of the formed biological material is different. To distinguish between the role of the flexibility of the stoichiometry and the change in the mean composition of organic material, we add a control state with fixed stoichiometry where  $CP = 121/1$  (henceforth denoted  $Ctrl_{121}$ ).

In order to explore the effects of variable stoichiometry, we make a sensitivity study where we apply changes to boundary conditions, individually and in combination (see Section 2.3.3), that may be representative of changes that occurred during glacial periods. All experiments are listed in Table 1.

The applied changes in boundary conditions are

- 10 – physical perturbations (colder climate):
  - radiative forcing corresponding to  $LGM$   $CO_2 = 185$  ppm
  - zonal albedo profile representative of  $LGM$  (calculated from the LGM climate simulation of Davies-Barnard et al., 2017)
- physical perturbations (weaker overturning):
- 15 – reduced wind forcing over the Southern Ocean (Lauderdale et al., 2013, e.g.,) and north of  $35^\circ N$  (see Section 2.3.1).
- biological perturbations:
  - changed remineralisation length scale (e.g., Matsumoto, 2007; Chikamoto et al., 2012; Menviel et al., 2012)
  - increased dust forcing, as simulated for  $LGM$  (regridded from Mahowald et al., 2006)

By applying the above perturbations, we aim to achieve some of the characteristics of the Last Glacial Maximum (LGM) ocean, which appears to have had a global average ocean temperature ( $\overline{T_{dec}}$ )  $2.7^\circ C$  colder than the Holocene (Headly and Severinghaus, 2007), a weakly ventilated deep ocean (e.g., Menviel et al., 2017) and a more efficient biological pump (e.g., Sarmiento and Toggweiler, 1984; Martin, 1990; Sigman and Boyle, 2000). We also aim to increase carbon retention in the deep ocean (Muglia et al., 2018).

The physical perturbations serve to achieve a colder climate (e.g.,  $\overline{T_{dec}}$  cools by  $2.1^\circ C$  c.f.  $Ctrl$ ), thus nearly 80 % of the observed  $2.7^\circ C$ , see Section 3.2.1) and weaker overturning (see Section 3.2.2 and Fig. 2) with a longer residence time of the Antarctic Bottom Water (AABW) cell compared to  $Ctrl$ . Colder conditions achieve a stronger solubility pump, thereby strengthening the retention of carbon in the deep ocean. As the physical perturbations affect the ocean circulation and temperature, they thereby affect biological productivity, e.g. through changed rates in nutrient upwelling and slower growth in colder water (Ridgwell et al., 2007).

30 The biological perturbations serve to achieve a more efficient biological pump, which is connected with increased retention of nutrients and carbon in the deep ocean, and lower surface nutrient concentrations in productive regions (see Sections 3.2.3

thus the global ocean carbon storage is larger than in  $Ctrl_{RED}$ . This also suggest that a perturbation, which increases ocean storage of P through the biological pump, could cause storage of 15 (i.e. 121-106) more carbon atoms in simulations using GAM compared to RED, simply because the average composition of the formed biological material is different. To distinguish between the role of the flexibility of the stoichiometry and the change in the mean composition of organic material, we add a control state with fixed stoichiometry where  $CP = 121/1$  (henceforth denoted  $Ctrl_{121}$ ).

In order to explore the effects of variable stoichiometry, we make a sensitivity study where we apply changes to boundary conditions, individually and in combination (see Section 2.3.3), that may be representative of changes that occurred during glacial periods. All experiments are listed in Table 1.

The applied changes in boundary conditions are

- 10 – physical perturbations (colder climate):
  - radiative forcing corresponding to  $LGM$   $CO_2 = 185$  ppm
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- biological perturbations:
  - changed remineralisation length scale (e.g., Matsumoto, 2007; Chikamoto et al., 2012; Menviel et al., 2012)
  - increased dust forcing, as simulated for  $LGM$  (regridded from Mahowald et al., 2006)

By applying the above perturbations, we aim to approach, but not fully resolve, some of the characteristics of the Last Glacial Maximum (LGM) ocean, which appears to have had a global average ocean temperature ( $\overline{T_{dec}}$ )  $2.57 \pm 0.24^\circ C$  colder than the Holocene (Bereiter et al., 2018), a weakly ventilated deep ocean (e.g., Menviel et al., 2017) and a more efficient biological pump (e.g., Sarmiento and Toggweiler, 1984; Martin, 1990; Sigman and Boyle, 2000). We also aim to increase carbon retention in the deep ocean (Muglia et al., 2018).

The physical perturbations serve to achieve a colder climate ( $\overline{T_{dec}}$  cools by  $2.1^\circ C$  c.f.  $Ctrl$ ), thus 80 % of the observed  $2.6^\circ C$ , see Section 3.2.1) and weaker overturning (see Section 3.2.2 and Fig. 2) with a longer residence time of the Antarctic Bottom Water (AABW) cell compared to  $Ctrl$ . Colder conditions achieve a stronger solubility pump, thereby strengthening the retention of carbon in the deep ocean. As the physical perturbations affect the ocean circulation and temperature, they thereby affect the nutrient distribution, and the rates of nutrient upwelling and biological growth (slower growth in colder water). They thereby affect the biological productivity (Ridgwell et al., 2007).

30 The biological perturbations serve to achieve a more efficient biological pump, which is connected with increased retention of nutrients and carbon in the deep ocean, and lower surface nutrient concentrations in productive regions (see Sections 3.2.3

and 3.2.4). With flexible stoichiometry, lower surface nutrient concentrations results in a higher  $C/P$  ratio, further increasing the export production, and thereby the carbon retention in the deep ocean. In our experiments, we show that the flexible stoichiometry amplifies the response of the biological pump to both physical and biological perturbations.

The perturbations and the experiments are described in detail in Sections 2.3.1–2.3.3.

### 5 2.3.1 Physical perturbations

We change the physical conditions for climate by changing radiative forcing and albedo to LGM-like conditions and denote these changes *LGMphys*. We set the radiative forcing in the model to correspond to an atmosphere with 185 ppm  $\text{CO}_2$  instead of 278. However, we allow the  $p\text{CO}_2^{\text{atm}}$  to freely evolve (starting from the value of 278 ppm of the *Ctrl* state atmosphere) in response to the cooler climate. For albedo, we apply a zonal *LGM* albedo profile (calculated from the LGM climate simulation of Davies-Barnard et al., 2017). Assumptions of a simple zonal profile instead of e.g. a 2D field re-gridded from PMIP LGM simulations allows for a better consistency with the original zonal mean albedo profile developed for the modern configuration of GENIE (Marsh et al., 2011). Together, the changes in radiative forcing and albedo causes the global ocean average temperature ( $\overline{T}_{\text{occ}}$ ) to decrease by 2.1°C compared to *Ctrl* (see Section 3.2.1).

To achieve a longer residence time of the AABW water mass, and an associated increase in carbon and nutrient retention, we apply weaker winds (denoted  $WNA \times 0.5$ ). We use the Southern Ocean wind profile of Lauderdale et al. (2013), where the peak westerly wind strength at 50°S has been reduced half compared to the control state (see Section 2.3.3). The winds north and south of the peak are reduced accordingly to give a continuous profile (see Fig. 2 a of Lauderdale et al., 2013). The result is a weaker overturning (see Table 2) and a longer residence time of the AABW (see Section 4.5) as is expected for the glacial ocean (e.g., Menviel et al., 2017). Thus, this approach is justifiable in a model of reduced complexity. However, there are studies suggesting that the Southern Ocean winds may in fact have been stronger during glacial times (Sime et al., 2013; Kohfeld et al., 2013; Sime et al., 2016). To avoid an expansion of the NADW overturning cell that would be inconsistent with the glacial ocean (e.g., Curry and Oppo, 2005), winds north of 35°N are also gradually reduced so that the wind strength north of 50°N is reduced by half compared to the control state.

### 2.3.2 Biological perturbations

It has been hypothesised that the cooling of the glacial ocean led to a deepening of the remineralisation length scale (henceforth denoted RLS) in the ocean, and thereby more efficient retention of organic carbon in the deep ocean (e.g., Matsumoto, 2007; Chikamoto et al., 2012), which in turn caused a lowering of  $p\text{CO}_2^{\text{atm}}$ . However, Menviel et al. (2012) find that such a deepening results in model changes in export production (i.e. the amount of C captured by primary production that leaves the surface ocean without being remineralised) in poor agreement with paleo-proxies. Deeper remineralisation also results in increased nutrient retention in the deep ocean, thus causing changes in surface nutrient fields and in  $C/P$  ratios of *GAM*. We test the effect of changes in RLS by multiplying the model default RLS by a factor  $Y$  ( $RLS \times Y$ , see Section 2.3.3).

Increased dust forcing leads to increased iron (*Fe*) availability. This allows for increased productivity (and hence more efficient usage of other nutrients) in the high-nutrient, low-chlorophyll (HNLC) regions in the North Pacific, Equatorial Pacific

and 3.2.4). With flexible stoichiometry, lower surface nutrient concentrations results in a higher  $C/P$  ratio, further increasing the export production, and thereby the carbon retention in the deep ocean. In our experiments, we show that the flexible stoichiometry amplifies the response of the biological pump to both physical and biological perturbations.

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### 2.3.2 Biological perturbations

In the ocean, phytoplankton growth rates and remineralisation of particulate organic carbon are processes that both work more slowly at colder temperatures (Eppley, 1972; Laws et al., 2000). Cooling of the ocean would thus lead to decreased production of particulate organic matter (POC), and simultaneously to a slower degradation of POC, with competing effects on export production (i.e. the amount of C captured by primary production that leaves the surface ocean without being remineralised) (Matsumoto, 2007). However, Matsumoto (2007) shows that the effect of slower remineralisation dominates the effect on export production. It has therefore been hypothesised that the cooling of the glacial ocean led to a deepening of the remineralisation

and Southern Ocean, where iron (Fe) is the limiting micronutrient (e.g., Martin, 1990). The variable stoichiometry in *GAM* is expected to be influential if the concentrations of *P* decrease in such regions as a result of increased Fe availability. This process may hence be of importance in a glacial scenario where dust forcing increases as a result of the drier conditions (e.g., Martin, 1990). We apply the regridded LGM dust fields of Mahowald et al. (2006) and denote this change *LGMdust*.

### 2.3.3 Sensitivity experiments and combined simulations

In the sensitivity study, for each of the three *C/P* parametrisations, we first change one forcing at a time (see Table 1). We run simulations where we apply individually the LGM boundary conditions for radiative forcing (*LGMrf*), albedo (*LGMalb*) and dust (*LGMdust*) and one simulation with halved wind stress near the poles (-50 and 50°N) (*WNS* × 0.5). For the remineralisation length scale (RLS), we test a range of values of the multiplication factor  $RLS \times fr$ , where  $fr = \{0.75, 1.25, 1.75\}$ .

10 This allows us to test the sensitivity to deep ocean retention of organic carbon.

We then run simulations where we combine several changes in forcing. We get a colder climate simulation (*LGMphy*) by combining *LGMrf* and *LGMalb*. In simulation *Acomb*, we combine *LGMrf*, *LGMalb*, *LGMdust*, and  $RLS \times 1.25$  (see Table 1). Kwon et al. (2009) show that small changes in remineralisation depth can cause substantial changes in  $pCO_2^{atm}$ .

15 With the RLS deepening of 25%, we keep the corresponding changes in  $pCO_2^{atm}$  from exceeding the  $\approx 20 - 30$  ppm obtained in other studies (Matsumoto, 2007; Menviel et al., 2012). We finally run a glacial-like simulation *GLcomb* (see Section 3.3), which is similar to *Acomb* but also includes the change in wind stress  $WNS \times 0.5$ . The achieved *GLcomb* model state has a colder climate (see Table 2), reduced deep ocean ventilation and more carbon retention in the deep ocean compared to the control state.

## 2.4 Observations

20 For comparison and validation of model results, we use records of ocean state variables from observations of modern data and proxy data from the LGM.

Modern data of ocean temperature, oxygen and nutrients are retrieved from the World Ocean Atlas 2013 (Locarnini et al., 2013; Garcia et al., 2014b, a) and we use the proxy estimates of LGM ocean temperature from Headly and Severinghaus (2007). Average modern day strength of the Atlantic meridional overturning circulation (AMOC) is estimated by McCarthy et al. (2015) from the RAPID-MOCHA array at 26 °N.

25 We use model-data comparison of benthic  $\delta^{13}C$  to assess the statistical similarity (correlation) between both the model control state and glacial-like state (see Section 2.3) to benthic  $\delta^{13}C$  data representing the Late Holocene (0-6 ka, HOL) and Last Glacial Maximum (19-23 ka, LGM), respectively Peterson et al. (2014). Locations of core sites can be seen in Fig. S.1. (see also Fig. 1 in Peterson et al. (2014)). Note that LGM benthic  $\delta^{13}C$  is more  $^{13}C$ -depleted than the Holocene due to the addition of  $^{13}C$ -depleted terrestrial carbon to the glacial ocean (Shackleton, 1977; Curry et al., 1988; Duplessy et al., 1988), which is not simulated in our model experiments. Therefore, to compare our glacial-like simulations (*GLcomb*) to LGM observations, we subtract a Holocene-LGM global average difference of 0.32 ‰ (Gebbie et al., 2015) from the *GLcomb* experiments. Gebbie et al. (2015) state that the wide range of error for the estimate of glacial-to-modern change in benthic  $\delta^{13}C$  of  $0.32 \pm 0.20$  ‰.

length scale (henceforth denoted RLS) in the ocean, and thereby more efficient retention of organic carbon in the deep ocean (Matsumoto, 2007; Chikamoto et al., 2012), which in turn caused a lowering of  $pCO_2^{atm}$ . Menviel et al. (2012) find that such a deepening results in model changes in export production in poor agreement with paleo-proxies, while Chikamoto et al. (2012) find improved model agreement with the glacial proxy records of export production and stable carbon isotopes for

5 temperature-dependent growth rates and remineralisation. Deeper remineralisation also results in increased nutrient retention in the deep ocean, thus causing changes in surface nutrient fields and in *C/P* ratios of *GAM*. We test the effect of changes in RLS by multiplying the model default RLS by a factor  $Y$  ( $RLS \times Y$ ; see Section 2.3.3).

Increased dust forcing leads to increased iron (Fe) availability. This allows for increased productivity (and hence more efficient usage of other nutrients) in the high-nutrient, low-chlorophyll (HNLC) regions in the North Pacific, Equatorial Pacific and

10 Southern Ocean, where iron (Fe) is the limiting micronutrient (Martin, 1990; Moore et al., 2013). The variable stoichiometry in *GAM* is expected to be influential if the concentrations of *P* decrease in such regions as a result of increased Fe availability. This process may hence be of importance in a glacial scenario where dust forcing increases as a result of the drier conditions (Martin, 1990; Moore et al., 2013). We apply the regridded LGM dust fields of Mahowald et al. (2006) and denote this change *LGMdust*.

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Modern data of ocean temperature, oxygen and nutrients are retrieved from the World Ocean Atlas 2018 (Locarnini et al., 2018; Garcia et al., 2018c, b) and we use the proxy estimates of LGM ocean temperature from (Bereiter et al., 2018). Average



suffers from a lack of observations in all ocean basins but the Atlantic. Therefore, we place more emphasis on the results of the model–data comparison in the Atlantic than in the Indo–Pacific sector.

## 2.5 Nutrient utilisation efficiency

The extent to which biology succeeds to use the available nutrients can be determined by calculating the nutrient utilisation efficiency  $\overline{P^*}$  (Ito and Follows, 2005; Ödalen et al., 2018),

$$\overline{P^*} = \frac{P_{rem}}{P_{tot}} \quad (2)$$

which is the fraction of remineralised ( $P_{reg}$ ) to total ( $P_{tot}$ ) nutrients (in this case,  $PO_4$ ) in the ocean. Overlines denote global averages. Remineralised nutrients have been transported from the surface to the interior ocean by the biological pump, and  $P_{rem}$  is given by

$$P_{rem} = P_{tot} - P_{pre} \quad (3)$$

Here,  $P_{pre}$  is preformed  $PO_4$  – the concentration of  $PO_4$  that was present in the water parcel as it sank, thus the fraction that was not used by biology in the surface ocean. In cGENIE, the concentration of preformed tracers is set in the surface ocean and then passively advected through the ocean interior (Ödalen et al., 2018). The biological pump also captures carbon, and a similar relationship can be used for concentrations of DIC, where

$$DIC_{rem} = DIC_{tot} - DIC_{pre} \quad (4)$$

$DIC_{rem}$  is used to compute the ocean storage of remineralised acidic carbon ( $AC_{rem}$ , see Appendix A).  $AC_{rem}$  is biological carbon that entered the ocean in the form of  $CO_2$  in soft tissue (as opposed to carbonates in hard tissue), measured independent of oxygen consumption and/or remineralised phosphate.

In cGENIE,  $P_{pre}$  and  $DIC_{pre}$  are modelled as passive tracers (Ödalen et al. (2018)). Hence, we can use the model output for  $P_{pre}$  in Eq. 3 to compute  $\overline{P^*}$  (Eq. 2).

In a model with fixed Redfield ratio,  $\overline{P^*}$  determines the effect of the biological pump on  $pCO_2^{atm}$ . For example, it has been found that a higher  $\overline{P^*}$  in the initial state gives a lower potential for drawdown of  $pCO_2^{atm}$  in response to similar perturbations (Marinov et al., 2008; Ödalen et al., 2018). However, with variable stoichiometry this is no longer true, since the amount of carbon retained in the deep ocean is not necessarily proportional to  $\overline{P^*}$ .

modern day strength of the Atlantic meridional overturning circulation (AMOC) is estimated by McCarthy et al. (2015) from the RAPID-MOCHA array at 26 °N.

We use model–data comparison of benthic  $\delta^{13}C$  to assess the statistical similarity (correlation) between both the model control state and glacial–like state (see Section 2.3) to benthic  $\delta^{13}C$  data representing the Late Holocene (0–6 ka, HOL) and Last Glacial Maximum (19–23 ka, LGM), respectively Peterson et al. (2014). Locations of core sites can be seen in Fig. S.1 (see also Fig. 1 in Peterson et al. (2014)). Note that LGM benthic  $\delta^{13}C$  is more  $^{13}C$ -depleted than the Holocene due to the addition of  $^{13}C$ -depleted terrestrial carbon to the glacial ocean (Shackleton, 1977; Curry et al., 1988; Duplessy et al., 1988), which is not simulated in our model experiments. Therefore, to compare our glacial–like simulations (*GLcomb*) to LGM observations, we subtract a Holocene–LGM global average difference of 0.32 ‰ (Gebbie et al., 2015) from the *GLcomb* experiments. Gebbie et al. (2015) state that the wide range of error for the estimate of glacial–to–modern change in benthic  $\delta^{13}C$  of  $0.32 \pm 0.20\%$  suffers from a lack of observations in all ocean basins but the Atlantic. Therefore, we place more emphasis on the results of the model–data comparison in the Atlantic than in the Indo–Pacific sector.

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which is the fraction of remineralised ( $P_{reg}$ ) to total ( $P_{tot}$ ) nutrients (in this case,  $PO_4$ ) in the ocean. Overlines denote global averages. Remineralised nutrients have been transported from the surface to the interior ocean by the biological pump, and  $P_{rem}$  is given by

$$P_{rem} = P_{tot} - P_{pre} \quad (3)$$

Here,  $P_{pre}$  is preformed  $PO_4$  – the concentration of  $PO_4$  that was present in the water parcel as it sank, thus the fraction that was not used by biology in the surface ocean. In cGENIE, the concentration of preformed tracers is set in the surface ocean and then passively advected through the ocean interior (Ödalen et al., 2018). The biological pump also captures carbon, and a similar relationship can be used for concentrations of DIC, where

$$DIC_{rem} = DIC_{tot} - DIC_{pre} \quad (4)$$

$DIC_{rem}$  is used to compute the ocean storage of remineralised acidic carbon ( $AC_{rem}$ , see Appendix A).  $AC_{rem}$  is biological carbon that entered the ocean in the form of  $CO_2$  in soft tissue (as opposed to carbonates in hard tissue), measured independent of oxygen consumption and/or remineralised phosphate.

### 3 Results

#### 3.1 Control states

##### 3.1.1 Ocean temperature and circulation

As the three control states,  $Ctrl_{RED}$ ,  $Ctrl_{GAM}$  and  $Ctrl_{I21}$  are driven by the same physical forcings and have the same  $pCO_2^{atm}$ , they have the same ocean circulation pattern (Fig. 2 a, c, e and Table 2, Table S.2) and climate (exemplified by global ocean average temperature ( $\overline{T_{occ}}$ ) in Table 2 and Table S.2). The surface ocean nutrient fields are fairly similar, with small differences due to the different C/P parametrisations (compare Fig. 3 a, and Fig. S.2). The strength of the Atlantic meridional overturning circulation (AMOC), diagnosed in the model as the maximum of the Atlantic meridional overturning streamfunction deeper than 1000 m, is 14 Sv ( $1SV = 1 \cdot 10^6 m^3 s^{-1}$ ) in all control states (Table 2, Table S.2). Results from the RAPID-MOCHA array at 26°N suggest an average AMOC strength of  $17.2 \pm 0.9$  Sv (McCarthy et al., 2015), thus our control state AMOC is a little bit weaker than in present day climate. The observational estimate for  $\overline{T_{occ}}$  according to the World Ocean Atlas 2013 (Locarnini et al., 2013) is 3.49 °C, thus comparable to the 3.56 °C of our  $Ctrl$  simulations. The surface nutrient concentrations of our control state  $Ctrl_{GAM}$  (Fig. 3 a) compare reasonably well with observed surface ocean concentrations of  $PO_4$  (Fig. 3 c), with some underestimation in the Pacific equatorial region, the North Pacific ocean, and the Labrador Sea. The agreement with observations is better for  $Ctrl_{GAM}$  than for  $Ctrl_{RED}$  (Fig. S.2).

##### 3.1.2 Surface nutrient distribution and C/P ratios

In Fig. 3 we see that surface  $PO_4$  fields (left hand column) and the corresponding fields of surface C/P ratios (as given by Eq. 1, right hand column) of  $Ctrl_{GAM}$  (panels a, b) and of observations (panels c, d) are similar in their pattern as well as in the magnitudes of values. Note that high concentrations of  $PO_4$  correspond to low C/P ratios, and vice versa. The highest observed  $PO_4$  concentrations in the Northern and equatorial Pacific are not fully reproduced by the model, but the pattern is well reproduced. In the surface C/P field of  $Ctrl_{GAM}$  (Fig. 3 b) we see the signature of very high nutrient concentrations in the Southern Ocean ( $> 1 \mu mol L^{-1}$ , Fig. 3 b) as a band of low ratios, with the most extreme values near the Antarctic continent, as seen in observations (Fig. 3 d).

The nutrient utilisation efficiency  $\overline{P^*}$  (Eq. 2) in the three control states differs by a few percent; 0.43, 0.46 and 0.42 in  $Ctrl_{RED}$ ,  $Ctrl_{GAM}$  and  $Ctrl_{I21}$  respectively (Table 2). The fraction of  $DIC_{rem}$  in  $DIC_{tot}$  (see Section 2.5, Eq. 4, Table S.1) is 0.065, 0.077 and 0.072 in  $Ctrl_{RED}$ ,  $Ctrl_{GAM}$  and  $Ctrl_{I21}$  respectively.

##### 3.1.3 Ocean dissolved $O_2$

The most apparent difference between  $Ctrl_{RED}$  and  $Ctrl_{GAM}$  is in deep ocean oxygen concentrations, where the global ocean average dissolved  $O_2$  concentration ( $\overline{O_2}$ ) in  $Ctrl_{GAM}$  ( $144 \mu mol kg^{-1}$ ) is lower than in  $Ctrl_{RED}$  and  $Ctrl_{I21}$  (166 and  $171 \mu mol kg^{-1}$ , respectively). Compared to observations (World Ocean Atlas 2013, Fig. 4 a–b), both  $Ctrl_{RED}$  (Fig. 4 c–d) and  $Ctrl_{GAM}$  (Fig. 4 e–f) agree reasonably well with the real ocean.  $Ctrl_{GAM}$  appears to capture better than  $Ctrl_{RED}$  the

In cGENIE,  $P_{pre}$  and  $DIC_{pre}$  are modelled as passive tracers (Ödalen et al. (2018)). Hence, we can use the model output for  $P_{pre}$  in Eq. 3 to compute  $\overline{P^*}$  (Eq. 2).

In a model with fixed Redfield ratio,  $\overline{P^*}$  determines the effect of the biological pump on  $pCO_2^{atm}$ . For example, it has been found that a higher  $\overline{P^*}$  in the initial state gives a lower potential for drawdown of  $pCO_2^{atm}$  in response to similar perturbations (Marinov et al., 2008; Ödalen et al., 2018). However, with variable stoichiometry this is no longer true, since the amount of carbon retained in the deep ocean is not necessarily proportional to  $\overline{P^*}$ .

### 3 Results

#### 3.1 Control states

##### 3.1.1 Ocean temperature and circulation

As the three control states,  $Ctrl_{RED}$ ,  $Ctrl_{GAM}$  and  $Ctrl_{I21}$  are driven by the same physical forcings and have the same  $pCO_2^{atm}$ , they have the same ocean circulation pattern (Fig. 2 a, c, e and Table 2, Table S.2) and climate (exemplified by global ocean average temperature ( $\overline{T_{occ}}$ ) in Table 2 and Table S.2). The surface ocean nutrient fields are fairly similar, with small differences due to the different C/P parametrisations (compare Fig. 3 a, and Fig. S.2). The strength of the Atlantic meridional overturning circulation (AMOC), diagnosed in the model as the maximum of the Atlantic meridional overturning streamfunction deeper than 1000 m, is 14 Sv ( $1SV = 1 \cdot 10^6 m^3 s^{-1}$ ) in all control states (Table 2, Table S.2). Results from the RAPID-MOCHA array at 26°N suggest an average AMOC strength of  $17.2 \pm 0.9$  Sv (McCarthy et al., 2015), thus our control state AMOC is a little bit weaker than in present day climate. The observational estimate for  $\overline{T_{occ}}$  according to the World Ocean Atlas 2018 (Locarnini et al., 2018) is 3.49 °C, thus comparable to the 3.56 °C of our  $Ctrl$  simulations. The surface nutrient concentrations of our control state  $Ctrl_{GAM}$  (Fig. 3 a) compare reasonably well with observed surface ocean concentrations of  $PO_4$  (Fig. 3 c), with some underestimation in the Pacific equatorial region, the North Pacific ocean, and the Labrador Sea. The agreement with observations is better for  $Ctrl_{GAM}$  than for  $Ctrl_{RED}$  (Fig. S.2).

##### 3.1.2 Surface nutrient distribution and C/P ratios

In Fig. 3 we see that surface  $PO_4$  fields (left hand column) and the corresponding fields of surface C/P ratios (as given by Eq. 1, right hand column) of  $Ctrl_{GAM}$  (panels a, b) and of observations (panels c, d) are similar in their pattern as well as in the magnitudes of values. Note that high concentrations of  $PO_4$  correspond to low C/P ratios, and vice versa. The highest observed  $PO_4$  concentrations in the Northern and equatorial Pacific are not fully reproduced by the model, but the pattern is well reproduced. In the surface C/P field of  $Ctrl_{GAM}$  (Fig. 3 b) we see the signature of very high nutrient concentrations in the Southern Ocean ( $> 1 \mu mol L^{-1}$ , Fig. 3 b) as a band of low ratios, with the most extreme values near the Antarctic continent, as seen in observations (Fig. 3 d).

equatorial oxygen minimum in the Atlantic basin, but goes too low in the North Pacific. In  $Ctrl_{GAM}$  (Fig. 4 f), the North Pacific is markedly lower in oxygen than in  $Ctrl_{RED}$  (Fig. 4 d) and even anoxic in the oxygen minimum zone (OMZ). This should be kept in mind when analysing the oxygen sections of the glacial-like states  $GLcomb_{RED}$  (Fig. 4 g-h) and  $GLcomb_{GAM}$  (Fig. 4 i-j). Global averages for dissolved  $O_2$  are given in Table 2.

### 5 3.1.4 Ocean $\delta^{13}C$

By comparing  $Ctrl_{RED}$   $\delta^{13}C$  and Holocene (0–6 ka, HOL) benthic  $\delta^{13}C$  values, we estimate a global model–data correlation of 0.78 (Table S.3). The modern-day Atlantic Ocean has a distinctive spatial  $\delta^{13}C$  pattern (Fig. 5 a, Fig. S.1) with  $^{13}C$ -enriched values in the intermediate depth (<2 km) North Atlantic and Nordic Seas and  $^{13}C$ -depleted values in the deep (>2.5 km) South Atlantic. While the model produces a weaker gradient than the observed HOL Atlantic Ocean (corr. 0.50, Table S.3) the model correlates well with Eastern Atlantic  $\delta^{13}C$  records (Fig. S.1). For the Indo-Pacific, the weaker benthic  $\delta^{13}C$  gradient is well represented by the model (Fig. 5 e). This pattern emerges mainly due to  $^{13}C$ -depleted, biologically sourced carbon that is accumulated in the weak circulation region of the interior North Pacific (e.g., Matsumoto et al., 2002). However, Indo-Pacific  $\delta^{13}C$  values of  $Ctrl_{RED}$  are overall lower than the HOL observations. The overall model–data correlation for the Indo-Pacific is 0.39 (Table S.3). Comparing the control states of the  $RED$  and  $GAM$  model versions,  $\delta^{13}C$  patterns (Fig. 5 a, e and Fig. S.3, a, e) and model–data correlations with HOL observations (Table S.3) are similar between the model versions, with somewhat lower correlations for  $GAM$ .

### 3.2 Sensitivity experiments

The applied changes listed in Table 1 cause changes in e.g. ocean overturning, temperature, surface nutrient distributions and biological productivity, which result in changed  $pCO_2^{atm}$ . The resulting steady state global average values for temperature ( $\overline{T_{oce}}$ ), dissolved oxygen ( $\overline{O_2}$ ), and nutrient utilisation efficiency  $\overline{P^*}$ , as well as the maximum and minimum of the Atlantic meridional overturning streamfunction, are listed in Table 2.

#### 3.2.1 Radiative forcing and albedo

In the simulations where radiative forcing and albedo are changed to represent LGM conditions ( $LGM_{rf} + LGM_{alb} = LGM_{phy}$ ), the reductions in  $pCO_2^{atm}$  are similar in the  $RED$  and the  $GAM$  model versions. In  $LGM_{phy}$ , the resulting  $pCO_2^{atm}$  is 245.4 and 244.9 ppm respectively, thus a reduction of 33 ppm compared to the  $Ctrl$  278 ppm (Fig. 6). Here, variable  $C/P$  does not impact the results, because changes in the surface nutrient distribution (Fig. 7 a), and the associated changes in  $C/P$  (Fig. 8 a), are limited to very high latitudes where productivity is already low in the control state, due to low temperatures and a lack of light and iron. The drawdown of  $pCO_2^{atm}$  can mainly be attributed to the increase in solubility carbon ( $C_{solv}$ ) due to ocean cooling, and to an increase in sea ice, which prevents air–sea gas exchange and therefore causes an increase in disequilibrium carbon ( $C_{dis}$ ) (Ódalen et al., 2018). Ocean cooling amounts to 2.1°C in  $LGM_{phy}$  compared to  $Ctrl$  ( $\overline{T_{oce}}$  in Table 2). In cGENIE, the increase in  $C_{solv}$  associated with ocean cooling corresponds to  $\approx 7 \pm 1.5$  ppm °C<sup>-1</sup>

The nutrient utilisation efficiency  $\overline{P^*}$  (Eq. 2) in the three control states differs by a few percent; 0.43, 0.46 and 0.42 in  $Ctrl_{RED}$ ,  $Ctrl_{GAM}$  and  $Ctrl_{121}$  respectively (Table 2). The fraction of  $DIC_{rem}$  in  $DIC_{tot}$  (see Section 2.5, Eq. 4, Table S.1) is 0.065, 0.077 and 0.072 in  $Ctrl_{RED}$ ,  $Ctrl_{GAM}$  and  $Ctrl_{121}$  respectively.

### 3.1.3 Ocean dissolved $O_2$

5 The most apparent difference between  $Ctrl_{RED}$  and  $Ctrl_{GAM}$  is in deep ocean oxygen concentrations, where the global ocean average dissolved  $O_2$  concentration ( $\overline{O_2}$ ) in  $Ctrl_{GAM}$  ( $144 \mu mol kg^{-1}$ ) is lower than in  $Ctrl_{RED}$  and  $Ctrl_{121}$  (166 and 152  $\mu mol kg^{-1}$ , respectively). Compared to observations (World Ocean Atlas 2013, Fig. 4 a–b), both  $Ctrl_{RED}$  (Fig. 4 c–d) and  $Ctrl_{GAM}$  (Fig. 4 e–f) agree reasonably well with the real ocean.  $Ctrl_{GAM}$  appears to capture better than  $Ctrl_{RED}$  the equatorial oxygen minimum in the Atlantic basin, but goes too low in the North Pacific. In  $Ctrl_{GAM}$  (Fig. 4 f), the North Pacific is markedly lower in oxygen than in  $Ctrl_{RED}$  (Fig. 4 d) and even anoxic in the oxygen minimum zone (OMZ). This should be kept in mind when analysing the oxygen sections of the glacial-like states  $GLcomb_{RED}$  (Fig. 4 g–h) and  $GLcomb_{GAM}$  (Fig. 4 i–j). Global averages for dissolved  $O_2$  are given in Table 2.

### 3.1.4 Ocean $\delta^{13}C$

By comparing  $Ctrl_{RED}$   $\delta^{13}C$  and Holocene (0–6 ka, HOL) benthic  $\delta^{13}C$  values, we estimate a global model–data correlation of 0.78 (Table S.3). The modern-day Atlantic Ocean has a distinctive spatial  $\delta^{13}C$  pattern (Fig. 5 a, Fig. S.1) with  $^{13}C$ -enriched values in the intermediate depth (<2 km) North Atlantic and Nordic Seas and  $^{13}C$ -depleted values in the deep (>2.5 km) South Atlantic. While the model produces a weaker gradient than the observed HOL Atlantic Ocean (corr. 0.50, Table S.3) the model correlates well with Eastern Atlantic  $\delta^{13}C$  records (Fig. S.1). For the Indo-Pacific, the weaker benthic  $\delta^{13}C$  gradient is well represented by the model (Fig. 5 e). This pattern emerges mainly due to  $^{13}C$ -depleted, biologically sourced carbon that is accumulated in the weak circulation region of the interior North Pacific (Matsumoto et al., 2002). However, Indo-Pacific  $\delta^{13}C$  values of  $Ctrl_{RED}$  are overall lower than the HOL observations. The overall model–data correlation for the Indo-Pacific is 0.39 (Table S.3). Comparing the control states of the  $RED$  and  $GAM$  model versions,  $\delta^{13}C$  patterns (Fig. 5 a, e and Fig. S.3 a, e) and model–data correlations with HOL observations (Table S.3) are similar between the model versions, with somewhat lower correlations for  $GAM$ .

### 25 3.2 Sensitivity experiments

The applied changes listed in Table 1 cause changes in ocean characteristics such as overturning circulation, temperature, surface nutrient distributions and biological productivity, which result in changed  $pCO_2^{atm}$ . The resulting steady state global average values for temperature ( $\overline{T_{oce}}$ ), dissolved oxygen ( $\overline{O_2}$ ), and nutrient utilisation efficiency  $\overline{P^*}$ , as well as the maximum and minimum of the Atlantic meridional overturning streamfunction, are listed in Table 2.

(Ódalen et al., 2018, supplementary Fig. S.1). Thus, in *LGMphy*  $C_{sat,T}$  and  $C_{dis}$  should contribute roughly 40 and 60 % respectively of the change in  $pCO_2^{atm}$ . Note that cGENIE underestimates the true effect of ocean cooling on solubility, due to a temperature restriction on the solubility constants (Ódalen et al., 2018). This temperature restriction limits solubility from changing below 2.0 °C. In this case, the solubility effect on  $pCO_2^{atm}$  of reducing  $T_{occ}$  by 2.1 °C (from 3.6 °C to 1.5°C,  $\approx 15$  ppm) is thus comparable to only 1.6 °C of cooling (from 3.6 °C to 2.0 °C,  $\approx 11$  ppm), and the solubility effect is underestimated by  $\approx 4$  ppm.

### 3.2.2 Reduced wind forcing

When the peak of Southern Ocean (henceforth SO) winds is reduced, the strength of the overturning circulation of AABW decreases (see difference in Southern Hemisphere overturning streamfunction between Fig. 2 a and b). Thus, given that the volume of AABW does not change, its residence time increases. This also means that the upwelling nutrient-rich water in the SO stays a longer time near the surface and loses more nutrients before being subducted. This decreases the SO concentration of preformed phosphate in  $WNS \times 0.5_{RED}$  compared to *Ctrl*, as seen in Fig. 7 b, and increases the nutrient utilisation efficiency  $\overline{P^*}$  (Table 2, Fig. 9). This leads to a drawdown of  $pCO_2^{atm}$  of 12.9 ppm compared to *Ctrl\_{RED}* (Fig. 6). As the nutrient concentration in the SO decreases (Fig. 7 b), the flexible *C/P* ratio (Fig. 8 b) leads to an increased carbon capture efficiency in *GAM* compared to *RED* (see  $GLcomb-Ctrl$  of biologically sourced carbon ( $AC_{rem}$ ) in Fig. 9), which is partly compensated by a reverse effect in the Pacific equatorial region. Consequently, in  $WSN \times 0.5_{GAM}$ , we get a reduction of  $pCO_2^{atm}$  of 16.3 ppm compared to *Ctrl\_{GAM}* (Fig. 6). Hence, for halved peak wind stress at  $\pm 50^\circ N$ , the flexible stoichiometry increases the drawdown by  $\approx 26$  %. In a simulation with reduced wind stress and fixed *C/P* stoichiometry of 121/1 ( $WNS \times 0.5_{121}$ ), we get a  $pCO_2^{atm}$  of 263.5 ppm, thus a drawdown of 14.5 ppm. This indicates that, in this case, about half of the effect of the variable stoichiometry can be attributed to a difference in the mean *C/P* composition of the organic material between the control states *Ctrl\_{RED}* and *Ctrl\_{GAM}*.

### 3.2.3 Remineralisation length scale

When the remineralisation length scale (RLS) increases, the biological material reaches deeper before it is remineralised, and it takes longer for it to be returned to the surface. Therefore, more of the biologically sourced carbon ( $AC_{rem}$ ) and nutrients are present in the deep ocean at any given time, leading to an increase in  $\overline{P^*}$  (Table 2, Fig. 9) and a decrease in  $pCO_2^{atm}$  (Fig. 6). The deeper we make the RLS, the bigger the drawdown of  $pCO_2^{atm}$  – in  $RLS \times 1.25_{RED}$  and  $RLS \times 1.75_{RED}$   $pCO_2^{atm}$  decreases by 14 and 33 ppm, respectively, compared to *Ctrl\_{RED}*. In *GAM*, the drawdown in each experiment is increased by an additional  $\approx 30$  %, thus  $RLS \times 1.25_{GAM}$  and  $RLS \times 1.75_{GAM}$  see a reduction of  $pCO_2^{atm}$  of 18 and 44 ppm, respectively, compared to *Ctrl\_{GAM}* (Table S.2). Our changes in RLS cause very small, but global, changes in surface nutrients (ex.  $RLS \times 1.25$  in Fig. 7 c), which, through the small resulting changes in *C/P* (Fig. 8 c), still contribute to the additional drawdown of  $pCO_2^{atm}$  in *GAM*. Experiments with deeper RLS in 121 ( $RLS \times 1.25_{121}$  and  $RLS \times 1.75_{121}$ ), suggest that about 40 % of the observed  $pCO_2^{atm}$  differences can again be attributed to the difference in export flux average *C/P* in the control state.

### 3.2.1 Radiative forcing and albedo

In the simulations where radiative forcing and albedo are changed to represent LGM conditions ( $LGMrf + LGMalb = LGMphy$ ), the reductions in  $pCO_2^{atm}$  are similar in the *RED* and the *GAM* model versions. In *LGMphy*, the resulting  $pCO_2^{atm}$  is 245.4 and 244.9 ppm respectively, thus a reduction of 33 ppm compared to the *Ctrl* 278 ppm (Fig. 6). Here, variable *C/P* does not impact the results, because changes in the surface nutrient distribution (Fig. 7 a), and the associated changes in *C/P* (Fig. 8 a), are limited to very high latitudes where productivity is already low in the control state, due to low temperatures and a lack of light and iron. The drawdown of  $pCO_2^{atm}$  can mainly be attributed to the increase in solubility carbon ( $C_{sat,T}$ ) due to ocean cooling, and to an increase in sea ice, which prevents air-sea gas exchange and therefore causes an increase in disequilibrium carbon ( $C_{dis}$ ) (Ódalen et al., 2018). Ocean cooling amounts to 2.1 °C in *LGMphy* compared to *Ctrl* ( $T_{occ}$  in Table 2). In cGENIE, the increase in  $C_{sat,T}$  associated with ocean cooling corresponds to  $\sim 7 \pm 1.5$  ppm °C<sup>-1</sup> (Ódalen et al., 2018, supplementary Fig. S.1). Thus, in *LGMphy*  $C_{sat,T}$  and  $C_{dis}$  should contribute roughly 40 and 60 % respectively of the change in  $pCO_2^{atm}$ . Note that cGENIE underestimates the true effect of ocean cooling on solubility, due to a temperature restriction on the solubility constants (Ódalen et al., 2018). This temperature restriction limits solubility from changing below 2.0 °C. In this case, the solubility effect on  $pCO_2^{atm}$  of reducing  $T_{occ}$  by 2.1 °C (from 3.6 °C to 1.5°C,  $\approx 15$  ppm) is thus comparable to only 1.6 °C of cooling (from 3.6 °C to 2.0 °C,  $\approx 11$  ppm), and the solubility effect is underestimated by  $\approx 4$  ppm. As we do not change salinity, we are simultaneously likely to overestimate the increase in solubility between *Ctrl* and a glacial-like state, by  $\sim 6$  ppm (Kohfeld and Ridgwell, 2009). This effect is consistent for any choice of *C/P* parametrisation, and is therefore not explored further.

### 3.2.2 Reduced wind forcing

When the peak of Southern Ocean (henceforth SO) winds is reduced, the strength of the overturning circulation of AABW decreases (see difference in Southern Hemisphere overturning streamfunction between Fig. 2 a and b). Thus, given that the volume of AABW does not change, its residence time increases. This also means that the upwelling nutrient-rich water in the SO stays a longer time near the surface and loses more nutrients before being subducted. This decreases the SO concentration of preformed phosphate in  $WNS \times 0.5_{RED}$  compared to *Ctrl*, as seen in Fig. 7 b, and increases the nutrient utilisation efficiency  $\overline{P^*}$  (Table 2, Fig. 9). This leads to a drawdown of  $pCO_2^{atm}$  of 12.9 ppm compared to *Ctrl\_{RED}* (Fig. 6). As the nutrient concentration in the SO decreases (Fig. 7 b), the flexible *C/P* ratio (Fig. 8 b) leads to an increased carbon capture efficiency in *GAM* compared to *RED* (see  $GLcomb-Ctrl$  of biologically sourced carbon ( $AC_{rem}$ ) in Fig. 9), which is partly compensated by a reverse effect in the Pacific equatorial region. Consequently, in  $WSN \times 0.5_{GAM}$ , we get a reduction of  $pCO_2^{atm}$  of 16.3 ppm compared to *Ctrl\_{GAM}* (Fig. 6). Hence, for halved peak wind stress at  $\pm 50^\circ N$ , the flexible stoichiometry increases the drawdown by  $\approx 26$  %.

In a sensitivity test where we make the RLS 25 % shallower (which would be representative of a warmer climate c.f. *Ctrl*), the  $pCO_2^{atm}$  increases by 18 and 23 ppm in *RED* and *GAM* respectively compared to their control states (see  $RLS \times 0.75_{RED}$  and  $RLS \times 0.75_{GAM}$  in Table S.2.). Interestingly, the response in  $pCO_2^{atm}$  is again  $\approx 30$  % larger in *GAM*. The variable stoichiometry thus amplifies the effect on  $pCO_2^{atm}$  by any change in RLS.

### 3.2.4 Dust forcing

The simulations with LGM dust forcing (*LGMdust*, Table 1) show the largest difference in  $pCO_2^{atm}$  between the *RED* and the *GAM*. In *LGMdust\_{RED}*,  $pCO_2^{atm}$  decreases by 16 ppm compared to *Ctrl\_{RED}*, whereas *LGMdust\_{GAM}* sees a reduction of 21 ppm compared to *Ctrl\_{GAM}* (Fig. 6). The drawdown is thus  $\approx 30$  % larger with variable stoichiometry.  $\approx 10$  % can be explained by a change in average composition of the exported organic material (see *LGMdust\_{121}* in Table S.2., where the drawdown is 18 ppm, and  $\approx 10$  % larger than in *LGMdust\_{RED}*).

As anticipated, the iron added by the dust forcing allows more efficient usage of P in the HNLC-regions, which increases  $\overline{P^*}$  and the ocean storage of biologically sourced carbon (Table 2, Fig. 9). This reduces the surface nutrient concentrations in these areas (Fig. 7 d). In the *GAM* model version, this is followed by increased C/P ratios in these areas (Fig. 8 d), resulting in a lower  $pCO_2^{atm}$  in *LGMdust\_{GAM}* than in *LGMdust\_{RED}*. The largest anomalies in  $PO_4$  concentrations, and consequently in C/P, are observed in subantarctic zone of the Southern Ocean, particularly in the Atlantic and Indian sectors. This subantarctic increase in biological efficiency is consistent with radionuclide proxy data from the LGM (e.g., Kumar et al., 1995; Kohfeld et al., 2005).

### 3.3 Combined experiments

We show the results of two different combined simulations; *Acomb* and *GLcomb*. *GLcomb* is the “glacial-like” simulation, which combines all the sensitivity experiments (Table 1). *Acomb* omits the reduction in wind stress.

#### 3.3.1 Ocean temperature and circulation

In the glacial-like simulations, *GLcomb\_{RED}* and *GLcomb\_{GAM}*, the global average ocean temperature ( $\overline{T_{occ}}$ ) is 1.7 °C lower than in the respective control states (Table 2). Headly and Severinghaus (2007) estimate LGM  $\overline{T_{occ}}$  to have been  $2.6 \pm 0.6$  °C colder than the modern ocean. *GLcomb* is thus just outside the one standard deviation limit of the warm end of this estimate.

In *Acomb*,  $\overline{T_{occ}}$  is 2.1 °C cooler than *Ctrl*, thus this simulation falls within the uncertainty of the Headly and Severinghaus (2007) estimate for the LGM.

Ocean overturning circulation weakens in *GLcomb* compared to *Ctrl* (Fig. 2, Table 2), mainly as a result of the wind stress reduction. For example, the AMOC (here measured as the maximum of the Atlantic overturning streamfunction) reduces in strength by  $\approx 15$  %, from 14 Sv to 12 Sv (Table 2). The global meridional overturning stream function reveals that the SO overturning cell sees a reduction in transport (Fig. 2 d), which is associated with weaker upwelling and thus longer residence

#### 3.2.3 Remineralisation length scale

When the remineralisation length scale (RLS) increases, the biological material reaches deeper before it is remineralised, and it takes longer for it to be returned to the surface. Therefore, more of the biologically sourced carbon ( $AC_{rem}$ ) and nutrients are present in the deep ocean at any given time, leading to an increase in  $\overline{P^*}$  (Table 2, Fig. 9) and a decrease in  $pCO_2^{atm}$  (Fig. 6). The deeper we make the RLS, the bigger the drawdown of  $pCO_2^{atm}$  – in  $RLS \times 1.25_{RED}$  and  $RLS \times 1.75_{RED}$   $pCO_2^{atm}$  decreases by 14 and 33 ppm, respectively, compared to *Ctrl\_{RED}*. In *GAM*, the drawdown in each experiment is increased by an additional  $\approx 30$  %, thus  $RLS \times 1.25_{GAM}$  and  $RLS \times 1.75_{GAM}$  see a reduction of  $pCO_2^{atm}$  of 18 and 44 ppm, respectively, compared to *Ctrl\_{GAM}* (Table S.2). Our changes in RLS cause very small, but global, changes in  $PO_4$  concentrations (global average anomaly =  $-0.016 \mu M$ ,  $RLS \times 1.25$  in Fig. 7 c), which, through the small resulting changes in C/P (Fig. 8 c), still contribute to the additional drawdown of  $pCO_2^{atm}$  in *GAM*.

In a sensitivity test where we make the RLS 25 % shallower (which would be representative of a warmer climate c.f. *Ctrl*), the  $pCO_2^{atm}$  increases by 18 and 23 ppm in *RED* and *GAM* respectively compared to their control states (see  $RLS \times 0.75_{RED}$  and  $RLS \times 0.75_{GAM}$  in Table S.2.). Interestingly, the response in  $pCO_2^{atm}$  is again  $\approx 30$  % larger in *GAM*. The variable stoichiometry thus amplifies the effect on  $pCO_2^{atm}$  by any change in RLS. The potential implications of this result for warm climate scenarios is further discussed in Section 4.1.

#### 3.2.4 Dust forcing

The simulations with LGM dust forcing (*LGMdust*, Table 1) show the largest difference in  $pCO_2^{atm}$  between the *RED* and the *GAM*. In *LGMdust\_{RED}*,  $pCO_2^{atm}$  decreases by 16 ppm compared to *Ctrl\_{RED}*, whereas *LGMdust\_{GAM}* sees a reduction of 21 ppm compared to *Ctrl\_{GAM}* (Fig. 6). The drawdown is thus  $\approx 30$  % larger with variable stoichiometry. About a third ( $\approx 10$  % of  $\approx 30$  %) of the increase in drawdown can be explained by a change in average C/P composition of the organic material that is exported out of the surface ocean (see Section 4.4).

As anticipated, the iron added by the dust forcing allows more efficient usage of P in the HNLC-regions, which increases the ocean storage of biologically sourced carbon  $P_{rem}$  (thus,  $P^*$  increases, Table 2, Fig. 9). This reduces the surface nutrient concentrations in these areas (Fig. 7 d). In the *GAM* model version, this is followed by increased C/P ratios in these areas (Fig. 8 d), resulting in a lower  $pCO_2^{atm}$  in *LGMdust\_{GAM}* than in *LGMdust\_{RED}*. The largest anomalies in  $PO_4$  concentrations, and consequently in C/P, are observed in subantarctic zone of the Southern Ocean, particularly in the Atlantic and Indian sectors. This subantarctic increase in biological efficiency is consistent with radionuclide proxy data ( $^{10}Be$ ,  $^{230}Th$ ,  $^{231}Pa$ ) from the LGM (e.g., Kumar et al., 1995; Kohfeld et al., 2005).

#### 3.3 Combined experiments

We show the results of two different combined simulations; *Acomb* and *GLcomb*. *GLcomb* is the “glacial-like” simulation, which combines all the sensitivity experiments (Table 1). *Acomb* omits the reduction in wind stress.

time for AABW, as hypothesised for the glacial ocean (e.g., Menviel et al., 2017). In *Acomb*, where the wind stress is kept at modern values, the ocean overturning circulation remains similar to the control state (Table 2).

### 3.3.2 Surface nutrient distribution and C/P ratios

In the surface nutrient anomalies ( $GLcomb - Ctrl$ , shown for *GAM* in Fig. 7 f), we see the strongest response in the Southern Ocean, with different effects south and north of the so-called biogeochemical divide described by Marinov et al. (2006). Marinov et al. (2006) show that the air–sea balance of  $CO_2$  is dominated by processes in the waters close to Antarctica, whereas global export production is instead controlled by the biological pump and circulation in the Subantarctic region. The border between these two regimes is referred to as the biogeochemical divide. South of the biogeochemical divide, close to the Antarctic continent, we see an increase in  $GLcomb$  nutrient concentrations compared to *Ctrl* (Fig. 7 f), which coincides with an increase in sea-ice in this area (not shown). Colder conditions due to changed albedo and radiative forcing, with more sea ice than in the control state, cause a reduction in biological production, leaving more unused P in the surface layer (Fig. 7 a). North of the biogeochemical divide, increased aeolian dust flux increases the productivity of the biology, which reduces P in the surface compared to the control (Fig. 7 d). In combination with circulation changes, resulting from the reduced SO wind stress (Fig. 7 b), and deeper remineralisation (Fig. 7 c), P concentrations in the Subantarctic region are strongly reduced (Fig. 7 f). In the North and Equatorial Pacific, there is also a reduction of P (Fig. 7 f), mainly due to the increased dust flux (Fig. 7 d). There is an increase in P seen in the Arctic, again coincident with an increase in sea ice in the same area. As a result of these changes, we see strong positive anomalies in C/P in the HNLC-regions, and negative anomalies in the highest latitude bands (Fig. 8 f). The organic matter that is exported out of the upper layer (henceforth referred to as export production) in  $GLcomb_{GAM}$  has a global average C/P ratio of 134/1.

### 3.3.3 Ocean dissolved $O_2$

Despite colder conditions, which allow for more dissolution of  $O_2$ , the reduction in  $\overline{O_2}$  is evident in the  $GLcomb$ -simulations (Fig. 4). This mirrors the increase of  $AC_{rem}$  (Fig. 9). The  $\overline{O_2}$  reduction is about 50 % larger in *GAM* compared to *RED*. As the initial state  $Ctrl_{GAM}$  is already lower in oxygen than  $Ctrl_{RED}$  ( $144 \mu mol kg^{-1}$  compared to  $166 \mu mol kg^{-1}$ ), and variable stoichiometry allows for additional ocean storage of organic carbon, the end state  $\overline{O_2}$  is drastically lower in  $GLcomb_{GAM}$  ( $74 \mu mol kg^{-1}$ ) compared to  $GLcomb_{RED}$  ( $122 \mu mol kg^{-1}$ ) and  $GLcomb_{121}$  ( $124 \mu mol kg^{-1}$ ).

### 3.3.4 Ocean $\delta^{13}C$

In  $GLcomb_{RED}$  (contours in Fig. 5 b,d), the Atlantic North–South gradient in  $\delta^{13}C$  is stronger than in  $Ctrl_{RED}$  (contours in Fig. 5 a,c). This strong gradient is not observed in the Holocene Atlantic  $\delta^{13}C$ -data (dots in Fig. 5 a,b), but is prominent in the LGM time slice (dots in Fig. 5 c,d). The LGM observations are well reproduced in  $GLcomb_{red}$  (corr. 0.62, Table S.3.), especially in the East Atlantic (corr. 0.77). When we correct  $GLcomb_{RED}$  for the absence of injected terrestrial carbon, we see clear similarities with LGM observations (Fig. 5 d), though the southernmost cores still indicate more  $^{13}C$ -depleted conditions

### 3.3.1 Ocean temperature and circulation

In the glacial-like simulations,  $GLcomb_{RED}$  and  $GLcomb_{GAM}$ , the global average ocean temperature ( $\overline{T_{oce}}$ ) is  $1.7^\circ C$  lower than in the respective control states (Table 2). Headly and Severinghaus (2007) estimate LGM  $\overline{T_{oce}}$  to have been  $2.7 \pm 0.6^\circ C$  colder than the modern ocean, while a more recent estimate by Bereiter et al. (2018) constrains  $\overline{T_{oce}}$  to  $2.57 \pm 0.24$ .  $GLcomb$  is thus just outside the one standard deviation limit of the warm end of the Headly and Severinghaus (2007) estimate for the LGM. In *Acomb*,  $\overline{T_{oce}}$  is  $2.1^\circ C$  cooler than *Ctrl*, thus this simulation falls within the uncertainty of the Headly and Severinghaus (2007) estimate. Compared to the Bereiter et al. (2018) estimate, our combined experiments  $GLcomb$  and *Acomb* achieve 64 and 82 % of the glacial–interglacial difference in  $\overline{T_{oce}}$ , respectively. As anticipated, our combined forcings do not induce a full glacial maximum state, but a state with glacial-like climate conditions.

Ocean overturning circulation weakens in  $GLcomb$  compared to *Ctrl* (Fig. 2, Table 2), mainly as a result of the wind stress reduction. For example, the AMOC (here measured as the maximum of the Atlantic overturning streamfunction) reduces in strength by  $\sim 15\%$ , from 14 Sv to 12 Sv (Table 2). The global meridional overturning stream function reveals that the SO overturning cell sees a reduction in transport (Fig. 2 d), which is associated with weaker upwelling and thus longer residence time for AABW, as hypothesised for the glacial ocean (e.g., Menviel et al., 2017; Skinner et al., 2017). In *Acomb*, where the wind stress is kept at modern values, the ocean overturning circulation remains similar to the control state (Table 2).

### 3.3.2 Surface nutrient distribution and C/P ratios

In the surface nutrient anomalies ( $GLcomb - Ctrl$ , shown for *GAM* in Fig. 7 f), we see the strongest response in the Southern Ocean, with different effects south and north of the so-called biogeochemical divide described by Marinov et al. (2006). Marinov et al. (2006) show that the air–sea balance of  $CO_2$  is dominated by processes in the waters close to Antarctica, whereas global export production is instead controlled by the biological pump and circulation in the Subantarctic region. The border between these two regimes is referred to as the biogeochemical divide. South of the biogeochemical divide, close to the Antarctic continent, we see an increase in  $GLcomb$  nutrient concentrations compared to *Ctrl* (Fig. 7 f), which coincides with an increase in sea-ice in this area (not shown). Colder conditions due to changed albedo and radiative forcing, with more sea ice than in the control state, cause a reduction in biological production, leaving more unused P in the surface layer (Fig. 7 a). North of the biogeochemical divide, increased aeolian dust flux increases the productivity of the biology, which reduces P in the surface compared to the control (Fig. 7 d). In combination with circulation changes, resulting from the reduced SO wind stress (Fig. 7 b), and deeper remineralisation (Fig. 7 c), P concentrations in the Subantarctic region are strongly reduced (Fig. 7 f). In the North and Equatorial Pacific, there is also a reduction of P (Fig. 7 f), mainly due to the increased dust flux (Fig. 7 d). There is an increase in P seen in the Arctic, again coincident with an increase in sea ice in the same area. As a result of these changes, we see strong positive anomalies in C/P in the HNLC-regions, and negative anomalies in the highest latitude bands (Fig. 8 f). The organic matter that is exported out of the upper layer (henceforth referred to as export production) in  $GLcomb_{GAM}$  has a global average C/P ratio of 134/1.

than the model. In the Indo-Pacific,  $GLcomb_{RED}$  is too  $^{13}C$ -depleted compared to LGM observations, particularly with the correction for the absence of a terrestrial signal (Fig. 5 h), and the model–data correlation is poor (0.05). For the Indo-Pacific, the model–data correlation for Holocene data is similar between  $GLcomb_{RED}$  and  $Ctrl_{RED}$  (0.24 and 0.39 respectively, Table S.3). This suggests that the poor correlation with LGM data is simply due to our changes in forcings being insufficient to achieve the required rearrangements in Indo-Pacific circulation patterns. In  $GLcomb$ , similarly as in  $Ctrl$ , there is very little difference between the  $RED$  and  $GAM$  model versions in terms of  $\delta^{13}C$  patterns (compare Fig. 5 d,h to Fig. S.3. d,h) and model–data correlations (Table S.3). However, there are overall lower values of  $\delta^{13}C$  in  $GAM$ , reflecting the larger storage of biologically sourced carbon in the deep ocean in this model version.

### 3.3.5 Atmospheric $CO_2$

In the combined experiments  $Acomb$  and  $GLcomb$ ,  $pCO_2^{atm}$  decreases strongly compared to the control state (–56 to –80 ppm, Fig. 6). This is partly a result of colder conditions (Table 2), which lead to increased solubility for  $CO_2$  in sea water, and also cause increased  $C_{ice}$ , because of expanded sea ice cover (not shown) which restricts air–sea gas exchange. This slows down the equilibration of the  $CO_2$ -rich upwelling water with the atmosphere before it is subducted into the deep ocean. Changes in biological production (see Section 3.3.2) and storage of biologically sourced carbon, Fig. 9, also contribute strongly to the reduced  $pCO_2^{atm}$ . In  $GLcomb_{RED}$  and  $GLcomb_{GAM}$ , we achieve drawdown of  $pCO_2^{atm}$  of 64 and 80 ppm, respectively, from the 278 ppm of the control states (Fig. 6). This corresponds to an increase in ocean carbon storage of 139 PgC and 173 PgC, respectively (Table S.1). The drawdown is thus 25 % larger in  $GAM$  than in  $RED$ . If we compare this to  $GLcomb_{121}$  (drawdown of 72 ppm, Fig. 6), we see that about half (8 ppm) of this can be attributed to increased average C/P composition of exported organic material compared to  $Ctrl$ . In  $Acomb$ , where the perturbation in wind stress is omitted, drawdown of  $CO_2$  is smaller than in  $GLcomb$ , but still 14 % larger in  $Acomb_{GAM}$  than in  $Acomb_{RED}$  (56 and 63 ppm, respectively, see Fig. 6). Here, 12 out of the 14 % difference in  $pCO_2^{atm}$  can be attributed to a change in average C/P, thus almost the full extent of the change. As shown above, for the individual perturbation simulations, as well as for  $GLcomb$ , only half of the change in  $pCO_2^{atm}$  is due to changed average C/P. Thus, the effects of the perturbations do not add linearly.

## 4 Discussion

### 4.1 Accounting for variable C/P in ocean carbon cycle models

The representation of ocean biology in GCMs tends to be over-simplified (Le Quééré et al., 2005a) and the development of the models is often held back by constraints imposed by maintaining the computational efficiency of the model. The Galbraith and Martiny (2015) model is simple and based on nutrient variables that are already present in biogeochemical models (nitrate and phosphate). By implementing the  $GAM$  parametrisation, or possibly a power law as that described by (Tanioka and Matsumoto, 2017), an additional facet of the complexity of ocean biology can be implicitly accounted for at a relatively small computational cost. The approach taken by both Galbraith and Martiny (2015) and Tanioka and Matsumoto (2017) is to adapt

### 3.3.3 Ocean dissolved $O_2$

Despite colder conditions, which allow for more dissolution of  $O_2$ , the reduction in  $\overline{O_2}$  is evident in the  $GLcomb$ -simulations (Fig. 4). This mirrors the increase of  $AC_{rem}$  (Fig. 9). The  $\overline{O_2}$  reduction is about 50 % larger in  $GAM$  compared to  $RED$ . As the initial state  $Ctrl_{GAM}$  is already lower in oxygen than  $Ctrl_{RED}$  ( $144 \mu mol kg^{-1}$  compared to  $166 \mu mol kg^{-1}$ ), and variable stoichiometry allows for additional ocean storage of organic carbon, the end state  $\overline{O_2}$  is drastically lower in  $GLcomb_{GAM}$  ( $74 \mu mol kg^{-1}$ ) compared to  $GLcomb_{RED}$  ( $122 \mu mol kg^{-1}$ ).

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### 3.3.5 Atmospheric $CO_2$

In the combined experiments  $Acomb$  and  $GLcomb$ ,  $pCO_2^{atm}$  decreases strongly compared to the control state (reduction of between –56 to –80 ppm, Fig. 6). This is partly a result of colder conditions (Table 2), which lead to increased solubility for  $CO_2$  in sea water and an expanded sea-ice cover (Figure S.4) which restricts air–sea gas exchange. The latter slows down the equilibration of the  $CO_2$ -rich upwelling water with the atmosphere before it is subducted into the deep ocean, and thus causes increased  $C_{ice}$ . In  $Acomb$  and  $GLcomb$ , changes in biological production (see Section 3.3.2) and storage of biologically sourced carbon (Fig. 9) also contribute strongly to the reduced  $pCO_2^{atm}$ .

The combined experiments show a striking difference in  $pCO_2^{atm}$  between the model versions  $RED$  and  $GAM$ ; in  $GLcomb_{RED}$  and  $GLcomb_{GAM}$ , we achieve drawdown of  $pCO_2^{atm}$  of –64 and –80 ppm, respectively, from the 278 ppm of the control states (Fig. 6). This corresponds to an increase in ocean carbon storage of 139 PgC and 173 PgC, respectively (Table S.1). The drawdown is thus 25 % larger in  $GAM$  than in  $RED$ . In  $Acomb$ , where the perturbation in wind stress is omitted, drawdown



a function to all the available species-independent observations. This means that they account for the adaptation of plankton to the surrounding conditions, both in terms of species composition and individuals being more frugal in low nutrient conditions. This is one of the main advantages of such an approach, as it can be applied in a model without different plankton functional types, which is what we use here. Ganopolski and Brovkin (2017) appear to succeed with full glacial-interglacial CO<sub>2</sub> cycles in CLIMBER-2, which does not have flexible stoichiometry for primary producers, but which has a temperature limitation on growth and explicit phyto- and zooplankton with different C uptake rates. This combination may perhaps achieve a similar response in carbon export in their simulations, when moving into a colder climate, as the flexible stoichiometry does in our simulations. The next step to approach a more realistic modelling of the biological pump would be to include a representation of preferential remineralisation of nutrients (e.g., Kolowith et al., 2001; Letscher and Moore, 2015), but this goes beyond the scope of the present study.

One drawback of the Galbraith and Martiny (2015) approach is that it assumes that the C/P ratio continues to increase continuously with increasing [PO<sub>4</sub>]. Thus, GAM does not account for the effects on C/P of temperature and light and the associated non-linear effects that could be of importance in e.g. the Southern Ocean (e.g., Yvon-Durocher et al., 2015; Tanioka and Matsumoto, 2017; Moreno et al., 2018), where [PO<sub>4</sub>] is very high. Up to [PO<sub>4</sub>] = 1.7 μM, the GAM parametrisation fits the binned observational data well (see Fig. 1 and S2 Galbraith and Martiny, 2015). To account for the lack of observational data at higher [PO<sub>4</sub>], we have tested the effect of saturation of the C/P ratio at higher [PO<sub>4</sub>] in *Ctrl* and *GLcomb* simulations where we kept C/P = 55/1 at [PO<sub>4</sub>] > 1.7 μM. The increase in ocean carbon storage and decrease in pCO<sub>2</sub><sup>atm</sup> between the *Ctrl* and *GLcomb* are nearly identical with GAM, thus saturation of the C/P ratio at very high [PO<sub>4</sub>] causes no noticeable impact on our results.

#### 4.2 Implications of changed average C/P

Part of the observed difference in pCO<sub>2</sub><sup>atm</sup> between *GLcomb<sub>RED</sub>* and *GLcomb<sub>GAM</sub>* results from a difference in global average C/P in the control states (*Ctrl<sub>RED</sub>* and *Ctrl<sub>GAM</sub>*). In *Ctrl<sub>GAM</sub>*, the average C/P in the export production is close to 121/1, instead of 106/1 as in *Ctrl<sub>RED</sub>*. We illustrate the consequences of this difference by running parallel simulations with fixed C/P of 121/1 (model version 121). Depending on the change in forcing, the simulations with 121 indicate that between 1/3 and 2/3 of the difference in drawdown between *RED* and *GAM* is due to a change in the average C/P (Fig. 6). This could have implications for model intercomparison projects, if they compare results from models that use different versions of fixed stoichiometry – e.g. models that apply Anderson and Sarmiento (1994) or Takahashi et al. (1985) stoichiometries, compared to those that use Redfield (1963). The problem with different stoichiometry assumptions in models is extensively discussed by Paulmier et al. (2009). Our study shows a direct consequence of such differences, with different model response to the same perturbation. Note that *Ctrl<sub>GAM</sub>* has a larger inventory of DIC as well as C<sub>soft</sub> compared to *Ctrl<sub>RED</sub>*. Yet, the effect of applying the same perturbation results in a larger drawdown of CO<sub>2</sub> in *GAM* than in *RED*. This is opposite of the conclusions of Ödalen et al. (2018). The reason is that the flexible stoichiometry in effect increases the drawdown potential, which more than compensates for the increased carbon inventory in the control state. In *GLcomb<sub>GAM</sub>*, the C/P in global

of pCO<sub>2</sub><sup>atm</sup> is smaller than in *GLcomb* and the difference between model versions is less pronounced, but there is still a 14 % difference between *Acomb<sub>RED</sub>* and *Acomb<sub>GAM</sub>* (–56 and –63 ppm, respectively (Fig. 6).

## 4 Discussion

### 4.1 Accounting for variable C/P in ocean carbon cycle models

The representation of ocean biology in General Circulation Models (GCMs) tends to be over-simplified (Le Quéré et al., 2005a) and the development of the models is often held back by constraints imposed by maintaining the computational efficiency of the model. The Galbraith and Martiny (2015) empirical model is simple and based on nutrient variables that are already present in biogeochemical models (nitrate and phosphate). By implementing the GAM parametrisation, or possibly a power law as that described by (Tanioka and Matsumoto, 2017), an additional facet of the complexity of ocean biology can be implicitly accounted for at a relatively small computational cost. Previous model ensemble studies have shown that this type of dynamical response of the biology to changes in the modelled ocean state can improve the model's ability to realistically simulate ocean biogeochemistry (Buchanan et al., 2018). In pre-industrial and future simulations, respectively, Buchanan et al. (2018) and Tanioka and Matsumoto (2017) find that the flexible stoichiometry acts to stabilise the response of ocean DIC to changes in the physical (circulation) state. In our glacial-like simulations, we find that the response of ocean DIC, and thus pCO<sub>2</sub><sup>atm</sup>, to the combined perturbations is greater in the simulations with flexible stoichiometry. Nonetheless, our study confirms the potential importance of dynamical biological response for the outcome of model studies.

The approach taken by both Galbraith and Martiny (2015) and Tanioka and Matsumoto (2017) is to adapt a function to all the available species-independent observations. This means that they account for the adaptation of plankton to the surrounding conditions, both in terms of species composition and individuals being more frugal in low nutrient conditions. This is one of the main advantages of such an approach, as it can be applied in a model without different plankton functional types, which is what we use here. Ganopolski and Brovkin (2017) appear to succeed with full glacial-interglacial CO<sub>2</sub> cycles in CLIMBER-2, which does not have flexible stoichiometry for primary producers, but which has a temperature limitation on growth and explicit phyto- and zooplankton with different C uptake rates. This combination may perhaps achieve a similar response in carbon export in their simulations, when moving into a colder climate, as the flexible stoichiometry does in our simulations. The next step to approach a more realistic modelling of the biological pump would be to include a representation of preferential remineralisation of nutrients (e.g., Kolowith et al., 2001; Letscher and Moore, 2015), but this goes beyond the scope of the present study.

One drawback of the Galbraith and Martiny (2015) approach is that it assumes that the C/P ratio continues to increase continuously with increasing [PO<sub>4</sub>]. As such, in a high surface [PO<sub>4</sub>] region like the Southern Ocean, GAM does not represent the effects on C/P of temperature and light, and the associated non-linear effects, that could be of importance here (e.g., Yvon-Durocher et al., 2015; Tanioka and Matsumoto, 2017; Moreno et al., 2018). Up to [PO<sub>4</sub>] = 1.7 μM, the GAM parametrisation fits the binned observational data well (see Fig. 1 and S2 Galbraith and Martiny, 2015). To account for the lack of observational data at higher [PO<sub>4</sub>], we have tested the effect of saturation of the C/P ratio at higher [PO<sub>4</sub>] in *Ctrl* and *GLcomb* simulations



where we kept  $CP = 55/1$  at  $[PO_4] > 1.7\mu M$ . The increase in ocean carbon storage and decrease in  $pCO_2^{atm}$  between the *Ctrl* and *GLcomb* are nearly identical with *GAM*, thus saturation of the *CP* ratio at very high  $[PO_4]$  causes no noticeable impact on our results.

Our sensitivity experiments  $RLS \times 0.75$  and  $RLS \times 1.25$ , reveal that the response in  $pCO_2^{atm}$  to the perturbation is enhanced in *GAM* compared to *RED* for both increased and decreased *RLS*. While increased *RLS* would be an effect of ocean cooling, and thus of interest for glacial studies, reduced *RLS* would be a consequence of ocean warming (Matsumoto, 2007). Matsumoto (2007) describes how decreased *RLS* would have a positive feedback on  $pCO_2^{atm}$  in future warming climate. Our results imply that flexible *CP* could have a further re-inforcing effect on this feedback. It would therefore be of interest to apply a parametrisation of flexible *CP* in models used for simulations of future climate feedbacks.

#### 4.2 De-coupling of biologically sourced carbon and nutrient utilisation efficiency

Many studies have suggested increased ocean storage of organic carbon as a potentially important contributor to the low glacial  $pCO_2^{atm}$  (e.g., Sarmiento and Toggweiler, 1984; Martin, 1990; Archer et al., 2000; Sigman and Boyle, 2000). However, biological production depends on water temperature (Eppley, 1972) and decreases in cold conditions. This temperature effect is parametrised in cGENIE as a local temperature-dependent uptake rate modifier proportional to  $e^{(T_i/15-9^\circ C)}$ , and we see overall reduced productivity in our cold climate simulations (see e.g. *LGM<sub>phy</sub>*, Table S.1). As the climate cools, the temperature effect leads to a decrease in biological productivity and a subsequent decrease in  $\overline{P^*}$  (see *LGM<sub>phy</sub>* in Fig. 9). If productivity decreases, other mechanisms are needed to offset this decrease, if the total ocean storage of organic carbon is to increase. Mechanisms that can contribute to increased deep ocean carbon retention are for example reduced SO overturning circulation (increased residence time of the AABW, Menviel et al., 2017) and deeper remineralisation (Matsumoto, 2007; Chikamoto et al., 2012), which we apply through our perturbations in winds (Section 3.2.2) and *RLS* (Section 3.2.3). From our results, it is evident that variable stoichiometry can be another contributing factor. In our simulations, global average export production decreases, both in terms of *POP* (particulate organic phosphorus) and *POC* (particulate organic carbon), by 15 % between *Ctrl<sub>RED</sub>* and *GLcomb<sub>RED</sub>* because of the colder climate. However, the variable stoichiometry in *GAM* partly offsets this decrease in biological carbon capture - while the export production in terms of *POP* decreases by 17 %, the corresponding decrease in *POC* is only 10 %. Thus, in *GLcomb<sub>GAM</sub>* we achieve an increase in ocean inventory of remineralised carbon, which exceeds the one of *GLcomb<sub>RED</sub>* (Fig. 9).

In summary, we suggest this is a result of changes in surface P fields (see Fig. 7)

Due to the competing effects between decreased export production and increased retention that are introduced by the different forcing components, the net change in  $P_{rem}$ , and thus in  $\overline{P^*}$ , is very small when moving from the control state (*Ctrl*) to the glacial-like state (*GLcomb*) (Fig. 9). In the fixed stoichiometry case (*RED*), there is a small net increase in  $\overline{P^*}$  of 0.020 in *GLcomb* compared to *Ctrl*, which is linearly related to a small increase in storage of  $AC_{rem}$  in the ocean. In the case with variable stoichiometry (*GAM*), there is instead a very small decrease in  $\overline{P^*}$  of 0.003. With a linear response, we would thus expect a decrease in storage of  $AC_{rem}$ , as well. Instead, we see a reasonably large increase in global average  $AC_{rem}$ .

average export production increases from 121/1 to 134/1, which reflects the increased storage of organic carbon allowed by the flexible stoichiometry.

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Due to the competing effects between decreased export production and increased retention, the overall change in  $\overline{P^*}$  is very small when moving from the control state ( $Ctrl$ ) to a glacial-like state ( $GLcomb$ ) (Fig. 9). In the fixed stoichiometry case ( $RED$ ), there is a small net increase in  $\overline{P^*}$  of 0.020 in  $GLcomb$  compared to  $Ctrl$ , which is linearly related to a small increase in storage of  $AC_{rem}$  in the ocean. In the case with variable stoichiometry ( $GAM$ ), there is instead a very small decrease in  $\overline{P^*}$  of 0.003. With a linear response, we would thus expect a decrease in storage of  $AC_{rem}$  as well. Instead, we see a reasonably large increase in global average  $AC_{rem}$ .

This can be explained by the non-linearity introduced by the local variability in C/P. The reduced  $pCO_2^{atm}$  in  $GLcomb$ , compared to the control state 278 ppm, is partly due to the biological pump being more efficient in some key (HNLC) regions. In these regions, there is a reduction of the surface nutrient concentration in  $GLcomb$  compared to  $Ctrl$ . When C/P increases with decreased surface layer P concentration, as it does in  $GAM$ , this further strengthens the biological pump in these key regions, resulting in a non-linear relationship between storage of remineralised phosphate and biologically sourced carbon (Fig. 9). From this, we conclude that, in a system where stoichiometry is variable on a local scale, ocean storage of biologically sourced  $CO_2$  can change while the amount of remineralised nutrients remains constant.

The reduced  $pCO_2^{atm}$  in  $GLcomb_{GAM}$ , compared to  $GLcomb_{RED}$ , can be explained by the non-linearity introduced by the local variability in C/P. When changes in ocean circulation, remineralisation depth and dust deposition cause the local nutrient availability in the surface waters to change, this affects the elemental composition of the exported organic material. In  $GLcomb$ , there is a reduction of the surface layer P concentration compared to  $Ctrl$  in some key (HNLC) regions. In  $GAM$ , this decrease in surface P results in an increase in C/P. This further strengthens the biological pump in these key regions, resulting in a non-linear relationship between storage of remineralised phosphate and biologically sourced carbon (Fig. 9). In  $Ctrl_{GAM}$ , the average elemental C/P composition is 121/1. In  $GLcomb_{GAM}$ , this average is 134/1. This means that even though the same amount of P is exported to the deep ocean, the organic molecules carry more carbon, which is released in the deep ocean during remineralisation. In  $Ctrl_{GAM}$ , the global average concentration of  $P_{rem}$  is  $1.16 \mu mol kg^{-1}$  (c.f.  $1.17 \mu mol kg^{-1}$  in  $GLcomb_{GAM}$ ). By increasing the average C/P composition of  $1.16 \mu mol kg^{-1}$  organic molecules from 121 to 134 (i.e. by 13 units), this causes an increase in  $C_{soft}$  by  $\sim 15 \mu mol kg^{-1}$ , which corresponds to the observed increase in  $AC_{rem}$ . From this, we conclude that, in a system where stoichiometry is variable on a local scale, ocean storage of biologically sourced  $CO_2$  can change while the amount of remineralised nutrients remains constant.

Note also that  $Ctrl_{GAM}$  has a larger inventory of DIC as well as  $C_{soft}$  compared to  $Ctrl_{RED}$ . Ödalen et al. (2018) found that drawdown of  $pCO_2^{atm}$  in response to a perturbation is larger when the control state has a smaller inventory of DIC and  $C_{soft}$ . Yet, the effect of applying the same perturbation results in a larger drawdown of  $pCO_2^{atm}$  in  $GAM$  than in  $RED$ . This is opposite of the conclusions of Ödalen et al. (2018). The reason is that the flexible stoichiometry in effect increases the drawdown potential, which more than compensates for the increased carbon inventory in the control state. In  $GLcomb_{GAM}$ , the C/P in global average export production increases from the control 121/1 to 134/1, which reflects the increased storage of organic carbon allowed by the flexible stoichiometry.

#### 4.3 Implications of flexible C/P for deep ocean oxygen

Studies have shown that deep ocean  $O_2$  concentrations were lower during the LGM than in the Holocene (e.g., Bradtmiller et al., 2010; Jaccard and Galbraith, 2012; Galbraith and Jaccard, 2015). Here, we discuss implications of using flexible C/P for the model's ability to reproduce ocean oxygen patterns and concentrations in the different time periods.

In the Atlantic,  $Ctrl_{GAM}$  (Fig. 4 e) reproduces the observed extent of the Oxygen Minimum Zone (OMZ) (Fig. 4 a) better than  $Ctrl_{RED}$  (Fig. 4 c) does. In the Pacific Ocean, the  $O_2$  gradient in the observations (Fig. 4 b) is more gradual compared to that of the control states (Fig. d, f), but the core of the OMZ is well reproduced by the model. The forcings applied to  $GLcomb$  are not sufficient to reproduce a full glacial state. Still, we do get a vertical expansion of the OMZ in  $GLcomb_{RED}$  (Fig. 4 h) compared to  $Ctrl_{RED}$  (Fig. 4 c), in agreement with the findings of Hoogakker et al. (2018). In  $GLcomb_{GAM}$ , oxygen depletion is too extensive (see below), but the tendency of vertical expansion compared to the control state is present here as well.

In our glacial-like states, we see a significant reduction of  $O_2$  compared to the control state in both  $RED$  and  $GAM$  (Fig. 4 d and e). This response is expected when we apply increased dust deposition and deeper remineralisation (Galbraith and Jaccard, 2015), and the direction of the overall response of deep ocean  $O_2$  to the glacial-like forcings is in line with observations. The reduction in  $O_2$  is stronger in  $GAM$ , due to the larger storage of respired carbon in this model version.

#### 4.4 Implications of flexible C/P for deep ocean oxygen

As shown by e.g. Bradtmiller et al. (2010); Jaccard and Galbraith (2012); Galbraith and Jaccard (2015), deep ocean  $O_2$  concentrations were lower during the LGM than in the Holocene. In our glacial-like states, we see a significant reduction of  $O_2$  in both RED and GAM (Fig. 4 d and e), which is expected when we apply increased dust deposition and deeper remineralisation (Galbraith and Jaccard, 2015). The reduction is stronger in GAM, due to the larger storage of respired carbon in this model version.

As illustrated by simulations in Galbraith and de Lavergne (2018), variable stoichiometry in itself is not always sufficient to achieve widespread deep ocean de-oxygenation in a model under glacial-like climate change. De-oxygenation is also dependent on e.g. deep water formation characteristics of the model (Galbraith and de Lavergne, 2018). It should be noted that  $Ctrl_{GAM}$  (Fig. 4 c) displays deeper oxygen minima in the oxygen minimum zones of both the Atlantic equatorial region and the North Pacific compared to what is seen in  $Ctrl_{RED}$  (Fig. 4 b). In  $Ctrl_{GAM}$ , a large part of the interior North Pacific is anoxic (Fig. 4 c), while observations (Fig. 4 a) indicate very low oxygen levels, but not anoxia. If this parametrisation of variable stoichiometry is to be used in cGENIE in future studies, we suggest some re-tuning (e.g. by reducing the global average concentration of nutrients) to improve the representation of observed ocean oxygen concentrations in the modern control state.

#### 4.5 What can we learn from the model-data comparison of $\delta^{13}C$ ?

The model-data comparison in  $\delta^{13}C$  (Section 3.1.4) suggests that the  $Ctrl$  simulations are overall well correlated with Holocene benthic  $\delta^{13}C$  data (HOL in Table S.3). For the Atlantic, the correlation of the  $Ctrl$  simulations is higher with the LGM benthic  $\delta^{13}C$  (LGM in Table S.3) than with HOL. However, the standard deviations (STDs) suggest that the Atlantic North-South gradient is not as strong as in an LGM ocean state and thus more similar to the modern ocean. When we apply our combined forcings in the  $GLcomb$  simulations, we achieve a stronger  $\delta^{13}C$  gradient in the Atlantic, allowing for a closer match with LGM data in terms of STDs. A stronger gradient in  $\delta^{13}C$  and more depleted suggest weaker ventilation of the deep ocean. The poor correlation in the Indo-Pacific, which we assume to be partly due to sparse mid-ocean observations for almost 70% of the ocean volume, makes the global statistics for LGM observations difficult to interpret.

Each of the two observational datasets (HOL and LGM) display similar correlations across the two model simulations. This implies that our changes in forcings do not achieve any obvious changes in water mass distribution. The applied changes affect the chemical and biological conditions for ocean carbon storage, such as temperature and nutrient availability, more than the physical conditions, such as water mass volume and turnover time. To achieve a full glacial state with cGENIE, with a more glacial-like water mass distribution, additional physical forcings (freshwater, mixing etc.) are likely to be required. The very small differences between RED and GAM suggests that using variable stoichiometry does not impact our ability to achieve the  $\delta^{13}C$  patterns seen in observational data. However, we note that some retuning of the modern control state is recommended before cGENIE with variable stoichiometry is used in other studies.

Finally, it should be noted that  $Ctrl_{GAM}$  (Fig. 4 c) displays deeper oxygen minima in the oxygen minimum zones of both the Atlantic equatorial region and the North Pacific compared to what is seen in  $Ctrl_{RED}$  (Fig. 4 b), and in observations.

In  $Ctrl_{GAM}$ , a large part of the interior North Pacific is anoxic (Fig. 4 c), while observations (Fig. 4 a) indicate very low oxygen levels, but not anoxia. As illustrated by simulations in Galbraith and de Lavergne (2018), variable stoichiometry in itself is not always sufficient to achieve widespread deep ocean de-oxygenation in a model under glacial-like climate change. Among other factors, model ocean oxygen conditions are also dependent on deep water formation characteristics of the model (Galbraith and de Lavergne, 2018). The deep water formation characteristics of a model affects the amount of time available for remineralisation and, consequently, the oxygen consumption. In addition, due to a lack of resolution deep water formation in climate models generally happens as open water convection, rather than as dense plumes along slopes (Heuzé et al., 2013). This may cause too much oxygen to be entrained into the deep ocean Galbraith and de Lavergne (2018). In cGENIE, this effect is small enough not to cancel the increased  $O_2$  consumption caused by the higher average C/P in  $Ctrl_{GAM}$  compared to  $Ctrl_{RED}$ .

In summary, the GAM version of the model reproduces quantitatively the observed  $O_2$  patterns of both the LGM and the Holocene, but with too low concentrations. If this parametrisation of variable stoichiometry is to be used in cGENIE in future studies, we suggest some re-tuning, for example by reducing the global average concentration of nutrients, to improve the representation of observed modern-day ocean  $O_2$  concentrations in the GAM control state.

#### 4.4 Effect of modified but fixed C/P

Part of the observed difference in  $pCO_2^{atm}$  between  $GLcomb_{RED}$  and  $GLcomb_{GAM}$  results from a difference in global average C/P in the control states ( $Ctrl_{RED}$  and  $Ctrl_{GAM}$ ). In  $Ctrl_{GAM}$ , the average C/P in the export production is close to 121/1, instead of 106/1 as in  $Ctrl_{RED}$ . We illustrate the consequences of this difference by running parallel simulations with fixed C/P of 121/1 (model version 121).

In a simulation with reduced wind stress ( $WNS \times 0.5_{121}$ ),  $pCO_2^{atm}$  is reduced by  $-14.5$  ppm compared to  $Ctrl_{RED}$  (Table S.2). The corresponding  $pCO_2^{atm}$  drawdown in  $WNS \times 0.5_{RED}$  and  $WNS \times 0.5_{GAM}$  is  $-12.9$ , and  $-16.3$  ppm, respectively. This indicates that, for the reduced wind stress case, about half of the enhanced drawdown achieved by the flexible stoichiometry can be attributed to a difference in the mean C/P composition of the organic material between the control states  $Ctrl_{RED}$  and  $Ctrl_{GAM}$ . Similarly, for the enhanced dust deposition experiments,  $LGM_{dust121}$  explains about 1/3 of the difference in  $pCO_2^{atm}$  between  $LGM_{dust_{RED}}$  and  $LGM_{dust_{GAM}}$  (Table S.2). In the combined experiment  $GLcomb$ , we can attribute about half ( $-8$  ppm of  $-17$  ppm) of the observed difference in drawdown between RED and GAM to the difference in control state average C/P. In  $Acomb$ , the control state difference in C/P accounts for about 2/3 of the difference between model versions ( $-5$  ppm of  $-8$  ppm). As shown above, the individual perturbation simulations and  $GLcomb$  have smaller fractions of the change in  $pCO_2^{atm}$  that are due to changed average C/P. As shown above, the simulations with 121 indicate that, depending on the change in forcing, between 1/3 and 2/3 of the difference in drawdown between RED and GAM is due to the difference in average C/P between the control states (Fig. 6, Table S.2). From this, we conclude that the effects of the perturbations do not add linearly.

As outlined in Section 4.3, an increase in *C/P* reduces deep ocean  $O_2$  concentrations, through an increase in regenerated carbon. In this respect, the 121 experiments fall between the corresponding *RED* and *GAM* experiments. For example, the global ocean average  $O_2$  concentration,  $\overline{O_2}$ , in *Ctrl*<sub>121</sub> is  $152 \mu\text{mol kg}^{-3}$ , which is lower than *Ctrl*<sub>RED</sub> ( $166 \mu\text{mol kg}^{-3}$ ), but higher than *Ctrl*<sub>GAM</sub> ( $144 \mu\text{mol kg}^{-3}$ ). Similarly, *GLcomb*<sub>121</sub> has a lower  $\overline{O_2}$  than *GLcomb*<sub>RED</sub> (96 compared to 122  $\mu\text{mol kg}^{-3}$ ), but higher than *GLcomb*<sub>GAM</sub> ( $74 \mu\text{mol kg}^{-3}$ ).

The observed effects of modified average *C/P* could have implications for model intercomparison projects, if they compare results from models that use different versions of fixed stoichiometry (for example, Anderson and Sarmiento (1994) or Takahashi et al. (1985) stoichiometries, compared to Redfield (1963)). The problem with different stoichiometry assumptions in models is extensively discussed by Paulmier et al. (2009). Our study shows a direct consequence of such differences, with different model response to the same perturbation.

#### 4.5 What can we learn from the model–data comparison of $\delta^{13}C$ ?

Proxy records of benthic  $\delta^{13}C$  indicate a change in ocean  $\delta^{13}C$  across the deglaciation. The whole ocean deglacial change has been estimated to  $\sim 0.35 \text{‰}$  (Peterson et al., 2014; Peterson and Lisiecki, 2018), and the surface–to–deep gradient weakened (shown in numerous studies, see e.g. Curry et al., 1988; Duplessy et al., 1988; Curry and Oppo, 2005; Herguera et al., 2010; Peterson and Lisiecki, 2018, and references therein). Here we compare model ocean  $\delta^{13}C$  of our simulations to the benthic  $\delta^{13}C$  records, to see how well the simulations capture the observed patterns, and if there is a difference in model–data correlation between *RED* and *GAM*.

The model–data comparison in  $\delta^{13}C$  (Section 3.1.4) suggests that the *Ctrl* simulations are overall well correlated with Holocene benthic  $\delta^{13}C$  data (HOL in Table S.3). For the Atlantic, the correlation of the *Ctrl* simulations is higher with the LGM benthic  $\delta^{13}C$  (LGM in Table S.3) than with HOL. However, the standard deviations (STDs) suggest that the Atlantic North–South gradient is not as strong as in an LGM ocean state and thus more similar to the modern ocean.

When we apply our combined forcings in the *GLcomb* simulations, we achieve a stronger  $\delta^{13}C$  gradient in the Atlantic, allowing for a closer match with LGM data in terms of STDs. A stronger gradient in  $\delta^{13}C$  and more depleted suggest weaker ventilation of the deep ocean. The poor correlation in the Indo–Pacific, which may be partly due to sparse mid–ocean observations for almost 70% of the ocean volume, makes the global statistics for LGM observations difficult to interpret. The forcings applied to *GLcomb* are factors that are likely to be important for the glacial ocean circulation and biogeochemistry. However, these forcings are not sufficient to reproduce a full glacial state (i.e. the use of the term *glacial–like simulations*, rather than *LGM simulation*). Other forcings that have shown to be important for modelling of glacial  $\delta^{13}C$  are, for example, brine rejection (Bouttes et al., 2010, 2011), and freshwater forcing (Schmittner et al., 2002; Hewitt et al., 2006; Bouttes et al., 2012). The fact that some important forcings are missing is likely the main cause for the model–data discrepancy, and the reason for why we do not achieve a glacial Pacific Ocean circulation consistent with observed  $\delta^{13}C$  patterns.

Each of the two observational datasets (HOL and LGM) display similar correlations across the two model simulations. The correlation of the HOL  $\delta^{13}C$  records with *Ctrl*<sub>RED</sub>, *Ctrl*<sub>GAM</sub>, *GLcomb*<sub>RED</sub>, and *GLcomb*<sub>GAM</sub> is in all cases between 0.76–0.78. Meanwhile, the correlation of LGM  $\delta^{13}C$  records with the same four simulations is in all cases between 0.55–0.58.

## 5 Conclusions

In this paper, we examine the potential role of variable stoichiometry in biological production for glacial ocean CO<sub>2</sub> storage. We show that flexible C/P composition of organic matter allows a stronger response of  $pCO_2^{atm}$  to glacial-like changes in climate, remineralisation length scale and aeolian dust flux. We conclude that variable stoichiometry may be important for glacial ocean CO<sub>2</sub> storage and for achieving the full extent of drawdown of atmospheric CO<sub>2</sub> in model simulations. In the experiment *GLcomb<sub>RED</sub>*, with glacial-like climate and Redfield stoichiometry (Redfield, 1963), ocean carbon storage increases by 139 PgC and atmospheric CO<sub>2</sub> decreases by 64 ppm. In *GLcomb<sub>GAM</sub>*, with glacial-like climate changes and variable stoichiometry, the corresponding numbers are 173 PgC and 80 ppm. Hence, the drawdown of atmospheric CO<sub>2</sub> increases by 25 % when C/P is variable.

About half of the increased drawdown of CO<sub>2</sub> results from different global average C/P in the export production. In addition, flexible stoichiometry allows increased carbon capture through the biological pump, while maintaining or even decreasing the fraction of remineralised to total nutrients in the deep ocean. With fixed stoichiometry, an increase in remineralised carbon is inevitably tied to a corresponding increase in remineralised nutrients.

We apply variable C/P parametrised as a simple function of the surface water concentration of PO<sub>4</sub>, as suggested by Galbraith and Martiny (2015). Tanioka and Matsumoto (2017) suggest that it is unrealistic for C/P to continue to increase indefinitely with increased [PO<sub>4</sub>], and therefore suggest a more complex power law function, which takes into account saturation of the C/P ratio at high concentrations of PO<sub>4</sub>. However, we found that saturation of the C/P ratio at concentrations higher than the observational upper bound of 1.7 μM causes no noticeable impact on our results.

The representation of flexible stoichiometry used in this study (Galbraith and Martiny, 2015) can be used without large increases in computational cost. It makes it possible to take into account, to first approximation, the complex biological changes that occur in the ocean during long-timescale climate change scenarios (see e.g. McNerney and Wing, 2011). We show here that, for glacial-interglacial cycles, this complexity contributes to changes in atmospheric CO<sub>2</sub> through flexible C/P ratios.

**Code and data availability.** The code for the cGENIE.muffin model is hosted on GitHub. The specific version used in this paper, tagged as release v0.9.5, can be obtained at <https://github.com/derpycode/cgenie.muffin/releases/tag/v0.9.5> and is assigned a DOI 10.5281/zenodo.3235761 (cGENIE release v0.9.5, 2019).

Configuration files for the specific experiments presented in the paper can be found in the directory cgenie.muffin/genie-userconfgs/MS/odalenetal.BG.2019. Details of the different experiments, plus the command line needed to run each one, are given in readme.txt.

A corresponding user manual detailing software installation and configuration, plus cGENIE.muffin model tutorials, is available from <https://github.com/derpycode/muffin/doc/releases/tag/1.9.1b> and is assigned a DOI 10.5281/zenodo.1407658. (cGENIE release 1.9.1b, 2018) Datasets are available upon request (e-mail to malin.odalenetal@misu.su.se).

As our *GLcomb*-simulations still correlate so well with the HOL dataset, this suggests the applied forcings have not caused these simulations to be clearly different from *Ctrl* in terms of water mass distribution. For the same reason, the correlation with LGM δ<sup>13</sup>C records does not significantly improve from *Ctrl* to *GLcomb*. The water mass distribution in cGENIE is strongly constrained by the resolution of the model, especially in the vertical. Changes in temperature and salinity that should cause changes in water mass volume may not be sufficient to allow a water mass to extend to the next vertical level of the model. As a consequence, while the gradient between water masses may become more or less pronounced, the interface of water masses may still remain at the same depth. The applied changes affect the chemical and biological conditions for ocean carbon storage, such as CO<sub>2</sub> solubility (temperature dependent) and nutrient availability, more than the physical conditions, such as water mass volume and turnover time. To achieve a full glacial state with cGENIE, with a more glacial-like water mass distribution, additional physical forcings (see above) are likely to be required.

How δ<sup>13</sup>C is represented in cGENIE is detailed in Appendix B. The very small differences between *RED* and *GAM* suggests that using variable stoichiometry does not impact our ability to represent the δ<sup>13</sup>C patterns seen in observational data. However, we note that some retuning of the modern control state is recommended before cGENIE with variable stoichiometry is used in other studies.

## 15 Conclusions

In this paper, we examine the potential role of variable stoichiometry in biological production for glacial ocean CO<sub>2</sub> storage. We show that flexible C/P composition of organic matter allows a stronger response of  $pCO_2^{atm}$  to glacial-like changes in climate, remineralisation length scale and aeolian dust flux. We conclude that variable stoichiometry may be important for glacial ocean CO<sub>2</sub> storage and for achieving the full extent of drawdown of atmospheric CO<sub>2</sub> in model simulations. In the experiment *GLcomb<sub>RED</sub>*, with glacial-like climate and Redfield stoichiometry (Redfield, 1963), ocean carbon storage increases by 139 PgC and atmospheric CO<sub>2</sub> decreases by 64 ppm. In *GLcomb<sub>GAM</sub>*, with glacial-like climate changes and variable stoichiometry, the corresponding numbers are 173 PgC and 80 ppm. Hence, the drawdown of atmospheric CO<sub>2</sub> increases by 25 % when C/P is variable.

About half of the increased drawdown of CO<sub>2</sub> results from different global average C/P in the export production. In addition, flexible stoichiometry allows increased carbon capture through the biological pump, while maintaining or even decreasing the fraction of remineralised to total nutrients in the deep ocean. With fixed stoichiometry, an increase in remineralised carbon is inevitably tied to a corresponding increase in remineralised nutrients.

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#### Appendix A: Regenerated acidic carbon

Carbon enters the ocean mainly in the form of CO<sub>2</sub> and dissolved carbonate. Despite this, the major fraction of carbon in the ocean resides as bicarbonate ions. The source related state variables acidic and basic carbon (AC and BC, respectively) allow us to separate the ocean DIC inventory into the sources of CO<sub>2</sub> (AC) and dissolved carbonate (BC). The concept of the sourced related state variables was first described by Walin et al. (2014).

AC and BC are defined from DIC and alkalinity (ALK) as

$$AC = DIC - \frac{1}{2}ALK \quad (A1)$$

$$BC = \frac{1}{2}ALK \quad (A2)$$

10 Total AC and BC include all ocean sources of carbon, including e.g. river runoff, air-sea gas exchange, the biological pump etc.

To isolate the CO<sub>2</sub> that was supplied to the ocean via biological soft tissue, we make use of the separation of DIC and ALK into their preformed and remineralised fractions (see Section 2.5). Thus, we then compute the remineralised acidic carbon ( $AC_{rem}$ ) as

$$15 \quad AC_{rem} = DIC_{rem} - \frac{1}{2}ALK_{rem} \quad (A3)$$

*Author contributions.* M. Ödalen, J. Nycander, K. I. C. Oliver and A. Ridgwell designed the model experiments. A. Ridgwell developed the original cGENIE model code. M. Ödalen and K. I. C. Oliver adapted the model code and forcings for the experimental design. M. Ödalen performed the model simulations and produced the tables and figures. C. D. Peterson provided expertise on ocean  $\delta^{13}C$  analysis. M. Ödalen prepared the manuscript with contributions from all co-authors.

20 *Competing interests.* No competing interests are present.

*Acknowledgements.* The model simulations were performed on resources provided by the Swedish National Infrastructure for Computing (SNIC) at the National Supercomputer Centre (NSC), Sweden. MÖ would like to acknowledge support from the Bolin Centre for Climate Research, Research Areas 1 and 6. AR was supported by a Heising-Simons Foundation award, and by EU grant ERC 2013-CoG-617313.

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5 Flexible C/P also has the potential to be an additional positive feedback of ocean warming on  $pCO_2^{atm}$  in future climate.

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20 AC and BC are defined from DIC and alkalinity (ALK) as

$$AC = DIC - \frac{1}{2}ALK \quad (A1)$$

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Total AC and BC include all ocean sources of carbon, including (but not limited to) river runoff, air-sea gas exchange, and the biological pump.

25 To isolate the CO<sub>2</sub> that was supplied to the ocean via biological soft tissue, we make use of the separation of DIC and ALK into their preformed and remineralised fractions (see Section 2.5). Thus, we then compute the remineralised acidic carbon ( $AC_{rem}$ ) as

$$AC_{rem} = DIC_{rem} - \frac{1}{2}ALK_{rem} \quad (A3)$$

## Appendix B: $\delta^{13}C$ in cGENIE

cGENIE represents  $^{13}C$  as an explicit tracer (separate from and in addition to bulk carbon) in the model, tracking its concentration in all the same gaseous, dissolved, and solid forms that carbon exists in, reporting  $\delta^{13}C$  in ‰ relative to the standard VPDB. The current scheme is based on that described in Ridgwell (2001) and updated as described in Ridgwell et al. (2007) and is evaluated for the modern ocean (alongside simulated  $\Delta^{14}C$ ) in cGENIE, in Turner and Ridgwell (2016).

In the aqueous phase, the isotopic partitioning of carbon between  $CO_2(aq)$ ,  $HCO_3^-$ , and  $CO_3^{2-}$  is resolved and follows Zeebe and Wolf-Gladrow (2001) (their Section 3.2). The empirical fractionation factors used are from Zhang et al. (1995). The air-sea fractionation scheme follows that of Marchal et al. (1998) with the individual fractionation factors again taken from Zhang et al. (1995).

For the isotopic composition of organic carbon ( $\delta^{13}C_{POC}$ ), the model of Rau et al. (1996) is adapted, assuming that the isotopic signature of exported POC reflects that of phytoplankton biomass. Following Ridgwell (2001), the full equation of Rau et al. (1996) is simplified to:

$$\delta^{13}C_{POC} = \delta^{13}C_{CO_2(aq)} - \epsilon_f + (\epsilon_f - \epsilon_d) \cdot \frac{K_Q}{[CO_2(aq)]} \quad (B1)$$

where  $[CO_2(aq)]$  is the ambient concentration of aqueous  $CO_2$  and  $\delta^{13}C_{aq}$  is its isotopic composition.  $K_Q$  is a temperature-only dependent approximation of the full cell-dependent size and growth rate parameterization in the Rau et al. (1996) model (see Ridgwell, 2001). We take an intermediate value for the enzymatic isotope fractionation factor associated with intracellular C fixation ( $\epsilon_f$ ) of -25‰ following Rau et al. (1996, 1997), and assume a temperature-invariant value for  $\epsilon_d$  of 0.7‰.

The result of applying this scheme in cGENIE, is a zonal mean profile characterized by  $\delta^{13}C_{POC}$  of -22 to -21‰ in the tropics, declining with increasing latitude to reach -28 to -30‰ in the Southern Ocean. This latitudinal pattern is comparable to measurements made on suspended particulate organic matter as discussed in Ridgwell (2001).

For  $^{13}C$  fractionation into biogenic carbonates at the ocean surface (e.g. foraminiferal tests, and coccolithophorid coccoliths), cGENIE follows Mook (1986) and employs a simple temperature-dependent fractionation between the  $\delta^{13}C$  of aqueous  $HCO_3^-$  and calcite.

*Author contributions.* M. Ódalen, J. Nycander, K. I. C. Oliver and A. Ridgwell designed the model experiments. A. Ridgwell developed the original cGENIE model code. M. Ódalen and K. I. C. Oliver adapted the model code and forcings for the experimental design. M. Ódalen performed the model simulations and produced the tables and figures. C. D. Peterson provided expertise on ocean  $\delta^{13}C$  analysis. M. Ódalen prepared the manuscript with contributions from all co-authors.

*Competing interests.* No competing interests are present.

*Acknowledgements.* The authors thank Pierce James Buchanan and one anonymous referee for their helpful comments which improved the paper. Model simulations were performed on resources provided by the Swedish National Infrastructure for Computing (SNIC) at the National Supercomputer Centre (NSC), Sweden. MÖ would like to acknowledge support from the Bolin Centre for Climate Research, Research Areas 1 and 6. AR was supported by a Heising-Simons Foundation award, and by EU grant ERC 2013-CoG-617313.



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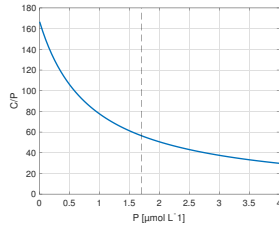
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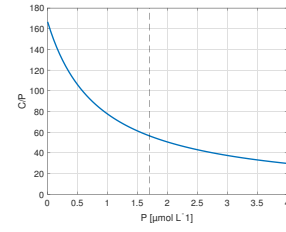
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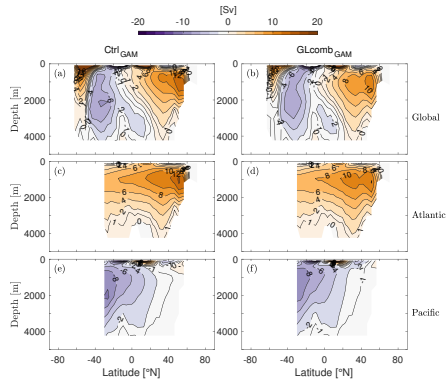
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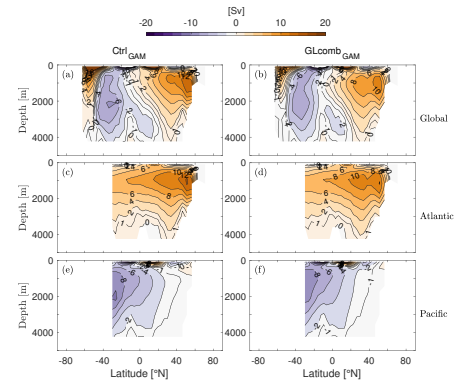
**Figure 1.** Flexible stoichiometry  $C/P$  (y-axis) dependent on the P-concentration [ $\mu\text{mol L}^{-1}$ ] (x-axis), as described by Eq. 1. Here, we extend the relationship beyond the observational interval  $0\text{--}1.7 \mu\text{mol L}^{-1}$  (bounded by dashed line) which form the basis of the relation derived by Galbraith and Martiny (2015).



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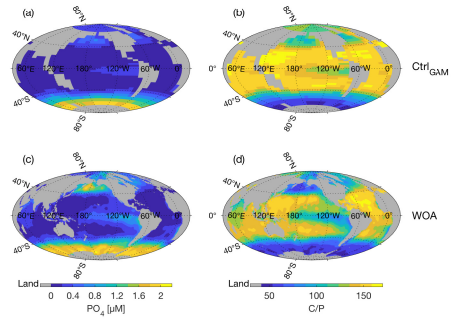


**Figure 2.** The eulerian component of the Global (panels a, b), Atlantic (panels c, d), and Pacific (panels e, f) ocean meridional overturning streamfunction ( $1 \text{ Sv} = 10^6 \text{ m}^3 \text{ s}^{-1}$ ) of *Ctrl\_GAM* (panels a, c, e) and *GLcomb\_GAM* (panels b, d, f). Note that the eddy-induced transport of tracers is taken into account through a skew-diffusive flux (Griffies, 1998) that is present in the velocity fields used to compute the eulerian stream function.

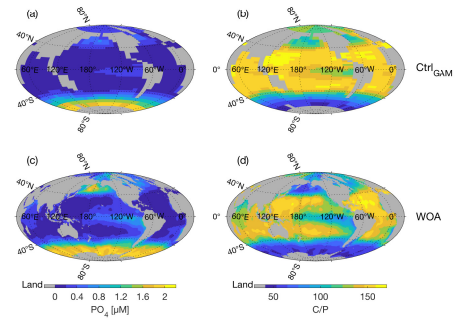


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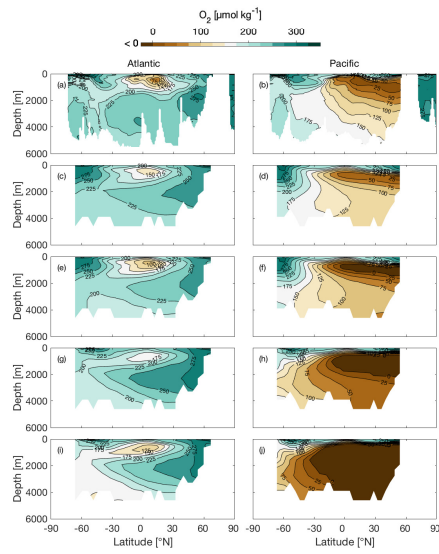




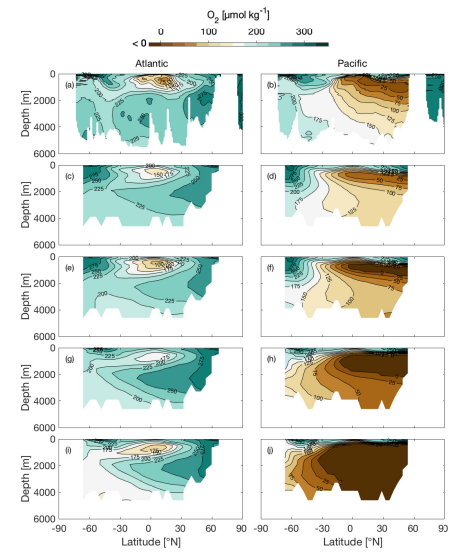
**Figure 3.** Surface  $PO_4$  concentration ( $\mu M$ ) (left hand column) and corresponding C/P as calculated using parametrisation of Galbraith and Martiny (2015) (right column). Panels show in *Ctrl\_GAM* (a, b) and observations (World Ocean Atlas 2013, Garcia et al., 2014a) (c, d).



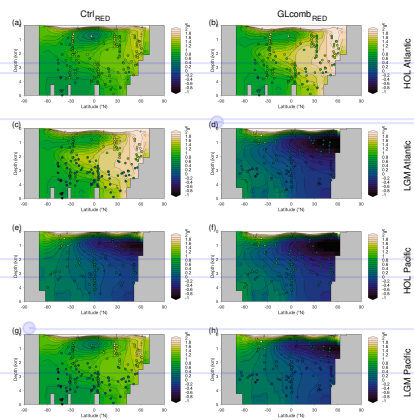
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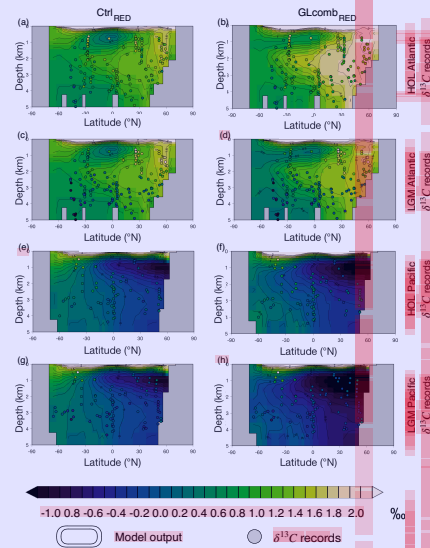
**Figure 4.** Sections of  $O_2$  concentration ( $\mu\text{mol kg}^{-1}$ ) along  $25^\circ\text{W}$  in the Atlantic basin (left hand column) and along  $135^\circ\text{W}$  in the Pacific basin (right hand column). Panels show observations (World Ocean Atlas 2013, Garcia et al., 2014b) (a, b), and model states *CtrlRED* (c, d), *CtrlGAM* (e, f), *GLcombRED* (g, h) and *GLcombGAM* (i, j).



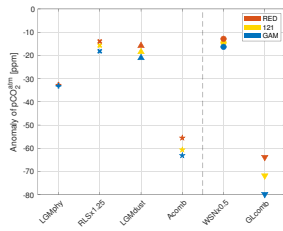
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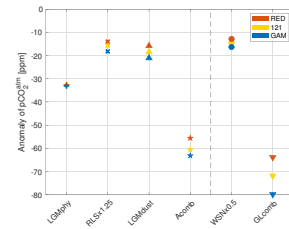
**Figure 5.** Model ocean  $\delta^{13}C$  (contours) compared to the two time slices (HOL and LGM) of observed benthic  $\delta^{13}C$  (circles) of Peterson et al. (2014). Left hand column shows  $Ctrl_{RED}$  (panels a, c, e, g) and right hand column shows  $GLcomb_{RED}$  (panels b, d, f, h). The rows show, from top to bottom, a-b) HOL Atlantic, c-d) LGM Atlantic, e-f) HOL Pacific, g-h) LGM Pacific. Note that, when we compare  $GLcomb_{RED}$  to LGM observations (panels d and h), a constant of 0.32 ‰ is subtracted from  $GLcomb_{RED}$  data, to account for terrestrial release of  $\delta^{13}C$ -depleted terrestrial carbon. The corresponding comparison for model version GAM is shown in Fig. S.3.



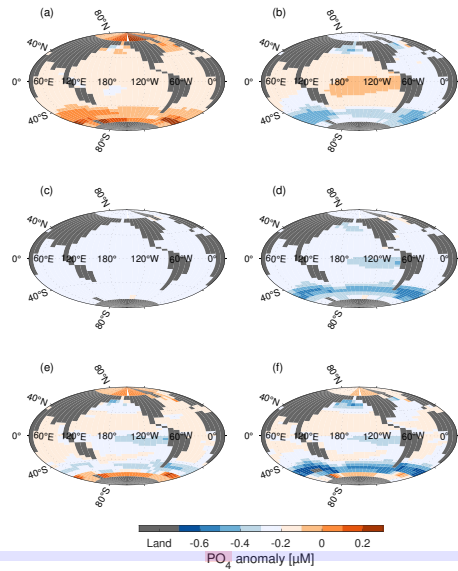
**Figure 5.** Model ocean  $\delta^{13}C$  (contours) compared to the two proxy record time slices (HOL and LGM) of benthic  $\delta^{13}C$  (circles) of Peterson et al. (2014). The upper half of the figure shows the Atlantic Ocean (panels a-d), while the lower half shows the Pacific Ocean (panels e-h). The columns represent the model simulations ( $Ctrl_{RED}$  or  $Ctrl_{GAM}$ ), while each row represents one of the proxy record time slices (HOL or LGM). The left hand column shows  $Ctrl_{RED}$  (panels a, c, e, g) and the right hand column shows  $GLcomb_{RED}$  (panels b, d, f, h). The rows show, from top to bottom, a-b) HOL Atlantic, c-d) LGM Atlantic, e-f) HOL Pacific, g-h) LGM Pacific. Note that, before we compare  $GLcomb_{RED}$  to LGM observations (panels d and h), a constant of 0.32 ‰ is subtracted from the simulated  $\delta^{13}C$ , to account for terrestrial release of  $\delta^{13}C$ -depleted terrestrial carbon which is not modelled. The corresponding comparison for model version GAM is shown in Fig. S.3.



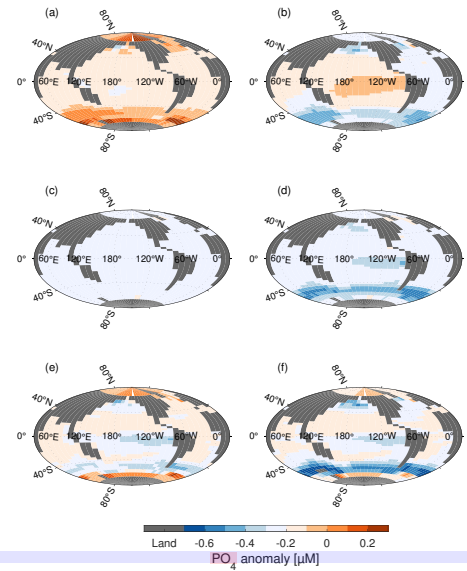
**Figure 6.** Resulting CO<sub>2</sub> anomaly, with respect to the control state 278 ppm, of the sensitivity experiments *LGMphy* (plus-symbol), *RLS* × 1.25 (×-symbol), *LGMdust* (upward arrowheads), and *WSN* × 0.5 (circles), and of the combined experiments *Acomb* (stars) and *GLcomb* (downward arrowheads). Results of the different model versions *RED*, 121 and *GAM* are shown in red, yellow and blue, respectively. The vertical dashed line separates simulations without (left) and with (right) wind perturbation.



**Figure 6.** Resulting CO<sub>2</sub> anomaly, with respect to the control state 278 ppm, of the sensitivity experiments *LGMphy* (plus-symbol), *RLS* × 1.25 (×-symbol), *LGMdust* (upward arrowheads), and *WSN* × 0.5 (circles), and of the combined experiments *Acomb* (stars) and *GLcomb* (downward arrowheads). Results of the different model versions *RED*, 121 and *GAM* are shown in red, yellow and blue, respectively. The vertical dashed line separates simulations without (left) and with (right) wind perturbation.



**Figure 7.** Surface  $PO_4$  anomaly [ $\mu M$ ], with respect to surface concentration of  $PO_4$  in  $Ctrl_{GAM}$  (Fig. 3a), for a)  $LGM_{phy_{GAM}}$ , b)  $WSN \times 0.5_{GAM}$  c)  $RLS \times 1.25_{GAM}$ , d)  $LGM_{dust_{GAM}}$ , e)  $Acomb_{GAM}$ , f)  $GLcomb_{GAM}$ . Changes in surface nutrient fields are similar for all three model versions ( $RED$ ,  $GAM$ , 121), thus only  $GAM$  is shown.



**Figure 7.** Surface  $PO_4$  anomaly [ $\mu M$ ], with respect to surface concentration of  $PO_4$  in  $Ctrl_{GAM}$  (Fig. 3a), for a)  $LGM_{phy_{GAM}}$ , b)  $WSN \times 0.5_{GAM}$  c)  $RLS \times 1.25_{GAM}$ , d)  $LGM_{dust_{GAM}}$ , e)  $Acomb_{GAM}$ , f)  $GLcomb_{GAM}$ . Changes in surface nutrient fields are similar for all three model versions ( $RED$ ,  $GAM$ , 121), thus only  $GAM$  is shown.

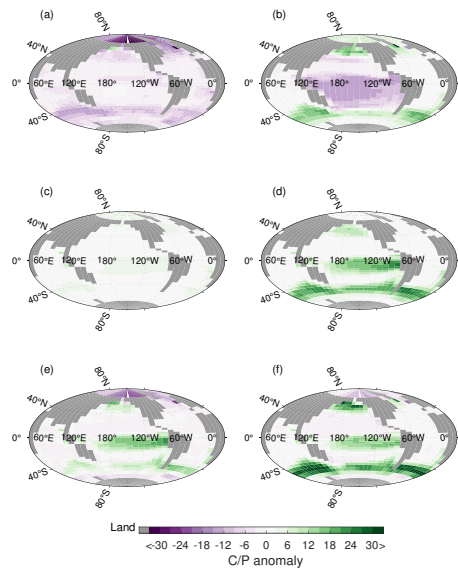


Figure 8. Surface  $C/P$  anomaly, with respect to  $CP$  of  $Ctrl_{GAM}$  (Fig. 3b), for a)  $LGM_{phy_{GAM}}$ , b)  $WSN \times 0.5_{GAM}$  c)  $RLS \times 1.25_{GAM}$ , d)  $LGM_{dust_{GAM}}$ , e)  $Acamb_{GAM}$ , f)  $GLcomb_{GAM}$ .

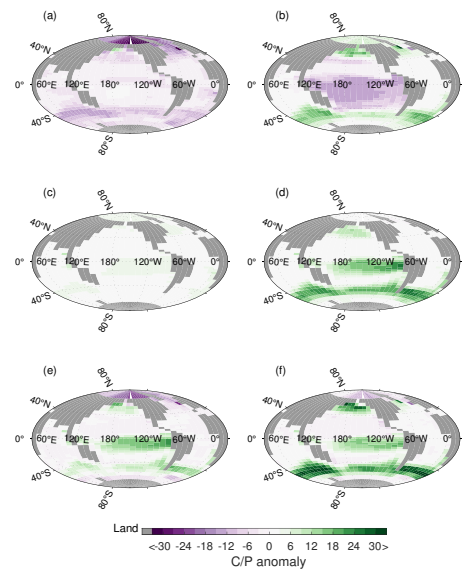
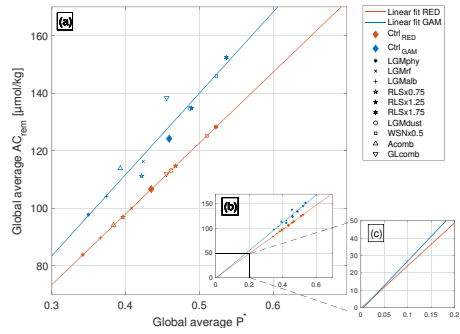
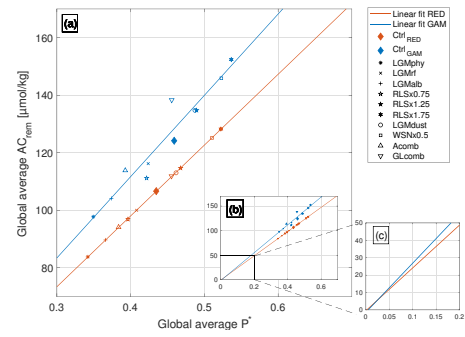


Figure 8. Surface  $C/P$  anomaly, with respect to  $CP$  of  $Ctrl_{GAM}$  (Fig. 3b), for a)  $LGM_{phy_{GAM}}$ , b)  $WSN \times 0.5_{GAM}$  c)  $RLS \times 1.25_{GAM}$ , d)  $LGM_{dust_{GAM}}$ , e)  $Acamb_{GAM}$ , f)  $GLcomb_{GAM}$ .



**Figure 9.** Remineralised acidic carbon ( $AC_{rem} = DIC_{rem} - (1/2) * ALK_{rem}$ , see Appendix A) as a function of  $P^*$ . Simulations using model versions *RED* and *GAM* are shown in red and blue, respectively. Different symbols indicate the sensitivity experiments, listed in the panel on the right hand side. Red and blue lines show linear least-squares fits to the separate ensembles for *RED* and *GAM*. Panels illustrate a) the deviation from the least-squares fit of the *GAM* ensemble as opposed to the *RED* ensemble, b) the linear fits extrapolated to origo, and c) a zoom-in around the origin, where the *RED* (red) line goes through the origin, while the *GAM* (blue) does not.



**Figure 9.** Remineralised acidic carbon ( $AC_{rem} = DIC_{rem} - (1/2) * ALK_{rem}$ , see Appendix A) as a function of  $P^*$ . Simulations using model versions *RED* and *GAM* are shown in red and blue, respectively. Different symbols indicate the sensitivity experiments, listed in the panel on the right hand side. Red and blue lines show linear least-squares fits to the separate ensembles for *RED* and *GAM*. Panels illustrate a) the deviation from the least-squares fit of the *GAM* ensemble as opposed to the *RED* ensemble, b) the linear fits extrapolated to origo, and c) a zoom-in around the origin, where the *RED* (red) line goes through the origin, while the *GAM* (blue) does not.

**Table 1.** List of experiments. Ensemble member acronyms, short descriptions of what the simulation tests, and specifications of parameter settings for each ensemble member. The  $pCO_2^{sim}$  is either prescribed to pre-industrial (PI) = 278 ppm, or freely varying with changes in climate and ocean circulation. The radiative forcing is either coupled to the  $pCO_2^{sim}$  of the atmospheric chemistry module of the model, or fixed at a value corresponding  $pCO_2^{sim} = 185$  ppm. The zonal albedo profile is either representative of modern/PI conditions or of the LGM. The wind stress is either modern/PI, or has an adjusted peak in wind stress at  $\pm 50^\circ$  N. The modern/PI remanualisation length scale (RLS) is 590 m. If RLS is changed, it is multiplied by a factor  $f_r$ . Dust forcing is either modern/PI or representative of LGM. Each experiment is conducted using model versions **MIROC5** CP fixed at 106/1 (Reifeld, 1963), denoted **RED**, CP variable with surface ocean  $PO_4$  concentration (Galbraith and Martiny, 2015), denoted **GM15**, and CP fixed at 12/1 (denoted 121, see Section 2.3).

Ensemble member	Short description	$pCO_2^{sim}$	Radiative forcing	Zonal albedo	Wind stress <sup>1</sup> at $\pm 50^\circ$ N	RLS <sup>2</sup> (m)	Dust forcing
<i>Ctrl</i>	Control	278 ppm (restored) variable	coupled to $pCO_2^{sim}$	modern/PI	modern/PI	590	modern/PI
<i>LGMrf</i>	LGM radiative forcing	185 ppm	fixed at	modern/PI	modern/PI	590	modern/PI
<i>LGMalb</i>	LGM zonal albedo	variable	coupled to $pCO_2^{sim}$	LGM <sup>3</sup>	modern/PI	590	modern/PI
<i>LGMphy</i>	LGMrf+ LGMalb	variable	fixed at	LGM	modern/PI	590	modern/PI
<i>WNS × 0.5</i>	Wind stress at $\pm 50^\circ$ N reduced	variable	coupled to $pCO_2^{sim}$	modern/PI	PI × 0.5	590	modern/PI
<i>RLS × f<sub>r</sub></i>	RLS changed by factor $f_r$	variable	coupled to $pCO_2^{sim}$	modern/PI	modern/PI	590 × $f_r$	modern/PI
<i>LGMdust</i>	LGM dust flux	variable	coupled to $pCO_2^{sim}$	modern/PI	modern/PI	590	LGM <sup>4</sup>
<i>GLcomb</i>	"Glacial-like" (GL) (all forcings)	variable	fixed at 185 ppm	LGM	PI × 0.5	590 × 1.25	LGM
<i>Acomb</i>	"GL" with PI wind	variable	fixed at 185 ppm	LGM	modern/PI	590 × 1.25	LGM

1) See Landerle et al. (2013) for example of reduced peak wind profile for the Southern Hemisphere.  
 2)  $f_r$  = multiplication factor for remanualisation length scale. We test multiplication factors between 0.75 and 1.75, corresponding to a change in RLS between -25 % to +75 %.  
 3) Calculated from HADCM3 LGM (21ka) simulation of Davies-Barnard et al. (2017)  
 4) Re-gridded LGM dust flux from Mahowald et al. (2006)

**Table 1.** List of experiments. Ensemble member acronyms, short descriptions of what the simulation tests, and specifications of parameter settings for each ensemble member. The  $pCO_2^{sim}$  is either prescribed to pre-industrial (PI) = 278 ppm, or freely varying with changes in climate and ocean circulation. The radiative forcing is either coupled to the  $pCO_2^{sim}$  of the atmospheric chemistry module of the model, or fixed at a value corresponding  $pCO_2^{sim} = 185$  ppm. The zonal albedo profile is either representative of modern/PI conditions or of the LGM. The wind stress is either modern/PI, or has an adjusted peak in wind stress at  $\pm 50^\circ$  N. The modern/PI remanualisation length scale (RLS) is 590 m. If RLS is changed, it is multiplied by a factor  $f_r$ . Dust forcing is either modern/PI or representative of LGM. Each experiment is conducted using model versions **MIROC5** CP fixed at 106/1 (Reifeld, 1963), denoted **RED**, CP variable with surface ocean  $PO_4$  concentration (Galbraith and Martiny, 2015), denoted **GM15**, and CP fixed at 12/1 (denoted 121, see Section 2.3).

Ensemble member	Short description	$pCO_2^{sim}$	Radiative forcing	Zonal albedo	Wind stress <sup>1</sup> at $\pm 50^\circ$ N	RLS <sup>2</sup> (m)	Dust forcing
<i>Ctrl</i>	Control	278 ppm (restored) variable	coupled to $pCO_2^{sim}$	modern/PI	modern/PI	590	modern/PI
<i>LGMrf</i>	LGM radiative forcing	185 ppm	fixed at	modern/PI	modern/PI	590	modern/PI
<i>LGMalb</i>	LGM zonal albedo	variable	coupled to $pCO_2^{sim}$	LGM <sup>3</sup>	modern/PI	590	modern/PI
<i>LGMphy</i>	LGMrf+ LGMalb	variable	fixed at 185 ppm	LGM	modern/PI	590	modern/PI
<i>WNS × 0.5</i>	Wind stress at $\pm 50^\circ$ N reduced	variable	coupled to $pCO_2^{sim}$	modern/PI	PI × 0.5	590	modern/PI
<i>RLS × f<sub>r</sub></i>	RLS changed by factor $f_r$	variable	coupled to $pCO_2^{sim}$	modern/PI	modern/PI	590 × $f_r$	modern/PI
<i>LGMdust</i>	LGM dust flux	variable	coupled to $pCO_2^{sim}$	modern/PI	modern/PI	590	LGM <sup>4</sup>
<i>GLcomb</i>	"Glacial-like" (GL) (all forcings)	variable	fixed at 185 ppm	LGM	PI × 0.5	590 × 1.25	LGM
<i>Acomb</i>	"GL" with PI wind	variable	fixed at 185 ppm	LGM	modern/PI	590 × 1.25	LGM

1) See Landerle et al. (2013) for example of reduced peak wind profile for the Southern Hemisphere.  
 2)  $f_r$  = multiplication factor for remanualisation length scale. We test multiplication factors between 0.75 and 1.75, corresponding to a change in RLS between -25 % to +75 %.  
 3) Calculated from HADCM3 LGM (21ka) simulation of Davies-Barnard et al. (2017)  
 4) Re-gridded LGM dust flux from Mahowald et al. (2006)



**Table 2.** Atmospheric  $CO_2$  ( $pCO_2^{atm}$ , ppm), global ocean averages of temperature ( $\overline{T_{occ}}$ , °C),  $\overline{P^*}$  and  $\overline{O_2}$  ( $\mu mol\ kg^{-1}$ ), and Atlantic overturning streamfunction ( $\psi$ , Sverdrups (SV)) maximum and minimum, for observations, and for selected ensemble members in each model version (RED/GAM). Observed modern day  $\overline{T_{occ}}$  and  $\overline{O_2}$  were computed using the World Ocean Atlas 2013 (Locarnini et al., 2013; Garcia et al., 2014b).  $\overline{P^*}$  for the modern day ocean is estimated by Ito and Follows (2005). Average modern day AMOC strength is estimated by McCarthy et al. (2015) from the RAPID-MOCHA array at 26 °N (corresponding to Atlantic  $\psi_{max}$  in the model). Note that observed  $pCO_2^{atm}$  is given for pre-industrial (PI) climate, as we do not model anthropogenic release of  $CO_2$ .

Ensemble member	$pCO_2^{atm}$ (ppm)	$\overline{T_{occ}}$ (°C)	$\overline{P^*}$	$\overline{O_2}$ ( $\mu mol\ kg^{-1}$ )	Atlantic $\psi_{max}$ (SV)	Atlantic $\psi_{min}$ (SV)	
Obs. modern	278 (PI)	3.49	0.36	169	17.2±0.9	-	
Ensemble member	version						
RED / GAM							
Ctrl	278.0 / 278.0	3.56 / 3.56	0.43 / 0.46	166 / 144	14.2 / 14.3	-0.8 / -0.7	
LGMphy	245.4 / 244.9	1.45 / 1.45	0.34 / 0.35	171 / 149	13.7 / 13.7	-0.4 / -0.4	
RLS × 1.25	264.0 / 262.3	3.50 / 3.49	0.47 / 0.49	155 / 129	14.4 / 14.5	-0.5 / -0.4	
LGMdust	262.2 / 256.9	3.48 / 3.47	0.46 / 0.49	152 / 124	14.4 / 14.5	-0.5 / -0.4	
WNS × 0.5	265.1 / 261.7	3.98 / 3.99	0.51 / 0.52	141 / 114	12.7 / 12.7	-0.8 / -0.7	
Acomb	222.5 / 214.9	1.45 / 1.45	0.48 / 0.39	148 / 116	13.7 / 13.7	-0.4 / -0.4	
GLEomb	214.1 / 198.2	1.94 / 1.91	0.46 / 0.46	122 / 74	12.0 / 12.1	-0.4 / -0.4	

**Table 2.** Atmospheric  $CO_2$  ( $pCO_2^{atm}$ , ppm), global ocean averages of temperature ( $\overline{T_{occ}}$ , °C),  $\overline{P^*}$  and  $\overline{O_2}$  ( $\mu mol\ kg^{-1}$ ), and Atlantic overturning streamfunction ( $\psi$ , Sverdrups (SV)) maximum and minimum north of 30 °N, for observations, and for selected ensemble members in each model version (RED/GAM). Observed modern day  $\overline{T_{occ}}$  and  $\overline{O_2}$  were computed using the World Ocean Atlas 2018 (Locarnini et al., 2018; Garcia et al., 2018b).  $\overline{P^*}$  for the modern day ocean is estimated by Ito and Follows (2005). Average modern day AMOC strength is estimated by McCarthy et al. (2015) from the RAPID-MOCHA array at 26 °N (corresponding to Atlantic  $\psi_{max}$  in the model). Note that observed  $pCO_2^{atm}$  is given for pre-industrial (PI) climate, as we do not model anthropogenic release of  $CO_2$ .

Ensemble member	$pCO_2^{atm}$ (ppm)	$\overline{T_{occ}}$ (°C)	$\overline{P^*}$	$\overline{O_2}$ ( $\mu mol\ kg^{-1}$ )	Atlantic $\psi_{max}$ (SV)	Atlantic $\psi_{min}$ (SV)
Obs. modern	278 (PI)	3.49	0.36	172	17.2±0.9	-
Ensemble member						
Ctrl <sub>RED</sub>	278.0	3.56	0.43	166	14.2	-0.8
Ctrl <sub>GAM</sub>	278.0	3.56	0.46	144	14.3	-0.7
LGMphy <sub>RED</sub>	245.4	1.45	0.34	171	13.7	-0.4
LGMphy <sub>GAM</sub>	244.9	1.45	0.35	149	13.7	-0.4
RLS × 1.25 <sub>RED</sub>	264.0	3.50	0.47	155	14.4	-0.5
RLS × 1.25 <sub>GAM</sub>	262.3	3.49	0.49	129	14.5	-0.4
LGMdust <sub>RED</sub>	262.2	3.48	0.46	152	14.4	-0.5
LGMdust <sub>GAM</sub>	256.9	3.47	0.49	124	14.5	-0.4
WNS × 0.5 <sub>RED</sub>	265.1	3.98	0.51	141	12.7	-0.8
WNS × 0.5 <sub>GAM</sub>	261.7	3.99	0.52	114	12.7	-0.7
Acomb <sub>RED</sub>	222.5	1.45	0.48	148	13.7	-0.4
Acomb <sub>GAM</sub>	214.9	1.45	0.39	116	13.7	-0.4
GLEomb <sub>RED</sub>	214.1	1.94	0.46	122	12.0	-0.4
GLEomb <sub>GAM</sub>	198.2	1.91	0.46	74	12.1	-0.4

## Variable C/P composition of organic production and its effect on ocean carbon storage in glacial model simulations

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<sup>1</sup>Department of Meteorology, Bolin Centre for Climate Research, Stockholm University, 106 91 Stockholm, Sweden

<sup>2</sup>Department of Earth Sciences, University of California–Riverside, Riverside, CA 92521, USA

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<sup>1</sup>Department of Meteorology, Bolin Centre for Climate Research, Stockholm University, 106 91 Stockholm, Sweden

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## S Supplementary material

This document includes supplementary figures and tables, containing data that is described or shown in other forms in the manuscript.

5 In Fig. S.1, the locations of core sites for observed benthic  $\delta^{13}C$  are indicated, and Holocene (HOL) observed benthic  $\delta^{13}C$  is compared to the bottom water ocean distribution of  $\delta^{13}C$  for *Ctrl<sub>RED</sub>*. The positions of observation sites are the same as in Peterson et al. (2014).

For comparison with Fig. 3a, we show the surface  $PO_4$  concentration ( $\mu M$ ) of the control state with fixed Redfield stoichiometry (*Ctrl<sub>RED</sub>*) (Fig. S.2).

10 For comparison with Fig. 5, which shows model ocean  $\delta^{13}C$  of model version *RED* compared to observations, we show the corresponding ocean sections for model version *GAM* (Fig. S.3).

The supplementary tables S.1 and S.2 list diagnostic variables for climate (Table S.1, model versions *RED* and *GAM*, all ensemble members), carbon and nutrients (Table S.2, all model versions, all ensemble members). Table S.3 lists model–data comparison statistics for the *Ctrl* and *GLcomb* simulations in each of the model versions *RED* and *GAM*, and for the two benthic  $\delta^{13}C$  data time slices HOL (0-6 ka) and LGM (19-23 ka).

## S Supplementary material

This document includes supplementary figures and tables, containing data that is described or shown in other forms in the manuscript.

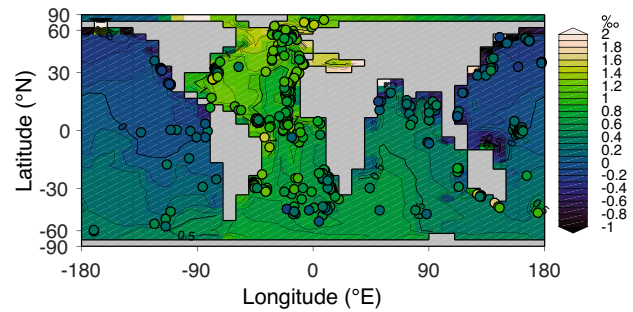
5 In Fig. S.1, the locations of core sites for observed benthic  $\delta^{13}C$  are indicated, and Holocene (HOL) observed benthic  $\delta^{13}C$  is compared to the bottom water ocean distribution of  $\delta^{13}C$  for *Ctrl<sub>RED</sub>*. The positions of observation sites are the same as in Peterson et al. (2014).

For comparison with Fig. 3a, we show the surface  $PO_4$  concentration ( $\mu M$ ) of the control state with fixed Redfield stoichiometry (*Ctrl<sub>RED</sub>*) (Fig. S.2).

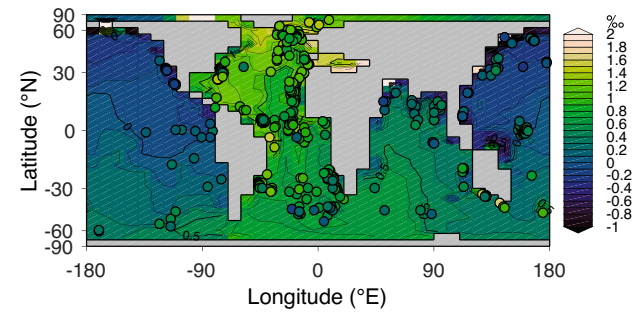
10 For comparison with Fig. 5, which shows model ocean  $\delta^{13}C$  of model version *RED* compared to observations, we show the corresponding ocean sections for model version *GAM* (Fig. S.3).

As an example of sea–ice cover expansion due to the applied glacial–like perturbations, we show the change in sea–ice cover between *Ctrl<sub>RED</sub>* and *GLcomb<sub>RED</sub>* (Fig. S.4).

15 The supplementary tables S.1 and S.2 list diagnostic variables for climate (Table S.1, model versions *RED* and *GAM*, all ensemble members), carbon and nutrients (Table S.2, all model versions, all ensemble members). Table S.3 lists model–data comparison statistics for the *Ctrl* and *GLcomb* simulations in each of the model versions *RED* and *GAM*, and for the two benthic  $\delta^{13}C$  data time slices HOL (0-6 ka) and LGM (19-23 ka).



**Figure S.1.** *Ctrl<sub>RED</sub>* bottom water ocean  $\delta^{13}C$  (contours) compared to the Holocene (HOL) time slice of observed benthic  $\delta^{13}C$  (circles) of Peterson et al. (2014).



**Figure S.1.** *Ctrl<sub>RED</sub>* bottom water ocean  $\delta^{13}C$  (contours) compared to the Holocene (HOL) time slice of observed benthic  $\delta^{13}C$  (circles) of Peterson et al. (2014).

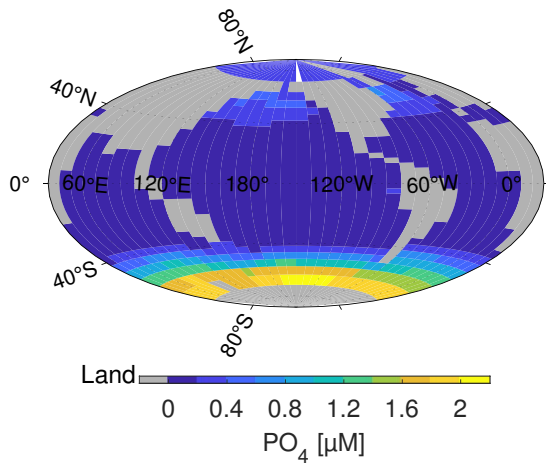


Figure S.2. Surface  $PO_4$  concentration ( $\mu M$ ) of the control state with fixed Redfield stoichiometry ( $Ctrl_{RED}$ ).

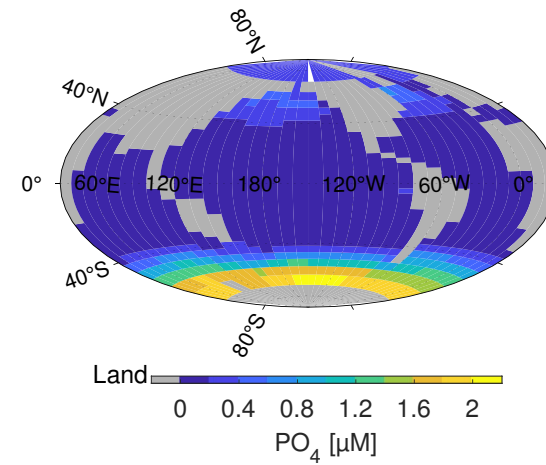
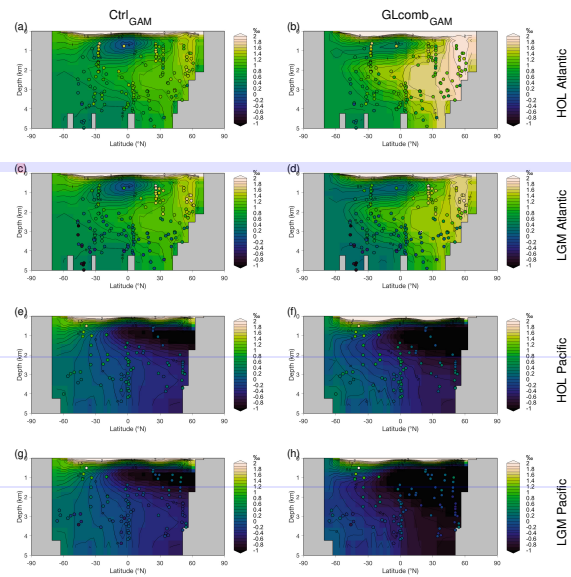
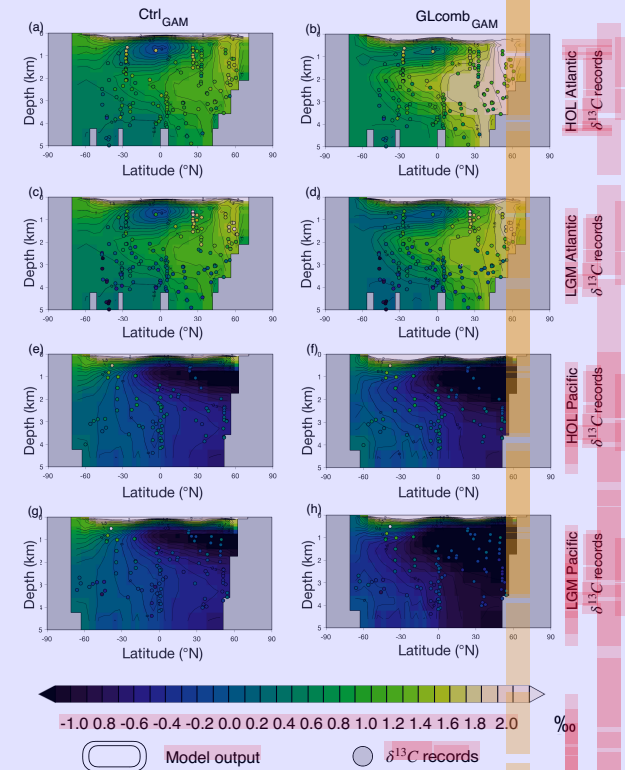


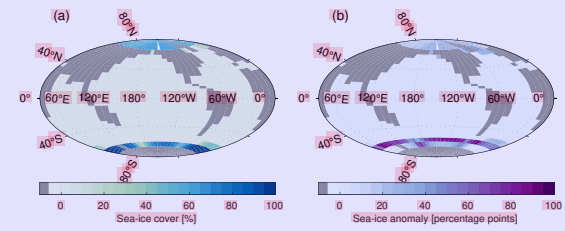
Figure S.2. Surface  $PO_4$  concentration ( $\mu M$ ) of the control state with fixed Redfield stoichiometry ( $Ctrl_{RED}$ ).



**Figure S.3.** Model ocean  $\delta^{13}C$  (contours) compared to the two time slices (HOL and LGM) of observed benthic  $\delta^{13}C$  (circles) of Peterson et al. (2014). **Left** hand column shows  $Ctrl_{GAM}$  (panels a, c, e, g) and right hand column shows  $GLcomb_{GAM}$  (panels b, d, f, h). The rows show, from top to bottom, a-b) HOL Atlantic, c-d) LGM Atlantic, e-f) HOL Pacific, g-h) LGM Pacific. Note that, when we compare  $GLcomb_{GAM}$  to LGM observations (panels d and h), a constant of 0.32 ‰ is subtracted from  $GLcomb_{GAM}$  data, to account for terrestrial release of  $\delta^{13}C$ -depleted terrestrial carbon.



**Figure S.3.** Model ocean  $\delta^{13}C$  (contours) compared to the two proxy record time slices (HOL and LGM) of benthic  $\delta^{13}C$  (circles) of Peterson et al. (2014). The upper half of the figure shows the Atlantic Ocean (panels a–d), while the lower half shows the Pacific Ocean (panels e–h). The columns represent the model simulations ( $Ctrl_{RED}$  or  $Ctrl_{GAM}$ ), while each row represents one of the proxy record time slices (HOL or LGM). The left hand column shows  $Ctrl_{GAM}$  (panels a, c, e, g) and the right hand column shows  $GLcomb_{GAM}$  (panels b, d, f, h). The rows show, from top to bottom, a-b) HOL Atlantic, c-d) LGM Atlantic, e-f) HOL Pacific, g-h) LGM Pacific. Note that, before we compare  $GLcomb_{RED}$  to LGM observations (panels d and h), a constant of 0.32 ‰ is subtracted from simulated  $\delta^{13}C$ , to account for terrestrial release of  $\delta^{13}C$ -depleted terrestrial carbon which is not modelled.



**Figure S.4.** a) Sea-ice cover (%) of  $Ctrl_{RED}$ , and b) the sea-ice anomaly  $Gcomb_{RED} - Ctrl_{RED}$  (percentage points).

**Table S.1.** Carbon and nutrient variables in control states (*Ctrl*) and ensemble members (Table 1) of model versions *RED* and *GAM*. The columns list global ocean values for C/P ratio in the export flux of organic matter (dimensionless quantity), total content of DIC ( $DIC_{cont}$ , PgC), average concentration of DIC ( $\overline{DIC}_{tot}$ ,  $\mu\text{molkg}^{-1}$ ), average concentration of remineralised DIC ( $\overline{DIC}_{rem}$ ,  $\mu\text{molkg}^{-1}$ ), average concentration of remineralised acidic carbon ( $\overline{AC}_{rem}$ ,  $\mu\text{molkg}^{-1}$ ), average concentration of  $PO_4$  ( $\overline{P}_{tot}$ ,  $\mu\text{molkg}^{-1}$ ), average concentration of remineralised  $PO_4$  ( $\overline{P}_{rem}$ ,  $\mu\text{molkg}^{-1}$ ) and average of the nutrient utilisation efficiency ( $\overline{P}^*$ ). The modern ocean observed C/P is given as determined by Anderson and Sarmiento (1994) and the global ocean carbon inventory ( $DIC_{cont}$ ) is estimated to 38,700 PgC (Stocker, 2014). The observational estimate for  $\overline{P}^*$  is given by Ito and Follows (2005).

Experiment acronym	C/P ratio	$DIC_{cont}$ (PgC)	$\overline{DIC}_{tot}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{DIC}_{rem}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{AC}_{rem}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{P}_{tot}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{P}_{rem}$ ( $\mu\text{molkg}^{-1}$ )	Global $\overline{P}^*$
Observ.	117 ± 14	~ 38,700	-	-	-	-	-	0.36
<i>Ctrl</i> <sub>RED</sub>	106.00	35,882	2,234.0	146.16	106.64	2.1520	0.9354	0.435
<i>Ctrl</i> <sub>GAM</sub>	120.85	36,134	2,249.7	172.28	124.17	2.1518	0.9877	0.459
<i>LGMrf</i> <sub>RED</sub>	106.0	35,910	2,235.7	136.32	99.982	2.1520	0.8783	0.408
<i>LGMrf</i> <sub>GAM</sub>	120.90	36,162	2,251.4	160.56	116.22	2.1518	0.9120	0.424
<i>LGMalb</i> <sub>RED</sub>	106.00	35,937	2,237.4	121.72	89.678	2.1522	0.7875	0.366
<i>LGMalb</i> <sub>GAM</sub>	121.15	36,192	2,253.3	143.32	104.12	2.1520	0.8045	0.374
<i>LGMphy</i> <sub>RED</sub>	106.00	35,953	2,238.4	113.33	83.791	2.1524	0.7358	0.342
<i>LGMphy</i> <sub>GAM</sub>	121.13	36,206	2,254.2	134.11	97.749	2.1521	0.7519	0.349
<i>WNS</i> × 0.5 <sub>RED</sub>	106.00	35,911	2,235.8	170.91	125.16	2.1524	1.0983	0.510
<i>WNS</i> × 0.5 <sub>GAM</sub>	124.75	36,170	2,251.9	201.96	145.91	2.1523	1.1257	0.523
<i>RLS</i> × 0.75 <sub>RED</sub>	106.00	35,843	2,231.5	141.81	96.857	2.1508	0.8525	0.396
<i>RLS</i> × 0.75 <sub>GAM</sub>	118.86	36,084	2,246.5	164.24	111.20	2.1505	0.9068	0.422
<i>RLS</i> × 1.25 <sub>RED</sub>	106.00	35,914	2,235.9	149.20	114.68	2.1526	1.0069	0.468
<i>RLS</i> × 1.25 <sub>GAM</sub>	122.69	36,175	2,252.2	177.94	134.76	2.1525	1.0534	0.455
<i>RLS</i> × 1.75 <sub>RED</sub>	106.00	35,956	2,238.6	156.51	128.25	2.1536	1.1250	0.522
<i>RLS</i> × 1.75 <sub>GAM</sub>	125.83	36,230	2,255.7	189.51	152.39	2.1535	1.1553	0.537

**Table S.1.** Carbon and nutrient variables in control states (*Ctrl*) and ensemble members (Table 1) of model versions *RED* and *GAM*. The columns list global ocean values for C/P ratio in the export flux of organic matter (dimensionless quantity), total content of DIC ( $DIC_{cont}$ , PgC), average concentration of DIC ( $\overline{DIC}_{tot}$ ,  $\mu\text{molkg}^{-1}$ ), average concentration of remineralised DIC ( $\overline{DIC}_{rem}$ ,  $\mu\text{molkg}^{-1}$ ), average concentration of remineralised acidic carbon ( $\overline{AC}_{rem}$ ,  $\mu\text{molkg}^{-1}$ ), average concentration of  $PO_4$  ( $\overline{P}_{tot}$ ,  $\mu\text{molkg}^{-1}$ ), average concentration of remineralised  $PO_4$  ( $\overline{P}_{rem}$ ,  $\mu\text{molkg}^{-1}$ ) and average of the nutrient utilisation efficiency ( $\overline{P}^*$ ). The modern ocean observed C/P is given as determined by Anderson and Sarmiento (1994) and the global ocean carbon inventory ( $DIC_{cont}$ ) is estimated to 38,700 PgC (Stocker, 2014). Observed modern day  $\overline{P}_{tot}$  was computed as a simple whole ocean average based on WOA18 (Garcia et al., 2018). The observational estimate for  $\overline{P}^*$  is given by Ito and Follows (2005).

Experiment acronym	C/P ratio	$DIC_{cont}$ (PgC)	$\overline{DIC}_{tot}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{DIC}_{rem}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{AC}_{rem}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{P}_{tot}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{P}_{rem}$ ( $\mu\text{molkg}^{-1}$ )	Global $\overline{P}^*$
Observ.	117 ± 14	~ 38,700	-	-	-	2.12	-	0.36
<i>Ctrl</i> <sub>RED</sub>	106.00	35,882	2,234.0	146.16	106.64	2.1520	0.9354	0.435
<i>Ctrl</i> <sub>GAM</sub>	120.85	36,134	2,249.7	172.28	124.17	2.1518	0.9877	0.459
<i>LGMrf</i> <sub>RED</sub>	106.0	35,910	2,235.7	136.32	99.982	2.1520	0.8783	0.408
<i>LGMrf</i> <sub>GAM</sub>	120.90	36,162	2,251.4	160.56	116.22	2.1518	0.9120	0.424
<i>LGMalb</i> <sub>RED</sub>	106.00	35,937	2,237.4	121.72	89.678	2.1522	0.7875	0.366
<i>LGMalb</i> <sub>GAM</sub>	121.15	36,192	2,253.3	143.32	104.12	2.1520	0.8045	0.374
<i>LGMphy</i> <sub>RED</sub>	106.00	35,953	2,238.4	113.33	83.791	2.1524	0.7358	0.342
<i>LGMphy</i> <sub>GAM</sub>	121.13	36,206	2,254.2	134.11	97.749	2.1521	0.7519	0.349
<i>WNS</i> × 0.5 <sub>RED</sub>	106.00	35,911	2,235.8	170.91	125.16	2.1524	1.0983	0.510
<i>WNS</i> × 0.5 <sub>GAM</sub>	124.75	36,170	2,251.9	201.96	145.91	2.1523	1.1257	0.523
<i>RLS</i> × 0.75 <sub>RED</sub>	106.00	35,843	2,231.5	141.81	96.857	2.1508	0.8525	0.396
<i>RLS</i> × 0.75 <sub>GAM</sub>	118.86	36,084	2,246.5	164.24	111.20	2.1505	0.9068	0.422
<i>RLS</i> × 1.25 <sub>RED</sub>	106.00	35,914	2,235.9	149.20	114.68	2.1526	1.0069	0.468
<i>RLS</i> × 1.25 <sub>GAM</sub>	122.69	36,175	2,252.2	177.94	134.76	2.1525	1.0534	0.455
<i>RLS</i> × 1.75 <sub>RED</sub>	106.00	35,956	2,238.6	156.51	128.25	2.1536	1.1250	0.522
<i>RLS</i> × 1.75 <sub>GAM</sub>	125.83	36,230	2,255.7	189.51	152.39	2.1535	1.1553	0.537



Table S.1. Continued.

Experiment acronym	C/P ratio	$DIC_{cont}$ (PgC)	$\overline{DIC}_{tot}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{DIC}_{rem}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{AC}_{rem}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{P}_{tot}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{P}_{rem}$ ( $\mu\text{molkg}^{-1}$ )	Global $\overline{P}^*$
<i>LGMdust<sub>RED</sub></i>	106.00	35,916	2,236.1	113.33	113.02	2.1515	0.9931	0.462
<i>LGMdust<sub>GAM</sub></i>	124.05	36,179	2,252.4	134.11	134.75	2.1512	1.0482	0.487
<i>Acomb<sub>RED</sub></i>	106.00	36,002	2,241.5	122.01	94.115	2.1528	0.8259	0.384
<i>Acomb<sub>GAM</sub></i>	125.61	36,270	2,258.2	150.58	113.85	2.1525	0.8452	0.393
<i>GLcomb<sub>RED</sub></i>	106.00	36,021	2,242.7	146.62	111.86	2.1537	0.9808	0.455
<i>GLcomb<sub>GAM</sub></i>	133.77	36,307	2,260.5	186.19	138.32	2.1534	0.9813	0.456

Table S.1. Continued.

Experiment acronym	C/P ratio	$DIC_{cont}$ (PgC)	$\overline{DIC}_{tot}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{DIC}_{rem}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{AC}_{rem}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{P}_{tot}$ ( $\mu\text{molkg}^{-1}$ )	$\overline{P}_{rem}$ ( $\mu\text{molkg}^{-1}$ )	Global $\overline{P}^*$
<i>LGMdust<sub>RED</sub></i>	106.00	35,916	2,236.1	113.33	113.02	2.1515	0.9931	0.462
<i>LGMdust<sub>GAM</sub></i>	124.05	36,179	2,252.4	134.11	134.75	2.1512	1.0482	0.487
<i>Acomb<sub>RED</sub></i>	106.00	36,002	2,241.5	122.01	94.115	2.1528	0.8259	0.384
<i>Acomb<sub>GAM</sub></i>	125.61	36,270	2,258.2	150.58	113.85	2.1525	0.8452	0.393
<i>GLcomb<sub>RED</sub></i>	106.00	36,021	2,242.7	146.62	111.86	2.1537	0.9808	0.455
<i>GLcomb<sub>GAM</sub></i>	133.77	36,307	2,260.5	186.19	138.32	2.1534	0.9813	0.456

**Table S.2.** Climatic variables for all control states (*Ctrl*) and ensemble members (Table 1). The variables are atmospheric  $CO_2$  ( $pCO_2^{atm}$ , ppm), global averages of temperature in the ocean ( $T_{avg}^{oce}$ , °C) and in the atmosphere ( $T_{avg}^{atm}$ , °C), transport in the Atlantic meridional overturning circulation (AMOC, Sv) and sea ice cover (%). The observational estimate for  $\overline{T_{oce}^{atm}}$  has been calculated using the World Ocean Atlas 2013 (Locarnini et al., 2013). Average modern day AMOC strength is estimated by McCarthy et al. (2015) from the RAPID-MOCHA array at 26° N. Modern day sea ice cover is given as an interval due to seasonal variability (Comiso, 2008). No observational estimate for  $\overline{T_{atm}^{atm}}$  is given, since modern atmospheric observations are strongly influenced by rising  $pCO_2^{atm}$  (Stocker, 2014).

Experiment acronym	$pCO_2^{atm}$ (ppm)	$\overline{T_{oce}^{atm}}$ (°C)	$\overline{T_{atm}^{atm}}$ (°C)	AMOC (Sv)	Sea ice (%)
Observ.	278	3.49	N/A	17.2±0.9	3 to 6
<i>Ctrl</i> <sub>RED</sub>	278.0	3.56	12.38	14.25	5.41
<i>Ctrl</i> <sub>GAM</sub>	278.0	3.57	12.38	14.27	5.42
<i>Ctrl</i> <sub>121</sub>	278.0	3.59	12.37	14.25	5.42
<i>LGM</i> <sub>rRED</sub>	265.2	2.89	10.46	14.99	7.38
<i>LGM</i> <sub>rGAM</sub>	265.5	2.90	10.46	14.97	7.35
<i>LGM</i> <sub>albRED</sub>	252.8	1.97	8.18	13.82	9.30
<i>LGM</i> <sub>albGAM</sub>	251.6	1.97	8.16	13.82	9.38
<i>LGM</i> <sub>phyRED</sub>	245.4	1.45	6.83	13.67	10.6
<i>LGM</i> <sub>phyGAM</sub>	244.9	1.45	6.84	13.66	10.6
<i>WNS</i> × 0.5 <sub>RED</sub>	265.1	3.98	12.12	12.66	5.68
<i>WNS</i> × 0.5 <sub>GAM</sub>	261.7	3.99	12.05	12.72	5.74
<i>WNS</i> × 0.5 <sub>121</sub>	263.5	3.97	12.09	12.66	5.69
<i>RLS</i> × 0.75 <sub>RED</sub>	295.8	3.64	12.66	14.13	5.21
<i>RLS</i> × 0.75 <sub>GAM</sub>	301.4	3.68	12.75	14.09	5.08
<i>RLS</i> × 0.75 <sub>121</sub>	298.7	3.65	12.71	14.13	5.14
<i>RLS</i> × 1.25 <sub>RED</sub>	264.0	3.50	12.13	14.44	5.68
<i>RLS</i> × 1.25 <sub>GAM</sub>	262.3	3.49	12.09	14.46	5.74
<i>RLS</i> × 1.25 <sub>121</sub>	259.8	3.49	12.05	14.46	5.78
<i>RLS</i> × 1.75 <sub>RED</sub>	244.7	3.38	11.77	14.55	6.06
<i>RLS</i> × 1.75 <sub>GAM</sub>	234.7	3.33	11.57	14.56	6.27
<i>RLS</i> × 1.75 <sub>121</sub>	240.6	3.36	11.69	14.59	6.14

**Table S.2.** Climatic variables for all control states (*Ctrl*) and ensemble members (Table 1). The variables are atmospheric  $CO_2$  ( $pCO_2^{atm}$ , ppm), global averages of temperature in the ocean ( $T_{avg}^{oce}$ , °C) and in the atmosphere ( $T_{avg}^{atm}$ , °C), transport in the Atlantic meridional overturning circulation (AMOC, Sv) and sea ice cover (%). The observational estimate for  $\overline{T_{oce}^{atm}}$  has been calculated using the World Ocean Atlas 2018 (Locarnini et al., 2018). Average modern day AMOC strength is estimated by McCarthy et al. (2015) from the RAPID-MOCHA array at 26° N. Modern day sea ice cover is given as an interval due to seasonal variability (Comiso, 2008). No observational estimate for  $\overline{T_{atm}^{atm}}$  is given, since modern atmospheric observations are strongly influenced by rising  $pCO_2^{atm}$  (Stocker, 2014).

Experiment acronym	$pCO_2^{atm}$ (ppm)	$\overline{T_{oce}^{atm}}$ (°C)	$\overline{T_{atm}^{atm}}$ (°C)	AMOC (Sv)	Sea ice (%)
Observ.	278	3.49	N/A	17.2±0.9	3 to 6
<i>Ctrl</i> <sub>RED</sub>	278.0	3.56	12.38	14.25	5.41
<i>Ctrl</i> <sub>GAM</sub>	278.0	3.57	12.38	14.27	5.42
<i>Ctrl</i> <sub>121</sub>	278.0	3.59	12.37	14.25	5.42
<i>LGM</i> <sub>rRED</sub>	265.2	2.89	10.46	14.99	7.38
<i>LGM</i> <sub>rGAM</sub>	265.5	2.90	10.46	14.97	7.35
<i>LGM</i> <sub>albRED</sub>	252.8	1.97	8.18	13.82	9.30
<i>LGM</i> <sub>albGAM</sub>	251.6	1.97	8.16	13.82	9.38
<i>LGM</i> <sub>phyRED</sub>	245.4	1.45	6.83	13.67	10.6
<i>LGM</i> <sub>phyGAM</sub>	244.9	1.45	6.84	13.66	10.6
<i>WNS</i> × 0.5 <sub>RED</sub>	265.1	3.98	12.12	12.66	5.68
<i>WNS</i> × 0.5 <sub>GAM</sub>	261.7	3.99	12.05	12.72	5.74
<i>WNS</i> × 0.5 <sub>121</sub>	263.5	3.97	12.09	12.66	5.69
<i>RLS</i> × 0.75 <sub>RED</sub>	295.8	3.64	12.66	14.13	5.21
<i>RLS</i> × 0.75 <sub>GAM</sub>	301.4	3.68	12.75	14.09	5.08
<i>RLS</i> × 0.75 <sub>121</sub>	298.7	3.65	12.71	14.13	5.14
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<i>RLS</i> × 1.25 <sub>GAM</sub>	262.3	3.49	12.09	14.46	5.74
<i>RLS</i> × 1.25 <sub>121</sub>	259.8	3.49	12.05	14.46	5.78
<i>RLS</i> × 1.75 <sub>RED</sub>	244.7	3.38	11.77	14.55	6.06
<i>RLS</i> × 1.75 <sub>GAM</sub>	234.7	3.33	11.57	14.56	6.27
<i>RLS</i> × 1.75 <sub>121</sub>	240.6	3.36	11.69	14.59	6.14

Table S.2. Continued.

Experiment acronym	$pCO_2^{atm}$ (ppm)	$T_{avg}^{oce}$ ( $^{\circ}C$ )	$T_{avg}^{atm}$ ( $^{\circ}C$ )	AMOC (Sv)	Sea ice (%)
<i>LGMdust<sub>RED</sub></i>	262.2	3.48	12.09	14.44	5.80
<i>LGMdust<sub>GAM</sub></i>	256.9	3.48	11.99	14.47	5.87
<i>LGMdust<sub>121</sub></i>	259.5	3.48	12.05	14.47	5.78
<i>Acomb<sub>RED</sub></i>	222.5	1.45	6.83	13.67	10.6
<i>Acomb<sub>GAM</sub></i>	214.9	1.45	6.84	13.66	10.6
<i>Acomb<sub>121</sub></i>	217.3	1.44	6.84	13.59	10.6
<i>GLcomb<sub>RED</sub></i>	214.9	1.94	6.86	12.05	10.2
<i>GLcomb<sub>GAM</sub></i>	198.2	1.91	6.85	12.09	10.3
<i>GLcomb<sub>121</sub></i>	206.2	1.93	6.86	12.02	10.3

Table S.2. Continued.

Experiment acronym	$pCO_2^{atm}$ (ppm)	$T_{avg}^{oce}$ ( $^{\circ}C$ )	$T_{avg}^{atm}$ ( $^{\circ}C$ )	AMOC (Sv)	Sea ice (%)
<i>LGMdust<sub>RED</sub></i>	262.2	3.48	12.09	14.44	5.80
<i>LGMdust<sub>GAM</sub></i>	256.9	3.48	11.99	14.47	5.87
<i>LGMdust<sub>121</sub></i>	259.5	3.48	12.05	14.47	5.78
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<i>GLcomb<sub>RED</sub></i>	214.9	1.94	6.86	12.05	10.2
<i>GLcomb<sub>GAM</sub></i>	198.2	1.91	6.85	12.09	10.3
<i>GLcomb<sub>121</sub></i>	206.2	1.93	6.86	12.02	10.3

**Table S.3.** Model–data comparison statistics for the *Ctrl* and *GLcomb* simulations in each of the model versions *RED* and *GAM*, and for the two benthic  $\delta^{13}C$  data time slices HOL (0-6 ka) and LGM (19-23 ka). Correlations are computed between benthic observations and model water mass  $\delta^{13}C$  in the grid cell corresponding to the observation depth. Standard deviations (STD) are the normalized values ( $STD_{model}/STD_{data}$ ), which are scaled by the number of observations.

Model – data	Global corr.	Global STD	Atlantic corr.	Atlantic STD	Indo–Pacific corr.	Indo–Pacific STD
<i>Ctrl</i> <sub>RED</sub> – HOL	0.78	1.23	0.50	0.83	0.39	0.81
<i>Ctrl</i> <sub>GAM</sub> – HOL	0.76	1.38	0.45	0.94	0.36	0.95
<i>GLcomb</i> <sub>RED</sub> – HOL	0.76	1.82	0.46	1.22	0.34	1.10
<i>GLcomb</i> <sub>GAM</sub> – HOL	0.76	2.11	0.44	1.46	0.33	1.31
<i>Ctrl</i> <sub>RED</sub> – LGM	0.58	0.96	0.64	0.43	0.06	0.83
<i>Ctrl</i> <sub>GAM</sub> – LGM	0.55	1.08	0.58	0.48	0.01	0.96
<i>GLcomb</i> <sub>RED</sub> – LGM	0.58	1.40	0.61	0.62	0.06	1.07
<i>GLcomb</i> <sub>GAM</sub> – LGM	0.57	1.62	0.60	0.74	0.02	1.28

**Table S.3.** Model–data comparison statistics for the *Ctrl* and *GLcomb* simulations in each of the model versions *RED* and *GAM*, and for the two benthic  $\delta^{13}C$  data time slices HOL (0-6 ka) and LGM (19-23 ka). Correlations are computed between benthic observations and model water mass  $\delta^{13}C$  in the grid cell corresponding to the observation depth. Standard deviations (STD) are the normalized values ( $STD_{model}/STD_{data}$ ), which are scaled by the number of observations.

Model – data	Global corr.	Global STD	Atlantic corr.	Atlantic STD	Indo–Pacific corr.	Indo–Pacific STD
<i>Ctrl</i> <sub>RED</sub> – HOL	0.78	1.23	0.50	0.83	0.39	0.81
<i>Ctrl</i> <sub>GAM</sub> – HOL	0.76	1.38	0.45	0.94	0.36	0.95
<i>GLcomb</i> <sub>RED</sub> – HOL	0.76	1.82	0.46	1.22	0.34	1.10
<i>GLcomb</i> <sub>GAM</sub> – HOL	0.76	2.11	0.44	1.46	0.33	1.31
<i>Ctrl</i> <sub>RED</sub> – LGM	0.58	0.96	0.64	0.43	0.06	0.83
<i>Ctrl</i> <sub>GAM</sub> – LGM	0.55	1.08	0.58	0.48	0.01	0.96
<i>GLcomb</i> <sub>RED</sub> – LGM	0.58	1.40	0.61	0.62	0.06	1.07
<i>GLcomb</i> <sub>GAM</sub> – LGM	0.57	1.62	0.60	0.74	0.02	1.28

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