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

   — *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).

   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 CO₂.*

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.

   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 GLcomb, by ∼ 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 ∼ 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 PO4 concentrations (global average anomaly = -0.016 µM) [...]

Sentence, now on p. 12, L. 8-9, has been changed to: Our changes in RLS cause very small, but global, changes in PO4 concentrations (global average anomaly = -0.016 µM, RLS × 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 × 0.75 and RLS × 1.25, reveal that the response in pCO2 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 pCO2 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 pCO2 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 × 1.25121 and RLS × 1.75121), suggest that about 40 % of the observed differences in pCO2 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),’

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

As \( P^{*} = \frac{P_{rem}}{P_{tot}} \), 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”**

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).**

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.*

– **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.**

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
the caption will also apply to Fig. S3. Also, it seems the referee may have misunderstood our subtraction of \(-0.32\%e\),
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 \%e 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 \(-0.32 \pm 0.20\%e\). 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\%e 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, \(P^* = \frac{P_{rem}}{P_{tot}}\), thus an increase in \(P_{rem}\) is analogous to an increase in \(P^*\).

As an increase in \(P^*\) 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. \(\psi_{m,in}\) in this table
is simply the minimum of the Atlantic overturning streamfunction below 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.

– **Section 2.4, p. 6, L. 22:**
  Typo, *retrained* 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).
  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”:**
  Typo, will be corrected.
  Sentence removed when information was moved to Section 4.4.
References


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 ‰ 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

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.

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.

One particularly important part of the manuscript that is not conveyed clearly is their diagnosis of CO₂ 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 CO₂ 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 CO₂ drawdown over a simple prescribed whole ocean increase. I would therefore advocate for the authors to make this more clear.

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 CO₂ 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 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, paloeproxy 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, CaCO₃ compensation and production rates, Fe fertilisation, increased N₂ 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.

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 contributers 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

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).

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.

On page 2, lines 5-6, we have added: ‘During deglaciation, radiocarbon evidence indicate that CO’$_2$ 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.
  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.
  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 (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.

  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.

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.

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.

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.

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 $\mu$molkg$^{-1}$, which is lower than Ctrl$_{RED}$ (166 $\mu$molkg$^{-1}$), but higher than Ctrl$_{GAM}$ (144 $\mu$molkg$^{-1}$).

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.’.

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).

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 \( pCO_2^{atm} \).

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 (\( \sim 10\% \) 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).

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).

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.

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 \( GL_{comb} \) and \( A_{comb} \) achieve 64 and 82 \% of the glacial–interglacial difference in \( T_{oce} \), respectively. As anticipated, our combined forcings do not induce a full glacial maximum state, but a state with glacial–like climate conditions.’

Page 12, lines 21–25 : Again, I am unsure how you are treating P:O\(_2\) remineralisation requirements in your variable stoichiometry experiments. I think this should be explained. It is also strange once again that your \( GL_{comb121} \) experiment is better oxygenated than your \( GL_{comb RED} \) experiment.

In remineralisation, there was an issue in the code which affected the C:O\(_2\) ratio in the 121–experiments. This made the P:O\(_2\) requirements appear strange, which PJB noticed. This has been corrected, and the 121–experiments re–run. After correction, C:O\(_2\) remains the same in all experiments, while the P:O\(_2\) ratio, as a result, changes between experiments. We will clarify this in the Methods section. After the correction described above, \( GL_{comb121} \) has a lower global average \( O_2 \) concentration than \( GL_{comb RED} \) (96 compared to 122 \( \mu \text{molkg}^{-1} \)), but higher than \( GL_{comb GAM} \) (74 \( \mu \text{molkg}^{-1} \)). 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\textsubscript{2} remains the same in all experiments. As a result, the P/O\textsubscript{2} 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\textsubscript{2}? 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\textsubscript{2}. Stephens & Keeling (2000) *The influence of Antarctic sea ice on glacial–interglacial CO\textsubscript{2} variations.* Nature. Kurahashi–Nakamura et al. (2007) *Compound effects of Antarctic sea ice on atmospheric pCO\textsubscript{2} change during glacial–interglacial cycle.* Geophysical Research Letters. Sun & Matsumoto (2010) *Effects of sea ice on atmospheric pCO\textsubscript{2}: 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 (GL\textsubscript{comb}–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\textsubscript{2}. 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\textsubscript{2}. 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.
This paragraph would benefit from being clearer in its findings of CO₂ 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.

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 pCO₂ atm, 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 Ódalen et al (2018)... which were? What did Ódalen et al (2018) do?

Here, lines 30–33 should read: Note that Ctrl\textsubscript{GAM} has a larger inventory of DIC, as well as C\textsubscript{soft}, compared to Ctrl\textsubscript{RED}. Ódalen et al. (2018) found that drawdown of CO\textsubscript{2} in response to a perturbation is larger when the control state has a smaller inventory of DIC and C\textsubscript{soft}. Yet, the effect of applying the same perturbation results in a larger drawdown of CO\textsubscript{2} in GAM than in RED. This is thus opposite of the conclusions of Ódalen 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 Ódalen et al. (2018) are clearly stated.

Added sentence ‘Ódalen et al. (2018) found that drawdown of CO\textsubscript{2} in response to a perturbation is larger when the control state has a smaller inventory of DIC and C\textsubscript{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\textsubscript{rem}) in GLcomb\textsubscript{GAM} compared to Ctrl\textsubscript{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\textsubscript{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\textsubscript{rem} compared to Ctrl\textsubscript{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\textsubscript{GAM}, the average elemental C/P composition is 121/1. In GLcomb\textsubscript{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\textsubscript{GAM}, the global average concentration of P\textsubscript{rem} is 1.16 \(\mu\text{molkg}^{-1}\) (c.f. 1.17 \(\mu\text{molkg}^{-1}\) in GLcomb\textsubscript{GAM}). By increasing the average C/P composition of 1.16 \(\mu\text{molkg}^{-1}\) organic molecules from 121 to 134 (i.e. by 13 units), this causes an increase in C\textsubscript{rem} by \(\sim 15 \mu\text{molkg}^{-1}\), which corresponds to the observed increase in C\textsubscript{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\textsubscript{rem} and P\textsubscript{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.

  - **I would like to see how variations in $P$:O$_2$ requirements were treated in this model.**
    C:O$_2$ requirements were meant to be held constant throughout the simulations, consequently causing changes in $P$:O$_2$. However, an inconsistency in the code caused C:O$_2$ requirements to change in the simulations of the 121–ensemble, causing an inconsistent behaviour of $P$:O$_2$. This has been corrected, as outlined above.
    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.’

  - **Also, can you please explain why the deep water formation characteristics of a model affects O$_2$?**
    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.
    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$_2$ consumption caused by the higher average C/P in Ctrl$_{GAM}$ compared to Ctrl$_{RED}$.’

  - **Overall, I find this section a bit sparse and I’m not entirely sure what the point of it is.**
    The section aims to discuss 1) to what extent our $GLcomb$ simulations reproduce proxy observations, in this case for O$_2$, and 2) to discuss one of the problems that arose from applying the flexible C/P in GENIE, i.e. that O$_2$ concentrations in Ctrl$_{GAM}$ 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.

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).


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 $GLcomb$ 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.’
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 CO₂, 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 δ¹³C change across the glaciation and into the Holocene? δ¹³C 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 δ¹³C data over the last 150000 years. Climate of the Past.)? Moreover, δ¹³C 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 δ¹³C and δ¹⁸O 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 δ¹³C across the deglaciation (whole ocean change 0.34 ± 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 δ¹³C 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.)

– (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 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.’

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”

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”.

– 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.

“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”?
  Yes, we will correct this to 0.003.
  Page 16, line 32: “0003” corrected to “0.003”


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 ‰ 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$_2$ 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–like model simulations

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Abstract. During the four most recent glacial maxima, atmospheric CO2 has been lowered by about 90–100 ppm with respect to interglacial concentrations. It is likely that most of the atmospheric CO2 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 CO2 storage.

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 increases when nutrient availability is scarce, as observations suggest, this has the potential to further increase glacial oceanic CO2 storage.

In response to changes in surface nutrient distributions, we perform a sensitivity study to test how a phosphate-concentration dependent C/P ratio influences the oceanic CO2 storage in an Earth system model of intermediate complexity (eGENIE). We carry out simulations of glacial-like changes in algae, 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 concentrations. While a flexible C/P ratio does not impact the model’s ability to simulate benthic δ13C patterns seen in observational data, our results indicate that, in production of organic matter, a flexible C/P ratio can further increase the oceanic storage of CO2 in glacial model simulations. Fast 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 CO2 concentrations.

1 Introduction

During the last four glacial maxima, atmospheric CO2 (hereafter pCO2) was lowered by 90–100 ppm compared to the interglacials (Pett, 1999; LeGrande et al., 2008). Due to the difference in size between the oceanic, terrestrial and atmospheric carbon...
reservoirs, where the oceanic reservoir is by far the largest with 99.9% of their summed carbon contents (e.g., Ciais et al., 2015). It is likely that most of the CO2 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., Schmittner and Toggweiler, 1986; Martin, 1990; Archer et al., 2000; Sigman and Boyle, 2000), subduction processes (Broecker, 1982b, 1983), changes in ocean circulation and sea ice cover (e.g., Boyle and Kipps, 1987; Dijkstra et al., 1980; Stephens and Keeling, 2000; Menviel et al., 2007). Extensive summaries of these processes, and examples of their interactions, are given by e.g., Broecker et al. (2007); Redfield and Ridgwell (2009); Hans 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 $\Delta^13C$ expected for a glacial.

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 model may affect the glacial downsink of $\Delta^13C$. 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 oceanic organic matter originally observed by Redfield (1963).

We investigate whether allowing for a flexible C/P stoichiometric ratio increases model ocean CO2 storage in a glacial-like climate. This possibility was suggested by e.g., Broecker (1982b), Archer et al. (2000) and Galbraith and Martray (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 Eggertsson and Galbraith (2018) and Galbraith and de Lavergne (2018), but their results were not analysed in terms of difference from a Redfield model version.

We conduct a sensitivity study, where we made 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 eGEMIE; an original version using the 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 stoichiometry of C/P and iron co-limitation (e.g., Galbraith and Martray, 2015). We show that flexible C/P stoichiometry allows for increased ocean carbon storage without decreasing the storage of preferred nutrients in the deep ocean.

2 Methods

2.1 Model description

eGEMIE is an Earth system model of intermediate complexity, with a 3D fractional–geocentric ocean (261 by 36 equal area horizontal grid, 16 depth levels), 2D energy–moisture balance atmosphere with prescribed wind fields, interactive atmospheric
each other. This is modelled using the average ratio of CIP of the ocean organic matter originally observed by Redfield (1963) (CIP = 1061), or adjustments to those suggested in follow-up studies (Takahashi et al., 1987; Anderson and Sarmiento, 1994).

We investigate whether allowing for a flexible CIP stoichiometric ratio increases model ocean CO₂ storage in a glacial-like climate. This possibility was suggested in studies by Broecker (1982b), Archer et al. (2000) and Galbraith and Marinov (2015), but the implications of Redfield versus flexible CIP 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 Eggertson and Galbraith (2010) and Galbraith and de Leeuw (2009), 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 stabilizing 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 deposition in one configuration to an interglacial control state. These 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 paleo-proxy evidence (Mortier et al., 2013; 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 (Mingram, 2007). These glacial climate results 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 the CO₂请大家注释：

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: GEnIE, an original version using fixed Redfield stoichiometry of CIP (Ridgwell et al., 2007) plus a co-limitation by iron (Tog Leadsley et al., 2016) for biological production, and a modified version using the non-Redfieldian, nutrient concentration dependent CIP stoichiometry suggested by Galbraith and Marinov (2015) and iron co-limitation.

We show that flexible CIP stoichiometry allows a larger glacial ocean CO₂ storage, as predicted by the two-model study of Galbraith and Marinov (2015). This 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 preferred nutrients in the deep ocean.

2 Methods

2.1 Model description

cGENIE is an Earth system model of intermediate complexity, with a 3D fractional–geostrophic ocean (36 × 36 equal area horizontal grid; 16 depth levels), 3D energy–moisture balance atmosphere with prescribed wind fields, interactive atmospheric chemistry, and ocean biogeochemistry. Model code and user handbook can be found in the cGENIE GitHub repository. cGENIE
chemistry and ocean biogeochemistry. Model code and input handbooks 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 \( P : C : N = 1 : 106 : 16:6 \), where \( P_2 \) is dissolved oxygen (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 Matrai, 2015; Yearn-Durocher et al., 2015; Tanaka and Matsumoto, 2017; Moreno et al., 2018). We test the importance of this variability for glacial ocean CO2 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 Matrai (2015) (Eq. 1). These two model versions are henceforth denoted RED and GAIM, respectively.

The flexible stoichiometry in GAIM depends on the ambient concentration of dissolved phosphate ([PO4]) in the water:

\[
P : C : N = 1 : \frac{[PO_4]}{130} + 0.0006 \text{ (mM)}^2.
\]

This relation shows that, when [PO4] is low, organisms bind more C per atom of P than they do under high [PO4] 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 [PO4]. In Section 3.1.2, Eq. 1 is also used to translate model surface [PO4] 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 (C/N/PO4) or variable (C/N/PO4) stoichiometry. The control states have a prescribed \( \mu^{(0)} \text{CO}_2 \) of 285 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 \( \text{C/N/PO4} \), the export flux of organic matter (see Ridgwell et al., 2007) has a global average C/P composition of 12:1:1 and

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thus the global ocean carbon storage is larger than in Ctrl(0°C). This also suggests 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 GAS 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 C/P = 121/1 (hereafter denoted Ctrl(sto)).

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 CO2 = 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 (Laudenbach et al., 2013, e.g.), and north of 35°N (see Section 2.3.1),
   - biological perturbations:
   - changed remineralisation length scale (e.g., Marumoto, 2007; Chikamoto et al., 2012; Manzoni et al., 2012)
   - increased dust forcing, as simulated for LGM (regressed from Mahowald et al., 2006)

By applying the above perturbations, we aim to achieve some of the characteristics of the Last Glacial Maximum (LGM).

20. ocean, which appears to have had a global average ocean temperature ($T_{ocean}$) 2.9°C colder than the Holocene (Hickey and Neumann, 2003), a weakly ventilated deep ocean (e.g., Manzoni et al., 2013) 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 (Higuera et al., 2008).

The physical perturbations serve to achieve a cooler climate (Fig. 2), i.e. cools by 2.1°C c.f. Ctrl, thus nearly 40% of the observed 2.9°C (see Section 2.3.1). Weaker overturning (see Section 2.3.2 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 (Balogh et al., 2007).

25. 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 2.3.3).
and 3.2.6). With flexible stoichiometry, lower surface nutrient concentrations result in a higher C/P ratio, further increasing the export production, and thereby the carbon sequestration 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 LGM(LPH). We set the radiative forcing in the model to correspond to an atmosphere with 185 ppm CO₂, instead of 278. However, we allow the p(CO₂) 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 Dutrieu-Barraud et al., 2017). Assumptions of a simple zonal profile instead of 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 (March et al., 2011). Together, the changes in radiative forcing and albedo causes the global ocean average temperature (T_ocean) to decrease by 2.3°C compared to Ctrl (see Section 2.3.1).

To achieve a longer residence time of the AABW water mass, and an associated increase in carbon and nutrient retention, we apply weaker winds (defined W_Na=0.5). We use the Southern Ocean wind profile of Lauthaler et al. (2013), where the peak windly 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 a continuous profile (see Fig. 2 of Lauthaler et al., 2013). The result is a weaker overturning (see Table 2) and a longer residence time of the AABW (see Section 4.3) as it is expected for the glacial ocean (e.g., Merlivat et al., 1975). 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 30°N is reduced by half compared to the control state.

5.2.3.2 Biological perturbations
It has been hypothesized that the cooling of the glacial ocean led to a deepening of the remineralization length scale (henceforth defined RLS) in the ocean, and thereby more efficient retention of organic carbon in the deep ocean (e.g., Manzoni, 2007; Chien et al., 2012), which in turn caused a lowering of p(CO₂). However, Merlivat et al. (2012) find that such a deepening results in model changes in export production (i.e. the amount of C exported by primary production that leaves the surface ocean without being remineralized) in poor agreement with palaeo-records. Deeper remineralization also results in increased nutrient retention in the deep ocean, thus causing changes in surface nutrient fields and in C/P ratios of G/LM. We test the effect of changes in RLS by multiplying the model default RLS by a factor 2 (RLS2) (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-chlrophyll (HNLC) regions in the North Pacific, Equatorial Pacific
and Southern Ocean, where iron (Fe) is the limiting microelement (e.g., Martin, 1990). The variable stoichiometry in GCM is expected to be influential if the concentrations of P increase in such regions as a result of increased Fe availability. This process may hence be of importance in a glaciated scenario where dust forcing increases as a result of the dust conditions (e.g., Martin, 1990). We apply the revised LGM dust fields of Malmqvist et al. (2006) and denote this change LGMalt.

5.2.3 Sensitivity experiments and combined simulations

In the sensitivity study, for each of the three CIP parametrisations, we first change one forcing at a time (see Table 1). We ran simulations where we apply individually the LGM boundary conditions for radiative forcing (LGMalt, f), albedo (LGMalt) and dust (LGMalt) and one simulation with halved wind stress near the poles (30° and 90°) (WMS NLS). For the remoralisation-length scale (RLS), we test a range of values of the multiplication factor RLS = 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 ran simulations where we combine several changes in forcing. We get a colder climate simulation (LGMalt) by combining LGMalt, f and LGMalt. In simulation Acrosb, we combine LGMalt, f, LGMalt, LGMalt, and BLS = 1.75 (see Table 1). Kwon et al. (2009) show that small changes in remoralisation depth can cause substantial changes in pCO2.

15. With the RLS deepening of 25%, we keep the corresponding changes in pCO2 from exceeding the 20–30 ppm obtained in other studies (Manzini et al., 2007; Mirov et al., 2012). We further use a glacial-like simulation (GLOresb) (see Section 3.3), which is similar to Acrosb but also includes the change in wind stress WMS NLS. The achieved GLOresb model state has a colder climate (see Table 7), 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 2005 (Locarnini et al., 2005; Garcia et al., 2010), and we use the proxy estimates of LGM ocean temperature from Healy and Stevenson (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 comparisons of benthic δ13C to assess the statistical similarity (correlation) between both the model control state and glacial-like state (see Section 2.3) to benthic δ13C data representing the Late Holocene (0–15 ka, RSL) and Last Glacial Maximum (19–23 ka, LGM), respectively, both estimated by Paterne et al. (2014). Location of core sites can be seen in Fig. S.1 (see also Fig. 1 in Paterne et al. (2014). Note that LGM benthic δ13C is more δ13C-depleted than the Holocene due to the addition of 14C-depleted terrigenous carbon to the glacial ocean (Shackleton, 1977; Curry et al., 1988; Delefesey et al., 1988), which is not simulated in our model experiments. Therefore, to compare our glacial-like simulations (GLOresb) with LGM observations, we subtract a Holocene-LGM global average difference of 0.32‰ (Gebbie et al., 2015) from the GLOresb experiments. Gebbie et al. (2015) state that the wide range of error for the estimate of glacial-to-modern change in benthic δ13C of 0.32 ± 0.26‰.
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 $\eta$ (Boo and Follows, 2005; O’Dalen et al., 2018):

$$\eta = \frac{P_{out}}{P_{in}}$$

which is the fraction of remineralised ($P_{out}$) to total ($P_{in}$) 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 $P_{out}$ is given by

$$P_{out} = P_{in} - P_{rem}$$

Here, $P_{rem}$ is performed $PO_4$ – 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 GENIE, the concentration of performed tracers is set in the surface ocean and then passively advected through the ocean interior. The biological pump also captures carbon, and a similar relationship can be used for concentrations of DIC, where

$$DIC_{out} = DIC_{in} - DIC_{rem}$$

DIC$_{out}$ is used to compute the ocean storage of remineralised acidic carbon ($AC_{out}$, see Appendix A). $AC_{out}$ 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 GENIE, $P_{rem}$ and DIC$_{rem}$ are modelled as passive tracers (O’Dalen et al., 2018). Hence, we can use the model output $P_{rem}$ in Eq. 3 to compute $\eta$ (Eq. 2).

In a model with fixed Redfield ratio, $\eta$ determines the effect of the biological pump on $\mu$CO$_2$. For example, it has been found that a higher $\eta$ in the initial state gives a lower potential for drawdown of $\mu$CO$_2$ in response to similar perturbations (Marinov et al., 2008; O’Dalen 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 $\eta$.

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 comparisons 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, H06) and Last Glacial Maximum (10-23 ka, LGM), respectively Paterson et al. (2014). Locations of core sites can be seen in Fig. S.1 (see also Fig. 1 in Paterson et al. (2014)). Note that LDM benthic $\delta^{13}$C is more $\delta^{13}$C-depleted than the Holocene due to the addition of $\delta^{13}$C-depleted terrestrial carbon to the glacial ocean (Shackleton, 1977; Curry et al., 1988; Delespesse et al., 1988), which is not simulated in our model experiments. Therefore, to compare our glacial-like simulations (GL000) in LGM observations, we subtract a Holocene-LGM global average difference of 0.32 % (Gribble et al., 2015) from the GL000 experiments. Gribble et al. (2015) state that the wide range of error for the estimate of glacial-to-modern change in benthic $\delta^{13}$C of 0.52 to 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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8
Results

3.1 Control states

3.1.1 Ocean temperature and circulation

As the three control states, Ctrl2013, Ctrl2015 and Ctrl2018, are driven by the same physical forcings and have the same
5 $\mu CO_2$, they have the same ocean circulation pattern (Fig. 2 a, c, e and Table 2, Table S.2) and climate (exemplified by
6 global ocean average temperature ($T_{mean}$) in Table 2 and Table S.2). The surface ocean nutrient fields are fairly similar, with
7 small differences due to the different C/P parametrizations (compare Fig. 3 a, c and Fig. S.2). The strength of the Atlantic
8 meridional overturning circulation (AMOC), diagnosed in the model as the maximum of the Atlantic meridional overturning
9 streamfunction deeper than 1000 m, is 14 Sverdrups (Sv) ($1 \times 10^{14} m^3 s^{-1}$) in all control states (Table 2, Table S.2). Results from the
10 RAPID-MOCHA array at 26°N suggest an average AMOC strength of 17 Sverdrups (Sv) (McCarthy et al., 2015), thus our control
11 state AMOC is a little bit weaker than in present day climate. The observational estimate for $T_{mean}$ according to the World
12 Ocean Atlas 2013 (Levitus et al., 2013) in 3.6°C, thus comparable to the 3.56°C of our Ctrl simulations. The surface nutrient
13 concentrations of our control state Ctrl2015 (Fig. 3 a) compare reasonably well with observed surface ocean concentrations of PO4 (Fig. 3 c), with some underestimated in the Pacific equatorial region, the North Pacific ocean, and the Labrador
14 Sea. The agreement with observations is better for Ctrl2018 than for Ctrl2013 (Fig. S.2).

3.1.2 Surface nutrient distribution and C/P ratios

In Fig. 3 we see that surface PO4 fields (left hand column) and the corresponding fields of surface C/P ratios (as given by
19 Eq. 1, right hand column) of Ctrl2013 (panels a, b) and of observations (panels c, d) are similar in their pattern as well as in
20 the magnitudes of values. Note that high concentrations of PO4 correspond to low C/P ratios, and vice versa. The highest
21 observed PO4 concentrations in the Northern and equatorial Pacific are not fully reproduced by the model, but the pattern is
22 well reproduced. In the surface C/P field of Ctrl2013 (Fig. 3 b) we see the signature of very high nutrient concentrations in the
23 Southern Ocean ($>500 m$), Fig. 3 b) as a band of low ratios, with the most extreme values near the Antarctic continent, as
24 seen in observations (Fig. 3 d).

The nutrient utilization efficiency ($\eta_{NUT}$) (Fig. 2) in the three control states differs by a few percent: 0.43, 0.46 and 0.42 in
25 Ctrl2013, Ctrl2015 and Ctrl2018, respectively (Table 2). The fraction of $DAC_{ocean}$ in $DAC_{total}$ (see Section 2.5, Eq. 4, Table
26 S.1) is 0.65, 0.677 and 0.672 in Ctrl2013, Ctrl2015 and Ctrl2018, respectively.

3.1.3 Ocean dissolved $O_2$

The most apparent difference between Ctrl2013 and Ctrl2015 is in deep ocean oxygen concentrations, where the global
29 ocean average dissolved $O_2$ concentration ($O_2$) in Ctrl2013 (Fig. 4 e) is lower than in Ctrl2013 and Ctrl2018 (Fig. 4 a and
30 Ctrl2015, respectively). Compared to observations (World Ocean Atlas 2013, Fig. 4 a-b), both Ctrl2015 (Fig. 4 c-d), and Ctrl2018 (Fig. 4 e-f) agree reasonably well with the real ocean. Ctrl2013 appears to capture better than Ctrl2015 the

In eGCE, $P_{min}$ and $DAC_{ocean}$ are modelled as passive tracers (Olåden et al. (2018)). Hence, we can use the model output for
35 $P_{min}$ in Eq. 3 to compute $\eta_{NUT}$ (Eq. 2).

In a model with fixed Redfield rates, $\eta_{NUT}$ determines the effect of the biological pump on $\mu CO_2$. For example, it has been
37 found that a higher $\eta_{NUT}$ in the initial state gives a lower potential for drawdown of $\mu CO_2$ in response to similar perturbations.

(Maynard et al., 2008; Olåden et al., 2016). However, with variable stoichiometry this is no longer true, since the amount of
39 carbon retained in the deep ocean is not necessarily proportional to $\eta_{NUT}$.

3 Results

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3.1.3 Ocean dissolved $O_2$

The most apparent difference between Ctrl2013 and Ctrl2015 is in deep ocean oxygen concentrations, where the global
34 ocean average dissolved $O_2$ concentration ($O_2$) in Ctrl2013 (Fig. 4 e) is lower than in Ctrl2013 and Ctrl2018 (Fig. 4 a and
35 Ctrl2015, respectively). Compared to observations (World Ocean Atlas 2013, Fig. 4 a-b), both Ctrl2015 (Fig. 4 c-d), and Ctrl2018 (Fig. 4 e-f) agree reasonably well with the real ocean. Ctrl2013 appears to capture better than Ctrl2015 the

In eGCE, $P_{min}$ and $DAC_{ocean}$ are modelled as passive tracers (Olåden et al. (2018)). Hence, we can use the model output for
40 $P_{min}$ in Eq. 3 to compute $\eta_{NUT}$ (Eq. 2).

In a model with fixed Redfield rates, $\eta_{NUT}$ determines the effect of the biological pump on $\mu CO_2$. For example, it has been
42 found that a higher $\eta_{NUT}$ in the initial state gives a lower potential for drawdown of $\mu CO_2$ in response to similar perturbations.

(Maynard et al., 2008; Olåden et al., 2016). However, with variable stoichiometry this is no longer true, since the amount of
44 carbon retained in the deep ocean is not necessarily proportional to $\eta_{NUT}$.
equatorial oxygen minimum in the Atlantic basin, but goes too low in the North Pacific. In $\text{Ctds}$s (Fig. 4-f), the North Pacific is markedly lower in oxygen than in $\text{Ctds}$s (Fig. 4-d) and even anoxic to the oxygen minimum zone (OMZ). This should be kept in mind when analyzing the oxygen sections of the glacial-like states $\text{GLCms}$ (Fig. 4-e) and $\text{GLCMs}$ (Fig. 4-f). Global averages for dissolved $O_2$ are given in Table 2.

3.3.4 Ocean $^{14}C$

By comparing $\text{Ctds}$s $^{14}C$ and Holocene ($0-6$ ka, HOLL) biogenic $^{14}C$ values, we estimate a global model-data correlation of $0.78$ (Table S.5). The modern-day Atlantic Ocean has a distinctive spatial $^{14}C$ pattern (Fig. 5-a) with $^{14}C$-enriched values in the intermediate depth ($\leq 2$ km) North Atlantic and Nordic Seas and $^{14}C$-depilited values in the deep ($\geq 25$ km) South Atlantic. While the model produces a weaker gradient than the observed HOLL Atlantic Ocean (core 0.50, Table S.6), the model correlates well with Eastern Atlantic $^{14}C$ records (Fig. S.10). For the Indo-Pacific, the weaker biogenic $^{14}C$ gradient is well represented by the model (Fig. 5-a). This pattern emerges mainly due to $^{14}C$-depleted, biologically sourced carbon that is accumulated in the weak circulation region of the Southern Ocean. (e.g., Matsumoto et al., 2002). However, Indo-Pacific $^{14}C$ values of $\text{Ctds}$s are overall lower than the HOLL observations. One overall model-data correlation for the Indo-Pacific is 0.49 (Table S.5). Comparing the control states of the RED and GAM model versions, $^{14}C$ patterns (Fig. 5-a, 5-c and Fig. S.10-a, c) and model-data correlations with HOLL observations (Table S.5) are similar between the model versions, with somewhat lower correlations for GAM.

3.2.1 Radiative forcing and algae

In the simulations where radiative forcing and algae are changed to represent LGM conditions ($LGM$): $f + LGM$($ab$) = $LGM$($p$,$\phi$), the reductions in $\text{pCO}_2$ are similar in the RED and GAM model versions. In $LGM$($p$,$\phi$), the resulting $\text{pCO}_2$ is 245.4 and 244.0 ppm respectively, thus a reduction of 33 ppm compared to the $Ctds$s 278 ppm (Fig. 6). Here, variable FIP does not impact the results, because changes in the surface nutrient distribution (Fig. 7-a), and the associated changes in $\text{Ctds}$s (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 decrease in $\text{pCO}_2$ can mainly be attributed to the increase in solubility carbon ($\text{C}_\text{s}$) due to ocean cooling, and to an increase in sea ice, which prevents air-sea gas exchange and therefore causes an increase in dissolved carbon ($\text{C}_\text{d}$) (Shalev et al., 2018). Ocean cooling amounts to 2.1 $^\circ$C in $LGM$($p$,$\phi$) compared to $Ctds$s (Table 2). In GENIE, the increase in $\text{C}_\text{d}$ is associated with ocean cooling corresponding to $\text{pCO}_2$ of 234 ppm.

The nutrient utilization efficiency $\phi$ (Fig. 2) in the three control states differs by a few percent: 0.43, 0.46 and 0.42 in $\text{Ctds}$s, $\text{Ctds}$s and $\text{Ctds}$s respectively (Table 2). The fraction of $\text{N}_\text{tot}$ in $\text{N}_\text{tot}$ (see Table 2, Fig. 4, Table S.11) is 0.06, 0.07 and 0.02 in $\text{Ctds}$s, $\text{Ctds}$s, and $\text{Ctds}$s respectively.

3.3.3 Ocean dissolved $O_2$

The most apparent difference between $\text{Ctds}$s and $\text{Ctds}$s is in deep ocean oxygen concentrations, where the global ocean average dissolved $O_2$ concentration (Table S.6) is lower than in $\text{Ctds}$s and $\text{Ctds}$s (0.8 and $O_2$) respectively. Compared to observations (World Ocean Atlas 2013), both $\text{Ctds}$s (Fig. 4-a) and $\text{Ctds}$s (Fig. 4-f) agree reasonably well with the real ocean. $\text{Ctds}$s appears to capture better than $\text{Ctds}$s the equatorial oxygen minimum in the Atlantic basin, but goes too low in the North Pacific. In $\text{Ctds}$s (Fig. 4-f), the North Pacific is markedly lower in oxygen than in $\text{Ctds}$s (Fig. 4-d) and even anoxic to the oxygen minimum zone (OMZ). This should be kept in mind when analyzing the oxygen sections of the glacial-like states $\text{GLCms}$ (Fig. 4-e) and $\text{GLCMs}$ (Fig. 4-f). Global averages for dissolved $O_2$ are given in Table 2.

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3.2.2 Hydrography

The applied changes listed in Table 1 cause changes in (a) ocean overturning, temperature, surface nutrient distributions and biological productivity, which result in changed $\text{pCO}_2$. The resulting steady-state global average values for temperature $\text{pCO}_2$ are given in Table 2.
(Oishi et al., 2018, supplementary Fig. S.1). Thus, in LGMphyC and CSM, the solution of pCO₂ is not constrained by a temperature restriction on the solubility constants (Oishi et al., 2018). This temperature restriction limits solubility from 10°C to 2°C. In this case, the solubility effect on pCO₂ is 0.01°C (from 3.6°C to 1.8°C, or 15 ppm) in total compared to only 1.6°C of cooling (from 3.6°C to 2.0°C, or 11 ppm), and the solubility effect is underestimated by 0.4 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 Figs. 2 and 4). 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 DASO₄-PO₄, compared to Ctrl, as seen in Fig. 7 b, and increases the nutrient utilisation efficiency. (Table 2, Fig. 9). This leads to a drawdown of pCO₂ by 12.9 ppm compared to Ctrl (Table 6). As the nutrient concentration in the SO decreases (Fig. 7 b), the solute CIP ratio (Fig. 8 b) leads to an increased carbon capture efficiency in GCM compared to R94 (and ELS+LSRCO₂) at the experimentally saturated carbon (ACSM) in Fig. 9, which is partly compensated by a lower CIP ratio in the Pacific equatorial region. Consequently, in WNS + SLOCE, we get a reduction of pCO₂ of 16.3 ppm compared to Ctrl (Fig. 6). Hence, for halved peak wind stress at 30°N, the solute CIP ratio increases the drawdown by 0.39 ppm. In a simulation with reduced wind stress and fixed CIP photoinhibition of 12% (WNS + SLOCE), we get a pCO₂ reduction of 26.5 ppm, but a drawdown of 14.8 ppm. This indicates that, in this case, about half of the effect of the variable is attributable to a difference in the mean CIP composition of the oceanic material between the control states Ctrl and CtrlCM.

### 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 (ACSM) and nutrients are present in the deep ocean at any given time, leading to an increase in pCO₂ (Table 2, Fig. 9) and a decrease in pCO₂ (Fig. 6). The deeper we make the RLS, the higher the drawdown of pCO₂ is in RLS + LS + LSCO₂ and RLS + LS + LSCO₂ + RLS + Lsrco₂. In GCM, the drawdown in each experiment is increased by an additional 39%, since RLS + Lsrco₂ and RLS + LS + LSCO₂, as a drawdown of pCO₂ of 14 and 18 ppm, respectively, compared to Ctrl + LSCO₂ (Table 5). One change in RLS causes very small, but global, changes in surface nutrients 25 ppm in RLS + Lsrco₂ (Fig. 7 c), which, through the small resulting changes in CIP (Fig. 8 c), will contribute to the additional drawdown of pCO₂ in GCM. Experiments with deeper RLS in 12% (RLS + Lsrco₂) and RLS + Lsrco₂ + RLS + Lsrco₂ suggest that about 40% of the observed pCO₂ differences can be attributed to the difference in export flux average CIP 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 (LGm = LGMf + LGMalt = LGMphyC), the reductions in pCO₂ are similar in the R94 and the GCM model versions. In LGMphyC, the resulting pCO₂ is 248.4 and 244.9 ppm respectively, thus a reduction of 32 ppm compared to Ctrl 219 ppm (Fig. 6). Here, variable CIP does not impact the results, because changes in the surface nutrient distribution (Fig. 7 a) and the associated changes in CIP (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 pCO₂ can mainly be attributed to the increase in solubility of CaCO₃ due to ocean cooling, and to an increase in sea ice, which prevents air-sea gas exchange and therefore causes an increase in dissolved carbon (CDSO₄-PO₄) (Oishi et al., 2018). Ocean cooling amounts to 2.1°C in LGMphyC compared to Ctrl (Table 2). In GENIE, the increase in CDSO₄-PO₄ associated with ocean cooling corresponds to ~27.0 ppm CO₂ (Oishi et al., 2018, supplementary Fig. S.1). Thus, in LGMphyC, CDSO₄-PO₄ and CCM should contribute roughly 40% and 60% respectively of the change in pCO₂. Note that GENIE underestimates the true effect of ocean cooling on solubility, due to a temperature restriction on the solubility constants (Oishi et al., 2018). This temperature restriction limits solubility from 2°C to 2°C. In this case, the solubility effect on pCO₂ is 0.01°C (from 3.6°C to 1.8°C, or 15 ppm) in total compared to only 1.6°C of cooling (from 3.6°C to 2.0°C, or 11 ppm), and the solubility effect is underestimated by 0.4 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 ~6 ppm (Kohfeld and Ridgwell, 2009). This effect is consistent for any choice of CIP parametrization, and is therefore not explored further.
In a sensitivity test where we make the RLS 25 % shallower (which would be representative of a warmer climate c.f. Ctrl), the δ13C‰ increases by 18 and 23 ppm in RED and GAM respectively compared to their control states (see Table 5, Table 6 and Table S.2.1). Interestingly, the response in δ13C‰ is again ~30 % larger in GAM. The variable stoichiometry thus amplifies the effect on δ13C‰ by any change in RLS.

5.3.2 Dust forcing

The simulations with LGM dust forcing (Table 1) show the largest difference in δ13C‰ between the RED and the GAM. In €\textit{LGM}C, δ13C‰ decreases by 16 ppm compared to CtrlC, whereas €\textit{LGM}C was a reduction of 21 ppm compared to CtrlC (Fig. 6). The drawdown is thus ~30 % larger with variable stoichiometry. This can be explained by a change in average composition of the deposited organic carbon (see Table 5). At the same time, the drawdowns in €\textit{LGM}C are 16 ppm and ~30 % larger than in €\textit{LGM}C.

As anticipated, the iron added by the dust forcing allows more efficient uptake of P in the HLNC regions, which increases CIP and the ocean storage of biologically sourced carbon (Table 2, Fig. 9). This reduces the surface nutrient concentrations in these areas (Fig. 7-8). In the GAM model version, this is followed by increased CIP ratios in these areas (Fig. 8 d), resulting in a lower δ13C‰ in €\textit{LGM}C than in €\textit{LGM}C. The largest assimilates in PIP, concentrations, and consequently in CIP, 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 radiocarbon proxy data from the LGM (e.g., Komar et al., 1995; Kohfeld et al., 2003).

3.3 Combined experiments

We show the results of two different combined simulations: €\textit{Acrol} and €\textit{GEoloch}. €\textit{GEoloch} is the "glacial-like" simulation, which combines all the sensitivity experiments (Table 1). €\textit{Acrol} omits the reduction in wind stress.

3.3.1 Ocean temperature and circulation

In the glacial-like simulations, €\textit{GeolochLGM} and €\textit{GeolochLGM}, the global average ocean temperature (\textit{T}°C) is 2°C cooler than in the respective control states (Table 2). Heaty and Severinghaus (2007) estimate LGM T°C to have been 4°C to 6°C colder than the modern ocean. €\textit{Geoloch} is thus just outside the one standard deviation limit of the warm end of this estimate. In €\textit{Acrol}, T°C is 2.1°C cooler than Ctrl, thus this simulation falls within the uncertainty of the Heaty and Severinghaus (2007) estimate for the LGM.

Ocean overturning circulation weakens in €\textit{Geoloch} 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 ~15 %, from 18 Sv to 12 Sv (Table 2). The global meridional overturning stream function reveals that the SO

20 overturning cell size a reduction in transport (Fig. 2 d), which is associated with weaker upwelling and the longer residence

3.2.3 Remineralization length scale

When the remineralization length scale (RLS) increases, the biological material reaches deeper before it is remineralized, and it takes longer for it to be returned to the surface. Therefore, more of the biologically sourced carbon (\textit{C_{B,biog}}) and nutrients are present in the deep ocean at any given time, leading to an increase in δ13C‰ (Table 2, Fig. 9) and a decrease in δ13C‰ (Fig. 6). The deeper we make the RLS, the bigger the drawdown of δ13C‰ in €\textit{RLS = 1000 km} and €\textit{RLS = 3800 km} decreases by 14 and 33 ppm, respectively, compared to CtrlC. In GAM, the drawdowns in each experiment is increased by an additional ~30 %, thus €\textit{RLS = 1000 km} and €\textit{RLS = 3800 km} for a reduction of δ13C‰ of 18 and 44 ppm, respectively, compared to CtrlC (Table S.2). Our changes in RLS cause very small, but global, changes in CIP concentrations (global average anomaly of ~0.05 ppm). €\textit{RLS = 1000 km} in Fig. 7 e), through the small resulting changes in CIP (Fig. 8 c), still contribute to the additional drawdown of δ13C‰ 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 δ13C‰ increases by 18 and 23 ppm in RED and GAM respectively compared to their control states (see Table 5). At the same time, the drawdowns in €\textit{RLS = 1000 km} are 16 ppm and ~30 % larger than in €\textit{RLS = 3800 km}.

As anticipated, the iron added by the dust forcing allows more efficient uptake of P in the HLNC regions, which increases CIP and the ocean storage of biologically sourced carbon (Table 2, Fig. 9). This reduces the surface nutrient concentrations in these areas (Fig. 7-8). In the GAM model version, this is followed by increased CIP ratios in these areas (Fig. 8 d), resulting in a lower δ13C‰ in €\textit{RLS = 1000 km} than in €\textit{RLS = 3800 km}. The largest assimilates in PIP, concentrations, and consequently in CIP, 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 radiocarbon proxy data from the LGM (e.g., Komar et al., 1995; Kohfeld et al., 2003).
time for AABW, as hypothesised for the glacial ocean (e.g., Martini et al., 2017) in Core 4, 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 (GLOMENG Ctrl. shown for GAM in Fig. 7 d), we see the strongest response in the Southern Ocean, with different effects north and south of the so-called biogeochemical divide described by Martini et al. (2006). Martini et al. (2006) show that the air-sea balance of CO₂ 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. 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 GLOMENG nutrient concentrations compared to Ctrl (Fig. 7 f), which coincides with

10 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 d). North of the biogeochemical divide, increased algal bloom 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 h), 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 h), mainly due to the increased dust flux (Fig. 7 d). There is an increase in P found 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 oceanic matter that is exported out of the upper layer (henceforth referred to as export production) in GLOMENG Ctrl. has a global average C/P ratio of 134/1.

3.3.3 Ocean dissolved O₂

Despite colder conditions, which allow for more dissolution of O₂, the reduction in O₂ is evident in the GLOMENG-simulations (Fig. 4). This mirrors the increase of Δ°Cmiss (Fig. 9). The O₂ reduction is about 30 % lower in GAM compared to SEED. As the initial state of C/exports is already lower in oxygen than O₂/exports W0, compared to O₂/exports Ctrl., and variable stoichiometry allows for additional ocean storage of organic carbon, the end state O₂ is drastically lower in GLOMENG Ctrl.

25 (280μmol/kg) compared to GLOMENG Ctrl. (320μmol/kg) and GLOMENG Ctrl. (290μmol/kg). O₂/exports Ctrl.

3.3.4 Oman Δ°C

In GLOMENG Ctrl. (contrasts in Fig. 5 a-d), the Atlantic North-South gradient in Δ°C is stronger than in Ctrl/GAM controls (Fig. 5 a-c). This strong gradient is not observed in the Holocene Atlantic Δ°C data in (Fig. 5 e-a), but prominent in the LGM time slice (dots in Fig. 5 c-d). The LGM observations are well reproduced in GLOMENG Ctrl. (cont. 0.62, Table S.5).

especially in the East Atlantic (cont. 0.77). When we correct GLOMENG Ctrl. for the absence of injected terrestrial carbon, we see clear similarities with LGM observations (Fig. 5 d). Though the southermost cores still indicate more 13C-depleted conditions
than the model. In the Indo-Pacific, \( \text{GLO} \) is too \(^{14}C \)-depleted compared to LGM observations, particularly with the correction for the absence of a terrestrial signal (Fig. 5 b), and the model-data correlation is poor (0.05). For the Indo-Pacific, the model-data correlation for Holocene data is similar between \( \text{GLO}_{\text{Hol}} \) and \( \text{CH} \) (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 \( \text{GLO}_{\text{Hol}} \), similarly as in CH, there is very little difference between the RED and GAM model versions in terms of \(^{14}C \) pathways (compare Fig. 5 a,b to Fig. 8.4 and 8.5 a,b) and model-data correlations (Table S 3). However, there are overall lower values of \(^{14}C \) in GAM, reflecting the larger storage of biologically sourced carbon in the deep ocean in this model version.

3.3.5 Atmospheric \(^{14}C \)

In the combined experiments \( \text{AcS} \) and \( \text{GLO}_{\text{Hol}} \), \(^{14}C \) decreases strongly compared to the control state (55 to 580 ppm, Fig. 6). This is partly a result of colder conditions (Table 2), which lead to increased solubility for \(^{14}C \) in sea water, and also cause increased \( \text{CO}_2 \) uptake because of expanded sea ice cover (not shown), which restricts air-sea gas exchange. This leads to an equilibrium of the \(^{14}C \)-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. 6, also contribute strongly to the reduced \(^{14}C \). In \( \text{GLO}_{\text{Hol}} \) and \( \text{GLO}_{\text{Hol}} \), we achieve drawdowns of \(^{14}C \) of 64 and 80 ppm, respectively, compared to 278 ppm of the control state (Fig. 6). This corresponds to an increase in ocean carbon storage of 1.9 gPg \( \text{C} \) and 1.7 gPg \( \text{C} \), respectively (Table S 1). The drawdown in \( \text{AcS} \) is thus 28% larger than in GAM than in RED. If we compare this to \( \text{GLO}_{\text{Hol}} \) (drawdown at 72 ppm, Fig. 6), we see that about half of the drawdown can be attributed to increased average \(^{14}C \) composition of oceanic organic material compared to RED. In AcS, where the perturbation in wind stress is added, drawdown of \(^{14}C \) is smaller than in \( \text{GLO}_{\text{Hol}} \) but still 14 % larger in \( \text{AcS} \) than in \( \text{AcS} \) (56 and 65 ppm, respectively, Fig. 6). Hence, 12 out of the 14 % difference in \(^{14}C \) can be attributed to a change in average \(^{14}C \) rather than the full extent of the change. The effects of the individual perturbation simulations are also shown in the combined experiments of \( \text{AcS} \) and \( \text{GLO}_{\text{Hol}} \). However, only half of the change in \(^{14}C \) is due to changed average \(^{14}C \). Thus, the effects of the perturbations do not add linearly.

4 Discussion

4.1 Accounting for variable \(^{14}C \) in ocean carbon cycle models

The representation of ocean biology in GCMs tends to be over-simplified (Le Quéré et al., 2005) and the development of the model is often held back by constraints imposed by maintaining the computational efficiency of the model. The Gaillardet and Martin (2013) 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 Tanaka and Maiuri, (2017), an additional facet of the complexity of ocean biology can be implicitly accounted for in a relatively small computational cost. The approach taken by both Gaillardet and Martin (2013) and Tanaka and Maiuri (2017) is to adapt
of $\Delta^{14}C$ is smaller than in $\Delta^{14}C_{GLam}$ and the difference between model versions is less pronounced, but there is still a 14% difference between $\Delta^{14}C_{GLam}$ and $\Delta^{14}C_{Gal}$. The difference is less pronounced in simulations with non-linear effects, such as the Southern Ocean. As such, there is a need for further improvements in 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 Tanaka and Matsumoto (2017) find that the flexible stoichiometry model 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 $\Delta^{14}C$, is limited to the combined perturbations 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 Galbreath and Martray (2015) and Tanaka and Matsumoto (2017) is to adapt a function to all the available species-dependent 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 frequent 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 see here. Galopoulou and Broin (2017) appear to succeed with full glacial-interglacial CO$_2$ cycles in CLIMBER-2, which does not have flexible stoichiometry for primary producers, but which has a temperature limitation on growth and explicit phytoplankton with different 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., Kellogg et al., 2001; Letcher and Moore, 2015), but this goes beyond the scope of this present study. One drawback of the Galbreath and Martray (2015) approach is that it assumes the C/P ratio continues to increase continuously with increasing [P]$_{w}$. Thus, [GAM] does not account for the effects on CIP of temperature and light and the associated non-linear effects that could be of importance in the Southern Ocean (e.g., Young-Dorsche et al., 2015; Tanaka and Matsumoto, 2017; Morono et al., 2018), where [P]$_{w}$ is very high. Up to [P]$_{w} = 15$mgL$^{-1}$, the [GAM] parameterisation fits the bound-observational data well (see Fig. 1 and S2 Galbreath and Martray, 2015). To account for the lack of observational data at higher [P]$_{w}$, we have tested the effect of saturation of the CIP ratio at [P]$_{w}$ of 15mgL$^{-1}$ in Orca and $\Delta^{14}C_{GLam}$ simulations where we kept CIP at [P]$_{w}$ > 15mgL$^{-1}$. The increase in ocean carbon storage and decrease in $\Delta^{14}C_{GLam}$ between the Orca and $\Delta^{14}C_{GLam}$ are nearly identical with [GAM], thus saturation of the CIP ratio at very high [P]$_{w}$ causes no noticeable impact on our results.

20 4.2 Implications of changed average CIP

Part of the observed difference in $\Delta^{14}C_{GLam}$ and $\Delta^{14}C_{Gal}$ results from a difference in global average CIP in the control states ($\Delta^{14}C_{Gal}$ and $\Delta^{14}C_{Gal}$). In $\Delta^{14}C_{Gal}$, the average CIP in the export production is close to 121%, instead of 100% as in $\Delta^{14}C_{Gal}$. We illustrate the consequences of this difference by running parallel simulations with fixed CIP of 121% (model version 121). Depending on the change in fixing, the simulations with 121 indicate that between 15% and 20% of the difference in d13C between REED and GAM is due to a change in the average CIP (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 Matsumoto (1996) or Takahashi et al. (1998) stoichiometries, compared to those that use Redfield (1958). The problems with different stoichiometry assumptions in models is extensively discussed by Pahler et al. (2008). Our study shows a direct consequence of such differences, with different model response in the same perturbation. Note that $\Delta^{14}C_{Gal}$ has a larger inventory of DIC as well as C$\varepsilon$P compared to $\Delta^{14}C_{Gal}$. Yet, the effect of applying the same perturbation results in a larger decrease of C$\varepsilon$P in GAM than in REED. This is opposite of the conclusions of Ohnuki et al. (2010). The reason is that the C-explicit stoichiometry in effect increases the d13C potential, which more than compensates for the increased carbon inventory in the control state. In $\Delta^{14}C_{GLam}$, the CIP in global
where we kept CIP = 5541 at [NO3] = 10 μM. The increase in ocean carbon storage and decrease in pCO2* between the Ctrl and GLoom_5 are nearly identical with GAM, thus saturation of the CIP ratio at high [NO3] causes no noticable impact on our results.

Our sensitivity experiments RLS = 0.75 and RLS = 1.25 reveal that the response in pCO2* to the perturbation is enhanced in GAM compared to RLS 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 (Murnane, 2007). Murnane (2007) describes how decreased RLS would have a positive feedback on pCO2* in future warming climates. Our results imply that flexible CIP could have a further no-refrigerant effect on this feedback. It would therefore be of interest to apply a parametrisation of flexible CIP 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 pCO2* (e.g., Sarmiento and Toggweiler, 1984; Martin, 1990; Archer et al., 2000; Sigman and Boyle, 2000). However, biological production depends on water temperature (Epplin, 1972) and decreases in cold conditions. This temperature effect is parametric in ORGANIC as a local temperature-dependent uptake rate multiplier proportional to $exp(T/30)$, and we see overall reduced productivity in our cold climate simulations (see e.g. LMHexp, Table 5.1). As the climate cools, the temperature effect leads to a decrease in biological productivity, and a subsequent decrease in P的日 (see LMHexp, 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), (Murnane et al., 2017) and deeper remineralisation (Murnane, 2007; Chikamoto et al., 2002), 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 PSSP (particulate organic phosphorus) and PSSC (particulate organic carbon), by 15% between Ctrl and GLoom_5, 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 PSSC decreases by 17%; the corresponding decrease in PSSP is only 10%. Thus, in GLoom_5 we achieve an increase in ocean inventory of remineralised carbon, which exceeds the one of GLoom_5 (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 $\Delta C_{\text{org}}$ and thus in $\Delta T$ is very small when moving from the control case (Ctrl) to the glacial-like state (GLoom_5) (Fig. 9). In the fixed stoichiometry case (RLS_5) there is a small net increase in $\Delta T$ of 0.02°C in GLoom_5 compared to Ctrl, which is linearly related to a small increase in storage of $\Delta C_{\text{org}}$ in the ocean. In the case with variable stoichiometry (GAM), there is instead a very small decrease in $\Delta T$ of 0.01°C. With a linear response, we would thus expect a decrease in storage of $\Delta C_{\text{org}}$ as well. Instead, we see a reasonable large increase in global average $\Delta C_{\text{org}}$. 

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average export production increases from 1220 to 1354, which reflects the increased storage of organic carbon allowed by the flexible bioturbation.

4.3 Decoupling 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 glaciated pCO\textsubscript{2} (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 parameterised in GLOM2 as a local temperature-dependent uptake rate modifying proportional to rGLOM2 with a small reduction in our cold climate simulations (see e.g. LGMmean, Table S.1). The climatic cools, the temperature effect leads to a decrease in biological productivity and a subsequent decrease in rGLOM2 in Fig. 9). If productivity decreases, other mechanisms are needed to offset this decrease, as the total ocean storage of organic carbon is to increase. Mechanisms that can contribute to increased deep ocean carbon retention are for example reduced M-O overturning circulation (increased residence time of the AAIB) and deeper remineralisation, 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 POPO (particulate organic phosphorus) and POPO (particulate organic carbon), by 15% between Ctrl and GLOMmean, 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 POPO increases by 17%; the corresponding decrease in POPO is only 10%. Thus, in GLOMmean, we achieve an increase in ocean inventory of remineralised carbon, which exceeds the one of GLOMmean (Fig. 9).

Due to the competing effects between decreased export production and increased retention, the small change in Tt is very small when moving from the control state (Ctrl) to a glacial-like state (GLOMmean) (Fig. 9). In the fixed stoichiometry case (BED), there is a small net increase in Tt of 0.02 in GLOMmean compared to Ctrl, which is linearly related to a small increase in storage of AC\textsubscript{AC} in the ocean. In the case with variable stoichiometry (GAM), there is instead a very small decrease in Tt of 0.005. With a linear relationship, we would thus expect a decrease in storage of AC\textsubscript{AC} as well. Instead, we see a reasonably large increase in global average AC\textsubscript{AC}.

This can be explained by the non-linearity introduced by the local variability in C. The reduced pCO\textsubscript{2} in GLOMmean, compared to the control state, 278 ppm, is partly due to the biological pump being more efficient in some key (HUMC) regions. In these regions, there is a reduction of the surface nutrient concentration in GLOMmean compared to Ctrl. When CIP increases with decreased surface layer P concentration, as it does in GAMA, 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\textsubscript{2} can change while the amount of remineralised nutrients remains constant.

5. The reduced pCO\textsubscript{2} in GLOMmean compared to GLOMmean can be explained by the non-linearity introduced by the local variability in C. When changes in ocean circulation, remineralisation depth and short deposition cause the local nutrient availability in the surface waters to change, this affects the elemental composition of the exported organic material. In GLOMmean, there is a reduction of the surface P/O ratio concentration compared to Ctrl in some key (HUMC) regions. In GLOMmean, this decrease in surface P/O results in an increase in C. 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 GLOMmean, the average elemental C/P composition is 1250, and GLOMmean this average C/P. 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, the global average concentration of pCO\textsubscript{2} is 378 ppm, which corresponds to the observed increase in AC\textsubscript{AC}. From this, we conclude that, in a system where stoichiometry is variable on a local scale, ocean storage of biologically sourced CO\textsubscript{2} can change while the amount of remineralised nutrients remains constant.

Note also that Ctrl has a larger inventory of AIC than GLOMmean compared to Ctrl. An overview of this is shown in Fig. 11. It is evident that the flexible bioturbation effect increases the drawdown potential, which more than compensates for the increased carbon inventory in the control state. In GLOMmean, the C/P in global average export production increases from the control state to 1354, which reflects the increased storage of organic carbon allowed by the flexible bioturbation.

4.2 Implications of flexible C/P for deep-ocean oxygen

Studies show that deep ocean O\textsubscript{2} concentrations were lower during the LGM than in the Holocene (e.g., Brandt, 2010; Jaccard and Galbraith, 2012; Galbraith and Jaccard, 2013). Here, we discuss implications of using flexible C/P for the model's ability to reproduce oxygen patterns and concentrations in the different time periods.

In the Atlantic, Ctrl (Fig. 4a) reproduces the observed extent of the Oxygen Minimum Zone (OMZ) (Fig. 4a) is better than Ctrl-G (Fig. 4g) shows. In the Pacific Ocean, the O\textsubscript{2} gradient in the observations (Fig. 4h) is larger compared to that of the control state (Fig. 4i) but the core of the OMZ is well reproduced by the model. The foraminifera applied in GLOM2 are not sufficient to reproduce a full glacial state. Still, we do get a vertical expansion of the OMZ in GLOMmean (Fig. 4a) compared to Ctrl (Fig. 4c) in agreement with the findings of Hopcroft et al. (2018). In GLOMmean, oxygen depletion is non-extreme (see below), but the tendency of vertical expansion compared to the control state is present in our model.

In our glacial-like states, we see a significant reduction of O\textsubscript{2} compared to the control state in both BED and GAMA (Fig. 4d and e). This response is expected when we apply increased dust deposition and deeper remineralisation (Galbraith and Jaccard, 2013) and the direction of the overall response of deep ocean O\textsubscript{2} to the glacial-like forcing is in line with observations. The reduction in O\textsubscript{2} is stronger in GAMA due to the larger storage of organic carbon in this model version.
4.4 Implications of flexible CIP for deep ocean oxygen

As shown by e.g. Bradtmiller et al. (2008), Jaccard and Galbraith (2012), Galbraith and Jaccard (2015), deep ocean O₂ concentrations were lower during the LGM than in the Holocene. In one glacial-like state, we see a significant reduction of O₂ in both REED and GAM (Fig. 4 d and e), which is unexpected 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 (2016), 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, 2016). It should be noted that CtrlHADAM (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 CtrlHADAM (Fig. 4 b) to CtrlHADAM, a large part of the interior North Pacific is anoxic (Fig. 4 e), while observations (Fig. 4 e) indicate very low oxygen levels, but not anoxia. If this parameterisation of variable stoichiometry is to be used in cGENIE in future studies, we suggest some 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 δ¹³C P?

The model-data comparison in δ¹³C P (Section 3.1.4) suggests that the Ctrl simulations are overall well correlated with Holocene benthic δ¹³C P data (HoC in Table 3.1.3) than with Holocene. 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 cGENIE simulations, we achieve a stronger δ¹³C P gradient in the Atlantic, allowing for a closer match with LGM data in terms of STDs. A stronger gradient in δ¹³C P 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 (Holocene and LGM) display similar correlations across the two model simulations. This implies that not changes in forcing is what affects any observed changes in water mass distribution. The applied changes affect the chemical and biological conditions for ocean carbon storage, such as nitrogen 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 (modern, among others) are likely to be required. The very small differences between REED and GAM suggest that using variable stoichiometry does not impact our ability to achieve

- the δ¹³C P patterns seen in observational data. However, we note that some tuning of the modern control state is recommended before cGENIE with variable stoichiometry is used in other studies.
As outlined in Section 4.3, an increase in CIP reduces deep ocean O\textsubscript{2} concentrations, through an increase in regenerated carbon. In this respect, the 123 experiments fall between the corresponding REd and GAM experiments. For example, the global mean average O\textsubscript{2} concentration, \textit{PICO2}, in \textit{CHL} to 152 \textit{m}ol\textsubscript{\textit{atm}} \textsuperscript{-3}, which is lower than \textit{CHLCPAM} 100 \textit{m}ol\textsubscript{\textit{atm}} \textsuperscript{-3}, but higher than \textit{CHLCPAM} 144 \textit{m}ol\textsubscript{\textit{atm}} \textsuperscript{-3}. Similarly, \textit{GLCENCPAM} has a lower O\textsubscript{2} than \textit{GLCENCPAM} 96 compared to 322 \textit{m}ol\textsubscript{\textit{atm}} \textsuperscript{-3}, but higher than \textit{GLCENCPAM} 176 \textit{m}ol\textsubscript{\textit{atm}} \textsuperscript{-3}.

The observed effects of modified average CIP could have implications for model intercomparison projects; if they compare results from models that use different versions of fixed straining (for example, Anderson and Sarmiento (1994) or Taka- hashi et al. (1985)) inconsistencies, compared to Redfield (1963). The problem with different straining assumptions in models is extensively discussed by Paulmier et al. (2009). One 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 $^{31}$C?

Proxy records of biogenic $^{31}$C indicate a change in ocean $\Delta^{31}$C across the salinity gap. The whole ocean salinity change has been estimated to be 735; S. (Peterson et al.; 1994; Peterson and Liñezki, 2018) and the surface-to-deep gradient weak-ened (shown in numerous studies; see e.g. Curry et al.; 1998; Duplessy et al.; 1998; Curry and Oppo, 2005; Herpaul et al.; 2010; Peterson and Liñezki, 2018). To test whether there is a difference in model-data correlation between REd and GAM:

The model-data comparison in $^{31}$C (Section 3.1.4) suggests that the CTR simulation is overall well correlated with Holocene biogenic $^{31}$C data (HOL, in Table S.3). For the Atlantic, the correlation of the CTR simulations is higher with the LGM biogenic $^{31}$C (14C, as shown 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 GLCEN simulations, we achieve a stronger $^{31}$C gradient in the Atlantic, allowing for a closer match with LGM data in terms of STDs. A stronger gradient in $^{31}$C and more depleted suggest weaker ventilation of the deep ocean. The poor correlation in the Indian-Pacific, which may be partly due to sparse high-latitude observ-
5 Conclusions

In this paper, we examine the potential role of variable stoichiometry in biological production for glacial ocean CO₂ storage. We show that flexible CIP composition of organic matter allows a stronger response of δ¹³Corg to glacial-like changes in climate, remineralisation length scale and acoustic drag due to the increased water mass. We conclude that variable stoichiometry is important for glacial ocean CO₂ storage and for achieving the full extent of drawdown of atmospheric CO₂ in model simulations. In the experiment GLOCEM1976, with glacial-like climate and Redfield stoichiometry (Redfield, 1963), ocean carbon storage increases by 139 Ppg and atmospheric CO₂ decreases by 64 ppm. In GLOCEM1983, with glacial-like climate changes and variable stoichiometry, the corresponding numbers are 173 Ppg and 88 ppm. Hence, the drawdown of atmospheric CO₂ increases by 25% when CIP is variable.

10 About half of the increased drawdown of CO₂ results from different global average CIP in the export production. In addition, flexible stoichiometry allows increased carbon capture through the biological pump, while maintaining or even decreasing the fraction of remineralisation 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 CIP parameterised as a simple function of the surface water concentration of PO₄, as suggested by Galbraith and Murtugudde (2015). Tanaka and Matsumoto (2017) suggest that it is unrealistic for CIP to continue to increase indefinitely with increased [PO₄], and therefore suggest a more complex power law function, which takes into account saturation of the CIP ratio at high concentrations of PO₄. However, we found that saturation of the CIP ratio at concentrations higher than the observational upper bound of 1.7 mmol causes no noticeable impact on our results.

The representation of flexible stoichiometry used in this study (Galbraith and Murtugudde, 2015) can be used without large computational cost. It makes it possible to take into account, to first approximation, the complex biological changes that occur in the ocean during long-time-scale climate change scenarios (see e.g. McManus and Wing, 2011). We show here that, for glacial-interglacial cycles, this complexity contributes to changes in atmospheric CO₂ through flexible CIP ratios.

Code and data available online: The code for the gGENIE 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/dietze/modelgENIE/releases/tag/v0.9.5 and is assigned a DOI 10.5281/zena-

25 Configuration files for the specific experiments presented in the paper can be found in the directory output_exp/fig1/00 exp_source/EXPision.10319. 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 gGENIE model tutorials, is available from https://github.com/dietze/modelgENIE/releases/tag/v0.9.5 and is assigned a DOI 10.5281/zenodo.1487588. (gGENIE release 1.9.5, 2019)

20 Datasets are available upon request (e-mail to mainak.saha@uni-mainz.de).

As our GLOCEM-simulations still correlate as well with the HCL data, this suggests the applied forcings have not caused these simulations to be clearly different from Cl30 in terms of water mass distribution. For the same reason, the correlation with LDM (PAG) runs does not significantly improve from Cl30 in GLOCEM. The water mass distribution in gGENIE 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 current level of the model's resolution. The surface water mass may become more or less prominent; however, interbasin exchanges in ocean circulation, such as the Atlantic Meridional Overturning Circulation, may still occur at the same depth. The applied changes affect the chemical and biological conditions for ocean carbon storage, such as CO₂ 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 gGENIE, with a more glacial-like water mass distribution, additional physical forcings (e.g. ice sheet) are likely to be required.

How (18O) is represented in gGENIE is detailed in Appendix B. The very small differences between RED and G4AM suggests that using variable stoichiometry does not impact our ability to represent the 18O patterns seen in observational data. However, we note that some tuning of the modern control state is recommended before gGENIE with variable stoichiometry is used in other studies.
Appendix A: Regenerated acidic carbon

Carbon enters the ocean mainly in the form of CO₂ 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 CO₂ (AC) and dissolved carbonate (BC). The concept of the source-related state variables was first described by Wallin et al. (2014).

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

\[ \text{AC} = \text{DIC} - \frac{1}{2} \text{ALK} \] (A1)

\[ \text{BC} = \frac{1}{2} \text{ALK} \] (A2)

15 Total AC and BC include all ocean source of carbon, including river runoff, air-sea gas exchange, the biological pump and air.

To isolate the CO₂ that was supplied to the ocean via biological soft tissue, we make use of the separation of DIC and ALK into their performed and remineralised fractions (see Section 2.5). Thus, we then compute the remineralised acidic carbon (\(\text{AC}_{\text{rem}}\)) as

\[ \text{AC}_{\text{rem}} = \text{DIC}_{\text{rem}} = \frac{1}{2} \text{ALK}_{\text{rem}} \] (A3)

Author contribs: M. Ödén, J. Nylander, K. J. C. Oliver and A. Ridgwell designed the model experiments. A. Ridgwell developed the original gCMINE model code. M. Ödénén and K. J. C. Oliver adapted the model code and fixtures for the experimental design. M. Ödén prepared the manuscript with contributions from all co-authors.

20 Competing interests. No competing interests are present.

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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. Milliman and Wang, 2011). We show here that, for glacial-interglacial cycles, this complexity contributes to changes in atmospheric CO₂ through flexible CIP ratios.

15 Flexible CIP also has the potential to be an additional positive feedback of ocean warming on CO₂ in future climate.

Code and data availability. The code for the gCMINE multi-fac 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/andyryder/gcmine-multi-fac/releases/tag/v0.9.5 and is assigned a DOI 10.5281/zenodo.3210761 (gCMINE release v0.9.5, 2019).

Configuration files for the specific experiments presented in the paper can be found in the directory
gcmine_multi_fac/source/CMIP6/decadal_BIG_2019. Details of the different experiments, plus the command line used to run each one, are given in readme.rst.

A corresponding user manual detailing software installation and configuration, plus gCMINE-multi-fac model tutorials, is available from https://github.com/andyryder/gcmine-multi-fac/releases/tag/v0.9.5 and is assigned a DOI 10.5281/zenodo.1407589. (gCMINE release 0.9.5, 2018)

Datasets are available upon request (e-mail to alix.sedler@uio.no).

Appendix A: Regenerated acidic carbon

Carbon enters the ocean mainly in the form of CO₂ 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 CO₂ (AC) and dissolved carbonate (BC). The concept of the source-related state variables was first described by Wallin et al. (2014).

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

\[ \text{AC} = \text{DIC} - \frac{1}{2} \text{ALK} \] (A1)

\[ \text{BC} = \frac{1}{2} \text{ALK} \] (A2)

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

To isolate the CO₂ that was supplied to the ocean via biological soft tissue, we make use of the separation of DIC and ALK into their performed and remineralised fractions (see Section 2.5). Thus, we then compute the remineralised acidic carbon (\(\text{AC}_{\text{rem}}\)) as

\[ \text{AC}_{\text{rem}} = \text{DIC}_{\text{rem}} = \frac{1}{2} \text{ALK}_{\text{rem}} \] (A3)
Appendix B: \( \delta^{14}C \) in eGENIE

eGENIE represents \( \delta^{14}C \) 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 \( \delta^{14}C \) 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. (2005) and is evaluated for the modern ocean (alongside simulated \( \delta^{14}C \) in eGENIE) in Turner and Ridgwell (2010).

In the aqueous phase, the isotopic partitioning of carbon between \( \text{CO}_2(aq) \), \( \text{HCO}_3^- \) and \( \text{CO}_3^{2-} \) is modelled and follows Zabkar and Wohlfarth (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. (1998).

10. For the isotopic composition of organic carbon (\( \delta^{14}C\text{org} \)), the model of Rau et al. (1996) is adopted, 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:

\[
\delta^{14}C\text{org} = \delta^{14}C\text{org}(\text{source}) - \left( \frac{\delta^{14}C\text{org}(\text{source}) - \delta^{14}C\text{org}(\text{ambient})}{\delta^{14}C\text{org}(\text{ambient})} \right) \times \frac{1}{1 + \alpha T}
\]

where \( \delta^{14}C\text{org}(\text{ambient}) \) is the ambient concentration of aqueous \( \text{CO}_2 \) and \( \delta^{14}C\text{org}(\text{source}) \) is its isotopic composition; \( \alpha T \) is a temperature-dependent approximation of the full cell-dependent size and growth rate parameterisation in the Rau et al. (1996) model (see Ridgwell, 2001). We take an intermediate value for the enzymatic isotopic fractionation factor associated with intracellular C-fixation \( \alpha = 0.25 \) following Rau et al. (1996, 1997) and assume a temperature-invariant value \( \alpha = 0.9 \% \).

The result of applying this scheme in eGENIE is a zonal mean profile characterized by \( \delta^{14}C\text{org} \) of \(-25 \% \) to \(-21 \% \) in the tropics, declining with increasing latitude to \(-28 \% \) 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 ISO\( ^{14}C \) fractionation into biogenic carbonates at the ocean surface (e.g. diatoms and coccolithophores in the ocean), eGENIE follows Menck (1986) and employs a simple temperature-dependent relationship between the \( \delta^{14}C \) of apatite and calcite.

Author contributions. M. Odle, J. Nylander, K. I. C. Oliver and A. Ridgwell designed the model experiments. A. Ridgwell developed the original eGENIE model code. M. Odle and K. I. C. Oliver adapted the model code for the experimental design. M. Odle performed the model simulations and produced the tables and figures. C. D. Peterson provided expertise on ocean \( ^{14}C \) analysis. M. Odle prepared the manuscript with contributions from all co-authors.

Competition interests. No competing interests are present.
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Figure 1: Flexible elasticity (MPa/m) dependent on the P-concentration [mol/l] (w- w- w- w- w-) as described by Eq. 1. Here, we found the relationship beyond the observational interval 0-5.7 [mol/l] (black line) which from the basis of the relation derived by Galliath and Marnot (2015).
Figure 2. The eddy component of the Global (panels a, b), Atlantic (panels c, d), and Pacific (panels e, f) ocean meridional overturning streamfunction (Sverdrups, Sv) of 
CrossSection (panels a, e) and CrossSection (panels b, f). Note that the eddy-induced transport of tracers is taken into account through a slow-diffusive flux (Griffies, 1990) that is present in the velocity fields used to compute the eddy stream function.
Figure 4. Sections of O$_2$ concentration (mol/m$^3$) along 25°W in the Atlantic basin (left hand column) and along 155°W in the Pacific basin (right hand column). Panels show observations (World Ocean Atlas 2013, Garcia et al., 2013b) (a, b), and model states CMAM2PC: a-b, CMAM_A1B (c, d), GLcontinental (e, h) and GLcontinental (f, j).
Figure 5. Model ocean δ¹³C (contours) compared to the two-pair model time series (HOK and LGM) of historical marine δ¹³C (circles) of Paterson et al. (2016). Left-hand column shows CMIP5 (panels a, c, e, g) and right-hand column shows CLIMB (panels b, d, f, h). The rows show, from top to bottom, (a/b) HOK Atlantic, (c/d) LGM Atlantic, (e/f) HOK Pacific, and (g/h) LGM Pacific. Note that while we compare CLIMB to LGM observations (panels d and h), a constant of 0.32% is subtracted from CLIMB to account for terrestrial release of δ¹³C-depleted terrestrial carbon. The corresponding comparisons for model versus GAM in shown in Fig. S.1.
Figure 6. Resulting CO$_2$ anomaly with respect to the control state 278 ppm, of the sensitivity experiments BLOOM (triangle), AFM-BLOOM (square), and BLOOM (circle), and of the combined experiments: AEC (star) and CL-Clim (downward arrowheads). Results of the different model versions: BLOOM, 121 and CAM are shown in red, yellow and blue, respectively. The vertical dashed line separates simulations without (left) and with (right) wind perturbation.
Figure 7. Surface PO4 anomaly [µM], with respect to surface concentration of PO4 in Ctrl (Fig. 3a) for a) AMMIL-1, b) AMMIL-2, c) AMMIL-3, d) AMMIL-4, e) AMMIL-5, f) AMMIL-6, g) AMMIL-7, h) AMMIL-8, i) AMMIL-9, j) AMMIL-10, k) AMMIL-11. 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 1960-1980 (Fig. 3b). a) RULG00.085, b) RGLG00.085, c) RUGL00.085, d) RGLG00.085, e) RUGL00.085, f) RUGL00.085.
Figure 9: Remotenedative carbon (ACO) as a function of 13C. Simulations using model versions RED and CAM 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 CAM. Panels illustrate a) the deviation from the least-squares fit of the CAM ensemble as opposed to the RED ensemble, b) the linear fit extrapolated to zero, and c) a zoom-in around the origin, where the RED (red) line goes through the origin, while the CAM (blue) does not.
Table 1. List of experiments. Experiment number corresponds to short descriptions of what the experiment does, and specifies details of parameter settings for each ensemble member. The $pCO_2$ is either prescribed to pre-industrial (P) or 2100 ppm, or finely varying with changes in climate and ocean circulation. The radiative forcing is either coupled to the $pCO_2$ of the atmospheric chemistry model of the model, or final at a single scenario, corresponding to a change in $pCO_2$ of 160 ppm. The aerosol profile is either representative of modern/1990 conditions or of the LGM. The wind stress is either modern/1990 or a single scenario, corresponding to a change in $pCO_2$ of 160 ppm.

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1) See last paragraph of Introduction text for the Southern Hemisphere.
2) f/r = fraction for a model run at different resolution.

Table 2. List of experiments. Experiment number corresponds to short descriptions of what the experiment does, and specifies details of parameter settings for each ensemble member. The $pCO_2$ is either prescribed to pre-industrial (P) or 2100 ppm, or finely varying with changes in climate and ocean circulation. The radiative forcing is either coupled to the $pCO_2$ of the atmospheric chemistry model of the model, or final at a single scenario, corresponding to a change in $pCO_2$ of 160 ppm. The aerosol profile is either representative of modern/1990 conditions or of the LGM. The wind stress is either modern/1990 or a single scenario, corresponding to a change in $pCO_2$ of 160 ppm.

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1) See last paragraph of Introduction text for the Southern Hemisphere.
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Table 2. Atmospheric CO₂ (pCO₂) [ppm], global mean averages of temperature (Tmean, °C), P̄, and Ō̂ (mixed kg⁻¹), and Atlantic overturning streamfunction (Φ). Overdrawn (NO) is maximum and minimum, but for observations, and for selected ensemble members in each model version (BIOGEOCHEM). Observed modern day Tmean and Ō̂ mix computed using the World Ocean Atlas 2018 (Lacan et al., 2008; Garcia et al., 2009). Activity modern day AMOC strength is estimated by McCarth et al. (2013) from the RAPID-MOCCHA array at 26°N (corresponding to Atlantic Ẇ̇Ċ̇̇̇ in the model). Note that observed pCO₂ [ppm] is given for pre-industrial (PI) climate, so we do not model anthropogenic release of CO₂.

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

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³School of Geographical Sciences, Bristol University, Bristol BS8 1SS, UK
⁴National Oceanography Centre, Southampton, University of Southampton, Southampton SO14 3ZH, United Kingdom

Correspondence: Malin Ödalen (malin.odalen@misu.su.se)
S Supplementary material

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

In Fig. S.1, the locations of core sites for observed benthic δ13C are indicated, and Holocene (HOL) observed benthic δ13C is compared to the bottom water ocean distribution of δ13C for CtrlRED. The positions of observation sites are the same as in Peterson et al. (2014).

For comparison with Fig. 3a, we show the surface PO4 concentration (μM) of the control state with fixed Redfield stoichiometry (CtrlRED) (Fig. S.2).

For comparison with Fig. 5, which shows model ocean δ13C 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 GLeenh simulations in each of the model versions RED and GAM, and for the two benthic δ13C data time slices HOL (0-6 ka) and LGM (19-23 ka).

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For comparison with Fig. 5, which shows model ocean δ13C 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 CtrlRED and GLeenh (Fig. S.4).

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 GLeenh simulations in each of the model versions RED and GAM, and for the two benthic δ13C data time slices HOL (0-6 ka) and LGM (19-23 ka).
Figure S1. CtrlADE bottom water ocean δ¹³C (contours) compared to the Holocene (HOL) time slice of observed benthic δ¹³C (circles) of Peterson et al. (2014).
Figure S.2: Surface $PO_4$ concentration ($\mu$M) of the control state with fixed Redfield stoichiometry ($C/16K/D$).
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). Left hand column shows $C^{\uparrow}$ ($a$, $c$, $e$, $g$) and right hand column shows $GLcomb_{\uparrow}$ ($b$, $d$, $f$, $h$). 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 $GLcomb_{\uparrow}$ to LGM observations (panels d and h), a constant of 0.32% is subtracted from $GLcomb_{\uparrow}$ 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 ($C^{\uparrow}$ or $GLcomb_{\uparrow}$), while each row represents one of the proxy record time slices (HOL or LGM). The left hand column shows $C^{\uparrow}$ ($a$, $c$, $e$, $g$) and the right hand column shows $GLcomb_{\uparrow}$ ($b$, $d$, $f$, $h$). 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 $GLcomb_{\uparrow}$ 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 and (b) the sea-ice anomaly Glomab – Ctrl (percentage points).
### Table S1. 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, Pmolekg⁻¹; average concentration of DIC (DIC, Pmolekg⁻¹), average concentration of remineralised DIC (DIC, Pmolekg⁻¹), average concentration of remineralised hydrogenocarbon (HOC, Pmolekg⁻¹), average concentration of PO₄ (PO₄, Pmolekg⁻¹), average concentration of remineralised PO₄ (PO₄, Pmolekg⁻¹), average concentration of remineralised hydrogenocarbon (HOC, Pmolekg⁻¹), and average of the nutrient utilisation efficiency (TP). The modern ocean observed C/P is given as determined by Anderson and Sammiento (1994) and the global ocean carbon inventory (DIC, Pmolekg⁻¹) is estimated to 38,700 Pmolekg⁻¹ (Stocker, 2014). The observational estimate for TP is given by Ino and Follows (2005).

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<th>DICmeas (Pmolekg⁻¹)</th>
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Table S.1. Continued.

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<td>$T_{sea}$ (°C)</td>
<td>AMOC (Sv)</td>
<td>Sea ice (%)</td>
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Table S.2. Climatic variables for all control states (Ctrl) and ensemble members (Table 1). The variables are atmospheric CO$_2$ (pCO$_2$ (ppm), global averages of temperature in the ocean ($T_{am}$, °C) and in the atmosphere ($T_{sea}$, °C), transport in the Atlantic meridional overturning circulation (AMOC, Sv) and sea ice cover (%). The observational estimate for $T_{am}$ 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 $T_{sea}$ is given, since modern atmospheric observations are strongly influenced by rising pCO$_2$. See Table S.2 for more details. (Stocker, 2014).
<table>
<thead>
<tr>
<th>Experiment Acronym</th>
<th>$pCO_2$ * (ppm)</th>
<th>$T_{sst}$ * (°C)</th>
<th>$T_{200m}$ (°C)</th>
<th>AMOC (Sv)</th>
<th>Sea Ice (%)</th>
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<td>14.44</td>
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<td>$Acorn_{RED}$</td>
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<td>6.83</td>
<td>13.67</td>
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<td>1.45</td>
<td>6.84</td>
<td>13.66</td>
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<td>6.86</td>
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Table S.2. Continued.

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<th>$T_{200m}$ (°C)</th>
<th>AMOC (Sv)</th>
<th>Sea Ice (%)</th>
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Table 5.3. 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 (6–8 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.

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References


Stocker, T.: Climate change 2013: the physical science basis: Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change, Cambridge University Press, 2014.

References


Stocker, T.: Climate change 2013: the physical science basis: Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change, Cambridge University Press, 2014.