

We thank the editor for her useful comments.

Dear Dr. Kemppinen,

Thank you for submitting the revised version of your manuscript entitled "Coupled climate-carbon cycle simulation of the Last Glacial Maximum atmospheric CO<sub>2</sub> decrease using a large ensemble of modern plausible parameter sets".

I have attentively read the responses to the referees' comments as well as your revised version. I would be happy to accept your manuscript for publication after the points listed below have been taken into account:

1) Figures 3 and 7: Please add land contours so that the maps can be read properly. Please note that this was asked upon first submission of the manuscript, and repeated during all stages of review. If needed, please have a look at "Ferret" (<https://ferretop.pmel.noaa.gov/Ferret/>), which would allow you to plot your data and add land contours on your maps easily.

The figures have been modified as suggested. In revising Fig. 3c, we also noticed that the range for the color bar was too low, leading to a portion of the North Atlantic having no colour. This error was introduced when changing the color bar as part of the previous revision, and has now been rectified.

2) The exact same sentence was added at the end of the abstract and conclusion. Please modify them and please make it clearer that oxygen and carbon isotopes are not simulated here.

We added "not evaluated in this study" behind carbon isotope and oxygen data in the abstract. The abstract now reads "An initial comparison of these dominant changes with observations and paleo-proxies other than carbon isotope and oxygen data (not evaluated directly in this study) suggests broad agreement. However, we advise more detailed comparisons in the future, and also note that, conceptually at least, our results can only be reconciled with carbon isotope and oxygen data if additional processes not included in our model are brought into play."

The conclusion now reads: "The dominant changes were broadly in agreement with observations and paleo-proxies other than carbon isotope and oxygen data, which we did not evaluate directly. However, we advise more detailed comparisons in future studies. It is also likely that our results can only be reconciled with carbon isotope and oxygen data if processes currently missing from our model are taken into account"

Other comments (lines and pages refer to the manuscript with track changes on):

- P19, L16-17: reformulate the iron fertilization part as it is not correct as is

**We have changed this sentence to make it clearer that iron fertilization = stimulation of iron-limited biological pump**

- P19, L 24-25: As far as I know stronger westerly winds over the North Atlantic have not been put forward as a possible mechanism to decrease atmospheric CO<sub>2</sub> over G-IG cycles.

**It is true that Muglia and Schmittner do not make any direct connection between wind stress and CO<sub>2</sub> via the AMOC. We have removed this reference.**

- P21, L. 31; Please directly start as "Section 2 describes...."

**We have revised this section as suggested.**

- Section 2.4: When describing the different subsets, could you please add the names of the subsets in parathesis.

**We have revised this section as suggested**

- P28, L.31: Please move "however" to the beginning of the sentence

**Done**

- P38, L.12-14: To me, a difference of 0.1 Sv +/- 1.2 Sv indicate that there is no statistical difference

between the LGM and PRE Atlantic AABW.

**Agreed. We have rephrased this section accordingly.**

- P39, L. 3: Do you mean the northern limit of AABW? Why AMOC?

**Yes, this sentence should be about the AABW, we have removed the reference to AMOC.**

- P39, L. 6: please spell out "less than"

**Done**

- P43, L. 9-10: I assume here you are referring to an increase in terrestrial carbon due to reduced soil decomposition. Please use this term instead of "growth of biosphere land C"

**We have modified the sentence accordingly.**

- Section 3.2.2. Please read the recent manuscript by Jeltsch-Thommes et al. 2019, <https://www.clim-past-discuss.net/cp-2018-167/>

This is an interesting study, taking an ensemble of simulations that includes some of the processes (e.g. organic carbon weathering and burial) which we do not include, and looking at which ensemble members satisfy atm  $^{13}\text{C}$  + ocean  $^{13}\text{C}$  + deep pacific carbonate ion concentration + atm $\text{CO}_2$  constraints. Land C is almost invariably negative at the LGM. To acknowledge this important research we added the following sentence to section 3.2.6 (in addition to referencing the paper in Table 4 of section 3.2.2): "Yet, further research is required here as one recent study suggests that taking into account these missing processes would most likely not (the possibility is not completely ruled out) allow reconciliation of a positive  $\Delta\text{TerrC}$  with the observed mean glacial ocean  $\delta^{13}\text{C}$  value (Jeltsch-Thommes et al., 2018)".

- P47, L. 7: Please take out "biosphere"

**Done**

- Table 4: Please add at the beginning of the legend that the estimates shown are for LGM compared to PRE. Please add estimates of Delta TerrC of Jeltsch-Thommes et al. 2019 and Menviel et al., 2017 (Paleoceanography).

**Done. We also ordered the references by date in the legend, and changed "C12" to CI12 and "A15" to A15 for consistency throughout.**

- Table 5: I suppose you are referring to carbon stored under ice-sheets

**Yes, during the LGM we mean carbon stored under the Eurasian and Laurentide ice sheets. During preindustrial – it is the carbon in the corresponding grid cells. We have modified the legend of Table 5.**

- P53, L. 11: Please rephrase this sentence as its meaning is unclear.

**The sentence now reads: "As shown in Fig. 12, compared to ENS104, the POC flux decreases in ENS315 and ENS16 tend to be smaller and larger respectively"**

- Figure 14: Please spell out GWS in the legend.

**Done. We also noticed that the first sentence in section 3.2.4 read "glacial weathering factor". We changed this to "land-to-ocean bicarbonate flux scaling factor"**

- P61, L. 22-23: The impact of changes in marine productivity on the global oceanic  $\text{d}^{13}\text{C}$  is not that straightforward and would depend on the associated changes in remineralisation and burial. Enhanced accumulation of remineralised carbon in the deep ocean would lower  $\text{d}^{13}\text{C}$ .

**Yes, agreed. The text now reads: "These include reduced marine productivity (e.g. Zimov et al., 2009), as phytoplankton discriminate against  $^{13}\text{C}$  during photosynthesis, giving the marine organic carbon reservoir a**

low  $\delta^{13}\text{C}$ . However, we note that the sign of this impact would additionally depend on the associated changes in organic matter remineralisation and burial”.

- Last sentence of the conclusion: please modify as stated above.  
Done

**Uploaded Files validated** (11 Apr 2019) by Lorena Grabowski

5

10

15

20

# Coupled climate-carbon cycle simulation of the Last Glacial 5 Maximum atmospheric CO<sub>2</sub> decrease using a large ensemble of modern plausible parameter sets

Krista M.S. Kemppinen<sup>1</sup>, Philip B. Holden<sup>2</sup>, Neil R. Edwards<sup>2</sup>, Andy Ridgwell<sup>3,4</sup>, Andrew D. Friend<sup>1</sup>

10 <sup>1</sup>Department of Geography, University of Cambridge, Cambridge CB2 3EN, UK

<sup>2</sup>Environment, Earth and Ecosystem Sciences, The Open University, Milton Keynes, MK7 6AA, UK

<sup>3</sup>School of Geographical Sciences, Bristol University, Bristol BS8 1SS, UK

<sup>4</sup>Department of Earth Sciences, University of California, Riverside, California 92521, USA

15 *Correspondence to:* Krista M.S. Kemppinen (Krista.Kemppinen@asu.edu)

**Abstract.** During the Last Glacial Maximum (LGM), atmospheric CO<sub>2</sub> was around 90 ppmv lower than during the preindustrial period. The reasons for this decrease are most often elucidated through factorial experiments testing the impact of individual mechanisms. Due to uncertainty in our understanding of the real system, however, the different models used to  
20 conduct the experiments inevitably take on different parameter values, and different structures. In this paper, the objective therefore, is to take an uncertainty-based approach to investigating the LGM CO<sub>2</sub> drop by simulating it with a large ensemble of parameter sets, designed to allow for a wide range of large-scale feedback response strengths. Our aim is not to definitely explain the causes of the CO<sub>2</sub> drop but rather explore the range of possible responses. We find that the LGM CO<sub>2</sub> decrease tends to predominantly be associated with decreasing sea surface temperatures (SSTs), increasing sea ice area, a weakening of  
25 the Atlantic Meridional Overturning Circulation (AMOC), a strengthening of the Antarctic Bottom Water (AABW) cell in the Atlantic Ocean, a decreasing ocean biological productivity, an increasing CaCO<sub>3</sub> weathering flux, and an increasing deep-sea CaCO<sub>3</sub> burial flux. The majority of our simulations also predict an increase in terrestrial carbon, coupled with a decrease in ocean and increase in lithospheric carbon. We attribute the increase in terrestrial carbon to a slower soil respiration rate, as well as the preservation rather than destruction of carbon by the LGM ice sheets. An initial comparison of these dominant  
30 changes with observations and paleo-proxies other than carbon isotope and oxygen data ([not evaluated directly in this study](#)) suggests broad agreement. However, we advise more detailed comparisons in the future, and also note that, conceptually at least, our results can only be reconciled with carbon isotope and oxygen data if additional processes not included in our model are brought into play.

35

## 1 Introduction

5 Analyses of Antarctic ice core records suggest that the atmospheric CO<sub>2</sub> concentration at the Last Glacial Maximum (LGM), about 21 kyr ago, was around 190 ppmv, well below the preindustrial atmospheric concentration of around 280 ppmv. The most commonly accepted mechanisms to explain the atmospheric CO<sub>2</sub> decrease include lower sea surface temperatures, which increases the ocean CO<sub>2</sub> solubility (Martin et al., 2005; Menviel et al., 2012), ~~increased-enhanced ocean biological pump due to increased input of aeolian iron to the ocean~~~~iron-fertilization-of-ocean-phytoplankton-by-aeolian-dust-input~~(Bopp et al., 2003; 10 Oka et al., 2011; Jaccard et al., 2013; Ziegler et al., 2013; Martínez-García et al., 2014; Lambert et al., 2015), capping of air-sea gas exchange by expanding sea ice (Stephens and Keeling, 2000; Sun and Matsumoto, 2010; Chikamoto et al., 2012) and ocean circulation/stratification changes increasing the net CO<sub>2</sub> flux into the ocean (Adkins et al., 2002; Lynch-Stieglitz et al., 2007; Skinner et al., 2010; Lippold et al., 2012; Gebbie, 2014; Skinner et al., 2014; Tiedemann et al., 2015; de la Fuente et al., 2015; Freeman et al., 2015). These changes may in turn be due to a range of possible mechanisms such as increased brine rejection (Shin et al., 2003; Bouttes et al., 2010, 2011; Zhang et al., 2013; Ballarotta et al., 2014), a shift in/weakening of the 15 westerly wind belt over the Southern Ocean (Toggweiler et al., 2006; Anderson et al., 2009; Völker and Köhler, 2013), ~~stronger westerly winds over the North Atlantic (Muglia and Schmittner, 2015),~~ and a reduced or reversed buoyancy flux from the atmosphere to the ocean surface in the Southern Ocean (Watson and Garabato, 2006; Ferrari et al., 2014). A process that is conversely assumed to have contributed to increasing atmospheric CO<sub>2</sub> is increasing salinity and ocean total dissolved inorganic carbon (DIC) concentration in response to decreasing sea level (Ciais et al., 2013). 20

A dominant assumption is also that the terrestrial biosphere carbon inventory was reduced (Crowley et al., 1995; Adams and Faure, 1998; Ciais et al., 2012; Peterson et al., 2014), in line with independent estimates of an ocean carbon inventory that was enhanced by several hundred petagrams (Goodwin and Lauderdale, 2013; Sarnthein et al., 2013; Allen et al., 2015; Skinner et al., 2015; Schmittner and Somes, 2016). The decrease in terrestrial carbon is generally attributed to unfavourable climatic 25 conditions for photosynthesis, and the destruction of organic material by moving ice sheets (e.g. Otto et al., 2002; Prentice et al., 2011; Brovkin et al., 2012; O'ishi and Abe-Ouchi, 2013). The hypothesis that there was an increase in terrestrial carbon has, however, also been put forward (e.g. Zeng, 2003; Zimov, 2006), with some studies additionally suggesting little net change (e.g. Brovkin and Ganopolski, 2015). Processes proposed to be responsible for the terrestrial carbon increase include growth in 'inert' or permafrost carbon, slower 'active' soil respiration rates, continental shelf regrowth, and the preservation rather

than destruction of terrestrial biosphere carbon in areas to be covered by the expanding Laurentide and Eurasian ice sheets (Weitemeyer and Buffett, 2006; Franzén and Cropp, 2007; Zeng et al., 2007; Zimov et al., 2009; Zech et al., 2011).

Other mechanisms which may have affected the LGM atmospheric CO<sub>2</sub> change include changes in carbonate weathering rate, through its control on the ocean ALK:DIC ratio and consequently the solubility of CO<sub>2</sub> (Munhoven, 2002; Jones et al., 2002; Foster and Vance, 2006; Vance et al., 2009; Brovkin et al., 2012; Crocket et al., 2012; Lupker et al., 2013; Simmons et al., 2016). The change in carbonate weathering rate would in turn have been caused by lower sea level, exposing previously submerged rock, the presence of a greater amount of glacial flour, which is more susceptible to weathering (Kohfeld and Ridgwell, 2009), or potentially higher soil carbon content. The lower sea level may also have reduced shallow water carbonate deposition by decreasing the area of shallow ocean (Opdyke and Walker, 1992; Kleypas et al., 1997; Brovkin et al., 2007), and increased oceanic PO<sub>4</sub> inventory, alleviating the PO<sub>4</sub> limitation on marine production (Tamburini and Follmi, 2009; Wallmann, 2014, 2015). Other potential CO<sub>2</sub> mechanisms include decreasing dissolved organic carbon inventory due to a more stratified deep ocean (Ma and Tian, 2014), and reduced marine bacterial metabolic rate in response to lower ocean temperatures. The lower metabolic rate acts to decrease the return rate of DIC from the remineralisation of organic material, and hence the concentration of CO<sub>2</sub> at the ocean surface (Matsumoto et al., 2007; Roth et al., 2014). The net flux of CO<sub>2</sub> into the ocean may also have increased due to enhanced diatom production caused by the leakage of silicic acid trapped in the Southern Ocean (Matsumoto et al., 2002, 2014), or increased Si inventory, caused by increased input of Si from wind-born dust or enhanced weathering (Harrison, 2000; Tréguer and Pondaven, 2000).

Mechanisms put forward to explain the LGM atmospheric CO<sub>2</sub> decrease arise from paleo-data and model studies. The latter most often involve factorial experiments, introducing mechanisms one at a time. There is rarely any investigation of the impact of alternative assumptions regarding parameter values or model structure. An example of a relevant study is Bouttes et al., 2011, which varied model parameters controlling the importance of iron fertilisation, brine rejection and stratification-dependent diffusion in an ensemble setting, assessing the agreement of the model output with data. Here, our aim is conversely to take an uncertainty-based approach to investigating the LGM CO<sub>2</sub> drop by simulating it with a large ensemble of parameter sets designed to allow for a wide range of large-scale feedback response strengths (Holden et al., 2013a). The objective is not to definitely explain the causes of the CO<sub>2</sub> drop but rather explore the range of possible responses. By *responses* we mean physical and biogeochemical changes in the Earth System (e.g. change in global particulate organic carbon export flux) and how these might be linked to ΔCO<sub>2</sub> and to each other, rather than specific mechanisms (e.g. iron fertilisation). Knowledge of these relationships can in turn inform analysis, in the future, of the relationship between the ensemble parameters and model outputs, in order to isolate individual LGM CO<sub>2</sub> mechanisms. In this study, we furthermore seek to simulate the LGM atmospheric CO<sub>2</sub> drop with the simulated CO<sub>2</sub> feeding back to the simulated climate, which is still infrequently done in LGM CO<sub>2</sub> experiments, and the first time it is done with GENIE-1. Moreover, rather than assuming that terrestrial carbon is destroyed

by the LGM ice sheets, we assume that it is gradually buried. This assumption has not yet been implemented, in GENIE-1 or other models, in an equilibrium set-up.

5 Despite our ensemble varying many of the parameters thought to contribute to variability in glacial-interglacial atmospheric CO<sub>2</sub>, not all sources of uncertainty can be captured, and this is reflected in our simulated ΔCO<sub>2</sub> distribution. We estimate that up to ~60 ppmv of ΔCO<sub>2</sub> could be due to processes not included in our model and error in our process representations (see section 2.4 for details). We thus treat ΔCO<sub>2</sub> between ~-90 and -30 ppmv as “equally plausible”, and focus on describing the physical and biogeochemical changes seen in the subset of simulations with this ΔCO<sub>2</sub>. We also do an initial assessment of how the subset mean and/or dominant (in terms of sign) responses compare against observations and paleo-proxies, including temperature, sea ice, precipitation, AMOC & AABW cell strengths, terrestrial carbon, ocean carbon, particulate organic matter export and deep-sea CaCO<sub>3</sub> burial.

15 Finally, to test the robustness of relationships derived from the analysis of the ensemble subset with ΔCO<sub>2</sub> between ~-90 and -30 ppmv, we briefly compare the physical and biogeochemical changes seen therein with the changes seen in the ensemble with no ΔCO<sub>2</sub> filter, and the ensemble with a more negative ΔCO<sub>2</sub> filter (~-90 to -60 ppmv) (section 2.4). In general, the same dominant relationships between ΔCO<sub>2</sub> and the physical and biogeochemical changes are observed as in the subset with ΔCO<sub>2</sub> between ~-90 and -30 ppmv. In the case of the ensemble subset with ΔCO<sub>2</sub> between ~-90 and -60 ppmv, we additionally look at what proportion of the total terrestrial carbon change comes from within the ice sheet areas, and from there draw conclusions for the rest of the ensemble.

20 The paper is organised as follows. ~~The introduction section, Section 1, is followed by~~ Section 2, ~~which~~ describes the model, the ensemble, the simulation set-up and the ensemble subsets to be analysed. Section 3 is the results and discussion section, which includes a brief evaluation of the preindustrial (control) spin-up simulation to verify reproducibility of Holden et al., 2013a. The majority of the section is devoted to the LGM simulation: namely, diagnosis of the physical and biogeochemical changes (including potential causal relationships) seen in the subset with ΔCO<sub>2</sub> between ~-30 and -90 ppmv, and to a lesser extent, the ensemble with both more and less constrained ΔCO<sub>2</sub>. Comparison of the first subset against observations and paleo-proxies is also included. Section 4 provides the key conclusions.

## 2 Methods

### 2.1 The model

The GENIE-1 configuration is as described in Holden et al. (2013a). The physical model consists of a three-dimensional frictional geostrophic ocean model (GOLDSTEIN) coupled to a thermodynamic/dynamic sea ice model (Edwards and Marsh, 2005; Marsh et al., 2011) and a two-dimensional Energy-Moisture Balance Model (EMBM). Atmospheric tracers are a sub-component of the EMBM, with a simple module (ATCHEM) used to store the concentration of atmospheric gases and their relevant isotopic properties (Lenton et al., 2007). The model land surface physics and terrestrial carbon cycle are represented by ENTS (Williamson et al., 2006). The ocean biogeochemistry model (BIOGEM) is as described in Ridgwell et al. (2007) but includes a representation of iron cycling (Annan and Hargreaves, 2010), and the biological uptake scheme of Doney et al. (2006). The model sediments are represented by SEDGEM (Ridgwell and Hargreaves, 2007). GENIE-1 also includes a land surface weathering model, ROKGEM (Colbourn, 2011), which redistributes prescribed weathering fluxes according to a fixed river-routing scheme. The model is on a 36 x 36 equal-area horizontal grid, with 16 vertical levels in the ocean.

### 2.2 The simulation ensemble

The GENIE-1 ensemble consists of 471 parameter sets, varying 29 key model parameters over the ranges in Table 1. It derives from the 471-member emulator-filtered plausibility constrained ensemble of Holden et al. (2013a), which varies 24 active parameters and 1 dummy parameter (as a check against over-fitting). The parameter values in Holden et al. (2013a) were derived by building emulators of eight preindustrial climate metrics and applying a rejection sampling method known as approximate bayesian computation (ABC) to find parameter sets that the emulators predicted were modern plausible. Two parameters were later added to the ensemble, in Holden et al. (2013b), to describe the un-modelled response of clouds to global average temperature change (OL1), and the uncertain response of photosynthesis to changing atmospheric CO<sub>2</sub> concentration (VPC). The parameters are as described in Holden et al., 2013b. We add two further parameters here that represent uncertain processes specific to the LGM. The first (FFX) scales ice-sheet meltwater fluxes to account for uncertainty in un-modelled isostatic depression at the ice-bedrock interface due to ice sheet growth, and for assuming a fixed land-sea mask (Holden et al., 2010b). We vary the parameter in the ensemble to capture the uncertainty in the magnitude of the glacial sea level drop and its effects on the carbon cycle. The second (GWS) scales the global average preindustrial carbonate weathering rates for the LGM, to account for uncertainty in carbonate weathering and un-modelled shallow water carbonate deposition rate changes. For both FFX and GWS, uniform random values were derived using the generation function runif in R.



**Table 1. Ensemble parameters.** Ranges are from (a) Holden et al. (2013a), (b) Holden et al. (2013b), and (c) Holden et al. (2010b), with the exception of GWS (see main text). The table also precludes the dummy parameter.

Module	Code	Description	Range	Ref.
EMBM	AHD	Atmospheric heat diffusivity ( $\text{m}^2 \text{s}^{-1}$ )	1118875 to 4368143	a
	AMD	Atmospheric moisture diffusivity ( $\text{m}^2 \text{s}^{-1}$ )	50719 to 2852835	a
	APM	Atlantic-Pacific moisture flux scaling	0.1 to 2.0	a
	OL0	Clear skies OLR reduction ( $\text{W m}^{-2}$ )	2.6 to 10.0	a
GOLDSTEIN	OL1	OLR feedback ( $\text{W m}^{-2} \text{K}^{-1}$ )	-0.5 to 0.5	b
	OHD	Isopycnal diffusivity ( $\text{m}^2 \text{s}^{-1}$ )	312 to 5644	a
	OVD	Reference diapycnal diffusivity ( $\text{m}^2 \text{s}^{-1}$ )	0.00002 to 0.0002	a
	OP1	Power law for diapycnal diffusivity depth profile	0.008 to 1.5	a
SEA-ICE	ODC	Ocean inverse drag coefficient (days)	0.5 to 5.0	a
	WSF	Wind scale factor	1.0 to 3.0	a
	FFX	Freshwater flux scaling factor	1.0 to 2.0	c
	SID	Sea ice diffusivity ( $\text{m}^2 \text{s}^{-1}$ )	5671 to 99032	a
ENTS	VFC	Fractional vegetation dependence on vegetation carbon density ( $\text{m}^2 \text{kgC}^{-1}$ )	0.4 to 1.0	a
	VBP	Base rate of photosynthesis ( $\text{kgC m}^{-2} \text{yr}^{-1}$ )	3.0 to 5.5	a
	VRA	Vegetation respiration activation energy ( $\text{J mol}^{-1}$ )	24211 to 71926	a
	LLR	Leaf litter rate ( $\text{yr}^{-1}$ )	0.08 to 0.3	a
BIOGEM	SRT	Soil respiration activation temperature (K)	198 to 241	a
	VPC	Photosynthesis half-saturation to $\text{CO}_2$ (ppmv)	30 to 697	b
	PHS	$\text{PO}_4$ half-saturation concentration ( $\text{mol kg}^{-1}$ )	$5.3\text{e-}8$ to $9.9\text{e-}7$	a
	PRP	Initial proportion of POC export as recalcitrant fraction	0.01 to 0.1	a
	PRD	e-folding remineralisation depth of non-recalcitrant POC (m)	106 to 995	a
	RRS	Rain ratio scalar	0.02 to 0.1	a
	TCP	Thermodynamic calcification rate power	0.2 to 2.0	a
	PRC	Initial proportion of $\text{CaCO}_3$ export as recalcitrant fraction	0.1 to 1.0	a
	CRD	e-folding remineralisation depth of non-recalcitrant $\text{CaCO}_3$ (m)	314 to 2962	a
	FES	Iron solubility	0.001 to 0.01	a
ROKGEM	ASG	Air-sea gas exchange parameter	0.1 to 0.5	a
	GWS	Land-to-ocean bicarbonate flux scaling factor	0.5 to 1.5	n/a

### 2.3 Experimental set-up of the model

The preindustrial ensemble simulation results were repeated to verify reproducibility of Holden et al. (2013a). The simulations were performed in two stages, each lasting 10 kyr, on the Cambridge High Performance Computing (HPC) Cluster Darwin.

5 The first stage involved spinning up the model with atmospheric CO<sub>2</sub> concentration relaxed to 278 ppmv and a closed biogeochemistry system. This means that there are no sediment-ocean interactions and the model forces the CaCO<sub>3</sub> weathering and deep sea sediment burial rates into balance. An initial CaCO<sub>3</sub> weathering is initially prescribed but this is subsequently rescaled internally to balance the modelled CaCO<sub>3</sub> burial rate and conserve alkalinity. In the second stage, atmospheric CO<sub>2</sub> was allowed to evolve freely, with interacting oceans and sediments, and the CaCO<sub>3</sub> weathering rate is set equal to the CaCO<sub>3</sub> burial rate diagnosed from the end of stage 1. To allow the sediments to reach equilibrium as fast as possible, no bioturbation was modelled in either stage 1 or stage 2.

Each parameter set was then applied to LGM simulations. The modelled preindustrial equilibrium states were used as initial conditions and the ensemble members were integrated for 10 kyr, with freely evolving CO<sub>2</sub>. These 10 kyr simulations are variously referred to here as the “LGM equilibrium simulation” or “stage 3”, and the LGM equilibrium state refers to the end of stage 3 (see S1 for more details). After application to stages 2 and 3, the original 471 ensemble members were filtered to 315 ensemble members to exclude those simulations with a stage 2 atmospheric CO<sub>2</sub> concentration outside of the range 268 to 288 ppmv (c.f. Prentice et al., 2001), those that entered a snowball Earth state in stage 3 (global annual SAT between ~-68 and -57 °C), or those that showed evidence of numerical instability (c.f. Holden et al., 2013b).

20 Boundary conditions applied in the LGM simulations included orbital parameters (Berger, 1978) and aeolian dust deposition fields (Mahowald et al., 2006). The atmospheric CO<sub>2</sub> used in the radiative code is internally generated, rather than prescribed but the radiative forcing from dust, and gases other than CO<sub>2</sub> was neglected. The model also requires a detrital flux field to the sediments, containing contributions from opal and material from non-aeolian sources (Ridgwell and Hargreaves, 2007).  
25 Weathering fluxes from the preindustrial simulation were applied, scaled by GWS (the land-to-ocean bicarbonate flux scaling factor).

The representation of the ice sheets is as described in Holden et al. (2010b), using the terrestrial ice sheet fraction and orography from the ICE-4G reconstruction of Peltier (1994). Rather than initialising the ensemble with the ice sheet extent and orography at 21 kyr BP, the ice sheets are configured to grow from their preindustrial to LGM extent in 1 kyr, at the beginning of the LGM simulation (i.e. years 0-1 kyr) in order to account for the impact of sea level change on ocean tracers. Following Holden et al. (2010b), only the Laurentide and Eurasian Ice Sheets are allowed to change from their preindustrial form (accounting for

~ 80% of global ice sheet change), and we also route the freshwater to build the ice sheets from the Atlantic, Pacific and Arctic, assuming modern topography, rather than extracting it uniformly. As the ice sheets grow, grid cells on land are gradually covered by ice and any carbon that remains, or has accumulated, is preserved underneath (“buried”). Once the ice covers a grid cell, there is no more exchange between the land carbon in that grid cell and the atmosphere. Prior to being buried, however, it is subject to the same forcings as carbon in any other grid cell. To determine how sensitive the burial carbon amount (i.e. the amount of carbon that is available for preservation underneath the ice) is to the duration of ice sheet build-up, we test the impact of varying the latter from 1 to 10 kyr for one ensemble member (extending the total simulation length to 11 kyr). Our assumption is that if the difference is negligible, applying the same ensemble member to a transient simulation of the full glacial cycle (and therefore a more realistic ice sheet build-up history) would not have yielded a dramatically different burial carbon inventory. We find that increasing the ice sheet build-up duration indeed changes the burial carbon amount only marginally: an increase of ~34 PgC. A limitation, however, is that we do not have a way of testing if the response of other ensemble members would be equally subdued.

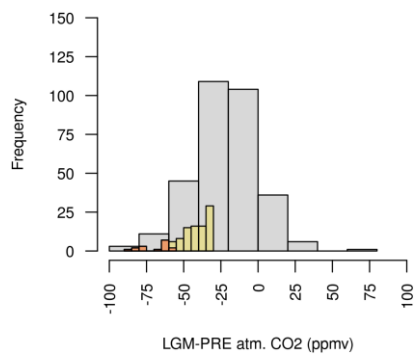
#### 2.4 Ensemble subsets

Although our ensemble varies many of the parameters thought to contribute to variability in glacial-interglacial atmospheric  $\text{CO}_2$ , not all sources of uncertainty can be captured. We estimate, based on our expert opinion, that up to ~60 ppmv of  $\Delta\text{CO}_2$  could be due to error in our process representations and processes not included in our model, such as changing marine bacterial metabolic rate, wind speed (via its effect on gas transfer) and Si fertilization. This is not a comprehensive assessment, however, as our model also does not include processes such as the effect of changing winds on ocean circulation (Toggweiler et al., 2006), Si leakage (Matsumoto et al., 2002, 2013, 2014), the effect of decreasing SSTs on  $\text{CaCO}_3$  production (Iglesias-Rodriguez et al., 2002), or changing oceanic  $\text{PO}_4$  inventory (Menviel et al., 2012). We focus our analyses on the subset of the ensemble with  $\Delta\text{CO}_2$  between ~-90 and -30 ppmv (Table 2), treating each value in this range as equally plausible. To test the robustness of diagnosed relationships, we also briefly compare the response of this subset ( $\text{ENS}_{104}$ ) with the response of the ensemble with no  $\Delta\text{CO}_2$  filter ( $\text{ENS}_{315}$ ), and the response of the ensemble with a more negative  $\Delta\text{CO}_2$  filter ( $\text{ENS}_{16}$ ). In  $\text{ENS}_{16}$  this second subset, the upper  $\Delta\text{CO}_2$  limit is set to ~-60 ppmv, roughly equivalent to allowing for an extra atmospheric  $\text{CO}_2$  decrease due to changing marine bacterial metabolic rate, wind speed (via its effect on gas transfer) and Si fertilization, between the best and upper estimate of Kohfeld and Ridgwell (2009). The  $\Delta\text{CO}_2$  distribution in each subset or ensemble is shown in Fig. 1.

**Table 2. Ensemble subsets, including  $\Delta\text{CO}_2$  and number of members in each.**

Ensemble	$\Delta\text{CO}_2$ range (ppmv)	Number of members
ENS <sub>315</sub>	-88 to 74	315
ENS <sub>104</sub>	-88 to -30	104
ENS <sub>16</sub>	-88 to -59	16

5



10

**Fig. 1. LGM change in atmospheric CO<sub>2</sub> distribution.** The ENS<sub>315</sub> response is shown in grey, the ENS<sub>104</sub> ensemble response in yellow and the ENS<sub>16</sub> ensemble response in orange. The same colour legend applies to all figures in the manuscript.

15

### 3 Results and discussion

#### 3.1 Preindustrial simulations

Comparison of the preindustrial response of ENS<sub>315</sub> (i.e. the original, non-ΔCO<sub>2</sub> filtered ensemble) against the preindustrial ensemble response of Holden et al., 2013a confirms that the two are very similar. We additionally evaluate ENS<sub>315</sub> against a few additional preindustrial metrics (see S2) and find responses that can be deemed plausible, following the design principles for the ensemble, outlined in Holden et al., 2013a.

#### 3.2 LGM simulations

##### 3.2.1 Climate, sea level and ocean circulation

###### Temperature

The ENS<sub>104</sub> mean LGM surface air temperature (SAT) anomaly (ΔSAT) is  $-4.6 \pm 1.7$ , and the range is  $-2.5$  to  $-10.4$  °C. The mean is close to the observed ΔSAT of  $-4 \pm 1$  °C (Annan and Hargreaves, 2013), and the range roughly equivalent to the range of previous model-based estimates (Kim et al., 2003; Masson-Delmotte et al., 2006; Schneider von Deimling et al., 2006; Braconnot et al., 2007; Holden et al., 2010a; Brady et al., 2013). The ENS<sub>104</sub> mean LGM SST anomaly (ΔSST) is  $-1.8 \pm 0.8$  °C, and the range is  $-4.5$  and  $-0.7$  °C. The mean is again close to an observational data-constrained model estimate (Schmittner et al. (2011), and within the range of estimates inferred from proxy data (MARGO Project Members 2009 in Masson-Delmotte et al., 2013). There is a positive correlation between ΔSAT and ΔCO<sub>2</sub> ( $r = 0.75$ , 0.05 significance level hereforth), most likely reflecting the radiative impact of atmospheric CO<sub>2</sub> on SAT, as well as the effect of changing SAT on ΔCO<sub>2</sub>. As suggested above, decreasing SST may contribute to decreasing CO<sub>2</sub> via the CO<sub>2</sub> solubility temperature dependence. Changing SAT may also affect ΔCO<sub>2</sub> via its effects on sea ice, ocean circulation, terrestrial and marine productivity (see below). The positive correlation is reproduced in ENS<sub>315</sub> ( $r = 0.74$ ), and as shown in Fig. 2, ΔSAT and ΔSST tend to be less negative in ENS<sub>315</sub> than in ENS<sub>104</sub>. In ENS<sub>16</sub>, ΔSAT and ΔSST are from the extreme or at least lower end of the ENS<sub>104</sub> range.

The ENS<sub>104</sub> mean ΔSAT and ΔSST spatial distributions are shown in Fig. 3. In line with observations (Annan and Hargreaves, 2013), the largest SAT decreases ( $> 10$  °C) are simulated over the Laurentide and Eurasian Ice Sheets. The equator to pole temperature gradient is also broadly reproduced. The largest SST decreases ( $\geq 4$  °C) are found in the North Atlantic and northeast Pacific, with more limited cooling ( $\leq -2$  °C) in the tropics and polar regions, again consistent with observations. However, the largest SST decreases ought to, however, also be found in the southern hemisphere mid-latitudes whereas the simulated cooling is more moderate.

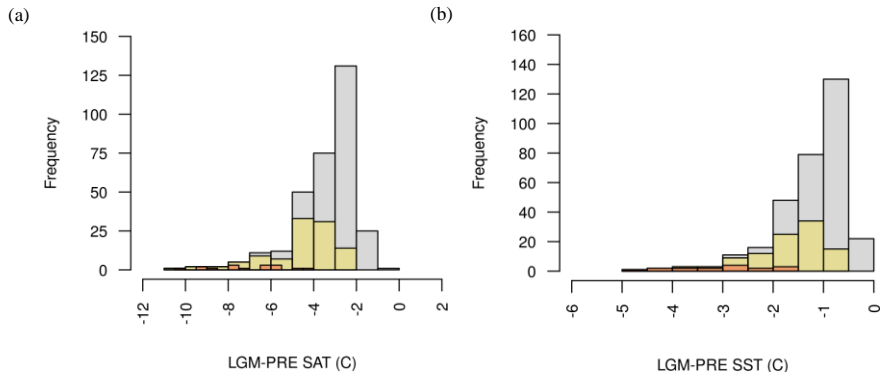
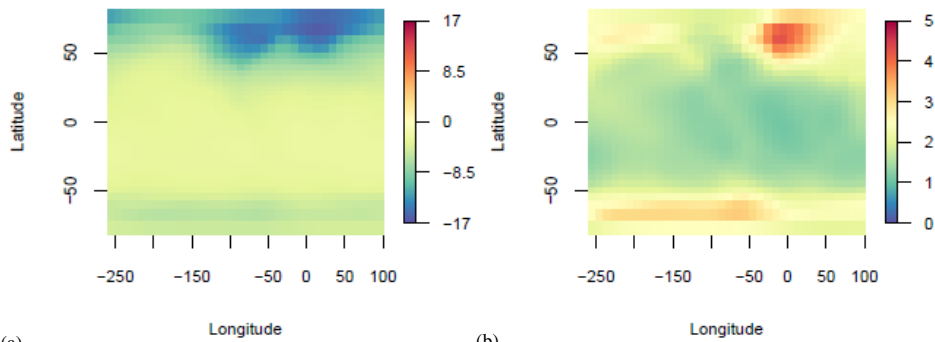


Fig. 2. LGM change in surface air temperature and sea surface temperature (a-b) distributions.

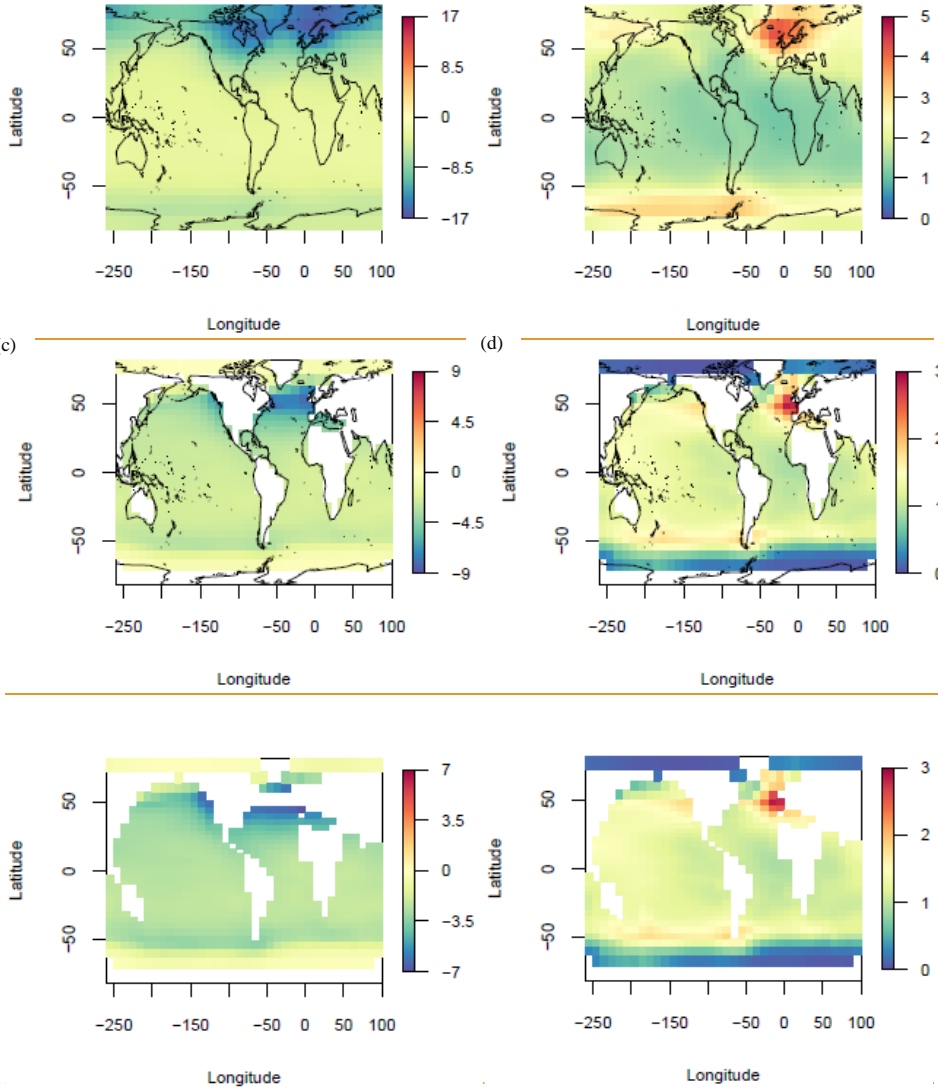
5



10 (a)

(b)

14



5 Fig. 3. LGM change in surface air temperature (a-b) and sea surface temperature (c-d) ( $^{\circ}\text{C}$ ) ENS<sub>104</sub> mean (left) and standard deviation (right).

### Salinity

- 5 The ENS<sub>104</sub> mean percentage increase in LGM salinity (and DIC, ALK, PO<sub>4</sub>, etc) due to decreasing sea level is  $2.84 \pm 0.62$  %S and the range is 2 to 4 %S. There is no significant relationship between %S and  $\Delta\text{CO}_2$  in either ENS<sub>104</sub> or ENS<sub>315</sub>, and the distribution of %S is similar in ENS<sub>104</sub> and in both ENS<sub>315</sub> and ENS<sub>16</sub> (Fig. 4).

10

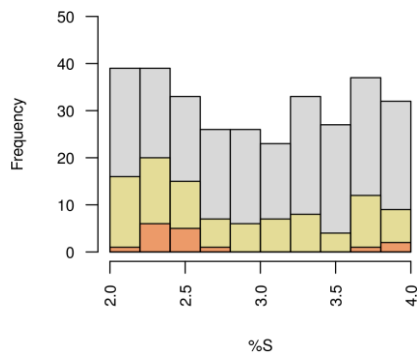


Fig. 4. Percentage increase in LGM salinity due to decreasing sea level distribution.

15

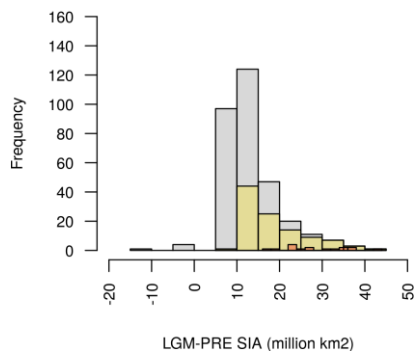
### Sea ice

- The ENS<sub>104</sub> mean LGM global annual sea ice area anomaly ( $\Delta\text{SIA}$ ) is  $18.6 \pm 7.4$  million km<sup>2</sup>, and the range is 9.9 to 44 million km<sup>2</sup>. There is a negative correlation between  $\Delta\text{SIA}$  and  $\Delta\text{SAT}$  ( $r = -0.97$ ) and between  $\Delta\text{SIA}$  and  $\Delta\text{CO}_2$  ( $r = -0.74$ ). The negative correlation between  $\Delta\text{SIA}$  and  $\Delta\text{CO}_2$  likely reflects the impact of changing atmospheric CO<sub>2</sub> on  $\Delta\text{SIA}$  but may also include a smaller contribution from changing sea ice area to  $\Delta\text{CO}_2$ . Increasing LGM sea ice area could for instance have capped the outgassing of CO<sub>2</sub> from the ocean, particularly in the Southern Ocean, and also reduced the net ocean-atmosphere CO<sub>2</sub> flux by decreasing the AMOC strength (see below). The negative correlation between  $\Delta\text{SIA}$  and  $\Delta\text{SAT}$ , and



between  $\Delta SIA$  and  $\Delta CO_2$ , is reproduced in ENS<sub>315</sub> ( $r = -0.96$  and  $r = -0.74$  respectively).  $\Delta SIA$  in ENS<sub>104</sub> also tends to be higher than in ENS<sub>315</sub>, and smaller than in ENS<sub>16</sub> (Fig. 5).

As shown in Fig. 6, fractional sea ice cover increases in all regions where sea ice is present in preindustrial simulations, although the largest increases take place in the North Atlantic.

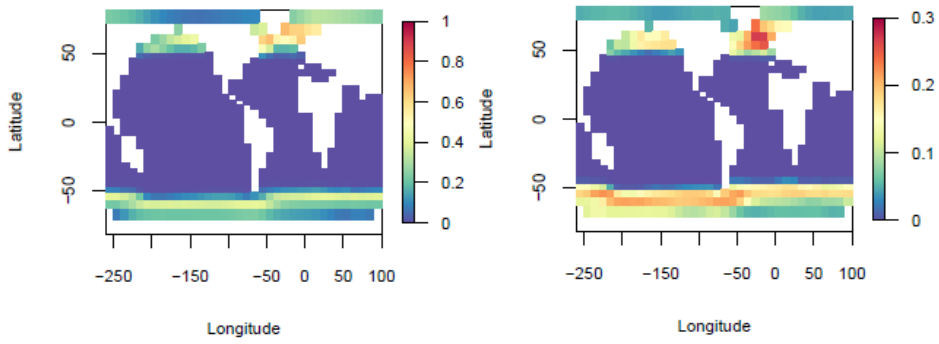


**Fig. 5. LGM change in global sea ice area distribution.**

15

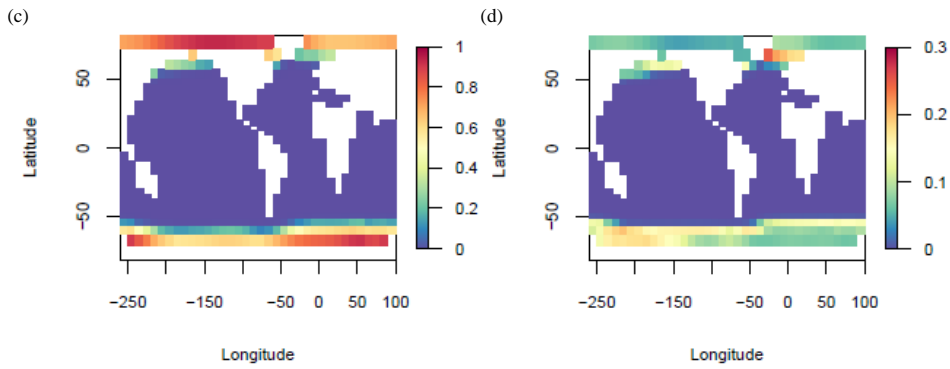
(a)

(b)



5

10



**Fig. 6. LGM-PRE (a-b) and PRE (c-d) fractional sea ice cover  $ENS_{10^4}$  means (left) and standard deviations (right).**

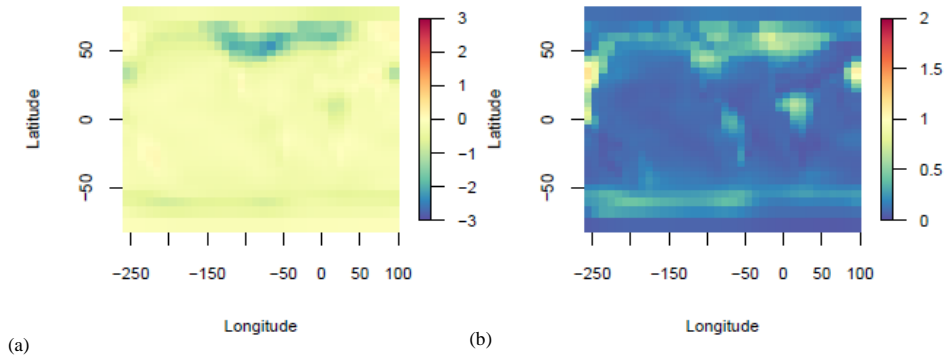
15

### Precipitation

The ENS<sub>104</sub> mean spatial distribution of the LGM precipitation rate anomaly ( $\Delta PP$ ) is shown in Fig. 7. The LGM changes are mostly negative but regions of positive  $\Delta PP$  do exist, notably over Siberia and Australia. The largest LGM precipitation decreases ( $> 1.5 \text{ mm day}^{-1}$ , with a maximum of  $2.25 \text{ mm day}^{-1}$ ) are found over northern North America, and from around the eastern North Atlantic to northwest Asia, coinciding with the location of the Laurentide and Eurasian Ice Sheets (and the largest increases in fractional sea ice cover) respectively. Relatively large precipitation decreases ( $> 0.75 \text{ mm day}^{-1}$ ) are also simulated in eastern Asia, equatorial Africa and other regions of enhanced fractional sea ice cover. Comparison against a pollen-based precipitation reconstruction (Bartlein et al., 2011; Alder and Hostetler, 2015) suggest that the simulated precipitation changes over Europe and equatorial Africa are of the right direction, while precipitation changes over western Siberia at least ought to be negative. The sign of the precipitation changes over North America is mostly consistent with observations, which record negative changes over most of the continent. However, positive changes, which are also observed, are not captured. Although not shown here, comparison of the ENS<sub>104</sub> mean against the ENS<sub>315</sub> mean suggests that the precipitation patterns in the two are very similar, but the decreases generally tend to be higher in the ENS<sub>104</sub> mean.

15 The precipitation decreases in ENS<sub>104</sub> conversely tend to be smaller than in ENS<sub>16</sub>.

20



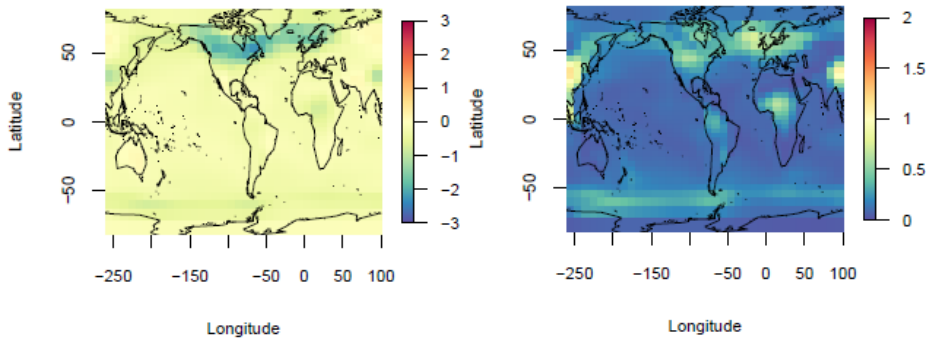


Fig. 7. LGM change in precipitation rate ( $\text{mm day}^{-1}$ ) ENS<sub>104</sub> mean (a) and standard deviation (b).

5

#### Ocean circulation

The ENS<sub>104</sub> mean LGM AMOC strength anomaly ( $\Delta\psi_{\text{max}}$ ) is  $-2.8 \pm 2.8$  Sv, and the range is -8 to 4.7 Sv (Fig. 8). These estimates lie at the low end of the  $\Delta\psi_{\text{max}}$  predicted by 9 PMIP2 (Weber et al., 2007) and 8 PMIP3 (Muglia and Schmittner, 2015) coupled model simulations. However, they do not include the more negative  $\Delta\psi_{\text{max}}$  predicted by Völker and Köhler (2013) for instance. The ENS<sub>104</sub> mean LGM-PRE AABW cell strength in the Atlantic Ocean ( $\Delta\psi_{\text{min}}$ ) is  $0.1 \pm 1.2$  Sv, which, A positive  $\Delta\psi_{\text{min}}$  here represents an LGM decrease in cell strength as we keep the original (negative) sign for anticlockwise flow of Antarctic water. A negative  $\Delta\psi_{\text{min}}$  conversely represents an LGM increase in cell strength. However, the difference between the LGM and PRE Atlantic AABW here is not statistically significant. The range of  $\Delta\psi_{\text{min}}$  is -4.3 to 4.3 Sv, roughly comparable to the range of  $\Delta\psi_{\text{min}}$  predicted in Weber et al. (2007) (see also Muglia and Schmittner, 2015), but excluding the much larger  $\psi_{\text{min}}$  increase predicted by Kim et al. (2003) for example. As shown in Fig. 9, the northern limits of the ENS<sub>104</sub> mean LGM AMOC and AABW cells is are roughly at the same latitudes as in the preindustrial simulations. The maximum depth reached by the ensemble mean AMOC base is also similar to preindustrial. Observations (Lynch-Stieglitz et al., 2007; Lippold et al., 2012; Gebbie, 2014; Böhm et al., 2015), conversely, suggest that the LGM AMOC shoaled to less than 2 km, raising its base depth by 2500 and 600 m at the north and south end of the return flow respectively. The LGM AABW, in turn, is thought to have filled the deep Atlantic below 2 km, reaching as far north as 65°N, which is ca. 25 degrees north of its modern northern limit (Oppo et al., 2015).

15

20

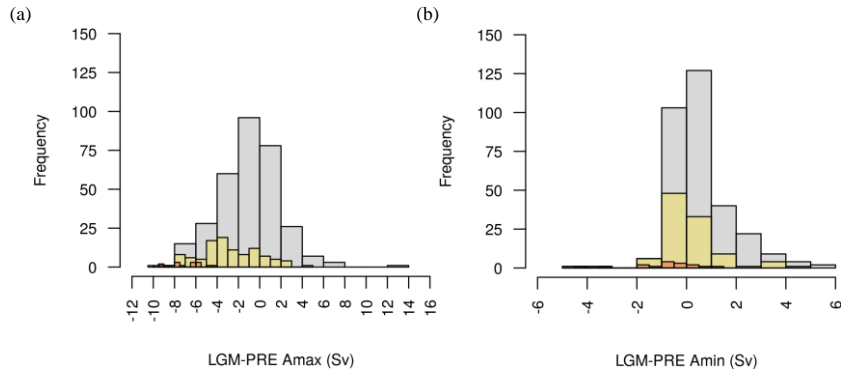
Although not shown here, the ENS<sub>16</sub> ensemble members tend to exhibit a shoaling of the AMOC and enhanced penetration of AABW. With regard to  $\Delta\psi_{\text{max}}$  and  $\Delta\psi_{\text{min}}$ , one can see from Fig. 8 that these tend to be more negative (i.e. weaker

AMOC and stronger AABW) than in ENS<sub>104</sub>. The  $\Delta\psi_{\max}$  and  $\Delta\psi_{\min}$  in ENS<sub>315</sub> tend to conversely be more positive. In ENS<sub>104</sub>, we also find a positive relationship between  $\Delta\psi_{\max}$  and  $\Delta\text{CO}_2$  ( $r = 0.57$ ) and a negative relationship between  $\Delta\psi_{\min}$  and  $\Delta\text{CO}_2$  ( $r = -0.42$ ). The relationships are reproduced in ENS<sub>315</sub> ( $r = 0.59$  and  $r = -0.36$  respectively). We additionally find, in both ENS<sub>104</sub> and ENS<sub>315</sub>, negative correlations between  $\Delta\psi_{\max}$  and  $\Delta\psi_{\min}$  ( $r = -0.62$  and  $-0.63$ ),  $\Delta\psi_{\min}$  and  $\Delta\text{SAT}$  ( $r = -0.4$  and  $-0.4$ ) and  $\Delta\psi_{\max}$  and  $\Delta\text{SIA}$  ( $r = -0.62$  and  $-0.66$ ), as well as positive correlations between  $\Delta\psi_{\max}$  and  $\Delta\text{SAT}$  ( $r = 0.68$  and  $0.66$ ), and  $\Delta\psi_{\min}$  and  $\Delta\text{SIA}$  ( $r = 0.37$  and  $0.42$ ). Based on these relationships, we hypothesise that increasing LGM AABW strength led to an expansion of the AABW cell. The latter in turn restricted the AMOC to lower depths, and reduced its overturning rate (e.g. Shin et al., 2003). The increase in AABW strength was likely driven by increases in sea ice enhancing brine rejection. Sea ice increases in the North Atlantic may have additionally weakened the AMOC cell by locally reducing deep convection.

The relationships between  $\Delta\psi_{\max}$ ,  $\Delta\psi_{\min}$  and  $\Delta\text{CO}_2$  are also consistent with increasing  $\psi_{\min}$  (decreasing  $\psi_{\max}$ ) contributing to decreasing atmospheric  $\text{CO}_2$ . The replacement of NADW by AABW in the North Atlantic would, for instance, have led to a dissolution of deep sea sediment  $\text{CaCO}_3$  due to AABW having a lower bottom water  $\text{CO}_3^{2-}$  concentration than NADW (see e.g. Yu et al., 2014). The increased  $\text{CaCO}_3$  dissolution flux would in turn have raised the whole ocean alkalinity, lowering the atmospheric  $\text{CO}_2$ . Enhanced AABW production would also have caused the deep ocean to become more stratified, allowing more DIC to accumulate at depth, and promoting further  $\text{CaCO}_3$  dissolution. A decrease in NADW formation could have additionally lowered atmospheric  $\text{CO}_2$  by reducing  $\text{CO}_2$  outgassing at the ocean surface, and reducing the burial rate of deep sea  $\text{CaCO}_3$  due to the concomitant increase in deep sea DIC accumulation. Further investigation is, however, required to confirm these causal relationships.

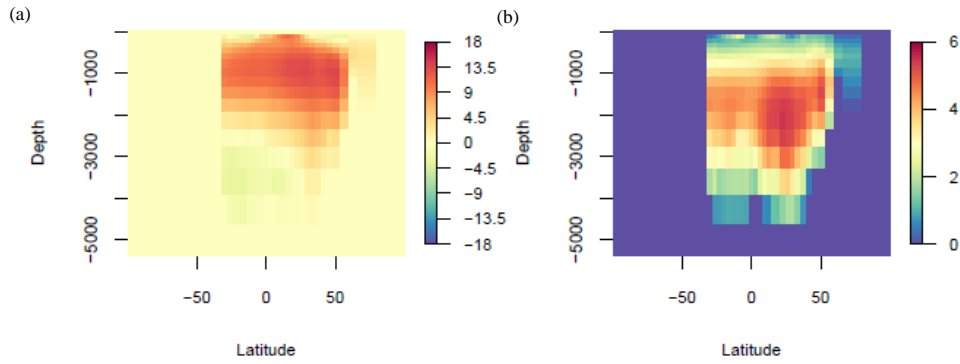
25

30



**Fig. 8. LGM change in  $\psi_{\max}$  and  $\psi_{\min}$  (a-b) distributions.**

5



10

15

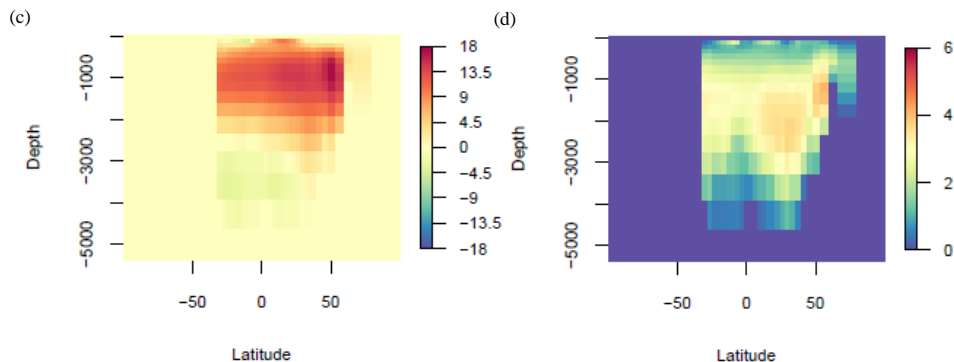
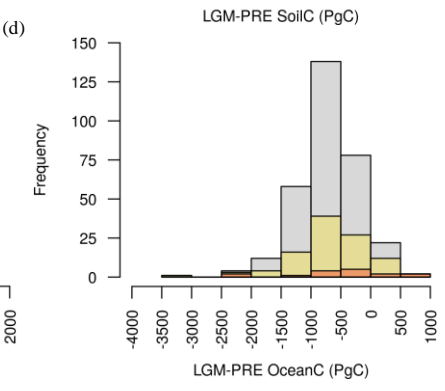
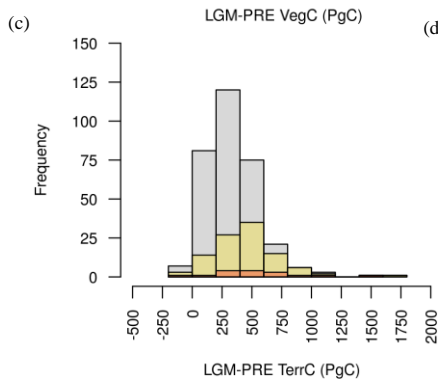
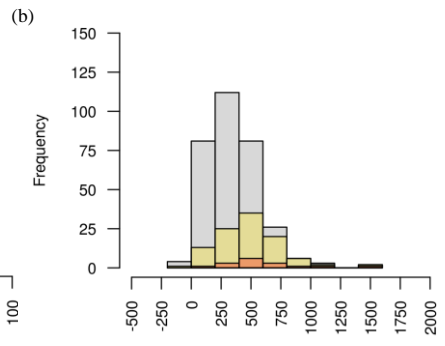
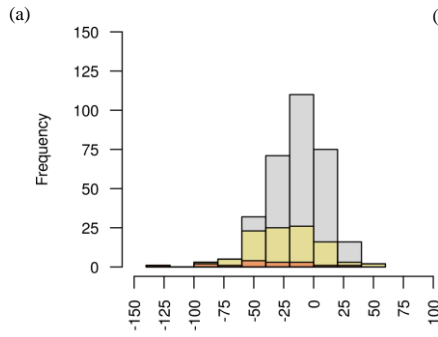


Fig. 9. LGM (a-b) and PRE (c-d) Atlantic overturning stream functions (Sv) ENS<sub>104</sub> means (left) and standard deviations (right).

### 3.2.2 Terrestrial biosphere, ocean and lithospheric carbon

As shown in Fig. 10, most of the ensemble members in ENS<sub>104</sub> predict an LGM increase in terrestrial biosphere ( $\Delta\text{TerrC}$ ), and lithospheric<sup>1</sup> ( $\Delta\text{LithC}$ ) carbon inventory and a decrease in ocean carbon inventory ( $\Delta\text{OceanC}$ ). The remaining ensemble members predict one of four other scenarios of carbon partitioning, with the second most common scenario (11% of ensemble members) being increasing terrestrial carbon and decreasing ocean and lithospheric carbon (Table 3). Similar patterns can also be observed in ENS<sub>315</sub> and ENS<sub>16</sub>. A likely explanation for scenario 1 (increase in terrestrial biosphere and lithospheric carbon, decrease in ocean carbon) is that [the growth of biosphere land carbon reduced soil decomposition](#) (see below) causes a flux of CO<sub>2</sub> from the atmosphere to the land, leading to an immediate outgassing of CO<sub>2</sub> from the ocean to remove the atmospheric pCO<sub>2</sub> difference. The CO<sub>2</sub> outgassing also leads to an increase in surface [CO<sub>3</sub><sup>2-</sup>] and subsequently deep ocean [CO<sub>3</sub><sup>2-</sup>], which reduces CaCO<sub>3</sub> dissolution (and increases lithospheric carbon). The increase in CaCO<sub>3</sub> burial in turn decreases [CO<sub>3</sub><sup>2-</sup>] and increases [CO<sub>2</sub>], which is communicated back to the surface, with a resultant increase in atmospheric CO<sub>2</sub> (Kohfeld and Ridgwell, 2009). The above explanation is of course only part of the explanation for this dominant carbon partitioning scenario, with physical mechanisms also expected to play a role, in addition to any changes in ocean productivity and changes in land carbonate weathering (see below).

<sup>1</sup> The  $\Delta\text{LithC}$  stems from changes in the deep-sea CaCO<sub>3</sub> burial flux and/or CaCO<sub>3</sub> weathering/shallow water deposition flux and was initially calculated to ensure that carbon was being conserved over the LGM simulation.



5

10

15



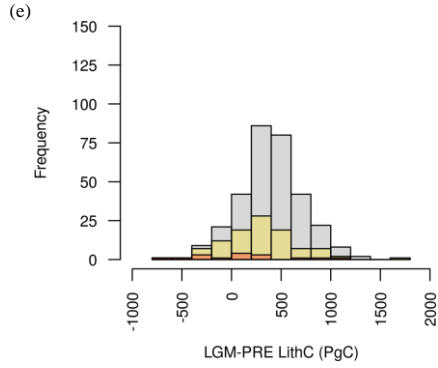


Fig. 10. LGM change in vegetation (a), soil (b), terrestrial (vegetation + soil) (c), ocean (d) and lithospheric (e) carbon inventory distributions.

Table 3. LGM-PRE carbon partitioning scenarios in ENS<sub>315</sub>, ENS<sub>104</sub> and ENS<sub>16</sub>.

Scenarios	ENS <sub>315</sub>		ENS <sub>104</sub>		ENS <sub>16</sub>	
	Total counts	(% of total)	Total counts	(% of total)	Total counts	(% of total)
1. $\Delta$ TerrC(+) $\Delta$ OceanC(-) $\Delta$ LithC(+)	279	(89)	82	(79)	10	(63)
2. $\Delta$ TerrC(+) $\Delta$ OceanC(+) $\Delta$ LithC(-)	16	(5)	11	(11)	3	(19)
3. $\Delta$ TerrC(+) $\Delta$ OceanC(-) $\Delta$ LithC(-)	11	(3)	8	(8)	2	(13)
4. $\Delta$ TerrC(-) $\Delta$ OceanC(+) $\Delta$ LithC(+)	1	(1)	1	(1)	0	(0)
5. $\Delta$ TerrC(-) $\Delta$ OceanC(+) $\Delta$ LithC(-)	5	(2)	2	(1)	1	(6)
6. $\Delta$ TerrC(-) $\Delta$ OceanC(-) $\Delta$ LithC(+)	1	(1)	0	(0)	0	(0)
7. $\Delta$ TerrC(+) $\Delta$ OceanC(+) $\Delta$ LithC(+)	2	(1)	0	(0)	0	(0)

The ENS<sub>104</sub> mean  $\Delta$ TerrC,  $\Delta$ OceanC and  $\Delta$ LithC, the signs of which are consistent with scenario 1, are reported in Table 4, alongside previous estimates from observational data- and model-based studies. From here we can see that the mean  $\Delta$ TerrC

is only aligned with a handful of estimates and no studies so far report a negative  $\Delta\text{OceanC}$ . Instead,  $\Delta\text{OceanC}$  is estimated to be positive, primarily based on carbon isotope data. The loss of hundreds of petagrams of carbon from the ocean in response to terrestrial carbon growth has, however, been previously proposed (e.g. Zimov et al., 2006). Moreover, if we assume that 90% of the atmospheric  $\text{CO}_2$  perturbation caused by the increase in terrestrial biosphere carbon reported in Table 4 gets removed by the ocean and sediments, the change in ocean carbon would be negative, even after adding the remaining carbon to be lost from the atmosphere to the ocean. We discuss what these results would likely mean for carbon isotope data in section 3.2.6.

The positive  $\Delta\text{TerrC}$  studies in Table 4 attribute the increase in terrestrial biosphere carbon to different factors: Zimov et al., 2009 and Zech et al., 2011 predict large increases in permafrost carbon while Zeng et al., 2003 ignores permafrost. Instead, the author attributes the glacial terrestrial carbon increase to the preservation rather than destruction of carbon in areas to be covered by the LGM ice sheets, lower soil respiration rates (in the active carbon pool) caused by a colder climate, as well as storage of carbon on exposed continental shelves. Here, neither the latter carbon accumulation mechanism, nor that of permafrost growth, are included. However, our model does attempt to capture the very slow rates of soil decomposition characteristic of permafrost (Williamson et al., 2006). We attribute the terrestrial carbon increase in our ensemble to a higher soil carbon inventory caused by a decreasing soil respiration rate. As can be seen from Fig. 10, vegetation carbon tends to conversely decrease at the LGM. As in Zeng (2003), we also do not assume that as the ice sheets expand over terrestrial carbon, they destroy it. The lack of this potential loss term means that our  $\Delta\text{TerrC}$  estimates may be higher than in many previous studies, irrespective of what the response of the terrestrial biosphere is to the LGM climate and  $\text{CO}_2$  forcings. Oishi and Abe-Ouchi (2011) for instance estimated that the LGM climate is responsible for the loss of 502 PgC of terrestrial carbon, while another 388 PgC is removed by the ice sheets. Zeng (2003) conversely proposed that 431 PgC is preserved under the ice sheets at the LGM. This number includes 315 PgC present during the interglacial, and another 116 PgC accumulated in response to the glacial climate forcings, prior to insulation of the terrestrial carbon from the atmosphere by the ice sheet coverage. Here, analysis of  $\text{ENS}_{16}$  suggests that during the 1000 years of LGM ice sheet build-up, the terrestrial carbon inventory in the areas to be occupied by the ice sheets increases by between 6 and 444 PgC, yielding LGM “ice-sheet or burial” carbon inventories between 318 and 1341 PgC (Table 5). This increase accounts for less than half of the total LGM change in terrestrial carbon (i.e.  $\Delta\text{TerrC}$ ) in the majority of simulations. However, if this burial carbon were to have been destroyed rather than preserved,  $\Delta\text{TerrC}$  would be negative in all but 3 simulations, as opposed to positive in all but one simulation (Table 5).

**Table 4. LGM-PI difference in terrestrial ( $-\Delta\text{TerrC}$ ), ocean ( $-\Delta\text{OceanC}$ ), and lithospheric ( $\Delta\text{LithC}$ ) carbon inventory (PgC) in this study ( $\text{ENS}_{104}$  mean, standard deviation and range) and previous studies.** CR95 = Crowley et al. (1995), AF98 = Adams and Faure (1998), Z03 = Zeng, 2003, ZI09 = Zimov et al. (2009), PR11 = Prentice et al. (2011), ZE11 = Zech et al. (2011), BR12 = Brovkin et al. (2012), C12 = Ciais et al. (2012), GL13 = Goodwin and Lauderdale (2013), OA13 = Oishi and Abe-Ouchi (2013), SA = Sarnthein et al. (2013), PE14 = Peterson et al. (2014), AL15 = Allen et al. (2015), BG15 = Brovkin and Ganopolski (2015), SK15 = Skinner et al. (2015), SS16 = Schmittner and Somes (2016), ME17 = Menviel et al. (2017), JE18 = Jeltsch-Thömmes et al., 2018.

PE14 = Peterson et al. (2014), OA13 = Oishi and Abe-Ouchi (2013), C12 = Ciais et al. (2012), Z03 = Zeng (2003), SA13 = Sarnthein et al. (2013), BG15 = Brovkin and Ganopolski (2015), PR11 = Prentice et al. (2011), SK15 = Skinner et al. (2015), SS16 = Schmittner and Somes (2016), GL13 = Goodwin and Lauderdale (2013), AL15 = Allen et al. (2015), CR95 = Crowley et al. (1995), AF98 = Adams and Faure (1998), BR12 = Brovkin et al. (2012), ZI09 = Zimov et al. (2009), ZE11 = Zech et al. (2011).

	This study	Previous studies	Ref.	Details
$\Delta$ TerrC	467.5 $\pm$ 286.5 [-51.6,1603.8]	[-1160, 530] -1500 <u>-850</u> [-694, -550] -600 -597 -511 <u>-378</u> -330  0  547  [200, 400] <1000 [730, 980] 687 654  [570, 970] 520  [510,670]	CR95	Pollen database
			AF98	Ecological data
			<u>JE18</u>	<u>Simulation with Bern3D</u>
			PR11	Simulation with LPX
			BR12	Simulation with CLIMBER-2
			OA13	Simulation with MIROC-LPJ
			PE14	Benthic foraminiferal $\delta^{13}\text{C}$ records
			<u>ME17</u>	<u>Simulation with LOVECLIM</u>
			C12	Benthic foraminiferal, ice core and terrestrial $\delta^{13}\text{C}$ records + simulation with LPJ land ecosystem model
		Z03	Simulation with a coupled atmosphere-land-ocean-carbon model	
		ZE11	Soil carbon measurements	
		ZI09	Soil carbon measurements	
$\Delta$ OceanC	-664 $\pm$ 626.9 [-3187.7, 662.4]	[730, 980] 687 654  [570, 970] 520  [510,670]	SA13	Ocean radiocarbon records
			SK15	Ocean radiocarbon records
			A15	Ocean $[\text{CO}_3^{2-}]$ reconstructions + benthic foraminiferal $\delta^{13}\text{C}$ records
			GL13	Ocean $[\text{CO}_3^{2-}]$ reconstructions
			C12	Benthic foraminiferal, ice core and terrestrial $\delta^{13}\text{C}$ records + simulation with LPJ land ecosystem model
			SS16	Simulation with MOBI 1.5 coupled to Uvic
$\Delta$ LithC	292.5 $\pm$ 373.9 [-654.9,1700.9]	n/a	n/a	n/a

Most of the terrestrial carbon increase in areas to be covered by the ice sheets in ENS<sub>16</sub> is due to soil carbon, with vegetation carbon decreasing in all but one simulation. The range of terrestrial carbon increases and the associated burial carbon amounts include Zeng (2003)'s estimates. Our LGM burial carbon estimates would also accommodate an additional 250-550 PgC (Franzen, 1994) from increased glacial peat accumulation (Zeng, 2003). No observational data-based estimates of the

LGM burial carbon inventory are available since only limited evidence exists for organic material being preserved by ice during glaciations (Franzen, 1994 and references in Weitemeyer and Buffett, and Zeng, 2007). Outside of the ice sheets, increases in the terrestrial carbon inventory in ENS<sub>16</sub> are mostly due to soil carbon, which increases in all simulations. Vegetation carbon, conversely, decreases in the majority of simulations. Our range of carbon changes outside of the ice sheet areas include the 198 PgC increase predicted by Zeng (2003) as a result of reduced soil respiration.

Although not evaluated directly, it is likely that similar ice sheet/non-ice sheet terrestrial carbon proportions than in ENS<sub>16</sub> are found in ENS<sub>104</sub> and ENS<sub>315</sub> because of the similar climate change distributions in all three instances (see earlier sections). Although not shown here, the spatial distribution of  $\Delta$ TerrC in ENS<sub>16</sub> is also similar to that of the ENS<sub>104</sub> (and ENS<sub>315</sub>) mean. The spatial distribution of  $\Delta$ TerrC in ENS<sub>104</sub> is shown in Fig. 11.

The largest increases in terrestrial carbon ( $\geq 20 \text{ kgC m}^{-2}$ ) are found in North America and Europe/western Asia, both within and south of the Laurentide and Eurasian ice sheet margins (Fig. 11). Regions with smaller but still relatively large ( $\geq 10 \text{ kgC m}^{-2}$ ) increases include the Andes and Patagonia regions, the southern tip of the African continent, eastern north Siberia and the grid cells just south of the Tibetan plateau. The largest LGM decreases in terrestrial carbon ( $\geq 10 \text{ kgC m}^{-2}$ ) conversely tend to be found in northwest North America, Beringia and the Tibetan plateau region. Other regions with relatively large ( $\geq 5 \text{ kgC m}^{-2}$ ) decreases include equatorial Africa and the deserts in central Asia. Everywhere else the LGM terrestrial carbon density increases by between 0 and  $10 \text{ kgC m}^{-2}$ . Comparison against paleoecological reconstruction studies (Crowley et al., 1995) suggests that the simulated terrestrial carbon changes within the Laurentide and Eurasian ice sheet areas are of the wrong sign, except in northwest North America, since these studies assume the complete destruction of vegetation and soils in ice sheet areas. Discrepancies between the ENS<sub>104</sub> and observations further arise from the rainforest regions, where the ensemble mean predicts terrestrial biosphere carbon density changes between  $-5$  and  $10 \text{ kgC m}^{-2}$ , well above observed changes of  $\sim -23 \text{ kgC m}^{-2}$ . It is important to note, however, that as suggested in Zeng (2007), the rate of decomposition of soil carbon at the LGM may have been slower than assumed in pollen data-based studies. The largest increases in terrestrial carbon density ( $\sim 40 \text{ kgC m}^{-2}$ ) produced by the ensemble mean are comparable to those found in areas with permafrost growth (Zimov et al., 2006). However, the peaks are potentially misplaced, being located within and south of the Laurentide and Eurasian ice sheet covered areas, rather than in eastern Siberia and Alaska. Alternatively, terrestrial carbon increases in eastern Siberia and Alaska are simply underestimated in the ensemble mean and large increases in terrestrial carbon indeed took place within the ice sheet areas during glacial periods.

The large LGM decreases in terrestrial carbon in northwest North America and adjacent Beringia are likely caused by precipitation decreasing comparatively more than SAT, and causing the decrease in photosynthesis to exceed the decrease in soil respiration. However, it is also noteworthy that, although not shown here, the regions with the largest decreases in

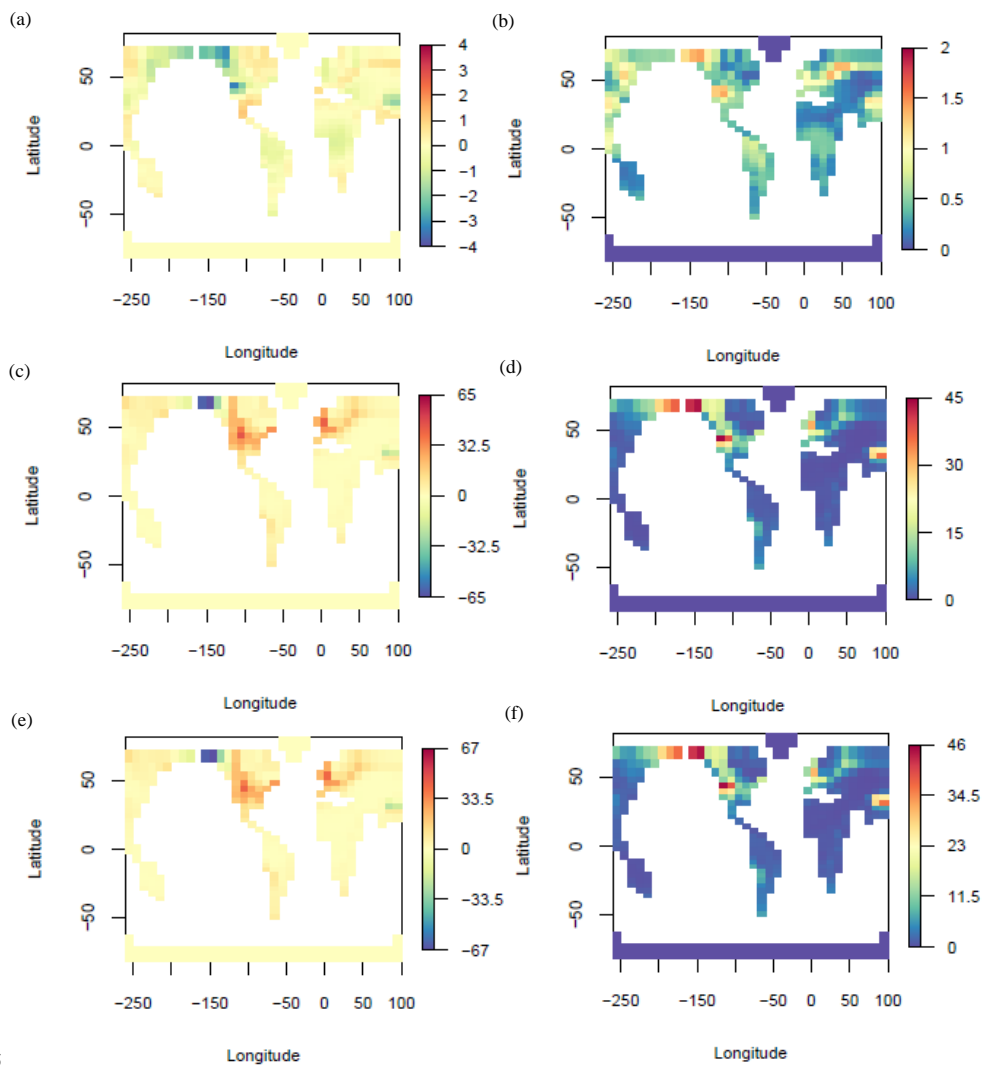
terrestrial carbon density, namely northwest North America, Beringia and the Tibetan plateau area, are also the regions with the largest terrestrial carbon densities in the preindustrial ENS<sub>315</sub> mean. We further note that the Tibetan soil carbon peak is overestimated in the latter, and the North American soil carbon peak misplaced, compared to observations. We attribute the first discrepancy to the lack of soil weathering in the model and the inclusion of land use effects in the observational data-based estimate (Holden et al., 2013b; Williamson et al., 2006). The second discrepancy is attributed to the lack of explicit representation of permafrost and the absence of moisture control on soil respiration.

**Table 5. Ice sheet and non-ice sheet terrestrial carbon stocks in ENS<sub>16</sub>.** Columns 2 and 5 show the amount of carbon stored ~~in ice sheet areas and under the ice sheets~~ in areas covered by the Eurasian and Laurentide Ice Sheets (“ice sheet”) during the preindustrial and LGM periods respectively. Column 3 is the difference between the two inventories. Column 4 is the LGM change in carbon in ice sheet areas expressed as percentage of the total LGM terrestrial carbon change. Column 6 is the LGM change in carbon outside of the ice sheets.

EM	PRE ice sheet	LGM-PRE ice sheet	% LGM-PRE Total land	LGM Burial	LGM-PRE non-ice sheet
442	456	117	51	573	111
873	896	444	29	1341	1089
511	677	262	32	939	567
99	372	33	20	405	130
871	404	149	26	553	425
786	502	131	21	633	486
107	540	86	22	626	310
701	549	161	36	710	283
801	707	275	39	982	423
219	312	6	16	318	-34
694	389	95	30	484	227
623	697	181	36	879	319
522	713	210	28	923	531
863	408	73	16	480	380
478	573	165	41	739	233
837	784	395	33	1179	796

15

20



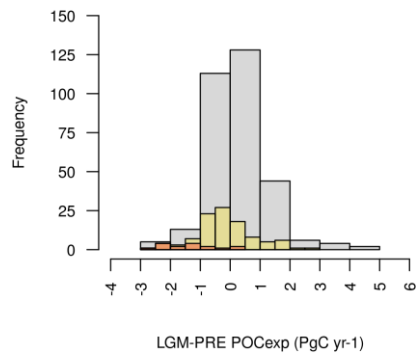
5

30

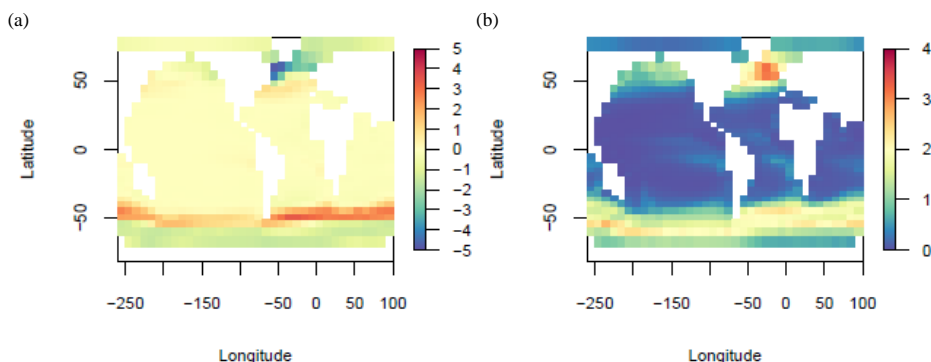
**Fig. 11. LGM vegetation (a-b), soil (c-d) and total terrestrial carbon changes (e-f) ENS<sub>104</sub> mean (left) and standard deviation (right). Units are kgC m<sup>-2</sup>.**

The ENS<sub>104</sub> mean LGM total POC export flux anomaly ( $\Delta\text{POC}_{\text{exp}}$ ) is  $-0.19 \pm 1 \text{ PgC yr}^{-1}$  and the range is -2.57 to 2.56  $\text{PgC yr}^{-1}$ , roughly consistent with previous model-based estimates (e.g. Brovkin et al., 2002; Bopp et al., 2003; Brovkin et al., 2007; Chikamoto et al., 2012; Palastanga et al., 2013; Schmittner and Some, 2016; Buchanan et al., 2016).

As shown in Fig. 12, compared to ENS<sub>104</sub>, the POC flux decreases in ENS<sub>315</sub> and ENS<sub>16</sub> tend to be smaller and larger respectively.  $\Delta\text{POC}_{\text{exp}}$  is positively correlated with  $\Delta\psi_{\text{max}}$  ( $r = 0.72$  and  $0.79$ ) and negatively correlated with  $\Delta\psi_{\text{min}}$  ( $r = -0.62$  and  $-0.58$ ) in both ENS<sub>104</sub> and ENS<sub>315</sub>. The correlations potentially suggest that decreasing AMOC strength and increasing AABW production lead to decreasing POC export. One possible mechanism is enhanced deep ocean stratification due to increasing AABW formation leading to not only more efficient trapping of DIC at depth (see above), but also nutrients and therefore reduced availability in the euphotic zone. All else held constant, a weaker and shallower AMOC cell would also inhibit the transfer of nutrients from the deep ocean to the surface. A negative correlation can additionally be found between  $\Delta\text{POC}_{\text{exp}}$  and  $\Delta\text{SIA}$  ( $r = -0.55$  and  $-0.6$ ), probably because no primary production occurs beneath the sea ice surface. Increasing sea ice area at the LGM therefore leads to decreasing POC export flux. This would also explain the largest ENS<sub>104</sub> mean decreases in POC export flux, shown in Fig. 13, coinciding with increases in sea ice fraction.



**Fig. 12. LGM change in POC export flux distributions.**



**Fig. 13. LGM surface POC export flux change ( $\text{molC m}^{-2} \text{yr}^{-1}$ ) ENS<sub>104</sub> mean (a) and standard deviation (b).**

The largest ENS<sub>104</sub> LGM *increases* in POC export flux conversely occur at around 50 °S, roughly in front of the Antarctic sea ice margins. Increases in POC export are also simulated close to the North Pacific and Atlantic sea ice margins, as well as in the eastern equatorial Pacific and the southwest Atlantic upwelling region. The increases in POC export flux at the sea

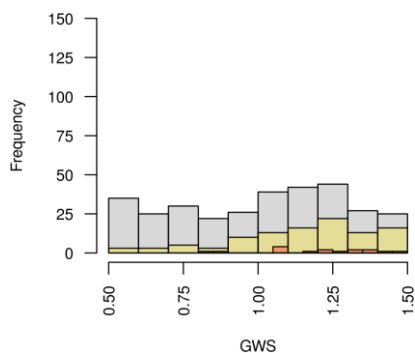
ice margins are likely caused by the advection of unutilised nutrients from underneath the sea ice. However, they may additionally be due to the enhanced iron availability from the increased supply of aeolian dust, particularly in the Southern Ocean and North Pacific since these are strongly limited by iron (Ridgwell et al., 2007). Iron fertilization may also explain the increases in POC export flux in the eastern equatorial Pacific and in the southwest Atlantic upwelling region. Comparison against observations suggests that the ensemble mean POC flux changes immediately north, and south of the Antarctic sea ice margins align with observations of increased and reduced marine productivity in the Subantarctic (~45 to 60 °N) and Southern Ocean respectively (Kohfeld et al., 2005; Kohfeld et al., 2013; Jaccard et al., 2013; Martínez-García et al., 2014). The simulated decreases in export flux in the Arctic and subarctic Atlantic (i.e. above ca. 50 °N), and the increases in export flux immediately south of 50°N are also in agreement with previous reconstructions (Kohfeld et al., 2005; Radi and de Vernal, 2008). The mostly lower LGM export fluxes at the equator and in the South Atlantic are conversely inconsistent with the observational data of Kohfeld et al., (2005). The decreases may be caused by the increases in productivity in HNLC regions reducing the phosphate (the other limiting nutrient in GENIE-1 besides iron) availability for photosynthesis in other regions. They may additionally be due to the model not simulating enhanced nutrient inventories in response to enhanced weathering or reduced shallower water deposition of organic matter. The model also does not vary wind speed which may have resulted in stronger tropical upwelling in the Atlantic at the LGM. The evidence is more ambiguous (or missing) for the



Pacific (Jaccard et al., 2010; Kohfeld and Chase, 2011; Kohfeld et al., 2005; Costa et al., 2016) and Indian Oceans (Kohfeld et al., 2005; Singh et al., 2011) and is therefore not discussed in more detail here.

### 5 3.2.4 Carbonate weathering and shallow water deposition

The ENS<sub>104</sub> mean land-to-ocean bicarbonate flux scaling factor glacial-weathering-factor (GWS) is  $1.16 \pm 0.24$  (corresponding to a percentage change in the land to ocean bicarbonate flux, %LOC, of 38.67), and the range is 0.52 to 1.5 (corresponding to a %LOC between -49.33 and 50). As shown in Fig. 14, the GWS in ENS<sub>104</sub> tends to be larger than in ENS<sub>315</sub> and smaller than in ENS<sub>16</sub>. There is also a negative correlation between GWS and  $\Delta\text{CO}_2$  ( $r = -0.52$ ) in ENS<sub>315</sub>, suggesting that increasing the input of bicarbonate to the ocean leads to a decrease in  $\text{CO}_2$  by raising the inventories of ALK and DIC in a 2:1 ratio. In ENS<sub>104</sub>, however,  $r$  is below the 0.05 significance level, suggesting that it is less important.

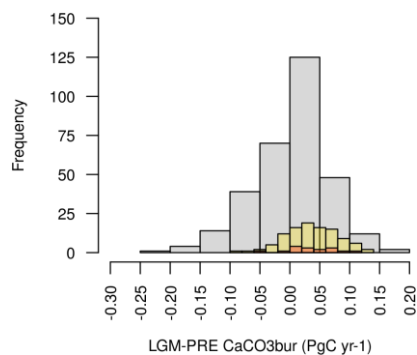


**Fig. 14. Land-to-ocean bicarbonate flux scaling factor (GWS)GWS distributions.**

### 3.2.5 Deep-sea carbonate burial

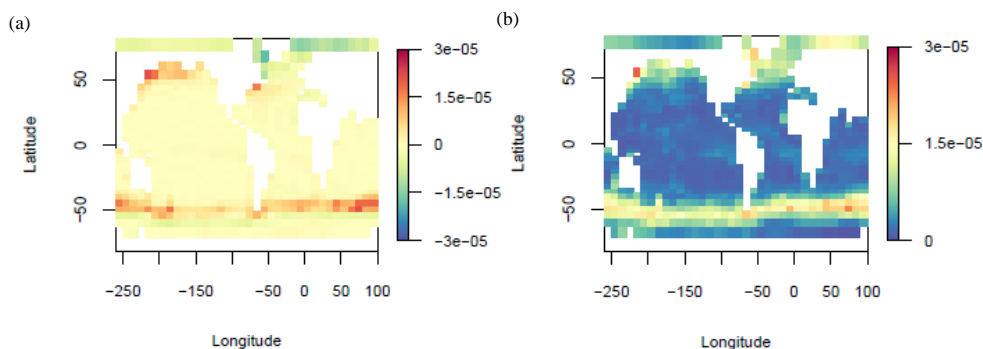
The ENS<sub>104</sub> mean global deep-sea  $\text{CaCO}_3$  burial flux anomaly ( $\Delta\text{CaCO}_{3\text{bur}}$ ) is  $0.036 \pm 0.045 \text{ PgC yr}^{-1}$  and the range is -0.098 to  $0.139 \text{ PgC yr}^{-1}$ . The mean value is ca. 3 times larger than the observed value (Catubig et al., 1998), although the latter still falls within the range of simulated values. As shown in Fig. 15,  $\Delta\text{CaCO}_{3\text{bur}}$  in ENS<sub>104</sub> tends to be higher than in ENS<sub>315</sub>, and lower than in ENS<sub>16</sub>. The change in global deep-sea  $\text{CaCO}_3$  burial flux anomaly is strongly determined by

GWS, as suggested by the positive correlation ( $r = 0.88$  and  $0.9$ ) between the two, in both  $ENS_{104}$  and  $ENS_{315}$ . Increasing %LOC (the percentage change in the land to ocean bicarbonate flux) should indeed enhance the  $CaCO_3$  burial flux as increasing ALK means the deep ocean  $CO_3^{2-}$  will eventually increase. The latter in turn would cause the saturation horizon to fall, allowing  $CaCO_3$  to accumulate over greater areas (which are now exposed to undersaturated waters) (Sigman and Boyle, 2000). The input of ALK to the surface ocean would also increase the rate of  $CaCO_3$  export production (enhancing the sediment deposition flux of  $CaCO_3$ ) since as discussed in Chikamoto et al. (2008), the latter is proportional to the production rate of POC (which is equal to the POC export flux), together with the sea surface saturation state with respect to  $CaCO_3$ , in GENIE-1. There is indeed also a positive correlation between %LOC and the global change in  $CaCO_3$  export ( $r = 0.27$  and  $0.4$ ), and between the latter and  $\Delta CaCO_{3bur}$  ( $r = 0.34$  and  $0.45$ ) in both  $ENS_{104}$  and  $ENS_{315}$ .



**Fig. 15. LGM change in deep sea sediment  $CaCO_3$  burial flux distributions.**

The  $ENS_{104}$  mean spatial distribution of  $\Delta CaCO_{3bur}$  is shown in Fig. 16. Relatively large increases in burial flux ( $\geq 0.5 \times 10^{-5} \text{ mol cm}^{-2} \text{ yr}^{-1}$ ) can be found at around  $50^\circ S$ , in the North Pacific, and to a lesser extent the North Atlantic. In other regions, the burial flux is significantly lower or negative, with the largest losses ( $\leq -0.5 \times 10^{-5} \text{ mol cm}^{-2} \text{ yr}^{-1}$ ) occurring the North Atlantic and arctic regions. The only exception is the western North Atlantic, which exhibits a large increase in burial. A comparison of the results against the reconstructions of Catubig et al., 1998 is somewhat difficult as the coverage is poor but overall  $CaCO_3$  burial was higher in the North Atlantic and the Pacific, and lower in the tropical and South Atlantic, and the Indian and Southern Ocean.



5 **Fig. 16. LGM deep sea  $\text{CaCO}_3$  burial rate change ( $\text{mol cm}^{-2} \text{yr}^{-1}$ )  $\text{ENS}_{104}$  mean (a) and standard deviation (b).**

### 3.2.6 Other paleo proxies

10 As shown in Table 4, a frequent argument for a lower glacial terrestrial carbon inventory is the reconstructed mean glacial ocean  $\delta^{13}\text{C}$  value of ca. 0.35‰ lower than present due to the fact that plants discriminate against  $^{13}\text{C}$  during photosynthesis. In our simulations conversely, it follows that the increase in glacial terrestrial carbon inventory would have resulted in an increase in ocean  $\delta^{13}\text{C}$ . Decreasing SSTs and increasing  $\text{CaCO}_3$  weathering would have, moreover, likely raised it further (in the first instance, by enhancing fractionation at the air-sea interface, and in the second instance, through the input of isotopically heavy weathering products). However, as noted in Zeng (2007), the interpretation of  $\delta^{13}\text{C}$  value can be complicated by factors such as the impact of enhanced glacial carbonate ion concentrations on  $\delta^{13}\text{C}$  in foraminera shells (Lea et al., 1999). In addition, there are other processes in our model which may have counteracted at least part of the increase in ocean  $\delta^{13}\text{C}$ . These include reduced marine productivity (e.g. Zimov et al., 2009), as phytoplankton discriminate against  $^{13}\text{C}$  during photosynthesis, giving the marine organic carbon reservoir a low  $\delta^{13}\text{C}$ . However, we note that the sign of this impact would additionally depend on the associated changes in organic matter remineralisation and burial. Another relevant process isThey also include greater sea ice area, which can lower the ocean  $\delta^{13}\text{C}$  by reducing the air-sea gas exchange, and therefore the net transfer of  $^{13}\text{C}$  into the ocean (Stephen and Keeling, 2000). We, moreover, propose that adding missing processes could have decreased ocean  $\delta^{13}\text{C}$  even further. These include weaker surface winds (while in our model these are fixed), again through reduced air-sea gas exchange (Menviel et al., 2015), as well as enhanced weathering

and reduced deposition of organic carbon at continental margins due to lower sea levels (Wallmann, 2014). Yet, further research is required here as one recent study suggests that taking into account these processes would most likely not (the possibility is not completely ruled out) allow reconciliation of a positive  $\Delta T_{err}C$  with the observed mean glacial ocean  $\delta^{13}C$  value (Jeltsch-Thommes et al., 2018). More importantly perhaps, however,

5 Missing processes would likely also be needed to reconcile our lower POC export fluxes with deep ocean oxygen records. These records tend to indicate there was a decrease in LGM deep ocean oxygen concentration (Jaccard et al., 2016). Lower POC export fluxes would conversely have resulted in an increase in deep ocean oxygen due to reduced oxygen consumption at depth. When observed over sufficiently large areas, lower oxygen concentrations can support the presence of an enhanced ocean carbon inventory as deoxygenation can be explained by reduced ocean ventilation (the sole input of oxygen is from  
10 the ocean surface) (Wagner and Hendy, 2015). The reduced ventilation is, in turn, assumed to have led to the accumulation of a significant amount of DIC in the ocean interior. Thus, explaining the lower deep ocean oxygen concentrations without having to reduce ocean ventilation as extensively as suggested by previous studies, would as a minimum likely require LGM export production to have increased rather than decreased. However, it may be possible to increase deep ocean oxygen consumption by increasing organic matter at depth but keeping the surface POC export flux constant. This would require  
15 adding missing processes such as increasing remineralisation depth with decreasing ocean temperature and increasing ballasting into our model (Kohfeld and Ridgwell, 2009; Menviel et al., 2012).

#### 4 Conclusions

We have used an uncertainty-based approach to investigating the LGM atmospheric  $CO_2$  drop by simulating it with a large  
20 ensemble of parameter sets and exploring the range of possible responses. Despite our ensemble varying many of the parameters thought to contribute to variability in glacial-interglacial atmospheric  $CO_2$ , we estimated that up to  $\sim 60$  ppmv of  $\Delta CO_2$  could be attributed to processes not included in our model and error in our process representations. As a result, we treated  $\Delta CO_2$  between  $\sim 90$  and  $-30$  ppmv as equally plausible, and focused on describing the responses of the subset of simulations  
25 with this  $\Delta CO_2$ . We found the range of responses to be large, including the presence of five different ways of achieving a plausible  $\Delta CO_2$  in terms of the sign of individual carbon reservoir changes. However, several dominant changes could be detected. Namely: the LGM atmospheric  $CO_2$  decrease tended to predominantly be associated with decreasing SSTs, increasing sea ice area, a weakening of the AMOC, a strengthening of the AABW cell in the Atlantic Ocean, a decreasing ocean biological productivity, an increasing  $CaCO_3$  weathering flux and an increasing deep-sea  $CaCO_3$  burial flux. The majority of our simulations also predicted an increase in terrestrial carbon, coupled with a decrease in ocean and an increase  
30 in lithospheric carbon. The increase in terrestrial carbon, which is uncommon in LGM simulations, was attributed to reduced soil respiration in response to the climate forcings, as well as our choice to preserve rather than destroy carbon that accumulates in ice sheet areas. The An initial comparison of these dominant changes with were broadly in agreement with observations and

paleo-proxies other than carbon isotope and oxygen data ~~suggests, which we did not evaluate directly, broad agreement.~~  
However, ~~more we advise more~~ detailed comparisons; in future studies, ~~it would be useful. We also suggest that, conceptually~~  
~~at least, it is also likely that~~ our results can only be reconciled with carbon isotope and oxygen data if ~~additional~~  
~~processes~~ ~~processes currently missing from~~ ~~not included in~~ our model are taken into account.

5

### Acknowledgements

This work made use of the Darwin Supercomputer of the University of Cambridge High Performance Computing Service (HPCS). K.M.S. Kempainen thanks staff at HPCS for their technical support, and Antara Banerjee and Alex Archibald for  
10 help with R. This manuscript was greatly improved by comments from an anonymous reviewer.

### References

- Adams, J. M. and Faure, H.: A new estimate of changing carbon storage on land since the last glacial maximum, based on  
global land ecosystem reconstruction, *Glob. Planet. Change*, 16–17, 3–24, doi:10.1016/S0921-8181(98)00003-4, 1998.
- 15 Adkins, J. F., McIntyre, K. and Schrag, D. P.: The Salinity, Temperature, and  $\delta^{18}\text{O}$  of the Glacial Deep Ocean, *Science*,  
298(November), 1769–1773, doi:10.1126/science.1076252, 2002.
- Alder, J. R. and Hostetler, S. W.: Global climate simulations at 3000-year intervals for the last 21 000 years with the GENMOM  
coupled atmosphere-ocean model, *Clim. Past*, 11(3), 449–471, doi:10.5194/cp-11-449-2015, 2015.
- Allen, K. A., Sikes, E. L., Hönisch, B., Elmore, A. C., Guilderson, T. P., Rosenthal, Y. and Anderson, R. F.: Southwest Pacific  
20 deep water carbonate chemistry linked to high southern latitude climate and atmospheric  $\text{CO}_2$  during the Last Glacial  
Termination, *Quat. Sci. Rev.*, 122, 180–191, doi:10.1016/j.quascirev.2015.05.007, 2015.
- Anderson, R. F., Ali, S., Bradtmiller, L. I., Nielsen, S. H. H., Fleisher, M. Q., Anderson, B. E. and Burckle, L. H.: Wind-  
Driven Upwelling in the Southern Ocean and the Deglacial Rise in Atmospheric  $\text{CO}_2$ , *Science*, 323(5920), 1443–1448,  
doi:10.1126/science.1167441, 2009.
- 25 Annan, J. D. and Hargreaves, J. C.: A new global reconstruction of temperature changes at the Last Glacial Maximum, *Clim.*  
*Past*, 9(1), 367–376, doi:10.5194/cp-9-367-2013, 2013. Annan, J. D. and Hargreaves, J. C.: Efficient identification of ocean  
thermodynamics in a physical/biogeochemical ocean model with an iterative Importance Sampling method, *Ocean Model.*,  
32(3–4), 205–215, doi:10.1016/j.ocemod.2010.02.003, 2010.
- Ballarotta, M., Falahat, S., Brodeau, L. and Döös, K.: On the glacial and interglacial thermohaline circulation and the associated  
30 transports of heat and freshwater, *Ocean Sci.*, 10(6), 907–921, doi:10.5194/os-10-907-2014, 2014.
- Bartlein, P. J., Harrison, S. P., Brewer, S., Connor, S., Davis, B. A. S., Gajewski, K., Guiot, J., Harrison-Prentice, T. I.,  
Henderson, A., Peyron, O., Prentice, I. C., Scholze, M., Seppä, H., Shuman, B., Sugita, S., Thompson, R. S., Viau, A. E.,  
Williams, J. and Wu, H.: Pollen-based continental climate reconstructions at 6 and 21 ka: A global synthesis, *Clim. Dyn.*,  
37(3), 775–802, doi:10.1007/s00382-010-0904-1, 2011.

- Berger, A.: Long-term variations of daily insolation and quaternary climatic changes, *J. Atmos. Sci.* 35(12), 2362–2367, 1978.
- Böhm, E., Lippold, J., Gutjahr, M., Frank, M., Blaser, P., Antz, B., Fohlmeister, J., Frank, N., Andersen, M. B. and Deininger, M.: Strong and deep Atlantic meridional overturning circulation during the last glacial cycle, *Nature*, 517(7534), 73–76, doi:10.1038/nature14059, 2015.
- 5 Bopp, L., Kohfeld, K. E., Le Quéré, C. and Aumont, O.: Dust impact on marine biota and atmospheric CO<sub>2</sub> during glacial periods, *Paleoceanography*, 18(2), 1046, doi:10.1029/2002PA000810, doi:10.1029/2002PA000810, 2003.
- Bouttes, N., Paillard, D. and Roche, D. M.: Impact of brine-induced stratification on the glacial carbon cycle, *Clim. Past*, 6(5), 575–589, doi:10.5194/cp-6-575-2010, 2010.
- Bouttes, N., Paillard, D., Roche, D. M., Brovkin, V. and Bopp, L.: Last Glacial Maximum CO<sub>2</sub> and δ<sup>13</sup>C successfully  
 10 reconciled, *Geophys. Res. Lett.*, 38(2), Citation No. L02705, doi:10.1029/2010gl044499, 2011.
- Brovkin, V. and Ganopolski, A.: The role of the terrestrial biosphere in CLIMBER-2 simulations of the last glacial CO<sub>2</sub> cycles. *Nova Acta Lc NF*, 121, 43-47, 2015.
- Brovkin, V., Hofmann, M., Bendtsen, J. and Ganopolski, A.: Ocean biology could control atmospheric delta C-13 during glacial-interglacial cycle, *Geochemistry Geophys. Geosystems*, 3, 22, doi:10.1029/2001gc000270, 2002.
- 15 Brovkin, V., Ganopolski, A., Archer, D. and Rahmstorf, S.: Lowering of glacial atmospheric CO<sub>2</sub> in response to changes on oceanic circulation and marine biogeochemistry, *Paleoceanography*, 22(4), doi:10.1029/2006PA001380, 2007.
- Brovkin, V., Ganopolski, A., Archer, D. and Munhoven, G.: Glacial CO<sub>2</sub> cycle as a succession of key physical and biogeochemical processes, *Clim. Past*, 8(1), 251–264, doi:10.5194/cp-8-251-2012, 2012.
- Buchanan, P. J., Matear, R. J., Lenton, A., Phipps, S. J., Chase, Z. and Etheridge, D.: The simulated climate of the Last Glacial  
 20 Maximum and insights into the global carbon cycle, *Clim. Past Discuss.*, 11(2), 1–45, doi:10.5194/cp-2016-73, 2016.
- Catubig, N. R., Archer, D. E., Francois, R., DeMenocal, P., Howard, W. and Yu, E. F.: Global deep-sea burial rate of calcium carbonate during the Last Glacial Maximum, *Paleoceanography*, 13(3), 298–310, doi:10.1029/98PA00609, 1998.
- Chikamoto, M. O., Matsumoto, K. and Ridgwell, A.: Response of deep-sea CaCO<sub>3</sub> sedimentation to Atlantic meridional overturning circulation shutdown, *J. Geophys. Res. Biogeosciences*, 113(3), doi:10.1029/2007JG000669, 2008.
- 25 Chikamoto, M. O., Abe-Ouchi, A., Oka, A., Ohgaito, R. and Timmermann, A.: Quantifying the ocean's role in glacial CO<sub>2</sub> reductions, *Clim. Past*, 8(2), 545–563, doi:10.5194/cp-8-545-2012, 2012.
- Ciais, P., Tagliabue, A., Cuntz, M., Bopp, L., Scholze, M., Hoffmann, G., Lourdou, A., Harrison, S. P., Prentice, I. C., Kelley, D. I., Koven, C. and Piao, S. L.: Large inert carbon pool in the terrestrial biosphere during the Last Glacial Maximum, *Nat. Geosci.*, 5(1), 74–79, doi:10.1038/ngeo1324, 2012.
- 30 Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., Jones, C., Quéré, C. Le, Myneni, R. B., Piao, S. and Thornton, P.: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change, *Chang. IPCC Clim.*, 465–570, doi:10.1017/CBO9781107415324.015, 2013.

- Colbourn, G.: Weathering effects on the carbon cycle in an Earth System Model, Ph.D. thesis, School of Environmental Sciences, University of East Anglia, United Kingdom, 2011.
- Costa, K. M., McManus, J. F., Anderson, R. F., Ren, H., Sigman, D. M., Winckler, G., Fleisher, M. Q., Marcantonio, F. and Ravelo, A. C.: No iron fertilization in the equatorial Pacific Ocean during the last ice age, *Nature*, 529(7587), 519–522, doi:10.1038/nature16453, 2016.
- 5 Crocket, K.C., Vance, D., Foster, G.L., Richards, D.A. and Tranter, M.: Continental weathering fluxes during the last glacial/interglacial cycle: insights from the marine sedimentary Pb isotope record at Orphan Knoll, NW Atlantic, *Quaternary Sci Rev* 38: 89–99. Doi: 10.1016/j.quascirev.2012.02.004, 2012.
- Crowley, T. J.: Ice Age terrestrial carbon changes revisited, *Global Biogeochem. Cycles*, 9(3), 377–389, doi:10.1029/95GB01107, 1995.
- 10 De La Fuente, M., Skinner, L., Calvo, E., Pelejero, C. and Cacho, I.: Increased reservoir ages and poorly ventilated deep waters inferred in the glacial Eastern Equatorial Pacific, *Nat. Commun.*, 6, doi:10.1038/ncomms8420, 2015.
- Doney, S. C., Lindsay, K., Fung, I. and John, J.: Natural variability in a stable, 1000-yr global coupled climate-carbon cycle simulation, *J. Clim.*, 19(13), 3033–3054, doi:10.1175/JCLI3783.1, 2006.
- 15 Durand, N., Deschamps, P., Bard, E., Hamelin, B., Camoin, G., Thomas, A. L., Henderson, G. M., Yokoyama, Y. and Matsuzaki, H.: Comparison of <sup>14</sup>C and U-Th Ages in Corals from IODP #310 Cores Offshore Tahiti, *Radiocarbon*, 55(4), 1947–1974, doi:10.2458/azu\_js\_rc.v55i2.16134, 2013.
- Edwards, N. R. and Marsh, R.: Uncertainties due to transport-parameter sensitivity in an efficient 3-D ocean-climate model, *Clim. Dyn.*, 24(4), 415–433, doi:10.1007/s00382-004-0508-8, 2005.
- 20 Ferrari, R., Jansen, M. F., Adkins, J. F., Burke, A., Stewart, A. L. and Thompson, A. F.: Antarctic sea ice control on ocean circulation in present and glacial climates, *Proc. Natl. Acad. Sci.*, 111(24), 8753–8758, doi:10.1073/pnas.1323922111, 2014.
- Foster, G. L. and Vance, D.: Negligible glacial-interglacial variation in continental chemical weathering rates, *Nature*, 444(7121), 918–921, doi:10.1038/nature05365, 2006.
- Franzen, L. G.: Are wetlands the key to the ice-age cycle enigma, *Ambio*, 23(4), 300–308, 1994.
- 25 Franzén, L.G. and Cropp, R.A.: The Peatland/ice age Hypothesis revised, adding a possible glacial pulse trigger. *Geogr. Ann.*, 89 A (4): 301–330, 2007.
- Freeman, E., Skinner, L. C., Tisserand, A., Dokken, T., Timmermann, A., Menviel, L. and Friedrich, T.: An Atlantic-Pacific ventilation seesaw across the last deglaciation, *Earth Planet. Sci. Lett.*, 424, 237–244, doi:10.1016/j.epsl.2015.05.032, 2015.
- Gebbie, G.: How much did Glacial North Atlantic Water shoal?, *Paleoceanography*, 29(3), 190–209, doi:10.1002/2013PA002557, 2014.
- 30 Goodwin, P. and Lauderdale, J. M.: Carbonate ion concentrations, ocean carbon storage, and atmospheric CO<sub>2</sub>, *Global Biogeochem. Cycles*, 27(3), 882–893, doi:10.1002/gbc.20078, 2013.
- Hain, M. P., Sigman, D. M. and Haug, G. H.: Shortcomings of the isolated abyssal reservoir model for deglacial radiocarbon changes in the mid-depth Indo-Pacific Ocean, *Geophys. Res. Lett.*, 38(4), doi:10.1029/2010GL046158, 2011.

- Harrison, K. G.: Role of increased marine silica input on paleo-pCO<sub>2</sub> levels, *Paleoceanography*, 15(3), 292–298, doi:10.1029/1999PA000427, 2000.
- Holden, P. B., Edwards, N. R., Oliver, K. I. C., Lenton, T. M. and Wilkinson, R. D.: A probabilistic calibration of climate sensitivity and terrestrial carbon change in GENIE-1, *Clim. Dyn.*, 35(5), 785–806, doi:10.1007/s00382-009-0630-8, 2010a.
- 5 Holden, P. B., Edwards, N. R., Wolff, E. W., Lang, N. J., Singarayer, J. S., Valdes, P. J. and Stocker, T. F.: Interhemispheric coupling, the West Antarctic Ice Sheet and warm Antarctic interglacials, *Clim. Past*, 6(4), 431–443, doi:10.5194/cp-6-431-2010, 2010b.
- Holden, P. B., Edwards, N. R., Müller, S. A., Oliver, K. I. C., Death, R. M. and Ridgwell, A.: Controls on the spatial distribution of oceanic  $\delta^{13}\text{C}_{\text{DIC}}$ , *Biogeosciences*, 10(3), 1815–1833, doi:10.5194/bg-10-1815-2013, 2013a.
- 10 Holden, P. B., Edwards, N. R., Gerten, D. and Schaphoff, S.: A model-based constraint on CO<sub>2</sub> fertilisation, *Biogeosciences*, 10(1), 339–355, doi:10.5194/bg-10-339-2013, 2013b.
- Houghton, J. T., Jenkins, G. J., Ephraums, J. J.: *Climate Change. The IPCC Scientific Assessment*. Cambridge University Press, Cambridge, 1990.
- Iglesias-Rodríguez, M. D., Brown, C. W., Doney, S. C., Kleypas, J., Kolber, D., Kolber, Z., Hayes, P. K. and Falkowski, P. G.: Representing key phytoplankton functional groups in ocean carbon cycle models: Coccolithophorids, *Global Biogeochem. Cycles*, 16(4), 47-1-47–20, doi:10.1029/2001GB001454, 2002.
- 15 Jaccard, S. L., Galbraith, E. D., Sigman, D. M. and Haug, G. H.: A pervasive link between Antarctic ice core and subarctic Pacific sediment records over the past 800 kyrs, *Quat. Sci. Rev.*, 29(1–2), 206–212, doi:10.1016/j.quascirev.2009.10.007, 2010.
- 20 Jaccard, S. L., Hayes, C. T., Martínez-García, A., Hodell, D. A., Anderson, R. F., Sigman, D. M. and Haug, G. H.: Two Modes of Change in Southern Ocean Productivity Over the Past Million Years, *Science*, 339(6126), 1419–1423, doi:10.1126/science.1227545, 2013.
- Jaccard, S. L., Galbraith, E. D., Martínez-García, A. and Anderson, R. F.: Covariation of deep Southern Ocean oxygenation and atmospheric CO<sub>2</sub> through the last ice age, *Nature*, 530(7589), 207–210, doi:10.1038/nature16514, 2016.
- 25 [Jeltsch-Thömmes, A., Battaglia, G., Cartapanis, O., Jaccard, S. L. and Joos, F.: A large increase in the carbon inventory of the land biosphere since the Last Glacial Maximum: constraints from multi-proxy data, \*Clim. Past Discuss.\*, doi: 10.5194/cp-2018-167, in review, 2018.](#)
- Jones, I. W., Munhoven, G., Tranter, M., Huybrechts, P. and Sharp, M. J.: Modelled glacial and non-glacial HCO<sub>3</sub><sup>-</sup>, Si and Ge fluxes since the LGM: Little potential for impact on atmospheric CO<sub>2</sub> concentrations and a potential proxy of continental chemical erosion, the marine Ge/Si ratio, *Glob. Planet. Change*, 33(1–2), 139–153, doi:10.1016/S0921-8181(02)00067-X, 2002.
- 30 Joos, F., Gerber, S., Prentice, I. C., Otto-Bliesner, B. L. and Valdes, P. J.: Transient simulations of Holocene atmospheric carbon dioxide and terrestrial carbon since the Last Glacial Maximum, *Global Biogeochem. Cycles*, 18(2), doi:10.1029/2003GB002156, 2004.

Formatted: Irish



- Kim, S.-J., Flato, G. and Boer, G.: A coupled climate model simulation of the Last Glacial Maximum, Part 2: approach to equilibrium, *Clim. Dyn.*, 20(6), 635–661, doi:10.1007/s00382-002-0292-2, 2003.
- Kleyvas, J. A.: Modeled estimates of global reef habitat and carbonate production since the last glacial maximum, *Paleoceanography*, 12(4), 533–545, doi:10.1029/97PA01134, 1997.
- 5 Kohfeld, K. E.: Role of Marine Biology in Glacial-Interglacial CO<sub>2</sub> Cycles, *Science*, 308(5718), 74–78, doi:10.1126/science.1105375, 2005.
- Kohfeld, K. E. and Chase, Z.: Controls on deglacial changes in biogenic fluxes in the North Pacific Ocean, *Quat. Sci. Rev.*, 30(23–24), 3350–3363, doi:10.1016/j.quascirev.2011.08.007, 2011.
- Kohfeld, K. E. and Ridgwell, A.: Glacial-Interglacial Variability in Atmospheric CO<sub>2</sub>, *Surf. Ocean. Atmos. Process.*, 251–286, doi:10.1029/2008GM000845, 2009.
- 10 Kohfeld, K. E., Graham, R. M., de Boer, A. M., Sime, L. C., Wolff, E. W., Le Quéré, C. and Bopp, L.: Southern Hemisphere westerly wind changes during the Last Glacial Maximum: Paleo-data synthesis, *Quat. Sci. Rev.*, 68, 76–95, doi:10.1016/j.quascirev.2013.01.017, 2013.
- Lambert, F., Tagliabue, A., Shaffer, G., Lamy, F., Winckler, G., Farias, L., Gallardo, L. and De Pol-Holz, R.: Dust fluxes and iron fertilization in Holocene and Last Glacial Maximum climates, *Geophys. Res. Lett.*, 42(14), 6014–6023, doi:10.1002/2015GL064250, 2015.
- 15 Lea, D. W., Bijma, J., Spero, H. J. and Archer, D.: Implications of a Carbonate Ion Effect on Shell Carbon and Oxygen Isotopes for Glacial Ocean Conditions, *Use Proxies Paleoceanogr. Examples from South Atl.*, 513–522, 1999.
- Lenton, T. M., Williamson, M. S., Edwards, N. R., Marsh, R., Price, A. R., Ridgwell, A. J., Shepherd, J. G. and Cox, S. J.: 20 Millennial timescale carbon cycle and climate change in an efficient Earth system model, *Clim. Dyn.*, 26(7–8), 687–711, doi:10.1007/s00382-006-0109-9, 2006.
- Lenton, T. M., Marsh, R., Price, A. R., Lunt, D. J., Aksenov, Y., Annan, J. D., Cooper-Chadwick, T., Cox, S. J., Edwards, N. R., Goswami, S., Hargreaves, J. C., Harris, P. P., Jiao, Z., Livina, V. N., Payne, A. J., Rutt, I. C., Shepherd, J. G., Valdes, P. J., Williams, G., Williamson, M. S. and Yool, A.: Effects of atmospheric dynamics and ocean resolution on bi-stability of the 25 thermohaline circulation examined using the Grid ENabled Integrated Earth system modelling (GENIE) framework, *Clim. Dyn.*, 29(6), 591–613, doi:10.1007/s00382-007-0254-9, 2007.
- Lippold, J., Luo, Y., Francois, R., Allen, S. E., Gherardi, J., Pichat, S., Hickey, B. and Schulz, H.: Strength and geometry of the glacial Atlantic Meridional Overturning Circulation, *Nat. Geosci.*, 5(11), 813–816, doi:10.1038/ngeo1608, 2012.
- Lupker, M., France-Lanord, C., Galy, V., Lavé, J. and Kudrass, H.: Increasing chemical weathering in the Himalayan system 30 since the Last Glacial Maximum, *Earth Planet. Sci. Lett.*, 365, 243–252, doi:10.1016/j.epsl.2013.01.038, 2013.
- Lynch-Stieglitz, J., Adkins, J. F., Curry, W. B., Dokken, T., Hall, I. R., Herguera, J. C., Hirschi, J. J.-M., Ivanova, E. V., Kissel, C., Marchal, O., Marchitto, T. M., McCave, I. N., McManus, J. F., Mulitza, S., Ninnemann, U., Peeters, F., Yu, E.-F. and Zahn, R.: Atlantic meridional overturning circulation during the Last Glacial Maximum., *Science*, 316(5821), 66–69, doi:10.1126/science.1137127, 2007.

- Ma, W. and Tian, J.: Modeling the contribution of dissolved organic carbon to carbon sequestration during the last glacial maximum, *Geo-Marine Lett.*, 34(5), doi:10.1007/s00367-014-0378-y, 2014.
- Mahowald, N. M., Muhs, D. R., Levis, S., Rasch, P. J., Yoshioka, M., Zender, C. S. and Luo, C.: Change in atmospheric mineral aerosols in response to climate: Last glacial period, preindustrial, modern, and doubled carbon dioxide climates, *J. Geophys. Res. Atmos.*, 111(10), doi:10.1029/2005JD006653, 2006.
- 5 Marsh, R., Muller, S. A., Yool, A., and Edwards, N. R.: Incorporation of the C-GOLDSTEIN efficient climate model into the GENIE framework: “eb go gs” configurations of GENIE, *Geosci. Model Dev.*, 4, 957–992, doi:10.5194/gmd-4-957-2011, 2011.
- Martin, P., Archer, D. and Lea, D. W.: Role of deep sea temperature in the carbon cycle during the last glacial, *Paleoceanography*, 20(2), 1–10, doi:10.1029/2003PA000914, 2005.
- 10 Martinez-Garcia, A., Sigman, D. M., Ren, H., Anderson, R. F., Straub, M., Hodell, D. A., Jaccard, S. L., Eglinton, T. I. and Haug, G. H.: Iron Fertilization of the Subantarctic Ocean During the Last Ice Age, *Science*, 343(6177), 1347–1350, doi:10.1126/science.1246848, 2014.
- Masson-Delmotte, V., Kageyama, M., Braconnot, P., Charbit, S., Krinner, G., Ritz, C., Guilyardi, E., Jouzel, J., Abe-Ouchi, A., Crucifix, M., Gladstone, R. M., Hewitt, C. D., Kitoh, A., LeGrande, A. N., Marti, O., Merkel, U., Motoi, T., Ohgaito, R., Otto-Bliesner, B., Peltier, W. R., Ross, I., Valdes, P. J., Vettoretti, G., Weber, S. L., Wolk, F. and Yu, Y.: Past and future polar amplification of climate change: Climate model intercomparisons and ice-core constraints, *Clim. Dyn.*, 26(5), 513–529, doi:10.1007/s00382-005-0081-9, 2006.
- 15 Matsumoto, K., Sarmiento, J. L. and Brzezinski, M. A.: Silicic acid leakage from the Southern Ocean: A possible explanation for glacial atmospheric  $p\text{CO}_2$ , *Global Biogeochem. Cycles*, 16(3), 5-1-5–23, doi:10.1029/2001GB001442, 2002.
- Matsumoto, K., Hashioka, T. and Yamanaka, Y.: Effect of temperature-dependent organic carbon decay on atmospheric  $p\text{CO}_2$ , *J. Geophys. Res. Biogeosciences*, 112(2), doi:10.1029/2006JG000187, 2007.
- Matsumoto, K., Tokos, K., Huston, A. and Joy-Warren, H.: MESMO 2: A mechanistic marine silica cycle and coupling to a simple terrestrial scheme, *Geosci. Model Dev.*, 6(2), 477–494, doi:10.5194/gmd-6-477-2013, 2013.
- 25 Matsumoto, K., Chase, Z. and Kohfeld, K.: Different mechanisms of silicic acid leakage and their biogeochemical consequences, *Paleoceanography*, 29(3), 238–254, doi:10.1002/2013PA002588, 2014.
- Menviel, L., Joos, F. and Ritz, S. P.: Simulating atmospheric  $\text{CO}_2$ ,  $13\text{C}$  and the marine carbon cycle during the Last Glacial-Interglacial cycle: Possible role for a deepening of the mean remineralization depth and an increase in the oceanic nutrient inventory, *Quat. Sci. Rev.*, 56, 46–68, doi:10.1016/j.quascirev.2012.09.012, 2012.
- 30 Menviel, L., Mouchet, A., Meissner, K. J., Joos, F. and England, M. H.: Impact of oceanic circulation changes on atmospheric  $\delta^{13}\text{CO}_2$ , *Global Biogeochem. Cycles*, 29(11), 1944–1961, doi:10.1002/2015GB005207, 2015.
- [Menviel, L., Yu, J., Joos, F., Mouchet, A., Meissner, K.J., and England, M.H.: Poorly ventilated deep ocean at the Last Glacial Maximum inferred from carbon isotopes: A data-model comparison study, \*Paleoceanography\*, 32, 2-17, doi: 10.1002/2016PA003024.](https://doi.org/10.1002/2016PA003024)

- Muglia, J. and Schmittner, A.: Glacial Atlantic overturning increased by wind stress in climate models, *Geophys. Res. Lett.*, 42(22), 9862–9869, doi:10.1002/2015GL064583, 2015.
- Munhoven, G.: Glacial - Interglacial changes of continental weathering: Estimates of the related CO<sub>2</sub> and HCO<sub>3</sub><sup>-</sup> flux variations and their uncertainties, *Glob. Planet. Change*, 33(1–2), 155–176, doi:10.1016/S0921-8181(02)00068-1, 2002.
- 5 O’Ishi, R. and Abe-Ouchi, A.: Influence of dynamic vegetation on climate change and terrestrial carbon storage in the Last Glacial Maximum, *Clim. Past*, 9(4), 1571–1587, doi:10.5194/cp-9-1571-2013, 2013.
- Oka, A., Abe-Ouchi, A., Chikamoto, M. O. and Ide, T.: Mechanisms controlling export production at the LGM: Effects of changes in oceanic physical fields and atmospheric dust deposition, *Global Biogeochem. Cycles*, 25, doi:10.1029/2009GB003628, 2011.
- 10 Opdyke, B. N. and Walker, J. C. G.: Return of the coral reef hypothesis: basin to shelf partitioning of CaCO<sub>3</sub> and its effect on atmospheric CO<sub>2</sub>, *Geology*, 20(8), 733–736, doi:10.1130/0091-7613(1992)020<0733:ROTCRH>2.3.CO;2, 1992.
- Oppo, D. W., Curry, W. B. and McManus, J. F.: What do benthic δ<sup>13</sup>C and δ<sup>18</sup>O data tell us about Atlantic circulation during Heinrich Stadial 1?, *Paleoceanography*, 30(4), 353–368, doi:10.1002/2014PA002667, 2015.
- Otto, D., Rasse, D., Kaplan, J., Warnant, P. and François, L.: Biospheric carbon stocks reconstructed at the Last Glacial Maximum: Comparison between general circulation models using prescribed and computed sea surface temperatures, *Glob. Planet. Change*, 33(1–2), 117–138, doi:10.1016/S0921-8181(02)00066-8, 2002.
- 15 Palastanga, V., Slomp, C. P. and Heinze, C.: Glacial-interglacial variability in ocean oxygen and phosphorus in a global biogeochemical model, *Biogeosciences*, 10(2), 945–958, doi:10.5194/bg-10-945-2013, 2013.
- Peltier, W. R.: Ice age paleotopography., *Science*, 265(5169), 195–201, doi:10.1126/science.265.5169.195, 1994.
- 20 Peterson, C. D., Lisiecki, L. E. and Stern, J. V.: Deglacial whole-ocean δ<sup>13</sup>C change estimated from 480 benthic foraminiferal records, *Paleoceanography*, 29(6), 549–563, doi:10.1002/2013PA002552, 2014.
- Prentice, I., Farquhar, G. and Fasham, M.: The carbon cycle and atmospheric carbon dioxide, *Clim. Chang. 2001 Sci. Basis*, 183–237, doi:10.1256/004316502320517344, 2001.
- Prentice, I., Harrison, S. and Bartlein, P.: Global vegetation and terrestrial carbon cycle changes after the last ice age, *New Phytol.*, 189(4), 988–998, doi:10.1111/j.1469-8137.2010.03620.x, 2011.
- 25 Radi, T. and de Vernal, A.: Last glacial maximum (LGM) primary productivity in the northern North Atlantic Ocean, *Can. J. Earth Sci.*, 45, 1299–1316, doi:10.1139/E08-059, 2008.
- Ridgwell, A. and Hargreaves, J. C.: Regulation of atmospheric CO<sub>2</sub> by deep-sea sediments in an Earth system model, *Global Biogeochem. Cycles*, 21(2), doi:10.1029/2006GB002764, 2007.
- 30 Ridgwell, A., Hargreaves, J. C., Edwards, N. R., Annan, J. D., Lenton, T. M., Marsh, R., Yool, A. and Watson, A.: Marine geochemical data assimilation in an efficient Earth System Model of global biogeochemical cycling, *Biogeosciences*, 4(4), 87–104, doi:10.5194/bg-4-87-2007, 2007.
- Roth, R., Ritz, S. P. and Joos, F.: Burial-nutrient feedbacks amplify the sensitivity of atmospheric carbon dioxide to changes in organic matter remineralisation, *Earth Syst. Dyn.*, 5(2), 321–343, doi:10.5194/esd-5-321-2014, 2014.

- Sarnthein, M., Schneider, B. and Grootes, P. M.: Peak glacial  $^{14}\text{C}$  ventilation ages suggest major draw-down of carbon into the abyssal ocean, *Clim. Past*, 9(6), 2595–2614, doi:10.5194/cp-9-2595-2013, 2013.
- Schmittner, A. and Somes, C. J.: Complementary constraints from carbon ( $^{13}\text{C}$ ) and nitrogen ( $^{15}\text{N}$ ) isotopes on the glacial ocean's soft-tissue biological pump, *Paleoceanography*, 31(6), 669–693, doi:10.1002/2015PA002905, 2016.
- 5 Schmittner, A., Urban, N. M., Shakun, J. D., Mahowald, N. M., Clark, P. U., Bartlein, P. J., Mix, A. C. and Rosell-Mele, A.: Climate Sensitivity Estimated from Temperature Reconstructions of the Last Glacial Maximum, *Science* (80-. ), 334(6061), 1385–1388, doi:10.1126/science.1203513, 2011.
- Shin, S.-I., Liu, Z., Otto-Bliesner, B., Brady, E., Kutzbach, J. and Harrison, S.: A Simulation of the Last Glacial Maximum climate using the NCAR-CCSM, *Clim. Dyn.*, 20(2), 127–151, doi:10.1007/s00382-002-0260-x, 2003.
- 10 Sigman, D. M. and Boyle, E. A.: Glacial/Interglacial Variations In Atmospheric Carbon Dioxide, *Nature*, 407(6806), 859–869, doi:10.1038/35038000, 2000.
- Simmons, C. T., Mysak, L. A., and Matthews, H. D.: An investigation of carbon cycle dynamics since the Last Glacial Maximum: Complex interactions between the terrestrial biosphere, weathering, ocean alkalinity, and  $\text{CO}_2$  radiative warming in an Earth system model of intermediate complexity, *Clim. Past Discuss.*, doi:10.5194/cp-2016-24, in review, 2016.
- 15 Singh, A. D., Jung, S. J. A., Darling, K., Ganeshram, R., Ivanochko, T. and Kroon, D.: Productivity collapses in the Arabian Sea during glacial cold phases, *Paleoceanography*, 26(3), doi:10.1029/2009PA001923, 2011.
- Skinner, L. C., Fallon, S., Waelbroeck, C., Michel, E. and Barker, S.: Ventilation of the Deep Southern Ocean and Deglacial  $\text{CO}_2$  Rise, *Science* (80-. ), 328(5982), 1147–1151, doi:10.1126/science.1183627, 2010.
- Skinner, L. C., Waelbroeck, C., Scrivner, A. E. and Fallon, S. J.: Radiocarbon evidence for alternating northern and southern  
20 sources of ventilation of the deep Atlantic carbon pool during the last deglaciation, *Proc. Natl. Acad. Sci.*, 111(15), 5480–5484, doi:10.1073/pnas.1400668111, 2014.
- Skinner, L., McCave, I. N., Carter, L., Fallon, S., Scrivner, A. E. and Primeau, F.: Reduced ventilation and enhanced magnitude of the deep Pacific carbon pool during the last glacial period, *Earth Planet. Sci. Lett.*, 411, 45–52, doi:10.1016/j.epsl.2014.11.024, 2015.
- 25 Stephens, B. B. and Keeling, R. F.: The influence of antarctic sea ice on glacial-interglacial  $\text{CO}_2$  variations, *Nature*, 404(6774), 171–174, doi:10.1038/35004556, 2000.
- Sun, X. and Matsumoto, K.: Effects of sea ice on atmospheric  $\text{pCO}_2$ : A revised view and implications for glacial and future climates, *J. Geophys. Res.*, 115(G2), 1–8, doi:10.1029/2009JG001023, 2010.
- Tamburini, F. and Föllmi, K. B.: Phosphorus burial in the ocean over glacial-interglacial time scales, *Biogeosciences*, 6(4),  
30 501–513, doi:10.5194/bg-6-501-2009, 2009.
- Tiedemann, R., Ronge, T., Lamy, F., Köhler, P., Frische, M., De Pol Holz, R., Pahnke, K., Alloway, B. V., Wacker, L. and Southon, J.: New Constraints on the Glacial Extent of the Pacific Carbon Pool and its Deglacial Outgassing, *Nova Acta Lc*, 121 (408), 229–233, 2015.

- Toggweiler, J. R., Russell, J. L. and Carson, S. R.: Midlatitude westerlies, atmospheric CO<sub>2</sub>, and climate change during the ice ages, *Paleoceanography*, 21(2), doi:10.1029/2005PA001154, 2006.
- Tréguer, P. and Pondaven, P.: Global change: Silica control of carbon dioxide, *Nature*, 486, 358–359, 2000.
- Vance, D., Teagle, D. A. H. and Foster, G. L.: Variable Quaternary chemical weathering fluxes and imbalances in marine geochemical budgets, *Nature*, 458(7237), 493–496, doi:10.1038/nature07828, 2009.
- Völker, C. and Köhler, P.: Responses of ocean circulation and carbon cycle to changes in the position of the Southern Hemisphere westerlies at Last Glacial Maximum, *Paleoceanography*, 28(4), 726–739, doi:10.1002/2013PA002556, 2013.
- Waelbroeck, C., Paul, A., Kucera, M., Rosell-Melé, A., Weinelt, M., Schneider, R., Mix, A. C., Abelmann, A., Armand, L., Bard, E., Barker, S., Barrows, T. T., Benway, H., Cacho, I., Chen, M. T., Cortijo, E., Crosta, X., De Vernal, A., Dokken, T., Duprat, J., Elderfield, H., Eynaud, F., Gersonde, R., Hayes, A., Henry, M., Hillaire-Marcel, C., Huang, C. C., Jansen, E., Juggins, S., Kallel, N., Kiefer, T., Kienast, M., Labeyrie, L., Leclaire, H., Londeix, L., Mangin, S., Matthiessen, J., Marret, F., Meland, M., Morey, A. E., Mulitza, S., Pflaumann, U., Pisias, N. G., Radi, T., Rochon, A., Rohling, E. J., Saffi, L., Schäfer-Neth, C., Solignac, S., Spero, H., Tachikawa, K. and Turon, J. L.: Constraints on the magnitude and patterns of ocean cooling at the Last Glacial Maximum, *Nat. Geosci.*, 2(2), 127–132, doi:10.1038/ngeo411, 2009.
- Wagner, M. and Hendy, I. L.: Trace metal evidence for a poorly ventilated glacial Southern Ocean, *Clim. Past Discuss.*, <https://doi.org/10.5194/cpd-11-637-2015>, 2015.
- Wallmann, K.: Is late Quaternary climate change governed by self-sustained oscillations in atmospheric CO<sub>2</sub>?, *Geochim. Cosmochim. Acta*, 132, 413–439, doi:10.1016/j.gca.2013.10.046, 2014.
- Wallmann, A.: Effects of Eustatic Sea-Level Change on Atmospheric CO<sub>2</sub> and Glacial Climate. *Nova Acta Lc NF*, 121, 241–245, 2015.
- Watson, A. J. and Naveira Garabato, A. C.: The role of Southern Ocean mixing and upwelling in glacial-interglacial atmospheric CO<sub>2</sub> change, *Tellus, Ser. B Chem. Phys. Meteorol.*, 58(1), 73–87, doi:10.1111/j.1600-0889.2005.00167.x, 2006.
- Weber, S. L., Drijfhout, S. S., Abe-Ouchi, A., Crucifix, M., Eby, M., Ganopolski, A., Murakami, S., Otto-Bliesner, B., and Peltier, W. R.: The modern and glacial overturning circulation in the Atlantic ocean in PMIP coupled model simulations, *Clim. Past*, 3, 51–64, <https://doi.org/10.5194/cp-3-51-2007>, 2007.
- Weitemeyer, K. A. and Buffett, B. A.: Accumulation and release of methane from clathrates below the Laurentide and Cordilleran ice sheets, *Global Planet Change*, 53(3), 176–187, 2006.
- Williamson, M. S., Lenton, T. M., Shepherd, J. G. and Edwards, N. R.: An efficient numerical terrestrial scheme (ENTS) for Earth system modelling, *Ecol. Modell.*, 198(3–4), 362–374, doi:10.1016/j.ecolmodel.2006.05.027, 2006.
- Yu, J., Anderson, R. and Rohling, E.: Deep Ocean Carbonate Chemistry and Glacial-Interglacial Atmospheric CO<sub>2</sub> Change, *Oceanography*, 27(1), 16–25, doi:10.5670/oceanog.2014.04, 2014.
- Zech, R., Huang, Y., Zech, M., Tarozo, R., and Zech, W.: High carbon sequestration in Siberian permafrost loess-paleosols during glacials, *Clim. Past*, 7, 501–509, doi:10.5194/cp-7-501-2011, 2011.

- Zeng, N.: Glacial-interglacial atmospheric CO<sub>2</sub> changes – the Glacial Burial Hypothesis. – *Advances in Atmospheric Sciences*, 20: 677–693, 2003.
- Zeng, N.: Quasi-100 ky glacial-interglacial cycles triggered by subglacial burial carbon release, *Clim. Past*, 3, 135–153, doi:10.5194/cpd-2-371-2006, 2007.
- 5 Zhang, X., Lohmann, G., Knorr, G., and Xu, X.: Different ocean states and transient characteristics in Last Glacial Maximum simulations and implications for deglaciation, *Clim. Past*, 9, 2319–2333, doi:10.5194/cp-9-2319-2013, 2013.
- Ziegler, M., Diz, P., Hall, I. R. and Zahn, R.: Millennial-scale changes in atmospheric CO<sub>2</sub> levels linked to the Southern Ocean carbon isotope gradient and dust flux, *Nat. Geosci.*, 6, 457–461, 2013.
- Zimov, S., Schuur, E. and III, F. C.: Permafrost and the global carbon budget, *Science*, 312(June), 1612–1613, 10 doi:10.1126/science.1128908, 2006.
- 10 Zimov, N. S., Zimov, S. A., Zimova, A. E., Zimova, G. M., Chuprynin, V. I., and Chapin, F. S.: Carbon storage in permafrost and soils of the mammoth tundra-steppe biome: Role in the global carbon budget, *Geophys. Res. Lett.*, 36, L02502, doi:10.1029/2008gl036332, 2009.