

# Sediment fluxes dominate glacial-interglacial changes in ocean carbon inventory: results from factorial simulations over the past 780,000 years

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**Abstract.** Atmospheric CO<sub>2</sub> concentrations ~~changed~~ varied over ice age cycles due to net exchange fluxes of carbon between land, ocean, ~~ocean sediments, atmosphere~~ marine sediments, lithosphere, and the ~~lithosphere. Marine sediment and ice cores preserved~~ atmosphere. Marine sediments and polar ice cores archived indirect biogeochemical evidence of these carbon transfers, which resulted from ~~sensitivities~~ poorly understood responses of the various carbon reservoirs to climate forcing, ~~many of which remain poorly understood. Numerical. Modelling~~ studies proved the potential of several physical and biogeochemical processes to impact atmospheric CO<sub>2</sub> under steady-state glacial conditions. Yet, it ~~is~~ remains unclear how much they affected carbon cycling during transient changes of repeated glacial cycles, and what role burial and release of sedimentary organic and inorganic carbon and nutrients played. Addressing this ~~uncertainty~~ knowledge gap, we produced a simulation ensemble of various idealized physical and biogeochemical carbon cycle forcings over the repeated glacial inception and terminations of the last 780 kyr with the Bern3D Earth system model of intermediate complexity ~~including, which includes~~ dynamic marine sediments. This ensemble allows for assessing transient carbon cycle changes due to these different forcings and gaining a process-based understanding of the ~~associated carbon fluxes and isotopic shifts~~ carbon fluxes resulting from the forcings, and the associated isotopic shifts that could serve as proxy data, in a continuously perturbed Earth system. We present results of the simulated Earth system dynamics in the non-equilibrium glacial cycles and a comparison with multiple proxy time series.

15 In our simulations ~~the ocean inventory changed by 200-1400 GtC and the atmospheric inventory by 1-150 GtC over the last deglaciation. DIC, the forcings cause sedimentary perturbations that have large effects on marine and atmospheric carbon storage. Dissolved Inorganic Carbon (DIC)~~ changes differ by a factor of up to 28 between simulations with and without interactive sediments, while CO<sub>2</sub> changes in the atmosphere are ~~at most up to~~ four times larger when interactive sediments are simulated. ~~Simulations with interactive sediments show no clear correlations between DIC or nutrient concentrations. The relationship between DIC (200-1400 GtC) and atmospheric CO<sub>2</sub> change (1-150 GtC) over the last deglaciation is strongly setup-dependent, highlighting the likely need for~~ need for considering multiple carbon reservoirs and multi-proxy analyses to ~~understand more robustly quantify~~ global carbon cycle changes during glacial cycles ~~in practice. Starting. Finally, initiating~~ transient simulations with an interglacial geologic carbon cycle balance causes isotopic drifts that require several 100 kyr to

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overcome, ~~and needs~~. These model drifts need to be considered when designing spin-up strategies.

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## 1 Introduction

During the Quaternary, the Earth's carbon cycle repeatedly shifted between low atmospheric CO<sub>2</sub> ~~concentrations~~ during glacial periods and elevated ~~concentrations~~ mixing ratios during interglacials in orbitally-paced cycles (Petit et al., 1999; Siegenthaler et al., 2005; Lüthi et al., 2008). The reconstructed evolution of atmospheric CO<sub>2</sub> ~~concentrations~~ from Antarctic ice cores aligns  
30 closely with temperature and ~~, with a delay, is lagged by~~ ice sheet extent, suggesting a close coupling of climate and the carbon cycle (e.g. Shackleton, 2000; Bereiter et al., 2015). Yet, simulating atmospheric CO<sub>2</sub> changes that are consistent with ~~reenstruected~~ reconstructed CO<sub>2</sub> and other proxy data is challenging because the observed carbon cycle changes were the result of complex Earth system responses to climate forcing (Schmittner, 2008).

Changing ocean chemistry is often attributed an important role in these cycles because of the considerable size of the marine  
35 carbon reservoir (Broecker, 1982a) and because reconstructions ~~imply smaller carbon stocks in vegetation and soils~~ show that overall there was likely less carbon stored on land (in vegetation, permafrost, peatlands and soils) at the Last Glacial Maximum (LGM) than during the current warm period (~~Lindgren et al., 2018; Jeltsch-Thömmes et al., 2019~~) (Yu et al., 2010; Lindgren et al., 2018; Je  
. A multitude of physical and biogeochemical processes have been assessed for their contribution to changes in the marine carbon storage on these timescales (~~e.g. Sigman et al., 2010; Fischer et al., 2010~~) (e.g. Kohfeld and Ridgwell, 2009; Sigman et al., 2010; Fisch  
40 , and their relative importance for the CO<sub>2</sub> difference between the ~~last glacial maximum~~ LGM and the late Holocene have been tested in numerical simulations with dynamic ocean models (e.g. Brovkin et al., 2012; Menviel et al., 2012). Changes in ocean circulation and increased CO<sub>2</sub> solubility due to lower temperatures contributed to the lower glacial atmospheric CO<sub>2</sub> concentration (Broecker, 1982a; Smith et al., 1999; Brovkin et al., 2007; Sigman et al., 2010; Fischer et al., 2010), while increased salinity and surface ocean dissolved inorganic carbon (DIC) concentrations due to lowered sea levels ~~added~~ tend to counteract  
45 this effect by stimulating CO<sub>2</sub> ~~back-outgassing~~ to the glacial atmosphere (Weiss, 1974; Broecker, 1982a; Brovkin et al., 2007). Furthermore, reduced ~~carbon-CO<sub>2</sub>~~ outgassing from the Southern Ocean due to a greater extent of sea ice isolating the surface ocean from the atmosphere, and enhanced stratification due to brine rejection during sea ice formation are other physical processes suggested to have affected the glacial carbon cycle (Stephens and Keeling, 2000; Bouttes et al., 2010).

~~Biogeochemical~~ Marine biogeochemical processes that lead to ~~increased ocean carbon storage include reduced~~ lower atmospheric  
50 CO<sub>2</sub> include a shift of organic carbon remineralization ~~rates in the colder ocean to greater depths~~, as well as increased export production due to increased nutrient supply from emerged shelves (phosphate) ~~, and~~ enhanced dust deposition (iron, silica) and ~~supply from the deep Southern Ocean~~ changes in Southern Ocean dynamics and nutrient utilization, which would have counteracted the effect of ~~low temperatures colder temperatures and large sea ice extent~~ on surface ocean ~~productivity and increased export production~~ export production and nutrient utilization (Broecker, 1982b; Martin, 1990; Pollock, 1997; Deutsch  
55 et al., 2004). In a (hypothetical) closed atmosphere-ocean system, the combination of these processes ~~result~~ results in increased

marine carbon storage during glacials, but not necessarily in ~~open systems (i.e. considering dynamic land and lithospheric carbon reservoirs)~~ (e.g. Buchanan et al., 2016; Kempainen et al., 2019).

~~Little is known about the changes of carbon stored as organic and inorganic carbon in a fourth reservoir: marine sediments and the lithosphere. It has since long been assumed~~ the open Earth system because the carbon removed from the surface ocean  
60 and atmosphere by these processes could have been sequestered in the water column as DIC or particulate carbon but also  
in marine sediments. Carbon can also be transferred to the land. Constraints on glacial atmospheric CO<sub>2</sub> can be reconciled  
with increased and decreased marine DIC inventory in an open system (Jeltsch-Thömmes et al., 2019; Kempainen et al., 2019)  
, though reproducing reconstructed carbon isotopic changes in atmosphere and ocean seems to require elevated DIC at the  
LGM (Jeltsch-Thömmes et al., 2019).

65 It is very probable that changing sedimentary carbonate and particulate organic carbon (POC) burial played a relevant role  
in glacial-interglacial carbon cycle changes by altering seawater carbonate chemistry, ~~particularly on continental shelves which~~  
~~would~~ carbonate ion concentrations, carbon isotope ratios, and oxygenation. Particularly, continental shelves have emerged  
from the ocean during glacial sea level low stands and provided new reef habitats and carbonate deposition environments  
during deglaciations and interglacials (e.g. Broecker, 1982b; Opdyke and Walker, 1992; Ridgwell et al., 2003; Brovkin et al.,  
70 2007; Menviel and Joos, 2012). Additionally, carbonate burial changes in the open ocean have been considered as ampli-  
fiers of marine carbon uptake (e.g. Archer and Maier-Reimer, 1994; Kohfeld and Ridgwell, 2009; Schneider et al., 2013;  
Roth et al., 2014; Kerr et al., 2017; Kobayashi et al., 2021). ~~Consistently, reconstructions~~ Organic carbon burial is also prone  
to vary in response to changes in the rain rate of POC sinking to the sea floor and altered oxygenation. Previous model  
simulations, that included POC burial, showed that interactive sediments greatly affect atmospheric CO<sub>2</sub> and carbon isotope  
75 variations through the burial-nutrient feedback, whereby enhanced burial of organic-bound carbon and nutrients reduces export  
production (Tschumi et al., 2011; Roth et al., 2014; Jeltsch-Thömmes et al., 2019; Jeltsch-Thömmes and Joos, 2023). Reconstructions  
of marine burial changes over the last glacial cycle suggest a reduction in ~~globally-averaged~~ globally-integrated inorganic car-  
bon burial (Cartapanis et al., 2018; Wood et al., 2023) during the last glacial period, but increased organic (Cartapanis et al.,  
2016) sedimentary carbon burial. The extents of both changes are uncertain due to the spatial heterogeneity of sedimentary  
80 burial and the inherently local nature of marine ~~sediment cores~~ archives, but possibly of comparable magnitude to terrestrial  
carbon stock changes (Cartapanis et al., 2016, 2018).

~~Previous model simulations, that included organic carbon burial, showed that interactive sediments greatly affect atmospheric~~  
~~CO<sub>2</sub> and carbon isotope amplitudes through the burial-nutrient feedback (Tschumi et al., 2011; Roth et al., 2014; Jeltsch-Thömmes et al., 2019).~~  
~~Dynamic sedimentary adjustment and imbalances in weathering-burial fluxes also increase the equilibration time of atmospheric~~  
85 ~~CO<sub>2</sub> by a factor of up to 20 to several tens of thousands of years and the resulting  $\delta^{13}\text{C}$  perturbations take hundreds of~~  
~~thousands of years to recover (Roth et al., 2014; Jeltsch-Thömmes et al., 2019; Jeltsch-Thömmes and Joos, 2023).~~ These find-  
ings demonstrate that organic and inorganic sedimentary changes and imbalances ~~between the weathering and burial fluxes to~~  
~~the consolidated sediments and lithosphere~~ with weathering fluxes need to be considered when quantifying carbon reservoir  
changes of the ocean, atmosphere, and land and interpreting the reconstructed changes in CO<sub>2</sub>, carbonate ion concentrations,  
90 isotopes, and nutrients over glacial cycles.

Model-based estimates of carbon and carbon isotope inventory differences between glacial and interglacial periods are complicated by temporal carbon cycle imbalances during the continuously evolving climate of glacial cycles. This is particularly challenging when simulating dynamic elemental cycling in and burial from reactive marine sediments and the input of elements by weathering and volcanic outgassing ~~and the loss of elements by burial in reactive sediments and the lithosphere~~, because of long-lasting re-equilibration and memory effects in carbon and nutrient fluxes and particularly isotopic changes (Tschumi et al., 2011; Jeltsch-Thömmes and Joos, 2020). ~~Importantly, sedimentary fluxes and related weathering-burial imbalances never reached true equilibrium during glacial cycles, which implies~~ Dynamic sedimentary adjustment, i.e. the equilibration of sedimentary dissolution and remineralization to changes in bottom water which slowly diffuse into sedimentary porewater, and imbalances between the supply (weathering) and loss (sedimentary burial) of carbon and nutrients also increase the equilibration time of atmospheric CO<sub>2</sub> by a factor of up to 20 to several tens of thousands of years and the resulting  $\delta^{13}\text{C}$  perturbations take hundreds of thousands of years to recover (Roth et al., 2014; Jeltsch-Thömmes et al., 2019; Jeltsch-Thömmes and Joos, 2020). Importantly, the equilibration time scales are longer than typical interglacials in the late Pleistocene, which opens up the possibility for memory effects that span several glacial cycles.

A caveat of several modeling studies attempting to quantify carbon reservoir sizes at the LGM is that they assume a steady state carbon cycle in a closed (atmosphere-ocean only) system and do not account for the history of environmental changes that pre-dated the LGM but could have introduced long-lasting memory effects. Transient simulations of ~~a whole an entire~~ glacial cycle with a fully dynamic marine and sedimentary carbon cycle showed that time lags in the carbon cycle response to orbital forcing add constraints for the identification of the processes that caused glacial CO<sub>2</sub> changes (Menviel et al., 2012). In particular, imbalances between marine carbon burial and continental weathering and the long marine residence time of phosphate delay the CO<sub>2</sub> increase during the temperature rise of deglaciations. ~~Transient Accounting for these long-term effects in their experimental design, transient~~ simulations of more than one glacial cycle showed that reconstructed atmospheric CO<sub>2</sub> and benthic marine  $\delta^{13}\text{C}$  changes over the last 400 kyr could be reasonably well simulated with a ~~combinations combination~~ of physical (radiative and ocean volume changes) and biogeochemical processes (~~carbonate chemistry and land carbon changes, temperature-dependent remineralization depth, additional nutrient supply during glacial~~ if (carbonate chemistry and land carbon changes, temperature-dependent remineralization depth, additional nutrient supply during glacial ~~Yet, shallow water carbonate burial changed too (Ganopolski and Brovkin, 2017). These burial changes were partially prescribed was prescribed and POC burial not included in the simulations, which begs the question how well the effect of the considered processes ~~can explain on~~ glacial-interglacial atmospheric CO<sub>2</sub> ~~change if sedimentary burial and surface ocean carbonate chemistry are entirely dynamically simulated. Simulations and carbon isotopic ratios changes if the sediments are dynamically~~ calculated. Recently, simulations of glacial-interglacial cycles beyond the Mid-Brunhes transition (~430 ka) were run with a box model (Köhler and Munhoven, 2020) and ~~purely physical models a purely physical model~~ (Stein et al., 2020) which are unable to capture transient and spatially heterogeneous interactive sediments. CLIMBER-2, a fully coupled intermediate-complexity Earth system model, was run stepwise over the last 3 Myr, but the results were not analysed for the carbon cycle dynamics (Willeit et al., 2019).~~

125 Here we examine systematically how the transient built-up and dissolution of marine sediments on glacial-interglacial  
timescales affects the carbon cycle changes produced by the various processes suggested to be relevant on these timescales, a  
gap left by previous studies. Instead of searching for the most likely scenario that reconciles the vast proxy evidence, we attempt  
to gain a more complete process understanding and overview of the proxy-relevant signals that these processes cause in the  
presence of weathering-burial imbalances. With this goal, we extend factorial simulations of multiple simplified physical and  
130 ~~biochemical~~ biogeochemical forcings in a marine sediment and isotope-enabled intermediate complexity Earth system model  
over the last 780 kyr ~~to understand how various processes affect carbon fluxes in response to continuously varying climate,~~  
~~and specifically how sediments affect the marine and atmospheric carbon cycle across repeated glacial cycles. To~~ and compare  
the resulting carbon and carbon isotopic signals to reconstructions. The long timescale is chosen to avoid biases resulting from  
steady state assumptions ~~, we simulated the last eight glacial cycles fully transiently, so that~~ and account for the possibility of  
135 memory effects under continuously varying climate and carbon cycle that could span multiple glacial cycles. Consequently,  
all carbon stores ~~at the beginning of the last glacial cycle~~ are achieved dynamically rather than being prescribed. ~~Specifically,~~  
~~we~~ We present two sets of simulations with and without interactive sediments to distinguish the role of interactive sediments  
in the carbon cycle changes caused by ~~these different forcings over repeated glacial cycles~~ the tested forcings over reoccurring  
glacial cycles of the last 780 kyr.

## 140 2 Methods

### 2.1 Bern3D v2.0s

We simulated the Earth system's transition through the last 780 kyr of glacial cycles with the intermediate complexity Earth  
system model Bern3D v2.0s, which has ~~a resolution of an irregular~~ 41×40 grid (lowest resolution: lat×lon = 5°×10° in  
the North Pacific, highest resolution: lat×lon = 3°×7° in the Equatorial Atlantic) in the horizontal and 32 logarithmically  
145 spaced ocean depth layers. The model combines modules for 3D physical ocean dynamics, marine biogeochemistry, ma-  
rine interactive sediments, and atmospheric energy-moisture balance. ~~The geostrophic-frictional balance ocean circulation is~~  
~~calculated explicitly (Edwards et al., 1998; Müller et al., 2006), and parameterizations are included to represent the effects of~~  
~~dia- and isopycnal diffusion and eddy-induced transport (Griffies, 1998). The NCEP/NCAR monthly wind stress climatology~~  
~~(Kalnay et al., 1996) is used to prescribe wind stress at the ocean surface. Atmosphere-ocean gas exchange and carbonate~~  
150 ~~chemistry are simulated according to the OCMIP-2 protocols (Najjar et al., 1999; Orr et al., 1999, 2017; Wanninkhof, 2014; Orr and Epital~~  
~~, and gas transfer velocities are scaled with wind speed (Krakauer et al., 2006). The global mean sea-air gas exchange was then~~  
~~reduced by 19% to achieve agreement with radiocarbon distribution estimates (Müller et al., 2008).~~

The physical ocean component transports tracers through the ocean by advection, convection, and diffusion. Euphotic zone  
production depends on temperature, light, sea ice cover, and nutrient (phosphate, iron, silica) availability ~~, with a full description~~  
155 ~~of the model biogeochemistry in Parekh et al. (2008); Tschumi et al. (2011) and of (Parekh et al., 2008; Tschumi et al., 2011)~~  
and explicitly calculates carbon isotope dynamics ~~in Jeltsch-Thömmes et al. (2019)~~ (Jeltsch-Thömmes et al., 2019). In our setup,  
a fraction of the particulate organic matter formed in the surface ocean is instantly remineralized following an oxygen con-

centration dependent version of the globally-uniform Martin curve (Battaglia and Joos, 2018) and particulate inorganic carbon and opal dissolution occurs according to globally-uniform e-folding profiles. The remaining solid particles reaching the sediment-ocean interface enter reactive sediments, where they are preserved, remineralized, or redissolved depending on dynamically calculated porewater chemistry, and mixed by bioturbation (Tschumi et al., 2011). ~~The sediment model includes CaCO<sub>3</sub> dissolution rates in the sediments are determined from the pore water saturation state, and POC remineralisation is parameterised by a linear dependence on porewater O<sub>2</sub> (Heinze et al., 1999; Tschumi et al., 2011). The model contains 10 layers and computes fluxes of carbon, nutrients, alkalinity, and isotopes between the ocean, reactive sediments, and the lithosphere. Loss fluxes to the lithosphere are compensated for at equilibrium of reactive sediments. As matter gets pushed downward out of the bottom layer ('sedimentary burial'), it is lost to the modelled inventories. These loss fluxes are at equilibrium compensated for by a corresponding solute input flux from weathering. The ocean model includes diagnostic tracers for preformed DIC and phosphate, which track the fractions of DIC and phosphate that are not incorporated into marine organic carbon during surface ocean production and into the coastal surface ocean. The (pre-industrial) land-sea mask and bathymetry are fixed throughout the spin-up and simulations.~~

## 2.2 Model spin-up with interglacial boundary conditions

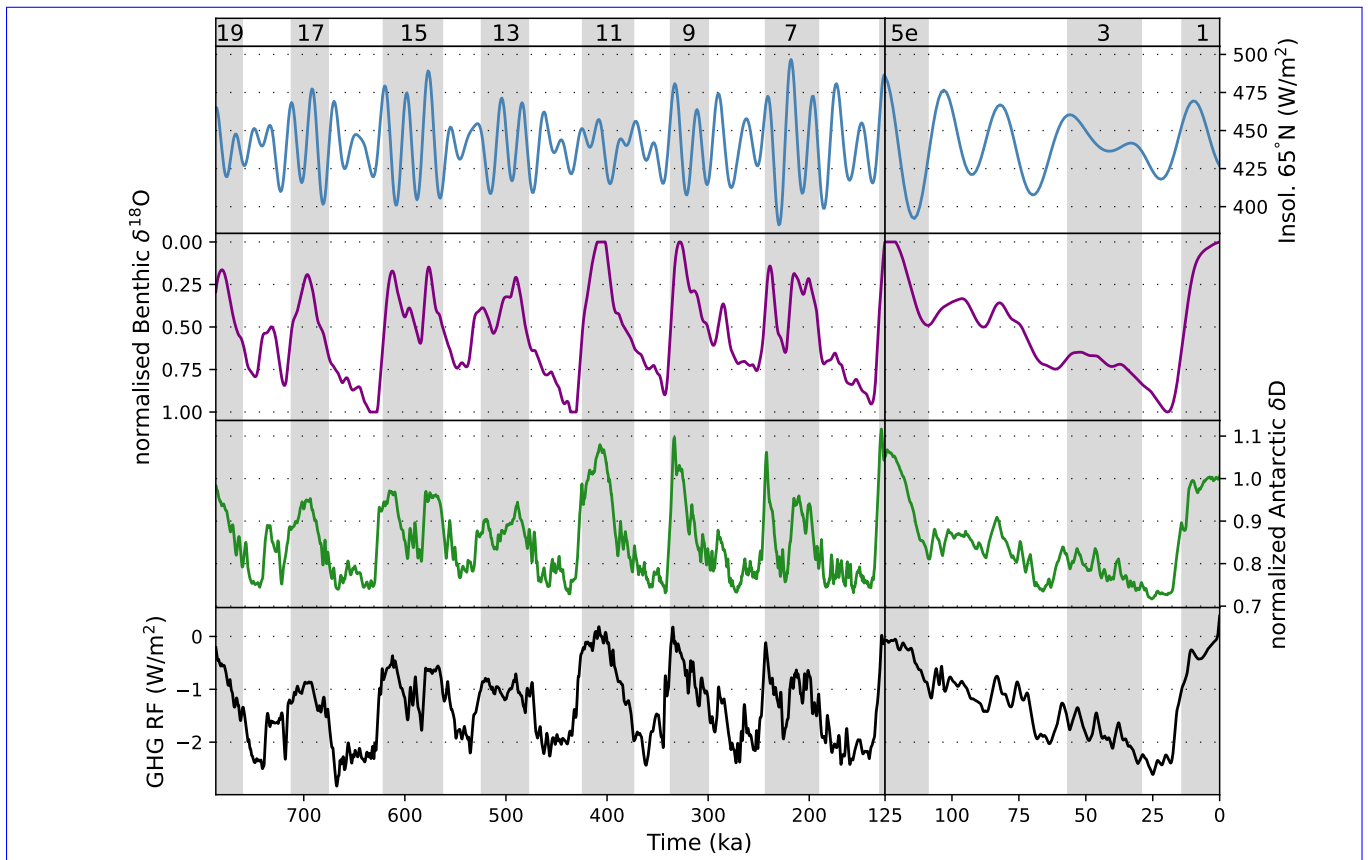
We spun up the model with pre-industrial boundary conditions in three stages, sequentially coupling all modules, ~~for computational efficiency.~~ First, we forced the ocean circulation and then the atmosphere-ocean carbon cycle as a closed system with pre-industrial climatic conditions and prescribed CO<sub>2</sub> ~~for 20 kyr.~~ In the next step, the sediment module is coupled and terrestrial solute supply (phosphate, alkalinity, DIC, DI<sup>13</sup>C and Si) to the ocean is ~~prescribed to balance loss to the lithosphere over set to dynamically balance the loss through sedimentary burial for 50 kyr. Then, this weathering input flux is diagnosed. At the end of this stage, the solute input flux required to balance sedimentary burial is diagnosed (Table S1) and kept constant thereafter for the rest of the spin up procedure and throughout our transient experiments.~~ Until this stage, atmospheric CO<sub>2</sub> and δ<sup>13</sup>C were prescribed. The spun up model for the pre-industrial was then run for 2000 years as an open system (freely evolving CO<sub>2</sub> and δ<sup>13</sup>C) with radiative forcing that varied linearly from PI to the slightly different MIS19 conditions, the starting point of our experiments. ~~The total length of the spin-up to this point was 72 kyr. To avoid large drifts in carbon isotopes and alkalinity (Jeltsch-Thömmes and Joos, 2023) (Jeltsch-Thömmes and Joos, 2023, explained at the end of our results section) in the simulations with the forcings that perturbed the carbon cycle the most (PO4, REMI, LAND, CO2T, BGC, ALL, described in the next section), we ran the fully-interactive model with the each respective forcing for three glacial cycles two glacial cycles (215 kyr) before starting our experiments. We discuss the relevance of initial conditions and imbalances of the geologic carbon cycle at the end of the manuscript. Model limitations due to constant terrestrial solute supply are discussed in SI.5.~~

## 2.3 Experimental design

~~We Data constraints on carbon cycle forcings are too sparse to know exact magnitudes and timings of the forcings that might have varied spatially and temporarily over the last eight glacial cycles. An inverse estimation of the forcings from the resulting proxy signals requires a different simulation ensemble and is beyond the scope of our study. Rather than trying to guess~~

the most proxy consistent forcing amplitudes and patterns, we designed seven simplified forcings (table 1), each with one exemplary magnitude, to simulate the effects of Earth system changes generic effects of processes that have been identified as glacial-interglacial carbon cycle drivers (similar to the study of long-term circulation changes in Adloff et al. (2023)): expanded Antarctic Bottom Water (AABW), here simulated by increased wind stress over the Southern Ocean, reduced sea-air gas exchange in the Southern ocean, reduced solar radiation due to increased dust and aerosol fluxes, enhanced supply of nutrients, reduced particulate organic carbon remineralization, lower rain ratio of particulate inorganic carbon (PIC,  $\text{CaCO}_3$ ) to particulate organic carbon (POC), and reduced terrestrial carbon storage during glacial times. Except for the orbital changes, which were calculated following Berger (1978); Berger and Loutre (1991) and the reconstructed  $\text{CO}_2$ ,  $\text{N}_2\text{O}$  and  $\text{CH}_4$  curves (Loulergue et al., 2008; Joos and Spahni, 2008; Bereiter et al., 2015; Etminan et al., 2016), which we used to calculate the radiative forcing of greenhouse gas changes, the amplitudes of the forcings were set to cause noticeable  $\text{CO}_2$  or circulation shifts, informed by previous studies (e.g. Tschumi et al., 2011; Menviel and Joos, 2012; Menviel et al., 2012; Jeltsch-Thömmes et al., 2019). We produced timeseries of these forcings by defining a maximum forcing amplitude for the LGM, a minimum for the Holocene and then modulating this amplitude by reconstructed relative changes in the temporal evolution of either Antarctic ice core  $\delta\text{D}$  (Jouzel et al., 2007) or benthic  $\delta^{18}\text{O}$  (Lisiecki and Raymo, 2005) for each year (Fig. 1). The choice of the isotope record for calculating the instantaneous forcing depends on whether we expect the forcing to evolve synchronously with temperature like  $\delta\text{D}$  or have a time lag similar to  $\delta^{18}\text{O}$ .

Forcing scenarios. Simulations are run in two configurations: the standard setup with interactive sediments and a closed-system setup without sediments (except PO4). (see section SI.5 for a discussion of the limitations). In all simulations, we prescribed the radiative effect of  $\text{CO}_2$  in the atmosphere, so that all simulations have the same radiative forcing from greenhouse gasses despite differences in simulated  $\text{CO}_2$ .



**Figure 1.** Forcing timeseries. Insolation changes ([top panel](#)) are calculated according to Berger (1978); Berger and Loutre (1991). The  $\delta^{18}\text{O}$  forcing ([second panel](#)) is the LR04 stack (Lisiecki and Raymo, 2005), smoothed by averaging over a 10000-year moving window and normalized to the LGM-PI difference. The  $\delta\text{D}$  forcing ([third panel](#)) is [taken](#) from Jouzel et al. (2007) and normalized to the LGM-PI difference. The radiative forcing (RF) of  $\text{CO}_2$ ,  $\text{N}_2\text{O}$  and  $\text{CH}_4$  ([greenhouse gasses 'GHG'](#), [bottom panel](#)) is calculated from Bereiter et al. (2015); Loulergue et al. (2008); Joos and Spahni (2008) following Etminan et al. (2016). [Gray shading indicate uneven Marine Isotope Stages \(MIS\).](#)

[Specifically, we performed one 'base' run with orbital and radiative forcing only, one model run for different forcings, each added to the base forcing, and combinations of the individual forcings to study non-linear effects that appear when processes interact. All of these experiments are run once with and once without interactive sediments, to examine the effect of sediment perturbations on the results. The forcings and their rationale are described below. The experiments are summarized in Table 1.](#)

215 The application of the standard forcing in simulation BASE ~~results~~ [causes temperature changes associated with orbital, albedo, and greenhouse gas changes which affect solubility, sea ice and circulation, e.g. slightly weakening AMOC \(by up to 4.5 Sv, Fig. S8\) and resulting](#) in younger deep water masses in the Atlantic and Pacific during the LGM than at the PI, [which is inconsistent with proxy data and thus indicates that additional Earth system changes must have occurred](#) (Pöpelmeier et al., 2020). To achieve an older glacial deep ocean ([diagnosed with an ideal age tracer](#)), we reduced the wind stress south of 48 °S by a maximum of 40% ~~temporally changing proportionally~~ [\(simulation SOWI\) temporally changing](#)

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proportionately to the  $\delta D$  change because we assume that wind strength over the Southern Ocean evolved without temporal lags to Antarctic temperature. As a result, the South Pacific downwelling is strengthened by up to 1.5 Sv locally in glacials, AMOC strength is further reduced by up to 1 Sv and the simulated deep ocean age is  $\sim 100$  years older in the LGM than in the PI, close to published model estimates (Schmittner, 2003). ~~Changing~~ In this set-up, ~~changing~~ wind stress only affects the circulation, not the piston velocity of gas exchange, which is forced by a wind-speed climatology. For an independent assessment of the effect of wind speed changes on sea-air gas exchange, we ~~added~~ performed a simulation in which we decreased the piston velocity in the Southern Ocean by a maximum of 40% (KGAS), also following the evolution of  $\delta D$ . ~~Finally~~ Next, we tested ~~a~~ an additional negative radiative forcing due to increased dust loads in the glacial atmosphere (e.g. Claquin et al., 2003) by reducing the total radiative forcing by a maximum of  $2.5 \text{ W/m}^2$  during the LGM to test the effects of stronger AMOC weakening (AERO), modulated by the  $\delta^{18}\text{O}$  record based on the reconstructed correlation between dust and  $\delta^{18}\text{O}$  (Winckler et al., 2008, similar to the study of long-term circulation changes in Adloff et al. (2023)). Under this forcing, the AMOC weakens by up to 12 Sv relative to PI during glacial maxima (the model behaviour to this forcing is described more extensively in the Supplementary Information) and water mass age rises to up to 1000 years in the deep North Atlantic as glacial deep water formation now only occurs in the Southern Ocean. In terms of biogeochemical forcings, we ~~added~~ mimicked a terrestrial carbon sink/source which ~~removes~~ by removing/emits/adding 500 PgC during deglaciation/ice age inception (Jeltsch-Thömmes et al., 2019) (LAND Jeltsch-Thömmes et al., 2019) and increased the marine phosphate inventory by 30% during the LGM glacial maxima by a globally-uniform supply of phosphate into the surface ocean (PO4). The timeseries of both forcings are proportional to  $\delta^{18}\text{O}$  changes, because we assume that both are lagging behind temperature changes due to continental ice-sheets and changing terrestrial environments. Effectively, our nutrient forcing reduces nutrient limitation globally. Rather than simulating the effects of different nutrient inputs in different regions (e.g. iron in the Southern Ocean, phosphate at shelves), we decided to group all these in one simulation with a global forcing because their net effect, increased export production, would be the same in our model, just in different regions. This is the only forcing that we did not apply to the model without interactive sediments because, while nutrients can be added to the surface ocean periodically, there is no simple way of artificially extracting nutrients from the ocean in return. We also reduced the speed of aerobic organic matter remineralization in the ocean by transitioning between the standard, pre-industrial Bern3D particle profile (Martin scaling) during interglacials and a linear profile in the first 2000 m of the water column (REMI, Fig. S9), following the  $\delta D$  record. ~~Finally~~, since we assume that remineralization changes happened synchronously with temperature change. Next, we reduced the PIC:POC rain ratio by 30/33% in the LGM and (PIPO) and similarly modulated the forcing timeseries with the  $\delta D$  record.

~~We performed one 'base' run with orbital and radiative forcing only, one model run for each individual biogeochemical forcing added to the base forcing and combinations of forcings to study non-linear effects of forcing combinations.~~ In addition we performed one run in which we let the model dynamically adjust/apply external alkalinity fluxes (in addition to the constant terrestrial solute supply applied in each simulation, see spin-up methodology) to restore the reconstructed atmospheric  $\text{CO}_2$  curve (CO2T). In this simulation, the model evaluates the difference between the simulated and reconstructed  $\text{CO}_2$  at each time step and adds or removes the marine alkalinity required to cause the necessary compensatory air-sea carbon flux from the surface ocean. Alkalinity changes, e.g. due to changes in shallow carbonate deposition or terrestrial weathering, are an effective

260 lever for atmospheric CO<sub>2</sub> change (e.g. Brovkin et al., 2007), and this additional run shows the long-term changes in marine biochemistry if ~~these processes were the dominant drivers~~ this was the dominant driver of glacial-interglacial atmospheric CO<sub>2</sub> change. ~~All simulations were started from the pre-industrial spin-up adjusted for MIS-19 radiative forcing. Climate change occurs only in response to the prescribed radiative forcing and not the simulated atmospheric CO<sub>2</sub> concentrations. To this set of 12 primary simulations, we added sensitivity experiments to assess biases induced by our experiment design: 1) We repeated the simulation ALL, including all forcings, with CO<sub>2</sub>-sensitive climate to study the impact of the CO<sub>2</sub>-climate feedback. 2) We repeated five simulations (REMI, PIPO, BGC, ALL, CO2T) starting from the transiently achieved MIS-15 Earth system state in their primary versions (215 kyr into the simulation) because they showed initial drifts in DIC and isotopes. We discuss the relevance of initial conditions and imbalances of the geologic carbon cycle at the end of the manuscript.~~

**Table 1.** Forcing scenarios. Simulations are run in two configurations: the standard setup with interactive sediments and a closed-system setup without sediments (except PO4).

ID	Description	LGM-PI amplitude	Modulating proxy
BASE	orbital changes + radiative effect of greenhouse gasses + ice sheet albedo		CO <sub>2</sub> , CH <sub>4</sub> , δ <sup>18</sup> O
SOWI	BASE + Wind stress strength over Southern Ocean (>48 °S)	-40%	δD
KGAS	BASE + gas transfer velocity in Southern Ocean	-40%	δD
AERO	BASE + Radiative forcing from dust particles	-2.5 W/m <sup>2</sup>	δ <sup>18</sup> O
PHYS	BASE + all physical forcings combined		
LAND	BASE + land C storage	-500 PgC	δ <sup>18</sup> O
REMI	BASE + linear glacial remineralization profile in upper 2000m	linear	δD
PIPO	BASE + PIC:POC changes	-0.33	δD
PO4	BASE + marine PO <sub>4</sub> reservoir	+30%	δ <sup>18</sup> O
BGC	BASE + all biogeochemical forcings combined		
ALL	BASE + all forcings combined		
CO2T	BASE + restoring reconstructed atm. CO <sub>2</sub> concentrations	-90 ppm	CO <sub>2</sub>

265 For the discussion of the simulations, we quantify the factorial effect of the simulated processes forcings on different carbon cycle metrics. In simulation BASE, only the standard forcing is active (see table 1), hence the factorial effect of the standard forcing forcing is equal to the simulated change:

$$f_{BASE} = \text{BASE}$$

In the simulations that combine the standard forcing with one other forcing, the factorial effect of the additional forcing is the  
270 difference between the respective simulation and BASE:

$$fFORC = FORC - fBASE$$

In simulations PHYS, BGC and ALL several forcings are combined. We use these simulations to determine non-linearities by calculating the difference between the results of these simulations and the linear addition of the individual effects of the active forcings:

$$275 \text{ ~~nlPHY~~nlPHY~~S~~ = PHYS - (fBASE + fKGAS + fSOWI + fAERO)$$

$$\text{nlBGC} = \text{BGC} - (fBASE + fREMI + fPO4 + fPIPO + fLAND)$$

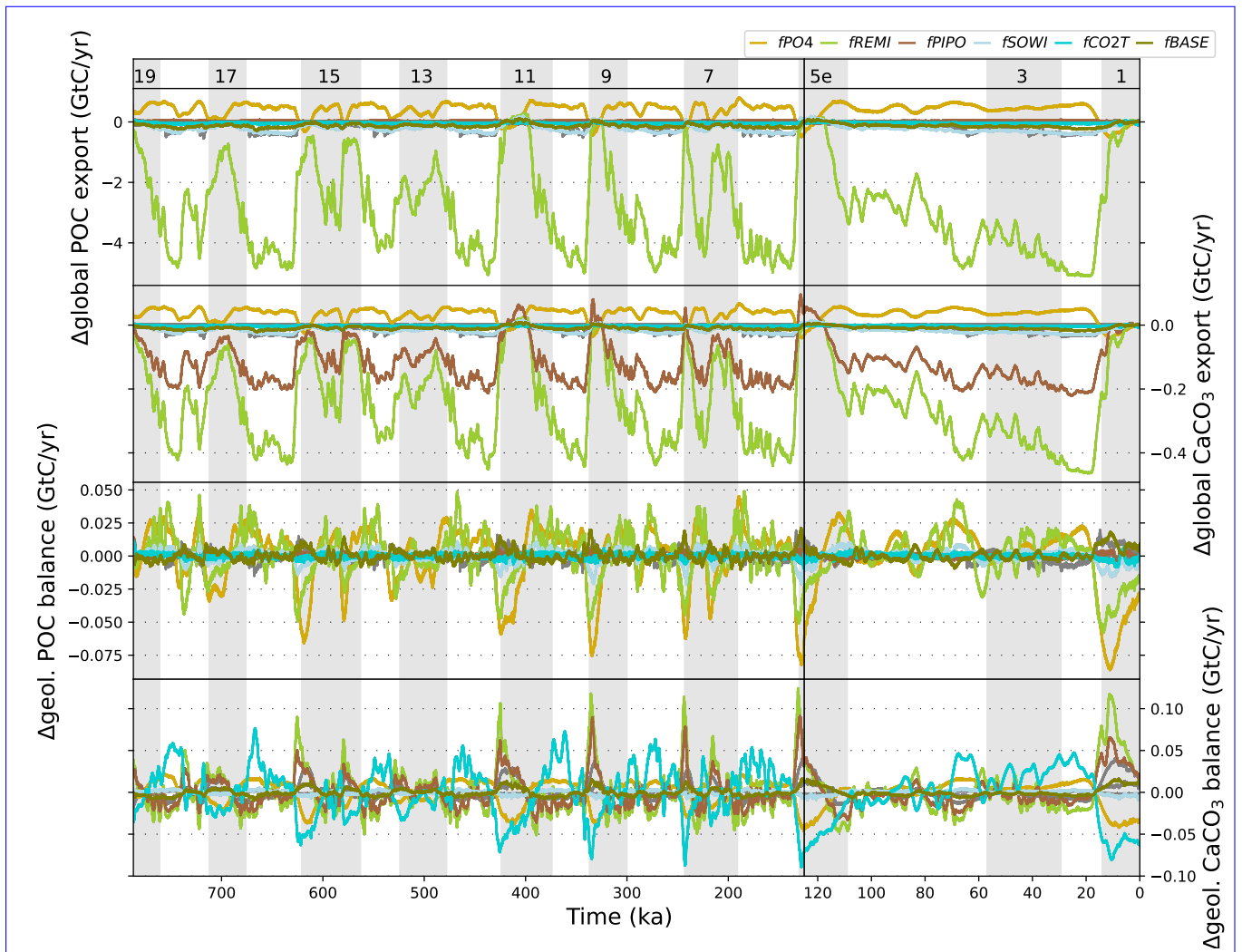
$$\text{nlADD} = \text{ALL} - \text{PHYPHYS} - \text{BGC} + \text{BASE}$$

$$\text{nlTOT} = \text{nlPHY} + \text{nlBGC} + \text{nlADD}$$

~~The impacts of ocean-sediment interactions and associated weathering-burial fluxes are quantified as differences between  
280 simulations with and without sediment module.~~

### 3 Results

The general response of marine biogeochemistry to the applied forcings has been tested and described in previous studies (e.g. Tschumi et al., 2008, 2011; Menviel and Joos, 2012; Menviel et al., 2012; Jeltsch-Thömmes et al., 2019; Jeltsch-Thömmes and Joos, here we therefore just provide a brief summary and focus more extensively on their effect on the sediments. A more detailed  
285 analysis of the model behaviour under each forcing is provided in the supplementary material.



**Figure 2.** Transient variations of atmospheric CO<sub>2</sub> concentrations as simulated POC and CaCO<sub>3</sub> export production and geologic imbalance (i.e. the difference between accumulation of these materials in PHYS, PO4, REMI, marine sediments and LAND the lithosphere minus the constant supply into the surface ocean that mimics terrestrial weathering and reconstructed by Bereiter et al. (2015) volcanism in our simulations) due to the applied forcings. Shown is are the deviation from factorial results for each simulation. The results that are explicitly mentioned in the pre-industrial value text are shown in colour, the others are shown in gray. Gray shading indicates uneven Marine Isotope stages MIS as indicated at the top of the figure. Dashed lines denote runs without sediment module (not available for PO4) See Fig. The same plots S10 for absolute changes in the other simulations are shown in S16.

The simulated amplitudes in CO<sub>2</sub> changes and their timings vary largely between simulations. The effect of dynamic sediments on the simulated atmospheric CO<sub>2</sub> strongly depends on the type of forcing. Interactive sediments have a negligible effect on atmospheric CO<sub>2</sub> changes. In our set-up, carbon exchange between the atmosphere, ocean, and sediments reacts to climatic and biogeochemical changes while weathering input fluxes of DIC, alkalinity, and PO<sub>4</sub><sup>3-</sup> are constant over time. Thus, a carbon flux imbalance arises in our simulations if only physical forcings are considered, but amplify glacial-interglacial

295 ~~CO<sub>2</sub>~~ in response to the applied forcings (Fig. 2 for factorial results, see Fig. S10 for absolute fluxes). All forcings except *fPO4* reduce global export production during glacial phases, either due to cooling and expanding sea ice or increased nutrient limitation. In addition to export production, the net C exchange between sediments and the ocean is changed by the applied forcings via changing benthic seawater composition, either through circulation, solubility, or biogeochemical changes. Cooling reduces global sediment accumulation rates of CaCO<sub>3</sub> and POC during glacial phases due to the reductions in export production (*fBASE*). In consequence, sequestration of CaCO<sub>3</sub> and POC from the reactive sediments (i.e. sedimentary burial) is also reduced in response to these forcings, since it is governed by the sedimentary mass accumulation rate. Instead, ~~reduced marine O<sub>2</sub> change under biochemical forcings~~, due to the deepened remineralization (*fREMI*), increases the preservation of sedimentary POC during glacials. Hence, POC accumulation is higher during glacial than interglacial phases, while the opposite temporal change occurs for CaCO<sub>3</sub> accumulation due to reduced CaCO<sub>3</sub> export production. Reduced nutrient limitation during glacial phases (*fPO4*) causes more, rather than less, export production during glacial phases. Increased ALK supply in simulation CO2T causes larger sedimentary CaCO<sub>3</sub> accumulation during glacial phases and dissolution events during deglaciations.

305 ~~The processes that cause the different model responses to the prescribed forcings have largely been described in other studies (e.g. Tschumi et al., 2008, 2011; Menviel and Joos, 2012; Menviel et al., 2012; Jeltsch-Thömmes et al., 2019; Jeltsch-Thömmes and Joos, 2019). How do the simulated sedimentary changes in our factorial setup compare in magnitude and sign with carbon cycle proxy records?~~

310 ~~We focus first on changes in the carbon stored as sedimentary organic and inorganic matter and changes in the benthic carbonate system, then DIC and atmospheric CO<sub>2</sub>, before discussing the simulated proxy signals in CO<sub>3</sub><sup>2-</sup> and are summarised in the SI to our manuscript, including a detailed analysis of the sedimentary changes simulated under the various forcings we tested~~  $\delta^{13}\text{C}$ . Individual proxy records were selected for their resolution or length. This is not an attempt at a comprehensive compilation of proxy records, nor an attempt to understand individual records in detail. Rather we aim to understand why the tested forcings do or do not reproduce prominent spatial or temporal patterns in the proxy records. It is also important to note that our simulations are designed to constrain the potential and plausibility of major contributions of the tested ~~processes~~ forcings to the observed glacial-interglacial atmospheric CO<sub>2</sub> changes, rather than reproducing a full, realistic scenario. ~~In their design, we prescribed the amplitudes and temporal evolution of each simulated process in a simplified way, while their true relative importance for glacial-interglacial carbon cycle changes remains still unknown and might have varied spatially and temporarily.~~ We therefore do not expect that any single simulation presented in our study captures all features of the reconstructed carbon cycle changes over glacial-interglacial cycles. Instead, we investigate the isolated ~~processes~~ forcings, which 320 occurred simultaneously in reality, and quantify their effects during eight consecutive glacial cycles. Comparing our results to proxy records, we can identify the dominant processes behind specific patterns in the reconstructions and the remaining challenges in reconciling the many carbon cycle reconstructions that are now available.

#### 4 ~~Comparison with carbon cycle reconstructions~~

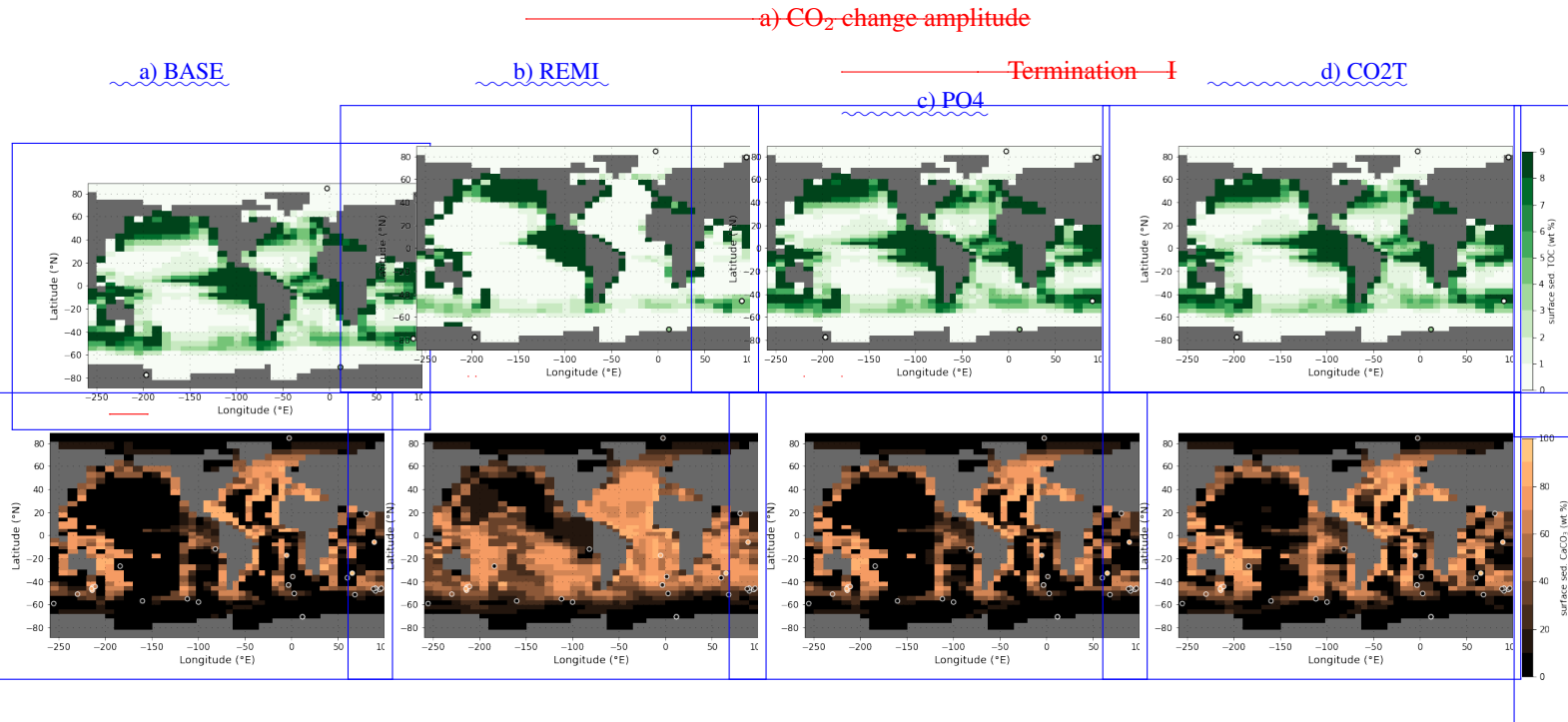
Summary Model-Data comparison. Shown are the factorial effects of the tested processes and their non-linearities in comparison with reconstructed LGM – Holocene differences in various proxy systems. The direction of each arrow indicates whether a difference is positive (pointing upwards, teal-coloured) or negative (pointing downwards, brown-coloured). The width of the arrows shows the size of the difference relative to the reconstruction in the uppermost row "Data". For POM export and global preformed nutrient concentrations, only qualitative reconstructions exist. Hence, the arrows showing simulated effects are normed by the biggest effect by any simulated process.

### 3.1 Sedimentary burial and $\text{CO}_3^{2-}$ concentrations

Table 4 provides a summary of the data-consistency of Reconstructions of global POC burial flux changes over the last glacial cycle (Cartapanis et al., 2016) indicate that POC burial was smallest during interglacials, and gradually rose during glacial phases until it peaked during the LGM.  $fSOWI$ ,  $fREMI$  and  $fPO4$  are the only effects which produce higher POC burial fluxes during glacial maxima than during interglacials (Fig. 2), and the factorial effects of each process we tested for selected carbon cycle proxies, and latter two are the only ones strong enough to overprint the opposite effect due to cooling ( $fBASE$ , Fig. S10). However, the non-linearities that arise when they are combined. The first row shows the reconstructed direction of LGM – Holocene differences, simulated increase in POC burial already occurs during the glacial inception, such that the highest burial rates persist throughout most of the glacial phase while in the reconstructions they remain close to the interglacial value through MIS4. Reconstructions of global  $\text{CaCO}_3$  burial changes over the last glacial cycle (Cartapanis et al., 2018) show that burial rates decreased in most ocean basins during glacial inception, while they increased in the Southern Ocean, resulting in only minor glacial-interglacial changes in the global average. Physical forcings (e.g.  $fSOWI$  in Fig. 2) do not affect  $\text{CaCO}_3$  burial rates during glacial inception, consistent with the reconstruction, while  $fPO4$  and  $fCO2T$  produce burial increases and  $fPIPO$  and the next lines show the direction and relative size (compared to the proxy signal) of changes induced by the various tested processes. The last three rows show the direction and relative size of non-linearities caused by three different combinations of the processes above. For many of the considered proxies, these non-linearities are larger than without interactive sediments (not shown) but still small compared to the effect of individual processes, especially when combining only physical processes. For some proxies, the non-linearities are not negligible but still smaller than the biggest effect of an individual process. Hence, in most cases, proxy changes provide a first-order constraint on the plausibility of large changes in individual processes.  $fBASE$ , the effect of temperature changes due to orbital, albedo and greenhouse gas changes, moves almost all proxy systems in the reconstructed direction (the directions of the arrows match), but almost never to the reconstructed extent (the widths of the arrows do not match). The only exception is strongly reduced export production in the polar Southern Ocean at the LGM, which in our model is predominantly driven by surface cooling and sea ice expansion regardless of which other processes were also changed. The mismatches in amplitudes of  $fBASE$  and reconstructed changes show that other processes must have affected the glacial carbon cycle, at least in our model. In the following sections, we expand on these model-data comparisons and discuss atmospheric  $\text{CO}_2$ , export production, the biological pump, sedimentary fluxes and carbon isotopes in more detail (see also section numbers at the bottom of table 4.  $fREMI$  produce decreases between MIS5 and MIS3. However, the physical forcings fail to decrease  $\text{CaCO}_3$  burial rates during MIS3 und MIS2.  $fREMI$  and

*f*PIPO decrease CaCO<sub>3</sub> burial during MIS3 and MIS2 but cause much larger burial events in MIS1 than reconstructed (Fig. 2, see also Figs S2, S4, S5, S6, S7).

### 360 3.2 Atmospheric CO<sub>2</sub>



**Figure 3.** Atmospheric CO<sub>2</sub> changes across deglaciations. a) Sedimentary POC and CaCO<sub>3</sub> fractions during LGM (Cartapanis et al., 2016; Wood et al., 2023) as reconstructed (circles) shows the factorial contributions to the mean glacial-interglacial CO<sub>2</sub> amplitude over the last five glacial terminations and in simulations PHYS, as well as the range between their minimum REMI, PO4 and maximum CO2T (underlying maps). Light colors indicate results without interactive sediments, full colors indicate results with interactive sediments. Shown are only data points that fall into the local benthic grid box of the model. The root mean square errors of simulated and maximum amplitudes over the last five deglaciations in the ice core record (Bereiter et al., 2015) reconstructed values are shown by the black (from left to right): 7.4 %, 3.3 %, 7.4 % and gray horizontal lines. b) 6.4 % for POC (top row) and 33.6 %, 31.5 %, 33.3 % and 34.4 % for CaCO<sub>3</sub> (bottom row) shows selected factors transiently over the last two terminations.

By design, CO<sub>2</sub> restoring causes marine carbon uptake and release that shape atmospheric CO<sub>2</sub> in line with observations. Most forcings increase the POC content of surface sediments (top 10 cm) during the LGM (Fig. 6, S6 sum of fBASE and fCO2T, S16), so here we focus on the CO<sub>2</sub> changes simulated by the other forcings. PO4, REMI and PIP0 produce the most consistent CO<sub>2</sub> difference between the LGM and PI with regard to the reconstructions (Fig. 6a). The timing of the lowest CO<sub>2</sub> values occurs during the coldest interval of glacial cycles, the glacial maxima, in all simulations except LAND3 (top row), the exception being fREMI, which decreases POC outside the East Pacific. However, too few reconstructions exist for depths that are consistent with our model bathymetry for a quantitative model-data comparison. For CaCO<sub>3</sub>, a few more data

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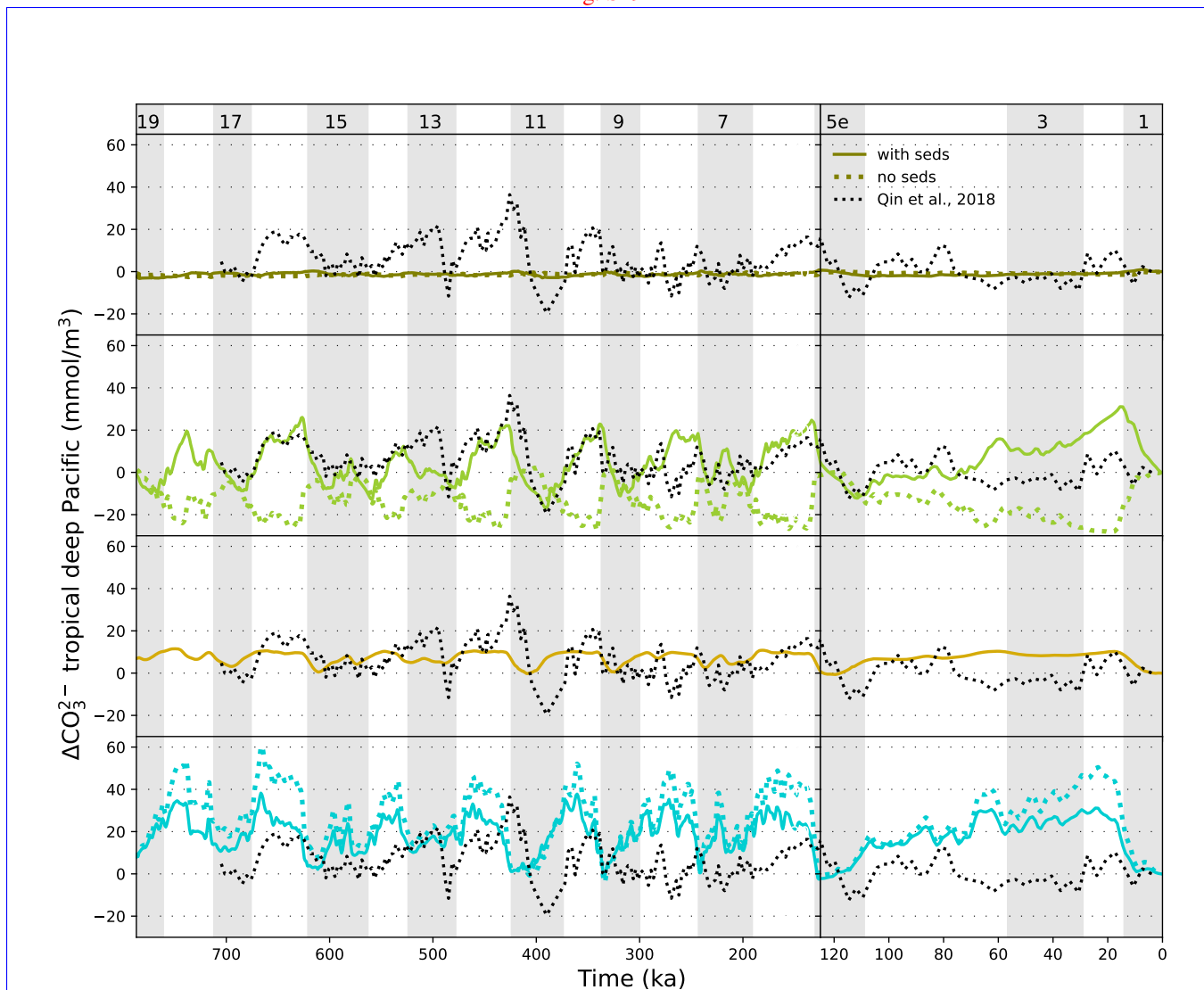
370 points fall within our benthic ocean grid cells. The cooling-related changes ( $fBASE$ ) included in all simulations reproduce a data-consistent carbonate compensation depth (CCD) in most of the Southern Hemisphere extra-tropics but a too high CCD in the tropical South Atlantic and Indian Ocean and a too low CCD off Peru (Fig. 3 bottom row). REMI better captures these tropical CCD changes but produces a too low extra-tropical CCD. These model-data differences indicate that different processes might explain the LGM sedimentary composition in different basins, which is not captured by our globally uniform forcings.

375 The model has been tuned to the pre-industrial  $CaCO_3$  distribution. However, in all simulations  $CO_2$  keeps increasing throughout interglacials when temperature is almost constant. In simulations PO4 and CO2T, this is a consequence of the proxy records used to scale the respective forcing – benthic  $\delta^{18}O$  for PO4 and  $CO_2$  for CO2T, which are not constant during interglacials (Fig. ??) our study late Holocene  $CaCO_3$  contents are the result of almost 800 kyr of transient simulation, which result in imbalances of the geologic carbon cycle at the simulation end even though the forcing is that of the Holocene (Table S2). Differences between the dynamically-achieved and observed pre-industrial sedimentary composition add context to the size of the simulated sedimentary fluxes and memory effects. The dynamically-evolved sedimentary POC content is similar across all simulations, while the  $CaCO_3$  content exhibits large-scale differences (Fig. S11, S12). Simulations with small sediment perturbations during the glacial cycle (e.g. SOWI, AERO and LAND, Fig. S12) result in  $CaCO_3$  contents that are similar to Holocene estimates. In simulations AERO, REMI and PIPO,  $CO_2$  lags the forcing by several thousand years during deglaciations and throughout interglacials (Fig. ?? and ??). In AERO, the lag is caused by the hysteresis behaviour of AMOC and exists in simulations with and without interactive sediments. In REMI and PIPO, the time lags are caused by weathering-burial imbalances, particularly a large build-up of alkalinity and DIC during large deglacial  $CaCO_3$  burial event results in higher sedimentary  $CaCO_3$  contents in the late Holocene than measured. Simulation CO2T, on the other hand, has less sedimentary  $CaCO_3$  content during the late Holocene than measured. This is the glacial phase which is only gradually reduced by enhanced  $CaCO_3$  result of strong dissolution due to forced alkalinity removal from the open ocean during deglaciations, mimicking e.g. coral reef building. It is therefore less likely that sedimentary  $CaCO_3$  burial during deglaciation (Fig. S18). The different correlations between temperature and  $CO_2$  in glacials and interglacials is also a feature of the ice core records (Brovkin et al., 2016), though the timing of peak interglacial  $CO_2$  concentrations and transient features of the atmospheric  $CO_2$  increase during deglaciations in the records is not necessarily reproduced in our idealised simulations with simplified forcings (Fig 6b, right panel). In most simulations, the weathering-burial disequilibrium, which builds up over the glacial phase, amplifies the glacial  $CO_2$  drawdown.

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Difference of the glacial-interglacial atmospheric CO<sub>2</sub> amplitude before and after the MBT in our simulations compared to that in the reconstructed CO<sub>2</sub> record (Bereiter et al., 2015). For the results of the simulations without interactive sediments see Fig-S19



**Figure 4.** Evolution of CO<sub>3</sub><sup>2-</sup> in the tropical deep Pacific as simulated for *f*<sub>BASE</sub>, *f*<sub>REMI</sub>, *f*<sub>PO4</sub> and *f*<sub>CO2T</sub> and reconstructed by Qin et al. (2018). The results of the other forcings are shown in Fig. S13.

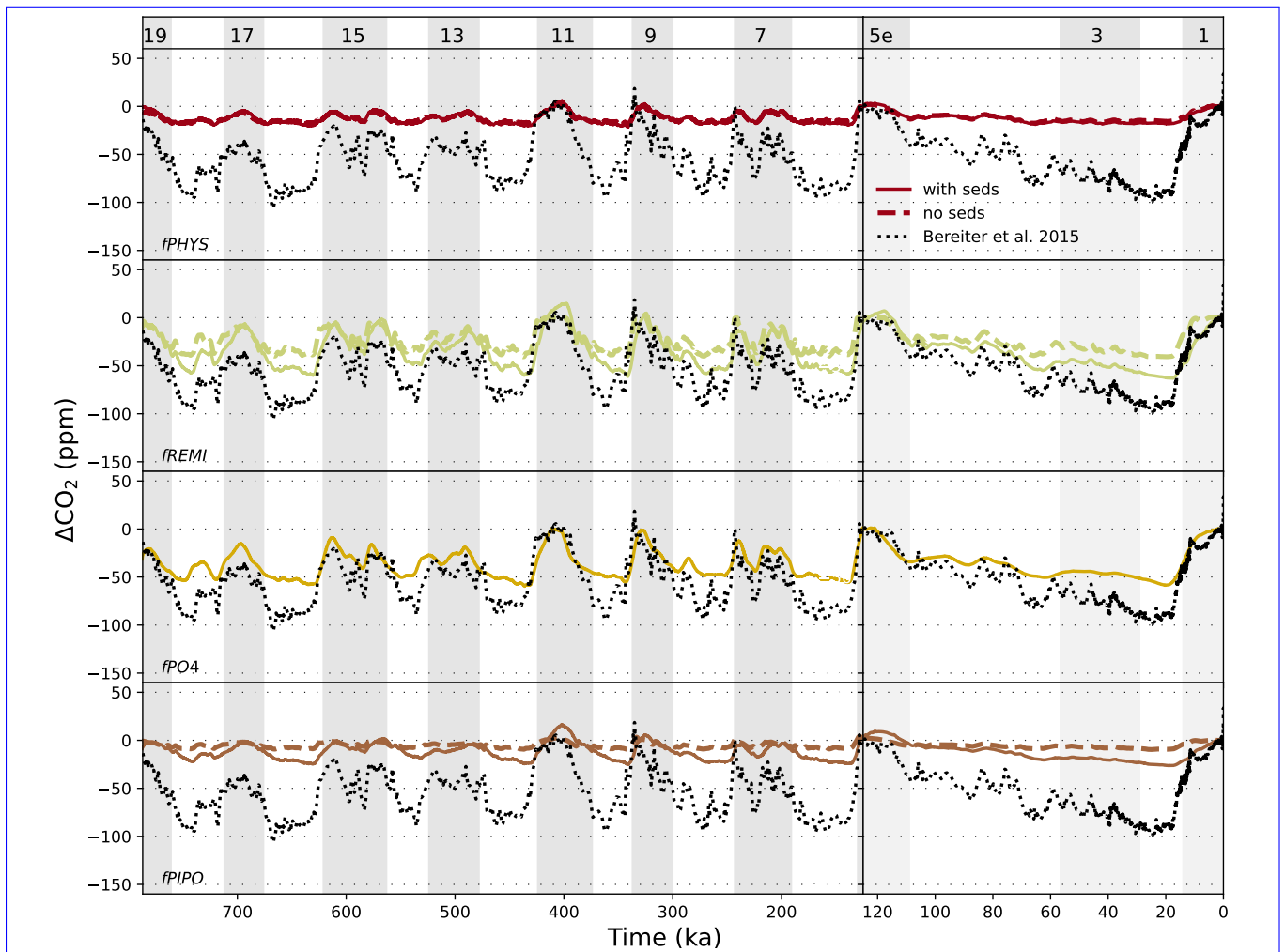
Burial-weathering imbalances also affect the difference between the Next, we address CO<sub>3</sub><sup>2-</sup> changes. Kerr et al. (2017) found a repeated pattern of low benthic CO<sub>3</sub><sup>2-</sup> in the tropical Pacific and Indian Ocean during interglacials and high CO<sub>3</sub><sup>2-</sup> during glacials (difference of 20-55 mmol/m<sup>3</sup>) throughout the last 500 kyrs. Qin et al. (2018) found that the same pattern extended over the last 700 kyrs. Physical forcings (*f*<sub>BASE</sub>, *f*<sub>KGAS</sub>, *f*<sub>SOWI</sub>, *f*<sub>AERO</sub>, *f*<sub>PHYS</sub>) and *f*<sub>PO4</sub> have little effect on deep Pacific CO<sub>3</sub><sup>2-</sup> over glacial cycles (Fig. 4, S13). Under the biogeochemical forcings (*f*<sub>REMI</sub>, *f*<sub>PO4</sub>, *f*<sub>PIPO</sub>,

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*fLAND*), the simulated glacial-interglacial  $\text{CO}_3^{2-}$  difference ranges from a few  $\text{mmol/m}^3$  to  $50 \text{ mmol/m}^3$ , and is caused by invasion of  $\text{CO}_2$  amplitudes of the last five glacial terminations compared to the glacial cycles before. Since maximum temperatures of interglacials were larger during the last four interglacials, the solubility of  $\text{CO}_2$  in seawater was lower, contributing to higher atmospheric  $\text{CO}_2$  levels. This creates a small direct response to the forced interglacial warming after the MBT under the standard forcing (*fBASE*,  $\sim 5 \text{ ppm}$ , Fig. ??). Wind-driven circulation into the ocean, ALK redistributions within the ocean, and weathering-burial imbalances due to changes of the carbonate export flux and carbonate compensation (Broecker and Peng, 1987, Fig. 4 and S13). *fREMI* and *fCO2T* cause the largest  $\text{CO}_3^{2-}$  changes in the deep equatorial Pacific. For the last glacial cycle, these simulated changes are larger than those reconstructed, suggesting that the forcings cause too large ALK re-distributions within the ocean or carbonate compensation during the last glacial cycle. Interestingly, however, during MIS13-MIS11 and the Mid-Brunhes transition, reconstructed  $\text{CO}_3^{2-}$  changes in the deep equatorial Pacific were larger than during the last glacial cycle (Qin et al., 2018, Fig. 4). *fCO2T* and *fREMI*, which produced larger-than-reconstructed  $\text{CO}_3^{2-}$  changes over the last glacial cycle produced  $\text{CO}_3^{2-}$  changes more similar to those reconstructed for MIS13-MIS11. The variability of  $\text{CO}_3^{2-}$  amplitudes between glacial cycles in the record is not reproduced by any of our forcings, but

While the reconstructed deep ocean  $\text{CO}_3^{2-}$  reservoir in the Pacific was relatively stable over the last deglaciation, a large  $\text{CO}_3^{2-}$  increase was reconstructed for the deep Atlantic (Qin et al., 2018; Yu et al., 2019). The different sensitivities of deep ocean  $\text{CO}_3^{2-}$  in the two basins is also apparent in all of our simulations (see examples in Fig. S14 and S15) and is the result of larger circulation and productivity changes in the Southern Ocean (SOWI) have a stronger effect, because in colder interglacials, the deep Pacific remains more isolated than during warm interglacials, preventing the release of an additional 5 ppm in the earlier glacial cycles. Reduced remineralization rates (REMI) and Atlantic than Pacific. However, circulation changes produce lower  $\text{CO}_3^{2-}$  in the deep sub-polar North Atlantic during the LGM, while reconstructions suggest higher  $\text{CO}_3^{2-}$  (Yu et al., 2019). Higher deep Atlantic  $\text{CO}_3^{2-}$  at the LGM requires increased nutrient supply during colder interglacials have the strongest individual effect on carbon storage differences across glacial cycles, each reducing the glacial-interglacial  $\text{CO}_2$  difference by 15 ppm in the early, colder glacial cycles. As already noted in the discussion of absolute  $\text{CO}_2$  concentrations, weathering-burial imbalances play a minor role for the simulated physical effects on the glacial-interglacial (*fPO4*), deeper remineralization (*fREMI*) or a net alkalinity input (*fCO2T*). These patterns appear with and without dynamic sediments in our simulations. Sediments mostly affect the amplitude and temporal evolution of deep  $\text{CO}_3^{2-}$  changes, not their spatial pattern (not shown).

### 3.2 Atmospheric $\text{CO}_2$



**Figure 5.** Transient variations of atmospheric CO<sub>2</sub> due to effects  $f_{PHYS}$ ,  $f_{PO4}$ ,  $f_{REMI}$ , and  $f_{PIPO}$  and reconstructed by Bereiter et al. (2015). Shown is the deviation from the pre-industrial value. Gray shading indicates uneven MIS as indicated at the top of the figure. Dashed lines denote runs without sediment module (not available for PO4). The same plots for the other simulations are shown in S16.

Interactive sediments have a negligible effect on atmospheric CO<sub>2</sub> amplitude but amplify the biochemical effects. In fact, only by including interactive sediments does our model simulate a shift in the MBT changes in our simulations with only physical forcings but largely alter glacial-interglacial CO<sub>2</sub> amplitude comparable to the observations change under biogeochemical forcings (Fig. ??). In most simulations, 5). Marine CO<sub>2</sub> uptake and reduced export production in the simulations with physical forcings causes a net dissolution/reduced deposition of sedimentary CaCO<sub>3</sub> deposition is reduced during glacials and marine alkalinity and DIC build up as a consequence. A large fraction of the glacial DIC pool is eventually incorporated into CaCO<sub>3</sub> and deposited during deglaciations, simultaneously drawing down alkalinity and thus releasing CO<sub>2</sub> to the atmosphere. One effect of interactive sediments is thus the larger of with little effect on outgassing. In simulations with biogeochemical forcings,

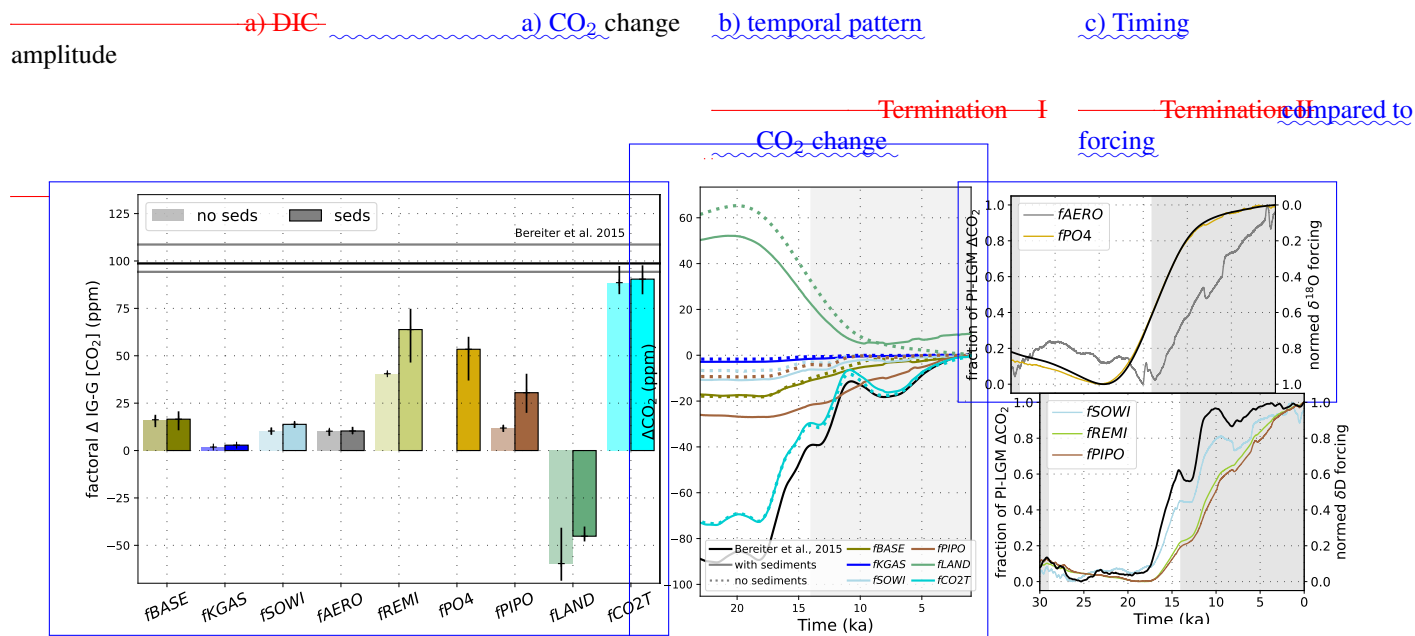
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~~the larger  $\text{CaCO}_3$  burial and alkalinity draw-down during bigger temperature rises at the onset of warm interglacials, which in our simulations is amplified by changes in PIC:POC (PIPO) and the remineralization profile (REMI) perturbations also have a larger effect on sea-air gas exchange. Another effect responsible for the larger  $\text{CO}_2$  amplitude changes under biochemical forcings is the reduction of sedimentary organic carbon burial rates during interglacials under in response to increased nutrient supply ( $\text{PO}_4$  ~~f~~  $\text{PO}_4$ ) or a flattened remineralization profile (REMI ~~f~~  $\text{REMI}$ ) during glacial phases. During deglaciations, sedimentary POC deposited during glacials is remineralized, which raises atmospheric  $\text{CO}_2$  in addition to the previously described alkalinity changes. The larger the temperature rise during deglaciation, the more POC is remineralized.~~

~~In summary, most of the simulated processes cause atmospheric  $\text{CO}_2$  increases during deglaciations, and the good matches with various features of reconstructed glacial-interglacial  $\text{CO}_2$  changes are produced by biochemical changes. Variations of the remineralization profile (simulation REMI) cause the largest deglacial  $\text{CO}_2$  change but at a slower pace than reconstructed. Nutrient supply changes in simulation  $\text{PO}_4$  cause the fastest deglacial  $\text{CO}_2$  rise but with a lower amplitude than REMI. All features of the reconstructed  $\text{CO}_2$  curve can artificially be achieved by changing external alkalinity fluxes ( $\text{CO}_2\text{T}$ ). However, the DIC and further reduces ALK, both contributing to enhanced  $\text{CO}_2$  changes in these simulations are caused by different mechanisms which also leave traces in the proxy record outgassing. We explore the forcing-specific differences in more detail by focusing exemplarily on the last deglaciation.~~

### **3.3 Marine DIC and the surface carbonate system**



**Figure 6.** Factorial DIC concentration Effects of individual forcings on deglacial atmospheric CO<sub>2</sub> changes for each process across deglaciations compared to reconstructions. In a) shows the factorial contribution of each process contributions to the mean glacial-interglacial CO<sub>2</sub> amplitude over the last five glacial terminations (excluding terminations before the Mid-Brunhes transition), as well as the range between their minimum and maximum. Light colours show the colors indicate results without dynamic-interactive sediments, and full colours show the contributions colors indicate results with dynamic-interactive sediments. In b) The mean, minimum and maximum amplitudes over the absolute temporal DIC evolution across two terminations is last five deglaciations in the ice core record (Bereiter et al., 2015) are shown for selected simulations with by the black and without interactive sediments gray horizontal lines. b) shows the factors discussed in the text transiently over the last termination. c) shows time lags between the factors and the respective forcing timeseries.

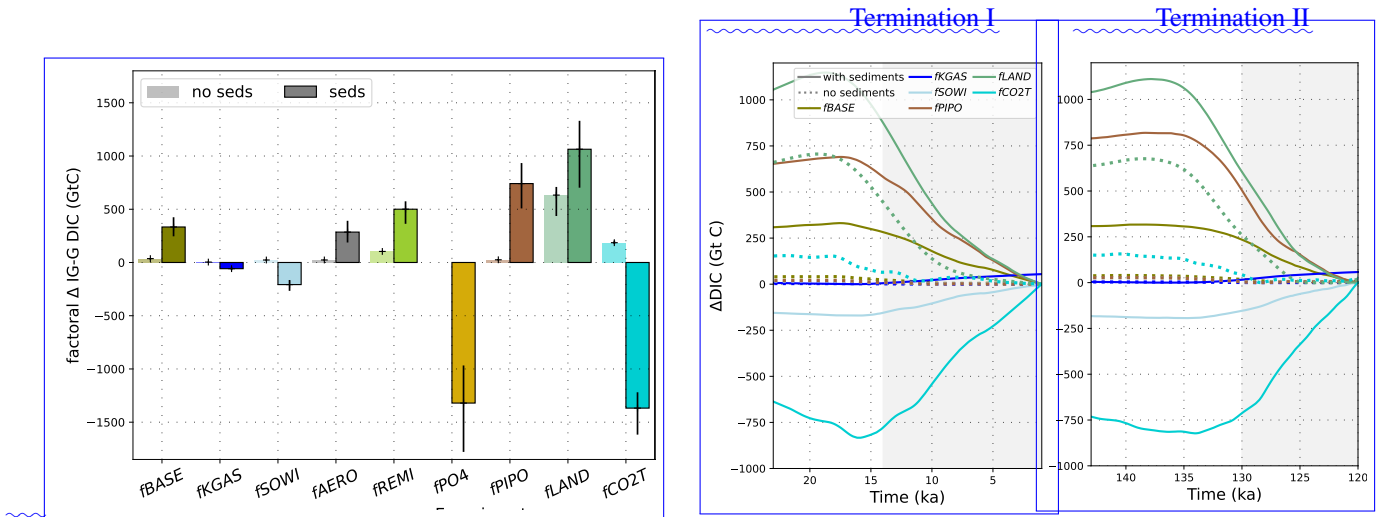
455 The simulated By design, CO<sub>2</sub> changes are the result of changes in carbon uptake in the surface ocean. All forcings strongly affect air-sea carbon fluxes in the Southern Ocean, by changing SST, sea ice, circulation, productivity and/or the carbonate system in the surface ocean. It has long been recognised that the Southern Ocean played an important role in glacial-interglacial changes in the partitioning of carbon between atmosphere and ocean (Wenk and Siegenthaler, 1985; Fischer et al., 2010). In addition to changes in the Southern Ocean, in our simulations surface carbonate system shifts in the non-polar oceans are required to achieve glacial-interglacial restoring causes marine carbon uptake that fills the gap between dynamic atmospheric CO<sub>2</sub> changes in BASE and reconstructions (Fig. 6, S6, S16), so here we focus on the other forcings. Biogeochemical forcings produce the largest CO<sub>2</sub> differences that are consistent with reconstructions. In simulations REMI, PO4 and CO2T, which produce the most data-consistent atmospheric CO<sub>2</sub> between the LGM and PI with regard to the reconstructions (Fig. 5, 6a). In these simulations, the weathering-burial disequilibrium, which builds up over the glacial phase, amplifies the deglacial CO<sub>2</sub> changes, such carbonate shifts occur. Surface ocean pH increases towards the glacial maximum, which is consistent with reconstructions (Fig. S18, Hönisch and Hemming, 2005; Shao et al., 2019). It is noteworthy that in simulation REMI with interactive sediments, surface ocean pH changes align closely with those in simulation CO2T, in which the model was forced

465 ~~to reproduce reconstructed atmospheric rise, particularly in *fREMI* and *fPIPO*. In both cases, sedimentary accumulation of  $\text{CaCO}_3$  spikes during deglaciation, due to increased  $\text{CaCO}_3$  export as the forcings wane (Fig. 2). The corresponding ALK reduction expels more  $\text{CO}_2$  changes. This alignment is visible throughout the glaciation up until the onset of the deglaciation, where pH changes in REMI lack behind those in CO2T. During from the surface ocean into the atmosphere. In the case of *fREMI*, this is further enhanced by a reduction in sedimentary POC accumulation during the deglaciation, pH changes~~  
470 ~~in simulation PO4 show the same speed as in CO2T, even though the amplitude is lower. This mirrors our results from the comparison of the simulated which reduces the C loss to the sediments. Under both forcings, the sedimentary processes that amplify the deglacial  $\text{CO}_2$  rise also reduce its speed and smooth out transient features of the  $\delta\text{D}$  record which are translated into transient atmospheric  $\text{CO}_2$  curves, which showed that REMI produced the most data-consistent changes in simulations without interactive sediments (Fig 6). These time lags are caused by the strengthened export production, which counteracts C degassing,~~  
475 ~~and a large build-up of alkalinity and DIC during the glacial phase (amplified by interactive sediments, Fig. S17) which is only gradually reduced by enhanced  $\text{CaCO}_3$  burial during deglaciations (Fig. S18). If instead export production and sedimentary C accumulation decrease during the deglaciations due to increased nutrient limitation (*fPO4*), the C previously incorporated into biogenic matter is outgassed from the surface ocean and no lag between  $\text{CO}_2$  changes during the glaciation but failed to reproduce the quick  $\text{CO}_2$  rise and the forcing emerges. Weathering-burial imbalances have a smaller effect on circulation-driven~~  
480 ~~deglacial  $\text{CO}_2$  release during the deglaciation. The spatial patterns of marine carbon uptake and release in our simulations are thus driven by combinations of physical and chemical processes. The net carbon fluxes into the ocean during glaciation and out of the ocean during deglaciation are roughly of equal magnitude in the Southern Ocean ( $>40^\circ\text{C-S}$ ) as in the rest of degassing (*fSOWI*, *fAERO*), regarding both amplitude and timing. However,  $\text{CO}_2$  also lags temperature in *fAERO* (with and without interactive sediments), due to the hysteresis of the ocean combined, but of opposite sign, under most forcings~~  
485 ~~and with and without interactive sediments AMOC. Enhanced Southern Ocean wind stress (*fSOWI*) is the only forcing in our simulation set that is able to create fast, transient  $\text{CO}_2$  releases despite weathering-burial imbalances. In all simulations except LAND, the lowest  $\text{CO}_2$  values occur during the coldest interval of glacial cycles, the glacial maxima (Fig. 5, S16). In all simulations in which the deglacial  $\text{CO}_2$  rise lags that of temperature,  $\text{CO}_2$  keeps rising throughout the Holocene. Only by including interactive sediments does our model simulate a shift in the MBT glacial-interglacial  $\text{CO}_2$  amplitude comparable to~~  
490 ~~the observations (Fig. ??S19, S20).~~

### 3.3 Marine DIC and the surface carbonate system

a) DIC change amplitude

b) temporal pattern



**Figure 7.** Factorial DIC concentration changes for each forcing over glacial cycles, from the highest or lowest DIC value during the glacial cycle, depending on which occurs earlier, to the other extreme. In a) factorial contribution of each forcing to the mean DIC amplitude over the last five glacial cycles, as well as the range between their minimum and maximum. Light colours show the without dynamic sediments, and full colours show the contributions with dynamic sediments. In b) the factorial contribution of selected forcings to the temporal DIC evolutions across two terminations is shown with and without interactive sediments.

Due to interactive sediments in our simulations, increased uptake or release of carbon in the surface ocean does not linearly correlate with DIC changes because marine carbon storage is also affected by changes in the deposition and dissolution fluxes of particulate carbon at the ocean-sediment interface. Interactive sediments affect marine carbon, alkalinity, and nutrient concentrations in two important ways: Firstly, sediments form a large **transient-dynamic** reservoir which can store and release large amounts of carbon and nutrients for hundreds to tens of thousands of years. Secondly, sedimentary mass accumulation, dissolution, and remineralization rates control **lithological-sedimentary** burial, the only permanent sink for carbon and nutrients in our simulations and the only mechanism **to-cause-imbalances-between-supply-from-weathering-and-sedimentary-burial-by-which-environmental-change-can-create-imbalances-with-the-prescribed-constant-solute-flux-from-land**. Fluxes into and out of the sediments respond to environmental change, in some cases on the timescale of water mass replacement or regional productivity changes. **Consequently, the-simulated-DIC-change-is-much-larger-than-the-simulated-change-in-atmospheric-carbon-under-physical-and-biochemical-forcings. In-our-simulations-the-ocean-inventory-changed-by-200-1400-GtC-and-the-atmospheric-inventory-by-1-150-GtC-over-the-last-deglaciation. DIC-changes-differ-by-a-factor-of-up-to-28-between-simulations-with-and-without-interactive-sediments, while-Carbon-fluxes-from-the-sediments-directly-affect-the-ocean, but-not-the-atmosphere, which-causes-different-amplitudes-in-the-simulated-DIC-and-atmospheric-CO<sub>2</sub>-changes-in-the-atmosphere-are-maximally-four-times-larger-when-interactive-sediments-are-considered (Figs-7, S3, changes-and-different-timings-of-carbon-accumulation-in-ocean-and-atmosphere. With-interactive-sediments, fBASE, fAERO, fREMI, fPIPO and fLAND produce highest DIC during**

glacial maxima and lowest DIC during interglacials as altered air-sea gas exchange and sediment accumulation result in a net influx of carbon into the ocean during glacial phases. However, while altered air-sea gas exchange still draws down atmospheric CO<sub>2</sub> under *fKGAS*, *fSOWI* and *fPO4*, larger changes to the sediment fluxes remove carbon from the glacial ocean (Fig. 2) and store excess carbon as carbonate and organic carbon in sediments instead of as DIC in the ocean. Consequently, the lowest DIC occurs during glacial maxima rather than during interglacials under these effects (Fig. S4, S5, S7, S23, S25, ??). *fCO2T* alters sedimentary carbonate preservation such that DIC extremes do not occur at the same time as atmospheric CO<sub>2</sub> extremes, but in between, i.e. the DIC maximum occurs during glaciation and the minimum during deglaciation (Fig. S6). Furthermore, the onset of the deglacial CO<sub>2</sub> rise in simulations with sediments does not always coincide with the onset of the deglacial DIC change, as is the case in simulations without sediments. This is simulated e.g. for terminations I and II in *LAND* and *CO2T* due to *fLAND* and *fCO2T* (Fig. S22), and for terminations I, II, III and IV in *PO4* and *ALL* due to *fPO4* and *fALL* (Fig. S21). This suggests that reconstructed DIC changes, e.g., based on radiocarbon (Sarnthein et al., 2013) may be uncertain and do not necessarily imply a comparable CO<sub>2</sub> drawdown from the atmosphere. In simulations *PO4* and *CO2T*, interactive sediments further produces the counter-intuitive result of reduced marine carbon storage during glacial maxima, because in these simulations excess carbon is stored in sediments as carbonate and organic carbon. In the following, we constrain these processes further with additional proxy data.

### 3.4 Export production changes during glacial-interglacial cycles

Export of biogenic matter from the surface ocean exerts a strong control on the carbonate system in the surface ocean and thus the sign and magnitude of the CO<sub>2</sub> flux across the sea-air interface (Volk and Hoffert, 1985). Decreasing temperatures, sea ice expansion, and curtailed nutrient supply due to a weakened circulation during glacials reduce export production in simulations with only physical forcings. In simulation *PO4*, the prescribed enhanced external nutrient input during glacial phases increases export production, while in simulation *REMI*, slowing remineralization rates in the surface ocean has the opposite effect by reducing the amount of nutrients in the surface. The lower PIC:POC ratio of simulation *PIPO* reduces export production of CaCO<sub>3</sub>.

a) *fBASE* *fPHYS* *fREMI* *fPIPO* *fPO4* *fCO2T* *fALL* *fSOWI* *fKGAS* *fLAND* *fCO2T*

— a) *fBASE* *fPHYS* *fREMI* *fPIPO* *fPO4* *fCO2T* *fALL* *fSOWI* *fKGAS* *fLAND* *fCO2T* between the LGM and the PI in simulations *BASE*, *PHYS*, *REMI*, *PIPO*, *PO4* and *CO2T* with interactive sediments. The filled triangles show the reconstructed sign and qualitative magnitude of change based on Kohfeld et al. (2005): black triangles show reconstructed decreases, white triangles show increases. Big triangles show big reconstructed changes, small triangles show small reconstructed changes.

Reviewing changes in various productivity proxies, Kohfeld et al. (2005) reconstructed spatial patterns of productivity changes between the Holocene and the LGM. Specifically, they found lower productivity in the polar oceans and increased productivity in the subpolar Southern Ocean and the tropical and subtropical Atlantic during the LGM. The direction of productivity changes in the Southern Ocean and upwelling areas in our simulations align with the reconstructions in most simulations, particularly with additional cooling and circulation slowdown with the physical forcings (Fig. ??). These changes induced by the physical forcing reduce productivity in the polar oceans and, to a lesser extent increase productivity elsewhere as nutrients are redistributed. AMOC weakening reduces productivity in the North Atlantic. Consequently, simulations that



contain a strong AMOC-weakening (AERO, PHYS) fail to reproduce the reconstructed strong productivity increases in the tropical and North Atlantic. Such a North Atlantic productivity increase is only simulated when AMOC changes are small or external nutrient supply into the North Atlantic is enhanced during glacials (simulation PO4). Increased external nutrient input during glacial phases causes large productivity increases in most of the extrapolar ocean, which is consistent with the reconstructions. The comparison of magnitudes of productivity change between our simulations and reconstructions is more uncertain than comparing the sign of change. Therefore, it must be noted that the standard forcing in BASE also produces small productivity increases in most extrapolar oceans. Yet, the resulting changes in surface ocean carbonate chemistry are far to small to cause data-consistent Across the tested processes, the corresponding ocean DIC inventory changes from glacial to interglacial are -1800–1400 GtC (Fig. 7) while the atmospheric inventory changes by -170–190 GtC (Fig. 6) over the the same period. For individual proceses, DIC changes differ by a factor of up to 28 between simulations with and without interactive sediments, while CO<sub>2</sub> changes, which are better reproduced in simulation PO4. Deepening the mean remineralization depth in simulation REMI produces the biggest mismatch between simulations and reconstructions of export production, although it captures the changes in atmospheric CO<sub>2</sub> well (see previous section). This mismatch indicates that the process behind the simulated carbonate system changes that produced the data-consistent CO<sub>2</sub> changes, large reductions in export production, is not compatible with productivity proxies and did likely not play a dominant role in the real world glacial carbon cycle changes in the atmosphere are maximally four times larger when interactive sediments are considered (Figs 7, 6).

### 3.4 The efficiency of the soft tissue pump during glacial-interglacial cycles

The interplay between export production and ocean circulation influences the strength of the soft tissue pump, i.e. the degree of nutrient depletion in the euphotic zone and the magnitude of the vertical nutrient and DIC gradients (Volk and Hoffert, 1985). Two approaches have been developed to quantify the efficiency of the soft tissue pump: nutrient utilization in the surface ocean Sarmiento (2006) and the fraction of regenerated nutrients in the ocean's interior (Ito and Follows, 2005). No direct proxy exists for these metrics across glacial cycles, but several proxies have been used to constrain their evolution indirectly (see reviews in Galbraith and Skinner, 2020; Sigman and Hain, 2024). Nutrient concentrations have been inferred directly from reconstructed  $\delta^{13}\text{C}$  of DIC and dissolved cadmium concentrations based on modern day correlations, and indirectly from export production reconstructions (e.g. Anderson et al., 2002). Hertzberg et al. (2016) inferred the vertical DIC gradient from the reconstructed vertical  $\delta^{13}\text{C}$  gradient, and (Yu et al., 2019) from the reconstructed vertical CO<sub>3</sub><sup>2-</sup> gradient. These studies suggested that the biological pump was more efficient during the last glacial maximum, i.e. that nutrient utilization was greater and that vertical gradients of DIC were larger in the Southern Ocean, South Pacific and Atlantic, Eastern Equatorial Pacific and North Atlantic. Tools have also been developed to infer regional to global changes in the soft tissue pump efficiency. The deep ocean oxygen concentrations provide constraints on the amount of deep ocean regenerated DIC (Galbraith and Jaccard, 2015) and Vollmer et al. (2022) inferred preformed phosphate concentrations from reconstructed AOU. These studies concluded that regenerated DIC was increased and preformed phosphate decreased in the deep ocean during the last glacial maximum, inferring a net increased efficiency of the global soft tissue pump.

575 Glacial-Interglacial amplitudes of  $\text{PO}_{4,reg}$  changes in all simulations. For BASE, the total amplitude is given, for the other simulations, the additional effect of each forcing to the standard forcing in BASE is shown. Error bars indicate the range of the amplitude across the last five deglaciations:

There are thus indirect proxy constraints for an increased efficiency of the soft tissue pump at the last glacial maximum. We set up one simulation, REMI, with reduced remineralization rates during periods of lower  $\delta\text{D}$  in the ice core record, 580 i.e. colder climate, which directly increases the soft tissue pump efficiency. As previously discussed, the resulting increased soft tissue pump efficiency in the glacial ocean has a large potential to draw down atmospheric  $\text{CO}_2$  and cause the reconstructed accumulation of respired carbon in the glacial ocean, consistent with other modelling studies (e.g. Menviel et al., 2012; Morée et al., 2021). Despite this large potential to cause  $\text{CO}_2$  changes, the soft tissue pump changes in REMI and SOWI do not produce proxy-consistent changes in export production (see above),  $\delta^{13}\text{C}$ ,  $\text{CO}_3^{2-}$  and The magnitude of these DIC changes depends 585 on the forcing strength, which varies between glacial cycles. The lukewarm interglacials of the first 350 kyr of our simulations do not restore the export fluxes and sedimentary  $\text{CaCO}_3$  burial (see table 4 and the next sections). A scenario of several simultaneously occurring processes with different effects on  $\text{CO}_2$  and nutrient concentrations over glacial cycles seems thus more likely than a dominance of soft tissue pump changes. Our simulations also show that a small contribution of soft tissue pump efficiency changes to atmospheric  $\text{CO}_2$  changes is not necessarily in contradiction with the proxy record, as processes 590 that alter the total inventories of nutrients and carbon in the ocean can affect nutrient distributions independently of atmospheric  $\text{CO}_2$ .

With and without interactive sediments, the soft tissue pump efficiency increase in simulation REMI results in increased nutrient utilization in the surface ocean and reduced preformed nutrients in the ocean's interior during glacial phases (Figs ??, 595 ??, ??). Although these metrics by definition do not scale linearly when we consider supply-burial imbalances of phosphate (Fig ??, ??), both metrics suggest that the simulated soft tissue pump efficiency increases during glaciation in REMI. However, the simulated accumulation of regenerated nutrients in the deep ocean is smaller with interactive sediments, even though the simulated glacial-interglacial  $\text{CO}_2$  changes are larger. Without interactive sediments, the vertical nutrient gradient during glacial phases is steepened primarily because a larger fraction of regenerated phosphate, released from decaying organic matter, accumulates in the ocean's interior. The accumulation of nutrients in the deep ocean is lower in the simulation with interactive 600 sediments because the resulting depletion of  $\text{O}_2$  in the deep ocean increases organic carbon burial, and thus phosphate and carbon removal from the ocean. In simulations in which atmospheric  $\text{CO}_2$  changes are dominated by processes other than changes in the soft tissue pump efficiency, changing vertical nutrient gradients can also anti-correlate with atmospheric  $\text{CO}_2$ , even in simulations with a constant marine nutrient inventory and no interactive sediments. For example, this is the case with the standard forcing (BASE) and alkalinity supply changes (CO2T): nutrient utilization and regenerated nutrient concentrations 605 are lower at glacial maxima (Fig. ??, ??) because of reduced export production in a colder ocean with increased sea ice cover. In simulation CO2T, marine alkalinity changes have large effects on atmospheric  $\text{CO}_2$ , while having a marginal effect on marine nutrient distributions (??) by changing the strength of the carbonate pump. preservation required to re-balance the geologic carbon cycle, and so marine DIC concentrations are persistently higher during 800-450 ka than at PI. Interglacials of the last

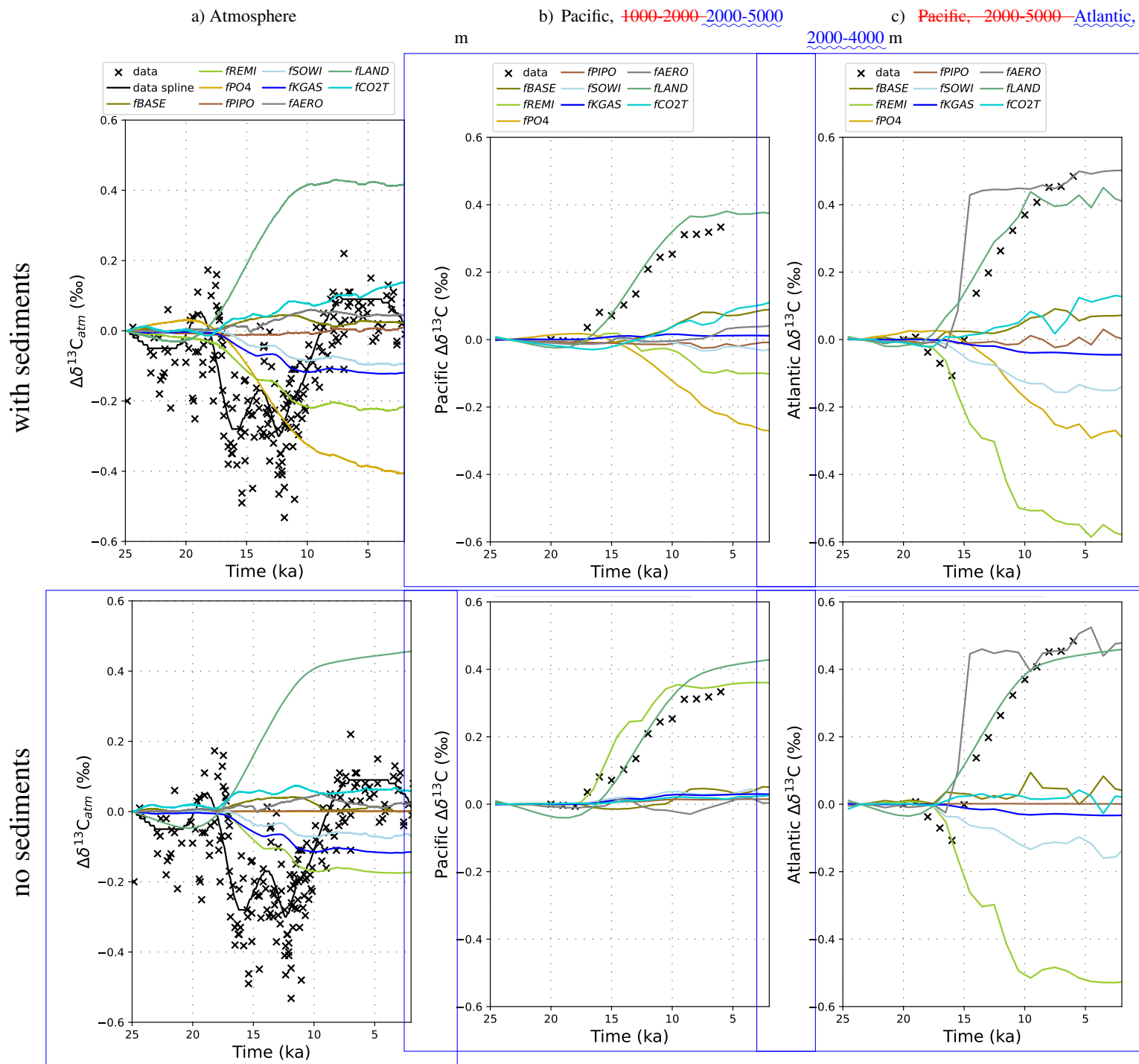
450 kyr of the simulation reduce DIC in the long-term because they are warm and long enough for increased carbon transfer  
610 into sediments and sediment burial.

### 3.4 $\delta^{13}\text{C}$ in the atmosphere and ocean

————— a) AERO ————— b) CO2T ————— c) LAND ————— d) PO4  
 $\delta^{13}\text{C}$  over the last recent glacial cycle in various reservoirs. Solid lines are simulations AERO, CO2T, LAND, and PO4. Dotted lines  
are reconstructions from the Pacific cores ODP 677 and ODP 847, combined and smoothed by Köhler and Bintanja (2008);  
615 regional stacks of sediment cores in the North and South Atlantic (Barth et al., 2018), and Talos Dome ice Eggleston et al. (2016)  
- Results for each individual forcing in an open and closed system are displayed in Fig. ??, ??, ??, ??, ??, ??.

$\delta^{13}\text{C}$  in the atmosphere and ocean is also affected by weathering-burial imbalances. Ice cores preserve the  $\delta^{13}\text{C}$  signature  
of atmospheric  $\text{CO}_2$  (Friedli et al., 1984), which showed large fluctuations during the last glacial cycle (Fig. 8), such as fluc-  
tuations of  $\sim 0.5\text{‰}$  during MIS 4 (71-57 ka, Fig. ??) and during the last deglaciation ( $\sim 18\text{-}8\text{ ka}$ ) (Eggleston et al., 2016).  
620 They also show a long-term trend of lower atmospheric  $\delta^{13}\text{C}$  during the Eemian than the Holocene (Schneider et al., 2013;  
Eggleston et al., 2016). ~~None of the forcings that we applied here produce all of the reconstructed features. In our simulations,~~  
~~the Reconstructions of  $\delta^{13}\text{C}$  changes in marine DIC show different trajectories in different ocean basins and water masses~~  
~~(Oliver et al., 2010; Peterson and Lisiecki, 2018). The  $\delta^{13}\text{C}$  signature of marine DIC in a given location and atmospheric  $\text{CO}_2$~~   
625 ~~is influenced by changes of carbon exchange with the ocean (and land in the case of LAND, BGC and ALL) and the spatial~~  
~~pattern of  $\delta^{13}\text{C}$  in the surface ocean processes which affect the whole marine carbon reservoir (e.g. changes in the size and~~  
~~composition of marine carbon input or output fluxes), as well as by changes in water mass distribution, export production, and~~  
~~isotopic fractionation during sea-air gas exchange and primary production (Jeltsch-Thömmes et al., 2019; Jeltsch-Thömmes and Joos, 2023~~  
~~, with any signal diluted by the 4-box land biosphere. With and without interactive sediments, the cooling induced by the~~  
~~standard forcing in simulation BASE leaves atmospheric  $\delta^{13}\text{C}$  virtually invariant except for minor positive excursions of~~  
630  ~~$\sim 0.05\text{‰}$  as the deep ocean is ventilated during deglaciations (Fig. ??). The largest  $\delta^{13}\text{C}$  variability (up to  $\pm 0.5\text{‰}$ ) is produced~~  
~~by changing organic matter remineralization (REMI) or organic carbon storage (PO4 and LAND). Yet, the gradual trend of~~  
~~reconstructed atmospheric  $\delta^{13}\text{C}$  over the last glacial cycle ( $\sim 0.5\text{‰}$  from inception to LGM) is only achieved in simulation~~  
~~PO4, the forcing with the biggest effect on sedimentary organic carbon storage (Fig. ??). LAND causes similar long-term~~  
~~changes but of the opposite sign. No simulation captures the large millennial-scale fluctuations in the reconstructions (Fig. 8).~~  
635 ~~Given our smoothed forcing and the absence of freshwater forcings, our simulations do not contain realistic millennial-scale~~  
~~circulation changes, which would likely be required to simulate these fluctuations (Tschumi et al., 2011; Menviel et al., 2015)~~  
~~None of the forcings that we applied here produce all of the reconstructed features. However, unlike in PO4, REMI and LAND,~~  
~~the maximum  $\delta^{13}\text{C}$  change produced by circulation and temperature changes (PHYS) is only of roughly half the amplitude~~  
~~of the  $\delta^{13}\text{C}$  swing during the deglaciation. It is established that a complex combination of processes is required to explain the~~  
640 ~~atmospheric  $\delta^{13}\text{C}$  record (e.g. Menviel et al., 2015) but a simulation over the last glacial period or the deglaciation accurately~~  
~~reproducing the reconstructions has not yet been achieved, and reconciling reconstructed with simulated atmospheric  $\delta^{13}\text{C}$~~

~~remains a major challenge for future work~~ they show the importance of considering weathering-burial imbalances in their interpretation.



**Figure 8.**  $\delta^{13}\text{C}$  over the last deglaciation in (a) the atmosphere, (b) intermediate-deep Pacific (120–266°E, -35–55°N) and (c) deep Pacific Atlantic (0–65°N) ocean. Lines are from simulations with an open-system simulation results. Crosses are reconstructions from Schmitt et al. (2012), Eggleston et al. (2016) and Peterson and Lisiecki (2018). All results are shown as differences from 24 ka. Results for with interactive sediments are shown in the closed-system-top row and results without sediments are displayed shown in Fig. ??the bottom row.

The Fig. 8 shows the factorial effects of the different forcings on atmospheric and marine  $\delta^{13}\text{C}$  signature of marine DIC in a given location is influenced by processes which affect the whole marine carbon reservoir (e.g. changes in the size and composition of marine carbon input or output fluxes), as well as by changes in water mass distribution and isotopic fractionation during sea-air gas exchange and primary production, which change the isotopic composition of local DIC (Jeltsch-Thömmes et al., 2019; Jeltsch-Thömmes and Joos, 2023). Changes to the whole marine carbon reservoir are the dominant cause of DIC changes in LAND and CO2T. In simulation LANDC across the last deglaciation in comparison to the reconstructed isotopic shifts in these reservoirs. Under *fLAND*,  $\delta^{13}\text{C}$  changes are driven by the simulated release of isotopically light land carbon (-24 ‰) during glacial inception and throughout the glacial, resulting in  $\delta^{13}\text{C}$  minima in all reservoirs during glacial maxima and large  $\delta^{13}\text{C}$  increases during deglaciation in response to land carbon uptake, with and without interactive sediments (Fig. ??, 8). Equally a This whole ocean shift is the dominant signal in  $\delta^{13}\text{C}_{DIC}$  decrease during the second half of the glacial phase, albeit of lower magnitude, occurred in simulation CO2T, driven by lower  $\text{CO}_2$  and a consequent shift in fractionation that causes increased incorporation of isotopically heavy carbon into biogenic export and burial and therefore removal of isotopically heavy carbon from the ocean (Fig. S6). Compared to LAND and CO2T, deep ocean  $\delta^{13}\text{C}$  changes were inverted in simulations REMI and PO4: deep ocean  $\delta^{13}\text{C}$  increased from glacial inception towards the glacial maximum records of the deep Pacific. In simulations without interactive sediments, *fREMI* also causes a similar shift in the deep Pacific, yet the shift is of opposite sign in simulations with interactive sediments due to the negative geologic POC balance during the deglaciation (Fig. ??, ??) as more POC is buried, removing isotopically light C from the system. In these simulations, during terminations (and in simulation PO4 also during interglacials), a decrease of  $\delta^{13}\text{C}$  is simulated in all dynamic carbon reservoirs as  $\text{CaCO}_3$  burial peaks temporarily and POC burial fluxes return to inter-glacial levels (Jeltsch-Thömmes et al., 2019). In addition, reduced POC fluxes to the sediments and increased ventilation of the deep ocean result in remineralization events of previously deposited sedimentary organic matter. While these tendencies of deep ocean  $\delta^{13}\text{C}$  occur globally in simulation PO4, they are restricted to the Atlantic, particularly the North Atlantic, in simulation REMI.

Because the sensitivities of 2). *fPO4* has a similar isotopic effect on the ocean as *fREMI* with sediments because it also leads to the release of sedimentary organic carbon during the deglaciation. Since the processes that affect  $\delta^{13}\text{C}_{\text{CO}_2}$  and  $\delta^{13}\text{C}_{DIC}$  are different, and  $\delta^{13}\text{C}_{DIC}$  varies between ocean basins, the forcings which best reproduce reconstructed evolution of  $\delta^{13}\text{C}$  changes also vary between atmosphere and ocean, and specific water masses. In the North Atlantic, nutrient input (PO4) and deepening of the remineralization depth (REMI) result in  $\delta^{13}\text{C}$  changes at intermediate depth that are similar to observations (green curve in Fig. ?? and Fig. ??). Yet, under these forcings deep ocean  $\delta^{13}\text{C}$  outside the North Atlantic does not evolve as reconstructed. Deep ocean  $\delta^{13}\text{C}$  in the Pacific and South Atlantic are best reproduced by alkalinity nudging (CO2T) and land carbon release (LAND, blue and yellow lines in Fig. ??). LAND and CO2T are also the only simulations with a persistent  $\delta^{13}\text{C}$  increase in the deep and abyssal Pacific during the last deglaciation, with LAND roughly reproducing the reconstructed amplitude (Fig. 8). The  $\delta^{13}\text{C}$  record of the deep North Atlantic is best reproduced by additional radiative cooling in simulation AERO, due to the resulting AMOC shoaling (purple curve in Fig. ??) (Oliver et al., 2010). This indicates that different processes were likely the dominant controls on  $\delta^{13}\text{C}$  regionally, even if they were not necessarily the dominant drivers of atmospheric  $\text{CO}_2$ . In our simulations, the simulated  $\delta^{13}\text{C}$  at intermediate depth in the North Atlantic is

680 most data-consistent in PO4, followed by AERO, the latter of which also reproduces the reconstructed changes in the deep Atlantic.  $\delta^{13}\text{C}$  at intermediate depth in the North Atlantic might thus have been dominated by changing export fluxes and circulation changes, while the latter dominated  $\delta^{13}\text{C}$ . The impact of interactive sediments also varies between water masses. For example, in the deep North Atlantic. In the deep Pacific and South Atlantic, Pacific accumulation of isotopically light  $\delta^{13}\text{C}$  as in simulation LAND likely dominated in the deep Pacific and South Atlantic. None of our simulations show lower marine benthic  $\delta^{13}\text{C}$  during the Eemian than during the Holocene, as reconstructed from marine sediments (Bengtson et al., 2021) and 685 which may be linked to changes in weathering fluxes not considered here.

### 3.5 Sedimentary burial and $\text{CO}_3^{2-}$ concentrations

Changes in the simulated sedimentary burial fluxes result in net transfers of up to 2000 PgC between the carbon pools of the ocean and sediments throughout a glacial cycle, while the net transfer between the ocean and atmosphere is roughly 200 PgC, and between the terrestrial biosphere and atmosphere on the order of 500-1000 PgC (Jeltsch-Thömmes et al., 2019). The carbon 690 cycle impact of glacial cycles was thus likely larger in the ocean than in the atmosphere (Roth et al., 2014; Buchanan et al., 2016), due to changes in sedimentary carbon storage. How realistic are the simulated fluxes?

————— a) POC burial ————— Simulated and reconstructed (Cartapanis et al., 2016, 2018) relative changes of global POC and  $\text{CaCO}_3$  burial changes over the last glacial cycle. Gray shading indicates odd isotope stages (MIS5e, MIS3 and MIS1).

695 Reconstructions of global POC burial flux changes over the last glacial cycle (Cartapanis et al., 2016) found that POC burial was smallest during interglacials, and gradually rose during glacial phases until it peaked during the LGM. LAND likely dominated (Fig. 8b) but must have over-compensated the sediment-enhanced isotopic effects of fREMI and fPO4, and cannot explain the reconstructed  $\text{CO}_2$  rise (Fig. ??a, see also simulated and reconstructed POC burial rates across the last glacial cycle in Figs S2, S4, S5, S6, S7). Simulations REMI and PO4 are the only single forcing simulations which produce 700 higher POC burial fluxes during glacial maxima than during interglacials. However, in these simulations, the simulated increase in POC burial already occurs during inception, such that the highest burial rates persist throughout most of the glacial phase while in the reconstructions they remain below the Holocene value until MIS2. PO4 also roughly reproduces the magnitude of POC burial changes during the last deglaciation but fails to produce the reconstructed low POC burial rates at the end of the Eemian. The large reconstructed POC burial reduction after the Eemian is only simulated when all biochemical forcings 705 are combined (BGC), and also then is not sustained into MIS4 as indicated by the reconstructions. The sedimentary record indicates that the glacial increase in POC burial occurred predominantly in the Southern Ocean (Cartapanis et al., 2016). In 6). In the deep North Atlantic, the model, surface ocean cooling and sea ice expansion reduce export production in the Southern Ocean during glacial inceptions, which reduces burial rates. External nutrient supply to the glacial Southern Ocean increases the flux of organic particles to the sediments relative to the other forcings and can counteract the climate-driven productivity 710 reductions. Simulation PO4 is thus the simulation which most closely aligns with the geographic pattern of reconstructed POC burial changes during glacial inceptions. In REMI, POC burial remains unchanged in the Southern Ocean and instead increased on continental margins in the Pacific and Indian Oceans. In either case, we have to recall that in our simulations the forcings are

simplified to be globally uniform, which might affect the spatial pattern of simulated burial changes. During deglaciations, the reconstructions show a strong decrease of POC burial in the Southern ocean, while most other ocean areas see burial increases during deglaciations. The latter are captured in most simulations, and are a response to surface ocean warming and enhanced upwelling of nutrients that previously accumulated in the deep ocean during the glacial, but the changes in the Southern Ocean are again best reproduced in simulation PO4.

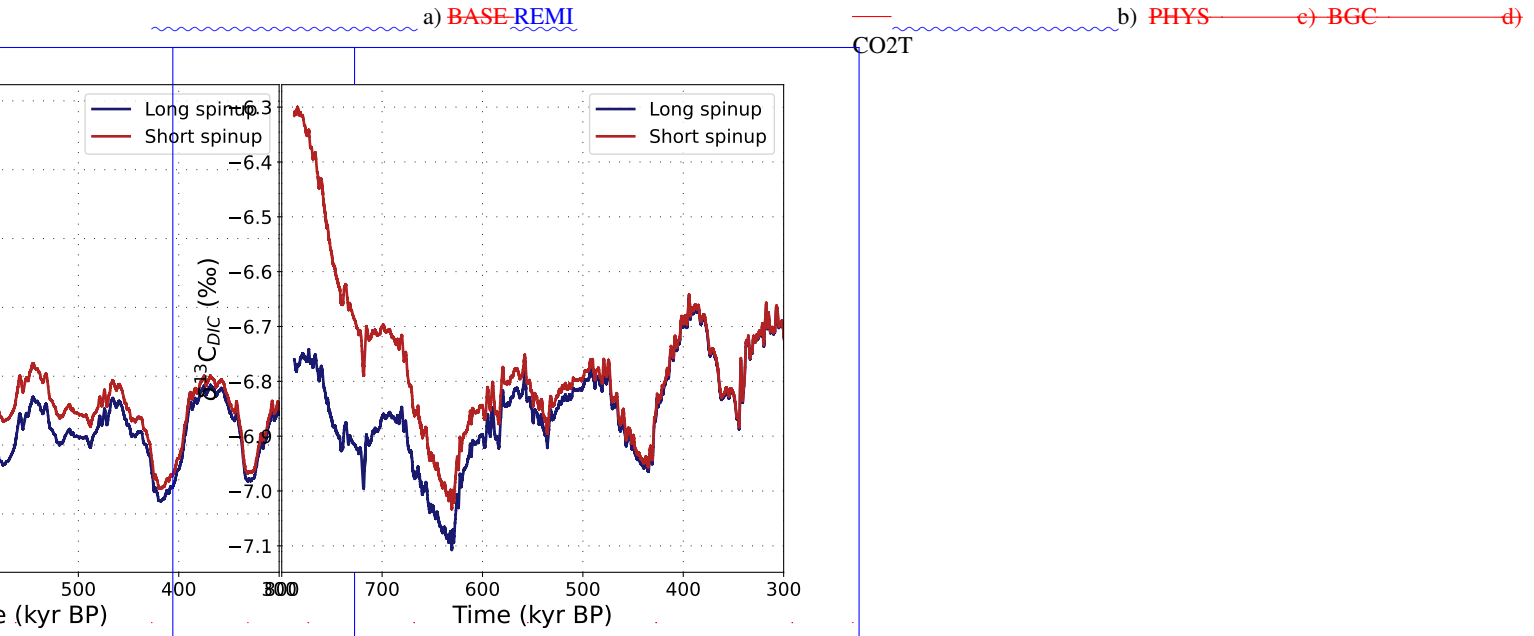
Reconstructions of global  $\text{CaCO}_3$  burial changes magnitude of the  $\delta^{13}\text{C}$  shift can also be reproduced by additional radiative cooling and the resulting AMOC shoaling due to *fAERO* (Fig. 8c) and the simulated isotopic shifts are less affected by interactive sediments.

In the atmosphere, the largest  $\delta^{13}\text{C}$  variability (up to  $\pm 0.5$  ‰) is also produced by *fLAND*, with and without interactive sediments, and by *fREMI* and *fPO4* in simulations with interactive sediments. In fact, the gradual trend of reconstructed atmospheric  $\delta^{13}\text{C}$  over the last glacial cycle (Cartapanis et al., 2018) show that burial rates decreased in most ocean basins during glacial inception, while they increased in the Southern Ocean, resulting in only minor glacial-interglacial changes in the global average. Physical forcings result in roughly constant  $\text{CaCO}_3$  burial rates during glacial inception, as suggested by the reconstruction, while simulations PO4 and CO2T display burial increases and all other simulations decreases between MIS5 and MIS3. The simulations of physical forcings also reproduces decreased  $\text{CaCO}_3$  burial rates starting in MIS4, though at a smaller amplitude than reconstructed ( $\sim 0.5$  ‰ from inception to LGM) is only achieved in *fPO4*, the forcing with the biggest effect on sedimentary organic carbon storage (Fig. ??b), while biochemical forcings produce much larger changes and mostly increased burial. The error in amplitude under biochemical forcings is particularly large during terminations (see also Figs S2, S4, S5, S6, S7). However, biochemical forcings produce more data-consistent spatial patterns of  $\text{CaCO}_3$  burial changes. Simulations PO4 and CO2T are the only setups which produced the reconstructed amplified  $\text{CaCO}_3$  burial in the Southern Ocean between MIS5 and MIS3 (Cartapanis et al., 2018). In PO4, burial rates increase due to increased productivity, and in CO2T due to higher sedimentary preservation in the open ocean (e.g. due to less deposition on shelves or more alkalinity input from weathering). In addition, burial rates continue to rise through the LGM in the Southern Ocean in both simulations, while the reconstructions show that burial rates decreased from MIS-3. It is possible that constraining nutrient supply to the Southern Ocean, e.g. by assuming that meteoric iron fertilization was the dominant nutrient forcing, could change the spatial pattern and result in more data-consistent burial changes during glacial inception. The reconstructed burial rate decline between MIS-3 and the LGM, which is missing in PO4, would then require that one of the other forcings became dominant over changes in nutrient supply. In our simulations, the other forcings all caused Southern Ocean  $\text{CaCO}_3$  burial rates to reach a minimum during the LGM, consistent with the reconstructions<sup>2</sup>). *fLAND* causes similar long-term changes but of the opposite sign. No simulation captures the large millennial-scale fluctuations in the reconstructions (Fig. 8). Given our smoothed forcing and the absence of freshwater forcings, our simulations do not contain realistic millennial-scale circulation changes, which would likely be required to simulate these fluctuations (Tschumi et al., 2011; Schmitt et al., 2012; Menviel et al., 2015). It is well-established that a complex combination of processes is required to explain the atmospheric  $\delta^{13}\text{C}$  record (e.g. Menviel et al., 2015) but a simulation over the last glacial period or the deglaciation accurately reproducing the reconstructions has not yet been achieved, and reconciling reconstructed with simulated atmospheric  $\delta^{13}\text{C}$  remains a major challenge for future work. However, our



simulations show that interactive sediments change the  $\delta^{13}\text{C}$  signals of Earth system changes on deglacial time scales and need to be considered in such future work, despite challenges associated with model spin-up as discussed next.

### 750 3.5 Long isotopic drifts due to weathering-burial imbalances



**Figure 9.** Sedimentary  $\text{CaCO}_3$  fraction during the late Holocene (top row Cartapanis et al., 2018) and LGM (bottom row Wood et al., 2023) as reconstructed (circles) and Comparison of simulated atmospheric  $\delta^{13}\text{C}$  in simulations BASE-REMI and CO2T when started from a 'short spinup', PHYS, i.e. a 70 kyr PI spinup followed by a 2 kyr adjustment to MIS19 conditions, BGC and CO2T (underlying maps) a 'long spinup', i.e. the short spinup plus 215 kyr of transiently simulated MIS19-MIS15.

Model-data comparison for the  $\text{CaCO}_3$  content of surface sediments is more challenging because of the simplified assumption of globally uniform detrital fluxes to the sediment and the coarse model resolution which does not resolve sea mounts and steep slopes. Yet, large-scale resemblance or mismatch of simulated and reconstructed sedimentary  $\text{CaCO}_3$  fraction can still offer some constraint on the reasonability of the simulated processes. For the LGM, the simulated distribution of sedimentary  $\text{CaCO}_3$  under the standard forcing (BASE) shows good agreement with the reconstructions by Wood et al. (2023) in most ocean basins. An important technical lesson of our simulations is that the long adjustment timescale in the geologic carbon cycle also presents an initialization problem, especially for carbon isotopes (Jeltsch-Thömmes and Joos, 2023). We started our experiments from MIS19, which was a colder interglacial than the the Holocene, and Holocene conditions were not reached during the lukewarm interglacials of the first 400 kyr of the simulations. In simulations with interactive sediments, the initial imbalance between weathering inputs derived from the pre-industrial spin-up and burial fluxes adjusting to the colder lukewarm interglacials and glacial states caused  $\delta^{13}\text{C}$  drifts during the first glacial cycles (Fig. 3). The low  $\text{CaCO}_3$  content at the North Pacific

margins is better simulated in REMI with slower remineralization rates in the surface ocean. Yet, no simulation reproduces the reconstructed low  $\text{CaCO}_3$  content in the North Atlantic and high  $\text{CaCO}_3$  content in the equatorial Pacific. The model has been tuned to the pre-industrial  $\text{CaCO}_3$  distribution, however, in our study late Holocene  $\text{CaCO}_3$  contents are the result of almost 800 kyr of transient simulation. The model-data match for the Holocene is relatively good for simulations with small sediment perturbations during the glacial cycle, especially simulations BASE, KGAS, SOWI, AERO and LAND, but also PO4 which does not produce a  $\text{CaCO}_3$  burial spike during deglaciations. In simulations REMI and PIPO, however,  $\text{CaCO}_3$  burial rates have not yet stabilised by the end of 9). Consequently, the simulations after the large  $\text{CaCO}_3$  burial event during the last deglaciation, resulting in much higher sedimentary  $\text{CaCO}_3$  contents in the Holocene than reconstructed. Simulation CO2T, on the other side, has less sedimentary  $\text{CaCO}_3$  content during the Holocene than reconstructed. This is the result of strong dissolution due to forced alkalinity removal from the ocean during deglaciations.

Evolution of  $\text{CO}_3^{2-}$  in the tropical deep Pacific as simulated in simulations BASE, PHYS, BGC and ALL and reconstructed by Qin et al. (2018). The results of the other forcings are shown in Fig. S13.

Comparing our simulation results to reconstructed  $\text{CO}_3^{2-}$  changes is another test of how realistic the simulated carbonate system changes during glacial cycles are. Kerr et al. (2017) found a repeated pattern of low benthic  $\text{CO}_3^{2-}$  in the tropical Pacific and Indian Ocean during interglacials and high  $\text{CO}_3^{2-}$  during glacials (difference of 20-55  $\text{mmol/m}^3$ ) across the last 500 kyrs. Qin et al. (2018) found that the same pattern extended over the last 700 kyrs. In our simulations with purely physical forcings (BASE, KGAS, SOWI, AERO, PHYS) and PO4 simulated glacial-interglacial  $\delta^{13}\text{C}$  signal over this period is altered by the long-term adjustment of the geologic carbon cycle. We addressed this issue by transiently simulating two full glacial cycles before starting the experiments. The magnitude of the initial imbalance in the geologic carbon cycle, and hence isotopic drift, depended on the simulated forcing and was largest in simulations REMI,  $\text{CO}_3^{2-}$  is almost constant over glacial cycles (Fig. 4, S13). In PIPO, LAND, REMI and PIPO and CO2T the simulated  $\text{CO}_3^{2-}$  changes are closer to the reconstructed magnitude.  $\text{CO}_3^{2-}$  maxima during glacial maxima are present in all simulations with interactive sediments, the glacial-interglacial difference ranging from a few  $\text{mmol/m}^3$  to 110  $\text{mmol/m}^3$ , and is caused by invasion of  $\text{CO}_2$  into the ocean and weathering-burial imbalances due to changes of the carbonate export flux and sediment dissolution (Fig. 4 and S13). In simulations without interactive sediments, this glacial  $\text{CO}_3^{2-}$  maximum is not simulated in PIPO, REMI and LAND. Importantly, the drift is a result of perturbing the sediment-weathering balance. The drift can therefore not be corrected for with a control simulation without forcing, because it only appears in the perturbed system. Instead, to avoid a drift, the experiment needs to start from an isotopically balanced geologic carbon cycle, which most commonly will require a long spin-up with a fully-coupled, open system, ideally over several glacial cycles especially when simulating large changes of the biological pump or marine carbonate system. We suggest that the size of the transient imbalance of the geologic carbon cycle, and thus the length of the required spin-up, could be minimized by balancing the geologic carbon cycle not for an interglacial state but for the mean burial fluxes over a full glacial cycle.

————— a) without sediments ————— b) with sediments



During the last deglaciation, reconstructions of  $\text{CO}_3^{2-}$  of The data references are provided at the deep equatorial Pacific showed only small variability, which is solely simulated with purely physical forcings or in simulations without interactive sediments (Fig. ??). The offset from the reconstructed glacial values and the large changes during the deglaciation suggest that all applied changes to nutrient supply (PO4) and remineralization (REMI) cause too large weathering-burial imbalances of alkalinity. While net alkalinity removal from the ocean during deglaciation (e.g. by shallow deposition, coral reef growth or strongly reduced weathering inputs) can cause widespread dissolution which might diminish excess accumulation of  $\text{CaCO}_3$  (see above), it cannot offset the strong  $\text{CO}_3^{2-}$  decrease which is not part of the reconstructions but caused by bottom of the applied nutrient and remineralization forcings table.

Interestingly, during MIS13-MIS11 and the Mid-Brunhes transition, reconstructed  $\text{CO}_3^{2-}$  changes in the deep equatorial Pacific were much larger than during the last glacial cycle (Fig. 4). Such variability of  $\text{CO}_3^{2-}$  amplitude between glacial cycles is not reproduced by any of our simulations, but simulations CO2T and REMI, which produced larger than reconstructed  $\text{CO}_3^{2-}$  changes over the last glacial cycle produced  $\text{CO}_3^{2-}$  changes more similar to those reconstructed for MIS13-MIS11 The direction of each arrow indicates whether a difference is positive (pointing upwards, teal-coloured) or negative (pointing downwards, brown-coloured).

a) fBASE Selected by fBASE effects on simulated LGM-PI differences in deep  $\text{CO}_3^{2-}$  (3500 m depth). The width of the arrows shows the size of the difference relative to the reconstruction in the uppermost row "Data". For POM export only qualitative reconstructions exist. Hence, the arrows showing simulated effects are normed by the biggest effect of any forcing.

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a) fBASE Selected by fBASE effects on simulated LGM-PI differences in deep  $\text{CO}_3^{2-}$  (3500 m depth). The width of the arrows shows the size of the difference relative to the reconstruction in the uppermost row "Data". For POM export only qualitative reconstructions exist. Hence, the arrows showing simulated effects are normed by the biggest effect of any forcing. **Table 2. Comparison** Quantified metrics of simulated the carbon cycle according to reconstructions and reconstructed (Yu et al., 2013)  $\text{CO}_3^{2-}$  changes model responses in our set of simulations with sediments. Shown are the deep-factorial effects of the tested forcings and their non-linearities in comparison with reconstructed differences (3500 m LGM minus Holocene) West Equatorial Pacific with over the last deglaciation (specific times of the comparisons vary slightly by proxy record, depending on temporal resolution and without dynamic sediments record length, and are indicated in the table header) in various proxy systems.

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While the reconstructed deep ocean  $\text{CO}_3^{2-}$  reservoir in the Pacific was relatively stable over the last deglaciation, a large  $\text{CO}_3^{2-}$  increase was reconstructed for Table 4 provides an overview of different proxy signals that are produced in by our factorial forcings, and the non-linearities that arise when they are combined, with interactive sediments over the last deglaciation. The first row shows the reconstructed direction of LGM - Holocene differences, and the next lines show the direction and relative size (compared to the proxy signal) of changes induced by the various tested forcings. The last four rows show the direction and relative size of non-linearities caused by three different combinations of the forcings above. For many of the considered proxies, the deep Atlantic Qin et al. (2018); Yu et al. (2019). The different sensitivities of deep ocean  $\text{CO}_3^{2-}$  in signals are strongly amplified by the dynamic weathering-burial imbalances, and also the non-linearities are larger with than without interactive sediments. However, the two-basins is also apparent in all of our simulations (see examples in Fig. ?? and S15) and is the result of larger circulation and productivity changes in the Atlantic than Pacific. However, circulation changes produce lower  $\text{CO}_3^{2-}$  in the deep subpolar North Atlantic during the LGM, while reconstructions suggest higher  $\text{CO}_3^{2-}$  (Yu et al., 2019). Higher deep Atlantic  $\text{CO}_3^{2-}$  at the LGM requires increased nutrient supply ( $\text{PO}_4$ ), deeper remineralization (REMI) or a net alkalinity input ( $\text{CO}_2\text{T}$ ). These patterns appear with and without dynamic sediments in our simulations. Sediments mostly affect the amplitude and temporal evolution of deep  $\text{CO}_3^{2-}$  changes, not their spatial pattern (not shown).

#### 810 4.1 Imbalances of the geologic carbon cycle

non-linearities are still small compared to the effect of individual biogeochemical forcings, and for some proxies of similar size as the effect of physical forcings. Hence, in most cases, proxy changes provide a first-order constraint on the plausibility of large changes in individual processes.  $f\text{BASE}$ , the effect of temperature changes due to orbital, albedo and greenhouse gas changes, moves almost all proxy systems in the reconstructed direction (the directions of the arrows match), but almost never to the reconstructed extent (the widths of the arrows do not match). It is only sufficient to explain strongly reduced export production in the polar Southern Ocean at the LGM, which in our model is predominantly driven by surface cooling and sea ice expansion regardless of which other processes also occurred.

The previous model-data comparison showed that weathering-burial imbalances increase the potential of many forcings to draw down  $\text{CO}_2$  during glacial periods and buffer carbon cycle changes during deglaciations. We identified two processes which are most effective at raising by which weathering-burial imbalances most effectively raise atmospheric  $\text{CO}_2$  during deglaciations in our simulations: Alkalinity removal and organic carbon remineralization. In simulations PIPO, REMI, BGC and ALL Under  $f\text{PIPO}$  and  $f\text{REMI}$  the combination of high alkalinity at the end of glacial phases and increased  $\text{CaCO}_3$  export production during deglaciation causes large transient  $\text{CaCO}_3$  deposition events in the open ocean (Fig. S252) which remove the excess glacial alkalinity and thus drive a large but slow continuous  $\text{CO}_2$  rise compared to the reconstruction. The marine DIC and alkalinity that built up over the previous glacial phase are too large to be removed instantly, and the resulting large deposition of  $\text{CaCO}_3$  during the deglaciation persists far into the interglacial. In consequence, these simulations produce poorer model-data matches for Holocene  $\text{CaCO}_3$  and marine  $\delta^{13}\text{C}$  distributions than the initial PI spinup (see Fig. ??,??). We also showed that the resulting  $\delta^{13}\text{C}$  and  $[\text{CO}_3^{2-}]$  changes signals in the deep Pacific are not consistent with reconstructions. In  $\text{CO}_2\text{T}$ , alkalinity removal is forced.  $f\text{CO}_2\text{T}$  shows the effect of forced alkalinity removal during glacialiations

830 to reproduce the reconstructed atmospheric CO<sub>2</sub> record, and can serve to study the effect of alkalinity removal through means other than deep ocean CaCO<sub>3</sub> burial (e.g. shallow deposition, coral reef growth, reduced terrestrial input) on other proxy systems. ~~In this simulation, This forcing causes deep ocean CaCO<sub>3</sub> dissolution occurs during the deglaciation and marine DIC increases, resulting in more proxy-consistent and increasing marine DIC during the deglaciation, moving  $\delta^{13}\text{C}$  changes~~ in the deep Pacific ~~but still in the proxy-consistent direction but still producing~~ a large mismatch in [CO<sub>3</sub><sup>2-</sup>]. ~~Alternatively, in~~  
835 ~~simulation PO4, the  $f_{\text{PO4}}$  results in a deglacial CO<sub>2</sub> rise is largely caused by due to~~ a reduction in export production and increased remineralization of sedimentary organic matter which accumulated during the previous glacial period ~~under reduced benthic O<sub>2</sub> concentrations~~. The resulting CO<sub>2</sub> increase is of similar amplitude as that ~~in simulation REMI due to  $f_{\text{REMI}}$~~  but happens faster, more consistent with the reconstruction. In addition, deep Pacific [CO<sub>3</sub><sup>2-</sup>] is less perturbed by this ~~process than in REMI or CO<sub>2</sub> effect than by  $f_{\text{REMI}}$  or  $f_{\text{CO2T}}$~~ , yet deep ocean  $\delta^{13}\text{C}$  is shifted in the wrong direction.

840 ~~There are several ways, however, in which the amplitude or regional pattern of the simulated changes might be biased by our experiment design. Firstly, by design our forcings are smooth in time and spatially uniform, which is a stark simplification. For example, the PO4 forcing ties nutrient supply to the  $\delta^{18}\text{O}$  record. The correlation between dust (iron source to the open ocean) concentrations in the EPICA Dome C ice core and benthic  $\delta^{18}\text{O}$  is of first order only and varies over the glacial cycle (Winckler et al., 2008). Several macro- and micronutrients were likely supplied to varying parts of the glacial ocean~~  
845 ~~(Broecker, 1982b; Martin, 1990; Pollock, 1997; Deutsch et al., 2004) and while dust flux changes seem to correlate globally (Kukla et al., 1990; Winckler et al., 2008), the timings and rates of other nutrient fluxes might in reality have varied temporally and spatially. Similarly, our other forcings might change more slowly over the deglaciation than the real processes they represent.~~

~~Another simplification in our experiment design is that the majority of our simulations assume temporally constant carbon~~  
850 ~~inputs although in reality these fluxes are climate sensitive (Munhoven, 2002). It is unlikely that removing this simplification could resolve the bias in simulated global carbon fluxes and reservoir size changes because it is estimated that global weathering rate changes during glacial cycles were small despite large local variability, possibly because they canceled out in the global mean (Jones et al., 2002; Von Blanckenburg et al., 2015; Frings, 2019; Börker et al., 2020). It was estimated that glacial-interglacial weathering flux changes altered atmospheric CO<sub>2</sub> by a maximum of 20 ppm (Köhler and Munhoven, 2020). Yet, the resulting~~  
855  ~~$\delta^{13}\text{C}$  perturbation could be larger because a global balance in carbon flux changes does not imply a balance in carbon isotope fluxes (Jeltsch-Thömmes and Joos, 2023). Additionally, there might have been non-linear changes in isotopic input fluxes during the simulated time period.~~

~~Finally, the imbalance between weathering and burial fluxes is also shaped by the sedimentation rate. In our simulations, sedimentation rates vary due to changes in biogenic export, yet accumulation of non-biogenic material remained constant. This~~  
860 ~~omission, however, does not seem to be the source of large errors. In a sensitivity experiment, we prescribed step-wise 30% increases and decreases of the non-biogenic flux in the PI steady state, which had only marginal effects on atmospheric CO<sub>2</sub>, DIC and sedimentary accumulation of biogenic particles (Fig. S1).~~

~~Regardless of which process or combination of processes we simulated, no simulation reached a weathering-burial equilibrium by the late Holocene. It seems likely that carbon burial in marine sediments was still adjusting to interglacial conditions at the~~

865 beginning of the industrial revolution. This is also indicated by the reconstructed changes in global sedimentary burial rates over the last glacial cycle, which suggest that burial fluxes changed throughout the Eemian and the current interglacial and only find apparent balances during the longer glacial phases (Fig S3, Cartapanis et al., 2016, 2018).

870 ~~\_\_\_\_\_ a) REMI \_\_\_\_\_ b) CO2T~~ Comparison of simulated atmospheric  $\delta^{13}\text{C}$  in simulations REMI and CO2T when started from a 'short spinup', i.e. a 50 kyr PI spinup followed by a 2 kyr adjustment to MIS19 conditions, and a 'long spinup', i.e. the short spinup plus 215 kyr of transiently simulated MIS19-MIS15.

On a technical note, the long adjustment timescale in the geologic carbon cycle also presented an initialization problem, especially for carbon isotopes (Jeltsch-Thömmes and Joos, 2023). We started our experiments from MIS19, which was a colder interglacial than the the Holocene, and Holocene conditions were not reached during the lukewarm interglacials of the first 400 kyr of the simulations. In simulations with interactive sediments, the initial imbalance between weathering inputs derived from the pre-industrial spin-up and burial fluxes adjusting to the colder lukewarm interglacials and glacial states caused  $\delta^{13}\text{C}$  drifts during the first glacial cycles (Fig. 9). Consequently, the simulated glacial-interglacial  $\delta^{13}\text{C}$  signal over this period is altered by the long-term adjustment of the geologic carbon cycle. We addressed this issue by transiently simulating two full glacial cycles before starting the experiments. The magnitude of the initial imbalance in the geologic carbon cycle, and hence isotopic drift, depended on the simulated forcing and was largest in simulations REMI, PIP0 and CO2T. Importantly, the drift is a result of perturbing the sediment-weathering balance. The drift can therefore not be corrected for with a control simulation without forcing, because it only appears in the perturbed system. Instead, to avoid a drift, the experiment needs to start from an isotopically balanced geologic carbon cycle, which most commonly will require a long spin-up with a fully-coupled, open system, ideally over several glacial cycles especially when simulating large changes of the biological pump or marine carbonate system. We suggest that the size of the transient imbalance of the geologic carbon cycle, and thus the length of the required spin-up, could be minimized by balancing the geologic carbon cycle not for an interglacial state but the mean burial fluxes over a full glacial cycle. Future work will have to test which combinations of these processes are most consistent with the wide range of available proxy data.

## 5 Discussion

It is well established that cooling and circulation changes altered sea-air gas exchange and increased deep ocean carbon storage by isolating it from the surface during glacial phases (e.g. Brovkin et al., 2007). Combined, these effects contribute to changes in atmospheric  $\text{CO}_2$  in our simulations that are comparable to Brovkin et al. (2012) (26 ppm compared to 30 ppm). Our simulations also capture some transient features of of sea-air gas exchange variability over the last glacial cycle that have been simulated by Brovkin et al. (2012). For example, we found a brief atmospheric  $\text{CO}_2$  increase between 110 and 90 ka due to circulation changes, but only in simulations in which AMOC has already weakened substantially by this point, i.e. those with feedbacks that amplify orbitally-driven cooling (e.g. increased aerosol load). Brovkin et al. (2012) showed that a higher vertical diffusivity in the Southern Ocean increases the sensitivity of the sea-air  $\text{CO}_2$  flux to sea ice changes. Raising the vertical diffusivity of ice-free areas by an order of magnitude in their model resulted in an additional  $\text{CO}_2$  draw-down of 10 ppm during

~~inception due to Southern Ocean cooling. We did not test the effect of such change in our simulations, but reducing the piston velocity in the Southern Ocean by up to 40 % in simulation KGAS caused an additional CO<sub>2</sub> draw-down of only ~2 ppm.~~

900 Isolating the deep Pacific through ~~increased~~reduced Southern Ocean wind forcing (~~simulation SOWI~~effect *f*SOWI) caused a glacial CO<sub>2</sub> decline by ~13 ppm, the biggest CO<sub>2</sub> draw-down on top of the effect orbital cooling (*f*BASE) of any isolated physical forcing that we tested. Tschumi et al. (2011) showed that this effect also has the potential to cause larger CO<sub>2</sub> draw-down with sedimentary amplification than simulated here. The idealised, strong reductions in wind speeds over the Southern Ocean prescribed by Tschumi et al. (2011) as a tuning knob for producing old deep ocean waters are unrealistic, but other processes could have contributed to increased isolation of the deep Pacific. Bouttes et al. (2011) showed that during glacial stages enhanced brine rejection during sea ice formation can isolate abyssal waters and cause atmospheric CO<sub>2</sub> and  $\delta^{13}\text{C}$  changes that are similar to those reconstructed. Enhanced brine rejection could thus have provided an additional physical process that increased the glacial marine carbon storage. The strength of this process, however, is only poorly constrained, and Ganopolski and Brovkin (2017) showed that, at a sufficient strength to significantly affect deep ocean carbon storage, this process creates  
905 bigger  $\Delta^{14}\text{C}$  anomalies in the deep ocean than reconstructed. Following (~~Menviel et al., 2011~~)Menviel et al. (2011), they also argue that the timing of increased sea ice formation and atmospheric CO<sub>2</sub> changes during the last deglaciation (Roberts et al., 2016) are not entirely consistent with a strong control of brine formation rates on marine carbon storage.

In further agreement with other modelling studies, e.g. Buchanan et al. (2016) and Morée et al. (2021), we find that changing the efficiency of the biological pumps (*f*REMI) is an efficient mechanism to achieve glacial-interglacial atmospheric  
915 CO<sub>2</sub> changes similar to those reconstructed from ice cores~~and to reproduce the reconstructed decreased preformed nutrient concentrations during glacial phases (Ito and Follows, 2005; Vollmer et al., 2022)~~. However, because of its large effects on deep Pacific [CO<sub>3</sub><sup>2-</sup>] and CaCO<sub>3</sub> accumulation during deglaciation it was unlikely the dominant carbon cycle change over the last glacial cycle. ~~Several biochemical forcings in addition to reduced remineralization in the surface ocean (REMI) substantially reduce atmospheric CO<sub>2</sub>, especially increased nutrient and alkalinity supply (PO<sub>4</sub>, CO<sub>2</sub>T). The low glacial DIC in the former simulations also shows that CO<sub>2</sub> removal from the atmosphere in theory does not need to result in increased DIC in the ocean. Instead, these biochemical forcings cause sedimentary changes that can store large amounts of carbon in inorganic and organic sedimentary matter.~~

A relevant role of marine sediments, particularly sedimentary CaCO<sub>3</sub>, in glacial-interglacial carbon cycle dynamics has long been discussed (e.g. Broecker, 1982b; Broecker and Peng, 1987; Opdyke and Walker, 1992; Archer and Maier-Reimer,  
925 1994; Raven and Falkowski, 1999) and shown in numerical experiments of differing physical and ~~biochemical~~biogeochemical complexities (Ridgwell et al., 2003; Joos et al., 2004; Tschumi et al., 2011; Menviel et al., 2012; Roth et al., 2014; Wallmann et al., 2016; Ganopolski and Brovkin, 2017; Jeltsch-Thömmes et al., 2019; Köhler and Munhoven, 2020; Stein et al., 2020; Kobayashi et al., 2021). In agreement with other studies (e.g. Ganopolski and Brovkin, 2017; Köhler and Munhoven, 2020), we find that changing marine alkalinity can produce large CO<sub>2</sub> changes. Organic carbon storage is less often considered  
930 in modelling studies, although it also showed significant changes across the last glacial cycle (Cartapanis et al., 2016). Out of the ~~processes forcings~~ we tested, ~~increased nutrient supply~~reduced nutrient limitation during glacial phases (~~simulation PO<sub>4</sub>~~*f*PO<sub>4</sub>) produces temporal and regional organic carbon deposition changes that were most consistent with the reconstruc-



tions. In this simulation, marine sediments turn into a strong carbon sink during cold phases. The simulated increased organic carbon deposition during glacial phases reproduces the reconstructed long-term trends in atmospheric and surface ocean  $\delta^{13}\text{C}$  during glacials, but ~~fails to simulate~~ is not sufficient in isolation to reproduce the reconstructed deep ocean  $\delta^{13}\text{C}$  changes in the Pacific and Atlantic. Thus, while sedimentary organic carbon burial could have provided a carbon sink during glacial phases, it must have been ~~small enough or be compensated by other isotopic forcings to not influence~~ operating alongside other processes to allow for the reconstructed benthic  $\delta^{13}\text{C}$  evolution. Interestingly, ~~our simulations with increased processes that increase~~ organic carbon burial during glacial phases (*fPO4*, *fREMI*) show that some of the deposited organic carbon can be returned to the ocean during deglaciations with a large potential to contribute to a fast post-glacial rise in atmospheric  $\text{CO}_2$ . In addition to carbon, nutrients are also removed from the ocean when organic matter is buried (Roth et al., 2014). Tschumi et al. (2011) demonstrated in their steady state experiments that increased organic nutrient burial enhances nutrient limitation on export production and reduces  $\text{CaCO}_3$  export, which increases surface alkalinity and amplifies the  $\text{CO}_2$  draw-down caused by the ~~removal~~ increased burial of organic carbon. ~~In simulation REMI~~ Under *fREMI*, this process operates transiently. Given the reconstructed increased organic carbon burial rates during glacial maxima, this could have been a relevant process over the last glacial cycles, though it might have been reduced in its efficiency ~~due to~~ by reductions in the PIC:POC of export production during glacial phases (Dymond and Lyle, 1985; Sigman and Boyle, 2000). Finally, sedimentary organic carbon oxidation can also regulate marine alkalinity by affecting sedimentary  $\text{CaCO}_3$  dissolution (Emerson and Bender, 1981; Sigman and Boyle, 2000). ~~The only simulation in our set which shows increased alkalinity fluxes out of the sediments~~, but this effect is not directly quantified in our setup. However, we can assess that increased sedimentary organic matter remineralization on a global scale during glacial phases ~~is LAND, in which terrestrial carbon release causes sedimentary dissolution. In all others, especially those which reproduce the reconstructed increase of~~ does not occur due to any of our tested forcings. On the contrary, the effects (*fPO4*, *fREMI*) that increase organic carbon burial during glacial maxima, a prominent feature of the reconstructions, decrease globally-averaged sedimentary remineralization rates ~~decrease~~ during glacial times. ~~Thus, remineralization-driven sedimentary dissolution does not contribute to the glacial-~~

A close relationship between DIC and  $\Delta^{14}\text{C}(\text{DIC})$  is found in modern deep ocean waters and this relationship has been used to reconstruct past DIC changes from radiocarbon reconstructions (Sarnthein et al., 2013). Sedimentary carbon fluxes can de-couple deep ocean  $\Delta^{14}\text{C}$  from DIC (Dinauer et al., 2020) and change DIC without altering sea-air carbon transfer, meaning that DIC changes do not necessarily imply a comparable  $\text{CO}_2$  draw-down in our simulations.-

change in the atmosphere. In all of our simulations with interactive sediments, the DIC inventory change over a glacial cycles is larger than the simultaneous atmospheric  $\text{CO}_2$  inventory perturbation because of changes in carbon reservoirs in sediments and weathering-burial imbalances. ~~In some~~ Changes in the simulated sedimentary burial fluxes result in net transfers of up to 2000 PgC between the carbon pools of the ocean and sediments throughout a glacial cycle, while the net loss of atmospheric C to reproduce the reconstructed glacial  $\text{CO}_2$  is roughly 200 PgC (Sigman and Boyle, 2000; Yu et al., 2010), and the net loss of terrestrial C is on the order of 500-1000 PgC (Jeltsch-Thömmes et al., 2019). The carbon cycle impact of glacial cycles was thus likely larger in the ocean than in the atmosphere (Roth et al., 2014; Buchanan et al., 2016), due to changes in sedimentary carbon storage. In some of our simulations, large DIC changes are produced by big ~~sedimentary~~

~~changes during glacials which cannot be restored during~~ sustained weathering-burial imbalances during glacials that cannot be compensated during the relatively short deglaciations and cause interglacial carbonate preservation patterns that are not consistent with observations (Fig. S11, S12). While this suggests that such a scenario is unrealistic, it does not generically preclude the possibility of large transient weathering-burial imbalances. Testing a wider range of forcing magnitudes and combinations with the same model but different set-up, ~~Morée et al. (2021)~~ Jeltsch-Thömmes et al. (2019) (the DIC results of which are published in the Appendix of Morée et al. (2021)) found a larger DIC change between the pre-industrial and LGM than simulated here ( $3900 \pm 550$  GtC compared to a maximum of  $1100 \pm 300$  GtC in Fig. 7) that is consistent with carbonate system proxy constraints. Combinations of the tested forcings thus allow for larger transient weathering-burial imbalances than produced by our simulation ensemble that can still be reconciled with carbonate system proxies. Some of the tested forcings also show lower glacial than inter-glacial DIC ( $fPO_4$ ,  $fCO_2T$ ) showing that  $CO_2$  removal from the atmosphere in theory does not need to result in increased DIC in the ocean. Instead, these biogeochemical forcings cause sedimentary changes that can store large amounts of carbon in inorganic and organic sedimentary matter. Kempainen et al. (2019) and Jeltsch-Thömmes et al. (2019) previously showed and discussed the possibility of a negative glacial DIC anomaly due to increased sedimentary storage. As found by Jeltsch-Thömmes et al. (2019), organic carbon burial extensive enough to cause a negative glacial DIC anomaly as due to  $fPO_4$ , produces large  $\delta^{13}C$  signals of opposite sign than reconstructed, and thus seem unlikely. In the study by Jeltsch-Thömmes et al. (2019), a negative glacial DIC anomaly due to alkalinity-driven  $CaCO_3$  accumulation is also inconsistent with the proxy record of the last 25 kyr. Consistently, we find that reconstructed deep Pacific  $[CO_3^{2-}]$  changes make a large-scale alkalinity-driven ( $fCO_2T$ ) glacial  $CaCO_3$  accumulation, which reduces atmospheric  $CO_2$  while also reducing DIC, unlikely because it causes larger deep Pacific  $[CO_3^{2-}]$  changes than reconstructed over the last deglaciation (Table 4). The isotopic signal of such large  $CaCO_3$  deposition, however, is smaller than that of POC burial changes and could more likely be overprinted by other processes (e.g. terrestrial carbon release and export production changes) to yield proxy-consistent evolutions (Table 4).

~~Regardless of the dominant carbon cycle change, like previous studies~~ It has long been suggested that sedimentary imbalances also contributed to the reconstructed interglacial sedimentary changes and  $CO_2$  rises after deglaciations (Broecker et al., 1999; Ridgwell et al., 2003). Consistently we find that  $CO_2$  degassing from the ocean persisted throughout deglaciations and into interglacials (e.g. Brovkin et al., 2012), and that the carbon cycle does not reach a new equilibrium before the next glacial inception (e.g. supply-burial imbalances in the late Holocene in Table S2). In our simulations AMOC hysteresis, sedimentary changes and  $\tau$ -delayed temperature responses, e.g. due to ice ~~shields~~ sheets (mimicked by scaling most forcings to the  $\delta^{18}O$  record), introduce memory effects which buffer deglacial carbon cycle reorganizations and cause continued  $CO_2$  rise throughout interglacials. For example, in  $PO_4$ , BGC and ALL, the simulations which best align with the reconstructed glacial-interglacial organic carbon burial changes, not all glacial organic matter is remineralised and carbonate dissolution continued throughout the interglacials. ~~It has long been suggested that sedimentary imbalances contributed to the observed interglacial sedimentary changes and  $CO_2$  rises~~ (Broecker et al., 1999; Ridgwell et al., 2003; Joos et al., 2004; Broecker and Stocker, 2006; Elsig et al., 2009; Menviel et al., 2012; Brovkin et al., 2012).

## 5 Conclusions

In response to different simulated carbon cycle forcings over the repeated glacial-interglacial cycles of the past 780 kyr in the Bern3D model, we found large sedimentary changes which substantially alter marine carbon and nutrient concentrations and spatial distributions. Our simulations show that ~~biochemical~~ biogeochemical forcings are required to perturb the sediments sufficiently to reproduce reconstructed burial changes and  $\text{CO}_3^{2-}$  variations, yet ~~other processes~~ compensating processes (e.g. shallow carbonate deposition) must have operated to reduce the buffering impact of this perturbation on the deglacial carbon cycle re-organization in order to match the speed of the associated carbon release. Our set of factorial simulations further leads to the following conclusions:

1010 Firstly, ocean-sediment interactions and related weathering-burial imbalances, including fluxes of nutrients, alkalinity, organic and inorganic carbon, tend to amplify glacial-interglacial  $\text{CO}_2$  change.

Secondly, ~~changes in the ocean inventory of DIC do not scale with changes in~~ the relationship between marine DIC and atmospheric  $\text{CO}_2$  but are ~~changes is not linear across the different forcings and~~ strongly influenced by sediment fluxes. For example, the potential addition of phosphate from exposed continental shelves causes ~~not only~~ a decrease in atmospheric  $\text{CO}_2$  ~~but also in ocean carbon inventory and marine DIC by increasing sedimentary carbon storage.~~ Factorial simulations yield ~~an average DIC change~~ changes in the ocean DIC inventory between -1340 to +1400 GtC and in the atmospheric  $\text{CO}_2$  changes ~~between -45 and 80 ppm (inventory between -96 and 180 GtC (-45 and 80 ppm))~~ over the last five deglaciations in response to individual prescribed physical and biogeochemical forcings. This suggests that approaches utilizing the relationship between radiocarbon and DIC from modern data to reconstruct the ocean's glacial DIC inventory and the postulated corresponding  $\text{CO}_2$  change from glacial radiocarbon data may be biased.

1020 Thirdly, ocean-sediment interactions strongly impact the evolution of important carbon cycle parameters such as  $\delta^{13}\text{C}(\text{DIC})$  and  $\delta^{13}\text{C}_{\text{CO}_2}$ ,  $\text{CO}_3^{2-}$ , export production,  $\text{CaCO}_3$  and POM burial fluxes, preformed and remineralized nutrient concentrations, and oxygen. The interpretation of the proxy records without consideration of weathering-burial imbalances and ocean-sediment interactions for both organic and inorganic carbon may lead to erroneous conclusions.

1025 We also showed that the long timescales of ocean-sediment interactions and the weathering-burial cycle pose substantial challenges for model spin ups-up because imbalances in the geologic carbon cycle can cause isotopic drifts at the beginning of simulations and which are not present in a control run. Depending on the initial isotopic imbalance, it takes up to 200 kyr for the drift to subside and the signal of the applied forcing to dominate the simulated transient  $\delta^{13}\text{C}$  changes. Further studies are needed to test whether  $\delta^{13}\text{C}$  can be spun up in more computationally-expensive models by combining them with lower-complexity models. In the absence of such a spin up strategy, open system simulations of glacial  $\delta^{13}\text{C}$  are likely strongly affected by these initial drifts.

*Data availability.* All simulation output necessary to produce the figures in this manuscript are available at <https://doi.org/10.5281/zenodo.11385608>

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1035 *Author contributions.* FP and AJT designed the simulations. AJT ran the simulations. MA processed the model output and drafted the manuscript. MA, AJT, FP, FJ and TFS interpreted the results and edited the manuscript.

*Competing interests.* The authors declare that they have no conflict of interest.

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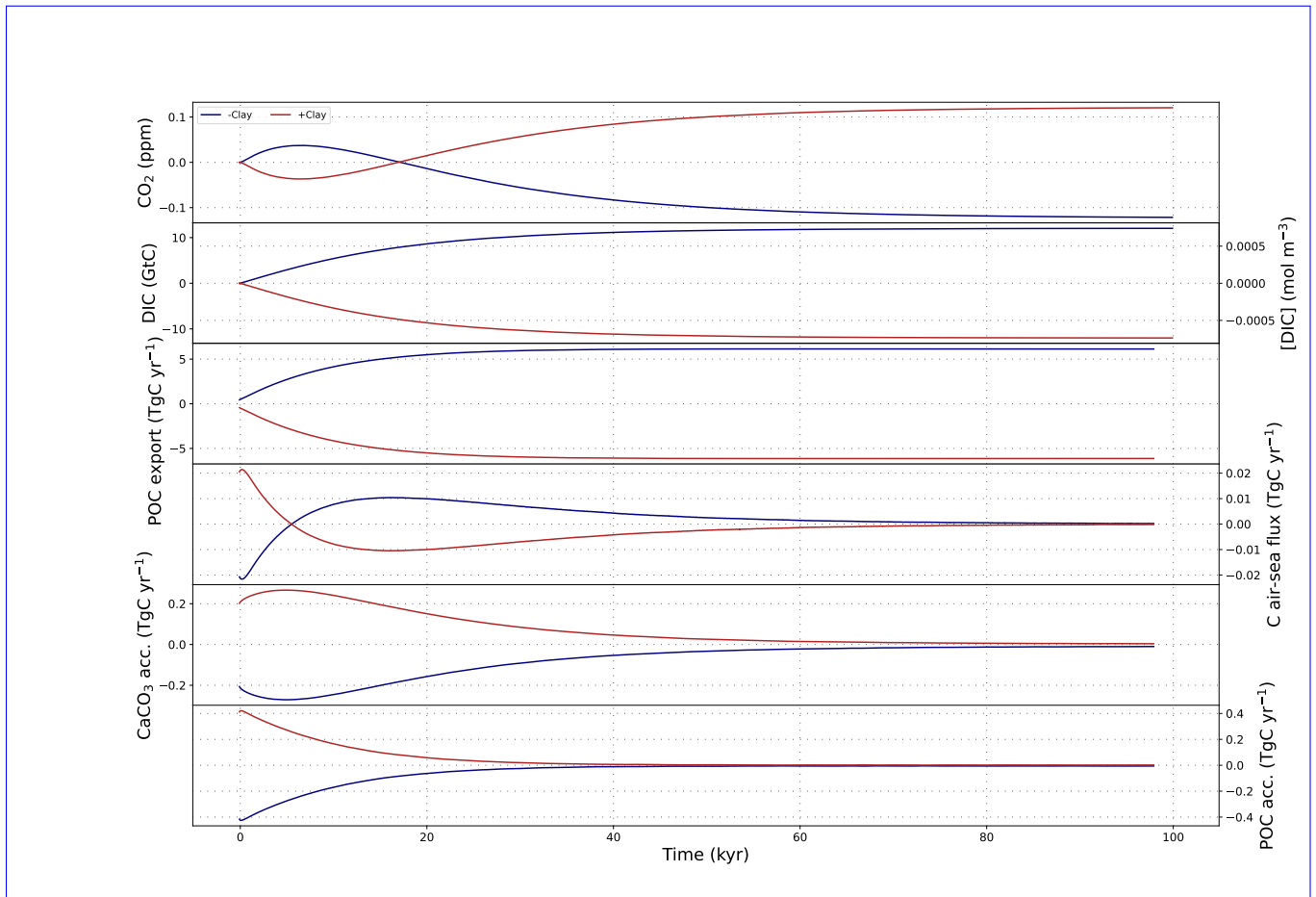
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## ~~Ocean circulation changes~~ Model limitations

The ocean circulation changes in all experiments due to the prescribed changes in insolation, radiative forcings from greenhouse gasses and land albedo. These forcings result in cyclic transitions between interglacial and glacial circulation states. The glacial states show a reduction of the Atlantic Meridional Overturning Circulation (AMOC) by up to 4.5 Sv and an increase of the shallow overturning cell in the equatorial Pacific north of the Equator of up to 1 Sv compared to the PI (Fig S8). Accordingly, water mass ages increase below 2000 m in the North Atlantic and decrease in the South Atlantic and Pacific during glacials. With additional wind stress reductions in the Southern Ocean (SO, <40°S, simulation SOWI), the South Pacific downwelling is strengthened by up to 1.5 Sv locally in glacials, and the AMOC strength further reduced by up to 1 Sv. The increased stratification in There are several ways in which the amplitude or regional pattern of the simulated changes might be biased by our experiment design. Firstly, by design our forcings are smooth in time and spatially uniform, which is a stark simplification. For example, the PO4 forcing ties nutrient supply to the  $\delta^{18}\text{O}$  record. The correlation between dust (iron source to the SO reduces upwelling and increases the water mass age throughout the Pacific and South Atlantic by up to 150 years. The slower AMOC also results in ~100 yr older waters below 2000 m in the North Atlantic. If instead of the wind stress the glacial radiative forcing is further reduced (by  $2.5 \text{ Wm}^{-2}$ , simulation AERO), AMOC weakens in all glacials by up to 12 Sv relative to PI during the glacial maxima (the model behaviour to this forcing is described more extensively in Adloff et al., 2023). The Pacific circulation is much less affected, showing only a small decrease (up to 1 Sv) in the Pacific Meridional Overturning Circulation (PMOC, here evaluated at 30degS). As a result of the AMOC collapse, the Atlantic water mass age increase caused by the standard forcing is amplified, with an aging of up to 1000 years in the deep North Atlantic as glacial deep water formation now only occurs in open ocean) concentrations in the EPICA Dome C ice core and benthic  $\delta^{18}\text{O}$  is of first order only and varies over the glacial cycle (Winckler et al., 2008). Several macro- and micronutrients were likely supplied to varying parts of the glacial ocean (Broecker, 1982b; Martin, 1990; Pollock, 1997; Deutsch et al., 2004) and while dust flux changes seem to correlate globally (Kukla et al., 1990; Winckler et al., 2008), the Southern Ocean timings and rates of other nutrient fluxes might in reality have varied temporally and spatially. Similarly, our other forcings might change more slowly over the deglaciation than the real processes they mimic.

Another simplification in our experiment design is that the majority of our simulations assume temporally constant terrestrial solute inputs although in reality these fluxes are climate sensitive (Munhoven, 2002). It is unlikely that removing this simplification would substantially alter the simulated global carbon fluxes and reservoir size changes because it is estimated that global weathering rate changes during glacial cycles were small despite large local variability, possibly because they canceled out in the global mean (Jones et al., 2002; Von Blanckenburg et al., 2015; Frings, 2019; Börker et al., 2020). It was estimated that glacial-interglacial weathering flux changes altered atmospheric  $\text{CO}_2$  by a maximum of 20 ppm (Köhler and Munhoven, 2020). Yet, the resulting  $\delta^{13}\text{C}$  perturbation could be larger because a global balance in carbon flux changes does not imply a balance in carbon isotope fluxes (Jeltsch-Thömmes and Joos, 2023). Additionally, there might have been non-linear changes in isotopic input fluxes during the simulated time period.

35 These circulation changes are largest in MIS-16a, 6a and 2, when the respective forcings are strongest, and also appear in interglacials that were colder than the PI, although at much smaller amplitude

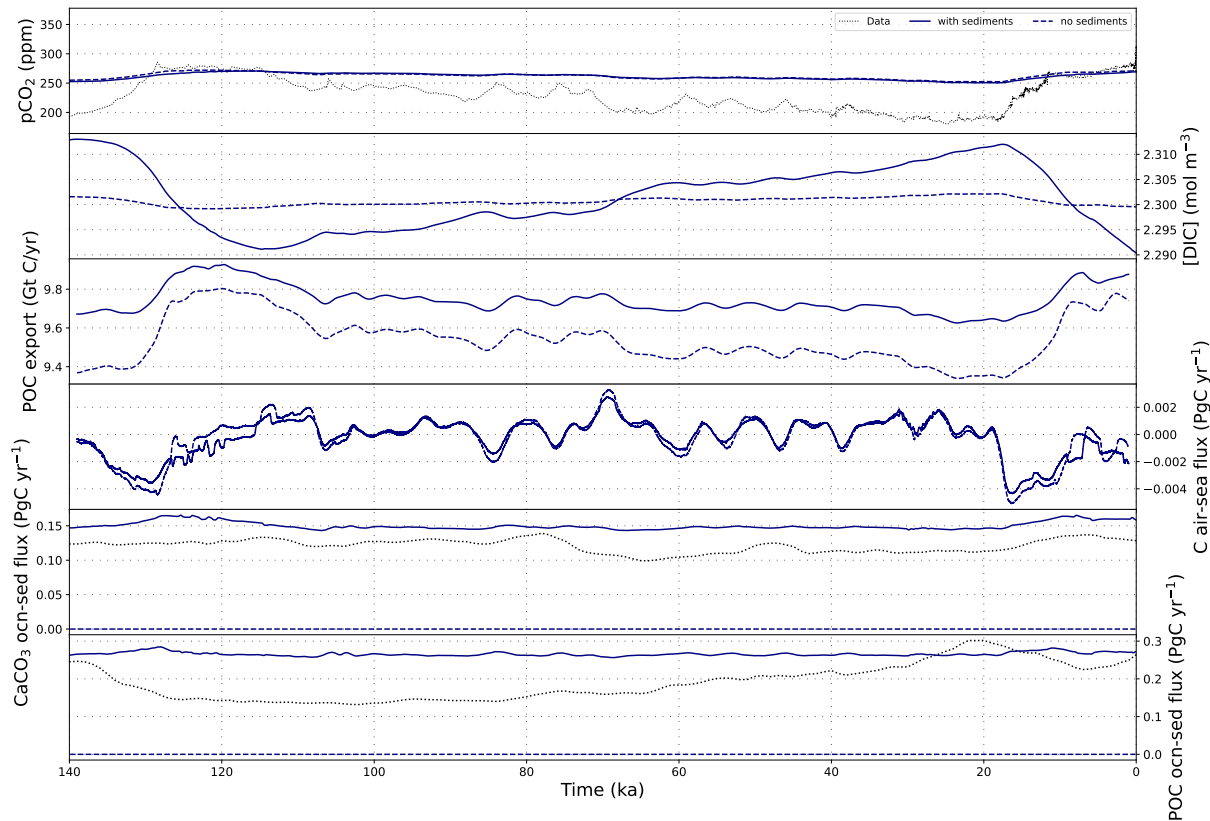


**Figure S1.** The effect of step changes of plus or minus 30% of the prescribed clay flux on atmospheric CO<sub>2</sub> concentrations, DIC and carbon fluxes over 100 kyr.

40 Finally, the imbalance between weathering and burial fluxes is also shaped by the sedimentation rate. In our simulations, sedimentation rates vary due to changes in biogenic export, yet accumulation of non-biogenic material was kept constant. This omission, however, is not a large error source, given that a separately prescribed step-wise 30% increase and decrease of the non-biogenic flux in the PI steady state had only marginal effects on atmospheric CO<sub>2</sub>, DIC and sedimentary accumulation of biogenic particles (Fig. S1).

### Effects of orbital, insolation and albedo changes on carbon fluxes

In the following, we examine the underlying glacial-interglacial carbon cycle changes and the effect of interactive sediments under each forcing. First we focus on the standard forcing, before discussing the effects of additional forcings.



**Figure S2.** Atmospheric CO<sub>2</sub> concentrations, DIC and carbon fluxes over the most recent full glacial cycle in simulation BASE with and without dynamic sediments.

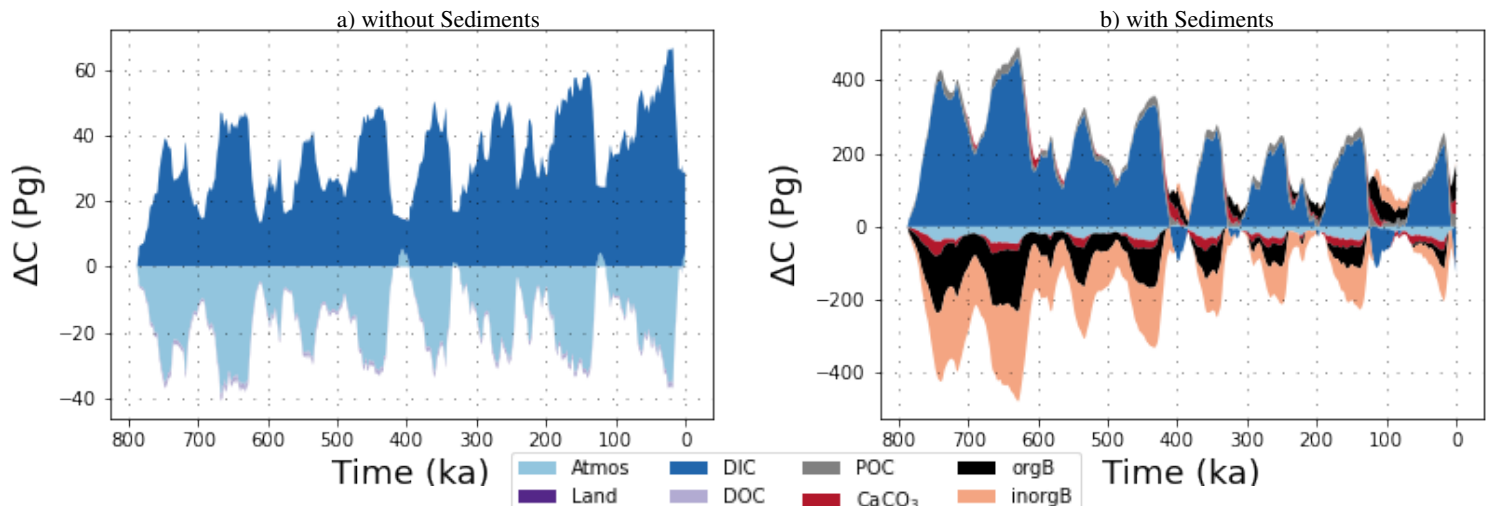
45 The dynamic circulation and climate affect the partitioning of carbon between the interactive carbon reservoirs in the model (atmosphere, ocean, reactive sediments and lithosphere). The applied forcings vary the CO<sub>2</sub> concentration gradient between air and seawater by modifying CO<sub>2</sub> solubility and surface ocean DIC and alkalinity concentrations. Without dynamic sediments (Fig S2), carbon in response moves between the atmosphere, the marine DIC and, to a lesser extent, DOC reservoirs in the ocean. With the standard forcing, CO<sub>2</sub> and O<sub>2</sub> solubilities increase during glacial phases because of the cooling surface ocean, leading to a steady marine uptake of carbon and oxygen from the atmosphere from peak interglacial through to the glacial maximum. The cooling reduces deep water formation rates in the North Atlantic and increases deep water formation in the Southern Ocean. These circulation changes increase the marine uptake of CO<sub>2</sub> while expanding sea ice prevents outgassing of marine CO<sub>2</sub> in the Southern Ocean. ~~Circulation changes also redistribute dissolved nutrients. Polar export production declines due to the amplified cooling in polar oceans and expanding sea ice, causing an overall productivity~~ Overall POC and CaCO<sub>3</sub> export fluxes decrease during glaciation despite increased primary productivity in mid-latitudes and sub-tropics due to the circulation-driven reduction of nutrient transport into the polar oceans. In reduced export production in the high latitudes, POC and CaCO<sub>3</sub> export fluxes decrease, predominantly due to sea ice growth, in places also because of reduced nutrient supply and

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lower temperatures. These export fluxes changes, particularly in the Southern Ocean, alter phosphate cycling: In interglacial states, high export fluxes effectively transfer phosphate from the photic zone to the intermediate ocean, where most exported POC is remineralized. Upwelling of intermediate water masses returns phosphate to the surface ocean. In glacial states, less of the phosphate upwelling in the Southern Ocean is incorporated into POC and exported to intermediate ocean depths. Instead, it is downwelled and incorporated into bottom waters. In consequence, the glacial deep ocean is enriched in preformed phosphate, while phosphate concentrations at intermediate depth decrease due to climate-driven export reduction. In the surface, reduced upwelling of nutrients and reduced nutrient uptake result in almost no net change of nutrient concentrations. During deglaciation, surface and deep waters warm and upwelling as well as export fluxes are restored. Hence, decreases in atmospheric CO<sub>2</sub> concentration during the onsets of glaciations are directly mirrored by increases in marine DIC and decreases in marine DOC, and the inverse occurs during deglaciation.

When interactive sediments are included in the simulations, export production and ocean chemistry changes ~~also~~ alter sediment burial and dissolution fluxes, resulting in more than 10x larger DIC fluctuations over a glacial cycle than in the ~~previous~~, closed system. Changes in net sea-air gas exchange across the glacial cycle ( $\sim 0.007$  PgC/yr) are smaller than changes in each POC and CaCO<sub>3</sub> burial rates ( $\sim 0.02$  PgC/yr). CaCO<sub>3</sub> burial is predominantly driven by productivity changes and peaks during interglacials. In glacials, CaCO<sub>3</sub> burial is reduced below areas with reduced euphotic zone CaCO<sub>3</sub> export, e.g. in the high latitudes, but additionally where CaCO<sub>3</sub> becomes unstable due lower temperatures or reduced pH due to increased sedimentary POC oxydation rates. The standard forcing is not sufficient to cause wide-spread O<sub>2</sub> depletion in the glacial deep ocean, hence under the standard forcing POC burial rates are driven by export production rates, with less/more burial in areas with reduced/increased POC export production, respectively. The exception is the upwelling zone in the Equatorial East Pacific and parts of the Indian Ocean, where increased POC export depletes benthic and sediment pore water O<sub>2</sub> during glacial phases. During deglaciations, sea ice recedes, ocean ventilation increases and the surface and intermediate oceans warm, fostering increased primary productivity. While productivity and POC burial increase quickly in the subpolar regions, POC burial rates in the Eastern Equatorial Pacific respond more slowly to the warming: Long turnover timescales of pore water O<sub>2</sub> in sediments and remineralisation of previously deposited POC delay the return of interglacial POC remineralisation rates relative to export rates from the surface ocean. Therefore, deglaciations are marked by faster productivity increases in the surface ocean than sedimentary POC remineralisation. This results in a 'sweet spot' during glacial terminations, when tropical POC burial is still higher than in the interglacial while extratropical POC export and burial has already recovered to interglacial levels, particularly during the last 400 kyr which show larger glacial-interglacial temperature contrasts and faster warming rates during deglaciations. This 'sweet spot' causes the maximum of global POC burial to occur during deglaciation, before the full interglacial.



**Figure S3.** Transient carbon reservoir size changes across the last 780kyr as simulated in simulations with the standard (orbital, radiation and albedo) forcings in simulation BASE with and without dynamic marine sediments. Shown are the size changes of atmospheric, terrestrial, marine (DIC and DOC), sedimentary (POC and  $\text{CaCO}_3$ ) and lithospheric (organic and inorganic) carbon storage. Note that the y-axis scale is an order of magnitude larger in b) than in a).

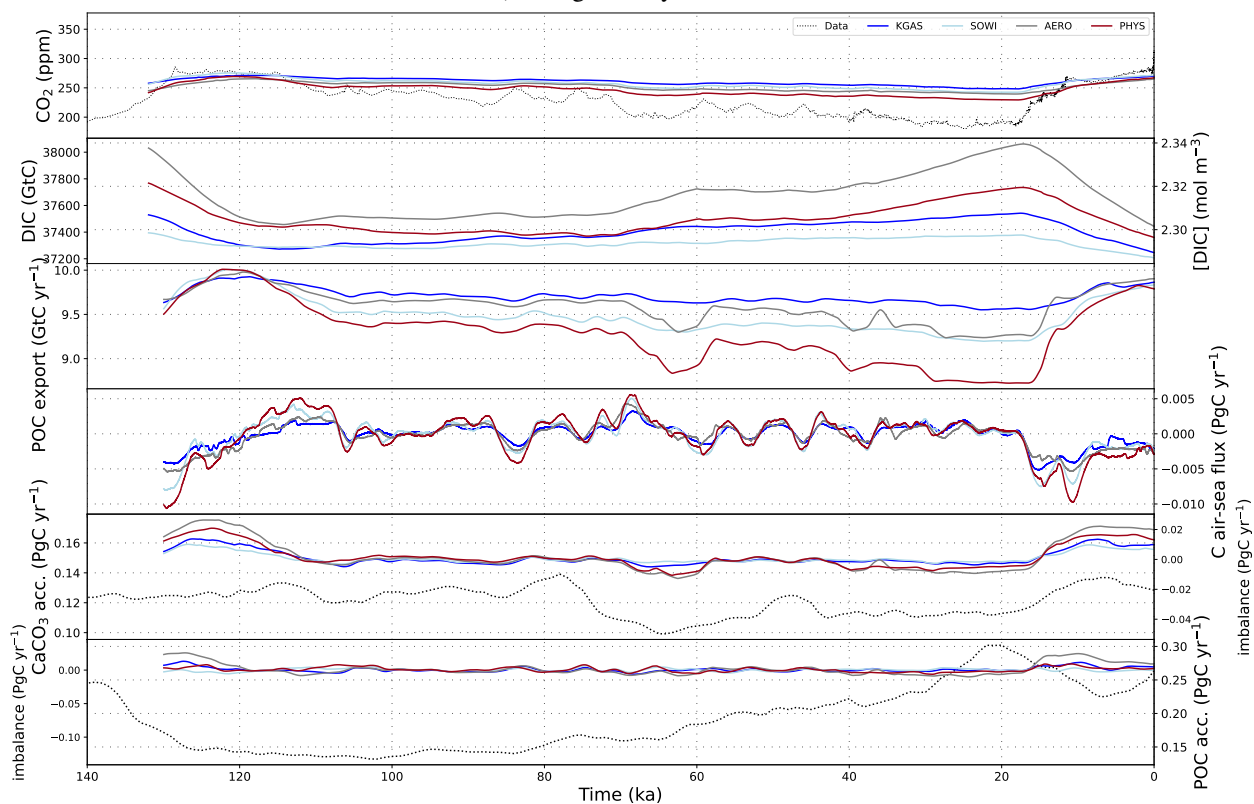
Introducing sediments (and a constant weathering flux) also changes carbon cycle dynamics over multiple glacial cycles. Fig S3 shows the transient changes in the simulated carbon reservoirs in simulation BASE over the entire simulated time period. In our set-up, carbon exchange between the atmosphere, ocean and sediments reacts to climatic and ~~biochemical~~ biogeochemical changes while weathering input fluxes of DIC, alkalinity and  $\text{PO}_4^{3-}$  are constant over time. A carbon flux imbalance arises during glacial phases in this open system. Under purely physical forcings, export fluxes from the photic zone decrease during glacial phases. Despite locally increased sedimentary POC preservation, global sediment accumulation rates decrease. In consequence, transfer-sequestration of  $\text{CaCO}_3$  and POC from the reactive sediments ~~to the lithosphere~~ (i.e. sediment burial) is reduced as well, since it is governed by the mass accumulation rate. The carbon which would have otherwise been buried instead accumulates as DIC in the ocean. Acceleration of sediment mass accumulation rates during glacial terminations increases ~~the carbon transfer into the lithosphere~~ sediment burial, which reduces marine DIC. The strength of these carbon cycle responses depends on the forcing strength, which varies between glacial cycles. The lukewarm interglacials of the first 350 kyr of our simulations do not restore the export fluxes and sedimentary  $\text{CaCO}_3$  preservation required to re-balance the geologic carbon cycle, and so marine DIC concentrations are persistently higher during 800-450ka than at PI. Interglacials of the last 450kyr of the simulation reduce DIC in the long-term because they are warm and long enough for increased carbon transfer into sediments and ~~the lithosphere~~ sediment burial.

### Effects of additional forcings and Earth system changes on carbon fluxes

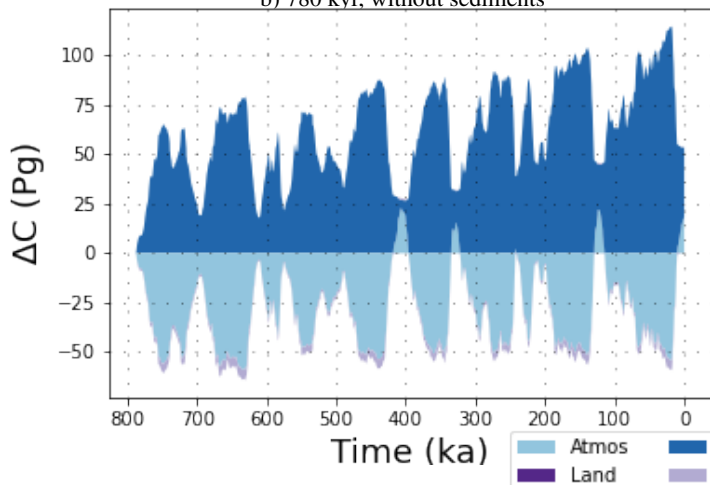
The previously described carbon cycle changes vary when further forcings and Earth system changes are applied.



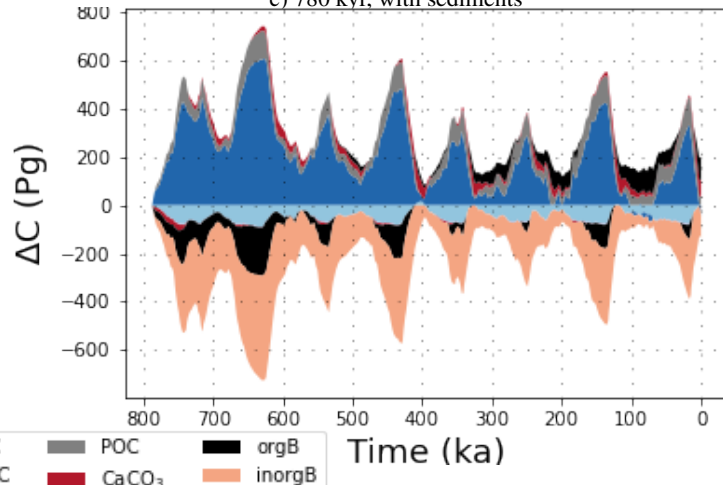
a) Last glacial cycle



b) 780 kyr, without sediments



c) 780 kyr, with sediments



**Figure S4.** a) Atmospheric CO<sub>2</sub> concentrations, DIC and carbon fluxes over the most recent full glacial cycle in simulations with additional physical forcings in an open system. b) Transient carbon reservoir size changes across the last 780 kyr as simulated with all additional physical forcings combined in a closed system and c) in an open system. Shown are the size changes of atmospheric, terrestrial, marine (DIC and DOC), sedimentary (POC and CaCO<sub>3</sub>) and lithospheric (organic and inorganic) carbon storage. Reservoir changes for individual forcings are displayed in Fig S23. Flux timeseries for simulations in a closed system are displayed in Fig S24.

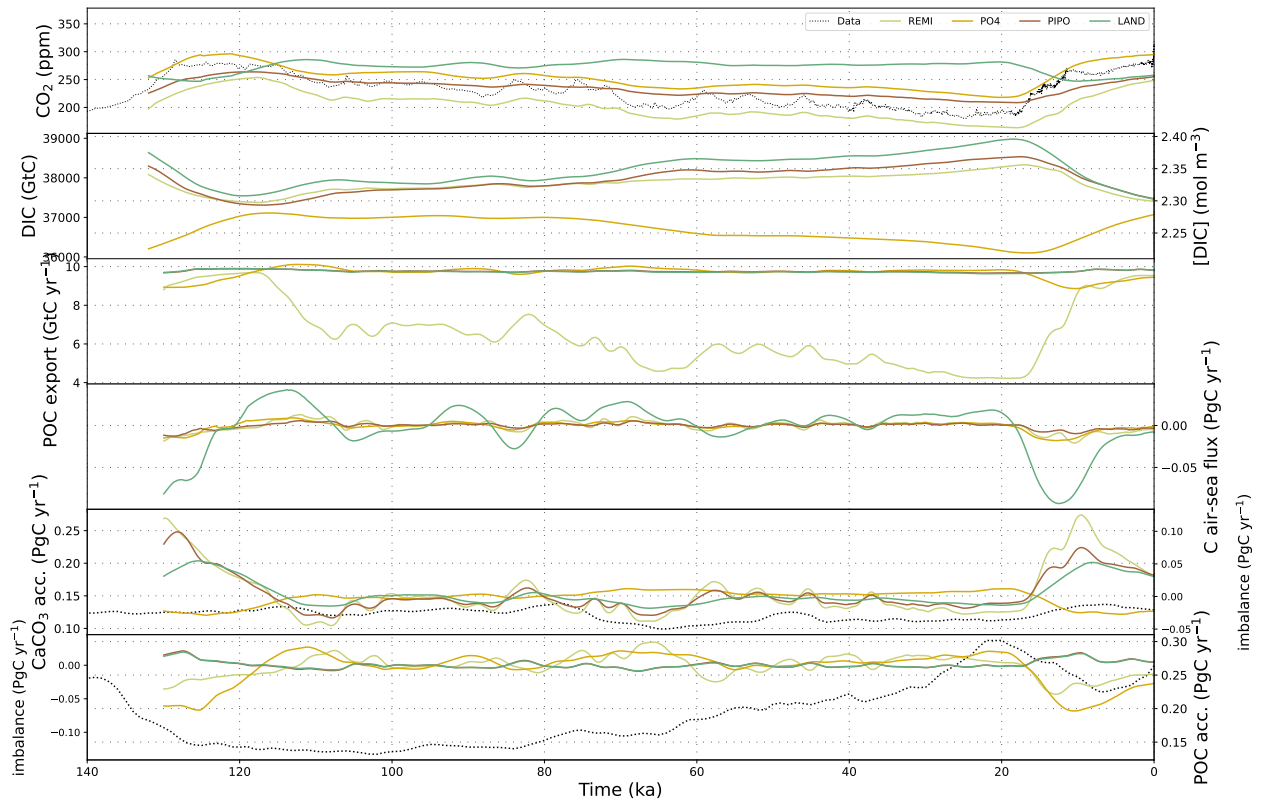
105 Additional physical forcings result in roughly 1.5x larger carbon fluxes (Fig. S4), partially by amplifying the processes under the standard forcing and partially by introducing additional ones. Additional reduction of wind stress in the Southern Ocean (simulation SOWI) leads to a stronger isolation of deep Pacific water masses, reducing benthic oxygen levels ~~and pH and increasing the carbon content of the glacial deep Pacific~~. With dynamic sediments, more organic matter and  $\text{CaCO}_3$  reaching the sediments is preserved due to the reduced oxygen concentrations, particularly in Pacific upwelling zones. This results in a larger net removal of nutrients and carbon from the ocean during glacial times which would have otherwise been released at intermediate depth. In consequence, wind stress forcing over the Southern Ocean reduces the carbon content of Pacific deep water when dynamic sediments are considered, despite an increase in water mass age. The re-ventilation of the deep Pacific during glacial termination leads to rising benthic oxygen concentrations. Due to the lower storage of dissolved nutrients and carbon in the glacial deep ocean, the potential to upwell nutrients during deglaciation is reduced, suppressing the spike in POC burial during terminations seen under the standard forcing and reducing PIC burial during these transition phases.

115 Reducing the transfer velocity of  $\text{CO}_2$  in the Southern Ocean during glacials (simulation KGAS) also reduces  $\text{CO}_2$  outgassing in the Southern Ocean which increases DIC in the deep Pacific but leaves ocean circulation unaffected, which reduces its global impact and, unlike the wind forcing, does not trap nutrients in the deep Pacific.

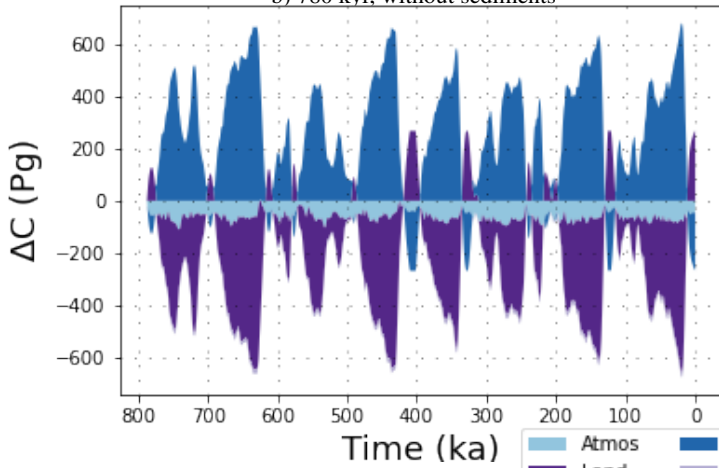
120 The AMOC slow-down in simulations with an additional reduction of incoming radiation during glacial phases and especially glacial maxima (e.g. via aerosol dimming, simulation AERO) creates an old, nutrient-rich and  $\text{O}_2$ -poor bottom water mass in the glacial Atlantic. Unlike with a vigorous AMOC, nutrients are not returned as quickly to the surface Atlantic but accumulate in the deep. The additional cooling combined with reduced nutrient supply reduces POC and  $\text{CaCO}_3$  export in the Atlantic. In the North, where sea ice extent is increased and temperatures drop the most, they cease entirely. Globally, the additional cooling increases  $\text{CO}_2$  and  $\text{O}_2$  solubility. Overall these effects increase glacial carbon storage in the deep ocean. With dynamic sediments, the reduced  $\text{CaCO}_3$  export in the North Atlantic raises the local lysocline, causing dissolution and increased marine DIC concentrations. The sudden shift in water masses when AMOC resumes during deglaciation amplifies the spike in burial rates observed under the standard forcing.

130 The different carbon and nutrient fluxes under these forcings change the total carbon and nutrient inventories in simulations with an open system, resulting in different DIC and nutrient concentrations at the start of the last glacial cycle and at the end of the runs.

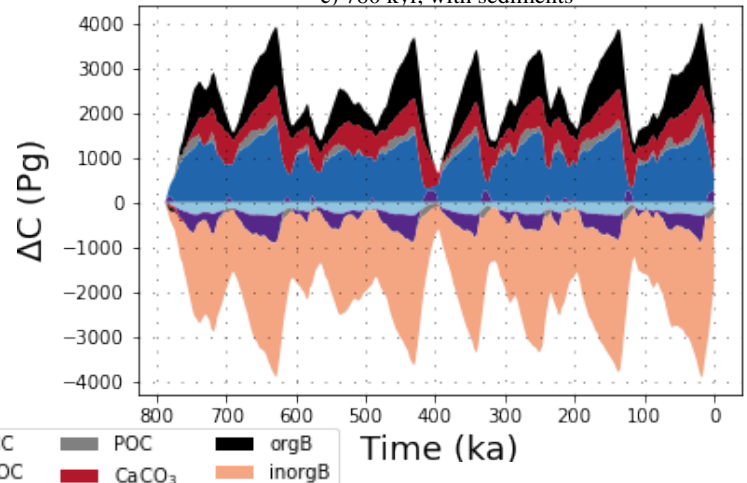
a) Last glacial cycle



b) 780 kyr. without sediments



c) 780 kyr. with sediments



**Figure S5.** a) Atmospheric  $\text{CO}_2$  concentrations, DIC and carbon fluxes over the most recent full glacial cycle in simulations with additional [biochemical-biogeochemical](#) forcings in an open system. b) Transient carbon reservoir size changes across the last 780 kyr as simulated with all additional [biochemical-biogeochemical](#) forcings combined in a closed system and c) in an open system. Shown are the size changes of atmospheric, terrestrial, marine (DIC and DOC), sedimentary (POC and  $\text{CaCO}_3$ ) and lithospheric (organic and inorganic) carbon storage. Reservoir changes for individual forcings are displayed in Fig S25 and ???. Flux timeseries for simulations in a closed system are displayed in Fig ??.

**Biochemical** Biogeochemical forcings affect carbon transfer primarily through the biological pump and the size of the terrestrial carbon sink. Nutrient inputs during glacial phases in simulation PO4 increase POC and CaCO<sub>3</sub> export, and sedimentary burial rates through increased sedimentary mass accumulation and lower O<sub>2</sub> concentrations in the deep ocean (Fig S5). During glacial termination, the prescribed nutrient supply to the surface ocean stops before the deep ocean is fully re-ventilated and the nutrients that accumulated in intermediate and deep water masses have returned to the surface. This delay results in low nutrient concentrations in the surface ocean, a transient drop in POC export, and consequentially burial fluxes. The reduced carbon burial raises DIC and increases the net carbon transfer from surface waters to the atmosphere during deglaciation. In consequence, when nutrients are added to a glacial ocean with responsive sediments, glacial phases become the dominant periods of organic and inorganic C transfer to the lithosphere sediment burial, reducing the accumulation of marine DIC and increasing the marine uptake of atmospheric CO<sub>2</sub> during glacial phases. This simulation PO4 yields the temporal CO<sub>2</sub> evolution which most closely resembles reconstructions from ice cores.

Reducing the PIC:POC ratio of export production during glacial phases (simulation PIPO) increases alkalinity in the surface ocean which enhances marine carbon uptake from the atmosphere, resulting in an additional CO<sub>2</sub> drawdown of up to ~10ppm without sediments. This effect is enhanced by 20ppm when dynamic sediments are considered. When the export production is tilted towards organic matter production in an ocean with interactive sediments, reduced CaCO<sub>3</sub> export during inceptions and glacial periods translate into reduced CaCO<sub>3</sub> burial rates. This leads to a shoaling of the carbonate compensation depth, a build-up of alkalinity in the ocean and increased carbon transfer from the atmosphere to the ocean. The reduced sedimentary carbonate accumulation reduces the total mass flux to the sediments. On extratropical continental slopes, the reduced mass accumulation slows organic carbon burial, retaining more nutrients in the ocean and decreasing O<sub>2</sub> concentrations through continued remineralization instead. On continental slopes under upwelling areas with high productivity, the reduced O<sub>2</sub> expands the O<sub>2</sub> minimum zones, an effect which outweighs the local reduction of carbonate export and results in higher POC burial rates despite less carbonate deposition. Restoration of the interglacial PIC:POC ratio during deglaciation then enhances sedimentary carbonate deposition in benthic waters with higher pH and larger O<sub>2</sub> minimum zones than under the standard forcing, increasing the temporal spikes in carbonate and POC burial. Reduced glacial PIC:POC increases CaCO<sub>3</sub> burial events during glacial terminations.

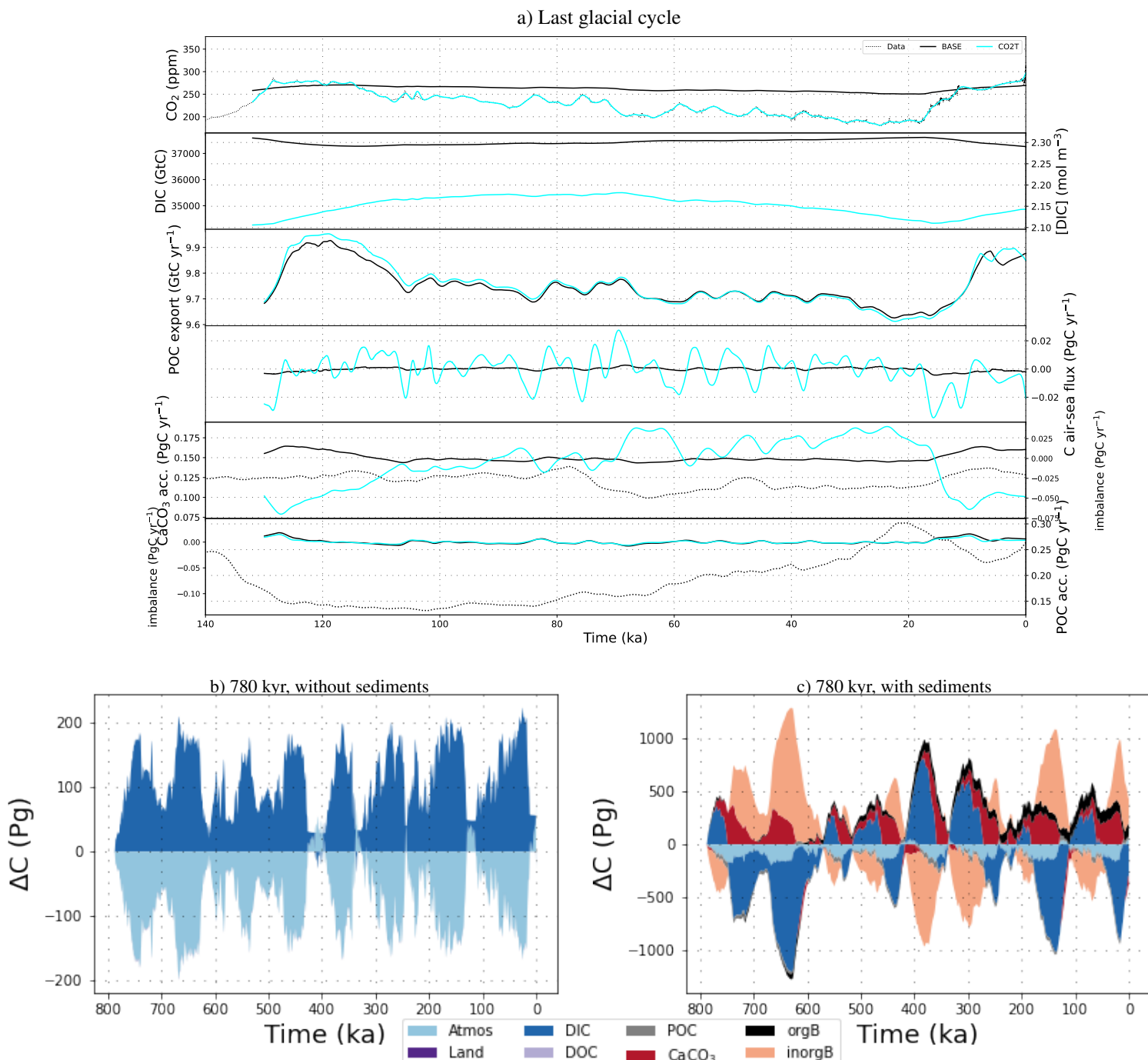
Lowering the remineralization depth of organic matter in the glacial water column (simulation REMI) leads to a net carbon and nutrient transfer from the surface ocean to intermediate and deep water masses, where more O<sub>2</sub> is consumed. Without dynamic sediments, the increased DIC concentrations in the deep ocean increases the carbon storage of the glacial ocean. In addition, the reduced dissolution of POC in the upper water column during glacials increases surface ocean pH and CO<sub>2</sub> uptake by the ocean. With dynamic sediments, the resulting reduction in deep ocean O<sub>2</sub> concentration increases POC preservation in sediments below high productivity zones, e.g. tropical continental margins and upwelling areas. Where the larger flux of POC reaching the sediments is not preserved, it is remineralized, reducing the stability of sedimentary CaCO<sub>3</sub>. Glacial inceptions are then characterized by increased POC and POP fluxes into the sediments and reduced CaCO<sub>3</sub> burial. During glacial terminations, POC is increasingly remineralized at shallower depth again, leading to reduced POC fluxes into the deep ocean and POC burial compared to the glacial phase. Surface ocean pH decreases and C is returned to the atmosphere. Compared to the standard

forcing, lowering the remineralization depth thus shifts the timing of maximal POC burial rates from the interglacial to the glacial and amplifies the transient spike in  $\text{CaCO}_3$  burial as increased nutrient supply during glacials does, but it also increases sedimentary  $\text{CaCO}_3$  dissolution during glacial phases.

170 Land carbon release to the atmosphere during glacial phases (simulation LAND) invades and acidifies the ocean due to increased atmospheric concentrations, growing the marine DIC reservoir during glacials with and without dynamic sediments, resulting in the biggest glacial marine DIC reservoirs across our simulations. When interactive sediments are considered, this marine carbon uptake reduces  $\text{CaCO}_3$  preservation and leads to a shoaling of the lysocline. During termination, as the external carbon addition subsides, the ocean vents carbon back into the atmosphere, transiently allowing for increased  $\text{CaCO}_3$  burial.

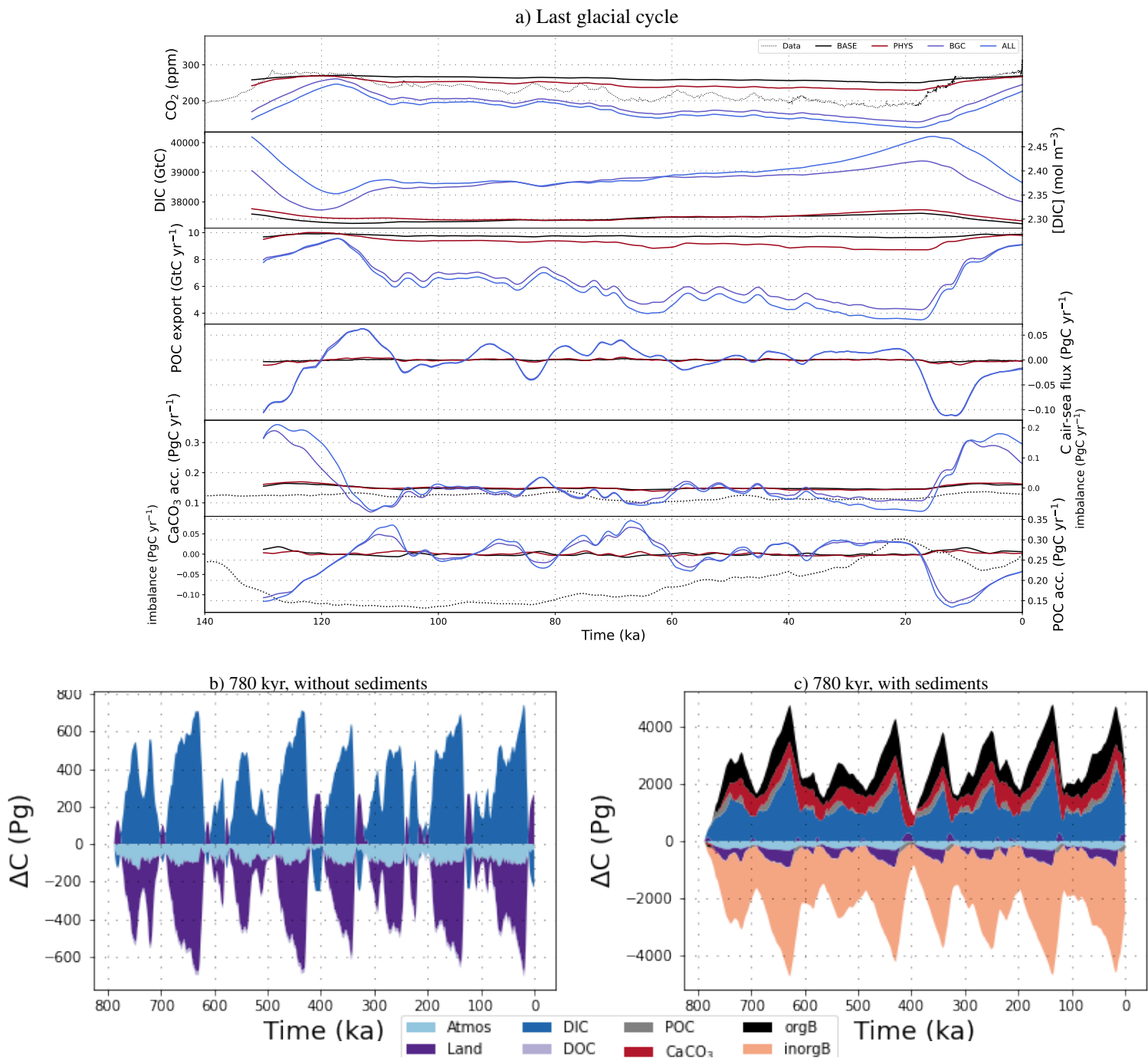
175 The previous paragraphs show that varying biogenic particle production in the surface ocean is only a relevant control on marine carbon storage changes when interactive sediments are simulated. Instead, lowering the main remineralization depth (simulation REMI) and adding terrestrial carbon release during glaciation (simulation LAND) strongly influence marine carbon storage with and without dynamic sediments. Without dynamic sediments, they double the marine carbon uptake during glacial periods. When including interactive sediments, all ~~biochemical~~ biogeochemical forcings have substantially larger effects on the carbon cycle than physical changes, with 5-10x larger carbon fluxes than under the standard forcing (Fig S5).

180  **$\text{CO}_2$  restoring and non-linear effects of combined forcings on carbon fluxes**



**Figure S6.** a) Atmospheric  $\text{CO}_2$  concentrations, DIC and carbon fluxes over the most recent full glacial cycle in simulations BASE and CO2T in an open system. b) Transient carbon reservoir size changes across the last 780 kyr as simulated with alkalinity nudging in a closed system and c) in an open system. Shown are the size changes of atmospheric, terrestrial, marine (DIC and DOC), sedimentary (POC and  $\text{CaCO}_3$ ) and lithospheric (organic and inorganic) carbon storage.

By design, the applied alkalinity nudging causes marine carbon uptake and release that shape atmospheric CO<sub>2</sub> in line with observations (Fig S6). As a consequence, the surface ocean is more alkaline in glacial times and more acidic during terminations than in the standard forcing, enabling increased marine carbon uptake. In simulations with dynamic sediments, CaCO<sub>3</sub> burial during cold phases is increased but the burial spike during terminations suppressed.



**Figure S7.** a) Atmospheric CO<sub>2</sub> concentrations, DIC and carbon fluxes over the most recent full glacial cycle in simulations with different combinations of additional forcings in an open system. b) Transient carbon reservoir size changes across the last 780 kyr as simulated with all additional forcings combined in a closed system and c) in an open system. Shown are the size changes of atmospheric, terrestrial, marine (DIC and DOC), sedimentary (POC and CaCO<sub>3</sub>) and lithospheric (organic and inorganic) carbon storage. Flux timeseries for simulations in a closed system are displayed in Fig ??.



185 The three tested physical forcings combine almost linearly in their effect on atmospheric CO<sub>2</sub>. Circulation change is dominated by radiation reductions, with strong AMOC weakening during glacials and some reduction of the PMOC, but less than in simulation SOWI because of increased sea ice cover in the Southern Ocean which limits the effect of wind stress changes. In consequence, the glacial deep ocean holds more nutrients when all forcings are combined: it has a large Atlantic reservoir due to sluggish overturning and a larger Pacific reservoir than in SOWI due to less organic carbon burial. During deglaciation, the  
190 release of these nutrients back into the surface ocean creates a larger productivity spike than when the forcings are applied individually, reducing marine [O<sub>2</sub>] further but causing only a minimal temporary reduction of <5 ppm in atmospheric CO<sub>2</sub> (Fig. S7). In simulations with interactive sediments, additional radiative forcing (AERO) and Southern Ocean wind forcing (SOWI) shift sedimentary CaCO<sub>3</sub> and POC accumulation rates in opposite directions. Yet, their effects on nutrient, temperature and oxygen distributions are almost additive.

195 While physical effects on carbon concentrations combine almost linearly, the combination of ~~biochemical~~biogeochemical forcings is non-linear because they directly alter production and dissolution patterns in opposing ways. Acidification of benthic water masses through external nutrient (PO<sub>4</sub>) and carbon (LAND) supply during glacials counteracts the benthic pH increase under a deepened remineralisation depth (REMI). When all ~~biochemical~~biogeochemical forcings are combined, net CaCO<sub>3</sub> fluxes into marine sediments are reduced during glacial maxima and increased during terminations, but the burial peak is  
200 delayed. ~~Biochemical~~Biogeochemical forcings dominate the carbon cycle response when all forcings are combined, except for the North Atlantic where circulation changes cause the biggest perturbation. The magnitude of the non-linearities that occur when all forcings are combined is similar to the combined effect of only the physical forcings.

### ~~Climate feedback effects~~

~~Atmospheric CO<sub>2</sub> concentrations, DIC and carbon fluxes over the most recent full glacial cycle in simulations with all additional forcings combined in an open system, with and without climate feedback.~~  
205

~~All simulations described so far were run with prescribed radiative forcing, i.e. without the radiative effect of simulated CO<sub>2</sub> changes. The benefit of this setup is that the climatic changes in the simulations are comparable, allowing to distinguish the carbon cycle effects of temperature change from the other physical and biochemical changes we simulated. At the same time, however, this simplified setup creates a bias by neglecting the climate feedback of carbon cycle changes. To assess the effect of this bias in the prescribed carbon cycle dynamics, we reran simulation ALL, which contains all tested forcings, with the carbon cycle climate feedback (ALL-Clim). The prescribed forcings in simulation ALL result in a glacial-interglacial CO<sub>2</sub> change that is 30% larger than in observations, but with absolute CO<sub>2</sub> values mostly below those reconstructed. Including the radiative effect of this CO<sub>2</sub> offset results in up to 2.5° colder glacial maxima. Simulation AERO showed that cooling has only limited effects on the carbon cycle. The additional cooling increases marine CO<sub>2</sub> uptake and reduces primary productivity, and consequently the amount of CaCO<sub>3</sub> and POC reaching the sediments, during glacial phases. The climate response to the  
215 simulated carbon cycle changes thus causes a net C and nutrient transfer into the ocean, increasing the peak glacial-interglacial atmospheric CO<sub>2</sub> difference by 10 ppm.~~

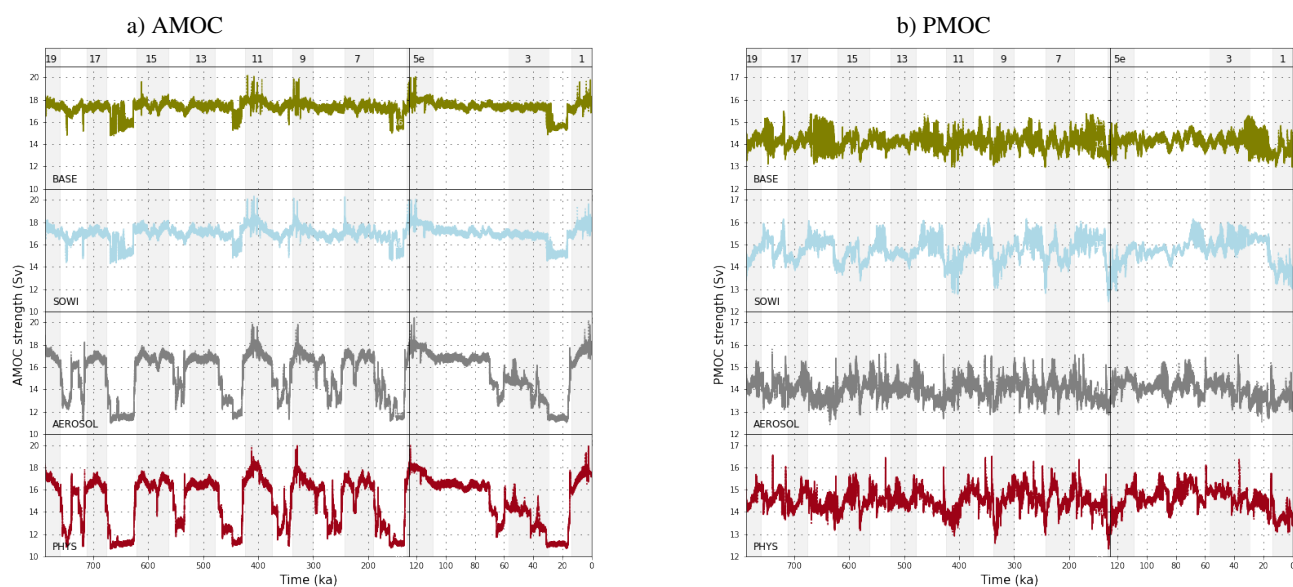
## Additional Figures

~~a) BASE, KGAS, SOWI, AERO~~

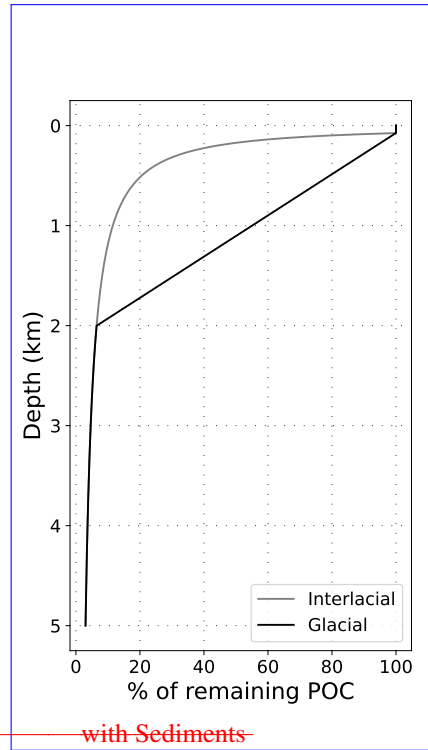
**Table S1.** Prescribed constant solute input into the surface ocean to balance steady-state interglacial sedimentary burial fluxes.

	<del>b) PIPO, BGC, ALL, CO2T</del> DIC (GtC/yr)	ALK (Tmol eq/yr)	$\text{PO}_4^{3-}$ (Tmol P/yr)	SiO (Tmol Si/yr)	$\text{DI}^{13}\text{C}$
heightBASE	0.414	21.61	0.19	4.52	

Transient variations of atmospheric  $\text{CO}_2$  concentrations as simulated in the simulations not shown in Fig. 5 in the main text, and as reconstructed by Bereiter et al. (2015). Shown is the deviation from the respective pre-industrial value.



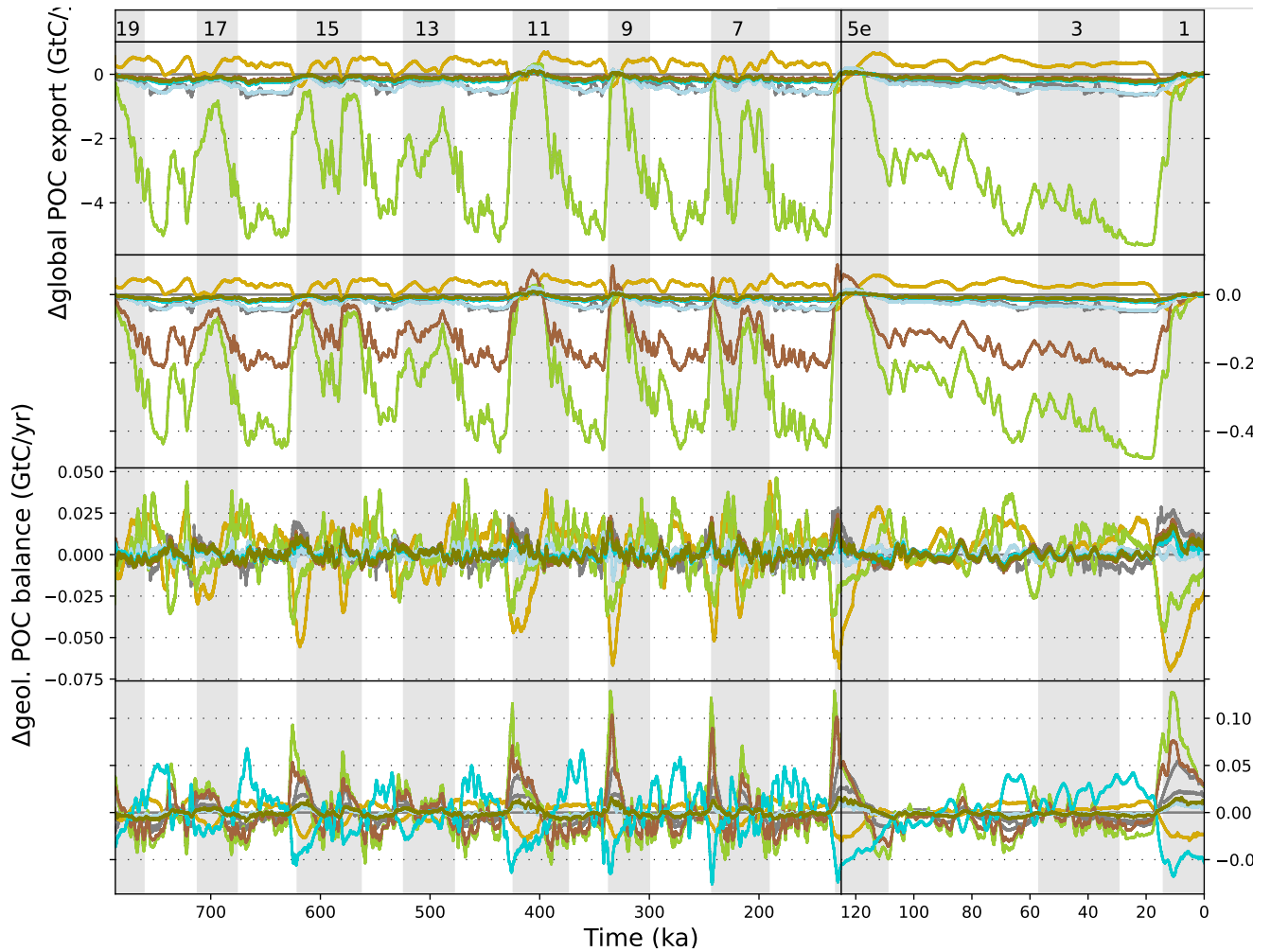
**Figure S8.** Transient variations of AMOC and PMOC strengths in simulations with different physical forcings.



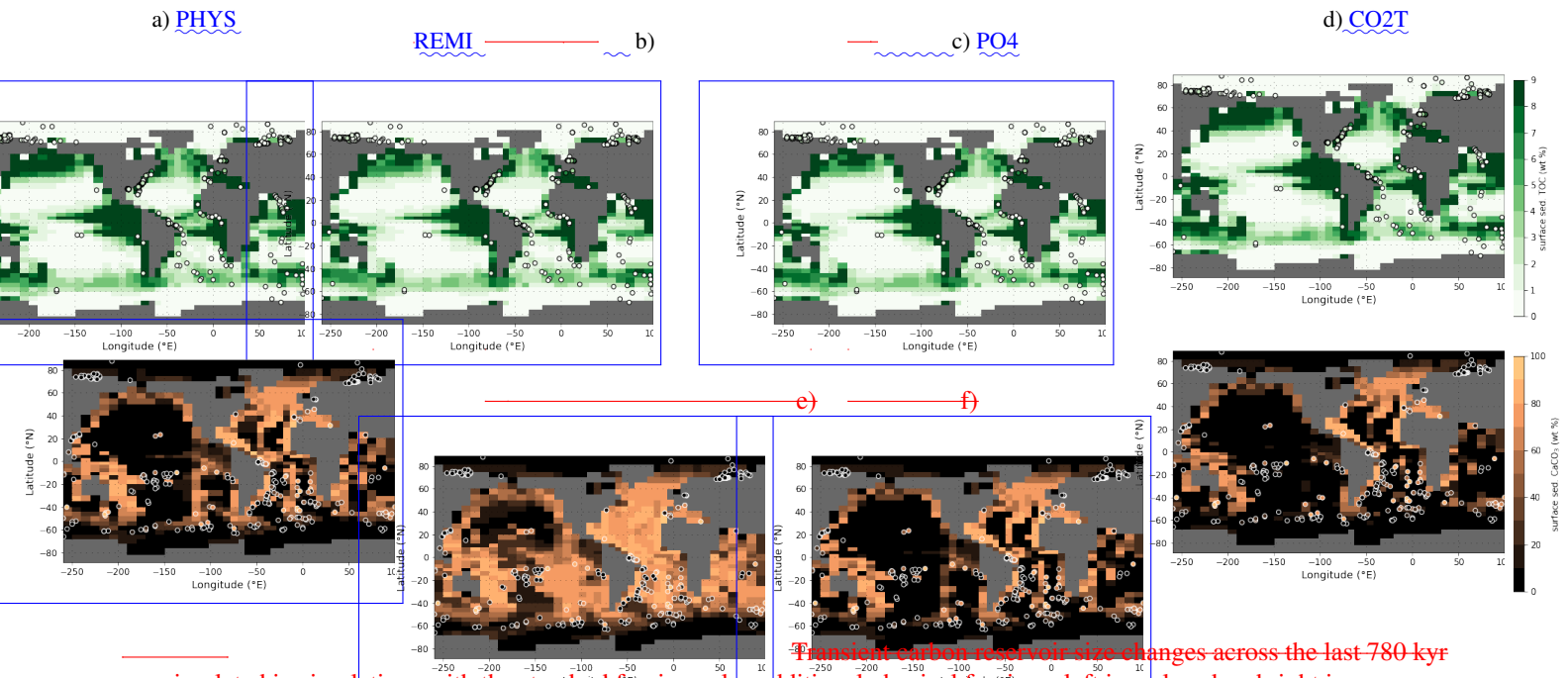
without Sediments

with Sediments

Figure S9. Comparison of the interglacial and glacial end-members of the prescribed remineralization profiles.

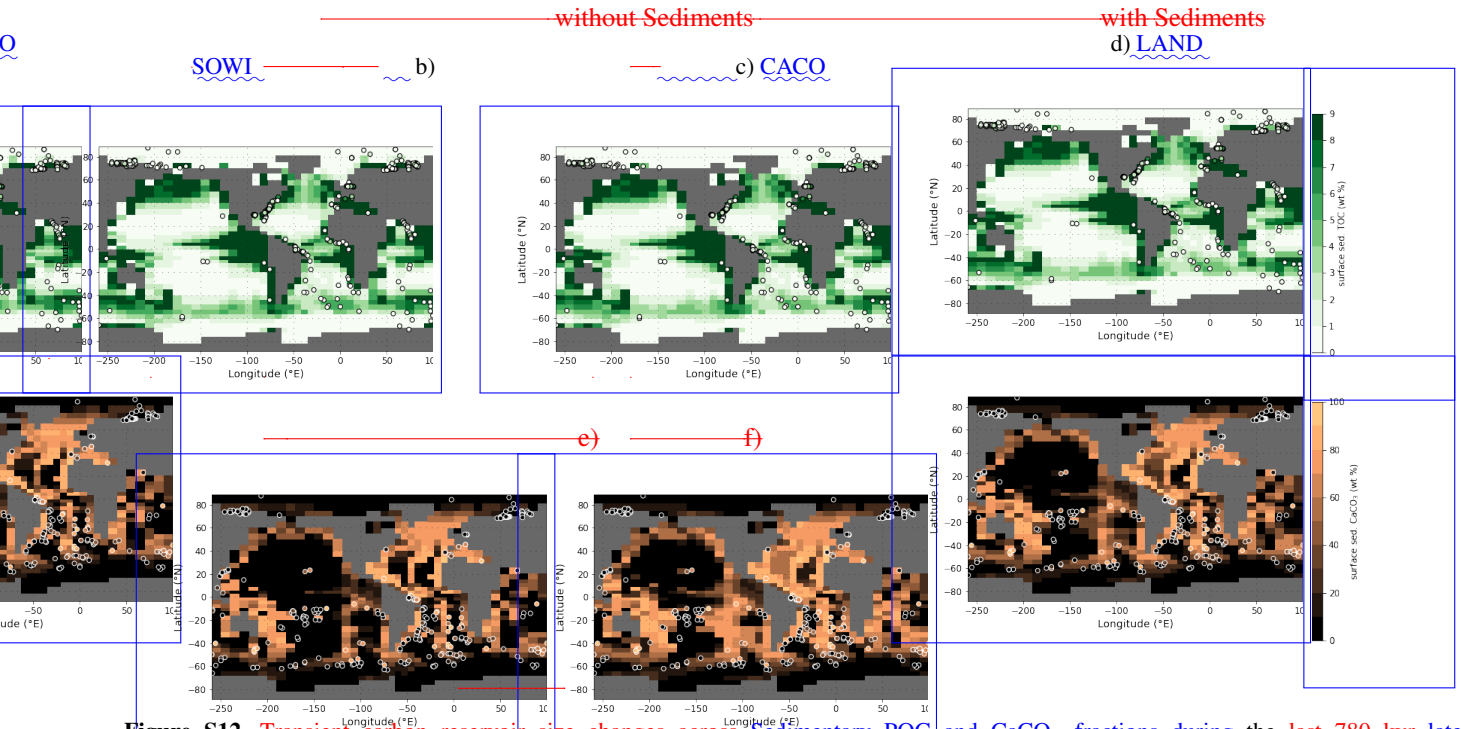


**Figure S10.** Transient variations of POC and  $\text{CaCO}_3$  export production and geologic imbalance (i.e. the difference between accumulation of these materials in marine sediments and the constant supply into the surface ocean that mimics terrestrial weathering in our simulations) due to the applied forcings. Shown are the absolute results for each simulation. The results that are explicitly mentioned in the text are shown in colour, the others are shown in gray. Gray shading indicates uneven MIS as indicated at the top of the figure.



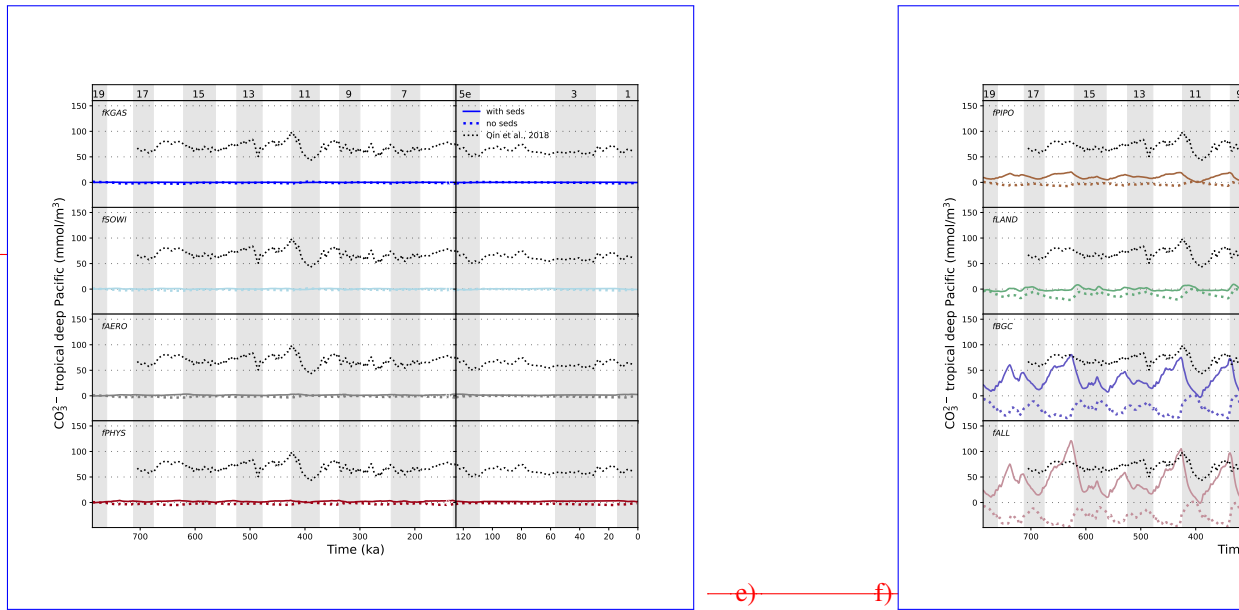
Transient carbon reservoir size changes across the last 780 kyr as simulated in simulations with the standard forcings plus additional physical forcings, left in a closed and right in an open system. Shown are the size changes of atmospheric, terrestrial, marine (DIC and DOC), sedimentary (POC and  $\text{CaCO}_3$ ) and lithospheric (organic and inorganic) carbon storage.

**Figure S11.** Atmospheric  $\text{CO}_2$  concentrations, DIC Sedimentary POC and carbon fluxes over  $\text{CaCO}_3$  fractions during the most recent full glacial-eyle late Holocene (Hayes et al., 2021) as reconstructed (circles) and in simulations with additional physical forcings PHYS, REMI, PO4 and without dynamic sediments CO2T (underlying maps). Shown are only data points that fall into the local benthic grid box of the model. The root mean square errors of simulated and reconstructed values are (from left to right): 7.6 %, 7.0 %, 7.6 % and 8.2 % for POC (top row) and 27.5 %, 25.7 %, 29.4 % and 31.4 % for  $\text{CaCO}_3$  (bottom row).



**Figure S12.** Transient carbon reservoir size changes across Sedimentary POC and CaCO<sub>3</sub> fractions during the last 780 kyr late Holocene (Hayes et al., 2021) as simulated-reconstructed (circles) and in simulations with the standard forcings plus additional biochemical forcings AERO, left in a closed SOWI, CACO and right in an open system LAND (underlying maps). Shown are only data points that fall into the size changes local benthic grid box of atmospheric the model. The root mean square errors of simulated and reconstructed values are (from left to right): 8.8 %, terrestrial 9.4 %, marine (DIC 7.6 % and DOC 7.6 % for POC (top row) and 27.2 %, sedimentary (POC 27.8 %, 26.2 % and 26.6 % for CaCO<sub>3</sub> ) and lithospheric (organic and inorganic bottom row) carbon storage.

without Sediments a)  $f_{CO2T}$ ,  $f_{KGAS}$ ,  $f_{SOWI}$ ,  $f_{AERO}$   
 b)  $f_{PIPO}$ ,  $f_{LAND}$ ,  $f_{BGC}$ ,  $f_{ALL}$  Sediments



Transient carbon reservoir size changes across the last 780 kyr

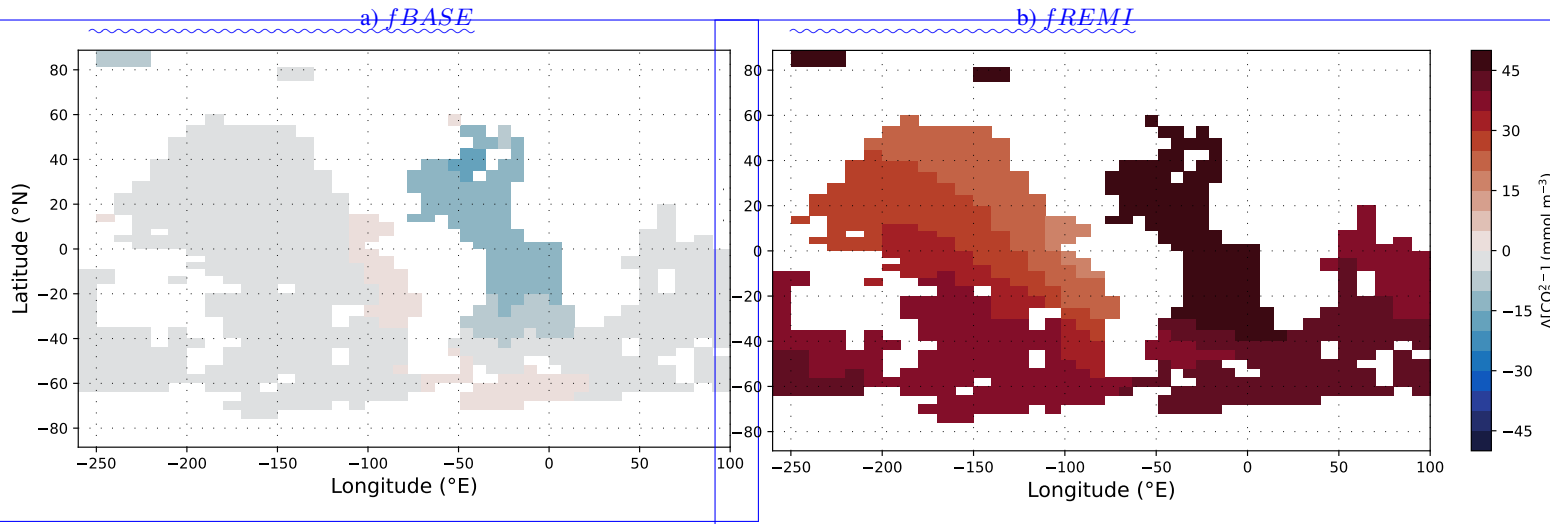
as simulated in simulations with the standard forcings plus terrestrial C fluxes, left in a closed and right in an open system.

Shown are the size changes of atmospheric, terrestrial, marine (DIC and DOC), sedimentary (POC and  $CaCO_3$ ) and lithospheric (organic and inorganic) carbon storage.

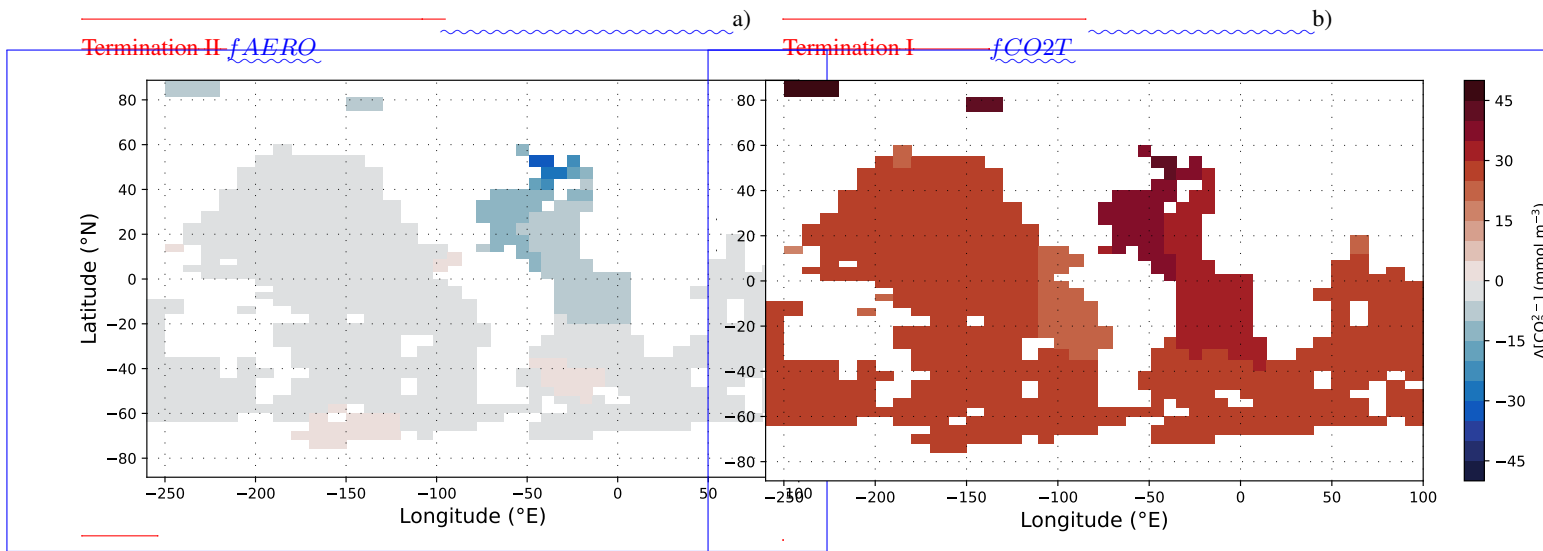
Atmospheric  $CO_2$  concentrations, DIC and carbon fluxes over the most recent full glacial cycle in simulations with additional biochemical forcings and without dynamic sediments.

Atmospheric  $CO_2$  concentrations, DIC and carbon fluxes over the most recent full glacial cycle in simulations with combinations of additional forcings and without dynamic sediments.

Figure S13. Transient variations of  $CO_3^{2-}$  in the tropical deep Pacific as simulated in simulations and reconstructed by Qin et al. (2018).

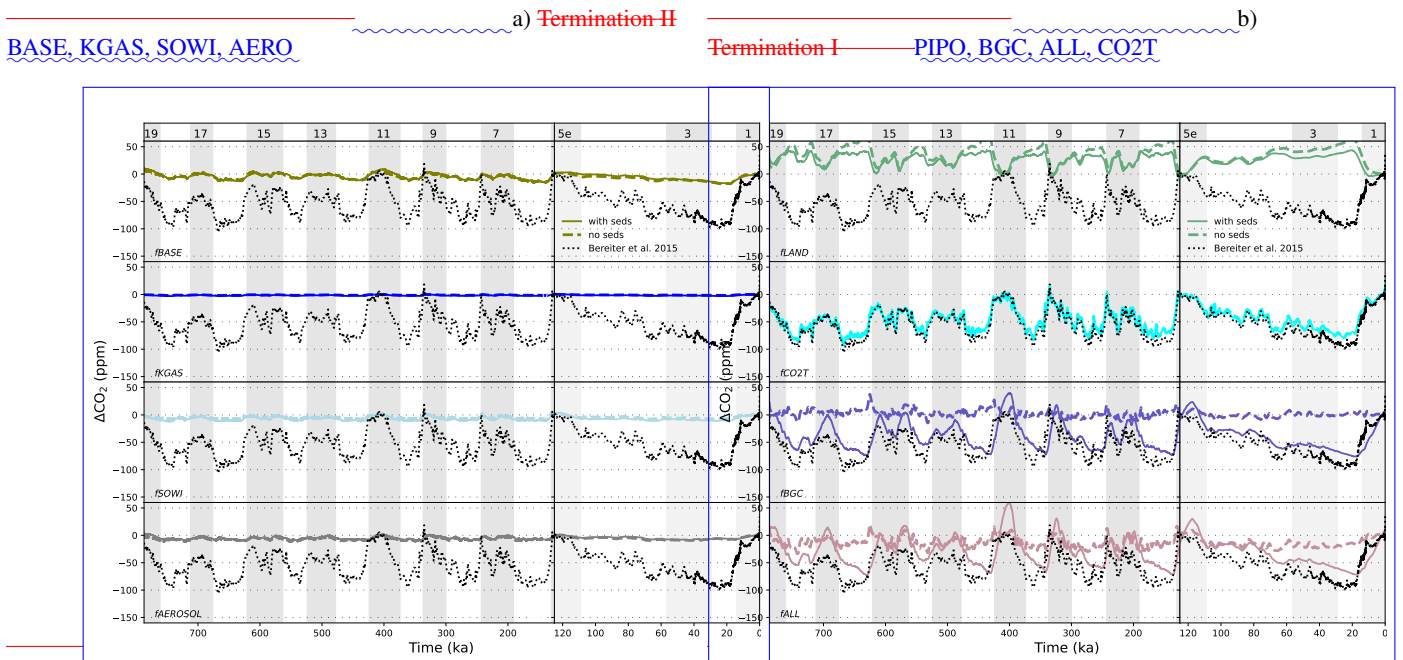


**Figure S14.** Difference of the glacial-interglacial atmospheric  $\text{CO}_2$  amplitude before and after the MBT in our simulations without interactive sediments compared to that Selected factorial effects on simulated LGM-PI differences in the reconstructed deep  $\text{CO}_2$  record (Bereiter et al., 2015, , horizontal black line)<sup>2</sup> (3500 m depth).

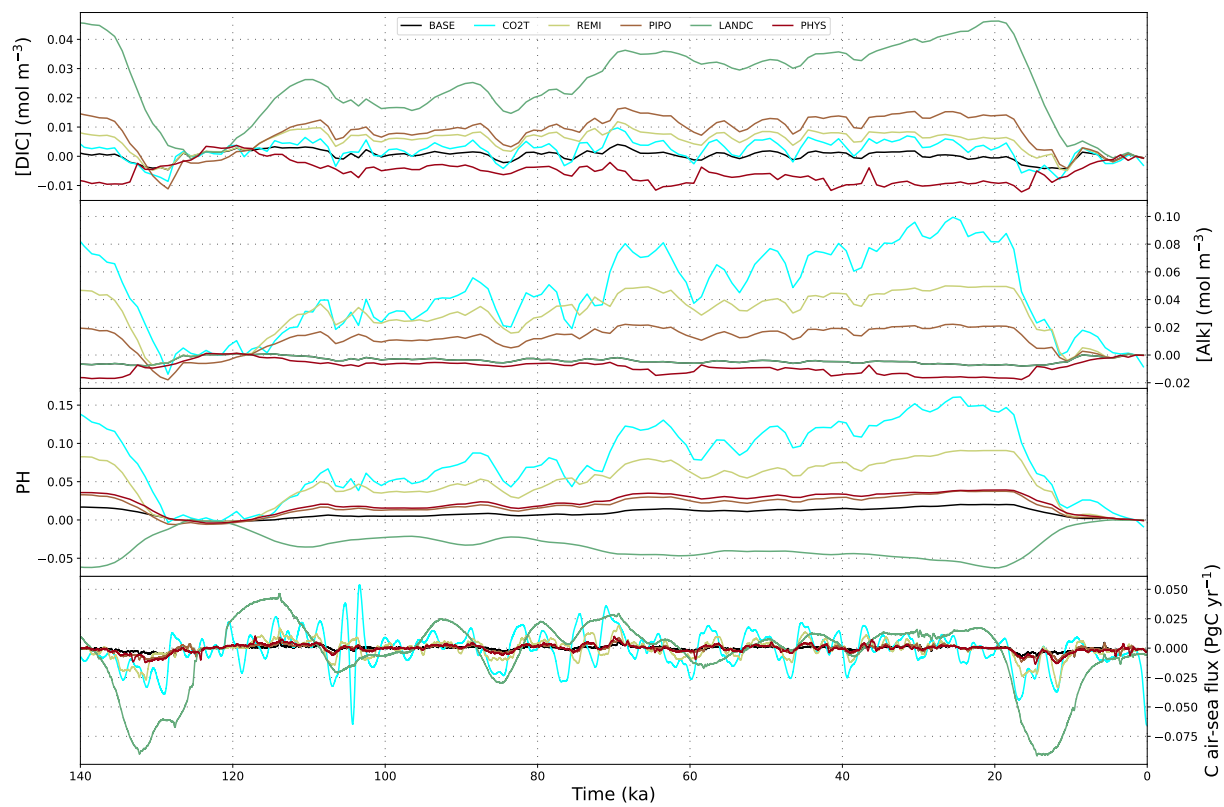


**Figure S15.**  $\delta^{18}\text{O}$ -derived scaling of the prescribed forcing and the resulting Selected factorial effects on simulated atmospheric  $\text{CO}_2$ , normalized by the respective PI-LGM  $\text{CO}_2$  difference, LGM-PI differences in selected simulations with interactive sediments (top row) and without interactive sediments deep  $\text{CO}_3^{2-}$  (bottom row 3500 m depth).

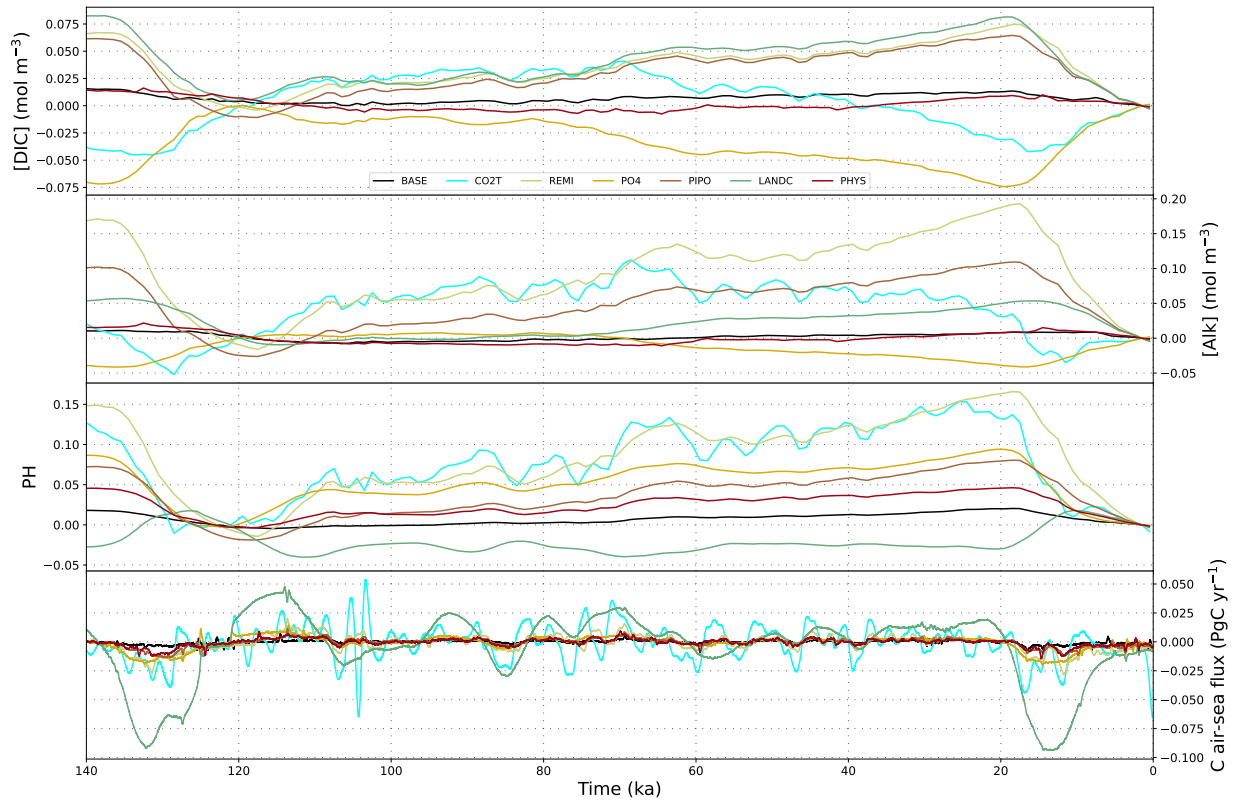




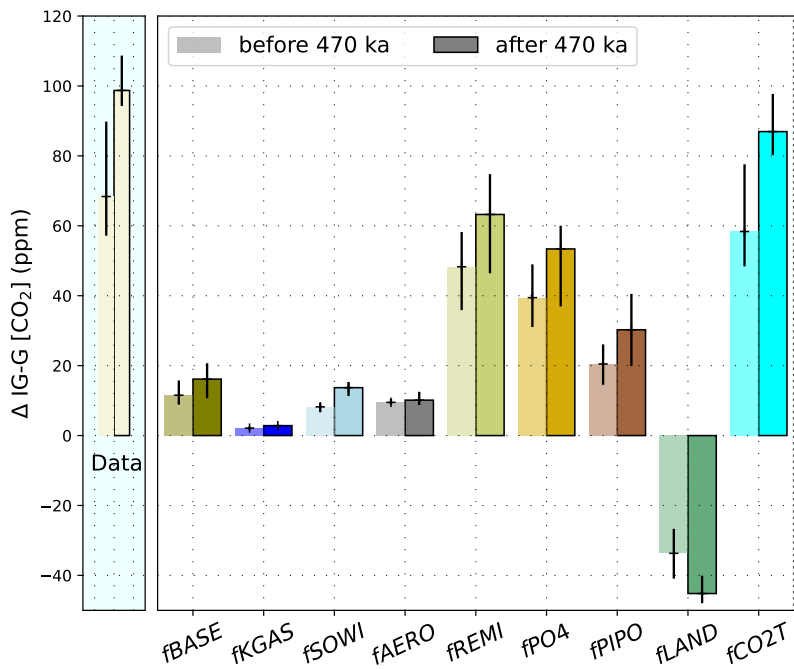
**Figure S16.**  $\delta D$ -derived scaling-Transient variations of the prescribed forcing and the resulting simulated atmospheric  $CO_2$  concentrations as simulated in the simulations not shown in Fig. 5 in the main text, normalized and as reconstructed by Bereiter et al. (2015). Shown is the deviation from the respective PI-LGM  $CO_2$  difference, in selected simulations with interactive sediments (top row) and without interactive sediments (bottom row) pre-industrial value.



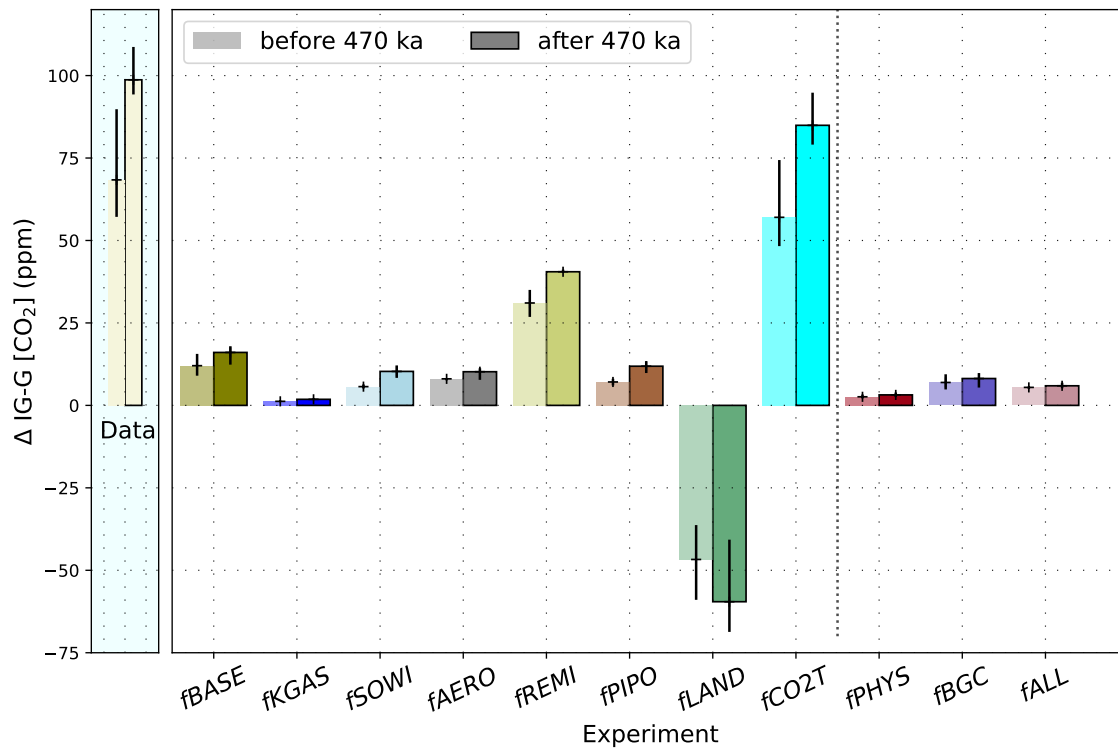
**Figure S17.** Globally-averaged changes in surface ocean carbonate system parameters in selected simulations without interactive sediments.



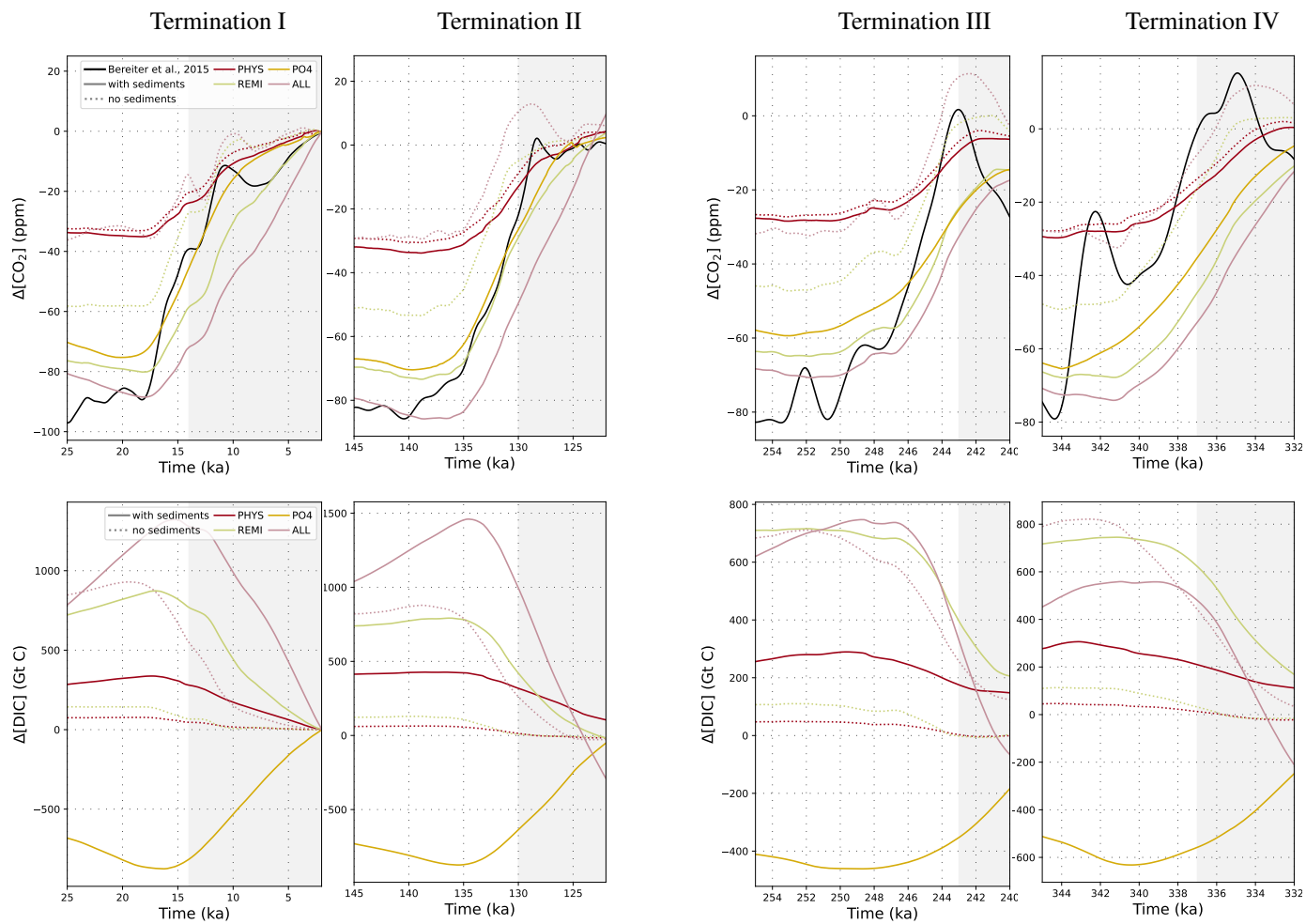
**Figure S18.** Globally-averaged changes in surface ocean carbonate system parameters in selected simulations with interactive sediments.



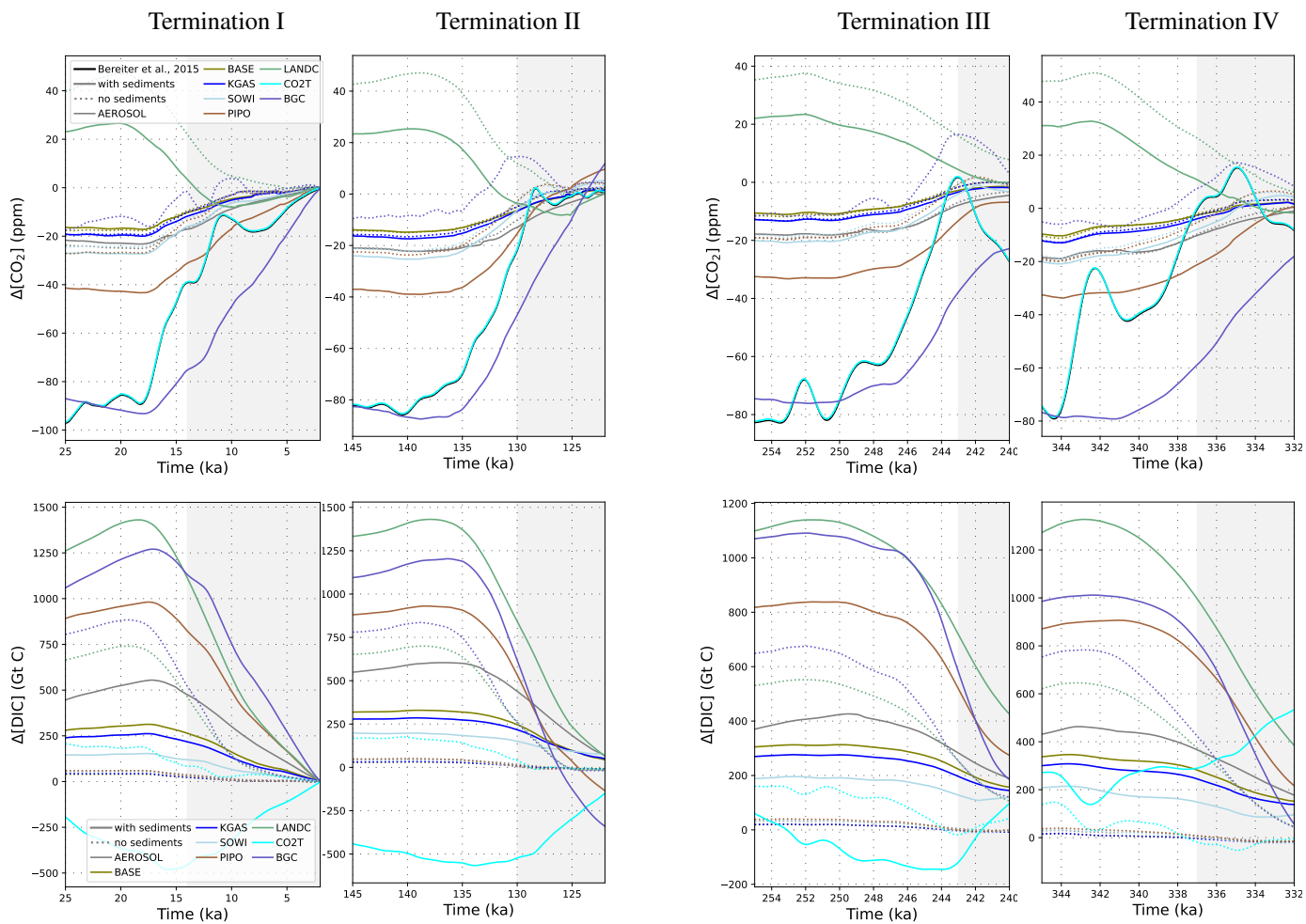
**Figure S19.** Difference of the glacial-interglacial atmospheric CO<sub>2</sub> amplitude before and after the MBT in our simulations compared to that in the reconstructed CO<sub>2</sub> record (Bereiter et al., 2015). For the results of the simulations without interactive sediments see Fig. S19



**Figure S20.** Difference of the glacial-interglacial atmospheric CO<sub>2</sub> amplitude before and after the MBT in our simulations without interactive sediments compared to that in the reconstructed CO<sub>2</sub> record (Bereiter et al., 2015, , horizontal black line).



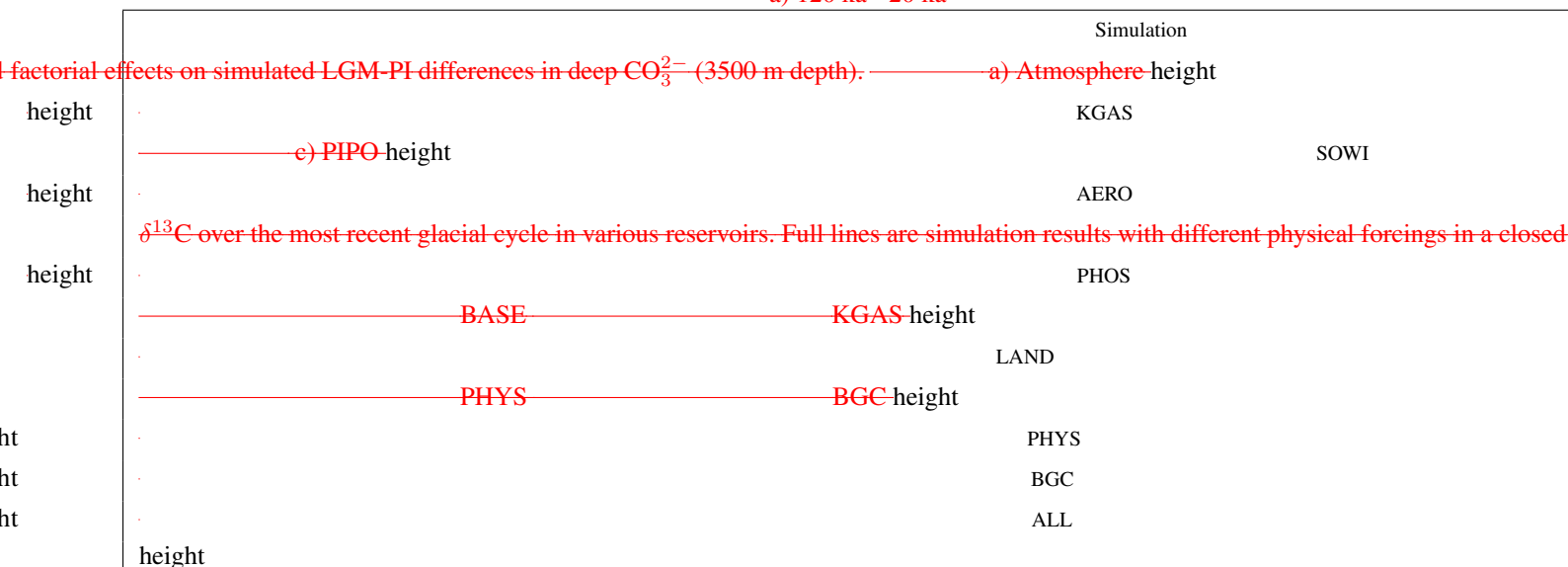
**Figure S21.** Reconstructed and simulated atmospheric  $\text{CO}_2$  changes (upper row) and simulated DIC changes (lower row) across the last four deglaciations.



**Figure S22.** Reconstructed and simulated atmospheric  $\text{CO}_2$  changes (upper row) and simulated DIC changes (lower row) across the last four deglaciations.

**Table S2.** Globally-averaged changes in surface ocean carbonate system parameters in selected simulations without interactive sediments Dynamical geologic carbon cycle imbalances (marine outputs - inputs) at the end of each simulation.

Globally-averaged changes in surface ocean carbonate system parameters in selected simulations with interactive sediments:  
 Globally-averaged changes in nutrient utilization in the surface ocean across the simulated 780 kyr.  
 Globally-averaged changes in  $PO_{4,pre}$  concentrations across the simulated 780 kyr.  
 The effect of step changes of plus or minus 30% of the prescribed clay flux on atmospheric  $CO_2$  concentrations, DIC and carbon fluxes over 100 kyr.  
 ————— a) 120 ka - 20 ka



Simulated (open system) and reconstructed (compilation from Pöppelmeier et al. (2023)) Holocene  $\delta^{13}C$  distribution Pacific.



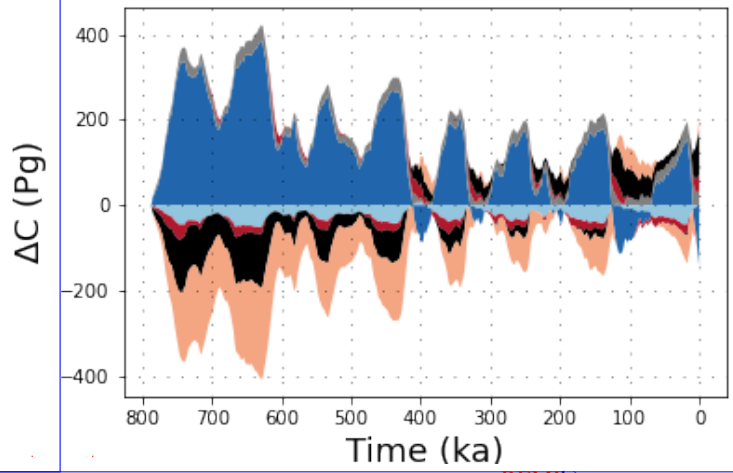
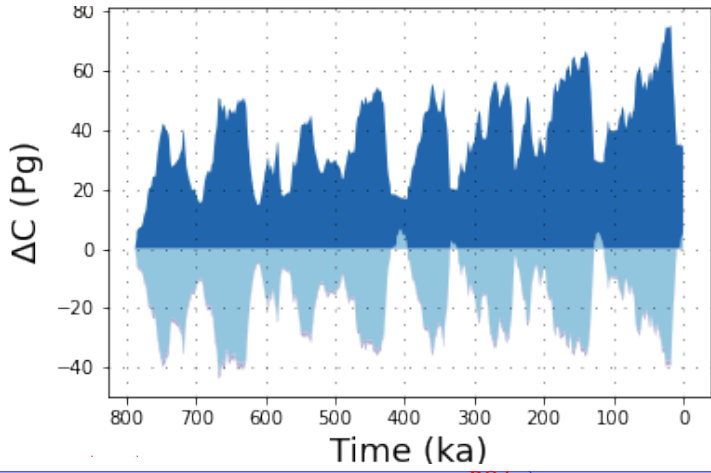
without Sediments

Sediments

BASE

KGAS

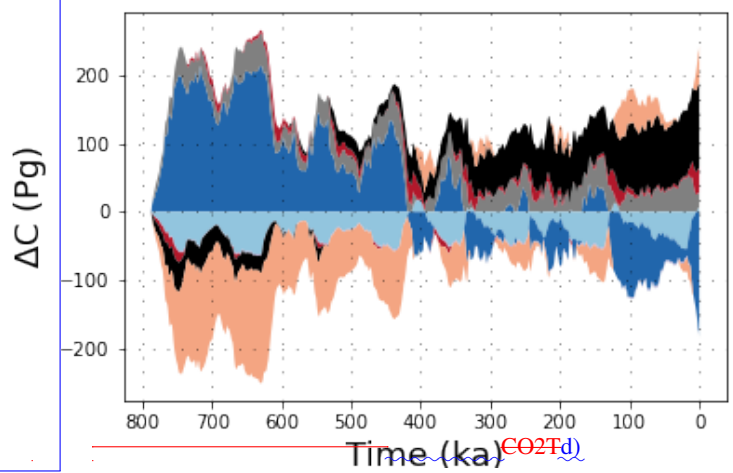
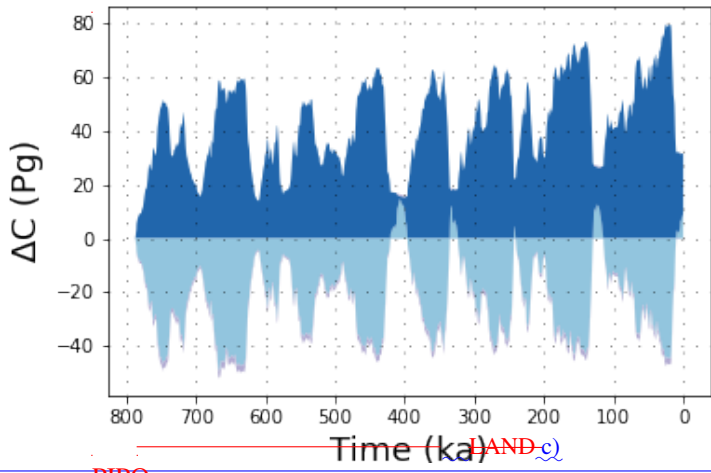
SOWI



AERO

PO4-a)

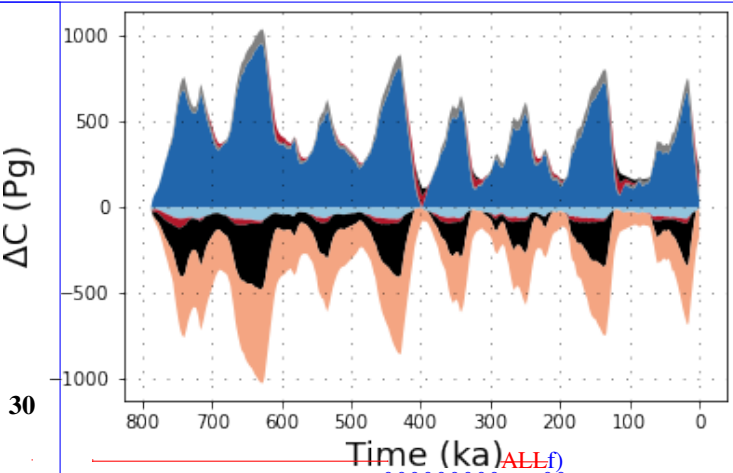
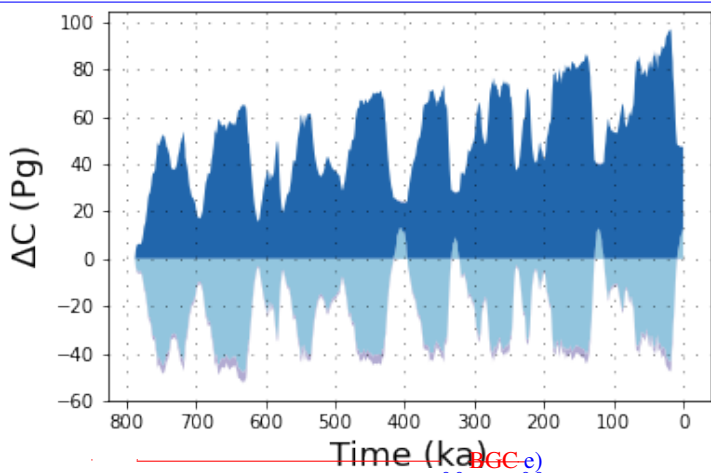
REMIB)



PIPO

LAND-c)

CO2T-d)

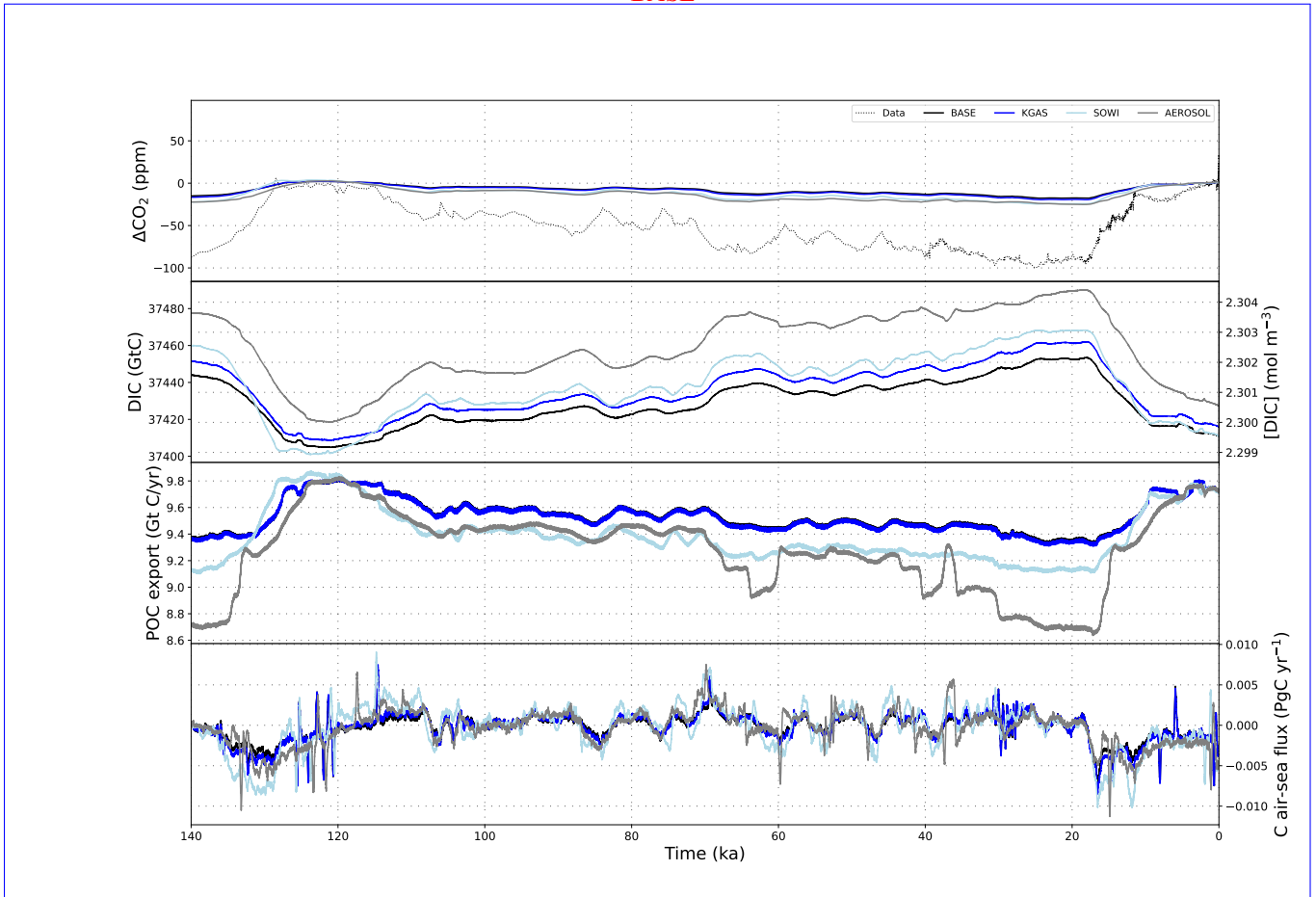


PHYS

IGC-e)

ALL-f)





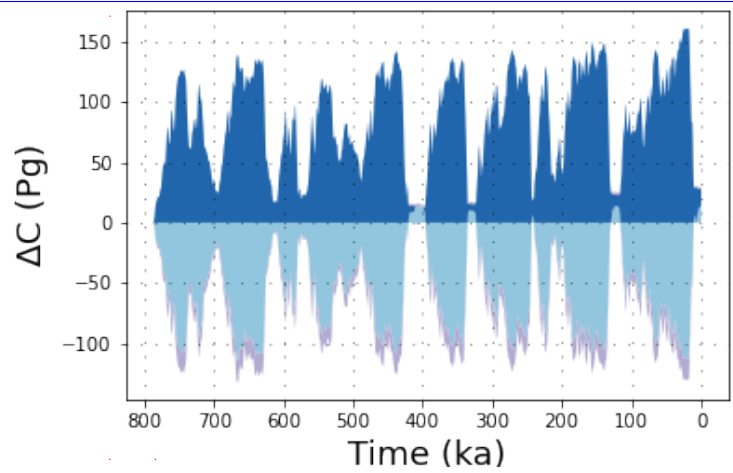
**Figure S24.** Atmospheric  $\text{CO}_2$  concentrations, DIC and carbon fluxes over the most recent full glacial cycle in simulations with additional physical forcings and without dynamic sediments.

Without Sediments

Sediments

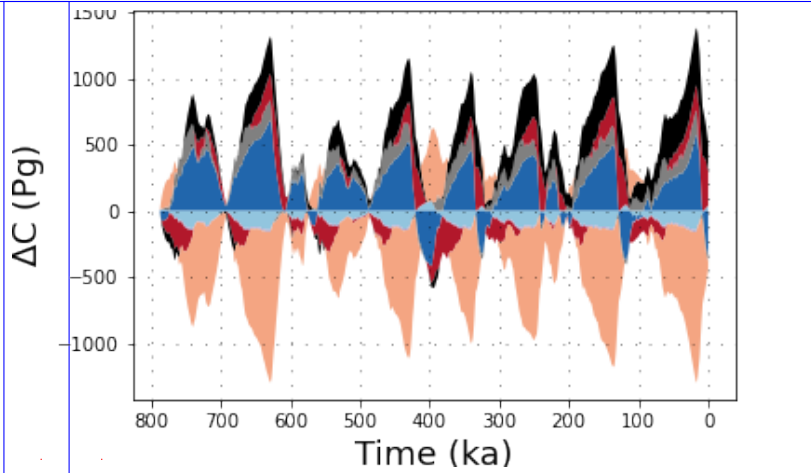
KGAS

SOWIwit

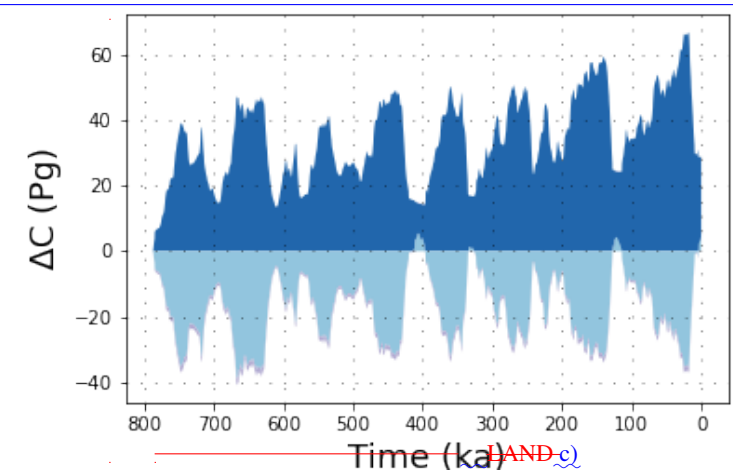


AERO

PO4-a)

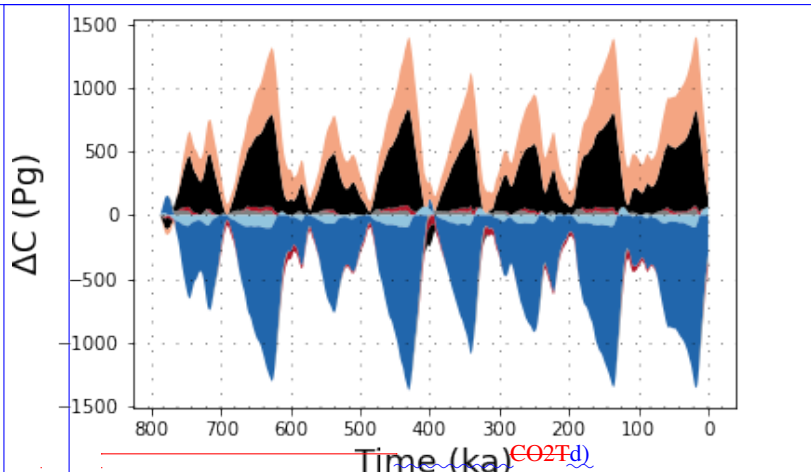


REMIb)

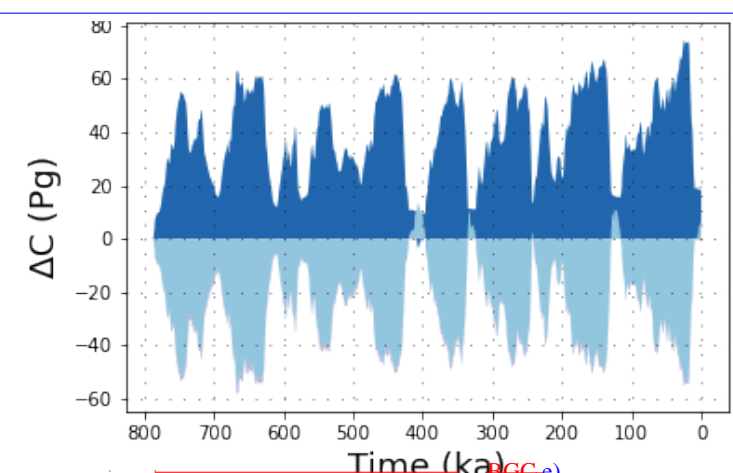


PIPG

LAND-c)

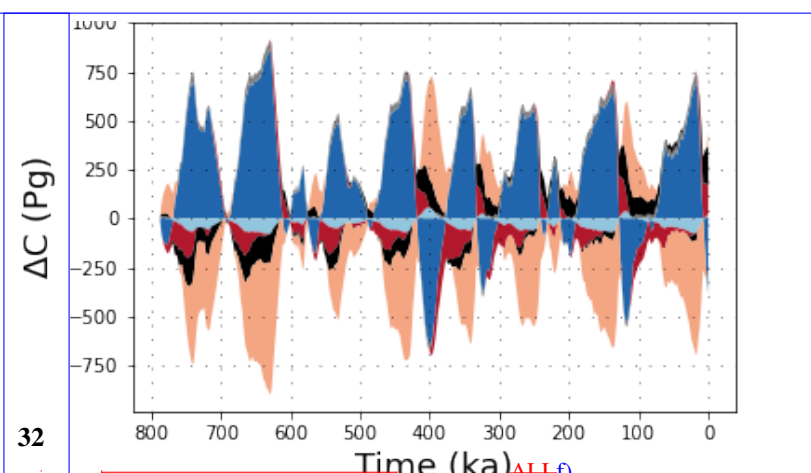


CO2Td)



PHYS

PGC-e)



32

ALLf)



↑ Support Model Data Comparison for simulations without interactive sediments