





REVIEW ARTICLE

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Ice sheets matter for the global carbon cycle

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The cycling of carbon on Earth exerts a fundamental influence upon the greenhouse gas content of the atmosphere, and hence global climate over millennia. Until recently, ice sheets were viewed as inert components of this cycle and largely disregarded in global models. Research in the past decade has transformed this view, demonstrating the existence of uniquely adapted microbial communities, high rates of biogeochemical/physical weathering in ice sheets and storage and cycling of organic carbon (>10⁴ Pg C) and nutrients. Here we assess the active role of ice sheets in the global carbon cycle and potential ramifications of enhanced melt and ice discharge in a warming world.

For a component of the Earth's system to impact the global carbon cycle, and potentially influence atmospheric concentrations of carbon dioxide or methane, it must either directly sequester and/or release carbon, or indirectly influence carbon uptake/release in other parts of the Earth system. The notion that ice sheets contain significant carbon stores has its roots in the early 2000s—the great ice sheets were hypothesised to advance over soil and vegetation carbon during glacial periods, with this fossil carbon being released back to the atmosphere once exposed by retreating ice during deglaciation¹. More recent work has highlighted the capacity of glacier surfaces to act as sinks for carbon-containing aerosols from anthropogenic or natural sources^{2,3}. However, both these mechanisms represent passive processes of carbon storage and release by glaciers. Only in the last 15 years have glacial systems started to be considered as active cyclers of carbon, arising from the discovery that they include a range of aquatic environments⁴ which host abundant and diverse populations of microorganisms⁵ and are hot spots for biogeochemical weathering⁶. These processes create the potential for ice sheets to directly or indirectly impact the global carbon cycle (Fig. 1). Direct impacts include the release of greenhouse gases (carbon dioxide, CO₂ and methane, CH₄) during the microbial respiration of organic matter (OM) stored within ice sheets. Examples of indirect impacts include the fertilisation of downstream ecosystems, promoted by either the release of nutrient-rich glacial meltwaters^{7–9} or by subglacial meltwater-induced upwelling of nutrient replete marine water at tidewater glacier margins^{10–14}. Ocean fertilisation by glaciers may be accompanied by significant CO₂ drawdown by phytoplankton, intensifying the biological pump^{15,16}.

The size of the carbon stores entombed in ice sheets^{1,17,18} and magnitude of nutrient supply to surface ocean waters by meltwaters and icebergs^{8,19} make it crucial to evaluate the role of ice sheets as open systems in regulating the global carbon cycle via the direct and indirect mechanisms identified in Fig. 1. Here, we draw upon advances over the last two decades to address the hypothesis that ice sheets have important direct and indirect impacts on the global carbon cycle (Fig. 1) at the present day, which are accentuated during periods of enhanced melt

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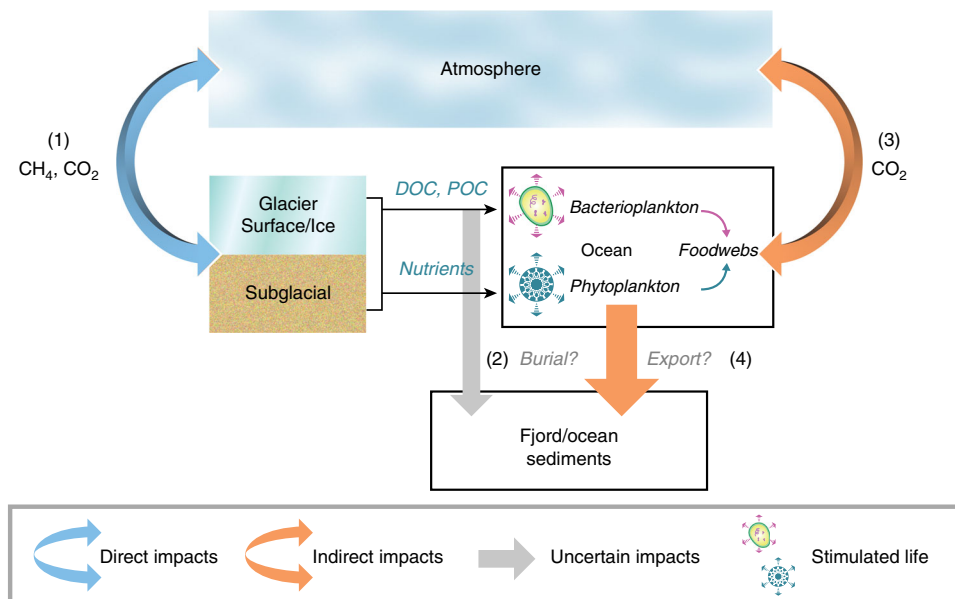


Fig. 1 Conceptual diagram of ice sheets in the global carbon cycle. The diagram indicates the potential direct and indirect impacts of ice sheets. (1) direct sequestration or emission of CO_2/CH_4 by microbial activity in ice sheets, (2) burial of terrestrial OM exported from ice sheets by rivers, (3) emission of CO_2 by respiration or uptake by primary production in the oceans (4) export production-OM produced by primary production which is not recycled before it sinks to the ocean floor

or ice discharge. In this Review, we first identify the key biogeochemical processes in ice sheets, and then go on to highlight in further discussions important indirect and direct impacts. We conclude this synthesis by evaluating the suggestion that ice sheets play a role in regulating the global carbon cycle with a novel analysis of the geological record over the last glacial-interglacial transition.

A paradigm shift in ice sheet biogeochemical cycling

In 1999, the first communities of microorganisms were discovered beneath a valley glacier in the Swiss Alps²⁰ driving a major shift in our world-view of glaciers and ice sheets as abiotic systems to extensive icy biomes⁵. Microbial communities have since been found ubiquitously in glacial systems⁵, ranging from sub-micron diameter liquid ice veins between ice crystals²¹ to large subglacial water bodies, such as Subglacial Lake Whillans situated 800 m beneath the West Antarctic Ice Sheet²². The survival of these seemingly diverse communities is due to their adaptation to a unique combination of physical and geochemical conditions that are not encountered anywhere else on Earth.

First, liquid water is abundant in ice sheets, generated by the melting of surface ice and snow and by geothermal/frictional heating and pressure melting of ice at the glacier bed. Surface melt is often widespread on the Greenland Ice Sheet and supplies melt to well-developed drainage systems at the ice sheet bed (where ice is at the pressure melting point)²³. These drainage systems evolve seasonally from slow-inefficient distributed drainage to fast-efficient drainage (e.g., channels), with residence times shifting from months to <1 day²³. In contrast, surface melt is largely absent in Antarctica, apart from in marginal locations^{24,25}. Nonetheless, the bed of the Antarctic Ice Sheet is hydrologically active, with subglacial lakes, swamps, channels and groundwater aquifers fed by the melting of basal ice layers⁴. Water flowing in such long residence time drainage systems here may take years to decades to emerge at the ice margin²⁶.

Second, the sliding of glaciers over their bedrock generates very fine, highly reactive rock flour by glacial crushing and grinding.

This is the source of a potent mixture of electron acceptors (e.g., oxidised forms of sulphur and iron such as sulphate and Fe(III)), electron donors (e.g., OM, hydrogen²⁷, as well as reduced elemental species such as Fe(II) in iron sulphide minerals), micro-nutrients and macro-nutrients, liberated by chemical dissolution. In the deep, dark and cold ecosystems beneath ice sheets, these rock-sourced redox pairs and nutrients promote the metabolism of a diverse mix of chemolithotrophic and chemoorganotrophic microorganisms, able to fix and supply autochthonous carbon to the wider subglacial ecosystem. In Antarctic Subglacial Lake Whillans, a large proportion of phylotypes in sediments were related to chemolithoautotrophic species that use reduced forms of sulphur, nitrogen and iron as energy sources²².

Third, as glaciers and ice sheets expand, they bury OM associated with soil, vegetation, lake and marine sediments. Furthermore, OM is deposited by aeolian processes onto the ice surface, originating from distant sources or from proximal surfaces surrounding the ice. This allochthonous material is supplemented by organic carbon fixed in situ by abundant autotrophic microorganisms in melting zones of ice sheet surfaces²², and thus, influences rates of ice melting by surface darkening (see Box 1)²⁸.

Diverse oxidising and reducing conditions evolve in response to patterns of water flow beneath ice sheets, from fast flowing oxic channels to slower drainage through anoxic or hypoxic sediments and subglacial lakes. These hydrogeochemical environments create niches for microbial colonisation and permit a diverse range of biogeochemical processes to be supported across the redox spectrum, including sulphide oxidation²⁹, denitrification^{30,31}, sulphate³², and iron reduction^{33,34} and methanogenesis^{35,36}. Well-developed hydrological systems, together with the release of icebergs via calving, create the potential for OM and nutrient transport out of the ice sheet and into downstream aquatic ecosystems (e.g., lakes, rivers, oceans). The release of fresh, buoyant subglacial meltwaters often some 100 s of m below the ocean surface at the margins of marine-terminating outlet glaciers also stimulates the upwelling of marine water and transport of associated nutrients to the ocean surface¹⁰⁻¹⁴. It is this combination of in situ microbial activity, dynamic processes

Box 1 | Microbial activity on ice sheet surfaces and the bioalbedo effect

The bioalbedo effect refers to the darkening effect of biological impurities on snow and ice¹⁷⁷. The melt zones of ice sheets are host to diverse communities of microorganisms that thrive during the summer months across a range of aqueous ecosystems including surface lakes, wet bare ice, snow and cryoconite holes (small cylindrical water-filled depressions, created by the solar heating of surface aggregates of mineral and organic particles and microbial cells, known as cryoconite)¹⁷⁸. Bare ice surfaces are dominated by ice algae¹⁷⁹, which are commonly green algae on the Greenland Ice Sheet^{179–181}. In cryoconite holes, the dominant active taxa are cyanobacteria and alpha-proteobacteria and/or beta-proteobacteria¹⁸². The activity of these microorganisms has recently drawn attention via the hypothesis that the biologically driven accumulation of OM accelerates ice melting, via its effect upon ice surface darkening^{28,183}. Net bioaccumulation depends upon the balance of CO₂ fixed from the atmosphere by phototrophs and CO₂ returned to the atmosphere by respiration, and is influenced by a wide range of physical and biogeochemical processes. Recent work on the Greenland Ice Sheet suggests that carbon fixation exceeds carbon consumption, making the ice sheet surface net autotrophic (i.e., a CO₂ sink^{113,183,184}) and enabling the accumulation of OM and pigmented algae¹⁷⁹. Autochthonous OM is supplemented by wind-blown material, which becomes biologically altered on the ice sheet surface by the release of exopolymeric substances which bind particles¹⁸⁵. The direct impact of the bioalbedo effect has yet to be fully quantified. However, initial investigations indicate that algal abundance on Greenland ice surfaces explains 70% of the variation ice reflectance, suggesting a significant impact of ice algae on ice surface albedo²⁸. The resultant early exposure of underlying dark (low albedo) glacial ice following snowmelt has the potential to further enhance glacier melting¹⁸⁶.

of meltwater export and glacial advance/retreat cycles that creates an active connection between ice sheets, the ocean and the atmosphere (Fig. 1) and which we explore in subsequent sections.

Ice sheets as nutrient factories

A unique combination of intense physical erosion, active biogeochemical cycling and high meltwater fluxes from glacier systems, as described in the previous section, point towards the importance of ice sheets as direct or indirect sources and processors of a wide range of life-essential elements. There are three potential impacts of this glacially exported nutrient within the marine environment. First, direct fertilisation by the glacially exported nutrients themselves, including inorganic forms of N (e.g., NH₄⁺, NO₃⁻, NO₂⁻) and P (PO₄³⁻), organic forms of N and P, Si and micronutrients such as Fe (Box 2, Supplementary Tables 1 and 2)³⁰. Second, indirect fertilisation by buoyant meltwater plumes entraining nutrient-rich marine waters as they rise up from depth^{11,13,14,37,38}. Finally, indirect impacts via benthic recycling and liberation of nutrients from glaci-marine sediments³⁹, which will in turn imprint upon upwelling oceanic waters. The release of nutrients to the surface ocean via these mechanisms has the potential to fertilise marine waters, stimulate changes in the plankton community composition⁴⁰ and enhance primary production, export production and CO₂ drawdown via the biological pump—an indirect impact on the carbon cycle. Deep ocean water and subglacial meltwaters tend to be enriched in different nutrient species, for example, subglacial meltwaters are enriched in crustal species such as Si and Fe but depleted in nitrate and phosphate, while deep marine waters are often enriched in nitrate and phosphate. Thus, the impacts of these two different mechanisms of nutrient release will be shaped by which nutrient they supply relative to that which is most limiting to phytoplankton.

By far the largest source of nutrients released directly via ice sheet meltwaters is the subglacial environment⁸, derived from bedrock by physical and biogeochemical weathering or from sequestered OM by biological activity⁴¹ (Box 2). Long flow paths (10 s to 1000 of km) result in enhanced meltwater residence times beneath ice sheets, which together with seasonally high meltwater pH (often > 8.5⁴²), promote the chemical dissolution and alteration of nutrient-rich minerals such as aluminosilicates and P-bearing apatite. Thus, meltwaters and icebergs exported from ice sheets are also often enriched in bioavailable forms of dissolved and particulate phosphorous and silicon^{42–44}. For example, yields of soluble reactive P generated in large ice sheet catchments are among the highest in the literature (17–27 kg P m⁻² a⁻¹)⁴², and an order of magnitude higher than from small valley glaciers^{45,46}.

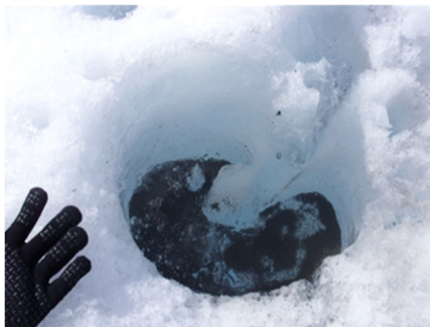
Total P fluxes are an order of magnitude higher than those for other world rivers, largely sourced from minerals such as fluorapatite⁴². This suggests that high physical and chemical erosion rates in ice sheets⁴⁷ are important in enhancing total P fluxes. Traditional notions of depressed silicate mineral weathering beneath small valley glaciers, inferred from low concentrations of dissolved Si in glacial runoff⁴⁸, may also not hold for large ice sheets⁴³. Recent work has shown significant concentrations of amorphous silicon (ASi) associated with suspended particulate matter in Greenland Ice Sheet runoff (~1% by mass). When this particulate component is included in total Greenland Ice Sheet Si fluxes via bulk runoff, the total flux rises by an order of magnitude to 50% of the total Arctic riverine Si flux⁴³. Potential formation mechanisms include either production of ASi during rock grinding, a chemically leached surface layer or a precipitated weathering crust arising from dissolution/re-precipitation on freshly ground and leached particles⁴³. Inclusion of ASi in total glacial Si fluxes has the potential to increase Si fluxes by an order of magnitude⁴³. Glacially sourced ASi is highly soluble in seawater and its export, together with DSi, has the potential to change the oceanic Si isotopic signature and inventory on glacial-interglacial timescales⁴⁹ and stimulate the productivity of diatoms and other siliceous organisms^{43,44,50}.

Perhaps one of the most well studied nutrients released from glaciers and ice sheets is iron (Fe). The liberation of bioavailable Fe from bedrock via biogeochemical weathering (see Box 2) is thought to be important in fertilising ocean basins where phytoplankton are limited by Fe availability (e.g., the Southern Ocean, NW Pacific Ocean)^{51,52}. A suite of microbially-mediated processes including silicate dissolution, sulphide oxidation⁵³ and dissimilatory iron reduction^{33,34} generate ice sheet runoff enriched in filterable (operationally defined here as Fe which passes through a 0.2 or 0.45 μm filter) and highly reactive particulate forms of iron^{54–56,57} that contain bioavailable Fe(II)^{58,59}. Icebergs are particularly important Fe exporters, containing enhanced concentrations of bioavailable (ascorbic acid extractable) iron (oxy)hydroxides (e.g., ferrihydrite) in iceberg rafted debris (IRD)¹⁹. There are likely important interactions between iron and other chemical species which are critical to consider within the context of wider ice sheet nutrient cycles, for example, the sorption of soluble reactive P (SRP) onto highly reactive Fe (oxy)hydroxide nanoparticles or colloids⁴².

In contrast to P, Si and Fe, concentrations of dissolved inorganic nitrogen in ice and snowmelt are low (nM to low μM)^{42,44} compared to deep ocean water (Supplementary Tables 1 and 2). While further NO₃⁻ and NH₄⁺ may be acquired by meltwaters in the subglacial environment by microbial activity, concentrations of dissolved N in glacial runoff are still in the low micromolar

Box 2 | Sources and cycling of nutrients**Atmospheric-derived nutrients**

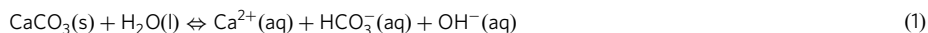
The annual deposition of snow and subsequent transformation to ice locks up atmospheric-derived nutrients, such as nitrate¹⁸⁷. Liberation of this ice-entombed nutrient is controlled by ice sheet hydrology and differs between ice sheets. On the Greenland Ice Sheet, atmospheric nutrients in snow and ice are released to surface meltwater streams in summer melt in the ablation zone^{31,187}. In zones of ice sheets where surface air temperatures are well below 0 °C (e.g., most of the Antarctic Ice Sheet), zero surface melting means that this atmospheric nutrient release does not occur until the ice is advected to melting zones of the ice sheet bed. An exception is found in marginal regions, such as the McMurdo Dry Valleys, where solar radiation-driven melting of debris entombed in surface glacier ice causes localised melting and meltwater release to streams²⁴.

**Ice sheet surfaces**

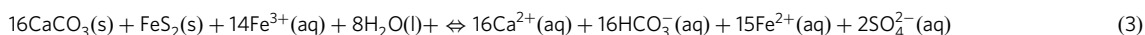
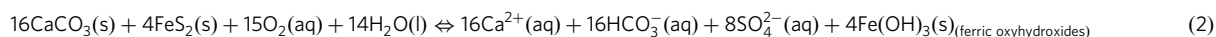
A wide range of ecosystems, such as cryoconite holes (see photo) on melting ice sheet surfaces, harbour productive microbiota with active nutrient cycling, including nitrogen fixation and nitrification^{7,188–190}. These microbial processes further enhance the nutrient content of meltwaters prior to their discharge either to the ice sheet bed via moulins or at the margin. While nitrate concentrations can be several μM, surface meltwaters generally have much lower concentrations of crustally derived species such as P, Si and Fe⁸.

Ice sheet beds

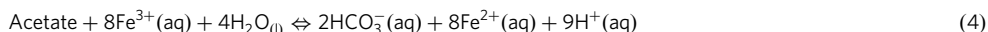
Physical processes are vital in promoting cycling of nutrients at ice sheet beds via: (1) production of fresh mineral surfaces by glacial grinding; and (2) OM cycling, including that of ancient overridden OM. The immense capacity of glaciers to erode their underlying bedrocks via a combination of plucking and abrasion, generates an abundant supply of very fine rock flour. This gives glacial meltwater rivers a distinctive milky appearance, visible as turbid plumes when they enter downstream fjord and coastal waters¹⁹¹. Such flour is highly geochemically reactive, due to its large surface area: volume ratio and the exposure of reactive minerals such as iron sulphides and carbonates⁴⁸. Traditionally, chemical weathering beneath ice sheets was assumed to be low to negligible¹⁹², but contemporary field studies in glacierised catchments indicate chemical weathering rates that exceed or are similar to the global mean⁴⁸. Marine-based work using paleo-proxies also indicates that sub-ice sheet chemical dissolution of rock material is enhanced during deglaciation (21–7 kyr B.P) when large expanses of glacial sediments become exposed as the ice retreats^{193,194}. The chemical weathering of glacial sediments is an important process driving the release of crustal nutrients, such as Si, P, Fe and other micronutrients in dissolved or bioavailable particulate forms. The first reaction to occur upon wetting of glacial flour is carbonate hydrolysis (e.g. hydrolysis of calcite, Eq. 1).



Further chemical dissolution, including that of silicate minerals, is fuelled by carbonation reactions (including via microbial CO₂ in some cases^{6,195}), by protons released during the (microbial) oxidation of sulphide minerals (e.g. coupled calcite dissolution/sulphide oxidation via oxic or anoxic mechanisms, Eqs. 2 and 3 respectively)^{29,53} or via other forms of microbial weathering (e.g., release of metabolites such as organic acids).



Silicate mineral dissolution generates dissolved Si in meltwaters, an important nutrient required by siliceous organisms such as diatoms and sponges. This process is thought to be enhanced beneath ice sheets relative to small valley glaciers, since long flow paths and prolonged meltwater residence times lead to the exhaustion of carbonate minerals in sediments or attainment of saturation with respect to calcite in meltwaters^{6,196}. Iron cycling is also important in glacial systems, via sulphide oxidation (oxic and anoxic)⁵³ and dissimilatory iron reduction³³ (Eqs. 2, 3 and 4, respectively).



OM buried beneath ice sheets during their formation, supplemented by new carbon production via chemolithoautotrophy¹⁹⁷, provides another important substrate for microbial nutrient cycling in wet-based zones of ice sheet beds. Ammonium is thought to be acquired by microbial mineralisation of OM, subsequently fuelling populations of nitrifiers^{22,198}. Heterotrophic respiration of subglacial OM utilising the full spectrum of electron acceptors along the redox continuum has been reported, including denitrification¹⁹⁸, iron reduction³³ (Eq. 4), sulphate reduction³² and methanogenesis^{35,36}.

range^{7,31}. The low N content of most bedrock types⁶⁰ also means that the concentrations of N associated with suspended particulate material in ice sheet runoff are often below detection limit of analytical methods.

Organic phases of key nutrients are important in some contexts within ice sheets, resulting from the cycling of allochthonous OM and production of autochthonous OM. The organic phases of particulate P and N are measurable in ice sheet runoff, but

comprise a much smaller proportion of the total N and P fluxes compared with those from Arctic rivers^{31,42}. In comparison, the dissolved organic components of N and P in ice sheet meltwaters can be significant, acquired via the activity of micro-organisms on the glacier surface and at the bed. For example, dissolved organic N (DON) comprised 50% of the total dissolved N load of Greenland Ice Sheet runoff³¹. Dissolved organic matter (DOM) may also act as an important stabiliser for key redox-sensitive or

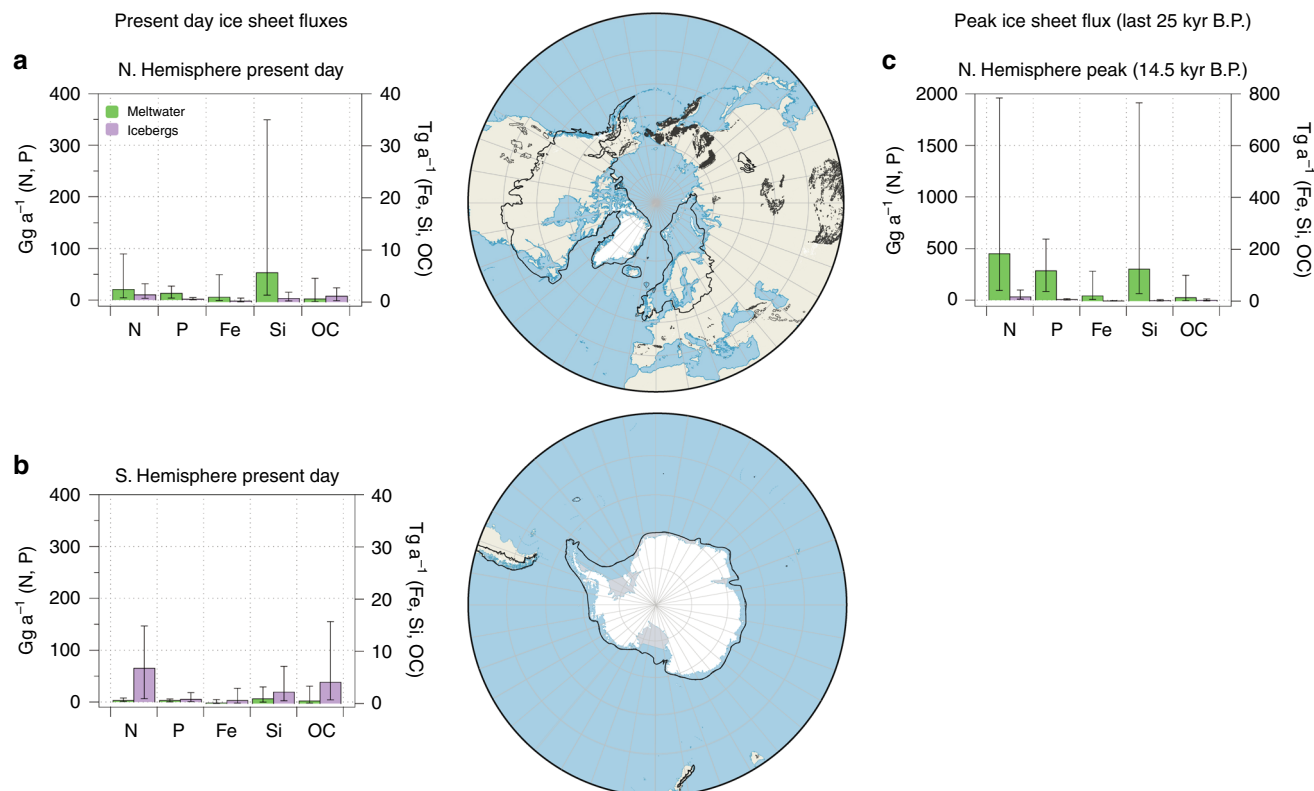


Fig. 2 Fluxes of nutrients and organic carbon. Fluxes of bioavailable nutrients and organic carbon associated with subglacial meltwater and ice discharge from (a) northern and (b) southern hemisphere ice sheets at the present day and (c) northern hemisphere ice sheets during Meltwater Pulse 1a (14.5 kyr B.P.). LGM extents of ice sheets in both hemispheres are indicated by a black line in the maps. Nutrient fluxes and their uncertainty refer to the following species: N = DIN + loosely sediment bound NH_4^+ (also including loosely bound NO_3^- for icebergs), P = DIP + bioavailable sediment bound P ($\text{MgCl}_2\text{-P}$ + NaOH-P), Fe = DFe ($<0.02 \mu\text{m}$) + CNFe (colloidal/nanoparticulate Fe, $0.02\text{--}0.45 \mu\text{m}$) + SSFe (sediment-bound ascorbic acid extractable nanoparticulate Fe, e.g., ferrihydrite), Si = DSi + ASi and OC = POC + DOC. All fluxes include minimum, maximum and mid-range estimates calculated from published estimates of the range of nutrient concentrations and freshwater fluxes. Please see Supplementary Methods for flux calculations, error bars and the full dataset (note the different y axis scales in Northern Hemisphere peak fluxes)

phase-sensitive trace elements such as iron. A direct relationship between dissolved organic carbon (DOC) and dissolved iron observed in sub-Antarctic meltwaters was attributed to the stabilisation of filterable Fe ($<0.45 \mu\text{m}$) by complexation with DOM⁵⁶, although further investigation is needed to determine if DOM-Fe linkage is important in glacial meltwaters.

Drawing upon previously published work we have generated the first global assessment of potential nutrient fluxes released directly from both ice sheets at the present day, also with indicative peak fluxes from northern hemisphere ice sheets during past periods of high melt rates, in this case, during Meltwater Pulse 1a at 14.5 kyr B.P. (see Supplementary Methods) (Fig. 2). The pattern that is immediately apparent from Fig. 2 is the important role of meltwater export in the northern hemisphere and of iceberg discharge in the south in delivering nutrients to the ocean—a reflection of the dominant water flux terms. Icebergs account for $>95\%$ of freshwater discharge from the Antarctic Ice Sheet and subglacial discharge dominates freshwater fluxes in the northern hemisphere, especially if most Greenland icebergs do not escape the extensive fjord systems⁶¹. High contemporary fluxes of bioavailable Fe and Si from ice sheets are observed (1.8 Tg a^{-1} Fe and 9.4 Tg a^{-1} Si), where $>60\%$ of these estimated Si and Fe fluxes are sourced from the Greenland Ice Sheet (Fig. 2, Supplementary Table 3). Present-day fluxes of Fe from the Greenland Ice Sheet are on a par with those associated with atmospheric dust to the North Atlantic⁵⁴

and Fe associated with Antarctic icebergs exceeds fluxes via aeolian dust to the Southern Ocean by three orders of magnitude⁶¹. Particulate material is the dominant flux term ($>95\%$ of Si and Fe) for these nutrient species^{8,62} (Fig. 2). Bioavailable P and N fluxes from ice sheets are generally an order of magnitude (Gg a^{-1}) lower than those for Fe, Si and organic carbon (OC, Tg a^{-1}). However, these estimates exclude the more refractory mineral forms of P associated with particles (e.g., fluorapatite), which display fluxes orders of magnitude higher than the traditionally ascribed bioavailable P flux (taken to include soluble reactive and loosely bound P and P associated with Al-Fe minerals P)⁴². Fluxes of bioavailable P from ice sheets at the present day are of a similar order of magnitude (25 Gg a^{-1}) to other riverine sources such as Arctic rivers (70 Gg a^{-1} bioavailable P)⁴². Present day N fluxes from ice sheets are moderate (100 Gg a^{-1} N, with 30 Gg a^{-1} from Greenland, 70 Gg a^{-1} from Antarctica) and exceed those from a major Arctic river (20 Gg a^{-1} for the Mackenzie River⁶³) (Supplementary Table 3). Fluxes of nutrients associated with glacially driven upwelling of marine water at ice sheet margins are still poorly known. Studies of single fjords and marine terminating systems suggest that they could be highly significant for N and P “pumping”, and moderately significant for Si¹⁰. For example, in Sermilik and Illulisat Fjords (E Greenland), P fluxes via upwelling are $2\text{--}9 \text{ Gg N a}^{-1}$ and those of N are $12\text{--}40 \text{ Gg P a}^{-1}$, compared with estimates of 15 Gg P a^{-1} and 30 Gg N a^{-1} via

meltwater and ice discharge from the entire Greenland Ice Sheet (Supplementary Table 3)¹⁴. For Si, upwelling fluxes are 14–66 Gg Si a⁻¹ for these fjords, compared with 6300 Gg a⁻¹ for the entire ice sheet (Supplementary Table 3)¹⁴.

Figure 2 indicates that nutrient fluxes from ice sheets were likely much higher during peak melt periods in the past, for example, during Meltwater Pulse 1a (MP1a at 14.5 ky B.P.), when freshwater fluxes were c. 20× higher for meltwater and 3× higher for icebergs in the northern hemisphere—reflecting high meltwater export during rapid disintegration of ice sheets over Northern Europe and America. Thus, the potential export of Si and Fe at this time was likely very high (126 Tg a⁻¹ and 21 Tg a⁻¹, respectively). This flux of Si is almost equivalent to the total global river discharge of Si during the same time interval, which is notable given that the primary source of Si in the oceans is riverine inputs⁴³. The impact of these boosted nutrient inputs on primary productivity in oceans bordering ice sheets during the last glaciation and glacial termination has been hinted at refs. ^{52,64,65}, but is poorly constrained and requires a comprehensive modelling study in its own right. What is known about the fate of glacially exported nutrients at the present day is examined in the following section.

Fate of glacially cycled nutrients

The fate of glacially exported or cycled nutrients and their impact on marine ecosystems depends upon a complex interplay of physical and biological processes, including proglacial/lake/fjord/estuarine filter effects (e.g., burial of reactive phases, benthic recycling, desorption/adsorption from particulates³⁹), advection by ocean currents⁶⁶, phytoplankton utilisation pathways^{67–69} and spatial patterns of phytoplankton nutrient limitation⁵¹. Observations of heightened biological activity in marine waters surrounding glaciers has been noted as early as 1938, when brown zones (representing turbid melt plumes) in front of tidewater glaciers were noted to be particularly productive regions for biota^{70,71}, with more recent research reinforcing this connection^{10,72}.

There is now compelling evidence for direct glacial nutrient fertilisation of marine ecosystems around the Antarctic Ice Sheet. Here, iron associated with subglacial meltwaters and icebergs is thought to stimulate enhanced marine primary productivity in the iron-limited Southern Ocean. Some of the highest concentrations of dissolved Fe in the Southern Ocean have been reported adjacent to Pine Island Glacier in the Amundsen Sea⁷³, and in the western Antarctic Peninsula⁷⁴, both inferred to derive from a glacier source. Modelling studies show that Southern Ocean primary productivity may be enhanced by up to 40% and export production by up to 30% by subglacial iron inputs^{15,75,76}. Satellite remote sensing studies also suggest that Antarctic meltwater may be an important source of iron to coastal polynyas⁷⁷ and that icebergs enhance primary productivity in the open and coastal Southern Ocean^{78,79}, confirming previous field observations of bioavailable iron in iceberg rafted sediments⁶¹.

In contrast, runoff from northern hemisphere ice sheets often enters fjords and complex estuarine environments, modulating total fluxes to the ocean via flocculation and scavenging^{38,80–82}. Recent studies suggest that direct inputs of nutrients from Greenlandic glaciers have a relatively small impact in stimulating fjord and coastal productivity because they do not supply large fluxes of nutrients (e.g., N and P) which limit phytoplankton in these waters and turbid melt plumes suppress productivity in the summer months¹⁰. Here, the most important influence of the ice sheet is heralded to be the pumping of N-replete and P-replete deep ocean water to the surface during the upwelling of buoyant subglacial meltwater at marine-terminating glacier margins^{10,13,14,37,44}. This indirect supply of nutrients has been

linked to spring and summer phytoplankton blooms, and supports fisheries in the coastal zone¹⁰. An exception may be the direct export of silicon (both dissolved and amorphous particulate phases) in glacial meltwaters⁸³, which has been demonstrated to support diatom blooms in Greenlandic fjords¹¹, corroborating previous studies suggesting high silica concentrations and high diatom abundance in glacially fed fjords and coastal waters⁸⁴.

While the impacts of glacially exported nutrients upon fjord and coastal productivity around Greenland may be limited, there is mounting evidence that there is a net export of glacial nutrients from land to the open ocean. For example, the concentrations of filterable and particulate iron in the surface waters at the mouths of Greenland fjords and in near coastal regions downstream of glacial meltwater inputs can be orders of magnitude higher than that in the open ocean^{38,81,85,86}. Radium isotopes measured on surface ocean waters off the coast of Greenland strongly suggest the rapid offshore transport of glacial particles into shelf waters and into the open ocean⁸³. Taking these inferences a step further, remote sensing and numerical modelling have showed a strong correlation between the timing and spatial extent of summer phytoplankton blooms in the Labrador Sea and the arrival of Greenland meltwater and subsequent patterns of advection via ocean currents¹⁶. The inferred driver for these summer (August, September) blooms is the advection of ice sheet derived Fe, which must be transported some 500 km offshore¹⁶. These summer/autumn blooms account for 40% of the annual net primary production for the region, indicating a process of regional significance¹⁶.

Increasing ice sheet freshwater discharge and glacier retreat⁸⁷ in the 21st century are predicted to be accompanied by rising nutrient and organic carbon export from ice sheets^{8,9}. However, this increase in glacially sourced nutrient fluxes may not be a simple linear function of the freshwater flux. For example, seasonal records of nutrient fluxes from a large Greenland outlet glacier in extreme melt years demonstrated that a doubling of glacial runoff was accompanied by a similar increase in dissolved nutrient loading⁸, but sediment-bound fluxes declined due to the intricate (supply-limited) relationship of particulate loading and bulk meltwater discharge⁸. Decreased glacier size, and hence erosion rates, may in fact also reduce sediment-bound nutrient export to the ocean, as seen for P export from two Greenland catchments of contrasting size⁴². In addition, expansion of the proglacial zone in land-terminating systems may drive fundamental shifts in microbial community size and composition and additional nutrient cycling steps may occur in proglacial aquatic ecosystems (e.g., lakes) prior to nutrient export to the ocean^{88,89}. In regions where marine ice retreats to land, changes in the mechanisms of freshwater (and nutrient) input to ocean waters may occur. Thus, there may be a shift from sub-surface to surface (turbid) meltwater flows¹⁰ at the land-ocean margin, and cessation of the entrainment of nutrient-replete ocean water by rising buoyant melt plumes from depth at marine margins. These changes are likely to lead to light limitation and reduced macronutrient (N and P) supply, respectively, in surface waters⁹⁰. They may explain the high biological productivity and fish catches found in the vicinity of fjords headed by marine terminating glaciers in Greenland compared with fjords dominated by land terminating glacier inputs¹⁰.

The above discussion highlights the importance of the fate of inorganic nutrients, supplied directly or indirectly via ice sheet meltwaters. However, ice sheets also act as significant stores of OM, which is either fixed by autotrophic microbial activity in situ²² or imported to the glacier system via wind-blown material (e.g., aeolian dust)³ or from biomes buried by ice during periods of glacial advance^{17,18}. The cycling of this OM within glaciers and ice sheets creates the potential for a series of more direct impacts on the global carbon cycle (Fig. 1), which are discussed in the next section.

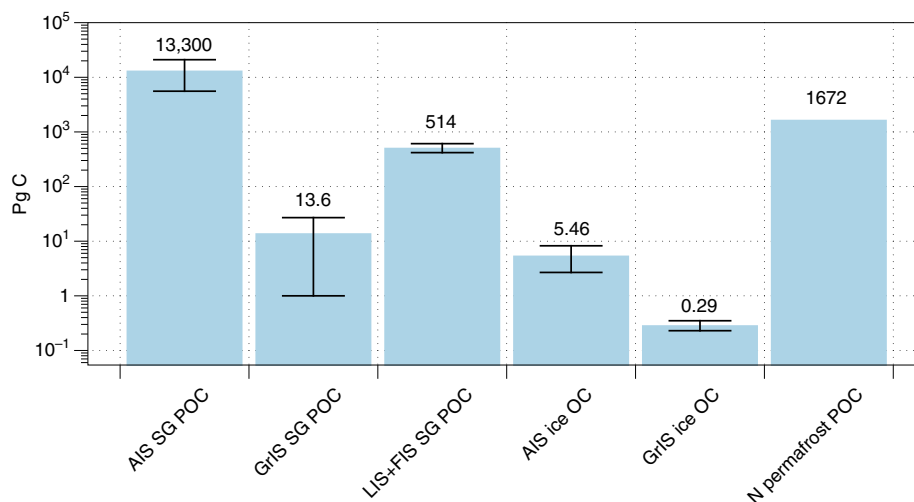


Fig. 3 Carbon inventories for present day and former ice sheets. Data presented includes minimum, mid-range and maximum estimates. Antarctic Subglacial POC (AIS SG POC), minimum estimates are calculated assuming a sediment depth of 1 km, sedimentary basin areas of 1×10^6 km² for WAIS and 2.5×10^6 km² for EAIS, a rock density of 2650 kg m⁻³, a porosity of 0.3 and a POC of 0.1%¹⁶⁹, maximum estimates are derived from ref. ¹⁶⁹, and mid-range values as the average between the two, Greenland Ice Sheet Subglacial POC (GrIS SG POC), minimum estimates calculated assuming a POC of c. 0.2%¹⁷⁰, sediment thicknesses of 0.1 m¹⁷¹ and a porosity of 0.4¹⁷², maximum estimates assuming a POC of 0.44%³⁶, sediment thicknesses of 2 m¹⁷¹ and a porosity of 0.3¹⁷² and mid-range values as the average between the two), Laurentide + Fennoscandian Ice Sheet Subglacial POC (LIS + FIS SG POC, minimum, maximum and mid-range estimates from ref. ¹⁸), Antarctic Ice Sheet englacial POC + DOC (AIS ice OC, mid-range, minimum and maximum values from ref. ⁹, where the min/max values only include DOC due to lack of data), Greenland Ice Sheet ice-bound POC + DOC (GrIS ice OC, mid-range, minimum and maximum values from ref. ⁹, where the min/max values only include DOC due to lack of data) and Northern hemisphere permafrost (N permafrost POC)⁹⁷

Ice sheets as dynamic carbon stores

Pre-existing soil, vegetation, lake and marine sediments, and associated OM, are overridden and incorporated into sediments beneath ice sheets as they form^{17,18}. Ice sheet surfaces may also act as extensive sinks for OM derived originally from terrestrial and anthropogenic sources^{3,91–93} or fixed via autotrophic biological activity⁹⁴ (see Box 1). Some carbon reservoirs in ice sheets are thought to be vast. For example the estimated mass of particulate organic carbon (POC) held in sediments beneath the Antarctic Ice Sheet (6000–21,000 Pg C)⁹⁵ is up to an order of magnitude greater than that associated with northern hemisphere permafrost⁹⁶ and 1–2 orders of magnitude greater than estimates for the former Laurentide Ice Sheet (514 Pg C)¹⁸ (Fig. 3, methods in caption). This reflects the presence of extensive and thick subglacial sedimentary basins in Antarctica, thought to contain fossil OM originating from ancient marine sediments⁹⁷. Smaller reserves of carbon are postulated to be present beneath the Greenland Ice Sheet (estimated at 0.5–27 Pg C, Fig. 3 for methods), where sediments are thinner but contain remains of ancient paleosols sequestered by the ice sheet during growth³⁶. Carbon storage estimates (Fig. 3) have large error bounds, primarily due to uncertainties in sediment thicknesses and organic carbon content beneath ice sheets. However, they dwarf estimates of carbon pools held in englacial ice as dissolved organic carbon (DOC) or POC (Fig. 3) which are estimated at <10 Pg C for both present day ice sheets⁹. Evidence for the presence of sedimentary OM beneath ice sheets is found in the preservation of ancient paleosols in basal sediments and bulk meltwaters of the Greenland Ice Sheet^{98,99} and the presence of marine sediments and their geochemical influences beneath the West Antarctic Ice Sheet and in the McMurdo Dry Valleys^{34,100}.

The fate of legacy OM beneath ice sheets is poorly known because of the inaccessibility of the subglacial environment. It is likely to include erosion and export of sedimentary OM (e.g., from soil, marine and lake sediments) from the ice sheet, storage in subglacial basins and frozen bed zones, and active respiration

via microbial activity to CO₂ or CH₄. These greenhouse gases may be consumed by further microbial activity, transported in the dissolved/gas phases within a subglacial hydrological system or stored as gas hydrate in sediments (for CH₄). Such processes of active carbon cycling create a direct link between ice sheets and carbon cycles of the atmosphere and oceans (Fig. 1) and are explored in the following sections.

Erosion of sedimentary organic matter and fluxes downstream.

Glacial erosion may lead to some OM removal or re-distribution over time beneath ice sheets. Indeed, where ice is warm at the bed and exhibits high rates of flow (e.g., close to the ice sheet margins), erosion rates could be considerable. For example, erosion rates of up to 0.6 mm a⁻¹ have been plausibly modelled for Antarctic ice stream tributaries¹⁰¹ and rates of up to 5 mm a⁻¹ are inferred at the margins of the Greenland Ice Sheet⁴⁷. However, erosion rates in inland regions of ice sheets must be much smaller to be compatible with the preservation of sedimentary basins, such as those found in Antarctica even after 30 Ma of glaciation¹⁰². Consistent with this are calculated erosion rates in East Antarctica of 0.04 mm a⁻¹ (Slessor Glacier¹⁰²) and 0.001 mm a⁻¹ (Lambert Basin¹⁰³). The erosion and export of organic carbon from the polar ice sheets has recently become pertinent to the global carbon cycle, because of the potential for this material to become buried in long term geological carbon sinks¹⁰⁴, such as the dark, oxygen-starved bottom waters of fjords¹⁰⁵. The global rate of carbon burial in fjords is estimated to be 18 Tg a⁻¹¹⁰⁵, but at many sites the proportions of old vs. newly produced OM are unknown. It is notable that the percentage organic carbon contents reported in Greenland fjord sediments (1.6%)¹⁰⁵ are orders of magnitude higher than those recorded in suspended particulate material exported in runoff from large Greenland outlet glaciers (<0.1%)¹⁰⁶.

The annual flux of DOC and POC in ice sheet meltwater and ice discharge is relatively small (present day total flux ~6 Tg C a⁻¹, including ice-rafted debris (IRD)) compared to the total reserve held in ice or sediments (Fig. 3) and is equivalent to approximately

10% of the DOC and POC export from Arctic rivers^{63,107}. Since erosion rates beneath ice sheets are generally low, material remaining under the ice is often old^{36,99}. For example, if we assume a subglacial POC store in Greenland of 27 Pg C (Fig. 3), it would take some tens of thousands of years to export all of this organic carbon via runoff (assuming meltwater export of POC and DOC at $<1 \text{ Tg a}^{-1}$ ¹⁰⁶). This is consistent with the observation that the ¹⁴C radiocarbon ages of bulk POC associated with suspended particulate material in Greenland runoff are old (5–9 kyr) and become progressively older through a melt season as the snowline retreats inland⁹⁹. We estimate that the amount of OC liberated via Antarctic subglacial meltwater discharge, is 0.17 Tg C a^{-1} as DOC and 0.33 Tg C a^{-1} as POC (using new data from Subglacial Lake Whillans for Antarctic DOC concentrations), which is comparable to previous estimates⁹ (see Supplementary Methods). DOC/POC release via Antarctic ice discharge is an order of magnitude higher at 4 Tg a^{-1} .

Although fluxes of DOC and POC are relatively small on a global scale ($<1\%$ global land-ocean fluxes), a growing number of studies have observed that glacier derived DOC and POC are highly bioavailable^{2,106}, and thus could be important in fuelling bacterial respiration in receiving aquatic ecosystems². Observation of radiocarbon depleted (i.e., pre-aged) organic carbon on glacier surfaces and in glacial runoff also suggests that glacially exported DOC is also paradoxically ancient^{3,92,93,108}. The source of this ancient DOC has been debated, as has the reason for its high bioavailability in comparison with non-glacial sources of DOC. Ice core data demonstrate a significant contribution of anthropogenic-derived carbon in glacier ice, concurrent with the onset of the industrial era^{109,110}. The molecular composition of OM within Alaskan and Tibetan glaciers indicates high relative contributions of condensed aromatics, which is consistent with the presence of combustion derived OM (i.e., black carbon)^{3,92,93}. Other studies have suggested an alternative explanation for aged DOC in glacial runoff (but not the glacier surface), arguing that it reflects cycling of overridden subglacial material (e.g., paleosols)¹⁰⁸ or glacial erosion and associated reactivation of ancient OM in bedrock¹¹¹. The high bioavailability of DOC emanating from glacial surfaces (and hence runoff) has been hypothesised to reflect OM sourced from the incomplete combustion of fossil fuels enriched in high abundances of nitrogen-rich aliphatic compounds³. However, more recent work also shows the potential role of microorganisms in cycling organic carbon to more bioavailable forms, giving rise to bioavailable DOC both on the glacier surface^{112,113} and at the glacier bed¹¹⁴. Future projections indicate that the total magnitude of DOC exported in glacier runoff between now and 2050 will be approximately 48 Tg C as annual glacier mass loss increases, particularly from mountain glaciers⁹. This increasing flux of glacier DOC provides a subsidy of bioavailable carbon to receiving streams, rivers, estuaries and coastal systems and will be disproportionately impactful in heavily glaciated coastal systems (e.g., Greenland, Gulf of Alaska, Patagonia) that are home to commercially important fisheries.

Microbial conversion of organic matter to greenhouse gases.

Sedimentary OM beneath ice sheets which is not eroded and exported from the glacier system is available as a substrate for subglacial microbial metabolism. An important fate for sedimentary OM buried beneath the ice is microbial respiration to greenhouse gases, and specifically CH₄, under the anaerobic conditions that are inferred from a small number of data points recovered from ice sheet beds^{22,115–117}. This may be supplemented by CH₄ generated during erosion of underlying bedrock

or from deep thermogenic sources in geothermally active zones⁹⁵, such as West Antarctica¹¹⁸. Supersaturated CH₄ concentrations of microbial origin have been reported recently in subglacial runoff draining from a small and much larger Greenlandic catchment^{115,117}, Antarctic Subglacial Lake Whillans¹¹⁶ and in low temperature (1–10 °C) anaerobic incubation experiments of subglacial sediment sampled from a range of glaciers^{36,95}. Concentrations of CH₄ >15 times greater than atmospheric values have also been recorded in air expelled with meltwater via subglacial channels at the margins of a large glacier in SW Greenland¹¹⁹. However, there is high uncertainty regarding the magnitude of sinks for the CH₄ produced, and how much CH₄ is oxidised to CO₂ before being released to the subglacial drainage system. This would reduce the positive radiative forcing associated with CH₄ emissions from ice sheets by approximately a factor of 20. In very long residence time (i.e., years) subglacial hydrological systems, such as Subglacial Lake Whillans, results suggest that most CH₄ generated in lake sediments is oxidised to CO₂ before reaching the lake water¹¹⁶. However, observations from the Greenland Ice Sheet indicate that if subglacial meltwaters/sediments are transported rapidly via efficient channels to the margin during summer melt, this oxidative sink is much reduced and lateral fluxes of CH₄ at the ice margin are high^{117,119} and rival those from other world rivers¹¹⁷. This suggests that subglacial hydrology is key in determining how much subglacial CH₄ is released to the atmosphere. This uncertainty regarding CH₄ export calls for wider study of CH₄ production and export from large glacier catchments draining ice sheets.

Fluxes of CH₄ in ice sheet runoff at the present day are poorly quantified. Conservative estimates via this manuscript suggest potential fluxes of $<1 \text{ Tg a}^{-1}$, employing modelled meltwater discharge from both ice sheets^{120,121} and concentrations of CH₄ measured in runoff from two end member estimates for subglacial meltwaters (min concentrations = $0.024 \mu\text{M}$ ¹¹⁶ and maximum concentrations of $83 \mu\text{M}$ ¹¹⁵). However, high pressure/low temperature conditions that typify the beds of thick ice sheets should favour methane hydrate formation^{17,95,122}, once saturation with respect to CH₄ is attained in sediment porewaters⁹⁵ (Box 3). Methane hydrate has yet to be directly detected beneath ice sheets, but numerical modelling suggests conditions conducive to its formation in Antarctic sedimentary basins and within the Greenland Ice Sheet interior, where ice and sediment thicknesses are $>1 \text{ km}$ ^{95,117}. There are numerous reports from marine sediments around the Antarctic Ice Sheet margin of high concentrations of CH₄ in sediment porewaters^{123–125} and active and relict cold seeps have been found off the Antarctic Peninsula and South Georgia^{126,127}. Recent drilling to marine sediments offshore from the Wilkes Land subglacial basin (via IODP cruise 318) showed extremely high concentrations of CH₄ in sediment cores (up to 43,000 ppm)¹²⁸. Such high concentrations were not found in cores further offshore. It is probable that these processes also prevail beneath the ice sheet, as indicated by the supersaturated CH₄ concentrations in Subglacial Lake Whillans, West Antarctica¹¹⁶ ($0.024 \mu\text{M}$ in lake waters to up to $300 \mu\text{M}$ in sediments).

There are substantial uncertainties regarding the magnitude of present day sub-ice sheet CH₄ hydrate reserves because of the difficulties of accessing sediments in subglacial sedimentary basins. Global subglacial methane hydrate stocks at the present day are likely to be dominated by those in Antarctic sedimentary basins (estimated at up to 300 Pg C as methane hydrate and free gas⁹⁵). At the LGM, the global sub-ice sheet hydrate reserve could have been much larger ($>500 \text{ Pg C}$, 20% of the present day marine hydrate stocks), with hydrate also present beneath former northern hemisphere ice sheets^{17,18,122} (see Fig. 4 for details and calculation methods). The vulnerability of Antarctic subglacial CH₄ hydrate reserves to

Box 3 | Subglacial methane hydrate

Methane hydrate (see inset image) is one of the three phases in which CH₄ may be present, the other two being dissolved methane and free gas. Two critical conditions are required for methane hydrate to form in sediments. First, saturation with respect to methane must be attained in sediment porewaters. Second, pressure and temperature conditions must be suitable for hydrate formation—where low temperatures and high pressures favour hydrate over free gas for the saturated phase. These temperature and ice thickness pre-requisites are easily attained beneath thick ice sheets, and recent work shows in situ microbial methane production in subglacial sediments^{35,36,115,116,168}. Methane hydrate itself comprises a methane molecule surrounded by a cage of water molecules, creating an ice-like structure. In marine sediments, methane hydrate may occupy up to a few percent of the sediment porosity. There are three additional factors that favour methane hydrate formation beneath ice sheets: a small and finite sulphate pool in subglacial sediments (via oxidation of sulphide minerals and/or overridden marine sediments) that reduces the potential for methane loss via Anaerobic Oxidation of Methane (AOM), frozen conditions creating a seal over the ice sheet bed, and finally glaciation periods of 10⁵-10⁶ years which promotes CH₄ accumulation in sediment porewaters.

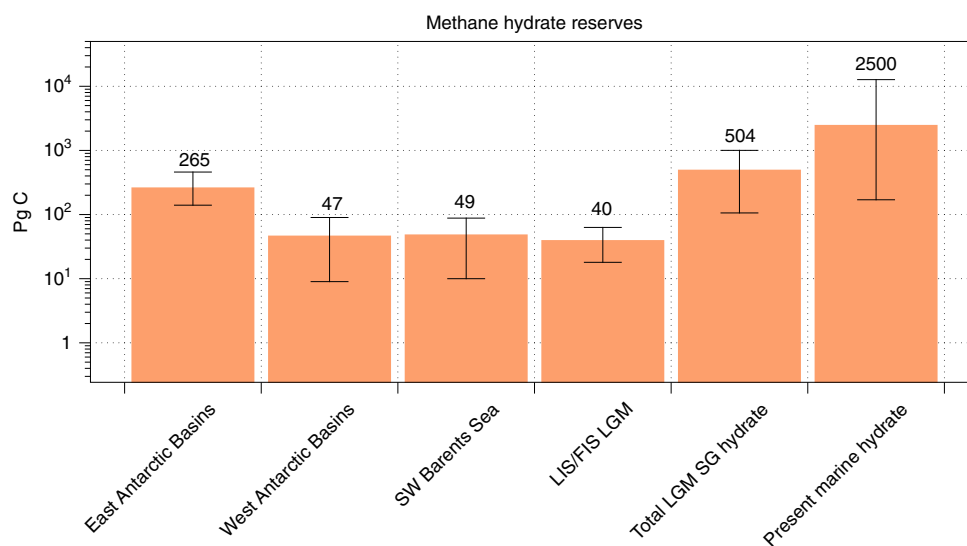
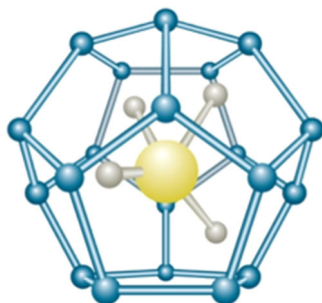


Fig. 4 Potential methane hydrate reserves beneath present and former ice sheets. Data presented includes minimum, mid-range and maximum estimates of carbon reserves. East Antarctic Ice Sheet sedimentary basin methane hydrate + free gas (AIS hydrate, minimum and maximum values taken from ref. ⁹⁶, with mid-range values as the average between the two), West Antarctic Ice Sheet sedimentary basin methane hydrate + free gas (WAIS hydrate, minimum and maximum estimates taken from ref. ⁹⁶, with mid-range values as the average between the two), the SW Barents Sea LGM hydrate¹⁶⁵ (mid-range values are the average of the minimum and maximum published values from ref. ¹⁶⁵), Laurentide and Fennoscandian Ice Sheet estimates of potential methane hydrate (minimum and mid-range estimates from estimates of methane hydrate carbon modelled in ref. ¹⁷, and maximum estimates taken from calculations in ref. ¹⁸) (LIS/FIS LGM), Total LGM subglacial (SG) hydrate + free gas (sum of all data presented, with SW Barents Sea estimates scaled to the entire formerly glaciated Barents Sea Shelf¹⁶⁵ hydrate scaled to the entire shelf), global present day marine methane hydrate, mid-range estimates (2500 Pg C) from ref. ¹⁷³, minimum and maximum estimates from ref. ¹⁷⁴ (170-12,700 Pg C)

destabilisation is high because of their predicted location around the continent’s periphery in sedimentary basins where ice thinning in a warming climate is probable. A priority for future ice sheet research is to establish the presence of methane hydrate beneath the Antarctic Ice Sheet, and to assess its vulnerability to destabilisation in a warming climate. Clues to this may be found in the paleo-record and are discussed below.

Back to the future

Global glacier volumes are predicted to decrease over the 21st century¹²⁹. The fastest present day relative net mass losses are apparent on mountain glaciers, but non-linear changes and high gross losses are expected for the Greenland and Antarctic ice sheets due to the collapse of floating ice tongues and marine ice sheet instability¹²⁹. The potential impacts of ice sheet melting

upon global sea level are well studied¹²⁹, but the impacts of thinning ice and enhanced freshwater fluxes upon local, regional and global carbon cycles (Fig. 1) are poorly constrained. Disentangling the complex set of interactions between these future changes in ice sheet mass balance and the carbon cycle is a challenging task—measurement programmes typically cover short time periods (years) relative to changes in warming climate (decades) and there is a dearth of mechanistic models capable of simulating biogeochemical processes within ice sheets and their wider ramifications. In the final section of this paper, we draw upon the geological record to explore possible biogeochemical impacts of melting ice sheets in the past in order to provide clues to potential impacts in a future warming world. In doing so, we introduce potential indirect (ocean fertilisation) and direct (e.g., CH₄ release from subglacial sedimentary basins) impacts of ice sheets on the global carbon cycle during past phases of ice sheet growth and retreat during the Quaternary (Fig. 1), which might form a strong focal point for future study.

Fertilisation impacts of ice sheets. Climate warming over the last glacial-interglacial transition was accompanied by the disappearance of ice sheets over much of northern Europe and America¹³⁰ and marginal retreat of the Antarctic Ice Sheet¹³¹. If indeed ice sheet freshwater export is a key source of nutrients for the world's oceans, then the geological record should hint at shifts in the productivity of ocean basins bordering ice sheets synchronous with changes in ice sheet freshwater inputs (e.g., meltwater, icebergs). To introduce this idea and to provide some testable hypotheses for future work, we turn our attention to the Fe-limited⁵¹ Southern Ocean over the last glacial-interglacial transition. Here, the productivity of phytoplankton is limited primarily by the availability of Fe in surface ocean waters, and variations in the Fe supply over glacial-interglacial cycles has been argued as a plausible driver for CO₂ drawdown¹³², via its influence upon the strength of the biological pump which controls carbon export to the deep ocean¹³³. Specifically, enhanced Fe supply to the Sub-Antarctic zone of the Southern Ocean, and associated changes in export production, has been linked to the step decreases in atmospheric CO₂ recorded in ice cores during the last glacial period, particularly during Marine Isotope Stages (MIS) 4/5 transition (c. 70 kyr B.P.) and around the LGM^{134–137}.

There are a number of potential Fe sources in the Southern Ocean fertilisation game, all with their own spatial and temporal complexities. These include aeolian dust¹³², coastal sediments^{138–141}, hydrothermal inputs¹⁴² and more recently, iceberg rafted debris (IRD)¹⁴³ and meltwater from the Antarctic Ice Sheet^{56,97,144}. Inferring the precise mechanism(s) driving Southern Ocean fertilisation at key periods of Earth's history is challenging, in part due to the overlapping geographical impacts of different Fe sources. For example, inputs of Fe from dust, coastal sediments or icebergs are often concentrated in the Atlantic Sector of the Southern Ocean, via transport off Patagonia (dust¹⁴⁵, including remobilised fine glacial sediments from Patagonian glaciers^{58,146}) and via ocean currents along the so called iceberg alley adjacent to the Antarctic Peninsula. In general, discerning the importance of each of these potential Fe sources involves correlating past CO₂ variations to reconstructions of iron/nutrient supply via elevated Fe inputs (the iron hypothesis¹³²) and associated proxies for export production (e.g., opal accumulation)¹⁴⁷.

Variation in aeolian dust supply to the Southern Ocean has attracted perhaps the greatest historical interest as an explanation for Fe fertilisation-driven changes in Southern Ocean productivity during the last glacial period, when enhanced inputs of wind-blown dust reflected changes in source area, as well as the strength and position of southern hemisphere westerlies¹⁴⁸. Supporting the dust

hypothesis for Southern Ocean fertilisation is the existence of excellent temporal records of past lithogenic fluxes (inferred to reflect dust inputs) to both the ice sheet¹⁴⁹ and to marine sediments^{136,150–152}, which lend themselves well to correlation with palaeo records of export production and atmospheric CO₂¹⁴⁹ (Fig. 5, Supplementary Fig. 2). For example, the EPICA Dome C ice core dust flux¹⁴⁹ record highlights the last glacial period as a period of enhanced dust transport (14 mg m⁻²), and therefore, of potential Fe fertilisation of the Southern Ocean¹⁴⁹. The fertilisation impacts of this Fe-bearing dust have been inferred in the SE Pacific and Atlantic (sub-Antarctic) sectors of the Southern Ocean at the LGM and have been linked to elevated rates of opal accumulation and overall export production^{136,137,148,150,153,154} (Fig. 5, Supplementary Fig. 2). They indicate Fe fertilisation of a northerly displaced opal belt—a zone of siliceous oozes and muds located between the Polar Front and the northern limit of seasonal sea ice which is associated with the upwelling of silica and nutrient-rich waters and relief of light limitation along the Antarctic Circumpolar Current (ACC) frontal system. In contrast, the Antarctic Zone of the Southern Ocean shows decreased opal export around the LGM^{137,155}. A dusty source for core-bound lithogenic material in marine cores is implied by presence of terrestrial n-alkanes in the same cores, ascribed to the input of plant leaf waxes associated with terrestrial inputs of dust¹⁵⁶.

A new player on the field of Southern Ocean Fe fertilisation is the Antarctic Ice Sheet. Early work on ice sheet contributions focussed upon iceberg rafted debris, which contains bioavailable Fe (oxy)hydroxide nanoparticles^{61,86} which are released from melting bergs as they drift often far offshore from the Antarctic continent^{19,143}. Estimates of the potential bioavailable (ascorbic acid extractable) Fe fluxes associated with Antarctic IRD at the present day (Fig. 5, Supplementary Fig. 2) are c. 600 Gg Fe a⁻¹ (range: 100–2900 Gg Fe a⁻¹) (Fig. 2, Supplementary Table 3). These compare with Antarctic bioavailable Fe fluxes associated with dust which are several orders of magnitude lower at 0.56 Gg Fe a⁻¹ for the present day⁶¹. More recently, ice shelf basal melt^{73,157}, surface melt⁵⁶, and subglacial meltwaters^{15,74,144} from the ice sheet have been proposed as potential sources of Fe to the Southern Ocean, but these melt (and Fe) inputs are likely limited to the coastal zone¹⁵.

Examination of records of IRD in several sub-Antarctic marine cores over the last glacial-interglacial transition^{158–160} (Fig. 5) suggest that Fe delivered by icebergs to the Southern Ocean could be an important segment of the deglacial Southern Ocean fertilisation, export production and CO₂ story. In particular, elevated IRD deposition is recorded in sub-Antarctic cores between 22 kyr and 17 kyr B.P. when Antarctic ice volume was at its highest¹⁶¹ (Fig. 5). There is insufficient confidence in past iceberg flux estimates from the Antarctic Ice Sheet to calculate LGM fluxes of iceberg hosted Fe. However, we know from marine cores that IRD fluxes to the Atlantic sector of the sub-Antarctic Southern Ocean around the LGM were x10–20 present day fluxes, which is consistent with more intense IRD fertilisation of sub-Antarctic waters at this time (Fig. 5). Together, these findings suggest that a combination of high ice discharge and slower iceberg melting due to colder sea surface temperatures¹⁵⁸ increased the supply of Fe-rich terrigenous material to sub-Antarctic waters during this interval, incidentally in a similar time frame to peak dust fluxes (Fig. 5). Later during deglaciation, we hypothesise that warmer ocean waters reduced iceberg transport offshore, such that Fe fertilisation of the sub-Antarctic zone substantially decreased and that of the Antarctic zone likely increased (Fig. 5).

It is difficult with the current data available to conclusively evaluate the role of iceberg-associated Fe in fertilising the Southern Ocean during the last glacial period alongside the more widely acclaimed dust. Certainly, the magnitude of present day

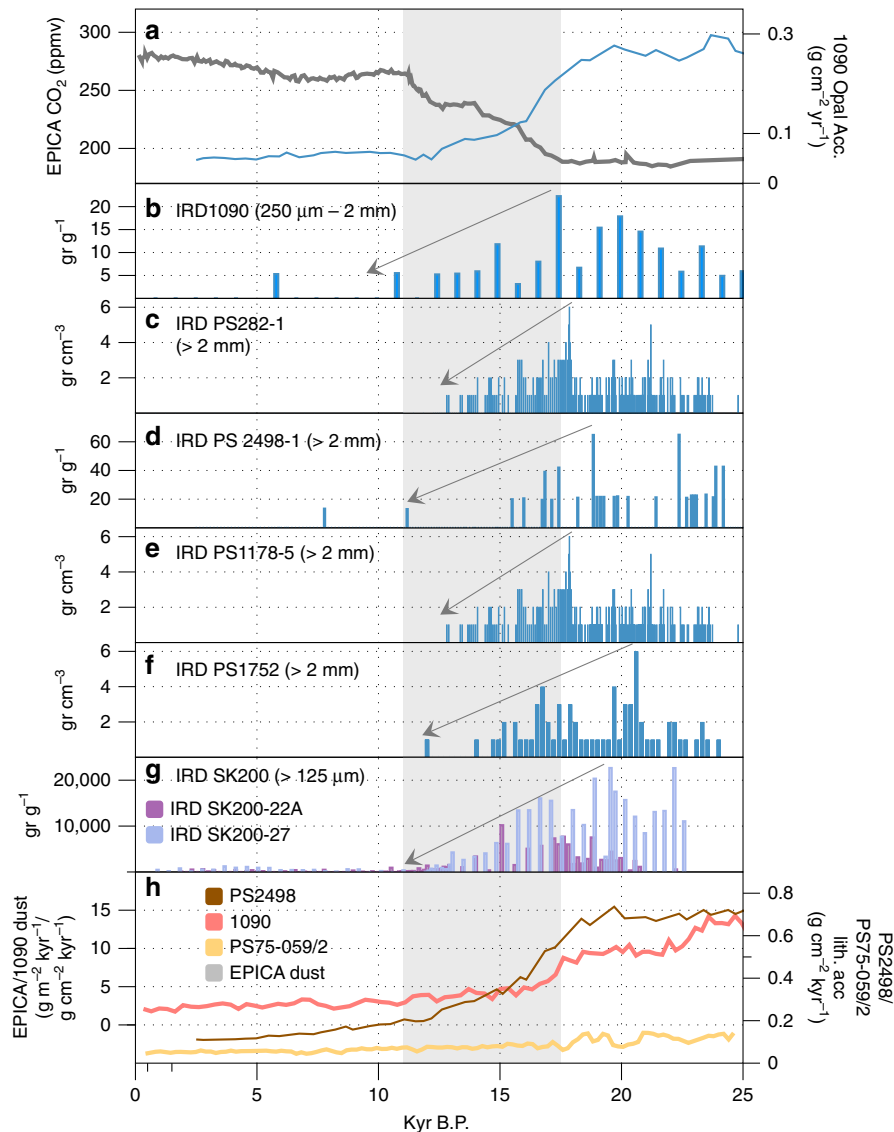


Fig. 5 Temporal variability in the Southern Ocean. Temporal variation in atmospheric CO₂, marine opal accumulation, Ice-rafted debris (IRD) and total lithogenic inputs to the Southern Ocean over the past 25 ka: **a** atmospheric CO₂ concentrations (EPICA Dome C, dark grey line) and opal accumulation in sub-Antarctic cores 1090/PS2498-1174 (blue line)¹⁵¹, **(b)** IRD in core 1090¹⁵⁹, **(c)** IRD in core PS282-1 where the IRD data are from ref. ¹⁶⁰ and the Depth/Age model is from Ref. ¹⁷⁵, **(d)** IRD in core PS2498-1 where the IRD data are from ref. ¹⁶⁰ and the Depth/Age model is from ref. ¹⁵¹, **(e)** IRD core PS1778-5, where the IRD data are from ref. ¹⁶⁰ and the Depth/Age model is from ref. ¹⁷⁶, **(f)**, IRD in core PS1752, where the IRD data are from ref. ¹⁶⁰ and the Depth/Age model is from ref. ¹⁷⁷, **g** IRD in cores SK200-22A and SK200-27 from the Indian Ocean sector of the Southern Ocean¹⁶¹. **h** Lithogenic fluxes to the Southern Ocean for marine cores 1090¹³⁷, PS2498-1¹⁵¹ and PS75-059/2¹⁵² alongside the EPICA Dome C dust flux record. The shaded area indicates the period of maximum CO₂ increase during deglaciation. See Supplementary Fig. 3 for core locations

IRD–Fe fluxes, when combined with the similarity in temporal and spatial patterns of IRD export and those for dust (Fig. 5), suggest that IRD may play a role in the Southern Ocean fertilisation story and warrants investigation. Unequivocally solving this mystery, however, requires a multi-pronged approach. First, it requires parallel study of a range of marine cores over a wide geographical area of the Southern Ocean to tease out the temporally variable contributions of both dust and IRD to the lithogenic flux record. Traditionally, IRD is assumed to account for the coarser fraction of lithogenic material in marine cores, which is variably defined (e.g., 250 µm–2 mm¹⁵⁸, >1 mm¹⁶², >125 µm¹⁶⁰). However, research on the grain size distribution of debris of glacial sediments, including those entombed in icebergs, often have an important fine (i.e., silt/clay) fraction^{61,163}. Thus, while the presence of larger particles

(e.g., sand) in marine cores might point towards IRD rather than dust inputs, the presence of silt/clays could reflect inputs from either IRD or dust. Geochemical provenance studies may help elucidate the precise origin of the lithogenic fraction in marine cores¹⁵⁰, as may the use of biomarkers. The presence of n-alkanes derived from leaf waxes in the lithogenic material in marine cores is often interpreted as indicative of a dusty source¹⁵⁶. While it seems unlikely that leaf waxes are present in sediments beneath the Antarctic Ice Sheet, the presence of these biomarkers in Antarctic IRD has not been evaluated. Finally, biogeochemical models have strong potential to reveal the magnitude of fertilisation impacts that could be possible in a glacial ocean via various Fe inputs, including dust and IRD. Model simulation of dust and ice sheet-sourced Fe impacts on Southern Ocean fertilisation and thus, productivity, have been attempted for a

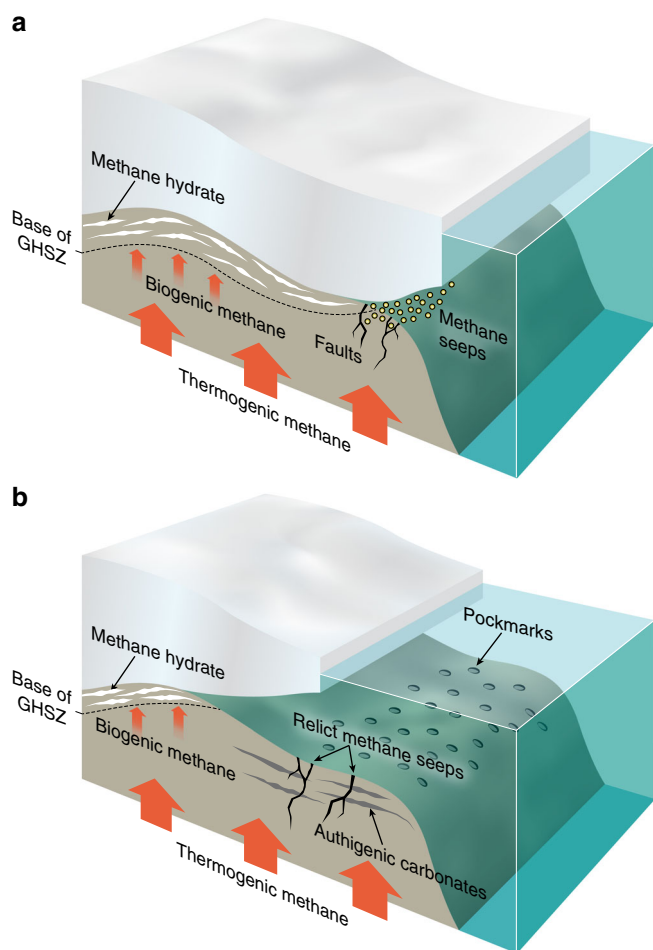


Fig. 6 Model of ice sheet impacts on hydrate reserves. A conceptual model illustrates the impact of ice sheet retreat and thinning on hydrate reserves beneath ice sheets, via their impact on the Gas Hydrate Stability Zone (GHSZ). **(a)** Conditions at peak glaciation, and **(b)** conditions after substantial ice sheet retreat. Following ice sheet retreat, relict features of hydrate destabilisation (e.g., authigenic carbonates, pock marks and relict cold seeps) may be evident on the formerly glaciated continental shelf

modern ocean and suggest strong influences by ice sheet Fe inputs^{15,75,76}. However, these simulations have not been conducted for an LGM ocean. Part of the challenge of conducting such model studies is the grave uncertainty regarding potential Fe fluxes from the ice sheet to the ocean, which need to be better constrained. In summary, determining the role of iceberg-borne Fe in fertilising the Southern Ocean is no simple task, but has the potential to reveal powerful insights regarding the relationship between Fe export from the ice sheet (via melt and icebergs) and export production in the Southern Ocean, which may become more pertinent in a future warming world.

Hydrate stability. Turning our attention to potential direct effects of ice sheets upon the global carbon cycle, we examine the geological record for past periods of methane hydrate destabilisation beneath ice sheets, and associated CH₄ release. Ice sheet thinning or retreat has the potential to dramatically alter in situ temperature and pressure conditions in sub-ice sheet sediments, triggering methane hydrate destabilisation and release of the resultant CH₄ gas to the atmosphere (Fig. 6). Non-linear changes in Greenland and Antarctic Ice Sheet extent and thickness, due to marine ice sheet instability have the potential to trigger such a response, but are difficult to predict¹²⁹. There is some evidence in marine sediments

located close to the former margin of former Eurasian Ice Sheets that past phases of ice sheet retreat have been associated with methane hydrate destabilisation in subglacial sediments. Abundant pockmarks and authigenic carbonate crusts aligned to the position of the former LGM Scandinavian Ice Sheet margin are observed both in the Barents Sea and off the coast of Norway^{122,164}. The former were interpreted to reflect fluid escape at the seafloor during (thermogenic) methane hydrate dissociation at depth, and the latter arise from AOM-driven saturation of sediment porewaters with respect to calcite. These features are contended to reflect CH₄ release as the ice overburden was removed during the last deglaciation^{122,164} and provide compelling evidence that hydrate forms beneath ice sheets and is destabilised as the ice thins and retreats, in this case over a period of ~10 kyr¹⁶⁴. Similar evidence has yet to be uncovered from the Antarctic Ice Sheet, where hydrate reservoirs are predicted at the present day⁹⁵. Ice thickness reductions in marginal areas of the Antarctic Ice Sheet during the last deglaciation were significant (e.g., 300–800 m in East Antarctica¹⁶⁵) and sufficient to destabilise potential subglacial hydrate reserves in these areas⁹⁵. The potential impacts of such release events on atmospheric CH₄ concentrations are unclear, and are complicated by the uncertainty regarding the fate of CH₄ in marine waters (e.g., oxidation to the less potent greenhouse gas, CO₂). For example, recent work off the coast of Svalbard has indicated that high CH₄ gas fluxes from the seafloor instead stimulate enhanced marine productivity, likely due to indirect transportation of nutrient-rich water and CO₂ (from dissociated CH₄) from depth. In this case, the negative radiative forcing exceeded positive radiative forcing associated with CH₄ release¹⁶⁶. Resolving the influence of these opposing influences is important in determining the net impact of subglacial CH₄ hydrate destabilisation on atmospheric CO₂. If the CH₄ is released to the atmosphere during non-linear ice retreat, it could impact the effectiveness of the UN Framework Convention on Climate Change emissions-based agreements to keep climate warming to a minimum of 2 °C by 2100.

Challenges and next steps. The balance of evidence presented in the previous sections supports our opening hypothesis that ice sheets have an important impact on local, regional and global carbon cycles via a suite of direct and indirect effects. The estimated magnitude of these effects is summarised in Fig. 7. Sub-Antarctic sedimentary basins represent by far the largest single store of POC within ice sheets (6000–21,000 Pg C), and ice sheets may also contain significant reserves of climatically sensitive methane hydrate (500 Pg C at the LGM). Export terms (POC and DOC in runoff/icebergs) are comparatively small (<10 Tg a⁻¹) but have potential regional importance for marine and lacustrine food webs due to the high lability of this material. The important indirect effect of meltwater and iceberg nutrient export upon the carbon cycle, via impacts on marine productivity, is illustrated by modelled 100 s Tg C a⁻¹ of export production in the Southern Ocean associated with iron export from the ice sheet which reduces outgassing from the Southern Ocean by 30%⁷⁶.

Scrutiny of the geological record also hints that these impacts were greater during periods of rapid ice sheet change over the last glacial-interglacial cycle. For example, a reduction in iceberg fluxes (and therefore, Fe) to the sub-Antarctic sector of the Southern Ocean from 20 to 11 kyr B.P. correlates in timing with the increase in atmospheric CO₂ recorded in the EPICA Dome C ice core (Figure 5). On the other side of the world, the observation of pock marks aligned to the position of former ice sheets are consistent with the release of CH₄ gas flares as the northern hemisphere deglaciated¹²². Despite these clues from the past, the impact of future climate warming in the Polar regions on the feedbacks between ice sheets and the global carbon cycle is highly

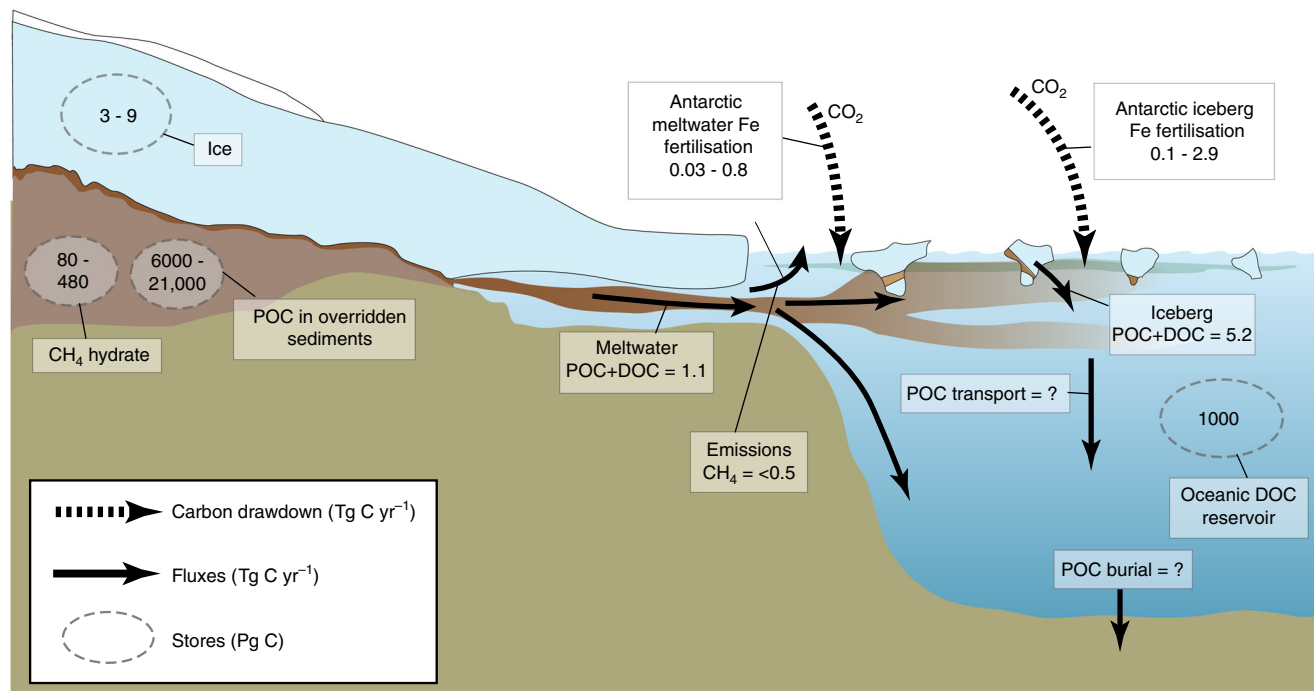


Fig. 7 Stores and fluxes in present day ice sheets. A summary diagram indicating stores and fluxes of nutrients for present day ice sheets, and the predicted impact on CO_2 (where data exists). The estimated size of carbon stores (Pg C) and Fluxes (Tg a^{-1})

uncertain. Predictions suggest that there may be increased fluxes of bioavailable nutrients to the ocean with rising freshwater discharge⁸ and destabilisation of hydrate reserves beneath ice sheets as ice thins^{17,95}. These two processes have opposing potential impacts upon atmospheric CO_2 concentrations, the former (nutrient fluxes to the ocean) acting as a negative feedback on warming and the latter (hydrate destabilisation) as a positive feedback. Discerning the relative importance of these impacts is hampered by a currently poor representation of ice sheet biogeochemical processes in global biogeochemical models due to gaps in data and understanding.

Thus, high uncertainty surrounds the estimates in Fig. 7, and future research must address several notable gaps in our current understanding, and hence predictive capabilities, of ice mass biogeochemical response to future warming. First, the basal regions of ice sheets are remote and challenging to access, and all predictions to date concerning the subglacial methane hydrate reserves or nutrient fertilisation potential, rely upon models calibrated to observations either in the laboratory or on smaller, more accessible valley glaciers. Direct access and sampling of deep subglacial aquatic environments such as subglacial lakes and sedimentary basins is essential, complemented by geophysical methods from which sub-ice conditions (e.g., hydrate) can be inferred. This requires a technological leap¹⁶⁷. Second, a shift in focus towards the downstream impact of ice sheets will help drive new understanding. This should encompass research spanning the full land-to-ocean continuum, together with paleo-environmental studies that seek to detect past changes in the ocean and/or atmosphere systems in response to biogeochemical perturbations related to ice sheets. Large-scale uncertainty, however, still centres upon the fate of nutrients in fjords, beneath ice shelves and in nearshore coastal environments and in constraining changes to nutrient fluxes from glacial runoff, icebergs and via meltwater induced upwelling as the freshwater flux increases. Last, coupled biogeochemical models, including feedbacks between the glacial cryosphere, atmosphere and oceans are required to test the sensitivity of carbon sinks or sources to

changes in the terrestrial cryosphere. From a field where life was thought absent until two decades ago, the possibility for new discovery is immense, but demands creativity, tenacity and technological investment in order to narrow current uncertainties and to reveal the true role of ice sheets in the global carbon cycle.

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Author contributions

J.L.W.–led the writing of the paper with contributions from co-authors. J.H. co-wrote the Section “Ice Sheets as Nutrient Factories” and drafted Figs. 2 and 7. L.T. undertook modelling of past ice sheet freshwater discharge to facilitate nutrient flux calculations from Northern Hemisphere ice sheets during Meltwater Pulse 1a, L.G.–input expertise on palaeo ice sheets and past freshwater fluxes, R.S.–co-wrote the Section “Ice Sheets as Dynamic Carbon Stores”, A.R.–contributed to writing of manuscript, K.K.–co-wrote “Back to the Future–fertilisation impacts of ice sheets”, including assistance with analysis of marine core data.

Additional information

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