Storage and release of organic carbon from glaciers and ice sheets

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Polar ice sheets and mountain glaciers, which cover roughly 11% of the Earth's land surface, store organic carbon from local and distant sources and then release it to downstream environments. Climate-driven changes to glacier runoff are expected to be larger than climate impacts on other components of the hydrological cycle, and may represent an important flux of organic carbon. A compilation of published data on dissolved organic carbon from glaciers across five continents reveals that mountain and polar glaciers represent a quantitatively important store of organic carbon. The Antarctic Ice Sheet is the repository of most of the roughly 6 petagrams (Pg) of organic carbon stored in glacier ice, but the annual release of glacier organic carbon is dominated by mountain glaciers in the case of dissolved organic carbon and the Greenland Ice Sheet in the case of particulate organic carbon. Climate change contributes to these fluxes: approximately 13% of the annual flux of glacier dissolved organic carbon is a result of glacier mass loss. These losses are expected to accelerate, leading to a cumulative loss of roughly 15 teragrams (Tg) of glacial dissolved organic carbon by 2050 due to climate change — equivalent to about half of the annual flux of dissolved organic carbon from the Amazon River. Thus, glaciers constitute a key link between terrestrial and aquatic carbon fluxes, and will be of increasing importance in land-to-ocean fluxes of organic carbon in glacierized regions.

laciers and ice sheets contain about 70% of Earth's freshwater, and ongoing mass loss from this ice reservoir is a major contributor to sea-level rise through the increased landto-ocean flux of freshwater^{1,2}. Glaciers are therefore a prominent component of the global hydrological cycle. However, it is only recently that glaciers have been recognized as unique ecosystems, and even as a biome, with potential implications for the global carbon cycle³⁻⁵. Glacier ecosystems accumulate organic carbon (OC) from in situ primary production as well as from the deposition of carbonaceous material derived from terrestrial and anthropogenic sources⁵⁻⁷. Organic carbon is released from glaciers through melt at the glacier surface that discharges at the glacier terminus into proglacial streams and fjords. Ice-locked OC can also enter marine and lacustrine environments through iceberg calving. The release of OC from glaciers into proglacial ecosystems has been quantified for a few isolated areas, including the Gulf of Alaska⁶, the European Alps⁷ and Greenland⁸. However, a comprehensive analysis of the total amount of OC stored in and released from glaciers on a regional and global basis is lacking. Such estimates are crucial to better constrain the role of glaciers in the global carbon cycle, especially as climate warming continues to reduce glacier ice stores.

We combine measurements of OC and ice volume from glaciers and ice sheets in mountain glaciers (MGL), the Greenland Ice Sheet (GIS), and the Antarctic Ice Sheet (AIS) to quantify the total mass of OC stored in the global terrestrial ice reservoir. In addition, we use current and future estimates of glacier mass balance and runoff to evaluate how the release of OC from glacier storage will change in coming decades. Because glacier runoff liberates highly biologically labile carbon^{6,7,9}, this information provides insight into how the productivity of proglacial aquatic ecosystems will be impacted by continued warming.

Organic carbon storage

Data on OC concentrations in glaciers are relatively sparse. We focus here on dissolved OC (DOC), which constitutes the bulk of glacier OC measurements and is the primary intermediary to carbon cycling¹⁰. We developed a database of glacier DOC concentrations containing more than 300 samples that span five continents (Fig. 1). The vast majority of samples were collected from MGL and the geographic distribution of samples is limited, particularly for the ice sheets (GIS and AIS) where there are relatively few glacier-associated DOC samples. Across all regions and glacier types, concentrations of DOC ranged from 0.01 to 43.2 mgC L⁻¹ with a grand mean of 0.97 mgC L⁻¹ (Fig. 2, Supplementary Table 1). The lowest DOC concentrations were reported from MGL ice cores in the European Alps with values of <0.05 mgC L⁻¹ (for example, ref. 11) and from old ice in the interior of GIS and AIS where DOC ranges from 0.02 to 0.04 mgC L⁻¹ (ref. 12). The highest DOC concentrations were found in basal ice and cryoconite holes reflecting localized accumulation of organic material from overrun OC13,14 and in-situ production¹⁵⁻¹⁷, respectively (Fig. 2, Supplementary Table 1). Average DOC concentration is significantly higher on the surface than in englacial ice for GIS (Mann–Whitney Test, P<0.01) and MGL (P<0.001) but not for AIS (P>0.05). Concentrations of DOC in englacial ice are significantly higher in MGL compared with GIS (P<0.01) but not compared with AIS (P>0.05; Fig. 2). However DOC data for AIS are strongly influenced by relatively high concentrations associated with marginal AIS glaciers within the McMurdo Dry Valleys (Supplementary Table 1). Thus, our findings are consistent with the idea that small glaciers and ice sheet margins receive higher inputs of external OC and demonstrate higher *in situ* productivity⁵.

Concentrations of DOC in englacial ice were used to calculate the global mass of DOC stored in glacier ice. The largest source of

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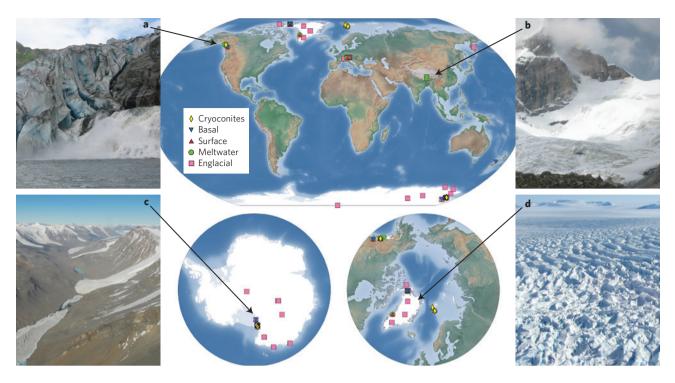


Figure 1 | Location of glacier DOC samples classified by type. a-d, Samples were collected from a wide variety of glacial environments including: Alaska (a), Tibet (b), Dry Valley glaciers in Antarctica (c), and the Greenland Ice Sheet (d).

uncertainty in this calculation is the concentration of DOC within englacial ice in AIS, which contains roughly 90% of the glacier ice on Earth. The majority of the measurements of DOC in englacial ice for AIS (>60%) are from Dry Valley glaciers that, although considered part of AIS rather than peripheral mountain glaciers¹⁸, are located in a polar desert with large ice free areas. The abundance of exposed soils in the Dry Valleys renders glaciers in this region non-representative of AIS as a whole. For example, mean englacial DOC concentrations are more than $2.5 \times$ higher for Dry Valley glaciers (0.40 mgC L⁻¹, n=11) compared to ice cores from the main AIS (0.15 mgC L⁻¹, n=8). Moreover, the mean concentration for the AIS ice cores included in our analysis falls near the centre of the range of DOC concentrations (0.02–0.32 mgC L⁻¹) reported for the Vostok ice core¹⁹, supporting the idea that these ice core data are representative of englacial DOC concentrations in AIS.

Excluding englacial ice data from the Dry Valleys and including only AIS ice-core data provides a conservative global estimate of glacier-stored DOC of 4.48 ± 2.79 PgC with 4.19 ± 2.78 Pg (93%) of glacier DOC stored in AIS, 0.22 ± 0.06 Pg (5%) in GIS, and 0.07 ± 0.01 Pg (2%) in MGL (Fig. 3a). Our estimate is somewhat higher than previous estimates of DOC storage in both Antarctica (3.3 Pg) and Greenland (0.3 Pg) that were based on a lower average DOC concentration (0.11 mgC L⁻¹) for AIS²⁰. A measure of the potential upper bound of DOC storage in AIS can be made by including englacial DOC data from the Dry Valleys, which increases the estimate of DOC storage in AIS to ~8.4 Pg, nearly doubling the global estimate of DOC stored in glacier ice.

A complete global glacier budget for OC requires estimating the storage of particulate OC (POC) in glacier ice. There are few measurements of POC in glacier ice compared with measurements of DOC, however a small number of studies report DOC:POC ratios in ice cores and englacial ice samples that can be used to estimate POC storage based on our estimates of glacier DOC stocks. Using POC concentrations for MGL and DOC:POC ratios for GIS and AIS (Methods), we estimate the global glacier POC store at 1.39 PgC, with 1.27 (91%) of glacier POC stored in AIS, 0.07 Pg (5%) in GIS, and 0.06 Pg (4%) in MGL.

Taken together, our estimates of DOC and POC in glacier ice suggest the global store of OC in glaciers and ice sheets is on the order of 6 Pg. In the context of cryospheric carbon storage, glacier OC storage is equivalent to ~6% of the total organic carbon pool in North American Arctic soils²¹. At the global scale, the store of glacier OC is small compared to the total amount of OC in permafrost soils (>1600 Pg)²². However, unlike OC in permafrost soils, OC released from glaciers, particularly as DOC, is rapidly transferred to proglacial aquatic ecosystems, bypassing potential biotic removal in soils²³. At the global scale glacier ice represents a significant, yet largely unrecognized hydrological reservoir of OC that merits consideration in studies addressing global riverine carbon dynamics and the land-to-ocean transport of OC (ref. 22).

Export of glacial organic carbon

Annual glacier runoff from the global ice reservoir through melting and iceberg calving is approximately 4,250 Gt yr⁻¹ (refs 24-26), while present-day annual glacier mass loss is estimated at 369-905 Gt yr⁻¹ globally²⁷. The ratio of these two aggregate values allows partitioning of the water flux from glaciers, with net mass changes accounting for only 10-20% of global glacier runoff and the bulk (80-90%) resulting from mass turnover (Box 1). Based on concentrations of DOC in glacier meltwater (Fig. 2, Supplementary Table 1), we estimate that global glacier runoff liberates 1.04 ± 0.18 TgC yr⁻¹ of DOC to proglacial freshwater and marine ecosystems, with the largest contribution $(0.58 \pm 0.07 \text{ TgC yr}^{-1} \text{ or } 56\%)$ coming from MGL compared to GIS $(0.22 \pm 0.04 \text{ TgC yr}^{-1})$ and AIS $(0.24 \pm 0.16 \text{ TgC yr}^{-1}; \text{ Fig. 3b})$. The global distribution of DOC export from glaciers is markedly different from the distribution of glacier DOC storage. The disproportionately high DOC export from GIS and MGL relative to the size of these ice reservoirs reflects higher rates of glacier mass turnover compared with AIS²⁸. Globally, approximately 0.14 TgC of the DOC released annually is associated with glacier mass loss, with the largest contribution from MGL and smaller contributions from the ice sheets consistent with a recent estimate for AIS²⁹. Thus, roughly 13% of the annual downstream flux of glacier DOC

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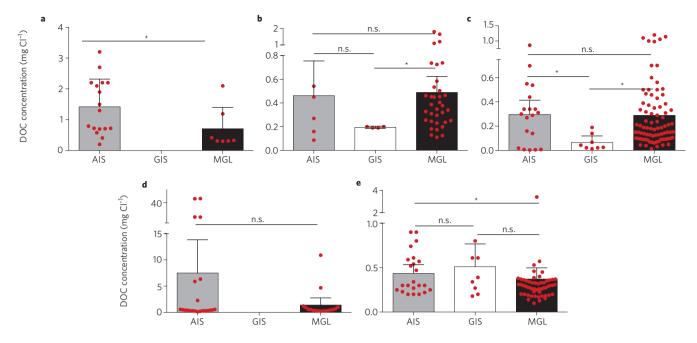


Figure 2 | **Glacier DOC concentrations. a-e**, Average concentration of DOC in cryoconites (**a**), surface (**b**), englacial (**c**) and basal ice (**d**) and in glacier melt water (**e**) for the AIS, GIS and MGL. Red dots indicate the single values for each entity. Horizontal lines indicate significance tests between groups with one asterisk referring to P < 0.05, two asterisks referring to P < 0.01, and n.s. denoting not significant (P > 0.05) based on the non-parametric Mann-Whitney test (two-tailed P). Error estimates are ±1 standard error.

constitutes a non-steady state flux that decreases the overall mass of DOC stored in glacier ice. The remainder of the DOC flux (87%) comes from annual mass turnover.

POC export from glaciers is closely tied to suspended sediment yields, which are dependent on many factors including: ice temperature, glacier hydrology, bedrock lithology, subglacial sediment stores, and glacier size³⁰. Moreover, glacier sediment yields vary by more than three orders of magnitude between polar glaciers (~10² t km⁻² yr⁻¹) and large valley glaciers in tectonically active regions (>105 t km⁻² yr⁻¹)³⁰ making it difficult to regionalize estimates of POC export from glaciers. The variability in glacier sediment export is reflected in POC data for glacier meltwater, with POC concentrations exceeding DOC concentrations by roughly an order of magnitude at GIS⁸, while being roughly equal for a small glacier in the European Alps³¹. Based on extremely limited POC data for glacier runoff, we estimate that glacier runoff releases nearly twice as much POC (1.97 Tg yr⁻¹) as DOC to downstream ecosystems. Greenland is the largest contributor to annual POC fluxes (1.19 Tg or 61% of the total glacier POC flux), followed by MGL (0.70 or 36%), while AIS contributes relatively little (0.07 Tg or 7%) because of low subglacial runoff.

On a global scale, our estimates suggest that the annual release of glacier OC to downstream freshwater and marine ecosystems is roughly 3 Tg. Our estimates of OC fluxes for GIS are higher than recent estimates⁸ for DOC (0.08 ± 0.02 TgC yr⁻¹) and POC (0.9 ± 0.2 TgC yr⁻¹) that neglected the englacial OC released via iceberg calving, which constitutes roughly 65% of the annual water flux from the GIS²⁴. In the context of land-to-ocean OC export, our estimates of the global fluxes of glacier OC liberated annually equate to ~0.6% of the global riverine flux of DOC to the coastal ocean³² and ~1% of the global POC flux³³.

A notable aspect regarding the magnitude of the ice-derived OC fluxes is that glacier-derived DOC is highly biologically available in comparison to DOC from other terrestrial sources (for example, soils, vascular plants), with 25-95% of DOC being readily metabolized by microbial heterotrophs in short-term laboratory bioassays^{6,7}. This suggests that glacial DOC entering aquatic ecosystems

is likely to stimulate heterotrophic metabolism and ultimately contribute to CO_2 outgassing to the atmosphere⁷. Furthermore, the high bioavailability of glacier DOC may prime the metabolism of apparently stable terrestrial DOC in downstream ecosystems³⁴. Thus, the biogeochemical role of DOC released from glaciers appears disproportionately relevant despite the modest magnitude of the flux on a global scale. This may be particularly true along heavily glacierized coastal margins, where glacier discharge dominates water fluxes into riverine and near-shore marine ecosystems, or in high-alpine valleys devoid of soils and vegetation.

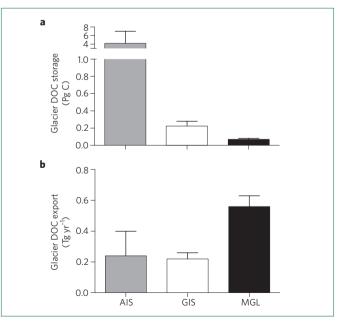


Figure 3 | Storage and flux of glacier DOC. Total glacier storage of DOC (a) and annual DOC export in glacier runoff (b) for MGL, GIS, and AIS. Error estimates are ±1 standard error.

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Box 1 | Glacier Runoff: Water and carbon.

Glacier runoff has been defined in various ways^{49,50}. Here we consider it the annual discharge of water (via melt, rain runoff, and calving) that is derived from precipitation deposited over the glacier footprint. Glacier runoff is comprised of two components: annual mass turnover and annual mass loss (Fig. B1). These components are analogous to the annual throughput of water transiting a reservoir and the change in water storage in the reservoir, respectively. The OC in glacier runoff is derived from three sources: englacial OC, surface deposition and production, and subglacial carbon.

Annual mass turnover is the mass (or volume) of water discharged from the glacier that is less than or equal to the net annual precipitation (that is, total precipitation minus sublimation and evaporation) deposited over the glacier footprint; this component does not change the glacier volume or the global store of OC in glacier ice.

Annual mass loss is the mass of water discharged from the glacier beyond net annual precipitation; this component depletes the global store of glacier ice and OC and contributes to sealevel rise. Future increases in glacier mass loss could increase the relative importance of this component of glacier runoff.

In a year when the glacier mass balance is positive, the annual mass turnover is less than net precipitation and the annual mass loss is negative, indicating a net mass gain of water and OC by the glacier.

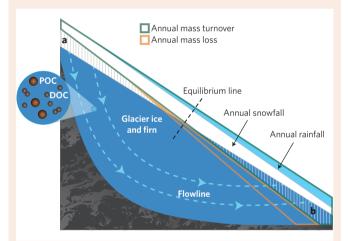


Figure B1 | Glacier mass turnover and runoff. Illustration of the different components of glacier runoff (annual mass turnover and annual mass loss) for a temperate mountain glacier. Glacier ice and firn are shown in blue along with the annual accumulation of snow (white) and rain (light blue) on the glacier surface. The mass of snow in wedge **a** is equal to the ice in wedge **b**, demonstrating that ice loss associated with annual mass turnover does not impact the total mass of the glacier.

Future of the glacier carbon store

The release of glacier OC in coming decades will be strongly influenced by shifts in surface mass balance and glacier dynamics. Ice loss from GIS and AIS is expected to continue increasing in coming decades^{35,36}. As a group, MGL are also projected to continue losing mass although the magnitude of this trend will vary strongly by region due to differences in glacierization and climate regime^{2,37}. Based on projections of glacier mass loss, we estimate that 15.34 Tg of DOC (an average of 0.43 TgC yr⁻¹) will be liberated from glacier storage by 2050, with the majority (9.68 Tg or 63%) coming from MGL. However, the total release of DOC from glaciers by 2050 will be substantially higher than this mass loss term because annual mass turnover through glaciers releases 0.9 TgDOC yr⁻¹. Conservatively projecting this mass turnover estimate forward yields an additional flux of 32.4 TgDOC to aquatic ecosystems by 2050. Thus, the overall magnitude of DOC released in glacier runoff by 2050 (~48 Tg) is equivalent to roughly 1.5 times the annual flux of DOC from the Amazon River³⁸. Analogous calculations for POC yield a total export of roughly 78 TgPOC by 2050, however the biological reactivity of this particulate OC has not been quantified, so it is unclear what proportion of this material will be readily metabolized in downstream ecosystems. Organic carbon exported as both DOC and POC from glaciers and ice sheets will continue to be dominated by mass turnover in coming decades despite projected increases in mass loss for MGL and the two ice sheets.

Our projected losses of OC from terrestrial ice storage are conservative because they assume concentrations of OC in glacier ice will remain constant and that increases in the overall flux of OC from glaciers will be driven solely by increased rates of glacier mass loss. However, there are several mechanisms by which concentrations of OC in glacier discharge could increase in the future including: increased primary production in glacier ecosystems associated with longer melt seasons and the expansion of snow free area on glaciers (currently estimated at 0.7×10^6 km² outside of Antarctica³⁹); increased deposition of carbonaceous material on glacier surfaces^{40,41}; and increased sediment (and POC) export associated with the potential transition from cold-based toward warm-based glaciers in high-latitude regions. Any increases in OC production or OC inputs to glaciers could partially mitigate the net loss of OC from glacier storage and increase future OC export from these ecosystems via both mass turnover and mass loss. Nonetheless, it is clear that in coming decades MGL will experience the single largest loss of glacier OC and that mass balance of glaciers will be an important driver in liberating POC and bioavailable DOC to high-latitude marine ecosystems, particularly those surrounding the major ice sheets that currently receive relatively limited land-to-ocean fluxes of organic carbon33,42.

Resolving uncertainties

Our global estimates of the storage and release of OC from glacier and ice sheet ecosystems contain substantial uncertainty. Nevertheless, they show that the vast majority of ice-locked OC is stored in the AIS and that the release of bioavailable glacier OC to downstream ecosystems is currently dominated by runoff from MGLs, which have high rates of mass turnover. Additional measurements of englacial OC from the ice sheets will help to better constrain global estimates of OC storage. Measurements of POC export from a wider range of glacial basins will allow for better quantification of the role of POC in the OC export budget of glaciers. From a glaciological standpoint, it is apparent that in addition to global net mass loss rates from glaciers, we need an improved understanding of mass balance components. Better quantitative estimates of factors such as net accumulation and ablation, including calving and meltwater runoff, will help us more accurately quantify the release of OC and other biogeochemically relevant materials from glaciers to downstream ecosystems.

Refining estimates of OC storage and loss from glaciers is critical for improving our understanding of the downstream biogeochemical and ecological impacts of glacier change. Glacier-derived OC has been shown to subsidize terrestrial^{43,44} and aquatic^{6,7,45} food webs, implying that future changes in glacier OC export may stimulate the metabolism of downstream ecosystems and alter their trophic structure. Ultimately, quantifying the magnitude and temporal dynamics of OC release from glaciers will improve our ability to predict changes in the biogeochemical coupling between glaciers and downstream ecosystems and deepen our insight into the role of glaciers in global carbon cycling.

Methods

Glacier OC storage. GIS and AIS represent the contiguous Greenland and Antarctic Ice Sheets. Following standard glaciological convention, MGL was defined to represent all mountain glaciers globally (including mountain glaciers around the peripheries of GIS and AIS)^{1,46}. Stores of glacier DOC ware calculated by multiplying average englacial DOC concentration for MGL, GIS and AIS by the total volume of ice for each^{46,47} and thus excludes glacier-associated DOC stored in subglacial (for example, overrun organic matter) and supraglacial (for example, cryoconite holes) environments:

MGL englacial $DOC_{AVG} \times MGL$ Volume = MGL DOC storage GIS englacial $DOC_{AVG} \times GIS$ Volume = GIS DOC storage AIS englacial $DOC_{AVG} \times AIS$ Volume = AIS DOC storage

where DOC_{AVG} indicates average englacial DOC concentrations calculated as the mean of all englacial DOC concentrations for MGL, GIS, and AIS (with the caveat that englacial DOC data from the McMurdo Dry Valleys were excluded from the AIS dataset because they were deemed non-representative of the main AIS). For englacial DOC data from ice cores, multiple samples from a single ice core were averaged to avoid a statistical bias towards intensively sampled glaciers. Error estimates for glacier DOC storage were calculated based on the standard error for englacial DOC data for mountain glaciers and the ice sheets and do not incorporate errors associated with estimates of ice volume.

The store of glacier POC in MGL was calculated in the same manner as DOC, by multiplying the mean englacial POC value (Supplementary Table S2) by the volume of ice in MGL. The stores of glacier POC in GIS and AIS were calculated by dividing DOC stores for the ice sheets by the mean DOC:POC ratio for polar ice and firn from GIS and AIS (Supplementary Table S2). The limited data for POC in glacier ice precluded calculating meaningful error estimates for glacier POC storage, which should be regarded as first order approximations.

The present day annual loss of DOC from the global glacier DOC store was calculated by multiplying contemporary rates of mass loss for glaciers in MGL, GIS, and AIS^{1,35} by the mean englacial DOC and POC concentration for each. Due to a lack of direct measurements, ratios of DOC:POC were used to estimate englacial POC concentrations for GIS and AIS. Future losses of glacier DOC and POC from storage were calculated in the same manner using projections of glacier mass loss for the period 2014–2050 for MGL, GIS and AIS^{24–26}.

Organic carbon in glacier runoff. Total DOC and POC fluxes in glacier runoff (Box 1) for mountain glaciers and the ice sheets were calculated based on the phase of runoff from each location. Glacier runoff (or discharge) from AIS occurs almost exclusively through iceberg calving, thus the masses of DOC and POC in runoff were calculated by multiplying the glacier discharge from AIS²⁶ by the concentration of DOC and POC in AIS englacial ice. In contrast, glacier runoff from GIS occurs via both calving (65%) and meltwater runoff (35%)²⁴ so the masses of DOC and POC in runoff were calculated using volume-weighted DOC and POC concentrations proportional to the amount of water lost as englacial ice (calving) versus meltwater. We estimated the partitioning of glacier runoff in MGL to be 70% meltwater and 30% calving⁴⁸ and similarly used volume-weighted DOC and POC concentrations based on this partitioning to calculate the masses of DOC and POC in glacier runoff from MGL. As with glacier storage, there were not sufficient data to calculate errors associated with our estimates of POC in glacial runoff. Thus, similar to glacier POC storage, the estimates of POC in glacier runoff off should be considered first order approximations (Supplementary Table S2).

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Author contributions

E.H., T.J.B., and R.G.M.S. conceived the study. All authors helped with compiling and analysing organic carbon and/or glaciological data and contributed to the writing of the paper.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence should be addressed to E.H.

Competing financial interests

The authors declare no competing financial interests.