

Long-term CO₂ production following permafrost thaw

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Thawing permafrost represents a poorly understood feedback mechanism of climate change in the Arctic, but with a potential impact owing to stored carbon being mobilized^{1–5}. We have quantified the long-term loss of carbon (C) from thawing permafrost in Northeast Greenland from 1996 to 2008 by combining repeated sediment sampling to assess changes in C stock and >12 years of CO₂ production in incubated permafrost samples. Field observations show that the active-layer thickness has increased by >1 cm yr^{–1} but thawing has not resulted in a detectable decline in C stocks. Laboratory mineralization rates at 5 °C resulted in a C loss between 9 and 75%, depending on drainage, highlighting the potential of fast mobilization of permafrost C under aerobic conditions, but also that C at near-saturated conditions may remain largely immobilized over decades. This is confirmed by a three-pool C dynamics model that projects a potential C loss between 13 and 77% for 50 years of incubation at 5 °C.

The Northern Hemisphere permafrost region contains approximately 1,700 Pg of organic C of which about 90% occurs in permafrost deposits¹. This C pool represents about 50% of the estimated global below-ground organic C pool¹. With the large amplitude of predicted Arctic climate change, this C pool has been used to imply a critical potential for global scale feedbacks from Arctic climate change if these C reservoirs are destabilized^{1,3}, but actual mobilization rates on decadal to century scales are unknown as well as the consistency on a circumpolar scale of the few studies reporting multiyear incubation results⁶. Long-term observations indicate that permafrost thawing in Northeast Greenland, measured as increasing active-layer depths, occurs at rates of more than 1 cm yr^{–1} (refs 4,7). In the present long-term incubation experiment we hypothesized that natural drainage associated with permafrost thawing would considerably increase the potential mineralization and the associated release of CO₂.

Sites included two different landforms (see Supplementary Figs S1–S3) with two different, but dominating, vegetation types⁷; a sandy ground moraine with a *Cassiope tetragona* heath vegetation covered in places by aeolian sediments and the lower part of a nivation site containing a large snow patch with wet grassland vegetation^{7–10}. These two sites differ in geomorphological activity, age, C-substrate quality and the environmental conditions controlling oxygen availability and pH as described in the Methods.

Depth and volume-specific samples from the active layer and top permafrost in Zackenberg (Northeast Greenland) were collected down to about 1 m depth in three replicate profiles in 1996 and

repeated in 2008 and 2012. In 2008, two permafrost cores were obtained down to at least 2 m depth at the same sites by drilling. Two Circumpolar Active Layer Monitoring Network (CALM) grids were established in 1996 in the two landforms studied here^{5,7}. Since then, thaw progression has been recorded based on regular probing throughout the summers.

Top permafrost samples ($n = 3$ per site) collected in 1996 at a depth of about 80–90 cm on the heath site and 60–70 cm on the wet grassland site were kept cold (<7 °C) and transported back to the laboratory for long-term incubation at 5 ± 1.5 °C. Each intact permafrost sample, consisting of 100–200 g soil, was incubated in glass jars with the top covered with Parafilm M with more than ten (<1 mm) holes to allow atmospheric conditions during incubation, but to limit evaporation. Subsamples from the wet grassland site were drained before incubation using a sand bath and leaving the samples to drain freely at 5 °C for 48 h to mimic natural drainage following thawing.

Subsamples of 2–3 g from each of the replicate intact permafrost samples were taken 22 times (between October 1996 and April 2009) and used for soil respiration measurements (roughly every six months). After being transferred to 12.5 ml incubator vials, samples were left for pre-incubation overnight and increasing CO₂ concentrations were measured three times the following day (over 8–10 h) using a ML GC82 (Mikrolab Aarhus A/S, Denmark). Six times during the 12.5-year incubation experiment, CO₂ production measurements were followed by measurements of total organic C and cold-water-extracted total dissolved C. Also, three times during the incubation experiment, the temperature-dependent CO₂ production was measured between 0 and 10 °C to assess any long-term adaptation to the incubation temperature of 5 °C.

In 2008 new top permafrost samples from the wet grassland vegetation site at Zackenberg as well as top permafrost samples (10–30 cm below permafrost table) from four other Arctic sites in Canada, West Greenland, North Greenland and Svalbard (Supplementary Table S1) were incubated under similar conditions as described above and used to assess CO₂ production over three years.

Results from Zackenberg (Fig. 1b and Supplementary Fig. S4) indicate that the active-layer thickness has increased significantly by 0.8 cm at the grassland site and 1.5 cm yr^{–1} at the heath site (1996–2012). This represents only a fraction of the permafrost degradation taking the high ice contents (40–80%) into account (Supplementary Fig. S5). Carbon stocks (to a depth of 1 m) were on the heath site 11.1 ± 2.3 kg C m² (mean $\pm$ standard deviation) in 1996, 10.8 ± 2.4 kg C m² in 2008 and 11.1 ± 2.4 kg C m² in

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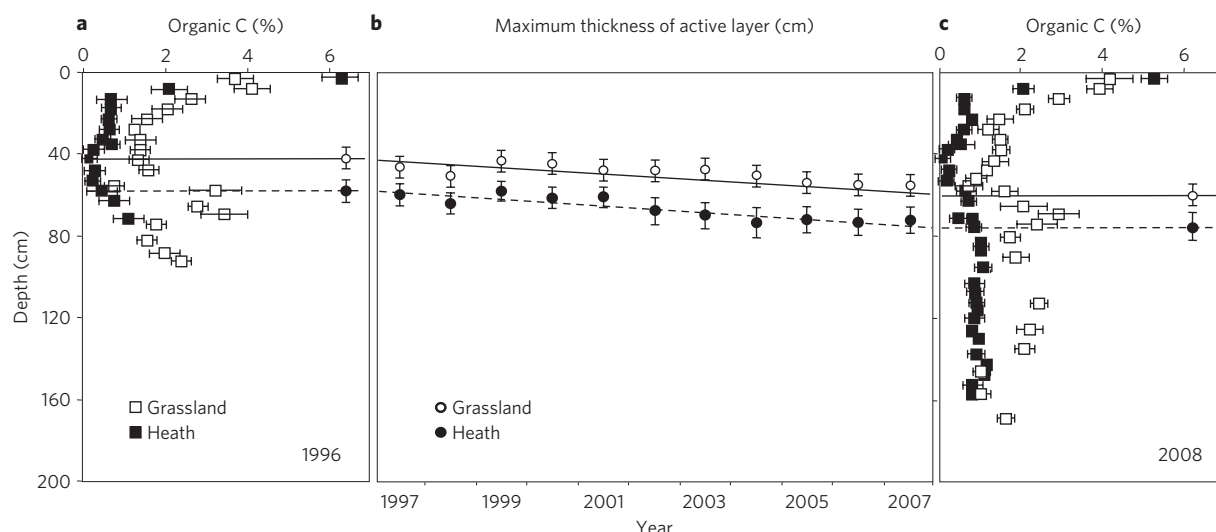


Figure 1 | Trends in permafrost thawing and soil organic C content. **a**, Soil organic C profiles (shown as squares) sampled in 1996 (%wt; 1 standard deviation shown as horizontal bars). The permafrost table is shown as horizontal lines (solid for the wet grassland site and dashed for the heath site). **b**, Maximum measured active-layer thickness (shown as circles) from 1996 to 2008 (one standard deviation shown for wet grassland $n = 24$ and for heath $n = 121$). Temporal trends in maximum thickness of the active layer from 1996 to 2008 are shown as linear regression lines (solid for the wet grassland site and dashed for the heath site, $p < 0.05$). **c**, Soil organic C profiles for 2008, using the same symbols as panel **a**.

2012, and on the wet grassland site $29.3 \pm 3.2 \text{ kg C m}^{-2}$ in 1996, $32.3 \pm 4.1 \text{ kg C m}^{-2}$ in 2008 and $31.6 \pm 4.0 \text{ kg C m}^{-2}$ in 2012 (based on solid bulk density and organic C content). The top 1 m C stocks reveal no detectable changes in total C from 1996 to 2012, as was also the case if only the 0.5–1 m depth interval was considered (Supplementary Fig. S6). But caution should be taken before generalizing this conclusion to a larger area as data only represent two landforms with very limited sampling and because soil collapse and ground surface lowering following thawing may change soil porosity and thus soil organic C stocks owing to physical changes following thawing. The newly thawed upper permafrost in the wet grassland indicates decreasing C concentrations, but not a significant loss in C stock.

Long-term incubations at 5°C (Fig. 2) over a period of >12 years reveal a loss of C as CO_2 equal to 55% of the initial C content ($>20\%$ in the first 21 months) of the top permafrost from the well-drained heath site, 9% loss in the top permafrost sample from the ambient wet grassland site and up to 75% loss at the drained top permafrost sample from the wet grassland site. This variation is considered representative of the variability of labile C linked to the original C source¹¹ and the important role of oxygen availability during incubation. A mass balance of the total C during the experiment indicates that the actual loss was 50%, 17% and 78%, respectively. This indicates a fair match between the C loss and the measured production of CO_2 . The ambient wet grassland samples were the exception; here anaerobic conditions probably resulted in CH_4 production as previously observed in Siberia⁶ and elsewhere^{12,13}. However, as CH_4 was not measured as part of this study, its importance on the net C loss remains unclear.

The constant incubation temperature at 5°C is significantly higher than under natural conditions. Ground temperature in a newly thawed permafrost layer will typically be peaking very close to 0°C for less than two months a year (August/September). Assuming a temperature-dependency of 2 ($Q_{10} = 2$; 70% respiration rate at 0°C as compared with 5°C , Supplementary Fig. S10) during two months a year; 144 months of incubation represents *in situ* conditions for roughly 100 calendar years. Similarly, *in situ* changes (1996–2008) represent 24 months in the laboratory. Based on a Q_{10} of 2, the expected amount of C being mineralized in

the field during 12 years can be calculated to be $<0.002 \text{ g C g}^{-1}$ soil (dry weight) under drained conditions and $<0.0004 \text{ g C g}^{-1}$ soil (dry weight) under wet conditions. These latter changes are too small to be detectable taking natural field variability into account, meaning that the incubation experiment confirms that it is unlikely to detect any significant changes in C stock over 12 years, if newly thawed permafrost layers remain near-saturated and close to 0°C .

A three-pool C model¹⁴ was used to deconvolute the total measured CO_2 production from the incubation study into pool-specific decay rates using inverse analysis (see C dynamics model performance and validation in Supplementary Methods). The total observed respiration rate is the sum of the three pool-specific respiration rates deriving from a fast, a slow and a passive C pool with turnover times <2 , ~ 3 –7 and $>4,000$ years, respectively. The percentage initial C pool loss (Fig. 2) was highest during the first four years and then declined slowly over time. During the whole incubation period most C being lost originated from the fast and slow C pool, as shown by the highest percentage initial C pool losses for these two pools (Fig. 2). However, small C losses from the passive C pool occurred during the whole incubation period (cumulative C loss of the passive C pool for the heath site was 0.25% at the end of the incubation and 1% after 50 incubation years, values were similar for the other sites). Based on estimated parameters from the three-pool model output (Supplementary Table S2), the decay rate of each C pool was used to extrapolate potential C losses for each soil type over 50 incubation years at 5°C (Supplementary Fig. S11). The dry ground moraine heath site has a potential for losing on average 58% (confidence interval: 47.6–68.8%) of initial C when estimating 50 incubation years and the drained nivation grassland site has a potential of 77% loss (confidence interval 62.6–92.0) if all incubation parameters remain constant. However, the C pool on the wet grassland site will largely remain (87%, confidence interval of 75–94.3) within 50 years of projected incubation. This marked difference in decomposition rates over a long period underlines the importance of oxygen availability and high ice content in permafrost soils.

The observations from the wet grassland site at Zackenberg are in line with four other Arctic locations with similar vegetation

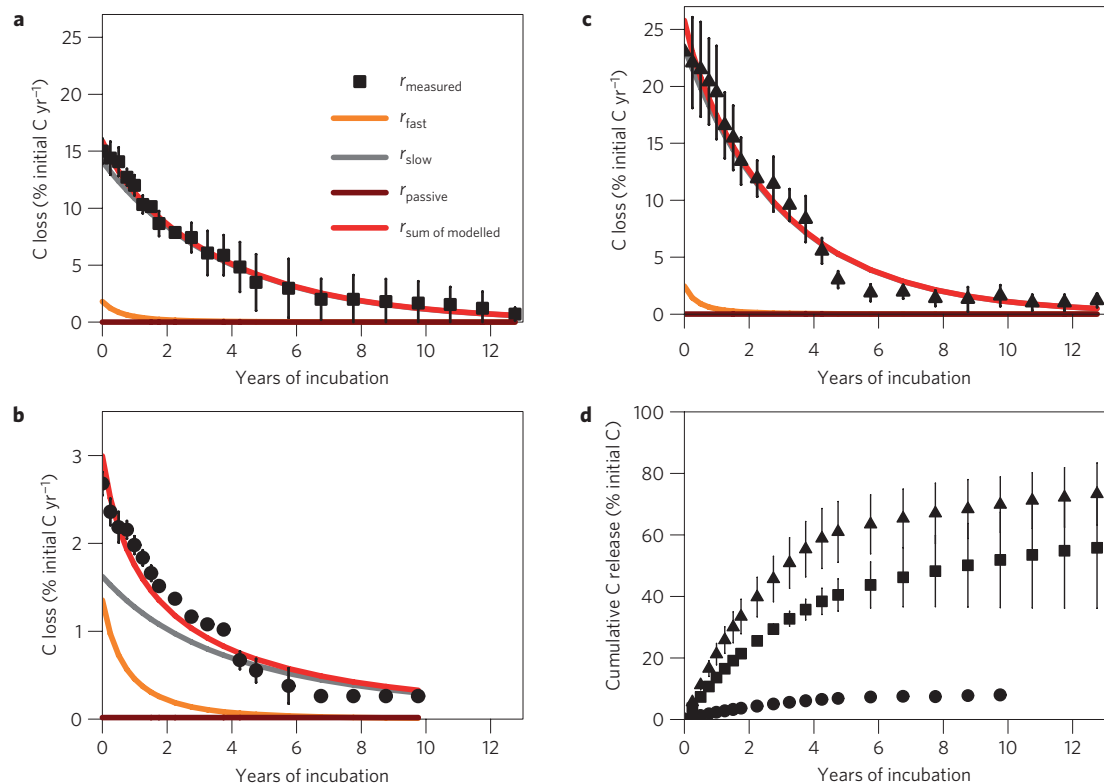


Figure 2 | C loss during a 12-year-long incubation at 5 °C. **a–c**, Observed and modelled C loss rate (r) in percentage of initial C per year calculated from respiration rates of long-term incubated permafrost samples at 5 °C for **(a)** heath site; **(b)** wet grassland site; and **(c)** drained grassland site. Observed values are represented with symbols (squares for heath site, circles for wet grassland site and triangles for drained grassland site) and modelled pool-specific C losses are shown with lines. Observed values represent the mean of three replicates and standard deviation. **d**, Cumulative C release as percentage of initial C for the three different sites, symbols are the same as in **a–c**.

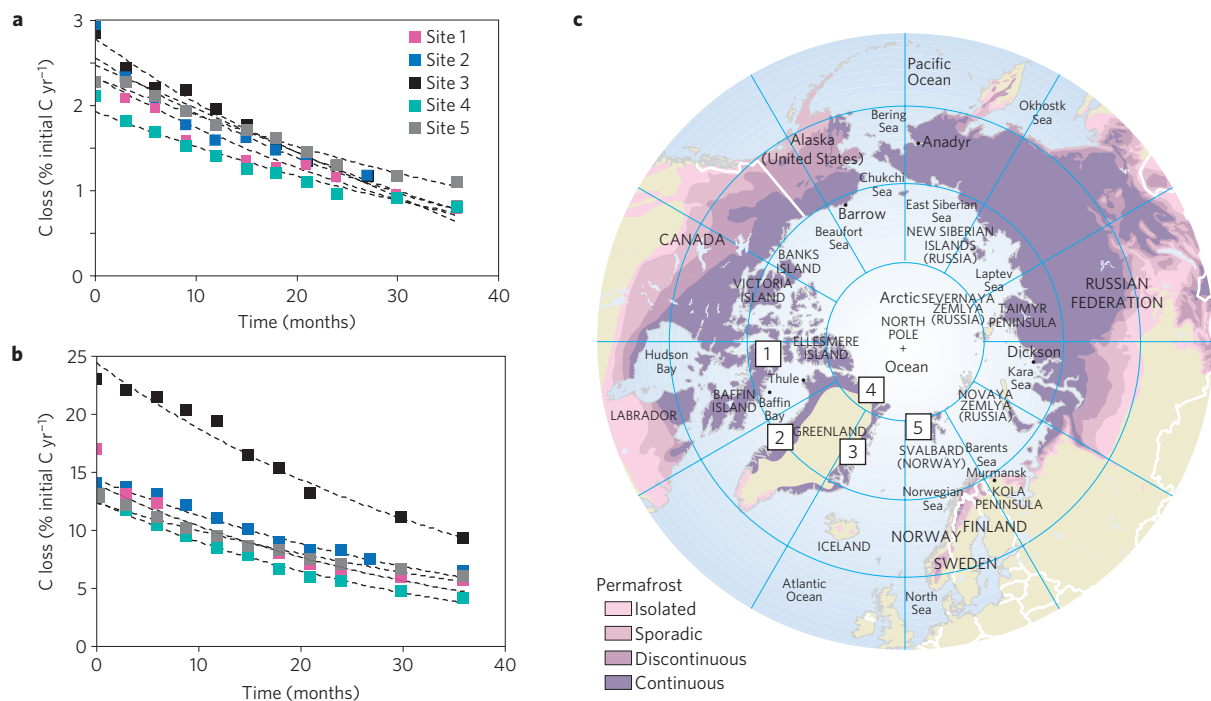


Figure 3 | C loss during a three-year-long incubation based on five sites **a–c**, Observed C loss in percentage of initial C per year based on CO_2 production rates during three years at 5 °C under **(a)** anaerobic and **(b)** aerobic incubation based on top permafrost samples collected at five Arctic grassland sites **(c)**. Panel **c** © International Permafrost Association.

(Fig. 3 and Supplementary Table S1). Although there is no direct link between present vegetation and permafrost C pools or lability, there is a surprising consistency in C pool loss rates. For aerobic conditions, Zackenberg (site 3B) is the site with the highest initial rate of C pool loss, which suggests that the general conclusion from this site is not underestimating a more regional tendency of permafrost C losses in the future. Only a few other studies are available for comparing results from our long-term incubations, however, the three-year incubation experiment using five Arctic sites reported here is comparable to a study based on Siberian permafrost⁶.

The top permafrost in Northeast Greenland is thawing at present, the active layer is deepening by more than 1 cm yr⁻¹ and long-term incubation reveals several C pools with contrasting turnover times. The future release of CO₂ associated with permafrost thawing will depend on both C substrate quality and long-term oxygen availability, ice contents and temperatures. Incubations at 5 °C reveal a loss of C in the form of CO₂ from 9 to 75% of the initial C content over 12 years (Fig. 2d), which is a fair approximation of the loss of C under natural conditions during the next 100 years given the assumptions that this material will remain near 0 °C for two months per year. Modelling results suggest that, during the next 50 incubation years at 5 °C, the long-term decomposition of permafrost C pools may lose up to 92% of the initial C under aerobic conditions and as little as 6% in the case of anaerobic conditions. Thus, we conclude that the long-term prediction of permafrost thawing in terms of CO₂ emissions can be made in a meaningful way only if the oxygen availability, controlled by water and ice contents and the long-term water balance, is also included in the assessment.

Methods

Study sites. Zackenbergdalen (74° 30' N, 20° 30' W) is a wide lowland valley dominated by Quaternary non-calcareous sediments with significant periglacial activity and continuous permafrost^{7–10}, with a mean annual air temperature of –9.5 °C (1996–2007). From the hillslopes towards the depressions, an increase in soil water content is seen from dry to wet conditions at the foot of the slopes owing to snow melt water being released during large parts of the summer. Roughly one-third of the lowland area in Zackenberg is poorly drained. Given the low summer precipitation, water availability during the growing season is mainly controlled by the location of large snow patches melting during the growing season, resulting in the distinct vegetation zonation around these. Sites included two contrasting landforms (see Supplementary Figs S1–S3) and dominating vegetation types⁷; *C. tetragona* heath on sandy ground moraine covered by aeolian sediments (representing 5–10% of the vegetated area) and wet grassland below a snow patch (representing 10–20% of the vegetated area). These two sites differ in geomorphological activity, age, C-substrate quality and the environmental conditions controlling oxygen availability and pH. The ground moraine heath site represents a stable landform with older organic layers at a depth of 40 cm associated with soil formation older than 3,000 years based on indirect dating of the podzolization period 7,400–3,000 years BP (ref. 8). In contrast, a mean sedimentation rate of 0.25 cm yr⁻¹ for the upper 47 cm on the wet grassland site suggests a much younger C deposition here. On the wet grassland site, the soil C pool in the top permafrost is mainly derived from graminoids providing potentially easily degradable C substrates compared with the recalcitrant litter of evergreen heath shrubs such as *Cassiope*¹¹. Finally, the heath site represents a landscape type with a potential of drainage following permafrost thawing, whereas the wet grassland site already represents a landscape depression that may receive additional melt water from the surroundings. Additional samples were collected from four other Arctic grassland vegetation sites in Canada, West Greenland, North Greenland and Svalbard (Supplementary Table S1).

Field measurements. Active-layer observations in Zackenberg (1997–2008) are based on two CALM grids in the two studied landforms. Here, thaw depths are determined by mechanical probing⁷. The flat ground moraine heath site consists of 121 points (entire ZERO-CALM1 grid), whereas for the wet grassland site only the wettest part of the ZERO-CALM2 grid is included consisting of 24 points. Observed changes in active-layer thickness from 1996 to 2008 represent minimum permafrost thawing rates because of the general lowering of the landscape (including the surface) following thawing of ice-rich permafrost.

Sampling was based on excavation of pits down to the frost table followed by drilling to obtain intact permafrost cores. Top permafrost cores were collected to a depth of 1 m in 1996 ($n = 3$ per site) using a metal core hammer and

adjacent similar cores to a depth of 1 m plus deeper cores ($n = 1$ per site) in 2008 by motorized hand-drilling equipment consisting of a Stihl drilling engine, an expandable drill string and a 40-cm-long core barrel with drill head. Sample lengths from 3 to 30 cm were packed in plastic bags in the field and immediately stored in a freezer box. Samples were kept below –5 °C at the Zackenberg Research Station and during transportation. Samples taken in 1996 for long-term incubation were kept cold (roughly 5 °C) until prepared for incubation. Volume-specific sampling allows element concentrations and ice content to be calculated as stocks.

Chemical analyses. As part of the long-term incubation, subsamples used for analysis of CO₂ production were subsequently analysed for total and dissolved C. Three replicates were pooled and hand-shaken for three minutes with distilled water (1:1 by mass) at 5 °C, centrifuged and the extracted soil water samples were filtered through Whatman GF-C glass-fibre filters, and the dissolved organic C was determined using a total organic C analyser (Dohrmann DC-80). Subsequently, samples were dried and crushed and the mean content of total organic soil C content was determined using an ELTRA SC-800 Carbon Determinator.

Three-pool carbon modelling. Total modelled soil respiration R is the sum of three pool-specific respiration rates, which were each simulated (equation (1)) as the pool-specific decay rate (k_i) multiplied by the total initial C pool (C_{tot}) multiplied by a fractionation coefficient (f_i) that describes the ratio of C pool i to the total C pool (equation (2)). The fraction of the passive C pool was calculated as the total C pool minus the sum of the fast and slow C pool fractions.

$$R = \sum_{i=1}^3 r_i = \sum_{i=1}^3 k_i C_{\text{tot}} f_i \quad (1)$$

$$f_i = \frac{C_i}{C_{\text{tot}}}, \sum_{i=1}^3 f_i = 1 \quad (2)$$

To better model pool-specific decomposition rates, we used data assimilation, which combines observed data and previous parameter knowledge with model structure to optimize parameter estimation (see Supplementary Table S2).

Statistics. Linear and nonlinear regression analyses have been used to test trends and variations reported to be significant only when $p < 0.05$. The temperature sensitivity (Q_{10}) was calculated using a first-order exponential fit¹⁵.

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Author contributions

B.E. initiated the experimental work in 1996 and compiled data and wrote most of the paper; A.M. carried out most of the chemistry analyses, C.S. and E.A.G.S. made the C dynamics model; B.E. and H.H.C. carried out the 2008 permafrost coring, L.B. was involved in the 2008 sampling and data analyses, H.H.C. initiated the 1996 ZERO-CALM monitoring as part of the GeoBasis programme and M.P.T. and C.S. were responsible for CALM measurements as part of the GeoBasis programme. All co-authors contributed to the writing.

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 and requests for materials should be addressed to B.E.

Competing financial interests

The authors declare no competing financial interests.