Biogenic volatile release from permafrost thaw is determined by the soil microbial sink

Warming in the Arctic accelerates thawing of permafrost-affected soils, which leads to a release of greenhouse gases to the atmosphere. We do not know whether permafrost thaw also releases non-methane volatile organic compounds that can contribute to both negative and positive radiative forcing on climate. Here we show using proton transfer reaction-time of flight–mass spectrometry that substantial amounts of ethanol and methanol and in total 316 organic ions were released from Greenlandic permafrost soils upon thaw in laboratory incubations. We demonstrate that the majority of this release is taken up in the active layer above. In an experiment using $^{14}$C-labeled ethanol and methanol, we demonstrate that these compounds are consumed by microorganisms. Our findings highlight that the thawing permafrost soils are not only a considerable source of volatile organic compounds but also that the active layer regulates their release into the atmosphere.
**Table 1 The most emitted compounds**

| Compound               | Mass-to-charge ratio | Emission rate (nmol g⁻¹ dw soil h⁻¹) | Relative abundance (%) |
|------------------------|----------------------|--------------------------------------|------------------------|
| Ethanol                | 47.049               | 1.345                                | 51.2                   |
| Methanol               | 33.033               | 0.673                                | 25.6                   |
| Acetaldehyde           | 45.033               | 0.198                                | 7.5                    |
| Acetone                | 59.049               | 0.134                                | 5.1                    |
| Formaldehyde           | 31.018               | 0.103                                | 3.9                    |
| Acetonitrile           | 42.034               | 0.062                                | 2.4                    |
| 2-Butanone             | 73.064               | 0.023                                | 0.9                    |
| 2-Butoxy/2-methyl-1-propane | 57.069               | 0.010                                | 0.4                    |
| Propyne/1,2-propadiene/cyclopropane | 41.038               | 0.009                                | 0.3                    |
| Cyclopropane/propane   | 43.054               | 0.008                                | 0.3                    |

Emission rate and relative abundance of the ten compounds released from permafrost soils in highest quantities is presented dw dry weight.
Disko Island, Greenland. dw dry weight

![Graphs](image)

**Fig. 1** Release of volatiles from thawing permafrost soils. The release of **a** ethanol, **b** methanol, and **c** other biogenic volatile organic compounds (BVOCs) over 43 h is shown for six permafrost soils (P1–P6) collected on Disko Island, Greenland. dw dry weight

compounds positively correlated with the dissolved organic carbon (DOC) and ammonium concentrations as well as the water content of permafrost (Fig. 2, Supplementary Fig. 2, 3). The variables showing strongest negative correlations with the emission rates were pH, microbial biomass, and water-extractable dissolved phosphorus concentration. Also total dissolved nitrogen and nitrate concentrations correlated negatively with the emission rates, although this was not significant for all BVOCs. For acetonitrile, bacterial abundance showed significant positive correlation (Supplementary Fig. 2).

**Uptake of volatiles from permafrost by active layer soil.** To assess whether the BVOCs released from thawing permafrost are likely to end up in the atmosphere or be retained in the active layer soil overlaying the permafrost, we performed an additional uptake experiment (from hereafter referred to as the Uptake experiment). BVOC release was measured for the permafrost soils alone as well as together with either the organic or mineral horizon of the active layer soil sharing the incubation atmosphere but without physical contact between the two soils. After 1 h at 6 °C, the first measurements showed that organic and mineral active layer soils took up 85% and 60% of the BVOCs released from the permafrost (See Fig. 3 for ethanol, methanol, and total other BVOCs and Supplementary Figs 4–6 for the most abundant other compounds). After 7 h, the relative uptake had increased to 98% and 86%, respectively.

**Mineralization of ethanol and methanol by soil microbes.** We went on to investigate whether microbial consumption of ethanol and methanol occurs in the studied mineral and organic active layer soil as well as the permafrost soil at low temperatures and realistic mixing ratios (from hereafter referred to as the Mineralization experiment). We injected 14C-labeled ethanol (2.3–3.6 ng g⁻¹ fresh weight soil) and methanol (1.1–1.8 ng g⁻¹ fresh weight soil) to the headspace of incubators with soil samples and followed over time the mineralization of the compounds to CO₂ at 6 °C.

The mineralization to CO₂ occurred faster and to a much higher extent for methanol compared to ethanol (Fig. 4). After 2 h, 3% of the added ethanol was mineralized to CO₂ in both organic and mineral soil layers, while 70% and 60% of the added methanol was mineralized in organic and mineral soils, respectively. Ultimately, about 95% of the added 14C-methanol was transformed into 14C-CO₂, while that was the case for only 15% of ethanol (Fig. 4). However, for both compounds, most of the mineralization occurred within the first 24 h followed by a low linear increase for the remaining incubation period. No 14C could be extracted with an organic solvent from the soils at the end of the experiment, suggesting that all the added 14C-labeled ethanol and methanol was either converted into 14C-CO₂ or incorporated into the microorganisms.

During the first 72 h, there was, in contrast to the active layer soils, hardly any mineralization of ethanol or methanol in the permafrost soils that had been thawed and stored at 4 °C 1 day prior to the experiment. Between 72 and 144 h, mineralization activity increased, and 45% of the 14C-methanol and 25% of the 14C-ethanol was mineralized.

To test whether the observed mineralization could be due to abiotic degradation of ethanol and methanol, we included soil samples sterilized by autoclaving in the experiment. In the sterilized samples, only 1% of the methanol and none of the ethanol was mineralized to CO₂ after 144 h.

**Discussion**

We have demonstrated that permafrost soils upon thaw release a variety of BVOCs with ethanol and methanol as the dominant compounds. The release rate of BVOCs peaked within the first 2 h of thaw and then declined over time. This rapid release and the subsequent decline in BVOC release has two potential explanations: previous production processes may have occurred in the frozen permafrost soil, slowly causing a buildup of immobilized BVOCs that were now released. Alternatively, the turnover
of a limited pool of labile carbon made available upon thaw, could cause an initially high microbial fermentation rate and a release of trace gases that decreases over time. In Arctic active layer soils, a large ethanol production has been shown to correlate with a depletion of labile carbon made available upon thaw. However, the rapid appearance of the release peak at low temperature (6 °C) points to a release of previously trapped gases rather than post-thaw microbial production, as earlier shown for methane.

Ethanol is produced from fermentative degradation of plant residuals in anoxic soils by microorganisms, facilitated by the enzymes pyruvic decarboxylase and alcohol dehydrogenase, while methanol can be formed by chemical and enzymatic demethylation of the methoxy groups of pectin in decaying plant cell walls. Furthermore, compounds such as ethanol, methanol, and acetone can be produced in non-enzymatic thermochemical Maillard reactions. Such reactions are, however, strongly temperature-dependent, and owing to the low incubation temperature used in our experiments, most likely only a minor part of the observed BVOC release is derived from abiotic processes.

DOC concentration, ammonium concentration, and water content of the permafrost were the soil properties correlating strongest with BVOC emissions during permafrost thaw, suggesting that the most fertile soils with potentially highest degree of anoxia due to waterlogging had the highest net production potential for the studied BVOCs. Microbial biomass and pH show a negative correlation with BVOC release, which can be due to an inverse relationship with water content of the soil as soils with a higher water content and therefore more anoxic conditions had lower pH and lower microbial biomass.

Despite the significant release of BVOCs from the thawing permafrost soils, it is likely that most of these compounds will never reach the atmosphere. In the Uptake experiment, both the mineral and organic horizon soil from the active layer took up the majority of the BVOCs released from the thawing permafrost. This uptake could be caused by BVOC sorption to soil particles and organic material, dissolution in the water phase for hydrophilic compounds, or microbial consumption. All three processes occur to some extent, but our PTR-TOF data suggest that microbial uptake was the major removal process. We observed that the relative BVOC uptake increased with time and that owes support to biotic rather than physico-chemical processes. In physico-chemical processes, the relative uptake would be expected to decrease rather than increase, as adsorption or dissolution would likely be reversible in contrast to microbial degradation of the compounds.

In the Mineralization experiment, we showed that added 14C-ethanol and 14C-methanol is rapidly converted to 14CO2. This conversion did not take place in sterilized soil samples indicating that it was in fact a result of microbial activity. Degradation of both ethanol and methanol started immediately in the active layer soils. The mineralization to CO2 occurred faster and to a higher extent for methanol compared to ethanol. However, at the end of the experiment, no 14C could be extracted from the soils, suggesting that also all of the added ethanol was quickly degraded microbially, just with a lower yield as CO2. A wide range of soil microorganisms utilize ethanol and methanol as a carbon and energy source under both oxic and anoxic conditions. The fact that these compounds were mineralized by microbes in the active layer soils is therefore not in itself surprising, but the fact that the microbes do degrade the low concentrations at a very high pace and with different 14CO2 yields is interesting. Both ethanol and methanol were degraded very fast (complete within 24 h and in the case of methanol probably much faster) but with different utilization strategies. Methanol seems to be used only as energy source (high 14CO2 yield), while ethanol is used mainly as a source of carbon for microbial growth and synthesis of molecules that are then slowly mineralized to CO2 (low 14CO2 yield). This is in agreement with the known degradation pathways of the two compounds. Methanol degrades through formaldehyde and formate to CO2, while ethanol is degraded through acetaldehyde to acetyl-CoA, which can be used as a building block for fatty acids, amino acids, etc.

As opposed to the active layer soils, degradation of ethanol and methanol in permafrost did not start until 72–144 h of incubation. This is in agreement with previous experiments with permafrost soil showing that microbial respiration starts to increase 3 days after thaw and peaks after 2 weeks. The initial lag phase can be explained by the fact that microorganisms may need some time to adjust to the new conditions and become active or that microbial growth was needed to obtain the increase in activity.

The fast and complete degradation of ethanol and methanol to CO2 in the active layer soils proves that the BVOC sink is primarily due to microbial mineralization rather than chemical or physical retention. In accordance with previous studies, we found higher microbial abundance in organic than in mineral horizon of the active layer soil (Table 2), which could explain the

![Table 2 Soil characteristics](image-url)
atmosphere, it is important to further address the processes of release during permafrost thaw. Regression coefficients of partial least squares regression (PLSR) models for the covariance between the measured soil variables and the accumulated release of ethanol and methanol during the first 5 h of permafrost thaw. All models had one PLS component. Positive regression coefficients indicate a positive relationship and negative ones a negative relationship. Error bars show ± confidence intervals (95%) of the regression coefficients. Significant factors are shown in green.

Methods

Site description. Permafrost cores and active layer soil samples were collected in early August 2015 in the Bløssedalen Valley, located on Disko Island in West Greenland (69°16′18.03′′N; 53°29′11.93′′W). The climate is Low Arctic and a climate station located near the sea level reveals a mean annual soil temperature at 5 cm depth of 0.9 °C (1991–2004) and an annual mean air temperature of −3.0 °C (1992–2012)

Permafrost and active layer sampling. Nine independent intact permafrost samples were sampled from pits by the use of sterilized steel pipes hammered into the permafrost ca. 10 cm below the permafrost table. The permafrost soils were kept frozen during transport to Copenhagen. In Copenhagen, the soil cores were homogenized into particles <1 cm³ in a freezer room using a hammer and a metal mesh (8 mm mesh size). Permafrost soils used in the Release and Uptake experiments were stored at −6 °C for 6 months, transported to the laboratory, and stored there at −18 °C for 10–15 days prior to the start of each experiment. Permafrost soils used in the Mineralization experiment were stored at −6 °C and thawed at 4 °C 1 day before the experiment.

Soil cores of the active layer were sampled by pushing a brass tube (diameter 4 cm) 10 cm into the soil after carefully removing the vegetation. The organic soil horizon (depth varied between 3 and 7 cm) was then separated from the mineral horizon. The active layer soils were stored at −6 °C and then thawed at 4 °C approximately 10 days prior to the start of each experiment. Shortly after the soils had thawed, they were gently homogenized by hand wearing gloves, followed by removal of roots and stones >3 mm in diameter.

Soil characterization. The frozen soil samples were thawed at 5 °C for 24 h prior to the chemical and microbial analysis. The samples were analyzed in duplicates as described below. Gravimetric soil water content was determined based on the water loss after drying at 70 °C for 24 h. Soil organic matter content was determined by loss on ignition at 550 °C for 6 h.

Microbial biomass estimation. For all soil types, triplicated 0.25 g DNA extraction subsamples were made using the PowerLyzer PowerSoil DNA Isolation Kit (MoBio, Carlsbad, California). For all soil types, triplicated 0.25 g DNA extraction subsamples were made using the PowerLyzer PowerSoil DNA Isolation Kit (MoBio, Carlsbad, California). Total fungal biomass was quantified based on the number of ITS2 gene copies obtained by targeting the fungal ITS2 nuclear ribosomal DNA region using forward primer gITS7 (GTGARTCATCGARTCTTTG) and reverse primer ITS4 (TCCTCCGGCTTATGATATGC) as described by Christiansen et al.

For all soil types, triplicated 0.25 g DNA extraction subsamples were made using the PowerLyzer PowerSoil DNA Isolation Kit (MoBio, Carlsbad, California). Total bacterial biomass was quantified based on the number of 16s gene copies obtained by quantitative PCR targeting the 16s rRNA sequence using forward primer 341F
and reverse primer 518 R (5′-ATTACGGGGCTGCTGG-3′) and 1 µl DNA template, as previously described by Feld et al.34. Soil characteristics in the active layer soils are presented in Supplementary Table 1.

**BVOC release from thawing permafrost.** For the BVOC measurements in the Release experiment, six 13-g fresh weight frozen permafrost soil samples were placed in polyester woven mesh bags (mesh size 515 micron) and incubated in 200 ml glass jars sealed by aluminium covered screw lids at 6 °C for 43 h. The glass
**Chemical composition determination.** The molecular formula was identified (ion mass range within ±3 mDa) with a combination of carbon, hydrogen, oxygen, and nitrogen atoms using the database created by Holzinger et al.35,37 and finally to provide output files with time-averaged (10 s) VOC mixing ratios of all detected mass peaks. VOC concentrations in blank samples were subtracted from those in the soil samples. The concentrations in the blanks were in general very low, suggesting minimal or no contamination from the zero air or used materials.

**Data processing.** Data from the PTR-TOF-MS was processed using the PTRWid software tool37. PTRWid was used to detect and identify mass peaks in the measurement spectrum, to calibrate the mass scale automatically, to convert the count rates of the detected compounds to VOC mixing ratios (following Holzinger et al.35), and finally to provide output files with time-averaged (10 s) VOC mixing ratios of all detected mass peaks. VOC concentrations in blank samples were subtracted from those in the soil samples. The concentrations in the blanks were in general very low, suggesting minimal or no contamination from the zero air or used materials.

**Calibration.** While the PTRWid software already applied a mass-dependent transmission efficiency of the detector (based on Cappellin et al.69) and a default reaction rate coefficient for the protonation in the drift tube when converting from count rate to mixing ratio, the accuracy can be improved when calibrating the instrument against a gas standard. The PTR-TOF-MS was calibrated against a gas standard mixture (ca. 1 ppmv, Ionicon Analytik, Innsbruck, Austria) at different concentrations by diluting the gas mixture with zero air (GC-U-b, Ionicon Analytik, Innsbruck, Austria) before, during, and after the experiments. Compound-specific calibration coefficients were averaged and applied for the whole period of the experiment for a number of compounds (Supplementary Table 2). The accuracy for estimation of the concentrations of the compounds without specific calibration standards was estimated to be ±40% for the ions with m/z <150 and ±60% for the ions with m/z above.

**BVOC mineralization experiment.** The mineralization rates of ethanol and methanol to CO2 were tested in organic, mineral, and permafrost layer soils using a recently developed method based on 14C-labeling (ref.41). Briefly, 6 g fresh weight (organic horizon) or 10 g (mineral horizon and permafrost) soil samples were weighed into 120 ml serum flasks in triplicates and incubated at 6 °C. In each flask, a glass vial containing 2.5 ml 1 M NaOH and 0.01 M NaHCO3 was placed to trap CO2 mineralized from 14C-labeled ethanol/methanol.

In the emissions from the incubators were sampled for 7 h and the technical setup was as described for the Release experiment.

**BVOC analysis instrumentation.** BVOC mixing ratios were measured using PTR-TOF-MS (PTR-TOF-MS 8000, Ionicon Analytik, Innsbruck, Austria). The PTR-TOF-MS was operated at 60 °C drift tube temperature, 2.20 hPa drift tube pressure, and 550 V drift tube voltage, which led to an E over N ratio (electric field E, number density N) of ca. 130 × 10−21 V m2. Compounds up to m/z = 130 Da were monitored at 1 Hz temporal resolution. The instrument provides a mass resolution >4000 m/Da (full width half maximum) and a detection limit <10 ppt (ref.35). The instrument was equipped with a heated PEEK capillary inlet system (operated at 60 °C) and a built-in permeation unit (PerMAsCaL; Ionicon Analytik, Innsbruck, Austria) which emitted 1,3-diiodobenzene (C6H4I2), which was used for an improved mass scale calibration by adding a continuous strong signal at a higher mass peak (i.e., m/z 203.943). Details about the PTR-TOF-MS technique are available from Lindinger et al.36 and Graus et al.33.

**Accumulated mineralization (% added 14C)**

- **ETHANOL**
  - Organic soil
  - Mineral soil
  - Permafrost soil

- **METHANOL**
  - Organic soil
  - Mineral soil
  - Permafrost soil

---

**Fig. 4 Microbial mineralization of ethanol and methanol.** Mean mineralization rates (n = 3) are shown for 14C-labeled a ethanol and b methanol in organic, mineral, and permafrost soils. Initial concentrations were approximately 3 and 1.5 µg kg−1 fresh weight soil for ethanol and methanol, respectively. The incubation temperature was 6 °C. Sterilized soil working as negative controls showed no mineralization. Error bars show standard error of the mean. Some error bars are smaller than the symbols.
biased as a fraction of the ethanol/methanol was dissolved in water or adsorbed to the soil.

The CO2-trap was exchanged through a needle syringe permanently installed in the septum at six time points during the experiment. To be able to differentiate between the trapped 14CO2 and the dissolved 13C-labeled ethanol/methanol, the CO2-trap was split in two. One ml of the CO2-trap was transferred to a 2 ml Eppendorf tube with 0.7 ml water and the other 1 ml of the CO2-trap was transferred to a 2 ml Eppendorf tube with 0.7 ml BaCl2 (1.7 M) to precipitate the trapped 14CO2 as Ba14CO3. The samples were then left for 5 h to react, followed by 2 min centrifugation at 12,000 x g, and then 1 ml from each tube was mixed with HiSafe 3 LSC-cocktail (Perkin Elmer, Waltham, MA) and counted for 30 min by liquid scintillation (Tri-Carb 2810 TR, PerkinElmer, Waltham, MA).

The last sample was taken after 144 h, and then 30 ml methanol was added to each flask through the permanently installed needle to extract any residual 13C-ethanol or -methanol. The samples were shaken for 24 h, and the supernatant was transferred to a 50 ml centrifuge tube and centrifuged for 10 min at 6000 x g. The amount of extractable 14C (non-degraded ethanol and methanol) was then determined in 3 ml supernatant by liquid scintillation counting.

Negative controls of each soil type were included in which the soil had been sterilized by autoclaving twice.

Statistical analyses. PLSR in SIMCA 13.0.3 (Umetrics, Umeå, Sweden) was used to assess for covariance between the permafrost soil characteristics and the emissions of the ten most emitted BVOCs. PLSR is a flexible multivariate technique used to predict a Y variable (here BVOC emission rate) with a number of X variables (here the soil characteristics presented in Table 2), which can be correlated. The data were centered and all variables were auto-scaled to unit variance to give equal importance for all variables. The one-component PLS models were cross-validated using six cross-validation groups.

For the Uptake experiment, the difference in BVOC release for permafrost alone as compared with permafrost soil together with organic or mineral soil was statistically tested in IBM SPSS Statistics (Version 22.0, IBM Corp., New York City, United States). The mean difference in BVOC release over time between incubations with and without active layer soil was tested in General Linear Model Univariate Analysis of Variance (ANOVA) with soil type (permafrost alone, organic plus permafrost soil, mineral plus permafrost soil) as a fixed factor and mean BVOC release over time as a dependent variable. Dunnett post hoc test was used for comparisons of the permafrost alone against permafrost with organic and mineral soils. The differences in the relative BVOC uptake between organic and mineral layer soils were tested with General Linear Model Repeated Measures ANOVA with time as a within-subjects factor and active layer type (organic or mineral) as a between-subjects factor.

Data availability. The authors declare that the data supporting this study are available within the paper and its Supplementary Information. All data are also available from the authors upon request.

Received: 13 February 2018 Accepted: 26 July 2018

Published online: 24 August 2018

References
1. Pfeilnas, J. et al. Biogenic volatile emissions from the soil. Plant Cell Environ. 37, 1866–1891 (2014).
2. Kreamshoj, M. et al. Large increases in Arctic biogenic volatile emissions are a direct effect of warming. Nat. Geosci. 9, 349–353 (2016).
3. Aaltonen, M. et al. Continuous VOC flux measurements on boreal forest floor. Plant Soil 369, 241–256 (2013).
4. Hugelius, G. et al. Improved estimates show large circumpolar stocks of permafrost carbon while quantifying substantial uncertainty ranges and identifying remaining data gaps. Biogeosciences 11, 4771–4822 (2014).
5. Gilbert, J. A., Hill, P. J., Dodd, C. E. R. & Laybourn-Parry, J. Demonstration of antifreeze protein activity in Antarctic lake bacteria. Microbiology 150, 171–180 (2004).
6. Feller, G. & Gerday, C. Psychrophilic enzymes: hot topics in cold adaptation. Nat. Rev. Microbiol. 1, 200–208 (2003).
7. Janssen, J. K. & Tas, N. The microbial ecology of permafrost. Nat. Rev. Microbiol. 12, 414–425 (2014).
8. Rivkina, E. et al. Microbial life in permafrost. Adv. Space Res. 33, 1215–1221 (2004).
9. Elberling, B., Christiansen, H. H. & Hansen, B. U. High nitrous oxide production from thawing permafrost. Nat. Geosci. 3, 506–506 (2010).
10. IPCC. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds Stocker, T. F. et al.) (Cambridge University Press, Cambridge and New York, NY, 2013).
11. Schuur, E. A. G. et al. Climate change and the permafrost carbon feedback. Nature 520, 171–179 (2015).
12. Jimenez, J. L. et al. Evolution of organic aerosols in the atmosphere. Science 326, 1525–1529 (2009).
13. Paasonen, P. et al. Warming-induced increase in aerosol number concentration likely to moderate climate change. Nat. Geosci. 6, 438–442 (2013).
14. Finlayson-Pitts, B. J. & Pitts, J. N. Jr. Chemistry of the Upper and Lower Atmosphere. (Academic Press, San Diego, 2000).
15. Quinn, P. K. et al. Short-lived pollutants in the Arctic: their climate impact and possible mitigation strategies. Atmos. Chem. Phys. 8, 1723–1735 (2008).
16. Turco, S. J. et al. Bacterial genome replication at subzero temperatures in permafrost. ISME J. 8, 139–149 (2014).
17. Rivkina, E. et al. Biogeochemistry of methane and methanogenic archaea in permafrost. FEMS Microbiol. Ecol. 61, 1–15 (2007).
18. Lacelle, D. et al. Geomicrobiology and occluded O2–CO2–Ar gas analyses then provide evidence of microbial respiration in ancient terrestrial ground ice. Earth Planet Sci. Lett. 306, 46–54 (2011).
observatory using a novel high mass resolution thermal-desorption proton-transfer-reaction mass-spectrometer (hr-TD-PTR-MS). Atmos. Chem. Phys. 10, 10111–10128 (2010).

39. Park, J.-H. et al. Active atmosphere-ecosystem exchange of the vast majority of detected volatile organic compounds. Science 341, 643–647 (2013).

40. Cappellin, L. et al. On quantitative determination of volatile organic compound concentrations using proton transfer reaction time-of-flight mass spectrometry. Environ. Sci. Technol. 46, 2283–2290 (2012).

41. Albers, C. N., Kramshøj, M. & Rinnan, R. Rapid mineralization of biogenic volatile organic compounds in temperate and Arctic soils. Biogeosciences 15, 3591–3601 (2018).

Acknowledgements

We gratefully acknowledge the financial support from the Danish Council for Independent Research | Natural Sciences, the Villum Foundation, the Danish National Research Foundation (CENPERM DNRF100), and the European Research Council (ERC) under the European Union’s Horizon 2020 research and innovation programme (grant agreement No. 771012). We thank Pia Bach Jakobsen for laboratory assistance with the mineralization experiment and Goshia Sylvester for assistance with the soil nutrient and microbial analyses. The Arctic Station (University of Copenhagen) is thanked for housing and supporting the logistics.

Author contributions

R.R., C.A.L., T.H. and M.K. designed the experiment. M.K. sampled the top soil and B.E. carried out the permafrost coring. M.K. and T.H. performed the Release and Uptake experiments. M.K. and C.A.L. performed the Mineralization experiment. M.K., R.R., R.H. and T.H. analyzed the data. M.K., R.R. and C.A.L. interpreted the data and wrote the article with contributions from all authors.

Additional information

Supplementary Information accompanies this paper at https://doi.org/10.1038/s41467-018-05824-y.

Competing interests: The authors declare no competing interests.

Reprints and permission information is available online at http://npg.nature.com/reprintsandpermissions/

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.