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LETTERS

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Potential carbon emissions dominated by carbon dioxide from thawed permafrost soils

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Increasing temperatures in northern high latitudes are causing permafrost to thaw[1], making large amounts of previously frozen organic matter vulnerable to microbial decomposition[2]. Permafrost thaw also creates a fragmented landscape of drier and wetter soil conditions[3,4] that determine the amount and form (carbon dioxide (CO_2), or methane (CH_4)) of carbon (C) released to the atmosphere. The rate and form of C release control the magnitude of the permafrost C feedback, so their relative contribution with a warming climate remains unclear[5,6]. We quantified the effect of increasing temperature and changes from aerobic to anaerobic soil conditions using 25 soil incubation studies from the permafrost zone. Here we show, using two separate meta-analyses, that a 10 °C increase in incubation temperature increased C release by a factor of 2.0 (95% confidence interval (CI), 1.8 to 2.2). Under aerobic incubation conditions, soils released 3.4 (95% CI, 2.2 to 5.2) times more C than under anaerobic conditions. Even when accounting for the higher heat trapping capacity of CH_4, soils released 2.3 (95% CI, 1.5 to 3.4) times more C under aerobic conditions. These results imply that permafrost ecosystems thawing under aerobic conditions and releasing CO_2 will strengthen the permafrost C feedback more than waterlogged systems releasing CO_2 and CH_4 for a given amount of C.

High-latitude ecosystems store almost twice as much C in soils than what is contained in the atmosphere[7,8]. As the global climate warms, northern high latitudes are experiencing rapid increases in temperature[9] that have the potential to not only increase C emissions from previously frozen C in permafrost and the active layer[10] but also to indirectly affect the C cycle through changes in regional and local hydrology. Warmer temperatures increase thawing of ice-rich permafrost and the melting of ground ice, which causes the land surface to collapse into the space that was previously filled by ice resulting in thermokarst terrain[11]. Permafrost thawing can also gradually increase active layer thickness (seasonally thawed ground), causing poorly drained soil conditions in lowlands or drier conditions in uplands where natural drainage can increase[3]. On the other hand, permafrost thaw and collapse can cause soils to become waterlogged where anaerobic conditions prevail and C is released in the form of CO_2 and CH_4. One major uncertainty in determining the climate forcing impact of permafrost ecosystems is understanding the relative magnitudes of the effects of shifting subsurface hydrology versus increasing temperatures on greenhouse gas release in permafrost ecosystems.

In addition to soil temperature and moisture, the chemical composition (for example, carbon to nitrogen ratio)[12], physical protection by soil minerals, microbial community dynamics, and other environmental controls, such as pH and nutrient availability, also impact the amount of C released to the atmosphere[13]. While temperature and soil moisture (that is, oxygen availability) are the most important changing environmental factors for future C release from permafrost, their effect size on C release has been poorly quantified.

Therefore, we used a meta-analysis approach to quantify the ratio of C release with a 10 °C increase in temperature, and between soils that were incubated aerobically and anaerobically (see Methods). We compiled a database of 25 incubation studies

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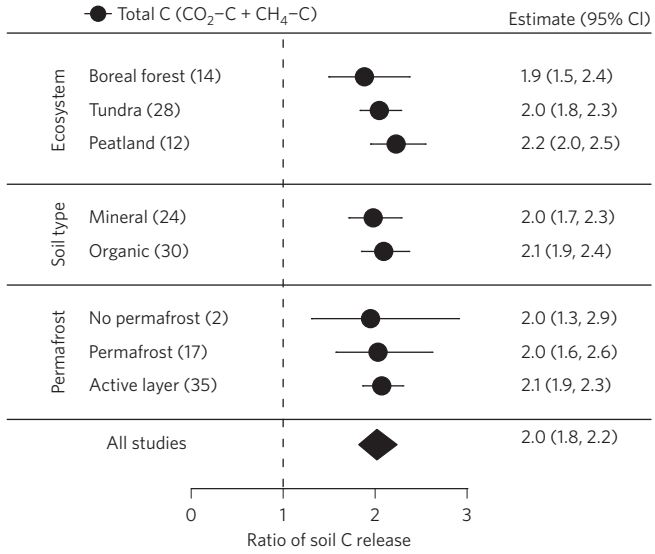

Figure 1 | Ratio of C release with a 10 °C increase in incubation temperature. Total C is the sum of CO_2-C and CH_4-C from aerobic and anaerobic incubations. Observations are split into different ecosystems, soil types and permafrost conditions. The numbers in brackets to the left represent numbers of observations for each subgroup. The numbers in brackets to the right represent the minimum and maximum range of the confidence interval for the ratio of soil C release in each ecosystem, soil type, and permafrost condition.

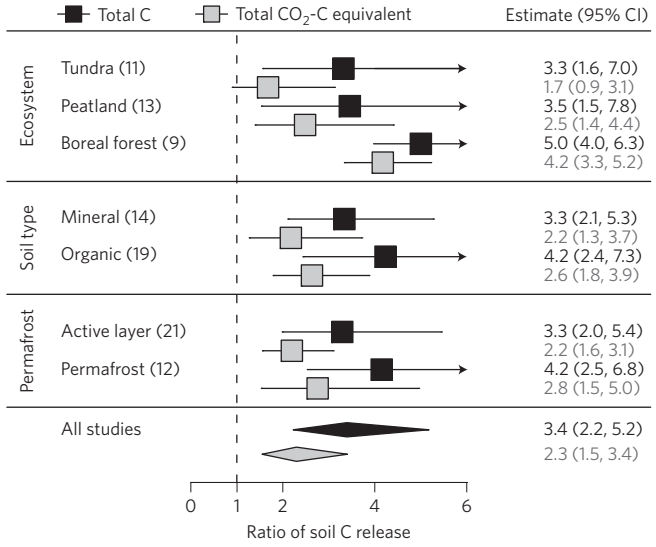

Figure 2 | Ratio of C release from permafrost-affected soils comparing aerobic to anaerobic incubation conditions. Total C is the sum of CO_2-C and CH_4-C whereas total CO_2-C equivalent is the sum of CO_2-C and CH_4-C expressed as CO_2-C equivalent (accounts for the higher GWP of CH_4). Observations are split into different ecosystems, soil types and permafrost conditions. The numbers in brackets to the left represent numbers of observations for each subgroup. The numbers in brackets to the right represent the minimum and maximum range of the confidence interval for the ratio of soil C release in each ecosystem, soil type, and permafrost condition. The arrow indicates that the confidence interval (CI) is wider than the space.

(Supplementary Table 1) that included soils from across the entire permafrost zone from three broad ecosystem types (boreal forest, peatland and tundra). Soils were collected from both the active layer and the permafrost layer, and all samples included in this synthesis were incubated at temperatures higher than or equal to −0.5 °C (Supplementary Table 1).

We quantified the warming capacity of C release from CO_2 and CH_4 under aerobic versus anaerobic conditions by accounting for both the amount of CO_2 and CH_4 produced and the relative global warming potential (GWP) of these two greenhouse gases. When investigating the climate forcing potential of soil decomposition in the permafrost zone, such a consideration is necessary as the GWP of CH_4 is 34 times higher than that of CO_2 on a 100-year timescale[14].

For the 21 incubation studies that used at least two incubation temperatures, a 10 °C increase in temperature (from 5 to 15 °C) resulted in an increase of net C release by a factor of 2.0 (95% CI, 1.8 to 2.2; Fig. 1, Supplementary Table 5). This pattern was consistent across boreal forest, peatland and tundra ecosystems as well as for mineral (%C < 20) and organic (%C > 20) soils and did not vary among soils that originated from the active layer or from the permafrost soil layer on the basis of Akaike's information criterion corrected for small sample sizes (AICc, Supplementary Table 10). Additionally, incubation duration and oxygen availability did not exhibit an effect of warming on C release (on the basis of AICc, Supplementary Table 10). It is a well-known fact that increasing temperatures enhance C release and our overall mean value of 2.0 is within the range of previously published literature within and outside the permafrost zone[15].

Carbon release under aerobic incubation conditions was on average 3.4 (95% CI, 2.2 to 5.2; Fig. 2, Supplementary Table 7) times higher than under anaerobic incubation conditions. The ratio of aerobic to anaerobic C release was not affected by ecosystem type, soil type, active layer or permafrost layer, incubation temperature or duration. The contribution of CH_4-C to total soil C release in anaerobic incubation studies was low (5.7% across all observations, 95% CI 2.7% to 8.7%; Fig. 3) but increased at higher incubation temperatures (on the basis of AICc, Supplementary Table 15). Methane production rates and emissions are known to be highly sensitive to temperature[16], and given that CH_4 exerts a greater influence on the climate than CO_2, this sensitivity will impact the strength of the permafrost C feedback as global temperatures rise. The contribution of CH_4-C to total soil C loss was higher during the incubation of tundra and peatland soils than in boreal forest soils (Supplementary Table 8), where CH_4 production was <4% of total C released under anaerobic conditions (Fig. 3). This may be related to the fact that tundra and peatland ecosystems experience anaerobic conditions more frequently in nature and thus are more likely to have established methanogenic communities[17]. Overall, the CH_4-C contribution to total C release in anaerobic incubations was too small to affect trends in the total soil C release in the incubations. We found that the aerobic incubations not only supported greater total soil C release, but were also associated with higher GWP of greenhouse gas (CO_2 and CH_4) release. Even when accounting for the 34 times higher GWP of CH_4 relative to CO_2, the ratio of aerobic to anaerobic CO_2-C equivalent (sum of CO_2-C plus CH_4-C expressed as CO_2-C equivalent) was 2.3 times higher in fully aerobic soils than under anaerobic conditions (Fig. 2). The contribution of CH_4-C calculated as CO_2-C equivalent to total CO_2-C equivalent increased to 21.7% (95% CI 13.4% to 30%) compared with when only accounting for CH_4-C, which shows that despite the relatively higher contribution of CH_4 when considering the global warming potential of both gases, CH_4-C still only contributes little to the overall C release.

The comparison of C release under aerobic and anaerobic incubation conditions provides important new results to constrain ecosystem and Earth system models and highlights the significance of anaerobic CO_2 production in incubation studies. However, it is important to keep in mind that incubation results do not equal *in situ* measurements of CO_2 and CH_4 emissions. Aerobic decomposition is the dominant C mineralization pathway in

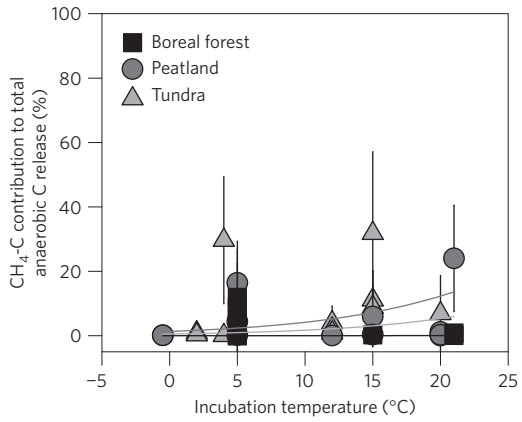

Figure 3 | Contribution of CH_4-C to total anaerobic C release for boreal forest, peatland and tundra ecosystems. Symbols represent observations from different studies and the error bars show standard deviation within an observation. Lines represent the average predicted relationship between CH_4-C contributions to total anaerobic C release and incubation temperature for the three given ecosystems.

unsaturated soils and produces CO_2 while anaerobic mineralization generates both CO_2 and CH_4. Net CH_4 emissions are the result of CH_4 production (anaerobic process) and consumption through CH_4 oxidation (largely aerobic process), while these incubation results reflect CH_4 production alone. Changes in CH_4 emissions from the permafrost zone have been attributed to changes in soil moisture, thermal conditions and vegetation shifts[18], and less to the increased availability of easily decomposable organic matter as the active layer thickens[19]. Additionally, maximum CH_4 production rates in incubation studies are sometimes reached after a lag time of a few days to months depending on incubation temperature, moisture content, ecosystem type, and sample depth[20]. Lag times for maximum CH_4 production in incubation studies occur because alternative electron acceptors (for example, nitrate, ferric iron and sulfate) are energetically favourable before methanogenic archaeal communities can establish. To evaluate the effect of a possible lag in CH_4 emissions in incubation studies, a sensitivity analysis (Supplementary Tables 17 and 18) was performed, which showed that even when including only those samples that had reached maximum CH_4 rates during the incubation (Supplementary Table 17) the contribution of CH_4-C to total anaerobic C release was low (average of 7.5%, 95% CI from 3.8 to 16.8, Supplementary Fig. 2). Additionally, there was no change in CH_4-C contribution to total soil C release under anaerobic conditions with incubation length (on the basis of AICc, Supplementary Table 15); however, under field conditions, it is possible that the contribution of CH_4 might be higher than what was found in the incubation studies. While lags in CH_4 emissions point towards the benefits of longer term incubation studies for quantifying lag effects, the overall interpretation of our comprehensive data set is not impacted by incubation length.

It follows from this analysis that whether northern landscapes will become wetter or drier under global change is a critical mechanism affecting the forms and amounts of C release. Changing surface hydrology due to permafrost thawing will produce a fragmented landscape of dry and wet ecosystems; and thus large uncertainties are associated with C release under changing hydrological conditions[3]. Another important factor is whether permafrost C (as it thaws) emerges in aerobic versus anaerobic environments even when surface hydrology stays constant. Globally increasing temperatures will affect drier soils in the Arctic much more than wetter soils owing to thermal properties with larger diurnal ranges in drained soils. Projected temperatures in the Arctic are expected to increase by 8.3 °C (±1.9 °C) for 2081–2100 compared with 1986–2005 when using the highest climate warming trajectory (Representative Concentration Pathway 8.5) which is 2.4 times the global average warming[21]. This increase in air temperature will not immediately be propagated into the soil and so the 10 °C increase is an upper limit.

It has been proposed that the response of C release to warming may be transient and weaken over time[22,23], which would affect the strength of the permafrost C feedback long term. Higher C losses under warming can be partially offset by increased plant C uptake during the growing season[23,24], feedbacks between living and decaying plant roots, and C stored in soil. Although plant communities in the Arctic are predicted to undergo structural, functional and compositional changes with climate change and boreal forests are expected to expand northwards[25], our study shows that the temperature effect on soil C mineralization rates varies little among different ecosystem types. Besides changing plant communities, various processes are involved with warmer temperatures, such as the stimulation of decomposition of older soil organic matter with higher plant activity[26], that are not accounted for in laboratory studies. Hence, our results should be viewed as a potential for increased soil C release under warmer temperatures, and not as an indicator of changes in net ecosystem C balance.

The existence of permafrost exerts a strong control on wetland distribution[27], and large changes in the areal extent of wetlands are expected as permafrost thaws[28]. Ponds and lakes are decreasing in number and area in the discontinuous and sporadic permafrost zone, while changes in the continuous permafrost zone are less consistent[29,30]. Besides a more gradual decrease of permafrost extent, abrupt thaw processes such as thermokarst formation[6] will change surface hydrology because of loss of ground ice (by melting followed by drainage). These abrupt thaw processes not only expose deep C stores to microbial breakdown but also determine whether decomposition releases CO_2 (aerobic mineralization) or CO_2 and CH_4 under anaerobic mineralization[6]. Broad-scale changes in landscape hydrology will lead to drier aerobic uplands after thaw of ice-poor permafrost, while thawing and collapsing of ice-rich permafrost will result in wetter lowlands. Therefore, the greater release of CO_2-C equivalent from permafrost-affected soils under aerobic conditions emphasizes the importance of monitoring and predicting changes in hydrology in a warming Arctic.

In this synthesis, we used two extreme scenarios to compare the effect of changing environmental conditions (a temperature increase of 10 °C and a change from aerobic to anaerobic soil conditions) on C release from permafrost-affected soils and showed that increasing temperatures have a large effect on CO_2 and CH_4 production but that changes in soil moisture conditions associated with permafrost thaw can exert even greater effects. As 3.4 times more soil C is mineralized under aerobic than anaerobic soil conditions, when permafrost thaws and drains, one unit of soil will have a more than three times higher impact on climate change than when the same unit of soil thaws under undrained (anaerobic) conditions. This implies that the permafrost C feedback to climate change could be stronger when a larger percentage of the permafrost zone undergoes thaw in dry and oxygen-rich environments, even under conditions where CO_2 is the dominant gas released to the atmosphere rather than CH_4.

Methods

Methods and any associated references are available in the online version of the paper.

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Author contributions

C.S. designed the study together with E.A.G.S.; C.S. compiled the database and extracted data from the literature with help from M.L. and S.M.N. M.K.-F.B. and C.S. performed the analysis. C.S. wrote the manuscript. All other authors either contributed data and provided input to the manuscript, or performed essential tasks in the field and laboratory for the included data sets.

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 C.S.

Competing financial interests

The authors declare no competing financial interests.

Methods

Permafrost incubation database. We compiled a database of soil incubation studies that used soils from the northern circumpolar permafrost zone. We searched the Web of Science for published incubation studies using the keywords 'incubation and permafrost and soil' or 'incubation and Arctic and soil' or 'incubation and boreal and permafrost' or 'incubation and tundra and permafrost' or 'incubation and peat* and permafrost' and 'decomposition and CO_2 or CH_4'. The database includes published data sets to the end of July 2014 as well as unpublished data sets that were acquired through an active solicitation with members of the Permafrost Carbon Network (http://www.permafrostcarbon.org). We screened the results for actual incubation studies following these criteria: incubation duration of more than 24 h; either C flux over time had to be available so we could calculate cumulative C release, or a cumulative C release value for the whole experimental period had to be reported; initial C content for individual samples had to be available; soils had to be incubated at a minimum of two constant incubation temperatures, or soils had to be incubated aerobically and anaerobically; for anaerobic incubations, the anaerobic headspace had to be created using oxygen-free gas (usually N_2 or He); and anaerobic samples needed to report CO_2 and CH_4. We identified a total of 25 studies that met all criteria, of which 21 had a temperature treatment and 10 incubated soils aerobically and anaerobically (Supplementary Table 1). The 21 incubation studies that used a temperature treatment could be either exclusively aerobic or anaerobic or both, so there is some overlap in the data sets (see Supplementary Table 1). Samples were considered aerobic when samples were incubated at field capacity and flushed with ambient air, under freely drained conditions, or kept at 50–60% moisture content. Samples were grouped into three different ecosystem types (boreal forest, peatland and tundra), which were assigned to soil samples on the basis of information from study authors. This approach led to multiple observations from individual studies (Supplementary Tables 2–4). Peatland samples could originate from the boreal or tundra zone and were assigned to a sample if the author had specifically called it a peatland. For most studies the original data set was made available by the author (for 21 out of 25); however, if the original data set was not available we extracted the mean cumulative C release from published figures and tables using GetData Graph Digitizer version 2.24 (Supplementary Table 1 identifies for which studies we extracted data).

Analysis. We calculated cumulative C release (for CO_2-C and CH_4-C) from original data (if available, Supplementary Table 1) by interpolating between successive measurements using linear interpolation and then summing up daily C release over the entire incubation period. We calculated C release as a percentage of total soil C to account for different initial C concentrations and to compare relative differences between various soil types. For comparison purposes we standardized total cumulative C release at 5 °C and 15 °C using the specific response to temperature (Q_{10}) for each sample pair but kept the given incubation temperature for the comparison between aerobic and anaerobic C release. Aerobic C release is aerobic CO_2-C, and anaerobic C release is the sum of anaerobic CO_2-C and CH_4-C. To account for the higher global warming potential (GWP) of CH_4 we converted CH_4-C into CO_2-C equivalent by multiplying CH_4-C by its most recent consensus GWP of 34 (includes climate–carbon feedback[14]) while also accounting for the different molecular weights of CO_2 and CH_4 because GWP is calculated on a weight basis for the two gases.

Response metric. Our effect size metric was the log ratio of the means ($\ln R$) with corresponding sampling variance (Supplementary Tables 2–4), which is a common measure of effect magnitude[31]. Equation (1) is used to calculate the ratio of C release with a 10 °C increase in temperature:

$$\ln R = \ln \frac{E_{(T+10)}}{E_T} \quad (1)$$

where E is the cumulative C release as CO_2-C plus CH_4-C, CH_4-C, or CO_2-C equivalent at 15 °C ($T+10$) and 5 °C (T). We use the term 'ratio of C release with a 10 °C increase in temperature' throughout the manuscript instead of Q_{10} for the purpose of comparing the effect sizes of changing environmental controls (temperature and aerobic to anaerobic incubation conditions) on C release.

For the difference in C release under aerobic versus anaerobic incubation conditions we used equation (2):

$$\ln R = \ln \frac{E_a}{E_{an}} \quad (2)$$

where E_a is the cumulative C release as CO_2-C and E_{an} as the sum of CO_2-C and CH_4-C or CO_2-C equivalent.

The natural log is used for the purpose of statistical tests but results in graphs and tables are back-transformed for easier interpretation. The variance (v) for E is calculated for temperature (equation (3)) as:

$$v = \frac{SD^2_{(T+10)}}{n_{(T+10)}E^2_{(T+10)}} + \frac{SD^2_{(T)}}{n_{(T)}E^2_{(T)}} \quad (3)$$

and for aerobic to anaerobic (equation (4)) as:

$$v = \frac{SD^2_{(a)}}{n_{(a)}E^2_{(a)}} + \frac{SD^2_{(an)}}{n_{(an)}E^2_{(an)}} \quad (4)$$

We used multilevel meta-analytic models that include a random term accounting for multiple observations originating from the same study[32]. By including a set of moderator variables in the models we accounted for the heterogeneity between studies and investigated the extent to which the moderators influenced the size of the true effect[33]. Our database allowed for the inclusion of the following moderator variables: ecosystem (boreal forest, peatland, and tundra); permafrost (active layer, no permafrost, and permafrost layer); soil type (organic, mineral); water treatment (aerobic or anaerobic incubation conditions, used only in the temperature meta-analysis); incubation length; and incubation temperature (used only in the aerobic to anaerobic meta-analysis). The rma.mv() function from the metafor[33] package in R was used to perform the meta-analyses. Considering all possible model subsets using maximum likelihood estimation and the glmulti[34] package in R, the best model was selected on the basis of Akaike's information criterion corrected for small sample sizes (AICc)[35] considering Δ_{AICc} values <10 in favour of the simpler model (Supplementary Tables 10–15). Taking all possible subsets of models into consideration, we calculated the relative importance of the various moderators, which is equal to the sum of the Akaike weights/probabilities for the models in which the moderator appears (Supplementary Table 16)[34]. The final model was fitted using restricted maximum likelihood and graphical validation tools were used to assess the underlying model assumptions of variance homogeneity (plots of the standardized residuals versus fitted values). None of the model validation plots indicated violation of the homoscedasticity or normality criterion. We provide information on the heterogeneity in each meta-analysis such as Q-test, and tau^2 in the Supplementary Methods (Supplementary Table 9). Meta-analyses and statistical modelling were done using R (ref. 36) version 3.2.3.

Outlier and influence diagnostics were performed for each meta-analysis by repeatedly fitting the model and leaving out one study at a time. A study was considered to be influential if its inclusion changed the overall model estimate by more than 15%. No influential study was detected in the temperature meta-analysis; however, ref. 37 in the aerobic to anaerobic meta-analysis was considered to be influential and therefore excluded from the main analysis. The main report shows results of meta-analyses without the influential study but we also performed meta-analyses including the influential study and report those values in Supplementary Table 7. Ref. 37 was flagged as influential because the mean anaerobic CO_2-C release was equal to or higher than the mean aerobic CO_2-C release, which contradicts the slower decomposition rates usually observed under anaerobic conditions. Carbon release under aerobic conditions was on average 3.39 times higher than under anaerobic incubation conditions when excluding the influential study and 2.77 times higher when including the influential study (Supplementary Table 7).

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