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LETTERS

# Temperature-controlled organic carbon mineralization in lake sediments

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**Peatlands, soils and the ocean floor are well-recognized as sites of organic carbon accumulation and represent important global carbon sinks[1,2]. Although the annual burial of organic carbon in lakes and reservoirs exceeds that of ocean sediments[3], these inland waters are components of the global carbon cycle that receive only limited attention[4–6]. Of the organic carbon that is being deposited onto the sediments, a certain proportion will be mineralized and the remainder will be buried over geological timescales. Here we assess the relationship between sediment organic carbon mineralization and temperature in a cross-system survey of boreal lakes in Sweden, and with input from a compilation of published data from a wide range of lakes that differ with respect to climate, productivity and organic carbon source. We find that the mineralization of organic carbon in lake sediments exhibits a strongly positive relationship with temperature, which suggests that warmer water temperatures lead to more mineralization and less organic carbon burial. Assuming that future organic carbon delivery to the lake sediments will be similar to that under present-day conditions, we estimate that temperature increases following the latest scenarios presented by the Intergovernmental Panel on Climate Change[7] could result in a 4–27 per cent (0.9–6.4 Tg C yr$^{-1}$) decrease in annual organic carbon burial in boreal lakes.**

The sequestration of organic carbon (OC) in the sediments of inland waters, both natural and artificial[3,8,9,10,11], is comparable to or even higher than in marine sediments[4] and soils[12–15]. Inland waters do not only bury OC, but are also active sites for the mineralization of considerable amounts of OC, originating from internal production or from the terrestrial environment[4,5,16]. The OC that reaches the lake sediment surface will partly be mineralized to $CO_2$ or $CH_4$ by heterotrophic microorganisms, and partly be buried in the sediments. The proportion that is buried (that is, OC burial per OC deposition onto the sediment surface) is termed the OC burial efficiency, while the fraction of the sediment OC that is lost through microbial processing is termed OC mineralization. As a consequence, the amount of OC that is eventually buried is a direct function of the burial efficiency[17]. The OC burial efficiency in lake sediments is related to oxygen exposure, but the effect of temperature on OC mineralization and burial remains unclear[17]. Relationships between lake sediment mineralization and temperature proposed so far are subject to confounding factors, such as lake depth, OC quality and lake trophic state[18,19]. In view of anthropogenic global warming and the substantial amount of OC buried in inland water sediments, it is critical to elucidate how temperature affects burial efficiency, to allow assessment of the future role of lakes as carbon sinks.

The boreal region contains roughly 30% of the global lakes[20,21] and is rich in OC[22]. Accordingly, boreal lake sediments contain 15% of the total carbon pool of the biome[22]. The Canadian boreal forest region alone could account for more than 10% of the global lake burial[5]. Northern latitudes, including the boreal zone, are expected to experience particularly severe warming[7,23], suggesting that temperature-dependence of sediment OC burial may be of particular importance at these latitudes.

We assessed the relationship between sediment OC mineralization and temperature in a cross-system survey of boreal lakes in central Sweden, and by compilation of published data from widely different lakes. We surveyed eight lakes with different trophic state and loading of terrestrial dissolved organic carbon (DOC) and total phosphorus ($P_{tot}$), enabling us to assess the relative importance of temperature versus lake trophic conditions and sediment organic matter characteristics. Sediment mineralization was measured as dissolved inorganic carbon production in undisturbed sediment cores, sampled along a depth gradient within each lake. In addition to the field survey, we also did experimental incubations of lake sediment in the laboratory to test the temperature sensitivity of sediment mineralization in contrasting lakes.

Mineralization of OC in the boreal lake sediments was strongly positively correlated with temperature ($r^2 = 0.61$, $P < 0.0001$, $n = 219$) and weakly correlated with the $P_{tot}$ concentration in the water ($r^2 = 0.14$, $P < 0.001$). There were statistically significant, but very weak, relationships between OC mineralization and indicators of OC degradability, such as the C:N and the C:P ratio of the sediment (respectively $r^2 = 0.027$, $P = 0.01$ and $r^2 = 0.028$, $P = 0.013$). There was no correlation between sediment OC mineralization and measures of elemental composition of the sediment organic matter (C, N, P concentrations; $r^2 = 0.002$, $P = 0.48$; $r^2 = 0.007$, $P = 0.23$; $r^2 = 0.005$, $P = 0.30$, respectively). A partial least square (PLS) regression of sediment OC mineralization against temperature, elemental composition of sediment organic matter (C:N and C:P ratios; concentration of C, N and P), and $P_{tot}$ concentration in the water column, explained a major fraction of the variance in the data set ($R^2Y = 0.66$; see Online Methods for nomenclature), and corroborated the dominant effect of temperature on OC mineralization in the sediment. Similarly, a multiple regression model predicted sediment OC mineralization from temperature ($T$) and total phosphorus concentration in the water column ($P_{tot,w}$) (OC mineralization $= -75.03 + 0.34\log P_{tot,w} + 31.21\log T$; $F(2, 216) = 193.67$; $P < 0.0001$; $n = 219$), but explained only a slightly higher proportion of the variability in OC mineralization compared to a model with temperature alone ($r^2 = 0.64$ versus $r^2 = 0.61$). Lastly, we also compared the partial correlation coefficients of the model terms for temperature ($r_{partial} = 0.76$; $n = 219$: $P < 0.0001$) and total phosphorus in the water column ($r_{partial} = 0.28$; $n = 219$; $P < 0.0001$), suggesting a strong effect of $T$ and a small, but significant effect of $P_{tot,w}$ on OC mineralization. Hence, OC mineralization rates were primarily explained by temperature, and the other studied variables were of subordinate importance.

We then added data of similar observations of temperature and sediment OC mineralization from a wide range of lakes that differ

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with respect to climate, productivity and OC source, based on a compilation of the published literature (Supplementary Notes). The combined data from the present study and the literature showed a positive correlation of sediment OC mineralization with temperature (Fig. 1a, $r^2 = 0.43$, $P < 0.0001$, $n = 574$), suggesting that the regulation of OC mineralization by temperature is valid for sediments of widely different lakes.

Additional laboratory experiments on sediments from lakes with contrasting sediment types demonstrate a direct controlling effect of temperature on sediment OC mineralization (Fig. 1b). The studied lakes are very different in terms of organic matter source and productivity: terrestrial organic matter dominated Svarttjärn sediment, while Vallentunasjön sediment was dominated by algal debris (Supplementary Methods). The response to temperature was very similar for both kinds of sediments (Fig. 1b), supporting the suggestion that temperature, rather than any potentially co-varying factor, caused the strong positive relationship between OC mineralization and temperature observed in the larger set of data (Fig. 1a).

We also compiled data on long-term net accumulation of OC in lake sediments based on syntheses of data at global and regional scales as well as estimates in individual lakes/sediment cores. Comparison of these data with the sediment carbon mineralization estimates reported above suggests that more than half of the OC that reaches the sediment is likely to be mineralized (Fig. 2). Sediment OC mineralization was on average 2.8 (median, 3.8) times higher than average global and regional estimates of long-term net accumulation of OC in lake sediments, and 5.1 (median, 6.4) times higher than long-term net accumulation determined from individual lakes or sediment cores. Thus, the estimated burial efficiency of about 20% is similar to the reported values of burial efficiency in lake sediments[17]. Hence, a large share of the OC deposited onto the sediments is mineralized, and, accordingly, a small change in mineralization (for example, due to increased temperature) may result in a drastic change in OC burial efficiency. To assess how far global warming may affect accumulation of OC in sediments, we investigated the consequences of global warming scenarios for OC burial.

On the basis of the temperature–sediment mineralization relationship in Fig. 1a, we estimated the effect of temperature on the OC burial for boreal lakes under different warming scenarios[7], assuming that the future deposition of OC to the lake bottoms will be similar to present-day conditions. Potential increase of OC delivery to the lake sediments could result in an increase in the amount of OC buried. However, the proportion of OC buried (that is, the burial efficiency) will be reduced in a warmer climate owing to a higher proportion of the sediment OC being mineralized. Even in cases of increased delivery of OC to the sediment owing to climate change, there will not be a corresponding increase in OC burial, as rising temperatures will increase OC mineralization and thereby lower OC burial efficiency (for more information, see Supplementary Methods and Supplementary Discussion). Our estimate is further based on the area of lake

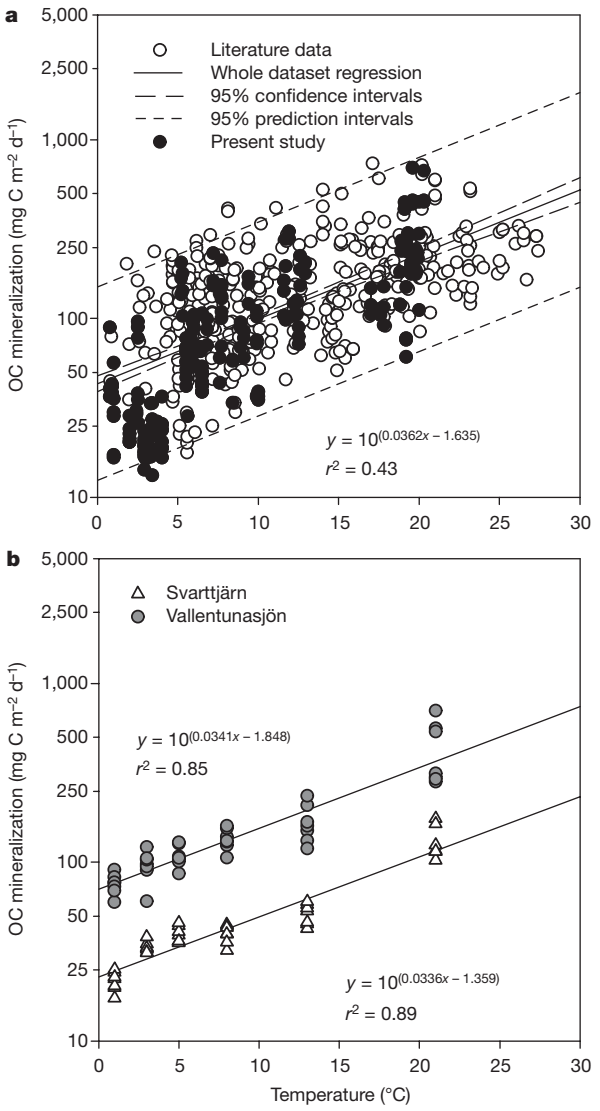


**Figure 1 | Temperature-dependent OC mineralization in lake sediments.** **a**, The relationship between sediment OC mineralization and temperature in the present study ($r^2 = 0.61$, $P < 0.0001$, $n = 219$), published literature ($r^2 = 0.26$, $P < 0.0001$, $n = 355$) (Supplementary Notes) and the two combined data sets, ($r^2 = 0.43$, $P < 0.0001$, $n = 574$), equation at lower right. **b**, OC mineralization measured under experimental manipulation of temperature in two extreme lakes in terms of the loading of the organic carbon—the humic Svarttjärn, equation at lower right, and the highly eutrophic Vallentunasjön, equation at upper left ($n = 42$ for each lake). The slopes were not statistically different (*t*-test, $P = 0.87$). The *y*-axis of the OC mineralization is represented on a log scale.

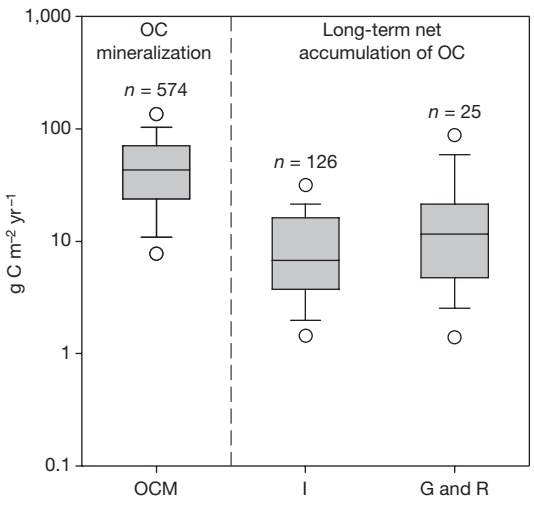


**Figure 2 | Mineralization and burial of OC in lakes.** Box plots representing sediment OC mineralization (OCM) and average long-term net accumulation of the organic carbon in lake sediments, representing global (G) and regional (R) as well as individual lake/sediment core estimates (I). The boundary of the box closest to zero indicates the 25th percentile, a line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles and open circles indicate 5th and 95th percentiles. OC mineralization data are derived from the present study ($n = 219$) as well as literature data ($n = 355$). Long-term net accumulation was obtained from literature[8,9,20] (Supplementary Notes). The *y*-axis is represented on a log scale.

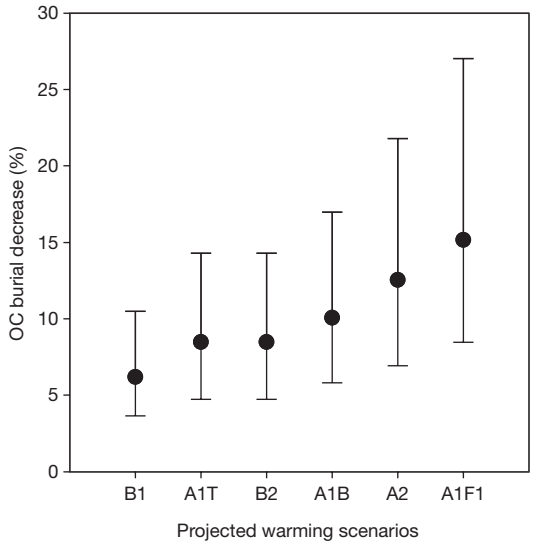


**Figure 3 | Organic carbon burial decrease.** The predicted percentage decrease in OC burial in lake sediments over the boreal zone under different climate warming scenarios by the end of the twenty-first century[7]: B1, A1T, B2, A1B, A2 and A1F1. Filled circles, decrease in OC burial based on the most likely scenarios for temperature change; vertical bars, response to a likely range of temperatures.

sediments expected to experience warming in direct proportion to increasing air temperatures via mixing of the water column. Different scenarios simulating a doubling in atmospheric $CO_2$ (refs 24, 25) predict consistently higher lake surface water temperatures but a somewhat variable response of bottom temperatures. These predictions have been confirmed by observations of strong surface water warming during the 2003 European heat wave[26]. About half of the total lake sediment area in the boreal zone has been estimated to be in contact with mixed surface water[27], a value that is supported by observations in 88 lakes in boreal Canada[28] and 25 lakes in boreal Sweden[29]. Hence, warmer air temperature will directly affect OC mineralization in about half of the sediment area.

The predicted increase in OC mineralization in sediments overlain by mixed water in response to global temperature under the most likely warming scenarios (that is, 1.8–4 °C)[7] resulted in a decrease in OC burial in boreal lake sediments in the range of 1.5–3.6 Tg C $yr^{-1}$. This represents a 6–15% decrease in OC burial in lake sediments over the boreal zone (Fig. 3). Applying the likely temperature range scenarios (that is, 1.1–6.4 °C)[7], the response of sediment mineralization to temperature resulted in a loss of 0.9–6.4 Tg C $yr^{-1}$, that is, a 4–27% decrease in lake sediment OC burial for the entire boreal zone (Fig. 3). This indicates that at the end of the twenty-first century[7], the strong temperature dependence of sediment OC mineralization may result in a significant decrease in the burial of OC in boreal lakes, and thereby in a concomitant increase in greenhouse gas emissions from lake sediments. We propose that this may be analogous to the recently discovered positive feedback on global warming caused by increased mineralization in peatlands of the Northern Hemisphere[30].

## METHODS SUMMARY

We surveyed eight lakes in central Sweden with different trophic status and receiving different amounts of terrestrial DOC (Supplementary Table 1). The lakes were sampled four times on a seasonal basis, between April 2007 and February 2008. Some of the lakes were thermally stratified during summer. However, our study includes only sediments overlain by oxygenated waters. Within each lake, intact sediment cores were sampled along a depth gradient and incubated *in situ* or at *in situ* temperatures. Incubations were carried out in the dark and start and end water samples were collected and analysed for the DIC (dissolved inorganic carbon) and methane concentration. Surface water samples were analysed for DOC concentration, absorbance and $P_{tot}$; for sediment, water content and concentration of C, N and P were measured. In a separate experimental set-up, sediment mineralization was measured in the laboratory under induced temperature changes. Sediment cores from two lakes with contrasting loadings of organic carbon were incubated in the dark at 1, 3, 5, 8, 13 and 21 °C. Sediment respiration was measured for the upper 5-cm layer of the sediment as DIC production in the dark. Full details are given in Methods and Supplementary Information.

**Full Methods** and any associated references are available in the online version of the paper at www.nature.com/nature.

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**Supplementary Information** is linked to the online version of the paper at www.nature.com/nature.

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## METHODS

**Sediment sampling and incubation.** Intact sediment cores were obtained with a UWITEC sediment corer. Three replicate sediment cores were sampled in the deepest, intermediate and shallow regions. The upper 10 cm layer was transferred to incubation cores (54 mm inner diameter) without visible disturbance of the sediment structure. A floating magnetic stirring bar allowed gentle mixing of the water column above the sediment using a magnet on the outside. After the cores were filled and closed (airtight, without any headspace) and before sampling, the water column was mixed with the magnet. For sampling, a mechanical system was used to press down the upper stopper of the incubation core, while simultaneously withdrawing the samples into a 50 ml syringe, thereby avoiding the intrusion of air into the sediment incubation core. Syringes were placed immediately on ice and analysed for DIC concentration in the laboratory within a few hours of sampling.

The sediment cores were incubated *in situ* at the sampling station in the dark. The incubation time varied between 24 and 69 h. During the winter sampling occasion, the sediment cores were processed in the laboratory, and were incubated for about 140 h in the dark and at *in situ* temperatures. These incubations were performed in special incubation chambers connected to external refrigerated/heated circulators (Julabo F25-ED). At the termination of the incubation, final water samples were taken and analysed in a similar way as initial samples for DIC.

**DIC measurements.** Measurements of the DIC concentration were performed on a Sievers 900 TOC analyser. The precision of the analytical method was $<1\%$ RSD (relative standard deviation) and accuracy of $\pm 2\%$ or 0.5 p.p.b. DIC.

**Sediment characteristics.** The upper layer of 0–5 cm was collected from three replicate cores at each station. Sub-samples were taken for C, N, P, water content and organic matter content. The sediment was dried at 105 °C. The C and N were analysed in an elemental analyser (NA 1500, Carlo Erba instruments). To determine sediment P content, dried sediment was ignited at 550 °C (ref. 31), followed by a subsequent P analysis of molybdate-reactive phosphate[32].

**Water column characteristics.** Depth profiles of temperature and oxygen concentration were measured with an OxyGuard Handy Delta oxygen meter. The concentration of $P_{tot}$ in the water was determined accordingly[32]. The concentration of DOC was analysed with a Sievers 900 TOC analyser.

**Literature data.** For literature searches we used the ISI (Web of Science) and ASFA (Aquatic Sciences and Fisheries Abstracts) databases. The published data that were considered in this study were restricted to studies carried out in undisturbed sediment cores. We collected 355 data points by digitizing of published graphs using Digitizelt 1.5.7 software. The oxygen uptake data provided in some references were converted to carbon units based on a respiratory quotient of 0.9 (ref. 33).

**Statistical analyses.** In order to consistently compare OC mineralization rates in sediments overlain by mixed (that is, oxygenated) water, any of the data indicating anoxic conditions near the sediments were excluded from the analysis. Thus, if oxygen concentration at the layer one metre above the sediment was less than $1\ mg\ l^{-1}$, incubation data were removed from the analysis. The same criterion was applied to the literature data. The contribution of other pathways of OC loss from the sediment such as $CH_4$ or DOC release was low (Supplementary Methods).

All data analysed by linear regression were log-transformed with the exception of ratios that were arcsine-transformed. To compare the linear regression slopes, we used the *t*-test approach[34]. We used PLS regression[35] in order to find out how different variables perform as predictors of sediment respiration. Compared to ordinary multiple linear regression, PLS is useful when there are several correlated responses in the data set, when variables deviate from normality or there is a smaller percentage of missing values. The results of a PLS analysis are displayed in the 'loadings plot', depicting the correlation structure among all factors and responses. The performance of the PLS model is expressed in the terms $R^2Y$ and $Q^2$. $R^2Y$ is comparable to $R^2$ in linear regression, and $Q^2$ is a measure of the predictive power of the model (the higher $Q^2$ values, the higher the performance of the model). Variables were transformed (log for volumetric data and arcsine for ratio) before modelling in order to increase model performance. All PLS modelling was done on SIMCA 12.0 software (Umetrics AB).

The variables identified as explaining most of the variance from the PLS analysis were used in a stepwise forward multiple regression model. All the variables were log-transformed in order to meet normality assumptions. Temperature data were expressed in K to avoid zero values. Other assumptions needed to meet the specification of the multiple regression analysis, such as multicollinearity or homogeneity of the error terms, were checked. The multiple regression modelling was performed in Statistica 8.0 software.


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CORRIGENDUM

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In Figure 1a and b of this Letter, the sign in the regression equations should have been a plus symbol, not a minus symbol. This does not affect the reported results or conclusions of the paper.