# Greenhouse gas production in low-latitude lake sediments responds strongly to warming

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Inland water sediments receive large quantities of terrestrial organic matter<sup>1-5</sup> and are globally important sites for organic carbon preservation<sup>5,6</sup>. Sediment organic matter mineralization is positively related to temperature across a wide range of high-latitude ecosystems<sup>6-10</sup>, but the situation in the tropics remains unclear. Here we assessed temperature effects on the biological production of CO<sub>2</sub> and CH<sub>4</sub> in anaerobic sediments of tropical lakes in the Amazon and boreal lakes in Sweden. On the basis of conservative regional warming projections until 2100 (ref. 11), we estimate that sediment CO2 and CH4 production will increase 9-61% above present rates. Combining the CO<sub>2</sub> and CH<sub>4</sub> as CO<sub>2</sub> equivalents (CO<sub>2</sub>eq; ref. 11), the predicted increase is 2.4-4.5 times higher in tropical than boreal sediments. Although the estimated lake area in low latitudes is 3.2 times smaller than that of the boreal zone, we estimate that the increase in gas production from tropical lake sediments would be on average 2.4 times higher for CO<sub>2</sub> and 2.8 times higher for CH<sub>4</sub>. The exponential temperature response of organic matter mineralization, coupled with higher increases in the proportion of CH<sub>4</sub> relative to CO<sub>2</sub> on warming, suggests that the production of greenhouse gases in tropical sediments will increase substantially. This represents a potential large-scale positive feedback to climate change.

Tropical and boreal biomes harbour approximately 50% of the lakes on Earth<sup>12</sup>. These inland waters emit substantial amounts of carbon dioxide (CO<sub>2</sub>; on the order of 0.5 Pg yr<sup>-1</sup>; refs 1,4,13,14) and methane (CH<sub>4</sub>; 70 Tg yr<sup>-1</sup>; ref. 15). Organic matter escapes mineralization through burial in lake sediments, representing a global carbon (C) sink<sup>13-15</sup>. Cold conditions are favouring organic carbon preservation in lakes at northern latitudes<sup>8-10,16</sup>, whereas warm inland waters show intense organic degradation supporting high C emissions to the atmosphere<sup>4,5,17,18</sup>.

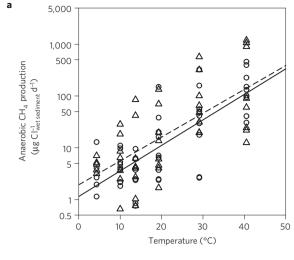
Temperature and organic carbon mineralization were recently shown to be strongly positively related in boreal lake sediments overlain by oxic water<sup>9</sup>. However, most freshwater sediments below the uppermost layer (typically a few millimetres) are anoxic<sup>19</sup>, where the anaerobic biological degradation of organic carbon releases not only CO<sub>2</sub> but also significant amounts of CH<sub>4</sub> (ref. 15). Although higher temperatures are also expected to increase metabolic responses<sup>20</sup>, the effects of changing temperatures on organic carbon mineralization can depend on several factors including organic matter characteristics (for example, the carbon–quality–temperature hypothesis)<sup>21</sup>. Thus, the temperature sensitivity of

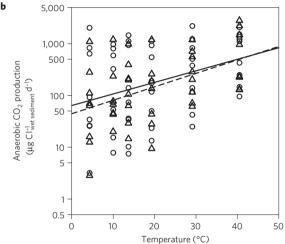
organic carbon stocks at high latitudes previously reported  $^{6-8,16}$  may not be valid in the tropics where temperature sensitivity data are much more scarce  $^{22}$ . We compared the anaerobic organic carbon mineralization to  $\mathrm{CO}_2$  and  $\mathrm{CH}_4$  in tropical and boreal lake sediments along a temperature gradient. We simultaneously sampled a wide range of lake sediments from both tropical and boreal zones (Supplementary Information and Supplementary Table 1). We assessed the temperature response of organic carbon mineralization to  $\mathrm{CO}_2$  and  $\mathrm{CH}_4$  in the different sediments in one integrated experiment to ensure that all sediments were treated similarly. The temperature range used for all sediments in the experiment was 4–40 °C, and the results were compared with expected temperature increases according to the conservative B1 Intergovernmental Panel on Climate Change (IPCC) scenario (see Supplementary Information for details).

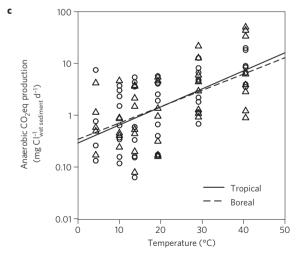
Anaerobic organic carbon mineralization increased exponentially with temperature (Fig. 1; that is, linear regressions of  $\log_{10}$  C gas production versus temperature; see Supplementary Information and Table 1 for further details). The temperature sensitivity of the anaerobic organic carbon mineralization was not significantly different between boreal and tropical lakes on the basis of the Wilcoxon rank-sum test for CH<sub>4</sub> (W=30, P=0.61), CO<sub>2</sub> (W=37, P=0.96) and CO<sub>2</sub>eq (W=41, P=0.67). This was confirmed using alternative statistical approaches including a t-test and one-way analysis of variance (P values were always >0.3 for both slopes and intercepts in the tropical and boreal equations given in Table 1). The temperature sensitivity varied among lakes (Supplementary Figs 1 and 2), but was on average not different between biomes.

On the basis of the slopes and intercepts reported in Table 1 and present annual average temperatures at the sediment surface of  $4\,^{\circ}\mathrm{C}$  for boreal and  $26\,^{\circ}\mathrm{C}$  for tropical sediments (see Supplementary Information for details), the anaerobic organic carbon mineralization would be 4.9-fold higher in tropical than in boreal sediments (expressed in  $\mathrm{CO}_2$  equivalent units to account for both  $\mathrm{CO}_2$  and  $\mathrm{CH}_4$ ; mg  $\mathrm{CO}_2\mathrm{eq}\,l_{\text{wetsediment}}^{-1}\,\mathrm{yr}^{-1}$ ). As anaerobic sediment mineralization dominates in most of the sediment volume, and because a similar exponential temperature dependence of organic carbon mineralization of sediments overlain by oxic water has been found previously9, the temperature sensitivity might be representative for overall sediment mineralization. This study addresses the temperature sensitivity of  $\mathrm{CO}_2$  and  $\mathrm{CH}_4$  gas production rates rather than fluxes to the atmosphere.

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**Figure 1**| **Temperature sensitivity of anaerobic CO<sub>2</sub> and CH<sub>4</sub> production in lake sediments. a-c,** CH<sub>4</sub> (a), CO<sub>2</sub> (b), and CO<sub>2</sub> equivalent (CO<sub>2</sub>eq; c) production for tropical (open circles) and boreal (triangles) sediments. Solid and dashed lines represent the fitted regressions (P < 0.05) for tropical and boreal lake sediments (see Table 1 for regression parameters). Note that units for CO<sub>2</sub> and CH<sub>4</sub> (mass of C) differ from CO<sub>2</sub>eq units (mass of CO<sub>2</sub> molecules).

Not all of the produced gas will reach the atmosphere, but the sediment production rates determine the potential for subsequent atmospheric emissions and climate feedbacks.

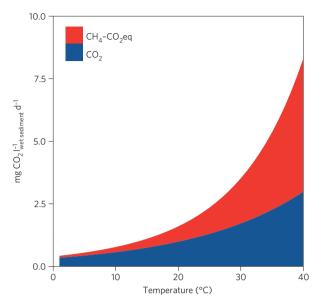


Figure 2 | Contribution of  $CO_2$  and  $CH_4$  to total  $CO_2$ eq production at different temperatures. The model is based on the temperature response equations using both tropical and boreal data in Table 1.

To estimate the relative effect of global warming over this century on anaerobic organic carbon mineralization in boreal and tropical lake sediments, we used the temperature-sediment mineralization relationships in Table 1, the present temperatures, and the projected temperature at the end of the century according to the IPCC B1 scenario11 (Supplementary Information). Under this scenario, the temperature response observed in this study was extrapolated to the estimated lake area fraction being shallow enough for transfer of atmospheric temperature increase to the sediment (see Supplementary Information for details). Relative to present levels, CO2, CH4 and CO2eq production rates across lakes is estimated to increase by 9-31, 20-61 and 14-40%, respectively (Table 2). However, in absolute terms, the increase is expected to be significantly higher in sediments of tropical lakes, as compared with boreal lakes. We find that the CO2 and CH4 production would increase at least 2.4-2.5 and 2.8-2.9 times more in tropical compared with boreal sediments, reaching a 3.0-3.2-fold higher increase in combined CO<sub>2</sub> and CH<sub>4</sub> production as CO<sub>2</sub>eq in tropical sediments. This result is robust to variability between lakes. When repeating the extrapolation using all combinations of the 25% and 75% quartiles of slopes and intercepts in the temperature responses for specific lakes (Supplementary Information), the CO<sub>2</sub>eq production increase in tropical sediments is 2.4–4.5 times higher than in boreal sediments.

The stronger temperature response of  $CH_4$  production relative to  $CO_2$ , and being evident at tropical temperatures, suggests a more powerful positive feedback on global warming than indicated by the  $CO_2$  production alone (Fig. 2). One possible explanation for this is that  $CH_4$  is increasingly produced from  $CO_2$  and  $H_2$  rather than from acetate at increasing temperatures, resulting in  $CO_2$  consumption by methanogenesis under warmer conditions<sup>23,24</sup>. The larger effect of warming in the tropics corresponds to exponential temperature responses for organic carbon mineralization reported at high latitudes<sup>9,16,25</sup> and highlights that small temperature changes in warm environments can result in greater effects than larger temperature changes in cold areas.

The difference in the tropical versus boreal temperature response is probably underestimated here for two reasons. First, the global tropical inundated area may be substantially larger than we assume<sup>4</sup>. Accordingly, a detailed survey of the average flooded area in the lowland Amazon alone, including lakes, rivers and wetlands<sup>26</sup>,

**Table 1**| Slopes (S) and intercepts (I) in the temperature response equations, the standard errors (s.e.m.) of S and I, and tests of differences between biomes for these parameters.

	Biome*	S	s.e.m. of S	I	s.e.m. of I	R <sup>2</sup>	P value	n
CH <sub>4</sub>	Tropical	0.049	0.006	0.060	0.14	0.59	< 0.001	48
	Boreal	0.046	0.008	0.28	0.19	0.44	< 0.001	44
	All data	0.047	0.005	0.17	0.11	0.51	< 0.001	94
CO <sub>2</sub>	Tropical	0.022	0.008	1.81	0.19	0.11	0.009	53
	Boreal	0.026	0.007	1.65	0.17	0.11	0.009	46
	All data	0.024	0.005	1.73	0.13	0.16	< 0.001	99
CO <sub>2</sub> equivalents	Tropical	0.035	0.007	-0.54	0.16	0.36	< 0.001	49
	Boreal	0.032	0.007	-0.47	0.18	0.30	< 0.001	42
	All data	0.033	0.004	-0.50	0.11	0.34	0.001	91

<sup>\*</sup>At the population level, slopes and intercepts for tropical and boreal regressions were not significantly different (see text for details). Therefore, a general equation based on both tropical and boreal data was made. The general equation format is  $\log_{10}(F) = S * T + I$ , where F is the formation rate of CH<sub>4</sub>, CO<sub>2</sub> (both as  $\mu g \, C \, I_{\text{wet sediment}}^{-1} \, d^{-1}$ ), or CO<sub>2</sub> equivalents (mg CO<sub>2</sub>  $I_{\text{wet sediment}}^{-1} \, d^{-1}$ ; note different units) and T is temperature (°C).

Table 2 | The predicted increase in anaerobic sediment production of CO<sub>2</sub>, CH<sub>4</sub> and CO<sub>2</sub>eq, relative to the current conditions, following a temperature change according to the IPCC B1 warming scenario projected for the year 2100.

Sediment source	CO <sub>2</sub> (%)	CH <sub>4</sub> (%)	CO <sub>2</sub> eq (%)
Tropical lakes	9-24	20-58	14-40
Boreal lakes	11-31	21-61	14-39

See Supplementary Information for calculation details.

reports an area substantially larger than the global tropical area used here. Second, we assumed a  $4\,^{\circ}$ C average present boreal temperature at the sediment surface, in spite of average air temperatures of between -5 and  $+5\,^{\circ}$ C over the boreal zone<sup>27</sup>, and without considering the near- or sub-zero temperatures under ice during winter in epilimnetic boreal sediments. All of these known uncertainties regarding areal estimates and present boreal sediment temperatures suggest that the difference in warming feedback between tropical and boreal sediment mineralization reported here is conservative.

Nevertheless, under warming scenarios with a lower predicted absolute temperature increase in the tropics than in northern ecosystems<sup>11</sup>, we show that the total organic carbon mineralization, and the proportion of mineralization that is channelled into CH<sub>4</sub> production, will most likely increase more in low- than in high-latitude lake sediments. Flooded areas in the warm tropics, including lakes and wetlands, are extensive sites for organic carbon decomposition and greenhouse gas emissions to the atmosphere<sup>4,18</sup>, which may even show hypoxia events in bottom waters near to the sediment<sup>28</sup>. Thus, these stocks of organic carbon may be particularly sensitive to small increases in temperature, thereby contributing to a potentially important positive feedback on global warming.

# Methods

A 10-cm surface layer of the sediment was sampled in Amazonian tropical and Swedish boreal lakes (n=9 and 8, respectively), encompassing a typical range of ecosystem types (see Supplementary Information for details). The experiments for both biomes were performed simultaneously in Sweden and were initiated within 9 days of sampling. Anoxic sediment slurries with a nitrogen gas headspace were incubated in 2,516 hermetically sealed 25-ml glass vials capped with 10-mm massive butyl rubber stoppers and maintained at six controlled temperatures (4.3, 10, 13.7, 19.3, 29.1, 40.5 °C) in the dark and inside boxes filled with water. After 0, 3, 6, 10, 20, 30 and 44 days of incubation, the vials (n=4 for each temperature and lake) were removed and biological activity stopped by acidification to pH <1.5. The headspace was then sampled, and the gas was

analysed for CO2 and CH4 concentrations using a 6890 Agilent gas chromatograph (Agilent Technologies) equipped with TCD and FID detectors and a nickel catalyst methanizer. Production rates were determined from the maximum significantly linear slope of the CO2 and CH4 concentrations for at least 3 consecutive samplings over 44 days. As a result of the acid preservation, CO<sub>2</sub> accumulation corresponds to formation of all inorganic carbon in the vials. Anaerobic organic carbon mineralization expressed as CO<sub>2</sub> equivalents (CO<sub>2</sub>eq) was calculated as the sum of the concentration of both CO2 and CH4 (in mass units) assuming a 25-fold greater radiative forcing for CH<sub>4</sub> (ref. 11). Production rates as CO2eq were then calculated as described for CO2 and CH4. The slope of the linear fit of log<sub>10</sub>-transformed production rates versus temperature was used as a measure of temperature sensitivity. The slopes of the above linear regression analyses, representing the temperature sensitivity of anaerobic organic carbon mineralization from tropical and boreal lakes, were compared using parallel approaches including the Wilcoxon rank-sum test, t-test and one-way analysis of variance (significance P < 0.05). The data were analysed using R software<sup>29</sup>. For full details regarding the lakes, experimental design, analytical methods, calculations and statistics, see Supplementary Information.

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### **Author contributions**

All authors contributed to the study design, conducted the experiment, interpreted data and wrote or commented on the manuscript. H.M. and L.P. also performed the sampling and most of the sample analyses.

### **Additional information**

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at <a href="https://www.nature.com/reprints">www.nature.com/reprints</a>. Correspondence and requests for materials should be addressed to H.M.

### **Competing financial interests**

The authors declare no competing financial interests.