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LETTERS

The effect of permafrost thaw on old carbon release and net carbon exchange from tundra

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Permafrost soils in boreal and Arctic ecosystems store almost twice as much carbon[1,2] as is currently present in the atmosphere[3]. Permafrost thaw and the microbial decomposition of previously frozen organic carbon is considered one of the most likely positive climate feedbacks from terrestrial ecosystems to the atmosphere in a warmer world[1,2,4–7]. The rate of carbon release from permafrost soils is highly uncertain, but it is crucial for predicting the strength and timing of this carbon-cycle feedback effect, and thus how important permafrost thaw will be for climate change this century and beyond[1,2,4–7]. Sustained transfers of carbon to the atmosphere that could cause a significant positive feedback to climate change must come from old carbon, which forms the bulk of the permafrost carbon pool that accumulated over thousands of years[8–11]. Here we measure net ecosystem carbon exchange and the radiocarbon age of ecosystem respiration in a tundra landscape undergoing permafrost thaw[12] to determine the influence of old carbon loss on ecosystem carbon balance. We find that areas that thawed over the past 15 years had 40 per cent more annual losses of old carbon than minimally thawed areas, but had overall net ecosystem carbon uptake as increased plant growth offset these losses. In contrast, areas that thawed decades earlier lost even more old carbon, a 78 per cent increase over minimally thawed areas; this old carbon loss contributed to overall net ecosystem carbon release despite increased plant growth. Our data document significant losses of soil carbon with permafrost thaw that, over decadal timescales, overwhelms increased plant carbon uptake[13–15] at rates that could make permafrost a large biospheric carbon source in a warmer world.

We measured ecosystem carbon (C) dynamics at a tundra site in Alaska where permafrost thaw has been documented since 1990, and was occurring in the area before that time, probably owing to regional climate change[12]. The Eight Mile Lake watershed is located in the northern foothills of the Alaska Range (Supplementary Information and Supplementary Fig. 1). Permafrost temperature has been monitored annually on a gentle north-facing slope in a 30-m-deep borehole that was installed in 1985 before the permafrost started to thaw[12]. Although permafrost thaw can sometimes result in water ponding, depending on local topography[16,17], this landscape consists largely of relatively well-drained uplands (Supplementary Fig. 2). Permafrost thaw at the local level occurs as a series of positive feedbacks between temperature change, ground subsidence, and hydrologic redistribution that causes further thawing in a spatially heterogeneous pattern generated by water flow paths. In this watershed, we monitored three sites that represented minimal, moderate and extensive amounts of change as a result of the duration of permafrost thaw, based on observations of ground subsidence, depth of thaw, historical ground temperature measurements, and historical and current photographs (Supplementary Table 1)[12,18–20]. Although an observational study cannot unequivocally rule out unknown preexisting differences across sites that might give rise to differences in carbon fluxes, all available historical evidence points to the soil and plant community originally being relatively similar across this hillslope. Here we assume that the site differences in onset of permafrost thaw are due to spatially random processes that occur at a local level as a series of positive feedbacks between temperature change, ground subsidence, hydrologic redistribution, and further thawing via thermal erosion from moving water, and therefore that the differences in permafrost thaw are the main driver of the differences in soil and plant community that we observe today. Across this gradient of thaw, we measured net carbon dioxide (CO_2) exchange between the tundra and the atmosphere over 3 years (Supplementary Figs 3 and 4), coupled with radiocarbon measurements (expressed as $\Delta^{14}C$) of respired C as a fingerprint for identifying the decomposition of old organic C that has been stored in these permafrost soils[21]. This is, to our knowledge, the first study to quantitatively demonstrate the link between old C emissions and ecosystem C losses.

The tundra ecosystem at Eight Mile Lake showed net C uptake during the summer months (June–August), with differences among sites and years (Mixed Model; site, $P = 0.053$; year, $P = 0.002$; site × year, $P = 0.473$). The moderate and extensive thaw sites trended towards greater C uptake, averaged across years, than the minimal thaw site (Tukey's pairwise comparisons; $P = 0.018$ and $P = 0.100$, respectively) (Fig. 1a). The pattern of significantly increased gross primary productivity at the moderate and extensive thaw sites, averaged across years for the full growing season (May–September), indicated that plant C uptake was stimulated by permafrost thaw (Supplementary Tables 2 and 3; Tukey's pairwise comparisons versus minimal thaw site; $P = 0.009$ and $P = 0.005$, respectively). Carbon gain in the summer was offset by net C loss in spring and autumn (May, September) (Fig. 1a) and during the winter (October–April) (Fig. 1b, Supplementary Table 2), when plant C uptake is low or absent while microbial decomposition proceeds even at subzero temperatures (Supplementary Fig. 4). Overall, C loss during winter accounted for 15–18% of ecosystem respiration (R_{eco}) on average across all sites. Winter C loss was large enough to switch the minimal and extensive sites, which were net C sinks in the growing season, to annual net C sources on average across years (Supplementary Table 2).

On an annual basis across years, the extensive thaw site had significantly higher R_{eco} ($P < 0.001$) with a trend towards greater total C loss than the minimal thaw site, while the moderate site had intermediate R_{eco} between the two (Supplementary Tables 2 and 3). The extensive thaw site was a net C source to the atmosphere, based on calculated annual net ecosystem C exchange, losing an average of $32 \pm 22\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (mean $\neq 0$, $P = 0.019$). However, there was significant interannual variability; this site lost $136\,\mathrm{g\,C\,m^{-2}}$ over the first two years of the study (Fig. 1c), but then gained

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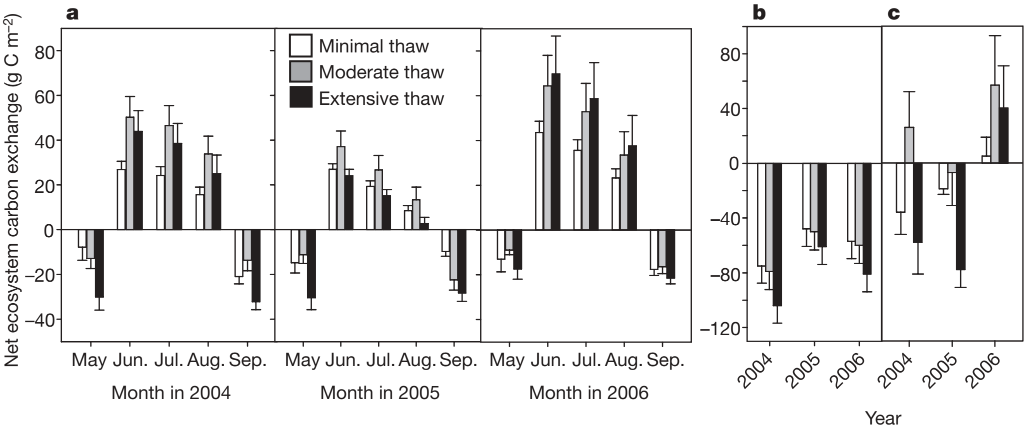

Figure 1 | Net exchange of CO$_2$ between tundra and the atmosphere for three sites that differ in the extent of permafrost thaw. **a**, For the growing season (May–September) over a 3-year period from 2004–06; **b**, for the winter (October–April); and **c**, on an annual basis, which is the net of the growing season and the winter. Values represent total C uptake (positive) or release (negative) per month (**a**), per winter (**b**) and per year (**c**). Data show mean ± s.e.

40 ± 31 g C m^{-2} in 2006. The moderate and minimal thaw sites had similar interannual variability, with greatest uptake in 2006. Overall, the minimal thaw site lost 17 ± 11 g C m^{-2} yr^{-1} but this value was not significantly different from neutral C balance (mean $\neq 0$, $P = 0.215$), while the moderate thaw site contrasted with the other two sites as a net sink of atmospheric C, gaining 25 ± 29 g C m^{-2} yr^{-1} (mean $\neq 0$, $P = 0.060$).

Flux measurements alone cannot determine the influence of permafrost C on ecosystem fluxes, but Δ^{14}C provides a fingerprint for determining the source of ecosystem C loss. Total R_{eco} is a mixture of CO$_2$ derived from three sources: plant metabolism, decomposition of recently dead plant tissue (recent detritus), and decomposition of older soil organic matter (old C). Each of these sources has a characteristic Δ^{14}C value as a result of radioactive decay combined with the recent change in atmospheric ^{14}C abundance caused by aboveground thermonuclear weapons testing (Supplementary Fig. 5a). Radiocarbon values of R_{eco} across sites were generally elevated relative to current atmospheric values, and on average they declined over the 3-year period (Fig. 2a). This R_{eco} Δ^{14}C pattern demonstrates the influence of (1) recent photosynthate, whose Δ^{14}C value is closely tied to the contemporary atmosphere that is currently declining by ~5‰ annually[22], and (2) decomposition of recently dead plant tissue that grew over the past several decades and thus contained elevated 'bomb' Δ^{14}C values. Also contributing to R_{eco} is the decomposition

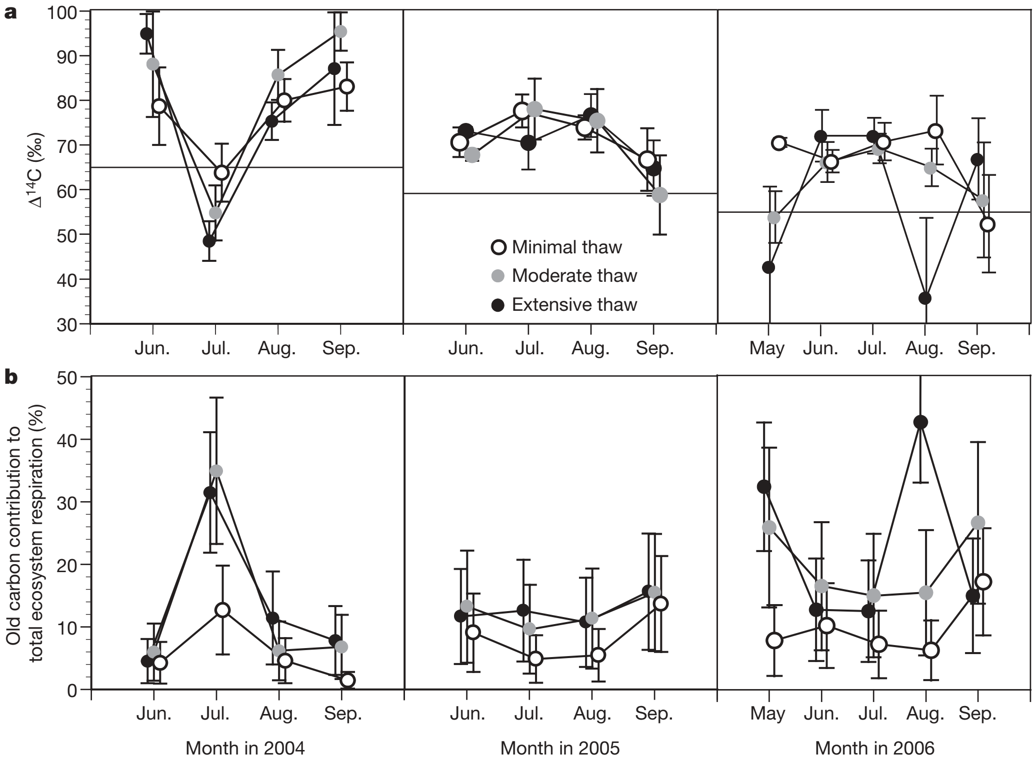

Figure 2 | Radiocarbon values of ecosystem respiration and the proportional contribution from old carbon for three sites that differ in the extent of permafrost thaw. **a**, Radiocarbon values (mean ± s.e.) of R_{eco} over a 3-year period from 2004–06. Horizontal lines across the graphs represent the average atmospheric value for each year. Radiocarbon is reported in Δ^{14}C units referenced to a 1890 wood standard defined as 0‰. **b**, Statistical partitioning estimate of the contribution of old C to R_{eco} (mean ± s.d.), based on Δ^{14}C measurements from incubations of surface soil, deep soil, and plants.

of old C with negative Δ^{14}C values as a result of radioactive decay. The imprint of old C is unequivocally observed in R_{eco} in months, or in sites, where R_{eco} Δ^{14}C values drop below the current atmospheric value (Fig. 2a), as it is the only CO_2 source pool that can lower R_{eco} Δ^{14}C values below that of the current atmosphere (Supplementary Fig. 5b).

Significant temporal variation in R_{eco} Δ^{14}C values ($P < 0.001$) is thought to reflect changes in the relative contribution of plant metabolism, recent detritus, and old C. To constrain the contribution of the three C sources to R_{eco}, we employed a statistical isotope mass balance approach using the laboratory incubations of plants and soil to estimate the proportional contribution of each source[23] (Supplementary Information, and Supplementary Table 4). The mean proportional contribution of deep C to growing season R_{eco} generally ranged from 7 ± 4% to 23 ± 9% (mean ± s.d.) across all sites and years, with individual site means reaching as high as 41 ± 10% at the extensive thaw site in particular months (Fig. 2b; Supplementary Table 5). If we combine the mean proportional contributions from old C loss with R_{eco} flux values (Supplementary Table 2), then the extensive and moderate thaw sites are projected to have lost an average of 63 and 47 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ respectively from the deep soil layers during the growing season; this was approximately 2 or 3 times greater than the deep C loss calculated for the minimal thaw site (22 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) (Fig. 3a). Applying a similar methodology to winter flux measurements increases the old C contribution to total annual R_{eco} at all sites, and reinforces the general pattern across sites of increasing old C loss with increased permafrost thaw (Supplementary Information, Supplementary Fig. 6).

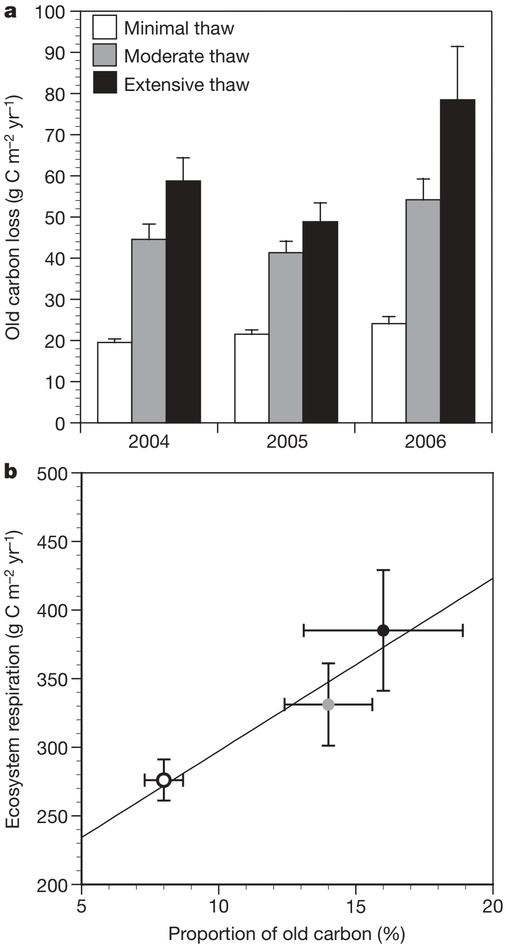

Figure 3 | Old carbon loss and its relationship to total ecosystem respiration for three sites that differ in the extent of permafrost thaw. **a**, Growing-season loss of old C from deeper in the soil profile, based on statistical partitioning estimates of mean proportional old C loss multiplied by R_{eco} flux measurements. Error bars represent the spatial variability of R_{eco} fluxes. **b**, The relationship between total R_{eco} and proportional old C loss for the growing season across sites. Error bars represent the interannual variability in C loss estimates; the regression line is shown for $n = 3$ sites.

Although our estimates of the proportional contribution of old C loss from statistical modelling can only be expressed as a possible range of values, the positive relationship observed between growing season R_{eco} and proportional old C loss across sites and years ($R^2 = 0.92$; Fig. 3b) supports the idea that the mean predicted contributions provide a reasonable picture of old C losses across sites. The relationship between these two independently estimated measurements across our gradient of sites shows that permafrost thaw and ground subsidence stimulates the release of old C, and that both the relative and absolute old C release increases with thawing. This observation confirms initial hypotheses regarding the response of permafrost C to warming[1,2,4–7,24]. More surprising is the finding that increased plant C uptake can offset the release of old C, at least in the initial decades of permafrost thaw.

How could these observed changes in flux have affected C stocks over time since thawing began at Eight Mile Lake? Our gradient of permafrost thaw provides some detail about decadal-scale trends. If C fluxes over time at a single site followed the trajectory observed across our gradient, the extensive thaw site would have accumulated an additional net 0.20 $\mathrm{kg\,C\,m^{-2}}$ over the first 15 years following thaw, even as old C deep in the soil was increasingly destabilized (Supplementary Information). Increased plant C uptake cannot fully offset continued increases in old C respiration, thus by the time the extensive thaw site reached the present-day state, it would have already lost an amount almost equivalent to the initial C gain (net gain since thawing initiated = 0.03 $\mathrm{kg\,C\,m^{-2}}$) and perhaps more than double that amount (net loss 0.32 $\mathrm{kg\,C\,m^{-2}}$), depending on the exact year that permafrost thaw initiated. Although these gains and losses are substantial, they are still small relative to the soil C stocks at this site, thus these changes would be impossible to detect with soil C stock measurements against background variability at this time.

Extending observed C exchange rates into the future must be done with caution, but provides insight into possible permafrost C losses and the feedback to climate change. Assuming that surface C gains and losses approach a dynamic equilibrium with the increased plant C uptake levels, the rate of old C loss at the extensive thaw site suggests that a net loss of 4.4–6.0 $\mathrm{kg\,C\,m^{-2}}$ is possible by the end of this century, or about 9.4–12.9% of the approximately 47 $\mathrm{kg\,C\,m^{-2}}$ contained in the 80-cm active layer of soil in the Eight Mile Lake watershed. Although our observations cannot account for future thawing that will expose a larger pool of permafrost C to decomposition, we can frame the observed C loss rate from our single gradient at Eight Mile watershed in a global context by applying this rate to the global surface permafrost C pool (818 Pg) to demonstrate that 0.8–1.1 $\mathrm{Pg\,C\,yr^{-1}}$ could be lost if surface permafrost thaws—as some models[25], albeit controversial[26], have predicted for this century (Supplementary Information). The actual emission rate will, of course, depend on future thaw rates, the forms of C gases released, and other positive and negative feedbacks to decomposition that may be expressed differently in the future or in different ecosystem types, such as changes in nutrient availability[27] and/or litter quality[28]. But the calculation is consistent with laboratory incubations of permafrost soil[29], and serves to illustrate that this biospheric feedback from permafrost C has the potential to be large as warming continues, and, at some point, could possibly be similar in magnitude to the current biospheric flux from land use change (1.5 ± 0.5 $\mathrm{Pg\,C\,yr^{-1}}$)[30].

METHODS SUMMARY

We measured net CO_2 exchange between tundra and the atmosphere over 3 years using a combination of static and automatic clear chambers. An infrared gas analyser measured chamber CO_2 concentrations to quantify ecosystem C exchange. Growing season measurements began within a week of snowmelt (early May), and ended at snowfall (end of September). During the winter, flux measurements were made either at the snow surface or in shallow snow pits on a campaign basis that covered all winter months over the study period. Growing season, winter and annual C exchange were estimated using gap filling with response functions to measured environmental variables, and by interpolating mean estimates between time points using continuous environmental measurements to understand whether these tundra sites were gaining or losing C. Gross primary productivity was estimated as the difference between the integrated net ecosystem exchange and R_{eco} values.

At monthly intervals during the growing season, we also collected ecosystem respiration CO_2 from dark chambers, as well as soil CO_2 from soil profile gas wells, for $\Delta^{14}C$ analysis. In the laboratory, CO_2 was then purified and analysed for $\Delta^{14}C$ using an accelerator mass spectrometer, while a subsample was analysed for $\delta^{13}C$ using an isotope ratio mass spectrometer. Radiocarbon provides an indication of the age of respired C, and thus can be used as a fingerprint for identifying the decomposition of old organic C that has been stored in these permafrost soils. We used these field $\Delta^{14}C$ measurements in combination with $\Delta^{14}C$ measured from soil and plant incubations to estimate the contribution from soil and plants to ecosystem respiration. To do this, we used two and three pool isotope mixing models to constrain the proportional contribution of the component sources to total ecosystem respiration, in particular to determine the contribution of old C to ecosystem C exchange.

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1. Schuur, E. A. G. *et al.* Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle. *Bioscience* **58,** 701–714 (2008).
2. Zimov, S. A., Schuur, E. A. G. & Chapin, F. S. Permafrost and the global carbon budget. *Science* **312,** 1612–1613 (2006).
3. Field, C. B., Sarmiento, J. & Hales, B. in *The First State of the Carbon Cycle Report (SOCCR) — Synthesis and Assessment Product 2.2* (eds King, A.W. *et al.)* 21–28 (National Oceanic and Atmospheric Administration, National Climatic Data Center, 2007).
4. Field, C. B., Lobell, D. B., Peters, H. A. & Chiariello, N. R. Feedbacks of terrestrial ecosystems to climate change. *Annu. Rev. Environ. Resour.* **32,** 1–29 (2007).
5. Davidson, E. A. & Janssens, I. A. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **440,** 165–173 (2006).
6. Heimann, M. & Reichstein, M. Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature* **451,** 289–292 (2008).
7. Oechel, W. C. *et al.* Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature* **361,** 520–523 (1993).
8. Harden, J. W., Sundquist, E. T., Stallard, R. F. & Mark, R. K. Dynamics of soil carbon during deglaciation of the Laurentide ice sheet. *Science* **258,** 1921–1924 (1992).
9. Schirrmeister, L. *et al.* Paleoenvironmental and paleoclimatic records from permafrost deposits in the Arctic region of Northern Siberia. *Quat. Int.* **89,** 97–118 (2002).
10. Zimov, S. A. *et al.* Permafrost carbon: Stock and decomposability of a globally significant carbon pool. *Geophys. Res. Lett.* **33,** doi:10.1029/2006GL027484 (2006).
11. Smith, L. C. *et al.* Siberian peatlands a net carbon sink and global methane source since the early Holocene. *Science* **303,** 353–356 (2004).
12. Osterkamp, T. E. Characteristics of the recent warming of permafrost in Alaska. *J. Geophys. Res.* **112** (F2), doi:10.1029/2006JF000578 (2007).
13. Myneni, R. B., Tucker, C. J., Asrar, G. & Keeling, C. D. Interannual variations in satellite-sensed vegetation index data from 1981 to 1991. *J. Geophys. Res.* **103** (D6), 6145–6160 (1998).
14. Sturm, M., Racine, C. & Tape, K. Climate change – Increasing shrub abundance in the Arctic. *Nature* **411,** 546–547 (2001).
15. Chapin, F. S. *et al.* Role of land-surface changes in Arctic summer warming. *Science* **310,** 657–660 (2005).
16. Oechel, W. C. *et al.* Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. *Nature* **406,** 978–981 (2000).
17. Vitt, D. H., Halsey, L. A. & Zoltai, S. C. The changing landscape of Canada's western boreal forest: The current dynamics of permafrost. *Can. J. For. Res.* **30,** 283–287 (2000).
18. Osterkamp, T. E. The recent warming of permafrost in Alaska. *Glob. Planet. Change* **49,** 187–202 (2005).
19. Osterkamp, T. E. & Romanovsky, V. E. Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost Periglac. Process.* **10,** 17–37 (1999).
20. Schuur, E. A. G., Crummer, K. G., Vogel, J. G. & Mack, M. C. Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra. *Ecosystems* **10,** 280–292 (2007).
21. Trumbore, S. Age of soil organic matter and soil respiration: Radiocarbon constraints on belowground C dynamics. *Ecol. Appl.* **10,** 399–411 (2000).
22. Levin, I. & Hesshaimer, V. Radiocarbon – A unique tracer of global carbon cycle dynamics. *Radiocarbon* **42,** 69–80 (2000).
23. Phillips, D. L. & Gregg, J. W. Source partitioning using stable isotopes: Coping with too many sources. *Oecologia* **136,** 261–269 (2003).
24. Shaver, G. R. *et al.* Global change and the carbon balance of Arctic ecosystems. *Bioscience* **42,** 433–441 (1992).
25. Lawrence, D. M. & Slater, A. G. A projection of severe near-surface permafrost degradation during the 21st century. *Geophys. Res. Lett.* **32,** L24401, doi:10.1029/2005GL025080 (2005).
26. Delisle, G. Near-surface permafrost degradation: How severe during the 21st century? *Geophys. Res. Lett.* **34** (9) doi:10.1029/2007GL029323 (2007).
27. Mack, M. C. *et al.* Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* **431,** 440–443 (2004).
28. Hobbie, S. E. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecol. Monogr.* **66,** 503–522 (1996).
29. Dutta, K., Schuur, E. A. G., Neff, J. C. & Zimov, S. A. Potential carbon release from permafrost soils of Northeastern Siberia. *Glob. Change Biol.* **12,** 2336–2351 (2006).
30. Canadell, J. G. *et al.* Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proc. Natl Acad. Sci. USA* **104,** 18866–18870 (2007).

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

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