LETTERS

Carbon respiration from subsurface peat accelerated by climate warming in the subarctic

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Among the largest uncertainties in current projections of future climate is the feedback between the terrestrial carbon cycle and climate[1]. Northern peatlands contain one-third of the world's soil organic carbon, equivalent to more than half the amount of carbon in the atmosphere[2]. Climate-warming-induced acceleration of carbon dioxide (CO_2) emissions through enhanced respiration of thick peat deposits, centuries to millennia old, may form a strong positive carbon cycle–climate feedback. The long-term temperature sensitivity of carbon in peatlands, especially at depth, remains uncertain, however, because of the short duration or correlative nature of field studies[3–5] and the disturbance associated with respiration measurements below the surface *in situ* or during laboratory incubations[6,7]. Here we combine non-disturbing *in situ* measurements of CO_2 respiration rates and isotopic (^{13}C) composition of respired CO_2 in two whole-ecosystem climate-manipulation experiments in a subarctic peatland. We show that approximately 1 °C warming accelerated total ecosystem respiration rates on average by 60% in spring and by 52% in summer and that this effect was sustained for at least eight years. While warming stimulated both short-term (plant-related) and longer-term (peat soil-related) carbon respiration processes, we find that at least 69% of the increase in respiration rate originated from carbon in peat towards the bottom (25–50 cm) of the active layer above the permafrost. Climate warming therefore accelerates respiration of the extensive, subsurface carbon reservoirs in peatlands to a much larger extent than was previously thought[6,7]. Assuming that our data from a single site are indicative of the direct response to warming of northern peatland soils on a global scale, we estimate that climate warming of about 1 °C over the next few decades could induce a global increase in heterotrophic respiration of 38–100 megatonnes of C per year. Our findings suggest a large, long-lasting, positive feedback of carbon stored in northern peatlands to the global climate system.

The long-term effect of climate warming on soil carbon in terrestrial ecosystems has been debated for more than a decade[8–13]. This controversy has focused primarily on upland mineral soils[5,13], for which enzyme kinetic theory, laboratory studies and multi-pool models have established the short-term intrinsic temperature sensitivity of soil respiration[8,12,14]. However, acclimation[9], fast depletion of labile carbon pools[8,10,12] or secondary environmental or ecological constraints[13,15] have caused limited or transient responses of soil respiration to long-term *in situ* experimental warming of these upland ecosystems and have obscured the temperature sensitivity of old (that is, long-term), recalcitrant carbon pools. The apparent sensitivity of soil carbon respiration to long-term climate warming thus depends strongly on the relative and absolute availability of recalcitrant substrates and the suite of environmental constraints to decomposition[13], which both differ with soil types and climatic conditions.

It is therefore surprising that the long-term *in situ* sensitivity to climate warming of one of the largest global stocks of old, recalcitrant organic carbon, residing in northern peatlands, has received far less attention[5,13]. Although northern peatlands cover only 2% of the land, their thick peat deposits contain one-third of the world's soil organic carbon[2]. Peat formation has withdrawn large amounts of CO_2 from the atmosphere for centuries to millennia as organic carbon was stabilized by increasing decay-resistance, anoxia and decreasing temperatures with depth or permafrost (Supplementary Fig. 1). It has been suggested[9,10] that soil organic carbon in cold regions may be highly sensitive to above-average current and predicted climate warming at northern high latitudes[16] because of the higher temperature sensitivity of soil respiration at low temperatures[3,8,17]. Furthermore, recalcitrant organic matter at depth might be more temperature sensitive than labile carbon at the surface because of its higher catabolic activation energy[12,14], although this remains controversial[7,18]. Because of the short duration or correlative nature of field studies[3–5] and disturbance artefacts of respiration measurements below the surface[6,7], it remains unclear whether northern peatland soil carbon, especially at depth (25–50 cm), is susceptible to long-term climate warming, and is at risk of causing long-lasting increased carbon losses to the atmosphere. Here we provide evidence that this may well be true.

We investigated the climate-change response of ecosystem respiration rates and of respiration processes related to short-term (autotrophic respiration and heterotrophic respiration of plant exudates) and medium- to longer-term (heterotrophic respiration of young, surface and older, subsurface peat) carbon cycles (Supplementary Fig. 1), using two whole-ecosystem climate-change experiments in a subarctic blanket-bog underlain by permafrost in Abisko, north Sweden (68° 21′ N, 18° 49′ E). We used open-top chambers (OTCs) to simulate changes in summer, winter and/or spring climate projected for the northern European subarctic during the coming decades[16] (Figs 1 and 2). The OTCs increased air[19] and soil temperatures (down to at least 20 cm depth) by up to about 1 °C in spring (May: between snow-melt and bud-break) and/or summer (June–September: growing season) and/or doubled the winter (October–April) snow depth[19], without consistently affecting soil moisture or active layer depth (Supplementary Information).

During the snow-free season (May–September) of years 4, 6, 7 and 8 of the long-term experiment, the doubled winter snow depth did not result in carry-over effects on spring or summer ecosystem respiration rates (Fig. 1). However, respiration rates increased strongly in response to warming by OTCs in spring (34–76%) or in summer
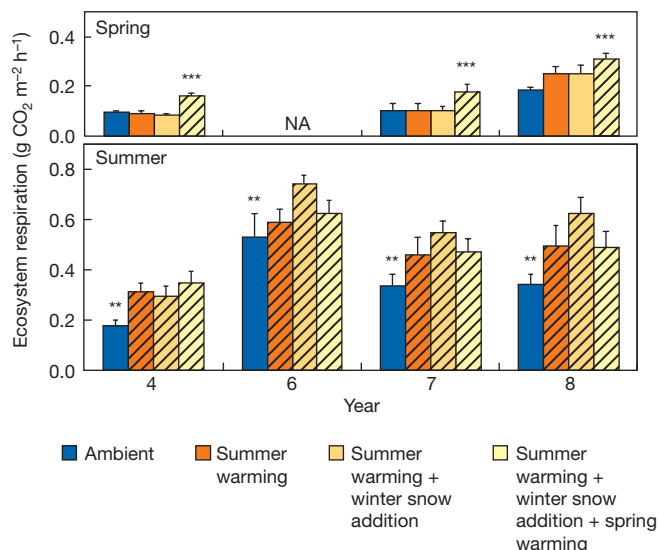
Figure 1 | Ecosystem respiration rates in a subarctic bog subjected to long-term experimental climate change or ambient conditions. Data were averaged separately for spring (May) and for summer (June–September). Hatched bars indicate passive warming with OTCs within the respective season. Error bars represent the standard error (s.e.) of residuals of treatments and blocks in spring, and the standard error of the mean (s.e.m.) of treatments in summer (one treatment replicate per block, $n = 5$ blocks). NA, no data available. Bars with asterisks differ significantly from bars without asterisks within the same season and year (planned orthogonal contrasts: **$P = 0.003$; ***$P = 0.001$).

(23–80%). In contrast to long-term studies in forest, meadow and tundra ecosystems[10,15,20], the warming effects did not decline towards the eighth year of the study (Fig. 1; year × treatment: $P = 0.53$ for spring, $P = 0.50$ for summer), indicating that climate warming has a long-lasting stimulating effect on CO_2-emission in subarctic peatlands.

To partition the sources of increased ecosystem respiration rates, we compared the effects of OTCs during the snow-free season between intact and trenched-plus-clipped parts of plots in a companion experiment. Heterotrophic respiration of peat (trenched-plus-clipped treatment) accounted for 70% of the total ecosystem respiration rate (intact treatment) and both heterotrophic and plant-related (aboveground, roots, rhizosphere) respiration rates

responded equally strongly to the warming treatment (Fig. 2). No change in their relative contribution was observed over the first year of the warming treatment, consistent with longer-term observations in other ecosystems[10,21]. This strongly suggests that heterotrophic respiration was responsible for the largest part of the increase in ecosystem respiration rates observed in the long-term experiment.

We further analysed the relative contribution of heterotrophic respiration of subsurface peat (25–50 cm depth, that is, the lower part of the active layer) to increased respiration rates in response to warming with a non-disturbing, *in situ* method, using the natural increase with peat depth of the $\delta^{13}C$ signatures of bulk C and respired CO_2 (Supplementary Fig. 2) and the overall $\delta^{13}C$ signature of CO_2 emitted from the plots. Because isotope discrimination during decomposition is dominated by the relative use by microbes of substrates differing in isotopic composition rather than by metabolic fractionation[22], a shift towards greater contribution of deeper peat to total respiration would be reflected as an increase in the overall $\delta^{13}C$ signature of CO_2 emitted in the field. Experimental warming increased the $\delta^{13}C$ signature of the respired CO_2 on average by 0.77‰ (Fig. 3), indicating a shift towards respiration of less-depleted carbon substrates. The effect was similar for heterotrophic respiration and total ecosystem respiration (Fig. 3), and therefore did not result from changes in photosynthetic fractionation by plants in response to aboveground environment[23]. Laboratory studies have shown that warming may decrease $\delta^{13}C$ signatures of respired CO_2 by 0.12–0.42‰ per °C owing to shifts towards decomposition of more depleted, recalcitrant substrates caused by microbial community changes[17]. Such changes in substrate use within peat layers may thus not explain, but may instead have partially obscured, the opposite, positive shift in $\delta^{13}C$ signature of respired CO_2 in our warming treatments. The clear increase in $\delta^{13}C$ signature of respired CO_2 after 1 or 7 years of experimental climate change (Fig. 3), compared with the 1.7‰ increase in $\delta^{13}C$ signature of bulk C over the upper 50 cm of peat (Supplementary Fig. 2), therefore strongly suggests that both short-term and long-term warming stimulated subsurface respiration disproportionately. Applying the range of temperature-related fractionation[17] to our data, we calculated that increased subsurface peat respiration was responsible for at least 69% of the increase in respiration rates in the warming treatments (Supplementary Information).
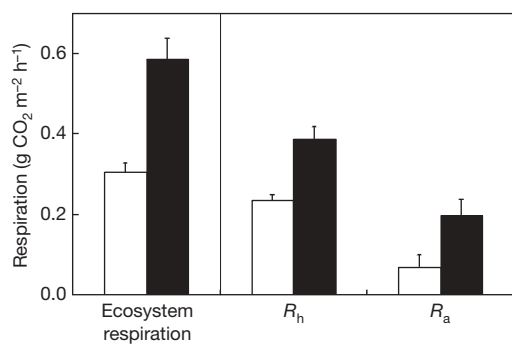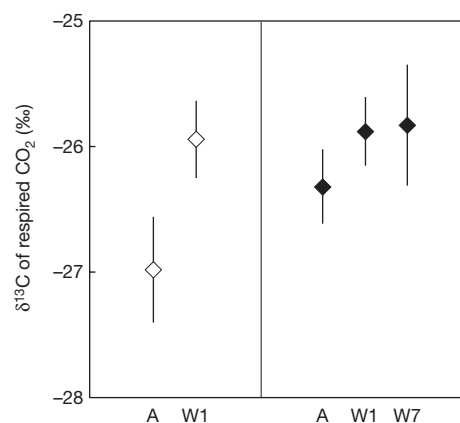

Figure 2 | Ecosystem respiration rates and their heterotrophic and plant-related components in a subarctic bog subjected to experimental warming or ambient conditions. Spring and summer warming (black bars) stimulated total ecosystem respiration ($P = 0.001$), and stimulated heterotrophic (R_h) and plant-related (R_a) respiration components equally ($P < 0.001$; warming × flux-component: $P = 0.65$) compared with ambient conditions (white bars). Response patterns remained unchanged over the first two experimental years (period × warming: $P = 0.41$ for ecosystem respiration, $P = 0.18$ for R_h and R_a), which were averaged. Error bars represent s.e.m. of treatments ($n = 5$ plots).

Figure 3 | Isotopic signatures of carbon respired as CO_2 in a subarctic bog subjected to experimental climate change or ambient conditions. Spring and summer warming (one year; W1) and spring and summer warming and winter snow addition (seven years; W7) increased $\delta^{13}C$ of respired CO_2 ($P = 0.032$) compared with ambient conditions (A). Climate-change duration did not affect $\delta^{13}C$ of respired CO_2 ($P = 0.93$). Climate-change effects on $\delta^{13}C$ of heterotrophic respiration (open symbols) and of total ecosystem respiration (filled symbols) did not differ (warming × flux-type: $P = 0.38$). Response patterns remained unchanged for four measurements (period × treatment: $P = 0.56$), which were averaged. Error bars represent s.e.m. of treatments ($n = 5$ plots).

Our data show for the first time that soil carbon respiration in a subarctic peatland, especially towards the bottom of the active layer, has a high, long-lasting sensitivity to climate warming. This contrasts with limited or transient soil respiration responses to *in situ* warming in other ecosystems, mostly on upland mineral soils[9,10,15,20], which were dominated by highly sensitive responses of plant-related respiration[24] and of fast-depleting, young, labile carbon[9,10,20,21]. In northern peatlands, fresh surface litter and plant-related respiration contribute proportionally less to total respiration than in most other ecosystems because of the large, old soil organic matter pool at depth[11,25]. This subsurface carbon sustained the accelerated respiration in our long-term warming treatments. Its vulnerability might be explained by a higher intrinsic temperature sensitivity of recalcitrant carbon[12,14] and be related to the presence of permafrost. Although our long-term climate manipulations did not alter the active layer depth (Supplementary Information), the progressively increasing thickness of unfrozen soil during the growing season continuously exposes deeper, highly temperature-sensitive carbon[3] to temperatures above freezing, a transition to which soil respiration is especially sensitive[3,8].

The net effect of climate warming on northern peatland carbon stocks will depend on the responses of both carbon losses from peat and carbon gains through new plant production (Supplementary Fig. 1). In the Arctic, ecosystem respiration is generally more sensitive to temperature than gross ecosystem productivity, especially in moss-dominated systems[26]. Biomass production of *Sphagnum* mosses, the primary peat-formers in peatlands, is also not enhanced in our and other ecosystem warming experiments[19,27], and expansion of productive woody shrubs in response to climate change, as observed in other tundra ecosystems[28], is hampered in peatlands by the fast vertical growth of *Sphagnum*[29]. We therefore expect that stimulation of carbon assimilation rates in peatlands will be modest compared with the observed strong increase in respiration rates.

The extensive reservoirs of organic carbon in northern peatlands are thus highly sensitive to climate warming. Indeed, large-scale, long-term observations across England and Wales have already shown dramatic declines in carbon content in peat soils, which are suggested to be linked to recent climate change[11]. Taking our data as indicative of the responses of undisturbed northern peatlands worldwide, we estimate that a mild growing-season temperature increase of about 1 °C during the coming decades[16], as simulated by our OTC treatments, may induce a global increase in heterotrophic respiration from northern peatlands of 38–100 megatonnes of C per year (1 megatonne = 10^{12} g) (Supplementary Information). This estimate is based on direct summer warming effects only, because the OTCs did not consistently affect other environmental conditions, for example, soil moisture or active layer depth (Supplementary Information). While permafrost thawing and, depending on initial moisture conditions, drying of peatlands might further increase peat respiration[5,13,30], the estimated potential extra global CO_2 emission based on direct warming alone is enough to offset much of the Kyoto Protocol target for greenhouse gas emission reductions for the whole European Union (92 megatonnes of C per year). In economic terms, this extra CO_2 emission would require an investment of €2.4–6.3 billion to compensate based on the current carbon allowance price of the EU Emissions Trading Scheme. Although our estimation may be crude, it clearly indicates the large, long-lasting potential feedback of increased respiration from northern peatlands to the global climate.

METHODS SUMMARY

Climate manipulations. In the long-term experiment (eight years), we combined changes in summer and/or spring temperatures, winter snow thickness, or ambient conditions (for the four treatment combinations used here, see Fig. 1). In the companion experiment (two years) we combined spring and summer warming or ambient conditions with aboveground manipulation of the vegetation of part of the plots, so as to be able to partition total ecosystem respiration (intact part) into heterotrophic respiration (trenched-plus-clipped part) and plant-related respiration (aboveground, roots, rhizosphere; difference between intact and trenched-plus-clipped parts). We used hexagonal OTCs that passively

increased temperatures by up to approximately 1 °C in both air[19] and soil (to a depth of at least 20 cm, Supplementary Information) when used in spring and/or summer and passively doubled snow depth[19] when used in winter, without consistently affecting soil moisture or active layer depth (Supplementary Information). Each treatment was replicated five times.

Respiration measurements. Respiration rates were measured over 120-s intervals with an infrared gas analyser coupled to a non-transparent respiration chamber placed on permanently installed collars, during the daytime on six to twenty occasions per year in the snow-free season (May–September) in years 4, 6, 7 and 8 of the long-term experiment and in years 1 and 2 of the companion experiment. Isotopic ($\delta^{13}C$) analyses of respired CO_2 were made by sampling air with accumulating CO_2 eight times from similar closed chambers installed for 30–60 min, on four occasions during the first and second seasons of the companion experiment and the seventh and eighth seasons of the long-term experiment. Samples were analysed with a gas chromatography-isotope ratio mass spectrometer (GC-IRMS), after which we estimated the $\delta^{13}C$ of the respired CO_2 from Keeling plots. The relative contribution of subsurface peat to the respiration rate increase in the OTC treatments was calculated using two end-member mixing models (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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Author Contributions R.A., T.V.C. and E.D. designed the long-term climate-change experiment. E.D. designed the companion experiment. E.D., R.A. and R.S.P.v.L. developed the carbon isotope methods. E.D., S.T., R.S.P.v.L., E.S and M.J.v.d.W. performed the respiration and environmental measurements in the field. E.D. and R.S.P.v.L. collected and analysed the stable isotope samples for the field and laboratory experiments. E.D., E.S., M.J.v.d.W. and S.T. performed the data analyses. E.D. wrote the manuscript, to which all authors contributed with discussion and text.

METHODS

Site. We performed two whole-ecosystem climate-change experiments in a subarctic blanket-bog in Abisko, north Sweden ($68°\,21'$ N, $18°\,49'$ E; ref. 19). Mean annual temperature is $-0.5\,°C$ with mean monthly temperatures ranging from $-10.7\,°C$ in January to $11.3\,°C$ in July. Mean total annual precipitation is 323 mm (Abisko Scientific Research Station Meteorological Station, 1971–2000 averages). The vegetation of the site is dominated by a continuous and homogeneous carpet of the peat moss *Sphagnum fuscum* (Schimp.) H. Klinggr. Other bryophytes and lichens are sparse. The vascular plant community is low and open (maximum shrub height ~15 cm, average cover ~20%), and consists mainly of crowberry, *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher, cloudberry, *Rubus chamaemorus* L., bog rosemary, *Andromeda polifolia* L., small cranberry, *Vaccinium microcarpum* (Turcz. ex Rupr.) Schmalh., dwarf birch, *Betula nana* L., bog whortleberry, *Vaccinium uliginosum* L. and Lapland small-reed, *Calamagrostis lapponica* (Wahlenb.) Hartm. The thickness of the organic peat layer is unknown but it extends at least to the top of the permafrost, which is present at the site at a depth of approximately 55 cm. The water table closely follows the decreasing thaw front during the summer, and because of the gently sloping aspect of the terrain the site is relatively dry and a true water table on top of the frozen peat layer is rare and below 30 cm depth during most of the summer. Because of the exposed location of the site at the shore of Lake Torneträsk, the ambient snow cover is relatively thin, reaching its maximum thickness of about 15 cm in February–March[19].

Climate manipulations. The experimental site was divided into five blocks, perpendicular to the direction of the slope, and all treatments were replicated once in each of these blocks. The long-term experiment, initiated in June 2000, consisted of six climate-change scenarios, each a different combination of presence or absence of transparent OTCs[19,31] (2.2 m in diameter) in spring, summer and winter. The OTCs passively altered temperatures and/or snow conditions in the different seasons (Supplementary Information), corresponding to predicted changes in climate for the coming decades in the northern European subarctic[16]. For the present study, we focused on four treatments: 'ambient'; 'summer warming'; 'summer warming + winter snow addition'; 'summer warming + winter snow addition + spring warming'.

The companion experiment consisted of an ambient and an OTC treatment during spring and summer, in factorial combination with aboveground vegetation manipulation. We cut 20-cm-deep trenches around ten 384 cm^2 patches of vegetation for the plant removal treatment, and installed stainless-steel collars (22-cm diameter, 10-cm deep), identical to the ones used for the respiration measurements, in early summer 2005. All living, aboveground vascular vegetation was clipped off and removed at peak biomass by the end of July, and the active parts of the dense *Sphagnum fuscum* carpet (1–2 cm) in September 2005. Aboveground litter was left in place. We minimized potential effects of decomposing cut-off roots on CO_2 fluxes by allowing 11 months to pass before starting the OTC treatment and the flux measurements, while the collars served as a barrier against in-growing roots[32], concentrated in the upper 10-cm of peat in subarctic peatlands[33]. Regrowth of shoots within the removal patches was therefore extremely rare, but was consistently removed. We installed a second collar at a short distance from the removal patch in each plot and left the vegetation intact. In early July 2006, the warming treatment of the companion experiment was initiated by placing OTCs (1.1 m diameter) over half of the plots, each containing a pair of undisturbed vegetation and a plant removal patch, while leaving the other pairs as ambient controls.

Respiration measurements. We investigated the effects of the climate manipulations on respiration rates in years 4, 6, 7 and 8 after initiation in the long-term experiment (2003, 2005–2007), and in years 1 and 2 (2006–2007) of the companion experiment. Respiration rates were measured on six to twenty occasions per year during the snow-free season (May–September), one to twelve occasions each month except in June 2003, May and June 2005 and July–September 2007. The isotopic composition of respired CO_2 was measured in all four treatment combinations of the companion experiment and in the 'summer warming + winter snow addition + spring warming' treatment of the long-term experiment on four occasions in July, August and September 2006 and May 2007. For both types of measurements, complete blocks were sampled consecutively between 10:00 h and 16:00 h, and each measurement occasion lasted for 1–3 days.

Respiration measurements were made with an infrared gas analyser (EGM-4; PP Systems) attached to a custom-made, non-transparent, vented soil respiration chamber (22-cm diameter, 24-cm height), which was placed onto permanently installed collars as described above, equipped with a water-seal. Chamber volumes were corrected for differences in the air volume above the *Sphagnum* surface contained within the respiration collar of each plot. After an equilibration period of 65 s, the CO_2 concentration in the chamber was measured at 5-s intervals for 2 min and used to calculate the respiration rate by linear regression.

For the isotopic analysis, air with accumulating CO_2 was sampled eight times at increasing intervals from closed respiration chambers similar to those described above, but equipped with a rubber septum port and no vent, placed on each plot for 30–60 min. Air was transferred directly with double-ended needles into 12-ml septum-capped glass vials (Exetainers, Labco Ltd), which had been flushed with N_2 and pre-evacuated. Immediately afterwards we collected a 5-ml sample and measured the CO_2 concentration with the infrared gas analyser. The gas samples in the glass vials were transported to our laboratory in Amsterdam and analysed for their isotopic composition with a gas chromatograph coupled to a stable isotope ratio mass spectrometer (Gasbench II and Delta^{plus}, ThermoFinnigan) within five days of sampling. The isotopic composition of respired CO_2 was estimated for each plot and each occasion from Keeling plots[34]. Carbon isotopic composition is reported in δ-notation $\delta^{13}C\,(‰) = 1{,}000 \times [(^{13}C/^{12}C)_{sample} - (^{13}C/^{12}C)_{standard}]/(^{13}C/^{12}C)_{standard}$, relative to the Vienna PeeDee Belemnite standard.

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