

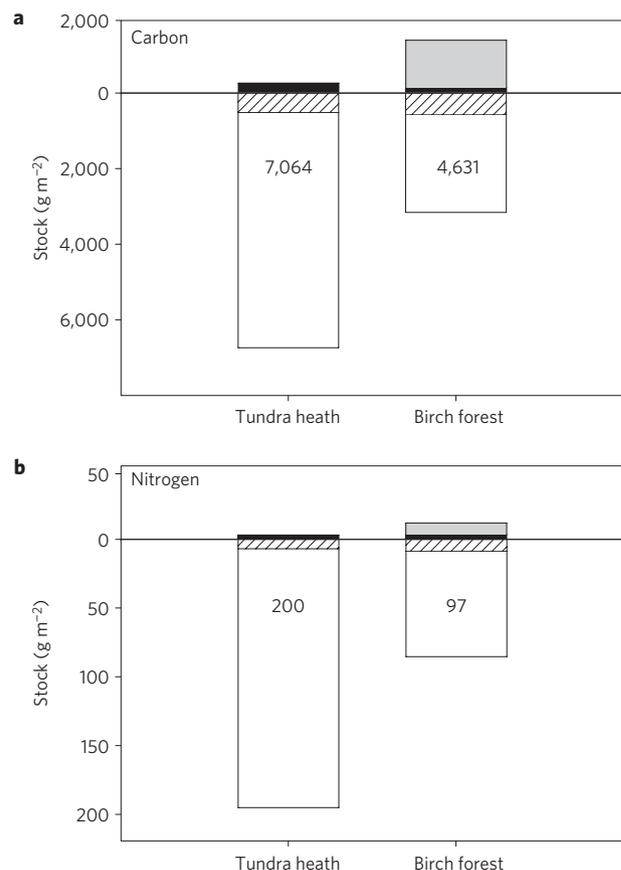
# A potential loss of carbon associated with greater plant growth in the European Arctic

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Rapid warming is expected to increase plant growth in the Arctic<sup>1</sup>, and result in trees gradually colonizing tundra<sup>2</sup>. Models predict that enhanced carbon (C) storage in plant biomass may help offset atmospheric CO<sub>2</sub> increases and reduce rates of climate change<sup>2–4</sup>. However, in some Arctic ecosystems, high plant productivity is associated with rapid cycling and low storage of soil C (refs 1,5,6); thus, as plant growth increases, soil C may be lost through enhanced decomposition. Here we show that, in northern Sweden, total ecosystem C storage is greater in tundra heath (owing to greater soil C stocks) than in more productive mountain-birch forest. Furthermore, we demonstrate that in the forest, high plant activity during the middle of the growing season stimulates the decomposition of older soil organic matter. Such a response, referred to as positive priming, helps explain the low soil C storage in the forest when compared with the tundra. We suggest that, as more productive forest communities colonize tundra, the decomposition of the large C stocks in tundra soils could be stimulated. Thus, counter-intuitively, increased plant growth in the European Arctic could result in C being released to the atmosphere, accelerating climate change.

High-latitude soils contain more C than the atmosphere<sup>7,8</sup>. As the Arctic is experiencing greater warming than other regions<sup>1</sup>, it is important to determine the vulnerability of these C stores. Large changes in plant productivity and community composition are already being observed<sup>2,3</sup>. With nitrogen (N) availability considered to limit plant productivity at high latitudes<sup>9</sup>, the possibility that sustained increases in productivity are coupled to the ability of some plant communities to stimulate (prime) decomposition and nutrient cycling needs to be considered<sup>10,11</sup>. Positive priming involves enhanced decomposition of older soil organic matter (SOM) pools following the supply of energy in new labile C inputs from plants. Priming effects are of particular interest in the Arctic owing to the fundamental changes in the productivity and distribution of plant communities that are taking place, and the fact that most C is stored below ground. Critically, our limited understanding of how plant–soil interactions control C storage in different Arctic ecosystems reduces our ability to predict whether C will be lost or gained as plant productivity increases in response to warming<sup>12</sup>.

In Fennoscandia, mountain-birch (*Betula pubescens* Ehrh. ssp. *czerepanovii* (Orlova) Hämet Ahti) forest forms the northern tree line, and is up to twice as productive as nearby tundra heath<sup>13</sup>. This type of forest has previously occupied areas at



**Figure 1 | C and N storage in the two ecosystems. a, C stocks. b, N stocks.** The stocks are divided into above-ground tree biomass (grey fill), above-ground shrub biomass (black fill), roots (diagonal hash fill) and soils down to the underlying parent material (white fill). Above-ground stocks are shown above the x axis; below-ground stocks are shown below the x axis. The total ecosystem stock values (g m<sup>-2</sup>) are provided within each soil bar. All differences between the two ecosystems (except root C and N stocks) were statistically significant ( $P < 0.001$ ).

much higher altitudes<sup>14</sup>, and has again been expanding uphill and northwards during recent decades, prompting suggestions that C storage in these areas has increased substantially<sup>15</sup>. However,

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**Table 1 | The  $^{14}\text{C}$  content of different soil depths in the two ecosystems, and carbon dioxide fluxes calculated using an established mean residence time approach<sup>30</sup>.**

Site	Horizon	Depth (cm)	$^{14}\text{C}$ (% modern)	Laboratory code	Mean residence time (yr)	C storage (kg C m <sup>-2</sup> )	C flux (g C m <sup>-2</sup> yr <sup>-1</sup> )	Contribution to flux (%)
Tundra heath	O	0–1	127.31 ± 0.55	SUERC-12116	20	0.52	26.2	48.0
	O	1–2	114.66 ± 0.50	SUERC-13099	50	0.55	11	20.1
	O	2–3.5	107.65 ± 0.47	SUERC-13100	100	0.77	7.7	14.1
	O	3.5–4.5	103.49 ± 0.45	SUERC-12117	200	0.62	3.1	5.7
	O	4.5–6.5	100.61*	-	300	1.48	4.9	9.0
	O	6.5–7.5	97.73 ± 0.43	SUERC-12118	500	0.83	1.7	3.1
Birch forest	O	0–1	135.32 ± 0.59	SUERC-12126	20	0.6	30.1	77.0
	O	1–2	111.87 ± 0.49	SUERC-12127	70	0.59	8.4	21.5
	E	2–5.5	88.09 ± 0.38	SUERC-12128	1,075	0.66	0.6	1.5

\*Data for this depth were calculated from an average of the layers immediately above and below. The  $^{14}\text{C}$  contents are presented with  $\pm 1\sigma$  analytical uncertainty and unique publication codes for each sample. Horizon labels are: O, organic; E, eluvial. Fluxes were calculated on the basis of the amount of C stored in each layer divided by its mean residence time, and then used to calculate the contribution to the total soil  $\text{CO}_2$  efflux.

such calculations fail to account for the fact that mountain-birch forests are generally characterized by low soil C storage<sup>16</sup>. In many areas of the Arctic, permafrost dynamics and waterlogging make it difficult to determine the extent to which the plant community, rather than the physical environment, influences soil C storage<sup>6</sup>. However, in mountainous parts of northern Fennoscandia, the soils are generally free-draining and permafrost is absent. Thus, the tundra heath/birch forest ecotone provides a model system for determining how decomposition is controlled in Arctic ecosystems of contrasting productivity.

Detecting priming effects *in situ* in natural ecosystems is challenging using conventional partitioning techniques (for example, trunk-girdling, trenching, root excising and stable C isotopes)<sup>17</sup>. However, nuclear weapons testing in the middle of the twentieth century enriched the atmosphere in radiocarbon (the bomb- $^{14}\text{C}$  peak). This provides a global tracer that can be used to distinguish between recent plant inputs (root respiration and decomposition of recently produced plant material) and the decomposition of organic matter that was produced over the past 50 years<sup>18</sup>, making it possible to determine how changes in plant activity affect decomposition in contrasting ecosystems.

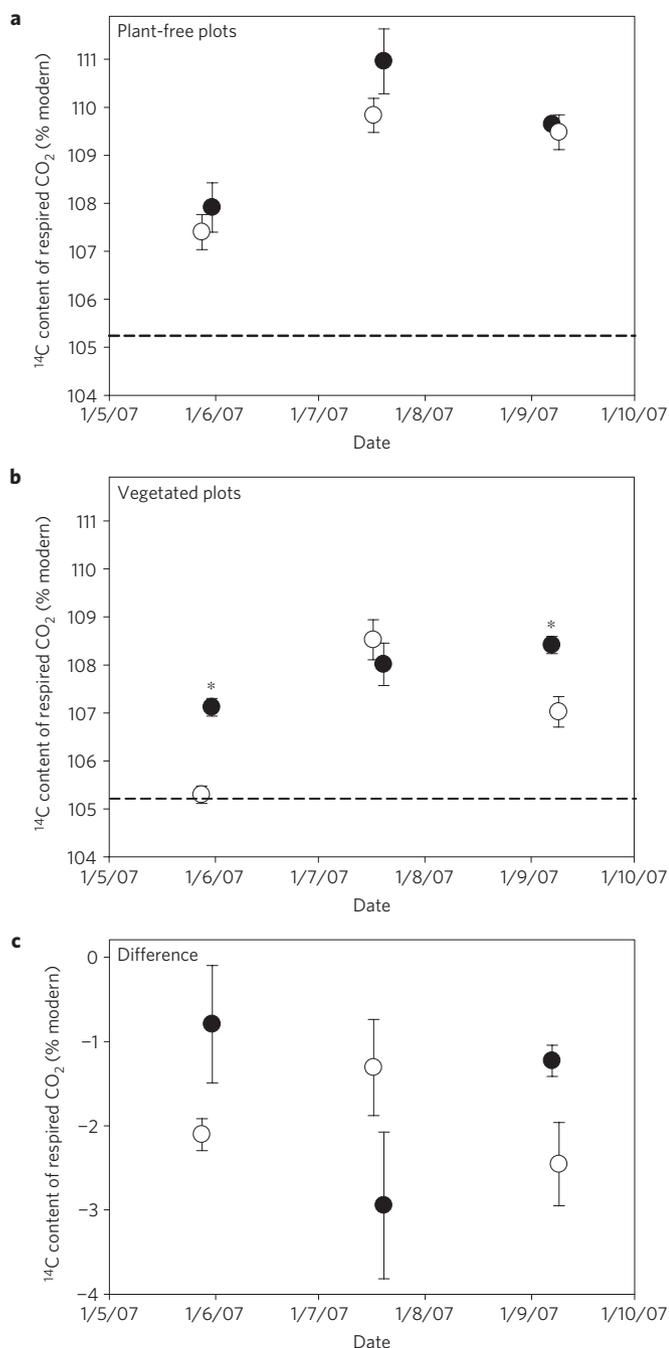
We carried out extensive surveys of above- and below-ground C and N stocks, as well as SOM  $^{14}\text{C}$  contents, in mountain-birch forest and tundra heath in Arctic Sweden. To determine how decomposition is controlled in the different ecosystems, we used an approach that measured the  $^{14}\text{C}$  content of  $\text{CO}_2$  being released from vegetated and plant-free plots, at different time points during the course of the growing season. Given that tundra plant species also form the understorey vegetation in the forest, the main difference between the vegetated plots at the two sites was the presence of mountain-birch roots in the forest, with most birch fine roots being present in the top few centimetres of the soil (organic horizon).

Total C and N storage was lower in the birch forest than on the tundra heath (Fig. 1), with the smaller stocks in soils (Supplementary Table S2) far outweighing the enhanced storage in plant biomass (Supplementary Table S1). The fact that these ecosystems are free-draining, and thus waterlogging does not inhibit rates of decomposition, meant that there was little C present that had been fixed before the 1950s (pre-bomb C), and the organic horizons were strongly enriched in bomb- $^{14}\text{C}$  (Table 1). Importantly, mean residence time modelling (see Supplementary Information) demonstrated that the depths dominated by pre-bomb levels of  $^{14}\text{C}$  (that is, <100% modern) contributed

only a small proportion of the overall respiratory flux in both ecosystems (Table 1; tundra heath = 3.1%, birch forest = 1.5%). This means that, in contrast to conventional radiocarbon dating, we can conclude that any increase in the  $^{14}\text{C}$  content of the  $\text{CO}_2$  being released from either ecosystem indicates that older C is being released, but that this C is decades (up to ~50 years old), rather than centuries, old.

The  $^{14}\text{C}$  content of the  $\text{CO}_2$  released from plant-free plots did not differ significantly between the tundra heath and birch forest at any point during the growing season (Fig. 2a). This indicates that, despite the differences between the soil profiles (Supplementary Table S2), in the absence of plants, the organic matter decomposing in the two ecosystems was of a similar age ( $P > 0.115$ ; Supplementary Table S4). In contrast, in vegetated plots, distinct differences were observed between the two ecosystems in terms of the seasonal pattern of  $^{14}\text{CO}_2$  release ( $P < 0.001$ ; Fig. 2b). On the tundra heath, the  $^{14}\text{C}$  content of the respired  $\text{CO}_2$  increased slightly during the course of the growing season. In contrast, in the forest the  $^{14}\text{C}$  content of the respired  $\text{CO}_2$  first increased between late May and July, before declining again by September. The pattern observed in the vegetated plots in the birch forest was unexpected, and critically, the fact that the release of the most  $^{14}\text{C}$ -enriched  $\text{CO}_2$  coincided with maximum plant activity suggests priming of older C by birch roots. We can conclude this for the following reasons.

Rates of photosynthesis (Supplementary Fig. S1), and therefore new C input, peaked mid season. Furthermore, partitioning calculations indicate that the contribution of plant respiration to  $\text{CO}_2$  release from the vegetated plots (Fig. 3c,d), and the contribution of roots to below-ground respiration (Supplementary Fig. S2), was also highest mid season. Plant respiration should have a  $^{14}\text{C}$  content similar to the contemporary atmosphere (105.25% modern in 2007). As the organic matter decomposing in both ecosystems was dominated by material enriched in bomb- $^{14}\text{C}$  (Table 1 and Fig. 2a), the difference in the  $^{14}\text{C}$  content of the  $\text{CO}_2$  released from the plant-free and vegetated plots was expected to be greatest mid season, and lower early and late in the growing season, as it was on the tundra heath (Fig. 2c); the high rate of plant respiration mid season, with an expected  $^{14}\text{C}$  content of ~105% modern, should have diluted the  $^{14}\text{C}$  content of the  $\text{CO}_2$  being released from the vegetated plots. In contrast, in the forest, the difference between vegetated and plant-free plots was greatest early and late in the growing season. To explain this result, high plant activity during July must have stimulated the decomposition of an



**Figure 2 | Seasonal variation in the  $^{14}\text{C}$  content of the respired  $\text{CO}_2$ .**

**a**, Plant-free plots. **b**, Vegetated plots. **c**, The difference between the two plot types (vegetated plots minus plant-free plots). Filled circles represent the tundra heath and open circles represent the birch forest. The horizontal dashed lines indicate the atmospheric  $^{14}\text{C}$  content in 2007. Error bars represent  $\pm 1$  s.e.m. ( $n = 3$ ). Significant differences ( $P < 0.05$ ) between ecosystems ( $t$ -test) on particular dates are indicated by asterisks. For the difference between plot types (**c**), a significant interaction ( $P = 0.044$ ) between ecosystem type and sampling date was observed (two-way repeated-measures analysis of variance).

older (bomb- $^{14}\text{C}$  enriched) pool of SOM. This provides evidence of a positive priming effect, and one that could not have been detected without the  $^{14}\text{CO}_2$  measurements.

Positive priming effects are often related to increased C transfer to the rhizosphere (the region of soil directly interacting with roots) stimulating the decomposition of older organic material,

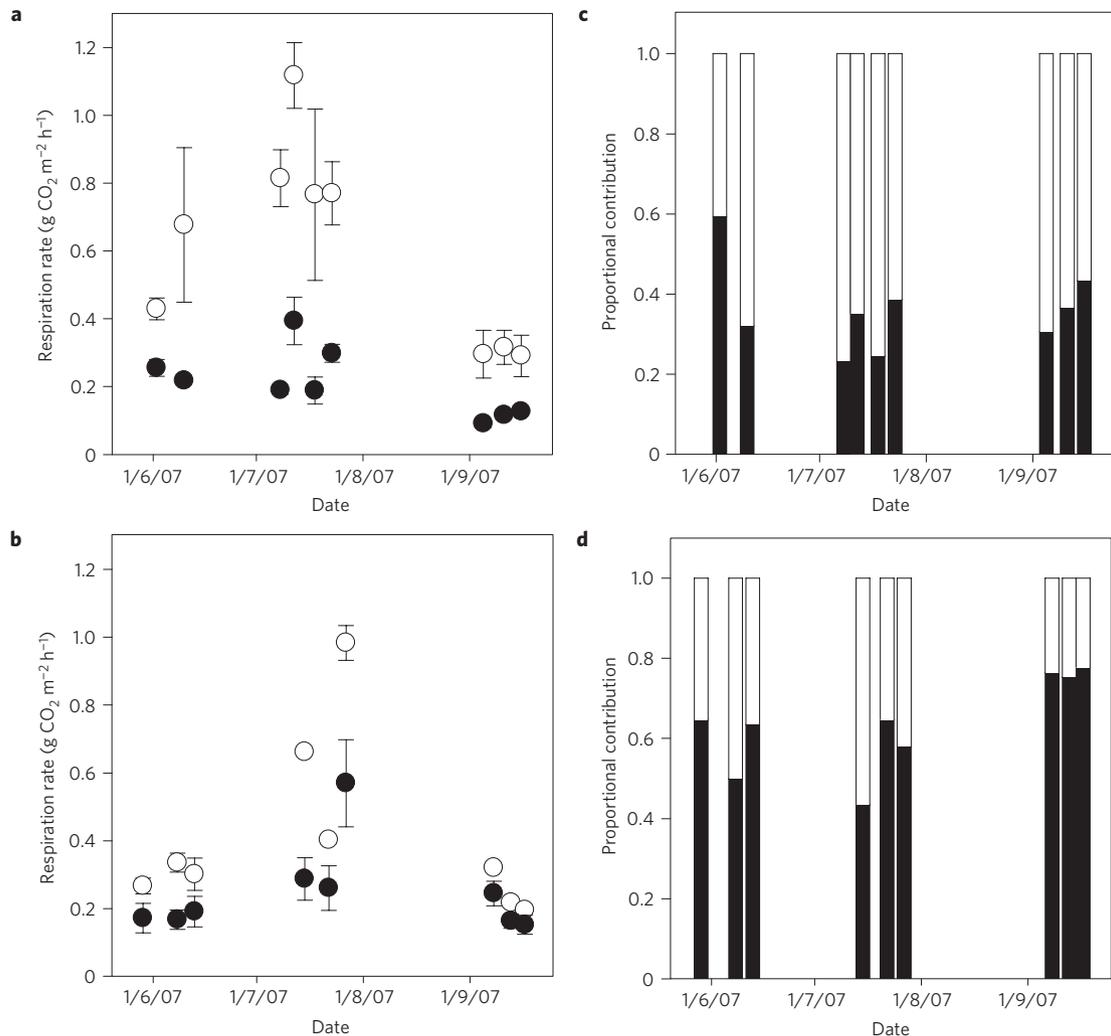
thus helping to meet the nutrient demand of plants during periods of peak activity<sup>19,20</sup>. Previous work in Scotland showed that planting *B. pubescens* on heather moorland reduced the mass of the organic horizon, whereas felling a mature birch forest resulted in organic matter accumulating<sup>21</sup>. However, it was suggested that birch transpiration, drying out the organic soils, may have caused those results. In our Swedish birch forest, no significant difference was observed between the moisture contents of vegetated and plant-free plots (Supplementary Table S5), and the thin organic horizon and low water-holding capacity of the mineral soil meant that moisture contents were never high enough to inhibit activity<sup>10</sup>. Thus, soil drying could not have been involved in the rhizosphere priming effects we observed, suggesting that increased C transfer to the rhizosphere mid season was the driving factor.

Further investigation into the exact mechanisms controlling the magnitude of rhizosphere priming effects in different plant communities is urgently required<sup>22</sup>. *Empetrum hermaphroditum* dominates the vascular plant community on the heath and is a key component of the forest understorey. *Empetrum* species have allelopathic properties that can negatively affect decomposition and nitrogen cycling<sup>23,24</sup>. Thus, the priming effect in the forest may be associated with increased C allocation to the birch rhizosphere to reduce the negative allelopathic effect of *Empetrum* on microbial activity and nutrient availability. In addition, the role contrasting types of mycorrhizal fungi play in rhizosphere priming remains poorly understood. Given that many of the key plant community shifts predicted for the Arctic involve increased dominance of ectomycorrhizal shrubs and trees (including birch)<sup>12</sup>, more research is required into the role ectomycorrhizal fungi play in rhizosphere priming effects.

Our analysis demonstrates that soil C and N stocks in mountain-birch forest are lower than in surrounding tundra heath, more than compensating for the increased C and N storage in tree biomass. Furthermore, with mountain-birch forests expanding in Fennoscandia, we suggest that positive priming of SOM decomposition may result in substantial losses of C from tundra soils following birch colonization, with these losses likely to exceed C gains in tree biomass. It should be noted though, that in this study, measurements were confined to the growing season. Thus, in addition to the priming effect observed, we cannot rule out differences in winter fluxes as a contributing factor to the lower soil C storage in the forest. Furthermore, at present, we are not able to estimate the potential rate of C loss. In Scotland, changes in organic horizon mass and C content after planting birch on heather moorland indicate that  $\sim 100 \text{ g C m}^{-2} \text{ yr}^{-1}$  may have been lost over a 20-year period<sup>21</sup>. Initial C stocks were higher in Scotland than in Sweden but the potential for rapid C release is clear. Experimental planting of mountain birch on tundra heath in northern Fennoscandia would help determine how rapidly C could be lost.

There is growing evidence from other high-latitude and -altitude ecosystems that the expansion of trees into tundra may not increase C storage as models predict<sup>4</sup>. The presence of Krummholz spruce or fir trees above the tree line is associated with reduced C storage in soils<sup>25</sup>, and in Alaska it has also been suggested that the expansion of boreal forest could result in a net loss of C, although this result was considered to be related more to changes in permafrost dynamics than the direct effects of the plant community<sup>6</sup>.

Plant communities in the Arctic are likely to change substantially during the twenty-first century. We suggest that the northward expansion of boreal forest will not enhance ecosystem C storage in Fennoscandia, but instead may lead to losses of soil C due to priming induced by C inputs from the roots of the colonizing trees. Critically, our results suggest that remotely sensed, plant-biomass inventories<sup>3,26</sup> may not be sufficient to determine the magnitude or



**Figure 3 | Respiration measurements and partitioning calculations.** **a, b**, The respiration rates measured from the vegetated (open circles) and plant-free (filled circles) plots during the 2007 growing season for the tundra heath (**a**) and for the birch forest (**b**). Mean respiration rates are shown,  $\pm 1$  s.e.m. ( $n = 3$ ). **c, d**, Stacked bars indicate the proportional contribution of soil (black) and vascular plant (white) respiration to respiration in the vegetated plots for the tundra heath (**c**) and for the birch forest (**d**). See Supplementary Information for partitioning calculations.

sign of changes in total C storage in Arctic ecosystems. Rather, we argue that a greater understanding of how plant–soil interactions control soil C storage is urgently required.

## Methods

**Field-site description.** We worked on both sides of the mountain-birch forest/tundra heath ecotone, near Abisko, northern Sweden. Moving uphill, our field sites were: an area near the uppermost limit of continuous birch forest (68° 19' 35" N, 18° 50' 00" E; elevation ~520 m) and an area of tundra heath immediately above the highest patch of mountain birch (68° 18' 07" N, 18° 51' 16" E; elevation ~710 m). The two sites were on the same hillside (same aspect) and both areas were on relatively flat terraces (slope < 5°) underlain by the same parent material—coarse glacial till. Thus, site selection ensured that the environmental conditions were as similar as possible. In the mountain-birch forest, as well as the *B. pubescens* ssp. *czerepanovii* trees, the understorey vegetation is dominated by the ericaceous dwarf shrubs *E. hermaphroditum* and *Vaccinium vitis-idaea*. The soil is a micro-podzol (spodosol) with a shallow organic layer, underlain by a blue-grey (Munsell chart: 10YR 5/1) eluvial (albic) horizon and a light-orange-coloured (Munsell chart: 10YR 4/3) illuvial (spodic) horizon (which is not always present) above coarse glacial till. On the tundra heath, the vascular plant community was strongly dominated by *E. hermaphroditum* with some *Vaccinium uliginosum* and *Betula nana*. The soil has a deeper organic horizon overlying coarse glacial till with large clasts and only occasional pockets of fine-grained material.

**Soil and plant sampling and analyses.** Soils surveys (see Supplementary Information) were used to identify the median soil horizon depths for each

ecosystem. At a representative location, a pit was dug, and the soil sampled with the minimum degree of compaction. The profile was cut into 1-cm-thick sections and analysed for <sup>13</sup>C and <sup>14</sup>C content at the NERC Radiocarbon Facility, UK (ref. 27). All <sup>14</sup>C results were normalized to a  $\delta^{13}\text{C}$  value of  $-25\text{‰}$  and expressed as a % modern and conventional radiocarbon ages (years before present; that is, relative to 1950; ref. 28).

Plant C and N stocks were obtained from destructive harvests of above-ground material (stems and leaves) from five 0.2 × 0.2 m plots placed in separate, representative plots of vegetation in each ecosystem, and live root material (judged by colour and elasticity), sorted from 4.5-cm-diameter, 25-cm-deep soil cores taken immediately after harvest (one core per plot). C and N stocks in tree stems were calculated on the basis of published biomass measurements, and C and N content values (see Supplementary Information).

**Experimental design and flux measurements.** During late summer 2006, three pairs of 50 × 50 cm plots were set up. Of each pair of plots, one was left as a control (vegetated plots), whereas in the other, all above-ground vascular plant material was removed by clipping. Trenches were also dug on all four sides of the clipped plots to sever links between any remaining live roots and photosynthetically active tissues (plant-free plots). For further details see Supplementary Information. At the centre of each plot, a respiration collar (7 cm tall and 16 cm in diameter) was established.

Net ecosystem exchange under ambient light at the vegetated and plant-free plots was measured using a portable infrared gas analyser (Model: EGM-4, PP Systems) connected to a transparent chamber (Model: CPY-2, PP Systems). To measure respiration, the chamber was darkened by covering it with thick black material. Soil temperature measurements at 2, 5 and 8 cm (digital thermometer, E.T.I.) and soil moisture measurements at 3 and 6 cm (Theta probe,

Model: ML2, Delta-T Devices) were taken around each collar during each flux measurement.

**<sup>14</sup>C sample collection and analysis.** On three occasions during the 2007 growing season (late May, mid July and mid September), an established sampling system<sup>29</sup> was used to collect samples of respired CO<sub>2</sub> for <sup>14</sup>C analysis (for further details see Supplementary Information and Supplementary Table S3). These CO<sub>2</sub> samples were purified and analysed for <sup>14</sup>C and <sup>13</sup>C at the NERC Radiocarbon Facility<sup>27,29</sup>.

**Data analysis.** Statistical analyses were carried out using SPSS (Version 11, SPSS Science) and data were checked for suitability for parametric analysis. Between-site differences in C and N stocks were investigated with *t*-tests. Repeated-measures analyses of variance (with date as the within-subject factor and ecosystem as the between-subject factor) were used to determine whether there was a significant difference between ecosystems in terms of the <sup>14</sup>C content of the CO<sub>2</sub> released from either the vegetated or plant-free plots.

Received 22 November 2011; accepted 9 May 2012;  
published online 17 June 2012

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## Acknowledgements

This work was carried out within the Natural Environment Research Council (NERC) funded Arctic Biosphere Atmosphere Coupling at Multiple Scales (ABACUS; [www.abacus-ipy.org](http://www.abacus-ipy.org)) project (a contribution to International Polar Year 2007–2008) under grants NE/D005833/1 and NE/D005884/1. We are grateful for the help of the staff at the Abisko Scientific Research Station. We thank L. English for assisting with the laboratory analyses, and J. Zaragoza-Castells and A. Bennett for their helpful comments on the manuscript.

## Author contributions

P.A.W., I.P.H., D.W.H. and M.S. designed the study. Soil surveys were carried out by I.P.H., M.S. and P.A.W., and <sup>14</sup>CO<sub>2</sub> collection and analysis was led by M.H.G. The plant community surveys were designed and carried out by B.J.F., V.L.S. and G.K.P. All authors contributed to writing the manuscript.

## Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on [www.nature.com/natureclimatechange](http://www.nature.com/natureclimatechange). Reprints and permissions information is available online at [www.nature.com/reprints](http://www.nature.com/reprints). Correspondence and requests for materials should be addressed to I.P.H.