Vascular plants promote ancient peatland carbon loss with climate warming

Tom N. Walker[1,2,3*], Mark H. Garnett[4], Susan E. Ward[2], Simon Oakley[3], Richard D. Bardgett[1] and Nicholas J. Ostle[2,3]

1. Faculty of Life Sciences, Michael Smith Building, The University of Manchester, Oxford Road, Manchester, M13 9PT, UK
2. Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster, LA1 4YQ, UK
3. Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster, LA1 4AP, UK
4. NERC Radiocarbon Facility, Scottish Enterprise Technology Park, Rankine Avenue, East Kilbride, Glasgow, G75 0QF, UK

* Corresponding Address: Department of Microbiology & Ecosystem Science, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

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Running title

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Abstract

Northern peatlands have accumulated one third of the Earth's soil carbon stock since the last Ice Age. Rapid warming across northern biomes threatens to accelerate rates of peatland ecosystem respiration. Despite compensatory increases in net primary production, greater ecosystem respiration could signal the release of ancient, century- to millennia-old carbon from the peatland organic matter stock. Warming has already been shown to promote ancient peatland carbon release, but, despite the key role of vegetation in carbon dynamics, little is known about how plants influence the source of peatland ecosystem respiration. Here, we address this issue using *in situ* ^{14}C measurements of ecosystem respiration on an established peatland warming and vegetation manipulation experiment. Results show that warming of approximately 1 °C promotes respiration of ancient peatland carbon (up to 2100 years old) when dwarf-shrubs or graminoids are present, an effect not observed when only bryophytes are present. We demonstrate that warming likely promotes ancient peatland carbon release *via* its control over organic inputs from vascular plants. Our findings suggest that dwarf-shrubs and graminoids prime microbial decomposition of previously 'locked-up' organic matter from potentially deep in the peat profile, facilitating liberation of ancient carbon as CO_2. Furthermore, such plant-induced peat respiration could contribute up to 40 % of ecosystem CO_2 emissions. If consistent across other sub-arctic and arctic ecosystems, this represents a considerable fraction of ecosystem respiration that is currently not acknowledged by global carbon cycle models. ~~.~~Ultimately, greater contribution of ancient carbon to ecosystem respiration may signal the loss of a previously stable peatland carbon pool, creating potential feedbacks to future climate change.

Introduction

Ecosystem respiration is the largest land to atmosphere carbon dioxide (CO_2) flux, accounting for more than half of all biospheric CO_2 emissions (IPCC, 2013). Climate warming is expected to increase ecosystem respiration globally (Davidson & Janssens, 2006; IPCC, 2013), but the magnitude of its impact will depend on additional factors that may themselves be temperature dependent (Davidson & Janssens, 2006; Metcalfe *et al.*, 2011). One such factor is vegetation, with shifts in plant community structure being reported in many biomes in response to climate change (Parmesan & Yohe, 2003; Elmendorf *et al.*, 2012). Vegetation is fundamental to terrestrial ecosystem carbon dynamics, being the source of photosynthetic carbon for the soil food web. It has been suggested that warming effects on plant growth and vegetation composition may drive greater uptake of atmospheric CO_2, offsetting losses caused by ecosystem respiration (Qian *et al.*, 2010; IPCC, 2013). However, ecosystem respiration has two components, autotrophic (plant) and heterotrophic (soil) respiration, that respond differently to climate and vegetation change (Dorrepaal *et al.*, 2009; Hartley *et al.*, 2012; Hicks Pries *et al.*, 2013). An increase in plant respiration is usually tightly coupled to an accompanying increase in photosynthesis (Hicks Pries *et al.*, 2013), resulting in faster CO_2 turnover but no change in net ecosystem CO_2 flux. Soil respiration, however, can increase independently of any compensatory responses in plant production (Hartley *et al.*, 2012). Given that the Earth's soils represent carbon that has been fixed and stored over several millennia, soil respiration encompasses the degradation of organic compounds with ages spanning from minutes to centuries. A greater proportional contribution of ancient carbon to soil respiration could thus signal a long-term loss of stable (Bosatta & Ågren, 1999), previously 'locked-up', organic matter from soil, irrespective of net ecosystem CO_2 flux (Dorrepaal *et al.*, 2009; Hartley *et al.*, 2012).

Northern peatlands are critical to the global carbon cycle, being the largest terrestrial organic carbon store and vulnerable to rapid temperature change (Dise, 2009; IPCC, 2013). Warming in these ecosystems has been shown to drive loss of ancient carbon from peat through ecosystem respiration (Dorrepaal *et al.*, 2009). However, vegetation composition can additionally alter the response of peatland ecosystem respiration to warming, due to different vegetation types varying in productivity (Ward *et al.*, 2013; Walker *et al.*, 2015), root and litter inputs (Cornelissen *et al.*, 2007; Ward *et al.*, 2015) and plant-microbe associations (Read *et al.*, 2004; Stępniewska & Goraj, 2014). Northern peatlands are dominated by four vegetation types, namely bryophytes, graminoids, dwarf-shrubs and trees (not naturally present in UK peatlands) (Rodwell, 1991), which differ considerably in their ecophysiological traits. For example, *Sphagnum* moss species produce decay-resistant litter that promotes low rates of soil respiration (Dorrepaal *et al.*, 2005), but are expected to have limited influence at the ecosystem level due to their low productivity relative to dwarf-shrubs and graminoids (Walker *et al.*, 2015). By comparison, the ubiquitous graminoid *Eriophorum vaginatum* grows rapidly and generates litter that is decomposable (Trinder *et al.*, 2008), leading to greater rates of decomposition and short-term carbon turnover (Ward *et al.*, 2009, 2015). Climate warming has been shown to increase ecosystem respiration relative to graminoid photosynthesis (Ward *et al.*, 2013), suggesting that increased dominance of graminoids in peatlands could accelerate carbon loss and create a positive feedback to climate change. In contrast, the dominant UK dwarf-shrub *Calluna vulgaris* has been shown to suppress activity throughout the soil food web (Ward *et al.*, 2015), and to reduce rates of soil respiration (Ward *et al.*, 2009). While the mechanism explaining the inhibitory effect of *C. vulgaris* on microbial activity is currently unclear, warming has been shown to cause the greatest increase in net ecosystem CO_2 uptake when dwarf-shrubs are present (Ward *et al.*, 2013), suggesting that greater dwarf-shrub growth in response to warming increases carbon sequestration. This

98 is in agreement with observations that warming-driven expansions of dwarf-shrubs in arctic
99 ecosystems increase net primary production (Qian *et al.*, 2010; Pearson *et al.*, 2013).
100 However, vascular plant production has also been associated with priming in the arctic,
101 leading to decomposition of ancient soil carbon (Hartley *et al.*, 2012). Moreover, studies in
102 northern peatlands have likewise shown that the presence of vegetation facilitates the
103 liberation of ancient carbon from peat (Hardie *et al.*, 2009). Ultimately, changes in the
104 composition of vegetation have the potential to amplify or diminish warming effects on
105 decomposition of ancient, previously 'locked-up', organic matter from peat. Nevertheless,
106 almost nothing is currently known about how changes in peatland vegetation composition
107 affect the source and age of peatland ecosystem respiration.
108
109 Numerous destructive methods exist for partitioning ecosystem respiration into component
110 sources (e.g. root exclusion, girdling and trenching; Kuzyakov, 2006). However, all cause
111 perturbations to the plant-soil system and none are able to explicitly determine CO_2 age.
112 Atomic bomb testing in the mid 20th Century caused a pulse of radiocarbon in the atmosphere,
113 known as the bomb-$^{14}CO_2$ spike (Levin *et al.*, 2010), which has been falling since then from a
114 value of approximately 190 %Modern to a contemporary value of 103 %Modern. The bomb-
115 $^{14}CO_2$ spike can be used to estimate the contribution of recent carbon (less than one year since
116 fixation; 103 %Modern), years- to decades-old carbon (104 %Modern to 190 %Modern) and
117 ancient carbon (e.g. centuries- to millennia-old; below 100 %Modern) to respired CO_2
118 (Hardie *et al.*, 2009; Hartley *et al.*, 2012; Hicks Pries *et al.*, 2013). While ecosystem
119 respiration represents carbon respired from a range of sources, radiocarbon measurements can
120 be coupled with isotope mass balance approaches that use the flux and isotopic signature of
121 ecosystem respiration to distinguish between plant and soil respiration (e.g. Hardie *et al.*,

2009; Hartley *et al.*, 2012). Together, these techniques represent a powerful tool for assessing warming and vegetation effects on the source of carbon respired from any ecosystem.

Here, we used an established peatland warming and vegetation manipulation experiment (Ward *et al.*, 2013) coupled with *in situ* ^{14}C measurements of ecosystem respiration to determine the effects of warming and different vegetation types on ancient peatland carbon release. Specifically, we tested the hypothesis that warming promotes the release of ancient, pre-bomb $^{14}CO_2$ spike, carbon through ecosystem respiration, and that its effects are modified by vegetation composition.

Materials & Methods

Study site and experimental design

The experiment was located on a sub-arctic blanket peat site in northern England (55°64'N, 2°45'W; altitude 550 m). Mean annual temperature is 6.0 °C and mean annual precipitation is 2016 mm (14 y average; UK Environmental Change Network). The vegetation community consists of three plant functional types, namely dwarf-shrubs, graminoids and bryophytes. We established a fully factorial climate warming and vegetation removal experiment in 2009 (Ward *et al.*, 2013). Vegetation manipulations were implemented by removing selected aboveground vegetation to create plots (1.5 m^2) containing none (bare), all combinations of one or two plant functional types and a fully vegetated control. A warming treatment was added to half of the plots using passive open top chambers (Marion *et al.*, 1997), generating ambient and elevated temperature versions of every vegetation treatment. For this study, we used ambient and elevated bare, single vegetation type and fully vegetated treatments from three replicate blocks. Ecosystem respiration and $^{14}CO_2$ data were collected in July 2013 (n = 3), alongside associated measurements of water table height (manual readings from dipwells), air temperature in the vegetation canopy and soil temperature at 5 cm below the surface (Hobo Pendant loggers, Onset, UK). Air temperature and precipitation during this growing season were within 0.15 °C and 0.01 mm of the 2000 to 2013 average, respectively (Supplementary Fig. S1). Additional measurements of ecosystem respiration taken during the 2009, 2010 and 2012 growing seasons also confirmed that 2013 measurements represented consistent interannual responses (Supplementary Fig. S2).

Ecosystem respiration flux measurements

Measurements of CO_2 were taken by enclosing permanent airtight collars (h = 10 cm; d = 30 cm) installed at the surface-peat interface with dark chambers (h = 35 cm). Ecosystem

156 respiration flux was measured in July 2013 using an infrared gas analyser (2 min closure time;
157 EGM-4, PP Systems, USA) (Ward *et al.*, 2013) and determined using a linear regression
158 approach that corrected for collar area, enclosure volume and air temperature (Gray *et al.*,
159 2013; Ward *et al.*, 2013).
160
161 *Radiocarbon sampling and analysis*
162 Samples were collected for ^{14}C analysis from the same chambers immediately after ecosystem
163 respiration measurements using an established molecular sieve sampling system (Hardie *et al.*,
164 2005; Hartley *et al.*, 2012). Enclosed chambers were first scrubbed of atmospheric CO_2 and
165 left to allow build-up of respired CO_2. After CO_2 accumulation (over 1000 ppm), chamber air
166 was circulated through a system containing a zeolite molecular sieve cartridge (type 13X, 1.6
167 mm pellets, Sigma-Aldrich, UK) to capture CO_2. Samples were returned to the NERC
168 Radiocarbon Facility (East Kilbride, Scotland), where CO_2 was thermally recovered (425 °C),
169 cryogenically purified and split into aliquots. One aliquot was concentrated onto a graphite
170 target and analysed for ^{14}C by accelerator mass spectrometry at the Scottish Universities
171 Environmental Research Centre (SUERC, East Kilbride, Scotland). Following convention[29],
172 ^{14}C data were normalised to -25 ‰ $\delta^{13}C$ to correct for mass-dependent isotopic fractionation
173 using:
174
175 (1)

$$N = S \times \left(\frac{1 + (-25 \div 10^3}{1 + \left(\delta^{13}C_S \div 10^3\right)} \right)$$

176
177 Where N is the normalised $^{14}C/^{13}C$ ratio of the sample, S is the raw $^{14}C/^{13}C$ ratio of the sample
178 and $\delta^{13}C_S$ is the $^{13}C/^{12}C$ ratio (‰) of the sample as reported *via* analysis from a dual isotope

ratio mass spectrometer. Normalised data were expressed (%Modern) with reference to the activity of the NBS Oxalic Acid international radiocarbon standard using:

(2)

$$\%\text{Modern} = \left(\frac{\text{N}}{\text{O}}\right) \times 100$$

Where O is the $^{14}C/^{13}C$ ratio of the standard normalised to -19 ‰ $\delta^{13}C$ (Supplementary Table S1). Another aliquot was analysed for $^{13}C/^{12}C$ on a dual input isotope ratio mass spectrometer (Thermo Fisher Delta V, Germany), expressed as ‰ relative to the Vienna PDB standard.

To correct for any atmospheric CO_2 that may have leaked into the chambers during sampling, we used $\delta^{13}C$ data to calculate the proportion of atmospheric CO_2 in measured samples (Gaudinski *et al.*, 2000):

(3)

$$\text{Air} = \frac{(\delta_s - \delta_k)}{(\delta_a - \delta_k)}$$

Where δ_S is the sample $\delta^{13}C$ value (‰), δ_a is the atmospheric $\delta^{13}C$ value (measured at -9 ‰ at time of sampling) and δ_k is the sample $\delta^{13}C$ value in the absence of any atmospheric contamination (‰). We derived δ_k using Keeling plots generated separately for different treatments (Supplementary Fig. S3). Sample ^{14}C contents were then corrected for atmospheric contamination using:

(4)

$$\Delta_{cn} = \frac{\Delta_n - (\mathrm{Air} \times \Delta_a)}{(1 - \mathrm{Air})}$$

Where Δ_{cn}, Δ_n and Δ_a are the ^{14}C contents (%Modern) of the corrected sample, uncorrected sample and atmosphere (measured at 103 %Modern at time of sampling), respectively (Gaudinski *et al.*, 2000).

Two-component partitioning calculations

We used a two-component isotope mass balance (Gaudinski *et al.*, 2000; Hardie *et al.*, 2009) to determine whether any vegetation type facilitated additional respiration from peat. Specifically, we described ecosystem respiration in different treatments as the product of peat respiration (i.e. ecosystem respiration in the absence of plants) versus plant respiration (i.e. pure plant respiration plus additional peat respiration induced by the presence of plants):

(5) $$(\Delta_e \times f_e) = (\Delta_p \times f_p) + (\Delta_s \times f_s)$$

Where Δ_p, Δ_e and Δ_s are the ^{14}C contents (%Modern) of plant respiration, ecosystem respiration and peat respiration, respectively, and f_p, f_e and f_s are their fluxes (mg CO_2-C m^{-2} h^{-1}). We assumed that the ^{14}C content and flux of bare treatment respiration represented that of peat respiration, and that plant respiration flux could be calculated as:

(6) $$f_p = f_e - f_s$$

In doing so, we were able to derive the ^{14}C content (age) of plant respiration as the only unknown in Equation 5:

225 (7) $$\Delta_p = ((\Delta_e \times f_e) - (\Delta_s \times f_s)) / f_p$$

226

227 We expressed plant respiration ^{14}C content both as %Modern and as a radiocarbon age (years
228 BP, where 0 years BP = AD 1950 (Stuvier & Polach, 1977)), the latter based on the
229 radioactive decay rate of ^{14}C (Equation 8). Following convention, plant respiration ^{14}C
230 contents greater than 100 %Modern were described as 'modern' (i.e. between AD1950 and
231 present day).

232

233 (8) $$\text{years BP} = -8033 \times \ln(\Delta_p / 100)$$

234

235 As autotrophs, plants respire carbon derived almost exclusively from recent photosynthesis,
236 so pure plant respiration has a ^{14}C content of approximately 103 %Modern (at the time of
237 sampling; see Supplementary Information for supporting data). Any deviation of plant
238 respiration ^{14}C content away from this signature therefore represents dilution by an additional,
239 older, source of respiration (i.e. plant-induced peat respiration), and the magnitude of this
240 deviation approximates the minimum mean age of the additional source.

241

242 Partitioning calculations were similarly performed on $\delta^{13}C$ data (Dorrepaal *et al.*, 2009) to
243 determine the $\delta^{13}C$ value of plant respiration in different treatments, using:

244

245 (9) $$\delta_p = ((\delta_e \times f_e) - (\delta_s \times f_s)) / f_p$$

246

247 Where δ_p, δ_e and δ_s are the $\delta^{13}C$ values (‰) of plant respiration, ecosystem respiration and
248 peat respiration, respectively.

249

All partitioning calculations were performed at the treatment level (n = 3), using means for ^{14}C content (Hardie *et al.*, 2009) and data generated by Keeling plots for $\delta^{13}C$ to correct for atmospheric contamination (Supplementary Fig. S3; Dorrepaal *et al.*, 2009). Using this approach, we were able to characterise vegetation and warming effects on the presence, minimum age (^{14}C content) and potential origin ($\delta^{13}C$ value; Dorrepaal *et al.*, 2009; Billett *et al.*, 2012) of plant-induced peat respiration.

Modelling plant-induced peat respiration flux

Where plant-induced peat respiration occurred, we estimated its potential absolute flux (mg CO_2-C m^{-2} h^{-1}) by expanding the two-component mass balance approach to distinguish between pure plant respiration and plant-induced peat respiration (Hardie *et al.*, 2009):

$$(\Delta_e \times f_e) = (\Delta_{pl} \times f_{pl}) + (\Delta_i \times f_i) + (\Delta_s \times f_s) \quad (10)$$

Where Δ_{pl} and Δ_i are the ^{14}C contents (%Modern) of pure plant respiration and plant-induced peat respiration, respectively, and f_{pl} and f_i are their fluxes (mg CO_2-C m^{-2} h^{-1}). We assumed that the ^{14}C content and flux of bare treatment respiration represented that of peat respiration, that the ^{14}C content of pure plant respiration was 103 %Modern (see Supplementary Information) and that the fluxes of plant-induced peat respiration and pure plant respiration could be calculated using Equations 11 and 12, respectively.

$$f_i = (f_p / 100) \times a \quad (11)$$

$$f_{pl} = f_p - f_i \quad (12)$$

Where a is the contribution (%) of plant-induced peat respiration flux to plant respiration flux. Unique solutions were not possible due to the presence of too many unknowns, so we modelled scenarios where the contribution of plant-induced peat respiration was between 10 and 50 % of the plant respiration flux (10 % intervals).

Through this, we derived a range of possible fluxes (mg CO_2-C m^{-2} h^{-1}) for plant-induced peat respiration, which were considered plausible if corresponding ^{14}C contents indicated a source of respiration that was fixed less than 5000 years BP (based on the approximate age of basal peat at the site; Billett *et al.*, 2012).

Statistical analysis

Linear mixed effects models were undertaken in R (R Development Core Team, Austria) using the package "nlme" to test for effects of warming, vegetation type and their interaction on ecosystem respiration flux and ^{14}C content. For ecosystem respiration flux we included a random term for block, and for ^{14}C content we included random terms for block and sample temperature (mean of internal chamber temperature during enclosure; measured with Hobo Pendant Loggers, Onset, UK). In all cases, model assumptions were scrutinised using fitted values versus residuals plots and QQ plots; where necessary, response variables were $\log_{10}$ transformed and models were refined to account for unequal variance between levels of explanatory variables (Zuur *et al.*, 2010). Significance of fixed effects was determined using single term deletions coupled with likelihood ratio (LR) tests, retaining variables in models with $P < 0.05$.

To determine whether observed responses of ecosystem respiration ^{14}C content occurred due to changes in microclimate, we used Pearson's Product Moment Correlations to test for

300 significant associations between ecosystem respiration ^{14}C content (%Modern) and air
301 temperature (ºC), soil temperature (ºC) and water table height (cm below surface) irrespective
302 of experimental treatment. Finally, we used a Pearson Product Moment Correlation to
303 determine whether older modelled plant respiration ages (i.e. lower ^{14}C content) were
304 significantly associated with carbon from deeper in the peat profile (i.e. higher $\delta^{13}C$ value;
305 Dorrepaal *et al.*, 2009; Billett *et al.*, 2012).
306

Results

Warming and vegetation effects on ecosystem respiration flux and ^{14}C content

Ecosystem respiration flux (Fig. 1a) was greatest when either dwarf-shrubs or graminoids were present (LR = 36.6, d.f. = 4,12, $P < 0.0001$), being increased by 145 % and 144 % relative to the bare and bryophyte only treatments, respectively. By comparison, ecosystem respiration flux did not significantly differ between the bare and bryophyte only treatments. Warming significantly increased ecosystem respiration flux in the bare (by 111 %) and dwarf-shrub only (by 63 %) treatments (LR = 12.3, d.f. = 4,16, $P = 0.0156$), but had no effect in the bryophyte, graminoid only or fully vegetated treatments.

Ecosystem respiration ^{14}C content (%Modern; Fig. 1b) was reduced in the presence of vegetation (LR = 37.1, d.f. = 4,13, $P < 0.0001$). Warming decreased ecosystem respiration ^{14}C content by 2 %Modern in the dwarf-shrub only treatment and increased it by 1 %Modern in the fully vegetated treatment (LR = 15.8, d.f. = 4,18, $P = 0.0034$). Warming did not affect ecosystem respiration ^{14}C content in the bare, bryophyte only or graminoid only treatments. When considered irrespective of experimental treatment, we found that ecosystem respiration ^{14}C content was not significantly associated with air temperature ($r = 0.22$, d.f. = 24, $P = 0.2704$), soil temperature ($r = 0.10$, d.f. = 17, $P = 0.6694$) or water table height ($r = -0.05$, d.f. = 28, $P = 0.7817$). This means that warming had the greatest effect on peat ^{14}C release *via* its influence on vegetation.

Warming and vegetation effects on plant-induced peat respiration

Two-component partitioning calculations showed that modelled plant respiration deviated from a pure plant respiration signature (i.e. 103 %Modern) in all but the warmed bryophyte only treatment (Table 1), indicating that vegetation facilitated plant-induced peat respiration

in these treatments. At ambient temperature the mean age of plant respiration only deviated considerably from a pure plant signature (i.e. 103 %Modern) in the bryophyte only treatment (Fig. 2). Specifically, plant respiration in the ambient bryophyte only treatment had a mean age of 412 years BP (94.8 %Modern), whereas in the ambient dwarf-shrub only treatment it had a mean age of 40 years (99.5 %Modern) and was modern in the ambient graminoid only and fully vegetated treatments (104.0 to 101.5 %Modern, respectively).

Warming facilitated plant-induced peat respiration when dwarf-shrubs or graminoids were present, an effect not observed when only bryophytes were present (Table 1). Dwarf-shrubs had a larger effect than graminoids, in that warming increased the mean age (Fig. 2) of plant respiration by approximately 900 years in the dwarf-shrub only treatment (i.e. a reduction of 10.9 %Modern) and by approximately 300 years in the graminoid only treatment (i.e. a reduction of 7.6 %Modern). However, the strongest warming effect on the mean age of plant respiration was observed when both dwarf-shrubs and graminoids were present in the fully vegetated treatment, where it increased by approximately 2100 years under warming (i.e. a reduction of 24.1 %Modern).

The mean $\delta^{13}C$ value of plant respiration did not strongly differ between vegetation types at ambient temperature (Table 1). However, warming increased the mean $\delta^{13}C$ value of plant respiration by 6.4 ‰ in the dwarf-shrub only treatment and by 5.9 ‰ in the graminoid only treatment, and its effect was greatest in the fully vegetated treatment where it increased the mean $\delta^{13}C$ value of plant respiration by 14.3 ‰. We also found a significant negative correlation between the modelled ^{14}C content (%Modern) and $\delta^{13}C$ value (‰) of plant respiration irrespective of experimental treatment (r = -0.82, d.f. = 5, P = 0.0253), with warmed plots possessing lower ^{14}C contents and higher $\delta^{13}C$ values (Fig. 3).

Three-component partitioning calculations showed that modelled fluxes of plant-induced peat respiration (Table 2) were lowest in the ambient bryophyte only treatment, ranging from 6.1 mg CO_2-C m^{-2} h^{-1} to 15.3 mg CO_2-C m^{-2} h^{-1} (assuming a 20 % to 50 % contribution to the total plant respiration flux, respectively). Modelled fluxes of plant-induced peat respiration were highest when all vegetation types were present at between 16.5 mg CO_2-C m^{-2} h^{-1} (10 % contribution) and 82.6 mg CO_2-C m^{-2} h^{-1} (50 % contribution), but were also high in the graminoid only treatment at between 14.9 mg CO_2-C m^{-2} h^{-1} (10 % contribution) and 69.4 mg CO_2-C m^{-2} h^{-1} (50 % contribution).

Warming increased the minimum proportional contribution of plant-induced peat respiration to total plant respiration when vascular plants were present (Table 2), an effect not observed in the bryophyte only treatment. Specifically, the contribution of plant-induced peat respiration increased from a minimum of 10 to 20 % in the graminoid only treatment, from 10 to 30 % in the dwarf-shrub only treatment and from 10 to 50 % in the fully vegetated treatment. Despite this, warming reduced modelled fluxes of plant-induced peat respiration in all but the dwarf-shrub only treatment, where they increased to between 26.5 mg CO_2-C m^{-2} h^{-1} (30 % contribution) and 44.2 mg CO_2-C m^{-2} h^{-1} (50 % contribution).

376 **Discussion**

377 There is mounting concern that rapid warming in northern peatlands is causing liberation of
378 ancient carbon from peat, raising questions about the future fate of the peatland carbon stock
379 (Dorrepaal *et al.*, 2009; Hicks Pries *et al.*, 2013). In this study, we show that warming effects
380 on the source of peatland ecosystem respiration are dependent on vegetation composition. We
381 demonstrate that warming of approximately 1 ºC triggers respiration of ancient peatland
382 carbon when dwarf-shrubs or graminoids are present, and that this effect is negated when
383 bryophytes are alone in the plant community. While measurements were taken on a single
384 sampling date, and hence must be interpreted with caution, both climate and CO_2 fluxes
385 during sampling were representative of five-year trends (Supplementary Figs S1 & S2). This
386 study consequently reveals that warming effects on ancient peatland carbon release vary with
387 vegetation composition, and furthermore that its effects only occur in the presence of vascular
388 plants. Such plant-induced peat respiration represents a significant contribution to ecosystem
389 respiration and a source of CO_2 to the atmosphere that, if consistent across peatland
390 ecosystems, is currently not considered by the majority of Earth System Models.
391
392 We found that ecosystem respiration ^{14}C content decreased in the presence of all vegetation
393 types, with fully vegetated plots respiring CO_2 with a ^{14}C concentration most similar to that of
394 the contemporary atmosphere. This confirms that the assimilation of modern photosynthetic
395 carbon by the plant community directly influences the source of peatland ecosystem
396 respiration. Further, warming only affected ecosystem respiration ^{14}C content when dwarf-
397 shrubs were present (i.e. the dwarf-shrub only and fully vegetated treatments), having no
398 effect on the ^{14}C content of bare peat respiration despite significantly raising CO_2 efflux.
399 Together, these findings show that dwarf-shrubs, and to some extent graminoids, influence
400 warming effects on the source of ecosystem respiration. At the same time, ecosystem

401 respiration flux was greatest when either graminoids or dwarf-shrubs were present, further
402 illustrating the key role of vascular plants in regulating peatland CO_2 fluxes (e.g. Ward *et al.*,
403 2013). Our discovery is supported by five years of CO_2 flux data from the same experiment
404 (Supplementary Fig. S2), suggesting that this is a long-term response with no acclimation to
405 either warming or vegetation change (Hartley *et al.*, 2008; Dorrepaal *et al.*, 2009). Two
406 scenarios could explain the reduction in ecosystem respiration ^{14}C content observed in
407 vegetated treatments. First, vegetation may increase the proportional contribution of recently
408 fixed carbon to ecosystem respiration, diluting its ^{14}C content towards that of the
409 contemporary atmosphere. This could occur *via* either greater plant respiration or enhanced
410 mineralisation of recent root inputs by soil microbes. Under this scenario, vegetation would
411 only affect the turnover of modern CO_2, having no bearing on ancient carbon release. Second,
412 vegetation may also prime microbial mineralisation of ancient carbon already present in peat
413 (i.e. below 100 %Modern), the release of which would also dilute the ^{14}C content of
414 ecosystem respiration. Under this scenario, vegetation would facilitate ancient carbon release,
415 with potential consequences for the fate of the peatland carbon stock.
416
417 Using mass balance approaches to distinguish between alternative scenarios, we found
418 contrasting effects of bryophytes and vascular plants on the source of peatland ecosystem
419 respiration. The presence of any vegetation induced additional peat respiration at ambient
420 temperature. However, warming triggered respiration of ancient carbon exclusively when
421 dwarf-shrubs or graminoids (i.e. vascular plants) were present, halting it entirely in the
422 bryophyte only treatment. Specifically, warming in vascular plant treatments increased both
423 the mean age of plant-induced peat respiration by up to 2100 years and its minimum
424 proportional contribution to plant respiration by up to 40 % (i.e. from 10 % to 50 % in the
425 fully vegetated treatment; Table 2). Through this, we reveal that the occurrence of vascular

plants facilitates warming-driven liberation of ancient peatland carbon. Dwarf-shrubs had the strongest effect, facilitating respiration with a mean age of approximately 1000 to 2100 years old under warming, potentially at a rate of between 25 and 44 mg CO_2-C m^{-2} h^{-1}. Since both climate and CO_2 fluxes during sampling were broadly representative of five-year trends (Supplementary Figs S1 & S2), this suggests a considerable loss of ancient, possibly stable (Bosatta & Ågren, 1999), carbon from northern peatlands. Despite this, we found that absolute fluxes of ecosystem respiration on the day of measurement were unaffected by warming in the bryophyte, graminoid and fully vegetated treatments. Warming-driven increases in the age of plant-induced peat respiration were thus accompanied by declines in absolute fluxes of plant-induced peat respiration in these treatments. This was most evident in the bryophyte only treatment, where warming reversed a small loss (6 to 15 mg CO_2-C m^{-2} h^{-1}) of approximately 400-year-old carbon that occurred in this treatment at ambient temperature. However, in real terms, ecosystem respiration was 1.5 to 3 times lower in the bryophyte only treatment than in any other vegetated treatment, further indicating that vascular plants have the greatest influence over ancient peatland carbon release. Indeed, warming in the dwarf-shrub only treatment increased ecosystem respiration flux, resulting in a higher plant-induced peat respiration flux (27 to 44 mg CO_2-C^{-2} h^{-1}) while also increasing its mean age by approximately 1000 years. Together, these findings indicate that vascular plants, and particularly dwarf-shrubs, facilitate a greater contribution of ancient peatland carbon to ecosystem respiration under climate warming, albeit it at a lower absolute rate on this sampling date. Given that the long-term sequestration of modern photosynthetic carbon as soil organic matter is far from certain (Conant *et al.*, 2011), such a shift in the source of respired CO_2 may signal the loss of a previously stable carbon pool.

450 Several mechanisms have been proposed to explain warming effects on peat, or soil
451 respiration, reflecting both its direct action on belowground microclimate and its indirect
452 action *via* changes to plant physiology (Davidson & Janssens, 2006; Fontaine *et al.*, 2007;
453 Dorrepaal *et al.*, 2009; Metcalfe *et al.*, 2011). In this study, our results imply that vegetation is
454 mostly responsible since we found no correlations between ecosystem respiration ^{14}C content
455 and air temperature, soil temperature or water table height. This is further supported by our
456 observation that warming had no effect on ecosystem respiration ^{14}C content in the absence of
457 vegetation. There is strong evidence that plants are able to prime organic matter
458 decomposition (Fontaine *et al.*, 2007; Hartley *et al.*, 2012; Lindén *et al.*, 2014), for instance
459 by increasing microbial activity or intensifying nutrient competition within the soil food web.
460 We suggest that priming occurs under warming when vascular plants are present, and that this
461 response is especially strong with dwarf-shrubs due to associated mycorrhizae facilitating
462 decomposition of recalcitrant, older (Bosatta & Ågren, 1999; Fontaine *et al.*, 2007) carbon
463 (Read *et al.*, 2004). Bryophytes, as rootless organisms, cannot similarly prime decomposition,
464 and did not facilitate release of ancient carbon under warming in this study. The priming
465 effects caused by vascular plants may even penetrate deep into the peat profile, for two
466 reasons. First, plant-induced peat respiration was at least twice as old as acrotelm (root-zone)
467 peat previously sampled from the same site (Hardie *et al.*, 2007). Second, warming increased
468 the modelled $\delta^{13}C$ value of plant respiration in vascular plant treatments, and we also found
469 that older (^{14}C-depleted) respiration was significantly $\delta^{13}C$-enriched. This suggests that
470 warming increases the contribution of deep peat carbon to ecosystem respiration in the
471 presence of vascular plants (Dorrepaal *et al.*, 2009; Billett *et al.*, 2012). While $\delta^{13}C$-enriched
472 respiration under rooting plants could alternatively be caused by transport of CO_2 associated
473 with methanogenesis (Stępniewska & Goraj, 2014), this is unlikely to be responsible here,

474 since graminoids, which are key methane conduits (Gray *et al.*, 2013), had weaker effects on
475 ancient carbon release than dwarf-shrubs.
476
477 While priming in mineral soils is well documented, there is currently no consensus on its
478 occurrence in organic soils (e.g. Hartley *et al.*, 2012; Lindén *et al.*, 2014; Linkosalmi *et al.*,
479 2015). Here, we present *in situ* evidence that vascular plants can prime decomposition of
480 existing organic matter in peatlands, and moreover that they can also facilitate warming-
481 driven release of ancient carbon. Defining such persistent plant-induced peat respiration as
482 'priming', however, should be done with caution, especially given that priming usually refers
483 to pulses of respiration caused by episodic release of carbon into soil. Indeed, plant-induced
484 peat respiration in this study comprised a significant fraction of ecosystem respiration even in
485 the fully vegetated treatment at ambient temperature (i.e. normal conditions). Regardless, it is
486 apparent from these and other findings that vascular plants are key mediators of organic
487 matter decomposition in many ecosystems, yet Earth System Models currently do not
488 acknowledge any form of plant-induced peat (or soil) respiration (Ostle *et al.*, 2009; Lou *et al.*,
489 2015). If such fluxes are universal across peatland and other sub-arctic and arctic ecosystems,
490 we suggest that their incorporation into global carbon cycle models may greatly improve
491 long-term predictions of soil carbon stocks, and, through this, future climate change.
492
493 In conclusion, we show that climate warming in peatlands promotes ancient carbon release
494 through ecosystem respiration, and that this effect is facilitated by the presence of vascular
495 plants. More work is now needed to determine the impacts of this discovery on the long-term
496 persistence of previously 'locked-up' carbon in peatlands, particularly given previous findings
497 that warming causes the greatest increase in net CO_2 sink strength when dwarf-shrubs are
498 present in these shrub dominated ecosystems (Ward *et al.*, 2013). Nevertheless, our findings

499 have implications for feedbacks to the climate system due to both rising temperatures (IPCC,
500 2013) and the global significance of the peatland carbon stock (Dise, 2009). At the same time,
501 vascular plant expansions are dominating vegetation change across many northern biomes
502 (Elmendorf *et al.*, 2012; Pearson *et al.*, 2013). As such, this study raises questions about the
503 fate of carbon stored not only in peatlands, but also in other high latitude ecosystems that
504 have potential to feed back to climate change.

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511

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615 **Supporting Information Captions**

616 Supporting information: determining pure plant respiration ^{14}C content; Supplementary

617 Tables S1, S2; Supplementary Figs S1-3.

618

619 **Tables**

620 Table 1. The modelled age (^{14}C content) and potential source ($\delta^{13}C$ value) of combined plant
621 and plant-induced peat respiration.

622

	^{14}C content		**$\delta^{13}C$ value**	
	Ambient	**Elevated**	**Ambient**	**Elevated**
	%Modern	%Modern	‰	‰
Bryophytes	94.8	-[1]	-30.6	-[1]
Graminoids	104.0	96.4	-27.0	-21.1
Dwarf-Shrubs	99.5	88.6	-27.4	-21.0
Fully vegetated	101.5	77.4	-29.5	-15.2

623 [1] Bryophytes prevented any plant-induced peat respiration at elevated temperature (Supplementary Methods)

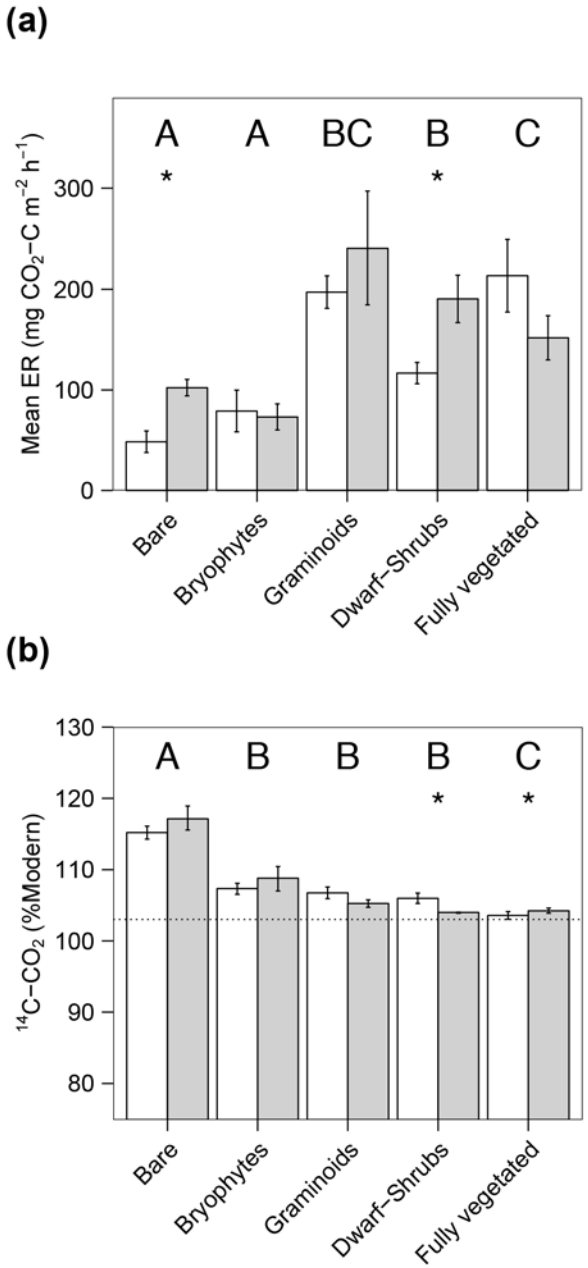
624 Table 2. The modelled flux (mg CO_2-C m^{-2} h^{-1}) of plant-induced peat respiration under
625 scenarios where it represents 10 to 50 % of the plant respiration flux. Missing values indicate
626 scenarios in which modelled plant-induced peat respiration ^{14}C contents were implausible (i.e.
627 greater than 5000 years BP; Billett *et al.*, 2012), and fluxes in parentheses indicate scenarios
628 in which modelled plant-induced peat respiration ^{14}C contents were modern (i.e. >
629 100 %Modern).
630

Contribution to flux (%)	**Bryophytes**		**Graminoids**		**Dwarf-Shrubs**		**Fully vegetated**	
	Ambient	Elevated[†]	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
10	-	n.a.	(14.9)	-	6.8	-	16.5	-
20	6.1	n.a.	(29.8)	27.7	13.7	-	33.0	-
30	9.2	n.a.	(44.7)	41.6	20.5	26.5	49.6	-
40	12.2	n.a.	(59.5)	55.5	27.3	35.3	66.1	-
50	15.3	n.a.	(74.4)	69.4	34.2	44.2	82.6	24.8

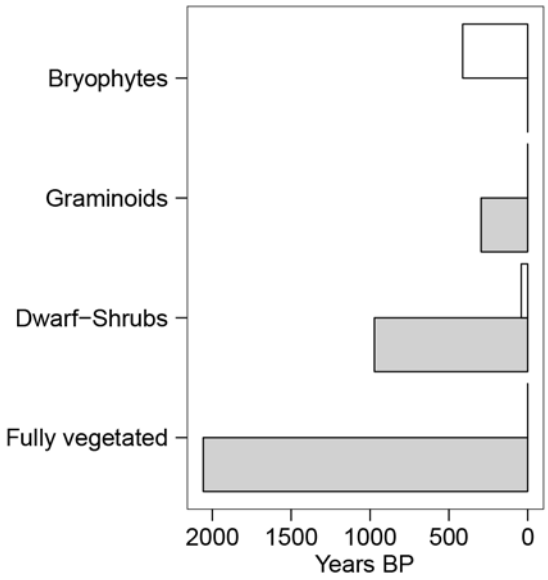
631 [†] Bryophytes prevented any plant-induced peat respiration occurring at elevated temperature
632

Figures

Fig. 1. Warming and vegetation effects on the size and source of ecosystem respiration. Mean (± SE) ecosystem respiration (ER) (a) flux (mg CO_2-C m^{-2} h^{-1}) and (b) ^{14}C content (%Modern) under different vegetation treatments and an ambient (white) or elevated (grey) warming treatment. Significant differences (P < 0.05) are shown by different letters for vegetation type and by a '*' for warming. For (b), changes in ^{14}C content towards that of the contemporary atmosphere (dotted line; 103 %Modern) could be driven by plant respiration (~ 103 %Modern) or by plants promoting mineralisation of ancient (< 100 %Modern) peat carbon.



641 **Fig. 2. Warming and vegetation effects on ancient peatland carbon release.** The modelled
642 mean radiocarbon age of plant respiration (years BP) under different vegetation treatments
643 and an ambient (white) or elevated (grey) warming treatment. Deviations from a modern
644 signature indicate the presence of plant-induced peat respiration, and the magnitude of this
645 deviation approximates the mean minimum age of the additional carbon source. Bryophytes
646 prevented any plant-induced peat respiration at elevated temperature.



647
648
649
650

Fig. 3. Relationship between the age and potential source of combined plant and plant-induced respiration. Age (^{14}C content; %Modern) and source (δ^{13}C value; ‰) were derived at the treatment level using a partitioning approach and are displayed as either ambient (white) or elevated (grey) temperature. There was a significant relationship between age and source (Pearson Product Moment Correlation: r = -0.82, d.f. = 5, P = 0.0253).