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Contact CEH NORA team at
noraceh@ceh.ac.uk

1 **Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation**
2 **composition**

3

4 Authors with email addresses. (Affiliations as number suffix – see below)

5 **Susan E. Ward**^{1,2} Email: s.e.ward@lancaster.ac.uk

6 **Nicholas J. Ostle**² Email: no@ceh.ac.uk

7 **Simon Oakley**² Email: soak@ceh.ac.uk

8 **Helen Quirk**¹ Email: h.quirk@lancaster.ac.uk

9 **Peter A. Henrys**² Email: pehn@ceh.ac.uk

10 **Richard D. Bardgett**^{1,3} . Email: richard.bardgett@manchester.ac.uk.

11 Affiliations:

12 1. Soil and Ecosystem Ecology Laboratory, Lancaster Environment Centre, Lancaster
13 University, Bailrigg, Lancaster, LA1 4YQ, UK.

14 2. Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue,
15 Bailrigg, Lancaster, LA1 4AP, UK.

16 3. Faculty of Life Sciences, Michael Smith Building, The University of Manchester, Oxford
17 Road, Manchester, M13 9PT, UK.

18

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37 Corresponding Author

38 Susan E Ward. Email: s.e.ward@lancaster.ac.uk. Tel: +44 (0) 1524 510531.

39

40 Authorship statement.

41 RDB and NJO conceived and designed the experiment, with input into the design from SEW.

42 SEW, SO, HQ performed the study, collected the data, and analysed the samples. SEW and

43 PAH analysed the data, and SEW, RDB, NO wrote the paper, to which all authors

44 contributed with discussions and text.

45

46 **ABSTRACT**

47 Understanding the effects of warming on greenhouse gas feedbacks to climate change
48 represents a major global challenge. Most research has focused on direct effects of warming,
49 without considering how concurrent changes in plant communities may alter such effects.
50 Here, we combined vegetation manipulations with warming to investigate their interactive
51 effects on greenhouse gas emissions from peatland. We found that although warming
52 consistently increased respiration, the effect on net ecosystem CO₂ exchange depended on
53 vegetation composition. The greatest increase in CO₂ sink strength after warming was when
54 shrubs were present, and the greatest decrease when graminoids were present. CH₄ was more
55 strongly controlled by vegetation composition than by warming, with largest emissions from
56 graminoid communities. Our results show that plant community composition is a significant
57 modulator of greenhouse gas emissions and their response to warming, and suggest that
58 vegetation change could alter peatland carbon sink strength under future climate change.

59

60 **INTRODUCTION**

61 There is growing concern about how biosphere carbon dynamics will respond to expected
62 climate change, with evidence suggesting that atmospheric warming will increase soil
63 respiration and greenhouse gas feedbacks (Bardgett *et al.* 2008; Craine *et al.* 2010). At the
64 same time, terrestrial ecosystems are being subjected to increasing environmental pressures
65 and human demands that are affecting vegetation community composition and diversity
66 globally (Thuiller *et al.* 2005; Stevens *et al.* 2010). Despite widespread recognition that both
67 climate and vegetation change can act independently as drivers of ecosystem carbon
68 dynamics (De Deyn *et al.* 2008; Dorrepaal *et al.* 2009), we know little about the potential role
69 in the carbon cycle of interactions between them (Bardgett *et al.* 2013). Indeed, experiments
70 that explore the independent and interactive effects of abiotic and biotic factors as controls
71 over ecosystem functioning are few (Hooper *et al.* 2005; Kardol *et al.* 2010), despite the
72 suggestion that the magnitude of effects of vegetation change on ecosystem processes can be
73 comparable to that of environmental change (Hooper *et al.* 2012; Tilman *et al.* 2012).

74

75 Carbon rich peatlands provide an ideal model system in which to examine the influence of
76 warming and vegetation change on ecosystem greenhouse gas emissions; they have a
77 relatively simple plant community structure, are recognised as important global sinks and
78 sources of the greenhouse gases CO₂ and CH₄ respectively, and are vulnerable to land use
79 and climate change (Dise 2009). Climate change models predict that northern latitude
80 peatlands will be subjected to higher temperatures with longer growing seasons (IPCC 2007),
81 and that this change will be accompanied by an increase in vascular plants at the expense of
82 bryophytes and lichens (Walker *et al.* 2006; Gallego-Sala & Prentice 2013). Recent work has
83 shown that experimental warming can significantly increase rates of peatland ecosystem
84 respiration (Dorrepaal *et al.* 2009; Briones *et al.* 2010), and that drought can induce carbon

85 loss *via* changes in soil enzyme activity (Fenner & Freeman 2011). Other peatland studies
86 suggest that there are key differences in the ecophysiological traits of dominant plant
87 functional groups, that have a strong regulatory role in ecosystem carbon dynamics (Ward *et*
88 *al.* 2012). Despite this, it is not known whether changes in plant community structure, and
89 the presence or absence of dominant peatland plant functional groups (*i.e.*, shrubs,
90 graminoids and bryophytes), will modify the impact of warming on ecosystem greenhouse
91 gas fluxes. This represents a serious knowledge gap, given that most plant communities
92 globally are subject to both vegetation and climate change, but their combined impact on
93 greenhouse gas fluxes is not known.

94

95 To redress this gap in knowledge, we established a unique field experiment in spring 2008
96 with the aim of examining the independent and interactive effects of warming and plant
97 functional composition on greenhouse gas exchange in a peatland ecosystem. We used a
98 plant removal approach to manipulate vegetation composition (Diaz *et al.* 2003; Wardle &
99 Zackrisson 2005) from an area of ombrotrophic blanket bog in northern England. Vegetation
100 manipulations included removal of all possible combinations of the three dominant plant
101 functional groups, namely ericoid shrubs, graminoids (sedges), and bryophytes/lichens.
102 Warming was induced passively on half of the experimental plots, using randomly allocated
103 hexagonal open-top chambers (OTCs) (Marion *et al.* 1997) which increased air temperatures
104 by approximately 1°C over the mid-day period. We present results from field measurements
105 of greenhouse gas fluxes, namely net ecosystem exchange (NEE) of CO₂, ecosystem
106 respiration, CH₄ and N₂O fluxes for all times of year spanning two growing seasons. We
107 show that, although rates of ecosystem respiration were consistently increased by warming
108 across all vegetation types, the effect of warming on NEE, once differences in photosynthetic
109 uptake of CO₂ were taken into account, was dependent on plant community composition.

110 More specifically, the greatest increase in CO₂ sink strength after warming was observed
111 when shrubs only (dominated by *Calluna vulgaris*) were present. Also, warming reduced
112 mean CO₂ sink strength in the presence of graminoids, and increased CO₂ sink strength when
113 graminoids were absent. In addition, we found that the efflux of CH₄ was more strongly
114 controlled by plant community composition than by warming, with largest emissions coming
115 from sedge (*Eriophorum vaginatum*) dominated communities. Taken together, these findings
116 highlight the importance of plant community composition as a driver of carbon cycling
117 processes, and show that plant community composition can modulate the effects of warming
118 on net ecosystem exchange of CO₂.

119

120 **MATERIALS AND METHODS**

121

122 **Study site.**

123 The study site was situated on an area of ombrotrophic blanket bog within the Moor House
124 National Nature Reserve in northern England (54°65' N, 2°45' W). The site altitude was
125 550m, the mean annual temperature is 5.8°C, and the mean annual precipitation 2048mm
126 (UK Environmental Change Network, www.data.ecn.ac.uk). The mean depth of peat at the
127 site was 1.17m (± 0.01), and the mean pH 4.07 (± 0.01). Abiotic conditions, including air
128 and soil temperature, solar radiation, photosynthetically active radiation and rainfall at the
129 site were recorded by the Moor House automated weather station (www.ecn.ac.uk)
130 (Supporting information, Table S1).

131

132 **Vegetation manipulation and climate warming.**

133 Vegetation removals were undertaken by hand, from areas measuring 1.5 x 1.5m, separated
134 by a buffer zone of at least 1m from adjoining plant removal plots. Shoots of shrubs and
135 graminoids were cut back to litter layer level, and all green (photosynthetic) tissues of
136 bryophytes were removed, taking care to minimise disturbance of the soil and remaining
137 vegetation types. Wooden boardwalks were installed on two sides of each removal plot, to
138 allow access to the sampling plots without damage by trampling. Plots were left to settle for
139 a year before sampling to minimise effects of decomposition from roots. The use of this
140 plant removal approach allowed us to measure the effects of plant functional groups *in situ* in
141 their natural environment (Diaz *et al.* 2003). The plant functional group manipulations were
142 from the three dominant vegetation types present: ericoid dwarf-shrubs (S), dominated by
143 *Calluna vulgaris* (L.) Hull; graminoids (G), dominated by the sedge *Eriophorum vaginatum*
144 L; and bryophytes/lichens (B) dominated by feather mosses (*Hypnum jutlandicum* Holm. &

145 Warncke; *Pleurozium schreberi* (Brid.) Mitt.) and *Sphagnum* mosses. There were 8 different
146 plant manipulations: a control with all vegetation present, three single groups (S, G or B),
147 three double groups (S&G, S&B, G&B) and a treatment where all above ground vegetation
148 was removed. The experiment site had four blocks, containing randomly arranged warmed
149 and non-warmed replicates of each plant manipulation treatment (n = 64).

150

151 Warming was achieved passively using hexagonal OTCs based on the ITEX design (Marion
152 *et al.* 1997), modified for peatland vegetation by the addition of a 20cm high vertical
153 galvanised steel base, on to which the transparent top sections were fixed using cable ties.
154 Each transparent section making up the hexagonal OTC measured 80cm along the bottom
155 edge, 62.5cm along the top edge and 40cm height, to give an internal diameter of 1m²,
156 avoiding edge effects. The transparent material was 2mm thick Liteglaze clear acrylic sheet
157 (Ariel plastics, UK), which allows 92% light transmission. The open-topped chamber
158 method offers a robust means to examine effects of warming in remote environments, without
159 the need for a power supply, and has been used frequently in arctic and peatland ecosystems
160 (Walker *et al.* 2006; Dorrepaal *et al.* 2009). This methodology has its limitations, most
161 notably that OTCs can act as a physical barrier to wind (Marion *et al.* 1997), which, in
162 addition to changing temperature, has the potential to alter the width of the boundary layer
163 and hence the concentration of CO₂ surrounding photosynthesising leaves, thereby affecting
164 rates of photosynthetic uptake of carbon. Despite these limitations, the technique provides a
165 valid and useful way of quantitatively comparing the effects of warming between
166 experimental vegetation removal treatments in the field.

167

168 The OTCs were fixed in place one month prior to commencement of sampling. Air
169 temperatures at vegetation canopy height were recorded using temperature loggers (Lascar

170 Electronics, Salisbury, UK). Water table levels were measured from dip-wells made of 1m
171 long perforated PVC pipe, installed in each of the 64 experimental plots. On average, the
172 OTC's increased mean air temperatures by 0.88°C and 0.72°C over the midday period
173 (during the gas sampling period between 11:00 and 14:00 hrs), for the growing and non-
174 growing season respectively. Over 24 hours, the mean increase in temperature was 0.46°C
175 and 0.21°C for the growing and non-growing seasons. We found no evidence of any
176 difference in water table draw-down due to warming ($F_{1,1476} = 0.2$, $P = 0.87$), or due to
177 vegetation type ($F_{1,1476} = 0.9$, $P = 0.33$). For full details of the abiotic conditions during all
178 sampling dates, see Table S1.

179

180 **Greenhouse gas flux measurements.**

181 In each sampling plot, a 30 cm diameter, 10cm high gas sampling base ring was fitted in
182 place at 5cm depth, with care taken to minimise disturbance and to avoid severance of large
183 plant roots. Boardwalks installed on two sides of each experimental plot allowed access to
184 the sampling areas without compressing the surrounding peat, which could have created
185 physical movement of gases. Measurements of CO₂ exchange were made over 120-s
186 intervals with a PP systems EGM4 portable IRGA coupled to a customised chamber lid,
187 30cm diameter and 35cm height (Ward *et al.* 2007). We used the dark and light flux method
188 for ecosystem respiration and net CO₂ flux respectively (Ward *et al.* 2007). Measurements
189 were taken between 11:00 and 14:00 hours from June 2009 to August 2010, at approximately
190 monthly intervals during the growing season, and bi-monthly at other times. For CH₄ and
191 N₂O, bi-monthly gas samples were collected on closure of the chamber lid and at three
192 additional time points up to 30 minutes closure. Gas samples (10ml) were taken from the
193 chamber headspace using a gas syringe, and injected into evacuated 3ml exetainers (Labco,
194 UK) for storage prior to analysis. Concentrations of CH₄ and N₂O were analysed by gas

195 chromatography, using Perkin Elmer Autosystem XL GCs with a flame ionisation detector
196 for CH₄ and electron capture detector for N₂O. GC detection limits were better than 0.2 ppm
197 for all gases. For each sample, 2.5ml of gas was injected into the GC using an HTA
198 Autosampler. Results were calibrated against certified gas standards, comprising 500ppm
199 CO₂, 10ppm CH₄ and 1ppm N₂O (BOC, UK). All fluxes were adjusted for field sampling
200 temperature, headspace volume and chamber area (Holland *et al.* 1999), and calculated by
201 linear regression using all time points sampled (Levy *et al.* 2012).

202

203 **Soil properties**

204 Peat cores measuring 3cm diameter and 10cm depth were collected from each field plot in
205 July of the final year of gas sampling, in order to gain a measure of microbial biomass and
206 the availability of dissolved organic carbon (DOC) and nitrogen (DON) in the peat. Peat was
207 homogenised and hand sorted to remove any root material, then analysed for microbial
208 biomass C and N using fumigation-extraction, and water extractable DOC and DON using
209 methods described in Ward *et al.* (2007).

210

211 **Statistics.**

212 Data were checked for normality using residual plots method, and log-transformed where
213 necessary before analysis. The effects of experimental warming and vegetation
214 manipulations, and their interactions, were analysed by repeated measures ANOVA, using
215 SAS Enterprise Guide 4, with sampling date nested within sampling block as random effects.
216 Vegetation effects were analysed as the presence and absence of each of the three plant
217 functional groups (shrubs, graminoids and bryophytes), and effects of vegetation diversity
218 were analysed based on the number of plant functional groups present. After confirming a
219 three way interaction between season, warming and plant functional group, data were

Plants modulate warming effects on GHG fluxes

220 analysed as 2 separate models: 1) growing season data; and 2) non growing season data, with
221 growing season defined as when the mean air temperature is greater than 6°C.

222

223 **RESULTS**224 **CO₂**

225 Our results show that the effect of warming on NEE of CO₂ was modulated by the removal of
226 different plant functional groups in the experimental communities (Fig 1, Table 1). A
227 significant interaction ($F_{1,744} = 6.4$, $P = 0.0126$) between warming and plant functional group
228 removal on NEE was observed during the growing season (*i.e.* when average air temperature
229 was $> 6^{\circ}\text{C}$). More specifically, mean CO₂ sink strength increased by 55% with warming in
230 plots where shrubs were the only plant functional group present, and by 36% when shrubs
231 were present with bryophytes, but without graminoids (Fig. 1). In the presence of
232 graminoids, however, mean CO₂ sink strength was reduced by 20% with warming, whereas
233 in the absence of graminoids, mean CO₂ sink strength was increased by 43% with warming.
234 Vegetation diversity also influenced NEE ($F_{3,744} = 18.3$, $P < 0.0001$), with strongest effects
235 seen when comparing non-vegetated plots with those containing 2 or 3 plant functional
236 groups, but there were no interactions between vegetation diversity and warming (Supporting
237 information, Table S2).

238

239 Ecosystem respiration rates were consistently raised by warming across all vegetation
240 treatments (Fig. 2), but there were no detectable interactions of warming with the removal of
241 shrubs, graminoids or bryophytes (Table 1). Across all vegetation removal treatments,
242 warming of $\sim 1^{\circ}\text{C}$ over the year increased rates of ecosystem respiration in warmed relative to
243 non-warmed treatment plots by a mean of 47% and 49%, during the growing and non-
244 growing seasons respectively ($F_{1,734} = 49.8$, $P < 0.0001$; $F_{1,227} = 10.1$, $P = 0.002$). There were
245 also highly significant effects of shrub, graminoid, and bryophyte removal on ecosystem
246 respiration rates, with strongest effects during the growing season, and interactions observed
247 between graminoids and the other plant functional groups (Table 1). The highest rates of

248 respiration were measured in the presence of vascular plants, and there was a greater
249 reduction in respiration from the removal of shrubs than from the removal of graminoids.
250 When bryophytes were removed, rates of respiration increased, however this effect was only
251 observed during the growing season (Table 1). Significantly lower rates of respiration were
252 measured for bare plots compared to those with one or more plant functional group present
253 ($F_{3,734} = 21.1$, $P < 0.0001$), but there was no interaction of vegetation diversity with warming
254 (Supporting information, Table S2).

255

256 **CH₄ and N₂O**

257 We found that vegetation composition, particularly the presence of graminoids, was a
258 stronger factor than warming in regulating peatland CH₄ fluxes (Fig. 3, Table 1), and that the
259 presence and absence of graminoids and shrubs interacted to affect net CH₄ exchange all year
260 round. Emissions of CH₄ were higher in the presence relative to absence of graminoids, but
261 lower in the presence relative to absence of shrubs. We measured the highest CH₄ fluxes
262 when graminoids (the sedge, *Eriophorum vaginatum*) were present without shrubs and
263 without bryophytes (Fig. 3). Warming effects on CH₄ efflux were only significant during the
264 growing season ($F_{1,251} = 5.6$, $P = 0.02$), but we detected no interactive effect of warming with
265 vegetation removal on ecosystem CH₄ emissions for any of the three plant functional groups
266 (Table 1). Outside the growing season, the peatland was seen to be a small sink for CH₄ in
267 the absence of vegetation, and when shrubs and bryophytes only were present in warmed
268 plots (Fig. 3).

269

270 For N₂O, we found no significant effect of warming either during ($F_{1,167} = 0.0$, $P = 0.92$) or
271 outside the growing season ($F_{1,167} = 2.5$, $P = 0.12$), although there was a trend for a greater
272 N₂O sink in warmed plots during the non-growing season (Fig. 4, Table 1). During the

273 growing season we detected an interactive effect between shrubs and bryophytes, whereby
274 the greatest mean sink for N₂O was measured when shrubs were present and bryophytes had
275 been removed. There were no interactions between warming and vegetation removal, and no
276 significant effect of plant diversity on N₂O flux.

277

278 **Soil properties**

279 Warming increased concentrations of DOC ($F_{1,64} = 6.1, P = 0.02$) and DON ($F_{1,64} = 7.0, P =$
280 0.01) in soil solution by 13% and 15% respectively (Table 2). Vegetation change was found
281 to have a stronger effect on DOC and DON than warming, with the removal of shrubs
282 increasing concentrations of DOC ($F_{1,64} = 22.4, P < 0.0001$) and DON ($F_{1,64} = 21.0, P <$
283 0.0001) by 21%. In contrast, the graminoid or bryophyte removal had no detectable effect on
284 DOC or DON, and no interactions between warming and vegetation change were detected
285 (Supporting information, Table S3). Microbial biomass C and N did not respond to warming,
286 although microbial N was affected by vegetation change: microbial biomass N was greatest
287 when both shrubs and bryophytes were removed (Supporting information, Table S3), and
288 microbial C:N ratio was 14% lower when shrubs were removed ($F_{1,64} = 5.4, P = 0.02$).

289

290 **DISCUSSION**

291 It has long been recognised that carbon cycling processes in peatlands are highly sensitive to
292 changes in climate (Dise 2009; Dorrepaal *et al.* 2009), and there is growing evidence that
293 climate driven vegetation change in peatland and high latitude ecosystems is leading to an
294 increase in vascular plants at the expense of bryophytes (Walker *et al.* 2006; Gallego-Sala &
295 Prentice 2013). However, despite these concurrent changes in climate and vegetation, their
296 interactive effects on greenhouse gas fluxes are virtually unknown. We, therefore, set out to
297 examine the independent and interactive effects of warming and plant functional composition
298 on greenhouse gas exchange in a peatland ecosystem, using a unique field plant manipulation
299 and warming experiment. Our findings provide the first evidence that the response of
300 peatland greenhouse gas exchange to warming is both modulated and strongly controlled by
301 plant community composition.

302

303 Our results show that removal of different plant functional groups in the experimental
304 communities modulated the effects of warming on NEE of CO₂. In particular, we found that,
305 during the growing season, a significantly greater increase in net CO₂ sink strength with
306 warming was seen in the presence of shrubs when graminoids were absent, whereas warming
307 had the opposite effect in the presence of graminoids. As the main terrestrial exchange of
308 carbon from peatlands is as CO₂ (Roulet *et al.* 2007), quantifying NEE of CO₂ allows us to
309 get a measure of the net ecosystem carbon balance of the system, and how this is affected by
310 warming and vegetation community composition. The clear interactive effect of warming
311 and plant functional group removal on NEE during the growing season (*i.e.* when average air
312 temperature was > 6°C), suggests that responses were dependent on feedbacks from actively
313 growing plants, supporting the idea that the composition of actively growing peatland
314 vegetation is a key modulator of the response of ecosystem CO₂ fluxes to climate change. In

315 contrast, although ecosystem respiration rates were consistently raised by warming across all
316 vegetation treatments, no such interaction of warming with vegetation composition was
317 detected. Given the similarity of the respiration responses of different plant functional groups
318 to warming, we propose that observed differences in NEE are largely attributable to
319 differences in photosynthetic CO₂ uptake, with shrubs growing alone, or shrubs with
320 bryophytes, showing the greatest increase in photosynthesis relative to respiration and hence,
321 increased net CO₂ sink strength, with warming. In contrast, in the presence of graminoids,
322 warming led to a greater increase in rates of respiration relative to photosynthesis, leading to
323 a reduction in net CO₂ sink strength. Differences in rates of assimilation of CO₂ and
324 translocation of new photosynthates below-ground have previously been observed among
325 dominant peatland plant functional groups (Ward *et al.* 2012), with vascular plants (shrubs
326 and graminoids) showing greater rates of CO₂ assimilation and transfer relative to
327 bryophytes. This significant positive effect of warming on photosynthetic drawdown of CO₂
328 by shrubs is likely to be a consequence of their characteristic ecophysiological traits related to
329 resource acquisition, including associations with ericoid mycorrhizal fungi (Read *et al.* 2004),
330 and canopy height and bushy growth habit, which makes them better placed to intercept light
331 and to shade vegetation beneath their canopy.

332

333 Another explanation for the differences in warming response of NEE across plant functional
334 groups might be associated shifts in microbial communities in the peat, which could
335 ultimately affect the balance between CO₂ uptake and release under warming (Bardgett *et al.*
336 2008). It is known that shrubs and graminoids in peatlands differ in the rate that they allocate
337 photosynthetic carbon below-ground (Ward *et al.* 2009; Ward *et al.* 2012), and such
338 differences in allocation are likely to affect the quality and quantity of exudates released from
339 roots, to mycorrhizal fungi, and ultimately to soil, thereby affecting the composition and

340 activity of microbial communities (De Deyn *et al.* 2008; Bardgett *et al.* 2013). Also,
341 observed differences in the photosynthetic response of plant functional groups to warming are
342 likely to have altered carbon flux to roots and rates of root exudation, thereby further
343 contributing to shifts in the composition and activity of microbial communities across
344 vegetation treatments, and potentially explaining differential responses of NEE to warming.
345 We did not measure soil microbial community structure in this study, but we did find, albeit
346 at one sample date, that microbial C:N was significantly affected by shrub removal, which
347 could be indicative of a change in microbial communities. This is perhaps due to the high
348 concentrations of phenolic compounds (Hattenschwiler & Vitousek 2000; Freeman *et al.*
349 2001) and the presence of mycorrhizal fungi (Read *et al.* 2004; Orwin *et al.* 2011) associated
350 with ericoid shrubs. More studies are clearly needed to unravel the mechanisms by which
351 differences in vegetation modulate responses of NEE to warming, including studies on the
352 potential role of shifts in microbial communities as determinants of the response of NEE to
353 warming.

354

355 The mean increase in rates of ecosystem respiration in response to $\sim 1^{\circ}\text{C}$ warming, of 47-
356 49%, is consistent with other studies of warming effects in peatlands, observed in the field
357 (Dorrepaal *et al.* 2009) and laboratory (Kim *et al.* 2012). As with our findings for NEE of
358 CO_2 , the greatest effects of vegetation composition were observed during the growing season,
359 with the highest respiration rates being measured when vascular plants (*i.e.*, shrubs and
360 graminoids) were present in the plant community. We also observed warming effects on
361 concentrations of DOC and DON in soil solution, which were found to be higher in soils
362 from the warmed than unwarmed plots at the peak of the growing season, which is likely
363 indicative of an increase in microbial activity in response to warming. Although the effects
364 of warming and vegetation composition on ecosystem respiration were found to be

365 independent, our findings do highlight the importance of both warming and actively growing
366 vegetation in controlling the release of CO₂ to the atmosphere by respiration.

367

368 Peatlands are a globally important source of CH₄ (Baird *et al.* 2009) and previous work has
369 shown that both warming (van Winden *et al.* 2012) and vegetation (Levy *et al.* 2012; Gray *et*
370 *al.* 2013) can have a measureable effects on ecosystem CH₄ emissions. Our study provides
371 the first *in situ* field experimental evidence that vegetation composition is a stronger factor
372 than ~ 1°C warming in regulating peatland CH₄ fluxes. As with our findings for CO₂, the
373 effects of vegetation community composition were stronger during the growing season than
374 for the rest of the year, which again, highlights the key role that actively growing vegetation
375 can play in controlling GHG exchange. The relatively greater levels of CH₄ efflux when the
376 graminoid *Eriophorum vaginatum* was present, may be explained by the recognised
377 functional traits of this wetland sedge, namely the presence of aerenchymous tissues which
378 act as a conduit for CH₄ from the catotelm (Strack *et al.* 2006; Green & Baird 2012). In
379 addition, differences in the quality and quantity of root exudates entering the soil from
380 contrasting plant functional groups (De Deyn *et al.* 2008) are likely to affect the activity of
381 methanogenic bacteria in the peat, as well as respiration processes. Sedges in particular have
382 been associated with enhanced CH₄ production due to an increased supply of available
383 substrates, particularly acetate, to methanogens (Bellisario *et al.* 1999; Hornibrook 2009; Lai
384 2009), providing an additional explanation for the increased CH₄ emissions we observed in
385 the presence of graminoids. Interestingly, we observed that the system was a small sink for
386 CH₄ in the absence of vegetation, and also when shrubs and bryophytes only were present in
387 warmed plots outside the growing season. This implies that, even out of the growing season,
388 the presence of vegetation is still exerting controls on CH₄ emissions, through either changes
389 in microbial activity, or differences in physical conditions. Although peatlands are associated

390 with greater CH₄ productivity than consumption, there is some evidence of CH₄ consumption
391 in peat, particularly by methylocystis-related species (Kolb & Horn 2012).

392

393 Whereas previous peatland observations of high CH₄ emissions from sedge dominated
394 communities come from contrasting physical habitats (Strack *et al.* 2006; McNamara *et al.*
395 2008), our plant manipulation approach allowed us to compare plant functional groups in the
396 same habitat, providing new evidence of the importance of vegetation composition in
397 controlling CH₄ emissions. Although warming did increase the mean CH₄ efflux for all
398 vegetation manipulation treatments by 90% during the growing season, these effects were
399 much weaker than those observed due to vegetation composition, and we found no statistical
400 evidence that warming effects differed between vegetation types.

401

402 Atmospheric exchange of N₂O, the third greenhouse gas measured in this study, was
403 relatively low, as would be expected in nutrient poor ecosystems such as peatlands (Reay *et al.*
404 2012). These small fluxes, which varied between net emissions and net uptake (Fig. 4),
405 are typical of northern ombrotrophic peatlands (Drewer *et al.* 2010). Despite this, vegetation
406 composition was found to impact on sink strength for N₂O during the growing season, being
407 greatest when shrubs were present and bryophytes had been removed. Unlike for other
408 greenhouse gases, however, we detected no response of warming on N₂O, aside a weak
409 increase in N₂O sink strength, suggesting that climate warming is unlikely to affect the
410 atmospheric exchange of N₂O in peatland in this N poor blanket peatland. In contrast, studies
411 of N₂O emissions from peatlands which are more nutrient-rich (Martikainen *et al.* 1993), or
412 which have patches of bare soil with high nitrate content due to cryoturbation (Repo *et al.*
413 2009), have shown that climate warming can have powerful effects on peat N₂O fluxes.

414

415 In conclusion, our findings provide evidence from a unique field manipulation experiment
416 that warming effects on greenhouse gas exchange in peatland are modulated by changes in
417 plant community composition, with the greatest increase in net CO₂ sink strength with
418 warming occurring when shrubs were present and graminoids were absent. A change in the
419 rate of greenhouse gas exchange with the atmosphere, brought about by increased domination
420 by vascular plants as peatlands warm, has the potential to feedback to global climate change
421 by exacerbating radiative forcing. Furthermore, the observed interaction of climate warming
422 with vegetation change could accelerate these feedbacks in peatland systems containing large
423 stocks of globally important carbon (Gallego-Sala & Prentice 2013). Whilst the mechanisms
424 that underlie our findings require further exploration, our results indicate that changes in
425 vegetation community composition can act as a strong determinant of climate change effects
426 on northern peatland carbon cycling. As such, these results highlight the importance of
427 considering biotic as well as abiotic climate induced changes when predicting the future
428 greenhouse gas sink/source strength of peatland ecosystems.

429

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437

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605

606

607 **SUPPORTING INFORMATION**

608 Additional supporting information may be downloaded via the online version of this article at
609 Wiley Online Library (www.ecologyletters.com).

610 **Table S1.** Abiotic conditions for all sampling dates.

611 **Table S2.** Effects of vegetation diversity on CO₂, CH₄ and N₂O.

612 **Table S3.** Statistical analysis for DOC, DON and microbial biomass C and N.

613

614 **TABLES**

615 **Table 1.** Statistical analysis for the effects of, and interactions between, warming and the
616 presence/absence of plant functional groups on CO₂, CH₄ and N₂O fluxes by seasons: a)
617 growing season May to September, b) non-growing season October to April.

618

619 Table 1

Source of variation	a) Growing season (May – Sept)			b) Non-growing season (Oct – April)		
	df	f	p	df	f	p
<i>Net ecosystem CO₂ exchange (mg m⁻² h⁻¹)</i>			(n = 744)			(n = 229)
Warming	1	0.0	0.86	1	3.1	0.08
Shrub presence/absence	1	151.4	<0.0001	1	21.1	<0.0001
Graminoid presence/absence	1	17.1	<0.0001	1	2.8	0.10
Bryophyte presence/absence	1	0.1	0.82	1	1.6	0.21
Warmed x shrub	1	0.5	0.48	1	2.5	0.12
Warmed x graminoid	1	8.0	0.005	1	0.0	0.97
Warmed x bryophyte	1	0.4	0.52	1	1.5	0.22
Shrub x graminoid	1	13.4	0.0004	1	0.0	0.95
Shrub x bryophyte	1	2.7	0.10	1	1.7	0.20
Graminoid x bryophyte	1	2.9	0.09	1	1.9	0.18
Warmed x shrub x graminoid	1	6.4	0.01	1	0.1	0.81
Warmed x shrub x bryophyte	1	0.0	0.87	1	1.4	0.25
Warmed x graminoid x bryophyte	1	0.2	0.67	1	0.1	0.77
<i>Ecosystem respiration (mg m⁻² h⁻¹)</i>			(n = 734)			(n = 227)
Warming	1	49.8	<0.0001	1	10.1	0.002
Shrub presence/absence	1	164.7	<0.0001	1	22.6	<0.0001
Graminoid presence/absence	1	32.8	<0.0001	1	6.1	0.016
Bryophyte presence/absence	1	5.4	0.022	1	0.4	0.55
Warmed x shrub	1	1.0	0.31	1	0.5	0.51
Warmed x graminoid	1	0.2	0.63	1	0.2	0.69
Warmed x bryophyte	1	0.5	0.50	1	0.1	0.72
Shrub x graminoid	1	14.3	0.0002	1	2.4	0.12
Shrub x bryophyte	1	0.0	0.90	1	1.3	0.26
Graminoid x bryophyte	1	19.3	<0.0001	1	2.0	0.16
(no significant 3 way interactions)						
<i>CH₄ (mg m⁻² h⁻¹)</i>			(n = 251)			(n = 218)
Warming	1	5.6	0.02	1	0.3	0.58
Shrub presence/absence	1	9.9	0.002	1	1.5	0.22
Graminoid presence/absence	1	10.1	0.002	1	15.9	0.0001
Bryophyte presence/absence	1	2.2	0.14	1	2.4	0.12
Warmed x shrub	1	0.1	0.78	1	2.8	0.10
Warmed x graminoid	1	0.4	0.55	1	0.6	0.44
Warmed x bryophyte	1	0.1	0.70	1	1.2	0.28
Shrub x graminoid	1	8.5	0.005	1	13.9	0.0003
Shrub x bryophyte	1	0.0	0.92	1	2.4	0.12
Graminoid x bryophyte	1	1.3	0.26	1	10.5	0.002
(no significant 3 way interactions)						
<i>N₂O (mg m⁻² hr⁻¹)</i>			(n = 164)			(n = 167)
Warming	1	0.0	0.92	1	2.5	0.12
Shrub presence/absence	1	0.1	0.82	1	0.5	0.50
Graminoid presence/absence	1	0.7	0.39	1	1.3	0.27
Bryophyte presence/absence	1	0.2	0.65	1	1.1	0.29
Warmed x shrub	1	0.1	0.76	1	2.2	0.14
Warmed x graminoid	1	1.1	0.31	1	0.2	0.63
Warmed x bryophyte	1	0.4	0.55	1	1.4	0.25
Shrub x graminoid	1	1.0	0.32	1	0.8	0.37
Shrub x bryophyte	1	4.2	0.04	1	0.4	0.51
Graminoid x bryophyte	1	0.1	0.71	1	0.2	0.63
(no significant 3 way interactions)						

621 **Table 2.** DOC and DON in soil solution, and microbial biomass C and N in soils, sampled
 622 during the growing season. Values are means +/- s.e.

Vegetation type	DOC ($\mu\text{g C g dry wt soil}^{-1}$)	DON ($\mu\text{g N g dry wt soil}^{-1}$)	Microbial Biomass C ($\text{mg C g dry wt soil}^{-1}$)	Microbial Biomass N ($\text{mg N g dry wt soil}^{-1}$)
<i>Non-warmed</i>				
Control	1304 (± 188)	686 (± 99)	19.3 (± 2.7)	3.2 (± 0.2)
Shrub only	1514 (± 131)	814 (± 76)	11.8 (± 3.4)	2.6 (± 0.6)
Graminoid only	2135 (± 237)	1164 (± 199)	13.6 (± 2.6)	3.5 (± 0.6)
Bryophyte only	2115 (± 205)	1185 (± 128)	14.7 (± 2.6)	3.3 (± 0.5)
Shrub + Graminoid	1357 (± 179)	726 (± 86)	17.0 (± 1.3)	3.0 (± 0.2)
Shrub + Bryophyte	1928 (± 170)	1018 (± 79)	18.3 (± 2.2)	3.7 (± 0.5)
Graminoid + Bryophyte	2141 (± 161)	1128 (± 84)	13.5 (± 1.9)	2.5 (± 0.2)
No vegetation	2020 (± 306)	1065 (± 157)	16.8 (± 1.6)	3.4 (± 0.5)
<i>Warmed</i>				
Control	1901 (± 267)	1169 (± 235)	16.0 (± 0.9)	3.1 (± 0.2)
Shrub only	2331 (± 166)	1216 (± 98)	10.7 (± 1.9)	2.2 (± 0.7)
Graminoid only	2096 (± 149)	1108 (± 81)	11.7 (± 0.8)	3.0 (± 0.4)
Bryophyte only	1900 (± 56)	1026 (± 31)	9.2 (± 1.8)	2.1 (± 0.6)
Shrub + Graminoid	1722 (± 240)	951 (± 123)	16.8 (± 1.0)	3.0 (± 0.8)
Shrub + Bryophyte	1531 (± 104)	789 (± 51)	15.8 (± 3.2)	3.6 (± 1.3)
Graminoid + Bryophyte	2376 (± 134)	1302 (± 83)	17.2 (± 0.8)	3.7 (± 0.5)
No vegetation	2502 (± 336)	1363 (± 145)	13.7 (± 0.8)	3.6 (± 0.4)

623

624 **FIGURE LEGENDS**

625 **Figure 1. Net ecosystem CO₂ exchange from the plant manipulation and warming**

626 **experiment.** Data are means (mg CO₂ m⁻² hr⁻¹) for all sampling dates +/- standard error.

627 White bars are for non-warmed and black bars are for warmed experimental field plots. Data

628 are split between: growing season of May to September (left), and non-growing season of

629 October to April (right). Negative values represent a net sink and positive values represent a

630 net source for CO₂.

631

632 **Figure 2. Ecosystem respiration from the plant manipulation and warming experiment.**

633 Data are means (mg CO₂ m⁻² hr⁻¹) for all sampling dates +/- standard error. White bars are

634 for non-warmed and black bars are for warmed experimental field plots. Data are split

635 between: growing season of May to September (left), and non-growing season of October to

636 April (right).

637

638 **Figure 3. Methane flux from the plant manipulation and warming experiment.** Data are

639 means (mg CH₄ m⁻² hr⁻¹) for all sampling dates +/- standard error. White bars are for non-

640 warmed and black bars are for warmed experimental field plots. Data are split between:

641 growing season of May to September (left), and non-growing season of October to April

642 (right).

643

644 **Figure 4. Nitrous oxide flux from the plant manipulation and warming experiment.**

645 Data are means (mg N₂O m⁻² hr⁻¹) for all sampling dates +/- standard error. White bars are

646 for non-warmed and black bars are for warmed experimental field plots. Data are split

647 between: growing season of May to September (left), and non-growing season of October to

648 April (right).







