

Plant functional type indirectly affects peatland carbon fluxes and their sensitivity to environmental change

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Abstract

The sensitivity of peatland carbon (C) fluxes to changes in climate and hydrology are uncertain due to the complex interactions between plants and peat properties. In this study we examine how peat cores taken from under three plant functional types (PFT) (bryophyte, graminoid and ericoid) differ in their biotic and abiotic properties and how this indirectly modulates the response of C fluxes to environmental change. Peat cores taken from under three PFTs had their aboveground vegetation removed to exclude direct plant-mediated effects, and were incubated in a temperature × water table factorial experiment at 12, 14 and 16°C (air temperature) with the water table level –25, –15 or –5 cm below the peat surface. Carbon dioxide (CO₂) and methane (CH₄) fluxes were measured over 11 months. Emissions of CO₂ and CH₄ increased with temperature, with strong positive (CH₄) and negative (CO₂) interactions with increasing water table level. There were significant effects of removed PFT on the environmental sensitivity of CH₄, but not CO₂ fluxes. CH₄ emissions were greatest in peat with graminoid PFT removed at the warmest temperature but these indirect effects were not explained by peat abiotic or biotic properties, which did not differ between PFTs. These results show that climate change-induced expansion of graminoids in northern peatlands will have direct and indirect effects on C fluxes and the stability of peatland C stores. These responses will be determined by the interactive effects of vegetation composition, hydrology and warming on methane-cycling microbial communities.

Highlights

- Peatland carbon flux strength under a changing climate is influenced by PFT.
- Peat from under graminoid PFT emits more methane than peat from under bryophyte or ericoid PFT.

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- Prior PFT cover influenced methane emissions, but did not affect peat abiotic or biotic properties.
- Increases in graminoid cover with climate change could indirectly increase peatland methane fluxes.

KEYWORDS

carbon cycling, climate change, greenhouse gas emissions, methane, peat, plant functional type

1 | INTRODUCTION

Northern peatlands are an important part of the global carbon (C) cycle. The total carbon stored has been estimated at 500 ± 100 Gt C using a diversity of methods (Yu, 2012); however, a recent paper has estimated a stock of 1,055 Gt C (Nichols & Peteet, 2019), a figure strongly disputed (Ratcliffe, Peng, Nijp, & Nilsson, 2020; Yu et al., 2019). Climate and land-use change are increasing the vulnerability of these critical C stores through effects on hydrology and vegetation, which are key regulators of peatland C cycling (Armstrong, Waldron, Whitaker, & Ostle, 2014; Limpens et al., 2008; Turetsky et al., 2014). By 2070 in the UK, climate change is predicted to increase surface air temperature by 0.9 – 5.4°C and alter precipitation by -47% to $+2\%$ in summer and -1 to $+35\%$ in winter (relative to the 1981–2000 baseline in UKCP18), with uncertain impacts on peatlands (IPCC, 2013; Met Office, 2019; Raftery, Zimmer, Frierson, Start, & Liu, 2017; Spahni, Joos, Stocker, Steinacher, & Yu, 2013). Land-use change also has the potential to alter peatland temperature and water table depth. For example, peat extraction, drainage or land-use change to agriculture or forestry, can lower the water table significantly (Price, Heathwaite, & Baird, 2003; Smith et al., 2016; Wilson et al., 2010), whereas the deployment of wind farms on a UK peatland and on agricultural land in Texas, USA, have been shown to cause 0.2 – 0.7°C warming of the land surface at night due to impacts on energy and airflow through the windfarm and diurnal differences in the stability of the boundary layer (Armstrong et al., 2016; Zhou et al., 2012). As a consequence, climate and land-use change will influence peatland C cycling, with implications for C storage and release (Gallego-Sala & Prentice, 2013; Smith et al., 2016).

Temperature and water table depth interact to regulate peatland greenhouse gas (GHG) fluxes, with well-documented effects in both mesocosm and field studies (e.g. Limpens et al., 2008; Samson et al., 2018; Turetsky et al., 2014). For example, greater CO_2 and CH_4 emissions were observed with warming in peat mesocosms with high and low water table levels (Moore & Dalva, 1997; Scanlon & Moore, 2000). Also, a 1°C annual increase in

temperature increased respiration by up to 60% in a field manipulation of an Arctic blanket peatland (Dorrepaal et al., 2009), whereas 0.5 – 1°C warming increased CH_4 fluxes by 80, 8 and 75% under raised, control and lowered (± 10 cm) water tables, respectively, in an *in situ* manipulation of an Alaskan peatland (Turetsky et al., 2008).

In addition to the direct effects of climate and hydrology on peatland C cycling and autogenic hydrological feedbacks that occur within peatlands (Waddington et al., 2015), changes in temperature and water table also indirectly influence C cycling through changes in the relative abundance and productivity of dominant plant functional types (PFTs; bryophyte, graminoid and ericoid) (Gavazov et al., 2018; Laine et al., 2011; Riutta, Korrensalo, Laine, Laine, & Tuittila, 2020). Warmer and drier conditions are predicted to favour a shift from bryophyte to vascular plant dominance (Buttler et al., 2015; Dieleman, Branfireun, McLaughlin, & Lindo, 2015; Walker, Ward, Ostle, & Bardgett, 2015), with implications for microclimates and GHG emissions (Gavazov et al., 2018; Radu & Duval, 2018; Robroek et al., 2015; Ward et al., 2013). However, a mechanistic explanation of PFT effects on the sensitivity of the peatland C balance to environmental change remains elusive (Robroek et al., 2016).

The regulatory role of PFTs in peatland C dynamics is defined by specific traits that influence the assimilation and processing of C (Armstrong, Waldron, Ostle, Richardson, & Whitaker, 2015). Living vegetation can directly affect GHG fluxes by moderating the influence of climate on CO_2 uptake through growth, in addition to moderating CO_2 and CH_4 release through differences in plant physiology between PFTs, which affect decomposition and gas transport (Greenup, Bradford, McNamara, Ineson, & Lee, 2000). However, PFT can also indirectly affect C fluxes through differences in the quality and quantity of rhizodeposits and plant litter entering the soil (De Deyn, Cornelissen, & Bardgett, 2008; Dieleman, Branfireun, & Lindo, 2017), which influence the abiotic and biotic properties of peat (Chronakova, Barta, Kastovska, Urbanova, & Picek, 2019; Robroek et al., 2015; Robroek et al., 2016; Ward, Bardgett, McNamara, & Ostle, 2009).

Separating the direct and indirect effects of living and decomposing plants on peatland C dynamics is complex and has received little attention (Armstrong et al., 2015; Kuiper, Mooij, Bragazza, & Robroek, 2014; Wiedermann, Kane, Potvin, & Lilleskov, 2017). Yet, quantifying these effects and their interactions with changing water tables and temperatures is critical to resolve the impacts of future climate change on GHG fluxes and ultimately peatland C balances.

Here we investigated whether the sensitivity of CO₂ and CH₄ fluxes to temperature and water table level was modulated by the past presence of three dominant PFTs (bryophyte, graminoid and ericoid) by removing the vegetation prior to investigating their environmental sensitivity. We hypothesized that (H1) small-scale changes in temperature and water table level will interact to differentially affect peatland CO₂ and CH₄ fluxes. We expected CO₂ fluxes to increase with warmer temperatures and lower water tables and CH₄ fluxes to increase with warmer temperatures and higher water tables. Given these interactions, we hypothesized that (H2) PFT effects on peat properties will result in differential sensitivity of CO₂ and CH₄ fluxes to temperature and water table level, with fluxes enhanced from peat with graminoid PFT cover removed compared to ericoid and bryophyte PFTs. This was expected given the lower concentrations of recalcitrant C compounds in plant litter of graminoid species, compared to ericoid and bryophyte PFTs (Bragazza, Parisod, Buttler, & Bardgett, 2013; Dieleman et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Study site

A blanket bog at Black Law Wind Farm, Lanarkshire, UK (55° 46' 01" N 03° 44' 20" W), was used as the study site. The blanket bog peatland has accumulated since the end of the last ice age on an underlying stratum of glacier boulder clay. The boulder clay deposits cover the solid geology, known to consist predominantly of limestone coal formations and extrusive igneous rock. The elevation ranges from 250 to 320 m above sea level, with a mean annual maximum temperature of 10.7°C, minimum 4.4°C, and mean annual precipitation of 1,093 mm (data from Salsburgh Met Office weather station) (Richardson, 2014). This blanket bog is typical of UK peatlands in terms of microtopography (hummock and hollow) and vegetation (National Vegetation Community M19 *Calluna vulgaris* – *Eriophorum vaginatum* blanket mire) (Armstrong et al., 2015; Rodwell, 2000),

with relatively low temperatures minimizing vegetation change over time. Peat depth across the whole site was highly variable, ranging from 23 to 350 cm, with peat depth in the sampling area approximately 320 cm (Armstrong et al., 2015). The blanket bog has been grazed for many years, with the sampling area selected to avoid areas disturbed by the wind farm installation in 2005 (Armstrong et al., 2015). In May 2011, a 10-m² area of blanket bog was marked out for sampling, which had a clear hummock and hollow formation with well-defined patches and areas of the three dominant plant species: *Sphagnum capillifolium* (hollow), *Eriophorum vaginatum* (hummock) and *Calluna vulgaris* (hummock), representing bryophyte, graminoid and ericoid PFTs, respectively. A single area of blanket bog was used to reduce variance among the replicate cores. In total, 108 intact cores (in PVC pipes, 11 cm diameter, 30 cm depth) were collected from beneath three dominant plant species (36 of each PFT) within the 10-m² plot. A number of discrete sampling areas within the 10-m² plot were selected for each PFT on the basis that the peat had continuous cover of the relevant PFT with at least a 10-cm buffer of vegetation around cores sampled (e.g., for bryophyte PFT cores, six hollows were sampled with five to seven cores per hollow). Peat cores were extracted by inserting sections of PVC pipe into the ground and excavating. Vegetation was removed from the core surface and intact cores were bagged, transported to the laboratory and stored at 4°C for 3 months prior to the start of the experiment.

2.2 | Experimental design

A fully factorial experiment was established using peat cores taken from under the three PFTs, incubated at three temperatures, with three water table levels and replicated four times. Twelve peat cores from under each PFT were randomly selected and placed into each of three walk-in controlled temperature rooms and incubated at 12, 14 and 16°C (air temperature). The temperature range was chosen in order to simulate conditions at the field site during summer (i.e., the period of maximum rates of GHG uptake and release), as well as small-scale temperature changes which could result from global climate change and land-use change (Armstrong et al., 2014; IPCC, 2013). At each temperature, 12 peat cores from under each PFT were randomly assigned a water table level treatment, measured as depth below the peat surface: low (–25 cm), intermediate (–15 cm) or high (–5 cm). These water table levels were chosen as they are typical of the water table

dynamic range at this site (Waldron et al., unpublished data; Limpens et al., 2008).

To control and monitor water table levels, the base of each PVC pipe was sealed using a PVC disc and silicone adhesive sealant, with tubing inserted near the base of each pipe and fixed along its length to enable monitoring of water table depth throughout the experiment. Water table levels were manipulated with the addition of deionised water during a 2-week adjustment period and maintained throughout the experiment. Peat cores were incubated for 322 days, with CO₂ and CH₄ fluxes measured six times at 0, 7, 35, 154, 223 and 322 days after the start of the experiment. This sampling frequency was selected to capture longer-term impacts of treatments on GHG fluxes. To measure CO₂ and CH₄ flux rates, an opaque collar (12 cm diameter, 10 cm height) with a detachable lid was attached to the top of each core with silicone adhesive sealant (the mean headspace volume was 642 cm³). Headspace samples (10 ml) were collected through a rubber septum in each chamber lid, using a syringe fitted with a 0.5-mm needle that was flushed three times before filling. The headspace was sampled at four time-points: immediately after sealing the lid and then every 10 min (4 × 10 mL samples = 6.2% of headspace volume). All headspace samples were stored in pre-evacuated 3-ml exetainers (Labco, Lampeter, UK) and analysed for CO₂ and CH₄ concentration on a (Perkin Elmer, Waltham, Massachusetts, USA) Autosystem XL GC with FID and methaniser. Full details of GC conditions are described in Case, McNamara, Reay, and Whitaker (2012). Results were calibrated against two certified gas standards of 500 and 4,000 ppm CO₂, and 1 and 10 ppm CH₄. Gas fluxes (CO₂ or CH₄-C g m⁻² day⁻¹) were checked for linearity (>0.9 regression coefficient) and calculated from the change in chamber concentration, air temperature, chamber volume and area measurements (Holland et al., 1999).

2.3 | Peat abiotic and biotic properties

Additional peat samples (four replicates for each PFT) were taken under the three different PFTs in the same 10-m² sampling area in May 2011 (using 5-cm diameter, 15-cm-long PVC cores) to quantify differences in peat physicochemical properties and microbial community composition. Peat samples were analysed for pH (fresh peat:H₂O, 1:2.5 v:v), with the total C and N content of peat and the C:N ratio evaluated from 0.1 g homogenized and oven-dried (105°C) subsamples using a LECO Truspec CN Analyser (LECO Corporation, St. Joseph, Michigan, USA).

Peat microbial community composition was assessed by extraction of phospholipid fatty acids (PLFA) from 0.5-g

subsamples of freeze-dried peat using a modified Bligh-Dyer extraction (Bardgett, Hobbs, & Frostegard, 1996). PLFAs were separated from other lipids using an aminopropyl solid phase extraction cartridge (Phenomenex, Torrance, California, USA) and gas chromatography was carried out on an Agilent Technologies 6,890 N GC with a CP-Sil 5 CB fused silica capillary column (Agilent Technologies, Santa Clara, California, USA). Biomarkers were used for bacteria (*i*15:0, *a*15:0, 15:0, *i*16:0, 16:1 ω 9, 16:1 ω 7 t, *i*17:0, *a*17:0, 17:0, *cy*17:0, 18:1 ω 7 and *cy*19:0) and saprotrophic fungi (18:1 ω 6 and 18:2 ω 6, 9) (Bardgett et al., 1996; Whitaker et al., 2014). Total PLFA concentration was calculated from all identified PLFAs (those listed above and 14:0, 16:1, 16:1 ω 5, 16:0, 17:1 ω 8, 7Me-17:0, br17:0, br18:0, 18:1 ω 5, 18:0, 19:1). The ratio of fungal to bacterial PLFAs (F:B) was taken to represent the relative abundance of these groups.

2.4 | Statistical analysis

One-way ANOVA was used to test the effect of removed PFT on peat physicochemical properties and microbial community composition (SAS V9.1, Enterprise Guide 4.0). Repeated measures ANOVA was performed for hypotheses 1 and 2, to test the interactive effects of temperature, water table level and removed PFT on CO₂ and CH₄ fluxes over time. All data were checked for normality and the residuals checked for homogeneity of variance, with natural log transformations applied to CO₂ and CH₄ data before final analysis. Throughout the text, “significant” is attributed to $p < .05$.

3 | RESULTS

3.1 | CO₂ responses to temperature, water table and removed PFT

Temperature and water table interacted significantly to affect CO₂ fluxes ($p = .0008$, Table 1). Fluxes increased with rising temperature and lowering of the water table, with this response strongest at the warmest temperature (Figure 1). Average CO₂ fluxes among all treatments and time-points ranged from 0.12 ± 0.09 to 1.37 ± 0.12 CO₂-C g m⁻² day⁻¹, typically declining over the course of the experiment (Figure 2). This effect was more pronounced at lower temperatures (time*temp, $p < .0001$, Table 1); for instance, at 12°C average CO₂ fluxes decreased by 25% during the 11 months incubation, whereas at 16°C there was a 10% decrease (Figure 2). Effects of water table (WT) also varied significantly over the course of the experiment (WT*time, $p = .0004$), with CO₂ fluxes decreasing over time by a greater degree under raised water tables (Table 1, Figure 2).

Parameters	df	CO ₂		CH ₄	
		F	p	F	p
T (temperature, °C)	2	64.00	<.0001	8.74	.0003
WT (water table level)	2	30.34	<.0001	17.81	<.0001
PFT (plant functional type)	2		NS	10.32	<.0001
D (time within 332-day period)	5	21.49	<.0001	14.64	<.0001
T*WT	4	4.97	.0008	3.24	.0146
T*PFT	4		NS	3.01	.0210
WT*PFT	4		NS	3.99	.0046
D*T	10	4.30	<.0001	2.98	.0013
D*WT	10	3.28	.0004	7.25	<.0001
D*PFT	10		NS	3.12	.0008

Abbreviations: *df*, degree of freedom; NS, not significant.

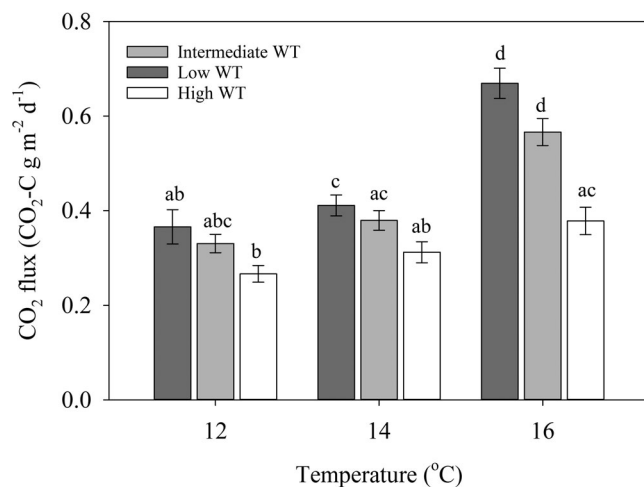


FIGURE 1 Interactive effects of temperature (°C) and water table (WT) on peat CO₂ fluxes (CO₂-C g m⁻² day⁻¹). Water table (WT) level: low = -25 cm, intermediate = -15 cm, high = -5 cm beneath peat surface. Data are means (averaged over 322 days and for removed PFT) ± standard error. Significant differences between treatments are shown by different lower case letters (where $p < .05$)

Removed PFT did not significantly affect CO₂ fluxes during the 11-month experiment as a main or interactive effect (Table 1), but there were significant positive interactions between temperature and removed PFT at individual time-points within the first month of incubations at day 0 ($F_{[2,626]} = 3.75$, $p = .0076$), day 7 ($F_{(2,626)} = 3.10$, $p = .0198$) and day 35 ($F_{(2,626)} = 3.82$, $p = .0067$, data not shown). During this time, increasing temperature had the greatest positive effect on CO₂ fluxes from peat cores with graminoid PFT removed, compared to ericoid and bryophyte PFT treatments (Figure 2).

TABLE 1 Main and interactive effects of temperature (T), water table level (WT), removed PFT and time (D) on CO₂ (CO₂-C g m⁻² day⁻¹) and CH₄ fluxes (CH₄-C g m⁻² day⁻¹) analysed by repeated measures ANOVA

3.2 | CH₄ responses to temperature, water table and removed PFT

Temperature, water table and removed PFT together influenced CH₄ fluxes, with significant two-way interactions between all treatments (Table 1, T*WT, T*PFT, WT*PFT, $p \leq .021$). At low water tables, temperature and PFT had no effect upon CH₄ fluxes, which were small, averaging 0.0001 CH₄-C g m⁻² day⁻¹, with some CH₄ consumption observed (Figure 3). In contrast, at an intermediate and high water table, CH₄ fluxes varied significantly with temperature (WT*Temp, $p = .0146$) and removed PFT (WT*PFT, $p = .0046$, Table 1). At these water table levels, CH₄ fluxes were greater at 12 and 16°C compared to 14°C regardless of PFT treatment. However, the magnitude of these fluxes varied significantly, with removed PFT (Table 1) being 4- to 30-fold greater in the cores with graminoid PFT removed compared with those with bryophyte and ericoid PFTs removed.

CH₄ fluxes over the course of the experiment were highly variable, ranging from -0.011 ± 0.004 to 1.54 ± 0.69 g CH₄-C m⁻² day⁻¹, with CH₄ fluxes typically greatest from 0 to 35 days, then low through the remainder of the experiment (Figure 3). There were significant pairwise interactions between time and temperature, water table and removed PFT ($p < .002$, Table 1), with CH₄ fluxes from peat taken under graminoids greatest at day 0 in the high water table treatments at 12 and 16°C, but not 14°C (Figure 3). For peat with bryophyte and ericoid PFTs removed, time had a negligible effect upon CH₄ fluxes across all temperature and water table treatments, with low average CH₄ fluxes throughout the incubation period (bryophyte 0.020 ± 0.009 , ericoid 0.006 ± 0.003 g CH₄-C m⁻² day⁻¹), in contrast to graminoids (0.097 ± 0.038 g CH₄-C m⁻² day⁻¹; Figure 3).

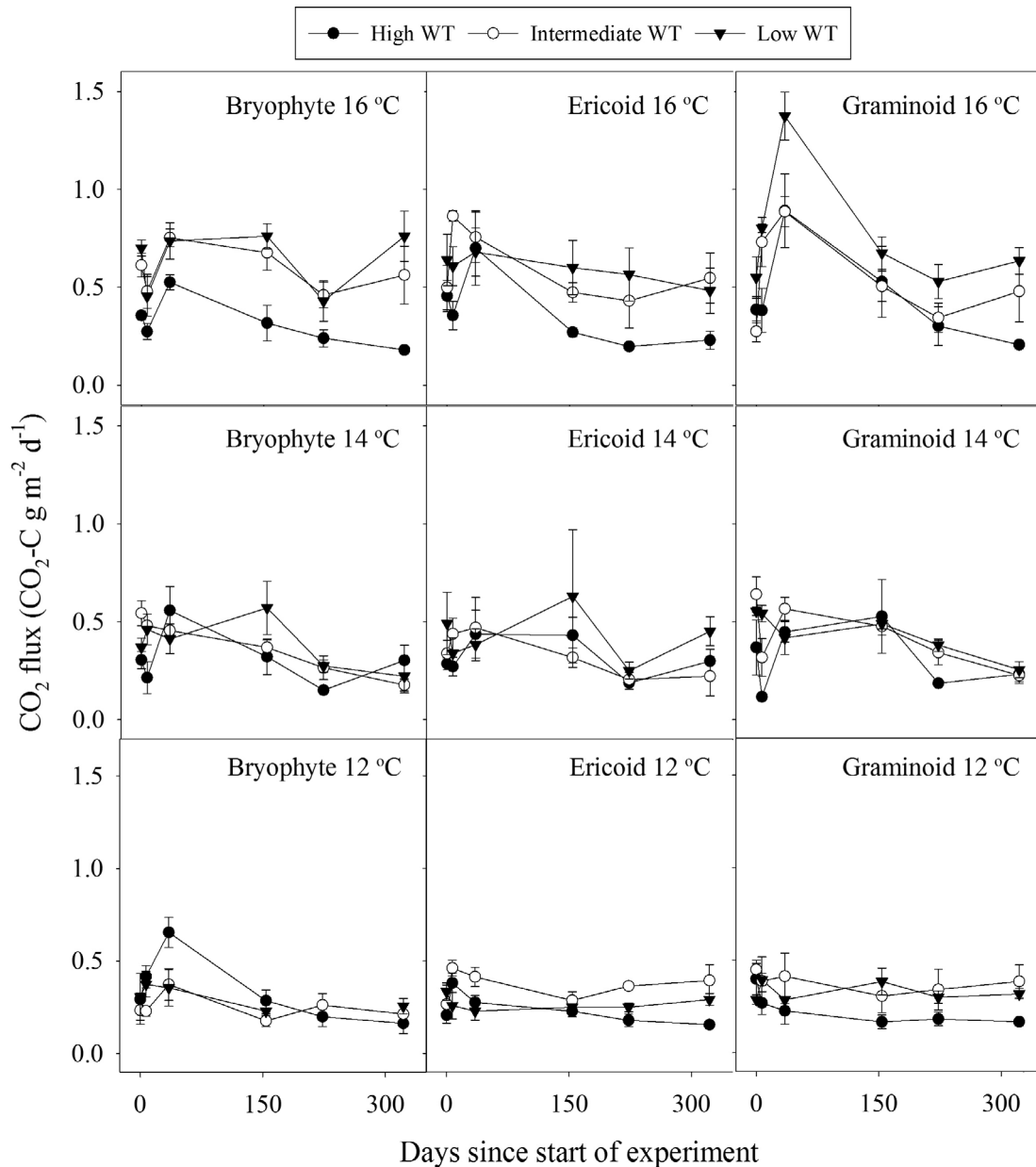


FIGURE 2 Interactive effects of temperature, water table (WT) and removed PFT (bryophyte, ericoid and graminoid) on CO_2 fluxes ($\text{CO}_2\text{-C g m}^{-2} \text{ day}^{-1}$) sampled over 322 days. Water table level: low = -25 cm, intermediate = -15 cm, high = -5 cm beneath peat surface. Data represent mean \pm standard error ($n = 4$)

3.3 | The effect of PFT on peat abiotic and biotic properties

Peat pH, total C and N content and C:N ratio were not significantly different between peats taken from under the three PFTs (Table 2). Measures of microbial community composition (total, fungal and bacterial PLFAs and fungal:bacterial PLFAs) were also not significantly different between peat cores taken from under the three PFTs; however, there was a trend of greater fungal to bacterial ratios in peat with ericoid PFT removed compared to the graminoid and bryophyte PFT (Table 2). This difference

was not statistically significant, possibly due to the relatively low level of replication ($n = 4$).

4 | DISCUSSION

In northern peatlands PFT is known to influence C dynamics, with the direct effects of living vegetation on C fluxes well studied and described (e.g., Laine et al., 2011; Robroek et al., 2015; Ward et al., 2013). However, the effects of different PFTs on the abiotic and biotic properties of peat may also indirectly affect C fluxes and their

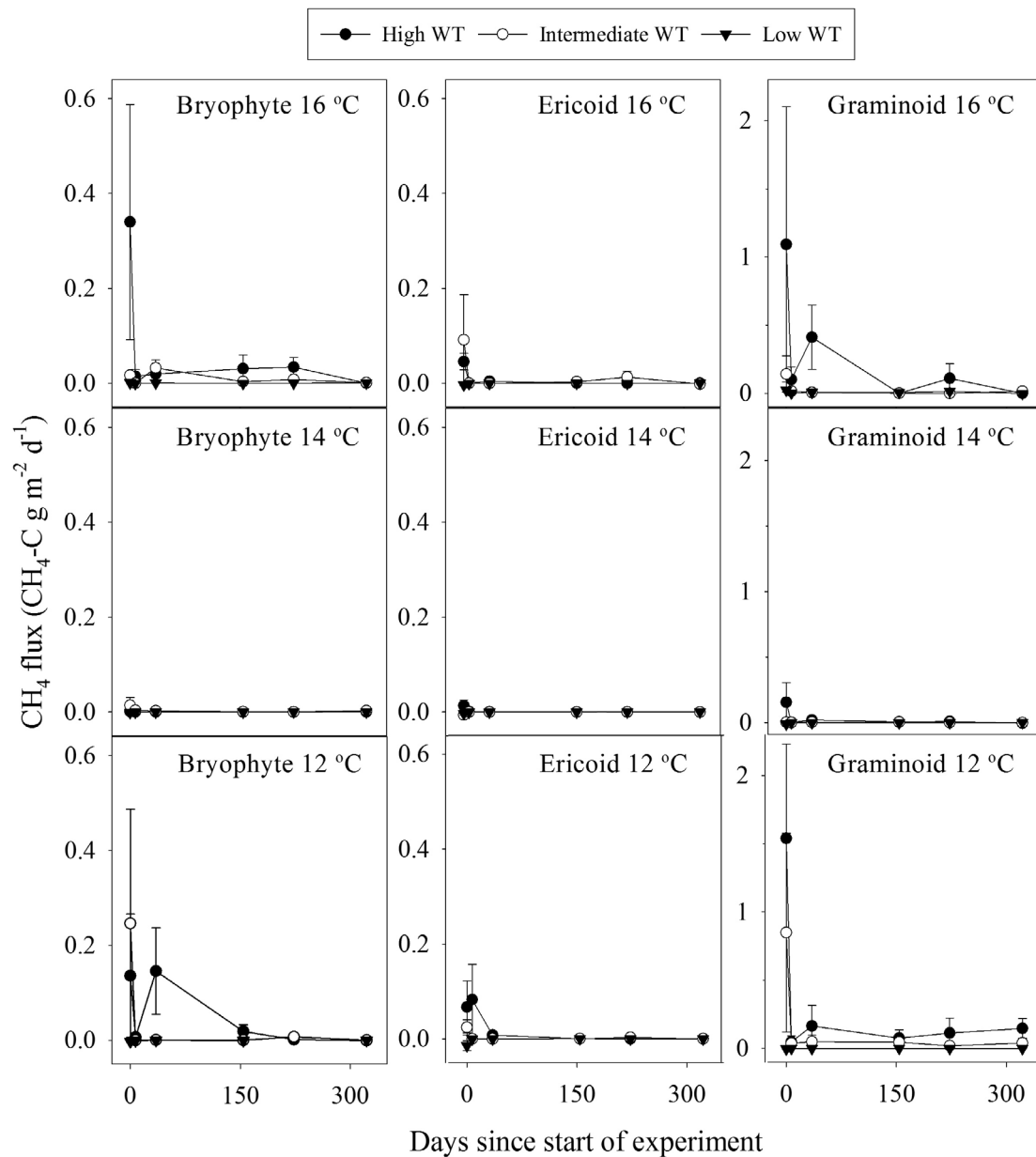


FIGURE 3 Interactive effects of temperature ($^{\circ}\text{C}$), water table (WT) and removed PFT (bryophyte, ericoid and graminoid) on CH_4 fluxes ($\text{CH}_4\text{-C g m}^{-2} \text{ day}^{-1}$) sampled over 322 days. Water table (WT) level: low = -25 cm, intermediate = -15 cm, high = -5 cm beneath peat surface. Data represent mean \pm standard error ($n = 4$); note different y-axis for graminoid PFT

sensitivity to environmental change. We investigated the effects of past PFT cover on the sensitivity of peatland C fluxes to temperature and water table over a period of 11 months in peat cores with the vegetation removed. In support of hypothesis 1, temperature and water table were major controls on GHG fluxes. Warmer and dryer conditions produced greater CO_2 fluxes but there were negligible effects of removed PFT; warming did stimulate CO_2 fluxes in peat more with graminoid PFT removed but only during the first month of the incubation. For CH_4 the response was more complex, with interactions between temperature, water table and removed PFT all influencing

CH_4 fluxes; the greatest fluxes were observed at the start of the incubation period, in peat cores previously populated by graminoids, thus partially supporting hypothesis 2.

4.1 | Temperature and water table regulation of C fluxes

Increases in CO_2 emissions in response to lowered water tables and increased temperatures have been observed in a range of mesocosm and field studies where intact vegetation has been removed, with similar ranges reported to

TABLE 2 Abiotic and biotic properties of peat from under each PFT, sampled prior to the experiment

Peat properties	Units	Removed PFT		
		Bryophyte	Graminoid	Ericoid
pH		4.06 ± 0.06	4.14 ± 0.10	4.07 ± 0.07
Total C content	%	40.84 ± 1.06	40.51 ± 1.36	40.30 ± 0.79
Total N content	%	0.99 ± 0.08	1.03 ± 0.05	1.00 ± 0.09
C:N		42.32 ± 3.85	39.42 ± 2.23	40.99 ± 2.63
Total PLFA	µg g ⁻¹ dwt soil	101.6 ± 21.9	132.2 ± 23.7	135.2 ± 31.6
Fungal PLFA	µg g ⁻¹ dwt soil	16.96 ± 5.22	21.13 ± 4.27	33.66 ± 8.59
Bacterial PLFA	µg g ⁻¹ dwt soil	43.4 ± 9.92	59.54 ± 10.27	60.35 ± 11.66
F:B PLFA		0.40 ± 0.08	0.35 ± 0.02	0.55 ± 0.08

Note: Data represent mean ± standard error ($n = 4$). One-way ANOVA revealed no significant differences in abiotic and biotic properties between peat taken from under the three PFTs ($p > .05$).

those observed here (Moore & Dalva, 1997; Silvola, Alm, Ahlholm, Nykanen, & Martikainen, 1996; Yavitt, Williams, & Wieder, 1997). The magnitude of water table and temperature effects on CO₂ fluxes has also been shown to vary with peatland trophic status, with peat CO₂ fluxes reported here in the range expected for an ombrotrophic bog (Silvola et al., 1996). These increases in CO₂ emissions with warming and drying are attributed to the stimulation of heterotrophic decomposition and hydrolytic enzyme activity and correspond with strong seasonal and climatic controls on peatland CO₂ fluxes measured across a range of northern peatlands (Armstrong et al., 2015; Dorrepaal et al., 2009).

Water table and temperature have also been identified as dominant controls on peatland CH₄ fluxes across a wide range of laboratory and *in situ* studies (Ballantyne, Hribljan, Pypker, & Chimner, 2014; Gill, Giasson, Yu, & Finzi, 2017; Turetsky et al., 2008). Net CH₄ fluxes from peat cores strongly increased with temperature (5 to 25°C range) under constant high water table (van Winden, Reichart, McNamara, Benthien, & Damsté, 2012). In contrast, 3 years of *in situ* warming in wet and drier boreal fens reduced CH₄ emissions overall, but with contrasting effects of drying and warming on methane production and methane oxidation (Peltoniemi et al., 2016). Here we observed that CH₄ fluxes were negligible and insensitive to temperature at low water table, but in intermediate and high water table treatments there were non-linear responses to warming (Figure 3); elevated CH₄ fluxes were observed at 12 and 16°C in some treatment combinations but very low fluxes were detected at 14°C across all treatments. It is hypothesized that higher temperatures can promote increased methanogenesis, but lowered water tables may offset increased CH₄ emissions through a greater capacity for methane oxidation (Estop-Aragones & Blodau, 2012; Nielsen et al., 2019). It is

possible that these counter-balanced effects of warming and drying on methane oxidation and production could partially explain the non-linear effects of temperature we observed, but this cannot be concluded definitively without DNA analysis of the peat microbial community. Nevertheless, our data do indicate that small-scale changes in temperature (±2°C) and water table (±10 cm), relevant to climate change scenarios, can exert a significant influence over GHG emissions.

4.2 | Interactions between abiotic controls and removed PFT

Temperature, hydrology and vegetation are known to independently exert control over ecosystem C dynamics in peatlands (Turetsky et al., 2014). There is also evidence that increasing prevalence of vascular plants can increase CO₂ and CH₄ emissions and alter their sensitivity to temperature and water table level (Leroy et al., 2017; Wiedermann et al., 2017). Here we found limited effects of removed PFT on CO₂ emissions and their environmental sensitivity; CO₂ emissions were stimulated by warming in graminoid PFT cores but only during the first month of the incubation, with non-significant main and interactive effects. Peat with graminoid PFT removed also emitted significantly more CH₄ on average, than peat with bryophyte and ericoid PFTs removed across all water table and temperature treatments (Figure 3), with CH₄ fluxes more strongly regulated by removed PFT than temperature (Table 1). This is consistent with a 1°C peatland warming experiment (Ward et al., 2013) and flux measurements in the intact Scottish peatland studied here, where vegetation composition was the strongest predictor of CH₄ flux measured *in situ* (Armstrong et al., 2015). CH₄ fluxes from ericoid and bryophyte PFT

cores in this study with live vegetation removed (0.006 and 0.02 g CH₄-C m⁻² day⁻¹, respectively) were similar in magnitude to those from *in situ* studies of ombrotrophic peat bogs including live vegetation, which ranged from 0.002 to 0.04 g CH₄-C m⁻² day⁻¹ (Armstrong et al., 2015; Laine et al., 2011; Ward et al., 2013). However, average CH₄ fluxes from the graminoid PFT cores (0.10 g CH₄-C m⁻² day⁻¹) were significantly greater than in *in situ* studies in comparative peatlands (0.02–0.04 g CH₄-C m⁻² day⁻¹) (Armstrong et al., 2015; Ward et al., 2013), driven by very large fluxes within the first month of incubation in some treatments.

Strong relationships between graminoid species and CH₄ fluxes have been observed previously in studies that included living vegetation, with greater CH₄ fluxes from graminoid- than from bryophyte- or ericoid-dominated peat (Armstrong et al., 2015; Greenup et al., 2000; Strack et al., 2017), and increased temperature sensitivity of CH₄ fluxes from mixed graminoid and bryophyte vegetation, compared to bryophytes alone (Leroy et al., 2017). This has been partly attributed to the presence of aerenchyma in graminoids; for example, *Carex* and *Eriophorum* spp., which act as conduits for CH₄ produced within the peat. Graminoids also produce more easily decomposed litter in comparison to ericoid and bryophyte species, leading to greater concentrations of labile C in graminoid-dominated peat (Dieleman et al., 2017; Robroek et al., 2015; Robroek et al., 2016). This might be responsible for the greater CH₄ fluxes we observed during the first month of incubation, as labile C from graminoid litter would continue to be mineralized by microbes (Weedon et al., 2013). Without living plants to replenish the labile C pool, microbial activity would become limited by the labile C remaining in the peat from beneath each PFT, possibly resulting in the observed decline in CO₂ and CH₄ fluxes over the duration of the experiment (Figures 2, 3). The higher CH₄ fluxes from peat taken from under graminoids, and the enhanced temperature sensitivity of CO₂ fluxes in these same treatments during the first month of the experiment, therefore indicate that decaying graminoid litter may be an important contributor to enhanced CH₄ fluxes observed in the field (Strack et al., 2017).

Peatland plant species are known to shape peat properties through their above- and belowground functional traits (Palozzi & Lindo, 2017). We hypothesized that the three removed PFTs, would have differentially affected the abiotic and biotic properties of the peat and as a consequence influenced the sensitivity of peat C fluxes to temperature and water table. However, we found no significant differences in peat abiotic properties, microbial community composition or abundance between the peat cores with different PFTs removed

(Table 2). This appears at odds with our finding that prior graminoid PFT cover resulted in greater and more sensitive CH₄ fluxes compared to cores taken from under bryophyte and ericoid PFTs. It is also surprising that no difference in microbial community composition or abundance was detected between removed PFTs, as a more extensive survey of this peatland reported lower fungal to bacterial ratios (lower fungal abundance) in peat from beneath graminoid compared to ericoid PFTs (Richardson, 2014), consistent with the increased lability of graminoid litter (Dieleman et al., 2017; Strack et al., 2017). It is possible that changes in microbial communities among PFT treatments were not detected due to use of PLFA analysis, which cannot detect changes in specific functional groups such as methanogens and methanotrophs, unlike DNA analysis. Elsewhere, dominant PFTs have been shown to influence methane-cycling communities, with consequences for CH₄ fluxes (Chronakova et al., 2019; Robroek et al., 2015). Removal of graminoid and ericoid PFTs from peatland plots reduced bacterial abundance and numbers of methanotrophs (Robroek et al., 2015). This decrease in methanotrophs in the absence of graminoids could explain the enhanced CH₄ fluxes and differential sensitivity to temperature and water table we observed in this study. It is likely that PFT has influenced other peat properties, which we did not measure, for example peat organic matter chemistry or the abundance of specific microbial taxa involved in methane production and oxidation. Increased concentrations of low-molecular-weight dissolved organic matter (DOM) moieties and decreased humic/lignin ratios of DOM were reported in peat cores where graminoids were retained versus removed (Robroek et al., 2015; Robroek et al., 2016). These properties can enhance methanogenic bacterial activity and promote degradation of complex DOM. Furthermore, peat monoliths populated solely by graminoids were found to have great C compound lability compared to bare peat or peat with Sphagnum cover (Dieleman et al., 2017). This suggests that labile C from root exudates or released from decomposing graminoid litter in high and intermediate water table conditions may be important in driving the enhanced CH₄ fluxes observed. It does not, however, explain why we did not observe parallel increases in CO₂ fluxes as a result of enhanced microbial activity (Robroek et al., 2015).

5 | CONCLUSION

Living and decomposing plants affect peatland C dynamics directly and indirectly, and this requires manipulative

experimentation to disentangle. Here we tested the indirect, belowground effects of PFT on peat C fluxes and demonstrated that expansion of vascular plants on peatlands, as a consequence of climate change, may increase the environmental sensitivity of peat CH₄ fluxes without necessarily causing detectable changes to peat biogeochemical properties. To improve our mechanistic understanding of this phenomenon we pose two questions raised by this study that warrant further research: (a) How and why does the methane-cycling community differ in peat populated by graminoid, bryophyte and ericoid species? (b) Are the non-linear effects of temperature on CH₄ fluxes due to differential responses of methanogens and methane-oxidizing bacteria to drying and warming, with responses mediated by the plant community? Addressing these questions would enable improved understanding of how changes in aboveground plant community composition will interact with longer-term effects below ground to determine the sensitivity of peatland C cycling to future climate and land-use change.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Study concept and design: H.R.R., J.W., S.W. and N.J.O. Experimental work and data analysis: H.R.R. Drafting of the manuscript: H.R.R. and J.W. Critical revision and contribution of intellectual content: J.W., S.W., A.A. and N.J.O. Study supervision: J.W., S.W. and N.J.O.

DATA AVAILABILITY STATEMENT

All data associated with this study are available from the Environmental Information Data Centre (eidc.ceh.ac.uk) and the data have been allocated a digital object identifier 10.5285/e15fbbab-1cdd-4509-81a3-aa050e927dd0 (Richardson et al., 2015).

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