

The effect of drainage ditches on vegetation diversity and CO₂ fluxes in a *Molinia caerulea*-dominated peatland

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ABSTRACT

Peatlands are recognized as important carbon stores; despite this, many have been drained for agricultural improvement. Drainage has been shown to lower water tables and alter vegetation composition, modifying primary productivity and decomposition, potentially initiating peat loss. To quantify CO₂ fluxes across whole landscapes, it is vital to understand how vegetation composition and CO₂ fluxes vary spatially in response to the pattern of drainage features. However, *Molinia caerulea*-dominated peatlands are poorly understood despite their widespread extent.

Photosynthesis (P_{G600}) and ecosystem respiration (R_{Eco}) were modelled (12 °C, 600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, greenness excess index of 60) using empirically derived parameters based on closed-chamber measurements collected over a growing season. Partitioned below-ground fluxes were also collected. Plots were arranged $\frac{1}{8}$, $\frac{1}{4}$ and $\frac{1}{2}$ the distance between adjacent ditches in two catchments located in Exmoor National Park, southwest England.

Water table depths were deepest closest to the ditch and non-significantly ($p=0.197$) shallower further away. Non-*Molinia* species coverage and the Simpson diversity index significantly decreased with water table depth ($p < 0.024$) and increased non-significantly ($p < 0.083$) away from the ditch. No CO₂ fluxes showed significant spatial distribution in response to drainage ditches, arguably due to insignificant spatial distribution of water tables and vegetation composition. Whilst R_{Eco} showed no significant spatial variation, P_{G600} varied significantly between sites ($p=0.012$), thereby controlling the spatial distribution of net ecosystem exchange between sites. As P_{G600} significantly co-varied with water table depths ($p=0.034$), determining the spatial distribution of water table depths may enable CO₂ fluxes to be estimated across *M. caerulea*-dominated landscapes. © 2015 The Authors. *Ecohydrology* published by John Wiley & Sons, Ltd.

KEY WORDS peatland; drainage; CO₂; *Molinia caerulea*; water table; vegetation composition

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INTRODUCTION

A small imbalance between primary productivity and decay within peatlands has led to the accumulation of large carbon stores (Yu *et al.*, 2010). However, many peatlands are subject to damaging land management practices, principally drainage for agriculture and forestry (Joosten and Clarke, 2002), which alter the balance between primary productivity and decomposition shifting peatlands towards CO₂ release (Gorham, 1991). Due to the recent addition of peatland restoration into the Kyoto Protocol, carbon markets may provide funding for peatland restoration (Bonn *et al.*, 2014); however, there are currently no appropriate default international emission factors for drained *Molinia caerulea*-dominated peatlands (Alm *et al.*,

1999b). Therefore, quantification of emissions from a wider range of vegetation and management types is required (Evans *et al.*, 2011).

Drainage ditches are frequently the main spatial feature within managed blanket bogs. They have been shown to lower the mean water table (Coulson *et al.*, 1990, Wilson *et al.*, 2010, Holden *et al.*, 2011), which in turn reduces species richness (Bellamy *et al.*, 2012), particularly affecting species dependent on high water levels including *Sphagnum*. *M. caerulea* thrives where water table depths fluctuate (Jefferies, 1915) and has encroached on many drained upland areas (Bunce and Barr, 1988). Although grasses have been shown to produce more biomass and uptake more carbon annually (Berendse, 1998, Otieno *et al.*, 2009, Ward *et al.*, 2009) than dwarf shrubs (e.g. *Erica tetralix* and *Calluna vulgaris*) and *Sphagnum*, the biomass produced is more labile and readily decomposed (Coulson and Butterfield, 1978, Berendse, 1998). Understanding how vegetation composition and CO₂ fluxes vary spatially in response to

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these features is therefore vital in upscaling CO₂ fluxes across the whole landscape through models. Using a combination of gas flux chambers and soil collars enables the measurement of both ecosystem and partitioned below-ground fluxes at discrete distances from drainage features. Such monitoring facilitates understanding of the variables driving spatial variation in CO₂ fluxes assisting upscaling (Laine *et al.*, 2006).

Most studies investigating the effect of drainage have compared pristine to drained areas of northern peatlands (Silvola *et al.*, 1996, Alm *et al.*, 1999a, Straková *et al.*, 2011b) as they sought to understand the broad effect of drainage in these ecosystems. Methane emissions (Minkkinen *et al.*, 1997) and nitrogen mineralization (Tarvainen *et al.*, 2013) have been shown to be greater near or in a drainage ditch compared with half-way between ditches. Studies on CO₂ exchange have compared microforms within drained peatlands (Komulainen *et al.*, 1999) or microforms along natural hydrological gradients (Laine *et al.*, 2007) rather than investigate the explicit role of the drainage features.

It is hypothesized that proximity to drainage ditches will influence water table depths, which will affect vegetation composition and primary productivity and consequently CO₂ fluxes (ecosystem respiration; photosynthesis; and total, heterotrophic and autotrophic below-ground respiration) in a drained *M. caerulea*-dominated peatland. The following paper tests this hypothesis in two drained, temperate, maritime blanket bogs in the UK.

STUDY SITES

The study sites were located in Exmoor National Park, southwest England, in two *M. caerulea*-dominated head-water catchments subject to extensive drainage: Aclands (49°46'51.66N 3°48'44.4W) and Spooners (49°46'51.44N 3°44'52.9W) (Figure 1). Drainage ditches of variable size, up to 0.5 m wide and 0.5 m deep, were hand dug since the 1830s (Hegarty and Toms, 2009). Between the 1960s and 1980s, larger machine-dug ditches (>1.5 m wide) targeted specific areas, for example, spring lines (Mills *et al.*, 2010). Both catchments have been classed as UK National Vegetation Classification M25: *M. caerulea*–*Potentilla erecta* mires (Rodwell, 1991). Long-term (1981–2010) average annual rainfall at nearby Liscombe (UK Meteorological Office, 2012) (51°05'23N 003°36'27W) totals 1445 mm with mean monthly temperature ranging from 1.1 °C in February rising to 18.6 °C in July and August.

Within each catchment, six pairs of sites were chosen to encompass the expected variation in altitude, aspect, slope, peat depth and ditch dimensions (Table I). As the ditches are unevenly spaced, plots were located on transects perpendicular to the ditch at 1/8, 1/4 and 1/2 of the distance between the ditch being monitored and the adjacent ditch. Proportional distances from the ditch were chosen to test

whether CO₂ fluxes could be upscaled for the whole peatland rather than discrete bands either side of a drainage ditch despite the known variations between sites. Locations are shown in Figure 1c and d ($n=36$).

METHOD

Net ecosystem exchange measurements

Net ecosystem exchange (NEE) was measured from three pairs of plots located 1/8, 1/4 and 1/2 distance from the ditch at each site ($n=6$) – a total of 36 plots. A 55 × 55 × 25 cm Perspex gas flux chamber was rested on permanently installed 50 cm tall legs with a plastic skirt weighted down by a heavy chain to form an airtight seal with the soil surface [following Shaver *et al.* (2007) and Street *et al.* (2007)]. An EGM-4 infrared gas analyser (PP Systems, Hitchin, UK) measured CO₂ concentration every 10 s for 2 min concurrently with chamber temperature and photosynthetic active radiation (PAR) (Skye Instruments, Llandrindod Wells, UK). CO₂ flux measurements were taken at full light, full dark, and ~60%, ~40% and ~10% light levels using a combination of shade cloths. Chamber air temperature was not directly controlled. Measurements were alternated between brighter and darker light levels to minimize any heating/shading effects. Neither condensation in the chamber, which reduces transparency, nor high humidity, which alters gas diffusion from the leaves, was noted over the sample period due to the abnormally cool weather conditions. The chamber was removed between measurements to restore ambient conditions. The net CO₂ exchange at each light level was calculated from the linear change in CO₂ concentration in the chamber (Pumpanen *et al.* 2004). The headspace volume was estimated by measuring the height from the ground to the base in a grid of nine points added to the chamber volume. The water table depth below the peat surface and soil temperature at 5 cm were also measured at every plot ($n=36$).

Vegetation greenness

Vegetation colour, in particular the ratio of green to red and/or blue, has been shown to vary seasonally and be useful as a proxy for vegetation phenology (Richardson *et al.*, 2007, Migliavacca *et al.*, 2011) and health (Mizunuma *et al.*, 2013). Downward facing true colour photographs of the vegetated NEE plots ($n=36$) were collected on ten occasions between 20/06/2012 and 25/10/2012 ($n=282$). Due to equipment bulk, images were not collected on the same day as CO₂ flux measurements. Between 22 and 36 plots were photographed on each occasion, except 10/8/2012 when only eight images were collected. Images were taken 116 cm above the ground using a Canon EOS-10D with a 28 mm fixed lens set to autofocus and fully automatic aperture and shutter speed. The mean red (DN_{Red}) and green (DN_{Green}) colour values for the images collected were determined using MATLAB R2011b

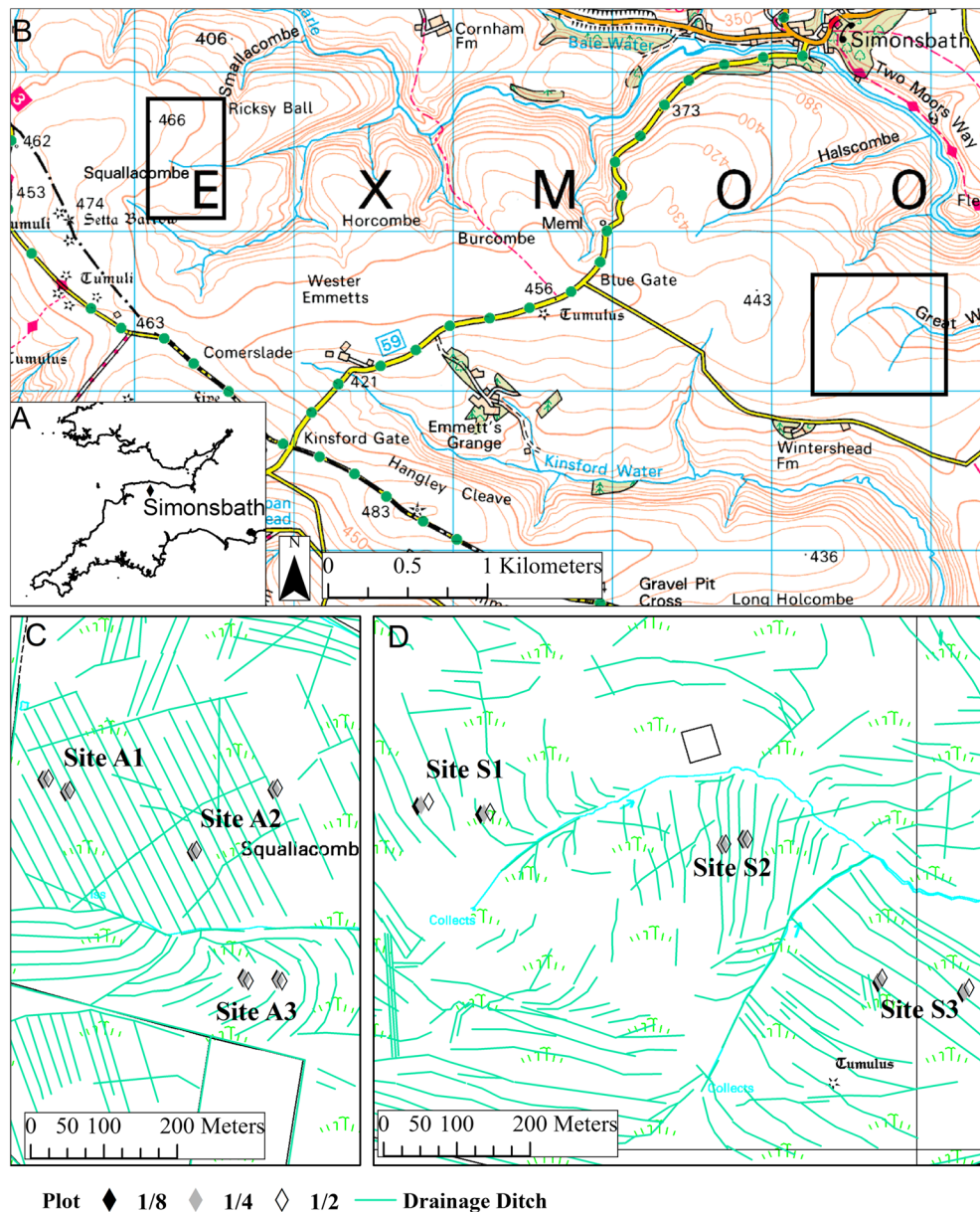


Figure 1. Location of Aclands and Spooners study catchments (b) within the southwest of England (a). Location of study sites within Aclands (c) and Spooners (d) study catchments. Coastline shapefile (Ordnance Survey 2008a), 1:50 000 Ordnance Survey Map (Ordnance Survey 2008d) 1:10 000 Ordnance Survey Map (Ordnance Survey 2008b, c).

(Mathworks Inc, Natick, MA, USA). The greenness excess index (GEI) has been shown to be useful as an indicator of spring green up (Richardson *et al.*, 2007, Migliavacca *et al.*, 2011). It was calculated for each image where $GEI = (DN_{Green} - DN_{Red}) / (DN_{Green} + DN_{Red})$. A daily GEI timeseries was modelled for each catchment using a third order Fourier series.

Net ecosystem exchange modelling

NEE measurements were collected approximately monthly over the growing season from 16/05/2012 to 19/09/2012 ($n=163$ sets). A complete set of measurements ($n=36$, a

'sampling round') took between 5 and 14 days dependent on weather conditions; to remove this temporal variability, photosynthesis and ecosystem respiration were modelled [Equations (1) and (2)] using all data collected for each plot ($n=36$). R_{Eco} was assumed to be equivalent to NEE under dark conditions, and gross photosynthesis (P_G) was calculated as the difference between average R_{Eco} (two measurements taken in dark conditions) and NEE measured at different light levels.

Equation (1): photosynthesis model

$$P_G = \frac{P_1 \cdot GEI \cdot I}{k_1 + I} + a \cdot \exp^{-b/r_s} \quad (1)$$

Table I. Site properties of experimental sites at Aclands and Spooners.

Site	Replicate	Mean peat depth ^a (cm)	Mean ditch width (cm)	Mean ditch depth ^b (cm)	Distance from ditch to downgradient ditch ^c (m)	Altitude ^d (m)	Slope (°) ^d	Aspect	Direction of ditch ^d (°)	Ditch direction with respect to slope
S1	R	22	58	24	37.8	425	4		144	Cross slope
	C	23	67	18	43.9	418	5	ESE	150	
S2	R	71	84	42	12.5	397	5		2	Down slope
	C	56	80	45	15.4	395	6	NE	0	
S2	R	29	38	24	29.3	405	5		302	Down slope
	C	29	42	24	32.8	407	5	N	300	
A1	R	33	25	14	22.4	442	2		20	Down slope
	C	38	32	20	20.3	443	2	NE	10	
A2	R	40	40	26	19.1	446	4		154	Down slope
	C	43	43	21	19.1	448	4	SE	150	
A3	R	30	50	18	18.3	463	3		144	Down slope
	C	36	42	18	18.7	461	3	SE	151	

^a Measured during dipwell installation from base of peat ($n=3$).

^b Measured from base of ditch to tussock shoulder.

^c Measured using tape measure.

^d From LiDAR.

where P_1 is the maximum rate of photosynthesis ($\mu\text{gC m}^{-2} \text{s}^{-1}$), GEI is the modelled greenness excess index, I is the incident PAR ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$), k_1 is the half-saturation coefficient ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$), T_5 is the soil temperature at a depth of 5 cm ($^{\circ}\text{C}$), and a (dimensionless) and b ($^{\circ}\text{C}^{-1}$) are empirically derived coefficients describing an Arrhenius (Arrhenius 1898) response to temperature.

Equation (2): ecosystem respiration model

$$R_{\text{Eco}} = c \cdot \exp^{-d/T_5} + e \cdot \exp\left(-0.5 \left(\frac{T_5 - T_{\text{Opt}}}{T_{\text{Tot}}}\right)^2\right) \quad (2)$$

where T_5 , T_{Opt} and T_{Tot} are the measured, optimum and maximum tolerable soil temperature at a depth of 5 cm ($^{\circ}\text{C}$); and c (dimensionless), d ($^{\circ}\text{C}^{-1}$) and e (dimensionless) are empirically derived coefficients describing an Arrhenius (Arrhenius, 1898) response to temperature; and e is an empirically derived coefficient describing a Gaussian temperature response.

R_{Eco} and P_{G600} were then calculated for a soil temperature of 12°C , GEI of 60 and PAR of $600 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ using the empirically derived parameters (Supplementary Material Table 1). A PAR of $600 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ was selected as it lay within the range of PAR observed, and most plots were light saturated at this PAR, enabling photosynthetic efficiency to be compared between locations.

Soil CO_2 efflux measurements

At each plot, four polyvinyl chloride (PVC) collars (16 cm diameter, 8 cm high) were placed on and sealed to the surface of the peat using non-setting putty (Evo-Stik 'Plumbers Mait'). Collars, installed in March 2012, were located between 0.5 and 2 m downgradient of the NEE

plots. Above-ground vegetation was removed by regular clipping from all PVC collars, enabling the measurement of below-ground fluxes only. In addition, circular 20 cm deep trenches (56 cm diameter) were cut around half the collars to sever live roots, allowing the below-ground heterotrophic component to be measured. The collars with only above-ground vegetation removed were used to measure total below-ground respiration. Trenches 20 cm deep were considered sufficient as although cord roots are 15–45 cm long (Jefferies, 1915), most of the root biomass is concentrated nearer the surface (Taylor *et al.*, 2001). For each plot, the two replicates of each treatment were averaged to produce a single value. Autotrophic respiration (including root respiration and microbial respiration of root exudates) was calculated from the difference between average total ($n \leq 2$) and average heterotrophic below-ground respiration ($n \leq 2$) measured at each location for each sampling round (complete set of measurements from 144 collars).

CO_2 measurements ($n=222$) were taken in a semi-randomized pattern approximately every 3 weeks from 16/04/2012 to 26/10/2012. Data collected between 16/04/2012 and 25/05/2012 were excluded due to obvious treatment effects. CO_2 flux was measured over 2 min using an EGM-4 infrared gas analyser and a CPY-4 canopy assimilation chamber (PP Systems, Hitchin, UK). At the same time as CO_2 flux measurements were made, the depth of the water table below the peat surface and soil temperature 5 cm were measured at each plot ($n=36$).

As below-ground respiration has been shown to be strongly controlled by soil temperature (Lloyd and Taylor, 1994), which varies diurnally, adjusting soil respiration to a fixed temperature removes this temporal variability. The

mean soil temperature at 5 cm (T) (°C) and the mean respiration rate (R_T) for each sample day at each site ($n=6$) ($\mu\text{mol m}^{-2} \text{s}^{-1}$) were regressed [Equation (3)], and the Q_{10} (the increase in respiration rate for a 10°C increase in temperature) was calculated.

Equation (3)

$$\ln R_T = \ln R_{10} + \frac{\ln Q_{10}}{10} (T - 10) \quad (3)$$

By using the Q_{10} values calculated by Equation (3) for total, heterotrophic and autotrophic below-ground respiration for each site (refer to Table 2 in the supporting information), all respiration rates were normalized to 10°C (r_{10}) [Equation (4)].

Equation (4)

$$r_{10} = R_t \cdot Q_{10}^{10-t/10} \quad (4)$$

where r_{10} is the temperature-adjusted respiration at 10°C for a measured respiration rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$) (R_t) at a given location ($n=1$) at temperature t °C and Q_{10} as mentioned previously.

Vegetation composition and primary productivity

Annual net primary productivity (ANPP) was measured in late August by destructive harvest of a 55 × 55 cm plot ($n=36$) approximately 2 m downgradient of the NEE plot. Vegetation composition of vascular plants and bryophytes (% cover) of the NEE plot was estimated by visual inspection in August. As 14/18 of the species present were observed in less than six locations, the total percentage cover of non-*Molinia* species was calculated. The number of species present at each location was counted to derive the species richness. The inverse Simpson diversity index [Equation (5)] was also calculated. This determines the probability that two individuals randomly selected from a sample will be of the same species. D increases from 1 to n as diversity increases.

Equation (5): inverse Simpson diversity index

$$D = 1 / \left(\frac{\sum n(n-1)}{N(N-1)} \right) \quad (5)$$

Published Ellenberg's moisture indicator values (Hill *et al.*, 1999) were assigned to all species identified where these species have been classified. These ranged from 6 (moist to damp, e.g. *Vaccinium myrtillus* and *Gallium saxatile*) to 9 (wet, e.g. *Narthecium ossifragum* and *Sphagnum fallax*); *M. caerulea* has a value of 8 (damp to wet). Ellenberg's moisture indicator values for the classified species present at each location were averaged to give the Ellenberg's moisture indicator value.

Statistical analysis

To test for spatial variation, a two-way analysis of variance (ANOVA) was carried out on seasonal mean water table depths, measured vegetation indices, P_{G600} and R_{Eco} with site, proportional distance from the ditch and proportional distance from the ditch nested within site as between-subject effects. A repeated-measures ANOVA was carried out on below-ground respiration rates, with site or proportional distance from the ditch (plot) as between-subject factors and sampling round (time) as a within-subject factor. *Post hoc* least squares difference tests were carried out to identify statistically different groups. Linear and quadratic regressions were carried out to test for a relationship between distance from the ditch and water table depth, measured vegetation indices, P_{G600} , R_{Eco} and below-ground respiration. The most significant relationships are reported.

It was expected that spatial variation in CO₂ fluxes would be driven primarily by variation in water table depth and/or vegetation composition. Water table depth and vegetation indices (percentage cover of *Molinia*, leaf litter and non-*Molinia* species, ANPP, species richness, inverse Simpson diversity index and Ellenberg's moisture indicator values) were regressed against CO₂ fluxes (modelled ecosystem respiration, modelled photosynthesis, seasonal mean total, heterotrophic and autotrophic below-ground respiration at 10°C for each location). All statistical analyses were performed with SPSS 19 (SPSS Inc., Chicago, Illinois, USA).

RESULTS

Spatial variation with distance from a drainage ditch

Water table depth was deepest closest to the ditch (1/8 distance) and became shallower at 1/2 distance (Figure 2a), but the difference was not significant ($p=0.197$, Table III). Although vegetation properties showed variation (Table II; Table 3 in the supporting information), analysis of variance indicated none varied significantly with proportional distance from the ditch (Table III). Both percentage coverage of non-*Molinia* species and the Simpson diversity index were lower at 1/8 distance than at 1/2 distance (Figure 2d and e). However, the difference between proportional distances from the ditch (Table III) was not significant ($p=0.083$ and $p=0.076$ for non-*Molinia* and the Simpson diversity index, respectively). Species richness (Figure 2f) also showed a non-significant increase at greater proportional distance from the ditch but no significant relationship with absolute distance from the ditch ($p=0.135$). ANPP, percentage cover of leaf litter and *Molinia* were lowest at 1/4 distance (Figure 2g, h and i), but showed no significant differences between proportional distances from the ditch (Table III) or from the absolute distances from the ditch (Table V).

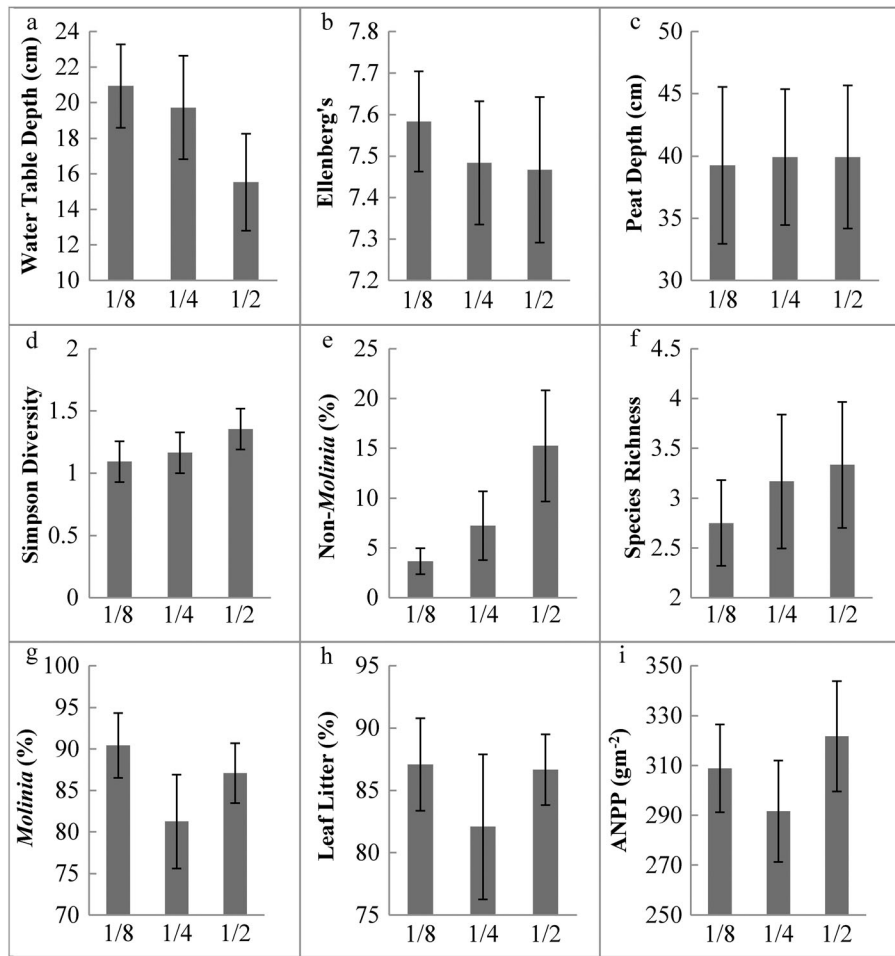


Figure 2. Variation with proportional distance from the ditch in (a) water table depth (cm below-ground surface), (b) Ellenberg's moisture indicator values, (c) peat thickness (cm), (d) inverse Simpson diversity index, (e) percentage coverage of non-*Molinia* species, (f) species richness, (g) percentage coverage of *Molinia*, (h) percentage coverage of leaf litter and (i) annual net primary productivity (ANPP) (g m^{-2}). $n = 12$. Error bars are one standard error.

Table II. Mean and standard error (in brackets) for different sites and proportional distances from the ditch.

	Distance from the ditch (m)	Water table depth (cm)	<i>Molinia</i> (%)	Leaf litter (%)	Non- <i>Molinia</i> (%)	ANPP (g m^{-2})	Species richness	Simpson diversity	
Proportional distance from the Ditch	1/8	3.01 (0.34)	21 (2)	90 (4)	87 (4)	4 (1)	309 (18)	2.8 (0.4)	1.1 (0.0)
	1/4	6.04 (0.70)	20 (3)	81 (6)	82 (6)	7 (3)	292 (20)	3.2 (0.7)	1.2 (0.1)
	1/2	12.07 (1.39)	16 (3)	87 (4)	87 (3)	15 (6)	322 (22)	3.3 (0.6)	1.4 (0.1)
Site	A1	.	15 (1)	88 (5)	87 (2)	5 (2)	295 (22)	3.8 (0.9)	1.1 (0.0)
	A2	.	31 (3)	83 (7)	89 (3)	3 (2)	281 (19)	2.3 (0.7)	1.1 (0.0)
	A3	.	14 (3)	83 (6)	85 (3)	6 (2)	299 (32)	4.0 (0.8)	1.1 (0.0)
	S1	.	11 (1)	88 (6)	80 (7)	21 (9)	294 (34)	4.0 (1.0)	1.5 (0.2)
	S2	.	21 (5)	78 (9)	100 (0)	6 (5)	373 (27)	1.7 (0.3)	1.1 (0.01)
	S3	.	20 (2)	97 (3)	71 (9)	12 (8)	303 (26)	2.7 (0.8)	1.3 (0.2)
Total	Mean	7.04 (0.82)	19 (2)	86 (3)	85 (2)	9 (2)	307 (11)	3.1 (0.3)	1.2 (0.1)
	Min	1.56	2	40	35	0	199	1.0	1.0
	Max	21.95	40	100	100	53	488	8.0	2.3

ANPP, annual net primary productivity.

Table III. Two-way analysis of variance for mean water table depth, vegetation indices, peat depth and modelled ecosystem respiration (R_{Eco}) and photosynthesis at 600 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ (P_{G600}) ($\mu\text{gC m}^{-2}\text{s}^{-1}$) at all locations ($n=36$) with site, proportional distance from the ditch (plot) and proportional distance from the ditch nested within site as between-subject variables.

	Source	SS	df	MS	<i>F</i>	<i>p</i>
Water table depth	Site	1 479	5	296	5.4	0.003
	Plot	194	2	97	1.8	0.197
	Plot(site)	367	10	37	0.7	0.734
% <i>Molinia</i>	Site	1 265	5	253	1.2	0.334
	Plot	517	2	258	1.3	0.307
	Plot(site)	3 000	10	300	1.5	0.231
% leaf litter	Site	2 822	5	564	3.0	0.040
	Plot	185	2	92	0.5	0.623
	Plot(site)	1 115	10	112	0.6	0.805
% non- <i>Molinia</i>	Site	1 365	5	273	1.9	0.154
	Plot	844	2	422	2.9	0.083
	Plot(site)	1 894	10	189	1.3	0.309
ANPP	Site	32 970	5	6 594	1.4	0.284
	Plot	5 498	2	2 749	0.6	0.586
	Plot(site)	41 057	10	4 106	0.8	0.591
Species richness	Site	30	5	6.0	1.8	0.162
	Plot	2	2	1.1	0.3	0.725
	Plot(site)	47	10	4.7	1.4	0.246
Inverse Simpson diversity index	Site	0.7	5	0.1	1.9	0.146
	Plot	0.4	2	0.2	3.0	0.076
	Plot(site)	1.1	10	0.1	1.4	0.246
Ellenberg's moisture indicator value	Site	2.2	5	0.4	2.0	0.135
	Plot	0.1	2	0.0	0.2	0.814
	Plot(site)	2.5	10	0.2	1.1	0.421
Peat depth	Site	11 547	5	2 309	24	0.000
	Plot	3.5	2	1.8	0.02	0.982
	Plot(site)	235	10	23.5	0.2	0.986
R_{Eco}	Plot	215	2	108	0.4	0.678
	Site	477	5	95	0.4	0.874
	Plot(site)	2 807	10	281	1.0	0.453
P_{G600}	Plot	877	2	438	0.3	0.760
	Site	31 947	5	6 389	4.1	0.012
	Plot(site)	21 522	10	2 152	1.4	0.269

Values where $p < 0.050$ are shaded dark grey.

SS, sum of squares; df, degrees of freedom; MS, mean sum of squares; *F*, *F* ratio; *p*, significance.

Average Ellenberg's moisture indicator values were greater at $\frac{1}{8}$ distance than at $\frac{1}{2}$ distance (Figure 2b), indicating a drier plant community further away from the ditch, which contrasts with the measured water table depths (Figure 2a). Ellenberg's moisture indicator values ranged from 6.6 to 8.5 with a mean of 7.5 (constantly moist or damp but not wet) and showed a non-significant positive relationship ($r^2=0.08$, $p=0.105$) to water table depth, indicating drier conditions (lower Ellenberg's moisture indicator values) occurring where the water table was closer to the soil surface. Ellenberg's moisture indicator values could not be used as indicators of moisture conditions and were therefore excluded from further investigation.

Neither modelled P_{G600} nor R_{Eco} varied significantly with proportional distance from the ditch (Table III) or absolute distance from the ditch (Table V). P_{G600} was greatest furthest from the ditch and least at $\frac{1}{4}$ distance (Figure 3a) whilst R_{Eco} increased non-significantly between

closest to the ditch and $\frac{1}{4}$ distance (Figure 3a). The interaction term between site and proportional distance from the ditch was not significant for either P_{G600} or R_{Eco} (Table III), indicating that the effect of proportional distance from the ditch did not depend on which site was being analysed. No below-ground respiration source varied significantly with proportional distance from the ditch (Table IV) or absolute distance from the ditch (Table V). However, they were all greatest at $\frac{1}{4}$ distance with $\frac{1}{2}$ distance smallest (Figure 4a).

Spatial variation between sites

Water table depth, percentage coverage of leaf litter and peat depth all varied significantly between sites (Table III). Site A2 was drier and site S1 wetter than all the other sites (Table II). Peat depth was also significantly greater at site S2 than at all the other sites (Table I). The sites could be divided into two groups based on the percentage coverage

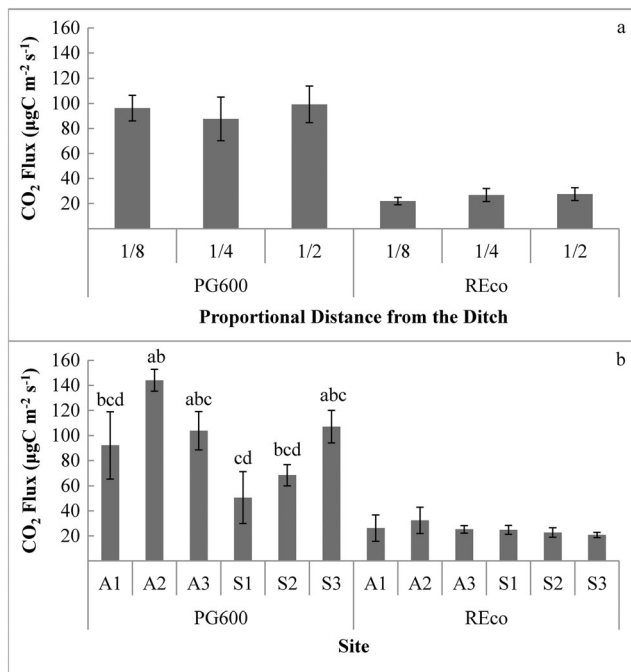


Figure 3. Variation in modelled photosynthesis (P_{G600}) ($\mu\text{gC m}^{-2} \text{s}^{-1}$) and ecosystem respiration (R_{Eco}) ($\mu\text{gC m}^{-2} \text{s}^{-1}$) with (a) proportional distance from the ditch and (b) site. Error bars are one standard error. Letters denote statistically significant groups $p = 0.012$.

of leaf litter, those with $\geq 85\%$ coverage (A1, A2, A3 and S2) and those with $\leq 85\%$ coverage (A3, S1 and S3) (Table II). The interaction term between site and proportional distance from the ditch was not significant for any of the spatial variables tested (Table III), indicating that, for example, the effect of proportional distance from the ditch

on water table depth did not depend on which site was being analysed.

P_{G600} varied significantly between sites (Figure 3b), with photosynthesis at site A2 greater than at sites S1 and S2 with the other sites intermediate. Sites A2 and S1 were also the driest and wettest, respectively (Table II). Ecosystem respiration was also greatest at site A2 but did not vary significantly between sites (Table III). Total and heterotrophic below-ground respiration showed similar spatial variation between sites with respiration greatest at S1 and least at A2, whereas autotrophic respiration was greatest at S3 and least at A3. Only heterotrophic respiration varied significantly between sites (Table IV) with site S1 having significantly greater respiration than all the other sites (Figure 4b). The significant interaction term between site and sampling round (time) for heterotrophic respiration (Table IV) indicates that heterotrophic respiration varied differently over time dependent on which site was being analysed.

Drivers of spatial variability

Percentage cover of non-*Molinia* species and the inverse Simpson diversity index both showed a significant negative covariance with water table depth (Table V). Greater diversity and more non-*Molinia* species occurred where the water table depth was closer to the surface.

Water table depth showed a significant positive covariance (Table V) with P_{G600} ; greater photosynthesis occurred where the water table was deeper. No other CO_2 fluxes co-varied with water table depth. P_{G600} showed no significant relationships with ANPP or vegetation composition indices (*Molinia*, non-*Molinia*, leaf litter, species richness or inverse Simpson diversity index) (Table V).

Table IV. Repeated-measures analysis of variance results for total, heterotrophic and autotrophic below-ground respiration adjusted to 10 °C.

Respiration source	Effect	SS	df	MS	F	p
Total at 10 °C	Time	3.60	2.05	1.75	10.60	0.000
	Site	1.42	5.00	0.28	1.32	0.283
	Plot	0.18	2.00	0.09	0.38	0.689
	Time × site	2.53	10.25	0.25	1.49	0.163
	Time × plot	0.72	4.54	0.16	1.00	0.421
Heterotrophic at 10 °C	Time	3.24	3.56	0.91	17.36	0.000
	Site	1.05	5.00	0.21	3.28	0.018
	Plot	0.01	2.00	0.01	0.07	0.937
	Time × site	1.92	18.22	0.11	2.67	0.001
	Time × plot	0.06	7.13	0.01	0.15	0.994
Autotrophic at 10 °C	Time	0.43	2.80	0.15	1.13	0.342
	Site	0.71	5.00	0.14	0.70	0.626
	Plot	0.10	2.00	0.05	0.25	0.781
	Time × site	2.26	13.98	0.16	1.19	0.298
	Time × plot	0.93	5.76	0.16	1.21	0.309

Proportional distance from the ditch (plot) and site were between-subject effects, and sampling round (time) was a within-subject effect. Values where $p < 0.050$ are shaded dark grey.

SS, sum of squares; df, degrees of freedom; MS, mean sum of squares; F, F ratio; p, significance.

Table V. Regression coefficients (r^2) and significance (in brackets) of linear regression between water table depth (cm below-ground surface) and annual net primary productivity (ANPP), peat thickness and vegetation indices.

	Water table depth (cm)	ANPP (g m^{-2})	<i>Molinia</i> (%)	Non- <i>Molinia</i> species (%)	Leaf litter (%)	Species richness	Simpson diversity	Inverse Simpson diversity	Peat thickness (cm)
Water table depth (cm)	0.13 (0.034) +	0.01 (0.662) +	0.06 (0.169) -	0.15 (0.021) -	0.03 (0.322) +	0.16 (0.087) -	0.14 (0.024) -	0.08 (0.106) +	
P_{G600}	0.01 (0.511) +	0.00 (0.896) +	0.03 (0.322) +	0.01 (0.479) +	0.00 (0.913) -	0.00 (0.850) -	0.02 (0.459) -	0.00 (0.884) -	
R_{Eco}	0.01 (0.613) -	0.01 (0.595) +	0.07 (0.132) -	0.04 (0.256) -	0.01 (0.534) +	0.10 (0.062) -	0.04 (0.268) -	0.01 (0.641) -	
R_{Tot}	0.05 (0.172) -	0.01 (0.646) -	0.04 (0.224) +	0.00 (0.923) +	0.15 (0.021) -	0.00 (0.746) +	0.00 (0.881) +	0.00 (0.856) -	
R_{Het}	0.00 (0.934) +	0.08 (0.096) -	0.01 (0.582) -	0.02 (0.440) +	0.07 (0.109) -	0.03 (0.332) +	0.02 (0.396) +	0.11 (0.046) -	
R_{Aut}		0.09 (0.587) +	0.09 (0.077) +	0.04 (0.709) -	0.05 (0.181) -	0.00 (0.940) -	0.00 (0.719) -	0.03 (0.327) +	

Regression coefficients (r^2) and significance (in brackets) of linear regression between modelled photosynthesis at 600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (P_{G600}), modelled ecosystem respiration (R_{Eco}), total (R_{Tot}), heterotrophic (R_{Het}) and autotrophic (R_{Aut}) below-ground respiration at 10 °C and water table depth, annual net primary productivity (ANPP), peat thickness and vegetation indices ($n=36$). Values where $p < 0.050$ are shaded dark grey. + denotes positive covariance, whereas - denotes negative covariance.

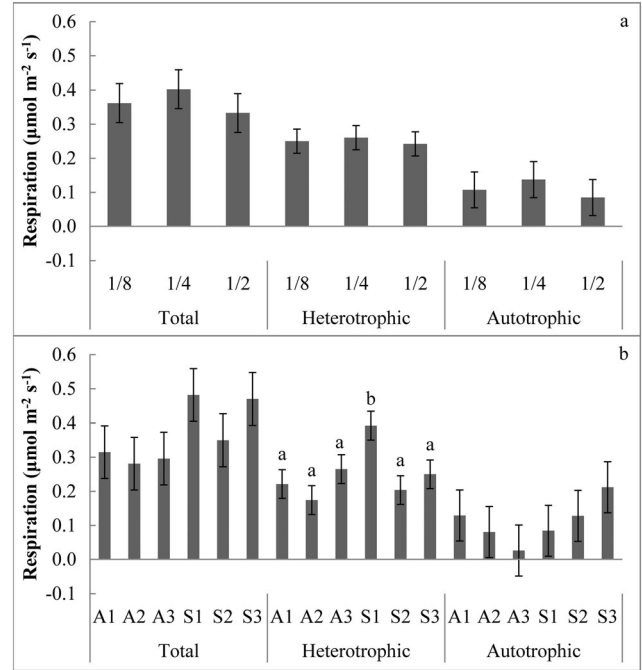


Figure 4. Variation in total, heterotrophic and autotrophic below-ground respiration at 10 °C ($\mu\text{mol m}^{-2} \text{s}^{-1}$) with (a) proportional distance from the ditch and (b) site. Error bars are one standard error. Letters denote statistically significant groups $p=0.018$.

R_{Eco} and autotrophic respiration showed no significant relationships with any of the variables tested (Table V). However, autotrophic respiration showed some level of co-variation ($r^2=0.09$, $p=0.077$) with percentage cover of *Molinia*; autotrophic respiration was greater where there was more *Molinia* coverage. Heterotrophic respiration significantly co-varied ($r^2=0.11$, $p=0.046$) with peat thickness with greater respiration where the peat was thinner (Table V) whilst total soil respiration was significantly greater ($r^2=0.15$, $p=0.021$) where there was less coverage of leaf litter.

DISCUSSION

Drainage ditches, water table depths and vegetation

The drainage features on Exmoor although small (typically <0.5 m wide and <0.5 m deep) penetrate deep into the shallow peat [Exmoor average 0.33 m (Bowes, 2006)] and are regularly spaced (approximately 20 m) (Figure 1), making them important spatial features governing ecohydrological processes in these uplands (Grand-Clement *et al.*, 2013). The mean water table was deeper closer to the ditch than at $1/2$ distance (Figure 2a), but the significant variability between sites (Table III) was such that the difference between proportional distances from the ditch was not significant. Differences between sites may have been due to a combination of different site

conditions (e.g. peat thickness, ditch direction etc.) as well as the distance between adjacent ditches and hence absolute distance of $\frac{1}{8}$, $\frac{1}{4}$ and $\frac{1}{2}$ plots from the ditch. On different ditches within the same catchments, Luscombe (2014) found water table depths to be deeper nearer the ditch, but that distance from the ditch explained only 13.6% of the observed spatial variance. Fine-scale topography and position up or down slope of the ditch altered the effect of proximity to a ditch. On deeper *Eriophorum vaginatum*, *Deschampia myrtilloides* and *M. caerulea*-dominated peatlands, Holden *et al.* (2011) also found water table depth to be deeper closest to the ditch with the effect localized within a few metres due to the low hydraulic conductivity of peat. However, when comparing 1.5 m to 6 m from the ditch in a *C. vulgaris*–*E. vaginatum* upland blanket bog, Coulson *et al.* (1990) found no significant difference in water table depths, possibly due to high rainfall conditions.

This non-significant variation in water table depth may explain why there was no significant (Table III) variation in percentage coverage of non-*Molinia* species and the inverse Simpson diversity index. Coulson *et al.* (1990) found coverage of *C. vulgaris* to increase away from the ditch with a concurrent decrease in grass species in two low-altitude British blanket bogs where they observed difference in water table depths, but in two higher altitude, higher rainfall bogs where no variation in water table depth was observed, there was no significant change in vegetation composition.

Site, water table depths and vegetation

Given the range of average water table depths for each site in this study (11–34 cm) (Table II), and previous work, a greater range of vegetation communities across the sites studied would be expected. For example, a 22 to –2 cm range in mean water table depth affected a change in vegetation from *E. vaginatum* to *Scheuchzeria palustris* in an undisturbed Finnish fen (Riutta *et al.*, 2007). In this study, *M. caerulea* ($86 \pm 3\%$) dominated with minimal non-*Molinia* species present ($9 \pm 2\%$). This vegetation composition reflects deeper water table depths under wet conditions, the competitive nature of *Molinia*, its ability to flourish where water table depths fluctuate (Jefferies, 1915) and tendency to exclude other plants (Taylor *et al.*, 2001). Minimal variability in vegetation composition would be expected to limit the magnitude of variation possible in CO₂ both between sites and with distance from the ditch.

Across all locations, more non-*Molinia* species ($r^2 = 0.15$, $p = 0.021$), greater species richness ($r^2 = 0.16$, $p = 0.087$) and higher diversity ($r^2 = 0.14$, $p = 0.024$) occurred where the water table depth was closer to the surface (Table V), indicating that *Molinia* may be less dominant where water tables are shallower enabling other species to grow. This

finding is similar to that of Laine *et al.* (2007) who found species richness to decrease as water table depths dropped below approximately 10 cm in an undisturbed Irish blanket bog.

Other studies in pristine peatlands (Laine *et al.*, 2007, Maanavilja *et al.*, 2011) found vascular green area to increase as water tables fell and vegetation composition changed. In this study, ANPP was not affected by water table depth (Table V). Again, this most likely reflects the greater vegetation diversity and wetter conditions within these studies compared with that observed on Exmoor. Rutter (1955) found mean water table depth to determine the shape of the *Molinia* tussock and the vegetation composition present in a wet heath. It is known that vegetation structure varies with wetness in these catchments (Luscombe *et al.*, 2014). However, in this study, mean water table depth did not relate to percentage coverage of *Molinia* (Table V). It may be that the vegetation survey failed to capture structural variation as the long spreading leaves covered most of the plot, resulting in limited variation in *Molinia* cover between locations ($86 \pm 3\%$).

Bellamy *et al.* (2012) found a wet vegetation index (based on vegetation with an Ellenberg's moisture indicator value of 8–10) to be lowest 0.5 m from the ditch in a blanket bog and increase with distance from the ditch. Conversely, an index of drier vegetation (Ellenberg's moisture indicator values of 4–7) was highest close to the ditch and decreased with distance. In the current study, Ellenberg's moisture indicator values decreased (non-significantly) with increased distance from the ditch, indicating wetter conditions nearer the ditch (Figure 2b). They also increased where water table depths were closer to the surface; contrary to expectations given, Ellenberg's moisture indicator values range from 1 (extreme dryness) to 12 (submerged plants) (Hill *et al.*, 1999), demonstrating that Ellenberg's moisture indicator values are not appropriate as a proxy for wetness in this relatively dry and low diversity environment where only *N. ossifragum* (9) and *S. fallax* (9) had higher indicator values than *M. caerulea* (8).

Spatial variability of CO₂ fluxes

CO₂ fluxes from the *Molinia*-covered peatland did not vary significantly with proportional distance from the ditch (Tables III, IV), arguably due to limited variation in either water table depth (Figure 2a) or vegetation composition (Figure 2d–g). In other studies where spatial features such as ditches have been explicitly monitored, clear differences in functional responses have been measured – e.g. ephemeral erosional gullies in a British blanket bog have been shown to have significantly higher ecosystem respiration (McNamara *et al.*, 2008, Clay *et al.*, 2012) and photosynthesis (Clay *et al.*, 2012) than the surrounding blanket bog. These gullies were

deeper (up to 3 m) and wider (5–9 m) and had a greater effect on both water table depth and vegetation community than the smaller drainage ditches of Exmoor. It is likely that CO₂ fluxes varied across ephemeral erosional gullies due to the spatial variation in vegetation and vegetation cover with the greatest rates of photosynthesis and ecosystem respiration from *Eriophorum* communities and lowest fluxes from bare peat.

Photosynthesis weakly ($r^2=0.13$, $p=0.034$) co-varied with water table depth; greater photosynthesis occurred where the water table was deeper. This may have occurred as drier conditions encourage greater above-ground biomass (Murphy and Moore, 2010) or promote increased coverage by graminoids, which have been shown to have higher NEE rates than mosses (Otieno *et al.*, 2009) and *C. vulgaris* (Aerts, 1990). Although the cover of non-*Molinia* species was less where the water table was deeper (Table V), there was no significant relationship between P_{G600} and non-*Molinia* directly. In addition, P_{G600} showed no significant relationships with either ANPP or percentage coverage of *Molinia* (Table V). It is possible that despite adaptations to live in conditions of fluctuating water table depths (Taylor *et al.*, 2001), the conditions for *M. caerulea* were sub-optimum at the wetter locations (e.g. site S1), thus reducing photosynthesis.

Where water table depth has been found to control spatial variation in photosynthesis, fluxes have also been greater in drier microforms (Laine *et al.*, 2006, Maanavilja *et al.*, 2011, Schneider *et al.*, 2012). In such studies, there was clear differentiation in water table depths and vegetation community between microforms so it is less clear if variation in photosynthesis was due to water table depth, vegetation community or both. Conversely, Bubier *et al.* (2003) found different microforms to have similar rates of photosynthesis, despite variation in vegetation composition and water table depth, due to similar leaf biomass.

Where variation in photosynthetic rates have been assessed within microforms in a pristine Finnish fen, hummocks and *E. vaginatum* lawns and hollows were found to respond to water table depths but not *Carex* lawns (Riutta *et al.*, 2007). However, in a pristine Russian boreal peatland, *Carex* lawns showed the greatest within microform variability in photosynthesis driven by variation in vegetation composition and water table depth (Schneider *et al.*, 2012), indicating the uncertainty in assessing controls on photosynthesis within a microform.

Where ecosystem respiration has been found to vary between microforms in pristine peatlands (Bubier *et al.*, 2003, Laine *et al.*, 2006, Maanavilja *et al.*, 2011, Juszczak *et al.*, 2013), wetter areas had distinct vegetation communities and lower respiration rates. Again, the minimal variation in vegetation composition observed in this study may explain why there was no statistically significant spatial variation in ecosystem respiration

(Table III). This finding suggests that photosynthesis is the main control on the spatial distribution of NEE. Riutta *et al.* (2007) also found photosynthesis to vary more between communities than ecosystem respiration in a Finnish fen.

Peatland restoration programmes (Grand-Clement *et al.*,) typically aim to raise water tables and re-establish the ecohydrological structure and functionality of peatlands. Re-colonization by peat-forming *Sphagnum*-rich vegetation communities has been identified as particularly important to promote carbon sequestration (Lunt *et al.*, 2010). Raising mean water table depths may have no effect on heterotrophic respiration of the peat store but decrease photosynthesis (Table V) shifting the ecosystem towards a greater CO₂ source unless change in water table depth is sufficient to alter the vegetation composition (and leaf litter quantity and quality) beyond that observed in this study.

As below-ground autotrophic respiration is strongly dependent on photosynthesis (Metcalf *et al.*, 2011), it would be expected that autotrophic (root) respiration would mirror photosynthesis and be dependent on water table depth. Instead, photosynthesis (Figure 3) and autotrophic respiration (Figure 4) showed dissimilar spatial patterns and varied with different spatial variables (Table V), suggesting that autotrophic respiration was controlled by factors additional to photosynthetic activity, such as morphological differences in root biomass (Heinemeyer *et al.*, 2012), variation in the allocation of carbon between growth and maintenance (Bond-Lamberty *et al.*, 2004) and moisture and nutrient availability (Chapman and Thurlow, 1998). Autotrophic respiration showed the strongest ($r^2=0.09$) and most significant ($p=0.077$) co-variation with percentage cover of *Molinia*, with greater autotrophic respiration where there was more *Molinia* coverage. As above-ground and below-ground biomass have been shown to be linked (Murphy and Moore, 2010), it may be that where there is greater *Molinia* coverage, there is greater root biomass, resulting in increased root respiration and microbial respiration of root exudates.

Neither total nor heterotrophic below-ground respiration varied with water table depth (Table V). Jaatinen *et al.* (2008) found long-term (45 years) water table drawdown of a fen to increase total soil respiration rates in the driest areas; however, the decomposition potential of the substrate remained greater in the wetter areas. As the drainage ditches on Exmoor are over 150 years old, much of the labile organic matter will have already degraded (Bridgham and Richardson, 1992). This will have left a humified peat that, although potentially vulnerable to priming (Freeman *et al.*, 2004, Fontaine *et al.*, 2007), is less responsive to variation in water table depth than recently drained peat. Grand-Clement *et al.* (2014) found consistently low humic to fulvic acid ratios for dissolved organic carbon from these catchments, indicative of more humified peats.

It was expected that heterotrophic respiration would vary with changes in leaf litter quality and quantity (Straková *et al.*, 2011a). Heterotrophic respiration showed no significant co-variation with percentage coverage of non-*Molinia* or inverse Simpson diversity index (Table V), variables influencing litter quality or ANPP, a measure of litter quantity. This may be due to the limited variation in vegetation composition and ANPP observed (Table II). Instead, heterotrophic respiration significantly co-varied with peat thickness (Table V) with greater respiration occurring where peat was thinner. This finding is contrary to those of other studies where thinner peats were found to have lower heterotrophic respiration rates in a *C. vulgaris* blanket bog (Hardie *et al.*, 2009) and also where peat thickness was found to have little effect on heterotrophic respiration as most respiration occurred near the surface of the peat (Blodau *et al.*, 2007) primarily due to a lack of oxygen below the water table. There is no obvious explanation for this relationship.

Where microforms or spatial features were found to have distinct CO₂ fluxes, they have been mapped and used to upscale CO₂ fluxes across a landscape (Laine *et al.*, 2006, Riutta *et al.*, 2007, McNamara *et al.*, 2008). In these *Molinia*-dominated peatlands, there was significant spatial variation (Table III) in P_{G600}. However, this was not directly associated with proportional distance from drainage ditches (Table III), so mapping these features cannot be used directly to upscale CO₂ fluxes in this landscape. Given the sparse vegetation in the ditches, it is unlikely that these would have large CO₂ fluxes; however, as these were not measured, it is currently unknown if these are important when estimating landscape scale fluxes.

CONCLUSION

Modelled CO₂ fluxes (photosynthesis and ecosystem respiration, total, heterotrophic and autotrophic below-ground respiration) showed no significant spatial distribution in response to drainage ditches, arguably due to a lack of significant spatial distribution in water table depths and minimal variation in vegetation composition (percentage cover of non-*Molinia* species and inverse Simpson diversity index).

Across all locations ($n=36$) where the average water table depth was closer to the surface, more non-*Molinia* species coverage, increased vegetation diversity and reduced P_{G600} occurred, indicating wetter conditions may be sub-optimum for *M. caerulea*. Our data emphasize that substantial reductions in heterotrophic respiration may not always occur following restoration, unless water tables rise to be consistently very close to the soil surface. As a consequence, raising mean water table depths through ecohydrological restoration may shift the ecosystem

towards greater CO₂ release unless the vegetation composition alters beyond that observed in this study.

Modelled P_{G600} showed significant spatial variation between sites and significantly co-varied with water table depth. This offers a potential means to estimate CO₂ fluxes at a landscape scale. Although water table depth showed variation between proportional distances from the ditch, the uncertainty is such that it should not be assumed that water table depth is distributed according to proportional distance from a drainage ditch. Therefore, other methods of determining the spatial distribution of water table depth, which may be only partially explained by ditch density, such as vegetation structure (Rutter, 1955) and thermal emissivity, (Luscombe *et al.* 2014) should be explored.

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