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Burning increases post-fire carbon emissions in a heathland and a raised bog, but experimental manipulation of fire severity has no effect

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Abstract

Large amounts of carbon are stored in northern peatlands. There is concern that greater wildfire severity following projected increases in summer drought will lead to higher post-fire carbon losses. We measured soil carbon dynamics in a *Calluna* heathland and a raised peat bog after experimentally manipulating fire severity. A gradient of fire severity was achieved by simulating drought in 2 × 2 m plots. Ecosystem respiration (ER), net ecosystem exchange (NEE), methane (CH_4) flux and concentration of dissolved organic carbon ([DOC], measured at the raised bog only) were measured for up to two years after burning. The response of these carbon fluxes to increased fire severity in drought plots was similar to plots burnt under ambient conditions associated with traditional managed burning. Averaged across all burnt plots, burning altered mean NEE from a net carbon sink at the heathland (-0.33 μmol CO_2 m^{-2} s^{-1} in unburnt plots) to a carbon source (0.50 μmol m^{-2} s^{-1} in burnt plots) and at the raised bog (-0.38 and 0.16 μmol m^{-2} s^{-1}, respectively). Burning also increased CH_4 flux at the raised bog (from 1.16 to 25.3 nmol m^{-2} s^{-1} in the summer, when it accounted for 79 % of the CO_2-equivalent emission). Burning had no significant effect on soil water [DOC].

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1. Introduction

Large amounts of carbon (C) are stored in northern peatlands (Leifeld and Menichetti, 2018), where it may be vulnerable to changes triggered by the projected warmer and drier climate (IPCC, 2014; Cook et al., 2014). Increased permafrost thaw, soil temperatures (Walker et al., 2018) and wildfire activity (Turetsky et al., 2015) could contribute to a positive feedback on climate change (Heimann and Reichstein, 2008).

High severity fire can directly impact belowground C stores by igniting peat or other organic soil layers (Davies et al., 2013; Kettridge et al., 2015). However, even where peat fuel moisture contents are high enough to prevent ignition ($>$ 150 %; Prat-Guitart et al., 2016) fire can alter processes controlling soil C dynamics. For example, fire-induced plant mortality can lower ecosystem respiration (ER) by reducing autotrophic respiration from aboveground structures and roots (Janssens et al., 2001; Moore et al., 2002), and through reduced microbial respiration due to a lower supply of root exudates (Artz, 2013). However, burning is also associated with warmer soils (Grau-Andrés et al., 2018a) that can lead to increased ER (Walker et al., 2018) and methane (CH_4) flux (Turetsky et al., 2014). In the longer term, post-fire changes in vegetation community composition (Grau-Andrés et al., 2019) may have the largest impact on soil C dynamics due to differences in C cycling between plant functional groups (Ward et al., 2009; Strack et al., 2017), including litter quality (Wardle et al., 2012) and transport mechanisms (e.g. aerenchymatous species can facilitate methane emission; Gray et al., 2013).

Wildfires can decrease the C sink in peatlands due to reduced primary productivity and increased respiration resulting from higher peat temperatures (Turetsky et al., 2002). However, these post-fire effects may be transient. Wieder et al. (2009) demonstrated that peatland C sequestration was greater than C loss

13 years after fire, as ground vegetation regenerated. In mature communities, net ecosystem exchange (NEE = ER minus photosynthesis) can increase with time since fire due to lower plant productivity (i.e. leads to a smaller carbon sink). For example, Ward et al. (2007) reported higher blanket bog NEE in plots unburnt for 50 years (ca. -0.25 μmol CO_2 m^{-2} s^{-1}) than in plots that had been burnt 9 years previously (ca. -0.55 μmol CO_2 m^{-2} s^{-1}). The effect of burning on CH_4 fluxes remains equivocal and evidence is limited. Studies following prescribed fires in UK peatlands have indicated either no short-term (< 3 years) change (Taylor, 2015) or a longer-term (9 years) decline in fluxes (Ward et al., 2007). CH_4 fluxes have also been observed to decline one year after wildfires (Davies et al., 2014). Fire effects on dissolved organic carbon concentration, [DOC], are also unclear: Ramchunder et al. (2013) found [DOC] to be higher in streams draining peatland catchments in the English Peat District that had a recent history of managed burning. However, studies completed at the plot level within the same ecosystem found no differences between burnt and unburnt areas (Armstrong et al., 2012; Clay et al., 2012). Methodological differences between catchment and plot studies have been proposed to explain the contradictory results (Holden et al., 2012), but definitive evidence of the mechanisms that might explain these differences is still lacking.

Peat bogs in the UK contain > 550 Tg C belowground, ca. 35 % of national belowground (upper 0.5 m) C stocks across terrestrial ecosystems (Ostle et al., 2009). Dwarf shrub heathlands also store a substantial amount of belowground C, 125 Tg or 7 % of national belowground C up to 0.5 m depth. These semi-natural habitats are often managed by traditional rotational burning (Allen et al., 2016) but are also prone to wildfires (Davies and Legg, 2016). Carbon deposits in heathlands may be vulnerable to fire because of these ecosystems lower resilience to drought compared to bogs (Davies et al., 2016; Grau-Andrés et al., 2018a). While dry conditions have been linked to higher fire severity (Grau-Andrés et al., 2018a), few studies have focused on the effect of variation in fire severity on post-fire belowground C dynamics. This is a significant gap in our understanding given the potential for increased fire severity across northern regions in response to climate change (Krawchuk et al., 2009; Cook et al., 2014). Thus, a greater understanding of the effects of fire severity on the potential impacts to soil C stores and soil C dynamics is needed to inform management strategies that minimise C loss.

We investigated the effect of fire severity on soil C dynamics using experimental fires in two contrasting UK habitats: an upland *Calluna vulgaris* (L.) Hull heathland and a lowland raised bog. Our objectives were to: (i) understand how soil carbon dynamics (ER, NEE, CH_4 flux and [DOC]) respond to a gradient of fire severity; and (ii) investigate how responses to fire vary across the sites' contrasting ecohydrological conditions.

2. Materials and methods

2.1. Experimental fires

The experiments were completed at two sites in Scotland (UK): an upland dry heath (Glen Tanar, 57.016°N, 2.974°W, elevation 460 m) actively managed for red grouse (*Lagopus lagopus scoticus* Latham, 1787) and a lowland raised bog (Braehead Moss, 55.740°N, 3.658°W, elevation 270 m) that is designated Special Area of Conservation but has historically experienced low intensity disturbance (grazing, cutting and peat extraction; SNH, 2012). Although both sites have similar vegetation structure, dominated by dense *Calluna vulgaris* (hereafter *Calluna*) and a continuous bryophyte layer (thinner at the heathland, mean ± SD = 3.7 ± 0.8 cm, than at the raised bog, 10.8 ± 3.7 cm), they lie at opposite ends of an ecohydrological gradient. Soils at the heathland are well-drained peaty podzols with an organic horizon < 10 cm, while the peat at the raised bog is up to 9 m deep and saturated throughout most of its profile, even at the drier south-eastern margin of the bog where the experiment was located. We completed ten experimental fires at the heathland and nine at the raised bog between September 2013 and November 2014. Within each experimental burn area, two 2 × 2 m rain-out shelters were installed three to four months before the fires, and two 2 × 2 m plots were delimited to be burnt under

Table 1: Mean (range, in parenthesis) fire-induced consumption of the moss and litter (M/L) layer and soil heating (at the soil surface, i.e. below the M/L layer, and 2 cm below) per treatment at the heathland site (Glen Tanar) and at the raised bog (Braehead Moss). From Grau-Andrés et al. (2018a).

Site	Fire severity	M/L consumption (cm)	Max T (ground, °C)	Max T (2 cm depth, °C)
GT	Low	0.7 (0–3.5)	31 (7–87)	13 (4–27)
	High	2.3 (0.4–5.4)	189 (9–661)	40 (5–254)
BM	Low	0.1 (0–0.8)	10 (8–17)	9 (7–11)
	High	1.4 (0–3.4)	15 (6–48)	10 (6–12)

ambient fuel moisture conditions. The combination of experimental drought and weather-induced variation in burning conditions led to a wide range of fire severity, measured as moss and litter layer consumption (using duff spikes) and soil heating (using thermocouple loggers). Mean fire severity was higher in plots subjected to the drought treatment (high fire severity plots) than those burnt under ambient conditions (low fire severity plots), and at the heathland than at the raised bog (Table 1). Full details of the experimental design, fire monitoring methods and fire severity differences between treatments and sites can be found in Grau-Andrés et al. (2018a).

2.2. Gas fluxes

The closed static non-steady-state chamber method was used to estimate CO_2 and CH_4 fluxes. Here, ground-atmosphere gas flux is calculated based on the gas concentration change with time in a closed volume (Levy et al., 2011). In each burnt location ("fire"), we inserted an opaque plastic collar into the ground at a randomly-chosen location in each low and high fire severity plot and in a nearby unburnt control location (n = five plots per fire). Collars were inserted at least two weeks before gas flux measurements began. A cylindrical clear plastic chamber (height = 0.46 m, diameter = 0.39 m) was secured to the collar with clamps prior to measurement. The chamber contained a five-volt fan for headspace mixing and air temperature and relative humidity sensors to allow measurement corrections. A photosynthetically active radiation (PAR) sensor was mounted on top of the chamber.

Due to instrument malfunction, we used two different analysers to measure the change of gas concentration in the chamber space: a Los Gatos Research Ultraportable Greenhouse Gas Analyser (CO_2, CH_4, H_2O; from August 2014 to April 2015) and a Vaisala GMP343 Carbon Dioxide Probe (CO_2 only; June to October 2015). Time since fire during the sampling period averaged 471 days (range: 123–744 days) for CO_2 and 357 days (123–588 days) for CH_4. Both instruments had a 1 s measurement rate. NEE, and CH_4 when the Los Gatos analyser was used, were estimated from measurements using the clear chamber, whilst ER was assessed by covering it with an opaque polyethylene cover. The chamber was vented between measurements. By convention, negative NEE values indicate a C sink. We used linear regression to calculate gas fluxes following Levy et al. (2011). Full details of chamber set up, sampling effort, weather during sampling and gas flux calculations are given in the Supplementary Material.

2.3. Dissolved Organic Carbon concentration

Measurement of soil water [DOC] was limited to the raised bog site as insufficient soil water could be sampled from the thin and free-draining soils of the heathland. Soil water was sampled using a network of PVC dip-wells with an internal diameter of 1.9 cm perforated at a frequency of 1–2 cm from 10 cm to 60 cm below the peat surface. Depth of the open part of the dip-well was designed to include water table fluctuation based on a pilot study, and was slightly shallower than in previous research on effects of burning on peatland [DOC] (ca. 0–100 cm; Clay et al., 2012; Worrall et al., 2013; Armstrong et al., 2015). We manually inserted a dip-well centrally in each low fire severity and each high fire severity plot and in two unburnt locations (controls) near each fire.

We took soil water samples approximately every two months from October 2013 to November 2015 (mean time since fire = 295 days, range = 5–731 days), emptying the dip-wells 24 hours beforehand. The position of the water table was recorded in relation to the top of the soil to the nearest cm. The samples were filtered within 24 h using pre-combusted 0.7 μm glass fibre filters (Fischerbrand) and stored in low-density polyethylene (LDPE) bottles in the dark at 3 °C for two to four months (unlikely to affect concentration; Gulliver et al., 2010) until the carbon concentration was analysed with a total carbon analyser (Thermolox^{TM}, Analytical Sciences).

2.4. Environmental variables

We recorded soil temperature and moisture content, and vegetation cover in the gas flux collars as these can be important drivers of variation in carbon dynamics. Soil temperature was measured using loggers (iButton^{TM}, Maxim Integrated) buried 2 cm below the top of the soil. Moisture content of the soil surface (approximately top 6 cm) was measured using a soil moisture meter (Hydrosense^{TM}, Campbell Scientific), taking three measurements near the location of each collar (details in Grau-Andrés, 2017). We visually estimated the percentage cover of plant functional groups (shrubs, graminoids and bryophytes) and type of substrate (litter and duff or bare organic soil, corresponding to soil horizons Oi and Oe/Oa; FAO, 2006) within the collars. Glen Tanar was surveyed in April 2015 and Braehead Moss in September 2015.

2.5. Data analysis

Our data is available online (Grau-Andrés et al., 2018b). R 3.4.2 (R Core Team, 2017) was used for all statistical analysis and plotting. Linear mixed effects models were fitted using the function "lme" in the package *nlme* (Pinheiro et al., 2015). The "r.squaredGLMM" function in *MuMIn* (Barton, 2015) was used to calculate marginal R^2 (variance explained by fixed effects) and conditional R^2 (variance explained by both fixed and random effects) (Nakagawa and Schielzeth, 2013; Johnson, 2014). Table 2 details the linear mixed effects models used to analyse the effect of fire severity on ER, NEE, DOC, vegetation group cover, soil temperature and soil moisture during the gas flux measurements. We fitted separate soil temperature and soil moisture models for each site, and separate vegetation cover models for each vegetation group.

Table 2: Linear mixed effects models used to test differences in carbon dynamics and environmental variables between fire severity treatments. Season excluded winter, except for DOC. Random effects were plot within fire for repeated measurements, and fire for single measurements.

Response	Fixed effects	Random effects
ER	Treatment × site × season	plot/fire
NEE	Treatment × site × season	plot/fire
DOC	Treatment × season	plot/fire
Vegetation type cover	Treatment × site	fire
Soil moisture	Treatment × season	plot/fire
Soil temperature	Treatment × season	plot/fire

To test for differences in ER and NEE between fire severity treatments (unburnt, low severity and high severity) within site (heathland and raised bog) and season (spring: March–May, summer: June–August, autumn: September–November), we performed multiple comparisons calculating 95 % confidence intervals of differences between means, using the variance of the full model and a Bonferroni-corrected t-value (3 treatments × 2 sites × 3 seasons = 18 comparisons). For the other variables, the function "glht" in *multcomp* (Hothorn et al., 2008) was used to perform simultaneous tests on differences between treatments within seasons (DOC, soil temperature and soil moisture) or within site (cover of plant functional groups). Homogeneity of variances among treatments was analysed using Levene's test as implemented in the R package *lawstat* (Gastwirth et al., 2017). A high abundance of zeros made statistical analysis of methane flux data unreliable; a graphical analysis based on boxplots is presented instead.

3. Results

3.1. Environmental variables

Burning led to warmer soils during gas flux sampling, both in the heathland (in spring and summer) and the raised bog (in summer) (Table 3). Post-fire increases in soil temperature were greater at the heathland, e.g. during summer, soil temperature in burnt plots, including low and high severity treatments, was 14.2 ± 2.8 °C (mean ± SD) compared to 11.1 ± 1.8 °C in unburnt plots. Summer burnt and unburnt soil temperatures at the raised bog were, by comparison, 13.9 ± 1.2 °C and 13.1 ± 0.6 °C respectively. No temperature differences between fire severity treatments were detected, except at the heathland during spring when soil in high fire severity plots was significantly warmer than in low severity plots.

Soil moisture content during the gas flux measurements was higher at the raised bog (330 ± 16 %) than at the heathland (275 ± 25 %), but differences between treatments within site were generally small. Only during spring at the heathland did high fire severity plots have significantly lower soil moisture content than unburnt plots (Table 3). There was some evidence that water table at the raised bog was lower in unburnt (20.6 ± 8.5 cm below the soil surface) than in burnt plots (16.0 ± 7.4 cm in low fire severity and 16.5 ± 9.7 cm in high fire severity plots) across all seasons (t-value = -1.8, p-value = 0.07). Differences between treatments within the same season were not significant.

Burning led to lower cover of shrubs in the gas flux collars (26.8 ± 24.7 % in unburnt and 7.1 ± 7.8 % in burnt plots across both sites). Cover of bryophytes was also reduced (80.2 ± 18.1 % in unburnt and 14.4 ± 20.2 % in burnt plots), while graminoids had similar cover in unburnt (4.0 ± 5.5 %) and burnt plots (4.8 ± 10.3 %) (Table 4). Low fire severity plots had similar cover of shrubs, graminoids and bryophytes to high severity plots. Litter cover was highest in low fire severity plots, and cover of duff/bare soil was highest in high severity plots.

3.2. Ecosystem respiration

Seasonal mean ER in unburnt plots at the heathland ranged between 0.58 (spring) and 1.7 μmol CO_2 m^{-2} s^{-1} (summer) (Figure 1). At the raised bog, mean ER in unburnt plots was slightly higher and ranged between 0.85 (spring) and 2.05 μmol m^{-2} s^{-1} (summer). ER was significantly higher in unburnt than in burnt plots for all seasons considered, both at the heathland and at the raised bog. ER in high fire severity plots was significantly greater than in low severity

Table 3: Mean (SD in parenthesis) of soil temperature and soil moisture (% dry weight) during gas flux measurements. Site was Glen Tanar (heathland) or Braehead Moss (raised bog). Different letters within the same row indicate statistically significant differences between fire severity plots ($\alpha = 0.05$; see Tables S2–S5 for model information).

Variable	Site	Season	Unburnt	Low fire severity	High fire severity
Soil T (°C)	GT	Spring	7.6 (0.7) a	11.1 (1.5) b	14.7 (3.2) c
		Summer	11.1 (1.8) a	13.8 (2.6) b	14.6 (3.1) b
		Autumn	7.9 (1.3) a	8.8 (2.0) a	8.9 (2.3) a
	BM	Spring	7.6 (1.1) a	8.0 (1.4) a	8.0 (1.3) a
		Summer	13.1 (0.6) a	13.8 (1.2) b	14.1 (1.2) b
		Autumn	9.3 (0.3) a	9.7 (0.6) a	9.6 (0.6) a
Soil moisture (%)	GT	Spring	270 (27) a	261 (19) ab	248 (23) b
		Summer	274 (29) a	283 (20) a	272 (24) a
		Autumn	285 (29) a	289 (21) a	282 (24) a
	BM	Spring	350 (30) a	334 (9) a	336 (10) a
		Summer	332 (8) a	327 (8) a	325 (25) a
		Autumn	329 (11) a	328 (10) a	330 (9) a

Table 4: Mean (range in parenthesis) cover of vegetation groups in gas flux collars for the different fire severity treatments. Site was Glen Tanar (heathland) or Braehead Moss (raised bog). Different letters within the same row indicate statistically significant differences between treatments ($\alpha = 0.05$; see Tables S6 and S7 for model information).

Site	Vegetation	Unburnt	Low fire severity	High fire severity
GT	Shrub	13.8 (0–30) a	8.4 (0–18) a	8.7 (2–22) a
	Graminoid	3.4 (0–10) a	3.2 (0–13) a	1.2 (0–7) a
	Bryophyte	81.1 (41–100) a	6.0 (0–35) b	4.3 (0–23) b
	Litter	13.0 (0–55) a	58.1 (8–99) b	25.1 (0–92) a
	Duff	5.1 (0–35) a	33.3 (0–94) b	70.6 (0–100) b
BM	Shrub	38.3 (3–84) a	2.4 (1–10) b	8.8 (0–40) b
	Graminoid	4.6 (0–15) a	5.4 (0–19) a	9.0 (0–70) a
	Bryophyte	79.3 (43–97) a	28.4 (1–87) b	17.8 (1–57) b
	Litter	18.0 (3–52) a	47.1 (3–92) a	28.0 (0–85) a
	Duff	2.4 (0–9) a	20.3 (0–90) a	52.0 (0–94) b

plots in autumn at the heathland (mean 0.87 ± 0.59 vs 0.52 ± 0.32 μmol m^{-2} s^{-1}), but all other differences between fire severity treatments within the same season and site were not statistically significant. Burning did not alter heterogeneity in ER as evidenced by the similar variances in burnt compared to unburnt plots, both at the heathland ($F_{1,39} = 2.1$, p-value = 0.16) and at the raised bog ($F_{1,43} = 2.2$, p-value = 0.15).

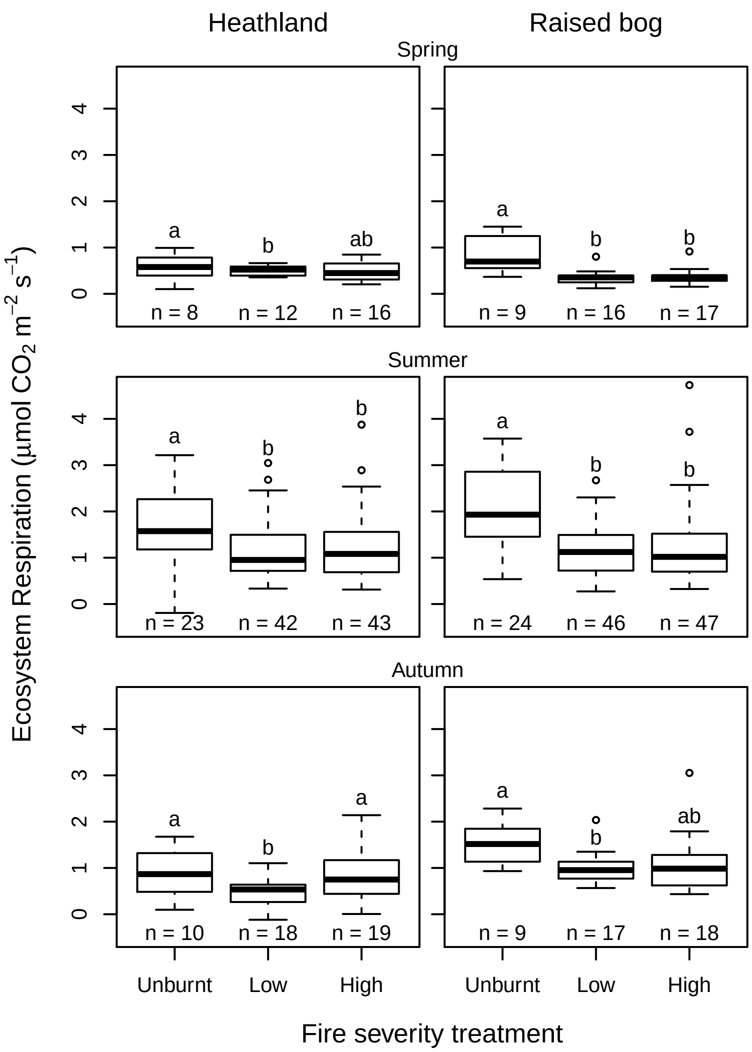

Figure 1: Ecosystem respiration per treatment, season and site. Box is the inter-quartile range and the thick line is the median; whiskers are data range excluding outliers (circles). n = number of observations. Within each season and site, different letters above the boxplots indicate statistically significant differences between treatments ($\alpha = 0.05$). Summary and inference statistics are provided in Tables S8 and S9.

3.3. Net ecosystem exchange

Seasonal mean NEE in unburnt plots at the heathland ranged between 0.18 μmol CO_2 m^{-2} s^{-1} in spring and -0.78 μmol m^{-2} s^{-1} in autumn (Figure 2). Seasonal mean NEE patterns in unburnt plots at the raised bog were similar and ranged between 0.18 (spring) and -0.64 (autumn) μmol m^{-2} s^{-1}. Overall, unburnt plots were a C sink, both at the heathland (mean -0.33 $\pm$ 1.7 μmol m^{-2} s^{-1}) and at the raised bog (mean -0.38 $\pm$ 0.75 μmol m^{-2} s^{-1}). In contrast, burnt plots were a net C source. Mean NEE of burnt plots across the sampling period was 0.50 $\pm$ 0.84 μmol m^{-2} s^{-1} at the heathland and 0.16 $\pm$ 0.86 μmol m^{-2} s^{-1} at the raised bog. In burnt plots, NEE was highest in summer rather than in spring (as in unburnt plots). Differences between low and high fire severity plots were not statistically significant. Burning reduced NEE heterogeneity at the heathland, as indicated by the significantly lower NEE variance in burnt compared to uburnt plots ($F_{1,39}$ = 20.1, p-value = < 0.001), but not at the raised bog ($F_{1,43}$ = 0.1, p-value = 0.8).

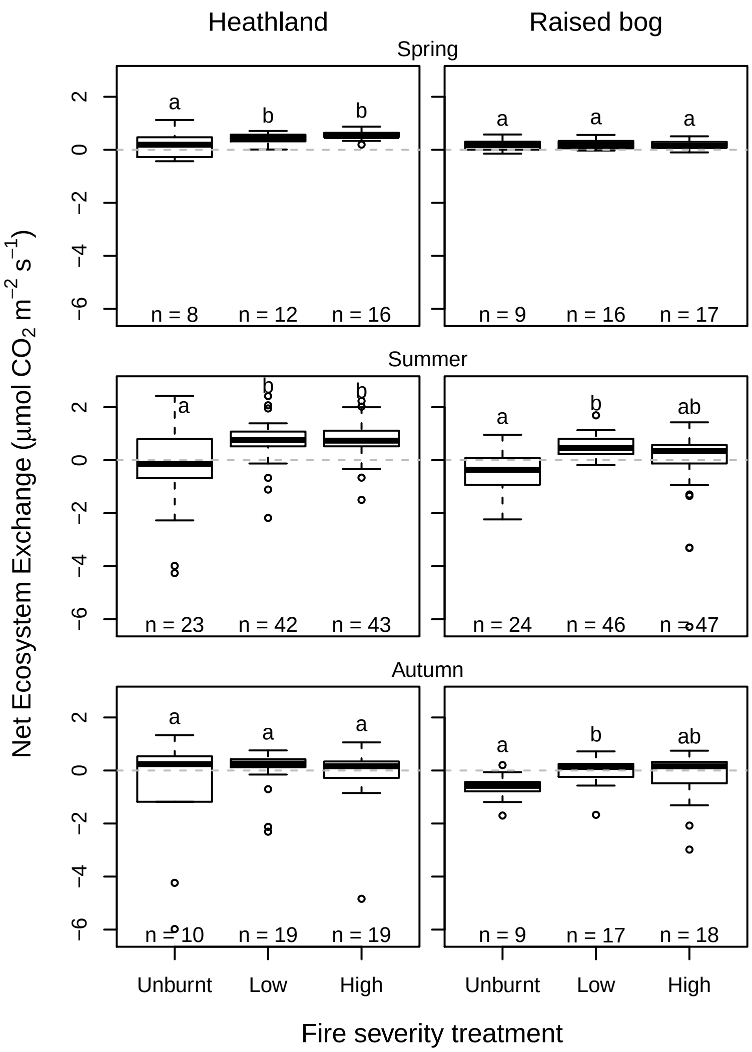

Figure 2: Net ecosystem exchange per treatment, season and site. Details as in Figure 1. Summary and inference statistics are provided in Tables S11 and S12.

3.4. Methane flux

Methane fluxes were generally negligible at the heathland although some larger fluxes were measured in unburnt plots during autumn (mean 1.4 ± 2.4 nmol m^{-2} s^{-1}; Figure 3). At the raised bog, mean CH_4 emissions in unburnt plots were 0.30 ± 1.14 nmol m^{-2} s^{-1} in spring and 1.10 ± 1.04 nmol m^{-2} s^{-1} in summer. Raised bog methane fluxes were larger in burnt than in unburnt plots, especially during the summer (25.3 ± 55.8 nmol m^{-2} s^{-1} in burnt plots). Variability in methane flux was also larger in burnt plots and in the summer, including three extreme measurements of 92, 168 and 212 nmol m^{-2} s^{-1}. Considering CH_4 has a global warming potential over 100 years 28 times greater than CO_2 (IPCC, 2014), summer CH_4 flux at the raised bog increased net CO_2-equivalent emission from burnt plots by 0.6–0.7 μmol m^{-2} s^{-1} (79 % of total summer flux). CH_4 contribution to CO_2-equivalent flux at the heathland was close to zero (see Figure S3 for details). Methane flux at the raised bog was similar in low (12.6 ± 41.1 nmol m^{-2} s^{-1}) and high severity plots (11.9 ± 34.7 nmol m^{-2} s^{-1}).

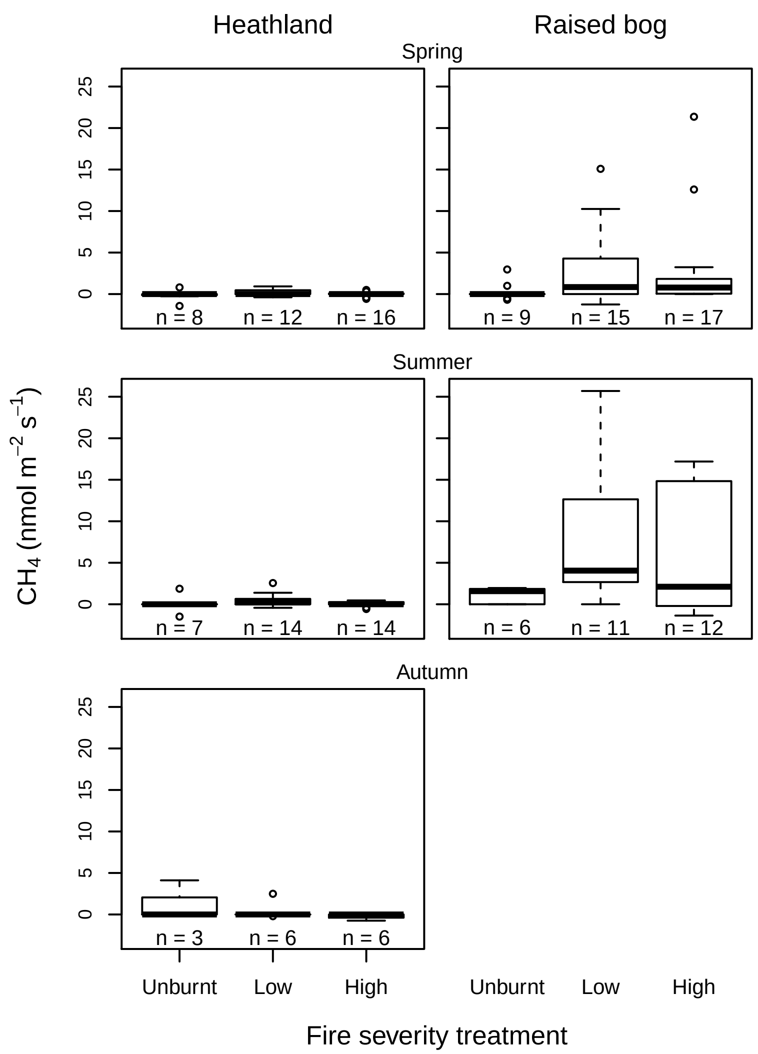

Figure 3: Methane flux per treatment, season and site. n = number of observations. Extreme summer measurements at the raised bog (92 and 168 nmol m^{-2} s^{-1} in high fire severity plots; 212 nmol m^{-2} s^{-1}, in a low fire severity plot) not shown. Summary statistics are provided in Table S14.

3.5. Dissolved organic carbon concentration

Burning had no statistically significant effect on soil water [DOC] within any season (Figure 4). [DOC] remained relatively constant across winter, spring and summer (124 ± 29 mg l^{-1}) but was significantly higher in autumn (149 ± 45 mg l^{-1}). Overall mean [DOC] was 137 ± 47 mg l^{-1} in unburnt plots, 128 ± 31 mg l^{-1} in low fire severity plots and 130 ± 33 mg l^{-1} in high fire severity plots. Variability was greater in unburnt plots than in burnt plots ($F_{1,47} = 9.0$, p-value $= 0.004$).

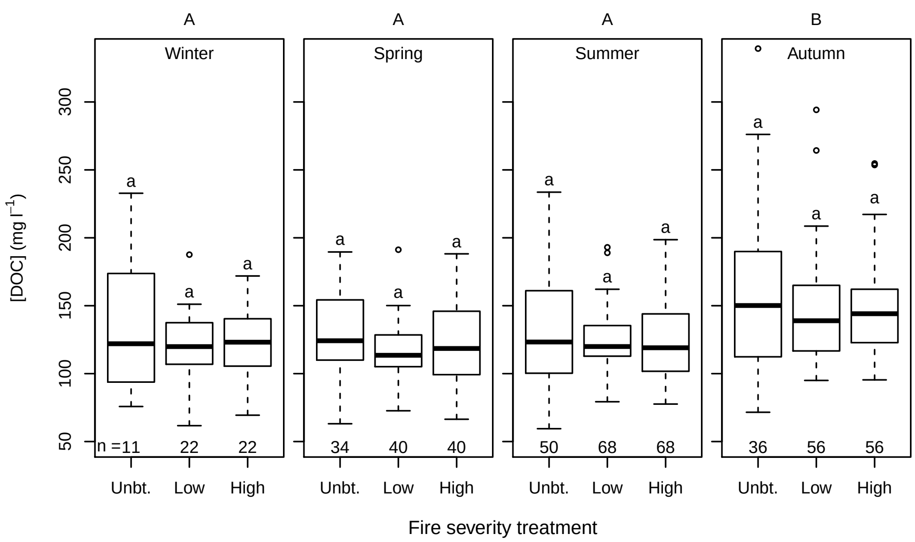

Figure 4: Concentration of dissolved organic carbon per treatment at the raised bog, grouped by season. Unbt. = unburnt. Number of observations are indicated below each boxplot. Within each season, different letters above the boxplots indicate statistically significant differences between treatments; capital letters refer to overall differences between seasons ($\alpha = 0.05$). Summary and inference statistics can be found in Tables S15–S18.

4. Discussion

4.1. Ecosystem Respiration

We found that burning decreased ER (Figure 1), probably due to reduced vegetation-induced respiratory processes, both heterotrophic and autotrophic

(Curiel-Yuste et al., 2004) and altered post-fire soil microbiology (Armas-Herrera et al., 2018). This contrasts with previous studies which have found no short-term (< 18 months) differences in ER between burnt and unburnt plots on an upland blanket bog at the Moor House Nature Reserve in northern England (Clay et al., 2010; Ward et al., 2012), and no short-term (< 3 years) effect of fire on ER on three sites across Scotland that included wet heath and blanket bog (Taylor, 2015). However, ER 9 years post-fire at Moor House was higher than in plots unburnt for 50 years (Ward et al., 2007), which may indicate that established post-fire vegetation promotes faster C cycling than mature communities (Wardle et al., 2012).

Generally, ER in higher compared to lower severity burns was similar, i.e. increased soil heating and consumption of the M/L layer (Grau-Andrés et al., 2018a) had little effect on post-fire respiration. Given the importance of fire severity in controlling post-fire soil microbiology (Dooley and Treseder, 2012; Ludwig et al., 2018), and the similar cover of vegetation functional groups in both burnt treatments (Table 4), the higher severity treatment may not have substantially altered soil microbial communities. Even in the high fire severity treatment in the heathland, where the highest fire severity was measured, average maximum soil temperature at 2 cm depth during the fire was less than 40 °C (Table 1), below the temperatures required to kill bacteria and fungi (ca. 90 °C, Neary et al., 1999). However, as ER at the heathland during autumn was greater in high fire severity plots than in low fire severity plots, there may have been an effect of fire severity on seasonal activity of the soil microbial community. Perhaps higher fire severity increased ER through stimulation of microbial activity by warmer soil (Walker et al., 2018) and greater nutrient availability due to an ash fertilisation effect (Dooley and Treseder, 2012). Such impacts might well only be detectable after the period of maximal microbial growth during the summer (Wardle, 1998).

Despite the low cover of shrubs in the gas flux collars in unburnt plots (Table 4) compared to that measured in a broader survey of post-fire vegetation response (Grau-Andrés et al., 2019), ER in unburnt plots was similar to previous studies. Such low shrub cover was likely a disturbance effect of collar insertion and was stronger at the heathland due to the longer, prostate *Calluna* stems at the site. Nevertheless, seasonal variation in ER in unburnt plots (0.58–1.7 μmol m^{-2} s^{-1} at the heathland, 0.85–2.05 μmol m^{-2} s^{-1} at the raised bog) was similar to other studies in UK shrub-dominated peatland, e.g. 0.8–2.3 μmol m^{-2} s^{-1} (Chapman and Thurlow, 1996), 1.2–2.7 μmol m^{-2} s^{-1} (Ward et al., 2007).

4.2. Net Ecosystem Exchange

Burning increased NEE (Figure 2). Considering the generally higher ER in unburnt plots, this means that burning induced a decrease in respiration but a larger decrease in photosynthesis resulting in a net increase in CO_2 emission. Reduced photosynthetic activity can be explained by fire-induced mortality of, and damage to, vascular and cryptogamic vegetation (Table 4). NEE was similar in low compared to high fire severity plots, i.e. increased fire-induced soil heating did not have any additional effects on soil microbiology above that associated with lower severity management fires. Furthermore, the altered ground vegetation and microclimate conditions in high fire severity plots, particularly at the heathland (e.g. higher cover of bare ground and warmer soil; Table 3) compared to low fire severity plots did not influence NEE.

Seasonal NEE variation in unburnt plots at the heathland (-0.78–0.18 μmol m^{-2} s^{-1}) showed a wider range than that previously reported for a temperate heath (-0.4 to -0.25 μmol m^{-2} s^{-1}; Larsen et al., 2007). Seasonal NEE patterns in unburnt plots at the raised bog (-0.64–0.18 μmol m^{-2} s^{-1}) were consistent with reports from UK peatlands (-0.95 to 0.01 μmol m^{-2} s^{-1}, Ward et al., 2007; -0.68 to -0.30 μmol m^{-2} s^{-1}, Armstrong et al., 2015). NEE was highest in spring in unburnt plots but in summer in burnt plots, showing that warmer weather (and higher PAR) induces a greater increase in photosynthesis than in respiration if vegetation cover is high (Larsen et al., 2007; Ward et al., 2007).

4.3. Methane

Burning increased post-fire CH_4 emission at the raised bog. Wildfires can reduce methanotroph activity in peat (Danilova et al., 2015) but the low fire-induced belowground heating at the raised bog (maximum soil temperature was 15 °C; Table 1) suggests that aboveground changes in vegetation were likely key in explaining differences in CH_4 flux between unburnt and burnt plots (Levy et al., 2012; Gray et al., 2013). For example, bryophytes can host symbiotic methanotrophic bacteria (Strack et al., 2017) and vascular plants have been linked to methanotroph abundance (Chen et al., 2008) and can promote methanotroph activity through diffusion of oxygen to the root zone (Ström et al., 2005). Vegetation can also influence CH_4 flux by facilitating its transport from anaerobic peat layers to the atmosphere, therefore bypassing methanotrophs. This is especially so with aerenchymatous species such as *Eriophorum vaginatum* L. (McNamara et al., 2008). In addition to a substantial reduction in shrub cover, burning increased cover of graminoids at the raised bog, dominated by *E. vaginatum*, from 4.6 % to 7.2 % (Table 4) and so this may have increased the flux. Vegetation can also have an effect on abiotic factors that are important controls on CH_4. The observed higher water table in burnt plots, presumably a result of lower evapotranspiration due to reduced plant cover (Wieder et al., 2009; Clay et al., 2012), could have enhanced soil anaerobic conditions and thus increased CH_4 production and decreased CH_4 consumption (Levy et al., 2012). We did not find evidence of a fire severity effect on CH_4 flux, likely a result of the overall low fire-induced soil heating and similar post-fire vegetation structure in low compared to high fire severity plots at the raised bog.

Our results differ from previous work in UK peatlands reporting reduced CH_4 production one year after fire (Davies et al., 2014) and no difference between burnt and unburnt plots up to three years after fire (Taylor, 2015). Longer-term research has observed lower CH_4 flux in plots unburnt for 9 years compared to plots unburnt for 50 years (Ward et al., 2007). Such disparity is probably related to the complexity of interrelated biotic and abiotic controls on carbon cycling (Armstrong et al., 2015) and to the heterogeneity of such controls in peatlands (Levy et al., 2012), including fire severity, thus making isolating fire effects difficult.

The largest CH_4 emissions were observed during the summer, indicating that soil temperature was an important controlling mechanism (Turetsky et al., 2014). The observed extreme summer CH_4 in burnt plots suggests burning may have facilitated episodic ebullition events. The mechanisms involved could be related to increased post-fire CH_4 production leading to a higher gas concentration in the soil thus promoting bubble formation, and/or to altered transport, e.g. as a result of changes in hydrology (Baird et al., 2004). Enhanced CH_4 production in burnt plots during the summer, in combination with the different mechanisms of transport and consumption that can control the flux, could explain the larger heterogeneity in CH_4 flux in burnt plots compared to unburnt. Even though summer CH_4 flux was 10 times lower than the positive NEE in burnt plots at the raised bog, its large global warming potential means it represented 79 % of the CO_2-equivalent flux.

Methane flux was negligible at the heathland in spring and summer, and only in autumn did unburnt plots show small emissions (Figure 3). Besides their lower C store, the thin soils of Glen Tanar probably did not support the anaerobic conditions needed for CH_4 production. Negative fluxes (-0.02 to -0.17 nmol m^{-2} s^{-1}) were recorded in spring and autumn, indicating some CH_4 consumption due to aerobic methanotrophic bacteria (Chen et al., 2008). CH_4 flux in unburnt plots was also small at the raised bog (e.g. 1.2 nmol m^{-2} s^{-1} during the summer) and at the lower end of those reported for peatlands across the UK (0.4–27.4, average 12.2 nmol m^{-2} s^{-1}; Levy et al., 2012). This could be because of the history of disturbance to the bog (limited grazing, burning and peat cutting; SNH, 2012) and the relatively drier location in the bog where the experiment took place.

4.4. Dissolved organic carbon concentration

Burning had no significant effect on mean soil water [DOC] at the raised bog, indicating that combined fire effects including fire-induced soil heating, decreased plant activity, altered soil thermal dynamics and hydrology were not important controls (Figure 4). Previous plot-level research on UK peatlands also found no long-term effect of burning on soil water [DOC] (Ward et al., 2007; Clay et al., 2009, 2012), although lower [DOC] was found in recently burnt plots (< 2 years) compared to *Calluna*-dominated plots (23.4 vs 42.0 mg l^{-1}) at a blanket bog in northern England (Armstrong et al., 2012). The lower variability in burnt plots compared to unburnt may be a consequence of the reduced contribution of spacially-variable plant photosynthate inputs to DOC compared to more homogenous belowground source (Moore, 2013). Mean seasonal soil water [DOC] at the raised bog ranged 120–155 mg l^{-1}, larger than averages reported for blanket peatlands in northern England (40 mg l^{-1}, Ward et al., 2007; 45 mg l^{-1}, Clay et al., 2009; 97.2 mg l^{-1}, Clay et al., 2012) and in Scotland (45 mg l^{-1}, Armstrong et al., 2015). [DOC] was higher in autumn, likely a result of increased DOC production during the summer and its flushing due to higher water tables in the autumn (Armstrong et al., 2015).

5. Conclusions

Burning decreased ecosystem respiration during the first two years following fires, but decreased photosynthesis more strongly. This resulted in higher net ecosystem exchange, and overall net CO_2 emission, compared to unburnt plots where there was net CO_2 assimilation. While mean net ecosystem exchange in unburnt plots was similar at the heathland and the raised bog (-0.33 and -0.38 μmol CO_2 m^{-2} s^{-1}, respectively), post-fire flux was larger at the heathland (0.50 vs 0.16 μmol m^{-2} s^{-1}). Methane flux was close to zero at the heathland. At the raised bog, burning increased methane flux. This was especially noticeable during summer (1.16 nmol m^{-2} s^{-1} in unburnt and 25.3 nmol m^{-2} s^{-1} in burnt plots), when methane flux represented most of the CO_2-equivalent flux. Although comparatively little CH_4 flux data were available, our results suggest a similar impact of burning on net carbon emission at the heathland and at the raised bog. Unlike for gaseous fluxes, burning did not induce short-term changes in dissolved organic carbon concentration at the raised bog. Generally, the effect of higher fire severity on soil carbon dynamics did not differ from regular managed burning. This suggests that increased fire severity within the range achieved in our experimental fires has a negligible effect on short-term soil carbon dynamics in *Calluna* heathlands and peatlands. However, it is important to note that alteration of short-term soil carbon dynamics is more likely where there is extensive consumption of ground fuels and/or ignition of organic soil layers as has been observed to occur during high severity peatland wildfires (Kettridge et al., 2015). Future studies should seek to assess carbon fluxes across a wider range of fire severities and for longer-periods post-burn.

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6. Supplementary material for "Burning increases post-fire carbon emissions in a heathland and a raised bog, but experimental manipulation of fire severity has no effect"

Contents

6.1. Gas flux sampling effort and weather

Table S1: Gas flux sampling effort, including sampling date, site (Glen Tanar and Braehead Moss), the gas analyser used (Los Gatos Research Ultra-Portable GHG analyser and Vaisala GMP343 Carbon Dioxide Probe), number of plots sampled (n), and mean (SD in parenthesis) air temperature, relative humidity and photosynthetic active radiation (in NEE measurements) during chamber deployments.

Date	Site	Instrument	n	Air T (°C)	RH (%)	PAR (μmol m^{-2} s^{-1})
2014-08-23	GT	LGR	20	14.7 (3.1)	79 (11.0)	816 (538)
2014-08-24	GT	LGR	15	19.8 (3.3)	64 (3.1)	799 (233)
2014-08-26	BM	LGR	20	26.0 (3.1)	64 (9.7)	1193 (319)
2014-08-27	BM	LGR	10	24.1 (1.6)	53 (2.8)	1217 (349)
2014-11-27	GT	LGR	5	4.9 (0.1)	99 (0.1)	20 (3)
2014-11-28	GT	LGR	10	6.2 (0.0)	99 (0.0)	61 (59)
2015-04-04	BM	LGR	23	14.8 (1.9)	83 (5.5)	582 (274)
2015-04-05	BM	LGR	19	22.7 (3.6)	68 (12.2)	1127 (428)
2015-04-18	GT	LGR	23	26.5 (2.3)	40 (4.9)	1207 (431)
2015-04-21	GT	LGR	13	25.9 (2.1)	38 (7.9)	1415 (113)
2015-06-27	BM	Vaisala	30	20.7 (2.9)	81 (5.2)	663 (459)
2015-06-28	BM	Vaisala	14	19.6 (2.7)	92 (4.5)	1114 (666)
2015-07-03	GT	Vaisala	18	26.5 (3.0)	68 (7.4)	1811 (341)
2015-07-04	GT	Vaisala	19	19.5 (2.9)	85 (5.2)	566 (398)
2015-08-09	BM	Vaisala	28	18.8 (1.7)	85 (4.9)	466 (158)
2015-08-10	BM	Vaisala	15	19.7 (2.4)	90 (5.0)	570 (287)
2015-08-15	GT	Vaisala	19	15.2 (3.8)	91 (4.7)	533 (416)
2015-08-16	GT	Vaisala	17	17.4 (1.3)	80 (4.4)	804 (170)
2015-09-24	GT	Vaisala	33	13.0 (3.4)	79 (9.6)	916 (481)
2015-10-09	BM	Vaisala	24	14.8 (1.3)	89 (2.5)	427 (116)
2015-10-10	BM	Vaisala	20	13.5 (0.7)	93 (1.6)	381 (96)

Figure S1: Closed chamber during net ecosystem exchange (NEE) and CH_4 flux measurements in Braehead Moss, with the Los Gatos Research analyser in operation.

6.2. Gas flux measurement and calculation

Each collar had an area of 0.0962 m^2, and mean height of 0.21 m (SD = 0.024 m) above ground. Mean headspace volume was 0.075 m^3, SD = 0.003 m^3. Closure times ranged between four and five minutes. The chamber was opened for ventilation for at least one minute prior to each measurement. Gas fluxes (F, μmol m^{-2} s^{-1}) were calculated (Levy et al., 2011; Equation 1) from the sequence of gas concentration measurements over time in each chamber closure.

$$F = \frac{dC}{dt_0} \cdot \frac{\rho V}{A} \tag{1}$$

where dC/dt_0 is the initial change in concentration (in μmol mol^{-1} s^{-1}) as estimated by a regression model, ρ is the air density (mol m^{-3}), V is the volume of the headspace (volume of the closed chamber and volume of the collar above the ground, in m^{-3}), and A is the area of ground delimited by the collar (m^{-2}).

Plastic tubing connected the Los Gatos analyser to the chamber and air was continually circulated with a pump integrated in the instrument, whilst the Vaisala passive analyser was mounted directly on top of the chamber. Tubing volume was negligible (< 0.1 % of headspace volume) and not considered for gas flux calculation. Increase in water vapour concentration in the chamber during the closure time has a dilution effect on the gas concentration measurement, and therefore water vapour needs to be accounted for and the gas concentration calculated on a dry air basis. The Los Gatos analyser corrected the concentration measurement internally. For the Vaisala analyser gas concentration measurements were corrected as follows:

$$C_{dry} = \frac{C_{moist}}{1 - C_{H_20}} \tag{2}$$

where C_{dry} and C_{moist} are CO_2 concentrations (in μmol mol^{-1}) in dry and moist air, respectively, and C_{H_20} is the water vapour concentration in mol mol^{-1}.

The initial change in concentration (dC/dt_0) can be estimated using a range of linear and non-linear modelling approaches (Levy et al., 2011). The simplest and most widely-used approach is linear regression, which provides an adequate estimate of initial change in concentration when the change in concentration is constant during the closure time, as was observed (Figure S2), and so linear regression was used. Gas flux estimates for which the 95 % confidence intervals of the regression line included zero were considered zero in order to exclude spurious estimates due to measurement inaccuracy. Air density (ρ) varies with pressure and air temperature, and was calculated using Equation 3.

$$\rho = \frac{P}{R \cdot T} \tag{3}$$

where ρ is air density (in mol m^{-3}), P is the air pressure (in Pa), R is the specific gas constant for dry air (in J kg^{-1} K^{-1}), and T is the average air temperature in the chamber (in K).

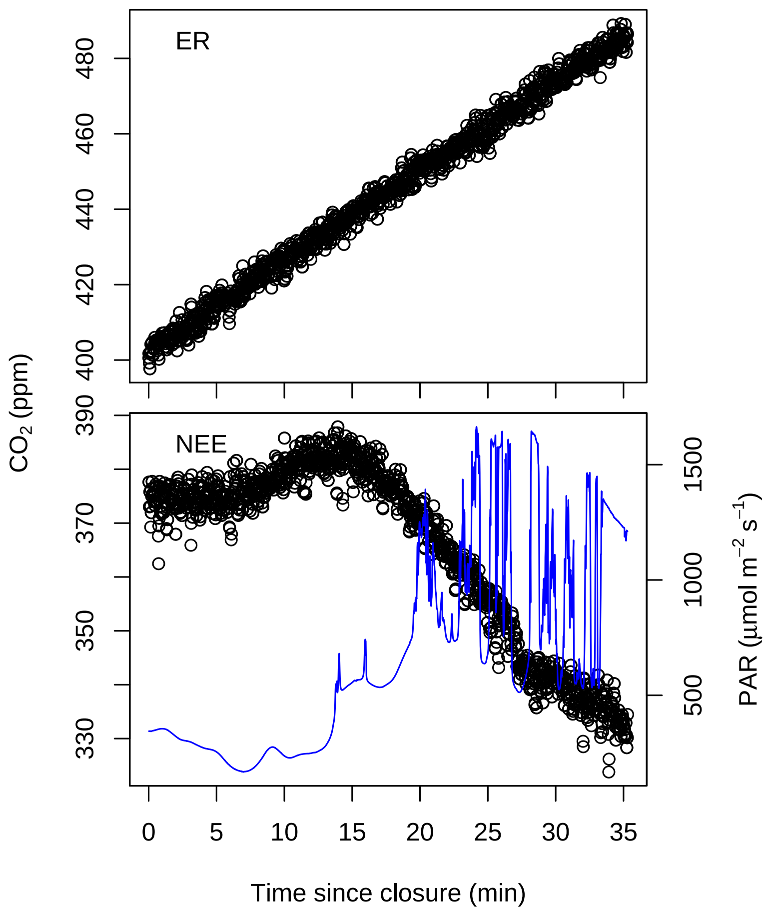

Figure S2: CO_2 concentration during two long closure deployments: one using a covered chamber (ecosystem respiration, ER, top plot, showing a linear increase in CO_2 concentration with time) and the other one with the uncovered clear chamber (net ecosystem exchange, NEE, bottom plot). Both measurements were completed in the same unburnt plot in Braehead Moss using the Vaisala instrument, in October 2015 (ER) and August 2015 (NEE). Photosynthetically active radiation (PAR, blue line) was included in the NEE plot to illustrate its effect on the balance between respiration and photosynthesis.

6.3. Soil temperature and soil moisture

Table S2: Details of the linear mixed effects models investigating the effect of the interaction between season ("Se": spring, summer and autumn), and fire severity (FS) treatment ("Tr": unburnt, low fire severity and high fire severity) on soil temperature during gas flux measurements. Separate models were fitted to each site (Glen Tanar and Braehead Moss). Plot within fire was included as a random effect. R^2 marginal and R^2 conditional were 0.51 and 0.57 (Glen Tanar) and 0.85 and 0.86 (Braehead Moss).

	Value	Std.Error	DF	t-value	p-value
	Glen Tanar				
(Intercept)	7.569	0.91	146	8.33	<0.001
Se(Summer)	3.546	0.98	146	3.61	<0.001
Se(Autumn)	0.492	1.03	146	0.48	0.634
Tr(Low-FS)	3.278	1.09	30	2.99	0.005
Tr(High-FS)	7.110	1.04	30	6.85	<0.001
Se(Summer) : Tr(Low-FS)	-0.506	1.26	146	-0.40	0.688
Se(Autumn) : Tr(Low-FS)	-2.559	1.31	146	-1.95	0.053
Se(Summer) : Tr(High-FS)	-3.518	1.21	146	-2.91	0.004
Se(Autumn) : Tr(High-FS)	-6.215	1.26	146	-4.92	<0.001
	Braehead Moss				
(Intercept)	7.571	0.35	153	21.56	<0.001
Se(Summer)	5.470	0.40	153	13.56	<0.001
Se(Autumn)	1.696	0.49	153	3.49	<0.001
Tr(Low-FS)	0.439	0.43	33	1.02	0.315
Tr(High-FS)	0.471	0.43	33	1.11	0.276
Se(Summer) : Tr(Low-FS)	0.349	0.50	153	0.70	0.488
Se(Autumn) : Tr(Low-FS)	-0.062	0.60	153	-0.10	0.918
Se(Summer) : Tr(High-FS)	0.545	0.50	153	1.09	0.276
Se(Autumn) : Tr(High-FS)	-0.123	0.60	153	-0.21	0.838

Table S3: Multiple comparisons of soil temperature between fire severity treatment levels within levels of season. See Table S2 for model details.

	Estimate	Std.Error	z-value	p-value
Glen Tanar				
spring:low-FS - unburnt	3.28	1.09	2.99	0.023
spring:high-FS - unburnt	7.11	1.04	6.85	<0.001
spring:high-FS - low-FS	3.83	0.92	4.18	<0.001
summer:low-FS - unburnt	2.77	0.62	4.47	<0.001
summer:high-FS - unburnt	3.59	0.62	5.82	<0.001
summer:high-FS - low-FS	0.82	0.52	1.58	0.582
autumn:low-FS - unburnt	0.72	0.72	1.00	0.924
autumn:high-FS - unburnt	0.90	0.72	1.25	0.809
autumn:high-FS - low-FS	0.18	0.60	0.30	1.000
Braehead Moss				
spring:low-FS - unburnt	0.44	0.43	1.02	0.916
spring:high-FS - unburnt	0.47	0.43	1.11	0.881
spring:high-FS - low-FS	0.03	0.36	0.09	1.000
summer:low-FS - unburnt	0.79	0.26	3.03	0.020
summer:high-FS - unburnt	1.02	0.26	3.92	<0.001
summer:high-FS - low-FS	0.23	0.21	1.06	0.900
autumn:low-FS - unburnt	0.38	0.43	0.88	0.957
autumn:high-FS - unburnt	0.35	0.42	0.83	0.969
autumn:high-FS - low-FS	-0.03	0.35	-0.08	1.000

Table S4: Details of the linear mixed effects models investigating the effect of the interaction between season ("Se": spring, summer and autumn), and fire severity treatment ("Tr": unburnt, low fire severity, high fire severity) on soil moisture content. Separate models were fitted to each site (Glen Tanar and Braehead Moss). Plot within fire was included as a random effect. R^2 marginal and R^2 conditional were 0.16 and 0.72 (Glen Tanar) and 0.13 and 0.61 (Braehead Moss).

	Value	Std.Error	DF	t-value	p-value
		Glen Tanar			
(Intercept)	270.081	7.83	146	34.49	<0.001
Se(Summer)	4.933	4.74	146	1.04	0.299
Se(Autumn)	13.196	5.57	146	2.37	0.019
Tr(Low-FS)	-8.088	6.44	30	-1.26	0.219
Tr(High-FS)	-21.649	6.19	30	-3.50	0.001
Se(Summer) : Tr(Low-FS)	15.093	6.08	146	2.48	0.014
Se(Autumn) : Tr(Low-FS)	13.332	7.05	146	1.89	0.061
Se(Summer) : Tr(High-FS)	18.577	5.83	146	3.19	0.002
Se(Autumn) : Tr(High-FS)	21.000	6.84	146	3.07	0.003
		Braehead Moss			
(Intercept)	339.991	3.01	151	113.05	<0.001
Se(Summer)	-8.082	2.43	151	-3.33	0.001
Se(Autumn)	-10.604	2.87	151	-3.70	<0.001
Tr(Low-FS)	-6.884	3.41	33	-2.02	0.052
Tr(High-FS)	-3.962	3.38	33	-1.17	0.249
Se(Summer) : Tr(Low-FS)	1.799	2.97	151	0.61	0.546
Se(Autumn) : Tr(Low-FS)	5.291	3.53	151	1.50	0.136
Se(Summer) : Tr(High-FS)	0.618	2.95	151	0.21	0.834
Se(Autumn) : Tr(High-FS)	4.639	3.50	151	1.33	0.186

Table S5: Multiple comparisons of soil moisture content between fire severity treatment levels within levels of season. See Table S4 for model details.

	Estimate	Std.Error	z-value	p-value
	Glen Tanar			
spring:low-FS - unburnt	-8.09	6.44	-1.26	0.756
spring:high-FS - unburnt	-21.65	6.19	-3.50	0.004
spring:high-FS - low-FS	-13.56	5.36	-2.53	0.081
summer:low-FS - unburnt	7.00	5.46	1.28	0.738
summer:high-FS - unburnt	-3.07	5.44	-0.56	0.993
summer:high-FS - low-FS	-10.08	4.51	-2.23	0.165
autumn:low-FS - unburnt	5.24	6.55	0.80	0.960
autumn:high-FS - unburnt	-0.65	6.51	-0.10	1.000
autumn:high-FS - low-FS	-5.89	5.41	-1.09	0.853
	Braehead Moss			
spring:low-FS - unburnt	-6.88	3.41	-2.02	0.250
spring:high-FS - unburnt	-3.96	3.38	-1.17	0.791
spring:high-FS - low-FS	2.92	2.76	1.06	0.857
summer:low-FS - unburnt	-5.08	2.69	-1.89	0.318
summer:high-FS - unburnt	-3.34	2.67	-1.25	0.743
summer:high-FS - low-FS	1.74	2.22	0.78	0.959
autumn:low-FS - unburnt	-1.59	3.30	-0.48	0.996
autumn:high-FS - unburnt	0.68	3.27	0.21	1.000
autumn:high-FS - low-FS	2.27	2.71	0.84	0.945

6.4. Post-fire vegetation cover

Table S6: Details of the linear mixed effects model investigating the effect of the interaction between site (Glen Tanar and Braehead Moss), and fire severity treatment ("Tr": unburnt, low fire severity and high fire severity) on cover of vegetation in gas flux collars. Separate models were fitted to each broad plant functional type / substrate cover. Response variables were log-transformed after adding a small constant to all values. Fire was included as a random effect.

	Value	Std.Error	DF	t-value	p-value	R^2m	R^2c
			Shrub				
(Intercept)	1.476	0.62	69	2.37	0.020	0.33	0.41
Tr(Low-FS)	0.267	0.66	69	0.41	0.686		
Tr(High-FS)	0.440	0.67	69	0.66	0.512		
Site(BM)	1.841	0.84	69	2.19	0.032		
Tr(Low-FS) : Site(BM)	-2.955	0.91	69	-3.26	0.002		
Tr(High-FS) : Site(BM)	-2.470	0.92	69	-2.69	0.009		
			Graminoid				
(Intercept)	-0.741	0.82	69	-0.90	0.371	0.06	0.20
Tr(Low-FS)	0.238	0.91	69	0.26	0.794		
Tr(High-FS)	-0.227	0.91	69	-0.25	0.804		
Site(BM)	0.411	1.07	69	0.38	0.703		
Tr(Low-FS) : Site(BM)	0.559	1.25	69	0.45	0.657		
Tr(High-FS) : Site(BM)	0.667	1.26	69	0.53	0.597		
			Bryophyte				
(Intercept)	4.374	0.10	69	42.32	<0.001	0.47	0.48
Tr(Low-FS)	-3.590	0.40	69	-9.08	<0.001		
Tr(High-FS)	-4.248	0.40	69	-10.54	<0.001		
Site(BM)	-0.052	0.12	69	-0.42	0.677		
Tr(Low-FS) : Site(BM)	1.864	0.55	69	3.39	0.001		
Tr(High-FS) : Site(BM)	2.120	0.55	69	3.82	<0.001		
			Litter				
(Intercept)	1.694	0.49	69	3.43	0.001	0.57	0.58
Tr(Low-FS)	2.166	0.54	69	4.02	<0.001		
Tr(High-FS)	-0.661	0.79	69	-0.84	0.403		
Site(BM)	0.934	0.68	69	1.38	0.172		
Tr(Low-FS) : Site(BM)	-1.252	0.74	69	-1.69	0.096		
Tr(High-FS) : Site(BM)	0.527	1.08	69	0.49	0.627		

		Duff					
(Intercept)	-0.698	0.76	69	-0.92	0.360	0.33	0.41
Tr(Low-FS)	3.490	0.89	69	3.94	<0.001		
Tr(High-FS)	4.302	0.83	69	5.21	<0.001		
Site(BM)	0.454	0.99	69	0.46	0.647		
Tr(Low-FS) : Site(BM)	-2.214	1.22	69	-1.81	0.075		
Tr(High-FS) : Site(BM)	-0.620	1.13	69	-0.55	0.587		

Table S7: Multiple comparisons of vegetation cover in gas flux collars between fire severity treatment levels within levels of season. See Table S6 for model details.

	Estimate	Std.Error	z-value	p-value
	Shrub			
GT:Low-FS - Unburnt	0.267	0.66	0.41	0.992
GT:High-FS - Unburnt	0.440	0.67	0.66	0.952
GT:High-FS - Low-FS	0.173	0.37	0.47	0.986
BM:Low-FS - Unburnt	-2.688	0.62	-4.31	<0.001
BM:High-FS - Unburnt	-2.030	0.63	-3.22	0.007
BM:High-FS - Low-FS	0.658	0.35	1.86	0.269
	Graminoid			
GT:Low-FS - Unburnt	0.238	0.91	0.26	0.999
GT:High-FS - Unburnt	-0.227	0.91	-0.25	0.999
GT:High-FS - Low-FS	-0.465	0.68	-0.69	0.946
BM:Low-FS - Unburnt	0.797	0.86	0.92	0.858
BM:High-FS - Unburnt	0.440	0.86	0.51	0.982
BM:High-FS - Low-FS	-0.357	0.65	-0.55	0.976
	Bryophyte			
GT:Low-FS - Unburnt	-3.590	0.40	-9.08	<0.001
GT:High-FS - Unburnt	-4.248	0.40	-10.54	<0.001
GT:High-FS - Low-FS	-0.658	0.55	-1.20	0.690
BM:Low-FS - Unburnt	-1.726	0.38	-4.51	<0.001
BM:High-FS - Unburnt	-2.128	0.38	-5.60	<0.001
BM:High-FS - Low-FS	-0.403	0.53	-0.76	0.919
	Litter			
GT:Low-FS - Unburnt	2.166	0.54	4.02	<0.001
GT:High-FS - Unburnt	-0.661	0.79	-0.84	0.891

GT:High-FS - Low-FS	-2.827	0.65	-4.34	<0.001
BM:Low-FS - Unburnt	0.914	0.51	1.79	0.306
BM:High-FS - Unburnt	-0.134	0.74	-0.18	1.000
BM:High-FS - Low-FS	-1.048	0.62	-1.70	0.358
	Duff			
GT:Low-FS - Unburnt	3.490	0.89	3.94	<0.001
GT:High-FS - Unburnt	4.302	0.83	5.21	<0.001
GT:High-FS - Low-FS	0.811	0.67	1.21	0.693
BM:Low-FS - Unburnt	1.276	0.84	1.51	0.485
BM:High-FS - Unburnt	3.682	0.78	4.73	<0.001
BM:High-FS - Low-FS	2.406	0.65	3.72	0.001

6.5. Ecosystem respiration

Table S8: Summary statistics of ecosystem respiration (μmol CO_2 m^{-2} s^{-1}) for different sites (Glen Tanar and Braehead Moss), seasons and fire severity treatments. n, number of observations.

Site	Season	Treatment	Mean (SD)	Min	Max	n
GT	Spring	Unburnt	0.58 (0.29)	0.10	0.99	8
		Low fire severity	0.51 (0.11)	0.36	0.66	12
		High fire severity	0.48 (0.21)	0.21	0.85	16
	Summer	Unburnt	1.71 (0.89)	-0.19	3.22	23
		Low fire severity	1.13 (0.65)	0.33	3.05	42
		High fire severity	1.22 (0.76)	0.31	3.87	43
	Autumn	Unburnt	0.88 (0.52)	0.10	1.67	10
		Low fire severity	0.52 (0.32)	-0.12	1.10	18
		High fire severity	0.87 (0.59)	0.01	2.14	19
BM	Spring	Unburnt	0.85 (0.40)	0.37	1.45	9
		Low fire severity	0.34 (0.16)	0.12	0.80	16
		High fire severity	0.37 (0.17)	0.15	0.91	17
	Summer	Unburnt	2.06 (0.86)	0.54	3.57	24
		Low fire severity	1.15 (0.56)	0.27	2.67	46
		High fire severity	1.22 (0.82)	0.32	4.73	47
	Autumn	Unburnt	1.53 (0.45)	0.93	2.28	9
		Low fire severity	0.98 (0.35)	0.57	2.04	17
		High fire severity	1.07 (0.62)	0.43	3.05	18

Table S9: Details of the linear mixed effects model investigating the effect of the interaction between season ("Se": Spring, Summer and Autumn), site (Glen Tanar and Braehead Moss) and fire severity treatment ("Tr": unburnt, low fire severity and high fire severity) on ecosystem respiration. R^2 marginal was 0.27 and R^2 conditional was 0.32.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.486	0.091	298	5.362	<0.001
Site(BM)	0.367	0.125	15	2.942	0.010
Tr(Low-FS)	0.002	0.108	63	0.017	0.987
Tr(High-FS)	-0.005	0.103	63	-0.047	0.963
Se(Summer)	1.235	0.156	298	7.895	<0.001
Se(Autumn)	0.431	0.160	298	2.699	0.007
Site(BM) : Tr(Low-FS)	-0.529	0.146	63	-3.616	<0.001
Site(BM) : Tr(High-FS)	-0.489	0.142	63	-3.451	0.001
Site(BM) : Se(Summer)	-0.033	0.218	298	-0.151	0.880
Site(BM) : Se(Autumn)	0.250	0.229	298	1.089	0.277
Tr(Low-FS) : Se(Summer)	-0.606	0.197	298	-3.078	0.002
Tr(High-FS) : Se(Summer)	-0.527	0.194	298	-2.723	0.007
Tr(Low-FS) : Se(Autumn)	-0.407	0.201	298	-2.022	0.044
Tr(High-FS) : Se(Autumn)	-0.081	0.197	298	-0.409	0.683
Site(BM) : Tr(Low-FS) : Se(Summer)	0.229	0.272	298	0.840	0.402
Site(BM) : Tr(High-FS) : Se(Summer)	0.178	0.270	298	0.660	0.510
Site(BM) : Tr(Low-FS) : Se(Autumn)	0.350	0.287	298	1.222	0.223
Site(BM) : Tr(High-FS) : Se(Autumn)	0.114	0.282	298	0.404	0.687

Table S10: Bonferroni-corrected 95 % confidence intervals for the difference in mean ecosystem respiration between fire severity treatments (unburnt, low fire severity and high fire severity) within site (Glen Tanar and Braehead Moss) and season. Model details in Table S9.

Site	Season	Unburnt vs Low-FS	Unburnt vs High-FS	Low-FS vs High-FS
GT	Spring	-0.14–0.17	-0.13–0.14	-0.11–0.16
	Summer	0.47–0.74	0.40–0.67	-0.06–0.20
	Autumn	0.14–0.59	-0.20–0.24	0.13–0.56
BM	Spring	0.34–0.71	0.31–0.67	-0.13–0.20
	Summer	0.73–1.10	0.65–1.02	-0.10–0.25
	Autumn	0.24–0.93	0.12–0.80	-0.19–0.44

6.6. Net ecosystem exchange

Table S11: Summary statistics of net ecosystem exchange (μmol CO_2 m^{-2} s^{-1}) for different sites (Glen Tanar and Braehead Moss), seasons and fire severity treatments. n, number of observations.

Site	Season	Treatment	Mean (SD)	Min	Max	n
GT	Spring	Unburnt	0.18 (0.53)	-0.43	1.13	8
		Low fire severity	0.43 (0.19)	0.01	0.71	12
		High fire severity	0.54 (0.17)	0.20	0.87	16
	Summer	Unburnt	-0.31 (1.66)	-4.26	2.42	23
		Low fire severity	0.72 (0.77)	-2.18	2.42	42
		High fire severity	0.81 (0.72)	-1.50	2.23	43
	Autumn	Unburnt	-0.78 (2.42)	-5.98	1.33	10
		Low fire severity	0.00 (0.84)	-2.31	0.76	19
		High fire severity	-0.17 (1.23)	-4.84	1.06	19
BM	Spring	Unburnt	0.18 (0.25)	-0.14	0.58	9
		Low fire severity	0.20 (0.16)	-0.03	0.56	16
		High fire severity	0.17 (0.16)	-0.10	0.51	17
	Summer	Unburnt	-0.49 (0.85)	-2.23	0.96	24
		Low fire severity	0.52 (0.37)	-0.18	1.69	46
		High fire severity	0.00 (1.32)	-6.28	1.43	47
	Autumn	Unburnt	-0.64 (0.57)	-1.70	0.20	9
		Low fire severity	0.00 (0.55)	-1.67	0.72	17
		High fire severity	-0.20 (0.99)	-2.98	0.75	18

Table S12: Details of the linear mixed effects model investigating the effect of the interaction between season ("Se": Spring, Summer and Autumn), site (Glen Tanar and Braehead Moss) and fire severity treatment ("Tr": unburnt, low fire severity and high fire severity) on net ecosystem exchange. R^2 marginal was 0.17 and R^2 conditional, 0.22.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.185	0.087	299	2.13	0.034
Site(BM)	-0.002	0.119	15	-0.02	0.984
Tr(Low-FS)	0.254	0.106	63	2.40	0.019
Tr(High-FS)	0.359	0.101	63	3.57	$<$0.001
Se(Summer)	-0.493	0.201	299	-2.46	0.015
Se(Autumn)	-1.009	0.357	299	-2.83	0.005
Site(BM) : Tr(Low-FS)	-0.227	0.143	63	-1.58	0.119
Site(BM) : Tr(High-FS)	-0.371	0.139	63	-2.67	0.010
Site(BM) : Se(Summer)	-0.178	0.280	299	-0.63	0.526
Site(BM) : Se(Autumn)	0.185	0.518	299	0.36	0.721
Tr(Low-FS) : Se(Summer)	0.774	0.251	299	3.08	0.002
Tr(High-FS) : Se(Summer)	0.752	0.248	299	3.03	0.003
Tr(Low-FS) : Se(Autumn)	0.548	0.442	299	1.24	0.216
Tr(High-FS) : Se(Autumn)	0.287	0.441	299	0.65	0.516
Site(BM) : Tr(Low-FS) : Se(Summer)	0.218	0.349	299	0.62	0.533
Site(BM) : Tr(High-FS) : Se(Summer)	-0.231	0.346	299	-0.67	0.504
Site(BM) : Tr(Low-FS) : Se(Autumn)	0.075	0.641	299	0.12	0.907
Site(BM) : Tr(High-FS) : Se(Autumn)	0.166	0.637	299	0.26	0.795

Table S13: Bonferroni-corrected 95 % confidence intervals for the difference in mean net ecosystem exchange between fire severity treatments (unburnt, low fire severity and high fire severity) within site (Glen Tanar and Braehead Moss) and season. Model details in Table S12.

Site	Season	Unburnt vs Low-FS	Unburnt vs High-FS	Low-FS vs High-FS
GT	Spring	0.10–0.40	0.23–0.49	-0.02–0.24
	Summer	0.84–1.20	0.94–1.29	-0.07–0.26
	Autumn	0.28–1.28	0.10–1.10	-0.28–0.67
BM	Spring	-0.16–0.20	-0.16–0.73	-0.13–0.19
	Summer	0.77–1.25	0.26–0.73	0.29–0.73
	Autumn	-0.13–1.42	-0.32–1.20	-0.49–0.90

6.7. Methane flux

Table S14: Summary statistics of methane flux (nmol CH_4 m^{-2} s^{-1}) for different sites (Glen Tanar and Braehead Moss), seasons and fire severity treatments. n, number of observations.

Site	Season	Treatment	Mean (SD)	Min	Max	n
GT	Spring	Unburnt	-0.11 (0.62)	-1.43	0.80	8
		Low fire severity	0.20 (0.39)	-0.39	0.92	12
		High fire severity	-0.02 (0.27)	-0.58	0.50	16
	Summer	Unburnt	0.06 (0.97)	-1.49	1.87	7
		Low fire severity	0.42 (0.78)	-0.43	2.56	14
		High fire severity	0.04 (0.28)	-0.57	0.46	14
	Autumn	Unburnt	1.37 (2.37)	0.00	4.11	3
		Low fire severity	0.38 (1.04)	-0.21	2.49	6
		High fire severity	-0.17 (0.33)	-0.75	0.13	6
BM	Spring	Unburnt	0.31 (1.10)	-0.68	2.96	9
		Low fire severity	2.95 (4.54)	-1.25	15.09	15
		High fire severity	2.84 (5.62)	0.00	21.36	17
	Summer	Unburnt	1.16 (0.92)	0.00	1.96	6
		Low fire severity	25.84 (62.18)	0.00	211.89	11
		High fire severity	24.74 (52.14)	-1.36	168.31	12

6.8. Net CO_2 equivalent flux

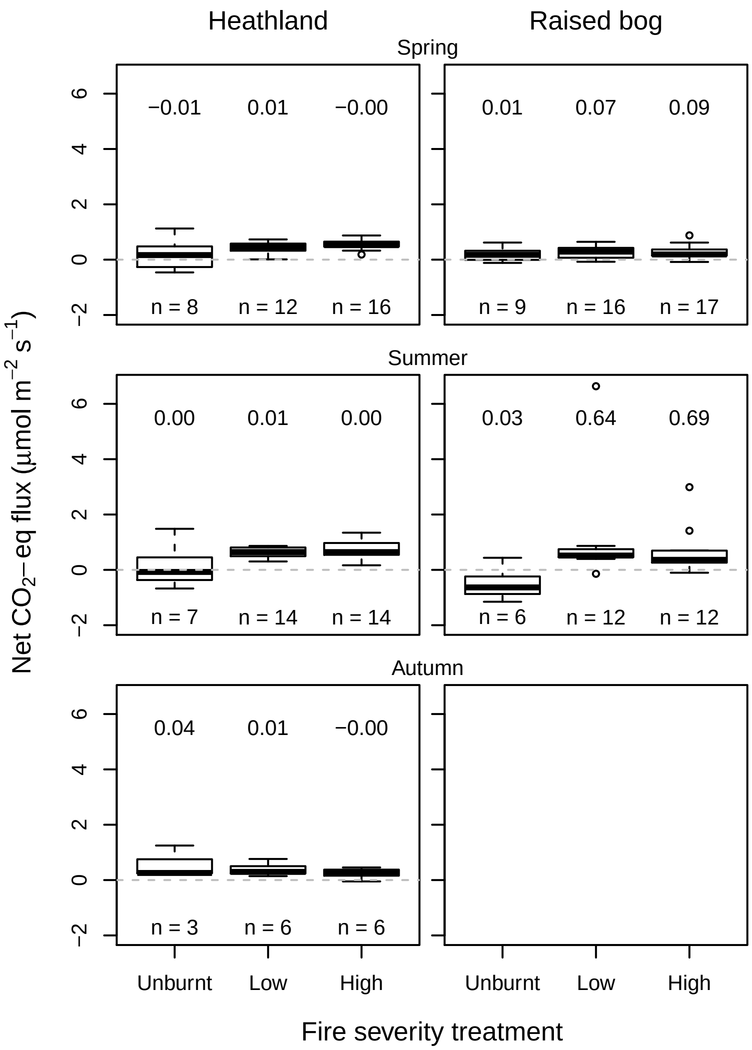

Figure S3: Net CO_2 equivalent flux incorporating CH_4 flux (multiplied by 28 as it has 28 times the global warming potential of CO_2; IPCC, 2014) and NEE flux measured at the same time, per treatment, season and site. Numbers above the boxplots indicate CO_2-eq increase compared to NEE (i.e. due to CH_4). n indicates number of observations.

6.9. Dissolved organic carbon

Table S15: Summary statistics of dissolved organic carbon concentration (mg l^{-1}) at Braehead Moss, for different seasons and treatments. n, number of observations.

Season	Treatment	Mean (SD)	Min	Max	n
Winter	Unburnt	134 (50)	76	233	10
	Low fire severity	120 (28)	62	188	22
	High fire severity	125 (31)	69	172	22
Spring	Unburnt	129 (34)	63	190	31
	Low fire severity	116 (22)	73	191	40
	High fire severity	122 (31)	66	188	40
Summer	Unburnt	130 (39)	59	234	50
	Low fire severity	124 (21)	79	193	68
	High fire severity	124 (27)	78	199	68
Autumn	Unburnt	156 (63)	72	339	33
	Low fire severity	146 (39)	95	294	56
	High fire severity	147 (37)	95	255	56

Table S16: Details of the linear mixed effects model investigating the effect of the interaction between season ("Se": spring, summer, autumn and winter), and fire severity treatment ("Tr": unburnt, low fire severity and high fire severity) on dissolved organic carbon concentration. R^2 marginal was 0.06 and R^2 conditional, 0.49.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	4.903	0.080	439	61.01	<0.001
Se(Spring)	-0.005	0.063	439	-0.08	0.933
Se(Summer)	-0.042	0.060	439	-0.69	0.488
Se(Autumn)	0.085	0.071	439	1.21	0.229
Tr(Low-FS)	-0.143	0.101	38	-1.41	0.166
Tr(High-FS)	-0.102	0.101	38	-1.01	0.318
Se(Spring) : Tr(Low-FS)	0.003	0.077	439	0.04	0.972
Se(Summer) : Tr(Low-FS)	0.103	0.073	439	1.42	0.157
Se(Autumn) : Tr(Low-FS)	0.120	0.086	439	1.39	0.165
Se(Spring) : Tr(High-FS)	-0.003	0.077	439	-0.03	0.974
Se(Summer) : Tr(High-FS)	0.052	0.073	439	0.71	0.477
Se(Autumn) : Tr(High-FS)	0.086	0.086	439	0.99	0.322

Table S17: Details of the linear mixed effects model investigating the effect of season on dissolved organic carbon concentration. R^2 marginal was 0.07 and R^2 conditional, 0.61.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	4.807	0.041	445	116.30	<0.001
seasonSpring	0.001	0.028	445	0.03	0.974
seasonSummer	0.023	0.026	445	0.89	0.375
seasonAutumn	0.171	0.027	445	6.42	<0.001

Table S18: Multiple comparisons of concentration of dissolved organic carbon between seasons. See Table S17 for model details.

	Estimate	Std. Error	z-value	p-value
Spring - Winter	0.00	0.03	0.03	1.000
Summer - Winter	0.02	0.03	0.89	0.808
Autumn - Winter	0.17	0.03	6.42	<0.001
Summer - Spring	0.02	0.02	1.10	0.686
Autumn - Spring	0.17	0.02	7.98	<0.001
Autumn - Summer	0.15	0.02	7.91	<0.001

References

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