



Research article

Leaving moss and litter layers undisturbed reduces the short-term environmental consequences of heathland managed burns



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ABSTRACT

Variation in the structure of ground fuels, i.e. the moss and litter (M/L) layer, may be an important control on fire severity in heather moorlands and thus influence vegetation regeneration and soil carbon dynamics. We completed experimental fires in a *Calluna vulgaris*-dominated heathland to study the role of the M/L layer in determining (i) fire-induced temperature pulses into the soil and (ii) post-fire soil thermal dynamics. Manually removing the M/L layer before burning increased fire-induced soil heating, both at the soil surface and 2 cm below. Burnt plots where the M/L layer was removed simulated the fuel structure after high severity fires where ground fuels are consumed but the soil does not ignite. Where the M/L layer was manually removed, either before or after the fire, post-fire soil thermal dynamics showed larger diurnal and seasonal variation, as well as similar patterns to those observed after wildfires, compared to burnt plots where the M/L layer was not manipulated. We used soil temperatures to explore potential changes in post-fire soil respiration. Simulated high fire severity (where the M/L layer was manually removed) increased estimates of soil respiration in warm months. With projected fire regimes shifting towards higher severity fires, our results can help land managers develop strategies to balance ecosystem services in *Calluna*-dominated habitats.

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1. Introduction

The severity of a fire was defined by Keeley (2009) as the direct, immediate fire effects such as degradation and loss of organic matter. Variation in severity can influence post-fire vegetation regeneration due to mechanisms occurring during the fire itself and altered post-fire environmental conditions. Immediate fire mechanisms include thermal damage to plant structures (Legg et al., 1992), and germination cues related to temperature pulses (Whittaker and Gimingham, 1962) and chemicals from smoke and ash (Bargmann et al., 2014). Altered post-fire environmental conditions include loss of nutrients (Rosenburgh et al., 2013), substrate change due consumption of ground fuels, e.g. the moss and litter (M/L) layers, during high severity fires (Davies et al., 2010), and changes to post-fire soil microclimate resulting from loss of

vegetation cover (Mallik, 1986; Brown et al., 2015). The latter is important as microclimate is a control on soil respiration and soil carbon dynamics (Lloyd and Taylor, 1994; Kettridge et al., 2012; Walker et al., 2016). Fire can also alter soil chemistry and structure (Granged et al., 2011) and soil microbiology (Ward et al., 2012; Fontúrbel et al., 2016), can be associated with increased rates of soil erosion (Fernández and Vega, 2016) and can lead to a loss of organic matter at high fire severities (Neary et al., 1999). Where ecosystems have peat or thick organic soils, the ignition of these during extremely severe fires can have considerable consequences for carbon storage and ecological function (Maltby et al., 1990; Davies et al., 2013; Turetsky et al., 2015).

Calluna vulgaris (L.) Hull (hereafter *Calluna*) dominated heathlands are internationally rare habitats of substantial conservation importance (Thompson et al., 1995). Typically found in north-west Europe, including Sweden, Norway, Denmark, the Netherlands, Italy and Spain, *Calluna* heathlands are perhaps best represented in the UK and Ireland (Gimingham, 1972). *Calluna* heathlands are semi-natural ecosystems that resulted from human land-use since the Mesolithic (Simmons and Innes, 1987). Management activities

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have included forest clearance, intensified grazing mainly from cattle and sheep, and burning to promote nutritious new growth for livestock (Webb, 1998). Anthropogenic fire played a significant role in the expansion and maintenance of *Calluna* heathlands (Dodgshon and Olsson, 2006).

Under a changing climate, it is projected that alterations to the seasonality of rainfall and warmer temperatures throughout heathlands' range will result in increased frequency and/or severity of summer drought (Murphy et al., 2009; Stocker et al., 2013; Cook et al., 2014). These climatic changes suggest the potential for increased wildfire activity (Westerling et al., 2006; Krawchuk et al., 2009) and higher severity wildfires that consume a larger proportion of ground fuels (Davies et al., 2016a). With many heathlands overlying peat deposits or organic soils that store substantial amounts of carbon (Bradley et al., 2005; Ostle et al., 2009), there is concern that higher severity fires could increase carbon emissions from both direct combustion and greater soil respiration resulting from an altered post-fire soil microclimate (Brown et al., 2015).

In the UK, managed burning remains a common, though controversial, practice and is particularly strongly associated with red grouse (*Lagopus lagopus scoticus* Latham) and deer (*Cervus elaphus* L.) management on sporting estates (Davies et al., 2016b). Current forms of management date back approximately 200 years and aim to increase *Calluna* productivity and forage quality, and to produce a range of habitat structures by burning narrow (ca. 30 m wide) strips to create a mosaic of different stand-ages (Allen et al., 2016). Such traditional burning can have benefits for habitat maintenance, biodiversity (Allen et al., 2016; Glaves et al., 2013) and fire risk reduction (Davies et al., 2008a). However, negative consequences have been noted for other ecosystem services such as carbon sequestration (Garnett et al., 2000) and stream water chemistry and ecology (Ramchunder et al., 2013). In order to minimise wildfire risk and reduce potentially negative ecological effects, managed burning is only permitted between, approximately, 1 October and 15 April (exact dates depend on country, altitude, etc.; see DEFRA, 2007; WAG, 2008; SEERAD, 2011). This means managers do not burn after mid-spring when heathland birds are nesting and when drier, warmer weather is likely to lead to difficult-to-control, high intensity fires.

On many heathlands *Calluna* forms dense, continuous stands (Gimingham, 1960) comprised of an upper canopy with a high proportion of live vegetation, a lower canopy with mainly dead foliage, a lower layer of dead and live stems without foliage and finally a M/L layer on top of a carbon-rich soil (Davies and Legg, 2011). During managed burns the M/L layer typically has a high fuel moisture content (>250%) and plays an important role in insulating soil from substantial temperature pulses, and possibly ignition, during the passage of a flaming fire-front (Davies and Legg, 2011). This often means that despite high fireline intensities, fire severity at the ground level, and thus impact on vegetation regeneration and soil properties, is low (Davies et al., 2009). However, where the moisture content of the M/L layer is below its ignition threshold (ca. 70%; Davies and Legg, 2011; Santana and Marrs, 2014), fuel available for combustion increases substantially, leading to higher soil heating (Bradstock and Auld, 1995) and difficulties with fire control (Davies et al., 2010).

Currently we have little quantitative evidence of how heathland fuel structure influences fire severity. In particular, additional knowledge of how the M/L layer controls fire-induced soil heating and post-fire soil thermal dynamics is needed. We investigated this by manipulating the structure of the M/L layer in experimental burn plots. Our objectives were to (i) quantify the role of the M/L layer in insulating soils from raised temperatures during managed burning, (ii) model post-fire soil thermal dynamics in relation to simulated variation in fire severity, and (iii) estimate the potential

effect of altered soil microclimate on soil respiration.

2. Material and methods

2.1. Study area

The experiment was completed at Glen Tanar Estate, Aberdeenshire, Scotland (latitude 57.013°N, longitude 2.957°W, elevation of 330 m a.s.l.). Weather records from 1994–2007 at Aboyne weather station, 13 km east of the site, elevation 130 m, show an average annual rainfall of 837 mm, mean summer temperature of 13.8 °C and mean winter temperature of 3.1 °C (Met Office, 2012).

Soils at the site are peaty podzols with a mean organic horizon depth of 9 cm. Vegetation is dominated by a dense and homogeneous canopy of mature (*sensu* Gimingham, 1989) *Calluna*, with *Erica cinerea* L., *Vaccinium myrtillus* L., *Trichophorum cespitosum* (L.) Hartm. and *Carex* spp. also common. Beneath the *Calluna* canopy we found a discontinuous layer of pleurocarpous mosses (dominant species: *Hypnum jutlandicum* Holmen and Warncke, and *Pleurozium schreberi* (Brid.) Mitt.) which are replaced by layers of *Calluna* litter where stand canopies were particularly dense. There are frequent wet flushes dominated by *Molinia caerulea* (L.) Moench, *Eriophorum vaginatum* L. and *Sphagnum* spp. More recently-burnt areas include patches of building phase *Calluna* and areas dominated by *Nardus stricta* L. and *M. caerulea*.

2.2. Experimental design and measurements

We completed seven experimental fires on four separate days between 12 and 26 April 2013. All fires were ignited with a drip torch, burnt as head fires (i.e. main fire spread direction was the same as wind direction) and covered an area of around 25 × 30 m. Within each fire we established six 1 × 1 m plots assigned to one of three treatments (each treatment replicated twice in each fire): (i) plots where the M/L layer was not manipulated, (ii) the M/L layer was removed after the fire, (iii) the M/L layer was removed before the fire. We manually removed the M/L layer down to the top of the O-horizon in the latter two fuel treatments. The treatments allowed us to quantify the effect of the M/L layer on fire-induced soil heating by comparing plots where the M/L layer was present at the time of burning versus plots where it had been removed. Furthermore, the treatments simulated fuel structure after low severity fires where M/L layer consumption is limited, and after higher severity where the M/L layer is consumed (Davies et al., 2016a), and thus allowed estimation of the effect of fire severity on post-fire soil thermal dynamics. The simulated approach is useful as when ground fuels become flammable (low moisture content), fuel available for combustion increases substantially (Davies et al., 2010), normal control methods have limited effectiveness and managed burning becomes too hazardous. This has limited the ability of previous research to capture a wide range of severities.

There can be substantial fine-scale (1 m²) spatial variability in the behaviour of surface fires (Bradstock and Auld, 1995; Thaxton and Platt, 2006; Davies et al., 2010). Our experimental design therefore followed the “microplot” approach for fire behaviour: plots within fires are treated as independent observations due to the significant variation in fire behaviour that results from interactions between heterogeneity in fuel structure, moisture content and fire weather (principally wind speed) during a burn (Fernandes et al., 2000). We assessed the validity of the microplot approach by partitioning the variance of fuel structure metrics (e.g. fuel load, bulk density, M/L layer thickness) in “within fires” and “between fires” components using a random effects model (see Table S1 in supplementary material). We used the non-destructive FuelRule method (Davies et al., 2008b), which is based on visual

obstruction of a banded measurement stick, to estimate plot fuel load and structure with five measurements taken in each plot. The method was calibrated using destructive sampling (full details are provided in Grau-Andrés, 2017).

To estimate fuel moisture content (FMC), immediately before each fire we sampled the top 2 cm of the soil, the top 2 cm of the M/L layer, dead *Calluna* shoots and live *Calluna* shoots (defined *sensu* Davies and Legg, 2011). We extracted a single soil core from a random location in each plot and calculated the FMC and dry bulk density of the top 2 cm of soil. We took M/L layer samples from three randomly-selected locations in each plot where the M/L layer had not been removed, and a single, integrated sample of live and dead *Calluna* FMC from each fire. Samples were dried in a fan-assisted oven at 80 °C for 48 h, and FMC expressed as percentage of dry weight.

During the burns we recorded ambient air temperature, relative humidity and wind speed using a Kestrel 4000 Wind Tracker mounted on a wind vane and 1.25 m tripod, i.e. at approximately mid-flame height. Fire rate of spread was estimated using Davies et al. (2009) empirical equation for *Calluna* moorlands based on wind speed, *Calluna* height and live *Calluna* moisture content. We used four “duff spikes” (metal spikes with a notch level with the M/L surface; e.g. Davies et al., 2010) per plot to estimate consumption of the M/L layer during the fires to the nearest 1 cm.

To assess temperature pulses from the passage of the fire front we buried two Hobo™ loggers connected to K-type twisted pair thermocouples in each plot. The thermocouples were located at the soil surface (i.e. below overlying layers of moss and litter in plots where these layers were not removed) and 2 cm below the top of the soil. Temperatures were recorded at 1 s intervals. In plots where it had not been removed, we measured the thickness of the M/L layer above the top thermocouple to the nearest 0.5 cm. Based on the thermocouple data we estimated five metrics of fire-induced soil heating (Table 1).

Post-fire soil thermal dynamics data were collected from two different experiments: the experimental fires and a series of wildfires. For the experimental fires, we buried iButton™ temperature loggers (0.5 °C accuracy, 2 h logging interval) 2 cm below the top of the soil. We buried a single iButton in a randomly-selected plot of each treatment in each of the seven fires. Next to each fire we also located an iButton in a single unburnt (control) plot. Temperatures were recorded from 26 April 2013 to 10 April 2014. We analysed post-fire soil thermal dynamics in three wildfires to assess whether our experimental manipulation of ground fuel structure led to fire effects similar to those seen in moderately-severe to severe wildfires. The three wildfires burnt *Calluna*-dominated heaths and/or bogs in northern England (Anglezarke, 53.658° N, 2.569° W; Wainstalls, 53.777° N, 1.928° W) and north-east Scotland (Finzean, 57.025° N, 2.702° W) between April 2011 and March 2012, capturing a range of variability in fire severity (e.g. ground fuel consumption ranged 0.4–1.0 kg m⁻²; Davies et al., 2016a). In each wildfire two paired plots were monitored, each

with an unburnt and a burnt subplot located either side of the perimeter of the fire. iButtons were used to record bi-hourly temperatures 2 cm below the top of the soil for approximately a month between August and September 2012. Soil types included rocky organic soils at Finzean and deep peat soils at the other sites. The potential effect of site, habitat type and fire behaviour were confounded in this experimental design but it still provides us with useful comparative data where information is otherwise lacking.

2.3. Data analysis

2.3.1. The role of the M/L layer in controlling fire-induced soil heating

All data analysis was performed in R 3.2.2 (R Core Team, 2015). Due to thermocouple malfunction, the number of observations was 41 at the soil surface and 38 two cm below. We examined differences in M/L layer consumption and fire-induced soil heating between burnt plots where the M/L layer was not removed, and plots where it was removed after the fire, to assess whether the two treatments could be grouped together in subsequent analyses. M/L layer consumption did not differ significantly between plots where the M/L layer was removed after the fire (average ± standard deviation was 0.21 ± 0.49 cm) versus where it was not manipulated (0.13 ± 0.38 cm). Where frequency of zeros was low and thus statistical testing was possible (i.e. soil heating metrics except time above 50 °C), differences were not significant (Table S2). Therefore, both treatments were combined into an “M/L layer present” group.

We investigated the effect of variation in ground fuel structure on fire-induced soil heating using linear mixed effects models that included an interaction between treatment (M/L layer present and removed) and depth of measurement (soil surface and 2 cm below) as fixed effects and fire as a random effect (function “lme” in the package *nlme*; Pinheiro et al., 2015). Response variables were logarithmically transformed, except for total heat, for which a square root transformation was used. Statistical analysis of time above 50 °C was not possible due to high abundance of zeros. Multiple comparisons (Hothorn et al., 2008) tested differences between treatments within measurement depth. We used the function “g.squaredGLMM” in the package *MuMIn* (Barton, 2015) to calculate the marginal R² (variance explained by fixed effects) and conditional R² (variance explained by both fixed and random effects) (Nakagawa and Schielzeth, 2013; Johnson, 2014).

To assess which environmental variables were most important in determining fire-induced soil heating in plots where the M/L layer was not removed, i.e. representative of normal managed burning in *Calluna* moorlands, we fitted separate linear fixed effects models for each temperature metric (Table 1, except for time above 50 °C due to high abundance of zeros) including interactions between measurement depth and each environmental variable as fixed effects and fire as a random effect. Available environmental variables measured at the plot level were total biomass above ground, M/L layer thickness, soil bulk density, M/L layer FMC and

Table 1
Fire-induced soil heating metrics calculated from temperature measurements at the soil surface and 2 cm below, from the start of the fire to 35 min after.

Variable	Details
Total heat (°C.s)	Measurement that integrates both the extent of temperature increase and its duration. Calculated as $\sum_{i=1}^{2100} (T_i - T_0)$, where T_i is the soil temperature at i seconds after the start of the fire and T_0 is the temperature before the start of the fire.
Maximum T (C)	Maximum soil temperature.
Heating and cooling rates (λ)	Exponential growth (heating) and exponential decay (cooling) constants (λ) associated with the rising and falling limbs of the temperature-time curves. λ were estimated fitting non-linear models of the type $T_i = T_0 \cdot e^{(\lambda \cdot i)}$, where T_i is temperature at time i (in minutes) and T_0 is the initial temperature, using the package <i>gnm</i> (Turner and Firth, 2015).
t above 50 °C (s)	Time that soil temperature was above the 50 °C threshold, associated with damage to, and mortality of, plant tissues (Granström and Schimmel, 1993; Massman et al., 2010) and stimulation of seed germination (Whittaker and Gimingham, 1962).

soil FMC. Soil bulk density and FMC were negatively correlated and, to avoid multicollinearity (Zuur et al., 2010), only soil FMC, *a priori* a stronger control on soil heating (Busse et al., 2010), was included in the initial models. Total heat was square root-transformed, and the other response variables were log-transformed. A constant variance structure accounted for the heterogeneity in variance between measurement depths. Akaike's Information Criterion (AIC) was used for model selection: terms that did not lower AIC by more than two units were sequentially removed (Symonds and Moussalli, 2010).

2.3.2. Effect of fire severity on post-fire soil thermal dynamics

Post-fire mean daily temperature (00:00 to 22:00) and daily temperature range, defined as the difference between maximum and minimum daily temperatures, were calculated using data from the iButtons. Simple harmonic regression (Cowpertwait and Metcalfe, 2009) was used to model mean daily temperature and daily temperature range separately in each treatment. We used linear mixed effects models that included sampling day and the sine and cosine terms of the harmonic expression as fixed effects:

$$MDT/DTR_{tr} (\text{°C}) \sim sday + \cos(2 \cdot \pi \cdot sday/365) + \sin(2 \cdot \pi \cdot sday/365) \quad (1)$$

where mean daily temperature (MDT) or daily temperature range (DTR) in treatment *tr* is a function of the sampling day *sday* (1, 25 April 2013, to 350, 10 April 2014) and a cosine and sine term. Fire was included as a random effect and temporal correlation of the data (continuous bi-hourly measurements at the same location) was accounted for with an autocorrelation structure of order 1 (function "corAR1" in package *nlme*). We calculated amplitude (vertical distance from the centreline to the wave maximum, in °C) and phase (horizontal distance to a wave starting at sampling day 1, in days) that characterise the modelled sinusoids following Piegorsch and Bailer (2005). Uncertainty in amplitude and phase was estimated using the approximate variance of a function of random variables based on a Taylor expansion (Meyer, 1970). For both mean daily temperature and daily range, we computed 95% confidence intervals for the differences in amplitude between all pairs of treatment levels. We followed the same procedure for differences in phase.

We tested whether soil temperatures following experimental fires responded differently to changing weather conditions compared to soils burnt-over by wildfires. To allow comparison of data from the experimental fires with the paired plot data from the wildfires (which burnt different sites in different years) we took two approaches to defining paired plots from our experimental fire data: one pair included the unburnt plot and the plot where the M/L layer was not removed (defined as "low severity" treatment), and the second pair included the same unburnt plot and an average of the two plots where the M/L layer was removed (simulated "high severity"). For both the wildfires and the experimental burns, we calculated the difference between temperatures in the unburnt subplot and the burnt subplot in each paired plot. We only used data from the experimental fires where mean daily temperature in the unburnt plot was within the range of mean daily temperatures recorded in the unburnt wildfire subplots (6.6–15.4 °C). Post-fire changes in mean daily temperature were modelled as a function of mean daily temperature in the unburnt plot and the fire type associated with the paired plot (wildfire, low severity experimental fire and simulated high severity experimental fire). Mean daily temperature in the unburnt plot was used as a proxy for weather conditions, and was included in the model to account for the effect of weather on post-fire thermal dynamics. We fitted a random

slopes and intercept model with an interaction between mean daily temperature in the unburnt plot and fire type as fixed effects, paired plot as a random effect and an autocorrelation structure of order 1.

2.3.3. Effect of post-fire soil thermal dynamics on relative soil respiration

Given the key role of temperature in controlling metabolic rates, temperature-driven models are often used to estimate soil respiration (Del Grosso et al., 2005). We used Eq. (2) (Lloyd and Taylor, 1994) to explore the potential effect of observed changes in soil thermal dynamics on soil respiration.

$$R = R_{10} e^{308.56 \left(\frac{1}{56.02} - \frac{1}{T-227.13} \right)} \quad (2)$$

where R_{10} is the estimated respiration at 10 °C and T is the soil temperature in K. As R_{10} was unknown for the site, we used a unitless value of 1 and thus expressed estimates of respiration as the proportional change in respiration relative to that at 10 °C. We estimated relative respiration during the first year after the fire in each plot using the bi-hourly temperature measurements. The approach focuses on soil temperature and does not consider other drivers of soil respiration such as moisture content and substrate dynamics (Curriel Yuste et al., 2007) likely to change after burning (Ward et al., 2012). Thus, our estimates provide an indication of how post-fire soil respiration may change due to an altered soil thermal regime alone, and noting that potentially important interactions with other environmental variables were not explored. Average relative respiration estimates were calculated for each plot in each season (spring: March–May, summer: June–August, autumn: September–November, winter: December–February), providing seven averages (one per fire) for each treatment and season. The data were analysed using a linear mixed effects model including an interaction between treatment and season as fixed effects and fire as a random effect. We performed multiple comparisons tests using the function "glht" in the package *multcomp* (Hothorn et al., 2008).

3. Results

3.1. The role of the M/L layer in controlling fire-induced soil heating

M/L consumption in plots where the M/L layer was not removed before the fire was very low: 0.17 ± 0.44 cm. Soil heating, as measured by total heat, maximum temperature and time above 50 °C, was higher in plots where the M/L layer had been removed prior to the fire than in those where it was present during the burn (Table 2). Temperatures were also considerably higher at the soil surface compared to 2 cm below ground. The temperature time curves consistently showed a steep rising limb associated with the arrival of the fire front followed by a shallow falling limb related to residual flaming and smouldering combustion and the slow cool down of the heated soil mass (Fig. 1). For temperature residence, maximum temperature, rate of heating and rate of cooling, the statistically significant interaction between treatment and depth of measurement indicated that M/L layer removal had a larger effect at the top of the soil compared to 2 cm below (model details are provided in Table S3).

Fuel structure and moisture content of the different fuel layers was relatively homogenous across fires (Table 3). For plots where the M/L layer was not manipulated, the main controls on fire-induced soil heating were depth of measurement, the moisture content of the soil and the moisture content of the M/L layer,

Table 2
Mean and standard deviation (in parentheses) of fire-induced soil heating metrics by depth of measurement (soil surface and 2 cm below) and treatment (M/L layer present or removed). Within each variable and depth of measurement, different letters indicate statistically significant differences between treatments ($\alpha = 0.05$). Statistical testing details are provided in Tables S3 and S4.

Variable	2 cm		0 cm	
	M/L present	M/L removed	M/L present	M/L removed
Total heat ($^{\circ}\text{C}\cdot\text{s}$)	1895 (2256) a	4322 (3874) b	7791 (7012) a	20469 (10170) b
Maximum T ($^{\circ}\text{C}$)	7 (3) a	9 (4) b	21 (22) a	73 (34) b
Heating rate (λ)	0.02 (0.04) a	0.03 (0.04) b	0.8 (2) a	5 (4) b
Cooling rate (λ)	3e-05 (4e-05) a	0.003 (0.01) b	0.08 (0.1) a	0.5 (0.3) b
t above 50°C (s)	0 (0)	0 (0)	11.1 (34.2)	57.8 (57.7)

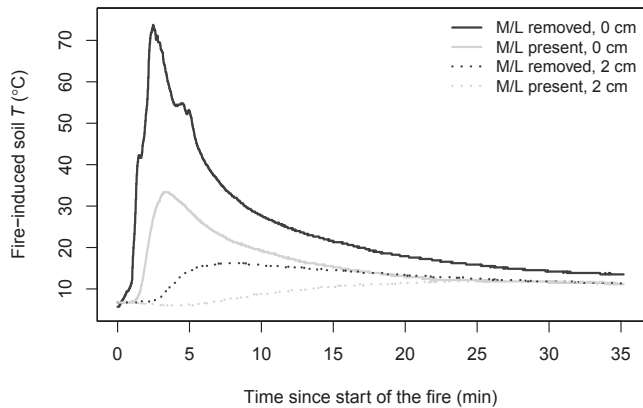


Fig. 1. Representative examples of fire-induced soil heating curves associated with plots where the M/L layer was present or removed at the time of the fire, at both measurement depths (soil surface and 2 cm below). Curves with the same colour belong to the same plot/treatment.

although the explanatory power of the models was low (Table 4).

3.2. Effect of fire severity on post-fire soil thermal dynamics

The harmonic expressions (Eq. (1)) had a significant effect in modelling mean daily temperature and daily temperature range (Table S3). Marginal R^2 (variance explained by fixed effects) ranged between 0.88 and 0.90 in mean daily temperature models and between 0.27 and 0.61 in daily temperature range models. Low marginal R^2 in daily temperature range models was associated with weak seasonal patterns in unburnt plots. Daily temperature range was highest in burnt plots where the M/L layer was manually removed, lowest in unburnt plots, and intermediate in burnt plots where the M/L layer was not removed (Fig. 2). Differences in daily temperature range between treatments were highest in summer (up to ca. 6°C) and lowest in winter (up to ca. 0.5°C). Mean daily temperature in burnt plots was higher than in unburnt in summer

Table 3
Summary of environmental variables associated with the experimental fires. M/L layer thickness and FMC refer to plots where the M/L layer was not removed.

Variable	n	Mean (SD)	Range
Fire rate of spread (m min^{-1})	7	7 (3.3)	3.7–12
Wind speed (m s^{-1})	7	3.3 (1.5)	1.9–6.3
Air temperature ($^{\circ}\text{C}$)	7	8.6 (2.6)	5.1–11.1
Relative humidity (%)	7	58 (12)	41–73
Live <i>Calluna</i> FMC (%)	7	81 (6)	74–92
Dead <i>Calluna</i> FMC (%)	7	15 (4)	13–23
<i>Calluna</i> height (cm)	42	51.3 (7.7)	31–65
Fuel load above moss (kg m^{-2})	42	1.5 (0.2)	1.0–1.9
M/L layer thickness (cm)	28	4.0 (1.9)	1.0–8.0
M/L layer FMC (%)	28	251 (77)	103–398
Soil FMC (%)	42	422 (88)	192–630
Soil bulk density (g cm^{-3})	42	0.1 (0.1)	0.02–0.4

Table 4
Optimal linear mixed effects models explaining variation in soil heating metrics as a function of depth of measurement (soil surface and 2 cm below) and moisture content of soil and of the M/L layer.

Response	DF	R^2_m	R^2_c	Fixed effect	t-value	p-value
Total heat ($^{\circ}\text{C}\cdot\text{s}$)	45	0.21	0.32	Depth	4.82	<0.001
				Soil FMC	2.35	0.023
Maximum T ($^{\circ}\text{C}$)	46	0.17	0.34	Depth	5.08	<0.001
Heating slope (λ)	46	0.10	0.34	Depth	3.41	0.001
Cooling slope (λ)	45	0.16	0.16	Depth	4.38	<0.001
				M/L layer FMC	-2.06	0.046

and spring and lower in autumn and winter. The removal of the M/L layer amplified the effect of burning and resulted in higher temperatures in spring and summer and lower temperatures in autumn and winter.

Mean daily temperature and daily temperature range were similar in burnt plots where the M/L layer was removed after the fire and in plots where it was removed before the fire. Comparisons

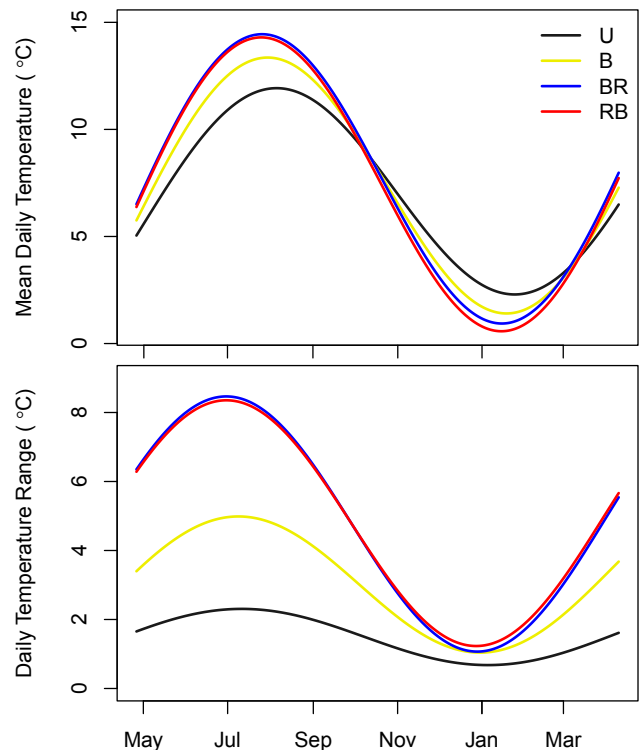


Fig. 2. Modelled mean daily temperature and daily temperature range (26 April 2013 to 10 April 2014) for unburnt plots (U), burnt plots (B), and burnt plots where the M/L layer was removed after (BR) and before the fire (RB). The harmonic linear mixed effects model included sampling day and the sine and cosine terms of the harmonic expression as fixed effects, and fire as a random effect.

between both treatments suggest that consumption of the *Calluna* canopy and removal of the M/L layer had an effect of a similar magnitude on soil thermal dynamics. For example, mean daily temperature in burnt plots was 1.6 °C higher than in unburnt in July, while it was approximately 2.6 °C higher in burnt plots where the M/L layer was removed. Similarly, daily temperature range in July was 2.6 °C higher in burnt than in unburnt plots and 5.9 °C higher in burnt plots where the M/L layer was removed than in unburnt.

Larger mean daily temperature amplitude in burnt plots where the M/L layer was removed indicated more extreme seasonal soil thermal dynamics (Table 5). The larger amplitude of the daily temperature range in the same plots indicated greater diurnal extremes. The negative phase for mean daily temperature and daily temperature range in burnt plots showed that annual patterns of soil thermal dynamics in these plots lead those of unburnt plots, i.e. maximum (summer) and minimum (winter) temperatures occurred 4–10 days earlier in the year in burnt compared to unburnt plots. Comparison of the 95% confidence intervals of the difference in amplitude between treatments revealed that seasonal patterns in mean daily temperature and in daily range were significantly different between all treatments except between plots where the M/L layer was removed before the fire and plots where it was removed afterwards. Patterns in phase differences were similar, except for mean daily temperature where phase was different in burnt plots where the M/L layer was removed before compared to after the fire.

Post-wildfire increases in mean daily soil temperature during warmer weather (as estimated by soil temperature in the unburnt plot) were similar to that observed after experimental fires in plots where the M/L layer was manually removed (p-value = 0.8), but significantly higher (p-value = 0.03) than in plots where the M/L layer was not removed (Fig. 3). Model details are provided in full in Table S6.

3.3. Effect of post-fire soil thermal dynamics on estimated soil respiration

Estimated relative soil respiration followed seasonal temperature patterns, with the highest values in summer and the lowest in winter (Fig. 4). The higher temperatures recorded in burnt plots where the M/L layer was removed led to significantly higher estimated relative respiration in the warmer summer months.

4. Discussion

4.1. The role of the M/L layer in controlling fire-induced soil heating

The effect of removing the M/L layer was similar across all measures of fire-induced soil heating: a small increase in the response variable at 2 cm depth and a substantial increase at the top of the soil (Table 2). For example, average maximum

Table 5

Amplitude and phase of the mean daily temperature and daily temperature range models (Fig. 2), for each fuel treatment. Variance in parenthesis. Same letters within columns indicate non-significant differences between fuel treatments, based on 95% confidence intervals. Phase is relative to that in unburnt: negative values indicate the sinusoidal wave is to the left (leading) the unburnt.

Treatment	Mean Daily Temperature		Daily Temperature Range	
	Amplitude (°C)	Phase (days)	Amplitude (°C)	Phase (days)
Unburnt	5.6 (0.01) a	0.0 (0.04) a	0.9 (0.001) a	0.0 (0.4) a
B	6.8 (0.01) b	-6.0 (0.01) b	2.2 (0.005) b	-4.0 (0.4) b
BR	7.7 (0.02) c	-9.9 (0.02) c	3.7 (0.01) c	-9.4 (0.5) c
RB	7.7 (0.02) c	-10.4 (0.03) d	3.6 (0.008) c	-9.8 (0.4) c

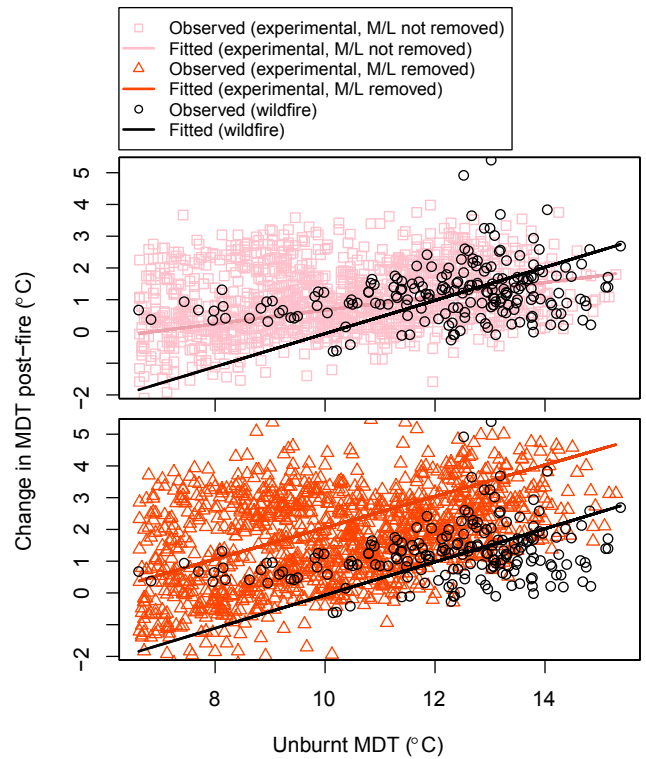


Fig. 3. Difference in post-fire soil mean daily temperature (MDT) between burnt and unburnt plots in experimental fires and wildfires versus MDT in the unburnt plot. (top) The M/L layer was not removed in burnt plots in experimental fires; (bottom) the M/L layer was manually removed in burnt plots in experimental fires. Fitted values from models including an interaction between unburnt MDT and fire type (wildfire, low severity experimental fire and simulated high severity experimental fire, i.e. where the M/L layer was removed) as a fixed effect are also shown.

temperature at the top of the soil was ca. 20 °C in burnt plots where the M/L layer was not removed compared to ca. 75 °C where it was removed. The insulating effect of the M/L layer was apparent from the increased heating and cooling rates in plots where the M/L layer was removed before the fire. Where the M/L layer was not removed,

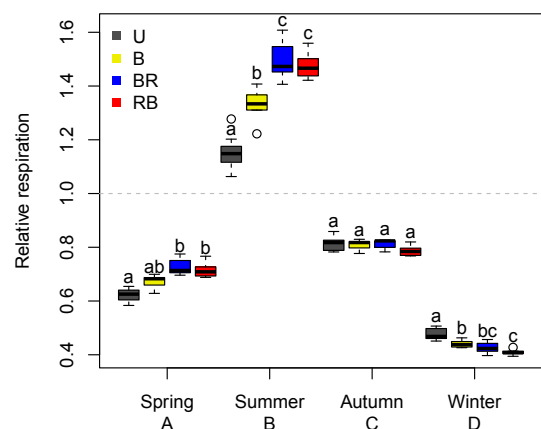


Fig. 4. Estimates of soil respiration relative to soil respiration at 10 °C, per season and treatment (codes follow Fig. 2). The height of the boxes indicate approximate first and third percentiles; the bar across is the median; the whiskers extend to most extreme datapoint within 1.5 times the interquartile range; circles are data outwith this range. Within each season, treatments with different lower-case letters are significantly different. Capital letters refer to overall differences between seasons ($\alpha = 0.05$). Statistical testing is reported in full in Table S7, Table S8 and Table S9.

i.e. conditions generally representative of managed burning in *Calluna* moorlands, the high M/L layer FMC (251%) limited the transmission of raised temperatures into the soil (Busse et al., 2010) and prevented the ignition of the M/L layer (Davies and Legg, 2011; Santana and Marrs, 2014). Soil and M/L layer moisture content explained some of the variation in soil heating, although overall model performance was low (Table 4). This is possibly due to a combination of the limited range of environmental and weather conditions under which we were able to safely complete our burns (Table 3) and the stochastic nature of fire behaviour and fuel structures at small temporal and/or spatial scales (Davies et al., 2010). Future research aiming to understand the effect of environmental variables on fire-induced soil heating more completely might benefit from greater variation in fuel structure, fuel moisture content and fire weather.

Although average soil maximum temperatures in plots where the M/L layer was removed were above the critical threshold for damage to rhizomes (55–59 °C) and seeds (65–75 °C) for common heathland species (Granström and Schimmel, 1993), the relatively short average time above 50 °C (around a minute) suggests extensive damage was unlikely (Mallik and Gimingham, 1985; Schimmel and Granström, 1996). Nevertheless, considering 70% of viable *Calluna* seeds in shallow organic soils are located in the upper 2 cm of the soil profile (Legg et al., 1992), the increased fire-induced soil heating observed in plots where the M/L layer was removed suggests thermal insulation from ground fuels can be an important control on post-fire vegetation response. Compared to low severity fires with limited M/L layer consumption and soil heating, moderately-high severity fires can promote regeneration of *Calluna* seeds through stronger germination cues from fire-induced temperature pulses (Whittaker and Gimingham, 1962), ash and smoke (Bargmann et al., 2014) and warmer soil during the growing season (Fig. 2). Furthermore, greater M/L layer consumption increases the area of bare soil thus improving the establishment of *Calluna* seeds (Davies et al., 2010). However, regeneration would decline sharply in high severity fires with extensive below-ground heating leading to seed mortality (Schimmel and Granström, 1996) and, in extremely severe wildfires, changes to soil structure and soil loss (Maltby et al., 1990; Davies et al., 2013).

4.2. Effect of fire severity on post-fire soil thermal dynamics

Differences in post-fire soil thermal dynamics between treatments can be explained by three main mechanisms: (i) the removal of the *Calluna* canopy and the M/L layer thus increasing solar radiation and air movement and facilitating heat exchange between soil and atmosphere (Barclay-Estrup, 1971); (ii) lower albedo in burnt plots, especially where the M/L layer was removed, due to the dark exposed soil (Chambers and Chapin, 2002); (iii) the alteration of soil moisture content, likely dependent on complex interactions between habitat, fire behaviour and weather. For example, depending on fire severity and soil characteristics, fire can create a water repellent layer that can reduce soil evaporation (Certini, 2005; Kettridge et al., 2015). Low near-surface moisture content can reduce latent heat fluxes and result in large diurnal temperature variations at the soil surface (upper 1.5 cm) (Kettridge et al., 2012). Comparison of soil thermal dynamics in unburnt plots, burnt plots and burnt plots where the M/L layer was manually removed indicates the contribution of the *Calluna* canopy and the M/L layer to alteration of post-fire thermal dynamics were of similar magnitude, i.e. the further increase in soil solar irradiation, exposure to air flow, reduced albedo and/or altered moisture regime from the removal of the M/L layer was comparable to that from burning.

The results suggest that soil thermal dynamics after high

severity fires where the M/L layer is consumed have both wider seasonal and diurnal ranges than after low severity fires where M/L layer consumption is low. The similarity in soil thermal dynamics between burnt plots where the M/L layer was manually removed after and before the fires can be explained by the high soil moisture content at the time of burning (mean 422%, Table 3), which was likely to have minimised the potential for soil scorching and the formation of hydrophobic surface layers (Certini, 2005). The change in soil thermal dynamics in burnt plots resulted in warmer soil temperatures during the growing season, especially in plots where the M/L layer was manually removed.

Higher mean and maximum daily temperatures, and lower minimum daily temperatures in recently burnt plots have been observed previously in heather moorlands (Brown et al., 2015). The post-wildfire soil temperature data we analysed, although short in duration and occurring within limited range of weather conditions, showed a relationship between mean daily soil temperature and prevailing weather conditions similar to that observed in experimental fires where the M/L layer was removed (Fig. 3). This may indicate that the combustion of the M/L layer in wildfires (Davies et al., 2016a) could be an important driver of increased alteration to post-fire soil thermal dynamics. However, further research needs to confirm this as differences in habitat and soil characteristics between our experimental and wildfire sites (e.g. soils were generally deeper and wetter at the wildfire sites), as well as differences in weather not accounted for by our model (solar radiation and precipitation), may also have contributed to differences in post-fire soil thermal dynamics.

4.3. Effect of post-fire soil thermal dynamics on estimated soil respiration

We used a simple model to form new testable hypotheses about how changes in soil temperature regimes could alter soil respiration (Fig. 4). This suggests that temperature differences should increase relative respiration in burnt plots compared to unburnt during the summer, when soil respiration is at its greatest (Falge et al., 2002). Furthermore, modelled soil respiration during the summer was highest in burnt plots where the M/L layer was manually removed. Therefore, a temperature-driven increase in soil respiration (Blodau et al., 2007; Dorrepaal et al., 2009) could result from high severity fires where the M/L layer is consumed. However, the potential implications of this for a sites' overall carbon balance is far from clear. For instance, higher soil temperatures could also result in increased Net Primary Productivity, which may offset increased respiration (Davidson and Janssens, 2006). In addition, the effect of an altered post-fire soil microclimate on the soil carbon budget is superimposed on changes in vegetation community composition, which is an important, though complex, control on soil carbon dynamics. For example, vascular plants can increase peatland soil respiration under warm conditions (Ward et al., 2013; Walker et al., 2016), whilst the inhibitory action of phenolics associated with shrubs can lower soil respiration (Wang et al., 2015). Community response to fire severity is therefore likely to be an important driver of carbon dynamics in *Calluna* heathlands, and could be key in determining the fate of large quantities of carbon stored in northern soils where higher severity fires are projected (Albertson et al., 2010). Our simple modelling exercise therefore points to important directions for future research but the hypothesised effects of changes in temperature regimes cannot be considered in isolation.

5. Conclusions

We found that the thickness and moisture content of the M/L

layer plays a critical role in controlling soil heating in *Calluna* heathland fires. Fire-induced soil heating increased significantly in the absence of the M/L layer overlaying the soil, although, due to high soil moisture content, temperatures remained at the lower end of those that could damage plant tissue. Post-fire soil thermal dynamics differed between levels of simulated fire severity. Thus with higher severity fires, where the M/L layer is consumed, soils will be warmer during summer with greater seasonal and diurnal temperature variation. The altered soil microclimate may increase soil respiration in the first years following burning. However, further information on effects of the severity of fires on below- and above-ground processes, including vegetation community response, is required to understand long-term consequences of a changing fire regime on the overall carbon balance. The results suggest that managed burning, aiming to rejuvenate *Calluna* heathlands whilst minimising soil carbon losses, should keep fire severity low to avoid consumption of the M/L layer by burning when the moisture content of the soil and the M/L layer are high.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jenvman.2017.08.017>.

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