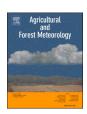
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No recovery of soil respiration four years after fire and post-fire management in a Nordic boreal forest

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ABSTRACT

The long-term carbon storage capacity of the boreal forest is under threat from the increasing frequency and intensity of wildfires. In addition to the direct carbon emissions during a fire, the burnt forest often turns into a net carbon emitter after fire, leading to large additional losses of carbon over several years. Understanding how quickly forests recover after a fire is therefore vital to predicting the effects of fire on the forest carbon balance. We present soil respiration and CH₄ fluxes, soil chemistry, microclimate and vegetation survey data from the first four years after a wildfire in a Pinus sylvestris forest in Sweden. This is an understudied part of the boreal biome where forest management decisions interact with disturbances to affect forest growth. We analysed how fire severity and post-fire salvage-logging affected soil carbon fluxes. The fire did not affect soil CH₄ uptake. However, soil respiration was significantly affected by the presence or absence of living trees after the fire and postfire forest management. Tree mortality due to the high-severity fire, or the salvage-logging of living trees after low-severity fire, led to immediate and significant decreases in soil respiration. Salvage-logging of dead trees after high-severity fire did not alter soil respiration compared to when the dead trees were left standing. However, it did significantly slow the regrowth of understory vegetation. Our results highlight that the impact of salvage-logging on the soil carbon fluxes depends on fire severity but that logging always slows the natural recovery of vegetation after fire. The soil CO2 fluxes did not show signs of recovery at any of the burnt sites during the first four years since the fire.

1. Introduction

Boreal forests store more carbon (C) than any other forest biome, but their C stores are at risk from increasingly frequent and severe wildfires. In 2018, an unprecedented number of forest fires broke out across Sweden due to prolonged drought, burning an area ten times larger than the annual mean (SOU, 2019). The increasing frequency of wildfires in these slow growing forests is reducing their capacity to accumulate and store C over the long-term, and is altering the vegetation communities that establish after a fire (Burrell et al., 2022; Mack et al., 2021; Walker et al., 2019).

During a fire, large amounts of C can be released into the

atmosphere. In addition, the burnt ecosystem may continue to be a net C emitter until newly established or surviving vegetation regrows sufficiently to turn the forest back into a C sink. These post-fire C losses can account for a significant proportion of the total C loss caused by forest fires (Ueyama et al., 2019). Forest floor respiration ($R_{\rm ff}$, i.e. the sum of autotrophic respiration from forest floor vegetation, tree roots and heterotrophic respiration from soil microbes) is the dominant component of post-fire ecosystem C emissions. In undisturbed Swedish boreal forests, Chi et al. (2021) found that $R_{\rm ff}$ contributes to 82 % of total ecosystem respiration and can be the main driver of differences in the annual net C balance between forest stands. Changes in $R_{\rm ff}$ become even more important in determining the net C balance of a stand after a fire

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because gross primary production (GPP) partly or completely stops immediately after a fire.

Soil respiration tends to decrease post-fire, especially after high-severity fire that causes high tree and understory mortality. This loss of vegetation not only reduces autotrophic respiration but also heterotrophic respiration since the root exudates that many microbes depend on are no longer produced. In addition, high soil burn severity can kill soil microbes and combust a large proportion of the soil organic layer, further reducing heterotrophic respiration (Xu et al., 2022; Zhou et al., 2023). In boreal North America, high-severity stand-replacing fires are typical (Rogers et al., 2015), and this type of fire has been the focus of most boreal forest fire research (Amiro et al., 2003; Köster et al., 2017; O'Neill et al., 2002).

In contrast, less is known about the impact of low-severity surface fires on forest carbon fluxes, even though these are typical across boreal Eurasia (Rogers et al., 2015). In boreal Eurasia, forests include tree species such as larch and Scots pine that are adapted to survive low-severity fire and prevent it from spreading into the forest canopy (Rogers et al., 2015). During a low-severity fire in these forests, the understory vegetation and part of the soil organic layer is burnt but most (if not all) trees survive. In a Chinese boreal forest, Hu et al. (2017) found that low-severity fire only caused a significant reduction in autotrophic, but not in heterotrophic respiration compared to unburnt plots, four to six years post-fire. This apparently more complex response of soil respiration to low-severity fire needs further investigation to help quantify how these fires affect the forest carbon budget across boreal Eurasia.

Fire can also affect the emission and uptake of methane (CH₄) by soil bacteria and vegetation. Dry, oxic soils act as a small CH₄ sink, consuming 5 % of all global CH₄ emissions (Saunois et al., 2020). There are fewer studies assessing the impact of fire on forest CH₄ fluxes than on CO₂ fluxes. Previous studies reported contrasting effects: increases (Burke et al., 1997; Jaatinen et al., 2004), decreases (Kulmala et al., 2014), and no significant effects (Köster et al., 2018) on soil CH₄ uptake after boreal forest fires. Soil physical characteristics have a large influence on how easy it is for CH₄ to diffuse into the soil and therefore on methane uptake (Ball et al., 1997). Since both fire and post-fire management of forest soils may affect soil structure, they may also lead to changes in soil CH₄ uptake. Measuring both soil respiration and methane fluxes after forest fires and how they change with time since fire is key to understanding how fast the forest C balance recovers post-fire.

Over half of the global boreal forest is managed (Astrup et al., 2018), vet few studies have explicitly considered how forest management after fire may affect the boreal forest C budget. Salvage-logging (cutting of burnt trees) is a common practice after fire in managed boreal forests (Nappi et al., 2011; Skogsstyrelsen, 2023) and an additional disturbance that may amplify the fire impacts (Leverkus et al., 2018). Neither Kelly et al. (2021) nor Parro et al. (2019) found significant differences in soil respiration between salvage-logged and unlogged forests in the first or 21st year after a stand-replacing fire, respectively. However, the impact of management after low-severity fire, the most common fire type in the intensively managed northern European boreal forest, has not previously been assessed. In addition to salvage-logging, various methods of site preparation may be used post-fire that further disturb the soil and thus affect the soil C fluxes. For example, exposure of the mineral soil by ploughing can decrease soil respiration due to reduced organic matter content and soil moisture (Strömgren and Mjöfors, 2012). On the other hand, soil mixing or mounding can increase soil CH4 emission due to increased organic matter availability for microbial activity (Sundqvist et al., 2014). Most research on the effects of site preparation on soil C fluxes in boreal forests has been performed after logging without fire, and thus our understanding of the interactive effect of fire and site preparation on soil C fluxes is limited.

Our study contributes to filling the research gaps identified above by analysing a time series of soil C flux measurements (soil respiration and CH₄) collected during the first four years after a major forest fire in

boreal Sweden. The extensive Ljusdal fire of 2018 enabled us to examine sites affected by low and high-severity fire, and with or without post-fire salvage-logging. This has provided us with unique insights into the impacts of both fire and management on post-fire forest recovery in an understudied part of the boreal forest. This study builds on a previous study, where data from the first post-fire year was analysed (Kelly et al., 2021). Here, we test four hypotheses: H1) soil respiration will decrease significantly after fire but more so after high-compared to low-severity fire, H2) soil respiration will decrease significantly after salvage-logging of low-severity fire sites but not after salvage-logging of high-severity fire sites, H3) soil respiration will increase significantly over time since the fire, H4) soil $\mathrm{CH_4}$ uptake will not change significantly after low- or high-severity fire or salvage-logging. We assess these hypotheses using several years of measurements of soil C fluxes, soil nutrient content, soil microclimate and vegetation regrowth.

2. Methods

2.1. Study area and design

The study area is in central Sweden (61°56′N 15°28′E, 220 m a.s.l) and had a mean annual temperature of 3.8 °C and mean annual precipitation of 652 mm during the study period 2019–2022 (SMHI, 2023; Ytterhogdal station 263 m a.s.l. and 40 km northwest of the site). It sits in a wide, flat valley, dominated by managed *Pinus sylvestris* forests with smaller areas of *Picea abies* and *Betula sp*. The understory vegetation consists of low shrubs (*Vaccinium vitis-idaea, Vaccinium myrtillus, Arctostaphylos uva-ursi, Empetrum nigrum, Calluna vulgaris*) and bryophytes (*Pleurozium schreberi, Dicranum* sp., *Polytrichum juniperinum, Cladonia* sp., *Cetraria* sp.). The soils are Podzols (WRB, 2015). The Ljusdal wildfire was ignited by lightning in July 2018 and burned 8995 ha, making it one of the largest Swedish forest fires of this and the last century (Drobyshev et al., 2015; SOU, 2019).

The burnt area included areas affected by high-severity and low-severity fire. Our definition of fire severity is based on the impact of the fire on the trees. We define high-severity fire as crowning fire leading to complete tree mortality, almost complete combustion of the understory vegetation and substantial consumption of the soil organic layer, whereas low-severity fire is defined as surface fire that almost all trees survive but which burns most of the soil organic layer and understory vegetation. Table 1 includes data on the thickness of the forest floor at each site. More details about the fire and study area can be found in Kelly et al. (2021).

After the fire, we established five sites in mature *Pinus sylvestris* stands that were affected by contrasting fire severity (high versus low) and post-fire management treatments (salvage-logging versus unlogged, replanted versus natural regeneration; Table 1, Fig. 1). Forest owners decided how their plots would be managed after the fire and we did not influence this decision, nor were we involved in carrying out the chosen post-fire treatments. We present the results from these sites split into three groups (note that the same site can be in multiple groups):

- 'Fire severity' group: comparing an unburnt site (UM) with a low-severity fire site (LM) and a high-severity fire site (HM). These three sites are all part of a nature reserve created after the fire. No salvage-logging occurred at LM or at HM and the sites have been allowed to regenerate naturally.
- 2. 'Salvage-logging after low-severity fire' group: comparing the LM site (unlogged) with a site that also experienced low-severity fire but was salvage-logged 10 months after the fire (SLM). In late spring 2019, soil scarification was performed, creating ridges where the charred and organic soil layers remained and furrows of exposed mineral soil. Seeds of *Pinus sylvestris* were spread after the soil scarification.
- 'Salvage-logging after high-severity fire' group: comparing the HM site (unlogged) with a site that experienced high-severity fire and was then salvage-logged (SHM). The SHM site was salvage-logged 6

fire and scarification.

Table 1 Description of the sites in the study area affected by the 2018 Ljusdal wildfire. Uncertainties are \pm SE. The forest floor refers to the combined litter layer (including bryophytes if present), charred layer (at the burnt sites only) and soil organic layer. The charred and total forest floor depth averages are based on 60 measurements per site and per layer taken in May 2019 except at SLM where they were measured in June 2020, see Section 2.4. *At SLM, two measurements of charred and total forest floor layer depth are given to represent the furrows with exposed mineral soil (0 mm forest floor and charred layer) and the ridges where forest floor remained after the

Description	UM	LM	нм	SLM	SHM
Site name	Unburnt Mature	Low-severity Mature	High-severity Mature	Salvage-logged, Low-severity Mature	Salvage-logged, High-severity Mature
Fire severity	No fire	Low	High	Low	High
Post-fire management	None (nature reserve)	Standing living trees with charring of the lower trunk, natural regeneration (nature reserve)	Standing dead burnt trees, natural regeneration (nature reserve)	Living trees salvage-logged within 10 months after fire, soil scarification and spreading of <i>Pinus sylvestris</i> seeds in late spring 2019 (commercial plantation)	Dead trees salvage-logged 6 months after fire, no soil preparation, <i>Pinus</i> sylvestris seedlings planted in spring 2020 (commercial plantation)
Charred forest floor layer depth (mm)*	0	8 ± 1	10 ± 0	$0,11\pm1$	9 ± 1
Total forest floor layer depth (mm)*	149 ± 4	37 ± 2	25 ± 1	$0,26\pm3$	23 ± 2
Tree age in 2018	60-70	70–90	~100	54	73
Mineral soil type	Sand	Sand	Sand	Silt loam	Sand

months after the fire, but it was not scarified. *Pinus* sylvestris seedlings were planted at SHM in 2020, two years after the fire.

We deliberately chose not to compare groups 2 and 3 since the salvage-logged sites in these two groups experienced different post-fire management treatments (i.e. scarification or not, spreading of seeds versus planting seedlings). The characteristics of all the sites are summarized in Table 1. All the sites except SLM are located within 1 km of each other whereas SLM is 3 km away from the other sites. As a result, all the sites experience the same weather conditions but SLM has a different soil mineral texture (silt loam) compared to the other sites (sand). Since we do not have pre-fire measurements at these sites, we assume that the unburnt site (UM) is representative of the pre-fire conditions at the sites. The first year of soil flux and chemistry data from sites UM, LM, HM and SHM are presented in Kelly et al. (2021), sapflow and tree growth data from UM and LM from two to four years post-fire in Dukat et al. (2024), eddy-covariance data from SLM from two to four years post-fire in Kelly et al. (2024) and soil fungal and bacterial growth and respiration data from UM, LM, HM and SHM during the second year post-fire in Soares, et al. (in review). The eddy-covariance measurements in Kelly et al. (2024) include the fluxes from the numerous tree seedlings which have become established at the SLM site since the fire. In the present study, only one of our soil flux collars at SLM included, by chance, a tree seedling. Our soil flux measurements thus capture only the soil and understory vegetation fluxes at the sites. At all our soil flux collars, the understory vegetation was small enough to fit inside the chamber.

2.2. Soil greenhouse gas fluxes

2.2.1. Measurements

Between 2019 and 2021, we conducted monthly manual soil CO_2 and CH_4 measurements with a dark chamber between June-September at all sites except SLM (where measurements started in 2020). We refer to these dark chamber CO_2 measurements as forest floor respiration ($R_{\rm ff}$) to highlight that they include respiration from the soil and from any understory vegetation growing in the collars. In 2022, we measured the fluxes only in July and August. The difference in the length of the sampling period had little effect on the soil greenhouse gas results: an analysis using only July–August data from all years (Fig. S1 and Tables S1 and S2) showed the same trends in the $R_{\rm ff}$ data and only minor differences in the CH_4 data as when the June-September data were included (Fig. 2a, c and Tables 2 and 3).

The soil flux measurements were conducted using a closed dynamic chamber on 10 collars per site in 2019 with an Ultraportable Greenhouse

Gas Analyser (model 915-0011, Los Gatos Research Inc.) and 12 collars per site in 2020-2022 with an LI-7810 Gas Analyser (LI-COR Environmental). Using different analysers may introduce some uncertainty in the comparison of the fluxes from different years but was unavoidable due to logistical challenges. However, the analysers were calibrated before the sampling rounds and the same chamber was used for all measurements in all years, which will have reduced this uncertainty. Furthermore, previous work has shown no significant differences in flux measurements between different models of closed dynamic chambers and gas analysers (Pumpanen et al., 2004). Both analysers recorded data at 1 Hz and offered high accuracy for both CO2 and CH4 concentration measurements. At all sites, 10 of the collars were arranged in two transects at 10 m intervals while the two additional collars were randomly placed within the site. As a result, the collars were located at varying distances to any remaining trees or tree stumps. To account for the soil scarification at SLM, five collars from the transects plus two random collars were located in the ridges with intact organic soil, while five collars were placed in the furrows of mineral soil. This distribution of the collars reflects the areal proportion of the ridges and furrows at SLM that cover about two-thirds and one-third of the site, respectively. We combined the data from the SLM collars in our main statistical analysis. Plots of the fluxes separated by soil type are available in Fig. S2.

The circular collars had a diameter of 16 cm and extended 10 cm into the soil. The dark chamber flux measurements followed the method and conversion from concentration to flux described in Kelly et al. (2021). These included using a 5 min chamber closure time, 150 s duration for the calculation of the linear regression of gas concentration versus time and selecting regressions with the highest R^2 where p < 0.001 and NRMSE < 0.2. After each flux measurement, the soil temperature at 5 cm depth was measured at two locations just outside the collar (thermometer HI98501 Hanna Instruments Ltd.) and the soil water content (SWC) integrated over 0-6 cm depth was measured at three locations (SM300 sensor in 2019, ML3 sensor in 2021-2022 with a HH2 moisture meter, Delta-T Devices Ltd.). These soil temperature measurements and air pressure measurements from SLM (EC100 barometer, Campbell Scientific, Inc.) were used as inputs to the ideal gas law to transform gas concentration into mass. Negative CO₂ or CH₄ fluxes indicate an uptake by the ecosystem whereas positive fluxes indicate emission to the atmosphere.

2.2.2. Analysis

We fit linear mixed-effects models to the soil flux data (one model per group and gas flux) to assess whether there were significant differences in $R_{\rm ff}$ and CH_4 fluxes between the sites within each group. The groups

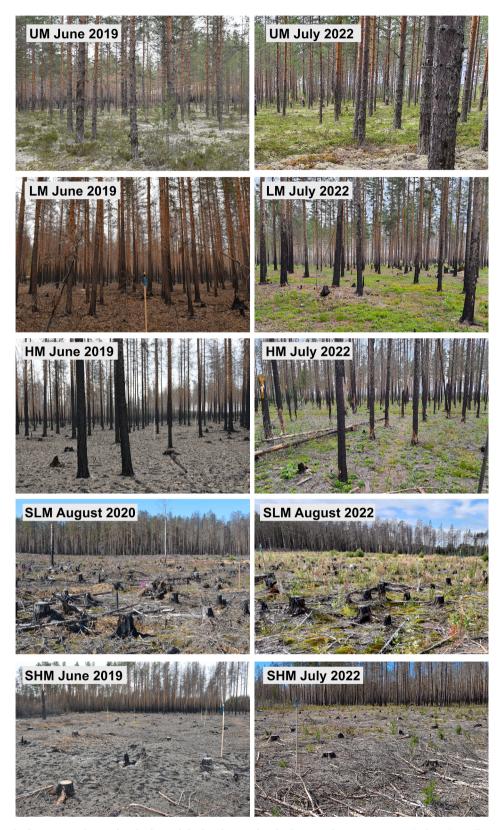


Fig. 1. Site photos from the first or second year after the fire and the fourth year after the fire. Site characteristics: UM (unburnt), LM (low-severity fire, living trees left standing), HM (high-severity fire, dead trees left standing), SLM (low-severity fire, living trees salvage-logged) and SHM (high-severity fire, dead trees salvage-logged).

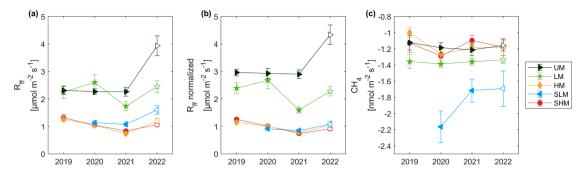


Fig. 2. Growing season means (\pm SE) of (a) forest floor respiration ($R_{\rm ff}$), (b) normalised $R_{\rm ff}$ ($R_{\rm ff,norm}$) and (c) soil CH₄ flux for 2019–2022. $R_{\rm ff,norm}$ is normalized to soil temperature of 15 °C and 10 % soil water content. The closed symbols represent years when site averages included June–September data (n = 40 per site in 2019 and n = 44 per site in 2020 and 2021) while the open symbols represent years when the site averages include July–August data (n = 24 per site in 2022). See also Table S3 for all means and SE per site and growing season. Site characteristics: UM (unburnt), LM (low-severity fire, living trees left standing), HM (high-severity fire, dead trees left standing), SLM (low-severity fire, living trees salvage-logged) and SHM (high-severity fire, dead trees salvage-logged).

Table 2 Results of ANOVAs on the mixed-effects models of the forest floor respiration flux data, 2019–2022 (n = 152 per site). Low + SL is low-severity fire followed by salvage-logging, High + SL is high-severity fire followed by salvage-logging. T_{soil} is soil temperature at 5 cm depth. Interactions were only included in the models if significant. The site \times Tsoil interaction was not significant in any model. df = numerator degrees of freedom, denominator degrees of freedom, $R_{marg}^2 = marginal R^2$ (variance explained by fixed effects), $R_{con}^2 = marginal R^2$ (variance explained by the fixed and random effects), $R_{con}^2 = marginal R^2$ (variance explained by the fixed and random effects), $R_{con}^2 = marginal R^2$ (variance explained by the fixed and random effects), $R_{con}^2 = marginal R^2$ (variance explained by the fixed and random effects), $R_{con}^2 = marginal R^2$ (variance explained by the fixed and random effects).

Group	Site			Tsoil			Time			$Site \times Time \\$			Model fit		
	df	F	p	df	F	P	df	F	p	df	F	p	R _{marg}	R _{con}	RMSE
Fire severity	2, 33	41.42	< 0.001	1, 438	320.25	< 0.001	1, 438	4.84	0.029	2, 438	8.82	< 0.001	0.49	0.67	0.34
Low + SL	1, 22	10.59	0.004	1, 213	115.27	< 0.001	1, 213	2.77	0.098	1, 213	7.34	0.007	0.33	0.70	0.33
High + SL	1, 22	0.01	0.934	1, 294	324.29	< 0.001	1, 294	35.31	< 0.001	-	-	-	0.46	0.55	0.29

Table 3 Results of ANOVAs on the mixed-effects models of the soil CH_4 flux data, 2019–2022 (n = 152 per site). Low + SL is low-severity fire followed by salvage-logging, High + SL is high-severity fire followed by salvage-logging. SWC is soil water content at 0–6 cm depth. Interactions were only included in the models if significant. df = numerator degrees of freedom, denominator degrees of freedom, $R_{marg}^2 = marginal R^2$ (variance explained by fixed effects), $R_{con}^2 = conditional R^2$ (variance explained by the fixed and random effects), RMSE = root mean square error (nmol CH_4 m⁻² s⁻¹). Statistically significant effects are marked in bold (p < 0.05).

Group Site		SWC			Time		$Site \times SWC$		Site × Time			Model fit						
	df	F	p	df	F	p	Df	F	p	df	F	p	df	F	p	R _{marg}	R _{con}	RMSE
Fire severity	2, 33	0.73	0.489	1, 440	139.63	<0.001	1, 440	0.38	0.540	-	-	-	-	-	-	0.15	0.56	0.26
Low + SL	1, 22	4.46	0.046	1, 212	19.93	<0.001	1, 212	4.34	0.038	1, 212	7.10	0.008	1, 212	7.01	0.009	0.18	0.57	0.43
High + SL	1, 22	0.07	0.789	1, 294	42.63	<0.001	1, 294	1.38	0.241	-	-	-	-	-	-	0.04	0.64	0.27

were (see Section 2.1): fire severity (UM, LM and HM), salvage-logging after low-severity fire (LM and SLM) and salvage-logging after highseverity fire (HM and SHM). For the Rff and CH4 fluxes, we modelled the data from every year between 2019 and 2022, using site and time since fire as fixed effects. Soil temperature at 5 cm depth (Tsoil) was included as a covariate in the R_{ff} models due to the strong relationship between T_{soil} and R_{ff}, whilst SWC was included as a covariate in the CH₄ models because of its strong relationship with CH₄ fluxes. We did not include both soil temperature and SWC in the same model to avoid issues of collinearity due to the strong correlation between these two factors. We included soil temperature and SWC as covariates in the models since they are key drivers of the soil fluxes (Davidson and Janssens, 2006; Smith et al., 2000). This also enabled testing for significant differences in the fluxes between sites at a specific SWC or soil temperature. All the fixed effects were centered at their mean value. Collar ID nested within site was included as a random effect to account for the multiple measurements per collar. Interactions between soil temperature or SWC and site or time since fire were only included in the models if significant. Rff data were log-transformed to ensure a normal distribution; this was not necessary for the CH₄ data. We included a

variance structure (VarIdent, described in Zuur et al., 2009) with site as the covariate in the models to account for the different variances in model residuals between sites. The model residuals met assumptions of equal variance and normal distribution. We followed the same steps in a separate analysis to model the $R_{\rm ff}$ and CH_4 fluxes at SLM, to assess whether the ridges and furrows created by the soil scarification had significantly different fluxes.

ANOVAs, followed by Tukey's post-hoc tests, were conducted on the models to establish whether there were significant differences in the fluxes between sites within each group and over time since the fire. All the mixed-effects model analysis was performed in R using the nlme package (Pinheiro et al., 2023). Model fit was described using marginal R^2 (R^2_{marg} , the variance explained by the fixed effects), conditional R^2 (R^2_{con} , the variance explained by the fixed and random effects) and root mean square error (RMSE) expressed in the units of the response variable. R^2_{marg} and R^2_{con} were calculated using the performance package (Lüdecke et al., 2021) based on Nakagawa and Schielzeth (2013).

When presenting the R_{ff} data, we show both R_{ff} and R_{ff} normalized ($R_{ff,norm}$) to 15 $^{\circ}C$ soil temperature and 10 % SWC, to eliminate the effects of variations in weather conditions during each sampling round.

The 15 °C value was chosen because it is close to the mean soil temperature across all measurements (16 °C) and has been used as a reference temperature previously (e.g., Lasslop et al., 2010) whilst the 10 % SWC is the mean SWC across all measurements. The $R_{\rm ff}$ normalization was based on a model from Carey et al. (2016) shown in the following equation:

$$\log (R_{\rm ff}) = a + bT_{\rm soil} + cT_{\rm soil}^2 + dSWC \tag{1}$$

 T_{soil} and SWC were from the manual measurements taken at the same time as the soil flux data, whilst a, b, c and d were fitted coefficients. Each site was modelled separately. Model R^2 for the soil respiration models was between 0.26 and 0.47. We did not normalize the CH_4 fluxes because the data were not well represented by any model.

2.3. Soil sampling and chemical analysis

Soils were sampled at all sites once per year at the start of the growing season (May or June) from 2019 to 2022. The entire forest floor layer, which includes the charred organic layer (when present), the soil uncharred organic layer, and any litter, mosses or lichens present was collected as a single sample within a 20 cm \times 20 cm square every 2 m along two 20 m-long transects within a few meters of the soil flux collars. In the centre of the 20 cm \times 20 cm square, a sample of the top 0–2 cm of the mineral layer was also collected. We sampled at different locations every year. The 20 samples of the forest floor layer were pooled to create four composite samples per site, and the same process was repeated for the mineral soil samples (see Kelly et al., 2021 for details). The forest floor and mineral soil composite samples were analysed for total content of carbon (C) and nitrogen (N) as well as C:N ratio: total concentrations of phosphorus (P), water-soluble C, phosphorus (P), ammonium (NH₄⁺), nitrate (NO₃) and bioavailable P (Melich P); effective cation exchange capacity (ECEC); electrical conductivity (EC) and pH. The protocols for the sample preparation and chemical analysis are described in Kelly et al. (2021). The total C and N content were determined using a total elemental analyser which provides the results as a percentage (i.e. proportion of sample mass that is C or N). No carbonates were present in the lithology of the study area, and no substantial amount of carbonates were found in the charred forest floor in the months following the fire (data not shown), so all soil carbon was assumed to be organic. Due to the small sample size per site and year, we did not perform any statistical tests on these data.

2.4. Microclimate

At UM, LM and SLM, soil temperature and soil moisture were monitored continuously during the whole study period with Campbell Scientific CS655 sensors (6 at each site, installed at 7.5 and 15 cm depth). Soil temperature probes also provided a shallow continuous measurement (3 cm, 7.5 cm, 15 cm depth, 107 Thermistors, Campbell Scientific, Inc.). At SLM, furrows of exposed mineral soil and ridges of intact burnt organic layer were monitored separately. Air temperature was measured at UM, LM and SLM using HygroVUE10 sensors (Campbell Scientific, Inc.) installed at 2 m height.

In addition, two TOMST TMS-4 loggers were installed at all sites (one at each end of the soil flux collar transect) to capture time series of soil temperature (7.5 cm depth), near-surface air temperatures (1.5 cm and 14 cm above the soil surface) and soil water content (2–13.5 cm depth). At SLM, four loggers were installed, two in the furrows and two in the ridges. The loggers were installed after soil thaw at the start of the 2022 growing season. The manufacture-provided sun shields were used above the 1.5 and 14 cm air temperature sensors. The loggers recorded data every 10 min.

To convert the raw soil moisture data from the TMS4-loggers to SWC, we calibrated the sensors by fitting a linear regression (R^2 between 0.48 and 0.81) against the CS655 sensor data at UM, LM and SLM. The TMS-4

data from HM and SHM were calibrated using the LM calibration curve because no CS655 sensors were installed at these sites. We only present the data from the TOMST TMS-4 loggers from 2022 in the main text because this is the only sensor and year from which we have data for all the sites. The longer-term data of air temperature, soil temperature and SWC from UM, LM and SLM are shown in Fig. S3.

2.5. Vegetation recovery

We surveyed the coverage of the understory vegetation at the burnt sites yearly in July 2020–2022 (unburnt site only in 2021–2022). Within a 25 cm \times 25 cm quadrat, the proportional cover of each vascular plant species and of all bryophytes was visually estimated following Delin (2021). We surveyed 12 quadrats per site along two transects of the same length, a few meters away from the soil flux collar transects. To estimate the total understory vegetation cover within the quadrat, we summed the cover from all vascular species and bryophytes in each quadrat.

To test for significant differences in proportional vegetation cover between the sites and over time since the fire within each site group, we modelled total vegetation cover (vascular plants and bryophytes, excluding *Pinus sylvestris* seedlings), as well as vascular plants and bryophytes separately using beta regressions (R package betareg, Cribari-Neto and Zeileis, 2010). To avoid values of 0 and 1 in beta regressions, we transformed proportional plant cover (P_{prop}) using:

$$Tprop = \left[P_{prop}(n-1) + 0.5 \right] / n \tag{2}$$

where n= the number of survey plots in the compared site group (Smithson and Verkuilen, 2006). We fitted one regression per plant and site group, using a log link function and site and year as dependent variables (their interaction was not significant). Chi-square likelihood ratio tests were then used to test for significant differences between the sites and years.

2.6. Linking the soil fluxes to the soil chemistry and understory vegetation

To further investigate the drivers of the $R_{\rm ff}$ and CH_4 fluxes, we produced a correlation matrix of the soil fluxes against the vegetation survey data (see Section 2.5) and soil chemistry variables from the forest floor layer (see Section 2.3) using spearman's rank since some variables were not normally distributed. All data were averaged on an annual scale. We pooled the data from all available sites and years to perform the correlations (2020–2022 for all sites, except UM which only had vegetation survey data from 2021 to 2022). Although this presents an issue of pseudo-replication and autocorrelation, pooling the data was the only way to have a sufficiently large sample size to analyse (n = 14; without pooling between n = 2–3 per site). We do not present p-values for this analysis and instead focus on interpreting the direction and strength of the correlations.

3. Results

3.1. Forest floor CO2 fluxes

Fire severity had a significant impact on forest floor respiration (R_{ff} , Table 2 and Fig. 3a). R_{ff} was significantly lower at HM (mean \pm SE $=1.03\pm0.04~\mu mol~m^{-2}~s^{-1}$) compared to both LM ($2.23\pm0.12~\mu mol~m^{-2}~s^{-1}$; Tukey test p<0.0001) and UM ($2.53\pm0.10~\mu mol~m^{-2}~s^{-1}; p<0.0001$) during the whole study period (Table S3). Significant differences in R_{ff} between LM and UM only appeared in the third and fourth years after fire (Tukey test p=0.03 and <0.0001, respectively), when R_{ff} was lower at LM than UM (Fig. 2a and b). As a result, there was a significant interaction between site and time since fire in the fire severity model (Table 2). R_{ff} at UM was much higher in 2022 compared to previous years. The high R_{ff} values at UM in 2022 were driven by a few

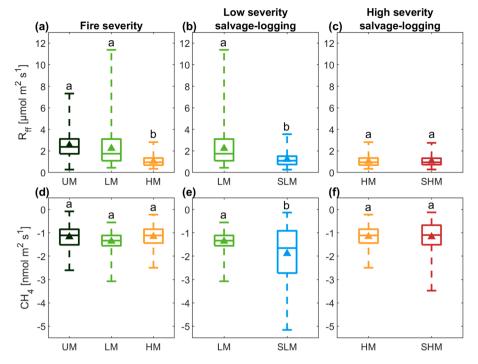


Fig. 3. Boxplots of all soil flux measurements from 2019 to 2022 (n = 152 per site), where different letters above the boxes indicate significant differences between the sites based on the ANOVA results in Tables 2 and 3 and Tukey post-hoc tests. Triangles show the mean flux and the boxplot whiskers show data minimum and maximum. (a-c) forest floor respiration ($R_{\rm ff}$) and (d-f) soil CH₄ flux. Data are divided into groups for fire severity (a, d), low-severity fire and salvage-logging (b, e) and high-severity fire and salvage-logging (c, f). Site characteristics: UM (unburnt), LM (low-severity fire, living trees left standing), HM (high-severity fire, dead trees left standing), SLM (low-severity fire, living trees salvage-logged) and SHM (high-severity fire, dead trees salvage-logged).

measurements of very high $R_{\rm ff}$ in August 2022. We could not find any fault with the measurements and therefore retained them in the analysis.

The salvage-logged, low-severity fire site (SLM) had consistently and significantly lower $R_{\rm ff}~(1.20\pm0.06~\mu{\rm mol~m}^{-2}~{\rm s}^{-1})$ than the low-severity fire site where the living trees had been left standing after the fire (LM; Figs. 3b and 2a, Table 2). There was a significant interaction between site and time since fire because the magnitude of the difference in $R_{\rm ff}$ between LM and SLM varied over time since the fire (Fig. 2a and b, Table 2). Within SLM, there was no significant difference in $R_{\rm ff}$ between collars on ridges versus furrows (ANOVA, p=0.51, Fig. S2).

After high-severity fire, salvage-logging (SHM; $1.05 \pm 0.04 \, \mu mol \, m^{-2} \, s^{-1}$) had no effect on R_{ff} compared to leaving the dead trees standing (HM; Fig. 3c; Table 2). Time since fire had a significant impact on R_{ff} at both sites: R_{ff} decreased during the first three years post-fire after which it started to increase again (Table 2, Fig. 2a).

3.2. Forest floor CH4 fluxes

All sites were CH₄ sinks during the entire study period (Fig. 2c, Table S3). The mean (\pm SE) CH₄ flux was -1.17 \pm 0.04 nmol m⁻² s⁻¹ at UM, -1.36 \pm 0.03 nmol m $^{\text{-2}}$ s $^{\text{-1}}$ at LM and -1.16 ± 0.03 nmol m $^{\text{-2}}$ s $^{\text{-1}}$ at HM, -1.89 ± 0.12 nmol m⁻² s⁻¹ at SLM and -1.17 ± 0.05 nmol m⁻² s⁻¹ at SHM. Neither fire severity nor salvage-logging after high-severity fire had a significant effect on the soil CH₄ fluxes (Fig. 3d, f, Table 3). However, after low-severity fire soil CH₄ uptake was significantly higher after salvage-logging (SLM) compared to leaving the trees standing (LM; Fig. 3e, Table 3). In the SLM/LM model, the differences in CH₄ flux between the sites varied significantly over time because CH₄ uptake was higher in 2020 than in 2021 at SLM (Table 3). At SLM, the collars located on ridges had significantly higher CH4 uptake than collars in furrows (ANOVA, p = 0.02, Fig. S2). All our CH₄ models had much higher conditional R² (which includes random and fixed effects) compared to marginal R² (only fixed effects; Table 3). This highlights the large variability in the CH₄ uptake between the collars at each site since collar ID was included as a random effect in the models.

3.2. Forest floor and mineral soil layer chemistry

In the forest floor layer, none of the nutrients showed a marked trend over time since fire (Fig. 4, Table S4). Many nutrients (bioavailable P, ECEC, water-soluble C, NH $_{+}^{+}$ C, N) showed large interannual variability within a site. Water-soluble C, water-soluble P, and EC (Fig. 4d, g, l) were notably higher at the unburnt site than at all the burnt sites. In addition, the low-severity fire site (LM) had higher water-soluble C, water-soluble P and EC compared to the high-severity burnt site (HM). For both salvage-logging groups (LM vs SLM and HM vs SHM), the salvage-logged site tended to have lower concentrations of water-soluble C and P and lower EC than at the unlogged site. The mineral soil layer had a similar chemical composition at all sites and over time after the fire (Fig. S4, Table S4). At all the sites, the concentration of all the nutrients except NO $_{3}$ and bioavailable P were markedly lower in the mineral soil layer than in the organic soil layer (Figs. 4, S4).

3.3. Microclimate

All sites had almost identical air temperatures at 14 cm above the soil surface (Fig. S5) with small differences appearing in mean daily air temperature at 1.5 cm (Fig. S5) and the largest differences between the sites in the soil temperature at 7.5 cm depth (Fig. 5a). These findings are echoed in the longer-term air temperature and soil temperature data from UM, LM and SLM shown in Figure S3.

Within the fire severity group (UM, LM and HM), HM experienced the largest range of soil temperatures, with maximum temperature exceeding that of the LM and UM sites by 3 $^{\circ}$ C (Fig. 5b). In spring 2022, the soil thawed at least two weeks earlier at the two burnt sites (HM and LM) than at the unburnt site (UM; Fig. 5a). During the peak growing season in July, the daily mean soil temperature was on average 2.3 $^{\circ}$ C higher at HM than at UM, and 0.6 $^{\circ}$ C higher at LM compared to UM. The

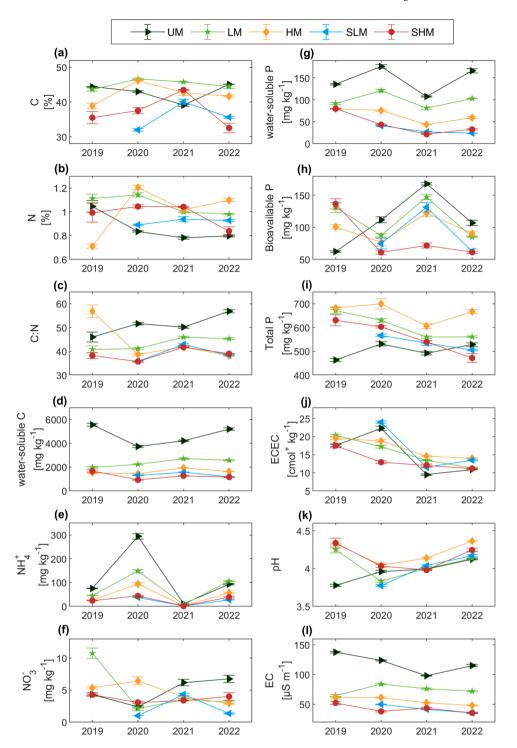


Fig. 4. Time series of mean (\pm SE) soil nutrient content in the forest floor layer at all sites in 2019–2022 (n = 4 per site and year), see Fig. S4 for the mineral layer results and Table S4 for the numerical data. Site characteristics: UM (unburnt), LM (low-severity fire, living trees left standing), HM (high-severity fire, dead trees left standing), SLM (low-severity fire, living trees salvage-logged) and SHM (high-severity fire, dead trees salvage-logged).

high-severity fire site had consistently lower soil moisture (SWC) than the low-severity and unburnt sites although the differences were very small (mean \pm SE of SWC at HM 5.4 \pm 0.01 % compared to 6.8 \pm 0.01 % at LM and 6.7 \pm 0.01 % at UM; Fig. 5c, and d and Table S5).

In both salvage-logging groups (LM vs SLM and HM vs SHM), the salvage-logged site experienced a larger range of soil temperatures than the unlogged site (Figs. 5b). The difference was especially pronounced at SLM, where the maximum temperature reached was 25.9 °C compared to 17.5 °C at LM. SHM reached 22.6 °C compared to 20.4 °C at HM.

Throughout the growing season, daily mean soil temperatures were higher at the salvage-logged than at the unlogged sites in both groups (Fig. 5a). SLM had much higher mean SWC than LM (22.2 \pm 0.01 % compared to 6.8 \pm 0.01 %; Fig. 5d and Table S5). In the high-severity group, the salvage-logged site had consistently lower daily mean SWC than the unlogged site, although the difference in average SWC was small (SHM mean = 3.1 \pm 0.01 %, HM mean = 5.4 \pm 0.01 %; Fig. 5c, d and Table S5).

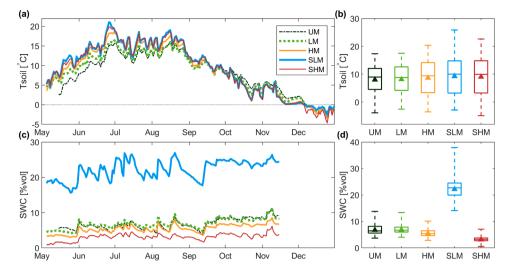


Fig. 5. (a) Daily mean soil temperature at 7.5 cm depth for all sites, (d) boxplot of all soil temperature measurements for all sites, (c) daily mean soil water content (SWC; when soil was not frozen) integrated over 2–13.5 cm depth for all sites, (d) boxplot of all SWC measurements for all sites. All data are from 2022 from TOMST TMS-4 sensors (two sensors per site except SLM which had four sensors). In the boxplots, triangles show the mean and whiskers show the data minimum and maximum. Site characteristics: UM (unburnt), LM (low-severity fire, living trees left standing), HM (high-severity fire, dead trees left standing), SLM (low-severity fire, living trees salvage-logged) and SHM (high-severity fire, dead trees salvage-logged).

3.4. Vegetation recovery

UM was not included in the statistical analysis of the fire severity group because there were fewer years of data available at UM, but for reference it is plotted in Fig. 6. Total vegetation cover, and in particular bryophyte cover, increased at UM between 2021 and 2022 (Fig. 6d, f). The large variability in vegetation cover between the two years at UM suggests that the variation over time in vegetation at the other sites may be partly due to factors other than the fire or post-fire management. Such factors could include the patchiness of the vegetation and differences in moisture availability (e.g., wet conditions proceeding the vegetation survey in 2022 may have made the bryophytes appear larger since they were full of water whereas in 2021 conditions were much

drier). The latter may explain why vegetation cover at SLM followed similar temporal trends as at UM, since SLM had the highest bryophyte cover of any of the burnt sites (Fig. 6d–f). However, the differences in mean total, vascular or bryophyte cover between the sites in each group were persistent across the years (Table S6).

Within the fire severity group (LM vs HM), LM had significantly higher total and vascular vegetation cover than HM (Fig. 6a, b, d, e, Table 4 and Table S6). LM was the burnt site with the highest total vegetation cover in 2022 ($26 \pm 6.8 \%$, Table S6). For the salvage-logging after low-severity fire group (LM vs SLM), there was no significant difference in total cover between the two sites because SLM had significantly lower vascular cover, but also significantly higher bryophyte cover than LM (Fig. 6a, b, c, Table 4). After high-severity fire and

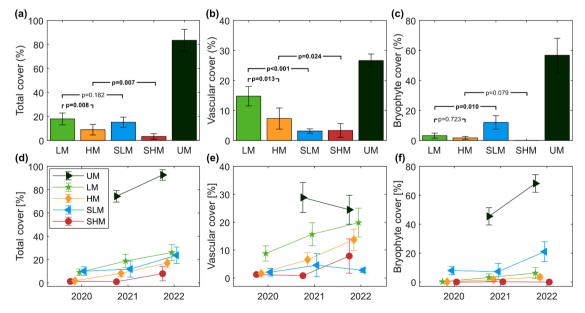


Fig. 6. Mean \pm SE of measurements from 2020–2022 combined (n = 36; UM only 2021–2022, n = 24) of (a) total vegetation cover, (b) vascular cover and (c) bryophyte cover in the understory. SHM mean and SE of bryophyte cover were <1 % and are not visible on the plot. *P*-values show results of chi-square tests for significant differences between sites within each group (LM vs HM, LM vs SLM, and HM vs SHM; Table 4). (d–f) annual mean \pm SE of measured total vegetation, vascular or bryophyte cover, respectively. Site characteristics: UM (unburnt), LM (low-severity fire, living trees left standing), HM (high-severity fire, dead trees left standing), SLM (low-severity fire, living trees salvage-logged) and SHM (high-severity fire, dead trees salvage-logged).

Table 4

Results of Chi-squared tests on the beta regressions of the total, vascular and bryophyte understory vegetation cover. Low + SL is low-severity fire followed by salvage-logging, High + SL is high-severity fire followed by salvage-logging. Note that the UM site was not included in the fire severity group because it had fewer years of data than the HM and LM sites. Statistically significant effects are marked in bold (p < 0.05).

Group	Site		Time		Model Fit		
	Chi-sq	p	Chi-sq	p	Pseudo R ²		
Total vegetation of	cover						
Fire severity	7.06	0.008	11.03	0.004	0.30		
Low + SL	1.78	0.182	7.58	0.023	0.17		
High + SL	7.30	0.007	6.30	0.043	0.26		
Vascular plants							
Fire severity	6.23	0.013	6.13	0.047	0.22		
Low + SL	18.85	< 0.001	2.13	0.345	0.37		
High + SL	5.10	0.024	4.36	0.113	0.21		
Bryophyte cover							
Fire severity	0.13	0.723	3.01	0.222	0.11		
Low + SL 6.68		0.010	5.67	0.059	0.28		
$High + SL \qquad \qquad 3.08 \qquad \qquad 0.$		0.079	1.81	0.405	0.14		

salvage-logging, the SHM site had the lowest total vegetation cover of all burnt sites (8 \pm 6.2 % in 2022) and significantly lower total and vascular vegetation cover than HM (Fig. 6a, b, Table 4 and Table S6). Total vegetation cover increased significantly between 2020 and 2022 for all 3 groups (Fig. 6d, Table 4). Only the fire severity group showed a significant increase in vascular cover over time and none of the groups had significant changes in bryophyte cover over time (Table 4, Fig. S6).

3.5. Relationships between the soil carbon fluxes, soil chemistry and understory vegetation

 $R_{\rm ff}$ was strongly (>0.6) positively correlated with vascular and total vegetation cover as well as soil NH_4^+ and water-soluble P concentrations

(Fig. 7). The soil CH₄ fluxes were not strongly correlated with any variable we tested. Vascular and total vegetation cover had strong positive correlations with water-soluble C while bryophyte cover was strongly but negatively related to soil N content. There were also strong, often positive, correlations between several of the soil chemistry variables relating to C and P concentrations and EC.

4. Discussion

4.1. Effects of fire severity on forest floor CO2 fluxes

We expected to see significant reductions in $R_{\rm ff}$ in the first years after both low- and high-severity fire (H1), yet we only observed significantly lower $R_{\rm ff}$ after high-severity fire. Our high-severity fire results are supported by other work in the European boreal forest, showing that soil respiration after high-severity fire was only 50 % or less of that measured in unburnt stands 1–21 years after fire (Ludwig et al., 2018; Parro et al., 2019). In their meta-analysis, Gui et al. (2023) also found a stronger and longer-lasting decrease in soil respiration after high-severity fire compared to low-severity fire in boreal forests globally.

It is surprising that $R_{\rm ff}$ remained so high for the first two years after the low-severity fire. After low- to moderate-severity fires across Sweden, microbial biomass decreased on average by 24 % in the first year post-fire compared to unburnt stands (Eckdahl et al., 2023). Indeed, laboratory measurements of soil samples taken from our sites in 2020 (two years post-fire) confirmed these findings, showing significantly lower heterotrophic respiration at both HM and LM compared to UM (Soares et al., in review). In addition, all the burnt sites had lower concentrations of water-soluble C (i.e. labile C) than the unburnt site in the four years since the fire and water-soluble C concentration was positively correlated to $R_{\rm ff}$ (Fig. 7). This suggests that the reduced availability of substrates for microbial activity at the burnt sites would have reduced their $R_{\rm ff}$. Furthermore, burnt soil organic matter is more

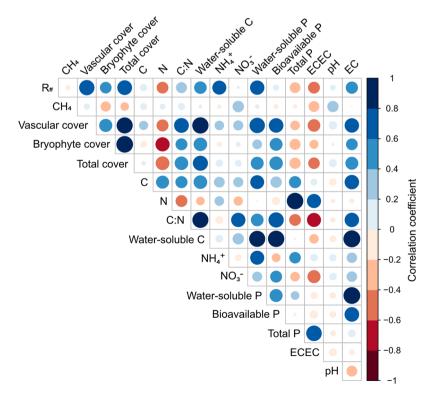


Fig. 7. Spearman's correlation coefficients of soil carbon fluxes ($R_{\rm fb}$, CH_4), vegetation cover and soil chemistry (from the forest floor layer), using annually averaged variables for all available years (2020–2022 for all sites except UM, 2021–2022) and all sites (n = 14). The size of the circles is proportional to the absolute value of the correlations.

resistant to decomposition, which should also have reduced $R_{\rm ff}$ at both HM and LM compared to UM (Pellegrini, 2022).

We hence conclude that the different behaviour of $R_{\rm ff}$ after high and low-severity fire at our sites likely results from changes in autotrophic respiration. The main difference between these two sites is the continuation of tree root respiration at LM (all trees survived the fire), whereas no tree root respiration occurred at HM (all trees died). *Pinus sylvestris* can experience significant root loss even after low-severity fire due to its shallow root distribution (Smirnova et al., 2008) and measurements of tree stem increment at the LM site suggest increased allocation of carbon to the roots since the fire (Dukat et al., 2024). Hence, the high $R_{\rm ff}$ at LM could be due to increased tree root growth to repair roots damaged by the fire. Although surface fires can cause delayed tree mortality, and thus decrease autotrophic respiration over time (Ribeiro-Kumara et al., 2022), we did not observe any tree mortality at LM during the four years following the fire.

In addition, we found significantly faster recovery of the understory vegetation cover at LM compared to HM since the fire (Fig. 6d) and total vegetation cover was strongly positively associated with $R_{\rm ff}$ (Fig. 7). This would have further contributed to increasing $R_{\rm ff}$ at LM compared to HM. Similarly, Singh et al. (2008) found that post-fire $R_{\rm ff}$ in boreal forests is strongly correlated with root biomass, emphasizing the importance of vegetation regrowth and autotrophic respiration in driving post-fire $R_{\rm ff}$. Furthermore, vascular cover was also very strongly and positively associated with water-soluble C concentration, indicating that the regrowth of vascular vegetation after fire was important for increasing the availability of root substrates which would have contributed to the heterotrophic component of $R_{\rm ff}$.

There are several factors that could help explain why Rff declined in the third and fourth years after low-severity fire compared to the unburnt site. August 2022 was especially rainy compared to previous years (see Fig. 2 in Dukat et al. (2024)), and the relatively moist soil conditions may have favoured vegetation growth and microbial activity at the unburnt site, resulting in very high average respiration at that site in 2022. Due to the negative effect of the fire on microbial biomass, substrate availability and understory vegetation cover at LM, soil respiration may not have responded as strongly to the favourable weather conditions and thus remained low compared to UM in 2022. In addition, tree growth was found to be more variable, and in some cases lower, at the LM site than at the UM site in the first four years after the fire (Dukat et al., 2024). Changes in carbon allocation and the availability of root exudates over time would have affected autotrophic respiration and may partly explain why the R_{ff} fluxes at LM showed large interannual variations. Fire can also introduce a nutrient pulse into soils (Bodí et al., 2014; Certini, 2005), which could have affected the Rff at LM. However, our soil chemistry data does not support this hypothesis because it does not show signs of a nutrient pulse or substantial declines in nutrient availability over time at the burnt sites.

4.2. Effects of salvage-logging after low-severity fire on forest floor CO_2 fluxes

The $R_{\rm ff}$ was significantly lower at the site where trees that survived a low-severity fire were salvage-logged (SLM) compared to a site where the living trees were left standing, thus confirming part of H2 (LM; Figs. 2a and 3b). The removal of the living trees stopped tree root respiration, a key component of soil respiration as discussed above, and therefore led to reduced $R_{\rm ff}$ at SLM compared to LM. Our results contrast with those of Kulmala et al. (2014) who observed increases in $R_{\rm ff}$ after a boreal forest clear-cut without fire, which they attributed to the higher soil temperatures and soil moisture caused by the clear-cut. Despite 8 °C higher maximum soil temperature and higher soil moisture availability at SLM compared to LM, and the significant effect of soil temperature on $R_{\rm ff}$ (Table 2), this did not result in higher $R_{\rm ff}$ at SLM than LM in our study. Our results thus highlight the negative effect of the fire and salvage-logging on $R_{\rm ff}$ which was not temperature-limited but was

instead limited by reduced autotrophic respiration, microbial biomass and substrate availability.

The scarification of the soil at SLM likely also reduced R_{ff}. When separating our Rff measurements between collars placed on areas with a remnant forest floor layer and areas where the mineral soil was exposed (Fig. S2), we found that areas with mineral soil had on average 12 % lower Rff, although the difference was not statistically significant. The furrows with exposed mineral soil had low water-soluble C availability (229 mg kg⁻¹ concentration in the mineral layer compared to 1352 mg kg-1 concentration in the forest floor layer at SLM; Figs. 4d and S4d), which would have impeded microbial activity. Similarly, in studies of the effects of soil preparation on boreal forest soil respiration, Pumpanen et al. (2004) and Strömgren and Mjöfors (2012) measured the lowest soil respiration in plots where bare mineral soil was exposed, which they attributed to the low organic matter content. In addition, the soil scarification likely enabled the establishment of Polytrichum spp. at SLM (the main bryophyte genus we observed at the site), by removing the organic soil layer and reducing competition from other vegetation (Bergstedt et al., 2008). As a result, bryophyte cover was significantly higher at SLM than LM (Fig. 6c).

It is important to note that although the salvage-logging of the living trees and soil scarification at SLM reduced $R_{\rm ff}$ after the fire compared to leaving the trees standing, SLM remained a net carbon source at the ecosystem level. An eddy covariance flux tower installed at SLM showed that the site emitted an average of 173 g C m⁻² per growing season during the first four growing seasons since the fire (Kelly et al., 2024). In comparison, the living trees that were left standing at LM were able to continue sequestering carbon at a rate of between 63 and 228 g C m⁻² yr⁻¹, despite reduced stem growth after the fire (Dukat, 2024).

4.3. Effects of salvage-logging after high-severity fire on forest floor ${\rm CO_2}$ fluxes

There were no significant differences in $R_{\rm ff}$ between the logged (SHM) and unlogged (HM) high-severity fire sites, thus confirming the 2nd part of H2 (Figs. 2a and 3c). Salvage-logging of dead trees therefore appears not to have any additional impact on $R_{\rm ff}$ compared to leaving the dead trees standing, and this did not change over the first four years since the fire. Although salvage-logging did lead to warmer soil, this did not affect the $R_{\rm ff}$. This could be due to the lack of substrates available for heterotrophic respiration at both sites (as discussed in Section 4.2). The similar $R_{\rm ff}$ at both sites could also reflect the balance between SHM having warmer soils (which would increase $R_{\rm ff}$) but significantly lower understory vascular vegetation regrowth (which would limit $R_{\rm ff}$), whereas HM had cooler soils but higher vascular vegetation regrowth.

R_{ff} at both sites declined significantly during the first 3 years after the fire. We assume that this was due to a decline in heterotrophic respiration, since autotrophic respiration could only have increased after the fire as vegetation recolonized both sites (Fig. 6d-f). The reduction in heterotrophic respiration over time could result from decreased substrate availability for microbial decomposition as any labile C and easily decomposable fine roots from the dead trees would have been decomposed rapidly after the fire (Berg and McClaugherty, 2020). In addition, fire transforms soil organic matter in multiple ways that make it harder to degrade after fire (Pellegrini et al., 2022).

4.4. No recovery of forest floor CO2 fluxes four years after fire

By the fourth year after the fire, $R_{\rm ff}$ and total understory vegetation cover were still substantially lower at all the burnt sites compared to the unburnt site. These differences were largest after high-severity fire and/or salvage-logging. None of the site groups we tested showed positive trends in $R_{\rm ff}$ over time since the fire, which contrasts with our original expectation in H3 that $R_{\rm ff}$ at the sites would start returning to pre-fire levels (like those at UM) over the four years since the fire. Our observations instead indicate that it may take many more years until $R_{\rm ff}$

recovers to pre-fire levels. Parro et al. (2019) found no significant difference in $R_{\rm ff}$ between 5 or 21 years after fire in Estonian *Pinus sylvestris* forests on sandy soils similar to our sites, and suggest that two decades may not provide sufficient time for $R_{\rm ff}$ to recover in such low fertility sites. Similarly, in their review of boreal forest $R_{\rm ff}$ fluxes after fire, Ribeiro-Kumara et al. (2020) found that it took between 10 and 30 years for $R_{\rm ff}$ to recover after fire. Since we have shown that tree respiration is such an important driver of $R_{\rm ff}$, the recovery time of $R_{\rm ff}$ will likely be tightly coupled to the time it takes for trees to regrow or recover from fire-related injuries, which in turn is linked to how the sites were managed after the fire (salvage-logged versus unlogged, planted seed-lings or seeds sown).

4.5. Effects of fire and salvage-logging on forest floor CH₄ fluxes

The soils at all our sites were CH₄ sinks (Fig. 2c), consuming CH₄ at a similar rate as reported for other Eurasian boreal forest fire sites (-1.1 to -1.3 nmol CH₄ m⁻² s⁻¹ in the first 5 years after fire; Köster et al., 2015, 2018). We did not find any effects of fire severity or salvage-logging after high-severity fire on the soil CH₄ fluxes in the first four years after the fire (Fig. 3d, f). Our results confirm previous findings by Kelly et al. (2021) who reasoned that the fire did not affect the mineral soil where most CH₄ consumption occurs, and hence did not impact the CH₄ fluxes. Similarly, Ribeiro-Kumara et al. (2020) found that fire had negligible effects on boreal forest soil CH₄ fluxes. Our results partly confirm H4.

On the other hand, there was significantly higher CH₄ uptake at the salvage-logged low-severity fire site (SLM) than at the unlogged low-severity fire site, which we did not expect (LM; Fig. 3e). Although SLM had the highest SWC of all our sites (Fig. 5d) and a finer-textured soil (Table 1) than the other sites, it also had the highest CH₄ uptake, which contrasts with previous findings that increasing SWC and decreasing soil particle size limit CH₄ diffusion into soil and therefore reduce CH₄ uptake (Ball et al., 1997; Smith et al., 2000). Köster et al. (2024) found that CH₄ uptake increased with increasing soil temperature in boreal forest soils after wildfire which could explain why CH₄ uptake was higher at SLM since it experienced much higher soil temperatures compared to LM as a result of the salvage-logging.

Although CH_4 uptake decreased significantly between 2020 and 2021 at SLM, this change was not related to changes in soil moisture or temperature conditions because they were similar in both years (not shown). In addition, because there were only weak correlations between CH_4 flux and all the soil chemistry variables, we cannot attribute the change in CH_4 uptake to changes in soil nutrient concentrations. We have not been able to identify the cause of the changes in the CH_4 fluxes over time at the SLM site.

The soil scarification at SLM led to significant variability in CH₄ uptake within the site, with higher uptake from the ridges of remaining organic soil than from the furrows with exposed mineral soil (Fig. S2). Our observations agree with findings from CH₄ measurements in agricultural soils which show that no-till soils can have significantly higher CH₄ uptake than tilled soils (Prajapati and Jacinthe, 2014). Tilling destroys the soil structure and reduces soil gas diffusivity, and thus limits CH₄ uptake. The same process likely also occurred during the soil scarification, reducing CH₄ uptake in the furrows.

4.6. Limitations

Our study is based on an opportunistic design as we could not control nor influence the wildfire or the post-fire forest management treatments. The wildfire burnt the study sites at different severities and the private owners of those sites independently decided which post-fire management approach to follow. Despite the inherent limitations of such a design, it did offer a unique opportunity as the UM, LM, HM, and SHM sites were all comparable and within less within less than 1000 m of each other. However, it was not possible to analyse the interaction

between fire severity and salvage-logging because the SHM and SLM sites were treated differently after they were salvage-logged (i.e. pine seedlings planted at SHM versus soil scarification and spreading of pine seeds at SLM). We also did not have an unburnt clear-cut site that would have made a full factorial design and allowed us to separate the effects of the salvage-logging and the fire. Future work at other sites should investigate these effects, their interaction and if possible compare burnt sites with and without soil scarification to better distinguish between the effects of the fire and post-fire treatment of the soil on the forest recovery.

The SLM site was located 3 km away from the other sites on loamy soil which increased the SWC at that site compared to all the others which were on sandy soils. In addition, furrows with exposed mineral soil at SLM retained more water and thus had higher SWC (not shown) than all other sites where the organic layer remained. Although these conditions impaired the comparison between SLM and LM slightly, our analysis of the $R_{\rm ff}$ data and vegetation cover still shows a significant impact of salvage-logging of living trees at SLM.

5. Conclusions

Forest floor respiration at our burnt *Pinus sylvestris* stands in central Sweden did not show any signs of recovery during the first four years post-fire. As forest floor respiration is tightly coupled to tree root activity, it is likely to take many more years before it reaches the levels observed at an unburnt control stand. Our results highlight that autotrophic respiration, in particular from tree roots, is the key driver forest floor respiration after fire (and salvage-logging). The effect of salvagelogging on forest floor respiration therefore depends on whether or not the trees survived the fire: if living trees are salvage-logged, this leads to a significant decline in forest floor respiration whereas if dead trees are salvage-logged, there is no further impact on the forest floor respiration. We also found that site preparation by scarification of the soil results in substantial differences in forest floor respiration and CH4 uptake because it disturbs the soil structure and removes organic material. Across our burnt sites, forest floor respiration was likely limited by reduced microbial biomass and substrate availability and therefore did not respond to increased post-fire or salvage-logging soil temperatures or to increased moisture availability during wetter periods. However, the soil methane sink we observed at all sites was not affected by the fire, confirming similar previous findings.

Although the reduction of forest floor CO_2 emissions by fire and/or salvage-logging may appear to be good news in the context of climate change, it is important to note that our measurements represent only part of the total ecosystem carbon balance. Fire and/or salvage-logging that cause tree mortality remove the main carbon sink from the forest ecosystem and thus turn these areas into carbon sources. Our results highlight the significant and persistent changes to forest floor carbon fluxes due to fire and choice of post-fire management strategy. Future work is needed to investigate the interaction effect between fire severity and salvage-logging and to more closely examine the effects of different site preparation methods on post-fire soil carbon fluxes and vegetation recovery in the boreal context.

Data availability

Data is available on Zenodo, doi:10.5281/zenodo.14833538.

CRediT authorship contribution statement

Julia Kelly: Writing – review & editing, Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis, Conceptualization. Stefan H. Doerr: Writing – review & editing, Investigation, Funding acquisition. Johan Ekroos: Writing – review & editing, Funding acquisition, Formal analysis. Theresa S. Ibáñez: Writing – review & editing, Investigation. Md. Rafikul Islam: Writing –

review & editing, Investigation. **Cristina Santín:** Writing – review & editing, Investigation, Funding acquisition. **Margarida Soares:** Writing – review & editing. **Natascha Kljun:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2025.110454.

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