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Boreal forest soil carbon fluxes one year after a wildfire: Effects of burn severity and management

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Abstract

The extreme 2018 hot drought that affected central and northern Europe led to the worst wildfire season in Sweden in over a century. The Ljusdal fire complex, the largest area burnt that year (8995 ha), offered a rare opportunity to quantify the combined impacts of wildfire and post-fire management on Scandinavian boreal forests. We present chamber measurements of soil CO_2 and CH_4 fluxes, soil microclimate and nutrient content from five *Pinus sylvestris* sites for the first growing season after the fire. We analysed the effects of three factors on forest soils: burn severity, salvage-logging and stand age. None of these caused significant differences in soil CH_4 uptake. Soil respiration, however, declined significantly after a high-severity fire (complete tree mortality) but not after a low-severity fire (no tree mortality), despite substantial losses of the organic layer. Tree root respiration is thus key in determining post-fire soil CO_2 emissions and may benefit, along with heterotrophic respiration, from the nutrient pulse after a low-severity fire. Salvage-logging after a high-severity fire had no significant effects on soil carbon fluxes, microclimate or nutrient content compared with leaving the dead trees standing, although differences are expected to emerge in the long term. In contrast, the impact of stand age was substantial: a young burnt stand experienced more extreme microclimate, lower soil nutrient supply and significantly lower soil respiration than a mature burnt stand, due to a thinner organic layer and the decade-long effects of a previous clear-cut and soil scarification. Disturbance history and burn severity are, therefore, important factors for predicting changes in the boreal forest carbon sink after wildfires. The presented short-term effects and ongoing monitoring will provide essential information for sustainable management strategies in response to the increasing risk of wildfire.

KEYWORDS
2018 drought, boreal forest, carbon fluxes, climate change, compound disturbance, forest fire, forest floor, harvesting, salvage-logging

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1 | INTRODUCTION

Wildfire is the main natural disturbance in boreal forests, and it influences the structure, diversity and carbon and energy balance of these ecosystems (Bond-Lamberty et al., 2007; De Groot et al., 2013; Zackrisson, 1977). The boreal region is a globally important store of carbon, accounting for approximately 20% of the carbon in terrestrial ecosystems, most of which is stored underground in organic soils (Bradshaw & Warkentin, 2015; IPCC, 2013). Wildfire directly impacts carbon stocks by consuming vegetation and soil organic matter (SOM; Bond-Lamberty et al., 2007; Walker et al., 2018). It also changes the abiotic environment (e.g. soil temperature and moisture availability) and the quantity and quality of available soil nutrients and organic matter (Certini, 2005; Santín et al., 2016). All of these fire-induced changes affect soil microbial activity and plant growth, which in turn control the exchange of carbon between the ecosystem and the atmosphere. As a result, the fluxes of two major greenhouse gases, carbon dioxide (CO_2) and methane (CH_4), are altered in the months to years following fire, which affects the ability of a forest to act as a greenhouse gas sink. To understand the mechanisms driving post-fire greenhouse gas exchange, it is crucial to measure soil microclimate, nutrient availability and greenhouse gas fluxes in situ after a fire.

There are several factors that influence the specific impacts of wildfire on forest ecosystems, including burn severity, pre- and post-fire forest management practices such as salvage-logging and stand age. Burn severity, which is related to the amount of vegetation and/or SOM consumed by fire (Keeley, 2009), affects the magnitude of the changes in soil carbon fluxes, microclimate and nutrient availability after fire. Autotrophic respiration declines with increasing burn severity due to increasing vegetation mortality and consequent reductions in root biomass and respiration (Hu et al., 2017). Heterotrophic respiration also declines with increasing burn severity due to larger losses of microbial biomass (Dooley & Treseder, 2012). Some microbial taxa are particularly vulnerable to high-severity fire because tree mortality stops the input of labile carbon to microbial communities via tree roots (Day et al., 2019; Pérez-Izquierdo et al., 2020). Soil temperature can increase after fire, especially after a high-severity fire, due to the removal of canopy shading, reductions in organic layer thickness and decreased surface albedo (Certini, 2005). Although higher soil temperatures generally stimulate decomposition, as a result of reductions in vegetation and microbial biomass, post-fire soil CO_2 fluxes may not respond to increases in soil temperature in the same way as unburnt soil (Allison et al., 2010; Waldrop & Harden, 2008). Little work has assessed the effect of burn severity on soil CH_4 fluxes in boreal regions, but Morishita et al. (2015) suggested that increased CH_4 uptake after a high-severity fire (compared with a low-severity fire) was due to higher soil temperatures.

In terms of soil nutrient availability, changes in the composition of SOM depend on the temperature reached in the soil and heating duration during a fire. The increasing loss of SOM at higher burn severities can reduce microbial activity and soil CO_2 fluxes (Ludwig et al., 2018; Santín et al., 2016). On the other hand, high combustion temperatures can increase bioavailable forms of nitrogen and phosphorus after fire, which can stimulate microbial activity and plant growth (Certini, 2005; Högberg et al., 2001; Lagerström et al., 2009).

Salvage-logging is a common management practice in many regions with commercial forestry and has recently emerged as the prevailing method after wildfires in Sweden. Harvesting stands affected by a disturbance allows for the retrieval of useable wood (if any) and replanting, increases safety and can reduce the risk of beetle or fungal attack or fire. However, salvage-logging is controversial because it can negatively impact many aspects of forest ecology (Lindenmayer et al., 2004). For example, dead trees and burnt wood can provide an important source of nutrients that are lost when trees are removed from a site (Marañón-Jiménez et al., 2013). In addition, salvage-logging has been shown to increase soil temperature and reduce soil moisture availability, which may make conditions less favourable for seedling establishment (Marcolin et al., 2019). Despite the prevalence of this management practice, there have been few assessments of the impact of salvage-logging on post-fire soil carbon fluxes. In the hemi-boreal pine forests of Estonia, Parro et al. (2019) found no effect of salvage-logging on soil CO_2 emission measured 5–21 years after wildfire. To our knowledge, the impact of salvage-logging on boreal soil CH_4 fluxes has not yet been quantified.

Another key factor determining the influence of fire on a forest ecosystem is stand age. Young stands have smaller aboveground carbon stocks than mature stands, which limits the amount of carbon lost during fire (Dieleman et al., 2020). However, young stands may also lose a larger proportion of the soil organic layer during combustion, compared with mature stands that have had time to accumulate a thicker organic layer between disturbances (Hoy et al., 2016; Walker et al., 2019). Differences in the depth of the organic layer after a fire could lead to differences in the soil carbon fluxes and microclimate between young and mature stands because the organic layer contains substrate for heterotrophic decomposition and regulates soil temperature and moisture content (Kasischke & Johnstone, 2005). Furthermore, it is important to consider not only the direct impacts of fire but also the amount of time since a previous disturbance. In particular, soil nutrient availability may decrease for multiple decades after a disturbance such as clear-cutting or wildfire, with more negative effects for sites affected by multiple disturbances (Bowd et al., 2019). Therefore, accounting for the impacts of stand age and disturbance history is vital in regions such as Scandinavia where the majority of forests are used for commercial wood production (KSLA, 2015; LUKE, 2018).

The summer of 2018 created a unique opportunity to study the impacts of wildfire and the factors discussed above on forest soils in a Scandinavian context. Sweden experienced extremely warm and dry weather conditions, which led to the worst wildfire season in the last 140 years (SOU, 2019). Across the whole country, 25,000 ha of forest burned in 2018, which is an area 10 times larger than the national annual average between 2000 and 2017 (SOU, 2019). The largest area burnt that year was the Ljusdal fire complex (see Section 2.1 for more details). We established five sites within this area that differed in terms of burn severity, salvage-logging (salvage-logged

and unlogged) and stand maturity. In this study, we assessed the impacts of these three factors on forest soil greenhouse gas fluxes, microclimate and nutrient availability during the first growing season after the fire.

2 | METHODS

2.1 | Study area and the Ljusdal fire complex

The study area was located in central Sweden (61°56′N, 15°28′E), 220 m a.s.l. in the municipality of Ljusdal (Figure 1a). Ljusdal was one of the areas worst affected by the 2018 wildfire season, where five fires accounted for 38% of the total burnt area across the country that season (Ljusdals kommun, 2018). On July 14, lightning strikes started two forest fires on either side of the Laforsen dam (Figure 1b,c). The fires were spread by wind, causing three new areas to ignite, although two were quickly put out, leaving three main forest fires that we here call the 'Ljusdal fire complex' (Figure 1b,c). The fire complex burned 8995 ha and took 21 days to be contained. It included a range of fire severities: some areas were burnt by high-intensity crowning fire, but the majority by low- to moderate-intensity fire, affecting only surface fuels and lower branches. Surface rather than crowning fire behaviour is typical in the Eurasian boreal forest (De Groot, Cantin, et al., 2013; Sitnov & Mokhov, 2018). Due to effective fire prevention and climatic conditions during the last 200 years, the annual area of forest burnt by wildfire in Sweden has been relatively low (a few thousand hectares), making the Ljusdal fire one of the largest of the last century (Drobyshev et al., 2015; SOU, 2019).

For the present study, we established five sites in 2019 in the southern part of the Ljusdal fire complex by the Laforsen dam (Figures 1d,e and 2). The study area was located in a wide and flat valley floor, with glaciofluvial and moraine deposits underlying the soil. The dominant forest tree species was pine (*Pinus sylvestris*), with smaller areas of spruce (*Picea abies*) and birch (*Betula* sp). The forest structure in our study area – small stands of different ages – is typical for Sweden, where 48% of the productive forest is owned by private individuals (with a mean plot size of ~50 ha; Skogsstyrelsen, 2018). The mean annual air temperature and total precipitation during the climate normal period 1991–2020 were 2.7°C and 648 mm, respectively, as recorded by the nearest national monitoring station (Ytterhogdal 263 m a.s.l., 40 km northwest of the site). In 2019, when our measurements were conducted, the mean annual air temperature and total precipitation were 3.3°C and 793 mm, respectively.

2.2 | Site descriptions

The five sites were located in an area <1 km², in *Pinus sylvestris* stands on poor, sandy soils (Figures 1d,e and 2; Table 1). To assess the impact of burn severity, we compared three sites: an area burnt by a high-severity fire (HM), another burnt by a low-severity fire (LM) and an unburnt site (UM). Burn severity was classified as either 100% tree mortality (high severity; scorching of tree canopies) or nearly 100%
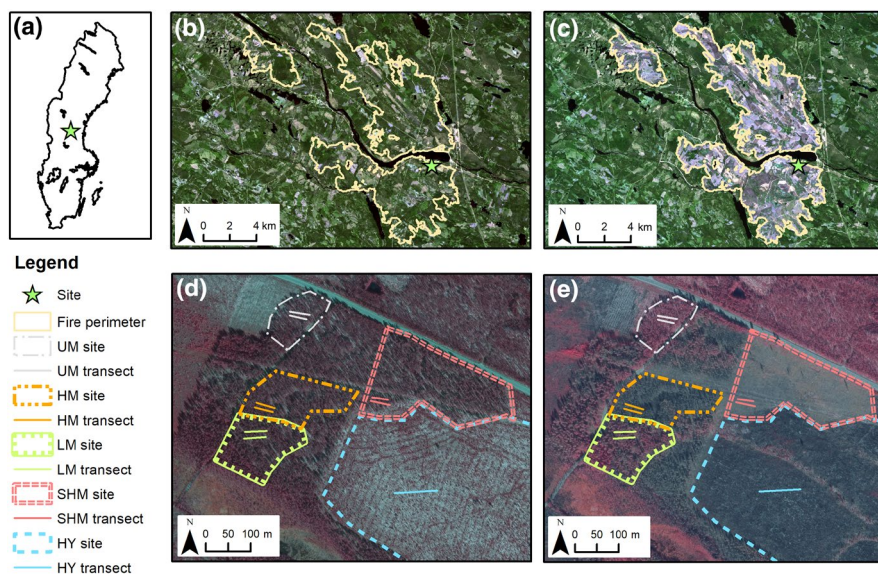

Legend
- ★ Site
- Fire perimeter
- UM site
- UM transect
- HM site
- HM transect
- LM site
- LM transect
- SHM site
- SHM transect
- HY site
- HY transect

FIGURE 1 (a) Star represents the location of the study area within Sweden (61°56′N, 15°28′E), (b) RGB satellite image from before the Ljusdal fire (July 2018) and (c) 1 year after in August 2019, the fire perimeter is outlined in yellow (d, e) false colour composite aerial photos of the sites from before the fire (August 2017) and after (September 2019) the fire and subsequent salvage-logging (at site SHM only), respectively. In (d, e) red and dark red colours represent living vegetation whilst blue colours represent bare soil, dead vegetation and asphalt. The perimeter of each site is outlined, as are the transects where the soil flux measurements were conducted. Site names: Unburnt Mature (UM), High severity Mature (HM), Low severity Mature (LM), Salvage-logged High severity Mature (SHM) and High severity Young (HY). Data sources: (a, d, e) © Lantmäteriet; (b, c) Sentinel-2 (European Space Agency) and © Skogsstyrelsen
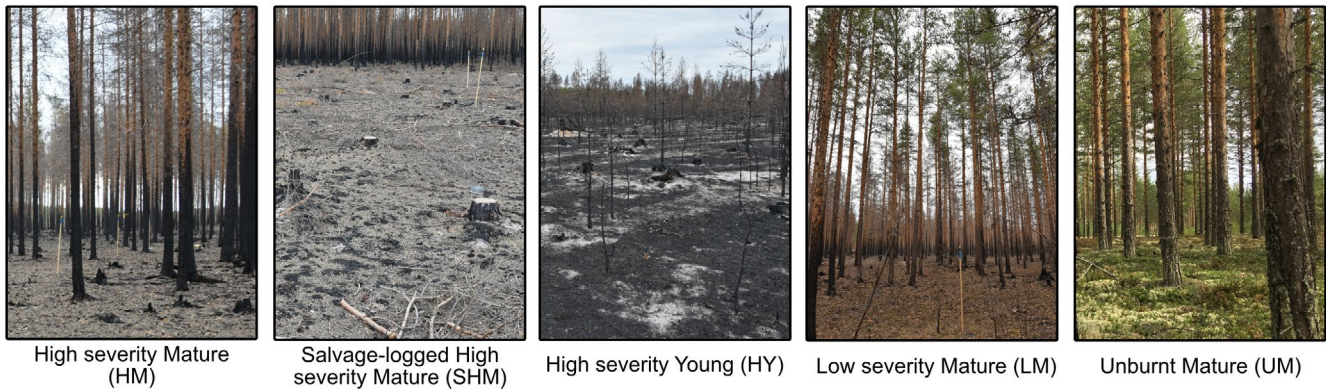
High severity Mature (HM) | Salvage-logged High severity Mature (SHM) | High severity Young (HY) | Low severity Mature (LM) | Unburnt Mature (UM)

FIGURE 2 Photos of the five sites, showing the effects of the fire on the soil and trees

TABLE 1 Post-fire site description

Description	Site				
	HM	SHM	HY	LM	UM
Site name	High severity Mature	Salvage-logged High severity Mature	High severity Young	Low severity Mature	Unburnt Mature
Burn severity	High	High	High	Low	No fire
Post-fire management	Standing burnt trees	Salvage-logged 5 months after fire	Standing burnt trees	Standing burnt trees	None
Charred organic layer depth (mm)	10 ± 0	9 ± 1	8 ± 1	8 ± 1	NA
Total organic layer depth (mm)	25 ± 1	23 ± 2	12 ± 1	37 ± 2	149 ± 4
Forest floor biomass (kg m^{-2})	1.77	2.24	1.33	2.41	3.34
Forest floor biomass loss (kg m^{-2})	1.57	1.10	Not known	0.93	0
Forest floor C loss (kg m^{-2})	0.80	0.69	Not known	0.43	0
Tree height (m)	17.4 ± 0.5	—	2.9 ± 0.3	19.3 ± 0.5	15.3 ± 0.4
DBH (cm)	20 ± 1	—	4 ± 1	24 ± 2	20 ± 1
Tree charring height (m)	3.8 ± 0.4	—	2.8 ± 0.1	2.1 ± 0.2	0
Trees ha^{-1}	594	—	984	484	688
Tree age in 2018 (years)	~100	73	10	~70	~60

Note: The total organic layer depth includes the thickness of the charred layer at the burnt sites. Uncertainties are described as ±SE.
Abbreviation: DBH, Diameter at Breast Height.

tree survival (low severity; tree canopy intact) one year after the fire. In 2019, the HM tree crowns still held burnt needles, whereas the LM tree crowns showed signs of needle regrowth. At the unburnt site (UM), the forest floor was covered by a dense layer of mosses and lichens (*Cladonia* spp., *Pleurozium schreberi*, *Cetraria* sp. and *Dicranum* sp.) and vascular plants (*Vaccinium vitis-idaea*, *V. myrtillus*, *V. uliginosum*, *Calluna vulgaris*, *Empetrum nigrum*, *Arctostaphylos uva-ursi* and *Avenella flexuosa*). At the burnt sites, the ground vegetation had been completely consumed by the fire. During the 2019 growing season, minor areas of *Vaccinium vitis-idaea* regrowth and some fungi fruiting bodies were visible. To assess the impact of salvage-logging, we compared two sites (both burnt at high severity), where one had been salvage-logged (SHM) in December 2018 (5 months after the fire), and at the other, the dead trees had been left standing (HM). No ground preparation was undertaken after the salvage-logging,

and we did not observe any soil compaction from the heavy machinery used for the logging. Finally, to assess the impact of stand maturity, we compared two sites (both burnt at high severity), where one stand was 10 years old (HY) and the other was ~100 years old (HM) at the time of the fire. The HY site had been clear-cut, which was followed by soil scarification and seeding in 2006 (i.e. 12 years before the fire).

Table 1 describes the sites and includes tree and soil characteristics, which were measured 1–2 years after the fire. Tree age was determined using forest inventories where available and otherwise tree rings. The soil measurements (charred and organic layer depth and biomass loads and loss) are described in Section 2.4. We note that some combinations of site characteristics (e.g. young salvage-logged or low-severity salvage-logged) were not present in our study area.

2.3 | Soil CO_2 and CH_4 flux measurements

We conducted manual dark chamber CO_2 (i.e. respiration) and CH_4 flux measurements of the soil and ground vegetation (the latter was only present at UM), which we refer to as 'soil fluxes'. In May 2019, 10 collars (circular, galvanized steel, 16 cm diameter, 10 cm depth) were placed along one or two transects at 10 m intervals at each of the five sites (see Figure 1d,e; Figure S1 for more details). The measurements were conducted in monthly campaigns between June and September 2019 (i.e. 1 year after the wildfire). For each campaign, 2–4 days with similar weather conditions were selected, and measurements started (ended) at least 2 h after (before) sunrise (sunset). We conducted a total of 200 measurements (40 per site) each for CO_2 and CH_4. Immediately after each flux measurement, we also measured soil temperature two times at three depths (1, 2 and 5 cm; handheld electronic thermometer HI98501 Hanna Instruments Ltd), and the volumetric soil water content (SWC) integrated over 0–5 cm depth (SM300 sensor and HH2 logger, Delta-T Devices Ltd) six times within 10 cm of each collar (i.e. outside the area covered by the chamber). The SWC measurements were converted to %vol based on the proportion of mineral or organic soil (using the total organic layer depth measurements in Table 1) in the top 5 cm of the soil.

The manual chamber measurements followed standard procedures (cf. Livingston & Hutchinson, 1995). A static chamber (16 cm diameter, 0.0045 m³ volume) was connected to an Ultra-portable Greenhouse Gas Analyzer (UGGA; Los Gatos Research, Inc.) to measure CO_2 and CH_4 concentration at 1 Hz during a 5 min chamber closure time. To convert the concentration measurements to fluxes, the slope of the linear regression of concentration over time (150 s duration) with the highest R^2 (>0.8 for CO_2 and >0.25 for CH_4 to avoid excluding low fluxes), and where $p \leq 0.001$ and Normalized Root Mean Square Error (NRMSE, normalized using the range of the measured values) <0.2, was selected. The slope and soil temperature for each collar and air pressure measurements from a nearby national monitoring station were used as inputs to the ideal gas law (see Supplementary Information for more details about the flux data processing). Although the observed CH_4 fluxes were low, they were above the minimum flux detection limit (0.0005 μmol m⁻² s⁻¹) of the UGGA for a chamber of our size (Sundqvist et al., 2014). As a result, we had a total of 199 CO_2 and 198 CH_4 flux measurements for our analysis.

2.4 | Soil sampling and laboratory chemical analysis

In May 2019, two 30-m parallel transects (Walker et al., 2018) for soil sampling and chemical analysis were established at the centre of each site to avoid border effects, but sufficiently far away (5–20 m) from the collar transects to avoid disturbing the gas flux measurements (see Figure S1). Every 2 m along both sides of each transect, the depths of the charred organic layer and the total organic layer (charred + uncharred) were measured, producing a total of 60 measurements per layer per site. At every 3 m, the entire organic layer was collected using a 20 cm × 20 cm sampling square. In addition, the

first 2 cm of the mineral soil below the organic layer was sampled. This resulted in 20 samples of the organic and mineral layers at each site. The samples were taken to the laboratory and oven-dried at a low temperature (40–45℃) until reaching a constant weight. Each of the organic layer samples was weighed for forest floor biomass estimations (Figure S1). The forest floor biomass loss was estimated for the HM, LM and SHM sites by calculating the difference between the mean biomass remaining at these sites compared with the UM site. Biomass loss could not be estimated for HY because there was no similar young, unburnt site with which to compare it with.

For the chemical analysis, four composite samples for each site were produced by pooling five soil samples from each transect (Figure S1). All samples were sieved (<2 mm) and homogenized, and a subsample was ground for further analysis. The total carbon (C) and nitrogen (N) concentrations were analysed using a total combustion analyser (TruSpec CHN Elemental Analyzer, LECO). The total phosphorous (P) concentrations were measured by colorimetry in a V360 spectrophotometer (JASCO) after acid digestion (U.S. EPA, 2007). The pH and electrical conductivity (EC) were also measured (sample:water ratio of 1:20; using a micropH 2000 meter and a GLP 31 meter, respectively, CRISON Instruments, S. A.).

For determination of water-soluble C, P, ammonium (NH_4^-) and nitrate (NO_3^-), the extracts were produced according to Ghani et al. (2003). The leachate was then used to measure water-soluble C and P (by colorimetry in a V360 spectrophotometer, JASCO), NH_4^- (by ion-selective electrode) and NO_3^- (ion chromatography). Bioavailable P was determined by the Mehlich 3 method (Mehlich, 1984) and measured by colorimetry.

To calculate the effective cation exchange capacity (ECEC), Ca^{2+}, Mg^{2+}, K^+, Na^+ and Al^{3+} concentrations were analysed using a Flame Atomic Absorption Spectrometer (PinAAcle 500, PerkinElmer) following the method by Helmke and Sparks (1996). The concentrations of these cations were then used to calculate the ECEC as follows: ECEC = (Ca + Mg + K + Na) + Al.

2.5 | Data analysis

We divided the sites into three groups and conducted separate statistical analyses to assess the effects of (a) burn severity, comparing UM (no fire), LM (low-severity fire) and HM (high-severity fire); (b) salvage-logging, comparing HM (unlogged) and SHM (salvage-logged); and (c) stand maturity, comparing HM (~100 years old) and HY (10 years old); on the soil nutrient availability, microclimate and soil CO_2 and CH_4 fluxes at each site.

Soil nutrient availability was analysed by plotting the mean and standard error (SE) of the composite soil samples (4 per site) of all chemical properties tested for each site (total C, total N, C:N ratio, water-soluble C, NH_4^-, NO_3^-, water-soluble P, bioavailable P, total P, ECEC, pH and EC) in the organic and mineral layers.

We also tested for significant differences in the soil temperature (2 cm depth) and SWC between the sites in each group. All data were tested for normality and equal variances using the Shapiro–Wilk test

and Levene's test, respectively. Log and square-root transformations were used if data did not meet assumptions of normality and/or were heteroscedastic. Depending on the outcomes of these two tests and the number of sites being compared, we used a one-way analysis of variance (ANOVA), Welch ANOVA, two-sample t-test or Wilcoxon rank sum test.

The soil CO_2 and CH_4 fluxes were analysed by fitting six linear mixed-effects models (one per group and gas flux) using the R package lme4 (R version 3.6.2; Bates et al., 2015; R Core Team, 2019). The fixed-effects estimates and pseudo-R^2 values (calculated according to Nakagawa & Schielzeth, 2013) are available in Table S1. All the fitted models met assumptions concerning normally distributed residuals, homoscedasticity and linearity. The CO_2 flux data were log transformed to satisfy assumptions of normality but this was not required for the CH_4 flux data. Site and soil temperature were used as fixed effects because our aim was to investigate differences in the fluxes between sites, and we wanted to control for the effects of soil temperature on the gas fluxes. Soil temperature at 2 cm depth was selected because the data were normally distributed, and this depth was within the soil organic layer at most of the sites. Collar ID (nested within site) was used as a random effect to account for the multiple measurements conducted on each collar. As SWC was correlated to soil temperature ($r = -0.69$ across all sites), we did not include SWC in the models. Significant differences between the site CO_2 or CH_4 fluxes (when soil temperature = site mean temperature) within each model were tested using ANOVAs with soil temperature as a continuous variable (Type III test for unbalanced data, Kenward–Roger method for calculating denominator degrees of freedom), followed by Tukey's post hoc tests. Since the ANOVAs tested for significant differences between the sites at the y-intercept (i.e. where soil temperature = 0℃), we centred the soil temperature data using the site means to ensure that the ANOVAs were conducted at an ecologically relevant temperature (rather than an extrapolation of the site gas fluxes at 0℃). We also checked whether the interaction between site and soil temperature was significant for each of the models, and it was only included if it was significant. To interpret the interaction effects between site and soil temperature, we plotted linear regressions (not the mixed-effects models discussed above) of the gas fluxes against soil temperature (2 cm depth) at each site. Interaction effects will be visible as non-parallel regression lines. In addition, linear regressions of the gas fluxes against SWC were plotted to examine the moisture sensitivity of the CO_2 and CH_4 fluxes at each site (see Figure S2).

3 | RESULTS

3.1 | Effects of burn severity on soil nutrients, microclimate and carbon fluxes

We compared the soil nutrient availability, microclimate and greenhouse gas fluxes between the high-severity fire site (HM), the low-severity fire site (LM) and the unburnt site (UM). All sites were mature stands at the time of the fire, and the trees were left standing after the fire (Table 1). The fire combusted a substantial portion of the organic layer at HM and LM (Table 1). The mean (±SE) total organic layer depth was 25 ± 1 mm and 37 ± 2 mm at HM and LM, respectively, indicating that the fire was more severe at HM than LM but not severe enough to remove the entire organic layer (UM: 149 ± 4 mm). The charred layer was similarly thick at both burnt sites (10 ± 4 mm at HM and 8 ± 1 mm at LM).

Soil nutrient concentrations in the organic layer, in particular C (total and water-soluble), total N, NH_4^- and P (water-soluble and bioavailable), were lower at HM than LM (Figure 3a,b,d,e,g,h). NO_3^- concentrations at LM (10.8 ± 0.7 mg kg^{-1}) were much higher than at any other site (4.3–6.7 mg kg^{-1}; Table S2). Both burnt sites had lower water-soluble C but higher bioavailable and total P concentrations than at UM (Figure 3d,h,i). For a full description of the soil nutrient content results (including those for the mineral soil layer), see Table S2 and Figure S3.

In terms of site microclimate, mean soil temperature was significantly higher at HM than UM, but there were no significant differences between HM-LM or LM-UM (note that the results should be treated with caution as the data were not normally distributed; Welch ANOVA and Games–Howell post hoc test, $F(2,75) = 4.41$, $p = 0.02$; Figure 4a). There were no significant differences in SWC between any of the sites, although UM had a larger range of SWC and a maximum SWC >11%vol higher than at the two burnt sites (Figure 4d). Monthly disaggregation of the SWC data showed that SWC was higher at UM than either of the burnt sites at the start and end of the growing season but that all the sites had similarly low SWC during the middle of the growing season (Figure S4).

The mean (±SE) soil CO_2 fluxes were significantly lower at HM (1.4 ± 0.1 µmol m^{-2} s^{-1}) compared with both LM (2.3 ± 0.2 µmol m^{-2} s^{-1}) and UM (2.3 ± 0.1 µmol m^{-2} s^{-1}; Figure 5a and Table 2). We note that these differences are not due to differences in the soil temperature between the sites as these effects were accounted for in the mixed-effects model. LM had higher (more negative) mean CH_4 uptake (−1.4 ± 0.1 × 10^{-3} µmol m^{-2} s^{-1}) compared with HM and UM (both −1.1 ± 0.1 × 10^{-3} µmol m^{-2} s^{-1}; Figure 5d), although the difference was not significant. In both the CO_2 and the CH_4 models, soil temperature (2 cm depth) had a significant effect on the fluxes (Table 2), and Figure 6a,b show increasing CO_2 emissions and CH_4 uptake with increasing soil temperature. In addition, the interaction effect between site and soil temperature was significant in the CH_4 model: CH_4 uptake increased more strongly with increasing soil temperature at UM compared with LM or HM (Table 2; Figure 6b).

3.2 | Effects of salvage-logging on soil nutrients, microclimate and carbon fluxes

The salvage-logged site (SHM) and the unlogged site where the dead trees had been left standing (HM) had comparable total
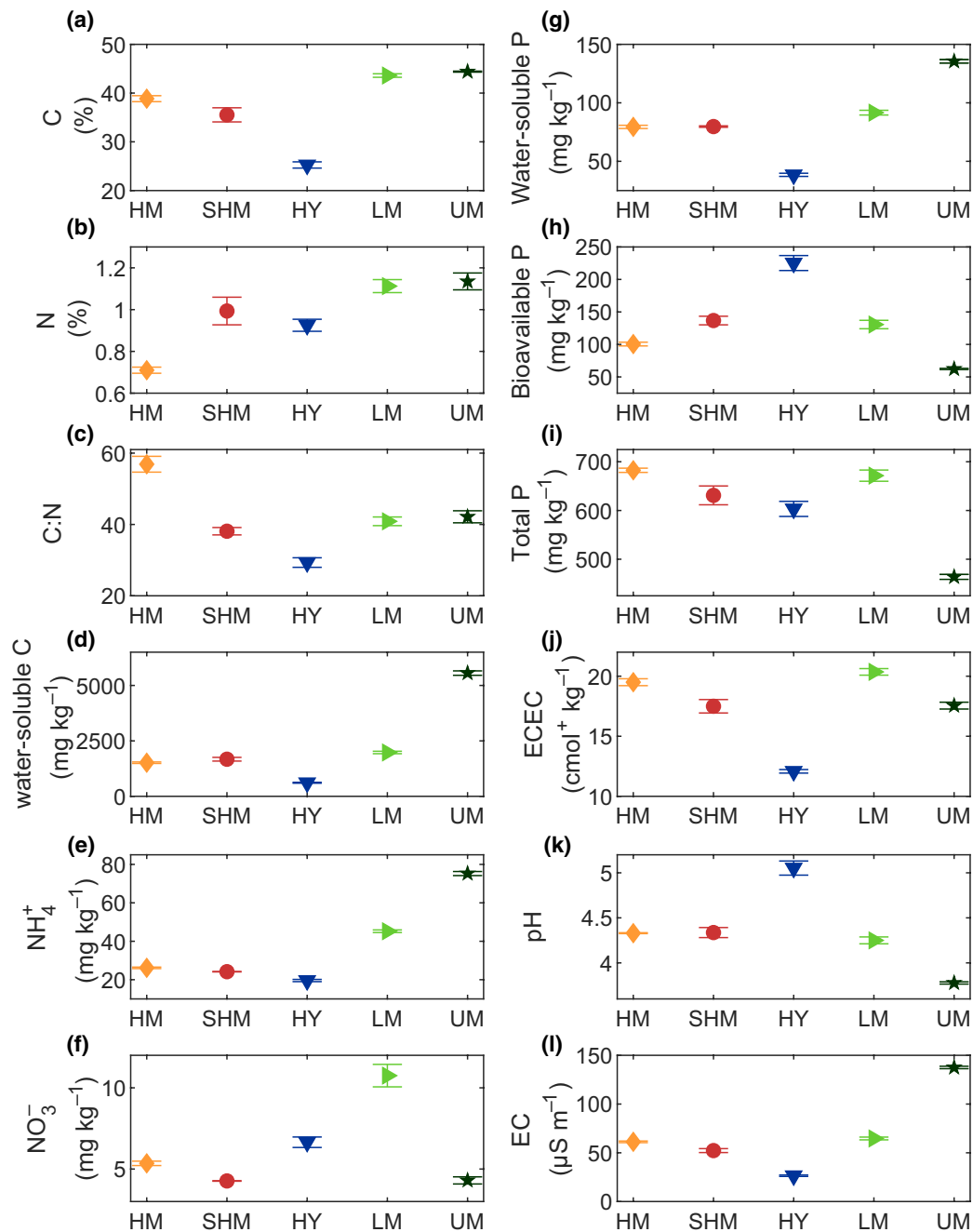
FIGURE 3 Mean ± SE of the soil chemical properties in the organic layer (mean of 4 composite samples) at all sites measured in May 2019. (a) total C content (b) total N content (c) C:N ratio (d) water-soluble C concentration (e) NH_4^- concentration (f) NO_3^- concentration (g) water-soluble P concentration (h) bioavailable P concentration (i) total P concentration (j) effective cation exchange capacity (k) pH (l) electrical conductivity. Site names: HM = High severity Mature, SHM = Salvage-logged High severity Mature, HY = High severity Young, LM = Low severity Mature and UM = Unburnt Mature

organic layer depth (mean ± SE: 23 ± 2 mm and 25 ± 1 mm, respectively) and charred organic layer depth (9 ± 1 mm and 10 ± 0 mm, respectively) after the high-severity fire (Table 1). There were only small differences in soil nutrient concentrations between the sites (Figure 3; Figure S3; Table S2). SHM had lower total C, C:N, NH_4^-, NO_3^-, total P and ECEC, but higher bioavailable P and total N in the organic layer compared with HM (Figure 3a-c,e,f,h-j; Table S2).

SHM experienced a larger soil temperature range and a maximum soil temperature 4°C higher than at HM (Figure 4b). However, neither median soil temperature (2 cm depth) nor mean SWC was significantly different between SHM and HM (Figure 4b,e). The sites also showed similar seasonal trends for both variables (Figure S4).

Furthermore, neither the mean soil CO_2 fluxes (1.3 ± 0.1 $\mu mol\,m^{-2}\,s^{-1}$ and 1.4 ± 0.1 $\mu mol\,m^{-2}\,s^{-1}$ at SHM and HM, respectively)
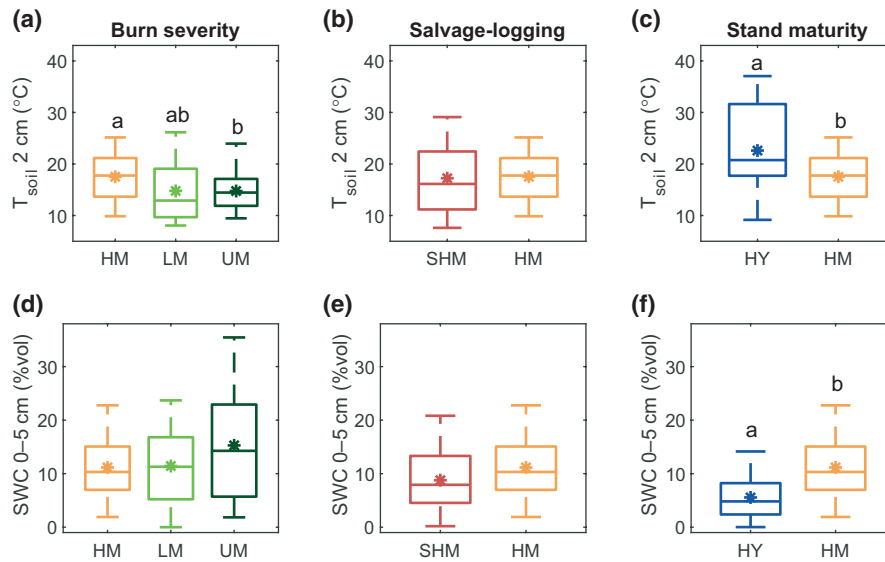
FIGURE 4 Site soil temperature (a–c) and soil water content (SWC; d–f) grouped according to burn severity (a, d), salvage-logging (b, e) and stand maturity (c, f). The boxes show the interquartile range, the middle line is the median and the asterisk is the mean. The lines extending above/below each box indicate the maximum/minimum data values. Different letters above each boxplot denote significant differences between the sites. Site names: HM = High severity Mature, LM = Low severity Mature, UM = Unburnt Mature, SHM = Salvage-logged High severity Mature and HY = High severity Young
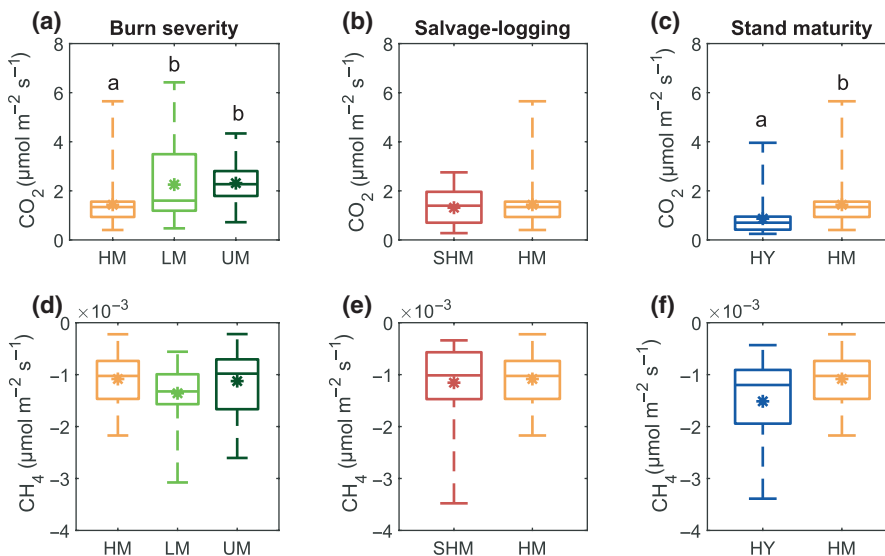

FIGURE 5 Site soil CO_2 (a–c) and CH_4 (d–f) fluxes grouped according to burn severity (a, d), salvage-logging (b, e) and stand maturity (c, f). The boxes show the interquartile range, the middle line is the median and the asterisk is the mean. The lines extending above/below each box indicate the maximum/minimum data values. Different letters above or below each boxplot denote significant differences in the fluxes between the sites (Tukey's post hoc test, $p \leq 0.05$). The corresponding ANOVA results are reported in Table 2. Site names: HM = High severity Mature, LM = Low severity Mature, UM = Unburnt Mature, SHM = Salvage-logged High severity Mature and HY = High severity Young

nor the mean CH_4 fluxes ($-1.2 \pm 0.1 \times 10^{-3}$ µmol m^{-2} s^{-1} and $-1.1 \pm 0.1 \times 10^{-3}$ µmol m^{-2} s^{-1} at SHM and HM, respectively) were significantly different between the two sites (Figure 5b,e; Table 2). These results were confirmed in the monthly flux time series (Figure S5). Both gas fluxes were significantly affected by soil temperature, but there was no significant interaction effect between site and soil temperature (Table 2). The relationship between the fluxes and SWC was also similar at both sites (Figure S2).

3.3 | Effects of stand maturity on soil nutrients, microclimate and carbon fluxes

Two sites were compared that differed in terms of stand age at the time of the fire: 10 years old (HY) versus ~100 years old (HM). Although we cannot be certain that the fire behaviour was directly comparable at the two sites (due to potential differences in pre-fire biomass or other factors), the charred organic layer was of similar

TABLE 2 Results of the ANOVAs on the mixed-effects models (one per group and gas flux), testing the effects of site and soil temperature (at 2 cm depth, continuous variable) on soil CO_2 and CH_4 fluxes (the interaction between site and soil temperature was only included if significant)

Group	Site			Soil temperature			Site × Soil temperature		
	$df^{a,b}$	F-value	p-value	$df^{a,b}$	F-value	p-value	$df^{a,b}$	F-value	p-value
Soil CO_2 flux									
Burn severity	2, 27.1	**9.947**	**<0.001**	1, 89.6	**160.874**	**<0.001**	—	—	—
Salvage-logging	1, 18.0	0.910	0.353	1, 59.4	**124.586**	**<0.001**	—	—	—
Stand maturity	1, 18.2	**20.844**	**<0.001**	1, 57.2	**206.258**	**<0.001**	1, 57.2	**8.172**	**0.006**
Soil CH_4 flux									
Burn severity	2, 27.4	3.125	0.059	1, 88	**128.222**	**<0.001**	2, 87.9	**7.359**	**0.001**
Salvage-logging	1, 17.8	0.086	0.772	1, 58.4	**19.688**	**<0.001**	—	—	—
Stand maturity	1, 18.1	1.599	0.222	1, 58.3	**82.480**	**<0.001**	—	—	—

Note: Tukey's post hoc tests results are reported in Figure 5. The groups are burn severity = UM, LM and HM; salvage-logging = SHM and HM; stand maturity = HY and HM. Bold *F*- and *p*-values are significant at $\alpha < 0.05$. Site names: HM = High severity Mature, SHM = Salvage-logged High severity Mature, HY = High severity Young, LM = Low severity Mature and UM = Unburnt Mature.

[a]Numerator degrees of freedom, denominator degrees of freedom.

[b]Not an integer because we used a model with ddf = 'Kenward–Roger' for unbalanced sample size.

thickness (mean ± SE: 8 ± 1 mm and 10 ± 0 mm at HY and HM, respectively), and there was complete tree mortality (i.e. high-severity fire) at both sites.

Our soil chemistry analyses showed that HY stood out from HM (and all the other sites) in many of the properties we tested (Figure 3; Figure S3; Table S2). In the organic layer, total C, C:N ratio, water-soluble C, NH_4^-, water-soluble P, ECEC and EC were lower at HY than at HM (or any other site; Figure 3a,c,d,e,g,j,l). In some cases, these differences were substantial, for example, total C content was 14% lower at HY compared with HM whilst water-soluble C was 900 mg kg^{-1} lower than at HM (Table S2). Bioavailable P and pH in the organic layer were also higher at HY than any other site (Figure 3h,k).

The soil at HY was significantly warmer (Wilcoxon rank sum test, $t = 1322$, $z = -2.72$, $p = 0.007$; Figure 4c) and drier (*t*-test, $t = 5.34$, 77 *df*, $p < 0.001$; Figure 4f) than at HM, throughout the growing season (Figure S2). Mean soil temperature (2 cm depth) was 5.1℃ higher at HY, whilst mean SWC was 5.6%vol lower at HY compared with HM. We observed that the soils at HY were darker than at the other burnt sites and that there was very little shading provided by the thin, burnt tree stems (Figure 2).

Despite the higher soil temperatures at HY, the soil CO_2 fluxes and their temperature sensitivity were significantly lower at HY compared with HM (mean CO_2 flux 0.9 ± 0.1 µmol m^{-2} s^{-1} and 1.4 ± 0.1 µmol m^{-2} s^{-1}, respectively; Table 2; Figures 5c and 6a). CH_4 uptake, which was greater at HY than HM (mean CH_4 flux −1.5 ± 0.1 × 10^{-3} µmol m^{-2} s^{-1} and −1.1 ± 0.1 × 10^{-3} µmol m^{-2} s^{-1}, respectively, Figure 5f; Table 2), was not significantly different between the two sites. There was a similar relationship between the CO_2 fluxes and SWC at both sites (Figure S2a), but the CH_4 uptake at HY decreased more with increasing SWC compared with HM (Figure S2b).

4 | DISCUSSION

4.1 | Impacts of burn severity

One year after the wildfire, we found significantly lower soil CO_2 fluxes at the high-severity fire site (HM) compared with the low-severity fire (LM) or unburnt (UM) sites. This finding is in agreement with the reported reductions in CO_2 emissions for several years after wildfire in boreal regions and their dependence on fire severity (e.g. Holden et al., 2016; Ludwig et al., 2018; Ribeiro-Kumara et al., 2020). The CO_2 fluxes at HM (mean 1.4 µmol CO_2 m^{-2} s^{-1}) were similar to those measured during the first growing season after a stand replacing fire in a Siberian larch forest (mean 1.1 µmol CO_2 m^{-2} s^{-1}; Köster et al., 2018). The CO_2 fluxes at LM (2.3 µmol CO_2 m^{-2} s^{-1}) also corresponded well with fluxes measured 1 year after low-severity fires in Alaskan black spruce and Siberian larch forests (2.2–2.3 µmol CO_2 m^{-2} s^{-1}; O'Neill et al., 2003; Sawamoto et al., 2000). The CO_2 fluxes at UM (between 0.7–4.3 µmol CO_2 m^{-2} s^{-1}) were generally lower but within the range reported for the growing season for two different 50-year-old Scots pine stands in Finland (~2–8 µmol CO_2 m^{-2} s^{-1} and ~1–6 µmol CO_2 m^{-2} s^{-1}; Pumpanen et al., 2015; Zha et al., 2007).

The low CO_2 fluxes at our high-severity burn site were likely due to the complete mortality of the trees and ground vegetation (i.e. shutdown of autotrophic respiration). The combustion of a large proportion of the organic layer (83% loss compared with UM) and reductions in labile and total C in the organic layer would also have caused heterotrophic respiration to decline. Indeed, the lower total C and N content at HM compared with LM is indicative of the higher combustion temperatures at HM that would have volatilized organic C and N, resulting in proportionally more mineral elements remaining the organic layer (Araya et al., 2017; Bodí et al., 2014). Furthermore, we noted that the soil CO_2 fluxes at HM were low
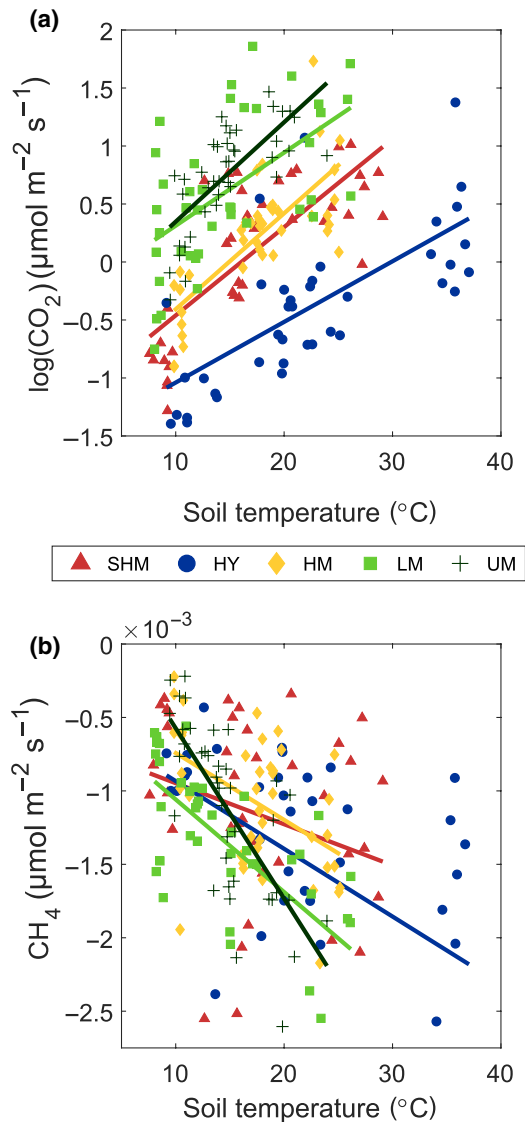
(a)

(b)

FIGURE 6 Linear regressions between (a) log(CO_2 flux) and (b) CH_4 flux and soil temperature at 2 cm depth at each site (see Table S3 for regression parameters). Site names: HM = High severity Mature, SHM = Salvage-logged High severity Mature, HY = High severity Young, LM = Low severity Mature and UM = Unburnt Mature

concluded that root biomass was more important in determining soil respiration than the depth of the soil organic layer. It is also possible that tree fine root production and turnover increased at LM because the fire increased the availability of soil nutrients and raised soil pH (Bryanin & Makoto, 2017; Yuan & Chen, 2010). In particular, our chemical analysis showed increased availability of P (total and bioavailable) at LM compared with UM. Higher labile P concentrations have been linked to increased microbial activity and soil respiration in a forest chronosequence in northern Sweden (Lagerström et al., 2009), whereas boreal forest fertilization studies have shown increased tree growth with P addition (Maynard et al., 2014). NO_3^- concentrations were also higher at LM than at any of the other sites, suggesting that microbial activity and thus nitrification were able to continue after the low-severity burn and/or that the presence of living trees and the remaining organic layer minimized NO_3^- losses at LM due to leaching. As a result, both autotrophic and heterotrophic CO_2 emissions at the site may have been stimulated, counteracting any reduction in the soil CO_2 fluxes due to the consumption of the organic layer (as seen at the HM site).

The mixed-effects model showed lower CH_4 uptake after a high-severity burn compared with a low-severity burn, but neither of these sites had significantly different CH_4 fluxes compared with the unburnt site due to the highly variable fluxes at UM. Similarly, Burke et al. (1997) found lower (but not significantly different) CH_4 uptake at a Canadian black spruce site during the first growing season after a high-severity burn compared with an unburnt site. We observed higher soil CH_4 uptake (mean -1.1×10^{-3} μmol CH_4 m^{-2} s^{-1}) at our high-severity fire site compared with Burke et al. (1997; -2.7×10^{-4} μmol CH_4 m^{-2} s^{-1}) but similar values to those reported by Köster et al. (2018; -1.3×10^{-3} μmol CH_4 m^{-2} s^{-1}) 1 year after a fire in a Siberian larch forest. Laboratory incubations of boreal forest soils have shown that CH_4 uptake is highest 2–20 cm deep in the mineral soil (Gulledge et al., 1997; Kulmala et al., 2014), whereas the impacts of wildfire are usually restricted to the surface and organic layers, as is the case in the present study (Köster et al., 2016; Waldrop & Harden, 2008). Soil moisture is one of the main factors impacting soil CH_4 fluxes because it affects the rate of CH_4 diffusion into soils and the pore space available for aerobic methane consumption (Smith et al., 2000). Although our results showed no significant differences in SWC (measured at the soil surface, 0–5 cm depth) between the sites as a result of burn severity, the UM site was better able to retain moisture in the spring and autumn than either of the burnt sites. Year-round flux measurements would be needed to examine whether differences in the CH_4 fluxes between the sites become more pronounced during the wetter parts of the year and whether they have a significant influence on the annual CH_4 uptake.

Soil carbon fluxes only represent part of the net ecosystem carbon balance, albeit an important one. We expect that measurements of the total ecosystem carbon fluxes would have revealed even larger differences between the sites as a result of burn severity. Despite the reductions in post-fire soil respiration at HM, tree mortality would make the site a net CO_2 source, whilst LM may remain a net sink due to the continued photosynthetic uptake by the surviving

despite mean soil temperatures 2.7°C higher than the other two sites, implying that heterotrophic respiration was more substrate-limited than temperature-limited, which was also observed by Allison et al. (2010) and Waldrop and Harden (2008) in their studies of the effects of fire on boreal forest soils.

The soil CO_2 fluxes were similar at the low-severity fire and unburnt sites despite a substantially reduced organic layer (75% loss compared with UM) and complete mortality of the ground vegetation at LM. As all trees survived the fire at LM 1 year after the fire, the soil CO_2 fluxes at this site included both heterotrophic and autotrophic respiration. Singh et al. (2008) observed a strong positive correlation between soil respiration and fine root biomass 6–28 years after wildfire at Canadian boreal forest sites and

trees. The net CH_4 balance would also differ at HM compared with the other two sites, since dead trees tend to emit less CH_4 than living trees (Covey & Megonigal, 2019), although it is not clear whether the sites are net sinks or sources of CH_4 without continuous ecosystem-scale flux measurements.

4.2 | Impacts of salvage-logging

There is little previous work comparing the impacts of alternative post-fire management strategies on forest soils and greenhouse gas fluxes, and the few available observations are not consistent. In the first year after a large Swedish wildfire in 2014, eddy covariance measurements by Gustafsson et al. (2019) showed higher ecosystem CO_2 emissions at a salvage-logged site compared with an unlogged site. During the first 3 years after fire in Mediterranean pine forests, Marañón-Jiménez et al. (2011) found lower, but not always significant, soil CO_2 fluxes at salvage-logged sites compared with sites where the dead trees were left standing. Studies of the effects of clear-cutting (without fire) on soil CO_2 fluxes in boreal forests are similarly inconclusive. Soil CO_2 fluxes have been found to increase, remain stable or decrease during the first growing season after harvesting, in part depending on whether logging residue was left on the ground and whether soil preparation had been carried out (Mallik & Hu, 1997; Pumpanen et al., 2004; Striegl & Wickland, 1998). One year after a high-severity burn, we found no significant effects of salvage-logging on soil CO_2 fluxes, CH_4 fluxes or soil microclimate, and only small differences in soil nutrient content, compared with leaving the dead trees standing (i.e. comparing SHM and HM). The similarity in the soil CO_2 fluxes may hence be partially due to the fact that the soils were not scarified and that only minor amounts of woody debris were left after the salvage-logging at SHM. However, if the salvage-logging had been conducted at a low-severity burn site, which is a common post-fire management practice in Sweden (although not elsewhere in the boreal region), we would expect the same impact as that of a high-severity burn, that is, not only decreased soil CO_2 fluxes but also the conversion of the site to a net CO_2 source due to reductions in photosynthetic carbon uptake.

Clear-cutting in boreal forests (not after fire) can turn forest soils from sinks to sources of CH_4 due to reductions in evapotranspiration and consequent increases in the water table (Sundqvist et al., 2014; Vestin et al., 2020) or soil compaction by heavy machinery (Strömgren et al., 2016; Teepe et al., 2004). However, we found no significant differences in SWC between the SHM and HM sites, and we did not observe any evidence of soil compaction at the SHM site. Furthermore, the remaining organic layer, which can act as a barrier to CH_4 diffusion, was a similar thickness at both sites (Saari et al., 1998). It is, hence, not surprising that no significant differences in the CH_4 fluxes were found.

Although salvage-logging after a high-severity fire did not immediately impact the soil carbon fluxes or nutrient availability, the removal of the dead trees may have long-term effects on these two processes and thus amplify differences in the net carbon balance

between SHM and HM. Dead trees can be a key source of nutrients, particularly C and N, that are released over many years, outlasting the short-term nutrient pulse from ash deposition immediately after a fire (Marañón-Jiménez & Castro, 2013). Having this nutrient source is significant given that C and N were reduced after a high-severity burn and boreal forests are often N-limited. On the other hand, heterotrophic respiration rates will be higher at HM than SHM over the long-term as the dead trees slowly decompose (Amiro et al., 2006).

4.3 | Impacts of stand age

Stand age had a clear impact on all the soil properties we tested (except CH_4 uptake), with the younger site (HY) experiencing significantly warmer and drier soils, lower nutrient supply and more substrate-limited soil respiration compared with the mature site (HM). All of these differences are likely related to the very thin organic layer remaining at HY, as a result of both its young age (i.e. less time to accumulate organic material) and the consumption of the soil surface during the high-severity fire. A thinner organic layer has a reduced ability to insulate the underlying mineral soil, thus driving up soil temperature and reducing moisture retention. Therefore, as well as being limited by very low concentrations of labile C, the shutdown of autotrophic respiration and the supply of root exudates from the trees, soil respiration at HY was also more likely to have been limited by water stress than at HM.

We note that our observations at HY not only reflect the young age of the stand but may also have been influenced by the clear-cut and soil scarification at HY, which occurred 12 years before the fire. In some cases, harvesting and/or soil scarification in boreal forests has not had any long-term impacts (10–20 years) on soil nutrient availability or has increased the availability of certain nutrients (Kishchuk et al., 2014; Simard et al., 2001). However, in Swedish Scots pine forests, Örlander et al. (1996) found that soil scarification led to reduced soil C and N concentrations up to 70 years after the disturbance (although it did not affect tree productivity), which supports our findings of lower C content in the organic layer at HY compared with all the other sites. Furthermore, Thiffault et al. (2007) noted that logged sites in Quebec had reduced ECEC concentrations compared with fire-affected sites 15–20 years after the disturbance, which fits with our observations of lower ECEC in the organic layer at HY compared with HM.

Forest stands subjected to multiple or compound disturbances can be more negatively affected than those exposed to single disturbance events (Bowd et al., 2019; Leverkus et al., 2018). We have analysed two forest stands affected by multiple disturbances: HY (clear-cut then fire) and SHM (fire then salvage-logging), but HY was more strongly affected (more extreme changes in microclimate, nutrient supply and soil respiration). These differences may have partly resulted from differences in the disturbance to the soil (e.g. soil scarification at HY but not at SHM) but also emphasize that stand age plays a key role in determining the response of a forest to disturbance. Our observations demonstrate the limited ability of young

stands to build up SOM and retain nutrients after a disturbance, which will have a long-term negative impact on ecosystem functioning and the carbon storage capacity of these stands (Walker et al., 2019). These findings are particularly significant in light of a global shift towards younger forests and more frequent and intense natural disturbances (McDowell et al., 2020).

4.4 | Limitations and opportunities

In the present study, we have compared a group of sites located within a 1 km^2 area. As a result of the close proximity of all our sites, we have eliminated undesired sources of variability that have complicated the interpretation of results in previous studies (e.g. differences in time since wildfire, landscape position, soil characteristics and weather). Nevertheless, despite concentrating on mature forest (with the exception of HY), the differences in the tree characteristics (i.e. tree height and stand density, Table 1) add some uncertainty to our comparisons between the sites. These uncertainties are, however, likely outweighed by the magnitude of the differences between the sites we compared (e.g. tree mortality vs. tree survival at HM and LM or logged vs. unlogged at SHM and HM).

Our study has highlighted clear differences in the soil carbon fluxes between the sites we investigated as a result of variations in burn severity and forest management. Accounting for such spatial variability is vital, particularly in Fennoscandia where the majority of forests are owned by private people in small holdings (typically 50 ha or less; KSLA, 2015; LUKE, 2018), creating a heterogeneous mosaic of forest ages and management practices. Our findings provide a basis for modelling and upscaling post-fire soil carbon fluxes across Fennoscandia. In addition, by capturing the response of forest soils within the first year of the fire and salvage-logging we have established a baseline against which future changes at the sites can be compared. Ongoing monitoring will reveal whether the direct impacts of the fire and management decisions translate into long-lasting differences between the sites.

4.5 | Future wildfire impacts

The length of the annual summer wildfire season is predicted to increase in Fennoscandia and, in our study area, could be 1 month longer by the end of the century (Kilpeläinen et al., 2010; MSB, 2013). Thus, although fire suppression has generally been highly effective, extreme wildfire seasons such as that experienced in 2018 are likely to become more common in the future. Our results suggest the increasing frequency of wildfires will reduce the forest soil carbon sink by limiting the time available for SOM to accumulate between disturbances. Furthermore, the burn severity of future fires will be a key determinant of soil CO_2 emissions during the initial post-fire years. Although soil CO_2 emissions may be reduced after high-severity fire compared with low-severity fire, at the ecosystem scale, stands affected by high-severity fire will become net sources of CO_2, whereas stands affected by low-severity fire will likely remain CO_2 sinks. Eddy covariance data or ecosystem modelling approaches are needed to estimate how the ecosystem scale carbon fluxes change after fire, in order to fully quantify the effects of fire on the forest carbon balance in Fennoscandia.

5 | CONCLUSIONS

We established five sites within the Ljusdal fire complex to assess how burn severity, immediate post-fire forest management (salvage-logging vs. letting the burnt trees stand) and stand age affected the forest soils 1 year after the fire. Our results show that a high-severity fire caused significant reductions in the soil CO_2 fluxes, higher soil temperature and pronounced differences in nutrient content compared with an unburnt site, whereas a low-severity fire only affected the soil nutrient content.

One year after the fire, salvage-logging after a high-severity fire had no additional impact on the soil compared with leaving the dead trees standing. We would, however, expect that salvage-logging after a low-severity fire would lead to significant changes in soil respiration due to the removal of living trees. Over the long term, and especially when considering the ecosystem-scale carbon fluxes, the differences between the salvage-logged and un-logged sites are very likely to become more pronounced as the burnt wood will increase CO_2 emissions and available nutrients at the unlogged sites.

The effect of post-fire salvage-logging on soil CH_4 fluxes has not been examined previously and we found, similarly to our analysis of burn severity and stand age, that it had no significant effect on CH_4 uptake in our study area. Finally, our results show that stand age is a key factor determining the effect of disturbances on forest stands and that the effects of clear-cutting and soil scarification more than a decade ago were still visible after the fire.

With climate change predicted to increase wildfire frequency across large parts of the boreal biome and the growing pressure from forest management, stands affected by multiple different disturbances with short return intervals are likely to become more common. Our results suggest that the soils in these forest stands are most at risk of losing their carbon storage capacity and nutrients vital to tree growth. Monitoring the long-term effects of disturbance and accounting for the management history of a site is, therefore, essential in order to estimate the carbon sink potential of managed boreal forests. Such work will help elucidate the effects of repeated disturbance on soil nutrient availability and greenhouse gas fluxes and can inform sustainable forest management practices.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author on reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.