Wildfire in Swedish boreal forests

Impacts of fire severity and salvage logging on tree seedling regeneration and the belowground system

Theresa Simona Ibáñez
Faculty of Forest Sciences
Department of Forest Ecology and Management
Umeå

SLU
SWEDISH UNIVERSITY
OF AGRICULTURAL
SCIENCES

DOCTORAL THESIS
Umeå 2022

Acta Universitatis Agriculturae Sueciae
2022:04

Cover photo: Theresa S. Ibáñez
Description of photograph: Tree seedling regeneration following wildfire.

ISSN 1652-6880
ISBN (print version) 978-91-7760-883-7
ISBN (electronic version) 978-91-7760-884-4

Umeå
Print: Original Tryckeri, Umeå, 2022

Wildfire in Swedish boreal forests - Impacts of fire severity and salvage logging on tree seedling regeneration and the belowground system

Abstract

Wildfires are projected to occur more frequently and become more severe as the climate warms. The increasing release of carbon to the atmosphere from more severe fires may contribute to climate warming, and thus initiate a positive feedback loop. Following wildfire, salvage logging is a common management practice, but the impact on soil and vegetation may vary depending on fire severity. Hence, it is important to understand how wildfire severity and salvage logging affect soil abiotic and biotic properties and tree seedling regeneration. Also, in the future, forest recovery from fire and salvage logging may be affected by climate warming. In this thesis, I have conducted laboratory and greenhouse experiments to investigate the abiotic and biotic effects of fire severity and post-fire management on biomass production of *Betula pendula*, *Picea abies* and *Pinus sylvestris* seedlings regenerated from seeds and associated soil processes. Further, I have performed a mesocosm field experiment to investigate the impacts of fire severity, salvage logging and experimental warming on *P. abies* and *P. sylvestris* nursery seedlings *in situ*, and undertaken field measurements of soil N transformation rates and C fluxes in stands of varying fire severity and management. This thesis shows that the effect of fire severity on the soil system is stronger than that of salvage logging and that the impact of salvage logging on forest regeneration varies depending on fire severity; these effects can further be directly or indirectly altered by experimental climate warming. This thesis also shows that the effect of soil abiotic and biotic properties following fire on tree seedling regeneration are species specific. Altogether, it contributes with new fundamental knowledge about the interactive effects of multiple drivers of seedling regeneration and soil processes in the post-fire boreal forest landscape. The conclusions of this thesis can be applied, in combination with other research, in decision making about management of boreal forest following wildfire.

Keywords: boreal forest, *B. pendula*, *P. abies*, plant-soil feedback, *P. sylvestris*, seedling regeneration, salvage logging, soil C fluxes, soil N transformation rates, wildfire

Author’s address: Theresa Simona Ibáñez, Swedish University of Agricultural Sciences, Department of Forest Ecology and Management, Umeå Sweden

Skogsbrand i svenska skogar - Effekter av brandhårdhet och avverkning av brandskadade träd på föryngring och markprocesser

Sammanfattning

Skogsbränder förväntas öka i frekvens och omfattning i framtiden i takt med att klimatet värms upp. Fler skogsbränder kan leda till ett ökat koldioxidutsläpp och en högre koldioxidhalt i atmosfären som i sin tur förstärker klimatuppvärmningen och som därmed initierar fler skogsbränder. Efter en skogsbrand är avverkning av brandskadade träd en vanlig åtgärd, men påverkan på mark och vegetation kan variera beroende på brandens svårighetsgrad. Därför är det viktigt att förstå hur kombinationen av brandhårdhet och avverkning påverkar markens abiotiska och biotiska egenskaper liksom föryngring av trädplantor. Det är också rimligt att tro att i framtiden kommer skogens återhämtning efter brand och avverkning också att påverkas av en ökad klimatuppvärmning. I min avhandling har jag genomfört laboratorie- och växthusexperiment för att undersöka hur de abiotiska och biotiska effekterna av brandens svårighetsgrad och skötselåtgärd (avverkning), påverkar tillväxt av *Betula pendula, Picea abies* och *Pinus sylvestris* plantor (föryngrade från frön) och de associerade markprocesserna. Vidare har jag utfört ett fältexperiment för att undersöka effekterna av brandhårdhet, avverkning av brandskadade träd och experimentell uppvärmning på *P. abies* och *P. sylvestris* träd från plantskoleplantor *in situ*, samt genomfört fältmätningar av flöden av kväve och kol i markbestånd av varierande brandhårdhet och skötselåtgärd. Min avhandling visar att brandhårdhet har ett starkare inflytande på markens omsättning av näringsämnen än vad avverkning av brandskadade träd har. Vidare varierar effekten av avverkning av brandskadade träd på skogsföryngringen beroende på brandhårdhet; dessa effekter kan ytterligare direkt eller indirekt förändras av en klimatuppvärmning. Min avhandling visar också att effekten av markens abiotiska och biotiska egenskaper efter brand på föryngring av trädplantor är artspecifik. Sammantaget bidrar denna avhandling med ny grundläggande kunskap om hur förändringar i vegetation, skogsavverkning och klimatuppvärmning efter skogsbrand av olika hårdhet interagerar med varandra och vilken betydelse dessa interaktioner har för förnyelse av plantor och markprocesser i det boreala skogslandskapet efter brand. Slutsatserna i denna avhandling kan tillämpas, i kombination med annan forskning, i beslutsfattande om skötsel av svenska skogar efter skogsbränder.

Nyckelord: avverkning av brandskadade träd, boreal skog, *B. pendula*, mark C-flöden, N-omvandlingsprocesser, *P. abies*, *P. sylvestris*, trädföryngring, växt-mark-återkoppling, skogsbrand

Författarens adress: Theresa Simona Ibáñez, Sveriges Lantbruksuniversitet Institutionen för Skogens Ekologi och Skötsel, Umeå, Sverige

Dedication

Till mina älskade föräldrar.

A tree with strong roots laughs at storms.
Malay proverb

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Ibáñez, T. S.*, Wardle D. A., Gundale, M. J., Nilsson, M-C. (2021). Effects of soil abiotic and biotic factors on tree seedling regeneration following a boreal forest wildfire. *Ecosystems*, pp 1-17. DOI: 10.1007/s10021-021-00666-0

II. Ibáñez, T. S.*, Rütting, T., Nilsson, M-C., Wardle, D. A., Gundale, M. J. Mid-term effects of wildfire and salvage logging on gross and net soil nitrogen transformation rates in a Swedish boreal forest (under review, Forest Ecology and Management)

III. Ibáñez, T. S.*, Gundale, M. J., Wardle, D. A., Strengbom, J., Barthelemy, H., Granath, G., Vishwanathan, K., Nilsson, M-C. Interactive effects of fire severity, salvage logging and climate warming on the regeneration of conifer nursery seedlings of different provenances (manuscript)

IV. Kelly, J., Ibáñez, T. S., Santín, C., Doerr, S. H., Nilsson, M-C., Holst, T., Lindroth, A., Kljun, N. (2021). Boreal forest soil carbon fluxes one year after a wildfire: effects of fire severity and management. *Global Change Biology*, 27 (17), pp 1-15. DOI: 10.1111/gcb.15721

Papers I and IV are published with open access.

*Corresponding author

The contribution of Theresa Simona Ibáñez to the papers included in this thesis was as follows:

I. Planned and designed the research with co-authors. Performed fieldwork, experiments and analyzed the data with support from DAW and MJG. Lead the writing of the manuscript and all authors contributed to revisions.

II. Planned and designed the research with co-authors. Performed fieldwork, experiments and analyzed data with support from TR, DAW and MJG. Lead the writing of the manuscript and all authors contributed to revisions.

III. Planned the research with MCN, MJG, DAW and JS. Performed fieldwork for seedlings data, harvested the experiment, and analyzed the data. Lead the writing of the manuscript with MCN, MJG and DAW contributed to revisions.

IV. Performed fieldwork for soil C fluxes measurements and part of microclimate data. Performed data analysis together with JK. Contributed to revisions of the manuscript.

1. Introduction

1.1 Wildfire in boreal forest

Wildfire is a natural disturbance in the boreal forest, and alters vegetation dynamics, regeneration, species diversity, soil properties and ecosystem functioning (Kuuluvainen and Rouvinen, 2000; Certini *et al*., 2005). Wildfire initiates secondary succession by eliminating fire-intolerant species, thereby enhancing space and nutrient availability for fire tolerant and pioneer species (Schimmel and Granström, 1996, DeLuca *et al*., 2002). Although the boreal forest is naturally adapted to wildfire, natural fire regimes have been altered because of climate change (Kasischke and Turetsky, 2006; Soja *et al*., 2007; Balshi *et al*., 2009; Ponomarev *et al*., 2016) and other anthropogenic actions such as suppression of natural wildfires (Guyette *et al*., 2002). Specifically, Sweden has during the last decade experienced a period of more intense wildfire than at any other time during the last century (Swedish Civil Contingencies Agency; https://ida.msb.se). More expansive and intense fires in boreal forests resulting from climate warming are likely to cause a higher loss of soil organic matter, more severe crown fires and higher tree mortality. These large fires are often stand replacing and are becoming much more frequent throughout the boreal region (Flannigan *et al*., 2009).

1.1.1 Climate warming and boreal forest wildfire

Fire behavior, i.e., burn probability, fire area, and fire intensity are all predicted to increase as the climate warms in much of the boreal region (de Groot *et al*., 2013), because of longer periods of extreme fire-promoting conditions, such as drought and warmer temperatures (Gillett *et al*., 2004). An increase in fire severity and impact from anthropogenic climate warming may initiate a positive feedback loop, whereby enhanced carbon release to the atmosphere may further enhance global warming (Field *et al*., 2007; Mack *et al*., 2011).

Figure 1. A low fire severity salvage logged site, with an open top chamber (OTC) positioned to test experimental warming on boreal forest tree seedling growth, studied in paper III. Photo: Theresa S. Ibáñez.

1.2 Salvage logging

Following wildfires, salvage logging is often performed, where dead and live scorched trees are removed from the area. This is often followed by soil preparation and replanting of a new production forest. Salvage logging has been shown to compact the soil (Pereira *et al*., 2018) and decrease the capacity of soils to retain water (Ginzburg and Steinberger, 2012). A removed canopy may also decrease the protection of seedlings against harsh temperatures, increase evapotranspiration and reduce soil moisture (Parro *et al*., 2015; Marcolin *et al*., 2019), and induce shift in fungal communities (Pérez-Izquierdo *et al*., 2021). However, the impact of salvage logging may vary depending on fire severity. There is therefore a need to understand the interactive effects of salvage logging and wildfire, partly because salvage logging is a common post-fire management activity, and few studies have addressed this issue.

1.3 Ecological processes following wildfire and salvage logging under climate warming

1.3.1 Tree seedling regeneration

Fires in boreal forests of Eurasia typically occur as low-intensity ground surface fires, to which many of the dominant tree species are adapted (de Groot *et al.*, 2013; Sitnov and Mokhov, 2018). Pioneer tree species such as *Pinus sylvestris* and *Betula pendula* regenerate by seeds that are dropped to the ground from surviving trees after wildfire, while *Picea abies*, which does not survive wildfires to the same extent, often recolonizes slowly by seeds that are transported from outside burnt areas (Granström, 1991; Hellberg *et al*., 2003). However, more intense stand replacing fires may change how boreal forest regenerates from wildfire disturbance (Johnstone *et al*., 2010; Alexander *et al*., 2018). Poor regeneration could be the consequence of the impact of fire on soil organic matter content (Czimczik *et al*., 2005) that can impair the functioning of soil microbial communities (Allison and Treseder 2011) and survivorship of mycorrhizal fungi (Dahlberg, 2002; Dahlberg *et al*., 2001).

Crown fires and salvage logging further opens stands up, and increases solar radiation at the ground level (Rogers *et al*., 2015), which may negatively affect regeneration of shade-tolerant species. Retention of live trees is on the other hand likely to enhance tree seedling regeneration and growth through greater turnover of soil organic nutrient pools, and this can be facilitated by their associated ectomycorrhizal fungi (Ibáñez *et al*., 2021; Peréz-Izquierdo *et al*., 2021). In contrast, logging may be beneficial for fast-growing shade-intolerant species and pioneer species because this reduces competition for light and nutrients from overstory trees (Beckage *et al*., 2008).

It is unclear how a warmer climate would affect tree seedling regeneration following wildfire and salvage logging, but key plant functional groups such as ericaceous dwarf shrubs are predicted to increase in quantity (as has been observed in tundra biomes) (Myers-Smith *et al*., 2011) which could impact seedling growth (Nilsson and Wardle 2005). This is due to several reasons such as alteration in litter decomposition rates, nutrient fluxes (De Long *et al.*, 2016), competition of nutrient resources and the production of allelochemicals against other plants (Nilsson, 1994; Jäderlund *et al.*, 1996). Hence, it is important to understand how the effects of salvage logging practices following wildfires of different intensities, and under a climate warming scenario, impact both natural and planted tree seedling regeneration (Figure 1).

1.3.2 Soil functioning

Nitrogen (N) is an important but highly limiting nutrient for plant growth in boreal forests (Högberg *et al.*, 2017). Wildfire can change N pools, either directly by volatilization which causes loss of N to the atmosphere (Certini, 2005) and combustion processes that increases the soil inorganic N pool of ammonium (NH_4^+) (Covington and Sackett, 1992), or indirectly by changing soil microbial activity (Köster *et al.*, 2021) that alters soil N transformation rates (i.e., mineralization, immobilization and nitrification processes). It is not yet fully understood how interactive effects of fire severity and salvage logging impact soil N transformation rates, even though this could in turn influence regenerating seedlings. Low severity fire retains live trees which, through uptake, can reduce loss of nitrate (NO_3^-) through leaching (Knicker, 2007). On the other hand, more severe stand-replacing fires combined with salvage logging may eliminate vegetation and greatly increase the risk on nutrient loss. Surface soil organic matter (SOM) is often more combusted after high severity fires or where smoldering occurs over extended periods (Homann *et al.*, 2011) relative to less intense fires, which can result in impairment or loss of ectomycorrhizal fungi which are important for nutrient turnover and plant growth (Day *et al.*, 2019).

Fire-induced changes in soil abiotic and biotic properties further alters carbon (C) pools in soil, aboveground biomass, and the atmosphere, partly because of alterations of C fluxes (i.e., fluxes of CO_2 and CH_4). The impact of high fire severity on soil respiration often results from a decline in autotrophic (root) respiration associated with high tree mortality (Hu *et al.*, 2017), and declines in heterotrophic (microbial) respiration from the loss of microbial biomass (Dooley and Treseder, 2012) and SOM (Keeley, 2009). As intervals between fires are projected to be shorter in the future (de Groot *et al.*, 2013), forest stands affected by multiple fire disturbances may potentially lose nutrient capital and thus show reduced soil nutrient availability (Bowd *et al.*, 2019). Therefore, stand age since the most recent fire disturbance, fire severity and salvage logging are important factors to observe for determining impacts on forest regeneration and the interactive effect of these are largely unexplored.

1.4 Objectives

The overall aim of this thesis is to understand how variation in wildfire severity and post-fire salvage logging practices affect tree seedling regeneration, and to understand how post-fire soil abiotic and biotic properties influence regeneration (Figure 2). To address this, I have used laboratory and greenhouse experiments to investigate effects of these factors on growth of *B. pendula*, *P. abies* and *P. sylvestris* seedlings grown from seeds (**paper I**) and various soil processes that drive plant nutrient supply (**paper II**) (Table 1). Further I have conducted a mesocosm field experiment to investigate the effect of fire severity, salvage logging and experimental warming on planted *P. abies* and *P. sylvestris* nursery seedlings in situ (**paper III**) and have undertaken field measurements of soil C fluxes in stands of varying fire severity and management (**paper IV**) (Table 1).

Altogether, this thesis disentangles how wildfire and salvage logging impact boreal forest tree seedling regeneration and soil properties, and offers insights about how these are altered by future climate factors such as intensified wildfires following climate warming and changes in understory vegetation. This thesis also addresses how wildfire interacts with salvage logging activities and thus contributes with fundamental knowledge needed for post-fire forest management.

All studies are conducted in, or used collected material from, the boreal forests of central Sweden. As such, the work for **papers I-III** has been performed in the Västmanland burn (following a wildfire in 2014), and **paper IV** has been conducted in the Ljusdal wildfire area burnt in 2018.

The main aim of each chapter in this thesis is:

I. To determine how the abiotic and biotic components of soil impact *B. pendula, P. abies* and *P. sylvestris* seedling growth when soils are subjected to different levels of burn severity (**paper I**).

II. To investigate how contrasting fire severity, and the interactive effects of fire and salvage logging, impacts soil N cycling processes four years after a wildfire (**paper II**).

III. To gain insights into how *P. abies* and *P. sylvestris* seedlings of different provenances may respond to fire severity and its interactions with experimental climate warming, ericaceous shrub presence and salvage logging (**paper III**).

IV. To evaluate the impacts of fire severity, salvage logging and stand maturity on forest soil greenhouse gas fluxes during the first growing season after the fire (**paper IV**).

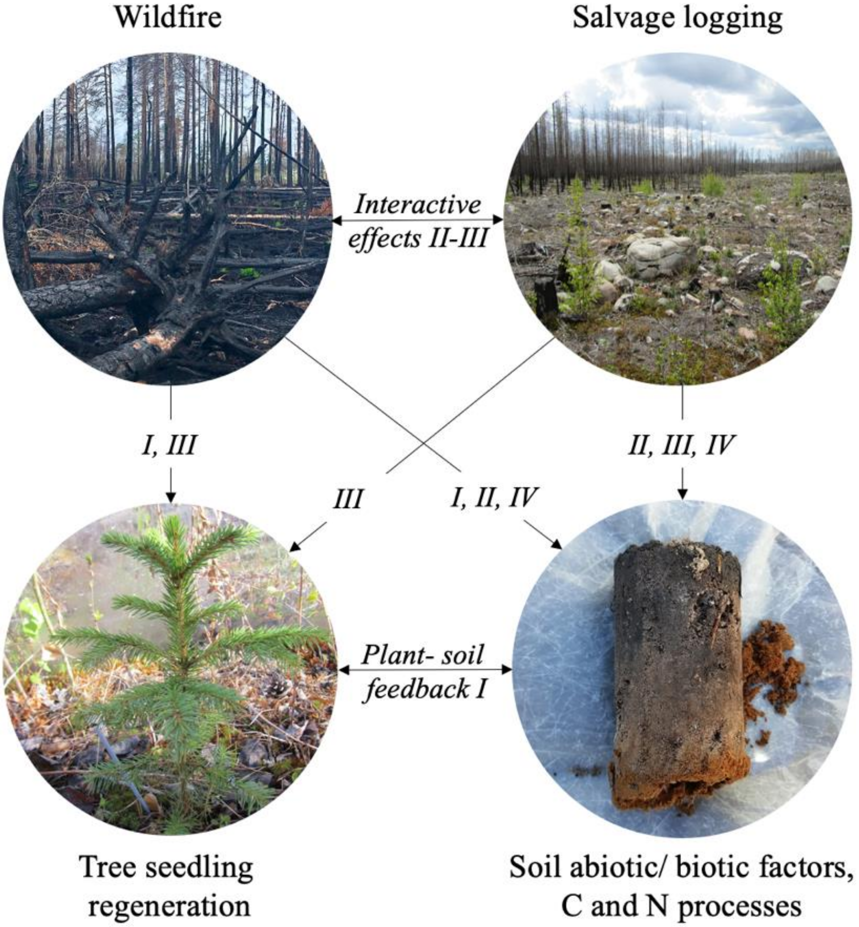


Figure 2. Conceptual framework of the direct, indirect and interactive effects of different disturbances (wildfire and salvage logging) on tree seedling regeneration (nursery seedlings planted in field and seedlings regenerated from seeds in a greenhouse) and soil system studied in this thesis. Roman numerals indicate the number of the corresponding paper. The arrows show the studied relationships between the factors and the direction of the arrows indicates factors that have an impact on tree seedlings regeneration or soil biota/ C and N processes. Text in italics explains the relation between the factors. Photos: Theresa S. Ibáñez.

2. Materials and methods

2.1 Study systems

For this thesis I have worked in two study systems in the Boreal forests of central Sweden (Figure 3).

2.1.1 The Västmanland burn

Mesocosm field studies and collection of materials for papers I-III were conducted in Västmanland (59°48’N, 16°06’E) where the Västmanland burn took place in July-August 2014 (Figure 3). The fire started due to a spark from a forestry machine and became increasingly intense because there was a long period of drought prior to the fire. The high amount of dry fuel, in combination with low air moisture and strong wind, made the fire spread quickly, and on the fifth day it developed into a severe crown fire with maximum speed of 80 m/min (Gustafsson *et al*., 2019). It burned over an area of 14 000 ha of forest land over just a few days (Lidskog *et al*., 2019). Variation in wind speeds during the fire resulted in a landscape of variable fire intensities (Figure 4). After the fire, a large portion of the burned area was set aside as a nature reserve. Portions of the burned area outside the nature reserve were salvage logged within weeks after the fire. Soils in the burned area are primarily podzols. Prior to the fire, stands were dominated by Scots pine (*Pinus sylvestris*) production forests with scattered Norway spruce (*Picea abies*) and birch (*Betula* spp.) trees, and with an understory vegetation dominated by ericaceous dwarf shrubs (*Vaccinium vitis-idaea, V. myrtillus* and *Calluna vulgaris*) and mosses (mainly *Pleurozium schreberi*). The mean annual air temperature in this region during the climate period of 1991-2020 was 6.3°C and total precipitation was 581 mm, recorded at the nearest meteorologic station in Sala 58 m.a.s.l (The Swedish Meteorology and Hydrological Institute [SMHI]).

2.1.2 The Ljusdal fire complex

For paper IV, field observations and the collection of materials were performed in a second study system in the municipality of Ljusdal (61°56′N, 15°28′E). The Ljusdal complex, consisted of three wildfires that started due to lightning strikes in July 2018, and they spread quickly because of dry fuel and wind (Figure 3). In total an area of 8 995 ha was burnt. Five months after the fire, parts of the burned area were salvage logged. The stands were located on glaciofluvial and moraine deposits under sandy soils. Prior to the fire, the area was managed as a *P. sylvestris* production forest with cohorts of varying ages (ranging from zero to 100 years), with scattered Norway spruce (*Picea abies*) and birch (*Betula* spp.). The understory vegetation prior to the fire consisted of mosses and lichens (*Cladonia* spp., *Pleurozium schreberi*, *Cetraria* sp. and *Dicranum* sp.), ericaceous shrubs (*Vaccinium vitis-idaea*, *V. myrtillus*, *V. uliginosum*, *Calluna vulgaris*, *Empetrum nigrum*, *Arctostaphylos uva-ursi*) and the grass *Avenella flexuosa*. The mean annual air temperature and total precipitation during the climate period of 1991-2020 was 2.7°C and 648 mm respectively, as recorded by the nearest national monitoring station in Ytterhogdal 263 m.a.s.l. (SMHI).

2.2 Experimental design

In the Västmanland burn, seven high and seven low fire severity stands (papers I-III), as well as seven nearby unburned stands (papers I, II) were used (Figure 4a, b, c). The stands that were selected were 40-50 years old pre-fire. Each burned stand was divided into a paired salvage logged and an unlogged site and measurements were made for these sites for papers II-III (Figure 4d). Further, for paper III, each site had four plots where two of these plots had open top chambers (OTCs) positioned as an experimental warming treatment and the other two had no OTCs and therefore experienced ambient temperatures (Figure 4e). For one of the two OTC plots, and for one of the two non-OTC plots, ericaceous shrubs were removed, while the others were left intact (paper III). Tree seedlings of *P. abies* and *P. sylvestris* of different provenances were planted in each plot (paper III) and were assessed for phenological and growth observations for three years. Soil samples were collected at the site level for estimations of total inorganic and organic nutrients. Parts of these soils were also used for a greenhouse experiment (paper I, unlogged sites of varying fire severity) and for estimations of soil N transformation rates (paper II, unlogged and salvage logged sites of varying fire severity).

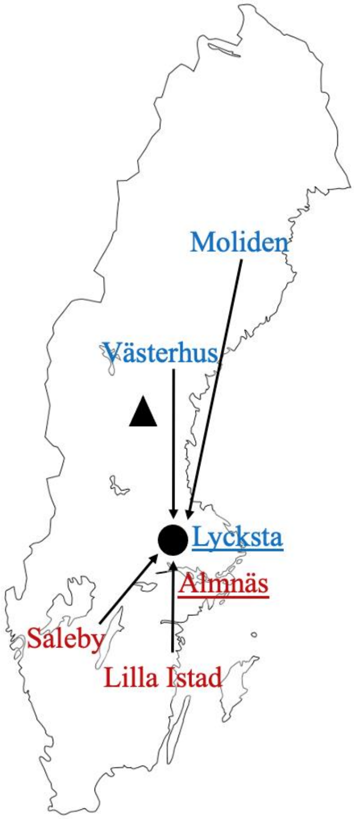


Figure 3. Map of Sweden. The circle indicates the location of the study area of the Västmanland burn that took place in 2014, and the triangle indicates the location of the study area of the Ljusdal fires that burned in 2018. Provenances of *Picea abies* are depicted in red and those of *Pinus sylvestris in blue*. Local populations are underlined. Arrows indicate the movement of different seedling provenances in Paper III. Figure created by Theresa S. Ibáñez.

The Ljusdal fire study area consisted of five stands, i.e., one unburned stand, one low fire severity stand, and three high fire severity stands. The high fire severity stands consisted of a mature forest (~100 years), a young forest (~10 years) and a salvage logged mature stand (photos of the stands are presented in paper IV). The unburned and low severity stands were both mature forests. In each stand there were ten fixed measuring points with circular collars attached to the ground for measurements of soil respiration. For both the Västmanland and Ljusdal study systems, high fire severity stands were characterized by high tree mortality (100%), whereas low fire severity stands had 70% of alive trees in the Västmanland burn and nearly 100% alive trees in the Ljusdal fire.

Figure 4. Photos from the Västmanland burn area, showing a high fire severity stand (a), low fire severity stand (b), unburned control stand (c), salvage logged site after crown fire with scattered regeneration of *Betula* spp. (d), and salvage logged site with open top chambers and colonization by *Chamaenerion angustifolium* (e). In the background of (d), an unlogged site of high fire severity is visible. Photos: Theresa S. Ibáñez.

2.3 Greenhouse experiments

Two greenhouse experiments were conducted to separate the effect of soil abiotic and biotic properties following wildfire on tree seedlings regenerated from seeds (paper I). Soil cores of ten cm depth from high, low and unburned stands were collected in September and October 2019 from high fire severity and low fire severity stands, as well as unburned stands, in the Västmanland burn. The soil was collected to the same depth (i.e., 10 cm) regardless of stand type, and the soil from different stand types therefore had different proportions of the organic soil layer versus underlying mineral soil (i.e., unburned stands consisted of only organic layer and the burned stands consisted of a mix of organic layer and mineral soil).

Figure 5. *Picea abies*, *P. sylvestris* and *B. pendula* seedlings studied in the greenhouse experiment (paper II) at the Wallenberg greenhouse at Umeå Plant Science Center. *Betula pendula* is at the front. Photo: Theresa S. Ibáñez.

Seeds of a genetic provenance that corresponded to our field area were obtained from the tree nursery Svenska Skogsplantor. The seeds were sown and germinated and seven days old seedlings of *P. abies*, *P. sylvestris* and *B. pendula* were planted in pots consisting of live soil of different fire severities for the first experiment. For the second experiment, the seedlings were planted in sterilized (gamma irradiated) soil that was reinoculated with live soil biota from the different fire severity stands (Figure 5). The second experiment therefore allowed separation of the effects of abiotic and biotic components of soil on trees seedlings regeneration. The seedlings were grown in the greenhouse for 4.5 months and thereafter harvested, oven-dried, and weighted to obtain aboveground, belowground, and total seedling biomass.

2.4 Fieldwork

2.4.1 Mesocosm experiment

A field mesocosm experiment was performed in the Västmanland burn area, where open top chambers (OTC) were positioned in stands of varying fire severity to test the effects of experimental warming on nursery tree seedlings of *P. sylvestris* and *P. abies* (Paper III). For each salvage logged and unlogged site at each stand, four plots were set up, two with OTCs installed and two without. Of these four plots, ericaceous shrubs were removed from two of them (one each with and without an OTC) on June 1-7, 2016, by gently pulling out their rhizomes to minimize disturbance in the soil and vegetation layer in two plots, and two were left intact (one with OTC and one without). The aboveground ericaceous shrubs were thereafter removed every month during the growing seasons between year 2017-2019.

Figure 6. The three provenances of *P. abies* (a) and *P. sylvestris* (b) studied in paper III. Photos: Theresa S. Ibáñez.

For each species, three seedling provenances were selected to represent one local provenance and two non-local provenances (Figure 6) while at the same time reflecting seedling transfer practices (i.e., those that are done to maximize biomass production) used in Swedish forestry. The total seedling height, shoot height, mortality, seedling damage (i.e., through dry bud, fungi, grazing) and bud set for spring and autumn were observed every month during the three growing seasons between year 2017-2019, and assessed as a response to the experimental treatment combinations. The seedlings were harvested in November 2019, oven- dried, and weighted to obtain aboveground biomass.

Figure 7. Soil respiration measurements with an Ultraportable greenhouse gas analyzer (UGGA) in a high fire severity stand in the Ljusdal fire area (paper IV). Photo: Natascha Kljun.

2.4.2 Soil C fluxes

During June to September 2019, one year after the Ljusdal fire, monthly measurements of soil C fluxes (i.e., uptake of CH_4 and release of CO_2 from the soil) at 10 positions in each of five different stands were performed with an Ultraportable greenhouse gas analyzer (UGGA) (Paper IV). At each of the ten positions per stand, a cylinder formed collar in metal was fixed into the soil. When measuring the soil C fluxes, a cylinder chamber was attached to each soil collar, which activated a closed system, and the concentration of CH_4 was decreased and CO_2 was increased from the ambient gas concentrations (Figure 7). Each measurement of soil C fluxes per collar was 5 minutes long and the linear increase of gas concentration in the chamber was further calculated. Simultaneous to each flux measurement, soil temperature and soil moisture at varying soil depths were measured.

2.4.3 Buried bag method

Net N transformation rates for the sites in Västmanland were obtained by collecting mineral soil cores from the different salvage logged and unlogged sites of varying fire severity (paper II). Five cores were placed in a polyethene bag, and then placed back in the hole they were removed from, in line with the “buried bag” net N mineralization assay (Gundale *et al.*, 2016), and left to incubate in the field for the growing season (Figure 8). In August 3-17, 2018, the buried bag cores were collected, 73 days after each bag was placed in the soil. Net N mineralization rates were obtained by calculating the inorganic N (NH_4^+ + NO_3^-) concentrations at 73 days minus that in the soil at zero days, divided by the incubation period of 73 days (Hart *et al.*, 1994).

Figure 8. Buried bag method for analyzing net N mineralization rates in mineral soil. The soil core (minus the soil organic layer) is placed in a sealed polyethene bag (a) and buried in the same hole from which the core was collected (b). The upper soil organic layer is then closing the hole and marked with a stick (c). Photos: Theresa S. Ibáñez.

2.5 Laboratory work

2.5.1 ^{15}N isotope pool dilution method

To measure gross soil N transformation rates (Figure 9), mineral soil from the different salvage logged and unlogged sites of varying fire severity were collected in the Västmanland fire area in August 2018 and brought to University of Gothenburg (paper II). Total NH_4^+ and total NO_3^- (^{14}N + ^{15}N) and $^{15}NH_4^+$ and $^{15}NO_3^-$ pools were measured at time zero and 24 hours after $^{15}NH_4$ or $^{15}NO_3^-$ injection. Gross N mineralization rates were calculated based on the rate of dilution of ^{15}N in the NH_4^+ pool, as unlabeled NH_4^+ is generated via mineralization from the organic N pool. The same calculation was performed for gross N nitrification, but here the ^{15}N labelled NO_3^- pool is diluted through new nitrification of unlabeled NH_4^+ (Hart *et al.*, 1994). The soil samples were extracted and filtered with 1 M KCl (Figure 10a), and analyzed with a SPINMAS, which is an instrument that prepares samples for inorganic nitrogen analysis and is connected to a quadrupole mass spectrometer (Figure 10b) (Stange *et al.*, 2007).

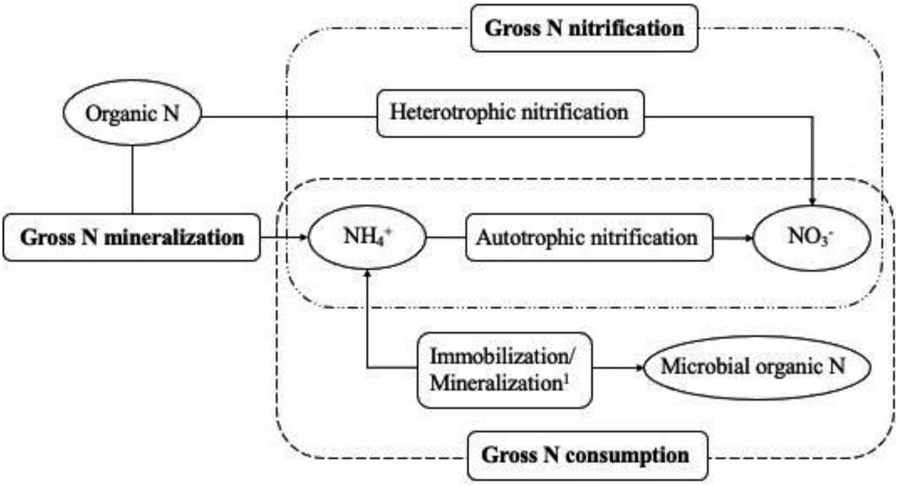


Figure 9. Schematic figure of soil nitrogen (N) cycling modified after Hart *et al.* (1994). The text in bold and the large dashed rectangles identify the transformations measured in paper II. Ellipses indicate the pools of different forms of N. Arrows indicate the direction of the process transforming N between the different pools of N.

[1] Nitrogen mineralization (microbial organic N to inorganic NH_4^+) is the reverse process of immobilization.

2.5.2 Relative microbial biomass

The substrate induced respiration (SIR) method was applied to determine the relative microbial biomass in both the mineral soil and the soil organic layer, for soils collected in the salvage logged and unlogged sites of varying fire severity at the Västmanland burn area (paper II). After the percentage of soil moisture was calculated and equalized among samples by either drying or rewetting the soil samples, a glucose solution was added and the soil was placed in sealed containers. The rate of CO_2 released from the soil was measured in the headspace of the containers using an infrared gas analyzer (EMG-4 Environmental Gas Monitor for CO_2). The increase in CO_2 concentration between one to three hours was used as a relative measure of active microbial biomass (Anderson and Domsch, 1978).

Figure 10. KCl extraction and filtration of mineral soil samples that have been isotopically labeled with ^{15}N (a). Adjustments of the SPINMAS instrument used for analyzing gross N transformation rates (b). Photos: Theresa S. Ibáñez (a), Gabriel Ibáñez (b).

2.5.3 Chemical properties of soils

Data for pH, inorganic nitrogen, Kjeldahl P and total C and N were obtained for all soils used in my thesis (papers I-IV). To determine pH, a solution- to soil ratio suspension of 0.01 M $CaCl_2$ was mixed with mineral soil (1:1) or organic soil (1:10) and left for one hour before pH was read (Thomas, 1996) (papers I, II). The pH and electrical conductivity (EC) for paper IV was measured with a sample to water ratio of 1:20; using a micropH 2000 meter and a GLP 31 meter, respectively (CRISON Instruments, S. A.). Concentrations of soil inorganic nitrogen (NH_4^+ and NO_3^-) were determined by extracting soil samples (papers I, III) and resin capsules (paper II) with 1 M KCl and further analyzing the extractions using standard colorimetric techniques with an autoanalyzer III Spectrophotometer (Omni Process, Solna, SE) (Gundale *et al*., 2016). Total concentrations of soil phosphorus (P) were determined by Kjeldahl acid digestion (G-189- 97 Rev. 3, multitest

MT7) using an Auto Analyzer 3 Spectrophotometer (Omniprocess, Solna, Sweden). Total soil carbon (C) and nitrogen (N) concentrations were determined by drying (70 C, 18 h) and grinding samples followed by dry combustion using an EA-IRMS Elemental Analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany).

2.6 Statistical analyses

The forest stands in the Västmanland burn area were classified into fire severity classes by using Principal Component Analysis (PCA) followed by K-mean clustering. For paper I, statistical analysis was performed by using split plot ANOVA with burn severity class (high, low and unburned) as a fixed factor and plant species (*P. abies, P. sylvestris* and *B. pendula*) as a sub-plot factor. For the second experiment we used a block design followed by split plot ANOVA with burn severity class and burn severity inoculum class as fixed factors and plant species as a sub-plot factor.

For paper II, response variables across three stand types of fire severity were compared by using One-Way ANOVA. A two-way split plot ANOVA (mixed effects model) was applied to evaluate how response variables responded to main and interactive effects of fire severity and post-fire management (salvage logged versus unlogged). Fire severity and post-fire treatment served as fixed factors, with post-fire treatment nested within fire severity, and stand ID serving as a random factor.

For paper III, a mixed model with a hierarchical design was used, where seedling total aboveground biomass served as the dependent variable and fire severity (high and low), salvage logging, warming (elevated, ambient), shrub removal and provenances were fixed factors. Each high and low fire severity stands had seven replicates each, and each of these stands had an ID that was paired with the level of fire severity (i.e., 3High or 5Low), which was in the model named “stand ID” and was included as a random factor. Further, to build the hierarchal levels of the experimental design in the model, we utilized random factors where salvage logging was nested within fire severity and warming and presence of shrub were randomized within each combination of fire severity and salvage logging. The model was tested in a mixed model ANOVA with the lmer4 R package.

For paper IV, soil CO_2 and CH_4 fluxes were analyzed by fitting six linear mixed-effects models consisting of one stand treatment factor (i.e., fire severity, salvage logging or stand maturity), per gas flux (i.e., CO_2 or CH_4), using the R package lme4. Each model had one treatment (fire severity, salvage logging or stand maturity) as a fixed factor, and soil temperature as continuous variable. The individual positions of measurement (i.e., the 10 collars per stand attached to the ground) were nested within each stand. When a statistically significant effect was found at $\alpha = 0.05$, Bonferroni (paper I) and Tukey’s post hoc test (papers II, III, IV) were used to explore pairwise differences between treatment means. SPSS version 24 (IBM Corp., Armonk, NY, USA) was used for the classification of the forest stands and for paper I, and R (R version 3.6.2; R Core Development Team, 2019) was used for papers II, III and IV.

Table 1. Overview of methodology included in each paper.

	Paper I	Paper II	Paper III	Paper IV
Study approach	Greenhouse experiment, laboratory analysis	Field observations, laboratory analysis	Field observations, Mesocosm, Laboratory analysis	Field observations, Laboratory analysis
Main treatment	Fire severity, soil sterilization	Fire severity, salvage logging	Fire severity, salvage logging, warming, presence of shrub	Fire severity, salvage logging, stand age
Wildfire severity	High, low, unburned	High, low, unburned	High, low	High, low, unburned
Response variable	Biomass of *P. abies*, *P. sylvestris* and *B. pendula* seedlings regenerated from seeds	Soil N transformation rates, relative microbial biomass	Biomass and growth of *P. abies* and *P. sylvestris* nursery seedlings of different provenances	Soil CH_4 and CO_2 fluxes, soil microclimate
Main methods	Controlled greenhouse, re-inoculation experiment using sterilized and non-sterilized soils	Buried bag method, Isotopic pool dilution method, substrate induced respiration (SIR)	Manipulative multi-factorial field experiment using OTCs and shrub removal in logged and unlogged sites of varying fire severity open top chamber	Soil respiration measured with Ultraportable greenhouse gas analyzer connected to closed chamber system
Chemical soil properties	Total C and N, Kjeldahl P, NH_4^+, NO_3^-, pH	Total C and N, NH_4^+ and NO_3^- in resin capsules, pH	C, N, NH_4^+, NO_3^-, pH	C, N, NH_4^+, NO_3^-, pH, water-soluble C, cation exchange capacity

3. Results and discussion

In this thesis, I investigated how soil N transformation rates, soil C fluxes, plant-soil interactions and tree seedling regeneration were influenced by wildfire severity, post-fire salvage logging, climate warming, and changes in understory vegetation. The main findings of the four papers are presented and discussed in this section, in which I link the results and new knowledge obtained from the individual papers with each other and with the overall aims of this thesis. In particular, emphasis is given on to understanding how salvage logging practices following wildfire of different severities affect tree seedling regeneration, and the circulation of soil nutrients between tree seedlings, microbial biomass and soil organic matter in the context of global warming and changes in understory vegetation.

3.1 Responses of the soil system were stronger from severe wildfire than by low intensity wildfire

Wildfires are known to immediately alter soil nutrients (NH_4^+ directly) by combustion processes (Covington and Sackett, 1992) followed by a short-term increase in NO_3^- production due to surviving or recovering nitrifying soil biota (Gundale *et al*., 2005). These effects make N more available for plant uptake. However, little is known about the mid-term effects (i.e., over four years) of wildfire severity on soil processes, which I studied in paper II. Further, as a consequence of microbial decomposer activity, CO_2 is emitted. This activity is affected by fire severity because mortality of trees can impair mycorrhizal communities (Peréz-Izquierdo *et al*., 2021), and severe fires can kill saprotrophic bacteria and fungi during combustion of the organic layer. Younger forests have a lower accumulation of the soil organic matter layer and younger trees are also more fire prone, and I therefore show in paper IV the importance of stand age when determining the effect of wildfire on soil C fluxes.

3.1.1 Wildfire altered soil N transformation rates

Four years after the Västmanland fire, severe burning increased the rate of gross soil N mineralization and ammonium consuming processes, i.e., immobilization and autotrophic nitrification (Figure 11a, b). Severe burning also decreased gross N nitrification rates (i.e., the sum of autotrophic and heterotrophic nitrification) relative to unburned soils (Figure 11c). Because gross N nitrification rates were an order of magnitude smaller than gross N consumption rates, immobilization is likely to have been the dominant pathway of gross N consumption (paper II). No alteration in net N transformation rates were observed.

Microbial immobilization can be stimulated by an increase in soil pH (Rousk *et al*., 2009), which could potentially explain the higher rates of N immobilization rates in soils of high fire severity (paper II). Laboratory measurements of SIR (substrate induced respiration; a measure of active soil microbial biomass) in mineral soil showed that the active microbial biomass was lower in burned soils than in unburned soils (paper II). This finding suggests nutrient immobilization therefore could be a function of microbial biomass change rather than absolute biomass, with immobilization being greatest when the microbial biomass is increasing over time. This would imply that soil microbial biomass was recovering after fire and thereby immobilizing N, while microbial biomass in unburned soils may have been more static or consisted of microbes with a slower turnover rate.

Overall, these results suggest that while fire causes a net loss of N from the site through organic matter combustion, it also leads to more N (per unit soil organic matter) being circulated between the non-living soil organic matter and the microbial biomass. This may serve to support higher plant growth in the long run, which could in turn lead to higher rates of new plant-derived organic matter input that would help soil organic matter stocks recover.

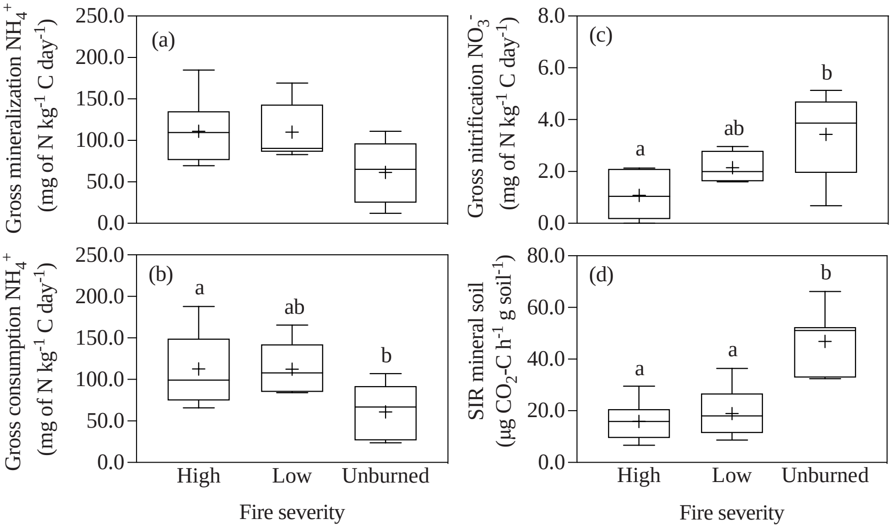


Figure 11. Mean (± SE) of gross mineralization of NH_4^+ (a), gross consumption of NH_4^+ (a) gross nitrification of NO_3^- (c) per unit soil C, and SIR (substrate induced respiration) in mineral soil (d) in soil from stands differing in fire severity (i.e., high, low or unburned). The boxes show the interquartile range, the middle line is the median and the plus sign 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 according to Tukey's post hoc post hoc tests at $P \leq 0.05$. The corresponding ANOVA results are reported in paper II. Sub-figure (a) showed significant ANOVA result at $P = 0.043$, but pairwise differences was not detected with Tukey's post hoc test.

3.1.2 High fire severity decreased soil C fluxes

Partly contrasting results of the response of microbial CO_2 respiration to fire were obtained from measurements in the laboratory using soil from the Västmanland fire area (paper II) versus field measurements in the Ljusdal fire area (paper IV). The laboratory measurements for the Västmanland burn showed microbial CO_2 respiration to be reduced in soil from both low and high fire stands compared to mineral soil from unburned stands four years post-fire (Figure 11d). In Ljusdal, one year after wildfire, high fire severity stands showed lower soil CO_2 respiration (both autotrophic root, and heterotrophic microbial respiration), compared to unburned and low fire severity stands (Figure 12) (paper IV). Here, both low fire severity and unburned stands had the same CO_2 fluxes despite a substantially thinner soil organic layer in the low fire severity stands compared to unburned due to consumption by fire. The different obtained results from the two study systems may be because the measurements were performed after different times following fire, as well as because different methods were used. If soil autotrophic respiration also would have been measured in the Västmanland burn, then the total soil CO_2 respiration potentially could have been higher in low fire severity soils, just as in the Ljusdal fire area where total CO_2 respiration was measured. Autotrophic respiration may therefore be important in determining post-fire soil CO_2 fluxes. In addition, the pulse of nutrients observed after the low intensity fire compared to after the severe intensity fire could benefit microbial activity, and hence enhance heterotrophic respiration in the low fire severity stand. From the Ljusdal study (paper IV), it was evident that stand age at the time of the wildfire also impacted the effect of fire on soil CO_2 respiration. Young stands have less time to build up the organic layer and retain nutrients after disturbance (Walker *et al.*, 2019). Young trees may also experience higher mortality (paper IV), which reduces autotrophic respiration, and heterotrophic respiration is also likely to be reduced given that the organic layer is almost completely consumed by the fire.

Overall, many of the C and N cycling responses measured in paper II and paper IV were more pronounced in the high fire severity treatments. However, this may only apply to mature forests, rather than to young forests, where multiple disturbances in young forests can in the short-term lead to reduced carbon storage capacity (Walker *et al.*, 2019). The potential future outcome for the severely burned and mature forests that I observed (in both the Västmanland and the Ljusdal fire areas) could be in line with a recent study from Alaska, which suggests that the more severe fires resulting from climate change lead to higher rates of soil C stock recovery in the longer term, despite initially resulting in higher soil C loss (Mack *et al.*, 2021) from loss of vegetation and lower nutrient turnover rates.

3.2 Responses of the soil system were more pronounced to changes in fire severity than salvage logging

Salvage logging is a common practice following wildfire in boreal forests (Leverkus *et al.*, 2018), and little is known about how it affects soil processes in boreal production forests in Sweden of varying fire severities. In paper II, I investigated the interactive effects of fire severity and salvage logging on soil N transformation rates, and in paper IV, I observed the impact of salvage logging after a severe fire on soil C fluxes. This focus is important because N is often considered the most limiting soil resource for forest growth in boreal forests (Högberg *et al.*, 2017), and results in a strong interaction between N and C cycles in these systems. Hence, changes in C and N cycling following wildfire and salvage logging are likely to be fundamental for driving plant growth and vegetation development following fire in boreal forests.

Salvage logging showed no effect on soil C fluxes (CH_4 or CO_2) one year post fire. In comparison, previous studies show contrasting results, i.e., eddy covariance measurements by Gustafsson *et al*. (2019) found higher emissions of ecosystem CO_2 in salvage logged stands, while Marañón-Jiménez *et al*. (2011) found lower soil CO_2 in salvage logged stands. In the study of paper IV (the Ljusdal fire area), salvage logging was only performed after high fire severity and the interactive effect of salvage logging and fire severity was therefore not tested in that paper. In Sweden, salvage logging is commonly used in post-fire management practice after low intensity fires. It would therefore have been interesting to also investigate the effect of salvage logging on soil CO_2 fluxes in low severity fires, where many trees survived the fire. I would have expected an alteration in soil respiration (compared to salvage logging after severe fire) because of the removal of living trees. The CO_2 fluxes of autotrophic root respiration and photosynthetic C uptake would have been impaired because of tree mortality, potentially turning the stand into a net CO_2 source.

In paper II, I found that salvage logging had no effect on soil N transformation rates four years post-fire at the Västmanland burn area. It was somewhat surprising that there was no alteration of gross N nitrification rates in the logged sites despite lower concentrations of NO_3^- adsorbed to resin capsules in mineral soil. One explanation could be that there was an uptake of NO_3^- by pioneer plant species in the logged sites (I observed high regeneration of *Betula* spp., four years post-fire), leading to no overall differences in gross N nitrification rates between logged and unlogged sites. Thus, increases in soil NO_3^- that have been shown to occur in response to fire and logging disturbance (Burns and Murdoch, 2005) may have declined four years post-disturbance because of the fast growth rate of regenerating species (Cui and Song, 2007).

Previous research in the Västmanland burn area by Peréz-Izquierdo *et al*. (2021) showed that the removal of live trees by salvage logging reduced ectomycorrhizal fungi, and it is therefore surprising that there was no corresponding alteration in soil N transformation rates in response to salvage logging found in paper II. One explanation could be that these processes may be mainly driven by bacteria and saprotrophic fungi, which could be better at carrying out soil C and N transformations than is the mycorrhizal fungal community (Maaroufi *et al*., 2019). Another explanation could be that any decline in ectomycorrhizal fungi could have been offset by an increase in bacteria and saprophytic fungi (as a consequence of the Gadgil effect; Gadgil and Gadgil, 1975), and this may have stabilized N and C cycling processes in response to logging.

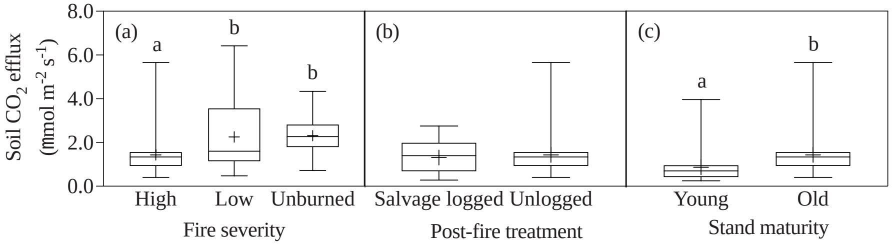


Figure 12. Soil CO_2 fluxes grouped according to responses to fire severity (a), salvage logging (b) and stand maturity (c). The boxes show the interquartile range, the middle line is the median and the plus sign is the mean. The lines extending above/below each box indicate the maximum/minimum data values. Different letters above or below each boxplot denote significant differences in the fluxes between the sites according to Tukey's post hoc post hoc tests at $P \leq 0.05$. The corresponding ANOVA results are reported in paper III.

Overall, these findings suggest that the soil processes studied in paper IV (the Ljusdal fire area, one year post-fire) were more resistant to salvage logging after severe fires, and for the soil processes studied in paper II (the Västmanland burn area, four years post-fire), this robustness was observed, but regardless of the level of fire severity. Alternatively, the results are an indication that any changes to soil processes that may have occurred in the short-term following salvage logging reverted back to the original state relatively quickly. Despite these findings, numerous other studies have shown that salvage logging can affect other ecosystem properties or processes. For example, a study conducted in a *P. sylvestris* forest in Italy (Marcolin *et al.*, 2019) showed that salvage logging enhances solar radiation at the ground, which increases soil temperature and decreases soil moisture, which could potentially impair forest regeneration. Marañón-Jiménez and Castro (2013) showed for a Mediterranean pine forest that salvage logging reduced SOM and nutrient availability. Further, salvage logging of dead trees may result in reduced C storage over time (Powers *et al.*, 2013).

3.3 Responses of tree seedling regeneration to wildfire and salvage logging were species specific

Lower intensity wildfires that occur as ground fires are more common than are stand replacing crown fires in Eurasian boreal forest (de Groot *et al.*, 2013; Sitnov and Mokhov, 2018), whereas stand replacing fires are more common in North America (Rogers *et al.*, 2015). However, with the changing climate and the predicted risk of more severe stand replacing fires throughout the circumboreal boreal forest zone in the future, there is a need to better understand the interactive effect of fire severity and salvage logging on forest regeneration. To fill this knowledge gap for Swedish boreal forests, in paper III, I investigated how nursery conifer seedlings of different provenances are affected by fire severity, salvage logging, experimental warming and changes in understory vegetation. In addition to this, in paper I, I set up a greenhouse experiment to separate the effects of abiotic and biotic soil properties on conifer and deciduous tree seedlings (regenerated from seeds) in soils that had been exposed to different fire severities (Figure 13). As climate warming is being accompanied by novel fire regimes in the boreal zone, there is a growing need to further understand the role played by both soil abiotic factors and the soil microbial community in promoting early seedling establishment under different fire scenarios.

3.3.1 Growth of nursery seedlings of conifers was the poorest in unlogged sites following low intensity wildfire

While I observed a small effect of salvage logging on the soil system in paper IV, I found an interactive effect of salvage logging and fire severity on the growth of nursery seedlings of *P. abies* and *P. sylvestris,* where both conifers grew worst in unlogged sites of low fire severity. The weaker response of seedling growth to non-logging in low fire severity stands could be because competition from the over- and understory vegetation may have also been stronger in these stands, such as from re-sprouting *Vaccinium vitis-idaea* (Table S2 in Paper III). Apart from that both species grew least in low fire severity unlogged sites, the two conifer species responded a bit different compared to each other. First, *P. sylvestris* seedlings grew best in salvage logged sites regardless of fire severity, and in high fire severity unlogged sites (Figure 14e). This effect occurred despite minor changes in total soil nutrients, and no changes in soil nutrients turnover between salvage logged and unlogged sites (paper II). With both crown fires and salvage logging opening up sites by eliminating canopy cover and tree stems, this suggests that enhanced light availability (and potentially also reduced resource competition from overstory trees) are important for promoting *P. sylvestris* tree seedling growth. Second, *P. abies* grew better in low fire severity salvage logged sites compared to low fire severity unlogged sites (Figure 14a). One explanation could be that salvage logged sites of low fire severity had high naturally regeneration of *B. pendula* as well as naturally regenerating *P. sylvestris* and *Populus tremula* (Table S2 in paper III), and the shade tolerant, late successional *P. abies* is known to grow well under a *B. pendula* canopy (Valkonen and Valsta, 2001). Overall, the study of paper III strengthens the idea of that the two conifer species are differently driven by abundance of light.

3.3.2 Soil biota from low fire severity stands enhance growth of conifer species in the greenhouse, but deciduous species may have an advantage after severe fire

The greenhouse study (paper I) showed that soil biota from low fire severity stands increased conifer (*P. abies* and *P. sylvestris*) seedling growth, while a deciduous tree species (*B. pendula*) was unresponsive to effects of soil biota (Figure 13b). This was shown in two greenhouse pot experiments with soils from high and low burn severity stands and from unburned stands, and the second of these experiments allowed separation of the effects on seedlings of soil abiotic and biotic properties in these stands through sterilization of soil followed by reinoculation of live biota. However, all three seedling species showed increased growth when grown in soils from unburned compared to burned stands for the first experiment, and in the second experiment all species responded positively to abiotic soil factors for the unburned stands. This occurred because unburned soil had higher amount of organic matter that could be mineralized and transferred to seedlings while the burned soil consisted of mostly mineral soil with fewer nutrients. Also, for the second experiment, sterilization of the soil released nutrients from the organic soil, which the unburned soil had the most of. I therefore suggest that the differences in availability of nutrients (i.e., abiotic soil properties) rather than in soil biota among soil types were the primary driver of growth differences for seedlings following wildfire in the greenhouse experiment.

When soils were re-inoculated with live soil, a positive response of biota from low fire severity soils was found for conifers, and particularly for *P. abies* (paper I), that grew larger from this treatment. This result may be explained by a higher survival of the overstory trees after a low severity fire, as well as survival of ectomycorrhizal fungi, which could have maintained the symbiotic relationship between the trees and the ectomycorrhizal community (Dahlberg, 2002; Pérez-Izquierdo *et al*., 2021). The soil from low fire severity stands that was brought into the greenhouse could then further initiate new symbiotic relations of ectomycorrhizal networks with regenerating seedlings, after a low compared to a high severity fire. Fire may also induce a functional shift in microbial community composition (Clemmensen *et al*., 2015) towards taxa that are more beneficial for seedling growth. Further, it is known that the community composition of ectomycorrhizal fungi associated with *P. abies and P. sylvestris* can overlap (Menkis *et al*., 2005), which could explain why seedlings of both conifers, but not *B. pendula*, responded positively to soil biota from low fire severity soils. Interestingly, the responses of the late successional and shade tolerant *P. abies* to soil biota were the most pronounced. In a field experiment, Stuiver *et al*. (2015) found strong support for *P. abies* responding more positively to soils from old forests than those from clear felled sites, which also supports the suggestion that ectomycorrhizal fungi have an important role for growth of *P. abies*.

Fast-colonizing deciduous tree species such as *B. pendula* (Hellberg *et al*., 2003; Gustafsson *et al*., 2019), that are effective at exploiting initial elevated levels of inorganic N resulting from fire disturbance (Gundale *et al*., 2005), are expected to become more abundant in the forested landscape if climate warming increases and higher burn severity conditions prevail (Mekonnen *et al*., 2019; Mack *et al*., 2021). The greenhouse experiments in paper I indicate that stand replacing (crown) wildfires may result in higher regeneration of *B. pendula*, even if the soil biota has been lost during fire.

High abundance of natural regeneration of *B. pendula* has previously been observed in burned (salvage logged) stands in the Västmanland burn area (Gustafsson *et al.*, 2021). Further, from the results of the greenhouse experiment, I suggest that stand replacing fires may result in poorer regeneration of conifers, unless the soil biota is maintained or has recovered from the disturbance. Hence, regeneration of conifers may be promoted when grown in soil with biota from low fire severity stands. These results suggest that plant-soil interactions are modified by wildfire severity, and that these responses are plant-species specific.

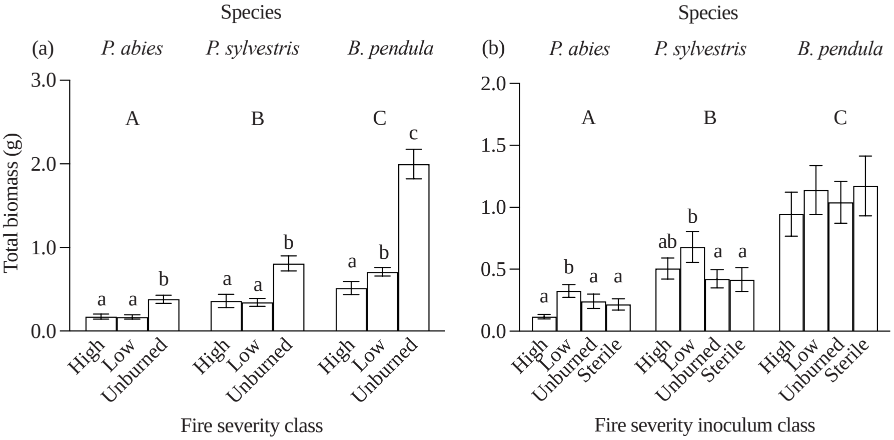


Figure 13. The Separated effects of soil abiotic (a) and biotic (b) components of soil of different fire severity. Mean ± SE of total biomass for tree seedlings of *Picea abies, Pinus sylvestris* and *Betula pendula* regenerated from seeds in a greenhouse experiment. Seedlings were grown on sterilized (gamma irradiated) soil, originating from stands differing in fire severity (that is, high, low and unburned), and with the sterilized soil then reinoculated with live soil from stands differing in fire severity (high, low and unburned) or with sterile soil. Different capital letters above bar groups indicate significant differences between plant species across fire severity inoculum class treatments, and small letters within bar groups indicate significant differences for fire severity classes (a) or fire severity inoculum class treatments (b) according to Bonferroni post hoc tests at $P \leq 0.05$. Corresponding ANOVA results (*F*- and *P*-values) are reported in paper I.

3.3.3 Severe wildfire impacts *P. sylvestris* seedling growth positively in the field but not in the greenhouse

In the field, I found a higher aboveground biomass of *P. sylvestris* nursery seedlings grown in high fire severity stands compared to when grown in low severity stands (paper III). In contrast to this, in the greenhouse experiment (paper I), I found no difference in growth of conifer seedlings between those planted in soils from stands of high versus low fire severity (Figure 13a). Instead, these seedlings grew the best in unburned soil. When soil abiotic and biotic factors were separated in the greenhouse experiment, the conifer seedlings grew best when subjected to biota from low fire severity soils (Figure 13b). However, these positive effects were not evident in the field experiment (paper III).

One explanation to help reconcile these disparate results between the field and greenhouse studies may be the constant light in the greenhouse experiment. In addition, the seedlings in the greenhouse were regenerated from seeds, and not nursed in pots with soil containing fertilizers and mycorrhizal fungi, as are nursery seedling produced for forest replanting, such as we used in the field study. The seedlings in the field might therefore have been less dependent on allocating resources to increase uptake of soil nutrients and were instead allocating resources to grow aboveground. This increase in growth for *P. sylvestris* was more pronounced in salvage logged sites of high fire severity since these sites were more exposed to light abundance. Seedlings grown without nutrient amendments in the greenhouse did potentially establish symbiotic relations with mycorrhizal fungi in the pots to enable nutrient uptake to a greater extent and much earlier than were the nursery seedlings that would have been established with nutrient additions. This pattern suggests that light conditions are relatively more important than are nutrient conditions for regulating seedling growth of *P. sylvestris* seedlings during the first few years after planting.

However, more information on naturally regenerated seedlings in field would help to establish a greater degree of accuracy on this matter. It remains to elucidate if the longer-term role of alive overstory trees with maintained soil biota after low severity fires has an impact on forest recovery, and whether or not this might be more important for naturally regenerated seedlings, and particularly that of *P. abies*.

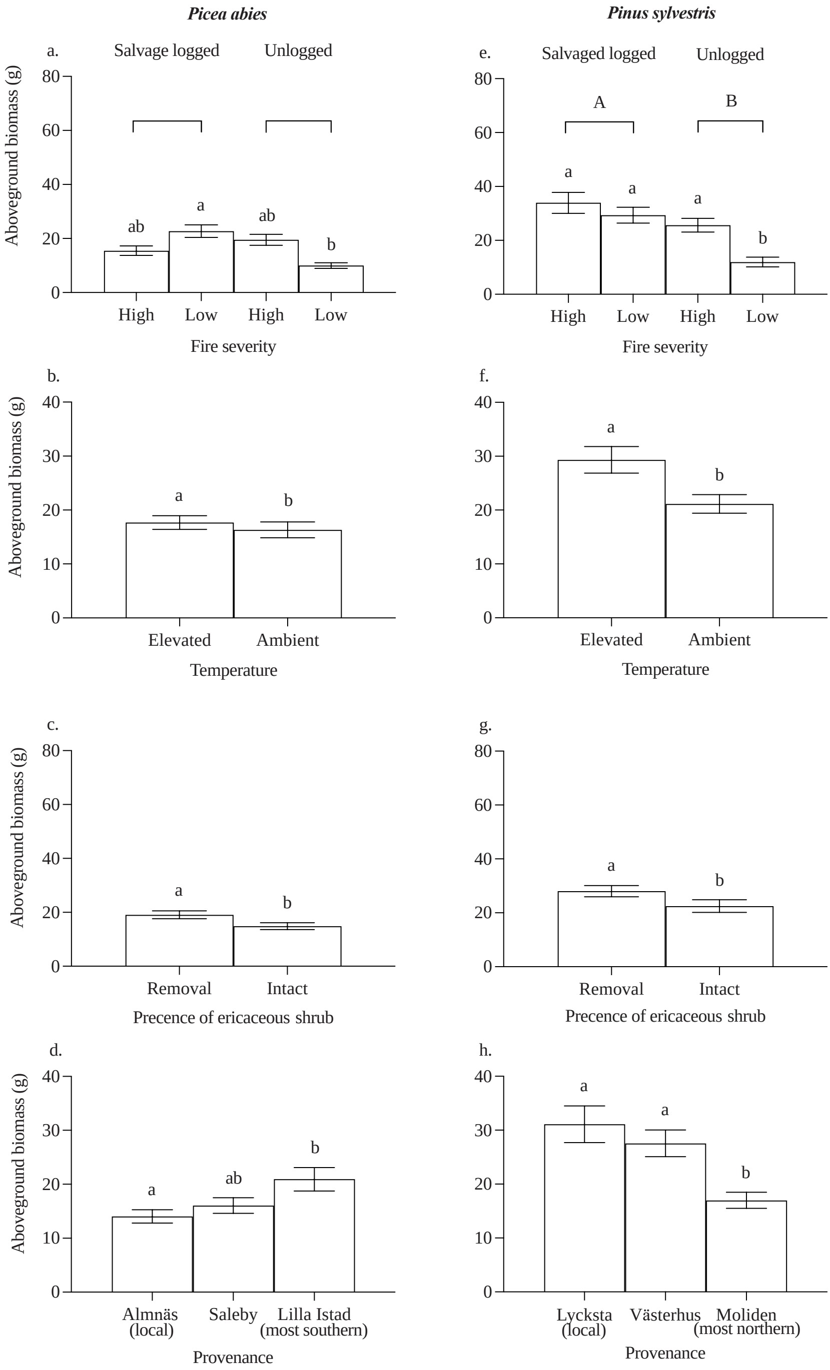

Picea abies
Pinus sylvestris
a.
Salvage logged
Unlogged
Aboveground biomass (g)
80
60
40
20
0
ab
a
ab
b
High
Low
High
Low
Fire severity
e.
Salvaged logged
Unlogged
A
B
a
a
a
b
High
Low
High
Low
Fire severity
b.
40
30
20
10
0
a
b
Elevated
Ambient
Temperature
f.
a
b
Elevated
Ambient
Temperature
c.
a
b
Removal
Intact
Precence of ericaceous shrub
g.
a
b
Removal
Intact
Precence of ericaceous shrub
d.
a
ab
b
Almnäs (local)
Saleby
Lilla Istad (most southern)
Provenance
h.
a
a
b
Lycksta (local)
Västerhus
Moliden (most northern)
Provenance

Figure 14. Mean ± SE of total aboveground biomass of *P. abies* (a-d) and *P. sylvestris* (e-h) nursery seedlings in field of the Västmanland burn, in response to fire severity and salvage logging (a, e), warming treatment (b, f), shrub removal and fire severity (c, g), of each provenance (d, h). Capital letters indicate statistical significance among pairs of bars and lower-case letters indicate significance among individual bars, according to Tukey's post hoc test at $P \leq 0.05$. Corresponding ANOVA results are reported in in paper IV.

3.4 Post-fire experimental warming enhances seedling growth

During the last decade Sweden has experienced a period of more intense wildfire than at any time during the last century (Swedish Civil Contingencies Agency; https://ida.msb.se) because of higher summer temperatures and longer periods of drought (Aakala *et al*., 2017, Granström 2018). Further, it is predicted that the warmer and longer growing season of northern forests resulting from climate warming will improve tree growth rates and ecosystem productivity (Bergh *et al*., 2003; Kellomäki *et al*., 2018; Devi *et al*., 2020), in part through elevated spring temperatures stimulating earlier bud burst and promoting photosynthesis and C assimilation capacity (Bergh *et al*., 2003). Sustained periods of droughts, greater fire severity and salvage logging may all impact the integrity of soils and capacity to maintain moisture (Marcolin *et al*., 2019) and understory vegetation abundance and composition. However, little is known about their interactive effects. I therefore wanted to test how post-fire experimental warming in salvage logged and unlogged sites affected the growth of planted *P. abies* and *P. sylvestris* nursery seedlings of different provenances, when fire severity varied, and in the presence or absence of understory shrubs.

Experimental warming increased aboveground seedling biomass for both conifer species independently of the other factors (i.e., fire severity, salvage logging, shrub removal) (paper III). This could be due to warming enhancing rates of nutrient cycling and supply in the soil (Hartley *et al*., 1999), or for *P. sylvestris*, promoting plant photosynthesis rates (Kurepin *et al*., 2018). It is somewhat surprising that warming increased the biomass and height of *P. abies* seedlings, because it is recognized from some greenhouse experiments that the genus *Picea* is vulnerable to warming because it has low plasticity in its photosynthetic and respiratory metabolism (Kurepin *et al*., 2018; Dusenge *et al*., 2020). These seedlings may have grown taller in the warming treatment to access light, because other plants (such as grasses and naturally established fast-growing deciduous trees) also grew taller in the warmed plots and therefore caused more severe competition for light. Overall, this study (paper IV) showed that warming increased seedlings aboveground biomass for both conifer species.

3.4.1 Tree seedlings provenances

Tree provenances are widely used in forestry in Northern Europe to enhance seedling survival and growth, and thus wood production (Handler *et al*., 2018; Hayatgheibi *et al*., 2020). In study III, I observed that when nursery seedlings of the most northerly provenance of *P. sylvestris* were moved south across a large latitudinal range to the study area, they grew worse than did the other provenances. One interesting finding was that when these *P. sylvestris* seedlings were also grown in plots subjected to experimental warming, they instead responded with enhanced height and grew the same as the other provenances (paper III). This finding, while preliminary, suggests that in a future warmer climate, *P. sylvestris* provenances could be moved substantially south (i.e., by 5° of latitude) than is typically used today, and still perform similarly to local provenances.

3.4.2 Presence of ericaceous shrubs

Key plant functional groups that survive fires may serve as competitors for regenerating tree seedlings. Further, climate warming is expected to enhance ericaceous shrub cover, which was shown in a tundra ecosystem by a study of Myers-Smith *et al*. (2011). These shrubs can be detrimental to seedling regeneration because they are strong resource competitors towards other plants, they can produce allelochemicals against other plants (Nilsson, 1994; Jäderlund *et al*., 1996), and they adversely affect litter decomposition and nutrient fluxes (De Long *et al*., 2016), all of which impair tree seedling regeneration and growth (Nilsson and Wardle, 2005). The growth of the seedlings observed in paper III decreased in the presence of ericaceous shrubs, however my data did not show any evidence that this effect was impacted or amplified by warming.

4. Conclusions and implications

The results of my thesis lead to several conclusions and the summary of my main findings are found in Table 2. First, this thesis shows that some soil N transformations responded to fire severity. Specifically, gross mineralization and consumption rates increased with increasing fire severity, and gross N nitrification decreased. I conclude that during the fire, when soil organic matter was combusted, there may be an initial net loss of N capital while at the same time more N will circulate between the different pools of inorganic and organic nitrogen (including the non-living soil organic matter and the microbial biomass). This circulation of nutrients may be beneficial for tree seedling regeneration, and could lead to a higher rate of organic matter building up during post-fire recovery as the seedlings grow and provide organic inputs over time. Given that some of the responses to burning of C and N cycling and growth of nursery tree seedlings in this thesis were most evident in the high burn severity stands, it is possible that a more severe wildfire may both cause a higher immediate C loss and a higher recovery rate of soil C stock over time.

Second, I observed that salvage logging had little impact on the measured soil processes in this study, i.e., on soil C fluxes after one year, and soil N transformation rates after four years post fire and logging practices. Salvage logging had, however, a greater impact on the regeneration of conifer nursery seedlings than on the soil processes. The two conifer species produced the least aboveground biomass when planted in unlogged sites of low fire severity. Further, *P. sylvestris* grew the best in sites where the canopy had been removed (by high fire severity or salvage logging), and biomass of *P. abies* was enhanced in sites that had been salvage logged and were of low fire severity. The fast-growing *P. sylvestris* enhanced in biomass when it had greater access to light and the shade tolerant late successional *P. abies* enhanced biomass when growing in the vicinity of naturally regenerated, fast-growing deciduous tree species. In addition, these varying responses of the two conifer species to salvage logging after high and low fire severity occurred despite no observed differences in nutrient turnover between salvage logged and unlogged sites. I therefore conclude that nursery tree seedling regeneration of *P. sylvestris* appeared to benefit from the enhanced light and reduced competition following wildfire and salvage logging, and that regeneration of *P. abies* is supported in salvage logged sites of low fire severity. However, in this thesis I do not address the question about overall ecosystem resilience of boreal forest ecosystems to salvage logging following wildfires of varying severities. Other parts of the ecosystem (e.g., mycorrhizal fungi) have shown to be severely affected by salvage logging (Pérez-Izquierdo *et al*., 2021) and to draw a conclusion about the overall impact of salvage logging; flora and fauna biodiversity, biotic and abiotic soil properties and processes of the ecosystem need to be considered across a variety of spatial and temporal (e.g., long term) scales.

Third, soil biota from low fire severity stands enhanced regeneration of *P. abies* and *P. sylvestris* seedlings from seeds in the greenhouse, while *B. pendula* growth was driven mainly by abiotic soil properties following wildfire. Thus, the results indicate that the biotic responses of seedling regenerated from seed were species specific. All species responded, however, positive to soil nutrients, since they all grew under the same light conditions and grew better in soils of unburned stands which had the highest concentrations of available nutrients. Altogether, this specific study (paper I) disentangled the effects of soil abiotic and biotic properties on boreal forest tree seedling regeneration following wildfire of varying severity. To my knowledge, no previous study in the boreal forest has explicitly addressed this issue. The findings of the greenhouse study contrast with the results for the field-planted *P. sylvestris* nursery seedlings, which showed higher growth when grown in high fire severity stands. Reconciling these two studies, it suggests that while light, nutrients, and soil microbes are all important for regeneration, light appears to be relatively more important.

Fourth, this thesis shows that warming directly increases seedling growth. Under experimental warming, an extreme southern movement of the northenmost *P. sylvestris* provenance grew just as well in total height as the other provenances that were moved within a latitude range that is suggested in forestry. This suggests that provenances may be less sensitive to translocation within a larger latitudinal range in a warming climate. However, climate warming might also indirectly affect tree seedling regeneration negatively, since warming is projected to increase the abundance of ericaceous shrubs, which may compete with tree seedlings for space and resources. In line with this, my data showed that shrubs had a negative impact on seedling growth, although I found no evidence that this negative effect was amplified by warming.

Finally, the findings of this thesis have important applied implications for research and management practice; (i) they increase our understanding of how regeneration and soil processes are altered following wildfire and salvage logging in Swedish boreal production forests. The data showed that factors such as light, competition, soil nutrients and soil biota served as important controls on forest regeneration after wildfire and salvage logging, and that these factors had varying impact on different tree species; and (ii), this thesis contributes with new knowledge (together with other research) needed for the application of post-fire management practice. In a changing environment, with warmer conditions and more frequent and intense fires, forest management practices need to consider these future conditions that prevail.

Table 2. Responses of tree seedling regeneration and soil processes to main and interactive effects of fire severity (high or low or unburned) and salvage logging (SL) or non-logging (NL), main effects of elevated (E) or ambient (A) temperature and removal (R) and presence (P) of ericaceous shrubs. Responses are marked with green arrow up (positive response), orange arrow down (negative response) or blue tilted arrow (intermediate effect, i.e., not statistically significant towards the other levels). Black circle indicates no observed response. Blank space means that the response was not tested for that specific factor.

		High fire severity[2]		Low fire severity[2]		Unburned	Warming		Ericaceous shrubs	
	Response variable	SL	NL	SL	NL	NL	E	A	R	P
Biomass of nursery seedlings in field	*Pinus sylvestris*	↑	↑	↑	↓		↑	↓	↑	↓
	Picea abies	↗	↗	↑	↓		↑	↓	↑	↓
Biomass of tree seedlings regenerated from seeds in greenhouse	Soil abiotic factors									
	Pinus sylvestris		↓		↓	↑				
	Picea abies		↓		↓	↑				
	Betula pendula		↓		↓	↑				
	Soil biotic factors									
	Pinus sylvestris		●		↑	↓				
	Picea abies		↓		↑	↓				
	Betula pendula		●		●	●				
Soil processes	Gross N mineralization rate	●	↑	●	↗	↓				
	Gross N consumption rate	●	↑	●	↗	↓				
	Gross N nitrification rate	●	↓	●	↗	↑				
	Soil CO_2 respiration	●	↓		↑	↑				
	Soil CH_4 uptake	●	●		●	●				
	SIR[1]	●	↓	●	↓	↑				
	NO_3^- resin capsule[3]	↓	↑	↓	↑					

[1] Substrate induced microbial respiration.

[2] Main effect of fire severity in unlogged sites or interactive effect between fire severity and salvage logging.

[3] No interactive effect and only main effect observed, where mineral soil NO_3^- concentrations were lower in salvage logged sites compared to unlogged.

References

Aakala, T., Pasanen, L., Helama, S., Vakkari, V., Drobyshev, I., Seppä, H., Kuuluvainen, T., Stivrins, N., Wallenius, T., Vasander, H., Holmström, L. (2018). Multiscale variation in drought controlled historical forest fire activity in the boreal forests of eastern Fennoscandia. Ecological Monographs, 88(1), 74-91. https://doi.org/10.1002/ecm.1276

Alexander, H. D., Natali, S. M., Loranty, M. M., Ludwig, S. M., Spektor, V. V., Davydov, S., Zimov, N., Trujillo, I., Mack, M. C. (2018). Impacts of increased soil burn severity on larch forest regeneration on permafrost soils of far northeastern Siberia. Forest Ecology and Management, 417, 144-153. http://doi.org/10.1016/j.foreco.2018.03.008

Allison, S. D., Treseder, K. K. (2011). Climate change feedbacks to microbial decomposition in boreal soils. Fungal Ecology, 4(6), 362-374. https://doi.org/10.1016/j.funeco.2011.01.003

Anderson, J. P. E., Domsch, K. H. (1978). A physiological method for the quantitative measurement of microbial biomass in soils. Soil biology and biochemistry, 10(3), 215-221. https://doi.org/10.1016/0038-0717(78)90099-8

Angelstam, P., Kuuluvainen, T. (2004). Boreal forest disturbance regimes, successional dynamics and landscape structures: a European perspective. Ecological Bulletins, 117-136.

Balshi, M.S., McGuire, A.D., Duffy, P., Flannigan, M., Walsh, J., Melillo, J. (2009). Assessing the response of area burned to changing climate in western boreal North America using a Multivariate Adaptive Regression Splines (MARS) approach. Global Change Biology, 15(3), 578-600. https://doi.org/10.1111/j.1365-2486.2008.01679.x

Beckage, B., Kloeppel, B. D., Yeakley, J. A., Taylor, S. F., Coleman, D. C. (2008). Differential effects of understory and overstory gaps on tree regeneration1. The Journal of the Torrey Botanical Society, 135(1), 1-11. https://doi.org/10.3159/07-RA-034.1

Bergh, J., Freeman, M., Sigurdsson, B., Kellomäki, S., Laitinen, K., Niinistö, S., Peltola, H., Linder, S. (2003). Modelling the short-term effects of climate change on the productivity of selected tree species in Nordic countries. Forest Ecology and Management, 183(1-3), 327-340. https://doi.org/10.1016/S0378-1127(03)00117-8

Bowd, E. J., Banks, S. C., Strong, C. L., Lindenmayer, D. B. (2019). Long-term impacts of wildfire and logging on forest soils. Nature Geoscience, 12(2), 113-118. https://doi.org/10.1038/s41561-018-0294-2

Burns, D. A., Murdoch, P. S. (2005). Effects of a clearcut on the net rates of nitrification and N mineralization in a northern hardwood forest, Catskill Mountains, New York, USA. Biogeochemistry, 72(1), 123-146. https://doi.org/10.1007/s10533-004-0355-z

Certini, G. (2005). Effects of fire on properties of forest soils: a review. Oecologia, 143(1), 1-10. https://doi.org/10.1007/s00442-004-1788-8

Clemmensen, K. E., Finlay, R. D., Dahlberg, A., Stenlid, J., Wardle, D. A., Lindahl, B. D. (2015). Carbon sequestration is related to mycorrhizal fungal community shifts during long-term succession in boreal forests. New Phytologist, 205(4), 1525-1536. https://doi.org/10.1111/nph.13208

Covington, W. W., Sackett, S. S. (1992). Soil mineral nitrogen changes following prescribed burning in ponderosa pine. Forest Ecology and Management, 54(1-4), 175-191. https://doi.org/10.1016/0378-1127(92)90011-W

Cui, X., Song, J. (2007). Soil NH 4+/NO 3− nitrogen characteristics in primary forests and the adaptability of some coniferous species. Frontiers of Forestry in China, 2(1), 1-10. https://doi.org/10.1007/s11461-007-0001-8

Czimczik, C. I., Schmidt, M. W. I., Schulze, E. D. (2005). Effects of increasing fire frequency on black carbon and organic matter in Podzols of Siberian Scots pine forests. European Journal of Soil Science, 56(3), 417. https://doi.org/10.1111/j.1365-2389.2004.00665.x

Dahlberg, A. (2002). Effects of fire on ectomycorrhizal fungi in Fennoscandian boreal forests. Silva Fennica, 36(1), 69-80.

Dahlberg, A., Schimmel, J., Taylor, A. F., Johannesson, H. (2001). Post-fire legacy of ectomycorrhizal fungal communities in the Swedish boreal forest in relation to fire severity and logging intensity. Biological Conservation 100(2), 151-161. https://doi.org/10.1016/S0006-3207(00)00230-5

Day, N. J., Dunfield K. E., Johnstone, J. F., Mack, M. C., Turetsky, M. R., Walker, X. J., Baltzer, J, L. (2019). Wildfire severity reduces richness and alters composition of soil fungal communities in boreal forests of western Canada. Global change biology 25(7), 2310-2324. https://doi.org/10.1111/gcb.14641

de Groot, W. J., Flannigan, M. D., Cantin, A. S. (2013). Climate change impacts on future boreal fire regimes. Forest Ecology and Management, 294, 35-44. https://doi.org/10.1016/j.foreco.2012.09.027

De Long, J. R., Dorrepaal, E., Kardol, P., Nilsson, M. C., Teuber, L. M., Wardle, D. A. (2016). Understory plant functional groups and litter species identity are stronger drivers of litter decomposition than warming along a boreal forest post-fire successional gradient. Soil Biology and Biochemistry, 98, 159-170. https://doi.org/10.1016/j.soilbio.2016.04.009

DeLuca, T., Nilsson, M.C., Zackrisson, O. (2002). Nitrogen mineralization and phenol accumulation along a fire chronosequence in northern Sweden. Oecologia, 133(2), 206-214. https://doi.org/10.1007/s00442-002-1025-2

Devi, N. M., Kukarskih, V. V., Galimova, A. A., Mazepa, V. S., Grigoriev, A. A. (2020). Climate change evidence in tree growth and stand productivity at the upper treeline ecotone in the Polar Ural Mountains. Forest Ecosystems, 7(1), 1-16. https://doi.org/10.1186/s40663-020-0216-9

Dooley, S. R., Treseder, K. K. (2012). The effect of fire on microbial biomass: a meta-analysis of field studies. Biogeochemistry 109, 49–61. https://doi.org/https://doi.org/10.1007/s10533-011-9633-8

Dusenge, M. E., Madhavji, S., Way, D. A. (2020). Contrasting acclimation responses to elevated CO_2 and warming between an evergreen and a deciduous boreal conifer. Global change biology, 26(6), 3639-3657. https://doi.org/10.1111/gcb.15084

Field, C. B., Lobell, D. B., Peters, H. A., Chiariello, N. R. (2007). Feedbacks of terrestrial ecosystems to climate change. Annual Review of Environment and Resources, 32, 1-29. https://doi.org/10.1146/annurev.energy.32.053006.141119

Flannigan, M., Stocks, B., Turetsky, M., Wotton, M. (2009). Impacts of climate change on fire activity and fire management in the circumboreal forest. Global change biology, 15(3), 549-560. https://doi.org/10.1111/j.1365-2486.2008.01660.x

Gadgil, P. D., Gadgil, R. L. (1975). Suppression of litter decomposition by mycorrhizal roots of Pinus radiata. New Zealand Forest Service.

Gillett, N.P., Weaver, A.J., Zwiers, F.W., Flannigan, M.D. (2004). Detecting the effect of climate change on Canadian forest fires. Geophysical Research Letters, 31(18). https://doi.org/10.1029/2004GL020876

Ginzburg, O., Steinberger, Y. (2012). Salvage logging versus natural regeneration post-fire practices in a forest: soil chemical and microbial aspects. Open Journal of Ecology, 2(1), 29-37. http://dx.doi.org/10.4236/oje.2012.21004

Granström A. (1991). Skogen efter branden. Skog & Forskning, 4(91), 32-38.

Granström, A. (2018). Brandsommaren 2018 - Vad hände och varför? Report. Karlstad, Sweden: MSB.

Gundale, M. J., DeLuca, T. H., Fiedler, C. E., Ramsey, P. W., Harrington, M. G., Gannon, J. E. (2005). Restoration treatments in a Montana ponderosa pine forest: effects on soil physical, chemical and biological properties. Forest Ecology and Management, 213(1– 3), 25–38. https://doi.org/10.1016/j.foreco.2005.03.015

Gundale, M. J., Nilsson, M. C., Pluchon, N., Wardle, D. A. (2016). The effect of biochar management on soil and plant community properties in a boreal forest. GCB Bioenergy, 8(4), 777-789. https://doi.org/10.1111/gcbb.12274

Gustafsson, L., Berglind, M., Granström, A., Grelle, A., Isacsson, G., Kjellander, P., Larsson, S., Lindh, M., Pettersson, L.B., Strengbom, J., Stridh, B., Sävström, T., Thor, G., Wikars, L-O., Mikusiński, G. (2019). Rapid ecological response and intensified knowledge accumulation following a north European mega-fire. Scandinavian Journal of Forest Research, 34(4), 234-253. https://doi.org/10.1080/02827581.2019.1603323

Gustafsson, L., Granath, G., Nohrstedt, H. Ö., Leverkus, A. B., Johansson, V. (2021). Burn severity and soil chemistry are weak drivers of early vegetation succession following a boreal mega-fire in a production forest landscape. Journal of Vegetation Science, 32(1), e12966. https://doi.org/10.1111/jvs.12966

Guyette, R. P., Muzika, R. M., Dey, D. C. (2002). Dynamics of an anthropogenic fire regime. *Ecosystems*, 5(5), 472-486. https://doi.org/10.1007/s10021-002-0115-7

Handler, S., Pike, C., St. Clair, B. (2018). Assisted Migration. USDA Forest Service Climate Change Resource Center. https://www.fs.usda.gov/ccrc/topics/assisted-migration

Hart, S. C., Stark, J. M., Davidson, E. A., Firestone, M. K. (1994). Nitrogen mineralization, immobilization, and nitrification. Methods of Soil Analysis: Part 2 Microbiological and Biochemical Properties, 5, 985-1018. https://doi.org/10.2136/sssabookser5.2.c42

Hartley, A. E., Neill, C., Melillo, J. M., Crabtree, R., & Bowles, F. P. (1999). Plant performance and soil nitrogen mineralization in response to simulated climate change in subarctic dwarf shrub heath. Oikos, 331-343. https://doi.org/10.2307/3546450

Hayatgheibi, H., Berlin, M., Haapanen, M., Kärkkäinen, K., Persson, T. (2020). Application of Transfer Effect Models for Predicting Growth and Survival of Genetically Selected Scots Pine Seed Sources in Sweden. Forests, 11(12), 1337. https://doi.org/10.3390/f11121337

Hellberg, E., Hörnberg, G., Östlund, L., Zackrisson, O. (2003). Vegetation dynamics and disturbance history in three deciduous forests in boreal Sweden. Journal of vegetation science, 14(2), 267-276. https://doi.org/10.1111/j.1654-1103.2003.tb02152.x

Homann, P. S., Bormann, B. T., Darbyshire, R. L., Morrissette, B. A. (2011). Forest soil carbon and nitrogen losses associated with wildfire and prescribed fire. Soil Science Society of America Journal, 75(5), 1926-1934. https://doi.org/10.2136/sssaj2010-0429

Hu, T., Sun, L., Hu, H., Weise, D. R., Guo, F. (2017). Soil Respiration of the Dahurian Larch (Larix gmelinii) Forest and the Response to Fire Disturbance in Da Xing'an Mountains, China. Scientific Reports, 7, 1–10. https://doi.org/10.1038/s41598-017-03325-4

Högberg, P., Näsholm, T., Franklin, O., Högberg, M. N. (2017). Tamm Review: On the nature of the nitrogen limitation to plant growth in Fennoscandian boreal forests. Forest Ecology and Management, 403, 161-185. https://doi.org/10.1016/j.foreco.2017.04.045

Ibáñez, T. S., Wardle, D. A., Gundale, M. J., Nilsson, M. C. (2021). Effects of Soil Abiotic and Biotic Factors on Tree Seedling Regeneration Following a Boreal Forest Wildfire. Ecosystems, 1-17. https://doi.org/10.1007/s10021-021-00666-0

Johnstone, J. F., Hollingsworth, T. N., Chapin III, F. S., Mack, M. C. (2010). Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Global Change Biology, 16(4), 1281-1295. https://doi.org/10.1111/j.1365-2486.2009.02051.x

Jäderlund, A., Zackrisson, O., Nilsson, M. C. (1996). Effects of bilberry (Vaccinium myrtillus L.) litter on seed germination and early seedling growth of four boreal tree species. Journal of Chemical Ecology, 22(5), 973-986. https://doi.org/10.1007/BF02029948

Kasischke, E. S., Turetsky, M. R. (2006). Recent changes in the fire regime across the North American boreal region—Spatial and temporal patterns of burning across Canada and Alaska. Geophysical research letters, 3(9). https://doi.org/10.1029/2006GL025677

Keeley, J. E., (2009). Fire intensity, fire severity and burn severity: A brief review and suggested usage. International Journal of Widlife Fire, 18, 116–126. https://doi.org/10.1071/WF07049

Kellomäki, S., Strandman, H., Heinonen, T., Asikainen, A., Venäläinen, A., Peltola, H. (2018). Temporal and spatial change in diameter growth of boreal Scots pine, Norway spruce, and birch under recent-generation (CMIP5) global climate model projections for the 21st century. Forests, 9(3), 118. https://doi.org/10.3390/f9030118

Knicker, H. (2007). How does fire affect the nature and stability of soil organic nitrogen and carbon? A review. Biogeochemistry, 85(1), 91-118. https://doi.org/10.1007/s10533-007-9104-4

Kuuluvainen, T., Rouvinen, S. (2000). Post-fire understory regeneration in boreal *Pinus sylvestris* forest sites with different fire histories. Journal of Vegetation Science, 11(6), 801-812. https://doi.org/10.2307/3236550

Kurepin, L. V., Stangl, Z. R., Ivanov, A. G., Bui, V., Mema, M., Hüner, N. P., Öquist, G., Way, D., Hurry, V. (2018). Contrasting acclimation abilities of two dominant boreal conifers to elevated CO_2 and temperature. Plant, cell & environment, 41(6), 1331-1345.

Köster, K., Aaltonen, H., Berninger, F., Heinonsalo, J., Köster, E., Ribeiro-Kumara, C., Sun, H., Tedersoo, L., Zhou, X., Pumpanen, J. (2021). Impacts of wildfire on soil microbiome in Boreal environments. Current Opinion in Environmental Science & Health, 100258. https://doi.org/10.1016/j.coesh.2021.100258

Leverkus, A. B., Lindenmayer, D. B., Thorn, S., Gustafsson, L. (2018). Salvage logging in the world’s forests: Interactions between natural disturbance and logging need recognition. Glob. Ecol. Biogeogr. 27, 1140–1154. https://doi.org/10.1111/geb.12772

Lidskog, R., Johansson, J., Sjödin, D. (2019). Wildfires, responsibility and trust: public understanding of Sweden's largest wildfire. Scandinavian Journal of Forest Research, 34(4), 319-328. https://doi.org/10.1080/02827581.2019.1598483

Maaroufi, N. I., Nordin, A., Palmqvist, K., Hasselquist, N. J., Forsmark, B., Rosenstock, N. P., Wallander, H., Gundale, M. J. (2019). Anthropogenic nitrogen enrichment enhances soil carbon accumulation by impacting saprotrophs rather than ectomycorrhizal fungal activity. Global change biology, 25(9), 2900-2914. https://doi.org/10.1111/gcb.14722

Mack, M. C., Bret-Harte, M. S., Hollingsworth, T. N., Jandt, R. R., Schuur, E. A., Shaver, G. R., Verbyla, D. L. (2011). Carbon loss from an unprecedented Arctic tundra wildfire. Nature, 475(7357), 489-492. https://doi.org/10.1038/nature10283

Mack, M. C., Walker, X. J., Johnstone, J. F., Alexander, H. D., Melvin, A. M., Jean, M., Miller, S. N. (2021). Carbon loss from boreal forest wildfires offset by increased dominance of deciduous trees. Science, 372(6539), 280-283. https://doi.org/10.1126/science.abf3903

Marañón-Jiménez, S., Castro, J. (2013). Effect of decomposing postfire coarse woody debris on soil fertility and nutrient availability in a Mediterranean ecosystem. Biogeochemistry, 112, 519–535. https://doi.org/10.1007/s10533-012-9744-x

Marañón-Jiménez, S., Castro, J., Kowalski, A. S., Serrano-Ortiz, P., Reverter, B. R., Sánchez-Cañete, E.P., Zamora, R. (2011). Post-fire soil respiration in relation to burnt wood management in a Mediterranean mountain ecosystem. Forest Ecology and Management, 261, 1436–1447. https://doi.org/10.1016/j.foreco.2011.01.030

Marcolin, E., Marzano, R., Vitali, A., Garbarino, M., Lingua, E. (2019). Post-fire management impact on natural forest regeneration through altered microsite conditions. Forests, 10. https://doi. org/10.3390/f10111014

Mekonnen, Z. A., Riley, W.J., Randerson, J. T., Grant, R. F., Rogers, B. M. (2019). Expansion of high-latitude deciduous forests driven by interactions between climate warming and fire. Nature plants, 5(9), 952-958. https://doi.org/10.1038/s41477-019-0495-8

Menkis, A., Vasiliauskas, R., Taylor, A. F., Stenlid, J., Finlay, R. (2005). Fungal communities in mycorrhizal roots of conifer seedlings in forest nurseries under different cultivation systems, assessed by morphotyping, direct sequencing and mycelial isolation. Mycorrhiza, 16(1), 33-41. https://doi.org/10.1007/s00572-005-0011-z

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., ... Hik, D. S. (2011). Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters, 6(4), 045509.

Nilsson, M. C. (1994). Separation of allelopathy and resource competition by the boreal dwarf shrub Empetrum hermaphroditum Hagerup. Oecologia, 98(1), 1-7.

Nilsson, M. C., Wardle, D. A. (2005). Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. Frontiers in Ecology and the Environment, 3(8), 421-428. https://doi.org/10.1890/1540-9295(2005)003[0421:UVAAFE]2.0.CO;2

Pereira, P., Francos, M., Brevik, E. C., Ubeda, X., Bogunovic, I. (2018). Post-fire soil management. Current Opinion in Environmental Science & Health, 5, 26-32. https://doi.org/10.1016/j.coesh.2018.04.002

Pérez-Izquierdo, L., Clemmensen, K. E., Strengbom, J., Granath, G., Wardle, D. A., Nilsson, M. C., Lindahl, B. D. (2021). Crown-fire severity is more important than ground-fire severity in determining soil fungal community development in the boreal forest. Journal of Ecology 109(1), 504-518. https://doi.org/10.1111/1365-2745.13529

Parro, K., Metslaid, M., Renel, G., Sims, A., Stanturf, J. A., Jõgiste, K., Köster, K. (2015). Impact of postfire management on forest regeneration in a managed hemiboreal forest, Estonia. Canadian Journal of Forest Research, 45(9), 1192–1197. https://doi.org/10.1139/cjfr-2014-0514

Ponomarev, E. I., Kharuk, V. I., Ranson, K. J. (2016). Wildfires dynamics in Siberian larch forests. Forests 7(6), 125. https://doi.org/10.3390/f7060125

Powers, E. M., Marshall, J. D., Zhang, J., Wei, L. (2013). Post-fire management regimes affect carbon sequestration and storage in a Sierra Nevada mixed conifer forest. Forest Ecology and Management, 291, 268-277. https://doi.org/10.1016/j.foreco.2012.07.038

Rogers, B. M., Soja, A. J., Goulden, M. L., Randerson, J. T. (2015). Influence of tree species on continental differences in boreal fires and climate feedbacks. Nature Geoscience, 8(3), 228-234. https://doi.org/10.1038/ngeo2352

Rousk, J., Brookes, P. C., Baath, E. (2009). Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. Applied and Environmental Microbiology, 75(6), 1589-1596. https://doi.org/10.1128/AEM.02775-08

Schimmel, J., Granstrom, A. (1996). Fire severity and vegetation response in the boreal Swedish forest. Ecology, 77(5), 1436-1450. https://doi.org/10.2307/2265541

Sitnov, S. A., Mokhov, I. I. (2018). A Comparative Analysis of the Characteristics of Active Fires in the Boreal Forests of Eurasia and North America Based on Satellite Data. Izvestiya, Atmospheric and Oceanic Physics, 54, 966–978. https://doi.org/10.1134/S0001433818090347

Soja, A. J., Tchebakova, N. M. French, N. H., Flannigan, M. D., Shugart, H. H., Stocks, B. J., Sukhinin, A. I., Parfenova, E. I., Chapin III, F. S., Stackhouse Jr., P. W. (2007). Climate-induced boreal forest change: predictions versus current observations. Global and Planetary Change, 56 (3-4), 274-296. https://doi.org/10.1016/j.gloplacha.2006.07.028

Stange, C. F., Spott, O., Apelt, B., Russow, R.W. (2007). Automated and rapid online determination of 15N abundance and concentration of ammonium, nitrite, or nitrate in aqueous samples by the SPINMAS technique. Isotopes in Environmental and Health Studies, 43(3), 227-236. https://doi.org/10.1080/10256010701550658

Stuiver, B. M. (2015). Stand Development Effects on N_2-fixation and Seedling Performance in Northern Boreal Forests. Doctoral thesis. Acta Universitatis agriculturae Sueciae, 2015:108, SLU.

Thomas, G.W. (1996). Chapter 16. Soil pH and Soil Acidity. In J. M. Bigham et al. (eds.) Soil Science, Society of America and American Society of Agronomy. Methods of Soil, Analysis. Part 3. (pp 475-490). Chemical Methods-SSSA Book Series no. 5.

Valkonen, S., Valsta, L. (2001). Productivity and economics of mixed two-storied spruce and birch stands in Southern Finland simulated with empirical models. Forest Ecology and Management, 140(2-3), 133-149. https://doi.org/10.1016/S0378-1127(00)00321-2

Walker, X. J., Baltzer, J. L., Cumming, S. G., Day, N. J., Ebert, C., Goetz, S., Johnstone, J. F., Potter, S., Rogers, B. M., Schuur, E. A. G., Turetsky, M. R., Mack, M. C. (2019). Increasing wildfires threaten historic carbon sink of boreal forest soils. Nature, 572, 520–523. https://doi.org/10.1038/s41586-019-1474-y

Populärvetenskaplig sammanfattning

Den globala uppvärmningen till följd av klimatförändringar bidrar till längre torkperioder. Detta ökar risken för att skogsbränder ska uppkomma, att skogarna brinner mer intensivt och att effekterna av bränderna blir större. Hur påverkas skogen av en kronbrand som dödat alla stora träd och där det mesta av det översta jordlagret brunnit upp och dödat svampar och bakterier (hög brandhårdhet), jämfört med om brandens effekter är mildare? Vilka är effekterna av den efterföljande avverkningen av brandskadad skog och vilken betydelse har brandhårdheten för effekten av avverkning på mark och växter? I min avhandling studerar jag hur föryngringen av tall, gran och vårtbjörk påverkas av avverkning av brandskadade träd när brandhårdheten varierat. Jag undersöker även hur dessa faktorer påverkar markprocesser så som mikrobiell omvandling (av svampar och bakterier) och tillgänglighet av kväve för en ny skogsregeneration.

Trädrötter och mykorrhizasvampar lever i symbios med varandra, där träd tar upp koldioxid från atmosfären och tillhandahåller svamparna med kol i utbyte mot kväve. Om träden dör (till följd av till exempel brand eller avverkning), påverkar detta mykorrhizasvamparna liksom utbytet av näring mellan träd, nya plantor och jord. Däremot medför döda stående träd att mer solljus kommer ned till marken och att resurskonkurrensen mellan stora träd och nya plantor minskar. Min avhandling visar i ett växthusförsök att efter en brand så är effekten av markens abiotiska (näring) och biotiska (mikroorganismers aktivitet) egenskaper på föryngring av trädplantor är artspecifik. Gran kan öka sin tillväxt i jord som har levande mikroorganismer, så som kan vara fallet i jord från skog som brunnit låg-intensivt med många överlevande stora träd. Björk tycks i mindre omfattning vara beroende av levande mikroorganismer och ökar istället i tillväxt när näringen i marken är hög.

Efter en skogsbrand är avverkning av brandskadade träd en vanlig åtgärd, vilket betyder att alla brandskadade träd förs bort från området och lämnar kvar ett kalhygge. Effekten av en sådan avverkning på mark och vegetation kan variera beroende på hur intensivt det har brunnit. Min avhandling visar att effekten av brandhårdhet på marken är större än effekten av avverkning av brandskadade träd. Min avhandling visar också att effekten av avverkning på skogsföryngringen varierar beroende på brandhårdhet. Dessa effekter kan ytterligare förstärkas av en klimatuppvärmning. Sammantaget bidrar min avhandling till ny kunskap till stöd för hur framtida skogar kan förvaltas i ett framtida scenario med ökande antal intensiva skogsbränder, till följd av ett förändrat klimat.

Acknowledgements

First thank you, whoever is reading my thesis, you make these written pages alive.

There are many people I met through these years in Umeå, whom I wish to thank. My supervisors, how lucky I feel to have been a part of your team. My main supervisor Marie-Charlotte, you have been a great mentor to me from the start - thank you for sharing your knowledge about boreal forests and for your constant support. Michael, thank you for your positive spirit and for being available to discuss anything at any time. David, thank you for your invaluable feedback on the manuscripts and for welcoming me to Singapore during my visit at NTU.

Further, I have worked with several people, and I am grateful to all of you. Morgan, it has been a pleasure to work with you in field, thank you for your patience and for being so eager to find solutions to problems. Thank you, Johannes (Forkman), for statistical feedback and discussions. Thank you, Margareta, Jenny, Abdul, Jonas, for your great work in the lab, to the staff at the library, at the Wallenberg greenhouse, the IT department at SLU in Umeå and to HR at FEM, for fast support when needed. A special thanks to Ulf, you were the first to welcome me at SLU, and you have been very supportive at HR. Thank you, Kelly for your great help in the lab and greenhouse, and thanks to everyone in the vegetation ecology lab group, for interesting discussions and talks. Thank you, Natascha, Julia, Louise and everyone in the Ljusdal fire ecology group, for excellent collaborations. Thank you, Tobias, for introducing me to the lab at GVC in Gothenburg during my visit and to Josefina, for helping me out when the SPINMAS stopped working. Thank you, Marie-Lou, Niklas, Malin and Alice, for fun times in field.

A big thanks to the PhDs, postdocs and friends in Umeå: Robert, Vicky, Zsofia, Alejandro, Johannes L., Felicia, Benjamin, Viktor, Lara, Joss, Susan, Betty, Kishore, Arvid, Artis, Stefan H., Roger, Malgorzata, Leslie, Lina and all old and new colleagues at SLU, for sharing this journey with me. A special thanks to Stefan P, for sharing the passion for salsa dancing and for answering kappa related questions, and to José for all the laughs and sharing great taste of music. Hélène - I am very grateful that you were always checking in on me.

During these past years in Umeå I have met friends at SLU, who had special impact on me. Thank you for entering my life and I hope to continue this friendship for many years, even if we will live in different corners of the world: Clydecia, you truly are one of a kind! You have been so friendly and helpful from the start. Simone, you became my first friend in Umeå - I miss you! Noelia, mi hermana española, I always feel positive after hanging out with you. Ruth, you social butterfly, thank you for being such an amazing and caring friend - the last two years in Umeå would not have been the same without you.

During my years in Umeå, I have had great support from the following close persons in my life and I made it because of you: Jossan, my best friend, you were always just a phone call away when I needed you and you mean the world to me. Zorro, my little partner in crime who always gives me unconditional love. Many ideas for the thesis came up during our long walks. Iona and Nataniel, who always make me laugh, Dad, thank you for supporting me to believe in myself, but also to accept my limitations in order to be happy. Mom, through all my phases in life you have always been there for me and I cannot thank you enough for that. Your constant questions of “did you eat something” or “did you sleep” were actually very nice to hear.

Last, my love, you supported me through my university studies, Ph.D. journey and throughout life. So Christian, now it is my turn to thank you for everything else.

I

Ecosystems
https://doi.org/10.1007/s10021-021-00666-0

ECOSYSTEMS

Effects of Soil Abiotic and Biotic Factors on Tree Seedling Regeneration Following a Boreal Forest Wildfire

Theresa S. Ibáñez,[1]* David A. Wardle,[2] Michael J. Gundale,[1] and Marie-Charlotte Nilsson[1]

[1]*Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden;* [2]*Asian School of the Environment, Nanyang Technological University, Singapore, Singapore*

ABSTRACT

Wildfire disturbance is important for tree regeneration in boreal ecosystems. A considerable amount of literature has been published on how wildfires affect boreal forest regeneration. However, we lack understanding about how soil-mediated effects of fire disturbance on seedlings occur via soil abiotic properties *versus* soil biota. We collected soil from stands with three different severities of burning (high, low and unburned) and conducted two greenhouse experiments to explore how seedlings of tree species (*Betula pendula*, *Pinus sylvestris* and *Picea abies*) performed in live soils and in sterilized soil inoculated by live soil from each of the three burning severities. Seedlings grown in live soil grew best in unburned soil. When sterilized soils were reinoculated with live soil, seedlings of *P. abies* and *P. sylvestris* grew better in soil from low burn severity stands than soil from either high severity or unburned stands, demonstrating that fire disturbance may favor post-fire regeneration of conifers in part due to the presence of soil biota that persists when fire severity is low or recovers quickly post-fire. *Betula pendula* did not respond to soil biota and was instead driven by changes in abiotic soil properties following fire. Our study provides strong evidence that high fire severity creates soil conditions that are adverse for seedling regeneration, but that low burn severity promotes soil biota that stimulates growth and potential regeneration of conifers. It also shows that species-specific responses to abiotic and biotic soil characteristics are altered by variation in fire severity. This has important implications for tree regeneration because it points to the role of plant–soil–microbial feedbacks in promoting successful establishment, and potentially successional trajectories and species dominance in boreal forests in the future as fire regimes become increasingly severe through climate change.

Key words: Abiotic and biotic soil characteristics; *Betula pendula*; Boreal forest; Burn severity; Climate change; *Picea abies*; *Pinus sylvestris*; Plant–soil interactions; Tree seedling regeneration; Wildfire.

Received 3 September 2020; accepted 30 May 2021

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-021-00666-0.

Author contributions All four authors planned and designed the research. TSI performed experiments and analyzed the data with support from DAW and MJG. TSI wrote the first draft of the manuscript, and all authors contributed substantially to revisions and gave final approval for publication. MCN administered the project and also acquired the funding.

**Corresponding author; e-mail:* theresa.ibanez@slu.se

HIGHLIGHTS

- High burn severity created conditions adverse for seedlings growth.
- Low burn severity promoted soil biota that enhanced growth of *Pinus sylvestris* and *Picea abies.*
- *Betula pendula* growth was driven by changes in abiotic soil properties.

INTRODUCTION

Fire is a recurrent natural disturbance in northern coniferous forests that controls vegetation dynamics, structure, diversity and function. While boreal forests are shaped by and adapted to fire, natural fire regimes are rapidly changing as a consequence of global climate change (Kasischke and Turetsky 2006; Soja and others 2007; Balshi and others 2009; Ponomarev and others 2016). For many parts of the boreal region, burn probability, fire area and fire intensity are projected to increase and become more common as the climate warms (de Groot and others 2013). This is in part due to increasing duration of extreme fire-promoting conditions, such as warmer temperatures (Gillett and others 2004). These changes in fire regime are predicted to alter plant and soil community structure and cause elevated tree mortality (Stephens and others 2013), alter soil organic matter content (Czimczik and others 2005) and alter functioning of soil microbial communities due to increased loss of organic material (Allison and Treseder 2011). More frequent and higher intensity fires are also likely to induce shifts in how boreal forests will regenerate and recover from fire disturbances (Johnstone and others 2010; Alexander and others 2018), in part as a consequence of fire-induced effects on loss of soil organic matter and survival of mycorrhizal fungi needed for tree seedling regeneration (Dahlberg and others 2001; Dahlberg 2002).

Fires in boreal forests of Eurasia typically occur as low-intensity ground surface fires, to which many of the dominant tree species are adapted (Angelstam and Kuuluvainen 2004). In Sweden, older Scots pine (*Pinus sylvestris*) trees frequently survive ground fire because of their thick bark and high crown base height (Zackrisson 1977; Hellberg and others 2003), and deciduous trees such as birch (*Betula pendula* and *Betula pubescens*) are well adapted to ground fires because the high position of the crown and their ability to resprout vegetatively after fire (Atkinson 1992). In contrast, Norway spruce (*Picea abies*) trees are usually consumed by fire because of their thin bark and low branches (Zackrisson 1977). Post-fire regeneration by *P. sylvestris* and *B. pendula* occurs from seeds that are dropped on site shortly after fire from surviving trees, and seeds of *B. pendula* can also be spread over long distances, while *P. abies* typically recolonizes slowly post-fire by seeds originating from outside burned areas. (Granström 1991; Hellberg and others 2003). Fire is often necessary for new forest tree cohorts to regenerate in these ecosystems (Lampainen and others 2004), and this is associated with the reduction or loss of understory vegetation and shifts in soil properties such as increased concentrations of inorganic nitrogen (that is, NH_4^+) (DeLuca and others 2002; Gómez-Rey and Gonzalez-Prieto 2013). However, the extent of post-fire tree regeneration is also regulated by soil burn severity (Bansal and others 2014), because higher severity burns cause greater loss of organic material and soil biota (Certini 2005) and higher mortality rates of trees which may lead to slower tree regeneration. Although much is already known about the impact of fire on plant mortality and post-fire successions in boreal forests, less is known about how variation in fire behavior and tree mortality impacts aboveground-belowground linkages and soil microbial communities, which may have important consequences for forest regeneration (but see Bergner and others 2004; Treseder and others 2004; Holden and others 2013; Sun and others 2015; Hewitt and others 2020).

Soil microorganisms, and notably saprotrophic microbes and ectomycorrhizal fungi, are critical components for nutrient turnover and seedling establishment and growth in boreal forest (Read and others 2004), and their response to fire disturbance can therefore impact on post-fire recovery of trees (Hewitt and others 2017). The extent to which the organic layer is combusted or lost from fire has major impacts on the soil biota and the speed of its post-fire recovery. Communities of ectomycorrhizal fungi can survive low burn severity fires when the organic layer is not completely consumed (Dahlberg 2002; Holden and others 2016). Survival and short-term recovery of ectomycorrhizal fungi may, however, depend not only on the remaining organic layer, but also on the degree of fire-induced mortality of overstory trees (Dahlberg 2002; Pérez-Izquierdo and others 2021). With regard to saprotrophic soil microbes, bacteria in general appear to be more resistant than fungi to fire because they are better adapted to resist fire-generated heat (Certini 2005; Mataix-Solera and others 2009). The release of organic nutrients after fire can stimulate the recovery rate of bacterial communities (Bárcenas-Moreno and others 2011), leading to accelerated short-term release of inorganic soil nutrients that favors tree regeneration. In contrast, higher burn severity may strongly reduce the microbial communities and thereby soil organic matter decomposition, reducing the availability of nutrients needed for tree growth (Holden and others 2016). In total, tree seedling responses to fire depend on how the fire affects both the soil microbes and the abiotic soil properties, as well as the interaction between them. However, the effects of belowground biotic and abiotic changes caused by fire on tree seedling regeneration have mostly been investigated in isolation from one another.

On 31 of July 2014, a large accidental wildfire in east-central Sweden, known as the Västmanland burn started (Gustafsson and others 2019). It was initiated and spread fast due to an extended period of unusually hot and dry weather; it burned more than 13,000 ha of forest and was the largest fire in Swedish modern history (Lidskog and others 2019). For a large part of this area, the fire was intense and caused widespread tree death and loss of the organic layer. Within this area, some forest stands were severely burned, some stands were less severely burned, and some stands were not burned at all, creating a mosaic of stands across the landscape with differing fire severity. We collected soils from forest stands of low burn severity, high burn severity and unburned stands for use in each of two greenhouse experiments that were set up to better understand how growth of three different seedling species (*P. abies*, *P. sylvestris*, *B. pendula*) respond to different burn severities. In the first greenhouse experiment we planted seedlings in live (non-sterile) soil from each burn severity class, and the difference in seedling growth between burn severity treatments could be due to either soil abiotic properties (that is, pH, nutrients, organic matter content, or texture) or biotic properties (that is, composition and biomass of organisms present); this experiment did not allow us to disentangle the role of these two mechanisms. In the second greenhouse experiment, we planted seedlings in sterilized soils that had been inoculated with live soil (that is, containing live soil biota) from each stand burn severity class. Doing this allowed us to separate how soil abiotic versus biotic properties influenced seedling growth and thus shed insights into the mechanisms underpinning the first experiment.

Through these two experiments, we sought to test how the abiotic and biotic components of soil impact tree seedling growth when soils are subjected to different levels of burn severity. For the first experiment, we hypothesized that seedlings will grow better in living soil from stands subjected to low burn severity relative to soils from either unburned or high burn severity stands. We expected this because burning would enhance nutrient availability (Wan and others 2001), and mild burning would enhance nutrient availability without impairing the ectomycorrhizal fungal community or stimulate succession of fire adapted fungal species. Further, we expected this effect to be greater for pioneering fast-growing species (*P. sylvestris* and *B. pendula*) that can better exploit these inorganic resources relative to late-successional species (*P. abies*) because of their rapid root growth and photosynthesis (Pumpanen and others 2009; Nilsson and others 2012). For our second experiment, we hypothesized that tree seedlings planted in sterilized soils would grow the largest when inoculated with soil from stands with live trees present (that is, stands subjected to low severity burning or unburned stands), and that this would occur irrespective of the burn severity class of the sterilized soil. We expected this because high burn severity soils should mostly lack live tree roots (Pérez-Izquierdo and others 2019) and thus are unlikely to harbor a living ectomycorrhizal fungal community (Dahlberg 2002; Pérez-Izquierdo and others 2021) that is essential for plant nutrient acquisition (Smith and Read 2008). Further, we expected that the positive effect of inoculation with unburned or low burn severity soils would be greatest for *P. sylvestris* seedlings because it was the dominant tree cover in these stands before and after fire, and would likely promote an ectomycorrhizal community that is most suitable for *P. sylvestris* and includes fire-adapted early colonizing fungi. Additionally, we would expect conifers to benefit from late-successional fungi present in unburned soils. Testing these hypotheses in combination contributes to a mechanistic understanding of how tree regeneration success following wildfire varies in response to burn severity in boreal forests, and how this is determined by abiotic versus biotic soil properties.

METHODS

Selection of Burn Severity Stands

Within the Västmanland burn, we selected 25 burned forest stands that were each about 0.25 ha and had undergone one thinning operation prior to the fire (stem density of $<$ 1000 stems per hectare); they were all on podzolized soils, had a site index of 22–24 m (that is, the estimated dominant height at age 100 years) and represented a gradient in burn severity. They occurred within an area of approximately 60 km^2, with each stand separated at least 300 m from all other stands. Prior to the fire, the stands were dominated (87%) by 40–50-year-old Scots pine (*P. sylvestris*) production forests with scattered (11%) Norway spruce (*P. abies*) and (2%) birch (*Betula* spp.) trees and an understory vegetation dominated by ericaceous dwarf shrubs (*Vaccinium vitis-idaea*, *V. myrtillus* and *Calluna vulgaris*) and mosses (mainly *Pleurozium schreberi*).

In April 2016, data for stand characteristics of the 25 burned stands were collected within a circular plot of 314 m^2 (radius = 10 m) in the center of each stand. Tree mortality was determined by visual inspection (for example, the lack of green needles present) and calculated as the percentage of dead trees versus all (dead and alive) trees within the plot. The number of trees with stem scorch visible (for example, trees that had bark that had fallen off the stem) was also counted. Flame length was determined as the average charring height of stems for 20 *P. sylvestris* trees per plot, and for these, the level of crown scorching (that is, the proportion of needles killed or consumed by fire throughout the whole crown) was also estimated. For each plot, the total organic (humus) depth (that is, Oa and Oe horizons) and the depth of the charred layer in the soil profile were measured at 25 random positions by vertically inserting a ruler in the ground. In addition, in four randomly allocated positions within each plot, the amount of charcoal deposited on the topsoil was collected within a circular area (radius = 8 cm) and converted to dry mass per area. With the use of these data (that is, tree mortality, flame height, stem scorch, crown scorch, humus depth, depth of charred soil, coarse charcoal on surface and fine charcoal on surface) for each of the 25 stands, we then classified the stands into burn severity classes by using Principal Component Analysis (PCA) followed by K-mean clustering. From this analysis we selected seven stands of high burn severity and seven stands of low burn severity for further use (Supporting Information Figure S1; Table S1). The major differences between high burn and low burn severity stands result from high burn stands having a higher tree mortality, larger flame height, a higher number of stem and crown scorches of trees and a larger reduction of humus thickness from humus combustion (Table 1). In addition, seven unburned stands distributed around the burned area (within 500 m of the fire perimeter) were also selected for this study. The three burn severity class stands (unburned, high burned and low burned in total 21 stands) were randomly distributed across the burned area, allowing each stand to serve as an independent replicate, with seven randomly distributed stands in each burn severity class. Prior to the fire, there were no major differences in mean tree height, tree basal area, tree biomass or tree species composition among burn severity classes (Pérez-Izquierdo and others, Unpublished Manuscript).

Soil Chemistry of Forest Stands

On May 22–26, 2018 we randomly collected five circular soil cores of mineral soil (radius = 5 cm; depth = 10 cm) and five circular soil cores of the organic layer (radius = 15 cm) to the full organic layer depth from each 21 stands. The organic (humus) layer included the Oa and Oe horizon, while the Oi horizon was excluded from the soil samples. The five soil cores were bulked to represent one sample per stand. Roots and small debris were removed from the soil. For a subsample of each sample, the total concentration of phosphorus (P) was determined by Kjeldahl acid digestion (G-189-97 Rev. 3, multitest MT7) using an Auto Analyzer 3 Spectrophotometer (Omniprocess, Solna, Sweden). Total soil carbon (C) and nitrogen (N) concentrations were analyzed by drying (70 °C, 18 h) and grinding samples followed by dry combustion using an EA-IRMS Elemental Analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). For another subsample, soil pH was determined by using a solution-to soil ratio suspension of 0.01 M $CaCl_2$ mixed with mineral soil (1:1) or humus (1:10) following Thomas (1996).

Greenhouse Experiment, Experimental Design and Soil Chemistry of Greenhouse Soil

We performed a greenhouse experiment using soils from each of the three burn severity classes of stands. From September 29 to October 2, 2017 we randomly collected approximately ten circular soil cores (radius = 5 cm; depth = 10 cm) within the 314 m^2 (radius = 10 m) circular area of each of the 21 stands. The different burn severities between stands resulted in variable thickness of the organic horizon, with high severity stands having little or no remaining humus (Mean 20.0 ± SE 1.7 mm), low burn severity stands having some organic layer (24.1 ± 1.9 mm) and unburned stands having thick organic layer (93.9 ± 5.5 mm). In order to

Table 1. Measures of Burn Severity of the Forest Stands.

Burn severity measures	df[1]	Burn severity class of forest stand		*F*-value	*P*-value
		High	Low		
Tree mortality (%)	1, 12	100.0 ± 0.0^{a}	32.1 ± 5.0^{b}	**186.85**	**< 0.001**
Flame height (m)	1, 12	6.8 ± 1.1^{a}	1.0 ± 0.1^{b}	**25.62**	**< 0.001**
Stem scorch (%)	1, 12	13.1 ± 3.6^{a}	2.9 ± 1.9^{b}	**6.48**	**0.026**
Crown scorch (%)	1, 12	99.4 ± 0.4^{a}	27.9 ± 2.4^{b}	**846.74**	**< 0.001**
Humus depth[2] (mm)	2, 18	20.0 ± 1.7^{a}	24.1 ± 1.9^{a}	**142.42**	**< 0.001**
Depth of charred soil profile layer (mm)	1, 12	10.3 ± 0.8^{a}	12.8 ± 0.8^{b}	**5.03**	**0.045**
Charcoal on soil surface (g/m^2)	1, 12	120 ± 25	75 ± 25	1.50	0.244

Mean ± SE.
Bold F- and P-values are significant at an alpha value of 0.05.
Numbers within rows accompanied by different letters differ significantly at $P \leq 0.05$ (following ANOVA).

[1] *Numerator degrees of freedom, denominator degrees of freedom.*

[2] *The mean ± SE depth of unburned humus was 93.9 ± 5.5 mm and was statistical significantly higher than both high and low burned soils at $P \leq 0.001$ (Bonferroni post hoc test following ANOVA).*

achieve a representative sample of the conditions that the roots of a developing seedling would experience, we sampled to a fixed depth (10 cm) at each site which included the humus that was present and the underlying mineral soil. As such, the proportion of organic (humus) soil to mineral soil varied across stands, with the highly burned sites having a low amount of humus relative to the unburned sites. For each stand, all the soil cores were bulked to create a single sample which was then passed twice through a 4.0-mm sieve, placed in a polyethylene bag and transported to Umeå in cooling boxes and stored at 2 °C until the start of the experiment on October 17, 2017. Two-thirds of the sieved soil from each stand was sent in cooling boxes to SynergyHealth (Etten-Leur, Netherlands), for gamma irradiation at a dose of 43.0–78.8 kGy. This sterilization treatment was chosen to effectively kill all the soil biota while creating minimal disturbance to physical soil structure (McNamara and others 2003).

To distinguish between the effects of soil biota and soil abiotic properties on seedling performance, two separate greenhouse experiments were set up in which tree seedlings were grown in the field collected soils. In the first experiment that tested for the effects of soil properties including live biota, we used unsterilized soil from the field sites to perform a factorial experiment consisting of three soil burn severity classes (that is, high burn, low burn and unburned) × three tree seedlings species (*P. abies*, *P. sylvestris*, or *B. pendula*) × seven replicates (that is, the seven stands per burn severity class), resulting in a total of 63 pots. For the second experiment that tested for the separated effects of soil biota and abiotic properties, we used sterilized soil originating from the same sites as the first experiment and applied soil community inoculation treatments consisting of live soil from each of the different burn severity classes (Figure 1). The experiment was set up in a factorial design in which pots were filled with sterilized soil from three burn severity classes (high burn, low burn or unburned) and planted with each of three plant species (*P. abies*, *P. sylvestris* or *B. pendula*); these soils then were inoculated with four burn severity inoculum class treatments. The four inoculum treatments consisted of live inoculum from each class, as well as a sterile control, resulting in 252 pots in total (Figure 1). The experimental units were randomly arranged into blocks, by including one stand of each burn severity class in each block. Thus, each block consisted of 12 pots (three burn severity classes × four burn severity inoculum classes). Because our research question was focused on local microbial communities and we aimed to generalize results from our experiment to the entire burned landscape we sampled, burn severity inoculum class derived from each stand was kept separate (Gundale and others 2017) and was randomly assigned to receiving soils originating from different stands (Gundale and others 2014). Our inoculation approach therefore followed experiment Type D described by Gundale and others (2017, 2019).

For both experiments, we used 800 ml pots (8 × 8 × 8.5 cm) with holes in the bottom to allow excess water drainage. Pots were filled with 2/3 experimental soil (that is, live soil for the first experiment; sterilized soil + live inoculum for the second experiment) and 1/3 with autoclaved quartz sand to improve drainage after watering. For the second experiment, 10% of the soil volume in each pot with sterilized soil was replaced with soil containing live biota (burn severity inoculum class treatments). This soil was also mixed with autoclaved quartz sand, resulting in an inoculation amount of approximately 6.6% of the total pot volume. Both unsterilized and sterilized soil from each stand, following mixing with quartz sand, was analyzed for nutrient concentration (NH_4^+, NO_3^+, PO_4^{3-}) using standard protocols (Gundale and others 2011).

All pots were set up on tables in a greenhouse and planted with *P. abies*, *P. sylvestris* or *B. pendula* seedlings. The seeds were obtained from tree nurseries in Sweden and consisted of genetic provenances that corresponded to our field sites. The seeds were sterilized in 5% hypochlorite and rinsed with deionized water and then placed on autoclaved quartz sand for pre-germination for seven days. Two seedlings per species were then planted in each pot, and after one month the smallest seedling was removed. During this first month new seedlings were planted if both seedlings in a pot died. After this period, 100% seedling survival was obtained. The tables were rotated once a week to avoid unwanted effects of greenhouse gradients. Both experiments were run for 4.5 months, and seedlings were watered every day with tap water. The ambient conditions within the greenhouse involved a 18:6 h light/dark photoperiod with a relative air humidity of 40%. The temperature ranged between 25 °C (day) and

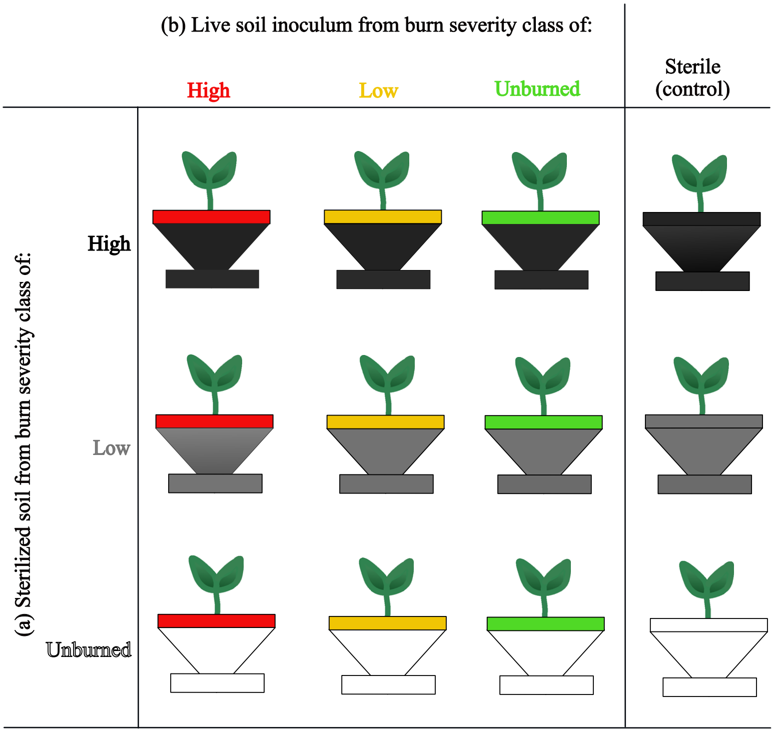


Figure 1. Schematic figure of Experiment 2, which aims to separate the soil biotic and abiotic effects of soils from forest stands subjected to high and low burn severity as well as from unburned stands on the growth of tree seedlings. **a** Pots with sterilized soil from high burn severity (black pots), low burn severity (gray pots) and unburned (white pots) stands receiving, **b** live soil inoculum from high severity (red), low severity (yellow) and unburned (green; top vertical) stands. Pots arranged vertically to the far right consist of sterile soil without added inoculum (sterile controls). Each pot was planted with seedling of *Picea abies*, *Pinus sylvestris* or *Betula pendula*. The 12 pots depicted represent one block for one species; in total seven blocks were set up for each of the three species. There were 12 (pots) × 3 (species) × 7 replicates (blocks), resulting in a total of 252 pots for this experiment. The percentage of total soil in each pot that was added live inoculum was 6.6%, except for the sterile control pots where it was 0%.

15 °C (night). At the end of the experiment we harvested the seedlings by eliminating soil from roots with water and cut the plant at the soil surface to separate aboveground from belowground biomass. Plants were put in paper bags and oven-dried at 65 °C for 48 h and weighed to obtain measures of aboveground, belowground and total biomass.

Statistical Analysis

For the first experiment, statistical analysis was performed by using split plot ANOVA with burn severity class as a fixed factor and plant species as a subplot factor. For the second experiment we used a blocked design followed by split plot ANOVA with burn severity class and burn severity inoculum class as fixed factors and plant species as a subplot factor. The sites were randomly selected in the field, and we therefore performed the data analysis with an assumption that the data is randomly distributed. To satisfy assumptions of homogeneity of variance, all data were $\log(x)$ transformed. Data for burn severity and soil characteristics of the forest stands, and nutrient concentrations in soil used in greenhouse, were analyzed using one-way ANOVA. For both experiments, stand characteristic and greenhouse soil data, Bonferroni post hoc test was used at $\alpha = 0.05$, to further explore pairwise differences between treatment means. All data were statistically analyzed in SPSS version 24 (IBM Corp., Armonk, NY, USA). Raw data are stored as Supplementary material (S3). Figure 1 was created in Affinity Designer 1.8.3.

RESULTS

Soil Chemical Properties

In 2018, four years after the fire, we found no significant differences in concentrations or ratios of total soil C, N, C:N and P in mineral soil or organic layer between stands of different burn severities (Table S2). Meanwhile, mineral soil pH of high burn severity stands (pH = 3.89 ± 0.06; mean ± SE) and low severity stands (pH = 3.78 ± 0.07) were both significantly higher than that for unburned stands (pH = 3.31 ± 0.12) but did not differ from each other ($F_{2,18} = 12.20$, P-value $\leq$ 0.001). For the humus, pH in low burn severity stands (pH = 3.30 ± 0.08) was significantly higher than for unburned stands (pH = 3.04 ± 0.04) ($F_{1,12} = 8.53$, P-value = 0.013); humus pH could not be determined for the high severity stands due to insufficient humus remaining as a consequence of the fire.

For the soil used for the greenhouse experiment, NH_4^+ and PO_4^{3-} were overall greatest in soil from the unburned stands, whereas NO_3^- was unresponsive to burn severity (Table 2; Figure 2). We also found that sterilization increased NH_4^+ in all soils with the strongest effects on unburned soil. Sterilization also increased soil concentrations of PO_4^{3-}, but only in unburned soil, and had no effect on NO_3^- (Table 2; Figure 2).

Greenhouse Experiments

In the first experiment in which we used unsterilized soil, both burn severity class and plant species identity significantly affected total, aboveground and belowground seedling biomass, and burn severity class also impacted the aboveground-to-belowground biomass ratio (Table 3); there were no interactive effects between these two factors. The effect of plant species identity was because *B. pendula* and *P. sylvestris* produced more aboveground and belowground biomass than did *P. abies* (Figure 3). For the burn severity class effect, seedling biomass were generally greater in the unburned soil compared to the high burn severity soil, with low burn severity soils often showing intermediate seedling growth (Figure 3). The aboveground-to-belowground biomass ratio was lowest in soil from the high burn severity stands, although this effect of burn severity was detected as significant only by the analysis of variance and not the post hoc analysis (Table 3; Figure 3d).

In the second experiment involving soil sterilization and inoculation of live biota, we found that burn severity class, burn severity inoculum class and plant species identity nearly always had significant effects on seedling total, aboveground and belowground biomass, and on the ratio of aboveground to belowground biomass (Table 4). The plant species effect occurred because *B. pendula* produced the most biomass, while *P. abies* produced the least; *B. pendula* seedlings also had the lowest aboveground-to-belowground biomass ratio (Figure 4). The burn severity effect occurred because seedling growth variables were always highest in unburned soils and usually least in high burn severity soils (Figure 4a–d). For the significant burn severity inoculum class effects, low burn severity inoculum class often stimulated the highest seedling biomass, and the aboveground-to-belowground biomass ratio, the most out of all inoculum classes (Figure 4e–h). The interactive effect of burn severity and plant species identity was significant for all variables except aboveground biomass (Table 4), which was due to the stronger overall pos-

Table 2. Results from Analysis of Variance Comparing Main and Interactive Effects of Burn Severity Class (BSC) and Sterilization (S), of Soil Used in the Greenhouse, for NO_3^-, NH_4^+ and PO_4^{3-}.

	df[1]	NO_3^-		NH_4^+		PO_4^{3-}	
		F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Burn severity class (BSC)	2, 18	2.470	0.099	**13.747**	**< 0.001**	**9.045**	**0.001**
Sterilization (S)	1, 12	3.457	0.071	**167.441**	**< 0.001**	**5.554**	**0.024**
BSC × S	2, 18	2.431	0.102	**17.864**	**< 0.001**	**6.010**	**0.006**

Bold F- and P-values are significant at an alpha value of 0.05.

[1] *Numerator degrees of freedom, denominator degrees of freedom.*

itive effect of burn severity on *B. pendula* biomass, and on the aboveground-to-belowground biomass ratio for *P. sylvestris* and *P. abies* (Figure 4a–d). We also observed a two-way interactive effect of burn severity inoculum class and plant species and a three-way interactive effect of these two variables and burn severity, on both aboveground biomass and the ratio of aboveground to belowground biomass (Table 4). The two-way interaction (Figure 4e–h) occurred because *B. pendula* responded less to burn severity inoculum class than did the two conifer species. Meanwhile, the three-way interaction occurred because the two conifer species responded stronger to low burn severity inoculum class when grown in the unburned soil compared to the other burn severity classes.

Discussion

We aimed to test how the abiotic and biotic properties of soil, collected from stands subjected to different burn severity, impact tree seedling growth. Overall, we found that effects of burn severity on both soil biotic and abiotic properties were important for seedling growth, but that effects of soil abiotic properties were overall more important, although seedlings of different tree species varied in their responses to only soil biotic properties. Our findings elucidate how fire may affect seedling performance via its effects on the soil and soil biota, thus providing insights into key mechanisms underlying tree regeneration after wildfire.

Effects of Non-sterile Burn Severity Soil on Tree Seedling Growth

In our first experiment, where live (non-sterile) soil from each stand was used, we found that both burn severity and plant species identity were important for explaining seedling growth. However, we did not find any interactive effect between burn severity and species identity, meaning that the three species responded similarly to the burn severity treatments. We found that all seedlings grew worse in high burn severity soils and best in unburned soils, with the fast-growing *P. sylvestris* and *B. pendula* seedlings achieving a higher final biomass than those of *P. abies*. These findings contradict those from field experiments showing ground burning of intermediate severity to be more beneficial to growth of pioneer species relative to their growth in unburned soil (Bansal and others 2014). In our study, there were no major differences in concentrations of NH_4^+, NO_3^- and PO_4^{3-} in live soils at the time of collection, probably because we collected our soils four years post-fire, and the expected flush of nutrients immediately following fire (Gundale and others 2005) may have dissipated. However, the greater seedling growth in unburned soils suggests higher nutrient availability in those soils, likely because these soils had a higher proportion of organic material that could be rapidly mineralized in the greenhouse environment.

The seedlings may also have grown largest in the unburned soils because these soils would likely support more ectomycorrhizal and saprotrophic fungi that would stimulate organic matter decomposition and plant access to nutrients which should benefit seedling growth (Holden and others 2016). It has also been suggested that high availability of C in the root zone from root exudates may stimulate bacterial breakdown of complex sources of N (Clarholm 1985), meaning that mineralization rates should be higher in soils with active plant roots. At the same time, lower growth of seedlings in high burn severity stands could be due not only to lower resource availability and loss of mutualistic biota, but also to greater levels of fungal pathogens (Hewitt and others 2016). However, our Experiment 1 is unable to separate between the likely abiotic and biotic mechanisms contributing to these effects.

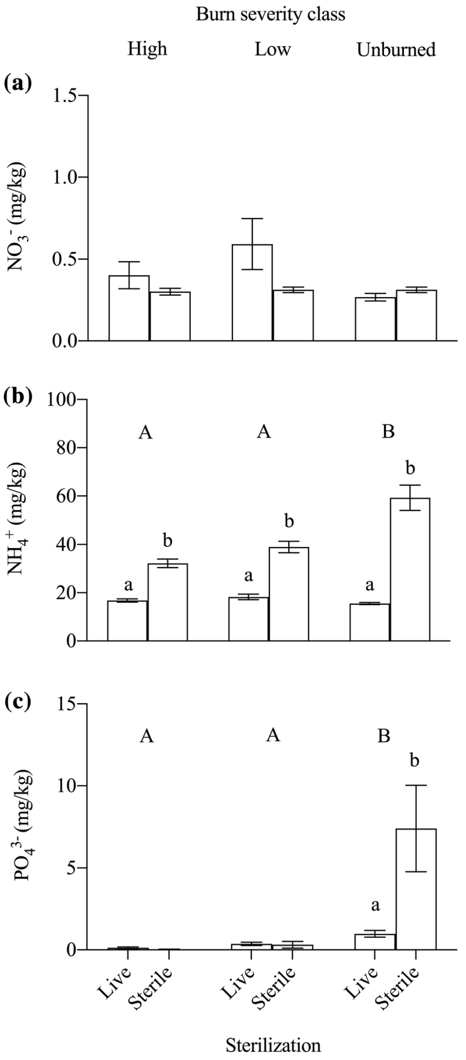


Figure 2. Mean ± SE of NO_3^- (**a**), NH_4^+ (**b**) and PO_4^{3-} (**c**) of live or sterilized mixtures of humus and mineral soil from different forest stand fire severity classes. All soil was mixed with autoclaved sand, at a 2:1 ratio. Different capital letters above pairs of bars indicate significant differences between burn severity classes, and different lower case letters indicate significant differences between live and sterile soil, according to Bonferroni post hoc tests at $P \le 0.05$. Corresponding two-way ANOVA results (*F*- and *P*-values) are reported in Table 2.

Our first experiment also revealed that increases in soil pH associated with fire could indirectly explain seedling growth response to fire, because the burned soil had both the highest soil pH and the lowest seedling growth. This may be because higher soil pH can disfavor communities of fungi (Day and others 2019), which would reduce the organic matter decomposition and therefore presumably decrease the availability of nutrients for plant growth (Smith and Read 2008). Our analysis further showed marginally significant statistical differences in seedling aboveground-to-belowground biomass ratios among soil burn severity treatments, and all species tended to have weakly lower ratios when grown in high burn severity soils compared to when grown in low severity and unburned soils, which could reflect greater soil resource limitation. Since the high burn severity soil had much less organic material than in the other soils, it is likely to contain fewer saprotrophic microbes and mycorrhizal fungi needed for promoting nutrient availability for the seedlings, which may have caused them to allocate more biomass to the rooting zone (Ledo and others 2018).

Separating Soil Biotic and Abiotic Influence on Seedling Growth

Our second experiment (Experiment 2) compared growth of seedlings in sterilized soils across the three burn severity treatments and in sterilized soils that had been reinoculated with live soils (that is, containing live soil biota) from each of the burn severity treatments. This set up enabled us to disentangle the effects of abiotic soil properties from that of live biota.

Similar to the first experiment, we found that burn severity had a highly significant influence on seedling growth of all species, in that seedlings in soil originating from unburned stands grew the most and those in soil from the high burn severity stands grew the least, even when soils were sterilized. We therefore suggest that the availability of nutrients (that is, abiotic soil properties) was the primary driver of growth differences among soils in both experiments. This effect may have occurred in Experiment 1 because there was more organic material in pots with unburned soil that could be mineralized and in Experiment 2 because the sterilization of the soil released nutrients of NH_4^+ and PO_4^{3-}. The higher PO_4^{3-} levels of sterilized unburned soil in our greenhouse experiment may also have contributed to higher uptake of NH_4^+ by seedlings. Blanes and others (2012) showed, although in a field experiment, that when limitation by P was alleviated, *Abies pinsapo* seedlings increased their N uptake. Although we cannot com-

Table 3. Results from Analysis of Variance Comparing the Main and Interactive Effects of Burn Severity Class (BSC) and Plant Species (PS) on the Total, Aboveground and Belowground Biomass Including the Ratio of Aboveground to Belowground Biomass.

	df[1]	Total biomass[2]		Aboveground biomass[2]		Belowground biomass[2]		Aboveground/belowground[2,3]	
		F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Burn severity class (BSC)	2, 18	**7.823**	**0.004**	**10.673**	**0.001**	**4.085**	**0.034**	**3.981**	**0.037**
Plant species (PS)	2, 36	**7.900**	**< 0.001**	**6.050**	**0.005**	**9.512**	**< 0.001**	3.071	0.059
BSC × PS	4, 36	1.115	0.365	0.857	0.499	1.215	0.321	0.308	0.997

Seedlings of Picea abies, Pinus sylvestris and Betula pendula were grown on unsterilized soils from three burn severity classes, that is, from stands of high or low burn severity, or from intact unburned stands.

Bold F- and P-values are significant at an alpha value of 0.05.

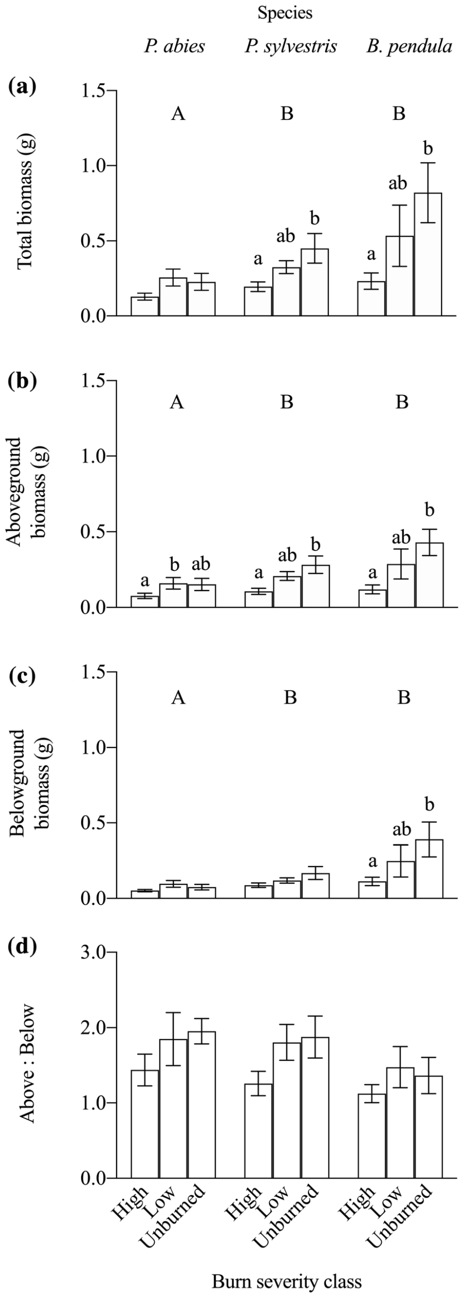
[1] *Numerator degrees of freedom, denominator degrees of freedom.*

[2] *Data were transformed (log(x)) prior to analysis.*

[3] *The ratio of aboveground to belowground biomass.*

pletely exclude the possibility that the responses to soil abiotic conditions could also be because of variation in soil physical properties across our stands, we believe this effect to be minimal and unlikely to vary much among our burn severity treatments. As such, the field collected soil was mixed with 1/3 autoclaved quartz sand to assure water drainage in each pot and to minimize the influence of variation of soil physical properties across our stands.

In partial agreement with our second hypothesis, we found that seedling growth was affected by addition of live inoculum from stands of different burn severities, but in a different way to what we observed for live soil in the first experiment. Specifically, for the two conifer species, we found stronger positive seedling growth responses when inoculum originated from low burn severity sites than from either unburned or high burn severity sites, pointing to the beneficial effects of a low intensity of burning. A possible mechanism is that soil microbes, including ectomycorrhizal fungi, can survive when the organic layer is not completely consumed in a low severity fire (Dahlberg 2002; Holden and others 2016; Day and others 2019), as opposed to in a high severity fire. Further, when overstory trees survive a low severity fire, these trees can maintain the symbiotic relationship with the ectomycorrhizal community (Dahlberg 2002; Pérez-Izquierdo and others 2019), which could allow new seedlings to easily develop new ectomycorrhizal networks after a low burn compared to after a high burn severity fire. Fire may also induce a functional shift in microbial community composition (Clemmensen and others 2015) toward taxa that are more beneficial for seedling growth. For example, Pérez-Izquierdo and others (2021) showed that soils of burned stands, from the same stands as those utilized in this study, were inhabited by ectomycorrhizal species of the genera *Sphaerosporella* and *Laccaria* that are known to be fire-adapted and possibly having a higher affinity for inorganic N (LeDuc and others 2013). It is therefore possible that these or other fire-resistant or fire-adapted ectomycorrhizal fungal species, when transferred to the unburned soils, would have benefitted seedlings by improving their access to inorganic N from this soil. Alternatively, non-mycorrhizal saprotrophs could also have contributed to these effects. As such, our results suggest that conifer tree seedlings are likely to be constrained by the availability of beneficial root associated soil biota (such as non-fire adapted ectomycorrhizal species) or particular saprotrophic microbes in sites that have experienced severe wildfire but not where fire has been less intense (Pérez-Izquierdo and others 2021). This could result in a slow post-fire recovery of important soil biota, and the tree seedlings that depend on them. Finally, soil inoculum from unburned soils had no positive effect on seedling growth of any species in our study. This inoculum is likely to host late-successional ectomycorrhizal fungi such as *Russula* and *Cortinarius* (Pérez-Izquierdo and others 2021) important for mobilizing nutrients bound in organic matter complexes (Lindahl and Tunlid 2015). When this inoculum was transplanted to burned soils in the greenhouse, it is plausible that they utilized host plants as their primary source of metabolic C (Corrêa and others 2011), and therefore drainage of C of seedling origin could have contributed to explain the lower biomass increment of



◀**Figure 3.** Mean ± SE of total biomass (**a**), aboveground biomass (**b**), belowground biomass (**c**) and the ratio of aboveground to belowground biomass (**d**) for tree seedlings of *Picea abies*, *Pinus sylvestris* and *Betula pendula*. Seedlings were grown on unsterilized soil originating from stands differing in burn severity (that is, high, low or unburned). Different capital letters above bars indicate significant differences between plant species across burn severity classes, and different lower case letters indicate significant differences between burn severity classes within species, according to Bonferroni post hoc tests at $P \leq 0.05$. Corresponding ANOVA results (*F*- and *P*-values) are reported in Table 3.

seedling grown in burned soils receiving unburned inoculum.

Contrary to our expectations, the late-successional *P. abies* showed the strongest positive response of all three species to soil inoculation (because it responded significantly more to inoculum from low severity burned stands than that from both high burned and unburned stands), with *P. sylvestris* showing an intermediate response, and *B. pendula* showing no response. We expected *P. sylvestris* to respond most strongly to soil burn severity inoculum because of the dominance of this species at our experimental sites, and because live adult trees often facilitate growth of regenerating tree seedlings of the same species (Jonsson and others 1999; Andivia and others 2018), in part through shared ectomycorrhizal connections. However, it is recognized that ectomycorrhizal communities associated with *P. abies* and *P. sylvestris* partially overlap (Menkis and others 2005), which could explain why seedlings of both conifers (but not *B. pendula*) responded positively to the low burn severity inoculum class relative to at least some of the other inoculum treatments. Our finding that *P. abies* and *P. sylvestris* do not perform well on highly burned soils in the absence of a live community of microorganisms may explain regeneration of conifers is sometimes disfavored following fire in Swedish forests (Elfving 1983; Kardell and Laestadius 1987). Unlike the two conifer species, *B. pendula* never responded to soil inoculation treatments. *B. pendula* is a fast-colonizing species on fire disturbed areas (Hellberg and others 2003; Gustafsson and others 2019), and its post-fire abundance has often been interpreted in terms of it being a good resource competitor (Dehlin and others 2004) that is effective at exploiting initial elevated levels of inorganic N resulting from fire disturbance (Gundale and others 2005). Findings from our study suggest *B. pendula*

Table 4. Results from Analysis of Variance Comparing the Main and Interactive Effects of Burn Severity Class (BSC), Burn Severity Inoculum Class (IC) and Plant Species (PS) on the Total, Aboveground and Belowground Tree Seedling Biomass, and the Ratio of Aboveground to Belowground Seedling Biomass.

	df[1]	Total biomass[2]		Aboveground biomass[2]		Belowground biomass[2]		Aboveground/belowground[2,3]	
		F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Burn severity class (BSC)	2, 66	**50.402**	**< 0.001**	**58.972**	**< 0.001**	**38.331**	**< 0.001**	**27.900**	**< 0.001**
Burn severity inoculum class (IC)	3, 66	**2.993**	**0.037**	**3.534**	**0.019**	2.002	0.122	**3.134**	**0.031**
Plant species (PS)	2, 144	**189.502**	**< 0.001**	**165.750**	**< 0.001**	**198.825**	**< 0.001**	**23.050**	**< 0.001**
BSC × IC	6, 66	1.331	0.256	1.235	0.300	1.362	0.243	0.174	0.983
BSC × PS	4, 144	**3.092**	**0.018**	1.717	0.149	**4.878**	**0.001**	**3.390**	**0.011**
IC × PS	6, 144	1.189	0.087	**2.703**	**0.016**	0.990	0.434	**2.701**	**0.016**
BSC × IC × PS	12, 144	1.469	0.142	**1.941**	**0.034**	1.167	0.312	**2.883**	**0.001**
Block	12, 66	**4.400**	**0.006**	**3.620**	**0.004**	**2.849**	**0.016**	1.972	0.082

Bold F- and P-values are significant at an alpha value of 0.05. Seedlings of Picea abies, Pinus sylvestris and Betula pendula were grown on sterilized (gamma irradiated) soils from three burn severity classes, that is, from stands with high or low burn severity, or, from unburned stands. In order to separate effects of abiotic drivers (burn severity) and biotic drivers (soil biota) on seedling growth, all sterilized soils were reinoculated with live soil from different classes (that is, stands with high burn severity, low burn severity or unburned) or with sterile soil.

[1] *Numerator degrees of freedom, denominator degrees of freedom.*

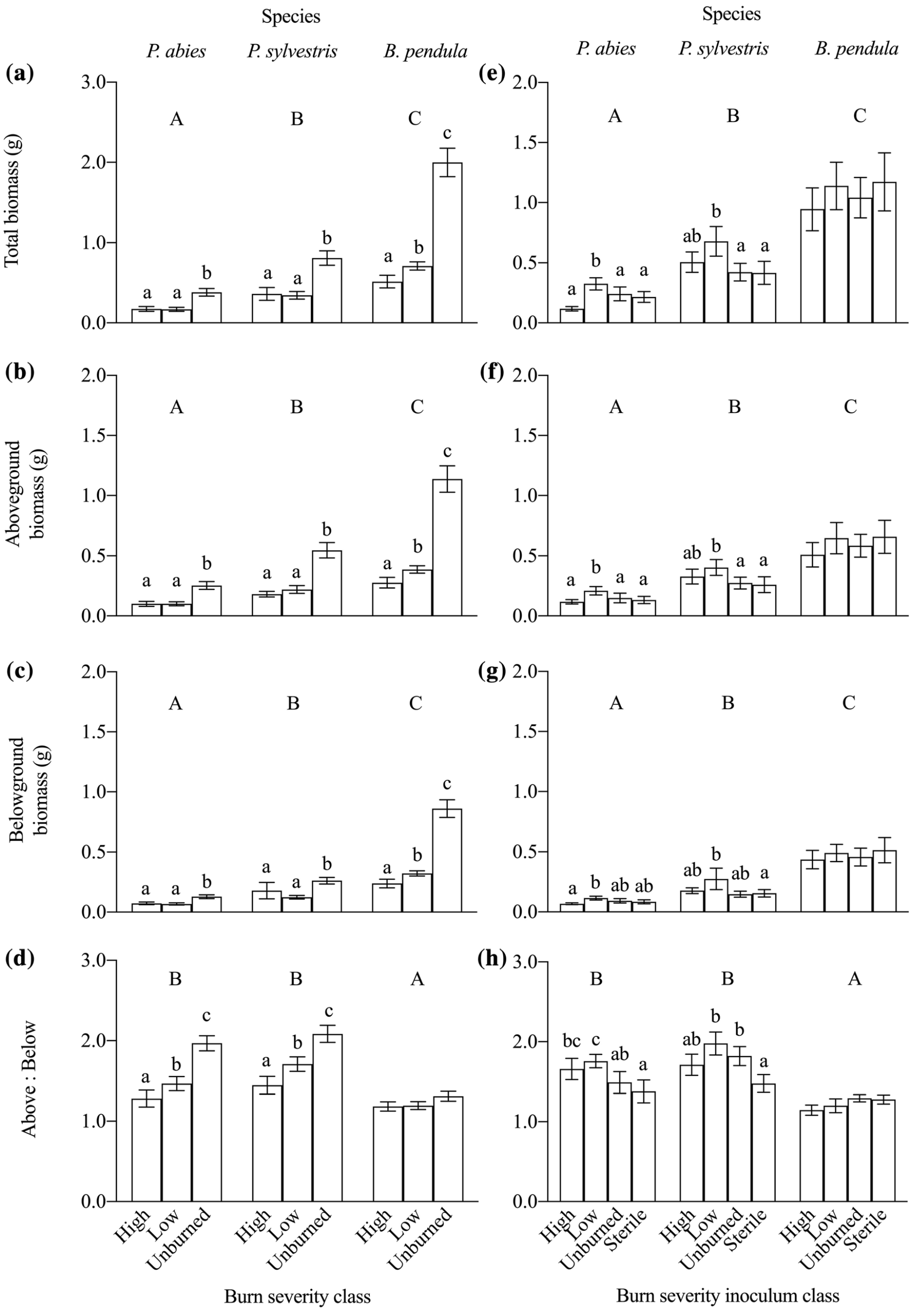
[2] *Data were transformed (log(x)) prior to analysis.*

[3] *The ratio of aboveground to belowground biomass.*

seedlings responded strongly to conditions of elevated nutrients and appeared less dependent than the conifers on ectomycorrhizal associations or other microorganisms for nutrient uptake during their establishment phase. However, this warrants further exploration given that mycorrhizal fungi have previously been shown to influence growth of *B. pendula* seedlings in boreal forests (Jonsson and others 2001). Deciduous trees such as *B. pendula* are expected to become more dominant in the forested landscape if climate warming increases and higher burn severity conditions prevail (Mekonnen and others 2019; Mack and others 2021). Our study suggests that this is mainly because *Betula pendula* seedlings are largely unresponsive to live soil biota and are therefore positioned to perform well directly after a fire in high burn severity sites even when the soil biota has been lost. *B. pendula* may not be disfavored from the absence of soil biota to the same extent as *P. sylvestris* and *P. abies* may be.

CONCLUSIONS

In this study we disentangled the effect of soil abiotic and biotic properties on tree seedling performance following wildfire to evaluate the effect of fire disturbance on the regeneration of boreal forests and shed light on the underlying mechanisms. Our results have several implications. First, they highlight that regeneration of *B. pendula* is unresponsive to changes in soil biota and is instead mostly driven by changes in abiotic soil properties. In contrast, both *P. abies* and *P. sylvestris* were responsive to soil biota from low burn severity soil relative to biota from the other soils; this demonstrates that low severity fire disturbances in part benefit post-fire regeneration of conifers due to the presence of specific soil biota that benefit from low burn severity fire. However, all seedlings responded positively when soil nutrients were elevated and grew well in the absence of biota, suggesting that soil nutrient conditions following fire would likely have an overriding importance for the regeneration success of all species shortly after fire. Second, studies such as ours can inform on strategic post-fire management decisions that involve restoration or assisted forest regeneration. When low burn severity fires occur, including during management procedures that incorporate prescribed burning prior to forest replanting, there is a need to consider its consequences for soil biota and how this biota in turn impacts on conifer seedling growth and regeneration. Finally, our work provides evidence of the relative importance of biotic and abiotic drivers of tree seedling regeneration following fire disturbance, and how these drivers are in turn


Species
P. abies
P. sylvestris
B. pendula
(a)
Total biomass (g)
3.0
2.0
1.0
0.0
A
B
C
a a b
a a b
a b c
(e)
2.0
1.5
1.0
0.5
0.0
A
B
C
a b a a
ab b a a
(b)
Aboveground biomass (g)
2.0
1.5
1.0
0.5
0.0
A
B
C
a a b
a a b
a b c
(f)
A
B
C
a b a a
ab b a a
(c)
Belowground biomass (g)
2.0
1.5
1.0
0.5
0.0
A
B
C
a a b
a a b
a b c
(g)
A
B
C
a b ab ab
ab b ab a
(d)
Above : Below
3.0
2.0
1.0
0.0
B
B
A
a b c
a b c
(h)
B
B
A
bc c ab a
ab b b a
High
Low
Unburned
High
Low
Unburned
High
Low
Unburned
Burn severity class
High
Low
Unburned
Sterile
High
Low
Unburned
Sterile
High
Low
Unburned
Sterile
Burn severity inoculum class

◀**Figure 4.** Mean ± SE of total biomass (**a**, **e**), aboveground biomass (**b**, **f**), belowground biomass (**c**, **g**), ratio of aboveground to belowground biomass (**d**, **h**) for tree seedlings of *Picea abies*, *Pinus sylvestris* and *Betula pendula*. Seedlings were grown on sterilized (gamma irradiated) soil, originating from stands differing in burn severity (that is, high, low and unburned), and with the sterilized soil then reinoculated with live soil from stands differing in burn severity (high, low and unburned) or with sterile soil. Different capital letters above bar groups indicate significant differences between plant species across burn severity inoculum class treatments, and small letters within bar groups indicate significant differences for burn severity classes (**a**–**d**) or burn severity inoculum class treatments (**e**–**h**) according to Bonferroni post hoc tests at $P \leq 0.05$. Corresponding ANOVA results (*F*- and *P*-values) are reported in Table 4.

impacted by burn severity. Understanding how burn severity impacts the interplay of these abiotic and biotic soil factors is of particular importance in understanding the mechanisms by which future climate change may influence forest regeneration, given that climate warming is expected to lead to both more frequent and more severe fires in the boreal region. As climate warming is being accompanied by novel fire behavior regimes, there is a growing need to further understand the role played by both soil abiotic factors and the soil microbial community in promoting early seedling establishment under different fire scenarios.

ACKNOWLEDGEMENTS

The research was funded by Formas (ID 2015-8544-30572-25) and a TC4F (Trees and Crops for the Future) grant to MCN. We wish to thank Kelley Gundale for assistance in the greenhouse, Morgan Karlsson and Marie-Lou Novene for assisting with the collection of soil samples and Marie-Lou Novene for laboratory help.

FUNDING

Open access funding provided by Swedish University of Agricultural Sciences.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

OPEN ACCESS

REFERENCES

Alexander HD, Natali SM, Loranty MM, Ludwig SM, Spektor VV, Davydov S, Zimov N, Trujillo I, Mack MC. 2018. Impacts of increased soil burn severity on larch forest regeneration on permafrost soils of far northeastern Siberia. Forest Ecology and Management 417:144–53. https://doi.org/10.1016/j.foreco.2018.03.008.

Allison SD, Treseder KK. 2011. Climate change feedbacks to microbial decomposition in boreal soils. Fungal Ecology 4(6):362–74. https://doi.org/10.1016/j.funeco.2011.01.003.

Andivia E, Madrigal-González J, Villar-Salvador P, Zavala MA. 2018. Do adult trees increase conspecific juvenile resilience to recurrent droughts? Implications for Forest Regeneration. Ecosphere 9(6):e02282. https://doi.org/10.1002/ecs2.2282.

Angelstam P, Kuuluvainen T. 2004. Boreal forest disturbance regimes, successional dynamics and landscape structures: a European perspective. Ecological Bulletins:117–36.

Atkinson MD. 1992. *Betula pendula* Roth (*B. verrucosa* Ehrh.) and *B. pubescens* Ehrh. Journal of Ecology 80:837–70. https://doi.org/10.2307/2260870.

Balshi MS, McGuire AD, Duffy P, Flannigan M, Walsh J, Melillo J. 2009. Assessing the response of area burned to changing climate in western boreal North America using a Multivariate Adaptive Regression Splines (MARS) approach. Global Change Biology 15(3):578–600. https://doi.org/10.1111/j.1365-2486.2008.01679.x.

Bansal S, Jochum T, Wardle DA, Nilsson MC. 2014. The interactive effects of surface-burn severity and canopy cover on conifer and broadleaf tree seedling ecophysiology. Canadian Journal of Forest Research 44(9):1032–41. https://doi.org/10.1139/cjfr-2014-0112.

Bárcenas-Moreno G, García-Orenes F, Mataix-Solera J, Mataix-Beneyto J, Bååth E. 2011. Soil microbial recolonisation after a fire in a Mediterranean forest. Biology and Fertility of Soils 47(3):261–72. https://doi.org/10.1007/s00374-010-0532-2.

Bergner B, Johnstone J, Treseder KK. 2004. Experimental warming and burn severity alter soil CO2 flux and soil functional groups in a recently burned boreal forest. Global Change Biology 10.12:1996–2004. https://onlinelibrary.wiley.com/doi/full/https://doi.org/10.1111/j.1365-2486.2004.00868.x

Blanes MC, Emmett BA, Viñegla B, Carreira JA. 2012. Alleviation of P limitation makes tree roots competitive for N against microbes in a N-saturated conifer forest: a test through P fertilization and 15N labelling. Soil Biology and Biochemistry 48:51–9. https://doi.org/10.1016/j.soilbio.2012.01.012.

Certini G. 2005. Effects of fire on properties of forest soils: a review. Oecologia 143(1):1–10. https://doi.org/10.1007/s00442-004-1788-8.

Clarholm M. 1985. Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. Soil Biology and Biochemistry 17(2):181–7. https://doi.org/10.1016/0038-0717(85)90113-0.

Clemmensen KE, Finlay RD, Dahlberg A, Stenlid J, Wardle DA, Lindahl BD. 2015. Carbon sequestration is related to mycorrhizal fungal community shifts during long-term succession in boreal forests. New Phytologist 205(4):1525–36. https://doi.org/10.1111/nph.13208.

Corrêa A, Hampp R, Magel E, Martins-Loução MA. 2011. Carbon allocation in ectomycorrhizal plants at limited and optimal N supply: an attempt at unraveling conflicting theories. Mycorrhiza 21(1):35–51. https://doi.org/10.1007/s00572-010-0309-3.

Czimczik CI, Schmidt MWI, Schulze ED. 2005. Effects of increasing fire frequency on black carbon and organic matter in Podzols of Siberian Scots pine forests. European Journal of Soil Science 56(3):417–28. https://doi.org/10.1111/j.1365-2389.2004.00665.x.

Dahlberg A. 2002. Effects of fire on ectomycorrhizal fungi in Fennoscandian boreal forests. Silva Fennica 36(1):69–80.

Dahlberg A, Schimmel J, Taylor AF, Johannesson H. 2001. Post-fire legacy of ectomycorrhizal fungal communities in the Swedish boreal forest in relation to fire severity and logging intensity. Biological Conservation 100(2):151–61. https://doi.org/10.1016/S0006-3207(00)00230-5.

Day NJ, Dunfield KE, Johnstone JF, Mack MC, Turetsky MR, Walker XJ, White AL, Baltzer JL. 2019. Wildfire severity reduces richness and alters composition of soil fungal communities in boreal forests of western Canada. Global Change Biology 25(7):2310–24. https://doi.org/10.1111/gcb.14641.

de Groot WJ, Flannigan MD, Cantin AS. 2013. Climate change impacts on future boreal fire regimes. Forest Ecology and Management 294:35–44. https://doi.org/10.1016/j.foreco.2012.09.027.

Dehlin H, Nilsson MC, Wardle DA, Shevtsova A. 2004. Effects of shading and humus fertility on growth, competition, and ectomycorrhizal colonization of boreal forest tree seedlings. Canadian Journal of Forest Research 34(12):2573–86. https://doi.org/10.1139/x04-143.

DeLuca T, Nilsson MC, Zackrisson O. 2002. Nitrogen mineralization and phenol accumulation along a fire chronosequence in northern Sweden. Oecologia 133(2):206–14. https://doi.org/10.1007/s00442-002-1025-2.

Elfving B. 1983. Den nya skogens produktion. Sveriges Skogsvårdsförbunds Tidskrift 83(4–5):7–16.

Gillett NP, Weaver AJ, Zwiers FW, Flannigan MD. 2004. Detecting the effect of climate change on Canadian forest fires. Geophysical Research Letters 31:18. https://doi.org/10.1029/2004GL020876.

Gómez-Rey MX, Gonzalez-Prieto SJ. 2013. Short-term impact of a wildfire on net and gross N transformation rates. Biology and Fertility of Soils 49(8):1065–75. https://doi.org/10.1007/s00374-013-0806-6.

Granström A. 1991. Skogen efter branden. Skog & Forskning 4(91):32–8.

Gundale MJ, DeLuca TH, Fiedler CE, Ramsey PW, Harrington MG, Gannon JE. 2005. Restoration treatments in a Montana ponderosa pine forest: effects on soil physical, chemical and biological properties. Forest Ecology and Management 213(1–3):25–38. https://doi.org/10.1016/j.foreco.2005.03.015.

Gundale MJ, Fajardo A, Lucas RW, Nilsson MC, Wardle DA. 2011. Resource heterogeneity does not explain the diversity–productivity relationship across a boreal island fertility gradient. Ecography 34(5):887–96. https://doi.org/10.1111/j.1600-0587.2011.06853.x.

Gundale MJ, Kardol P, Nilsson MC, Nilsson U, Lucas RW, Wardle DA. 2014. Interactions with soil biota shift from negative to positive when a tree species is moved outside its native range. New Phytologist 202(2):415–21. https://doi.org/10.1111/nph.12699.

Gundale MJ, Wardle DA, Kardol P, Nilsson MC. 2019. Comparison of plant–soil feedback experimental approaches for testing soil biotic interactions among ecosystems. New Phytologist 221(1):577–87. https://doi.org/10.1111/nph.15367.

Gundale MJ, Wardle DA, Kardol P, Van der Putten WH, Lucas RW. 2017. Soil handling methods should be selected based on research questions and goals. New Phytologist 216(1):18–23. https://doi.org/10.1111/nph.14659.

Gustafsson L, Berglind M, Granström A, Grelle A, Isacsson G, Kjellander P, Larsson S, Lindh M, Pettersson LB, Strengbom J, Stridh B, Sävström T, Thor G, Wikars LO, Mikusiński G. 2019. Rapid ecological response and intensified knowledge accumulation following a north European mega-fire. Scandinavian Journal of Forest Research 34(4):234–53. https://doi.org/10.1080/02827581.2019.1603323.

Hellberg E, Hörnberg G, Östlund L, Zackrisson O. 2003. Vegetation dynamics and disturbance history in three deciduous forests in boreal Sweden. Journal of Vegetation Science 14(2):267–76. https://doi.org/10.1111/j.1654-1103.2003.tb02152.x.

Hewitt RE, Chapin FS III, Hollingsworth TN, Mack MC, Rocha AV, Taylor DL. 2020. Limited overall impacts of ectomycorrhizal inoculation on recruitment of boreal trees into Arctic tundra following wildfire belie species-specific responses. PloS One 15(7):e0235932. https://doi.org/10.1371/journal.pone.0235932.

Hewitt RE, Chapin FS III, Hollingsworth TN, Taylor DL. 2017. The potential for mycobiont sharing between shrubs and seedlings to facilitate tree establishment after wildfire at Alaska arctic treeline. Molecular Ecology 26(14):3826–38. https://doi.org/10.1111/mec.14143.

Hewitt RE, Hollingsworth TN, Chapin FS III, Taylor DL. 2016. Fire-severity effects on plant–fungal interactions after a novel tundra wildfire disturbance: implications for arctic shrub and tree migration. BMC Ecology 16(1):1–11. https://doi.org/10.1186/s12898-016-0075-y.

Holden SR, Gutierrez A, Treseder KK. 2013. Changes in soil fungal communities, extracellular enzyme activities, and litter decomposition across a fire chronosequence in Alaskan boreal forests. Ecosystems 16(1):34–46. https://doi.org/10.1007/s10021-012-9594-3.

Holden SR, Rogers BM, Treseder KK, Randerson JT. 2016. Fire severity influences the response of soil microbes to a boreal forest fire. Environmental Research Letters 11(3):035004. https://doi.org/10.1088/1748-9326/11/3/035004.

Johnstone JF, Hollingsworth TN, Chapin FS III, Mack MC. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Global Change Biology 16(4):1281–95. https://doi.org/10.1111/j.1365-2486.2009.02051.x.

Jonsson L, Dahlberg A, Nilsson MC, Kårén O, Zackrisson O. 1999. Continuity of ectomycorrhizal fungi in self-regenerating boreal *Pinus sylvestris* forests studied by comparing mycobiont diversity on seedlings and mature trees. The New Phytologist 142(1):151–62. https://doi.org/10.1046/j.1469-8137.1999.00383.x.

Jonsson L, Nilsson MC, Wardle DA, Zackrisson O. 2001. Context dependent effects of ectomycorrhizal species richness on tree seedling productivity. Oikos 93(3):353–64. https://doi.org/10.1034/j.1600-0706.2001.930301.x.

Kardell L, Laestadius L. 1987. Longterm yield of Norway spruce (*Picea abies L.*) after prescribed burning. An example from Mid-Sweden. Sveriges Skogsvårdsförbunds Tidskrift (Sweden).

Kasischke ES, Turetsky MR. 2006. Recent changes in the fire regime across the North American boreal region—Spatial and temporal patterns of burning across Canada and Alaska. Geophysical Research Letters 3:9. https://doi.org/10.1029/2006GL025677.

Lampainen J, Kuuluvainen T, Wallenius TH, Karjalainen L, Vanha-Majamaa I. 2004. Long-term forest structure and regeneration after wildfire in Russian Karelia. Journal of Vegetation Science 15(2):245–56. https://doi.org/10.1111/j.1654-1103.2004.tb02259.x.

Ledo A, Paul KI, Burslem DFRP, Ewel JJ, Barton C, Battaglia M, Brooksbank K, Carter J, Eid TH, England JR, Fitzgerald A, Jonson J, Mencuccini M, Montagu KD, Montero G, Mugasha WA, Pinkard E, Roxburgh S, Ryan CM, Ruiz-Peinado R, Sochacki S, Specht A, Wildy D, Wirth C, Zerihun A, Chave J. 2018. Tree size and climatic water deficit control root to shoot ratio in individual trees globally. New Phytologist 217(1):8–11. https://doi.org/10.1111/nph.14863.

LeDuc SD, Lilleskov EA, Horton TR, Rothstein DE. 2013. Ectomycorrhizal fungal succession coincides with shifts in organic nitrogen availability and canopy closure in post-wildfire jack pine forests. Oecologia 172(1):257–69. https://doi.org/10.1007/s00442-012-2471-0.

Lidskog R, Johansson J, Sjödin D. 2019. Wildfires, responsibility and trust: public understanding of Sweden's largest wildfire. Scandinavian Journal of Forest. Research 34(4):319–28. https://doi.org/10.1080/02827581.2019.1598483.

Lindahl BD, Tunlid A. 2015. Ectomycorrhizal fungi–potential organic matter decomposers, yet not saprotrophs. New Phytologist 205(4):1443–7. https://doi.org/10.1111/nph.13201.

Mack MC, Walker XJ, Johnstone JF, Alexander HD, Melvin AM, Jean M, Miller SN. 2021. Carbon loss from boreal forest wildfires offset by increased dominance of deciduous trees. Science 372(6539):280–3. https://doi.org/10.1126/science.abf3903.

Mataix-Solera J, Guerrero C, García-Orenes F, Bárcenas GM, Torres MP. 2009. Forest fire effects on soil microbiology. Fire Effects on Soils and Restoration Strategies 5:133–75. https://doi.org/10.1201/9781439843338.

McNamara NP, Black HIJ, Beresford NA, Parekh NR. 2003. Effects of acute gamma irradiation on chemical, physical and biological properties of soils. Applied Soil Ecology 24(2):117–32. https://doi.org/10.1016/S0929-1393(03)00073-8.

Mekonnen ZA, Riley WJ, Randerson JT, Grant RF, Rogers BM. 2019. Expansion of high-latitude deciduous forests driven by interactions between climate warming and fire. Nature Plants 5(9):952–8. https://doi.org/10.1038/s41477-019-0495-8.

Menkis A, Vasiliauskas R, Taylor AF, Stenlid J, Finlay R. 2005. Fungal communities in mycorrhizal roots of conifer seedlings in forest nurseries under different cultivation systems, assessed by morphotyping, direct sequencing and mycelial isolation. Mycorrhiza 16(1):33–41. https://doi.org/10.1007/s00572-005-0011-z.

Nilsson U, Elfving B, Karlsson K. 2012. Productivity of Norway spruce compared to Scots pine in the interior of northern Sweden. Silva Fennica 46(2):197–209.

Pérez-Izquierdo L, Clemmensen KE, Strengbom J, Granath G, Wardle DA, Nilsson MC, Lindahl BD. 2021. Crown-fire severity is more important than ground-fire severity in determining soil fungal community development in the boreal forest. Journal of Ecology 109(1):504–18. https://doi.org/10.1111/1365-2745.13529.

Pérez-Izquierdo L, Clemmensen KE, Strengbom J, Nilsson MC, Lindahl BD. 2019. Quantification of tree fine roots by real-time PCR. Plant and Soil 440:1–8. https://doi.org/10.1007/s11104-019-04096-9.

Ponomarev EI, Kharuk VI, Ranson KJ. 2016. Wildfires dynamics in Siberian larch forests. Forests 7(6):125. https://doi.org/10.3390/f7060125.

Pumpanen JS, Heinonsalo J, Rasilo T, Hurme KR, Ilvesniemi H. 2009. Carbon balance and allocation of assimilated CO 2 in Scots pine, Norway spruce, and Silver birch seedlings determined with gas exchange measurements and 14 C pulse labelling. Trees 23(3):611–21. https://doi.org/10.1007/s00468-008-0306-8.

Read DJ, Leake JR, Perez-Moreno J. 2004. Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. Canadian Journal of Botany 82(8):1243–63. https://doi.org/10.1139/b04-123.

Smith SE, Read D. 2008. Mycorrhizal Symbiosis, 3rd edn. London: Academic press.

Soja AJ, Tchebakova NM, French NH, Flannigan MD, Shugart HH, Stocks BJ, Sukhinin AI, Parfenova EI, Chapin FS III, Stackhouse PW Jr. 2007. Climate-induced boreal forest change: predictions versus current observations. Global and Planetary Change 56(3–4):274–96. https://doi.org/10.1016/j.gloplacha.2006.07.028.

Stephens SL, Agee JK, Fule PZ, North MP, Romme WH, Swetnam TW, Turner MG. 2013. Managing forests and fire in changing climates. Science 342(6154):41–2. https://doi.org/10.1126/science.1240294.

Sun H, Santalahti M, Pumpanen J, Köster K, Berninger F, Raffaello T, Jumpponen A, Asiegbu FO, Heinonsalo J. 2015. Fungal Community Shifts in Structure and Function across a Boreal Forest Fire Chronosequence. Applied and Environmental Microbiology 81:7869–80. https://doi.org/10.1128/AEM.02063-15.

Thomas GW. 1996. Soil pH and soil acidity. Methods of soil analysis: part 3 chemical methods 5:475–90. https://doi.org/10.2136/sssabookser5.3.c16

Treseder KK, Mack MC, Cross A. 2004. Relationships among fires, fungi, and soil dynamics in Alaskan boreal forests. Ecological Applications 14(6):1826–38. https://doi.org/10.1890/03-5133.

Wan S, Hui D, Luo Y. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecological Applications 11(5):1349–65. https://doi.org/10.1890/1051-0761(2001)011[1349:FEONPA]2.0.CO;2.

Zackrisson O. 1977. Influence of forest fires on the North Swedish boreal forest. Oikos 29:22–32. https://doi.org/10.2307/3543289.

Supplementary material

Article title: **Effects of Soil Abiotic and Biotic Factors on Tree Seedling Regeneration Following a Boreal Forest Wildfire**

Authors: **Theresa S. Ibáñez, David A. Wardle, Michael J. Gundale, Marie-Charlotte Nilsson**

The following Supporting Information is available for this article:

Figure S1. Principal Component Analysis (PCA) plot of forest stands with different burn severity.

Table S1. Factor loadings of the burn severity variables.

Table S2. Soil nutrients in forest stands of different burn severity classes.

Electronic supplementary material S3. Raw data for all analyses.

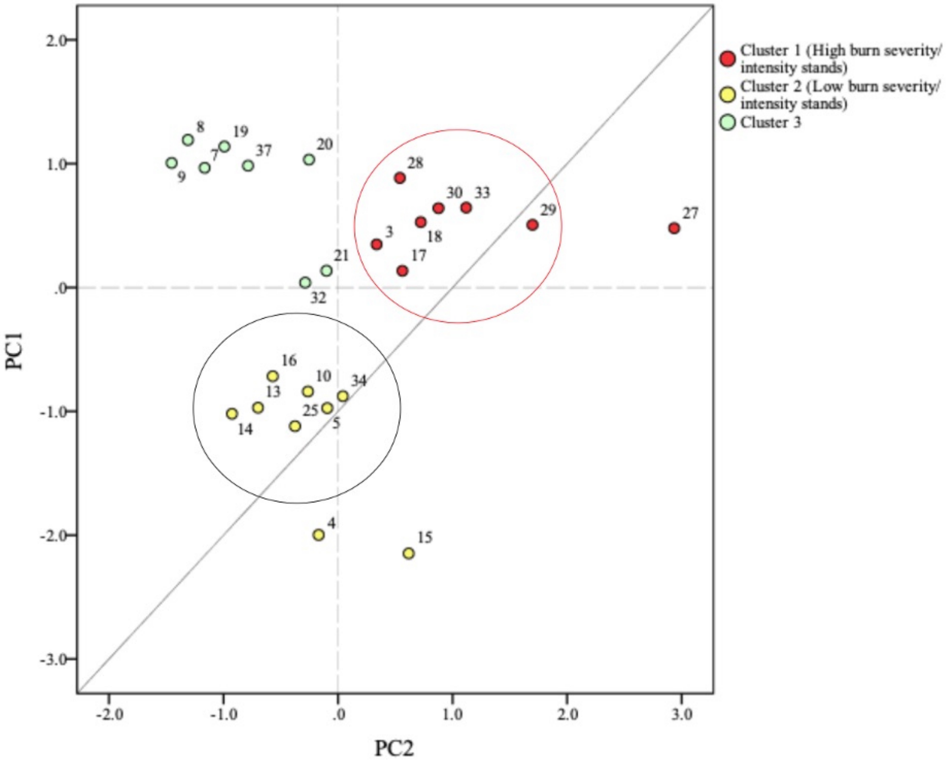


Figure S1. Forest stands plot from Principal Component Analysis (PCA), showing the scores for the two components (PC1 and PC2) describing data of burn severity of each of 25 forest stands. Data collected in the Västmanland burn area (N 59° 53′ 51″ N, 16° 8′ 19″ E). The first and second PCA axes explain 39.4% and 22.0% of the total variation of the data set. Groups of seven stands encircled are selected as high or low burn severity stands by K-mean clustering. The number next to each point refers to the identification of each stand. The burn severity variables and factor loadings in the PCA are presented in Table S1.

Table S1. Factor loadings of the burn severity variables for the two primary principal components (PC1 and PC2) in the PCA depicted in Fig. S1. For each row the bold number indicates the principal component to which it is most strongly aligned. The applied rotation method was Varimax with Kaiser Normalization, and the rotation was converged in three iterations.

Burn severity variable	PC1	PC2
Tree mortality	**0.930**	0.237
Flame height	**0.701**	0.584
Stem scorched	0.248	**0.730**
Crown scorched	**0.908**	0.257
Humus depth	0.359	**-0.761**
Depth of charred soil	-0.013	**-0.765**
Coarse charcoal on surface	**-0.547**	0.210
Fine charcoal on surface	**-0.183**	0.091
Variation explained (%)	39.4	22.0
Accumulated variation explained (%)	61.5	

Table S2. Total carbon (C) (g C per g dry mass), nitrogen (N) (g N per g dry mass), carbon:nitrogen ratio (C:N) and total Kjeldahl phosphorous (P) (%) in soils from forest stands of different burn severity classes. Mean ± SE. Analyses of variance (ANOVA) for mineral soil and independent t-test for organic layer. Alpha value of 0.05.

		Burn severity class of forest stand				
Nutrient	df[1]	High	Low	Unburned	*F* value	*P*-value
Mineral soil[2]						
C	2, 18	4.00 ± 0.52	4.22 ± 0.55	8.07 ±2.01	3.393	0.056
N	2, 18	0.14 ± 0.02	0.14 ± 0.02	0.27 ± 0.09	2.043	0.159
C:N	2, 18	29.25 ± 0.90	30.79 ± 1.04	32.73 ± 1.73	1.878	0.182
P	2, 18	0.03 ± 0.004	0.04 ± 0.01	0.13 ± 0.09	1.112	0.351
Organic layer[3]						
C	8.19	-	24.66 ± 1.53	32.16 ± 3.46	6.735	0.082
N	11	-	0.83 ± 0.07	0.98 ± 0.09	0.383	0.239
C:N	11	-	30.06 ± 1.43	32.78 ± 1.59	0.335	0.235
P	12	-	0.05 ± 0.002	0.09 ± 0.02	4.288	0.180

[1] Numerator degrees of freedom, denominator degrees of freedom for ANOVA and degrees of freedom for independent t-test.

[2] Analyses of variance (ANOVA)

[3] Indepentent t-test

IV

Received: 10 February 2021 | Accepted: 20 April 2021

DOI: 10.1111/gcb.15721

Global Change Biology WILEY

PRIMARY RESEARCH ARTICLE

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

Julia Kelly[1] | Theresa S. Ibáñez[2] | Cristina Santín[3,4] | Stefan H. Doerr[5] | Marie-Charlotte Nilsson[2] | Thomas Holst[6] | Anders Lindroth[6] | Natascha Kljun[1]

[1]Centre for Environmental and Climate Science, Lund University, Lund, Sweden

[2]Department of Forest Ecology and Management, Faculty of Forest Sciences, Swedish University of Agricultural Sciences, Umeå, Sweden

[3]Department of Biosciences, Swansea University, Swansea, Wales, UK

[4]Research Unit of Biodiversity, Spanish National Research Council, Mieres, Spain

[5]Department of Geography, Swansea University, Swansea, Wales, UK

[6]Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden

Correspondence

Julia Kelly, Centre for Environmental and Climate Science, Lund University, Sölvegatan 37, 223 62 Lund, Sweden.
Email: julia.kelly@cec.lu.se

Funding information

Swedish Strategic Research Area BECC, Biodiversity and Ecosystem Services in a Changing Climate, Grant/Award Number: 2018; Crafoordska Stiftelsen, Grant/Award Number: 20190763; Ramon y Cajal, Grant/Award Number: RYC2018-025797-I; Swedish Research Council Formas, Grant/Award Number: 2018-02700 and 2019-00836

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

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 hemiboreal 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℃ 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℃ and 793 mm, respectively.

2.2 | Site descriptions

The five sites were located in an area <1 km^2, 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%

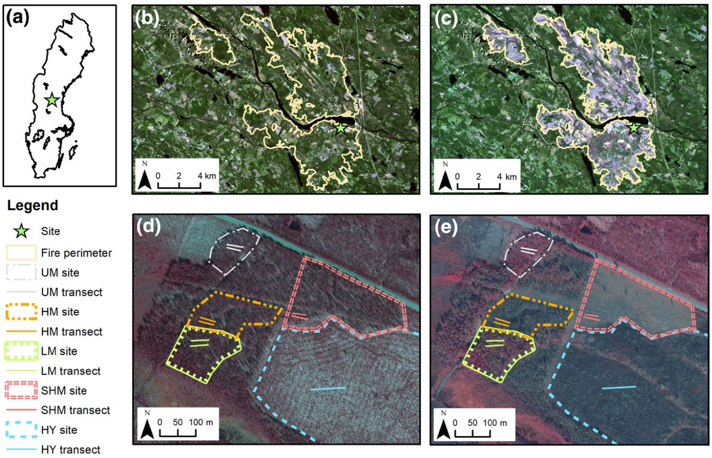
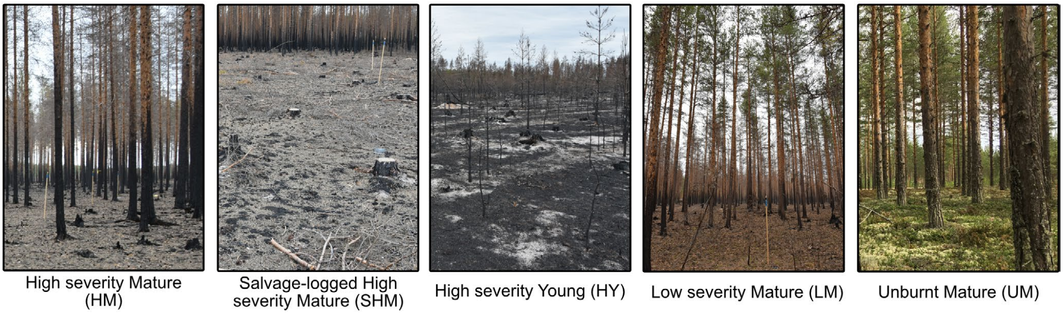


FIGURE 1 (a) Star represents the location of the study area within Sweden (61°56′N, 15°28′E), (b) RGB satellite image from before the Ljusdal fire (July 2018) and (c) 1 year after in August 2019, the fire perimeter is outlined in yellow (d, e) false colour composite aerial photos of the sites from before 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

	Site				
Description	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 m^3 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 $\mu mol\ m^{-2}\ s^{-1}$) 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

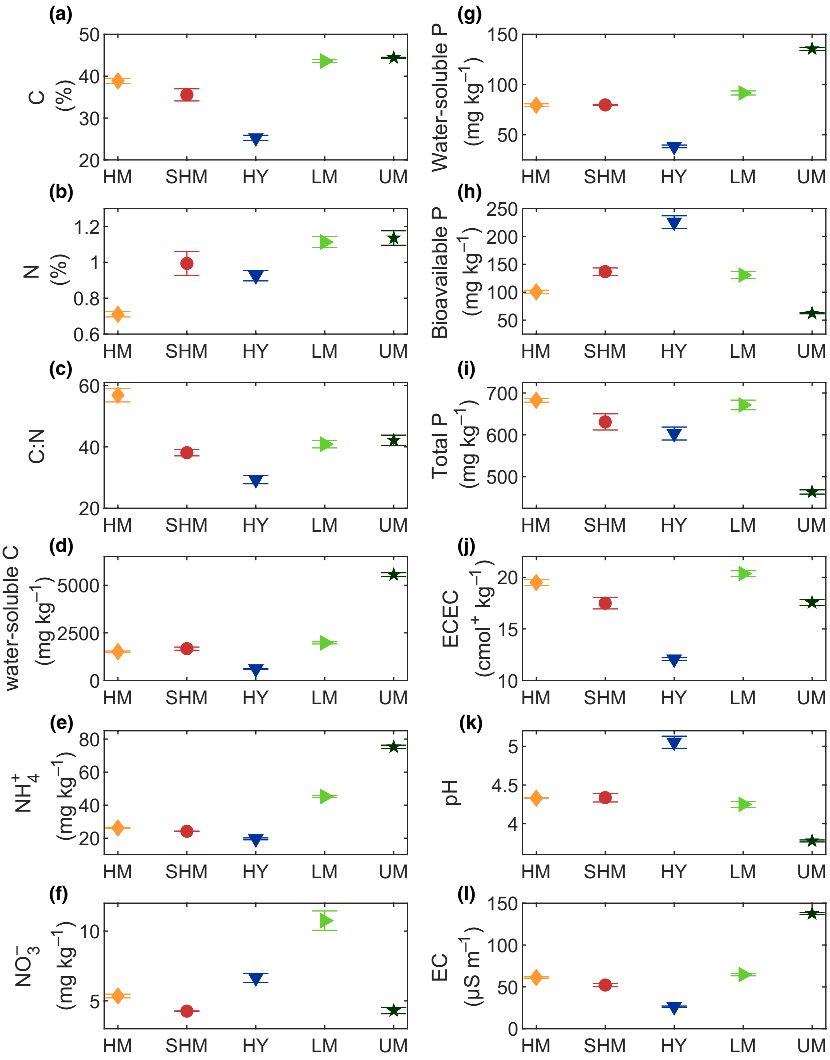


FIGURE 3 Mean ± SE of the soil chemical properties in the organic layer (mean of 4 composite samples) at all sites measured in May 2019. (a) total C content (b) total N content (c) C:N ratio (d) water-soluble C concentration (e) NH_4^- concentration (f) NO_3^- concentration (g) water-soluble P concentration (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 µmol m^{-2} s^{-1} and 1.4 ± 0.1 µmol m^{-2} s^{-1} at SHM and HM, respectively)

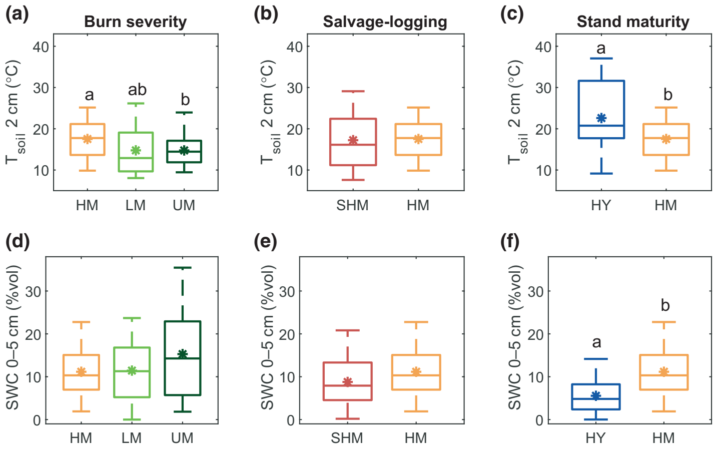


FIGURE 4 Site soil temperature (a–c) and soil water content (SWC; d–f) grouped according to burn severity (a, d), salvage-logging (b, e) and stand maturity (c, f). The boxes show the interquartile range, the middle line is the median and the asterisk is the mean. The lines extending above/below each 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

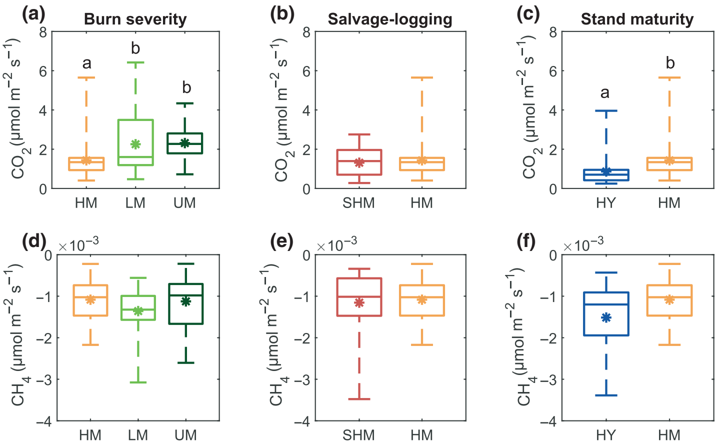


FIGURE 5 Site soil CO_2 (a–c) and CH_4 (d–f) fluxes grouped according to burn severity (a, d), salvage-logging (b, e) and stand maturity (c, f). The boxes show the interquartile range, the middle line is the median and the asterisk is the mean. The lines extending above/below each box indicate the maximum/minimum data values. Different letters above or below each boxplot denote significant differences in the fluxes between the sites (Tukey's post hoc test, $p \le 0.05$). 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)

	Site			Soil temperature			Site × Soil temperature		
Group	***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 $-1.5 \pm 0.1 \times 10^{-3}$ μmol m^{-2} s^{-1} and $-1.1 \pm 0.1 \times 10^{-3}$ μmol m^{-2} s^{-1}, 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

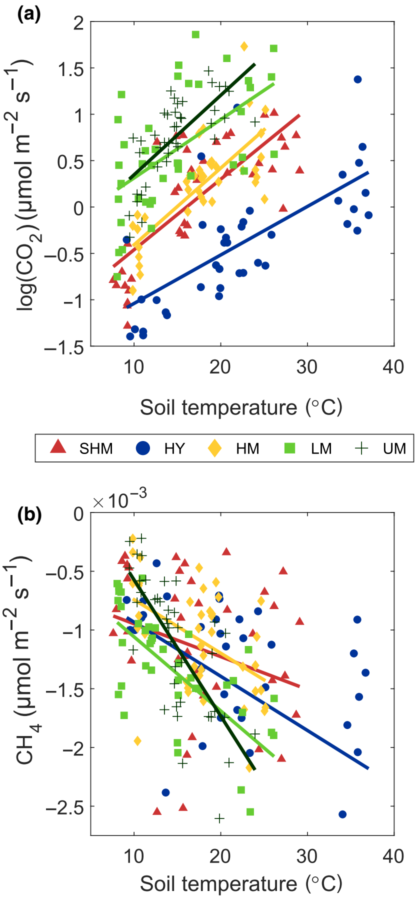


FIGURE 6 Linear regressions between (a) log(CO_2 flux) and (b) CH_4 flux and soil temperature at 2 cm depth at each site (see Table S3 for regression parameters). Site names: HM = High severity Mature, SHM = Salvage-logged High severity Mature, HY = High severity Young, LM = Low severity Mature and UM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

despite mean soil temperatures 2.7℃ 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 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 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 dryer 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 unlogged 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.

ACKNOWLEDGEMENTS

This project has been funded by Swedish Research Council Formas grants 2018-02700, 2019-00836, the strategic research program of the Crafoord Foundation grant 20190763, and the Swedish Strategic Research Area BECC (Biodiversity and Ecosystem Services in a Changing Climate). C.S. also received funding from the Spanish 'Ramon y Cajal' programme, Ref. N. RYC2018-025797-I. Jukka Kuivaniemi has been integral to the success of the project, and we thank him for facilitating access to the sites and tree-ring dating. We also thank him and Mårten Sörell for detailed information on the sites and forest management practices. We are grateful to Olle Olmårs for providing access to the HY and SHM sites, to Ellinor Delin for conducting a vegetation survey, to Niklas Båmstedt and Malin Blomberg for their assistance with the fieldwork and to Louise Andresen, for her insightful comments on the soil chemistry analysis.

DATA AVAILABILITY STATEMENT

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

ORCID

Julia Kelly https://orcid.org/0000-0002-7370-1401
Theresa S. Ibáñez https://orcid.org/0000-0003-2459-5945
Cristina Santín https://orcid.org/0000-0001-9901-2658
Stefan H. Doerr https://orcid.org/0000-0002-8700-9002
Marie-Charlotte Nilsson https://orcid.org/0000-0002-9254-2223
Thomas Holst https://orcid.org/0000-0002-3360-9395
Anders Lindroth https://orcid.org/0000-0002-7669-784X
Natascha Kljun https://orcid.org/0000-0001-9650-2184

REFERENCES

Allison, S. D., McGuire, K. L., & Treseder, K. K. (2010). Resistance of microbial and soil properties to warming treatment seven years after boreal fire. *Soil Biology & Biochemistry*, *42*, 1872–1878. https://doi.org/10.1016/j.soilbio.2010.07.011

Amiro, B. D., Barr, A. G., Black, T. A., Iwashita, H., Kljun, N., McCaughey, J. H., Morgenstern, K., Murayama, S., Nesic, Z., Orchansky, A. L., & Saigusa, N. (2006). Carbon, energy and water fluxes at mature and disturbed forest sites, Saskatchewan, Canada. *Agricultural and Forest Meteorology*, *136*, 237–251. https://doi.org/10.1016/j.agrformet.2004.11.012

Araya, S. N., Fogel, M. L., & Berhe, A. A. (2017). Thermal alteration of soil organic matter properties: A systematic study to infer response of Sierra Nevada climosequence soils to forest fires. *Soil*, *3*, 31–44. https://doi.org/10.5194/soil-3-31-2017

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*. https://doi.org/10.18637/jss.v067.i01

Bodí, M. B., Martin, D. A., Balfour, V. N., Santín, C., Doerr, S. H., Pereira, P., Cerdà, A., & Mataix-Solera, J. (2014). Wildland fire ash: Production, composition and eco-hydro-geomorphic effects. *Earth-Science Reviews*, *130*, 103–127. https://doi.org/10.1016/j.earscirev.2013.12.007

Bond-Lamberty, B., Peckham, S. D., Ahl, D. E., & Gower, S. T. (2007). Fire as the dominant driver of central Canadian boreal forest carbon balance. *Nature*, *450*, 89–92. https://doi.org/10.1038/nature06272

Bowd, E. J., Banks, S. C., Strong, C. L., & Lindenmayer, D. B. (2019). Long-term impacts of wildfire and logging on forest soils. *Nature Geoscience*, *12*, 113–118. https://doi.org/10.1038/s41561-018-0294-2

Bradshaw, C. J. A., & Warkentin, I. G. (2015). Global estimates of boreal forest carbon stocks and flux. *Global and Planetary Change*, *128*, 24–30. https://doi.org/10.1016/j.gloplacha.2015.02.004

Bryanin, S. V., & Makoto, K. (2017). Fire-derived charcoal affects fine root vitality in a post-fire Gmelin larch forest: field evidence. *Plant and Soil*, *416*, 409–418. https://doi.org/10.1007/s11104-017-3217-x

Burke, R. A., Zepp, R. G., Tarr, A., Miller, L., & Stocks, J. (1997). Effect of fire on soil-atmosphere exchange of methane boreal fluxes of carbon dioxide in Canadian boreal forest sites. *Journal of Geophysical Research*, *102*, 289–300. https://doi.org/10.1029/97JD01331

Certini, G. (2005). Effects of fire on properties of forest soils: A review. *Oecologia*, *143*, 1–10. https://doi.org/10.1007/s00442-004-1788-8

Covey, K. R., & Megonigal, J. P. (2019). Methane production and emissions in trees and forests. *New Phytologist*, *222*, 35–51. https://doi.org/10.1111/nph.15624

Day, N. J., Dunfield, K. E., Johnstone, J. F., Mack, M. C., Turetsky, M. R., Walker, X. J., White, A. L., & Baltzer, J. L. (2019). Wildfire severity reduces richness and alters composition of soil fungal communities in boreal forests of western Canada. *Global Change Biology*, *25*, 2310–2324. https://doi.org/10.1111/gcb.14641

De Groot, W. J., Cantin, A. S., Flannigan, M. D., Soja, A. J., Gowman, L. M., & Newbery, A. (2013). A comparison of Canadian and Russian boreal forest fire regimes. *Forest Ecology and Management*, *294*, 23–34. https://doi.org/10.1016/j.foreco.2012.07.033

De Groot, W. J., Flannigan, M. D., & Cantin, A. S. (2013). Climate change impacts on future boreal fire regimes. *Forest Ecology and Management*, *294*, 35–44. https://doi.org/10.1016/j.foreco.2012.09.027

Dieleman, C. M., Rogers, B. M., Potter, S., Veraverbeke, S., Johnstone, J. F., Laflamme, J., Solvik, K., Walker, X. J., Mack, M. C., & Turetsky, M. R. (2020). Wildfire combustion and carbon stocks in the southern Canadian boreal forest: Implications for a warming world. *Global Change Biology*, *26*, 6062–6079. https://doi.org/10.1111/gcb.15158

Dooley, S. R., & Treseder, K. K. (2012). The effect of fire on microbial biomass: A meta-analysis of field studies. *Biogeochemistry*, *109*, 49–61. https://doi.org/10.1007/s10533-011-9633-8

Drobyshev, I., Bergeron, Y., Linderholm, H. W., Granström, A., & Niklasson, M. (2015). A 700-year record of large fire years in northern Scandinavia shows large variability and increased frequency during the 1800s. *Journal of Quaternary Science*, *30*, 211–221. https://doi.org/10.1002/jqs.2765

Ghani, A., Dexter, M., & Perrott, K. W. (2003). Hot-water extractable carbon in soils: A sensitive measurement for determining impacts of fertilisation, grazing and cultivation. *Soil Biology & Biochemistry*, *35*, 1231–1243. https://doi.org/10.1016/S0038-0717(03)00186-X

Gulledge, J., Doyle, A. P., & Schimel, J. P. (1997). Different NH_4^+-inhibition patterns of soil CH_4 consumption: A result of distinct CH_4-oxidizer populations across sites. *Soil Biology & Biochemistry*, *29*, 13–21. https://doi.org/10.1016/S0038-0717(96)00265-9

Gustafsson, L., Berglind, M., Granström, A., Grelle, A., Isacsson, G., Kjellander, P., Larsson, S., Lindh, M., Pettersson, L. B., Strengbom, J., Stridh, B., Sävström, T., Thor, G., Wikars, L. O., & Mikusiński, G. (2019). Rapid ecological response and intensified knowledge accumulation following a north European mega-fire. *Scandinavian Journal of Forest Research*, *34*, 234–253. https://doi.org/10.1080/02827581.2019.1603323

Helmke, P. A., & Sparks, D. L. (1996). Lithium, sodium, potassium, rubidium, and cesium. In D. L. Sparks, A. L. Page, P. A. Helmke, R. H. Loeppert, P. Soltanpour, M. A. Tabatabai, C. T. Johnston, & M. E. Sumner (Eds.), *Methods of soil analysis: Part 3 chemical methods* (pp. 551–574). SSSA Book Series. Soil Science Society of America, Inc. and American Society of Agronomy, Inc. https://doi.org/10.2136/sssabookser5.3.c19

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg, G., Ottosson-Löfvenius, M., & Read, D. J. (2001). Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*, *411*, 789–792. https://doi.org/10.1038/35081058

Holden, S. R., Rogers, B. M., Treseder, K. K., & Randerson, J. T. (2016). Fire severity influences the response of soil microbes to a boreal forest fire. *Environmental Research Letters*, *11*. https://doi.org/10.1088/1748-9326/11/3/035004

Hoy, E. E., Turetsky, M. R., & Kasischke, E. S. (2016). More frequent burning increases vulnerability of Alaskan boreal black spruce forests. *Environmental Research Letters*, *11*. https://doi.org/10.1088/1748-9326/11/9/095001

Hu, T., Sun, L., Hu, H., Weise, D. R., & Guo, F. (2017). Soil respiration of the dahurian larch (*Larix gmelinii*) forest and the response to fire disturbance in Da Xing'an Mountains, China. *Scientific Reports*, *7*, 1–10. https://doi.org/10.1038/s41598-017-03325-4

IPCC. (2013). *Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.

Kasischke, E. S., & Johnstone, J. F. (2005). Variation in postfire organic layer thickness in a black spruce forest complex in interior Alaska and its effects on soil temperature and moisture. *Canadian Journal of Forest Research*, *35*, 2164–2177. https://doi.org/10.1139/x05-159

Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: A brief review and suggested usage. *International Journal of Wildland Fire*, *18*, 116–126. https://doi.org/10.1071/WF07049

Kilpeläinen, A., Kellomäki, S., Strandman, H., & Venäläinen, A. (2010). Climate change impacts on forest fire potential in boreal conditions in Finland. *Climatic Change*, *103*, 383–398. https://doi.org/10.1007/s10584-009-9788-7

Kishchuk, B. E., Thiffault, E., Lorente, M., Quideau, S., Keddy, T., & Sidders, D. (2014). Decadal soil and stand response to fire, harvest, and salvage-logging disturbances in the western boreal mixedwood forest of Alberta, Canada. *Canadian Journal of Forest Research*, *45*, 141–152. https://doi.org/10.1139/cjfr-2014-0148

Köster, E., Köster, K., Berninger, F., Prokushkin, A., Aaltonen, H., Zhou, X., & Pumpanen, J. (2018). Changes in fluxes of carbon dioxide and methane caused by fire in Siberian boreal forest with continuous permafrost. *Journal of Environmental Management*, *228*, 405–415. https://doi.org/10.1016/j.jenvman.2018.09.051

Köster, K., Köster, E., Orumaa, A., Parro, K., Jõgiste, K., Berninger, F., Pumpanen, J., & Metslaid, M. (2016). How time since forest fire affects stand structure, soil physical-chemical properties and soil CO_2 efflux in hemiboreal scots pine forest fire chronosequence? *Forests*, *7*. https://doi.org/10.3390/f7090201

KSLA. (2015). *Forests and forestry in Sweden*. Stockholm. https://doi.org/10.1007/BF00578267

Kulmala, L., Aaltonen, H., Berninger, F., Kieloaho, A. J., Levula, J., Bäck, J., Hari, P., Kolari, P., Korhonen, J. F. J., Kulmala, M., Nikinmaa, E., Pihlatie, M., Vesala, T., & Pumpanen, J. (2014). Changes in biogeochemistry and carbon fluxes in a boreal forest after the clear-cutting and partial burning of slash. *Agricultural & Forest Meteorology*, *188*, 33–44. https://doi.org/10.1016/j.agrformet.2013.12.003

Lagerström, A., Esberg, C., Wardle, D. A., & Giesler, R. (2009). Soil phosphorus and microbial response to a long-term wildfire chronosequence in northern Sweden. *Biogeochemistry*, *95*, 199–213. https://doi.org/10.1007/s10533-009-9331-y

Leverkus, A. B., Lindenmayer, D. B., Thorn, S., & Gustafsson, L. (2018). Salvage logging in the world's forests: Interactions between natural disturbance and logging need recognition. *Global Ecology and Biogeography*, *27*, 1140–1154. https://doi.org/10.1111/geb.12772

Lindenmayer, D. B., Foster, D. R., Franklin, J. F., Hunter, M. L., Noss, R. F., Schmiegelow, F. A., & Perry, D. (2004). Salvage harvesting policies after natural disturbance. *Science*, *303*, 1303. https://doi.org/10.1126/science.1093438

Livingston, G. P., & Hutchinson, G. L. (1995). Enclosure-based measurement of trace gas exchange: applications and sources of error. In P. A. Matson & R. C. Harriss (Eds.), *Biogenic trace gases: Measuring emissions from soil and water* (pp. 14–50). Wiley-Blackwell.

Ljusdals kommun. (2018). Bränderna i Ljusdal 2018. Ljusdal.

Ludwig, S. M., Alexander, H. D., Kielland, K., Mann, P. J., Natali, S. M., & Ruess, R. W. (2018). Fire severity effects on soil carbon and nutrients and microbial processes in a Siberian larch forest. *Global Change Biology*, *24*, 5841–5852. https://doi.org/10.1111/gcb.14455

LUKE. (2018). *Suomen metsätilastot*. Finnish Forest Statistics.

Mallik, A. U., & Hu, D. (1997). Soil respiration following site preparation treatments in boreal mixedwood forest. *Forest Ecology and Management*, *97*, 265–275. https://doi.org/10.1016/S0378-1127(97)00067-4

Marañón-Jiménez, S., & Castro, J. (2013). Effect of decomposing post-fire coarse woody debris on soil fertility and nutrient availability in a Mediterranean ecosystem. *Biogeochemistry*, *112*, 519–535. https://doi.org/10.1007/s10533-012-9744-x

Marañón-Jiménez, S., Castro, J., Fernández-Ondoño, E., & Zamora, R. (2013). Charred wood remaining after a wildfire as a reservoir of macro- and micronutrients in a Mediterranean pine forest. *International Journal of Wildland Fire*, *22*, 681–695. https://doi.org/10.1071/WF12030

Marañón-Jiménez, S., Castro, J., Kowalski, A. S., Serrano-Ortiz, P., Reverter, B. R., Sánchez-Cañete, E. P., & Zamora, R. (2011). Post-fire soil respiration in relation to burnt wood management in a Mediterranean mountain ecosystem. *Forest Ecology and Management*, *261*, 1436–1447. https://doi.org/10.1016/j.foreco.2011.01.030

Marcolin, E., Marzano, R., Vitali, A., Garbarino, M., & Lingua, E. (2019). Post-fire management impact on natural forest regeneration through altered microsite conditions. *Forests*, *10*. https://doi.org/10.3390/f10111014

Maynard, D. G., Paré, D., Thiffault, E., Lafleur, B., Hogg, K. E., & Kishchuk, B. (2014). How do natural disturbances and human activities affect soils and tree nutrition and growth in the Canadian boreal forest? *Environmental Reviews*, *22*, 161–178. https://doi.org/10.1139/er-2013-0057

McDowell, N. G., Allen, C. D., Anderson-Teixeira, K., Aukema, B. H., Bond-Lamberty, B., Chini, L., Clark, J. S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G. C., Jackson, R. B., Johnson, D. J., Kueppers, L., Lichstein, J. W., Ogle, K., Poulter, B., Pugh, T. A. M., Seidl, R., … Xu, C. (2020). Pervasive shifts in forest dynamics in a changing world. *Science*, *80*, 368. https://doi.org/10.1126/science.aaz9463

Mehlich, A. (1984). Mehlich 3 soil test extractant: A modification of Mehlich 2 extractant. *Communications in Soil Science and Plant Analysis*, *15*, 1409–1416. https://doi.org/10.1080/00103628409367568

Morishita, T., Noguchi, K., Kim, Y., Matsuura, Y., Morishita, T., Noguchi, K., Kim, Y., & Matsuura, Y. (2015). CO_2, CH_4 and N_2O fluxes of upland black spruce (*Picea mariana*) forest soils after forest fires of different intensity in interior Alaska. *Soil Science and Plant Nutrition*, *61*, 98–105. https://doi.org/10.1080/00380768.2014.963666

MSB. (2013). *Framtida perioder med hög risk för skogsbrand – Analyser av klimatscenarier*. Myndigheten för samhällsskydd och beredskap.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

O'Neill, K. P., Kasischke, E. S., & Richter, D. D. (2003). Seasonal and decadal patterns of soil carbon uptake and emission along an age sequence of burned black spruce stands in interior Alaska. *Journal of Geophysical Research*, *108*, 1–15. https://doi.org/10.1029/2001jd000443

Örlander, G., Egnell, G., & Albrektson, A. (1996). Long-term effects of site preparation on growth in Scots pine. *Forest Ecology and Management*, *86*, 27–37. https://doi.org/10.1016/S0378-1127(96)03797-8

Parro, K., Köster, K., Jõgiste, K., Seglinš, K., Sims, A., Stanturf, J. A., & Metslaid, M. (2019). Impact of post-fire management on soil respiration, carbon and nitrogen content in a managed hemiboreal forest. *Journal of Environmental Management*, *233*, 371–377. https://doi.org/10.1016/j.jenvman.2018.12.050

Pérez-Izquierdo, L., Clemmensen, K. E., Strengbom, J., Granath, G., Wardle, D. A., Nilsson, M., & Lindahl, B. D. (2020). Crown-fire severity is more important than ground-fire severity in determining soil fungal community development in the boreal forest. *Journal of Ecology*, *109*(1), 504–518. https://doi.org/10.1111/1365-2745.13529

Pumpanen, J., Kulmala, L., Lindén, A., Kolari, P., Nikinmaa, E., & Hari, P. (2015). Seasonal dynamics of autotrophic respiration in boreal forest soil estimated by continuous chamber measurements. *Boreal Environment Research*, *20*, 637–650.

Pumpanen, J., Westman, C. J., & Ilvesniemi, H. (2004). Soil CO_2 efflux from a podzolic forest soil before and after forest clear-cutting and site preparation. *Boreal Environment Research*, *9*, 199–212.

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Ribeiro-Kumara, C., Köster, E., Aaltonen, H., & Köster, K. (2020). How do forest fires affect soil greenhouse gas emissions in upland boreal forests? A review. *Environmental Research*, *184*, 109328. https://doi.org/10.1016/j.envres.2020.109328

Saari, A., Heiskanen, J., & Martikainen, P. J. (1998). Effect of the organic horizon on methane oxidation and uptake in soil of a boreal Scots pine forest. *FEMS Microbiology Ecology*, *26*, 245–255. https://doi.org/10.1016/S0168-6496(98)00040-3

Santín, C., Doerr, S. H., Merino, A., Bryant, R., & Loader, N. J. (2016). Forest floor chemical transformations in a boreal forest fire and their correlations with temperature and heating duration. *Geoderma*, *264*, 71–80. https://doi.org/10.1016/j.geoderma.2015.09.021

Sawamoto, T., Hatano, R., Yajima, T., Takahashi, K., & Isaev, A. P. (2000). Soil respiration in Siberian taiga ecosystems with different histories of forest fire. *Soil Science and Plant Nutrition*, *46*, 31–42. https://doi.org/10.1080/00380768.2000.10408759

Simard, D. G., Fyles, J. W., Paré, D., & Nguyen, T. (2001). Impacts of clearcut harvesting and wildfire on soil nutrient status in the Quebec boreal forest. *Canadian Journal of Soil Science*, *81*, 229–237. https://doi.org/10.4141/S00-028

Singh, S., Amiro, B. D., & Quideau, S. A. (2008). Effects of forest floor organic layer and root biomass on soil respiration following boreal forest fire. *Canadian Journal of Forest Research*, *38*, 647–655. https://doi.org/10.1139/X07-200

Sitnov, S. A., & Mokhov, I. I. (2018). A comparative analysis of the characteristics of active fires in the boreal forests of Eurasia and North America based on satellite data. *Izvestiya, Atmospheric and Oceanic Physics*, *54*, 966–978. https://doi.org/10.1134/S0001433818090347

Skogsstyrelsen. (2018). *Strukturstatistik: Statistik on skogsägande 2017*. Jönköping.

Smith, K. A., Dobbie, K. E., Ball, B. C., Bakken, L. R., Sitaula, B. K., Hansen, S., Brumme, R., Borken, W., Christensen, S., Priemé, A., Fowler, D., Macdonald, J. A., Skiba, U., Klemedtsson, L., Kasimir-Klemedtsson, A., Degórska, A., & Orlanski, P. (2000). Oxidation of atmospheric methane in Northern European soils, comparison with other ecosystems, and uncertainties in the global terrestrial sink. *Global Change Biology*, *6*, 791–803. https://doi.org/10.1046/j.1365-2486.2000.00356.x

SOU. (2019). *Skogsbränderna sommaren 2018*. Stockholm.

Striegl, R. G., & Wickland, K. P. (1998). Effects of a clear-cut harvest on soil respiration in a jack pine - lichen woodland. *Canadian Journal of Forest Research*, *28*, 534–539. https://doi.org/10.1139/cjfr-28-4-534

Strömgren, M., Hedwall, P. O., & Olsson, B. A. (2016). Effects of stump harvest and site preparation on N_2O and CH_4 emissions from boreal forest soils after clear-cutting. *Forest Ecology and Management*, *371*, 15–22. https://doi.org/10.1016/j.foreco.2016.03.019

Sundqvist, E., Vestin, P., Crill, P., Persson, T., & Lindroth, A. (2014). Short-term effects of thinning, clear-cutting and stump harvesting on methane exchange in a boreal forest. *Biogeosciences*, *11*, 6095–6105. https://doi.org/10.5194/bg-11-6095-2014

Teepe, R., Brumme, R., Beese, F., & Ludwig, B. (2004). Nitrous oxide emission and methane consumption following compaction of forest soils. *Soil Science Society of America Journal*, *68*, 605–611. https://doi.org/10.2136/sssaj2004.6050

Thiffault, E., Bélanger, N., Paré, D., & Munson, A. D. (2007). How do forest harvesting methods compare with wildfire? A case study of soil chemistry and tree nutrition in the boreal forest. *Canadian Journal of Forest Research*, *37*, 1658–1668. https://doi.org/10.1139/X07-031

U.S. EPA. (2007). *Method 3051A (SW-846): Microwave assisted acid digestion of sediments*. Sludges and Oils.

Vestin, P., Mölder, M., Kljun, N., Cai, Z., Hasan, A., Holst, J., Klemedtsson, L., & Lindroth, A. (2020). Impacts of clear-cutting of a boreal forest on carbon dioxide, methane and nitrous oxide fluxes. *Forests*, *11*, 1–28. https://doi.org/10.3390/f11090961

Waldrop, M. P., & Harden, J. W. (2008). Interactive effects of wildfire and permafrost on microbial communities and soil processes in an Alaskan black spruce forest. *Global Change Biology*, *14*, 2591–2602. https://doi.org/10.1111/j.1365-2486.2008.01661.x

Walker, X. J., Baltzer, J. L., Cumming, S. G., Day, N. J., Ebert, C., Goetz, S., Johnstone, J. F., Potter, S., Rogers, B. M., Schuur, E. A. G., Turetsky, M. R., & Mack, M. C. (2019). Increasing wildfires threaten historic carbon sink of boreal forest soils. *Nature*, *572*, 520–523. https://doi.org/10.1038/s41586-019-1474-y

Walker, X. J., Rogers, B. M., Baltzer, J. L., Cumming, S. G., Day, N. J., Goetz, S. J., Johnstone, J. F., Schuur, E. A. G., Turetsky, M. R., & Mack, M. C. (2018). Cross-scale controls on carbon emissions from boreal forest megafires. *Global Change Biology*, *24*, 4251–4265. https://doi.org/10.1111/gcb.14287

Yuan, Z. Y., & Chen, H. Y. H. (2010). Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: Literature review and meta-analyses. *Critical Reviews in Plant Sciences*, *29*, 204–221. https://doi.org/10.1080/07352689.2010.483579

Zackrisson, O. (1977). Influence of forest fires on the north Swedish boreal forest. *Oikos*, *29*, 22–32. https://doi.org/10.2307/3543289

Zha, T., Xing, Z., Wang, K. Y., Kellomäki, S., & Barr, A. G. (2007). Total and component carbon fluxes of a scots pine ecosystem from chamber measurements and eddy covariance. *Annals of Botany*, *99*, 345–353. https://doi.org/10.1093/aob/mcl266

SUPPORTING INFORMATION

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

How to cite this article: Kelly, J., Ibáñez, T. S., Santín, C., Doerr, S. H., Nilsson, M.-C., Holst, T., Lindroth, A., & Kljun, N. (2021). Boreal forest soil carbon fluxes one year after a wildfire: Effects of burn severity and management. *Global Change Biology*, 00, 1–15. https://doi.org/10.1111/gcb.15721

SUPPLEMENTARY INFORMATION

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

Julia Kelly*[1], Theresa S. Ibáñez[2], Cristina Santín[3,4], Stefan H. Doerr[5], Marie-Charlotte Nilsson[2], Thomas Holst[6], Anders Lindroth[6], Natascha Kljun[1]

*Corresponding author:

julia.kelly@cec.lu.se, Centre for Environmental and Climate Science, Lund University,
Sölvegatan 37, 223 62 Lund, Sweden

Affiliations:

[1]Centre for Environmental and Climate Science, Lund University, Lund, Sweden

[2]Department of Forest Ecology and Management, Faculty of Forest Sciences, Swedish University of Agricultural Sciences, Umeå, Sweden

[3]Department of Biosciences, Swansea University, Swansea, Wales, UK

[4]Research Unit of Biodiversity, Spanish National Research Council, Mieres, Spain

[5]Department of Geography, Swansea University, Swansea, Wales, UK

[6]Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden

Method for the manual dark CO_2 and CH_4 chamber measurements

At each of the five sites, 10 collars were placed 10 m apart along one or two transects (Figure 1d-e and Figure S1). One transect (90 m long) was used at the HY site to allow for comparison with data from an eddy covariance flux tower (not this study) whereas two transects (each 40 m long) were used at all the other (smaller) sites.

When calculating fluxes based on the concentration measurements, we adjusted the volume of the chamber based on the height of the soil surface or vegetation inside each collar. Linear regressions of the change in gas concentration over time were fitted over five windows of 150 seconds duration with intervals of 10-30 seconds between the start of each window. The first 30 seconds of each measurement were discarded to minimize the impact of pressure fluctuations that can occur during chamber closure (Davidson et al., 2002). For CO_2, the slope of the regression with the highest $R^2 > 0.8$, 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. If none of the five linear regressions passed the statistical thresholds, the concentration measurements were discarded. To calculate the flux, we used the selected slope, the soil temperature (5 cm depth) measured for each collar and air pressure measurements from a national monitoring station (58 km away from the site, measurements were adjusted to the elevation of the site) as inputs to the ideal gas law. Flux calculations for CH_4 followed the same procedure but the R^2 threshold was set to 0.25 to avoid excluding low fluxes (cf. Sundqvist et al., 2014).

Table S1. Mixed effects model formulas, fixed effects parameter estimates and pseudo-R^2 for linear mixed effects models. All models were fit using the lme4 package in R (R version 3.6.2; Bates et al., 2015; R Core Team, 2019). The fixed effects are site and T_{soil} (soil temperature at 2 cm depth), and the random effects are collar ID nested within site. The interaction between site and T_{soil} was only included if it was significant. The sites included within each model depend on the group being investigated: burn severity = UM, LM and HM; salvage-logging = SHM and HM; stand maturity = HY and HM. The pseudo-R_2 values were calculated according to Nakagawa and Schielzeth (2013), whereby $R^2_{GLMM(m)}$ is the marginal R^2 (variance explained by the fixed effects) and $R^2_{GLMM(c)}$ is the conditional R_2 (variance explained by the fixed and random effects). Site names: HM = High severity Mature, SHM = Salvage-logged High severity Mature, HY = High severity Young, LM = Low severity Mature and UM = Unburnt Mature.

Group	Formula	Fixed effects parameter estimates (± SE)	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
Burn severity	CO_2 ~ site + T_{soil} + (1|site:collar)	Intercept (UM) = -0.247 ± 0.026 HM = 0.110 ± 0.036 LM = -0.158 ± 0.036 T_{soil} = 0.031 ± 0.002	0.51	0.74
	CH_4 ~ site + T_{soil} + site * T_{soil} + (1|site:collar)	Intercept (UM) = $-1.241 \times 10^{-3} \pm 5.559 \times 10^{-5}$ HM = $1.184 \times 10^{-5} \pm 7.881 \times 10^{-5}$ LM = $1.636 \times 10^{-4} \pm 7.845 \times 10^{-5}$ T_{soil} = $-7.425 \times 10^{-5} \pm 6.553 \times 10^{-6}$ HM * T_{soil} = $-3.885 \times 10^{-5} \pm 1.049 \times 10^{-5}$ LM * T_{soil} = $2.792 \times 10^{-5} \pm 8.864 \times 10^{-6}$	0.44	0.66
Salvage-logging	CO_2 ~ site + T_{soil} + (1|site:collar)	Intercept (SLM) = 0.066 ± 0.023 HM = -0.022 ± 0.023 T_{soil} = 0.034 ± 0.003	0.58	0.64
	CH_4 ~ site + T_{soil} + (1|site:collar)	Intercept (SLM) = $-1.109 \times 10^{-3} \pm 1.026 \times 10^{-4}$ HM = $-3.012 \times 10^{-5} \pm 1.026 \times 10^{-4}$ T_{soil} = $-3.658 \times 10^{-5} \pm 8.244 \times 10^{-6}$	0.12	0.55
Stand maturity	CO_2 ~ site + T_{soil} + site * T_{soil} + (1|site:collar)	Intercept (HM) = -0.072 ± 0.035 HY = 0.160 ± 0.035 T_{soil} = 0.030 ± 0.002 HY*T_{soil} = 0.006 ± 0.002	0.62	0.86
	CH_4 ~ site + T_{soil} + (1|site:collar)	Intercept (HM) = $-1.224 \times 10^{-3} \pm 1.156 \times 10^{-4}$ HY = $1.461 \times 10^{-4} \pm 1.155 \times 10^{-4}$ T_{soil} = $-4.867 \times 10^{-5} \pm 5.357 \times 10^{-6}$	0.32	0.78

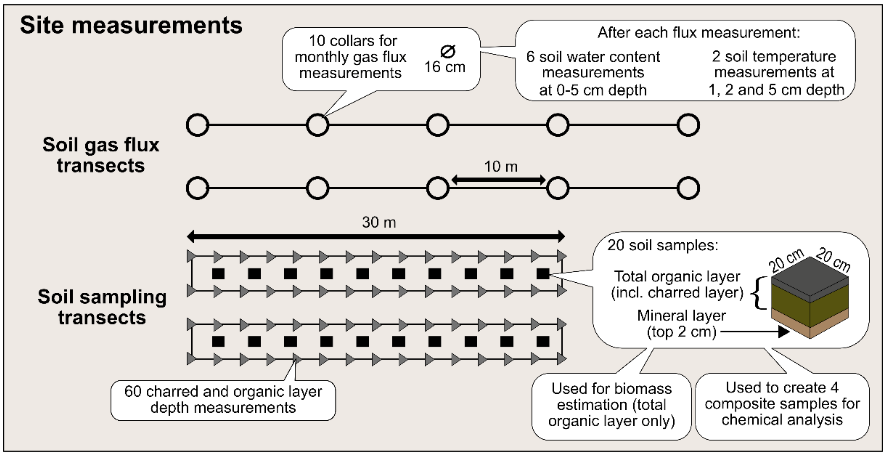


Figure S1. Layout of the soil gas flux and soil sampling transects at each site.

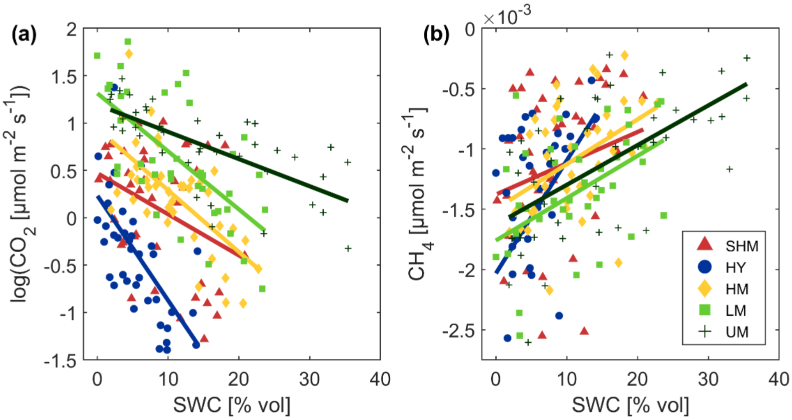


Figure S2. Linear regressions between log(CO$_2$ flux), CH$_4$ flux and soil water content at 0-5 cm depth at each site (see Table S4 for regression parameters). Site names: HM = High severity Mature, SHM = Salvage-logged High severity Mature, HY = High severity Young, LM = Low severity Mature and UM = Unburnt Mature.

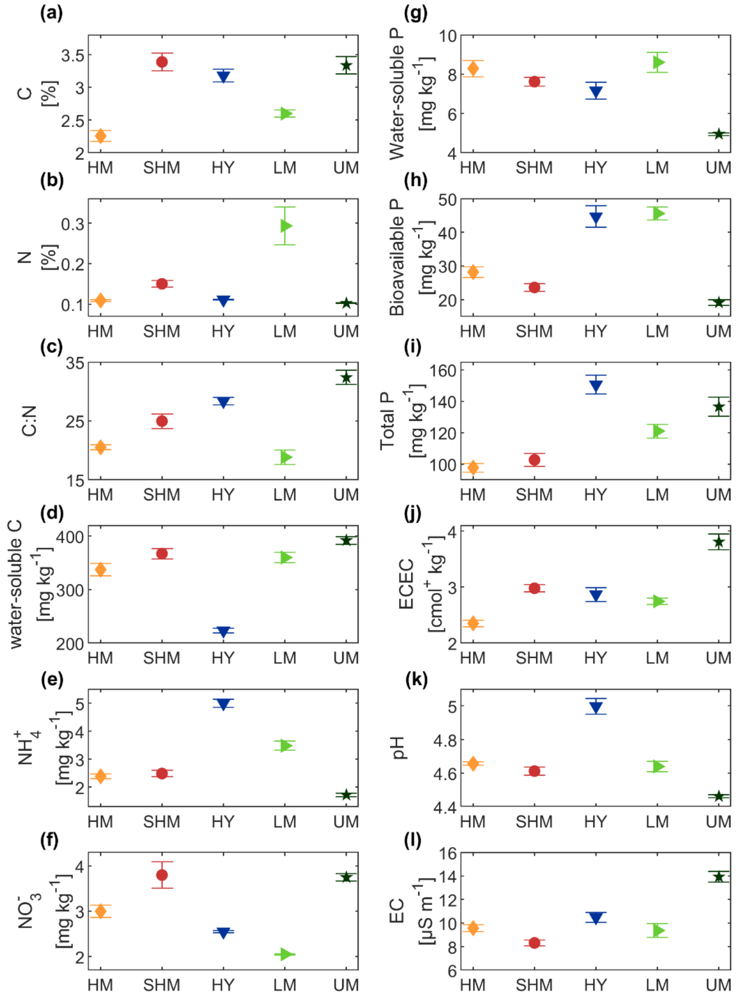


Figure S3. Mean ± SE of the soil chemical properties in the mineral layer (mean of 4 composite samples) at all sites measured in May 2019. Site names: HM = High severity Mature, SHM = Salvage-logged High severity Mature, HY = High severity Young, LM = Low severity Mature and UM = Unburnt Mature.

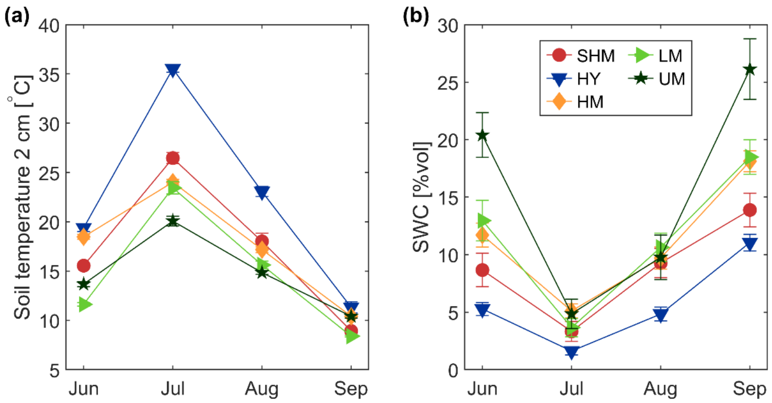


Figure S4. Monthly mean ± SE soil temperature (2 cm depth) and soil water content (SWC) at all sites in 2019. Site names: HM = High severity Mature, SHM = Salvage-logged High severity Mature, HY = High severity Young, LM = Low severity Mature and UM = Unburnt Mature.

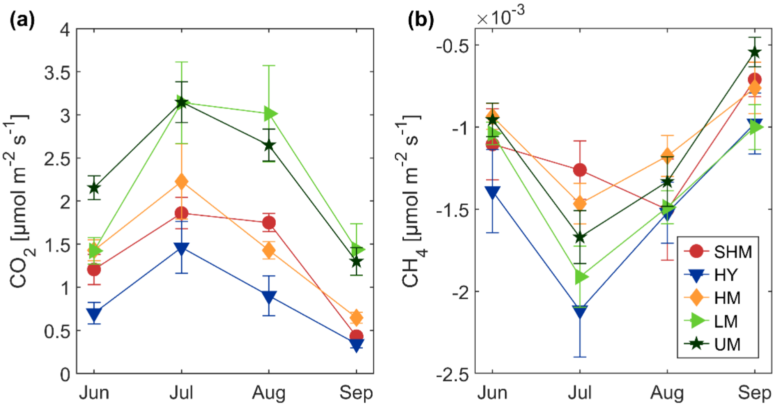


Figure S5. Monthly mean ± SE CO_2 and CH_4 fluxes at all sites in 2019. Site names: HM = High severity Mature, SHM = Salvage-logged High severity Mature, HY = High severity Young, LM = Low severity Mature and UM = Unburnt Mature.

Table S2. Mean (SE in brackets) of all the soil chemical properties tested at each site (4 composite samples) in the organic and mineral layers in May 2019. Ws = water-soluble, bio = bioavailable, tot = total, ECEC = effective cation exchange capacity, EC = 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.

Site	C (%)	N (%)	C:N	C_{ws} (mg kg^{-1})	NH_4^+ (mg kg^{-1})	NO_3^- (mg kg^{-1})	P_{ws} (mg kg^{-1})	P_{bio} (mg kg^{-1})	P_{tot} (mg kg^{-1})	ECEC (cmol$^+$ kg^{-1})	Ca (cmol$^+$ kg^{-1})	Mg (cmol$^+$ kg^{-1})	Na (cmol$^+$ kg^{-1})	K (cmol$^+$ kg^{-1})	Al (cmol$^+$ kg^{-1})	pH	EC (µS m^{-1})
Organic layer																	
HM	38.9 (0.6)	0.71 (0.01)	56.9 (2.2)	1516 (34)	26.2 (0.4)	5.4 (0.1)	79.4 (1.4)	100.6 (2.9)	683 (4)	19.50 (0.29)	13.31 (0.29)	2.42 (0.03)	0.18 (0.00)	2.07 (0.02)	1.52 (0.06)	4.33 (0.01)	61.3 (0.82)
SHM	35.5 (1.4)	0.99 (0.07)	38.1 (1.0)	1672 (84)	24.2 (0.1)	4.3 (0.0)	79.7 (0.6)	136.8 (6.6)	631 (19)	17.50 (0.56)	10.46 (0.30)	1.94 (0.08)	0.18 (0.00)	2.25 (0.08)	2.67 (0.36)	4.34 (0.06)	52.3 (2.03)
HY	25.3 (0.6)	0.93 (0.03)	29.3 (1.3)	612 (20)	19.6 (0.6)	6.7 (0.3)	38.5 (1.3)	225.3 (11.5)	603 (15)	12.08 (0.15)	9.12 (0.22)	1.09 (0.02)	0.12 (0.00)	0.92 (0.02)	0.85 (0.09)	5.05 (0.08)	26.5 (0.70)
LM	43.6 (0.4)	1.11 (0.03)	40.9 (1.2)	1977 (55)	45.2 (0.7)	10.8 (0.7)	91.6 (2.0)	130.6 (6.5)	672 (12)	20.36 (0.27)	14.35 (0.35)	2.40 (0.05)	0.21 (0.00)	2.06 (0.05)	1.35 (0.07)	4.25 (0.04)	64.7 (1.42)
UM	44.4 (0.1)	1.14 (0.04)	42.2 (1.7)	5557 (100)	75.3 (1.1)	4.3 (0.2)	135.5 (1.5)	62.3 (0.9)	464 (5)	17.55 (0.28)	11.41 (0.22)	2.01 (0.04)	0.20 (0.00)	2.72 (0.04)	1.10 (0.05)	3.78 (0.01)	137.5 (1.24)
Mineral layer																	
HM	2.3 (0.1)	0.11 (0.00)	20.5 (0.4)	338 (11)	2.4 (0.1)	3.0 (0.1)	8.3 (0.4)	28.2 (1.6)	98 (3)	2.35 (0.06)	0.82 (0.03)	0.16 (0.00)	0.03 (0.00)	0.16 (0.00)	1.19 (0.05)	4.66 (0.01)	9.6 (0.3)
SHM	3.4 (0.1)	0.15 (0.01)	25.0 (1.2)	367 (10)	2.5 (0.1)	3.8 (0.3)	7.6 (0.2)	23.6 (1.1)	103 (4)	2.98 (0.07)	0.71 (0.02)	0.17 (0.00)	0.07 (0.00)	0.17 (0.01)	1.87 (0.06)	4.61 (0.02)	8.3 (0.2)
HY	3.2 (0.1)	0.11 (0.00)	28.3 (0.6)	23 (4)	5.0 (0.1)	2.6 (0.0)	7.2 (0.4)	44.7 (3.2)	151 (6)	2.87 (0.12)	1.54 (0.13)	0.24 (0.02)	0.10 (0.00)	0.11 (0.01)	0.88 (0.04)	5.00 (0.05)	10.5 (0.4)
LM	2.6 (0.1)	0.29 (0.05)	18.8 (1.3)	360 (9)	3.5 (0.2)	2.1 (0.0)	8.9 (0.5)	45.6 (1.9)	121 (4)	2.75 (0.06)	1.11 (0.08)	0.17 (0.01)	0.03 (0.00)	0.19 (0.00)	1.24 (0.08)	4.64 (0.03)	9.4 (0.6)
UM	3.3 (0.1)	0.10 (0.00)	32.4 (1.2)	392 (7)	1.7 (0.1)	3.8 (0.1)	4.9 (0.1)	19.1 (0.9)	136 (6)	3.81 (0.14)	0.54 (0.00)	0.10 (0.00)	0.04 (0.00)	0.13 (0.00)	3.00 (0.13)	4.46 (0.01)	13.9 (0.5)

Table S3. Linear regression coefficients and goodness-of-fit statistics for log(CO_2 flux) and CH_4 flux against soil temperature (2 cm). Bold numbers are significant ($p < 0.05$). Site names: HM = High severity Mature, SHM = Salvage-logged High severity Mature, HY = High severity Young, LM = Low severity Mature and UM = Unburnt Mature.

Gas flux	Site	Slope	Intercept	R^2	RMSE
	HM	**0.083**	**-1.235**	0.59	0.350
	SHM	**0.076**	**-1.221**	0.57	0.435
CO_2	HY	**0.052**	**-1.562**	0.50	0.473
	LM	**0.063**	-0.317	0.32	0.536
	UM	**0.086**	**-0.510**	0.51	0.308
	HM	**-0.00005**	-0.00029	0.24	0.00041
	SHM	-0.00003	**-0.00067**	0.06	0.00070
CH_4	HY	**-0.00005**	-0.00047	0.25	0.00071
	LM	**-0.00006**	**-0.00043**	0.45	0.00041
	UM	**-0.00012**	**0.00059**	0.53	0.00040

Table S4. Linear regression coefficients and goodness-of-fit statistics for log(CO_2 flux) and CH_4 flux against soil water content (SWC).Bold numbers are significant ($p < 0.05$). Site names: HM = High severity Mature, SHM = Salvage-logged High severity Mature, HY = High severity Young, LM = Low severity Mature and UM = Unburnt Mature.

Gas flux	Site	Slope	Intercept	R^2	RMSE
	HM	**-0.065**	**0.941**	0.44	0.408
	SHM	**-0.043**	**0.471**	0.13	0.622
CO_2	HY	**-0.111**	0.234	0.40	0.515
	LM	**-0.061**	**1.314**	0.42	0.497
	UM	**-0.029**	**1.194**	0.47	0.320
	HM	**0.00004**	**-0.00150**	0.19	0.00042
	SHM	0.00003	**-0.00138**	0.04	0.00071
CH_4	HY	**0.00009**	**-0.00203**	0.19	0.00074
	LM	**0.00004**	**-0.00176**	0.19	0.00050
	UM	**0.00003**	**-0.00163**	0.35	0.00047

References

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67. https://doi.org/10.18637/jss.v067.i01

Davidson, E.., Savage, K., Verchot, L.., Navarro, R., 2002. Minimizing artifacts and biases in chamber-based measurements of soil respiration. Agric. For. Meteorol. 113, 21–37. https://doi.org/10.1016/S0168-1923(02)00100-4

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

R Core Team, 2019. R: A language and environment for statistical computing.

Sundqvist, E., Vestin, P., Crill, P., Persson, T., Lindroth, A., 2014. Short-term effects of thinning, clear-cutting and stump harvesting on methane exchange in a boreal forest. Biogeosciences 11, 6095–6105. https://doi.org/10.5194/bg-11-6095-2014