



Mid-term effects of wildfire and salvage logging on gross and net soil nitrogen transformation rates in a Swedish boreal forest

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ABSTRACT

Wildfires are natural and important disturbances of boreal forest ecosystems, and they are expected to increase in parts of the boreal zone through climate warming. There is a broad understanding of the immediate effects of fire on soil nitrogen (N) transformation rates, but less is known about these effects several years after fire. In July 2014, a large wildfire in the boreal forest zone of Central Sweden took place. Four years after the wildfire, we measured processes linked to the soil N cycle using the ¹⁵N pool dilution method (for gross N mineralization, consumption and nitrification) and the buried bags method (for net N mineralization), in soils from stands of different fire severity that had or had not been subjected to salvage logging. Gross N mineralization and consumption rates per unit carbon (C) increased by 81 % and 85 % respectively, in response to high fire severity, and nitrification rates per unit C basis decreased by 69 % in response to high fire severity, while net N mineralization was unresponsive. There was no difference in the effect of salvage logging across stands of differing fire severity on N transformation rates, although concentrations of resin adsorbed nitrate (NO₃) were overall 50 % lower in logged compared to unlogged stands. We also found that irrespective of burn severity, N immobilization rates exceeded N nitrification rates, and immobilization was therefore the dominant pathway of gross N consumption. Gross N consumption rates were higher in burned than unburned stands, despite there being a higher active microbial biomass in unburned soil, which suggests an even higher immobilization of N over time as the microbial biomass recovers following fire. Our study shows that soil N transformation rates were more affected by changes in fire severity than by salvage logging, and that four years after the fire many aspects of the N cycle did not differ between burned and unburned stands, suggesting substantial resilience of the N cycle to fire and salvage logging. However, we note that long term impact and many additional ecosystem properties or processes should be evaluated before concluding that salvage logging has no ecosystem impact. Furthermore, shortened fire regimes following climate warming accompanied with shorter intervals between salvage logging practices, could still impact the capability for the N cycle to recover after an intense fire. While wildfire in the boreal region results in a shift from nutrient conserving to nutrient demanding plant species, our results suggest this shift is dependent on a relatively short-lived pulse of higher N cycling processes that would have likely dissipated within a few years after the fire.

1. Introduction

Wildfires are an important disturbance agent in northern boreal forests, through promoting natural regeneration, and influencing biodiversity and vegetation dynamics. Fire can increase the loss of nitrogen (N) to the atmosphere through oxidation (Certini, 2005), but also enhance the short-term availability of soil nutrients through the

combustion of soil organic matter and the conversion of nutrients from organic to inorganic forms that are more available for plant uptake (Gundale et al., 2005). In addition to the release of nutrients from organic matter through both mineralization and nitrification, wildfire can also alter the transformations of soil nutrient pools that remain post-fire, either directly by the combustion and heat processes during the fire that increases the concentration of ammonium (NH₄⁺; Covington and

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Sackett, 1992), or indirectly by altering the composition and abundance and activity of soil organisms (Köster et al., 2021). Nitrogen is among the most important nutrients for plant growth globally, and its availability is often considered the most limiting soil resource for forest growth in boreal forests (Högberg et al., 2017). Hence, changes in N cycling following wildfire are likely to be fundamental for understanding plant growth and vegetation development following fire in boreal forests.

Anthropogenic actions have impacted natural fire regimes in the boreal zone, both by deliberate suppression of natural wildfire activity during the past century, and by indirectly promoting more extreme fire conditions through climate change (Knorr et al., 2016). These two processes have led to the current situation, where high fuel loads caused by fire suppression interact with extreme climate conditions, resulting in larger and more severe wildfires, which may in turn impact N cycling. Even though low severity wildfire causes some minor loss of N to the atmosphere via combustion, it seldom combusts large amounts of soil organic matter (SOM). Low severity wildfire therefore often results in a high rate of tree survival, where most of the original vegetation as well as microbial biomass is able to take up N released to the soil from the fire (through physiochemical processes and N mineralization), thus reducing its loss by leaching and water run-off (Stark and Hart, 1999; Knicker 2007). As most of the SOM remains after low severity wildfire, low fire severity stands support favorable conditions for growth and activity of ectomycorrhizal fungi, which promote nutrient turnover and retention (Day et al., 2019). Meanwhile, high severity fires often combust a substantial portion of surface SOM (Homann et al., 2011) and a large proportion of the total N capital in the soil is lost to the atmosphere through oxidation (Thornley and Canell, 2004), and can alter the composition of the following successional forest regrowth (Lecomte et al., 2006).

In addition to the impact of wildfire itself on soil nutrient transformations, wildfire is often followed by post-fire logging to recover damaged timber in many countries (referred to as “salvage logging”), which can also potentially impact soil nutrient transformation. Historically in Sweden, wildfires have been suppressed in production forests, but as severe wildfire is becoming more common, salvage logging is being implemented in both high and low severity burn areas. While wildfire itself can affect soil micro-climate, salvage logging can reduce the amount of shade on the forest understory and soil, hence, increases soil temperature and reduces soil moisture (Marcolin et al., 2019), and also disturbs or compacts soil (Pereira et al., 2018), which could potentially alter soil N mineralization rates. However, the effect of salvage logging may vary depending on the severity of the preceding fire. In low intensity wildfires, tree mortality may be very low, meaning that salvage logging can remove live trees that continue to provide an active supply of carbon to soils. Loss of these trees and their carbon inputs could modify soil microclimate (due to surface exposure) and impair microbial activity and growth (Pérez-Izquierdo et al., 2021), and potentially impact soil N transformations. High intensity wildfire can result in high tree mortality, and salvage logging of dead trees may have smaller direct effects on N transformation rates, especially in comparison to the consequences of large losses of organic matter and soil microbiota caused by the fire. There is a need to understand the interaction of salvage logging with wildfire, because salvage logging is a common post-fire management activity, and the impacts of salvage logging on nutrient cycling in boreal forests following fire remains largely unexplored.

Through this study we aimed to test how contrasting fire severity, and the interactive effects of fire and salvage logging, impact soil N cycling processes four years after a major wildfire in a Swedish boreal forest. To our knowledge, effects of fire severity and salvage logging on mid-term N transformation rates have not been previously assessed. We first hypothesized that high fire severity would lead to reductions in gross and net N mineralization and nitrification rates relative to unburned stands. This is because severe fire burns deeper into the organic soil layer, which should cause greater loss of both SOM and short-term

organic matter inputs from live trees (due to high direct tree mortality caused by the fire) and thus lower growth and activity of soil microbes involved in N transformations (Day et al., 2019). In contrast to high severity fire, we anticipated that low fire severity would enhance gross N mineralization rates, but reduce net N mineralization rates. We expected this because low severity fires combust relatively little soil organic matter, leaving behind abundant substrates for C and N mineralization, while also causing higher litter inputs through canopy scorching (versus more complete combustion in high fire severity stands). This would lead to higher gross N mineralization but reduced net N mineralization because of enhanced N immobilization by soil microbes that are able to utilize new organic C inputs. Secondly, we hypothesized that salvage logging would show an interactive effect with fire severity. This is because salvage logging should have little impact on N mineralization processes in high fire severity stands because the trees are dead, whereas in low fire severity stands where many trees survive the fire, the removal of living trees would have a larger impact on the N cycling processes. Specifically, because living trees continue to serve as a C source to ectomycorrhizal fungi and saprotrophs which are important drivers of carbon and nutrient cycling (Pérez-Izquierdo et al., 2021), we expected removal of these trees to cause gross N mineralization to decrease (because of less microbial activity), and net N mineralization to increase (due to less immobilization). Evaluating these hypotheses should help to enhance our knowledge of the effects of forest fire severity and its interactive effect with salvage logging on mid-term soil processes and N transformation rates.

2. Methods

2.1. Stand characteristics

For this study, we used 21 conifer forest stands (seven unburned, seven high fire severity and seven low fire severity), that were located within or near the nature reserve Hälleskogsbrännan, Västmanland, Sweden (latitude 59°53'51" N; longitude 16°8'19"E). This nature reserve was created after a large accidental wildfire that occurred in the area, starting on July 31, 2014. Over five days, a total area of 14 000 ha of forest was burned, and in some areas the fire was intense and quickly spread, resulting in larger areas of tree death and organic layer combustion (Gustafsson et al., 2019). Prior to the fire, the selected study stands were dominated by 40–50 year old *Pinus sylvestris* forests with interspersed *Picea abies* and *Betula pendula*. The understory vegetation was dominated by ericaceous dwarf shrubs, notably *Vaccinium vitis-idaea*, *V. myrtillus* and *Calluna vulgaris*, and the feather mosses *Pleurozium schreberi* and *Hylocomium splendens*. The mean annual air temperature in this region (data from the nearest meteorologic station in Sala 58 m.a.s.l.) during the climate period of 1991–2020 was 6.3°C and total precipitation was 581 mm (The Swedish Meteorology and Hydrological Institute [SMHI]). The soils were podzols, and each stand had a site productivity index of T22-24 m (i.e., a predicted height of trees of 22–24 m at an age of 100 years) and an approximate present age of around 50 years. Each of the 21 stands we selected (described below) were 0.25 ha in area and were production forests before the fire that had undergone their first thinning. The closest distance between each stand was 300 m and all stands occurred within an area of 60 km². Further details of the study system are presented in Table S1.

Data for stand characteristics was collected in April 2016, in order to classify the 21 stands into three categories based on their fire severity characteristics (i.e., high fire severity, low fire severity, and unburned). These 21 stands were selected from 50 initial stands based on the criteria that they had to show visible impacts from fire to the canopy and/or the soil surface, using satellite photos. Further, the selected stands had to be on similar underlying soil parent material as well as have comparable pre-fire stand age, management history, elevation (100 m.a.s.l.), and accessibility from forest roads. Following a field visit in May 2016, stands fulfilling the selection criteria above were further assessed for the

level of tree mortality. In brief, this involved collection of data for each stand on percentage of tree mortality, percentage of trees with stem scorches, flame length (i.e., the average charred height for 20 *P. sylvestris* trees per plot), the level of scorched crown (measured as the amount of needles that was consumed by fire per crown), remaining organic layer depth after fire, and amount of charcoal on the forest floor. These data were analysed with a Principal Component Analysis (PCA) with the statistical program SPSS version 24 (IBM Corp., Armonk, NY, USA) to classify the stands into fire severity categories (see Ibáñez et al., 2021 for further details). The high fire severity stands had a higher tree mortality, larger flame height, a higher number of stem and crown scorches of trees, than did the low fire severity stands. From this analysis, we assigned 7 of the 21 stands into each of the three categories. For the high fire severity and low fire severity stands, half of each stand was salvage logged immediately after fire using standard even-aged management harvesting techniques (i.e., all trees within the salvage logged area were harvested and removed from the area), as part of the fire rescue operation to prevent burn damaged trees from tipping over and blocking forest roads (Pérez-Izquierdo et al., 2021). Thus, for each of these burned stands, we created paired sampling plots, consisting of logged and unlogged portions of the stand, and we placed a single plot in each unburned stand (unlogged; Pérez-Izquierdo et al., 2021). This resulted in a total of 5 forest cover types and 35 sample plots in total ($n = 7$ of each type). We used this study system to measure a variety of N transformation rates. This included resin adsorbed NH_4^+ and NO_3^- , and net N mineralization and nitrification which were measured over a 73 day period in order to integrate the wide range of processes that influence these variables; whereas, gross N mineralization and nitrification rates were measured over the scale of hours to provide an instantaneous view of these primary transformation (described in further detail down below).

2.2. Net N mineralization rates

We collected three sets of mineral soil cores from all plots. The first two sets were used for determination of net N mineralization and nitrification rates, and this involved taking soil cores from all plots of all stands over May 23–26, 2018. For the first set of soil cores, we randomly collected five mineral soil cores (5 cm diameter by 10 cm depth, organic layer excluded if detected), and when the organic layer was not completely combusted or in unburned stands, we also collected five cores from the organic layer (30 cm diameter to full organic layer depth: 1–1.7 cm). The five mineral soil cores per plot were composited in the field, as were the five organic layer cores, yielding one bulked mineral soil and one organic layer sample per plot. Each mineral soil or organic layer sample was then passed twice using a 4 mm sieve and transported in cooler boxes to our laboratory facility in Umeå. In each plot a second set of five mineral soil cores adjacent to each of the five cores of the first set were also collected. Each of these five intact soil cores was placed in a polyethylene bag with 50 μm thickness, 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. In August 3–7, 2018, we returned to each plot, and collected the buried bag cores, 73 days after each bag was placed in the soil. We evaluated the net rates over this time scale because it provided an adequate period to assess the net balance between gross N mineralization, consumption, and nitrification that influence net values. The five buried soil cores for each plot were then bulked into one mineral soil sample per plot.

We measured NH_4^+ and NO_3^- in soil from the first set of soil cores as time zero and soil from the second set of soil cores (from bags that were buried) 73 days later. Soil from each set of cores from each plot was extracted with 1 M KCl, and analyzed for NH_4^+ and NO_3^- concentrations using standard colorimetric techniques with an autoanalyzer III Spectrophotometer (Omni Process, Solna, SE; Gundale et al., 2016). We obtained the net N mineralization rates by calculating the differences in

inorganic N ($\text{NH}_4^+ + \text{NO}_3^-$) over 73 days. (Hart et al., 1994). For each bulked soil sample, we also used 5 g subsample to determine gravimetric water content so the results could be expressed on a dry soil weight basis.

2.3. Gross N mineralization, consumption and nitrification rates

At the second soil sampling occasion (August 3–7, 2018), we collected a further third set of five mineral soil cores as described above adjacent to where the five initial cores were sampled within the plot. Half of this soil volume was transported to the University of Gothenburg for analyses of gross N mineralization, NH_4^+ consumption and N nitrification rates, and the other half was transported to our laboratory facility in Umeå for analyses of pH, microbial activity and nutrients. All was transported in cooler boxes.

Gross N mineralization and nitrification rates (Fig. 1) in mineral soil were determined by using the isotope ^{15}N pool dilution method developed by Kirkham and Bartholomew (1954). This involves adding ^{15}N isotope labelled NH_4^+ and NO_3^- to soil for measuring gross mineralization and nitrification rates, respectively. Briefly, total NH_4^+ and total NO_3^- ($^{14}\text{N} + ^{15}\text{N}$) and $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ pools are measured at time 30 min and 24 h after $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$ injection. This time scale was chosen because it minimized the possibility that labelled substrates would be consumed and mineralized, which could potentially obscure the pool dilution measurements. Gross N mineralization is calculated based on the rate of dilution of ^{15}N in the NH_4^+ pool, as unlabelled NH_4^+ is generated via mineralization from the organic N pool. The same calculation is performed for gross N nitrification, but here the ^{15}N labelled NO_3^- pool is diluted through new nitrification of unlabelled NH_4^+ (Hart et al., 1994).

For each of these analyses, the composite soil sample from each plot (from the third set of mineral soil cores) was subsampled so that 50 g field fresh soil was added to four 500 mL Simax jars, which were then sealed with parafilm that were punctured to allow gas exchange and incubated in a dark place at room temperature (20 °C) for 24 h. Isotopic labels were prepared as follows; for the $^{15}\text{NH}_4^+$ label, 76.71 mg of $(\text{NH}_4)_2\text{SO}_4$ was mixed with 200 mL of deionized water, and for the $^{15}\text{NO}_3^-$ label, 6.81 mg of KNO_3 was mixed with 200 mL of deionized water. For two of the four jars from each plot, we added 2 mL of $^{15}\text{NH}_4^+$ label to the soil; one of these was intended for 30 min incubation and the other for 24 h incubation. This resulted in 33% of $^{15}\text{NH}_4^+$ label relative to the ambient NH_4^+ pool per soil sample. For the other two jars we added 2 mL of $^{15}\text{NO}_3^-$ label to the soil, and again one was incubated for 30 min incubation and the other for 24 h. The added NO_3^- label consisted of 98% of the total NO_3^- pool. In Swedish boreal forests there are naturally very low concentrations of NO_3^- , and to measure gross nitrification rates we had to add this relatively high amount of $^{15}\text{NO}_3^-$ to be able to measure the process rate. The high amount of NO_3^- that is added to the pool of produced NO_3^- would not stimulate nitrification, but it would stimulate NO_3^- immobilization, hence this process rate therefore not calculated in this study. For each of the two jars harvested at 30 min, 1 M KCl was applied 30 min following label addition and the jars were then shaken for one hour at 120 rpm and allowed to settle for 20 min; this was followed by filtration. The remaining two jars were incubated for 24 h in a dark place at room temperature, and then extracted in the same way as the jars harvested after 30 min incubation. For the extracts from each jar, we determined the ^{15}N abundance and concentration of NH_4^+ and NO_3^- using SPINMAS (continuous-flow Quadrupole Mass Spectrometry for inorganic nitrogen connected to a Mass Spectrometer) (Stange et al., 2007). We then used the following formula described by Hart et al. (1994) to calculate the gross N mineralization rate:

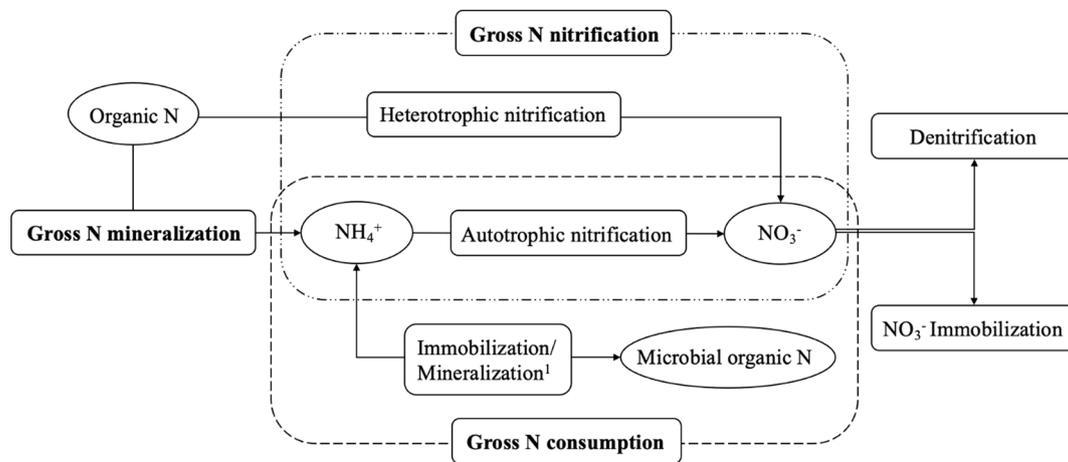


Fig. 1. Schematic figure of soil nitrogen (N) circulation, modified after [Hart et al. \(1994\)](#). The text in bold and the dashed rectangles identifies the transformations measured in this study. Ellipses indicate the pools of different forms of N. Arrows indicate the direction of the process transforming N between the different pools of N. ¹Nitrogen mineralization, i.e., organic N to inorganic ammonium (NH₄⁺) is the reverse process of NH₄⁺ immobilization.

$$\text{Gross N mineralization rate} = \frac{[\text{NH}_4^+]_{0h} - [\text{NH}_4^+]_{24h}}{24h} \times \frac{\log\left(\frac{\text{APE}_{0h}}{\text{APE}_{24h}}\right)}{\log\left(\frac{[\text{NH}_4^+]_{0h}}{[\text{NH}_4^+]_{24h}}\right)}$$

Where APE_{0h} is the atom percentage ¹⁵N excess of NH₄⁺, at 30 min after injection of the stable isotope, and APE_{24h} is the atom percentage ¹⁵N excess of NH₄⁺ at 24 h after injection. The concentration of NH₄⁺ is in mg kg⁻¹. The same formula was used to calculate gross N nitrification, but then APE and concentrations of NO₃⁻ were used. For calculations of gross NH₄⁺ consumption rate (the sum of immobilization, nitrification and other NH₄⁺ consuming processes, [Fig. 1](#)), the following formula was used:

$$\text{Gross NH}_4^+ \text{ consumption rate} = \text{gross N mineralization rate} - \frac{[\text{NH}_4^+]_{24h} - [\text{NH}_4^+]_{0h}}{24h}$$

2.4. Soil chemistry measurements

We measured the soil total C and N stored in the mineral soil and organic layer from the bulked sample of the third set of cores for each plot. This data set for total C and N was previously used and the methodology was previously described in [Ibáñez et al. \(2021\)](#). To determine pH in these soil cores, we used a solution-to-soil weight ratio suspension of 0.01 M CaCl₂ mixed with mineral soil (1:1) or organic soil (1:10). The suspension was mixed and left to stand for one hour before we read pH ([Thomas, 1996](#)).

In May 2018, ten ionic resin capsules (PST-1 Capsule, UNIBEST, Bozeman, USA) were placed in each plot in the soil to a depth of four cm beneath the mineral soil surface to measure accumulation of inorganic nitrogen over time. In August 2018, 73 days after placement, the capsules were collected and NH₄⁺ and NO₃⁻ were extracted from them by rinsing each capsule three times with 10 mL 1 M KCL ([Gundale et al., 2011](#)). The resin capsules were incubated in the field during the same time as the buried bag incubations that were used for obtaining net N mineralization rates. This time length was desirable because it provided an adequate period to assess the net balance between gross N mineralization, consumption, nitrification, plant uptake and leaching that may influence resin adsorbed nutrient concentrations ([Fajardo and Gundale, 2018](#); [Grau-Andrés et al., 2021](#)). These extracts were then analyzed for NH₄⁺ and NO₃⁻ concentrations using standard colorimetric techniques with an autoanalyzer III Spectrophotometer (Omni Process, Solna, SE; [Gundale et al., 2016](#)).

2.5. Microbial activity

We determined the relative microbial biomass in a subsample of each mineral and organic layer soil sample (collected August 3–7, 2018) using the substrate-induced respiration method (SIR) ([Anderson and Domsch, 1978](#)). First, we calculated the percent moisture content of each sample by measuring its wet weight and oven dry weight (60 °C for 48 h). Next, 10 g of dry weight equivalent soil was placed into a 100 mL Simax jar, and its water content adjusted to 150 % (dry weight basis) for organic and 20 % for mineral soil. Finally, a glucose solution was injected into each soil, which added 0.5 g of glucose per sample. Soils were incubated at room temperature (20 °C), and CO₂ concentration in the headspace was measured at 1 and 3 h after glucose addition, using an infrared gas analyzer (EMG-4 Environmental Gas Monitor for CO₂). The increase in CO₂ concentration from 1 to 3 h was used as a relative measure of active microbial biomass ([Anderson and Domsch, 1978](#)). This timescale of measurements was appropriate because it was long enough to assess a linear increase in respiration in response to glucose addition; yet was short enough to prevent added glucose from being fully consumed ([Gundale et al., 2016](#); [Pluchon et al., 2016](#)).

2.6. Statistical analyses

To test our first hypothesis, we compared response variables across three stand types of fire severity (unburned, low severity, and high severity wildfire) by using One-Way ANOVA (n = 7). When a statistically significant effect was found at α = 0.05, Tukey's post hoc test was used to explore pairwise differences between treatment means. For our second hypothesis we used a two-way split plot ANOVA (mixed effects model) to evaluate how response variables responded to main and interactive effects of fire severity (low severity versus high severity wildfire) 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. When statistical difference was obtained at α = 0.05, Tukey's post hoc was used to explore pairwise differences between treatment means. We tested the homogeneity of variance for the data used in the One-Way ANOVA and tested for normality of residuals for the mixed effects model. All data was statistically analysed in R (R version 3.6.2; R Core Development Team, 2019), using the R function aov() for the first hypothesis, and the R package lme4 followed by the R package emmeans for the mixed effects model for the second hypothesis. The figures were created with GraphPad Prism version 8.4.3 for Macintosh (GraphPad Software, La Jolla California USA).

2.7. Combination of observational and experimental approaches

This study combines both an experimental component (i.e., salvage logging which is a manipulated factor) and observational component (i.e., effects of wildfire, because we are capitalizing on a 'natural' experiment). In this light, while we can manipulate salvage logging ourselves, a wildfire never burns randomly in the landscape, and can vary due to pre-fire conditions. For this reason we have carefully examined the pre-fire conditions within the burned area (i.e., by assessing stand age, mean tree height, tree basal area, tree biomass and tree species composition; Table S1; Pérez-Izquierdo et al., Unpublished Manuscript) with the intention of selecting sites in which these properties are relatively constant to minimize confounding factors. Studies that include both observational and experimental factors, such as we have done, are commonly used in ecology to capitalize on the different strengths of the two approaches (Fukami and Wardle 2005; Kardol et al., 2018).

3. Results

3.1. Effects of fire severity on soil properties and N soil cycling

To test our first hypothesis, we evaluated the effects of fire severity (high, low or unburned) on soil properties and processes. We found no effect of fire severity on total N for both mineral and organic soil, and total C and C:N (by mass) for organic layer, however total C and C:N in mineral soil was highest in soil from unburned stands and lowest in soil from high severity burn stands (Table 1). For both mineral soil and organic layer, pH was lower in unburned stands than in burned stands (Table 1).

We found no effect of fire severity on concentrations of NH_4^+ or NO_3^- absorbed on ionic resin capsules that had been inserted into the mineral soil layer (Fig. 2a-b; Table 2). However, we found that both low and high fire severity reduced SIR in mineral soil relative to in the unburned stands (Fig. 2c-d; Table 2). There was insufficient organic layer remaining in the high severity burn stands to measure SIR in the organic layer, and SIR in the organic layer did not differ between low severity burned and unburned stands.

Fire severity had no effect on gross N mineralization and NH_4^+ consumption rates measured per unit soil weight (Fig. 3a-b, Table 3). Gross nitrification rates (per d.w. soil) were significantly affected by fire, with highest rates in unburned soil and lowest in high fire severity soil (Fig. 3c; Table 3). When gross N rates were expressed on a per unit C basis (i.e., indication of how stable or labile the soil organic nitrogen is) fire severity had a significant effect on gross N mineralization, NH_4^+ consumption and nitrification (Table 3). While gross mineralization was lower in the unburned treatment than in the burned stands (and this effect was significant according to the ANOVA), no differences among treatments were detected from post hoc testing (Fig. 3e). We also found

that NH_4^+ consumption rates were lowest in unburned soil (Fig. 3f). Gross nitrification per soil C was highest in unburned soil and lowest in high fire severity soil (Fig. 3g). There was no effect of fire severity on the net N mineralization rates (total inorganic N) whether expressed per d. w. soil or per total soil C (Fig. 3d, h; Table 3).

3.2. Interactive effects of salvage logging and burn severity on soil properties and N soil cycling

For our second hypothesis, we evaluated the main and interactive effects of fire severity (high and low) and post-fire treatment (salvage logged vs. unlogged stands) on soil properties and processes. There was no effect of fire severity, post-fire treatment, or their interaction on soil C, N, C:N, pH, or SIR (Fig. 4, Tables 4, 5). There was also no effect of any factor on the resin capsule data, other than that concentrations of NO_3^- absorbed on resin capsules in the mineral soil were lowest in stands that had been subjected to salvage logging (Fig. 4b, Table 4).

Fire severity, post-fire treatment, and their interaction had no effect on gross N mineralization and NH_4^+ consumption rates or on net inorganic mineralization rates, whether expressed per unit soil weight or per unit weight of soil C (Fig. 5a-b, d-f, h, Table 6). Gross N nitrification was significantly higher in low than in high fire severity stands both when expressed per unit soil weight and per unit weight of soil C, but was unaffected by post-fire treatment (salvage logging) (Fig. 5c, g; Table 6).

4. Discussion

We aimed to test the effects of fire severity (Hypothesis 1) and the interactive effects of fire severity and salvage logging (Hypothesis 2) on N transformation rates four years after wildfire. Overall, we found that fire positively increased gross N mineralization and consumption rates of NH_4^+ (when measured per unit total soil C), and that high fire severity decreased gross N nitrification rates. Further, we found that gross N nitrification was driven more by the degree of fire severity than by salvage logging practices. We now discuss these findings to develop insights about how wildfire and salvage logging affects boreal forest soil N transformation rates and what mechanisms are involved.

4.1. Effects of fire severity on soil properties and N soil cycling

4.1.1. Gross N mineralization

In contrast to our first hypothesis, we found that gross N mineralization rates on a per gram of soil basis was unresponsive to fire severity. However, when gross N mineralization was reported on a per unit C basis, we found significantly higher rates for burned soils than for unburned control soils. There was a lower C content (g C per g dry mass) in both high and low fire severity soils than in unburned soils, which explains why there was an effect of burning only when results were

Table 1

Mean values (\pm SE) and results from analysis of variance comparing the effect of fire severity (i.e., high, low or unburned) on total carbon (C), nitrogen (N), ratio of C:N and pH in mineral soils and the organic layer. C and N are presented as % of dry soil mass. Hyphens means that there was no organic material detected.

	df ¹	Fire severity categories of forest stand			F value	P-value
		High	Low	Unburned		
<i>Mineral soil</i>						
C	2, 17	4.00 \pm 0.52 ^a	4.22 \pm 0.55 ^a	6.07 \pm 0.22 ^b	5.361	0.016
N	2, 17	0.14 \pm 0.02	0.14 \pm 0.02	0.18 \pm 0.01	2.302	0.130
C:N	2, 17	29.25 \pm 0.90 ^a	30.79 \pm 1.04 ^{ab}	33.95 \pm 1.45 ^b	4.366	0.030
pH	2, 18	3.89 \pm 0.06 ^a	3.78 \pm 0.07 ^a	3.31 \pm 0.12 ^b	12.200	<0.001
<i>Organic layer</i>						
C	1, 11	–	22.83 \pm 2.24	31.26 \pm 3.95	3.721	0.080
N	1, 11	–	0.77 \pm 0.09	0.95 \pm 0.10	1.824	0.204
C:N	1, 11	–	29.80 \pm 1.23	32.85 \pm 1.88	1.944	0.191
pH	1, 12	–	3.30 \pm 0.08 ^a	3.04 \pm 0.04 ^b	8.527	0.013

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

¹ Numerator degrees of freedom, denominator degrees of freedom.

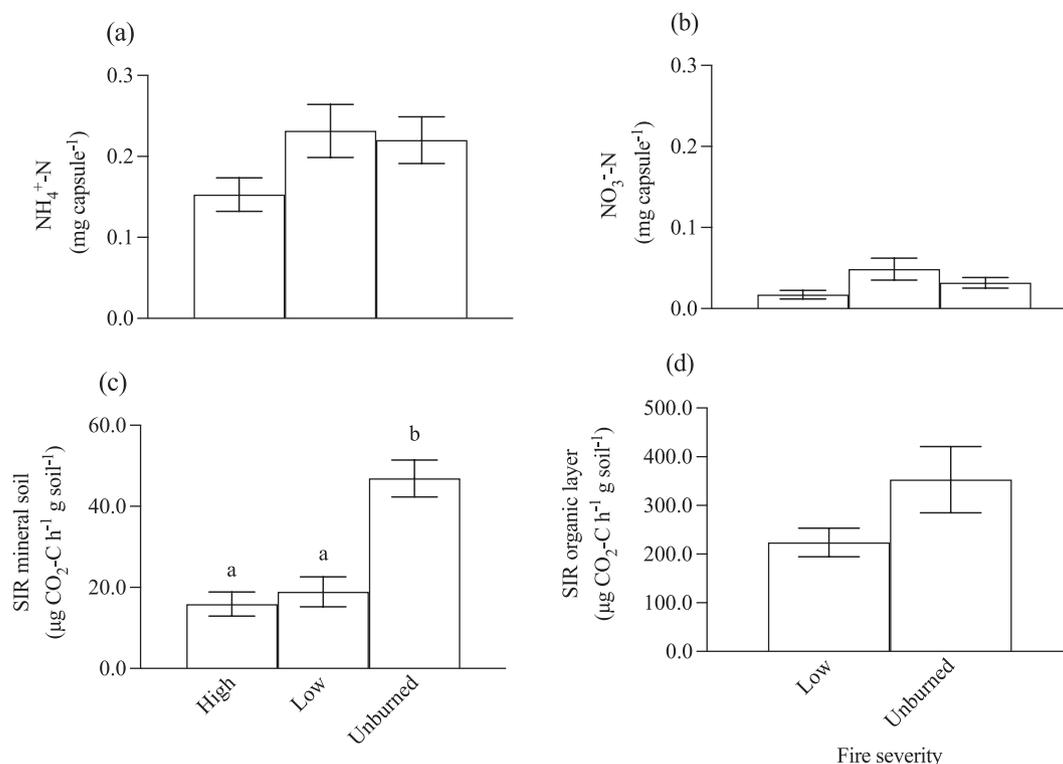


Fig. 2. Mean values (±SE) of ammonium (NH₄⁺) in resin capsules (a), nitrate (NO₃⁻) in resin capsules (b), substrate induced respiration (SIR) in mineral soil (c), and SIR in organic layer (d), in soil from stands differing in fire severity (i.e., high, low or unburned). Different letters above bars indicate significant differences between fire severity according to Tukey's post hoc tests at $P \leq 0.05$. Corresponding ANOVA results (F - and P - values) are reported in Table 2.

Table 2

Results from analysis of variance comparing the effect of fire severity (i.e., high, low or unburned) on concentrations of ammonium (NH₄⁺) and nitrate (NO₃⁻) per resin capsule in mineral soil, substrate induced respiration (SIR) in mineral soil and organic layer.

	Fire severity (FS)		
	df ¹	F -value	P -value
<i>Mineral soil</i>			
Resin capsule NH ₄ ⁺	2, 17	2.297	0.131
Resin capsule NO ₃ ⁻	2, 17	2.658	0.099
SIR	2, 18	20.340	<0.001
<i>Organic layer</i> ²			
SIR	1, 12	3.005	0.109

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

¹ Numerator degrees of freedom, denominator degrees of freedom.

² Excluding high fire severity soils because there was no organic material detected.

calculated on a per unit soil C basis. However, this result was inconsistent with our predictions that only low burn severity would have a stimulatory effect on gross N mineralization rates, and that high fire severity soils would reduce gross N mineralization rates. It is possible that higher gross N mineralization rates in burned soil could be because the fire improved the quality of the remaining SOM post-fire, which could make it more mineralizable (Merino et al., 2018).

4.1.2. Gross N consumption

We observed higher gross N consumption rates when expressed on a per unit C basis, but not per gram soil, in soils from high fire severity stands than in unburned soils, and intermediate rates in low fire severity stand soils. This pattern also contradicts our first hypothesis, as we expected soils from high and low severity stands to show lower and higher gross N transformation rates than those from unburned stands,

respectively. Our result is also inconsistent with Koyama et al. (2011), who found reduced NH₄⁺ consumption rates by soil microbes in burned than in unburned coniferous forests sites in North America, 26 months after wildfire. Gross N consumption is determined by both microbial immobilization of NH₄⁺ and autotrophic nitrification (Hart et al., 1994). Because gross N nitrification rates were an order of magnitude smaller than gross N consumption rates in our study, immobilization is likely to have been the dominant pathway of gross N consumption. Gross N immobilization in boreal forests is usually controlled to some degree by the C:N ratio of organic matter available to saprotrophs, with ratios above 30:1 generally causing a high microbial N demand. However, we found high burn severity mineral soils had lower C:N ratios than unburned soils, likely due to greater oxidation of C to CO₂ relative to mineralization of N (Bodí et al., 2014). This suggests that higher microbial immobilization was stimulated by some factor other than a shift in C:N ratio in high fire severity soils.

One factor that could stimulate higher microbial immobilization in high fire severity soil was that the increase in pH observed in these soils may have stimulated growth and activity of bacteria that are typically favored by increased soil pH (Rousk et al., 2009). Although our measures of SIR suggested that active microbial biomass was lower in burned soils, immobilization could potentially be more a function of microbial biomass change rather than absolute biomass, with immobilization being greatest when the microbial biomass is increasing over time. It could be 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. However, to confirm this, measurements on microbial biomass change over time in both treatment and control sites would be needed, which we did not assess in this study.

4.1.3. Net N mineralization

Our first hypothesis also predicted that net N mineralization would be reduced in response to fire, but our results instead showed no effects

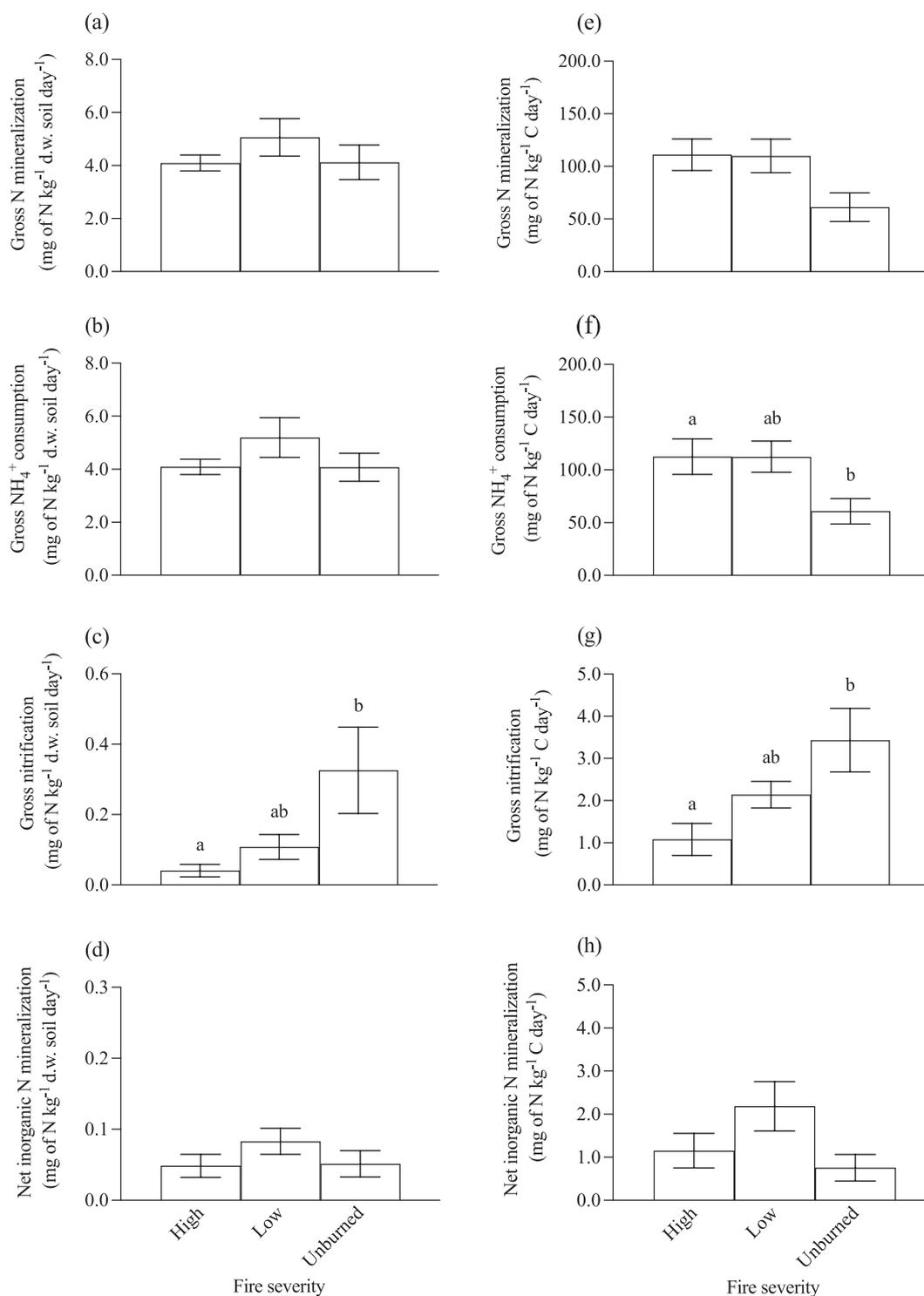


Fig. 3. Mean values (\pm SE) of gross nitrogen (N) mineralization (a,e), gross ammonium (NH_4^+) consumption (b,f), gross nitrification (c,g), and total net inorganic N mineralization rate (d,h), expressed per unit soil mass (a-d) and per unit soil C (e-h) in soil from stands differing in fire severity (i.e., high, low or unburned). Different letters above bars indicate significant differences between fire severity according to Tukey's post hoc tests at $P \leq 0.05$. Corresponding ANOVA results (F - and P -values) are reported in Table 3. Sub-figure (e) showed significant ANOVA result at $P = 0.043$, but pairwise differences was not detected with Tukey's post hoc test.

of fire severity on net N mineralization. Net N mineralization rates represent the balance between gross N mineralization and N consumption. The lack of net N mineralization response in our study could be explained by gross N mineralization and N consumption rates showing very similar responses to burning, which has also been observed elsewhere (Fernández-Fernández et al., 2017). However, a study from forests in Galicia, Spain (Prieto-Fernández et al., 1993) showed net N

mineralization to be higher in burned soil compared to unburned soil within a few weeks post-fire, but that the net N mineralization rate decreased after 11 weeks. The timescale of response found in that study could therefore explain why we saw no difference in net N mineralization rates in our stands four years post-fire.

Table 3

Results from analysis of variance comparing the effect of fire severity (i.e., high, low or unburned) on gross and net nitrogen (N) process rates in mineral soil.

	Fire severity (FS)		
	df ¹	F-value	P-value
<i>Process rate per unit soil mass (N kg⁻¹ dry weight soil day⁻¹)</i>			
Gross N mineralization	2, 16	0.237	0.792
Gross ammonium (NH ₄ ⁺) consumption	2, 16	0.413	0.668
Gross nitrification	2, 12	4.321	0.039
Net N mineralization	2, 15	1.076	0.366
<i>Process rate per unit soil carbon (C) (N kg⁻¹ C day⁻¹)</i>			
Gross N mineralization	2, 16	3.866	0.043
Gross NH ₄ ⁺ consumption	2, 16	4.229	0.034
Gross nitrification	2, 12	5.360	0.022
Net N mineralization	2, 15	2.696	0.100

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

¹ Numerator degrees of freedom, denominator degrees of freedom.

4.1.4. Gross N nitrification

Consistent with our first hypothesis, we found reduced gross N nitrification rates (which included both autotrophic and heterotrophic nitrification) in high burn severity stand soils compared to unburned stand soils, both when expressed per gram soil and per unit total C. In line with our result, Gómez-Rey and Gonzalez-Prieto (2013) showed

that gross nitrification rates were reduced one week following fire in a *P. sylvestris* planted forest in Galicia. However, our result is *inconsistent* with a study from Fernández-Fernández et al. (2017), who showed that fire resulted in increased gross N nitrification rate, six months after fire in a *Pinus pinaster* forest in Galicia. Thus, the reduced gross N nitrification rate we observed in response to fire does both contradict and confirm several other studies that have observed altered gross N nitrification rates over relatively short time scales. The supporting studies are presented on a per unit soil basis. In our study system, we did not find any differences in resin NH₄⁺ or NO₃⁻ concentrations between unburned and burned soil, despite gross nitrification rate being different. This is probably because gross N nitrification was a very small flux compared to most other N transformations (such as gross N mineralization and consumption), and because of several mechanisms that cause loss of soil NO₃⁻ (e.g., plant uptake, denitrification and more liable to leaching because NO₃⁻ is anionic). It is therefore not surprising that a significant increase in the relatively small gross N nitrification flux caused by burning did not translate into effects of burning on resin adsorbed NO₃⁻ pools. Potentially, there could also be significant gross NO₃⁻ immobilization, although this was not measured in our study.

4.2. Interactive effects of salvage logging and burn severity on soil properties and N soil cycling

We did not find significant interactive effects of fire severity and salvage logging on any measures of gross or net N transformation rate, which is inconsistent with our second hypothesis. However, we did find lower concentrations of NO₃⁻ adsorbed to resins in mineral soils of logged stands than of unlogged stands. Heavy logging equipment, such as that associated with salvage logging, has the potential to compact soils and thus reduce infiltration through the soil and the mobility of NO₃⁻ to resin capsules (Pereira et al., 2018). Alternatively, rain that lands directly on

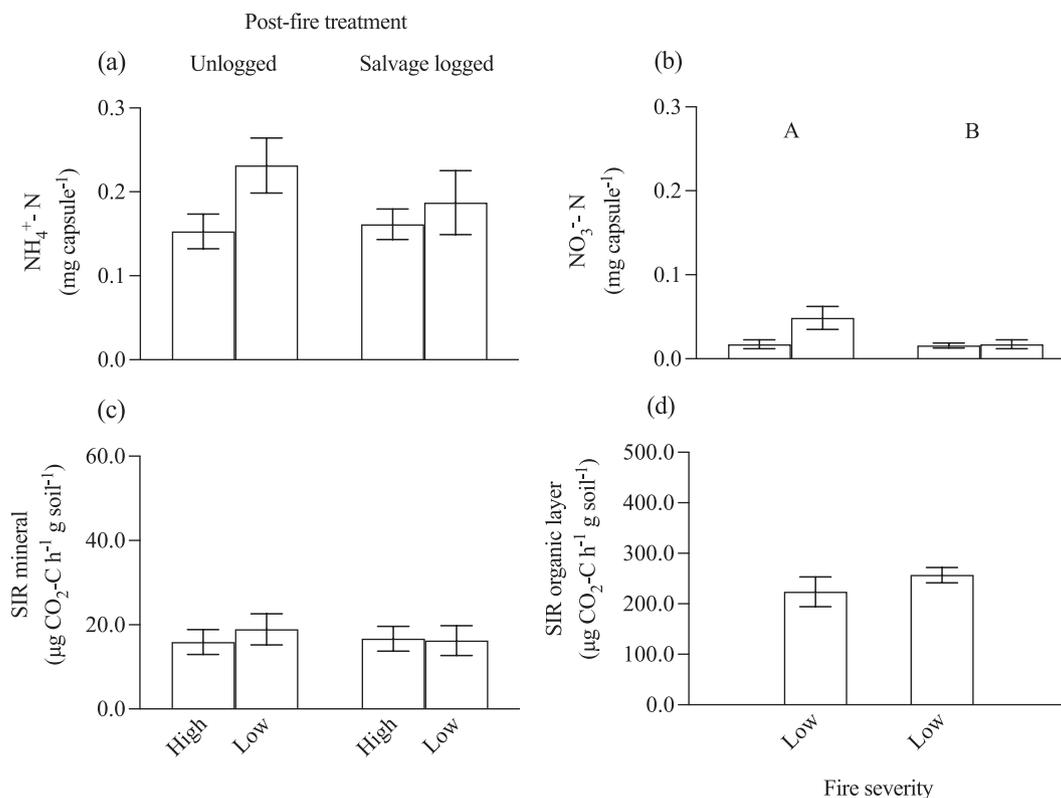


Fig. 4. Mean values (±SE) of ammonium (NH₄⁺) in resin capsules (a), nitrate (NO₃⁻) in resin capsules (b), substrate induced respiration (SIR) in mineral soil (c), and SIR in organic layer (d), in soil from stands differing in fire severity (i.e., high or low) and post-fire treatment (i.e., unlogged or salvage logged forest stands). Different letters above bars indicate significant differences between fire severity according to Tukey's post hoc tests at $P \leq 0.05$. Corresponding ANOVA results (F- and P-values) are reported in Table 4.

Table 4

Results from analysis of variance comparing the effect of fire severity (i.e., high or low) and post-fire treatment (i.e., unlogged or salvage logged) on nutrients of ammonium (NH_4^+) and nitrate (NO_3^-) in capsules in mineral soil, on total carbon (C), nitrogen (N), ratio of C:N, substrate induced respiration SIR and pH in mineral soil and organic layer. Hyphens means no data.

	Fire severity (FS)			Post-fire treatment (PFT)			FS × PFT		
	df ¹	F-value	P-value	df ¹	F-value	P-value	df ¹	F-value	P-value
<i>Mineral soil</i>									
Resin capsule NH_4^+	1, 11.3	3.052	0.108	1, 13.2	0.385	0.546	1, 13.2	0.807	0.385
Resin capsule NO_3^-	1, 11.5	3.980	0.070	1, 13	5.538	0.035	1, 13	3.193	0.097
C	1, 12	0.189	0.671	1, 12	0.227	0.643	1, 12	0.850	0.375
N	1, 12	0.285	0.603	1, 12	0.242	0.632	1, 12	0.611	0.450
C:N	1, 12	0.605	0.452	1, 12	0.550	0.473	1, 12	0.565	0.467
SIR	1, 10	0.082	0.781	1, 10	0.301	0.595	1, 10	0.679	0.429
pH	1, 12	2.875	0.116	1, 12	0.001	0.975	1, 12	0.006	0.942
<i>Organic layer</i>									
C	–	–	–	1, 12	0.287	0.602	–	–	–
N	–	–	–	1, 12	0.002	0.963	–	–	–
C:N	–	–	–	1, 12	1.357	0.267	–	–	–
SIR	–	–	–	1, 12	0.971	0.344	–	–	–
pH	–	–	–	1, 12	0.000	0.988	–	–	–

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

¹ Numerator degrees of freedom, denominator degrees of freedom.

Table 5

Mean values (\pm SE) of total nutrients and pH in mineral soil and organic layer in stands of different fire severity (i.e., high or low) and post-fire treatment (i.e., unlogged or salvage logged forest stands). Carbon (C) and nitrogen (N) are expressed as % of dry soil mass. Corresponding analysis of variance (ANOVA) results (F- and P- values) are reported in Table 4. Hyphens means no data.

	Fire severity and post-fire treatment categories of forest stand			
	High fire severity		Low fire severity	
	Unlogged	Salvage logging	Unlogged	Salvage logging
<i>Mineral soil</i>				
C	4.00 \pm 0.52	4.81 \pm 0.88	4.22 \pm 0.55	3.96 \pm 0.61
N	0.14 \pm 0.02	0.17 \pm 0.04	0.14 \pm 0.02	0.14 \pm 0.02
C:N	29.25 \pm 0.90	29.26 \pm 1.08	30.79 \pm 1.04	29.29 \pm 1.00
pH	3.89 \pm 0.06	3.89 \pm 0.09	3.78 \pm 0.07	3.77 \pm 0.05
<i>Organic layer</i>				
C	–	–	22.83 \pm 2.24	24.60 \pm 2.42
N	–	–	0.77 \pm 0.09	0.78 \pm 0.08
C:N	–	–	29.80 \pm 1.23	31.86 \pm 1.27
pH	–	–	3.30 \pm 0.08	3.30 \pm 0.05

the bare soil in logged stands after fire can break apart soil aggregates, leading to reduced infiltration and mobility of NO_3^- to resin capsules (Badía and Martí, 2008) and this can be specifically pronounced in high fire severity stands (Mataix-Solera et al., 2011). Standing live and dead trees in unlogged stands may intercept this falling rain and thus reduce its effects on those soil physical properties that regulate infiltration and run-off. Also, in bare soil, repeated wetting- drying cycles can lead to soil compaction, reducing water infiltration and NO_3^- mobility. Further, four years after the fire in our study area, we observed high regeneration of deciduous trees (mainly *Betula* spp.) in the logged areas compared to unlogged areas. Uptake of NO_3^- by these pioneer species may help explain why gross N nitrification did not differ between logged and unlogged stands, whereas differences in extractable NO_3^- did occur (Burns and Murdoch, 2005; Cui and Song, 2007). These findings can also help explain the regeneration of fast-growing recruitment of *Betula* on salvaged logged sites, given the responsiveness of *Betula* to inorganic N.

While we did not detect any effects of salvage logging on the soil processes that we measured, a recent study by Pérez-Izquierdo et al. (2021) performed in the same study area (five years post-fire) showed that in burned stands, salvage logging which removed trees that

survived the fire, caused a decline in ectomycorrhizal fungi. It is surprising that this change in the microbial community caused by salvage logging did not result in alteration of soil N transformations. This suggests that these processes may be largely driven by bacteria and saprotrophic fungi, which are better at carrying out these transformations than is the mycorrhizal fungal community (Maaroufi et al., 2019). Alternatively, any decline in ectomycorrhizal fungi could have been offset by an increase in bacteria and saprophytic fungi (i.e., the Gadgil effect; Gadgil and Gadgil, 1975), which may serve to maintain the N cycle even when the forest is disturbed by salvage logging.

In our study, we found few effects of salvage logging on the N cycle, suggesting that the N cycle is either resistant to change, or that any short-term changes that occurred returned to the original state relatively soon (<4 years) after salvage logging. Despite this finding, 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 enhanced solar radiation at the ground level, which increased soil temperature and decreased soil moisture at 5 cm depth, potentially impairing forest regeneration. Further, Marañón-Jiménez and Castro (2013) showed for a Mediterranean Pine forest that salvage logging after fire reduced SOM, nutrient availability and C storage over time (Powers et al., 2013). These studies suggest that a greater range of response variables need to be considered to evaluate the ecosystem impacts of salvage logging in Swedish forests. Furthermore, in our study system, salvage logging was performed directly after the fire event during a late Swedish summer month, when soils were relatively well drained. We suggest that other aspects of salvage logging research could focus on the timing of salvage logging activity in relation to soil water saturation. For example, salvage logging may have a different impact on soils and nutrient cycling processes than we observed, if performed during the autumn or spring when soils are typically near field capacity. This type of research would provide further information on how salvage logging may best be implemented to minimize impacts.

5. Conclusion

Previous research has focused on short-term (<3 years) and long-term (>10 years) effects of fire on N-cycling, while the mid-term effects (i.e., > 4 and < 10 years after fire) and the interactive effects between fire severity and salvage logging on N-cycling have been little studied. In our study, we focused on a time scale of four years after fire, which is some time after the initial post-fire flush of nutrients is known to occur. We found that over that timeframe severe fires increased gross

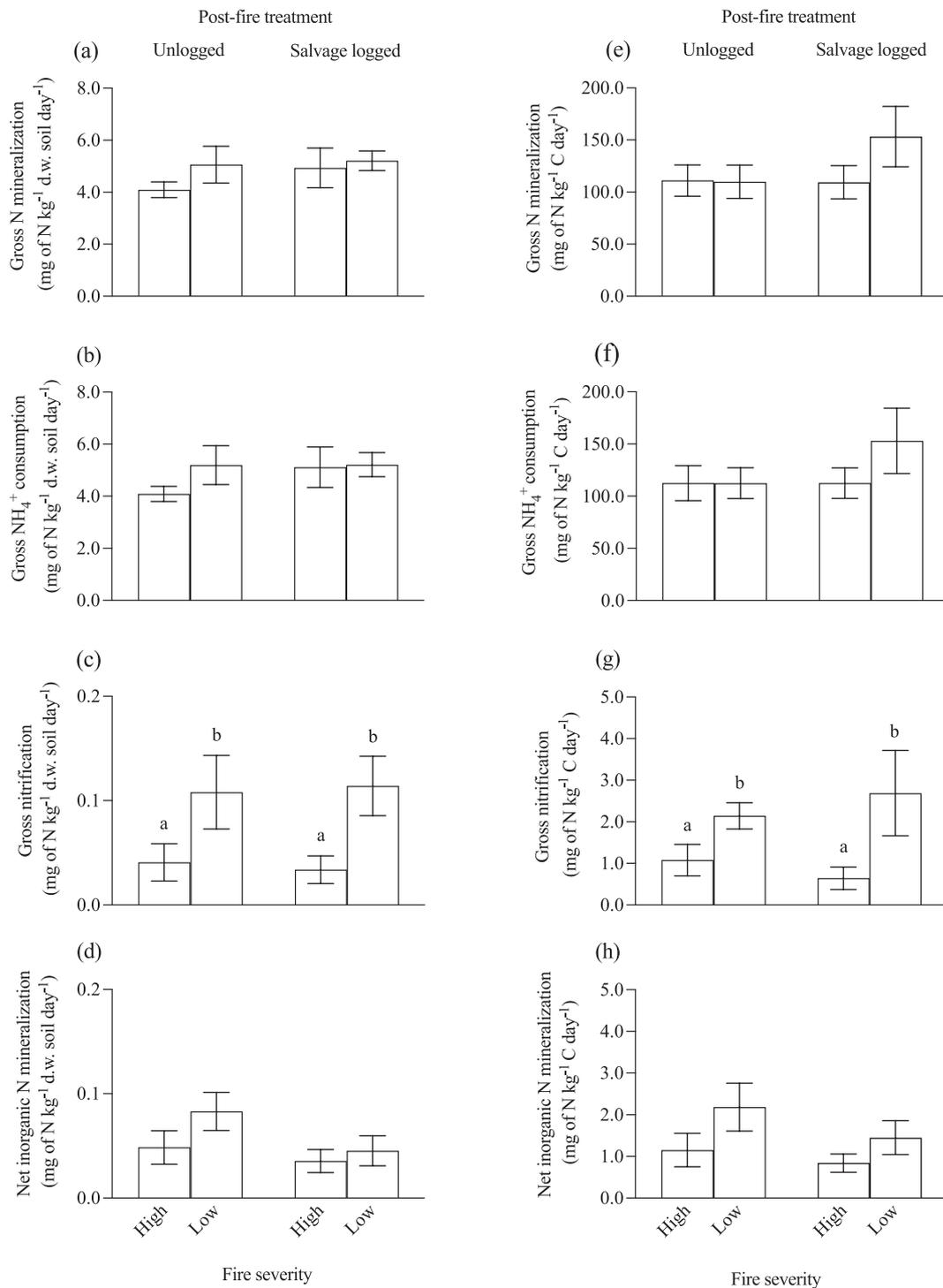


Fig. 5. Mean values (\pm SE) of gross nitrogen (N) mineralization (a,e), gross ammonium (NH₄⁺) consumption (b,f), gross nitrification (c,g), and total net inorganic N mineralization rate (d,h), expressed per unit soil mass (a-d) and per unit soil C (e-h) in soil from stands differing in fire severity (i.e., high, low or unburned) and post-fire treatment (i.e., forest stands or salvage logged stands). Different letters above bars indicate significant differences between fire severity according to Tukey's post hoc tests at $P \leq 0.05$. Corresponding ANOVA results (F - and P - values) are reported in Table 6.

N mineralization and consumption rates on a per unit soil C basis and decreased gross N nitrification rates on both a per unit soil C basis and dry soil basis, compared to unburned soils. This suggests 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 short-run, which could in turn lead to higher rates of new organic matter input that would help

soil organic matter stocks recover. Given that some of these N cycling responses were generally more pronounced in the high fire severity treatments, our findings suggest that high severity fires that are occurring as a result of climate change may also lead to higher rates of soil C stock recovery in the longer term, presumably by supporting deciduous species growth, despite initially resulting in higher soil C loss (Mack et al., 2021). We further found that N transformations on both a per unit soil C basis and dry soil basis were altered to a much greater degree by

Table 6

Results from analysis of variance comparing the effect of fire severity (i.e., high or low) and post-fire treatment (i.e., unlogged or salvage logged forest stands) on gross and net nitrogen (N) process rates in mineral soil.

	Fire severity (FS)			Post-fire treatment (PFT)			FS × PFT		
	df ¹	F-value	P-value	df ^{1,2}	F-value	P-value	df ¹	F-value	P-value
<i>Process rate per unit soil mass (N kg⁻¹ dry weight soil day⁻¹)</i>									
Gross N mineralization	1, 10	0.321	0.584	1, 10	1.743	0.216	1, 10	0.069	0.799
Gross ammonium (NH ₄ ⁺) consumption	1, 10	0.211	0.656	1, 10	2.198	0.169	1, 10	0.243	0.632
Gross nitrification	1, 7.7	6.533	0.035	1, 7.7	0.121	0.737	1, 7.7	0.006	0.942
Net inorganic N mineralization	1, 10	2.129	0.175	1, 10	2.784	0.126	1, 10	0.664	0.434
<i>Process rate per unit soil carbon (C) (N kg⁻¹ C day⁻¹)</i>									
Gross N mineralization	1, 10	1.267	0.287	1, 10	1.206	0.298	1, 10	1.412	0.262
Gross NH ₄ ⁺ consumption	1, 10	1.060	0.328	1, 10	1.075	0.324	1, 10	1.072	0.325
Gross nitrification	1, 7.7	7.206	0.029	1, 7.7	0.010	0.925	1, 7.7	0.723	0.421
Net inorganic N mineralization	1, 10	3.659	0.085	1, 10	1.995	0.188	1, 10	0.321	0.583

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

¹ Numerator degrees of freedom, denominator degrees of freedom.

fire severity than by salvage logging, and found little evidence for an interaction between these two factors. Our study hereby shows that four years post-fire there is little evidence that salvage logging has a strong impact on soil N transformations, at least within the environmental parameters of our study site, and in relation to the salvage logging techniques that were employed. While salvage logging may be performed primarily to preserve timber value, we found little support that it enhances nutrient cycling or availability that could potentially support higher rates of forest regrowth. Given that salvage logging removes wood that otherwise has important biodiversity habitat value, another management aspect of salvage logging that needs to be investigated is its long-term impact on biodiversity. Several studies have highlighted negative of salvage logging other aspects of ecosystem function or biodiversity that we did not consider in our study (Marañón-Jiménez and Castro, 2013; Powers et al., 2013; Marcolin et al., 2019; Pérez-Izquierdo et al., 2021), we therefore suggest that further research is needed to explore this additional management dimensions.

CRedit authorship contribution statement

T.S. Ibáñez: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Visualization, Writing - original draft, Writing - review & editing. **T. Rütting:** Formal analysis, Investigation, Methodology, Resources, Writing - review & editing. **M-C. Nilsson:** Conceptualization, Investigation, Funding acquisition, Methodology, Resources, Supervision, Writing - review & editing. **D.A. Wardle:** Conceptualization, Investigation, Methodology, Supervision, Writing - review & editing. **M.J. Gundale:** Conceptualization, Investigation, Methodology, Resources, Supervision, Writing - review & editing.

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Declaration of Competing Interest

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

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120240>.

References

- Anderson, J.P.E., Domsch, K.H., 1978. A physiological method for the quantitative measurement of microbial biomass in soils. *Soil Biol. Biochem.* 10 (3), 215–221. [https://doi.org/10.1016/0038-0717\(78\)90099-8](https://doi.org/10.1016/0038-0717(78)90099-8).
- Badía, D., Martí, C., 2008. Fire and rainfall energy effects on soil erosion and runoff generation in semi-arid forested lands. *Arid Land Research and Management* 22 (2), 93–108. <https://doi.org/10.1080/15324980801957721>.
- Bodí, M.B., Martín, 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 Sci. Rev.* 130, 103–127. <https://doi.org/10.1016/j.earscirev.2013.12.007>.
- 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>.
- Covington, W.W., Sackett, S.S., 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *For. Ecol. Manage.* 54 (1–4), 175–191. [https://doi.org/10.1016/0378-1127\(92\)90011-W](https://doi.org/10.1016/0378-1127(92)90011-W).
- Cui, X., Song, J., 2007. Soil NH₄⁺/NO₃⁻ 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>.
- 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. *Glob. Change Biol.* 25 (7), 2310–2324. <https://doi.org/10.1111/gcb.14641>.
- Fajardo, A., Gundale, M.J., 2018. Canopy cover type, and not fine-scale resource availability, explains native and exotic species richness in a landscape affected by anthropogenic fires and posterior land-use change. *Biol. Invasions* 20 (2), 385–398. <https://doi.org/10.1007/s10530-017-1539-5>.
- Fernández-Fernández, M., Rütting, T., González-Prieto, S., 2017. Effects of a high-severity wildfire and post-fire straw mulching on gross nitrogen dynamics in Mediterranean shrubland soil. *Geoderma* 305, 328–335. <https://doi.org/10.1016/j.geoderma.2017.06.023>.
- Fukami, T., Wardle, D.A., 2005. Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society B: Biological Sciences* 272 (1577), 2105–2115. <https://doi.org/10.1098/rspb.2005.3277>.
- Gadgil, P.D., Gadgil, R.L., 1975. Suppression of litter decomposition by mycorrhizal roots of *Pinus radiata*. *New Zealand Forest Service*.
- Gómez-Rey, M.X., Gonzalez-Prieto, S.J., 2013. Short-term impact of a wildfire on net and gross N transformation rates. *Biol. Fertil. Soils* 49 (8), 1065–1075. <https://doi.org/10.1007/s00374-013-0806-6>.
- 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. *For. Ecol. Manage.* 213 (1–3), 25–38. <https://doi.org/10.1016/j.foreco.2005.03.015>.
- Gundale, M.J., Deluca, T.H., Nordin, A., 2011. Bryophytes attenuate anthropogenic nitrogen inputs in boreal forests. *Glob. Change Biol.* 17 (8), 2743–2753. <https://doi.org/10.1111/j.1365-2486.2011.02407.x>.
- 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., Berglund, M., Granström, A., Grelle, A., Isacson, 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. *Scand. J. For. Res.* 34 (4), 234–253. <https://doi.org/10.1080/02827581.2019.1603323>.
- Grau-Andrés, R., Pingree, M.R.A., Oquist, M.G., Wardle, D.A., Nilsson, M.-C., Gundale, M. J., 2021. Biochar increases tree biomass in a managed boreal forest, but does not alter N₂O, CH₄, and CO₂ emissions. *GCB Bioenergy* 13 (8), 1329–1342. <https://doi.org/10.1111/gcb.12864>.
- 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>.
- 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 Sci. Soc. Am. J.* 75 (5), 1926–1934. <https://doi.org/10.2136/sssaj2010-0429>.
- 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. *For. Ecol. Manage.* 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* 25 (2), 471–487. <https://doi.org/10.1007/s10021-021-00666-0>.
- Kardol, P., Fanin, N., Wardle, D.A., 2018. Long-term effects of species loss on community properties across contrasting ecosystems. *Nature* 557 (7707), 710–713. <https://doi.org/10.1038/s41586-018-0138-7>.
- Kirkham, D.O.N., Bartholomew, W.V., 1954. Equations for following nutrient transformations in soil, utilizing tracer data. *Soil Sci. Soc. Am. J.* 18 (1), 33–34. <https://doi.org/10.2136/sssaj1954.03615995001800010009x>.
- 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>.
- Knorr, W., Arneeth, A., Jiang, L., 2016. Demographic controls of future global fire risk. *Nat. Clim. Change* 6 (8), 781–785. <https://doi.org/10.1038/nclimate2999>.
- Koyama, A., Stephan, K., Kavanagh, K.L., 2011. Fire effects on gross inorganic N transformation in riparian soils in coniferous forests of central Idaho, USA: wildfires v. prescribed fires. *International Journal of Wildland Fire* 21 (1), 69–78. <https://doi.org/10.1071/WF10132>.
- 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* 22, 100258. <https://doi.org/10.1016/j.coesh.2021.100258>.
- Lecomte, N., Simard, M., Bergeron, Y., 2006. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Québec. *Canada. Ecoscience* 13 (2), 152–163. <https://doi.org/10.2980/i1195-6860-13-2-152.1>.
- 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. *Glob. Change Biol.* 25 (9), 2900–2914. <https://doi.org/10.1111/gcb.14722>.
- 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 (1–3), 519–535. <https://doi.org/10.1007/s10533-012-9744-x>.
- 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 (11), 1014. <https://doi.org/10.3390/f10111014>.
- Mataix-Solera, J., Cerdà, A., Arcenegui, V., Jordán, A., Zavala, L.M., 2011. Fire effects on soil aggregation: a review. *Earth-Sci. Rev.* 109 (1–2), 44–60. <https://doi.org/10.1016/j.earscirev.2011.08.002>.
- Merino, A., Fonturbel, M.T., Fernández, C., Chávez-Vergara, B., García-Oliva, F., Vega, J. A., 2018. Inferring changes in soil organic matter in post-wildfire soil burn severity levels in a temperate climate. *Sci. Total Environ.* 627, 622–632. <https://doi.org/10.1016/j.scitotenv.2018.01.189>.
- 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., Gilliam, F., 2021. Crown-fire severity is more important than ground-fire severity in determining soil fungal community development in the boreal forest. *J. Ecol.* 109 (1), 504–518. <https://doi.org/10.1111/1365-2745.13529>.
- Pluchon, N., Vincent, A.G., Gundale, M.J., Nilsson, M.-C., Kardol, P., Wardle, D.A., 2016. The impact of charcoal and soil mixtures on decomposition and soil microbial communities in boreal forest. *Appl. Soil Ecol.* 99, 40–50. <https://doi.org/10.1016/j.apsoil.2015.11.020>.
- 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. *For. Ecol. Manage.* 291, 268–277. <https://doi.org/10.1016/j.foreco.2012.07.038>.
- Prieto-Fernández, Á., Villar, M.C., Carballas, M., Carballas, T., 1993. Short-term effects of a wildfire on the nitrogen status and its mineralization kinetics in an Atlantic forest soil. *Soil Biol. Biochem.* 25 (12), 1657–1664. [https://doi.org/10.1016/0038-0717\(93\)90167-A](https://doi.org/10.1016/0038-0717(93)90167-A).
- Rousk, J., Brookes, P.C., Baath, E., 2009. Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. *Appl. Environ. Microbiol.* 75 (6), 1589–1596. <https://doi.org/10.1128/AEM.02775-08>.
- 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. *Isot. Environ. Health Stud.* 43 (3), 227–236. <https://doi.org/10.1080/10256010701550658>.
- Stark, J.M., Hart, S.C. 1999. Effects of disturbance on microbial activity and N-cycling in forest and shrubland ecosystems. United states department of agriculture forest service general technical report PNW, 101-105.
- Thomas, G.W., 1996. Chapter 16. p 475-490. Soil pH and Soil Acidity. In: J. M. Bigham et al. (ed.) *Soil Science, Society of America and American Society of Agronomy. Methods of Soil Analysis. Part 3. Chemical Methods-SSSA Book Series no. 5.* Madison, WI.
- Thornley, J.H.M., Cannell, M.G.R., 2004. Long-term effects of fire frequency on carbon storage and productivity of boreal forests: a modeling study. *Tree Physiol.* 24 (7), 765–773. <https://doi.org/10.1093/treephys/24.7.765>.