Fire Severity Effects on Soil Carbon and Nutrients and Microbial Processes in a Siberian Larch Forest

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KEY WORDS

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Primary Research Article

ABSTRACT

Fire frequency and severity are increasing in tundra and boreal regions as climate warms, which can directly affect climate feedbacks by increasing carbon (C) emissions from combustion of the large soil C pool and indirectly via changes in vegetation, permafrost thaw, hydrology, and nutrient availability. To better understand the direct and indirect effects of changing fire regimes in northern ecosystems, we examined how differences in soil burn severity (i.e., extent of soil organic matter combustion) affect soil C, nitrogen (N), and phosphorus (P) availability and microbial processes over time. We created experimental burns of three fire severities (low, moderate, high) in a larch forest in the northeastern Siberian Arctic and analyzed soils at 1-day, 8-days, and 1-year post-fire. Labile dissolved C and N increased with increasing soil burn severity immediately (1-day) post-fire by up to an order of magnitude, but declined significantly 1-week later; both variables were comparable or lower than unburned soils by 1-year post-fire. Soil burn severity had no effect on P in the organic layer, but P increased with increasing

severity in mineral soil horizons. Most extracellular enzyme activities decreased by up to 70% with increasing soil burn severity. Increasing soil burn severity reduced soil respiration 1-year post-fire by 50%. However, increasing soil burn severity increased net N mineralization rates 1-year post-fire, which were 10-fold higher in the highest burn severity. While fires of high severity consumed approximately five times more soil C than those of low severity, soil C pools will also be driven by indirect effects of fire on soil processes. Our data suggest that despite an initial increase in labile C and nutrients with soil burn severity, soil respiration and extracellular activities related to the turnover of organic matter were greatly reduced, which may mitigate future C losses following fire.

INTRODUCTION

As the global climate continues to warm, wildfire frequency and severity are increasing in high latitudes (Flannigan *et al.* 2000; Kasischke *et al.* 2010). High latitude soils (to 3 m depth) store ~ 1,035 Pg C, representing a globally significant carbon (C) pool (Hugelius *et al.* 2014; Schuur *et al.* 2015). Fires have profound consequences for ecosystem biogeochemical cycling, both directly through the combustion of organic matter and indirectly through changing vegetation dynamics, physical environmental conditions, and resource availability (Bond-Lamberty *et al.* 2004; Mack *et al.* 2008). The indirect effects of fire on permafrost (permanently frozen ground) ecosystems can lead to climate feedbacks by altering C cycle processes, such as decomposition rates and primary productivity, and thawing previously frozen soil horizons (Schuur *et al.* 2008; Brown *et al.* 2015).

A substantial portion of fuel combustion from fires in high-latitudes comes from surface organic layers (Boby *et al.* 2010). The combustion of this insulating layer can lead to higher soil temperatures and thaw depths, and in some instances, ground subsidence (Brown *et al.* 2015). The collapse of permafrost following a fire can increase soil moisture as a result of localized ground subsidence, or it can decrease soil moisture by allowing drainage or lowering the water table with deeper thaw depths (Jorgenson & Osterkamp 2005; Brown *et al.* 2015). Soil temperature and moisture are often the most important abiotic factors influencing soil decomposition rates and soil respiration (Davidson & Janssens 2006; Natali *et al.* 2011, 2015). As such, fires can indirectly affect soil C cycling and feedback to climate change, through altering the conditions for decomposition and exposing previously frozen permafrost to decomposition.

Through combustion, fires alter soil organic matter (SOM) stoichiometry by reducing C and nitrogen (N) pools and redistributing phosphorus (P) in ash (Wang *et al.* 2012, Wan *et al.* 2001). Combustion also alters the composition of SOM by creating recalcitrant pyrogenic organic matter (Glaser *et al.* 2002) and changing the proportions of dissolved and labile organic matter (Martín et al. 2009, Wang et al. 2012). By altering the form and availability of nutrients, fires can indirectly contribute to the loss of C and nutrients from ecosystems through run-off of dissolved organic matter (DOM) and inorganic nutrients (Bayley *et al.* 1992; Lamontagne *et al.* 2000; Petrone *et al.* 2007) and as result, also affect nutrient limitation of the recovering vegetation and microbial communities (Shaver & Chapin 1995; Liang *et al.* 2014; Sullivan *et al.* 2015; Sistla *et al.* 2012).

Soil microbes act as the primary control on soil decomposition, mediating the type of C and nutrients released. Fire influences soil microbial abundance and activity indirectly through a variety of mechanisms, including alteration of soil moisture and nutrient availability, decreasing C quantity and quality, and increasing soil temperature and pH (Dooley & Treseder 2011). Boreal fires can reduce soil microbial biomass and soil respiration for up to 20 years post-fire, contributing to a negative feedback to warming (Dooley & Treseder 2011). Microbial access to nutrients, and in particular, the acquisition of resources through production of extracellular enzymes, which cleave substrates from organic matter and provide soluble forms of nutrients, is often the rate-limiting step of decomposition (Jones & Kielland 2002; German *et al.* 2011; Sinsabaugh & Shah 2012). However, the effects of fire on extracellular enzyme activity (EEA) are not well-understood; some high-latitude studies have shown that fire increases EEA (Gartner *et al.* 2012; Tas *et al.* 2014), while others have shown decreases (Waldrop & Harden 2008; Holden *et al.* 2013). These differences across studies may have been driven, in part, by different fire severities and recovery times.

In order to better understand the indirect effects of fire on ecosystem processes in high-latitudes, it is important to quantify the role of fire severity. Fire severity in high-latitudes is often measured as a function of canopy loss (if trees are present), soil organic layer loss, or both (Keeley 2009). Fire severity can be difficult to quantify and compare among fires and ecosystems due to uncertainty and variability in pre-fire organic layer depths. In this study, we conducted experimental burns across a range of soil burn severities (i.e., extent of combustion of the soil organic layer). We created four soil burn severity treatments (low, moderate, and high severity, plus an unburned control) within a sparse Cajander larch (*Larix cajanderi* Mayr.) forest near the boreal-tundra ecotone in far Northeastern Russia. Our objectives were to 1) assess the effects of soil burn severity on the soil environment (temperature, pH, moisture) and soil resources (amount and lability of C, N, and P); 2) understand the consequences of these changes for soil respiration and microbial EEA; and 3) determine how dynamic these effects are through time.

We hypothesized that dissolved and labile C and nutrient availability would increase with increasing soil burn severity as a result of incomplete SOM combustion immediately following the fires. We expected this effect to be short-lived due to leaching and export of labile and dissolved material. We hypothesized that increasing soil burn severity would immediately reduce microbial activity as a result of microbial mortality. However, we predicted after only a few days the microbial community would recover in response to warmer soils, higher pH and higher nutrient availability, resulting in higher microbial activities. We hypothesized that 1-year post-fire, higher soil burn severity would lead to lower total soil C and N, higher proportion of recalcitrant DOM, and lower microbial respiration and EEAs through suppressed microbial biomass.

METHODS

Study Area

This study was conducted in the Kolyma River watershed of Northeastern Russia, in a sparse larch forest near the boreal-tundra ecotone. The Kolyma River is underlain by continuous permafrost, and the area where the study was conducted is underlain by yedoma deposits that formed during the Pleistocene, which are characterized by high organic matter and ice content (Zimov *et al.* 2006). The Russian boreal forest is relatively understudied and little is known about vegetation and soil responses to fire (Alexander *et al.* 2012, 2018). The research site was located ~0.5 km east of the Northeast Science Station (NESS) near Cherskiy, Sahka Republic, Russia (68.74 °N, 161.40 °E), which is approximately 250-km north of the Arctic Circle and 130-km south of the Arctic Ocean. The mean annual temperature of the area is -11.6 °C, with summer temperatures averaging 12 °C and winter temperatures -33 °C (Alexander *et al.* 2012). Mean annual precipitation is 210 mm/year with approximately half falling during the summer as rain (Alexander *et al.* 2012). The fire return interval for the Russian Far East is estimated to be between 80-200 years (Ponomarev *et al.* 2016), with an annual burned area of ~2 Mha/yr

(Rogers *et al.* 2015). Vegetationat the study site can be characterized as a sparse Cajander larch forest (0.03 trees m^{-2}), with understory vegetation including deciduous shrubs (*Betula divaricate, B. exilis*, *Salix spp.* and *Alnus fruticosa*), evergreen shrubs (*Vaccinium vitisidaea, Arctous alpine, A. erytrocarpa, Empetrum androgynum, Pyrola grandiflora,* and *Rhododendron subarcticum*), herbs (*Carex appendiculata*), grasses (*Calamagrostis neglecta*), mosses (*Aulacomnium turgidum*), and lichens (*Cetraria cuculata* and *Cladina rangiferina*). Overstory trees were ~ 178 yr old and averaged 9 m tall and 16 cm in diameter at breast height (Alexander *et al.* 2018). Organic layer depths pre-burn averaged 10.3 ± 0.4 cm at the study site (Alexander *et al.* 2018). During the July sampling times, thaw depths averaged 23.4 ± 2.3 cm at the study site (Alexander *et al.* 2018).

Experimental Design and Burns

In July 2012, 16 experimental plots (2 x 2-m) were delineated along a gradually sloping hillside such that no plots were directly downhill from another. Plots were located ~ 2 m apart and at least 2 m from mature larch trees. Each plot was randomly assigned to a soil burn severity treatment: control (no burn),low, moderate, and high. Each plot had a 0.5-m wide buffer along each side that was clipped of aboveground vascular vegetation prior to burning to ensure consistency among treatment effects and to prevent fire spread. Our objective was to experimentally alter burn conditions (via fuel load manipulations) to represent the effects of different burn severities common in Siberian larch forests. Soil burn severity was assessed based on residual organic layer depth (i.e., organic layer remaining following fire): 2-4 cm (high), 6-8 cm (moderate), and > 10 cm (low) (Sofronov & Volokitina 2010). We focused on residual organic layer depth because of its ecological relevance, for example as a barrier to seedling recruitment and as a determinant of total soil organic matter pools which support microbial biomass and respiration (Dooley & Treseder 2011; Alexander *et al.* 2018), and biophysical relevance to belowground processes, for example as a control on soil moisture, soil temperature, and heat conductance (Hinzman *et al.* 1991). Furthermore,post-fire organic layer depth is a more accurate proxy of burn severity than categorical fuel loads because it allows for variability in severity between treatments and within treatments to be accounted for. Natural fuels collected from forested and riparian areas nearby were dried for several days and then applied to the plots to manipulate soil burn severity. Low severity treatments received 2.25 kg m^{-2} fine twigs (< 1 cm diameter) and leaves. The moderate severity treatments received

2 kg m^{-2} fine twigs and leaves, 2.5 kg m^{-2} small twigs (1-2 cm diameter), and 5 kg m^{-2} coarse twigs (2-5 cm diameter). The high severity treatments received 5.5 kg m^{-2} fine twigs and leaves, 5 kg m^{-2} small twigs, 5 kg m^{-2} coarse twigs, and 21.5 kg m^{-2} logs (> 5 cm diameter). Fuel loads were based on preliminary burn trials, which showed that these quantities were sufficient to create different levels of soil burn severity (Alexander *et al.* 2018). While fuel added to manipulate burn severity will also impact nutrient inputs, particularly P, the amount of P in added fuel (estimated at 0.0022-0.014 kg m^{-2}) was less than the amount resulting from combustion of natural fuels and organic matter (estimated 0.007-0.019 kg m^{-2}), assuming P concentrations of 0.006-0.16% in biomass (Son & Gower 1992) and 0.12% in the organic layer (Giesler *et al.* 2012; Beermann *et al.* 2015). Experimental burns were conducted on 6 and 7 July 2012 and were allowed to burn out naturally. Fires were started using fire starters comprised of dried hay-like material covered with parafilm. No outside fuel sources (beyond added biomass and fire starters) were used in these burns.

Soil Sampling and Analyses

Soil cores were collected from 12 of the experimental plots (three of each treatment, in order to preserve one set without any destructive sampling) at 1-day post-fire, 8-days post-fire, and 1-year post-fire. For each sampling time, three cores were collected from each plot at least 20 cm inward from the edge of the plot. Two depths were sampled at each time point: the organic layer and the top 10 cmof the mineral horizon. During the 1-year post-fire sampling, soils were also sampled from the bottom 10 cm of thawed mineral soil (depths were not significantly different across treatments and the end of the core averaged 51 cm below the organic layer). The organic layer depth was measured at each location where a core was taken. We collected three samples per plot per soil depth increment, and these sub-replicates were then pooled together and homogenized. We measured thaw depth 1-day, 6-days, and 1-year post-fire at five locations in each plot by pushing a thin metal probe in the ground until hitting frozen soil. Soil temperature was measured 1-year post-fire and recorded at these same locations using iButtons placed 5 cm deep. The five sub-replicates were averaged for statistical analyses.

Soils were subsampled for soil water content, water extractions, and extracellular enzyme assays within 24-hours of collection. Soil moisture was calculated as the percent change relative to soil wet mass, after drying at 100 °C until constant mass. Soil organic matter content was determined from ash-free dry mass after combusting at 500 °C for 4 hours. Soil pH was measured using 5 g soil in 25 ml DI water for organic samples and 10 g soil and 20 ml DI water for mineral samples, for the 1-day and 8-day sampling times. Soils were extracted with DI water similar to Tas *et al.* 2014, in a ratio of 50 ml water to 10 g soil, centrifuged at 6000 rpm for 10 min and then filtered using 0.7 μm filters. Water extractions were analyzed for dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) using a Shimadzu TOC-VCPH analyzer at NESS. Chromophoric dissolved organic matter (CDOM) was measured on water extractions using a spectrophotometer measuring absorbance across 200-800 nm. Specific UV absorbance at 254 nm (SUVA) and slope ratios (S_R) were then calculated following Helms *et al.* (2008). Higher SUVA values are indicative of more aromatic CDOM, which often corresponds to more recalcitrance to decomposition (Weishaar *et al.* 2003). Higher S_R values correspond to lower molecular weights of CDOM, which may suggest that these compounds are more labile (Helms *et al.* 2008). Water extractions were frozen until analyzed colorimetrically for NH_4^+, NO_3^-, and PO_4^{-3} on an Astoria autoanalyzer at Woods Hole Research Center in Falmouth, MA. Nitrate values were almost always below levels of detection (25 μg/l), and henceforth, we report dissolved inorganic nitrogen (DIN) as the sum of NH_4^+ and NO_3^-.

The potential activities of extracellular enzymes involved in C, N, and P acquisition were determined colorimetrically as described by Sinsabaugh *et al.* (1993). We assayed the activities of β-glucosidase, which breaks down cellulose providing glucose as a product, phenol oxidase, which decomposes lignin, leucine aminopeptidase, which degrades proteins and polypeptides, and acid phosphatase, which cleaves PO_4^{-3} groups from organic molecules. For each assay the following substrates (respectively) were dissolved in 50 mM sodium acetate buffer (pH 5): 5 mM pNP-β-glucopyranoside, 10 mM LDOPA, 2.5 mM leucine p-nitroanilide, and 5 mM pNP- PO_4^{-3}. We incubated 600 μl soil slurries with 400 μl of substrate for 4-24 hours at 17 °Cand measured the formation of the colored product with a microplate reader (Biotek Powerwave XS2) at NESS. Potential extracellular enzyme activities were assayed for organic samples at all sampling times and the mineral samples from

1-year post-fire.

Soil Incubations

Soils from the 1-year sampling time were incubated in the lab to measure soil respiration as well as net N mineralization rates. Two sets of 10 g subsamples were weighed fresh. The first set of subsamples was extracted with 2 M KCl within 24 hours and analyzed for DOC, TDN, NH_4^+, and NO_3^- in the same manner as the water extracts. The second set of field-moist subsamples was incubated in the dark at 17 °C. Moisture levels were maintained by weighing daily and adding DI water until sample mass returned to initial values. After 1 week, CO_2 flux over a 1 hour period was measured using an infrared gas analyzer (LICOR, 6262). After incubating for 2 weeks, soils were extracted with 2 M KCl. Net inorganic N mineralization rates were calculated as the DIN after incubating, minus the initial DIN measured on sub-samples prior to the incubation. Net organic N production rates were calculated similarly, using the difference between total dissolved nitrogen and DIN.

Statistical Analyses

We used mixed-effects models to determine the effects of soil burn severity and time on soil nutrient concentrations and microbial activities. Soil burn severity and time were used as fixed effects, with plot as the random effect to account for repeated sampling. We used post-fire organic layer depth as a metric of soil burn severity. We examined the effect of soil burn severity on the response variables described above by implementing linear mixed-effects models for regressions with post-fire organic layer depth as the explanatory variable. For response variables that did not have a linear relationship with post-fire organic layer depth, we used the soil burn severity treatments (control, low, moderate, high) as a categorical fixed effect. All statistical analyses were done using the statistics program “R” v2.7.0, with a family-wise significance level alpha = 0.05. P-values were adjusted for multiple comparisons using the Benjamini and Hochberg method. Model fitting was performed using the “lme” function from the “nlme” package for R using restricted maximum likelihood, and degrees of freedom were calculated using the inner-outer rule (Pinheiro *et al.* 2000). For those variables only measured at the 1-year sampling point, we used simple ANOVA (“aov” in R) and linear regression (“lm” in R) models. We assessed the assumptions of each model using QQ-normal plots of residuals and plots of residuals against fitted values to assess heteroscedasticity. Where necessary, data were log-transformed (used for DON, DOC, DIN, and

PO_4^{-3}) to achieve equal variance. We used plots of residuals against time to check for autocorrelation and used "varIdent" to model increasing residual variance with time (necessary for PO_4^{-3} only) to correct it. Where applicable, post-hoc Tukey's tests were run to determine pairwise differences. Errors presented in text and figures are standard errors.

RESULTS

Effectiveness of Soil Burn Severity Treatment

The experimental burn treatments were effective in creating a range of soil burn severities as measured by post-fire organic layer depths (ANOVA $F_{3,8}$=8.817, p<0.01; Table 1). Prior to the experimental burns, there were no statistical differences in thaw depth (23.4 ± 2.3 cm) or organic layer depths (10.3 ± 0.4 cm). The low severity treatment scorched the soil surface but barely consumed the organic layer. The moderate severity treatment consumed on average 50% of the organic layer, about 5 cm, while the high severity treatment consumed 75% of the organic layer. After the first year post-fire, there was also observable ground subsidence in the high severity treatment. By 6-days post-fire, thaw depths (which do not account for ground subsidence) in high severity plots were already thawed significantly deeper than the control plots and low severity treatment (ANOVA $F_{3,8}$=15.19, p<0.01; Table 1). Soil surface temperatures 1-year post-fire increased with soil burn severity up to 2°C above control treatments (ANOVA $F_{3,12}$=5.6, p=0.012; Table 1).

Table 1. Soil burn severity effects on thaw depth, organic layer depth, soil pH, and soil temperature; C = control, L = low severity, M = moderate severity, H = high severity. Values are means with standard error in parentheses. Letters denote significant differences from a post-hoc Tukey's HSD test across time and treatment. Temperature data are from Alexander *et al.* (2018).

		Relative thaw depth*	Organic layer depth (cm)	Soil temperature °C (5 cm depth)	Organic layer pH
1-day post-fire	C	1.00 (0.22)^{ae}	10.89 (1.28)^{ad}	no data	5.70 (0.14)^{a}
	L	1.15 (0.11)^{ae}	9.22 (2.06)^{abd}	no data	5.96 (0.12)^{ab}
	M	1.40 (0.03)^{ace}	6.33 (0.88)^{abc}	no data	6.07 (0.07)^{ab}
	H	1.59 (0.10)^{acd}	2.11 (0.22)^{c}	no data	6.59 (0.25)^{b}
1-week post-fire‡	C	1.36 (0.18)^{ac}	9.33 (1.33)^{abd}	no data	5.84 (0.16)^{ac}
	L	1.75 (0.14)^{cd}	7.83 (2.09)^{abcd}	no data	5.71 (0.06)^{a}
	M	1.97 (0.08)^{bd}	4.83 (0.33)^{bc}	no data	6.04 (0.16)^{ab}
	H	2.43 (0.01)^{b}	2.33 (0.19)^{c}	no data	6.46 (0.25)^{bc}
1-year post-fire	C	0.79 (0.06)^{e}	12.67 (0.67)^{d}	7.9 (0.14)^{a}	no data
	L	1.10 (0.20)^{ae}	11.33 (2.33)^{ad}	7.8 (0.2)^{a}	no data

M	1.50 (0.15)[ac]	6.17 (0.44)[abc]	8.5 (0.31)[ab]	no data
H	2.38 (0.11)[b]	4.70 (1.19)[bc]	9.8 (0.65)[b]	no data

* Thaw depth relative to pre-fire (day 0) measurements, e.g. 1 is no change, >1 is deeper, <1 is shallower. Average pre-fire thaw depth is 23.4 (2.3) cm.

‡ 1-week post-fire corresponds to 6-days for relative thaw depth and 8-days for organic layer depth.

1-Day Post-Fire

Soil moisture, soil organic matter content, and enzymatic activities of phosphatase and β-glucosidase decreased with increasing soil burn severity in the organic layer (Fig 1, Fig 4a-b, Table 2). Concentrations of DOC, DON, and DIN in the organic layer increased with soil burn severity up to approximately 4 times the concentration of the unburned soils (Fig 2a-c, Table 2). The activity of the extracellular enzyme, leucine aminopeptidase (Fig 4c, Table 2), and soil pH (Fig S1, Table 2) also increased with increasing soil burn severity. The slope ratio (S_R) of water-extractable CDOM from organic layer soils increased with soil burn severity (Fig 3, Table 2), indicating a greater proportion of low molecular weight compounds with increasing soil burn severity. SUVA values from the water-extractable CDOM decreased with soil burn severity (Fig S2), indicating lower average aromaticity. For all time points, SUVA showed a similar relationship as S_R, where low molecular weight DOM corresponds to low aromaticity (Fig S2, Table 2). Dissolved PO_4^{-3} (Fig 2d, Table 2) and phenol oxidase activity (Fig S3) in the organic layer were not significantly affected by soil burn severity. For the majority of response variables, the effects of soil burn severity were marginal or not detectable in the mineral horizons. The exceptions are DON and PO_4^{-3} concentrations in the top 10 cm of the mineral horizon, both of which increased with soil burn severity (Fig S4a-b).

Table 2. Linear mixed-effects model results from regressions with post-fire organic layer depth (continuous) as the explanatory variable across three sampling periods (time, categorical). The random effect accounts for repeated measures on plots through time. Bolded values are significant (p-value<0.05) after adjusting for multiple comparisons. Italicized values are significant before adjusting for multiple comparisons.

Response variable	Slope with post-fire organic layer depth	Difference 1-Day to 8-Days	Difference 1-Day to 1-Year	Interactions between slope and time	Degrees of freedom	Random effect variance: Intercept	Random effect variance: Residual
SOM	**1.9**	**-10.4**	**-10.2**	None	21	12.2	84.6
Soil moisture	**1.45**	**-5.7**	**-14.3**	None	21	6.8	23.6
pH	**-0.06**	-0.13	NA	NA	10	0.066	0.039
DOC*	**-0.10**	**-1.0**	**-2.6**	*1-Year: 0.13*	19	2.3E-10	0.21

SUVA	**0.007**	**0.07**	**0.14**	None	21	0.0008	0.0026
Slope Ratio	**-0.02**	**-0.14**	**-0.21**	*8-Days: 0.01* **1-Year: 0.02**	19	0.0006	0.0024
DON*	**-0.20**	**-1.1**	**-2.9**	*1-Year: 0.16*	19	2.2E-10	0.38
DIN*	**-0.19**	-0.3	**-3.2**	**1-Year: 0.33**	19	0.31	0.86
PO_4^{-3} *	-0.01	-0.43	0.30	None	21	0.77	0.46
β-glucosidase	**1.2**	**6.1**	3.7	None	21	14.4	44.9
Phosphatase†	**8.1**	22	-22	*1-Year: 3.8*	19	3.2E-16	5.3E-6
Leucine aminopeptidase	**-2.6**	**-30.6**	-18.2	*8-Days: 3.4* **1-Year:5.4**	18	74	123.2
Soil respiration per g soil	**5.7**	NA	NA	NA	10	NA	NA
Soil respiration per g SOM	**5.1**	NA	NA	NA	10	NA	NA

*Log transformed to correct unequal variance.

†Increasing variance with time modeled explicitly using varIdent.

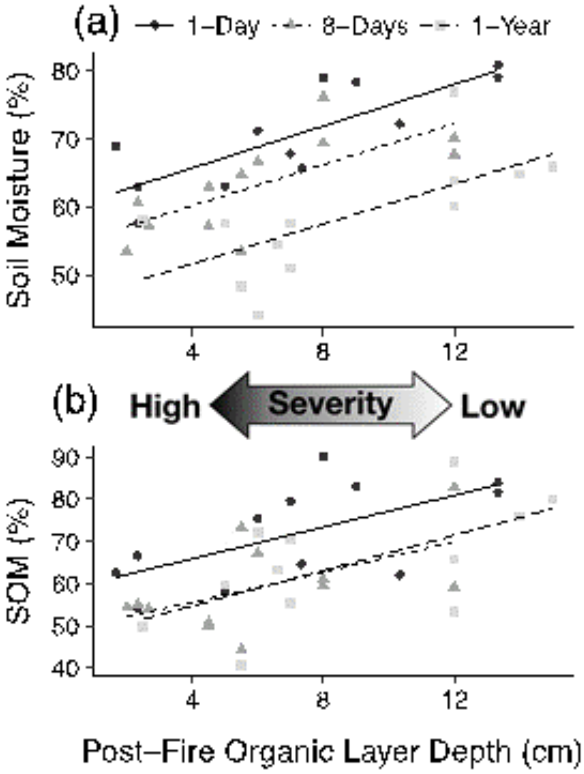

Fig. 1. Organic layer (a) % soil moisture of field-wet mass and (b) % soil organic matter (SOM), as a function of residual organic layer depth, along a soil burn severity gradient in a larch forest in Cherskiy, Russia. Regression lines are from a mixed effects model.

8-Days Post-Fire

Both soil moisture and soil organic matter content continued to have a negative relationship with soil burn severity, similar to 1-day post-fire (Fig 1, Table 2). Across treatments, concentrations of DOC and DON were reduced by half compared to 1-day post-fire, and the trend of increasing concentrations with soil burn severity remained the same (Fig 2a-b, Table 2). DIN showed the same magnitude and rate of increase with soil burn severity as 1-day post-fire (Fig 2c, Table 2). The S_R of water-extractable CDOM still increased with soil burn severity, though the magnitude of the slope and intercept decreased relative to 1-day post-fire (Fig 3, Table 2). Soil pH and the EEAs of phosphatase and β-glucosidase show the same relationships with soil burn severity as 1-day post-fire (Fig 4a-b, Fig S1, Table 2). Leucine aminopeptidase activity however no longer showed any effects from fire (Fig 4c, Table 2). Similar to 1-day post-fire, concentrations of dissolved PO_4^{-3} were not significantly affected by fire after 8 days (Fig 2d, Table 2). In the mineral horizon, there was a significant time by soil burn severity response; while DON increased with soil burn severity after one day, DON decreased with soil burn severity after 8-days following fire, (Fig S4a). Dissolved PO_4^{-3} in the mineral horizon had the same increasing trend with soil burn severity 8-days post-fire as 1-day post-fire (Fig S4b).

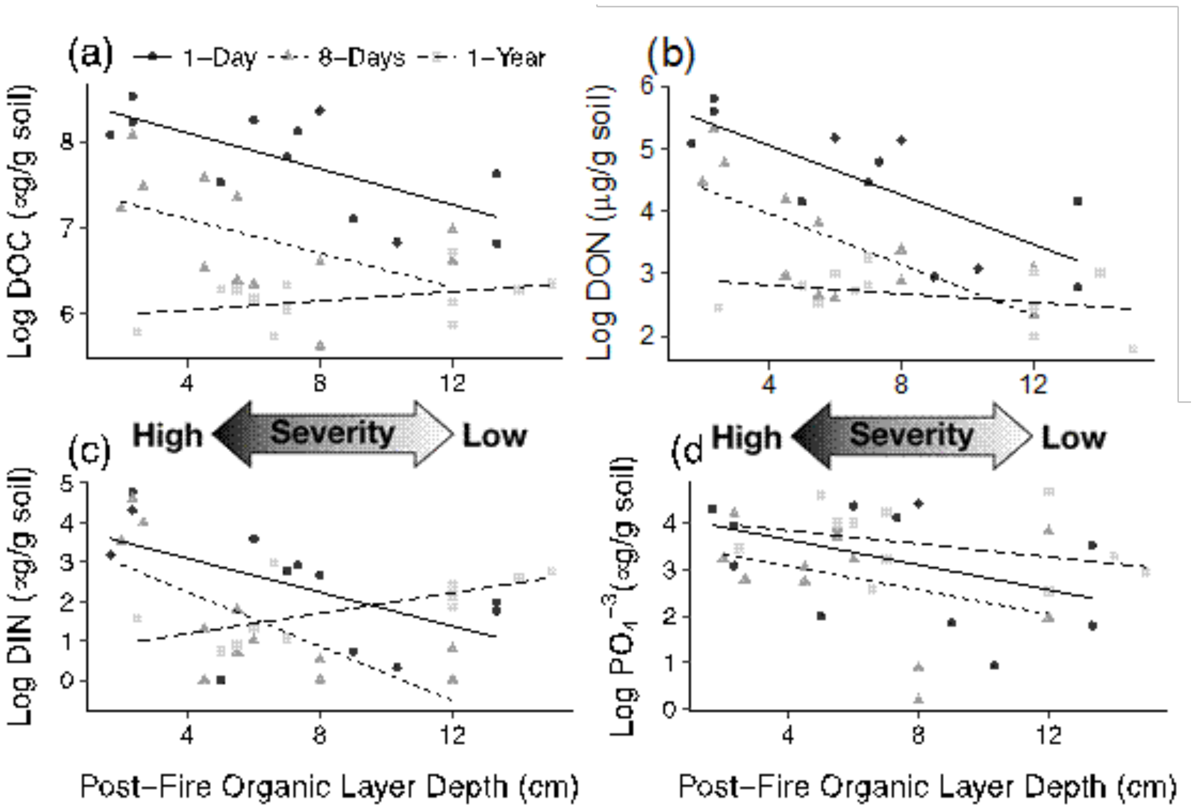

Fig. 2. Water-extractable nutrients in the organic layer along a soil burn severity gradient in a larch forest in Cherskiy, Russia. Dissolved organic carbon (DOC) concentration (a), dissolved organic nitrogen (DON) (b), dissolved inorganic nitrogen (DIN) (c), and dissolved PO_4^{-3} (d). Regression lines are from a mixed effects model.

1-Year Post-Fire

Soil moisture and soil organic C content in the organic layer still showed the same declining relationship with soil burn severity 1-year post-fire (Fig 1, Table 2). However, there were no longer detectable differences in DOC and DIN concentrations (Fig 2a-b, Table 2), or in the S_R of water-extractable CDOM (Fig 3, Table 2). Both DIN (Fig 2c, Table 2) and leucine aminopeptidase (Fig 4c, Table 2), which increased in the organic layer in the day and week following fire, declined with increasing soil burn severity after 1-year. The extracellular activities of phosphatase and β-glucosidase in the organic layer still showed the same declining trend with increasing soil burn severity after 1-year (Fig 4a-b, Table 2). Dissolved PO_4^{-3} concentrations in the organic layer remained unchanged (Fig 2d, Table 2). The only effect of soil burn severity in the top 10 cm of the mineral horizon was a decrease in DON with increasing soil burn severity (Fig S4a). In the base 10 cm of the thawed mineral horizon, there was a marginally significant increase in DOC, DON, and PO_4^{-3} with increasing soil burn severity (Fig S5).

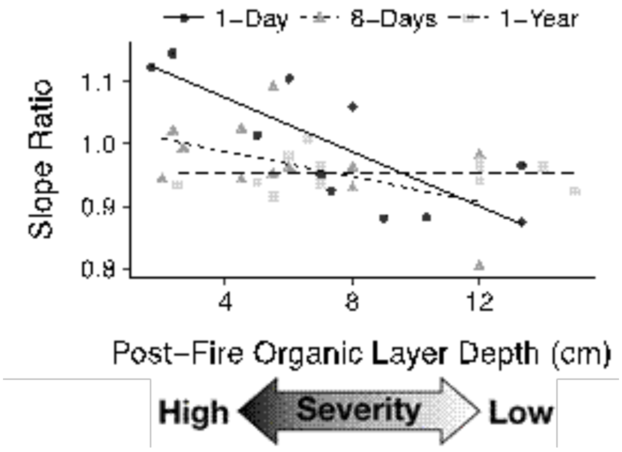

Fig. 3. Molecular weight as indicated by slope ratio, S_R, from water-extractable dissolved organic matter. Regression lines are from a mixed effects model.

Respiration of incubated organic layer soils collected one year following fire declined linearly with increasing soil burn severity, both when normalized to soil dry mass as well as soil organic matter content (Fig 5). In organic soils from all soil burn severity treatments, net production rates for DOC, DON, and DIN were near zero (Table 3). The control treatments had significantly lower net DOC and DON production rates and net DIN mineralization rates than all soil burn severities (Table 3).

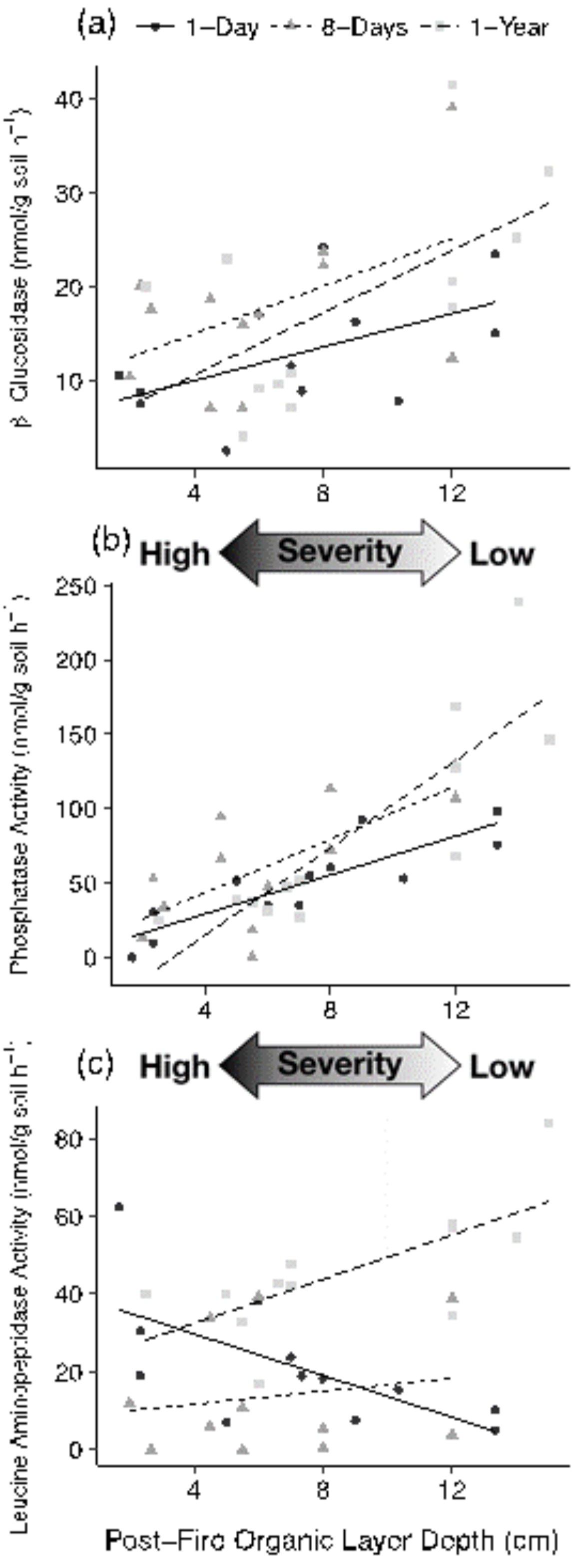

Fig. 4. Organic layer extracellular enzyme activity for (a) β-glucosidase, (b) phosphatase, and (c) leucine aminopeptidase, as a function of residual organic layer depth. Regression lines are from a mixed effects model.

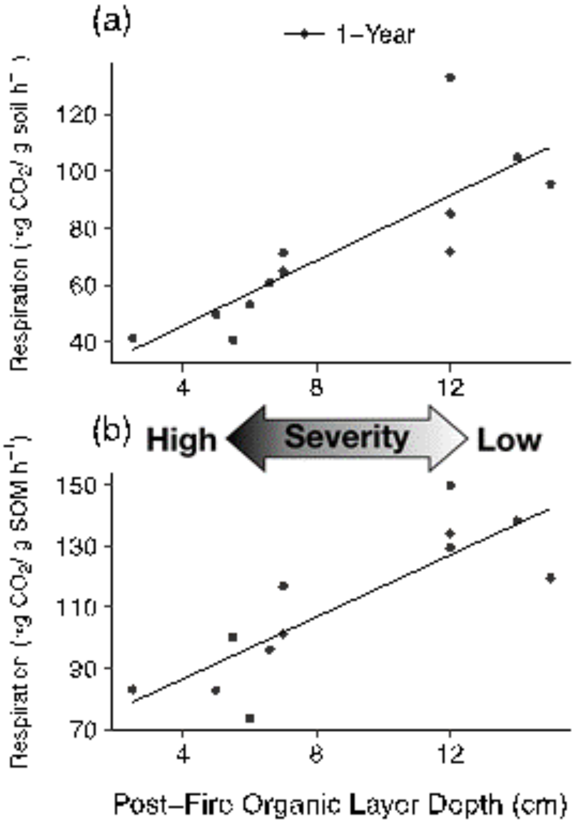

Fig. 5. Soil respiration 1-year post-fire, (a) normalized to soil mass, (b) normalized to soil organic matter. Regression lines are from a mixed effects model.

Table 3. Soil burn severity effects 1-year post-fire on net production rates of dissolved organic carbon dissolved organic nitrogen, and net mineralization rates of dissolved inorganic nitrogen in the organic layer; C = control, L = low severity, M = moderate severity, H = high severity. Values are means with standard error in parentheses. Letters denote significant differences from a post-hoc Tukey's HSD test after fitting an ANOVA.

Variable		Mean (SE)	Degrees of freedom	F-value
DOC net production rates	C	-99.3 (12.6)^{a}	3, 8	9.909
	L	15.8 (25.1)^{b}		
	M	-5.1 (15.8)^{b}		
	H	-6.0 (5.3)^{b}		
DON net production rates	C	-11.2 (2.3)^{a}	3, 8	10.8
	L	-1.4 (1.8)^{b}		
	M	-0.94 (0.40)^{b}		
	H	-1.1 (0.86)^{b}		
DIN net mineralization rates	C	-2.3 (0.58)^{a}	3, 8	7.4
	L	0.19 (0.59)^{b}		
	M	-0.75 (0.27)^{ab}		
	H	0.18 (0.075)^{b}		

DISCUSSION

Despite the global importance of soil C pools in high-latitudes, the effects of fire in Siberian forests remain understudied in comparison to North American boreal forests (Alexander *et al.* 2018). This study addressed this knowledge gap by quantifying a relationship between soil burn severity and changes in soil C, N, and P pools, soil respiration and EEAs related to the turnover of organic matter.

Effectiveness of Soil Burn Severity Treatment

The experimental burn treatments resulted in post-fire organic layer depths comparable to the range observed (2-10 cm) in Siberian larch forests (Sofronov & Volokitina 2010). These reductions in the insulating soil organic layer, combined with lower albedo from the charred soil surface, caused the deeper thaw depths and warmer soil temperatures observed with increasing soil burn severity (Table 1). The deeper thaw depths along with warmer soil temperatures contributed to the declining soil moisture in the total organic layer with increasing burn severity (Fig 1). Both increases and decreases in soil moisture following fires have been observed in other studies (Dooley & Treseder 2011), and though we saw a consistent decline in soil moisture with soil burn severity, we also observed localized subsidence in the highest burn severities that became saturated depressions, causing wetter soils in the deeper mineral layer (Alexander *et al.* 2018). This increase in thaw depths and changes in soil moisture exposed new soil horizons to decomposition and potential leaching of organic matter (Minsley *et al.* 2016).

1-Day Post-Fire

Incomplete combustion of organic matter can increase small molecular weight organic material and inorganic nutrient availability through pyrolysis. We measured a post-fire increase in DOC, DON, and DIN concentrations 1-day after burning (Fig 2a-c), a trend frequently described in other ecosystems (DeLuca & Zouhar 2000; Choromanska & DeLuca 2001, 2002; Bárcenas-Moreno *et al.* 2011) and that could explain the increases in stream nutrient export reported following fires in some boreal ecosystems (Bayley *et al.* 1992; Lamontagne *et al.* 2000; Petrone *et al.* 2007). Warmer temperatures can enhance rates of microbial N mineralization, but this is unlikely to have caused the magnitude of DIN increases we observed after only 1 day. The optimal temperatures for pyrolysis of organic N into mineral N is well below temperatures recorded during wildfires, and this is the likely cause of the higher DIN observed in this study (Clough *et al.* 2013).

Unlike C and N, we did not observe a significant increase in dissolved PO_4^{-3} with increasing soil burn severity, resulting in an uncoupling of dissolved P from C and N cycles in the organic layer after the fires (Fig 2d). However, there could have been an increase in available P in an unmeasured pool; PO_4^{-3} participates in numerous sorption reactions that would prevent extraction in water, but not necessarily immobilize it from the microbial community (Reddy *et al.* 1998). We also measured an increase in dissolved PO_4^{-3} and DON with increasing soil burn severity in the top 10 cm of the mineral horizon, (Fig S4), suggesting there was infiltration and leaching from ash and the organic horizon.

We observed higher DOM lability with increasing soil burn severity (Fig 3, Fig S2), perhaps due to the greater abundance of soil organic matter as a fuel source compared to lower latitude soils. In contrast, studies of changes in dissolved C pools following fires have described greater losses of labile than recalcitrant fractions (Jiménez Esquilín *et al.* 2008; Martín *et al.* 2009; Wang *et al.* 2012). We only examined the water extractable DOM fraction, and given that much of the C left behind from fire can be highly aromatic and hydrophobic, it is likely that the fraction of recalcitrant C pools also increased. However, the changes in DOM lability are important because they can support fast regrowth of the microbial community.

Our hypothesis that microbial activities would decline due to fire-induced mortality immediately post-fire was not supported because not all EEAs declined; while β-glucosidase and phosphatase declined, leucine aminopeptidase increased with soil burn severity (Fig 4). Alternatively, we propose that fire-driven changes in substrate availability caused induction-suppression responses in enzyme production. If the post-fire increase in low molecular weight compounds were easily assimilated, this may explain the reduction in β-glucosidase activity (Allison & Vitousek 2005). Likewise, phosphatase can be suppressed by higher P availability (Sinsabaugh & Shah 2012), which supports the possibility that P availability may have increased with soil burn severity, even though we did not observe significant changes in the water-extractable PO_4^{-3} pool. In contrast, when the availability of a *complex* nutrient increases (e.g., DON), we expect an increase in enzyme production for that target resource (Allison & Vitousek 2005) as was observed with increases in both DON and leucine aminopeptidase activity with soil burn severity (Fig 2b, 4c). These results are consistent with observations in other ecosystems where fire depresses microbial P demand and increases microbial N demand (Toberman *et al.* 2014).

8-Days to 1-Year Post-Fire

The initial effects of soil burn severity on dissolved C and nutrients were brief. After one week following fire, dissolved concentrations of C and nutrients were already declining and by 1-year post-fire there was no longer any effect of soil burn severity on DOM concentration or composition. This loss could be due to sorption, uptake, or infiltration and leaching of soil C and nutrients (Richardson & Marshall 1986; Hart *et al.* 2005). In a natural wildfire it is possible the higher nutrient availability would persist longer, since soils would experience runoff inputs from upslope in addition to downslope runoff losses. Given the transient nature of the post-fire nutrient increase, it is unlikely that recovering vegetation will benefit from this pulse, despite the strong N limitation in many terrestrial arctic and boreal ecosystems (Shaver & Chapin 1995; Liang *et al.* 2014; Sullivan *et al.* 2015).

Although DOM was similar in burned and unburned plots after only 1-year, EEAs were still affected by fire, which suggests that substrate availability is not enough to explain microbial responses to soil burn severity. There is evidence in other ecosystems that when N becomes scarce, soil microbes invest less in producing N-expensive extracellular enzymes (Sinsabaugh & Moorhead 1994; Schimel & Weintraub 2003; Allison & Vitousek 2005; Moorhead *et al.* 2013). Thus, the declining activities of β-glucosidase, leucine aminopeptidase, and phosphatase with increasing soil burn severity 1-year post-fire could be caused by the concurrent decline in DIN concentrations with increasing soil burn severity. It is important to note that the measured EEAs are potentials, with temperature held constant. Warmer temperatures measured *in situ* in the high and moderate severity treatments (Alexander *et al.* 2018) could compensate for smaller extracellular enzyme pools.

In this study, soil conditions following the fires changed in ways favorable to microbial growth (i.e., warmer and higher pH), but also in unfavorable ways (i.e., drier and contained less SOM). Fire has been shown to suppress soil microbial biomass for as long as 20 years post-fire in boreal ecosystems (Dooley & Treseder 2011). Lower active microbial biomass after fires has been attributed to the loss of SOM, N, and water stress (Hart *et al.* 2005). Less active microbial biomass with increasing soil burn severity could contribute to the declining EEAs and reduced rates of soil respiration that we observed 1-year post-fire. The decline in potential respiration rates in the soil organic layer with increasing soil burn severity represents a possible negative C feedback. However, the warmer soil temperatures and deeper thaw depths in the higher soil burn severities could increase soil respiration *in situ*.

Net production rates of DON, DIN, and DOC were not related to soil burn severity, but were altered by fire regardless of severity. Given the other evidence in this study for less active microbial biomass with increasing soil burn severity 1-year post-fire, the net increase in production rates was likely due to reduced immobilization rates as opposed to an increase in gross production rates. Given that wildfire severity is often heterogeneous, more research is needed to determine why processes respond differently to soil burn severity. For example,why EEAs relate linearly to soil burn severity but net N mineralization rates have a threshold change with fire presence.

This study quantitatively addressed the effects of soil burn severity in a Siberian larch forest, an understudied ecosystem particularly vulnerable to climate change with a disproportionately large role in soil C storage. Our findings suggest that higher soil burn severity in organic-rich permafrost ecosystems can create a substantial and immediate increase in N and C and increase the proportion of labile DOM. The longevity of this alteration was brief, with the majority of the pulse of N and C disappearing within days, thus it is not likely to alleviate nutrient limitation in recovering vegetation. Fire caused an uncoupling of P from C and N cycles through disparate changes in dissolved nutrients and by causing a strong and lasting decline in phosphatase activity. Despite the transience of the initial increase in dissolved N immediately post-fire, over the long-term, an increase in net N mineralization rates could lead to greater nutrient availability for primary production. However, a less active microbial biomass would also process SOM more slowly, and decreased rates of EEAs would result in slower nutrient turnover. Our results show that as soil burn severity increases, so too will the suppression of soil respiration, which represents an important mechanism that could mitigate initial C losses from fires in permafrost-dominated ecosystems.

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