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LETTER

Fire severity influences the response of soil microbes to a boreal forest fire

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Abstract

Wildfire activity is projected to increase in boreal forests as a result of climate warming. The consequences of increased wildfire activity for soil carbon (C) storage in boreal forests may depend on the sensitivity of soil microbes to fire severity, but microbial responses to boreal forest fire severity are not well known. Here, we combine remote sensing of fire severity and field sampling to characterize the response of soil microbial biomass per g soil, microbial respiration of CO_2 per g soil, and fungal groups to fire severity in a boreal forest ecosystem. We used remote sensing measurements of differenced normalized burn ratio from Landsat as a measure of fire severity. Our results demonstrate that fire severity controls soil microbial responses to boreal forest fires. In comparison to unburned stands, burned stands had a 52% and 56% reduction in soil microbial biomass and basal respiration, respectively. Within burned stands, we found that microbial biomass and basal respiration significantly declined with increasing fire severity. In addition, mycorrhizal taxa and basidiomycetes displayed particularly low tolerances for severe fire. Although wildfires result in the immediate loss of soil C, our study provides evidence that decreases in microbial biomass and respiration following high severity fires may reduce the capacity of the soil microbial community to decompose soil C over longer time scales. Therefore, models of C cycle responses to climate warming may need to represent the sensitivity of microbial biomass and fungal community composition to fire severity in boreal forests.

Introduction

Increases in wildfire activity are an element of global change in boreal forests. Surface temperatures in boreal forests have increased by ~2 °C in the past 100 years (Wendler and Shulski 2009, IPCC 2013), and one consequence of warming in boreal forests is an intensification of the fire regime. Climate warming and drying favor a boreal forest fire regime that is characterized by a greater number of extreme fire years with large fires that burn at high severity (Kasischke and Turetsky 2006, Turetsky *et al* 2011, de Groot *et al* 2013). Models of future wildfire activity in North American boreal forests predict substantial increases in fire season length (Flannigan *et al* 2013), burned area (Flannigan *et al* 2005, Balshi *et al* 2009), and fire severity (Flannigan *et al* 2013) during the 21st century.

The soils of boreal forests store up to 20% of global soil organic carbon (C) (Jobbagy and Jackson 2000, Tarnocai *et al* 2009), and these large soil C stocks may be altered by increases in wildfire activity. Conventional ecosystem theory of secondary succession predicts that microbial decomposition increases following boreal forest fires, and that the post-fire stimulation of microbial decomposition reduces soil C stocks (Harmon *et al* 2011). Microbial decomposition is predicted to increase because soil temperatures are higher in recently burned stands, and forest fires can create detritus that is available for decomposition. However, hypothesized increases in microbial decomposition are difficult to reconcile with the observed

responses of soil microbes to boreal forest fires. Microbial biomass (i.e., fungi + bacteria) and extracellular enzyme production have consistently been found to decline following boreal wildfires (Dooley and Treseder 2012). Moreover, plant litter has been shown to decompose more slowly in recently burned boreal forest stands (Holden *et al* 2013). These observations challenge the conventional view that soil microbial activity increases following boreal forest fires, and instead suggest that microbial responses to fire may exert a negative feedback on soil C stocks.

Fire severity may determine the degree to which soil microbes—and the ecosystem level processes that are regulated by soil microbes—are affected by boreal forest fires. Fire severity is defined here by the immediate impacts of a fire on the physical environment. Severe fires may be particularly destructive to soil microbial communities if their higher temperatures more effectively sterilize surface soils. Indeed, previous studies have found that higher severity fires can more strongly reduce microbial biomass (Fioretto *et al* 2005, Knelman *et al* 2015), fungal abundance (Bergner *et al* 2004), and fungal diversity (Hewitt *et al* 2013) and shift bacterial communities (Knelman *et al* 2015), compared to lower severity fires. In addition, severe fires can yield greater mortality for host plants of symbiotic microbes (e.g., mycorrhizal fungi). Indeed, Dahlberg *et al* (2001) found that ectomycorrhizal root colonization and diversity was lower in more severe burns in a Swedish boreal forest. The sensitivity of soil microbes to fire severity could, in turn, alter soil C storage in boreal forests. Saprotrophic fungi regulate C loss from boreal forest soils via the decomposition of organic matter in soil. On the other hand, mycorrhizal fungi regulate C gains to the soil by facilitating the transfer of nutrients to plant roots (Clemmensen *et al* 2013). Thus, the consequences of increased wildfire activity for soil C storage in boreal forests could depend on the sensitivities of each fungal group to fire severity.

Hewitt *et al* (2013) examined shifts in fungal community composition with fire severity in Alaskan tundra, and noted that relative abundance of dominant taxa tended to decline with fire severity. Nevertheless, sensitivities of fungal taxa to fire severity have not yet been documented in boreal forest. Recent studies on post-fire plant community composition indicate that fire severity influences the distributions of coniferous and deciduous trees in boreal forests (Johnstone *et al* 2010, Beck *et al* 2011). It is unclear whether fire severity will affect certain fungal groups more than others. Clarifying the response of soil fungal taxa to fire severity is essential for projecting the effects of increased wildfire activity on the large soil C stocks in boreal forests.

Here, we investigate the responses of soil microbial biomass, microbial respiration of CO_2, and fungal taxa to fire severity in a boreal forest ecosystem. To do so, we combined remote sensing of fire severity with field sampling of a fire scar in interior Alaska. We also sampled soil from unburned late successional control stands adjacent to the fire scar. We predicted that more severe fires would cause greater reductions in soil microbial biomass and respiration than low severity fires. In addition, we expected that taxonomic and functional groups of fungi would vary in their ability to tolerate severe fires.

Materials and methods

Site description

The Gilles Creek fire was a lightning-caused crown fire that occurred from 26 May−2 June 2010 in interior Alaska and burned ~8000 ha (figure 1(A)). Pre-fire vegetation types in the fire scar were aggregated from the LANDFIRE dataset (US Department of Interior G S 2009). The dominant vegetation type within the burn perimeter was black spruce forest (62%), followed by mixed white spruce-aspen forests (17%), and pure aspen (5%). Birch (*Betula nana* L.) and willow (*Salix* spp. L.) shrub stands were found in Southern areas of the perimeter (13% of the fire scar), although these were mostly left unburned. Soils are primarily Inceptisols. The local climate is cold and dry with a mean annual temperature of 2 °C and a mean annual precipitation of 303 mm.

Soil sampling

From 27 August to 31 August 2012, we collected soil samples from 19 sites within the Gilles Creek fire scar ($n = 15$ black spruce stands, 4 white spruce-aspen stands; supplementary table S1). Details are described in Rogers *et al* (2014). Burn sites were chosen to represent a range of fire severities. Sites were separated by at least 90 m. We also sampled from seven additional sites in late successional unburned control forests adjacent to the fire scar ($n = 4$ black spruce stands, 3 white spruce-aspen stands; supplementary table S1). Control sites were selected to match pre-fire vegetation structure and topography at the burned locations. Field sites were located between 120 and 700 m away from an access road traversing the center of the fire. At each site, we established a 2 m × 30 m transect (supplementary figure S1). We collected three soil cores along the transect—one at each end, and one in the middle. For each core, we sampled the entirety of the organic soil horizon using a 5 cm diameter soil corer. If present, fresh plant litter and live moss were removed prior to taking soil cores. Prior to sample collection at each site, the soil corer was pre-cleaned with soil from the site, so contamination between sites was unlikely.

Organic soils were separated into fibric (moderately decomposed plant material) and humic (highly decomposed, no recognizable plant parts) horizons following Boby *et al* (2010). In the unburned sites, the fibric horizon was ~6–7 cm thick on average, whereas

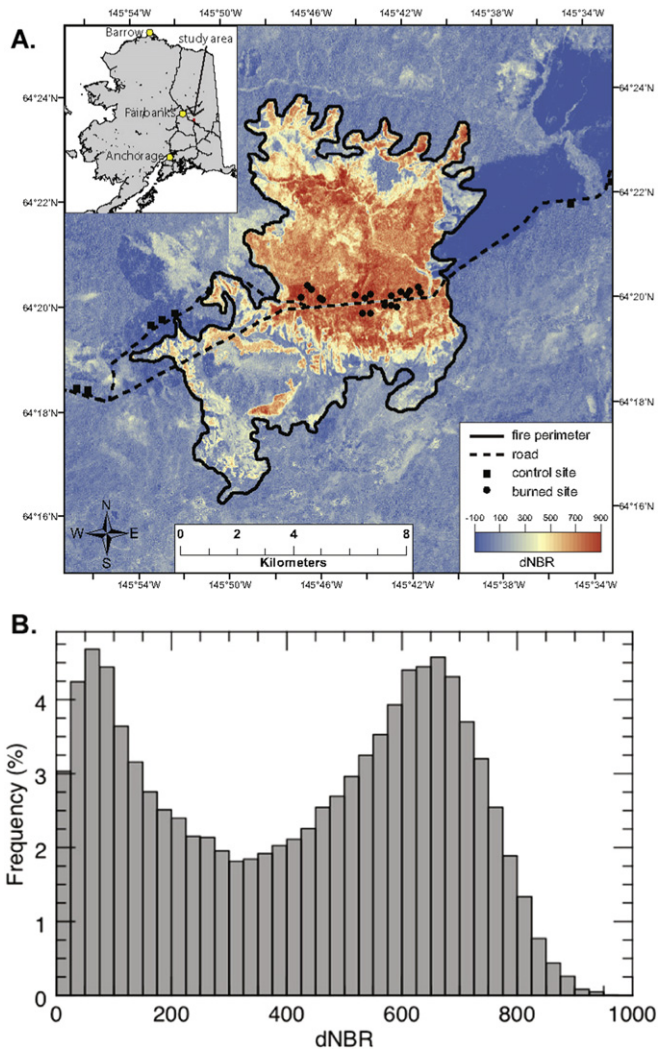

Figure 1. Map of the Gilles Creek fire scar in interior Alaska (A) and histogram of dNBR across the fire perimeter (B). Larger dNBR values indicate higher fire severity. dNBR was positively correlated with composite burn index (Rogers *et al* 2014). The fire perimeter was derived from the Monitoring Trends in Burn Severity database. Symbols represent sampling locations in the fire scar and adjacent unburned control forests.

the humic horizon averaged about 2 cm thick (Rogers *et al* 2014). Humic soils were not present at every site. We did not collect mineral soil, because previous work in the area demonstrated that microbial biomass in the mineral horizon was substantially lower than in the organic horizon and similar between burned and unburned sites (Holden *et al* 2013). At each site, we collected six additional soil cores that were used to determine the height and bulk density of the fibric and humic soil layers. Following collection, soils were immediately placed on ice, where they remained for a maximum of five days until they could be transported to UC Irvine (Irvine, CA, USA).

Upon return to UC Irvine, each horizon from each soil core was hand-homogenized and divided into subsamples that were stored at either 4 °C or –80 °C. Fibric soils and humic soils remained separate, and were analyzed separately. The subsamples stored at 4 °C were used to measure microbial biomass and respiration, and we began those incubations within 24 h of returning to UC Irvine. Fungal DNA was extracted from the –80 °C subsamples within two months.

Fire severity

We characterized fire severity at each site using the differenced normalized burn ratio (dNBR) derived from 30 m Landsat 5 Thematic Mapper (TM) imagery, exactly as described in Rogers *et al* (2014). A Level 1 georectified pre-fire image was selected from 3 August 2009 (path 68, row 15) and post-fire image from 3 September 2011 (path 67, row 15) from the USGS GLOVIS website (USGS 2012). We used the Landsat Ecosystem Disturbance Adaptive Processing System (LEDAPS) to obtain surface reflectance (Masek *et al* 2006). LEDAPS converts digital numbers, calibrates at-sensor radiance values, and corrects for atmospheric contamination using column water vapor from National Centers for Environmental Prediction reanalysis and ozone concentration from Total

Ozone Mapping Spectrometer data aboard the Nimbus-7, Meteor-3, and Earth Probe platforms. Topographic corrections were performed using a modified version of the rotation method following Rogers *et al* (2014). The normalized burn ratio (NBR) was calculated from each scene according to

$$\mathrm{NBR} = \frac{\rho_4 - \rho_7}{\rho_4 + \rho_7} \times 1000,$$

where ρ_4 = band 4 reflectance (0.76–0.90 μm) and ρ_7 = band 7 reflectance (2.08–2.35 μm). Because the post-fire scene contained a few distinct clouds that covered four control sites, we employed a gap-filling technique using NBR from an additional scene from 5 October 2011 (path 67, row 15). To account for seasonal phenology effects, domain-wide differences in NBR were first subtracted from the ancillary image (figure 1(A)). dNBR was calculated as

$$\mathrm{dNBR} = \mathrm{NBR}_{\mathrm{pre-fire}} - \mathrm{NBR}_{\mathrm{post-fire}}.$$

Site-level dNBR values were calculated from the average of 30 m pixels that contained our 2 m × 30 m transects (typically 2 to 3 pixels). Since sites were at least 90 m apart, no pixels covered more than one site.

As an additional metric of severity, we measured the composite burn index (CBI) for each site as detailed in Rogers *et al* (2014). The CBI is a rapid visual characterization of fire severity based on five forest strata (Kasischke *et al* 2008). We chose to measure CBI because it is a widely used metric in both research and fire management communities. We used a modified CBI protocol to account for the shorter stand structures of interior Alaska (Kasischke *et al* 2008). We assessed CBI for the entire 2 m × 30 m transect.

Soil microbial biomass

Active soil microbial biomass was measured using the substrate-induced respiration (SIR) method (Anderson and Domsch 1978). Because SIR measures respiration in response to labile substrate addition, SIR primarily characterizes the biomass of saprotrophic microbes, and does not necessarily include biomass of mycorrhizal fungi. One-gram soil (fresh weight) was placed in an airtight 40 ml glass vial. Subsamples from the fibric and humic layers of each soil core were incubated separately. Soil samples were amended with 0.1 ml glucose solution (10 mg glucose g^{-1} soil), and incubated at 22 °C for 4 h shaking at 100 r.p.m (Lavoie and Mack 2012). Headspace gas samples were collected at 2 and 4 h and CO_2 concentrations were determined using an infrared gas analyzer (PP Systems EGM-4, Amesbury, MA, USA). We converted CO_2 respiration to microbial biomass C (C_{mic}) using the equation C_{mic} (μg C_{mic} g^{-1} soil) = (μl CO_2 g^{-1} soil h^{-1}) × 40.04 + 0.37 (Anderson and Domsch 1978). In previous work with soils from this region, we found that the SIR method gave similar values of μg C_{mic} g^{-1} soil as the chloroform fumigation method. We scaled microbial biomass to a ground area basis using soil bulk densities and horizon depths.

Soil basal respiration

One-gram soil (fresh weight) was placed in an airtight 40 ml glass vial. Soils were incubated at 10 °C (similar to *in situ* soil temperatures during the growing season) for 24 h. Microbial respiration of CO_2 was measured at 2, 4, and 24 h by drawing headspace air samples from the incubation vials and injecting each sample into an infrared gas analyzer. Soil basal respiration was calculated as the change in CO_2 concentration per g soil per hour.

DNA sequencing and analysis

To manage project scope and monetary costs, we constrained DNA sequencing to one soil horizon only. We selected fibric soils, because humic soils were present in only a subset of our sites. DNA was extracted from a 0.25 g subsample of each fibric soil sample using the PowerSoil DNA extraction kit (MoBio, Carlsbad, CA, USA). Three DNA extractions were performed for each sample. On each extraction, we amplified fungal 18S DNA following the procedure described in Holden *et al* (2013). The triplicates were then pooled within each sample. Sequencing was performed on a Roche 454 Gene Sequencer at the Environmental Genomics Core Facility at the University of South Carolina (Columbia, SC, USA). Following pyrosequencing, DNA sequences were demultiplexed, quality filtered, and processed using QIIME v1.7.0 (Caporaso *et al* 2010). Low quality sequences were removed using QIIME's default settings. We obtained 10 427 high-quality DNA sequences, with an average of 193 sequences per soil sample. Samples with fewer than 100 quality DNA sequences were excluded from further analyses, and all remaining samples were rarefied to a sequencing depth of 100 sequences per sample prior to downstream analyses. This number of sequences per sample is not sufficient to fully characterize fungal diversity in our soil samples and thus we do not present analyses of fungal community composition. However, previous work suggests that this level of sequencing effort will allow us to identify the most abundant fungal taxa in each soil sample (Rousk *et al* 2010). DNA sequences were deposited in the National Center for Biotechnology Information Sequence Read Archive (accession number SRX376967).

DNA sequences were binned into phylotypes (hereafter, 'taxa') with 97% sequence similarity using the USEARCH algorithm (Edgar 2010). The 97% similarity cut-off corresponds to approximately the family level for the 18S region (Anderson *et al* 2003). USEARCH filters low abundance taxa and performs de novo and reference-based chimera detection using the program UCHIME (Edgar *et al* 2011). For reference-based chimera detection, we used a manually curated database of 18S sequences of fungi submitted to GenBank as part of the Assembling the Fungal Tree of Life (AFTOL) project (Lutzoni *et al* 2004).

Sequences identified as chimeric by both the de novo and reference-based detection methods were removed from all further analyses. We obtained 173 unique taxa. The most abundant sequence in each taxon was selected as its representative sequence. The closest taxonomic identity for each representative sequence was assigned by BLAST comparison against sequences contained within the aforementioned AFTOL database and GenBank (accessed 12/2015). Non-fungal taxa were removed from the dataset, and our final dataset included 156 unique fungal taxa.

Fungal taxa were assigned to putative functional groups (i.e., free-living filamentous, lichen, mycorrhizal, pathogen, or yeast) if they matched a family in which at least 90% of described taxa belonged to a single functional group, as reported in the FunGuild database (supplementary table S2) (Tedersoo *et al* 2010, Clemmensen *et al* 2013, Nguyen *et al* 2015). Ninety-eight taxa could not reliably be placed into a single functional group and were listed as unknown.

We calculated the 'fire severity tolerance' for each taxon as the average dNBR of the sites in which it was observed. We computed fire severity tolerance based on (1) presence/absence data and (2) weighted by the relative abundance of the taxon at the sites in which it was observed. Although these values were similar for most fungal taxa, to be conservative we present the fire severity tolerance based on the presence/absence data.

Statistics

We used analysis of variance (ANOVA) to detect significant differences in microbial biomass and basal respiration between burned and unburned soil samples. To test for significant relationships between fire severity and soil microbial biomass and respiration in burned black spruce stands, we used ordinary least squares regression with dNBR as the independent variable, and microbial biomass or basal respiration as the dependent variables. We did not perform regressions on data from burned white spruce-aspen stands given the low number of burned sites ($n = 4$). In all cases, fibric and humic soil data were analyzed separately. Microbial biomass, microbial respiration, and dNBR data were ranked prior to statistical analysis to minimize any undue influence of outliers.

We used analyses of variance to determine whether fire severity tolerance differed significantly among fungal phyla or among functional groups. We used phylum or functional group as the independent variable and fire severity tolerance (i.e., average dNBR) as the dependent variable. The unit of observation was individual fungal taxa. We used a Tukey post hoc test to detect pairwise differences between phyla or functional groups. Statistical analyses were conducted using Systat 13 (SPSS 2009).

Results

Remote sensing of fire severity

The Gilles Creek fire burned at a range of fire severities (figure 1(B)). The distribution of dNBR is bimodal, largely because low-lying black spruce and willow shrub stands in the Southern portion of the fire scar burned at low severity or were left unburned. Burned black spruce stands had a mean dNBR of 457. The mean dNBR in burned white spruce-aspen stands was 379.

Microbial biomass and soil basal respiration

Soil microbial biomass in fibric soil was significantly reduced in burned stands compared to unburned stands: by 53% in black spruce stands and 47% in white spruce-aspen stands (P(black spruce) = 0.0004, P(white spruce) = 0.013; figure 2(A)). In burned black spruce stands, we found that fire severity was negatively related to microbial biomass ($r^2 = 0.483$, $P = 0.002$; figure 2(B)). This pattern was conserved when microbial biomass was scaled to a ground area basis (supplementary figure S2). Likewise, we observed that soil basal respiration in fibric soil was significantly lower in burned stands (P(black spruce) = 0.003, P(white spruce) = 0.024; figure 2(C)), and basal respiration declined as a function of dNBR in burned black spruce stands ($r^2 = 0.544$, $P = 0.001$; figure 2(D)). Because our white spruce-aspen stands experienced a narrow range of fire severity—between 450 and 650 dNBR—we were unable to detect significant relationships between dNBR and microbial biomass or soil basal respiration there (supplementary figure S3). Microbial biomass and soil basal respiration in humic soil did not differ significantly between burned and unburned forests, and did not vary significantly with fire severity (supplementary figure S4).

Comparison with the CBI

In burned sites, the CBI was strongly positively correlated with dNBR (Rogers *et al* 2014). Accordingly, we observed comparable patterns between microbial biomass and soil basal respiration and CBI (figure 3).

Fire severity tolerance

Fungal phyla differed in their fire severity tolerance (ANOVA, $F_{6,114} = 2.827$, $P = 0.013$; figure 4(A)). Ascomycota and Basidiomycota were the two most abundant fungal phyla in our sequence data set, representing at least 43.6% and 27.6% of fungal taxa, respectively. Ascomycota displayed a significantly greater fire severity tolerance than did Basidiomycota ($P = 0.007$; figure 4(A)). The remaining phyla made up a small fraction of fungal taxa (combined relative abundance of 6.4%) and did not differ significantly in their fire severity tolerance (figure 4(A)).

Fungal functional groups also differed significantly in their fire severity tolerance (ANOVA, $F_{4,51} = 2.992$, $P = 0.027$; figure 4(B)). Specifically,

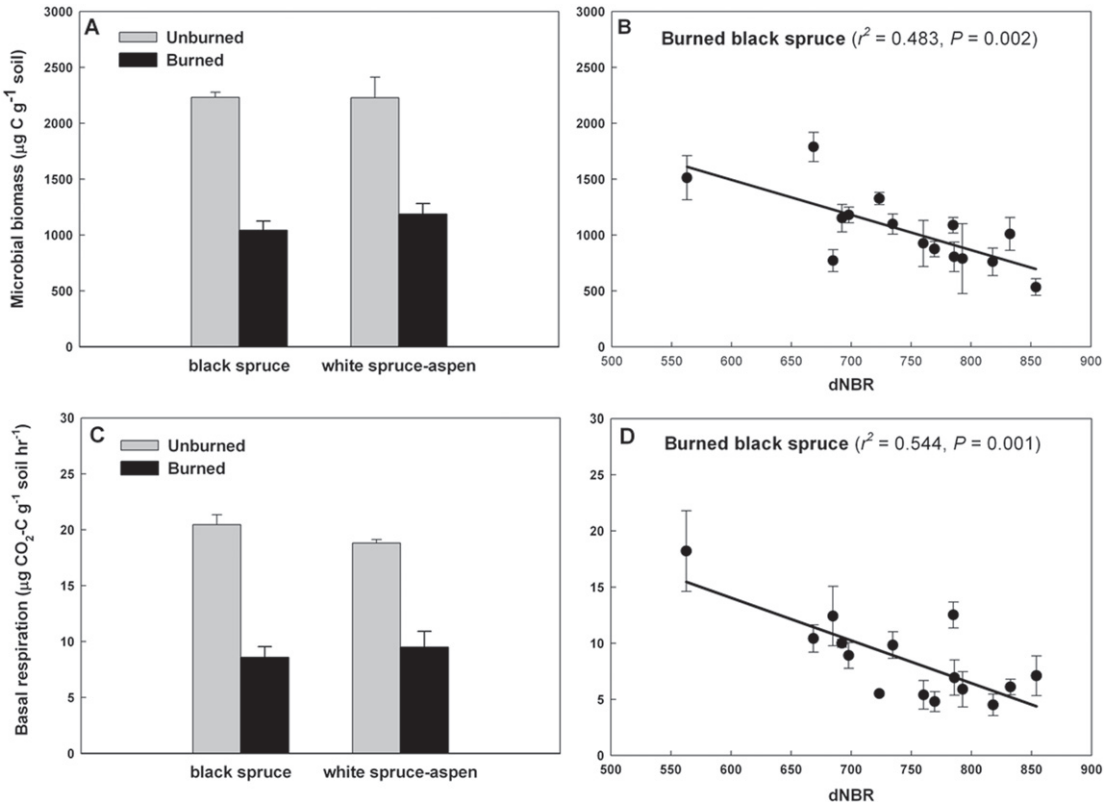

Figure 2. The effect of fire severity on fibric soil microbial biomass and basal respiration. In both black spruce and white spruce-aspen stands, microbial biomass (A) and basal respiration (C) were significantly lower in burned soils compared to unburned soils (microbial biomass: P(black spruce) $= 0.0004$, P(white spruce-aspen) $= 0.013$; basal respiration: P(black spruce) $= 0.003$, P(white spruce-aspen) $= 0.024$). Columns represent the mean value for all burned (n(black spruce) $= 15$, n(white spruce-aspen) $= 4$) and unburned (n(black spruce) $= 4$, n(white spruce-aspen) $= 3$) sampling locations. Microbial biomass and respiration declined with increasing fire severity in burned black spruce stands (B), (D). Symbols in (B) and (D) represent the mean of 3 soil cores from each burned black spruce stand. Lines are best-fit regressions for burned black spruce stands ($n = 15$). Error bars are ± 1 SEM.

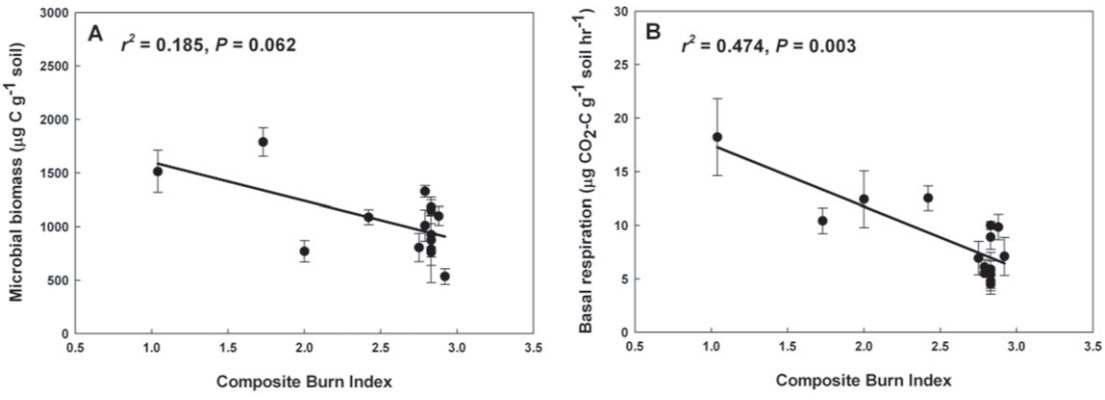

Figure 3. Microbial biomass (A) and basal respiration (B) in burned black spruce stands as a function of the Composite Burn Index (CBI), a visual ground-level assessment of fire severity. Black symbols represent the mean of 3 soil cores from each burned black spruce stand ($n = 15$). Lines are best-fit regressions. Error bars are $\pm$1SEM. We observed comparable microbial biomass and respiration responses to increasing fire severity when fire severity was measured visually.

mycorrhizal fungi exhibited significantly lower fire severity tolerance than did free-living filamentous fungi ($P = 0.043$; figure 4(B)). Free-living filamentous fungi were the most diverse functional group across all samples in our study (35 taxa), followed by mycorrhizal fungi (4 taxa), pathogens (9 taxa), yeasts (3 taxa), and lichenized fungi (5 taxa).

Discussion

Climate warming will likely increase the frequency, extent, and severity of wildfires in boreal forests. By combining remote sensing measurements of fire severity with field sampling of fungi (sensu Hewitt *et al* 2013), our study provides evidence that fire

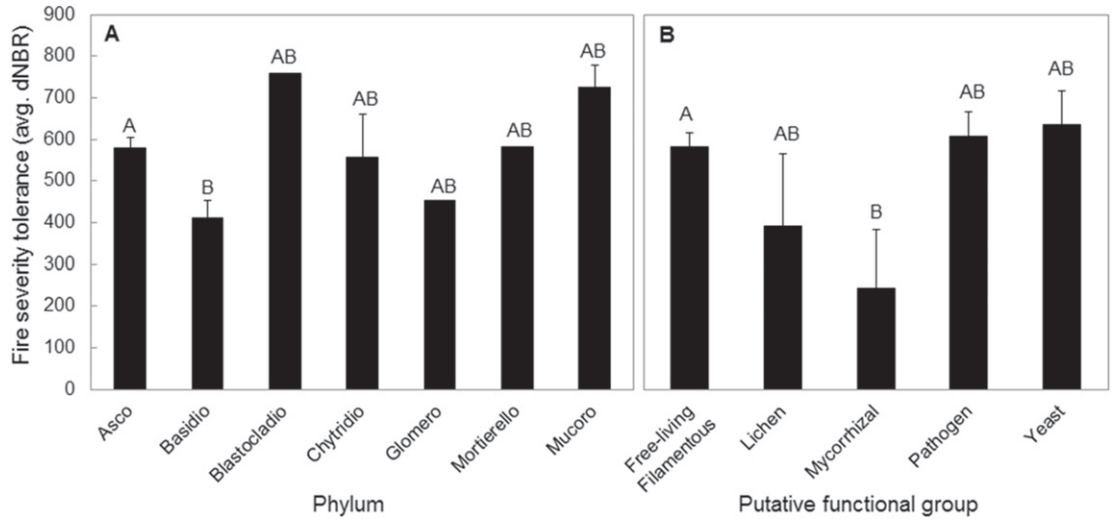

Figure 4. Fire severity tolerance for fungal phyla (A) and fungal functional groups (B). For each fungal taxon, fire severity tolerance was calculated as the average dNBR of all sites at which that taxon was detected. Fire severity tolerance differed significantly among fungal phyla ($P = 0.013$) and functional groups ($P = 0.027$). Different letters indicate significant differences in fire severity tolerance based on Tukey post hoc tests ($P < 0.05$). Error bars are ± 1 SEM.

severity controls soil microbial responses to boreal forest fires. We found that unburned boreal forest stands had some of the highest levels of soil microbial biomass and basal respiration within this study. Black spruce stands that burned at low severity had intermediate levels of microbial biomass and respiration. In contrast, stands that burned at higher severity had the lowest levels of microbial biomass. In addition, mycorrhizal taxa and members of the Basidiomycota were especially sensitive to fire severity. Severely burned stands (dNBR values >670) accounted for approximately 18.7% of the fire scar (figure 1(B)). These findings are consistent with our prediction that more severe fires would cause greater reductions in soil microbial biomass and shifts in fungal community composition.

In fibric soils, the observed decrease in microbial biomass with increasing dNBR may be attributable to higher soil temperatures during the fire. Soil heating trials have demonstrated that the survival of soil microbes decreases with increasing temperature, with complete sterilization around 200 °C (Dunn *et al* 1985, Serrasolsas and Khanna 1995, Debano *et al* 1998). Although we were unable to measure soil temperatures during the fire, it is probable that higher dNBR values corresponded to hotter fires that burned deeper into soils and increased soil temperatures more than low severity burns. dNBR has previously shown promising explanatory power for surface organic char in interior Alaska (Hudak *et al* 2007) and other metrics of fire severity (Epting *et al* 2005, Allen and Sorbel 2008, Hall *et al* 2008, Verbyla and Lord 2008, Barrett *et al* 2010, 2011, Soverel *et al* 2010), though not in all cases (Hoy *et al* 2008, Murphy *et al* 2008).

Previous studies that visually measured fire severity lend support to our finding that high severity fires elicit greater reductions in soil microbial biomass than low severity fires (Bergner *et al* 2004). Furthermore, soil invertebrates display similar declines in abundance with increasing fire severity (Wikars and Schimmel 2001, Malmström 2010). In humic soils, microbial biomass was not affected by burning or fire severity, potentially because these deeper soils were buffered from temperature changes during the fire (Certini 2005).

Soil basal respiration exhibited a similar response to fire severity as microbial biomass, with greater reductions in higher severity sites. These findings are not in agreement with hypothesized post-fire increases in microbial decomposition from classic ecosystem theory of secondary succession (Chapin *et al* 2011, Harmon *et al* 2011). Nevertheless, they are consistent with recent studies reporting that microbial respiration decreases or shows no change following boreal forest fires (Goulden *et al* 2011). Post-fire microbial respiration may have been limited by low microbial biomass, low water availability, or low soil C quality (Dooley and Treseder 2012).

An important consideration is that we measured microbial respiration in the laboratory under standardized conditions. Soil temperatures during the growing season have been found to increase by approximately 5 °C following boreal forest fires (Liu *et al* 2005). Assuming a Q_{10} value of ~2 for microbial respiration (Zhou *et al* 2009), soil temperature increases of this magnitude could substantially stimulate microbial respiration during the growing season. Therefore, we cannot rule out that higher *in situ* soil temperatures in burned stands might increase microbial respiration when measured in the field. However, given the observed reduction in soil microbial biomass, any increases in microbial respiration would

have to result from large increases in mass-specific respiration rates of soil microbes.

In addition to altering microbial biomass and basal respiration, fire severity differentially affected specific fungal groups. Previous studies have shown that fire severity can influence fungal communities in the Arctic (Hewitt *et al* 2013) and bacterial communities in temperate forests (Weber *et al* 2013). Our study suggests that fire severity can alter fungal communities in boreal forests as well. More severe burns tended to eliminate mycorrhizal fungi and basidiomycetes to a greater extent than other functional groups and phyla. Tree survival was low in the high severity burns (supplementary figure S5), which may have limited the availability of mycorrhizal host plants. In our study, most mycorrhizal taxa were ectomycorrhizal (supplementary table S2). Other studies have reported that ectomycorrhizal fungi are negatively affected by boreal forest fires, and this group can require up to 12–17 years to return to pre-fire abundance (Treseder *et al* 2004, Holden *et al* 2013). The current study expands on these findings by demonstrating that post-fire reductions in mycorrhizal fungi are contingent on fire severity.

The sensitivity of soil microbes to fire severity may affect C storage in boreal forests and influence feedbacks between increased wildfire activity and climate warming. We found that high severity burns affected taxa of the Basidiomycota more negatively than those in other phyla. The Basidiomycota includes saprotrophic fungi with well-developed capacities to degrade recalcitrant C compounds (Floudas *et al* 2012, Riley *et al* 2014). Our laboratory incubations indicated that in the short term, the biomass and respiration of saprotrophic microbes showed the greatest declines following higher severity fires. Reductions in the biomass of saprotrophic microbes after high severity fires likely decrease the rate of soil organic matter decomposition, slow the transfer of C from boreal forests soils to the atmosphere, and constitute a negative feedback to climate warming.

On the other hand, mycorrhizal fungi contribute to long-term C accumulation in boreal forest soils by facilitating the transfer of atmospheric C to soil and producing C compounds with long residence times in soil (Clemmensen *et al* 2013). Thus, reductions in mycorrhizal fungi after high severity fires may slow the rate of soil C accumulation in boreal forests and constitute a positive feedback to warming. High severity fires also promote increased deciduous tree cover in boreal forests, which has a biophysical cooling effect (Rogers *et al* 2013). Ultimately, the net climate feedback arising from increased boreal forest fire severity will likely be a balance between increased C and aerosol emissions from the fire itself, a decline in the biomass and respiration of saprotrophic microbes, potential decreases in soil C accumulation that result from reductions in mycorrhizal fungi, and the biophysical cooling effect associated with increased deciduous tree cover (Beck *et al* 2011). Potential positive and negative feedbacks between increased fire severity and climate warming that are mediated by soil microbes are not well accounted for in current Earth system models.

The results of our study should be considered with several caveats in mind. First, we sampled from a single fire scar in interior Alaska. Our findings may not be applicable to all boreal forest ecosystems, and may be particularly relevant for relatively dry upland boreal forests represented by this fire scar. Moreover, we sampled a limited the number of low severity burned black spruce stands. A larger sample size of low severity black spruce stands would have improved our ability to draw more precise inferences about the response of soil microbes across the lower end of the severity gradient. Nonetheless, our study suggests that fire severity can influence microbial dynamics two years after the fire, with potential consequences for carbon fluxes in that time frame. Longer-term effects are more difficult to predict, although the chronosequence study by Holden *et al* (2013) noted that fungal abundance, fungal community composition, and litter decomposition rates required at least 12 years to recover from fire in this system. Finally, we did not sample fungal community composition in humic soils. Given that microbial biomass and soil basal respiration did not change significantly with fire severity in that layer, it is possible that fungal community composition was likewise unaffected.

In conclusion, we found that fire severity controlled soil microbial biomass and basal respiration following boreal forest fires, and differentially affected fungal groups. High severity burn sites exhibited greater reductions in microbial biomass and respiration than did low severity burn sites. Fire severity has previously been shown to influence post-fire plant communities in boreal forests (Johnstone *et al* 2010). Our study provides evidence that fire severity also regulates responses of fungal groups, with mycorrhizal fungi and Basidiomycota displaying less tolerance for high fire severity. The sensitivity of fungal groups to fire severity may influence soil C storage in boreal forests and alter feedbacks between increased wildfire activity and climate warming, but these feedbacks are not well represented in current Earth system models. Our study has also demonstrated how remote sensing data can be used to scale up field studies on soil microbes and soil C dynamics following boreal wildfires. More broadly, remote sensing can be used to characterize other variables that are of interest to microbial ecologists, and further collaborations between microbial ecologists and the remote sensing community are likely to benefit studies on the abiotic drivers of soil microbial communities.

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