**Decreases in soil moisture and organic matter quality suppress microbial
decomposition following a boreal forest fire**

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ABSTRACT

Climate warming is projected to increase the frequency and severity of wildfires in boreal forests, and increased wildfire activity may alter the large soil carbon (C) stocks in boreal forests. Changes in boreal soil C stocks that result from increased wildfire activity will be regulated in part by the response of microbial decomposition to fire, but post-fire changes in microbial decomposition are poorly understood. Here, we investigate the response of microbial decomposition to a boreal forest fire in interior Alaska and test the mechanisms that control post-fire changes in microbial decomposition. We used a reciprocal transplant between a recently burned boreal forest stand and a late successional boreal forest stand to test how post-fire changes in abiotic conditions, soil organic matter (SOM) composition, and soil microbial communities influence microbial decomposition. We found that SOM decomposing at the burned site lost 30.9% less mass over two years than SOM decomposing at the unburned site, indicating that post-fire changes in abiotic conditions suppress microbial decomposition. Our results suggest that moisture availability is one abiotic factor that constrains microbial decomposition in recently burned forests. In addition, we observed that burned SOM decomposed more slowly than unburned SOM, but the exact nature of SOM changes in the recently burned stand are unclear. Finally, we found no evidence that post-fire changes in soil microbial community composition significantly affect decomposition. Taken together, our study has demonstrated that boreal forest fires can suppress microbial decomposition due to post-fire changes in abiotic factors and the composition of SOM. Models that predict the consequences of increased wildfires for C storage in boreal forests may increase their predictive power by incorporating the observed negative response of microbial decomposition to boreal wildfires.

Keywords: boreal forest; decomposition; forest fire; microbial respiration; reciprocal transplant; soil microbial community

1. INTRODUCTION

The soils of boreal forests store an estimated 150–191 Pg carbon (C), which accounts for approximately 20% of global soil organic C (Jobbagy and Jackson, 2000; Tarnocai et al., 2009). Given the large amount of C stored in the soils of boreal forests, there is substantial interest in predicting the impact of climate warming on soil C stocks in this region. Surface temperatures in boreal ecosystems have increased by approximately 2°C in the past 100 years, and these ecosystems are anticipated to warm by an additional 3–8°C in the next century (IPCC, 2013; Wendler and Shulski, 2009). One anticipated consequence of climate warming in boreal forests is an increase in wildfire activity.

Fires are a chronic global disturbance in boreal forests, but North American and Eurasian boreal forests experience distinct fire regimes. In North America, boreal forest fires are typically high-intensity crown fires that kill most trees, combust organic matter in surface soils, and initiate century-long vegetation succession. In contrast, Eurasian boreal forests fires are typically low-intensity surface fires that do not kill healthy trees (de Groot et al., 2013a; Rogers et al., 2015; Wooster and Zhang, 2004). Climate warming and summer drought are predicted to shift boreal forest fire dynamics in North America to a fire regime characterized by a greater number of extreme fire years with larger fires that burn at higher severity (de Groot et al., 2013b; Gillett et al., 2004; Turetsky et al., 2011). Models of future wildfire activity predict that the burned area in North American boreal forests could increase 2–5 times by the end of the 21st century (Balshi et al., 2009; Euskirchen et al., 2009; Flannigan et al., 2005). Increases in boreal wildfire activity

that result from climate warming may alter soil C stocks in boreal forests through direct and indirect mechanisms. Combustion of surface soils is a direct mechanism through which boreal forest fires alter soil C stocks. Indirectly, longer term changes in soil C stocks that result from increased boreal forest fires will be primarily mediated by post-fire changes in microbial decomposition.

Microbial decomposition governs the amount of soil C stored in an ecosystem, and the rate of decomposition is regulated by abiotic factors (i.e., temperature, moisture), the quantity and quality of soil organic matter (SOM) available for decomposition, and the soil microbial community (Aerts, 1997; Cornwell et al., 2008; Prescott, 2010; Swift et al., 1979). Classic ecosystem theory of secondary succession predicts that microbial decomposition increases following boreal forest fires (Chapin et al., 2011b; Harmon et al., 2011). Hypothesized post-fire increases in microbial decomposition are based on two critical assumptions. First, boreal forest fires create abiotic conditions that are more favorable to decomposition than the pre-fire abiotic conditions. Second, boreal forest fires increase the pool of labile C that is available to decomposer microbes. One estimate of microbial decomposition following a boreal forest fire concluded that the post-fire stimulation of microbial decomposition released as much C to the atmosphere as combustion emissions during the fire (Richter et al., 2000). Post-fire decomposition increases of this magnitude could substantially reduce soil C stocks and create a positive feedback between climate warming, wildfire occurrence, and C emissions from post-fire microbial decomposition.

However, hypothesized post-fire increases in microbial decomposition align poorly with the observed response of soil microbial communities to boreal forest fires. Numerous studies have found that boreal forest fires decrease soil microbial biomass (Dooley and Treseder, 2012;

Pietikainen and Fritze, 1995; Smith et al., 2008). Moreover, the recovery of microbial biomass following boreal forest fires can require more than a decade (Holden et al., 2013). Consistent with decreases in microbial biomass, the activity of microbial extracellular enzymes has been shown to decline following boreal forest fires (Waldrop and Harden, 2008). Furthermore, additional studies that have measured litter decomposition in burned and unburned forests have found slower rates of litter decay in recently burned stands (Brennan et al., 2009; Holden et al., 2013; Pietikainen and Fritze, 1993). These observations call into question hypothesized post-fire increases in microbial decomposition and the responsible mechanisms.

Microbial decomposition is predicted to increase following boreal forest fires in part because wildfires are assumed to create abiotic conditions that are favorable for decomposition. Cold temperatures and water-saturated soils in late successional boreal forests typically constrain the activity of decomposer microbes and lead to slow rates of decomposition (Van Cleve et al., 1983). Boreal forest fires of North America increase the amount of solar radiation that reaches the soil surface, because fires reduce canopy thickness and remove the insulating moss groundcover. As a consequence, growing season soil temperatures in the top 10 cm of soil in recently burned stands are typically 5–10°C higher than in late successional stands (Liu et al., 2005; Treseder et al., 2004). Post-fire increases in soil temperature can also be accompanied by decreases in soil moisture (Holden et al., 2013). Microbial decomposition is often highest at intermediate moisture levels, when soils are dry enough that oxygen availability is not limited but not so dry that microbes have insufficient access to water (Chapin et al., 2011a). Thus, post-fire changes in microbial decomposition may depend on the degree of soil drying following the fire.

Changes in the quantity and quality of SOM following boreal forest fires may also influence post-fire microbial decomposition. Here, we define SOM following Baldock and Broos (2011) as the sum of all natural and thermally altered biologically derived organic materials found in the soil or on the soil surface. Fires can potentially increase SOM through C inputs from root death and partially combusted aboveground vegetation. In addition, soil nutrients often increase after fires due to the deposition of nutrient rich ash on the soil surface (Harden et al., 2004; Wan et al., 2001). Increased nutrient availability in nutrient-poor boreal soils may alleviate microbial nutrient limitation and stimulate decomposition. The higher quality litter of early successional plants relative to late successional plants might also stimulate microbial decomposition. On the other hand, boreal forest fires usually combust feathermoss groundcover and the uppermost portion of the organic horizon and thus may actually reduce the pool of SOM that is available for decomposition (Turetsky et al., 2011). There is also evidence that fire combusts the more labile components of SOM and that the residual SOM is more enriched in complex molecules that are difficult for microbes to decompose (Czimczik et al., 2003; Harden et al., 2004; Neff et al., 2005). Finally, although early successional plant litter is often of higher quality, total plant litter inputs to soil are reduced in the first few years following boreal forest fires as vegetation recovers (Mack et al., 2008). The net response of microbial decomposition to post-fire changes in the quality and quantity of SOM is unclear.

In addition to abiotic factors and the characteristics of SOM, the soil microbial community exerts direct biotic control over decomposition. Indeed, recent studies have demonstrated that microbial community composition directly affects decomposition rates and CO₂ production (Allison et al., 2013; Reed and Martiny, 2013). Boreal forest fires have previously been shown to alter the composition of the soil microbial community. For example,

recently burned stands in interior Alaska were dominated by ascomycete fungi, while late successional stands had a high abundance of basidiomycete fungi (Holden et al., 2013). Bacterial community composition in boreal forests is also sensitive to disturbance by fire (Smith et al., 2008; Xiang et al., 2014). However, the consequences of post-fire changes in soil microbial communities for decomposition have not been previously investigated.

Overall, the response of microbial decomposition to boreal forest fires remains uncertain. This uncertainty hinders our ability to accurately predict C cycle and climate feedbacks that arise from increased wildfire activity (Allison and Treseder, 2011). Therefore, the goals of our study were to understand how microbial decomposition changes following high-intensity crown fires in boreal forests of North America and to examine the mechanisms that govern post-fire changes in microbial decomposition. We used a reciprocal transplant between a recently burned boreal forest stand and a late successional boreal forest stand to independently manipulate soil abiotic conditions, SOM, and the microbial community. We then measured the consequences for microbial decomposition. Contrary to classic ecosystem theory of secondary succession, but in line with the findings from recent studies, we hypothesized that post-fire changes in abiotic conditions would reduce the rate of microbial decomposition. In addition, we predicted that changes in SOM following boreal forest fires would negatively affect microbial decomposition. Finally, we expected that post-fire microbial community changes would influence decomposition.

2. MATERIALS AND METHODS

2.1. Study sites

Our study was conducted in a boreal forest ecosystem in interior Alaska near the Pogo Gold Mine in the Tanana Valley State Forest approximately 100 km east of Fairbanks. The local climate is cold and dry with a mean annual temperature of 2°C and a mean annual precipitation rate of 303 mm. Soils are primarily Inceptisols; permafrost is discontinuous in the region and was not present at the study sites.

We selected two study sites representative of a recently burned boreal forest stand and a late successional boreal forest stand. The recently burned stand (hereafter, burned site) was located within the Gilles Creek Fire scar (N 64°20.095', W 145°41.290'). The Gilles Creek fire was a lightning-caused crown fire that occurred from 26 May – 2 June 2010 and burned ~8000 ha. The Gilles Creek fire was characteristic of the high-intensity crown fires that occur in boreal forests of North America (Rogers et al., 2014). The dominant pre-fire vegetation in the fire scar was black spruce (*Picea mariana* B.S.P). The Gilles Creek fire burned at a range of fire severities, and our study site was located within a stand that experienced high fire severity (Rogers et al., 2014). At our study site, the fire caused complete stand mortality and combusted nearly 100% of tree needles, cones, fine branches, and understory vegetation. In addition, the fire combusted nearly 100% of feathermoss ground cover and burned into the organic soil horizon (Supplementary Table S1).

The late successional boreal forest stand (hereafter, unburned site) was located adjacent to the Gilles Creek fire scar (N 64°20.500', W 145°49.301'), and was selected to have similar climate, topography, potential biota, and parent material as the burned site. The unburned site had nearly 100% feathermoss groundcover, and the understory vegetation was dominated by deciduous shrubs, forbs, and graminoids (Holden et al., 2013). The unburned site did not burn in

the Gilles Creek fire because of a man-made firebreak. This firebreak was located ~1 km from our unburned study location.

2.2. Reciprocal transplant

We used a reciprocal transplant to test how post-fire changes in abiotic conditions, SOM composition, and soil microbial communities influence microbial decomposition following a boreal forest fire. We used “microbial cages” to independently manipulate the abiotic environment, the origin of SOM, and the origin of the soil microbial community. Microbial cages are similar to litterbags, but are constructed of nylon mesh with 0.45 μm pores (Millipore, Bradford, MA, USA). This pore size restricts the colonization of microbial cages by fungi and most bacteria from the environment, but allows for the passage of water and solutes. The efficacy of microbial cages has been demonstrated in prior studies (Allison et al., 2013; Reed and Martiny, 2013). Our experiment had 3 factors: abiotic environment (unburned or burned site), SOM origin (unburned or burned SOM), and soil microbial community origin (microbial community derived from unburned or burned site). These factors were manipulated in a fully factorial design, and we sampled microbial cages after 9, 12, and 24 months of decomposition. Each treatment combination was replicated 8 times per sampling date for a total of 192 microbial cages.

To manipulate the origin of decomposing SOM, we collected organic soil from the unburned and burned site in July 2011 (approximately 13 months after the fire). Soil organic matter was collected from 1 m $\times$ 1 m plots in 10 random locations at each site. At the unburned site, we collected the entirety of the fibric and mesic soil horizons, but we did not collect live or dead moss (hereafter, unburned SOM; Supplementary Table S1). At the burned site, we collected the residual fibric and mesic horizons that were left following the fire (hereafter, burned SOM;

Supplementary Table S1). This included SOM that had been charred in the fire and the underlying SOM that did not burn in the fire. The depth of burn varied across the burned site such that in some plots the fire combusted all of the fibric soil and in other plots there was unburned fibric soil. Our ten sampling locations captured this variation in the depth of burn. We choose to collect both charred SOM and the underlying unburned SOM from the burned site because we reasoned that this material together is primarily what fuels microbial decomposition following boreal forest fires. We estimate that ~50% of the SOM that we collected at the burned site had been charred in the fire. We refer to this material as “burned SOM” to indicate that it originated from the burned site and not because it was comprised completely of burned soil. Soil organic matter was collected by hand at each site, air dried, and homogenized by hand. Any sticks or rocks that were present in the SOM samples were removed.

We placed 2 g of dried SOM into 10 cm × 10 cm microbial cages. Microbial cages and SOM were sterilized with at least 22 kGy gamma irradiation. Sterility was verified by plating SOM on lysogeny broth and potato dextrose agar. Following sterilization, microbial cages were inoculated with soil microbes from either the unburned site or the burned site. Inoculum was prepared by mixing 1 g SOM in 1 L sterile deionized water and stirring for 5 minutes. Each microbial cage was inoculated with 1 ml of inoculum. We previously characterized the composition of the soil fungal community from the unburned and burned site, and we found that fungal communities between the two sites differed significantly in their proportional abundance of ascomycete and basidiomycete fungi (Holden et al., 2013).

Microbial cages were placed on the ground surface (i.e., not buried in the soil) in the unburned and burned site in 8 replicate blocks on 4 September 2011. Microbial cages were collected in batches of 64 on 9 May 2012, 29 August 2012, and 27 August 2013. Following

collection, we immediately measured the respiration of microbes decomposing SOM in the microbial cages (see section 2.4 below) and microbial cages were then placed on ice and transported to UC Irvine (Irvine, CA, USA). Microbial cages were stored at 4°C until processing. All microbial cages were processed within 72 hours of collection from the field.

2.3. Initial chemical composition of soil organic matter

We measured C and nitrogen (N) concentrations on 6 subsamples of unburned and burned SOM by combustion on an elemental analyzer (FlashEA 1112, Thermo Fisher Scientific, Waltham, MA, USA). In addition, we characterized the initial chemical composition of SOM from the unburned and burned site using solid-state ^{13}C nuclear magnetic resonance (NMR). For our ^{13}C -NMR work we used a Varian Infinity CMX 300 MHz NMR spectrometer at the William R. Wiley Environmental Molecular Sciences Laboratory at the Pacific Northwest National Laboratory. We obtained ^{13}C -NMR spectra for 3 subsamples of unburned and burned SOM. Each sample was packed in a 4-mm zirconia rotor and fitted with boron-nitride spacers and KEL-F (low carbon) caps. A ramped (^{13}C pulse) cross polarization magic angle spinning (CPMAS) pulse sequence was used. The contact time was 1 ms, the spinning rate was 10 kHz, and the decoupling field was 63-55 kHz. The ^{13}C chemical shifts were referenced to tetramethylsilane (0 ppm) using an external reference, hexametabenzene (HMB, 16.81 ppm). We took up to 50,000 scans for each sample. After Fourier transformation, we applied a line broadening of 100 Hz to all samples. The chemical composition of SOM can be inferred by dividing the ^{13}C -NMR spectra into seven chemical shift regions that correspond to seven functional groups (Baldock et al., 2004; Baldock et al., 1997) as Alkyl-C (0-45 ppm); N-alkyl, methoxyl (45-60 ppm); O-alkyl-C (60-95 ppm); di-O-alkyl (95-110 ppm); aromatic-C (110-160 ppm); phenolic (145-165 ppm); carboxyl-C (165-215 ppm). The proportion of C in each

functional group was computed by integrating the area under the individual peaks of the functional group region that was later divided by the total area under the entire spectrum (0-215 ppm) (Berhe et al., 2012; Swift, 1996; Waldrop et al., 2010). All spectra processing was performed using MestReC software (version 4.59, Universidad de Santiago de Compostela, Spain).

2.4. Microbial respiration

We used 0.5 L glass jars fitted with airtight sampling ports to measure the respiration of microbes decomposing SOM in each microbial cage. Immediately following collection, fresh plant litter and soil were gently removed from the exterior of the microbial cages, and microbial cages were incubated for 30 minutes. During the incubation we placed jars in a shallow trench in the organic horizon of the unburned or burned site in order to mimic the abiotic conditions experienced by microbial cages while in the field. After 30 minutes, headspace CO₂ concentrations were measured using an infrared gas analyzer (PP Systems EGM-4, Amesbury, MA, USA). We calculated microbial respiration as the change in CO₂ concentration over time ($\mu\text{g CO}_2\text{-C per g SOM per hour}$) with the initial CO₂ concentration being atmospheric (~395 ppm CO₂ at our study sites) and the final CO₂ concentration was measured after the 30 minute incubation.

2.5. Mass loss

Following collection, microbial cages were carefully examined for holes in the nylon mesh. Microbial cages that had been damaged during incubation in the field were excluded from further analysis. Damage to the microbial cages resulted primarily from UV degradation of the nylon mesh. All together, 8, 16, and 17 litterbags were discarded from the 9, 12, and 24 month collections, respectively. This represents 12.5%, 25.0%, and 26.6% of litterbags from each

collection date, respectively. The excluded litterbags were approximately evenly distributed among treatments (Supplementary Table S3). To measure mass loss, we determined the total wet mass of SOM in each bag. A subsample of SOM was dried at 65°C to constant mass and used to calculate moisture content and dry mass. Mass loss was determined as the difference between the initial dry mass and the final dry mass of SOM.

2.6. Microbial biomass

Active microbial biomass in microbial cages was measured using the substrate-induced respiration (SIR) method (Anderson and Domsch, 1978). A one-gram subsample of SOM (fresh weight) from each microbial cage was placed in an airtight 40 ml glass vial. 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 CO₂ concentrations were determined using an infrared gas analyzer. SIR responsive microbial biomass is expressed as µg CO₂-C per g SOM per hour.

2.7. Statistical analyses

We used Welch's *t* tests to detect significant differences in C, N, and percentage composition of chemical functional groups in unburned and burned SOM. The effects of abiotic environment, SOM origin, and microbial community origin on respiration, mass loss, moisture content of decomposing SOM, and microbial biomass were analyzed using a factorial mixed-model ANOVA with repeated measures (hereafter, overall ANOVA). The model included abiotic environment, SOM origin, microbial community origin, collection date, and their interactions as fixed effects. Subject nested within block was included as a random effect. We define subject as the set of 3 microbial cages with the same block, abiotic environment, SOM origin, and microbial community origin. Each subject was sampled once per sampling date. The

actual number of microbial cages per treatment per collection date varied from 5–8 because some microbial cages were damaged during incubation at the field sites. Therefore, significance tests were based on type III sums of squares to account for the unbalanced number of replicates (Hector et al., 2010; Shaw and Mitchell-Olds, 1993). If the fixed effects or their interactions were significant, we performed ANOVAs on each sampling date with block as a random effect (hereafter, post hoc ANOVA). If ANOVAs were significant, comparisons among means were analyzed by Tukey's HSD posthoc contrasts. Respiration data were square root transformed and moisture content data were arcsine square root transformed to improve normality and reduce heteroscedasticity. Statistical analyses were performed using the nlme and stats packages in the R software environment (R Core Development Team, 2011).

3. RESULTS

3.1. Abiotic environment effects

Overall, we found that post-fire changes in abiotic conditions had a negative effect on microbial decomposition. Soil organic matter decomposing at the burned site lost significantly less mass than SOM decomposing at the unburned site ($P = 0.031$ for abiotic environment effect, overall ANOVA; Table 1; Fig. 1a). After 24 months of decomposition, mass loss was $23.6\% \pm 0.7\%$ in the unburned site but only $16.3\% \pm 0.6\%$ in the burned site. In addition, the respiration of microbes decomposing SOM in microbial cages showed a significant abiotic environment by collection date interaction ($P = 0.028$, overall ANOVA; Table 1). Microbial cages decomposing at the burned site respired significantly less CO_2 than microbial cages from the unburned site after 9 ($P = 0.029$, post hoc ANOVA; Supplementary Table S2) and 24 ($P < 0.001$, post hoc ANOVA; Supplementary Table S2) months of decomposition. This effect was strongest after 24

months of decomposition, when respiration was reduced by 55.4% in burned site microbial cages. However, microbial respiration did not differ between the two sites after 12 months of decomposition (Fig. 2).

Similar to respiration, we found that the moisture content of decomposing SOM showed a significant abiotic environment by collection date interaction ($P < 0.001$, overall ANOVA; Table 1). At the 24 month collection, SOM at the burned site had 62.3% less moisture than SOM at the unburned site ($P < 0.001$, post hoc ANOVA; Supplementary Table S2; Fig. 3). At the 9 month collection in May 2012, SOM from both sites was relatively dry and did not differ significantly. In contrast, at the 12 month collection in August 2012, it rained on the day of sampling and the moisture content of decomposing SOM was relatively high and did not differ significantly between the two locations (Supplementary Table S2; Fig. 3).

The effect of abiotic conditions on soil microbial biomass was inconsistent throughout the course of the experiment. Microbial biomass did not differ between the unburned and burned site after 9 months of decomposition, but microbial biomass was significantly higher at the burned site after 12 months of decomposition ($P = 0.015$, post hoc ANOVA; Supplementary Table S2; Fig. 4a). On the other hand, microbial biomass was significantly higher at the unburned site after 24 months of decomposition ($P < 0.001$, post hoc ANOVA; Supplementary Table S2; Fig. 4a).

3.2. Soil organic matter effects

Soil organic matter from the unburned and burned site did not differ significantly in percentage C or N (%C: $t = 0.880$, $P = 0.405$; %N: $t = 1.302$, $P = 0.225$). In addition, we found no detectable differences in the chemical composition of unburned and burned SOM using ^{13}C NMR (Supplementary Fig. S1). Approximately 35% of unburned and burned SOM was

comprised of O-alkyl-C (Supplementary Fig. S1). Alkyl-C was the second most abundant chemical functional group, accounting for approximately 20% of SOM (Supplementary Fig. S1). Despite having no detectable differences in initial chemical composition, burned SOM (i.e., burned SOM and underlying unburned SOM collected from the burned site) overall had slightly, but significantly, lower moisture than unburned SOM ($P = 0.048$, overall ANOVA; Table 1; Supplementary Figure S2).

Although we did not detect differences in the initial chemical composition of SOM using ^{13}C NMR spectroscopy, we found some evidence that post-fire changes in SOM had a negative effect on microbial decomposition. For example, after 24 months of decomposition, burned SOM lost 18.2% less mass than unburned SOM ($P = 0.009$, post hoc ANOVA; Supplementary Table S2; Fig. 1b). In addition, the overall ANOVA indicated that there was a significant abiotic environment by SOM origin interaction ($P = 0.049$, overall ANOVA; Table 1). Specifically, we observed that burned SOM lost less mass than unburned SOM when both were decomposing at the unburned site (Fig. 1c). In addition, there was a strong effect of SOM origin on soil microbial biomass. Burned SOM had significantly lower microbial biomass than unburned SOM, and this pattern was consistent across each sampling date ($P < 0.001$, overall ANOVA; Table 1; Fig. 4b). However, we found no main effects or interactions of SOM origin on microbial respiration (Table 1).

3.3. Microbial community effects

There were no significant effects of microbial community origin on mass loss, respiration, moisture content, or soil microbial biomass (Table 1).

4. DISCUSSION

Climate warming will likely increase wildfire occurrence in boreal forests of North America, with uncertain consequences for microbial decomposition and soil C stocks (Turetsky et al., 2011). Our study is among the first to measure post-fire microbial decomposition of SOM in an Alaskan boreal forest. Contrary to predictions from classic ecosystem theory of secondary succession, we found that microbial decomposition was suppressed following a boreal forest fire. Furthermore, by independently manipulating abiotic conditions, the origin of SOM, and the origin of the soil microbial community, we were able to test the mechanisms that govern post-fire changes in microbial decomposition. Our results indicate that the rate of microbial decomposition is slower in the recently burned stand because of post-fire changes in abiotic conditions and the quality of SOM. We did not find evidence that changes in the composition of the soil microbial community that result from boreal forest fires influence post-fire microbial decomposition.

In support of our hypothesis that post-fire changes in abiotic conditions reduce the rate of microbial decomposition, we found that SOM decomposing at the recently burned site lost 30.9% less mass over the course of the experiment than SOM decomposing at the unburned site. Our data suggest that one abiotic factor that may constrain microbial decomposition in recently burned stands is water availability. For example, after 24 months of decomposition, we observed that SOM decomposing at the unburned site had more than twice the amount of moisture as SOM decomposing at the burned site. At our burned study site the fire combusted nearly 100% of the surface moss cover. After removal of this insulating moss layer, it is likely that soils in the burned stand dried out more quickly following precipitation events. Overall, we argue that soil microbes in the burned site were experiencing greater moisture stress. This assertion is supported by additional studies that have reported significant declines in soil moisture following boreal

forest fires (Harden et al., 2006; Holden et al., 2013; Waldrop and Harden, 2008). It is also important to note that the microbial cages in our study were placed on the ground surface and were thus quickly impacted by weather events, whereas SOM deeper in the soil profile might be more buffered from changes in the weather.

The respiration of microbes decomposing SOM in the microbial cages also suggests that water availability governs microbial activity following boreal forest fires. For example, we observed no difference in microbial respiration at the 12 month collection when both sites had a relatively high moisture content. On the other hand, the significant reduction in moisture at the burned site at the 24 month collection coincided with a greater than 50% drop in microbial respiration. Thus, even though recently burned boreal forest stands have higher soil temperatures (Liu et al., 2005), at our study site soil warming was accompanied by soil drying. Moisture availability appears to represent a greater constraint on microbial activity than soil temperature. This conclusion is consistent with a soil warming experiment located in a nearby mature boreal forest stand that observed moisture limitation of soil microbial activity with soil warming (Allison and Treseder, 2008). Moreover, soil moisture has previously been shown to govern microbial activity and litter decomposition in high latitude forests of North America (Brockett et al., 2012; Hackl et al., 2005; Prescott et al., 2004). Nevertheless, we cannot rule out that there may be additional unmeasured abiotic factors that differed between the unburned and burned site that are partially contributing to the patterns that we observed. Overall, our findings imply that we cannot accurately predict microbial decomposition rates in boreal forests from data on soil temperature alone.

We used ^{13}C NMR to characterize the molecular structure of unburned and burned SOM. This analysis indicated that approximately 60% of SOM from both sites was in alkyl-C and O-

411 alkyl-C functional groups. These functional groups correspond primarily to simple proteins,
412 lipids, and carbohydrates (Baldock et al., 2004; Baldock et al., 1992), and represent relatively
413 labile compounds that can be readily metabolized by microbes. The high proportional abundance
414 of labile compounds in SOM from both sites explains why we observed measurable mass loss of
415 SOM over the course of two years. However, as expected, SOM decomposed more slowly than
416 fresh plant litter, which typically loses 30–60% of its mass during the first year of decomposition
417 in boreal forests (Holden et al., 2013; Talbot and Treseder, 2012). We did not detect differences
418 in the abundance of chemical functional groups between unburned and burned SOM using ^{13}C
419 NMR, and SOM did not differ in total concentrations of C or N. This finding contradicts
420 previous studies that have reported decreases in C concentrations and changes in SOM chemistry
421 following boreal forest fires (Harden et al., 2004; Neff et al., 2005; Tas et al., 2014). One
422 important consideration is that our SOM sampling approach may have influenced our results. At
423 the burned site we chose to collect both burned SOM and the underlying unburned soil because
424 we reasoned that both of these materials are fueling microbial decomposition at the burned site.
425 The presence of unburned soil in our burned SOM sample might in part explain why we did not
426 observe significant differences in SOM chemistry between the two study sites. A second
427 consideration is that we collected SOM from the burned site approximately 13 months after the
428 fire. Given this time lapse, we may not have captured the more ephemeral soil changes that occur
429 following forest fires. For example, ash deposition on the soil surface can increase inorganic N
430 availability (Wan et al., 2001), but this increase is typically transient because recovering
431 vegetation and soil microbes can quickly assimilate this nutrient pulse. In the Gilles Creek fire
432 scar, the availability of NO_3^- returned to pre-fire levels within 3 months of the fire (Holden et al.,
433 2013). Therefore, our experiment captured the more long-lasting effects of fire on SOM rather

than the short-term effects. Similar studies comparing the decomposition rate of burned SOM collected at multiple depths and time points following a forest fire would advance our understanding of the effects of fire on SOM and the corresponding consequences for decomposition.

Although we did not detect differences in the chemical composition of SOM using ^{13}C NMR, we found some support for our hypothesis that changes in SOM following boreal forest fires negatively affect microbial decomposition. This effect was most evident after 24 months of decomposition, when burned SOM lost significantly less mass than unburned SOM. In addition, at the earlier stages of decomposition we observed that burned SOM lost less mass than unburned SOM when both were decomposing at the unburned site. Furthermore, burned SOM consistently had lower microbial biomass than unburned SOM.

There are several possible explanations for the observed negative effect of burned SOM on microbial decomposition. First, organic soil at the burned site was visibly charred from the fire, and this incomplete combustion very likely created refractory and oxidation-resistant C in SOM (González-Pérez et al., 2004). We may not have detected these compounds with ^{13}C NMR because we sampled the entirety of the fibric and mesic soil horizons at the burned site, but only ~50% of material was burned. Soil organic matter that remained unburned during the Gilles Creek fire may have diluted the signal from the charred SOM in our ^{13}C NMR analysis. Despite not being detected with ^{13}C NMR, any refractory and oxidation-resistant C in burned SOM may have had an inhibitory effect on microbial growth and decomposition. Second, we observed that burned SOM had significantly less moisture than unburned SOM, potentially because charring increases soil hydrophobicity (DeBano, 2000; O'Donnell et al., 2009). The lower moisture content of burned SOM may have exacerbated microbial moisture limitation at the burned site

and further suppressed decomposition. Overall, we found evidence that post-fire changes in SOM have a negative effect on microbial decomposition, but we were unable to identify the exact mechanism(s) through which post-fire changes in SOM suppress microbial decomposition. Post-fire changes in SOM and the consequences for microbial decomposition are an important topic for further research.

Contrary to our initial hypothesis that post-fire microbial community changes would influence decomposition, we observed no significant effects of microbial community origin on SOM mass loss or respiration. We previously demonstrated that soil fungal communities from the unburned and burned site differed in their relative abundance of ascomycete and basidiomycete fungi (Holden et al., 2013). However, these differences did not appear to affect the early stages of SOM decomposition. These findings imply that there may be some degree of functional redundancy among boreal soil fungi, and are consistent with the observation of functional redundancy from previous studies (Rousk et al., 2009; Setälä and McLean, 2004). It is also possible that, given a longer decomposition period, significant effects of fungal community composition would have emerged. We can also not rule out that there was migration of some bacteria from the environment into the microbial cages that affected decomposition rates. Previous decomposition experiments have found evidence for a “home field advantage” in which microbial communities decompose litter from their home site faster than litter from foreign sites (Ayres et al., 2009; Strickland et al., 2009). However, in our study we did not find any evidence for home field advantage. This discrepancy may stem from the fact that most studies that have found evidence for home field advantage have used plant litter types that vary substantially in their initial chemistry. Overall, in agreement with Cleveland et al. (2014), our data suggest that

abiotic factors and SOM quality are more important than microbial community composition in determining decomposition rates.

At the ecosystem level, it is important to consider the observed post-fire decrease in microbial decomposition relative to the amount of C emitted from soil combustion during the fire. A previous study in the Gilles Creek fire scar calculated that the fire emitted, on average, 1.36 kg C m^{-2} from soil combustion (Rogers et al., 2014). In comparison, at the 24 month collection date we observed a difference in microbial respiration between the unburned and burned site of $5.03 \mu\text{g CO}_2\text{-C g}^{-1} \text{ SOM hr}^{-1}$ (Fig. 2). Scaling this difference in respiration to a ground area basis using the site-wide values for soil bulk density and organic horizon depths presented in Rogers et al. (2014), this equates to a $116.94 \text{ mg C m}^{-2} \text{ hr}^{-1}$ reduction in microbial respiration at the burned site. Therefore, the observed reduction in microbial respiration is orders of magnitude smaller than soil combustion emissions during the fire. However, if the observed reduction in microbial respiration persists for several years of secondary succession, as suggested by Holden et al. (2013), then soil combustion emissions from the fire and post-fire reductions in microbial respiration might ultimately counterbalance one another. Year-round measurements of microbial respiration in unburned and burned boreal forest stands are needed in order to make direct comparisons between soil combustion emissions and post-fire changes in microbial decomposition.

The results of our study should be interpreted with several caveats in mind. For example, our study was conducted in a single boreal forest ecosystem and our fire treatment was not replicated. Thus, our findings may not be representative of all boreal forests. In particular, permafrost is discontinuous in our study area and permafrost was not present at our study sites. The presence of permafrost likely influences post-fire soil moisture and might moderate

microbial moisture limitation following boreal forest fires. Moreover, boreal forests underlain by permafrost generally burn at lower severity. Our study was also conducted following a high-intensity crown fire that is more characteristic of boreal forest fires in North America. It is possible that microbial decomposition would respond differently to the low-intensity surface fires that are characteristic of Eurasian boreal forests. Additional studies in a wide variety of fire scars across North American and Eurasia would further clarify the response of microbial decomposition to boreal wildfires. Our study was also conducted over the course of two years only, and a longer decomposition period might be required to observe all significant effects. Finally, we did not initiate our study until 13 months after the fire and our burned SOM samples contained both burned soil and the underlying unburned soil. This sampling scheme may have limited our ability to understand how post-fire changes in SOM chemistry affect microbial decomposition.

5. CONCLUSIONS

In conclusion, we found strong evidence that microbial decomposition was suppressed following a high-intensity crown fire in a boreal forest of interior Alaska. Although soil temperatures increase following boreal forest fires, our results indicate that microbial decomposition was inhibited because of post-fire decreases in soil moisture and the quality of SOM. These findings challenge the prediction from classic ecosystem theory of secondary succession that boreal forest fires stimulate microbial decomposition, and suggest there is not a positive feedback between climate warming, wildfire occurrence, and post-fire microbial decomposition in boreal forests of North America. Overall, the net effect of increased wildfires on soil C stocks in boreal forests will likely be a balance between increased combustion

emissions from fires and decreased C emissions from inhibited microbial decomposition following the fire. Therefore, Earth System Models that predict the impact of climate warming on C storage in boreal forests may need to account for the negative response of microbial decomposition to boreal forest fires despite increases in soil temperature.

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FIGURE LEGENDS

Figure 1. Percentage mass loss (mean $\pm$ SE) over time in response to abiotic conditions (A), SOM origin (B), and the interaction between abiotic conditions and SOM origin for the September 2012 sampling date (C). Asterisks (A-B) denote significant differences in percentage mass loss for a given date ($P < 0.05$ for post hoc ANOVA). Different letters (C) indicate significant differences in percentage mass loss among treatments ($P < 0.05$ for Tukey's HSD post hoc contrasts).

Figure 2. Microbial respiration (mean $\pm$ SE) over time in response to the abiotic environment. Asterisks denote significant differences in respiration between the unburned and burned site on a given date ($P < 0.05$ for post hoc ANOVA).

Figure 3. The moisture content of decomposing SOM (mean $\pm$ SE) over time in response to abiotic conditions. Asterisk denotes a significant difference in moisture content at the 24 month collection ($P < 0.05$ for post hoc ANOVA).

Figure 4. Soil microbial biomass (mean $\pm$ SE) over time in response to abiotic conditions (A) and SOM origin (B). Asterisks denote significant differences in microbial biomass on a given date ($P < 0.05$ for post hoc ANOVA).

TABLES

Table 1. Overall ANOVA statistics for factors affecting mass loss, microbial respiration, moisture content of decomposing SOM, and microbial biomass.

Factor	df	Mass loss		Respiration		Moisture content		Microbial Biomass	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Abiotic environment ^a (A)	1, 113	5.73	0.031	0.05	0.821	0.22	0.649	1.39	0.259
SOM origin ^b (S)	1, 113	0.73	0.396	0.23	0.633	3.99	0.048	20.85	<0.001
Microbe origin ^c (M)	1, 113	0.16	0.692	0.002	0.962	0.001	0.974	3.09	0.081
Collection date ^d (D)	2, 113	27.76	<0.001	4.04	0.021	474.70	<0.001	6.39	0.002
A × S	1, 113	3.96	0.049	0.001	0.988	2.46	0.120	0.68	0.412
A × M	1, 113	0.01	0.944	0.02	0.880	0.07	0.797	0.69	0.406
A × D	2, 113	1.47	0.233	3.70	0.028	100.37	<0.001	10.77	<0.001
S × M	1, 113	0.94	0.601	0.37	0.544	1.74	0.189	1.16	0.284
S × D	2, 113	3.71	0.028	1.64	0.200	0.91	0.408	1.81	0.181
M × D	2, 113	0.53	0.587	1.11	0.335	0.54	0.583	1.01	0.369
A × S × M	1, 113	1.88	0.173	0.01	0.939	1.74	0.190	0.37	0.544
A × S × D	2, 113	0.79	0.457	1.19	0.309	1.02	0.363	2.56	0.082
A × M × D	2, 113	0.02	0.976	0.68	0.508	0.38	0.685	0.38	0.686
S × M × D	2, 113	0.17	0.844	0.04	0.961	1.11	0.332	0.67	0.516
A × S × M × D	2, 113	0.47	0.626	0.02	0.984	0.64	0.528	0.88	0.417

Significant *P* values (< 0.05) are shown in bold

^a Abiotic environment refers to microbial cages decomposing at either the unburned or burned site

^b SOM origin refers to soil organic matter collected from either the unburned site or burned site

^c Microbe origin refers to soil microbial community inoculum derived from either the unburned or burned site

^d Litterbags were collected after 9, 12, and 24 months of decomposition

Figure 1

Figure2

Figure3

Figure4