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Fire severity mediates climate-driven shifts in understorey community composition of black spruce stands of interior Alaska

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Abstract

Question: How do pre-fire conditions (community composition and environmental characteristics) and climate-driven disturbance characteristics (fire severity) affect post-fire community composition in black spruce stands?

Location: Northern boreal forest, interior Alaska.

Methods: We compared plant community composition and environmental stand characteristics in 14 black spruce stands before and after multiple, naturally occurring wildfires. We used a combination of vegetation table sorting, univariate (ANOVA, paired *t*-tests), and multivariate (detrended correspondence analysis) statistics to determine the impact of fire severity and site moisture on community composition, dominant species and growth forms.

Results: Severe wildfires caused a 50% reduction in number of plant species in our study sites. The largest species loss, and therefore the greatest change in species composition, occurred in severely burned sites. This was due mostly to loss of non-vascular species (mosses and lichens) and evergreen shrubs. New species recruited most abundantly to severely burned sites, contributing to high species turnover on these sites. As well as the strong effect of fire severity, pre-fire and post-fire mineral soil pH had an effect on post-fire vegetation patterns, suggesting a legacy effect of site acidity. In contrast, pre-fire site moisture, which was a strong determinant of pre-fire community composition, showed no relationship with post-fire community composition. Site moisture was altered by fire, due to changes in permafrost, and therefore post-fire site moisture overrode pre-fire site moisture as a strong correlate.

Conclusions: In the rapidly warming climate of interior Alaska, changes in fire severity had more effect on post-fire community composition than did environmental factors (moisture and pH) that govern landscape patterns of unburned vegetation. This suggests that climate change effects on future community composition of black spruce forests may be mediated more strongly by fire severity than by current landscape patterns. Hence, models that represent the effects of climate change on boreal forests could improve their accuracy by including dynamic responses to fire disturbance.

Introduction

Climate in interior Alaska is warming as rapidly as any place on the planet, at twice the global average rate (ACIA 2005). Current effects of a warming climate in interior Alaska include permafrost degradation, wetland drying, and increases in the extent and severity of wildfire (Osterkamp & Romanovsky 1999; Hinzman et al. 2005; Kasischke & Turetsky 2006). These biophysical changes are expected to accelerate in the future, with potentially large effects on the structure and function of the boreal forest (Chapin et al. 2004). Thus, Alaska provides opportunities to study direct and indirect ecosystem response to

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warming. It also provides an opportunity to explore concepts and approaches that might prove valuable more broadly, as the effects of future warming become more pronounced in lower latitudes.

One significant projected effect of warming in interior Alaska is an increase in the frequency and severity of fires (Balshi et al. 2009). This change in fire regime is predicted to cause a switch in dominance from black spruce to more mixed-deciduous communities (Greene et al. 2007; Johnstone et al. 2010). Changes in the frequency and severity of fires could also alter the relative abundance and diversity of plant functional groups within black spruce communities by changing understorey species composition. Incorporating new understanding about the relative importance of pre-fire conditions, fire severity and post-fire environment on understorey species, particularly in response to an altered climate and fire regime, will improve our ability to model and predict vegetation responses.

Black spruce (*Picea mariana*) dominated stands are currently the most widespread forest type in the boreal forest of interior Alaska. Although understorey species in black spruce forests represent a small percentage of above-ground biomass, in northern latitudes, they account for a significant proportion of stand net primary productivity (Chapin 1983) and the majority of plant species diversity (Hollingsworth et al. 2006). Understorey species strongly influence the perpetuation of black spruce forests through their effects on physical environment and flammability (Roberts 2004; Nilssone & Wardle 2005). For example, thick *Sphagnum* spp. mats acidify the soil, insulate the ground to protect permafrost, increase water availability and sequester nutrients (Rochefort et al. 1990; Turetsky et al. 2010). In interior Alaska, black spruce forest succession and vegetation properties are tightly linked to fire disturbance due in part to the functional properties of black spruce (e.g. high flammability of the needles and post-fire seed dispersal from semi-serotinous cones), the rapid regeneration of many low shrubs associated with black spruce, and the accumulation of thick moss beneath black spruce canopies (Sigafoos 1957; Johnson et al. 2001). Black spruce stands typically experience stand-replacing fires that result in complete crown mortality, but variable organic matter consumption (Boby et al. 2010) and mortality of understorey plants (Viereck 1973). Establishment of overstorey species typically occurs within a decade after fire (Johnson 1992; Johnstone et al. 2004), but the influence of fire severity on the successional trajectory of understorey communities has not previously been studied.

Both physical environment and pre-fire community composition are likely to influence fire severity and post-fire succession. For example, fires burn more severely, remove more of the surface organic mat and expose mineral soil under dry weather conditions and in topographically dry sites. In turn, exposed mineral soil typically provides a more favourable seedbed for post-fire seedling establishment (Johnson 1992; Johnstone & Chapin 2006). In addition, morphological characteristics and life-history attributes of the pre-fire community influence fire severity through effects on site moisture, organic layer depth (Johnson 1992; Harden et al. 2006) and vegetation structure (Ryan 2002). Fire severity, in turn, affects patterns of plant mortality, post-fire regeneration and future stand characteristics (Johnstone et al. 2008). However, for the vast majority of naturally occurring fires, neither the pre- and post-fire community composition nor environmental characteristics are known and therefore cannot be used to evaluate their relative importance in determining the post-fire successional trajectory. Establishing the relationships between species composition, fire severity and site environment may enable us to identify the pre-fire characteristics that most strongly influence community successional trajectory.

In 2004 extensive wildfires burned 14 Alaskan black spruce stands that had previously been characterized both in terms of community composition and pre-fire environment (Hollingsworth et al. 2006). These stands burned under a range of fire severities, providing a unique opportunity to study relationships between fire severity, pre- and post-fire environmental conditions, pre- and post-fire community composition and community successional trajectories. Specifically, we were interested in: (1) describing changes in the post-fire environment as a result of wildfire; (2) describing the variation in species composition post-fire; (3) quantifying changes in species richness, growth form abundances and species abundances pre- to post-fire; and (4) determining the effect of pre-fire conditions, fire severity and post-fire conditions on post-fire plant community composition.

Methods

Site selection

In 2004, Alaska experienced the most extensive wildfires in recorded history. We sampled 14 black spruce-dominated sites that burned during these 2004 wildfires. These specific sites were chosen because they had been characterized *before* burning by Hollingsworth et al. (2006). The pre-fire sampling took place in 2001 and 2002. The study area, known as interior Alaska, is a region of discontinuous permafrost, with a continental climate and extreme temperatures. In Fairbanks, the average annual temperature is $-2.5°C$, the mean temperature in January is $-23.1°C$ and the mean temperature in July is $22.8°C$, based on temperature records from 1929 to 2000 (http://climate.gi.alaska.edu). The sites (designated 1–14) were

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dispersed across interior Alaska along three highways in three different wildfire complexes: the Taylor Highway (sites 1–8), the Dalton Highway (sites 9–10) and the Steese Highway (11–14) (Fig. 1). These sites burned between 19.06.2004 and 25.08.2004, ranged in elevation from 93–1022 m and varied in age between 66 years old and 176 years old. Pre-fire, these sites varied in black spruce basal area between 0.1 and 23.7 m^2 (Boby et al. 2010). We relocated all sites using GPS coordinates and a Trimble GeoExplorer 3.0 GPS unit and determined their burn severity (see details below) in early May 2005, as soon as the snow melted. Sites were then visited during mid-summer of 2005 and 2006 to observe short-term changes in species composition directly following wildfire. The original sites were variable in size, usually 50 m × 50 m, and were established using the centralized replicate sampling procedure (Mueller-Dombois & Ellenberg 1974). In 2005, a centre point was re-established at the exact pre-fire site centre for those sites where centre stakes had survived the fire. However, in four sites, the pre-fire centre stakes were not found, in three of these sites we located site boundary markers. Where we could not precisely relocate the centre stake or the fire had burned severely, we selected our centre point as close as possible to the original GPS location of that centre point (GPS accuracy of ± 5 m). Direct comparisons pre- to post-fire are very difficult in variable plot experimental designs. However, given the extremely low species richness of boreal forests (Chapin et al. 2004), and unpublished data (http://www.lter.uaf.edu/data_b.cfm) suggesting that species–area curves in black spruce communities peak between 15 m × 15 m plots and 50 m × 50 m plots, depending on topography, we felt confident that we were accurately capturing changes in species composition pre- to post-fire. Of the 14 sites chosen for the study, nine were classified as acidic black spruce/lichen (*Picea mariana/Cetraria islandica*) plant communities pre-fire. The remaining five sites were non-acidic (pH > 5.5) Black spruce/prickly rose/horsetail (*Picea mariana/Rosa acicularis/Equisetum* spp.) communities (Hollingsworth et al. 2006).

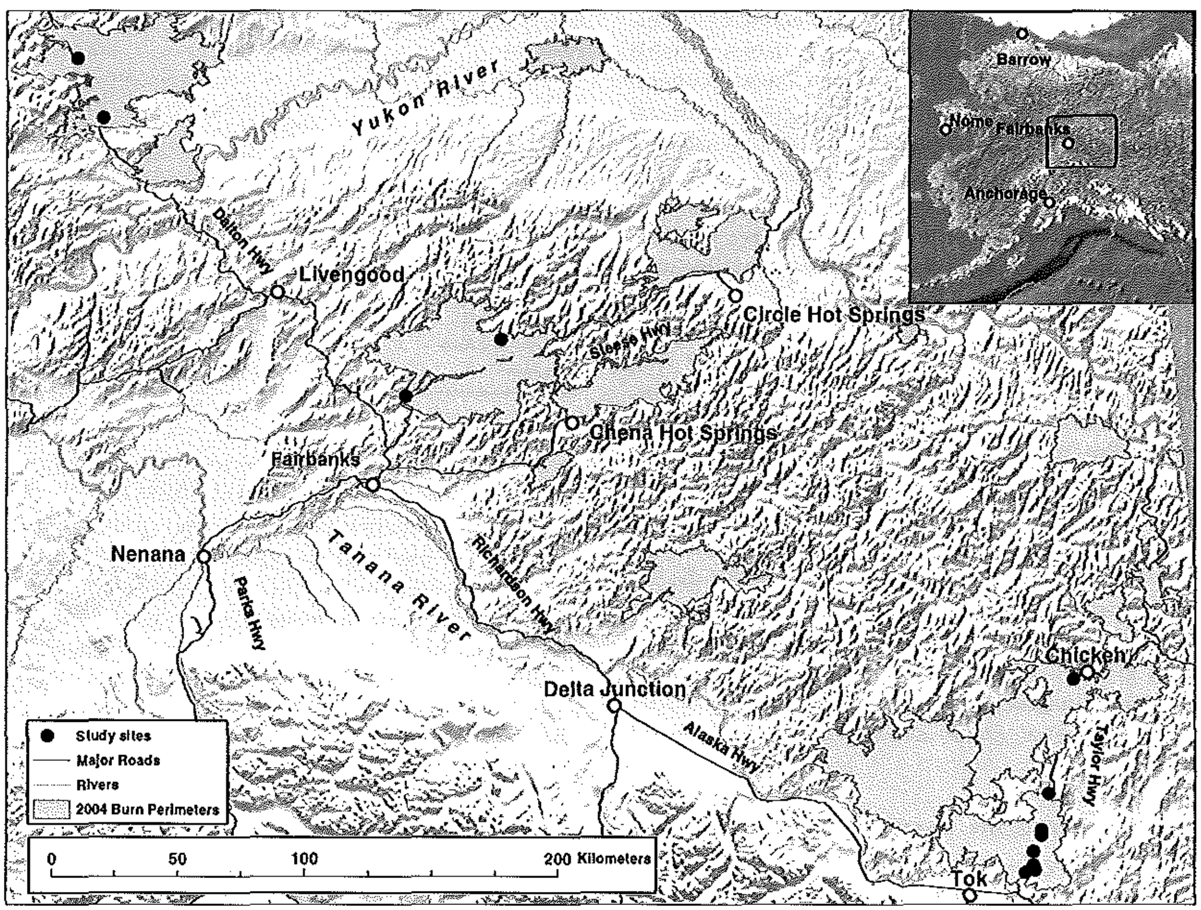

Fig. 1. The location and extent of the study area within Alaska (inset) showing the location of the sampled sites from the 2004 fires. Modified from Johnstone et al. (2010).

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Vegetation composition

To quantify vegetation composition after fire, a relève was conducted at each site in 30 m × 40 m plots during the summer of 2006, following the methods used to characterize pre-fire community composition in the same sites (Hollingsworth et al. 2006). The relève consisted of a list of all plant species present, both vascular and non-vascular, and an estimate of their percentage cover using the Braun-Blanquêt cover estimate scale (Braun-Blanquêt 1965). Each species encountered was recorded, and voucher specimens were collected and verified with the University of Alaska Fairbanks herbarium specimens. Vascular nomenclature follows Hultén (1968), with the exception of grasses (Welsh 1974) and members of the Salicaceae (Viereck & Little 1986). Non-vascular nomenclature follows Esslinger (1997) for lichens and Anderson (1990) and Anderson et al. (1990) for bryophytes.

Environmental and stand characteristics

Potential environmental variables correlated to pre-fire and post-fire community composition were collected during pre-fire community characterization and in mid-summer 2005, respectively (Table 1). The variables sampled included: slope, aspect, elevation, topographic position, site contour, parent material, micro-topography, surficial geology, presence of thermokarst, geomorphology, site moisture, mineral soil exposure (estimated across the entire site) and average organic layer depth (used to estimate fire consumption of the organic layer (Boby et al. 2010). In September, both pre- and post-fire, we took ten active layer measurements per site to estimate permafrost depth. Reconstruction of percentage organic loss (consumption) was estimated across all the 2004 fires based on adventitious roots of charred trees and is discussed fully in Boby et al. (2010). At each site, both pre- and post-fire, we dug a soil pit to a depth of 1 m or to frozen ground, and depth of soil layers was recorded. Soil samples were collected from the uppermost mineral horizon (usually between 30cm to 50cm below the soil surface for sites pre-fire and 10 cm to15 cm below the soil surface for sites post-fire). Mineral soils were sieved, dried at 50°C and characterized by the UAF Palmer Research Station in terms of mineral pH and texture (sand, silt and clay). For information on the scalars estimated pre-fire see Hollingsworth et al. (2006) and http://www.lter.uaf.edu/data_b.cfm.

Characterization of fire severity and site moisture

We characterized fire severity at each site using a composite burn index (CBI) (Key & Benson 2005) that estimates mortality and consumption of the canopy, tall shrub and ground layers. CBI is highly correlated with other measurements of fire severity such as residual organic matter and per cent combustion (Boby et al. 2010). Because 99% of each site experienced full canopy and tall shrub mortality, we used only the ground layer component of CBI to assign each site a fire severity rating (Johnstone et al. 2008). *Burn severity* at each site was rated as low, moderate or high (Table 1). *Site moisture* was determined through a combination of site topography, presence of permafrost and soil texture (Johnstone et al. 2008). First, using a previously established site moisture index based on site topography, we rated site moisture for each site. Then, site moisture was adjusted according to permafrost status at a site, where site moisture *increased* if shallow permafrost was present. Finally, site moisture was again adjusted based on the mineral soil texture at a site, where site moisture was *decreased* if shallow soils were sandy or gravelly (Johnstone et al. 2008). In this way, three

Table 1. Site variables measured, or estimated, and used in Pearson correlation coefficient analysis with DCA ordination axes. A value of "scalar" represents a categorical variable. na indicates that the variable was not measured or estimated. [1]Scalar defined in Johnstone et al. (2008). [2]Modified from Key & Benson (2005), where: Low severity = light char and/or less than 10% removal of the moss layer and low consumption of litter, fine, medium and heavy fuels). Moderate severity = moderate char and/or 10–50% removal of the moss layer, total consumption of litter and moderate char/consumption of fine, medium and heavy fuels). High severity = deep char and/or greater than 50% loss of the moss layer, complete consumption of litter, and high char/consumption of fine, medium and heavy fuels.

Environmental variable	Range pre-fire	Range post-fire
Site variables		
Age of oldest trees	66–176	na
Aspect	15–350	na
Elevation (m)	220–1022	na
Geomorphology	Scalar	na
Microtopography	Scalar	na
Presence of thermokarst	Scalar	Scalar
Topographic position	Scalar	na
Site contour	Scalar	na
Site moisture[1]	Scalar	Scalar
Slope (degrees)	1–12	na
Surficial geology	Scalar	na
Water flux	Scalar	Scalar
Soil characteristics		
% clay	5.6–49.2	2.4–22.4
% sand	0.24–77.2	16.8–52.2
% silt	9.3–62.0	35.4–70.8
Active layer depth (cm)	47.1– > 100	54.3– > 100
Organic layer depth (cm)	15.2–36.5	1.6–18.3
Parent material	scalar	na
Soil pH	4.11–6.72	4.6–6.1
Fire characteristics		
% Organics lost	na	31.7–89.5
Mineral exposure	na	Scalar
CBI score[2]	na	1.39–2.9

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variables (topography, permafrost status and soil texture) were incorporated into our site moisture classification.

Analytical methods

Changes in environment post-fire

We investigated changes in soil pH and site moisture pre- and post-fire at all the sites. These two environmental variables could be directly impacted by wildfire, and also indirectly affect post-fire vegetation patterns. Although site topography and soil texture will not change pre- to post-fire, permafrost status may, thus leading to changes in site moisture. We therefore also investigated changes in active layer depth pre- and post-fire. We used paired *t*-tests (SAS version 8, SAS Institute Inc., Cary NC, USA, 2000) to evaluate these changes.

Impact of fire severity and pre-fire environment on post-fire species composition

We performed detrended correspondence analysis (DCA) (PC-ORD version 5, MjM Software, Gleneden Beach, OR, USA, 2006) to evaluate the effects of fire severity and pre-fire site moisture on post-fire black spruce communities (67 species and 14 sites). Percentage of variance represented by the ordination axis was calculated by performing post-hoc tests using relative Euclidean distance analysis on the ordinated data. There were no sites with less than five species, and rare species were down-weighted. Ordination techniques are often used to describe patterns in multivariate dependent variables, such as species composition across multiple sites. In natural systems, where species composition and site factors are often dependent and environment cannot be controlled, correlation analysis is more appropriate than multiple regression, which assume a "response and predictor"-independent relationship (McCune & Grace 2002). Using Pearson correlation coefficients, we correlated ordination axes with 22 environmental variables (Table 1) and additional visual estimates of stand structure percentage seedlings, deciduous shrubs, evergreen shrubs, graminoids, forbs, mosses, lichens, litter, dead trees, rocks and water). These variables are different from the species compositional data because they are gross visual estimates of growth form percentage cover, and correlating them with species composition visually depicts the structure of sites. Important environmental variables were then visually interpreted with a biplot overlay, indicating the strength and direction of the correlations.

Changes in plant communities pre- to post-fire

We evaluated changes in plant communities at three scales: changes in individual species, change in growth forms and changes in overall species composition. Growth forms were defined as: evergreen shrubs, deciduous shrubs, graminoids, forbs, seedless vasculars, bryophytes and lichens, traditionally recognized by Arctic ecologists for predicting vegetation responses to ecosystem processes (Chapin et al. 1996).

We compared changes in species richness across all sites using paired *t*-tests (SAS version 8). We then evaluated changes in species abundance and frequency as a result of wildfire. The majority of this data set was non-normally distributed because not every species that occurred both pre- and post-fire occurred in every plot, or in the same plot pre- and post-fire. We therefore (1) dropped all species that did not occur both pre- and post-fire; (2) determined the remaining species that occurred in at least 60% of sites and were normally distributed; (3) compared the abundance values pre- and post-fire for those species using paired *t*-tests (SAS version 8); (4) with the remaining species that could not be analysed for changes in abundance, we corrected for the large number of zeros in the data by transforming all abundance data to presence (1) and absence (0); and finally (5) used a *G*-test (SAS version 8) to determine if there was a significant difference in the frequency before and after fire for these species.

We analysed growth form diversity of pre- and post-fire community composition in two ways: (1) overall growth form diversity based on species identity where each species was used only once regardless of how many sites in which it occurred or at what abundance, and (2) by looking at the change in species richness within each growth form pre- versus post-fire using site-specific data. We were not able to analyse changes in abundance of growth forms because each species cover is estimated based on Braun-Blanquét cover classes. The overall growth form diversity was analysed by grouping species into growth forms and then performing a paired *t*-test analysis in SAS version 8 on the number of species for each growth form pre- versus post-fire. We used ANOVA (JMP version 5, SAS Institute, Cary, NC, USA, 2001) to test for significant differences in growth form richness across fire severity levels. If there were significant changes in vegetation, we performed Tukey-Kramer post-hoc *t*-tests. Assumptions of ANOVA were met for these analyses.

We determined the overall change in species community composition within, as well as between, sites pre- to post-fire using a DCA ordination (PC-ORD V5) with 119 species and 28 sites. To determine the degree of change in vegetation composition experienced by an individual site pre- to post-fire, we determined the difference in ordination vector length for each site pre- to post-fire. Based on pre- and post-fire ordination scores, we calculated the vector length difference by using an individual site's pre-

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and post-fire ordination scores (X and Y scores) and subtracting the post-fire x and y coordinates from pre-fire coordinates. Values were then changed to absolute values. The difference in vector length value for each site was termed its "change in vector value," which described the degree of change in vegetation composition that the site experienced pre- to post-fire. The amount of vegetation composition change within a site could then be compared between sites, where the higher vector length change value reflected a greater change between pre- and post-fire community composition. To quantify this further, we used a two-way ANOVA (JMP 4.0) to test if there were differences in vector length between fire severity levels and pre-fire site moisture. If there were significant differences in vector length, we performed Tukey-Kramer post-hoc t-tests.

Results

Changes in post-fire environment

We found that, after fire, all sites decreased or did not change in mineral soil pH. In the non-acidic sites, mineral soil pH decreased significantly (pre-fire mean soil pH = 6.03 ± .34, post-fire mean soil pH = 5.63 ± .28, $P > 0.0001$). We did not find a correlation between pre-fire moisture and post-fire moisture. When pre- and post-fire site moisture classifications were compared, five sites remained at the same moisture classification, four sites were classified as drier and five sites were classified as wetter. Although not significant, we found that post-fire site moisture increased in sites that burned with high severity, whereas sites that burned with medium or low severity tended to decrease in site moisture. Of the 14 sites observed, 12 had permafrost pre-fire and ten had permafrost post-fire. All sites with permafrost increased in active layer depth, but not significantly (pre-fire mean active layer depth = 71.32 ± 5.65, post-fire mean active layer depth = 75.22 ± 5.40), however sites that experienced the greatest change in active layer depth (> 10-cm change) also showed changes in site moisture.

Post-fire species composition

The post-fire ordination showed substantial variation in community composition among sites (Fig. 2). Axis-I was negatively correlated with slope ($r = -0.619$), percentage deciduous shrubs ($r = -0.588$), elevation ($r = -0.547$) and percentage clay ($r = -0.518$). It was positively correlated with pre-fire pH ($r = 0.522$), percentage rock ($r = 0.521$), lichens ($r = 0.519$) and post-fire pH ($r = 0.483$). Axis-2 was highly correlated with percentage organic soil lost ($r = 0.640$), percentage forbs ($r = -0.609$), percentage residual organic (amount of organic matter remaining post-fire) ($r = 0.579$) and percentage mineral soil ($r = -0.548$). Based on these correlations, both Axis-1 and -2 are difficult to interpret, however it appears that sites at higher elevations and acidity occur on the left of the ordination, and Axis-2 represents a gradient in residual organic matter, with more severely burned sites (high mineral soils, low residual organic) at the bottom of the ordination.

Within the ordination space, sites were classified by measured fire severity (composite burn index) (Fig. 2). Along Axis-1, high-severity sites were grouped, based on similarity of species composition, on the right side of the ordination space, whereas moderate and low severity sites were distributed along the left side (Fig. 2). Along Axis-2, sites with measured (CBI) high-fire severity were located in the bottom half of ordination space, whereas moderate severity and low severity sites were widely distributed. It appears, therefore, that high severity sites had much more distinct species composition than moderate or low severity sites. No discernible pattern was evident between pre-fire site moisture and post-fire community composition; however, pre-fire pH (which correlates with pre-fire community composition; Hollingsworth et al. 2006) showed a slightly stronger correlation with post-fire composition than post-fire pH, suggesting a small legacy effect of pre-fire community composition on post-fire vegetation recovery. In summary, fire severity had a greater impact on post-fire community composition than did pre-fire site moisture. This effect of fire severity differentiated the community composition of severely burned sites from low and moderate severity sites.

Changes in community composition pre- to post-fire

We examined changes in conununity composition at three scales: species, growth form and overall community.

Shifts in species pre- to post-fire

In the 2 years post-fire, fire eliminated half the species from the sites we studied (53 of 105), representing a significant reduction in species richness ($P = < 0.001$, df = 13) and loss of species diversity post-fire as compared to mature black spruce communities (Table 2). Pre-fire the average species richness across sites was 35.5 ± 1.48 species/site, and post-fire the average species richness was 23.21 ± 1.38 species/site. However within 2 years, 17 new species (25% of the post-fire flora) appeared that had not been recorded at any of these sites before fire. Thirteen of those new species occurred in sites that burned with high severity, whereas only nine of them occurred in sites that burned with moderate or low severity (Table 2).

Of 50 species that occurred both pre- and post-fire, 13 showed significant changes in their presence/absence among the 14 study sites from pre- to post-fire (Table 3).

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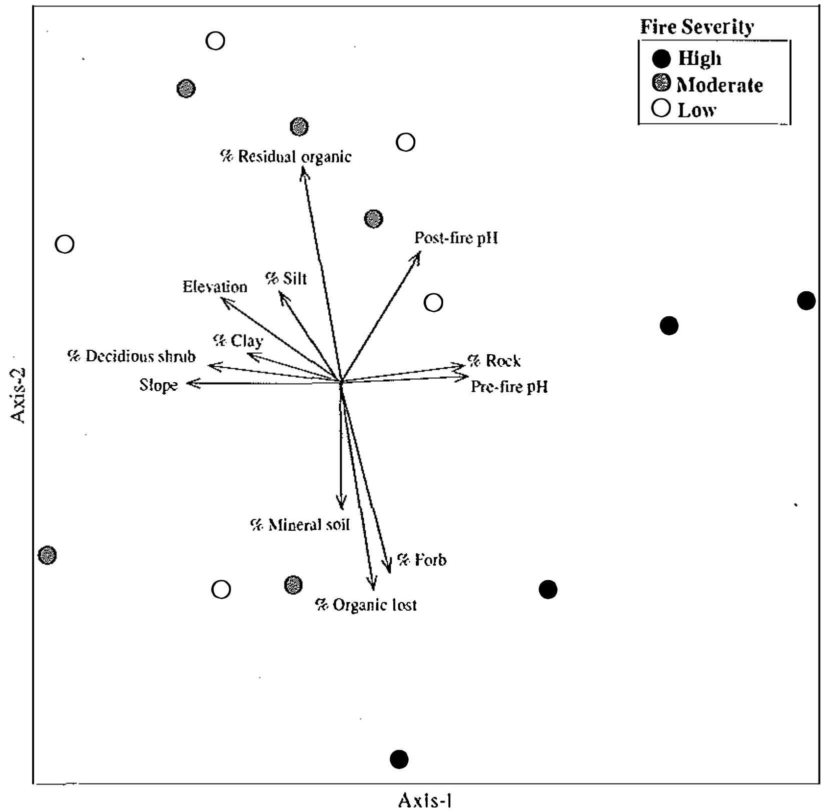

Fig. 2. The post-fire ordination grouped by fire severity. The total inertia for the DCA was 1.77, the gradient length of Axis-1 was 4.13 and the Axis-1 eigenvalue was 0.36. The gradient length of Axis-2 was 4.02 and the eigenvalue was 0.22. Vectors indicate the environmental variables that are most strongly correlated with the ordination axes (Pearson correlation coefficients ($r > 0.275$, as suggested by McCune & Grace 2002). Vector length and direction represent magnitude and direction of correlation, respectively.

Five lichen species four moss species, one evergreen shrub and one deciduous shrub significantly decreased in presence after the 2004 wildfires. Conversely, only one forb and one deciduous shrub significantly increased in presence after the 2004 wildfires.

Of the 50 species found pre- and post-fire, eight occurred in at least 60% of both pre- and post-fire sites. This enabled us to evaluate whether their abundance (rather than just presence/absence) changed significantly in response to fire. Of these eight species, *Ledum groenlandicum* ($P = 0.0017$ df = 13), *Vaccinium vitus-idaea* ($P < 0.0001$ df = 13) and *Vaccinium uliginosum* ($P < 0.0001$ df = 13) significantly decreased in abundance after the 2004 wildfires. None of the eight species showed a significant increase in abundance, although *Rubus chamaemorus*, *Petasites frigidus* and *Calamagrostis canadensis* tended to increase.

Shifts in growth forms pre- to post-fire

All species found in both pre- and post-fire communities were grouped into the following growth forms: deciduous shrub, evergreen shrub, graminoid, forb, seedless vascular, bryophyte or lichen. An ANOVA revealed decreases in the number of species of evergreen shrubs and lichens pre- to post-fire ($F = 2.36$, df = 6, $P = 0.04$ and $F = 4.5$, df = 6, $P = 0.029$ for evergreen shrubs and lichens, respectively) (Fig. 3). This difference was most pronounced in the number of lichen species found, with more pre-fire (34) than post-fire (nine). When sites were grouped by fire severity class, ANOVAs revealed that post-fire, only evergreen shrubs and bryophytes showed significant differences in species richness between the fire severity classes (Fig. 4), therefore, the effect of fire, regardless of severity, is high for lichens. There were significantly fewer evergreen species in sites that burned severely as compared to sites that burned at moderate ($F = 5.3$, df = 13, $P = 0.04$) or low severity ($F = 13.9$, df = 13, $P = 0.005$). Similarly, bryophytes had fewer species in severely burned than in low severity sites ($F = 6.44$, df = 13, $P = 0.032$) (Fig. 4). Pre-fire, there was no significant difference in evergreen and bryophyte species richness between the three severity classes (Fig. 4). Finally, there was a significant decrease in evergreen and bryophyte

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Table 2. Plant species distribution pre- and post-fire grouped by growth form. If a species occurred post-fire, the species distribution across fire severity classes are also indicated. Species labelled with "All" were observed across all severity classes.

Growth Form	Species observed Pre-fire ONLY	Species observed Post-fire ONLY	Fire severity class observed	Species found BOTH Pre AND Post-fire	Fire severity class observed
Deciduous shrubs	*Rubus arcticus*	*Salix alaxensis*	All	*Alnus viridus*	Moderate
	Salix arbusculoides	*Salix glauca*	All	*Alnus incana*	High
	Salix niphoclada	*Salix scouleriana*	All	*Betula glandulosa*	Moderate, Low
	Salix fuscens	*Rubus idaeus*	High, Moderate	*Betula nana*	All
				Dasiphora fruticosa	High
				Rosa acicularis	All
				Salix myrtillifolia	High
				Rubus chamaemorus	All
				Salix pulchra	All
				Spiraea beauverdiana	All
Evergreen shrubs	*Chamaedaphne calyculata*			*Arctostaphylos rubra*	High, Moderate
				Cornus canadensis	Moderate
				Empetrum nigrum	Moderate, Low
				Ledum decumbens	All
				Ledum groenlandicum	All
				Oxycoccus microcarpos	Moderate, Low
				Vaccinium vitis-idaea	All
				Vaccinium uliginosum	All
Graminoids	*Carex garberi*	*Arctagrostis latifolia*	High	*Calamagrostis canadensis*	All
	Carex vaginata	*Luzula rufescens*	High, Moderate	*Carex bigelowii*	All
	Luzula multiflora	*Poa pratense*	High	*Eriophorum vaginatum*	All
	Luzula parviflora	*Poa palustre*	Moderate, Low		
Forbs	*Drosera rotundifolia*	*Cardamine hyperborea*	High	*Chamerion angustifolium*	All
	Geocaulon lividum	*Corydalis sempervirens*	Moderate, Low	*Mertensia paniculata*	High, Moderate
	Moehringia lateriflora	*Chamerion glandulosum*	High	*Petasites frigidus*	All
	Petasites sagittatus	*Galium boreale*	High	*Polygonum bistorta*	Moderate
	Pinguicula villosa	*Polygonum alaskanum*	All	*Saussurea angustifolia*	All
	Platanthera hyperborea	*Senecio congestus*	High, Low		
	Pyrola asarifolia	*Stellaria longipes*	High, Low		
	Pyrola secunda				
	Ranunculus lapponicus				
Seedless vasculars	*Equisetum pratense*			*Equisetum arvense*	High, Moderate
	Lycopodium clavatum			*Equisetum scirpoides*	All
	Lycopodium complanatum			*Equisetum sylvaticum*	All
				Lycopodium annotinum	Moderate
Bryophytes	*Polytrichum juniperinum*	*Ceratodon purpureus*	All	*Aulacomnium palustre*	All
	Ptilium crista-castrensis	*Marchantia polymorpha*	All	*Aulacomnium turgidum*	Moderate, Low
	Sphagnum balticum			*Hylocomium splendens*	Moderate, Low
	Sphagnum fuscum			*Pleurozium schreberi*	Moderate, Low
	Sphagnum russowii			*Polytrichum commune*	All
				Polytrichum strictum	All
				Sphagnum angustifolium	Moderate, Low
				Sphagnum girgensohnii	Moderate, Low
				Sphagnum rubellum	Moderate
				Sphagnum warnstorfii	Moderate
				Tomenthypnum nitens	Moderate
Lichens	*Cetraria cuculata*			*Cetraria islandica*	Moderate
	Cetraria laevigata			*Cladina arbuscula*	Moderate, Low
	Cetraria nivalis			*Cladina rangiferina*	Moderate, Low
	Cladina stellaris			*Cladonia amaurocraea*	Moderate
	Cladina stygia			*Cladonia gracilis*	Moderate, Low
	Cladonia cenotea			*Cladonia uncialis*	Low
	Cladonia chlorophaea			*Nephroma arcticum*	Moderate, Low
	Cladonia coccifera			*Peltigera aphthosa*	Moderate, Low
	Cladonia cornuta			*Peltigera neopolydactyla*	Low
	Cladonia crispata				
	Cladonia deformis				
	Cladonia ecmocyna				
	Cladonia elongata				
	Cladonia fimbriata				
	Cladonia subfurcata				
	Cladonia sulphurina				
	Dactylina arctica				
	Masonhalea richardsonii				
	Nephroma expallidum				
	Peltigera leucophlebia				
	Peltigera canina				
	Peltigera malacea			*Pleurozium schreberi*	Moderate, Low
	Peltigera polydactyl				
	Peltigera scabrosa				
	Stereocaulon alpinum				
	Stereocaulon tomentum				

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Table 3. G-test of independence for differences in presence/absence from pre- to post-fire. Data reported only for species with significant differences.

Growth Form	Species	P-value	G-test value	Presence Pre- to Post-fire
Evergreen shrub	*Empetrum nigrum*	< .001	22	Decreased
Deciduous shrub	*Salix pulchra*	< .01	5.45	Increased
	Betula nana	< .05	4.27	Decreased
Forb	*Chamerion angustifolium*	< .001	25.71	Increased
Moss	*Aulacomnium palustre*	< .01	7.37	Decreased
	Hylocomium splendens	< .001	13.56	Decreased
	Pleurozium schreberi	< .001	11.04	Decreased
	Sphagnum rubellum	< .01	6.89	Decreased
Lichen	*Cetraria cucullata*	< .001	19.99	Decreased
	Cetraria islandica	< .001	19.99	Decreased
	Cladina arbuscula	< .001	25.71	Decreased
	Cladina gracilis	< .05	5.31	Decreased
	Nephroma arcticum	< .001	7.79	Decreased

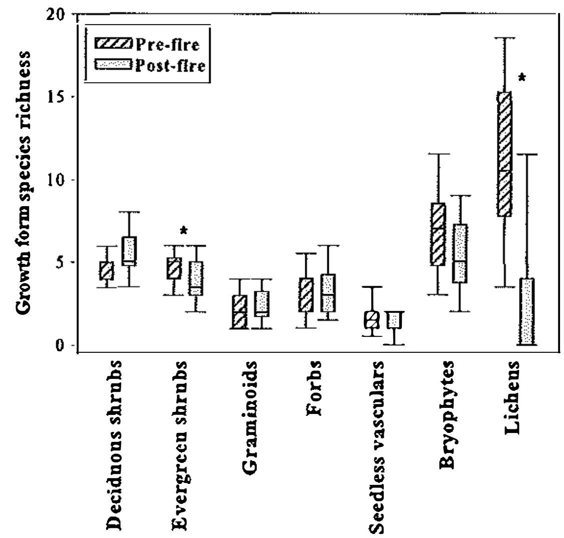

Fig. 3. The growth form species richness pre- and post-fire. *Indicates significant difference ($P < 0.05$) between pre- and post-fire species richness.

species richness pre- to post-fire in sites that experienced high severity fires ($F=7.8$, df = 13, $P=0.01$ and $F=2.3$, df = 13, $P=0.13$, for evergreen shrubs and bryophytes, respectively), whereas there was no significant difference in species richness pre- to post-fire in the sites that burned at moderate or low severity (Fig. 4).

Shifts in community composition pre- to post-fire

When pre- and post-fire communities were ordinated together, pre-burn sites clearly separated from the sites post-fire. Based on correlations with environmental variables, Axis-1 clearly represents a fire severity/vegetation loss gradient (Fig. 5). Axis-1 was negatively correlated with percentage deciduous shrub cover ($r = -0.612$), percentage evergreen shrub cover ($r = -0.473$) and percentage moss cover ($r = -0.421$), and positively correlated with percentage dead tree ($r=0.542$) and percentage forb ($r=0.504$). Axis-1 therefore represents the expected decrease in overall plant cover and increase in dead biomass post-fire. Axis-2 represents a complex soil acidity gradient related to site aspect, where it was positively correlated with site aspect ($r=0.544$) and percentage deciduous shrub cover ($r=0.427$) and negatively correlated with pH of the mineral soil ($r = -0.619$) (Fig. 5).

In general, sites that experienced moderate and low fire severity showed more similarity in overall plant community composition to their pre-fire composition, as compared to sites that experienced high fire severity (Fig. 5). To quantify the overall change in species composition at each site due to the 2004 wildfires, we evaluated the change in vector length between each site's pre-fire and post-fire ordination value. Based on an ANOVA, all 14 sites had some degree of change between pre- and post-fire composition ($F=2.82$, df = 13, $P=0.10$). High severity sites showed significantly greater change in community composition pre- to post-fire than did low severity sites (Tukey-Kramer's t-test post-hoc test: $P=0.045$, df = 13).

Discussion

Wildfire substantially altered plant cover and community composition in our 14 study sites. Previous studies have shown that pre-fire, black spruce vegetation composition is closely related to soil pH, stand structure and a complex drainage gradient (Hollingsworth et al. 2006). After fire and the resulting loss of stand structure, fire severity and post-fire site moisture assumed primary importance in explaining variation in community composition.

The fire-driven changes in community composition that we documented in 14 sites are consistent with patterns from previous comparisons between unburned and burned sites or inferred chronosequences across a variety of biomes. These previous studies showed that recently burned sites have low abundances of mosses, lichens and evergreen shrubs, and high abundance of graminoids and forbs (Schimmel & Granstrom 1996; Holt & Severns 2005; Johansson & Reich 2005; Lecomte et al. 2005). The lack of below-ground organs in bryophytes and lichens and the shallow roots and below-ground stems of most evergreen shrubs make these growth forms

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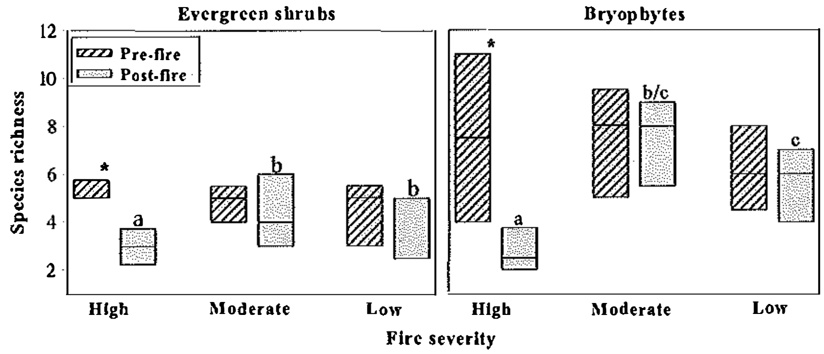

Fig. 4. The species richness for evergreen and bryophyte growth forms by fire severity class. Values with different letters (a, b or c) have significantly different ($P < 0.05$) means between fire severity level post-fire, and *indicates significant difference between pre-and post-fire richness.

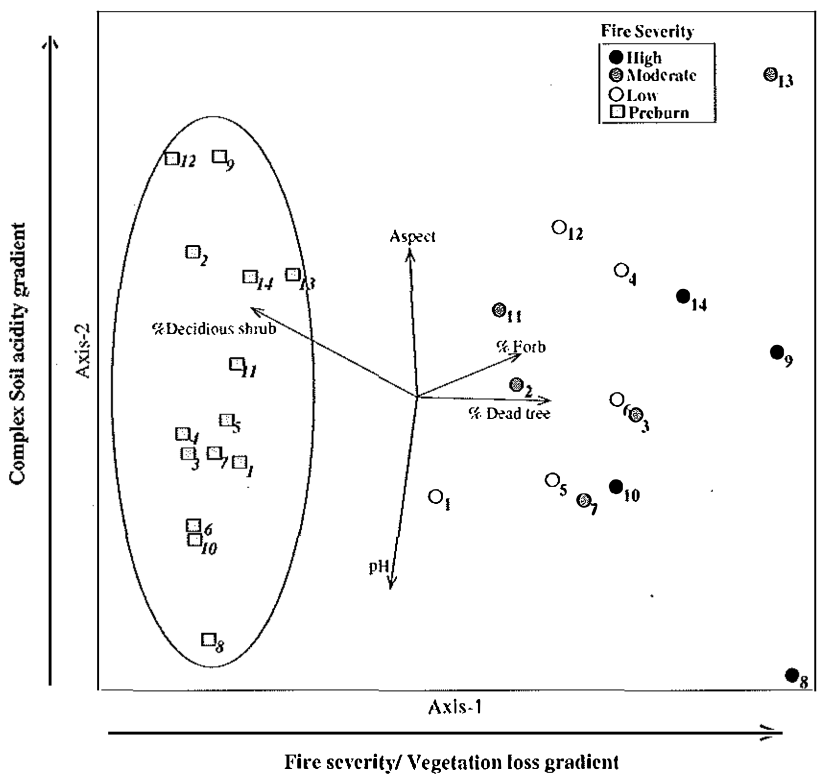

Fig. 5. The pre-fire/post-fire site ordination with pre-fire sites circled. Vectors indicate the environmental variables that are most strongly correlated with the ordination axes ($r > 0.275$) (Pearson correlation coefficients). The total inertia for the DCA ordination was 2.83, the gradient lengths for Axis-1 and -2 were 4.86 and 5.38, respectively, and the eigenvalues were 0.51 and 0.22 for Axis-1 and -2, respectively. Vector length and direction represent magnitude and direction of correlation, respectively.

particularly vulnerable to fire (Johnson 1992; Landhausser & Wein 1993). Some early successional bryophytes (e.g, *Ceratodon purpureus* and *Marchantia polymorpha*) recruited to our sites after fire, which is consistent with studies looking specifically at moss succession post-fire (Benscoter 2006; Turetsky et al. 2010).

The strong effect of fire severity that we observed on post-fire community composition parallels a switch from predominantly black spruce recruitment on low and moderately burned sites to predominantly deciduous tree recruitment on severely burned sites (Johnstone et al. 2010). Earlier studies in boreal Alaska and Canada have shown that successional trajectories are determined within the first decade after fire (Johnstone et al. 2004), indicating that the tree species observed immediately post-fire are indicative of long-term successional patterns.

Therefore, a shift from black spruce to deciduous tree recruitment on severely burned sites could alter successional trajectories and lead to greater abundance of deciduous forests on landscapes previously dominated by black spruce (Johnstone et al. 2010). Our results suggest that recent increases in fire severity (Kasischke & Turetsky 2006) would cause parallel shifts in overstorey and understorey community composition. The increase in grasses and forbs and decrease in evergreen shrubs, mosses and lichens that we observed on severely burned sites also characterizes the difference between current deciduous forests and black spruce forests in interior Alaska (Viereck et al. 1983). The growth forms that increase in severely burned sites are characterized by higher quality litter, more rapid nutrient cycling and greater nutrient requirement than the growth forms that decrease in these sites (Chapin et al. 1996; Hobbie 1996), so the parallel shifts in overstorey and understorey community composition could be linked by ecosystem processes as well as fire effects on post-fire recruitment.

Much to our surprise, *pre*-fire site moisture had no detectable effect on post-fire community composition (Figs 2 and 5), even though it was one of the two most important determinants of community composition before the sites burned (Hollingsworth et al. 2006). The lack of legacy effect of pre-fire moisture on post-fire community composition probably reflects the large loss of lichen and moss species after fire, since these are some of the most important determinants of pre-fire community composition (Hollingsworth et al. 2006). However, pre-fire moisture may have contributed indirectly to post-fire community composition through effects on fire severity (Kane et al. 2007), which strongly influenced post-fire composition. Pre-fire soil pH was correlated with post-fire community composition (Figs 2 and 5). This indicates a potential legacy effect of site acidity, which may exert an influence on vegetation development, despite fire severity. This acidity effect may be due in part to differences in underlying parent material, soil texture and pre-fire vegetation composition (Hollingsworth et al. 2006).

Our results indicate that *post*-fire moisture showed a slightly higher correlation with post-fire community composition than pre-fire moisture. This might indicate that the current environment strongly influenced community composition in both unburned vegetation (Hollingsworth et al. 2006) and post-fire vegetation (Johnstone et al. 2010), and also reinforces the strong link between fire severity and post-fire site moisture (Johnstone et al. 2008). In addition, there was no consistent trend between pre-fire and post-fire site moisture. Changes in site moisture among sites pre- to post-fire probably resulted from spatial variation in multiple factors that influence post-fire site moisture, including fire severity, permafrost thaw, loss of transpiring vegetation and loss of moisture-retaining mosses. The stronger effect of post-fire moisture on post-fire community composition suggests that severe-burning wildfires will substantially weaken the legacy effect of pre-fire vegetation on post-fire community composition.

The recent increases in extent and severity of wildfires in the Alaska and western Canada (Kasischke & Turetsky 2006; Duffy et al. 2007) are projected to continue (Flannigan et al. 2005; Soja et al. 2007). Such changes would radically alter both the controls on and the landscape patterns of community composition in the Alaskan boreal forest. In the past, strong legacy effects of residual organic matter after low and moderate severity fires resulted in relatively rapid return to pre-fire community composition (Viereck 1973; Chapin et al. 2004). Observed and projected increases in fire severity weaken this legacy effect (Johnstone et al. 2010), making sites more responsive to post-fire moisture and to landscape patterns of fire severity than to the environmental mosaic that governed pre-fire community composition (Figs 2 and 5; Johnstone et al. 2010). Most dynamic vegetation models assume that current community composition exerts a strong influence over future composition, modified by changes in climate and frequency of disturbance. In addition, few dynamic models allow the introduction of species not already within the species pool (e.g. Prentice et al. 1992). Our results suggest that characteristics of the disturbance itself (e.g. fire severity) could also exert strong control over the future landscape dynamics of Alaska's boreal forest, but also suggest a legacy effect of mineral soil pH (but not pre-fire site moisture) that influences the local species pool.

The differences in post-fire community composition that we observed between sites with high and moderate/low fire severity are functionally important. Severely burned stands had less cover of berry-producing species (*Vaccinium uliginosum, Vaccinium vitis-idaea, Empetrum nigrum*) and of lichens (an important winter forage for caribou) than other stands. These plant species are also less abundant in deciduous forests (Viereck et al. 1983) that are likely to develop from these severe burns (Johnstone et al. 2010). This suggests that increased fire severity might reduce the abundance of these important components of local subsistence economies (Nelson et al. 2008). However, the availability of other subsistence foods such as moose might increase in the deciduous-dominated stands that develop from severe burns (Nelson et al. 2008). The reduction in moss cover in severely burned stands and succeeding deciduous forests also has important implications through reduced insulation that allows permafrost to thaw and reduces rates of organic accumulation (Turetsky et al. 2010). These changes could reduce

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carbon sequestration by boreal forests and act as a positive feedback to climate warming.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Photo S1. A newly burned landscape in northern Alaska, with a fire burning in the background.

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