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# Variation in plant community composition and vegetation carbon pools a decade following a severe fire season in interior Alaska

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**Keywords**
Black spruce; Boreal forest; Deciduous; Depth of burn; Fire severity; Steady state; Successional trajectory; Understorey species composition; Vegetation carbon pools

**Nomenclature**
Johnson et al. (1995) for vascular plants;
Vitt et al. (1998) for nonvascular plants.

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## Abstract

**Questions:** How does fire severity, measured as depth of burn of ground layer fuels, control the regeneration of understorey species across black spruce-dominated stands varying in pre-fire organic layer depths? Are successional shifts from evergreen to deciduous understorey vegetation more likely to occur with greater depth of burn? Does a shift in understorey vegetation community towards more deciduous species influence carbon accumulation in vegetation biomass?

**Location:** Northern boreal forest, interior Alaska.

**Methods:** We sampled 32 stands in interior Alaska that burned in 2003 and 2004 in which depth of burn had been recorded soon after fire. In 2014 we characterized tree density, understorey vegetation composition, above- and below-ground vegetation carbon pools, and a suite of environmental variables. We used ANOVA and multivariate redundancy analysis models to analyse the dominant controls on vegetation composition and carbon pools.

**Results:** Fire severity was a strong control on post-fire tree and non-vascular species composition. Ten years post-fire, sites that experienced deeper burning of organic layers had a higher abundance of deciduous tree species, fire-adapted mosses, forbs and graminoids, and lower abundances of evergreen shrubs and *Sphagnum* mosses. Environmental variables (elevation, soil bulk density and mineral soil pH, moisture and temperature) served as important controls on tree and vascular understorey species composition. We found no evidence that carbon pools associated with recovering vegetation biomass were influenced by landscape position, fire severity or environmental variables.

**Conclusions:** Both fire frequency and depth of burn are projected to increase with a warmer climate in interior Alaska. These shifts in fire regime are expected to favour the regeneration of deciduous species over conifers, which have the potential to regulate successional pathways and large-scale trends in albedo, which both ultimately could influence ecosystem–climate feedbacks and dampen future fire cycles. Our results show that understorey species composition is controlled by fire severity, suggesting that more severe burning causes a decline in the self-replacement of conifer communities across a range of hydrologic settings. Overall, our results suggest a loss of resilience in black spruce forests in the face of a changing fire regime. However, we found no evidence that fire severity influences vegetation carbon pools 10 yrs post-fire, suggesting that there is less landscape variation in biomass carbon pools than in vegetation composition and succession during early post-fire succession.

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## Introduction

The climate in Alaska is warming at twice the global average (ACIA 2004) resulting in widespread consequences for ecosystems, including permafrost degradation, wetland drying and increasing extent and severity of wildfire (Osterkamp & Romanovsky 1999; Hinzman et al. 2005; Kasischke & Turetsky 2006; Turetsky et al. 2011). These changes to the biophysical environment have altered the structure and function of both boreal and tundra systems, often related to state changes in ecosystems that persist across multiple disturbance cycles (Chapin et al. 2004). For example, recent warming combined with chance dispersal following fire has allowed the northern expansion of lodgepole pine. Once established, these flammable trees continue to promote fire, which favours persistence of a pine-dominated state (Johnstone & Chapin 2003).

Wildfire is a very important natural disturbance in the boreal region (Payette 1992) and has played a vital role in boreal vegetation structure in North America for more than 5000 yrs (Lynch et al. 2003). However, during the 2000s, increases in the number of years with extensive fires have doubled the annual average burn area in interior Alaska relative to the previous five decades (Kasischke et al. 2010). These increases in area burned have been attributed to warmer summer temperatures and drier fuels (Kasischke et al. 2010). Warmer and drier conditions also allow for deeper burning into the organic soil layer (Chapin et al. 2010), particularly during late season fires (Turetsky et al. 2011).

Forests dominated by black spruce (*Picea mariana*) account for an estimated 60% of total forest cover in the boreal forest region of Alaska (Bonan 1991). In the discontinuous permafrost region, black spruce forests often are underlain by permafrost, which contributes to wet and cold conditions that constrain rates of decomposition and nutrient turnover, and thereby promote the development of thick organic layers (Van Cleve et al. 1991). Due to the long-term accumulation of these thick organic soil layers or peat, these black spruce forests play an important role in the global carbon cycle.

Variation in depth of burning at a given site has implications for vegetation succession following wildfire, contributing to two stable ecological states in interior Alaska: (1) a thick organic layer state characterized by coniferous black spruce stands; and (2) a shallow organic layer state characterized by deciduous aspen and birch (Johnstone et al. 2010a). Black spruce stands have low rates of evapotranspiration (Bonan 1991), understorey communities dominated by mosses that promote high water retention and build up of thick organic layers (Turetsky et al. 2010), and oftentimes have a near-surface permafrost layer that retards drainage (Jorgenson et al. 2010). The high moisture content of these systems inhibits deep burning, leaving residual organic soil that persists across multiple fire cycles. Black spruce tends to be more competitive than deciduous species when colonizing organic soils, in part because black spruce produces a large amount of seed from aerial seed banks, thereby ensuring some seed find suitable microsites for germination (Viereck 1983). Furthermore, larger-seeded, coniferous species have higher establishment potential in organic soils compared to smaller-seeded, deciduous species (Johnstone & Chapin 2006). In contrast, deciduous stands have shallow organic layers that burn more completely during wildfire, often exposing the mineral soil bed (Kasischke et al. 2000). Under these conditions, deciduous trees have a competitive advantage when re-colonizing. Early models of boreal succession suggested that fire promotes deciduous species during early succession, followed by shifts to conifer species in later successional stages (Van Cleve & Viereck 1981). However, more recent models of boreal succession emphasize the importance of black spruce self-replacement in areas where fires do not consume the entire soil organic layer (Johnstone et al. 2010b). Changes in the fire regime that cause an increase in organic layer burning can potentially cause shifts between the thick organic soil/conifer and the thin organic soil/deciduous states (Johnstone et al. 2010a). An increase in abundance of deciduous-dominated forests has local and regional importance due to potential implications for land–atmosphere energy exchange, increased nutrient cycling, increased plant productivity and altered wildlife habitat use (Johnstone et al. 2010a).

While the successional trajectory of tree species following wildfire in interior Alaska as a function of fire severity has been well documented (Kasischke & Johnstone 2005; Johnstone et al. 2010b; Shenoy et al. 2011), less is known about the effects of variation in fire severity on understorey vegetation. Bernhardt et al. (2011) showed that low-severity fires tended to favour the regeneration of a community similar to the pre-fire because many understorey species regenerate asexually after the fire from below-ground tissues. Because canopy closure occurs over 30–40 yrs of post-fire succession in these systems (relative to a fire rotation period of 80–140 yrs; Hart & Chen 2006), understorey species are likely to account for a large proportion of the total plant diversity and biomass pools for a significant portion of the fire-free period. Even in mature boreal stands, the productivity of mosses in the understorey is comparable or can even exceed that of black spruce productivity (Turetsky et al. 2010).

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The overall objective of this study is to examine relationships between fire severity and understorey vegetation community composition and re-growth across a variety of landscape positions. This study differs from other studies that have examined overstorey and/or understorey vegetation communities and carbon pools following wildfire because we sampled across a larger range of landscape settings, thus encompassing considerable landscape variation in pre-fire organic layer depths. Also, while other studies have focused on the trajectory of overstorey biomass pools following fire (e.g., Alexander et al. 2012), here we focus on understorey vascular and nonvascular species, given that these species play an important role in nutrient and energy cycling as well as potential post-fire vegetation shifts. We quantified understorey vegetation composition in black spruce-dominated sites that burned 10 or 11 yrs prior to our sampling. In all of our sites, pre-fire depth of the organic soil layer, as well as the depth of burn had been quantified soon after fire (Turetsky et al. 2011). This allowed us to explore whether increasing fire severity was associated with a reduction in black spruce self-replacement in favour of deciduous dominance post-fire. Studies have shown that species composition and densities in the first decade of post-fire succession are maintained through decades of stand development, regardless of pre-fire composition (Gutsell & Johnson 2002; Johnstone et al. 2004). Thus, while our sampling in this study is limited to a 10-yr post-fire window, it is likely that our results provide insight into longer-term successional patterns.

Based on previous studies, we predicted that increases in the fraction of organic soil consumed during fire would be related to declines in evergreen shrub understorey and *Sphagnum* moss abundance, and increases in the abundance of deciduous shrub understorey species. We also hypothesized that changes in species composition associated with fire severity would lead to changes in vegetation biomass and carbon pools. Specifically, we expected that vegetation communities in sites recovering from severe burning would have larger vegetation carbon pools due to the fast-growing nature of species found in these sites relative to the more conservative species associated with succession following less severe burning.

## Methods

### Study sites

This study took place in 32 sites in interior Alaska that had undergone 10 yrs of post-fire succession. We selected a subset of the sites used by Turetsky et al. (2011), with a focus on capturing the extent of variation in depth of burn, site moisture levels, topographic positions and geographic distribution across the landscape (Appendix S1). All study sites are located in the Interior Highlands Ecoregion (http://www.epa.gov/wed/pages/ecoregions.htm) of Alaska, which is characterized by discontinuous permafrost, a continental climate and temperature extremes ranging from −70 to +35 °C (Hinzman et al. 2006). The study sites were all dominated by black spruce prior to burning in 2003 or 2004. Pre-fire stand density ranged from 800–13 455 trees·ha$^{-1}$ (Kasischke et al. 2008a). To account for site characteristics related to topography, the 32 sites were evenly distributed on north-facing slopes, south-facing slopes, dry ridge tops and poorly drained lowlands.

During the summer of 2004, interior Alaska experienced the hottest and driest weather since 1940 (Alaska Climate Research Center 2009). These conditions resulted in widespread fires that consumed 2.7 million ha of forest, representing the largest annual burned area in Alaska's 58-yr fire record (Todd & Jewkes 2006). Study sites were originally established the following spring (May 2005) in areas that were accessible from the Taylor, Steese and Dalton Highways. In addition to sites that burned in 2004, four sites where chosen from the Erikson fire, which burned in 2003. For this study, all of the 32 study sites were revisited in summer 2014 for vegetation and soil sampling.

### Vegetation composition measurements

Understorey species abundance in each site was measured using the point intercept method, which has been proven to yield more objective and precise estimates of plant cover than ocular estimates of percentage cover (Godínez-Alvarez et al. 2009).

At each site, a 50-m baseline transect was established along a randomly chosen geographic bearing. Three 30-m transects were established perpendicular to the 50-m transect: one at the centre at the 25-m mark and two on either side of the centre at randomly generated distances >5 m away from the centre point. Understorey species (Table 1) abundance was measured using the point intercept method per Jonasson (1983) along all three transects, with a pin being dropped every meter. Species abundance was calculated using the following formula:

$$\text{Species abundance}\ (\%\ \text{cover}) = \left(\frac{\text{number of hits per species}}{\text{total number of hits}}\right) \times 100.$$

Overstorey tree (*Populus tremuloides*, *Betula neoalaskana*, *P. mariana*, *Larix laricina*) and tall shrub (*Alnus crispa*, *Betula* spp., *Salix* spp.) species were measured as stems·m$^{-2}$. It is recognized that 50 yrs post-fire these may not all be considered canopy species but, at 10 yrs post-fire all stems >75-cm tall were counted as they are likely to shade out and influence understorey species composition. Analysis involving deciduous tree species used only *P. tremuloides*,

**Table 1.** Plant species found across all sites with corresponding growth form.

| Growth Form | Species | |
|---|---|---|
| Deciduous Shrub | *Betula glandulosa* | |
| | *Rubus chamaemorus* | |
| | *Rubus idaeus* | |
| | *Spiraea beauverdiana* | |
| Evergreen Shrub | *Arctostaphylos rubra* | *Ledum groenlandicum* |
| | *Chamaedaphne calyculata* | *Oxycoccus microcarpos* |
| | *Cornus canadensis* | *Vaccinium uliginosum* |
| | *Empetrum nigrum* | *Vaccinium vitis-idaea* |
| | *Ledum decumbens* | |
| Graminoid | *Carex bigelowii* | |
| | *Eriophorum vaginatum* | |
| | *Poa palustre* | |
| | *Poa pratense* | |
| Forbs | *Chamerion angustifolium* | |
| | *Drosera rotundifolia* | |
| | *Mertensia paniculata* | |
| | *Petasites frigidus* | |
| | *Petasites sagittatus* | |
| | *Polygonum alaskanum* | |
| Seedless Vascular | *Equisetum arvense* | |
| | *Equisetum scirpoides* | |
| | *Equisetum sylvaticum* | |
| Bryophytes | *Aulacomnium palustre* | *Polytrichum strictum* |
| | *Bryum pseudotriquetrum* | *Sphagnum angustifolium* |
| | *Ceratodon purpureus* | *Sphagnum capillifolium* |
| | *Hylocomium splendens* | *Sphagnum girgensohnii* |
| | *Pleurozium schreberi* | *Tomenthypnum nitens* |
| | *Polytrichum juniperinum* | |
| Lichens | *Cladonia gracilis* | |
| | *Cetraria nivalis* | |
| | *Cetraria cucullata* | |

*A. crispa* and *B. neoalaskana* as they are the dominant species in mature deciduous forests (Johnstone et al. 2010b). Along each of the three 30-m transects, established perpendicular to the 50-m baseline and used for measuring understorey species, the species and accompanying basal diameter were recorded for all individuals within 1 m on either side of the transect, giving a total sampling area of 60 $m^2$ per transect. Counting stems of all species and dividing by the total sampling area of 180 $m^2$ determined total stem density per site.

## Fire severity

Depth of burn data were taken from Turetsky et al. (2011) and were represented in three ways: (1) the depth of organic soil consumed during the fire; (2) the depth of the post-fire organic soil layer; and (3) the fraction of organic soil consumed during the fire. Briefly, depth of burn during fire was quantified using the uppermost adventitious roots of black spruce trees as a marker of pre-fire organic layer depth (Kasischke et al. 2008b; Boby et al. 2010). This approach to measuring fire severity has been used in a variety of stands in Alaska (Boby et al. 2010) and has been compared to combustion rods installed in controlled burn conditions (Kasischke et al. 2008b). Depth of organic soil consumed during fire was estimated by measuring the distance from the uppermost adventitious root down to the top of the post-fire organic soil layer, with the uppermost adventitious root being a marker of pre-fire organic soil depth. Post-fire organic layer depth was determined by digging 25 soils pits along the established transects and measuring from the top of the organic soil horizon to the top of the first mineral soil horizon. Fraction of organic soil consumed during the fire is the ratio of depth of burn to pre-fire organic layer depth (the sum of depth of organic soil consumed during the fire and post-fire organic layer depth). Full details on methodologies employed at these sites are found in Kasischke et al. (2008b) and Turetsky et al. (2011).

## Environmental variables

Mineral soil moisture, temperature and pH were sampled in all sites during the same 3-d rain-free period in early August, thereby avoiding variation associated with seasonal trends of soil warming/drying or weather. These variables were measured seven times along a 30-m transect laid along a randomly generated bearing. Mineral soil temperature and moisture where measured at the top of the mineral horizon. Soil pH was measured by collecting mineral soil and creating a 1:1 slurry with distilled water in the laboratory and measuring pH using a Vernier pH probe (Sarasota, FL, US). Elevation was measure using a Garmin Legend H hand-held GPS unit (Schaffhausen, CH). Light availability was assessed through canopy openness. Hemispherical photos were taken at ground level and at 1 m, at the end of each transect, totalling six photos per site. Photos were taken using a Nikon D3100 camera (Tokyo, JP) with a Sigma 360, 4.5-mm fisheye lens. Canopy photos were assessed for percentage of canopy openness using Gap Light Analyzer (GLA) v 2.0 (Cary Institute for Ecosystem Studies, Milbrook, NY, US). Mean canopy openness at ground level and 1 m was calculated per site. Organic soil bulk density was determined from soil cores 4.75 cm in diameter that were taken from the top of the organic soil layer down to the mineral soil layer (cores containing char were cut at the char layer). Six soil cores were taken in each site at the end of the three parallel transects. Cores were sliced vertically in half and placed in a drying oven at 65 °C for 48 hr. The moisture content of the core was determined as (wet weight of half core − dry weight of half core)/wet weight of half core. Water content of the whole core was then calculated by multiplying moisture content by the wet weight of the whole core. The dry weight of the whole core was then calculated by subtracting the water content of the whole core from the wet weight of the whole core. Final bulk density was then calculated by dividing the dry weight of the whole core by volume of the core.

### Biomass accumulation

To sample above-ground biomass, a wooden frame measuring 0.5 m × 0.5 m was laid down at the end of each 30-m transect for a total of six plots per site. All understorey plant species <1 m in height inside the frame were destructively harvested. Vegetation was sorted, air dried and packed in paper bags by functional types (deciduous shrub, evergreen shrub, graminoid, forb, moss, lichen). In the laboratory, samples were placed in a drying oven at 60 °C for a minimum of 12 hr. Samples were assumed to be 50% carbon by dry biomass (Schlesinger & Bernhardt 2013).

In the centre of each vegetation clip plot a soil core, 4.75 cm in diameter, was taken from the top of the organic soil down to the mineral layer. In the laboratory the core was split in half vertically down the centre. Half of the core was placed in a #10 sieve with a #270 sieve underneath. Cores were picked of roots, which were separated by class (dead roots, forb roots, live roots, all other roots), although analysed together for total below-ground biomass. The sieve was then covered and shaken for 2 min. Remaining roots were then picked and separated. This process was repeated one more time and the #270 sieve was examined for forb roots. The remaining core was then placed in a bin filled with deionized water, and roots from the floating core were separated by class. All roots were then placed in a drying over for 48 hr at 65 °C and re-weighed for dry mass. Samples were assumed to be 50% carbon by dry biomass.

### Statistical analysis

All statistical analysis was performed in R (R Foundation for Statistical Computing, Vienna, AT). Here, we report statistics from multivariate analysis of understorey species abundance and present the data in a univariate form. Multivariate analysis was used to allow us to determine the effect of fire severity while also testing for other controls on vegetation communities, including a suite of environmental variables. In all multivariate analyses, species abundance data were 4th root- and Hellinger-transformed, given that the data contained many zeros (Legendre & Gallagher 2001). Environmental variables were log-transformed in order to achieve normality. For analyses of species abundance, fire event name (representative of different geographic locations and time of fire) was considered a random variable to account for stochastic differences among fires or differences in fire weather that were beyond the scope of this study.

To test the effects of depth of burn, environment and post-fire tree recruitment on understorey regeneration, we performed redundancy analysis (RDA; Legendre & Gallagher 2001). RDA is a form of constrained ordination that examines how much of the variation in one set of variables explains the variation in another set of variables. It is the multivariate analogue to multiple linear regression. In addition, we determined the effects of depth of burn, environment and post-fire tree recruitment on both vascular and nonvascular functional group composition. Variation decomposition was then used to partition the variation in the response table with respect to the explanatory matrices, and we reported the adjusted $R^2$, and display these results with univariate figures. Finally, forward selection was used to determine the strength of each explanatory variable within a given matrix then visually interpreted with a biplot.

Landscape position can be used as a proxy for soil moisture as flat uplands receive high amounts of insolation and are drier because of down-slope movement of soil water compared to wetter lowlands that receive run-off from upland areas. South-facing slopes are generally drier than north-facing slopes due to increased solar radiation. As such, ANOVA was used to determine if landscape position (north-facing slope, south-facing slope, flat upland or lowland), used as a proxy for soil drainage, significantly influenced the size of the vegetation carbon pools, followed by a *post-hoc* Tukey's HSD comparison of means test.

The RDA analysis was used to determine the relative influence of environment, canopy tree species density, understorey composition and fire severity on the size of the vegetation carbon pool. Due to the large number of understorey species, a PCA reduced the amount of information into axes explaining most of the variation present in the original species matrix. Axes with eigenvalues >2 were used in the subsequent RDA analysis. Given that the axes from the vascular and nonvascular species matrix were not significant predictors of vegetation carbon pools, we did not interpret those PCA axes.

Figure 1 provides an overview of all significant controls on species composition and vegetation carbon pools. All possible combinations of interactions were tested and only the significant ones are displayed here. The adjusted $R^2$ is shown for each interaction to indicate the strength of that control on species composition.

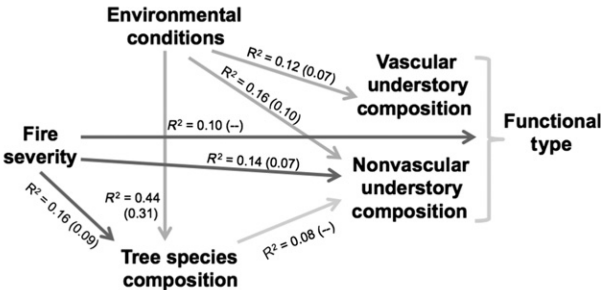

**Fig. 1.** Diagram illustrating the significant controls on species composition and vegetation carbon pools (shown with arrows) with the associated adjusted $R^2$ and pure effect provided in brackets. We were unable to determine pure effect for the relationship between fire severity and functional type, and tree species composition and nonvascular species composition due to statistical artifacts from correlations.

## Results

### Controls on understorey species abundance 10 yrs post-fire

We used vegetation composition, fire severity and environmental variables to test the controls on understorey species abundance 10 yrs post-fire. Environmental variables, which varied between sites, were not significantly influenced by fire severity (Fig. 1). As predicted, fraction of organic layer consumed was related to the tree stand density ($R^2$ = 0.16, $P < 0.05$). Ordination of post-fire vegetation data showed that deciduous tree abundance increased with fraction of organic soil consumed. The abundance of deciduous stems (Fig. 2a), primarily *P. tremuloides* and *B. neoalaskana,* was higher in sites with shallower post-fire organic layer depths, as well as sites that had a larger fraction of organic soil consumed during the fire. Forward selection did not identify a significant relationship between fire severity and black spruce stem density. Environmental variables were also a significant control on tree species abundance ($R^2$ = 0.43, $P < 0.001$). Using forward selection, we identified elevation as the dominant environmental control on tree species abundance, in particular the abundance of *Salix* spp. at 220–940 m a.s.l. (Fig. 3). This indicates that deciduous recruitment, while dependent on fire severity, is also highly dependent on environmental conditions that are not influenced by fire.

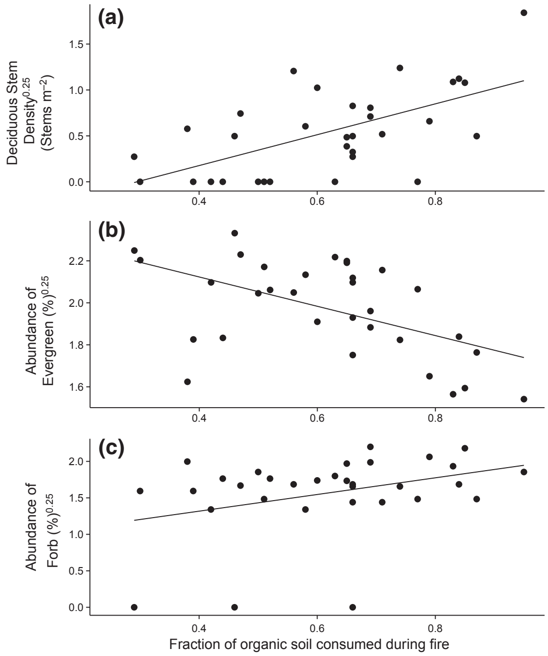

**Fig. 2.** Relationship between fraction of organic soil consumed and (**a**) deciduous tree stem density, (**b**) abundance of understorey evergreen shrub species, (**c**) and abundance of understorey forb species.

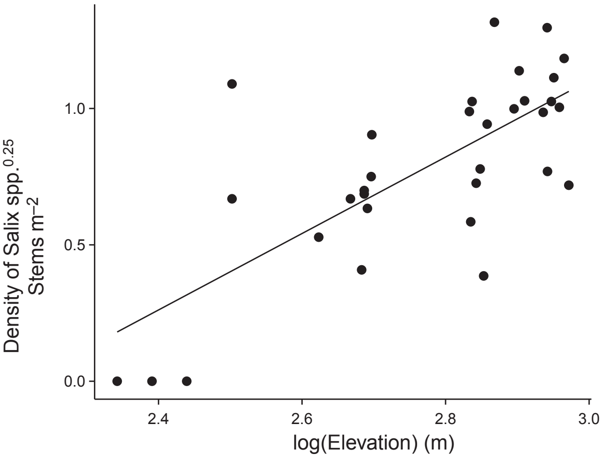

**Fig. 3.** Relationship between the density of *Salix* spp. (stems·m$^{-2}$) and elevation (m).

The RDA analysis revealed that fire severity was not related to total vascular understorey species abundance. However, fire severity significantly influenced understorey species abundances at the level of plant functional types ($R^2$ = 0.10, $P < 0.01$). Evergreen shrub species abundances (i.e. *Ledum decumbens, Vaccinium uliginosum* and *Vaccinium vitis-idaea)* were negatively related to the amount of organic soil consumed during the fire (Fig. 2b). Alternatively, forb abundance (i.e. *Chamerion angustifolium*) increased as the fraction of organic soil consumed increased (Fig. 2c). Environmental variables also influenced vascular understorey species abundances ($R^2$ = 0.12, $P < 0.05$). Forward selection identified elevation and mineral soil pH as the most influential environmental variables in this analysis ($P < 0.05$). However, neither mineral soil pH nor elevation was affected by fire severity. This suggests that the environment serves as a strong control on understorey vascular species composition, independent of landscape variation in fire severity.

The RDA analysis revealed that fire severity was the strongest control on the abundance of nonvascular understorey species ($R^2 = 0.14$, $P < 0.05$). Fire-intolerant species such as *Sphagnum* spp. decreased in abundance with increasing fraction of organic soil consumed (Fig. 4a; $R^2 = 0.32$, $P < 0.001$), while fire-adapted species increased in abundance (Fig. 4b). Nonvascular species were also related to tree species abundances ($R^2 = 0.08$, $P < 0.05$). Forward selection identified *P. tremuloides* as an influential tree species on nonvascular understorey species, as the abundance of fire-adapted moss species (*Polytrichum strictum* and *Ceratodon purpureus*) increased with increased *P. tremuloides* abundances. Environmental conditions were also related to nonvascular understorey species abundances ($R^2 = 0.16$, $P < 0.05$). Forward selection identified soil bulk density as the most influential environmental variable in this analysis ($P < 0.05$). Soil bulk density was not affected by fire severity, suggesting that this is a control on nonvascular understorey species that is independent of fire severity.

### Recovery of vegetation carbon pools following wildfire

Biomass accumulation data were used to test the effects of fire severity of above-ground and below-ground vegetation carbon pools. Above-ground and below-ground vegetation carbon pools averaged 1.63 ± 0.21 and 1.68 ± 0.13 $\text{MgC}\cdot\text{ha}^{-1}$, respectively. Across all landscape positions, carbon pools associated with roots were approximately half of the total vegetation carbon pool. Lowlands had the largest below-ground plant carbon pools (Fig. 5).

Total, above-ground, and below-ground vegetation carbon did not vary among landscape positions (Fig 5; total vegetation biomass: $F_{[3,27]} = 0.2704$, $P > 0.05$; above-ground biomass: $F_{[3,27]} = 1.017$, $P > 0.05$, below-ground biomass: $F_{[3,27]} = 2.334$, $P > 0.05$). Deciduous shrub biomass accounted for the largest proportion of above-ground vegetation biomass in all landscape positions except lowlands ($F_{[5,185]} = 9.83$, $P < 0.05$). In lowlands, evergreen shrubs accounted for the largest proportion of the above-ground vegetation biomass pool.

The RDA analysis revealed no relationships between vegetation carbon pools and fire severity metrics or environmental parameters. We also found no relationships between carbon pools and tree abundance and understorey abundances at both the species and plant functional level.

## Discussion

Recent literature has suggested that increases in fire frequency (Kasischke & Turetsky 2006; Bond-Lamberty et al. 2007) and depth of burning (Johnstone & Chapin 2006; Turetsky et al. 2011) could alter the resiliency of boreal forests. Following severe fires that remove a large portion of the organic soil layer, a coniferous stand may move from

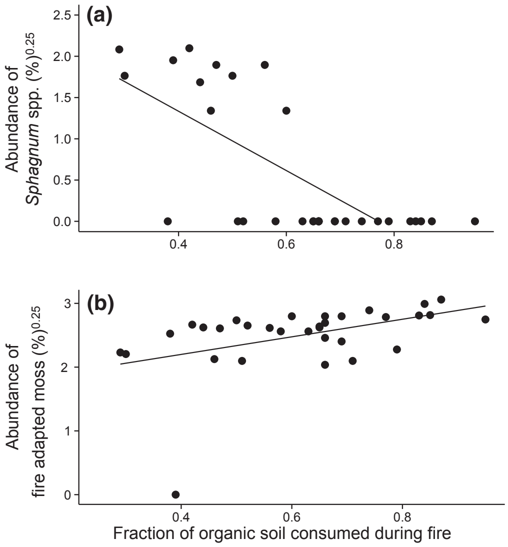

**Fig. 4.** Relationship between fraction of organic soil consumed during the fire and (**a**) abundance of *Sphagnum* spp. mosses and (**b**) abundance of fire-adapted mosses.

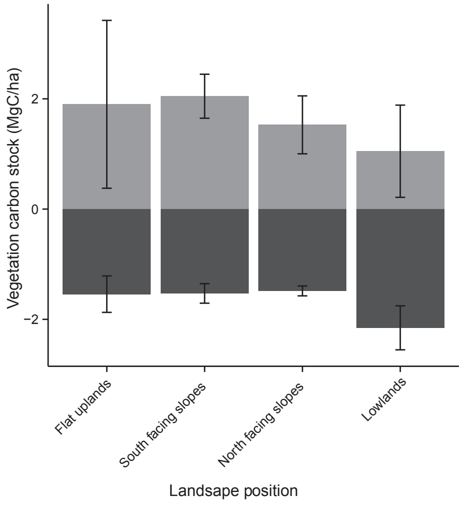

**Fig. 5.** Mean above-ground (white) and below-ground (dark grey) vegetation carbon pool by landscape position, ordered from driest to wettest. Positive values are above-ground carbon stocks while negative values indicate below-ground carbon stocks. There was no significant difference in total, above-ground or below-ground vegetation carbon pool between landscape positions.

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a domain of self-replacement to a new successional trajectory of increasing dominance by deciduous species. This state change occurs because deciduous species are more competitive in colonizing very shallow organic soil layers or mineral soils exposed by combustion (Johnstone et al. 2010b). Turetsky et al. (2011) report a series of Alaskan black spruce stands that burned during a severe fire year (2004). By sampling across a range of landscape conditions as well as early vs late season fire activity, they documented a range of depth of burn and resulting ecosystem carbon losses. In this study, our objective was to determine relationships between the amount of organic soil consumed during the 2004 fires and patterns of understorey plant succession over the subsequent 10-yr period. We were primarily interested in understanding whether these relationships were consistent across a range of topographic positions, including upland and lowland forests.

Our results show that the fraction of organic soil consumed during the fire explains a significant amount of variation in understorey species abundances 10 yrs post-fire. For example, we found that increasing fraction of organic soil consumed during fire was associated with decreases in the abundance of *Sphagnum* mosses and evergreen shrubs. Because these two functional groups are important in maintaining thick organic layers that lead to self-replacing conifer stands (Johnstone et al. 2010a), declines in their abundance support the hypothesis that increasing fire severity promotes a deciduous state (Johnstone & Chapin 2006).

Surprisingly, the trend between fire severity and deciduous cover was consistent across all landscape positions, and we found no evidence of an interaction between landscape position and vegetation composition. We had hypothesized that lowlands, which tend not to experience deep burning, would not display the same trends as upland systems. Instead, we found relatively consistent response of vegetation across a range of topography and soil moisture conditions driven primarily by the fraction of organic soil consumed during the fire.

Our results emphasize the dynamic nature of the moss layer during early stages of post-fire succession. In mature sites, S*phagnum* mosses, which are known to have low thermal conductivity, high porosity and higher water-holding capacity than feather mosses (Donnell et al. 2008), inhibit deep burning and allow residual organic soils to persist across multiple fire rotations (Turetsky et al. 2012). As expected, our results show that *Sphagnum* abundance declines with increases in the fraction of organic soil consumed, indicating that declines in *Sphagnum* abundance begin once approximately 40% of the organic soil is consumed during the fire. Once 65% of the organic layer is consumed, *Sphagnum* mosses were no longer present across the suite of sites sampled in this study. This suggests that if depth of burn increases as predicted (Turetsky et al. 2011), then *Sphagnum* mosses may not persist across multiple fire rotations, thereby promoting shallower organic soils that support a deciduous domain. Not surprisingly, declines in *Sphagnum moss* abundance were positively correlated with increases in the abundance of fire-adapted mosses such as *P. strictum* and *C. purpureus*. In contrast to *Sphagnum* spp., these mosses tend to have high turnover rates and support little water retention (Turetsky et al. 2012), thereby contributing to drier soil conditions that tend to support deeper burning during fire events.

Similarly, we found that declines in evergreen shrub species, due to increased fraction of organic soil consumed, were positively correlated with increases in graminoid and forb species. This is important, given that these functional groups have very different turnover rates and water-holding capacities. Evergreen shrub species have low evapotranspiration rates (Bonan 1991; Liu et al. 2005) and poor litter quality that support slow rates of decomposition (Van Cleve & Viereck 1981). In contrast, graminoid and forb species have higher litter quality, more rapid nutrient cycling and rapid decomposition (Chapin et al. 1996; Hobbie 1996). A switch from an evergreen shrub-dominated understorey to a graminoid-/forb-dominated understorey will likely lead to faster nutrient cycling and the persistence of shallow organic layer domains and deciduous forests.

Together, our results highlight the importance of understorey communities in the ecosystem state changes associated with boreal wildfire regimes (Johnstone et al. 2010a). Though consideration of ‘conifer’ and ‘deciduous’ domains emphasize canopy dynamics, both moss and herbaceous components of the understorey can play important roles in the resistance of conifer forests to deep burning (as is the case for *Sphagnum* and feather mosses). Conversely, understorey species such as graminoids can help promote deciduous cover by contributing to fast nutrient cycles. Overall, the interaction between fire severity and both the understorey and canopy vegetation communities are expected to influence future regimes. Compared to coniferous stands, deciduous stands have lower canopy bulk density, less flammable resins and reduced abundance of ground fuels, all of which contribute to lower flammability (Johnson 1992; Hely et al. 2000). By having a lower potential to burn, deciduous stands may reduce fire activity in general or may act as partial fire breaks, thereby reducing the potential for fire to spread across the landscape (Amiro et al. 2001). Deciduous vegetation has a higher albedo than conifer vegetation, which is important to post-fire net radiative balance (Randerson et al. 2006). Increasing deciduous extent may also lead to less flammable fuel accumulation in the landscape, thereby creating a dampening effect on future fire cycles (Cumming 2001; Duffy et al. 2007). On the other hand, given the right fire weather conditions, deciduous fuels will readily combust and not act as a fire break (Flannigan et al. 2005). Thus, understanding how changes in vegetation as a result of changing fire activity will influence future warming or disturbance regimes remains a key area of future research.

We predicted that large carbon losses associated with severe burning could be offset quickly by the rapid productivity of deciduous species. Surprisingly, we found no relationships between fire severity, landscape characteristics and the size of vegetation carbon pools 10 yrs post-fire. Our results are contrary to those of Alexander et al. (2012), who found that 20–59-yr-old stands undergoing shifts from black spruce to deciduous dominance were associated with larger above-ground carbon pools. While we focused on biomass associated with understorey species <1 m in height, Alexander et al. (2012) focused on trees >1.5 m in height with basal area ranging from 3.6 to 12.2 $cm^2 \cdot m^{-2}$. Our results show that the re-growth of the understorey biomass pool is relatively uniform across the landscape and across fire conditions.

Previous work from Turetsky et al. (2011) estimated that soil carbon loss in these sites during the Alaska fires of 2004 was approximately 29.48 ± 13.19 and 49.93 ± 26.47 $MgC \cdot ha^{-1}$ in early vs late season fires, respectively. Ten years post-fire, our results show that the understorey vegetation carbon pool stores 3.36 ± 1.54 $MgC \cdot ha^{-1}$ in sites that experienced early season burning and 2.87 ± 0.91 $MgC \cdot ha^{-1}$ in sites that burned during late season fires. This suggests that approximately 11% of the carbon lost during the combustion of the organic layer has been regained in the vegetation over the past decade in early season fire sites, while only 5% of ecosystem carbon losses have been regained in the vegetation following late season fire activity. Understanding these patterns of plant carbon uptake is important for understanding longer-term turnover and development of soil carbon pools (Melvin et al. 2015).

Our data, in combination with other published studies on post-fire vegetation carbon stocks, suggest that it would take approximately 50 yrs to re-accumulate the carbon lost during organic layer combustion (Fig. 6), in comparison to current fire return intervals in this region of between 80 and 120 yrs (Hart & Chen 2006). Increasing fire frequency, severity or late season burning could cause ecosystems to be a net source of carbon to the atmosphere across multiple fire cycles. However, this will only occur if there is sufficient organic soil to burn. Eventually, thick organic layers will be consumed, and the remaining shallow organic soils or exposed mineral soils will remain and persist post-fire. On the other hand, Alexander et al. (2012) found that shifts from black spruce stands to higher deciduous cover lead to a substantial increase in above-ground carbon accumulation in intermediate-aged stands. Despite these rapid rates of plant biomass accumulation, it is unclear how long this carbon could be preserved in this ecosystem state with fast turnover rates (relative to the conifer domain), and whether ultimately much of this carbon will be transferred to soil layers. Thus, while it is clear that carbon losses associated with combustion as well as carbon gains via plant re-growth will be altered in a warming world, the balance between these processes will depend on a variety of factors, such as fire behaviour, but also plant traits and post-fire nutrient cycling.

**Fig. 6.** Change in total vegetation carbon pools with time following fire in black spruce stands. Data are from this study and from published literature values. We fitted a polynomic relationship to the data ($y = -0.0022x^2 + 0.9222x - 5.317, R^2 = 0.92329$).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Location, environmental conditions and organic layer depths of sites sampled during the 2015 field season.