

Predicting Ecosystem Resilience to Fire from Tree Ring Analysis in Black Spruce Forests

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ABSTRACT

Climate change has increased the occurrence, severity, and impact of disturbances on forested ecosystems worldwide, resulting in a need to identify factors that contribute to an ecosystem's resilience or capacity to recover from disturbance. Forest resilience to disturbance may decline with climate change if mature trees are able to persist under stressful environmental conditions that do not permit successful recruitment and survival after a disturbance. In this study, we used the change in proportional representation of black spruce pre- to post-fire as a surrogate for resilience. We explored links between patterns of resilience and tree ring signals of drought stress across topographic moisture gradients within the boreal forest. We sampled 72 recently (2004) burned stands of black spruce in interior Alaska (USA); the relative dominance of black spruce after fire ranged from almost no change (high resilience) to a 90% decrease (low resilience). Variance partitioning analysis indi-

cated that resilience was related to site environmental characteristics and climate-growth responses, with no unique contribution of pre-fire stand composition. The largest shifts in post-fire species composition occurred in sites that experienced the compounding effects of pre-fire drought stress and shallow post-fire organic layer thickness. These sites were generally located at warmer and drier landscape positions, suggesting they are less resilient to disturbance than sites in cool and moist locations. Climate-growth responses can provide an estimate of stand environmental stress to climate change and as such are a valuable tool for predicting landscape variations in forest ecosystem resilience.

Key words: resilience; climate change; drought stress; fire severity; dendroecology; *Picea mariana*; boreal forest; seedling regeneration.

INTRODUCTION

Forest ecosystem types and species distributions are fundamentally linked to climate and are expected

to alter in response to climate change (Trumbore and others 2015). Unprecedented rates of climate warming over the past decade have increased forest drought stress and mortality worldwide (Allen and others 2010). However, the most dramatic shifts in forested ecosystems are not expected to be in direct response to climate change, but are more likely to stem from climate change acting in concert with disturbance (Ghazoul and others 2015). Disturbances can significantly alter forest ecosystem structure, growth, and successional trajectories (McCullough and others 1998). As environmental

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conditions continue to change, the occurrence, severity, and impact of disturbances on forested ecosystems are increasing across the globe (Flannigan and others 2009; Turner 2010; Seidl and others 2014). Therefore, there is a need to identify factors that may signal changes in the ability of forested ecosystems to recover from disturbance.

Resilience theory is a useful framework to study the impacts of climate change on forested ecosystems. We define resilience as the ability of an ecosystem to absorb disturbance, re-organize, and maintain structural and functional integrity (Folke 2006). When the ecosystem's resilience is exceeded, it will transform to a new state that has different properties, functions, and feedbacks, and from which the probability of return to the previous state is low (Folke 2006). Depending on the ecosystem and the factors influencing resilience, shifts to new states can be gradual or abrupt. Environmental stresses can act to decrease ecosystem resilience and in the face of disturbance cause abrupt changes in stability domains (Rappport and Whitford 1999). The ability to detect changes in ecological resilience prior to disturbance is central for predicting changes in ecosystem stability under rapid climate change and novel environmental conditions (Scheffer and Carpenter 2003; Reyer and others 2015).

The boreal forest is an excellent system to study changes in ecosystem resilience to climate change and disturbance. Boreal forests have warmed at nearly twice the rate of the global average during the last 30 years (IPCC 2013). Large fires are common in the boreal forest (Johnson 1992), and this biome is considered highly vulnerable to shifts in vegetation communities as climate continues to change (Gonzalez and others 2010). In addition, forest composition in regions of frequent fire is heavily influenced by patterns of recovery immediately after disturbance (Gutsell and Johnson 2002; Johnstone and others 2004; Shenoy and others 2011), making it possible to infer changes to resilience within a few years. Shifts in vegetation communities are also influenced by pre-disturbance species composition and landscape variation in environmental conditions (Thompson and others 2009). Therefore, changes in resilience are unlikely to be homogenous across the landscape and there is substantial uncertainty regarding the factors contributing to possible threshold changes in boreal forest stability.

In this study, we examine landscape variations in forest resilience to disturbance throughout interior Alaska, an area that has undergone significant warming in the last three decades (Wolken and

others 2011; IPCC 2013). Warmer and drier growing conditions have resulted in drought stress across regional and topographic moisture gradients in forests of black spruce (*Picea mariana*) in Alaska (Walker and Johnstone 2014; Walker and others 2015). Stress signals in conifer tree growth may indicate declines in boreal forest resilience if mature trees currently survive in environments that do not permit successful post-fire recruitment and survival (Bouchon and Arseneault 2004). Post-fire regeneration is affected by microclimate conditions corresponding with topographic position (Johnstone and others 2010b; Dodson and Root 2013) and directly influenced by temperature and precipitation regimes (Hogg and Wein 2005). Additionally, disturbances can rapidly change environmental condition which might exceed a tree species tolerance limits for establishment (Astrom and others 2007). For serotinous species like black spruce, a strong correlation between pre-fire species basal area and post-fire seed production typically leads to stand self-replacement after fire (Van Cleve and Viereck 1981; Greene and Johnson 1999). Return intervals for fire in Alaskan spruce forests are typically around 100 years and thus are rarely long enough to permit relay patterns of canopy dominance (Van Cleve and Viereck 1981; Johnstone and others 2010a). Instead, changes in canopy composition are often triggered by disturbance, and in the initial decade after fire the relative abundance of seedlings is strongly predictive of future canopy composition (Gutsell and Johnson 2002; Johnstone and others 2004; Shenoy and others 2011). Thus, changes in the proportion of black spruce before and after fire are a reasonable proxy for ecosystem resilience, as this measurement directly estimates potential shifts from black spruce to deciduous canopy dominance over the next fire-free period. Furthermore, once canopy composition has changed, the new composition is likely to be perpetuated in future fire cycles by the same regeneration feedbacks that have maintained stable cycles of black spruce dominance in the past (Greene and Johnson 1999; Johnstone and others 2010a). Shifts from black spruce to a more deciduous-dominated landscape will affect climate-albedo feedbacks, nutrient cycling and plant productivity, future fire regimes, wildlife habitat, and natural resources for subsistence (Chapin and others 2010).

We tested the relative influence of pre-fire stand composition, environmental factors, and the growth-climate relationships of trees prior to fire (an indication of pre-disturbance stress) on our estimate of resilience. We hypothesized that legacy

effects of pre-fire vegetation and constraints imposed by site-level environmental conditions could be important controls on post-fire regeneration patterns in these forests; if these vary in a predictable way across the landscape, they may provide a tool for estimating future resilience of black spruce forests. We further anticipated that growth-climate responses could be a useful indicator of stand vulnerability to state changes under climate change and predicted that stands experiencing the greatest degree of pre-fire drought stress would show the largest post-fire compositional change (least resilience to disturbance). Our analysis provides insight on how ecological resilience is influenced by pre-fire composition, climate sensitivity of the pre-fire forest, and environmental factors across broad landscape gradients in a single forest type.

METHODS

Study Area

Our study area was the boreal forests that lie south of the Brooks Range and north of the Alaskan Range in interior Alaska, USA. Forests stands in the uplands of this region are principally dominated by black spruce, intermixed with patches of trembling

aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) (Van Cleve and Viereck 1981). Based on climate records from Fairbanks, Alaska, the average annual temperature is -2.5°C , mean monthly temperatures range from -23.1°C in January to $+22.8^{\circ}\text{C}$ in July, and there is a relatively short growing season of 135 days or less (Hinzman and others 2005). Annual precipitation is low and decreases from west to east, averaging 286 mm y^{-1} , 35% of which falls as snow (Hinzman and others 2005). The majority (75–80%) of the boreal forest in interior Alaska is underlain by permafrost (Osterkamp and Romanovsky 1999); permafrost tends to be absent from south-facing slopes and floodplains (Van Cleve and others 1983).

Field and Laboratory Methods

We established 72 sites within three large burned areas that arose from multiple fire ignitions in 2004 (Figure 1). Within each burn complex, we established 24 sites dominated by black spruce prior to burning. We established 12 pure black spruce sites that were stratified by landscape position, with three sites each of moist lowland (M), north-facing midslope (N), south-facing midslope (S), and dry upland (D) positions within each burn complex. In addition, we established six sites each in mixed

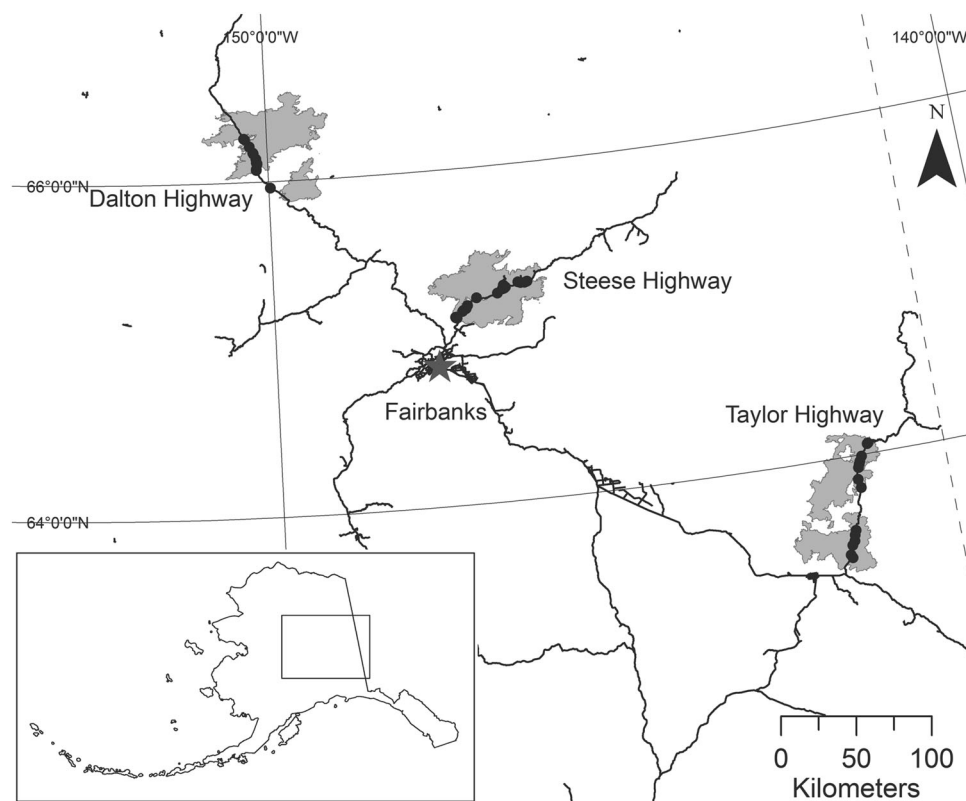


Figure 1. Location of 72 study sites (black dots), located in three separate 2004 burn complexes (gray), along the Dalton, Steese, and Taylor Highways in the region surrounding the city of Fairbanks (star) in interior Alaska.

trembling aspen/black spruce stands (TA) and mixed paper birch/black spruce stands (PB), which were generally located in drier and warmer landscape positions within the burn complexes. To randomize site selection, we carried out an initial reconnaissance that identified all areas (~2–3 times larger than a site) that had mixed tree species composition or that were black spruce dominated and fit the predetermined broad-scale landscape positions and that ranged from 100 m to 1 km from the road. We then randomly selected a subset of all identified locations to sample. Although tree mortality from fire was close to 100%, fires rarely consumed all the branches or bark on a tree (Boby and others 2010); fire-killed tree species were easily identifiable with well-preserved stems when sites were sampled in the summers of 2012 or 2013.

Each site consisted of two parallel 30 m transects separated by 20 m. At each site, we recorded latitude, longitude, and elevation in the center of the 30 m × 20 m area with a handheld GPS, and the slope and aspect with a clinometer and compass. Using these measurements, we calculated a unitless index of heat load that takes into account topographic and latitudinal effects on incoming solar radiation (McCune and Keon 2002). Soil texture class was assessed in the field by hand texturing the uppermost mineral horizon, following the Canadian System of Soil Classification (Branch and others 1987). Understory composition was noted, in particular the presence of indicator species outlined by Hollingsworth and others (2006). Based on understory composition, topography, and drainage conditions adjusted for soil texture, site moisture classes were estimated on a six-point scale, ranging from xeric to subhygric (Johnstone and others 2008).

We estimated pre-fire and post-fire stem density and forest composition by measuring pre-fire (burned) trees and newly established seedlings. We counted all standing or fallen pre-fire trees and measured diameter at breast height (dbh) on all individuals taller than 1.4 m that were originally rooted in two parallel 2 m × 30 m belt transects. We used these data to estimate total density (stems ha⁻¹) and basal area (m² tree area ha⁻¹) of each tree species prior to the fire. To estimate post-fire regeneration, we surveyed all sites for newly established seedlings of post-fire origin. Seedlings were counted within ten randomly positioned 1 m × 1 m quadrats along the two parallel transects for a total sample area of 10 m² per study site. The number and species of all post-fire seedlings, including resprouting stems (distinguishable by size and presence of pre-fire stems), were recorded for

each quadrat and averaged by unit area to determine species-specific seedling densities at each site. Using the pre- and post-fire stem densities, we then calculated the proportion of spruce stems relative to total stems in both the pre-fire and post-fire stand.

At each site, we collected 10 stem disks, ranging in diameter from 2 to 20 cm, at the standard height of 1.4 m from pre-fire black spruce trees randomly selected along the two transects. Stem disks were sanded with increasingly finer sandpaper up to 400 grit to produce visible rings (Cook and Kairiukstis 1990). Annual rings widths were measured on two radii per stem disk (WINDENDRO version 2012c, resolution 0.001 mm). We visually cross-dated each tree ring series against master chronologies developed for each site and region. We quality-checked our cross-dating using COFECHA version 6.06 (Grissino-Mayer 2001).

Growth–Climate Responses

Climate data for each of our study regions was characterized based on spatially interpolated mean monthly temperature and total monthly precipitation for the period 1975–2003 (as per Walker and Johnstone 2014). We calculated a monthly climatic moisture index (CMI) from total monthly precipitation minus monthly potential evapotranspiration (PET), a function of temperature (Hogg 1997). High CMI values signify high moisture availability. Detrending of ring-width chronologies and growth–climate analyses were completed using the R statistical language (R Development Core Team 2012) and followed the methods outlined in Walker and Johnstone (2014) and Walker and others (2015). We calculated bootstrapped correlations of detrended, individual ring-width chronologies with monthly temperature and precipitation over a 17 month climatic window, extending from April of the year preceding growth to August of the current year of growth (1975–2003). From these correlations, we categorized the growth response of each individual tree to temperature and precipitation as positive, negative, mixed, or no response and then calculated the proportion of trees in each temperature and precipitation category for each site (see details in Walker and others 2015). As our previous analyses indicated temperature induced moisture stress in these forest stands pre-fire (Walker and Johnstone 2014), we used the proportion of trees responding negatively to temperature and the proportion responding positively to precipitation as two indicators of stand-level drought stress. Proportion, rather than average site-level response, was used to

account for individual tree growth–climate responses within sites.

We estimated the sensitivity of tree growth to climate at each site using bootstrapped correlations of mean ring-width chronologies for each site and mean monthly temperatures, total monthly precipitation, or monthly CMI. This resulted in 51 radial growth correlations to monthly climate parameters at each site. For subsequent analyses, we used only those growth–climate correlations that elicited a significant response in at least 20% of the sites and that were not highly collinear (Spearman’s rank correlation $\rho > 0.6$). Our selection process resulted in five variables associated with CMI that represented the strongest and most widespread relationships between site-level patterns of tree growth and monthly climate.

Data Analysis

Data analyses were performed using the R statistical language (R Development Core Team 2012). As a proxy for ecosystem resilience, we estimated the change in tree composition (black spruce dominance) after fire as the difference in the proportion of total trees that were black spruce in the pre-fire vs. post-fire stand at the same site. Negative values represent a decrease in the proportion of black spruce trees in the post-fire stand. Using the proportional change in black spruce, rather than spruce or deciduous seedling densities, captures the possible change in species composition following fire. Furthermore, seedling densities are often much higher compared to mature stem density and change over time through self-thinning (Johnson and Fryer 1989), making proportional change in composition a more meaningful measure of resilience than post-fire seedling densities.

We assessed three sets of explanatory variables as potential predictors of the change in black spruce dominance: measures of (a) pre-fire stand composition (pre-fire; 7 variables), (b) site environmental conditions (site; 9 variables), and (c) dendroclimatic variables (dendro; 8 variables) (Table 1). In addition to the two climate–growth responder categories and the five climate–growth correlations (see above), we included average radial growth from 1975 to 2003 for each of the site chronologies in the dendro explanatory matrix (Table 1). We included latitude in the site explanatory matrix to account for the spatial non-independence of sites distributed across three distinct burn scars.

We completed variation partitioning with partial regression using the function ‘varpart’ in the

package ‘vegan’ (Oksanen and others 2013) to determine how variables associated with pre-fire stand composition, site environmental conditions, and dendroclimatic responses (Table 1) were related to changes in black spruce dominance after fire. A stepwise selection process, using model adjusted R^2 and variable retention at a permutation value of $p = 0.05$ (Blanchet and others 2008), identified individual variables within each of three explanatory datasets that were significantly associated with variation in the proportional change of black spruce. We determined the relative influence of each set of explanatory variables by calculating the shared and unique variation explained by the significant variables. The unique variation is the portion of variation accounted for after controlling for all other measured variables. The shared variation is the explained variation that is common to more than one set of explanatory datasets (Legendre and Legendre 2012).

We used boosted regression tree analysis (BRT) in the packages ‘gbm’ (Ridgeway and others 2015) and ‘dismo’ (Hijmans and others 2013) to determine the most important variables explaining the proportional change in black spruce, evaluate potential thresholds in the effects of these explanatory variables, and examine their functional responses. To avoid over-fitting, we only included the explanatory variables that were significant based on the variable partitioning analysis (see above) and removed an additional four variables that were correlated to other explanatory variables (Spearman’s $\rho > 0.4$; Table 1). We fit BRT models using fivefold cross-validation to identify the optimum number of trees (Elith and others 2008) and the following parameters: Gaussian error distribution, a learning rate of 0.001, a bag fraction of 0.5, and tree complexity of three. Next, we used a stepwise selection process that began with the set of candidate predictor variables (Table 1) and tested if the model could be simplified based on changes in the cross-validation (cv) deviance (Elith and others 2008). The lowest cv deviance was obtained by dropping five of the nine predictor variables. We subsequently found no substantial change in cv deviance when tree complexity was reduced to model only main effects, and partial dependencies between response variables and covariates were constrained to monotonic relationships. We used this simplest model form for the final model. We examined the relative influence of the predictor variables by creating partial dependency plots, which represent the effects of each variable on the change in proportion of black spruce after accounting for the average

Table 1. Variables Included in the Three Explanatory Matrices of Pre-fire Composition, Site, and Dendroclimatic Variables for Variance Partitioning Analysis (*), Boosted Regression Tree Analysis (+), and Mixed Effect Models (#)

Matrix	Variable	Units	Mean \pm SD	Range
Pre-fire composition variables	Black spruce density	stems/m ²	0.40 \pm 0.26	0.002–1.18
	Black spruce basal area**#	m ² /ha	8.88 \pm 6.70	0.02–34.55
	Trembling aspen density*	stems/m ²	0.04 \pm 0.07	0–0.25
	Trembling aspen basal area	m ² /ha	4.04 \pm 13.40	0–84.31
	Paper birch density	stems/m ²	0.03 \pm 0.05	0–0.23
	Paper birch basal area*	m ² /ha	1.48 \pm 3.07	0–14.82
	Total deciduous density	stems/m ²	0.06 \pm 0.08	0–0.28
	Latitude**+	radians	1.14 \pm 0.02	1.11–1.17
	Moisture class (1–6)	unitless	2.56 \pm 1.40	1–6
	Elevation (m.a.s.l)**+	m.a.s.l	457.3 \pm 225.9	111–898
Site variables	Slope (radians)*	radians	0.13 \pm 0.13	0–0.47
	Aspect (radians)*	radians	1.39 \pm 0.82	0.21–3.12
	Heat load**+	unitless	–1.54 \pm 0.98	–2.79 to 0.29
	pH**+	unitless	5.69 \pm 0.66	4.45–7.60
	Organic layer depth**#	cm	9.63 \pm 7.55	1.00–41.80
	Mean stand age (ring count at DBH)	years	56.95 \pm 19.81	31.10–131.30
	CMI previous July	Correlation	0.29 \pm 0.17	–0.13 to 0.68
	CMI previous August	Correlation	0.26 \pm 0.19	–0.18 to 0.62
	CMI current April	Correlation	0.30 \pm 0.18	–0.13 to 0.60
	CMI current May**#	Correlation	0.31 \pm 0.16	–0.24 to 0.60
Dendroclimatic variables	CMI current August**+	Correlation	0.25 \pm 0.14	–0.05 to 0.49
	Proportion of trees responding negatively to temperature (prop temp neg)**+	Proportion	0.56 \pm 0.21	0–1
	Proportion of trees responding positively to precipitation (prop precip pos)	Proportion	0.35 \pm 0.19	0–0.86
	Average radial growth (1970–2003)	mm	0.44 \pm 0.22	0.12–0.95

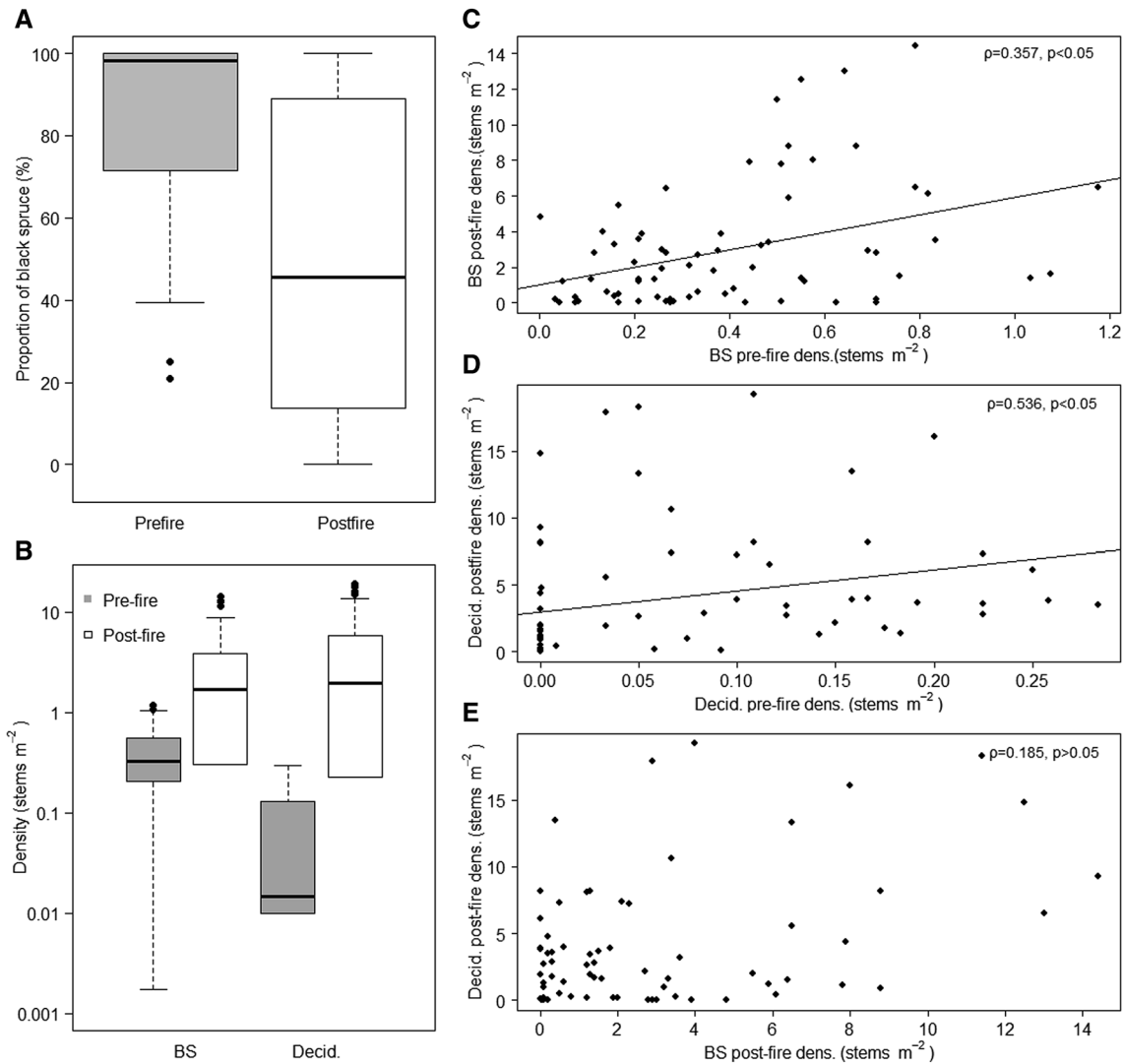


Figure 2. Plots showing: **A** the distribution of the proportion of black spruce trees (%) in the pre-fire and post-fire stands, **B** the distribution of pre-fire (gray boxes) and post-fire (white boxes) stem densities of black spruce and deciduous trees (y-axis is potted on a log₁₀ scale), and the relationships between: **C** pre-fire and post-fire black spruce density, **D** pre-fire and post-fire deciduous density, and **E** post-fire seedling densities of black spruce and deciduous trees.

effects of the other variables included in the BRT model (Elith and others 2008).

To determine how ecosystem resilience may vary among topo-edaphic categories, we assessed how our site type categories related to the proportional change in black spruce and the most important variables explaining this change (identified with the BRT model). We tested the statistical significance of differences between means using a mixed model approach in the ‘lme4’ package (Bates and others 2015) with the change in black spruce proportions and the top three most important variables (Table 1) identified in the BRT analysis as response variables. Variability due to individual sites within site categories was set as a random effect. To visu-

alize the differences between sites, we created boxplots of each of the variables stratified by site type.

RESULTS

Black spruce forests are widespread in interior Alaska, and the 72 sites we sampled in three 2004 Alaskan burn complexes (Figure 1) captured a broad gradient in environmental conditions, pre-fire stand density and composition, and radial growth responses to climate (Table 1). Radial growth and growth responses to climate varied across our study sites. Average radial growth of black spruce from 1975 to 2003 ranged from less

Table 2. Explanatory Variables Selected By Stepwise Selection for Variance Partitioning Models of the Change in Proportion of Black Spruce After Fire

Explanatory set	Variable	R ²
Pre-fire	Trembling aspen density	0.029
	Black spruce basal area	0.015
	Paper birch basal area	0.005
	R ² full model	0.078
Site	Organic layer depth	0.179
	Aspect	0.103
	pH	0.001
	Heat load	-0.003
	Slope	-0.002
	Elevation	0.008
	Latitude	-0.013
	R ² full model	0.308
	Dendro	CMI current May
CMI current August		0.032
Prop temp neg		-0.007
R ² full model		0.153

Variables are listed in order of decreasing statistical significance in the full model. The adjusted R² are for the univariate relationships with bolded values indicating significance ($p < 0.05$). R² for the model with all selected variables is also included.

than 1.5 mm y⁻¹ in stands on north-facing slopes and moist lowlands to more than 9 mm y⁻¹ on south-facing slopes and in mixed black spruce–deciduous stands. Of all the growth–climate responses examined, correlations with CMI in the previous and current growing season were the strongest, eliciting significant responses in over 40% of the stands (Online Appendix 1). Specifically, correlations with CMI in May of the current growing season were significant in over 50% of stands and on average, radial growth was positively correlated ($r = 0.32$) to this climate parameter. A positive response to CMI in May signifies that radial tree growth is greater when more moisture is available in the spring. The strongest positive responses were in dry upland sites and mixed black spruce–deciduous stands. Within most stands, the majority of trees responded negatively to temperature, and a smaller proportion also responded positively to precipitation (Table 1).

Pre-fire tree species composition and density varied across our study sites. Black spruce stems comprised on average 98% of stems in black spruce stands and 65% of stems in mixed stands before the 2004 fires. The density of black spruce stems in pre-fire stands ranged from near zero, on a sparsely treed north-facing slope, to 1.7 stems m⁻² in a mixed stand (Figure 2). The density of deciduous

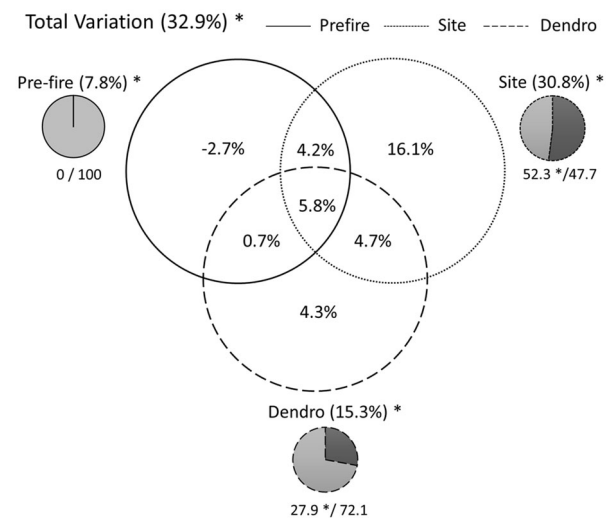


Figure 3. Venn diagram showing partitioning of variation in the change in proportion of black spruce after fire in relation to three explanatory datasets. The non-overlapping sections represent the proportion of unique explained variation, and the overlapping sections represent the shared portion of explained variation for each explanatory dataset in relation to the response variable. Additional pie charts show the total variation (in parentheses) partitioned into unique and shared variation (%) explained by each explanatory dataset of pre-fire stand composition, site characteristics, and dendroclimatic responses of the pre-fire stand. See Table 1 for specific variables within each explanatory variable set. The significance (*) is based on adjusted R² values with $p < 0.05$. Note: the significance of the shared variation of each explanatory dataset cannot be tested.

trees in pre-fire stands was near zero in all the black spruce sites and reached a maximum of 0.28 stems m⁻² in the mixed stands. Although few mature deciduous trees were encountered in the pre-fire pure black spruce stands, we observed many post-fire deciduous seedlings. The relative proportion of black spruce trees to total trees decreased from pre-fire to post-fire (Figure 2A) in over 85% of sites. As expected for young stands that have not yet experienced self-thinning, post-fire stem densities of both black spruce and deciduous trees (trembling aspen and paper birch combined) were greater than pre-fire stem densities (Figure 2B). Post-fire spruce density was positively correlated with pre-fire spruce density ($\rho = 0.357$, $p < 0.05$) (Figure 2C). Similarly, post-fire deciduous density was positively correlated with pre-fire deciduous density ($\rho = 0.536$, $p < 0.05$) (Figure 2D). However, we did not observe any significant relationship between post-fire densities of spruce and deciduous seedlings ($p > 0.05$) (Figure 2E).

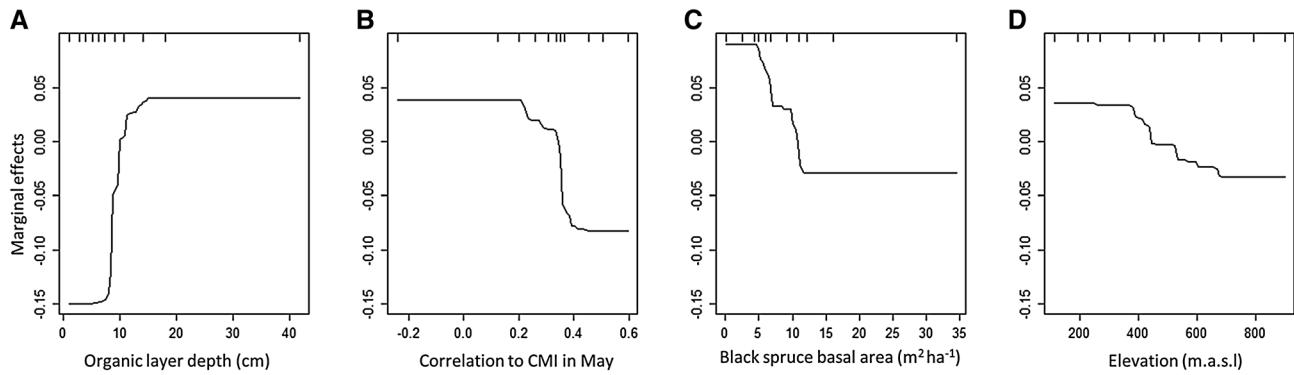


Figure 4. Partial dependency plots based on output from a boosted regression tree (BRT) model that explained 25% of the variation in the change in proportion of black spruce after fire. *Plots* represent the marginal effects of: **A** organic layer depth (relative influence: 42.3%), **B** radial growth correlation to climate moisture index in May of the current growing season (relative influence: 22.9%), **C** black spruce pre-fire basal area (relative influence: 22.5%), and **D** elevation (relative influence: 12.3%), when all other variables are held constant. The BRT included only main effects and was constrained to monotonicity. *Tick marks* at the top of each plot represent the 10% quantiles of the explanatory variable distributions.

In modeling the change in proportional representation of black spruce pre- to post-fire, initial stepwise selection chose three of seven pre-fire stand composition variables, seven of ten site variables, and three of eight dendroclimatic response variables (Table 2). The variance partitioning model with all explanatory datasets explained almost 33% of the variation in the response variable (Figure 3). Only the explanatory datasets of site and dendroclimatic variables had significant total and unique explanatory contributions; pre-fire stand composition explained 7.8% of the variation, but had no unique explanatory contributions (Figure 3).

The final model of the BRT analysis explained 25% of the variation in the change in proportional representation of black spruce pre- to post-fire. This model consisted of four of the possible nine predictor variables, modeled with only the main effects, and was constrained to monotonicity. Of the four explanatory variables included in the final BRT model, post-fire residual organic layer depth had the strongest relative influence (Figure 4). Growth response to CMI in May, pre-fire black spruce basal area, and elevation also contributed to explaining the proportional change in black spruce composition (Figure 4). Partial dependency plots indicate that the greatest change in black spruce occurred at sites with thin post-fire organic layers, a positive response to CMI in May, a relatively large black spruce basal area, and located at slightly higher elevations (Figure 4).

In exploring how our predetermined site type classification corresponded to the change in black spruce proportions, we found that the south (S) and mixed spruce–deciduous (TA and PB) stands experienced the greatest amount of composition

change (Table 3 and Figure 5). Organic layer depth varied among site types, with the lowest depth in mixed (TA and PB) stands, and greatest depth in moist (M) stands. Pre-fire stands also differed in black spruce basal area among site types, with the lowest in moist sites. Although site types were specifically selected to capture a topographic gradient in moisture availability, stand-level correlations between tree rings and May CMI were similar and largely positive among all site types (Table 3 and Figure 5).

DISCUSSION

Patterns of black spruce recovery after fire across our study landscape were related to environmental gradients and tree ring indicators of climatic stress. We observed a decrease in the proportion of spruce relative to total trees from the pre-fire to the post-fire stand in nearly all examined stands, indicating shifts from black spruce dominated stands to mixed or deciduous-dominated stands. However, these shifts were not uniform across the landscape. Forest stands most likely to show the largest change in black spruce dominance, and therefore the lowest resilience to disturbance, were those that had relatively thin post-fire organic layer depths and showed dendroclimatic indications of recent drought stress. These sites were generally located at warmer and drier landscape positions, suggesting a landscape pattern of lower resilience to disturbance compared to sites in cool and moist locations. Our results suggest that changes in ecological resilience and post-disturbance successional trajectories have a deterministic component that is likely to vary in a predictable way at the landscape scale.

Table 3. Mixed Effect Models to Test for Differences Among Site Types in Observed Changes in Black Spruce Proportion After Fire, as well as Measures of Post-fire Organic Layer Depth, Pre-fire Black Spruce Basal Area, and Pre-fire Stand Response to May CMI (Current Year)

Model coefficients (site types)	Black spruce proportion (1 to -1)	Organic layer depth (cm)	Black spruce basal area (m ² /ha)	Correlation to May CMI
Intercept (Dry)	-0.237 ± 0.079	12.290 ± 1.961	12.026 ± 1.969	0.305 ± 0.049
North	-0.042 ± 0.112	3.690 ± 2.772	-5.442 ± 2.783	-0.102 ± 0.069
South	-0.156 ± 0.096	-3.367 ± 2.772	1.893 ± 2.783	0.055 ± 0.069
Moist	0.161 ± 0.096	-5.967 ± 2.772	-9.224 ± 2.783	-0.102 ± 0.069
Trembling aspen	-0.230 ± 0.097	-7.533 ± 2.401	-5.390 ± 2.410	0.065 ± 0.060
Paper birch	-0.182 ± 0.097	-6.252 ± 2.401	-0.787 ± 2.410	0.035 ± 0.060

Bolded values indicate significance ($p < 0.05$).

Ecological resilience is the ability of an ecosystem to recover structural and functional integrity after disturbance (Folke 2006). However, the dynamics of disturbance and recovery in forested ecosystems often exceed the timescales of ecological field studies, making measurements of ecological resilience extremely difficult. In this study, we evaluated forest resilience based on patterns of early seedling regeneration that we assume reflect the composition of future forest stands. Although we expect sites with high seedling densities to undergo self-thinning, repeated observations after fire across a range of black spruce stands indicate that the relative abundance of species in the initial 3- to 7-year period of post-disturbance regeneration is maintained through 2–3 decades of succession (Gutsell and Johnson 2002; Johnstone and others 2004; Shenoy and others 2011). Furthermore, detailed stand age reconstructions in western boreal forests indicate that for at least a century of successional development the canopies of conifer and mixed stands are composed of trees that recruited shortly after fire (Johnson and others 1994; Gutsell and Johnson 2002). The short duration of the post-fire recruitment window is strongly influenced by the decrease in seedbed quality associated with post-fire recovery and regeneration of understory moss and vegetation, which effectively impairs continuous seedling establishment and results in relatively even aged stands (Johnstone and Chapin III 2006). Delayed recruitment is severely constrained by poor seedbeds (Brown and Johnstone 2012) and suppression of growth in the forest understory (Johnson and others 1994) and is unlikely to alter the patterns we observed in initial post-fire forest composition. Alternatively, it is possible that the mixed black spruce/deciduous stands could undergo relay succession, during which deciduous trees may initially dominate but their shorter life spans and shade intolerance would lead to increasing spruce dominance over time. However, aging of mixed stands in interior Alaska indicate that canopy succession to spruce dominance is rare even after more than 200 years (Kurkowski and others 2008). This, in combination with the relatively short fire cycle of boreal forests (<150 years) (Kasischke and others 2010), indicates that the initial post-fire patterns of forest composition are likely to persist.

A primary factor underlying resilience of northern boreal black spruce forests through several fire cycles is how fire affects soil organic layer depth. Historically, low-severity fires in moist and cool black spruce forests likely left a considerable portion of the organic layer intact (Johnstone and

others 2010a). For successful establishment to occur on the partially combusted surface organic layers, a high seed input is needed, such as that from the aerial seed bank stored in black spruce semi-serotinous cones. Small seeded deciduous species, such as aspen and birch, are rarely able to establish on this low-quality seedbed (Johnstone and Chapin III 2006; Greene and others 2007). However, with increasing fire frequency, extent, and severity in response to warmer temperatures and more frequent droughts (Xiao and Zhuang 2007; Wotton and others 2010), shifts in boreal vegetation from a spruce to a broadleaf-dominated landscape have occurred (Beck and others 2011). Specifically, when severe fires consume a large portion of the organic layer, leaving an average of less than 5–10 cm depth, deciduous trees can establish at much higher densities (Johnstone and others 2010a). We found a similar threshold, where stands with less than about 10 cm depth experienced the greatest change in proportion of black spruce. However, post-fire organic layer depth is

not only a function of fire consumption but it is also associated with the pre-fire organic layer depth (Johnstone and others 2010a) and thus represents a combination of fire history and environmental conditions at the site. In terms of our predetermined site types, we found that post-fire organic layer depth was greatest in moist sites. Moist sites with deep organic layers are of poor quality for deciduous establishment and success, suggesting that these areas might be less vulnerable to a change in successional trajectory following disturbance.

Although fire characteristics such as high severity can decrease ecosystem resilience to disturbance, changes in climate that affect regeneration conditions may also affect resilience. We used tree ring responses to climate as an indication of the climate effects on potential recruitment and found that the radial growth response to CMI in May of the current growing season was a significant predictor of ecosystem resilience. A strong positive response to CMI in May signifies that high moisture

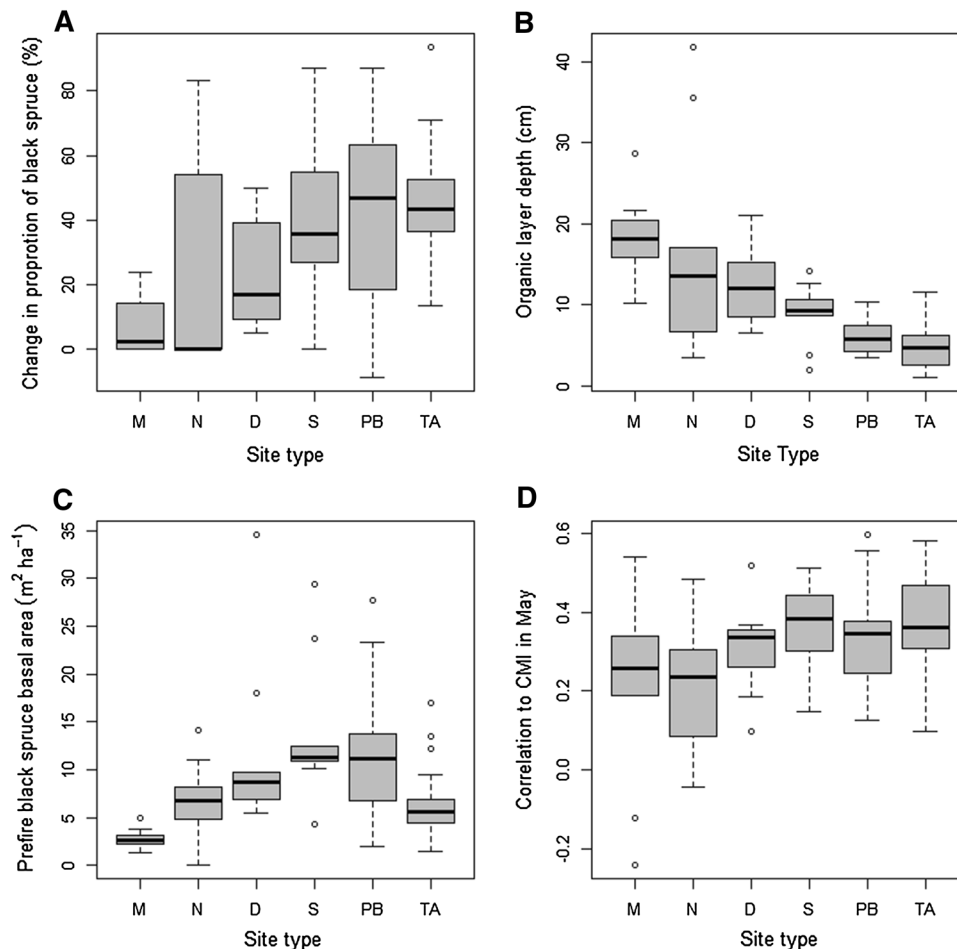


Figure 5. Boxplots showing the variability between site types (*M* moist, *N* north, *D* dry, *S* south, *PB* paper birch, *TA* trembling aspen) for each of: **A** change in black spruce proportion (%), **B** organic layer depth (cm), **C** black spruce pre-fire basal area ($\text{m}^2 \text{ha}^{-1}$), and **D** the stand response to CMI in current may (correlation coefficient).

availability in the early growing season results in increased radial growth or alternatively low moisture results in reduced radial growth. This response can be explained by warm air temperatures in spring increasing the evaporative demand of leaves during a period when low soil temperatures constrain water uptake (Berg and Chapin III 1994). Stands that were drought stressed (that is, ring widths positively correlated to CMI; Walker and others 2015) experienced the greatest change in composition from pre-fire to post-fire. This suggests that post-fire seedling recruitment and survival is inhibited by stressful environmental conditions where mature black spruce trees are able to survive. Furthermore, these results highlight that growth–climate responses of pre-fire trees are a useful tool for predicting changes in ecological resilience. Our results are consistent with a study of post-fire recovery of white spruce stands in south central Yukon (Canada), where the greatest change in composition after fire coincided with sites where pre-fire ring widths were negatively correlated with summer temperatures (Johnstone and others 2010b).

Despite pre-fire stand composition being an overall poor predictor of ecosystem resilience, our BRT models predicted that stands with relatively higher pre-fire black spruce basal area were more likely to shift to deciduous dominance. Stands with high pre-fire black spruce basal area were found in warmer and drier landscape positions and/or in association with deciduous species. The presence of deciduous trees in the pre-fire stand provides a bud bank for asexual regeneration and facilitates rapid post-fire colonization (Greene and Johnson 1999; Chen and others 2009). In our study, sites with even a few deciduous trees present in the pre-fire stand experienced a large decrease in the proportion of black spruce to deciduous trees following fire. However, sites with no pre-fire deciduous trees were capable of shifting to deciduous dominance similar in magnitude to those with pre-fire deciduous trees. Legacy effects of pre-fire vegetation appeared to be much less important than the effects of fire and environmental conditions in controlling post-fire regeneration patterns in these black spruce forests.

CONCLUSION

Historically, the boreal forest has undergone abrupt changes in species composition associated with climate change and disturbance. Warm periods in interior Alaska that increased fire frequency during the past 5000 years resulted in more deciduous

cover compared to cooler periods with fewer fires that were dominated by black spruce (Kelly and others 2013). Overall, the fire and climate regimes in boreal forest of interior Alaska have been suitable to maintain persistent cycles of black spruce self-replacement for the past 5–6000 years, indicating substantial ecosystem resilience (Chapin and others 2010, Kelly and others 2013). However, climate and the associated effects of climate on the fire regime are already beyond the historical range of variability (Kelly and others 2013). As such, black spruce ecosystems may experience widespread state changes in response to disturbance.

Here we observed shifts in successional trajectories from the previous fire cycle that highlight a loss of ecosystem resilience to disturbance in some of these black spruce forests. Areas most vulnerable to a loss of resilience had shallow post-fire organic layers, suggesting more severe fire, in combination with pre-disturbance drought stress, which indicates stressful environmental conditions for regeneration. As models project continued climate change and increased fire severity, frequency, and size (de Groot and others 2013), we can expect a loss of boreal forest ecosystem resilience to disturbance from fire. However, this loss of resilience will likely be confounded with environmental heterogeneity, and we therefore do not expect a uniform loss of resilience across the landscape. Specifically, areas most vulnerable to post-disturbance compositional change are those located at warmer and drier landscape positions and sites at the wetter and cooler end of the spectrum may be more resilient to disturbance. As climate change continues, increases in aridity, drought stress, and decreasing ecosystem resilience are of serious concern not only for the boreal forest but for forested ecosystems worldwide (Ghazoul and others 2015; Trumbore and others 2015). We believe our results are relevant not only for forecasting and managing the effects of a substantially altered boreal landscape, but the methods employed in this study might be useful for predicting vulnerability of other forested ecosystems. In particular, landscape patterns of tree sensitivity to climate factors may be useful to identify where on the landscape we can expect climate change to decrease resilience and lead to ecological surprises under future disturbance.

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