

Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest

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Abstract

Predicting plant community responses to changing environmental conditions is a key element of forecasting and mitigating the effects of global change. Disturbance can play an important role in these dynamics, by initiating cycles of secondary succession and generating opportunities for communities of long-lived organisms to reorganize in alternative configurations. This study used landscape-scale variations in environmental conditions, stand structure, and disturbance from an extreme fire year in Alaska to examine how these factors affected successional trajectories in boreal forests dominated by black spruce. Because fire intervals in interior Alaska are typically too short to allow relay succession, the initial cohorts of seedlings that recruit after fire largely determine future canopy composition. Consequently, in a dynamically stable landscape, postfire tree seedling composition should resemble that of the prefire forest stands, with little net change in tree composition after fire. Seedling recruitment data from 90 burned stands indicated that postfire establishment of black spruce was strongly linked to environmental conditions and was highest at sites that were moist and had high densities of prefire spruce. Although deciduous broadleaf trees were absent from most prefire stands, deciduous trees recruited from seed at many sites and were most abundant at sites where the fires burned severely, consuming much of the surface organic layer. Comparison of pre- and postfire tree composition in the burned stands indicated that the expected trajectory of black spruce self-replacement was typical only at moist sites that burned with low fire severity. At severely burned sites, deciduous trees dominated the postfire tree seedling community, suggesting these sites will follow alternative, deciduous-dominated trajectories of succession. Increases in the severity of boreal fires with climate warming may catalyze shifts to an increasingly deciduous-dominated landscape, substantially altering landscape dynamics and ecosystem services in this part of the boreal forest.

Keywords: *Betula neoalaskana*, boosted regression trees, composite burn index, fire severity, *Picea mariana*, *Populus tremuloides*, postfire succession, seedling recruitment, topography

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Introduction

Although environment clearly exerts a strong control over potential plant community composition (e.g. Whittaker, 1975), there is often substantial variation in communities that is poorly predicted by environmental factors. For example, communities dominated by species with significant overlap in their environmental and

ecological niches have the potential to reorganize into multiple alternative states after disturbance (Law & Morton, 1993). Accumulating evidence suggests that initial conditions and legacies of past disturbance can play key roles in determining community composition (Dublin *et al.*, 1990; Foster *et al.*, 1998) and may prevent the formation of equilibrium communities predicted from environmental niches (Camill & Clark, 2000). A nonequilibrium perspective on community dynamics is increasingly warranted under current pressures of rapid climatic and land-use change, where the interactions of historical contingency and threshold responses may generate unexpected ecosystem trajectories (Scheffer *et al.*, 2001; Higgins *et al.*, 2002).

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Much of our understanding of patterns of ecological succession is built from studies of ecological chronosequences, where communities of different ages are compared under the assumption of equivalent initial starting conditions and successional trajectories (Van Cleve *et al.*, 1991; Johnson & Miyanishi, 2008). However, this approach is poorly suited to assessing the effects of postdisturbance conditions and initial community assembly, which may be critical in determining trajectories of ecosystem succession (Fastie, 1995; Davis *et al.*, 1998). Today ecologists are being challenged to predict the future dynamics of ecological communities under conditions of rapid environmental change and novel ecological conditions (Peterson *et al.*, 2003). Under these circumstances, even long-term studies seem unlikely to provide adequate or timely information on the range of successional dynamics that may emerge from new combinations of environmental, disturbance, and biotic conditions. Research aimed at understanding ecological responses to a range of initial starting conditions, including the potential for threshold responses, is one way to meet the challenge of predicting ecological responses under a changing environment.

In the boreal forests of North America, there is substantial modeling and empirical evidence that fire, the most widespread agent of disturbance (Payette, 1992; is likely to increase in extent and severity with climate warming (Gillett *et al.*, 2004; Flannigan *et al.*, 2005; Balshi *et al.*, 2009). How can we predict forest responses to what are likely to be historically unusual combinations of fire and environmental conditions? For boreal forests with stand-replacement fire and few shade-tolerant canopy species, much can be learned about the patterns of future forests from studies of early, postfire community reorganization (Lavoie & Sirois, 1998; Peters *et al.*, 2005). Boreal forests with frequent, stand-replacing fire are usually dominated by a single cohort of a few tree species that establish simultaneously after fire but differ in their rates of growth to the forest canopy (Gutsell & Johnson, 2002; Schulze *et al.*, 2005). The majority of these trees recruit within 3–6 years after fire, and this period of initial recruitment constitutes a short and critical window of community reorganization after disturbance (Johnstone *et al.*, 2004; Peters *et al.*, 2005). Consequently, patterns of seedling composition and density established within a few years after fire are strong predictors of the initial successional trajectory of a forest (Johnstone *et al.*, 2004). For boreal forest stands where fire cycles are typically <100 years, such as those in western North America (Yarie, 1981; Larsen, 1997), this initial cohort will likely determine canopy composition for the duration of the fire-free interval. As a result, early assessment of postfire tree recruitment can provide a useful means to link initial,

postdisturbance conditions to future successional development of a forest.

The successional recovery of vegetation after fire in boreal forests is often assumed to follow a paradigm of community replacement across fire cycles, whereby fire initiates a change in the stage but not the trajectory of succession (Dix & Swan, 1971; Heinzelman, 1981; Van Cleve & Viereck, 1981). This pattern of repeatable successional cycles is believed to be driven by two mechanisms: (1) stable abiotic conditions that interact with physiological tolerances to determine species distributions across environmental gradients (Whittaker, 1975; Van Cleve & Viereck, 1981), and (2) positive neighbor effects that favor the re-establishment of dominant species after disturbance (Dix & Swan, 1971; Frelich & Reich, 1999). Much of boreal North America is dominated by serotinous conifers that rely on large quantities of seed produced from aerial seedbanks to ensure ample reproduction after fire on poor quality, organic seedbeds (Johnstone & Chapin, 2006a; Greene *et al.*, 2007). In contrast, small-seeded deciduous broadleaf species are able to recruit from seed only on high-quality, mineral soil seedbeds (Johnstone & Chapin, 2006a; Greene *et al.*, 2007) and instead rely primarily on asexual resprouting to regenerate after fire (Greene & Johnson, 1999). Species traits such as litter quantity and quality or evapotranspiration of dominant conifer or broadleaf trees further modify environmental conditions in ways that support their continued dominance (Van Cleve & Viereck, 1981). Together, positive regeneration feedbacks and species effects on their local environment help maintain a high resilience of local forest composition to changing disturbance and environmental conditions (Chapin *et al.*, 2004).

Disturbances may play a key role in overcoming resilience and shaping long-term responses of ecosystems to environmental change (Payette & Gagnon, 1985; Clark *et al.*, 1996; Arseneault & Sirois, 2004; Chapin *et al.*, 2004). Patch-scale variations in patterns of fire behavior and severity are important in driving patterns of vegetation recovery across a range of boreal forests (Arseneault, 2001; Rydgren *et al.*, 2004; Johnstone & Kasischke, 2005). However, fire impacts on successional trajectories are likely to be contingent on a number of landscape factors, including abiotic conditions, spatial contingencies, and prefire vegetation legacies (Turner *et al.*, 2003). Consequently, predicting the responses of forest ecosystems to directional changes in climate and fire is a complex problem in heterogeneous landscapes. Because experiments that incorporate realistic landscape heterogeneity are extremely difficult to implement, carefully designed observational studies may be the best way to examine the interacting roles of landscape processes and disturbances in driving

ecological dynamics (Holling & Allen, 2002; Peters *et al.*, 2004).

In this study, we relate landscape-scale variations in environmental factors, fire conditions, and vegetation legacies to patterns of postfire recovery to examine how these variables affect the development of different successional trajectories in boreal forests. Data on early postfire tree recruitment were collected for burned black spruce forests following an extreme fire year in interior Alaska. We used these data to test whether patterns of recovery were consistent with expectations of black spruce self-replacement after fire and to assess the conditions under which conifer recovery may be disrupted to initiate alternative trajectories of forest succession.

Materials and methods

Study area

Our study area in the upland boreal forests of interior Alaska is bounded by the Alaska Range (63°N) to the south, the Brooks Range and latitudinal treeline (67°N) to the north, the Dalton Highway (150°W) to the west, and the Alaska/Canada border (142°W) to the east (Fig. 1). The region is characterized by gently sloping uplands, has a continental climate, and is underlain by frequent but discontinuous permafrost. Much of the

forested area is dominated by black spruce [*Picea mariana* (Mill.) B.S.P.], a semiserotinous conifer that occurs throughout boreal North America (Viereck, 1983; Hollingsworth *et al.*, 2006). We focused our study specifically on this forest type. Stands of deciduous broadleaf trees, primarily trembling aspen (*Populus tremuloides* Michx.), and Alaskan paper birch (*Betula neoalaskana* Sarg.) dominate local patches within a matrix of upland spruce forests in interior Alaska (Viereck, 1983; Calef *et al.*, 2005).

Climate records indicate that the summer of 2004 was one of the hottest and driest summers recorded since 1940 for interior Alaska (Alaska Climate Research Center, 2009). Widespread fires in 2004 burned 2.7 million ha of forest in interior Alaska, representing the largest annual area burned in Alaska's 58-year fire record (Todd & Jewkes, 2006). The fires of 2004 burned into late August, and we established our study sites in the following spring (May, 2005), immediately after snow melt. We identified areas of the 2004 burns that were accessible from sections of the Taylor, Steese, and Dalton Highways in interior Alaska (Fig. 1). We carried out an initial reconnaissance of the burned areas to estimate the range of forest and fire conditions available in each of the three burn complexes. We then selectively identified 90 sites (~30 sites in each burn complex) that encompassed the range of fire severities, site moisture, topographic positions, and geographic dispersion that

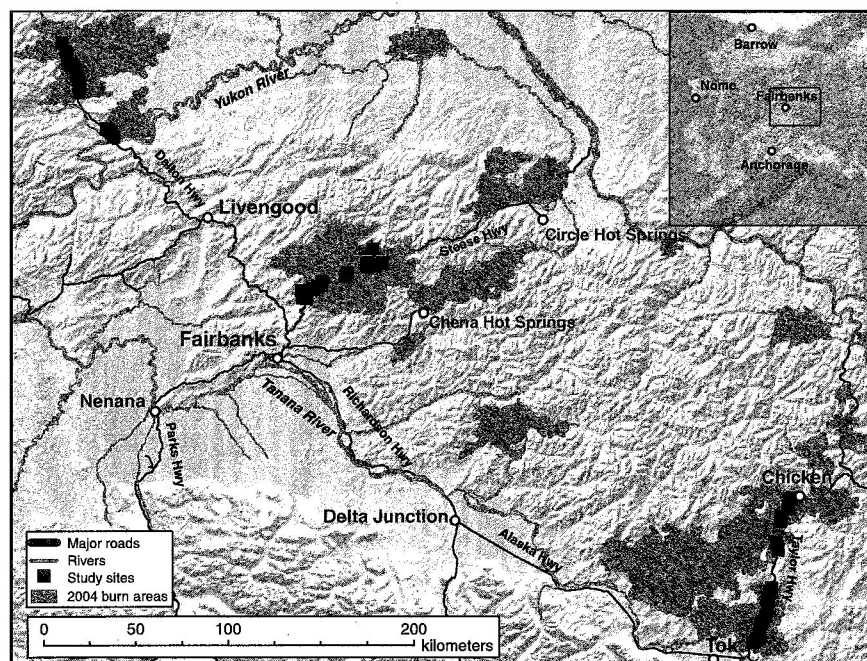


Fig. 1 Map of the study sites in interior Alaska (modified from Johnstone *et al.*, 2009). Solid gray polygons indicate areas that were burned in 2004. Study sites ($n = 90$) are shown as filled black squares in fires that intersected the Dalton, Steese, and Taylor highways. Because of the small scale of the map, symbols overlap for some sites.

we encountered in burned black spruce forests. We selected locations that we could reach within a 15min walk (600 m) of the road. All sites were dominated by a black spruce overstory before burning. The prefire communities included subtypes ranging from moist acidic or nonacidic forests with an understory dominated by *Eriophorum vaginatum* L. tussocks, to nonacidic dry forests and elevational black spruce treeline (Hollingsworth *et al.*, 2006). Tree mortality assessed in 2005 ranged from 30% to 100%, with most sites (82/90) having at least 95% canopy mortality.

Field measurements

At each site, we selected and permanently marked a 30m x 30m sample area that was representative of a large (at least 0.25ha), relatively homogeneous burned stand. In 2005, we measured elevation, latitude, and longitude at the plot center point with a GPS receiver, and slope and aspect using a compass and inclinometer. This information was used to calculate an index of the relative solar insolation received at each site on the summer solstice (Bennie *et al.*, 2006). Site moisture classes were estimated on a six-point scale, ranging from xeric to subhygric, based on topography-controlled drainage conditions and adjusted for soil texture and presence of near-surface permafrost (Johnstone *et al.*, 2008).

Stand characteristics of the prefire forest were measured in 2006 in two parallel 2m x 30m belt-transects. For each prefire tree rooted within the belt-transect, we measured the diameter at breast height (DBH) if the stem was > 1.4m height, or tallied the number of stems for stems < 1.4m height. Species were distinguished by trunk, branch, and cone morphology. Stems that branched above the ground surface were counted as a single stem, and the largest stem was measured for DBH. Fallen stems were included if originally rooted in the plot. Trees considered to be dead before the 2004 fire - based on extensive charring of the sapwood - were excluded from the analysis. From these data, we calculated the total density (stems ha⁻¹, including all heights) and tree basal area (stem area ha⁻¹ of trees > 1.4m height) of each tree species in the prefire stand.

We estimated stand age from ring counts of five black spruce trees that were dominant or subdominant in the prefire tree canopy. Although the exact age is difficult to determine from ring counts in black spruce (DesRochers & Gagnon, 1997), they provide a useful estimate of the minimum age of a stem. We sampled stem disks as close to the stem base as possible to minimize bias in estimating tree ages (Vasiliauskas & Chen, 2002). Stem disks were dried, sanded, and rings were counted under a binocular microscope. For most of the sampled

stands (63/90), spruce ring counts from the five sampled trees clustered within a decade of each other, and we took the age of the oldest stem as the estimate of stand age. For stands (19/90) with two age cohorts, we estimated the stand age based on the youngest cluster (> 2 stems) of stems aged within a decade of each other (i.e. the most recent burn). A small number of stands (8/90) showed no clustering of stem ages, and we estimated the age of the stand as the age of the oldest tree. Of these stands, five were located close to elevational treeline.

We estimated the distance from the plot edge to the nearest unburned stand of > 20 live deciduous trees by pacing distances < 200 m or visually estimating (calibrated with measured road distances) for distances > 200m. Because measurement error probably increased with distance to seed source, we classified distance estimates into eight semilogarithmic classes, starting at 0 m and with breaking points between classes at 50, 100, 200, 400, 800, 1600, and 3000 m.

We measured fire severity in May-June, 2005 using two ordinal metrics: (1) the Composite Burn Index (CBI), and (2) a canopy-severity index. CBI is a semi-quantitative index that provides a synthetic metric of fire severity in burned forests (Key & Benson, 2005). The CBI estimates fuel consumption and mortality in five strata from the ground layer to the forest canopy. Because of the high levels of aboveground plant mortality in this crown-fire system, much of the variation in our estimates of CBI was attributable to variations in the consumption of surface ground fuels (Baby, 2007). We also estimated canopy severity separately with a stand-level index that focused on canopy dominant and subdominant trees, where 1 = low consumption, with many needles remaining; 2 = low to moderate, with few needles but most small twigs remaining; 3 = moderate, with few small twigs remaining but many branches; 4 = moderate to high, with many lower canopy branches consumed; and 5 = high, with most branches and cones consumed.

To assess the efficacy of CBI in capturing variations in fire severity that affect postfire seedbed quality, we also measured organic layer thickness and organic soil cover, as these have previously been shown to strongly influence seedling recruitment success (Johnstone & Chapin, 2006a; Greene *et al.*, 2007). The depth of the residual, postfire organic layer was measured at 11 randomly selected points along a transect through the site. Relative cover of bare organic soil (burned fibric and humic layers and dead moss) was recorded using point-intercept samples with 60 points site⁻¹.

In June 2008, the start of the fourth growing season after the 2004 fires, we surveyed all sites for newly established seedlings of postfire origin. Seedlings were

counted in 20, 50 cm x 50 cm quadrats for a total sample area of 5 m² study site⁻¹. Quadrat locations were determined by repeated, 'blind' tossing of a quadrat, or were laid out at random points along parallel transects in a subset of 39 sites. The number and species of all postfire seedlings were recorded in each quadrat, including resprouting stems. Seedling counts were averaged and standardized by unit area to obtain one estimate of average seedling density for each species at a site.

Data analysis

We developed models to predict postfire tree seedling recruitment using boosted regression tree analysis, which is a machine-learning approach based on classification and regression trees (De'ath, 2007; Elith *et al.*, 2008). Machine learning methods have been increasingly advocated for ecological analyses because of their flexibility in modeling complex nonlinear relationships and interactions without the restrictive assumptions of parametric statistics (Olden *et al.*, 2008). Boosted regression trees (BRT) fit into a general class of analyses that use randomization and machine learning to generate multiple, simple models that are aggregated to improve model stability and predictive capacity (Prasad *et al.*, 2006; Cutler *et al.*, 2007; De'ath, 2007). This method uses the iterative partitioning approach of regression trees, but reduces predictive error by 'boosting' initial models with additional, sequential trees that model the residuals in randomized subsets of the data (Friedman, 2001; De'ath, 2007; Elith *et al.*, 2008). We selected BRT analysis because of its flexibility in incorporating different data types, relatively transparent approach, and interpretability of output in describing relationships between dependent and independent variables (Prasad *et al.*, 2006; De'ath, 2007; Elith *et al.*, 2008). In comparative analyses of ecological datasets, BRT models often outperform alternative statistical approaches in terms of both predictive accuracy and interpretability (Leathwick *et al.*, 2006; Prasad *et al.*, 2006; Cutler *et al.*, 2007).

We used BRT models to predict variations in three postfire parameters: seedling densities of black spruce, seedling density (including resprouts) of deciduous tree species (aspen and birch), and the proportion of postfire seedlings that were spruce. Seedling densities (seedlings m⁻²) were first transformed using $10 \log_{10}(x + c)$, where c was equal to the lowest observed value (0.2). For the analysis of the spruce proportion of seedlings, we included only those sites where seedlings were present. We also found that the performance of our models was significantly affected by the presence of a single outlier plot, where one quadrat in a high elevation site had an anomalously high count of birch seedlings, and all other quadrats had zero seedlings. We felt

that the site-level regeneration was poorly represented by the averages across quadrats, and removed this site from the analysis. Consequently, model fitting of spruce and deciduous recruitment patterns was based on $n = 89$ samples, and the spruce proportion model used $n = 74$ samples.

BRT, like many other statistical approaches, are vulnerable to model overfitting when input variables are highly correlated (Olden *et al.*, 2008). To reduce the potential for collinearity in predictor variables to bias the model results, we used a conservative approach to variable selection that included elimination of highly correlated variables from the input dataset (e.g. Parisien & Moritz, 2009). We first selected candidate predictor variables based on *a priori* hypotheses of factors likely to affect patterns of boreal tree regeneration (Table 1). Within a given category, we then selected a limited set of predictor variables that we believed represented distinct control factors and that we determined statistically were not strongly correlated with other input variables in the model ($p < 0.6$). Because our data did not consistently conform to the assumptions of parametric statistics, we used the nonparametric rank correlation coefficient, Spearman's ρ (Conover, 1999) to describe bivariate relations between variables. Where there were several surrogate variables that were highly correlated, we selected the variable with the strongest bivariate correlations with seedling densities, and excluded the surrogates from the model selection process.

Spatial autocorrelation effects were represented in the models by site latitude and a categorical factor coding the three burns. We expected that the key environmental factors influencing regeneration patterns would be local climate and moisture (Hollingsworth *et al.*, 2006; Kurkowski *et al.*, 2008). Climate effects were represented by indicator variables that have been strongly linked to variations in temperature and overall climate severity: latitude and elevation (Holtmeier & Broll, 2005), and slope/aspect effects on potential insolation (Van Cleve *et al.*, 1991; McCune & Keon, 2002). Topographic and soil effects on moisture availability, which also influence the distribution of boreal plant communities (Van Cleve *et al.*, 1991), are represented here by our site-moisture index. Prefire vegetation is expected to be a strong predictor of postfire recruitment, both due to effects on seed and bud-banks (Greene & Johnson, 1999; Chen *et al.*, 2009) and as an indicator of site suitability for a species (Van Cleve & Viereck, 1981). We represented prefire spruce using both density, to indicate previous recruitment success, and basal area, which has been shown elsewhere to predict seed availability (Greene & Johnson, 1999). Prefire deciduous trees were represented by a Boolean indicator of presence/absence, as the presence of even a few prefire

Table 1 Summary of candidate predictor variables used in developing the regression tree analyses of postfire regeneration

Category	Variable name*	Scale (units)	Mean $\pm$ SD (range) [†]
Spatial	Burn‡§¶	Nominal	–
	Latitude‡§¶	Continuous (°N)	65.0 $\pm$ 1.0° (63.4–66.3°)
Environmental	Elevation‡§¶	Continuous (m above sea level)	493 $\pm$ 250 (93–1022)
	Insolation‡§¶	Continuous (proportion)	0.73 $\pm$ 0.06 (0.52–0.86)
	Moisture class‡§¶	Ordinal (ranks)	3 (1–6)
Prefire vegetation	Prefire spruce density‡¶	Continuous (stems m ⁻²)	0.80 $\pm$ 0.57 (0.01–2.38)
	Prefire spruce basal area‡	Continuous (cm ² m ⁻²)	9.0 $\pm$ 6.5 (0.0–27.3)
	Prefire presence of deciduous§¶	Ordinal, boolean (presence/absence)	–
Fire effects	Stand age‡¶	Continuous (years since fire)	91 $\pm$ 31 (29–186)
	Distance to unburned deciduous§¶	Ordinal (ranks)	4 (0–7)
	Canopy fire severity rank‡¶	Ordinal (ranks)	2 (1–5)
	Composite burn index (CBI)‡§¶	Continuous (unitless)	2.19 $\pm$ 1.34 (1.30–2.93)

Variables are listed as having a primary association to one of four general categories of spatial, environmental, prefire vegetation, and fire effects, but may also be linked to variation within other categories.

*Symbols next to a variable name indicate which models included it as a candidate variable.

†Median and range are given for ordinal variables.

‡Black spruce seedling density.

§Deciduous seedling density.

¶Spruce proportion of seedlings.

aspen has been shown to be sufficient for abundant asexual regeneration (Lavertu *et al.*, 1994).

We also included variables to represent different aspects of the fire regime: fire frequency, spatial configuration, and severity (Table 1) (Turner *et al.*, 2001). We measured fire frequency as the length of the previous fire return interval, estimated here by the age of a burned stand (Johnstone & Chapin, 2006b). The spatial configuration of a fire and consequent impacts on seed dispersal to a burned site were represented by distance to live deciduous stands (Greene & Johnson, 1999). We did not include distance to live spruce stands, as black spruce is a semiserotinous conifer that typically depends on on-site seed for regeneration (Greene & Johnson, 1999). Effects of fire severity on local seed availability for black spruce were estimated by the canopy severity rank, which should capture the effects of canopy fuel consumption on seed viability in the aerial seedbank (de Groot *et al.*, 2004; Johnstone *et al.*, 2009). CBI was included as a more general metric of fire severity that incorporated effects of canopy, understory,

and surface fuel consumption (Key & Benson, 2005). It is important to note that variations in CBI were not independent of site moisture ($r = -0.49$, $P < 0.001$, $n = 89$), so our models cannot definitively separate out the effects of fire severity and site moisture on tree regeneration. The correlation between CBI and site moisture represents the strongest intercorrelation between the predictor variables included in our models.

All statistical analyses were performed in R (R Development Core Team, 2006; R Foundation for Statistical Computing, Vienna, Austria), using the 'GBM' and 'GBMPLUS' packages for BRT analysis. We started our BRT analysis with an initial set of calibration runs that fit a large number of sequential trees (De'ath, 2007; Elith *et al.*, 2008). We plotted test error against number of trees, and set the learning rate to a value that resulted in average test error being minimized at approximately 1000 trees (Elith *et al.*, 2008). All of our models were subsequently fit with the following metaparameters: Gaussian error distribution, a learning rate of 0.003–0.005, 800–1000 trees, a bag fraction of 0.5, and fivefold

cross-validation. Model fit was evaluated by comparing training and test data to assess predictive error. These parameters were selected following rules suggested for optimization of BRT model performance in ecological studies (De'ath, 2007; Elith *et al.*, 2008).

We fit BRTs to our response data using a stepwise process that started with the full suite of hypothesized predictor variables (Table 1) with up to three-way interactions. We then compared the predictive error and residual plots from this most-complex model with alternative models obtained by sequential simplification (Elith *et al.*, 2008). We eliminated variables in reverse order of their relative influence, until subsequent elimination caused a notable ($> 2\%$) increase in prediction error (PE). We also tested the elimination of variables where the direction of the main effects was contrary to our prior expectations, suggesting spurious effects due to model overfitting. These variables were removed only when their estimated relative importance in the model was $< 5\%$. Once the model had been reduced to the smallest number of variables, we tested whether fitting the model with a reduced number of interactions (two-way or only main effects) caused a notable increase in PE. Finally, we assessed whether PE was increased by constraining the partial dependencies of responses to explanatory variables to be monotonic (De'ath, 2007). At each stage, we examined residual plots to ensure that model fit was not degrading with the process of model Simplification and retained variables whose removal led to the generation of nonrandom pattern in the residuals.

We interpreted the results from the best BRT model by examining the relative influence of variables and plotting the partial dependencies of responses to individual predictor variables (De'ath, 2007; Elith *et al.*, 2008). Partial dependency plots provide a tool for interpreting the functional effects of each variable in the model by representing a variable's marginal effects on the response, after accounting for the average effects of other variables in the model (Friedman, 2001). The relative influence, or importance, of individual predictor variables in the model was also estimated from the sum of squared improvements associated with that variable, averaged across all trees in the boosted model (Friedman, 2001; De'ath, 2007; Elith *et al.*, 2008).

Results

All of the sites sampled in this study were dominated by black spruce before they burned (Fig. 2a). Most sites had no deciduous broadleaf trees present in the prefire stand, although we sampled two stands that had a mix of black spruce and aspen, and there were 32 stands that had at least one deciduous tree in the prefire stand

(Fig. 2a). Stands with prefire deciduous trees showed a similar range of stand ages (30–175 years) to those with only spruce in the prefire stand (29–186 years).

The density of prefire black spruce ranged from close to zero (open stands near treeline with only one to two trees encountered in 60m^2 subplots) to densely treed stands with up to 2.4stems m^{-2} . The median density of spruce in the prefire stands was 0.7stems m^{-2} , which is close to the median of 0.6stem m^{-2} observed for spruce seedlings in the postfire stands. Postfire spruce density was positively correlated with total prefire spruce density ($\rho = 0.39, P < 0.001, n = 89$; Fig. 2b), not correlated with total, prefire spruce basal area ($\rho = -0.06, P = 0.6$), and showed a weak negative correlation with standing, prefire spruce basal area ($\rho = -0.29, P = 0.004$). Postfire spruce densities had an order of magnitude larger range than prefire density, with a maximum of 22stems m^{-2} . Despite the sparse abundance of prefire deciduous trees, we observed a large range of postfire deciduous stem densities, from 0 to 230stems m^{-2} with a median of 2.2stems m^{-2} . There were a number of stands that had very low recruitment of both spruce and deciduous seedlings, and 15 of the 90 sampled stands showed zero postfire seedling recruitment (Fig. 2c).

Analysis with BRT indicated that elevation had the strongest influence on postfire densities of spruce seedlings, followed by prefire spruce density and site moisture (Fig. 3). CBI and stand age had weaker effects on spruce density, but could not be removed from the model without increasing PE. Partial dependencies from the fitted model indicate that, when other variables were held constant, high spruce densities were most likely to be found at lower elevations, in stands with high prefire spruce density, and at moist sites (Fig. 3). Higher spruce recruitment was also more likely when fire severity was high, and stands were close to 100 years or more in age. Forcing the marginal effects in the model to be monotonic had little effect on the overall shape of the estimated effects (Fig. 3). Including two-way interactions in the model accounted for a reduction of $\sim 4\%$ of the relative PE and allowed the model to include weak interactions between moisture and CBI, and elevation and prefire spruce. The PE of the final model was 0.54, indicating that it was able to predict nearly half of the observed variation in log-transformed spruce densities.

In contrast to the spruce model, fire severity (CBI) accounted for over 50% of the relative influence on deciduous seedling density in the best deciduous model (Fig. 4). Elevation had a moderate effect on deciduous recruitment, and latitude, moisture, and distance to the nearest unburned deciduous stand had relatively weak effects. Partial dependency plots indicate that deciduous recruitment was highest at high levels of fire

severity (CBI), low elevations, more southern latitudes, moist sites, and close to a live deciduous stand (Fig. 4). As in the spruce model, constraining the marginal relationships to be monotonic had little effect on shape of the estimated response function. Including two-way interactions in the model accounted for a reduction of $\sim 2\%$ of the relative FE and allowed the model to include weak interactions of elevation with latitude and CBI in affecting deciduous seedling density. The PE of the deciduous model ($PE = 0.44$) indicated that the model captured over half of the observed variation in log-transformed deciduous seedling density.

The fitted models predicting black spruce and deciduous recruitment had several variables in common that showed similar functional relationships but differed in their relative influence between the models. For example, both spruce and deciduous seedling densities responded negatively to increases in elevation, and positively to increases in fire severity and site moisture. In order to understand what factors impact the relative composition of postfire recruitment, and subsequent successional trajectory, we also fitted a third model to predict variations in the proportion of postfire seedlings that were spruce. Although spruce and deciduous seedling densities were correlated ($\rho = 0.43$, $P < 0.001$, Fig. 2c), there was a wide range in the relative dominance of spruce vs. deciduous seedlings observed in the postfire sites. Notably, although only 36% of prefire stands contained deciduous trees and only 3% were codominated by deciduous trees, a large proportion of the sites with successful seedling recruitment (58%) had postfire communities where over 75% of the tree seedlings were deciduous aspen or birch.

Regression tree analysis indicated that fire severity (CBI) had a dominant influence on the proportion of postfire seedlings that were spruce. This effect greatly exceeded the relative influence of stand age, moisture,

prefire spruce density, and latitude (Fig. 5). The lower sensitivity of conifers to fire severity (Fig. 3) and poor ability of deciduous species to recruit under low fire severity (Fig. 4) translated into a steep threshold response of relative spruce dominance to variation in fire

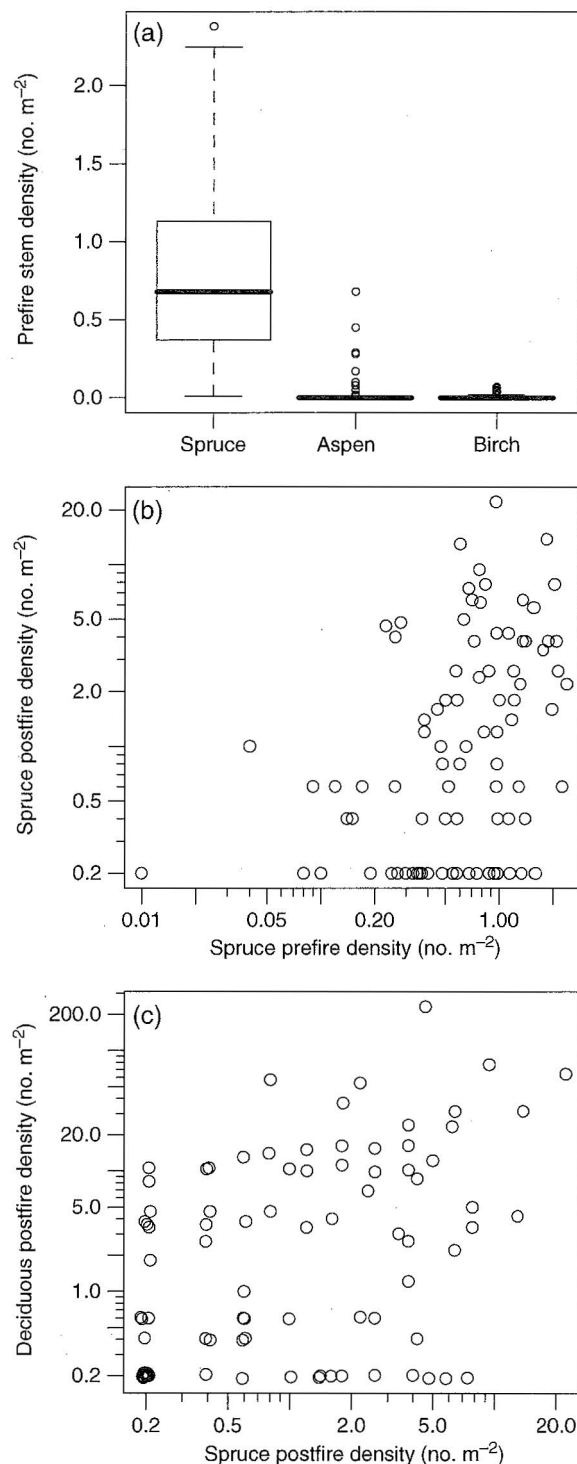


Fig. 2 Descriptive plots showing the observed distribution of pre- and postfire stem densities (no. stems m⁻²) in the sampled stands ($n = 89$). (a) Boxplots showing the observed density of total prefire stems of black spruce, trembling aspen, and paper birch that were alive when the stand burned. Boxes and whiskers encompass 25–75% and 5–95% quantiles of the data, respectively, with the median indicated by a dark horizontal line and outliers shown as dots. (b) The relationship between prefire (x-axis) and postfire (y-axis) densities of black spruce. Note that both axes are plotted on a log₁₀ scale, and a constant of 0.2 has been added to the postfire densities. (c) Relationships between postfire densities of black spruce and deciduous tree seedlings. Both axes are plotted on a log₁₀ scale, with an added constant of 0.2, and random jitter has been added to distinguish overlapping points. There are 15 points clustered near the origin, representing sites where no postfire seedlings were observed.

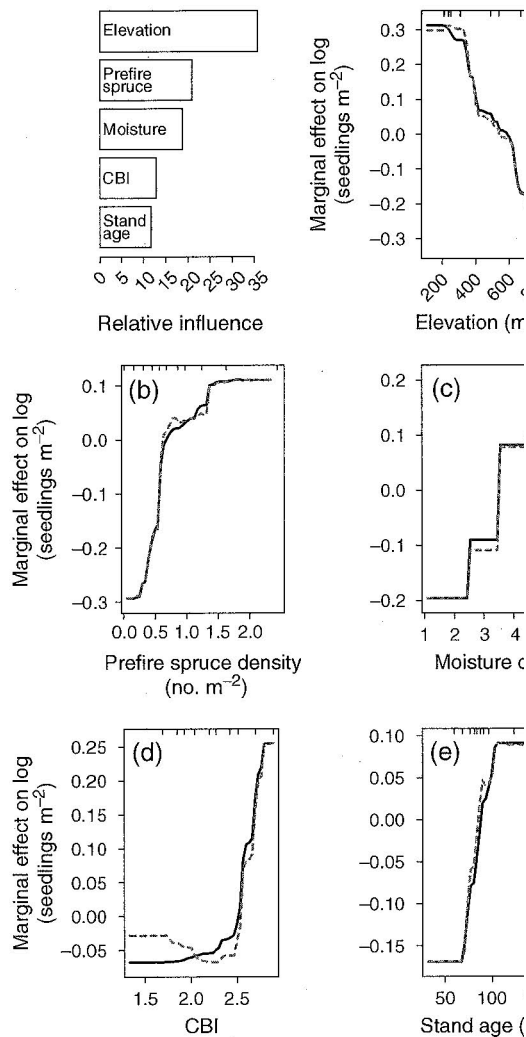


Fig. 3 Relative influence and partial dependency plots for variables in a boosted regression tree predicting seedling densities of black spruce ($\log_{10}$ seedlings m^{-2}). Partial dependency plots (a–e) represent the estimated marginal effect of a variable on y when all other variables are held at their average. Marginal effects were constrained in the model to be monotonic; gray lines indicate the partial dependency without this constraint. Tick marks at the top of a–e indicate the deciles (10% quantiles) of the observed distribution of continuous predictor variables. Results are presented for the simplest model that minimized prediction error (PE = 0.54).

severity (Fig. 5). Both partial dependency plots (Fig. 5) and bivariate correlations (Fig. 6) indicated that regenerating stands were more likely to be dominated by spruce when fire severity was below an approximate threshold of $\text{CBI} \gg 2$, and were likely to be dominated by deciduous seedlings above that value. Variations in CBI primarily reflected differences in postfire seedbed conditions, and high values of CBI generally indicated

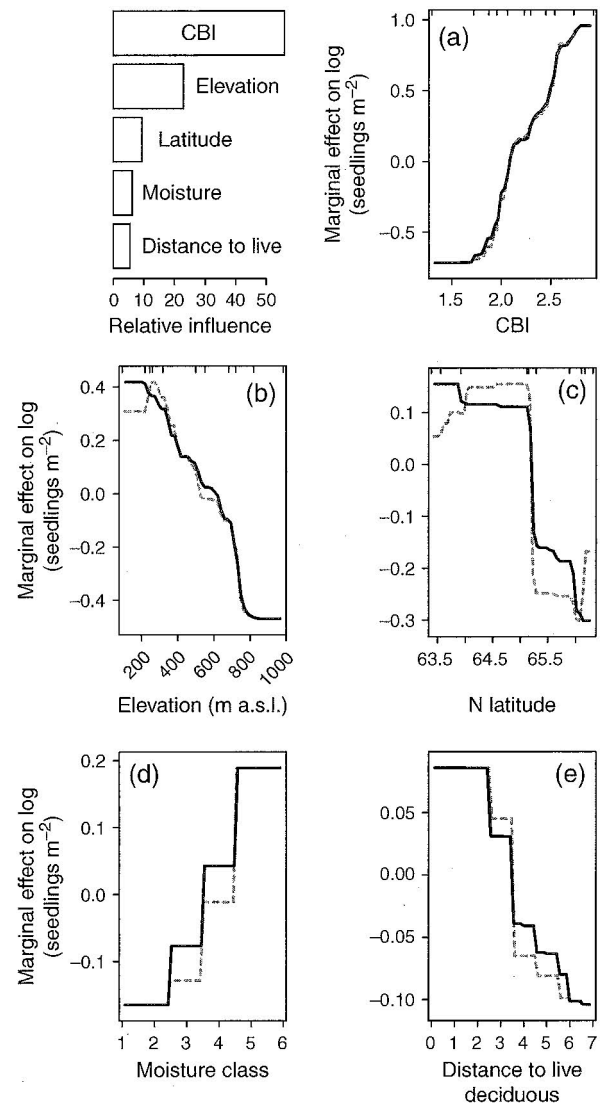


Fig. 4 Relative influence and partial dependency plots for variables in a boosted regression tree predicting seedling densities of deciduous broadleaf trees ($\log_{10}$ seedlings m^{-2}). Partial dependency plots (a–e) represent the estimated marginal effect of a variable on y when all other variables are held at their average. Marginal effects were constrained in the model to be monotonic; gray lines indicate the partial dependency without this constraint. Tick marks at the top of a–e indicate the deciles (10% quantiles) of the observed distribution of continuous predictor variables. Results are presented for the simplest model that minimized prediction error (PE = 0.44).

that sites had lower cover of organic surface layers and comparatively shallow organic layers (Fig. 6). The negative correlation between the proportion of spruce seedlings and CBI likely reflects the positive correlation with organic layer depth and, to a lesser degree, percent cover of organic soil (Fig. 6). High values of CBI were

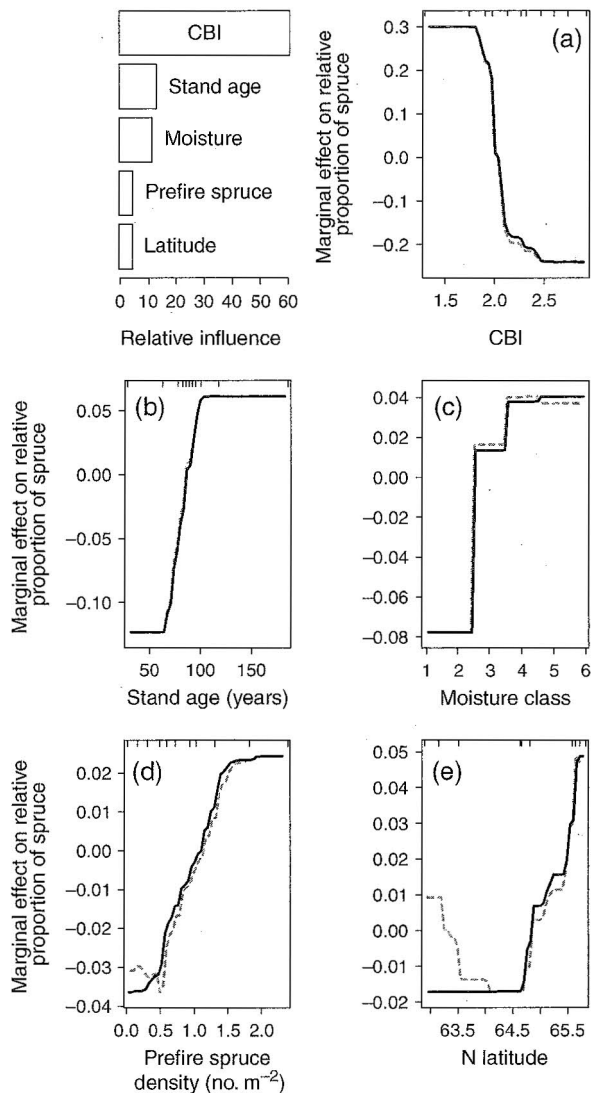


Fig. 5 Relative influence and partial dependency plots for variables in a boosted regression tree predicting relative spruce dominance, or the proportion of total seedlings that were black spruce. Partial dependency plots (a–e) represent the estimated marginal effect of a variable on y when all other variables are held at their average. Marginal effects were constrained in the model to be monotonic; gray lines indicate the partial dependency without this constraint. Tick marks at the top of a–e indicate the deciles (10% quantiles) of the observed distribution of continuous predictor variables. Results are presented for the simplest model that minimized prediction error (PE = 0.42).

also associated with high levels of canopy severity ($p=0.41$, $P<0.001$, $n=89$, data not shown), but there was no relationship between canopy severity rank and the relative proportion of spruce seedlings ($p=-0.06$, $P=0.56$, $n=72$).

The likelihood of observing a high proportion of spruce seedlings also increased when the prefire stand

was close to or over 100 years in age and the site was mesic or moist (Fig. 5). The density of prefire spruce and site latitude had positive, but relatively minor effects on postfire spruce dominance. Although the species-specific models indicated that both spruce and deciduous species were sensitive to elevation effects on recruitment, elevation did not emerge as a key factor predicting the relative abundance of the two groups. Second-order interactions accounted for a reduction of $\sim 3\%$ of the relative PE and allowed the model to include weak interactions between CBI and moisture class in affecting the proportion of spruce seedlings. The fitted model was able to explain over half of the variation in the relative dominance of postfire seedling communities (final PE = 0.42).

Discussion

The results of this study indicate that successional trajectories in black spruce forests are highly sensitive to variations in disturbance regime, contrary to the reigning paradigm of steady-state, self-replacement succession dynamics. Physical environmental constraints and, to a secondary degree, vegetation legacies are factors that favor the resilience of black spruce forests to fire disturbance. However, shifts in the fire regime to more severe or more frequent fires can interrupt stable cycles of black spruce dominance and favor the development of alternate successional trajectories dominated by deciduous broadleaf species. Changes in fire regime are not likely to affect all parts of a landscape equally, and landscape positions that are cool and moist may be relatively protected from the effects of increased fire severity or frequency (Johnstone & Chapin, 2006a; Kane *et al.*, 2007). Our data suggest that spruce forests are most vulnerable to a shift in successional trajectories caused by severe fires when they are on moderate- to well-drained sites. These relationships help us anticipate the changes in landscape forest cover that may arise if fires become more severe or frequent with future climate change (Gillett *et al.*, 2004; Flannigan *et al.*, 2005; Balshi *et al.*, 2009). A change in dominant forest cover from conifer to deciduous broadleaf species could have a cooling effect on local climate (less energy absorption, and greater transpiration) (Chapin *et al.*, 2005), reduce forest flammability and fire spread (Cumming, 2001), and alter spatial patterns of human subsistence activities (Nelson *et al.*, 2008). The relationships that we demonstrate for current landscape-scale patterns of seedling regeneration after fire provide a strong empirical basis for predicting the types of changes in forest dynamics that are likely to unfold in the coming century and therefore

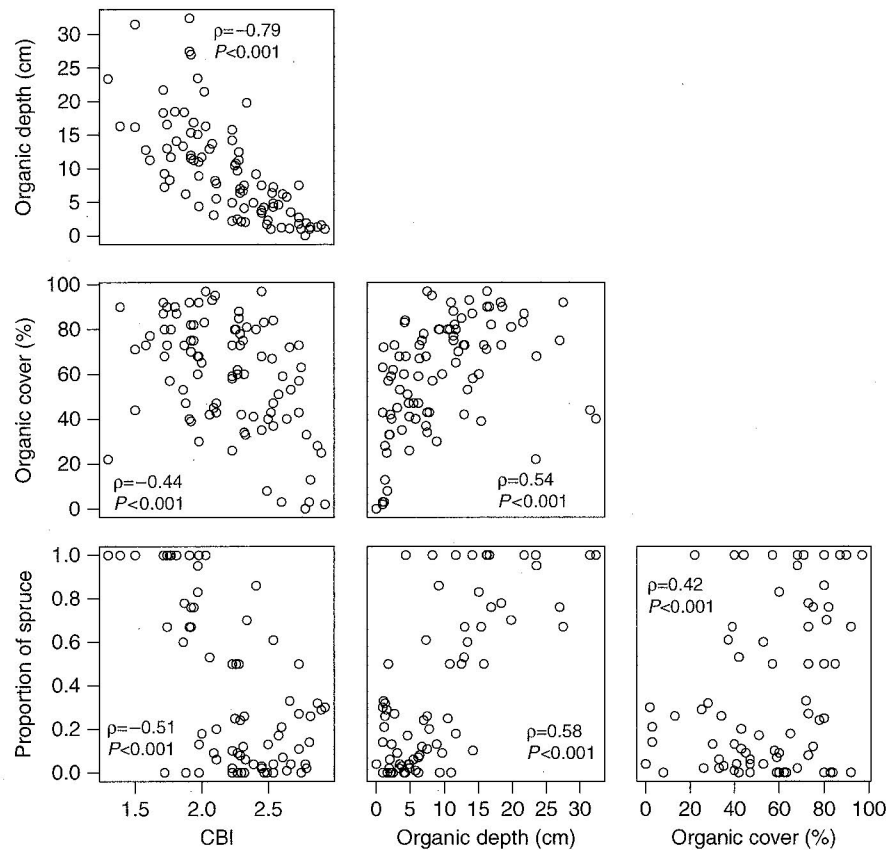


Fig. 6 Bivariate scatterplots showing relationships between the proportion of black spruce in the postfire seedling community ($n = 72$), and variables representing fire severity (Composite Burn Index, or CBI) and its effects on postfire seedbeds [depth of the residual organic layer (cm) and percent cover of organic layers; $n = 89$]. Each point represents the value for a site. Relationships between variables are summarized in each plot by the rank correlation coefficient (ρ) and its associated P -value.

the management choices facing northern residents (Chapin *et al.*, 2008).

Data on seedling recruitment in the 2004 burns indicate that fire conditions, particularly high-severity fire, can break through the legacy lock of spruce dominance and catalyze a shift to alternate, deciduous-dominated trajectories of succession. Although black spruce regeneration was only moderately sensitive to effects of fire severity (CBI) or fire return interval, fire severity had a strong and dominant influence on the recruitment of deciduous trees and thus the composition of the postfire seedling community. The difference in the sensitivity of spruce vs. deciduous recruitment to fire severity likely reflects differences in seed size, as larger-seeded conifers have a much greater ability to establish seedlings on poor-quality, organic seedbeds than small-seeded, deciduous species (Johnstone & Chapin, 2006a; Greene *et al.*, 2007). Sites that burned with high fire severity were more likely to have thin organic layers and exposed mineral soil, and the change in seedbed quality allowed deciduous seedlings to

dominate postfire regeneration in severely burned sites. This effect was reinforced at sites that burned at a young age, as spruce recruitment was reduced but deciduous recruitment was not affected. Previous studies have shown that short disturbance intervals lead to low seed availability and poor regeneration of serotinous conifers, but have little effect on deciduous recruitment (Jasinski & Payette, 2005; Johnstone & Chapin, 2006b). Our results indicate that high-severity fires and, to a lesser extent, shorter fire return intervals alter the playing field of postfire spruce succession and allow deciduous species to expand their dominance in stands that were formerly spruce-dominated.

Physical environmental factors had a strong influence on densities of spruce and deciduous seedlings, but had only weak effects on relative species dominance. Black spruce and deciduous recruitment both responded negatively to increased elevation, suggesting that both are sensitive to the harsh environmental conditions found at higher elevations (Holtmeier & Broll, 2005). Site moisture had a positive effect in both models, but

influenced spruce recruitment more than it did deciduous recruitment. Consequently, moist sites favoured spruce seedlings over those of deciduous broadleaves, as did higher latitudes, where evapotranspiration is reduced. We hypothesized that spruce recruitment would be favored on north-facing slopes due to low solar insolation (e.g. Kurkowski *et al.*, 2008), but insolation was never selected as an important factor in our models. The overall picture of environmental effects on postfire succession that emerged from our analysis was that spruce forests showed the strongest potential for self-replacement in mesic-to-moist stands and at higher latitudes. These effects are consistent with the location of our sites close to latitudinal and elevational treelines and observed patterns of self-replacement succession of black spruce in cool, moist sites (Van Cleve & Viereck, 1981; Kurkowski *et al.*, 2008).

Successional paradigms for northern black spruce forests suggest that burned stands should rapidly regenerate a new cohort of spruce seedlings, leading to stand self-replacement with little intervening change in forest composition (Dix & Swan, 1971; Van Cleve & Viereck, 1981; Kurkowski *et al.*, 2008). Black spruce trees have semiserotinous cones that produce a flush of local seed dispersed soon after a fire (Viereck, 1983). This provides black spruce with a substantial recruitment advantage over other, nonserotinous trees at sites with thick organic seedbeds because these seedbeds typically require a high seed: seedling ratio for successful recruitment (Johnstone & Chapin, 2006a; Greene *et al.*, 2007). Seed production and seedling densities of serotinous conifers have been shown to be proportional to prefire basal area in more southern boreal forests (Greene & Johnson, 1999; Greene *et al.*, 2004; Chen *et al.*, 2009). Detailed measurements of postfire seed rain made at a subset of our sites did reveal a positive relationship between total seed rain and standing basal area of prefire spruce, but the impact of basal area on viable seed rain was largely obscured by strong negative effects of canopy fire severity on seed viability (Johnstone *et al.*, 2009). It is likely that the high levels of canopy severity observed in many of our study plots reduced seed viability and thereby weakened the functional relationship between prefire basal area and regeneration potential of black spruce (Greene & Johnson, 1999). It is possible that the positive relationship we observed between spruce pre- and postfire densities reflects a legacy of similar environmental conditions for spruce regeneration following past and recent fire events, rather than a legacy of seed availability. In either case, this relationship indicates some level of system resilience, as it suggests that postfire spruce regeneration has a tendency to resemble recruitment patterns from the previous fire interval. However, our models

ascribe relatively little weight to this relationship in determining seedling dominance, indicating that legacy effects of prefire spruce abundance are insufficient to maintain spruce-to-spruce self-replacement cycles under the full range of conditions found in the 2004 fires.

We also expected deciduous recruitment to show legacy effects of prefire vegetation, as deciduous trees in the prefire stand provide a bud-bank for asexual regeneration (Lavertu *et al.*, 1994; Greene & Johnson, 1999). However, our results indicated that stands with prefire deciduous trees were no more likely to support postfire deciduous seedlings than stands that contained only spruce when they burned. This is consistent with our observations that most deciduous seedlings recruited from seed rather than asexual regeneration. Deciduous seedling densities declined with the estimated distance to patches of live deciduous trees, but again, this effect was relatively minor compared with the effects of fire and environmental conditions. Consequently, our data suggest that observed patterns of spruce and deciduous recruitment were driven most strongly by the physical conditions associated with fire and environmental conditions, rather than strong legacy effects caused by seed or bud availability.

Shifts in the dominance of spruce vs. deciduous tree seedlings have long-term consequences for successional trajectories and future forest composition. Although sites with high seedling densities are likely to experience self-thinning (Westoby, 1984), long-term observations indicate that compositional patterns established shortly after fire are good predictors of relative composition two or three decades later (Johnstone *et al.*, 2004). Careful aging of mixed stands of black spruce and deciduous trees in interior Alaska shows little evidence of canopy succession to spruce dominance even after >200 years (Fastie *et al.*, 2003; Kurkowski *et al.*, 2008). In situations where relay succession from deciduous to conifer species has been observed, mortality of individual deciduous trees in the forest canopy appears to require at least 50–70 years, and about 200 years for canopy replacement of deciduous broadleaves by conifers (Bergeron, 2000; De Grandpre *et al.*, 2000; Schulze *et al.*, 2005). With fire cycles in the boreal forests of western North America typically <100 years (Yarie, 1981; Larsen, 1997), there is unlikely to be sufficient time for many stands that regenerate to deciduous forest to return to black spruce dominance before they burn again. Although preferential herbivory on deciduous species by moose (*Alces alces*) or snowshoe hare (*Lepus americanus*) can have strong effects on tree composition during early succession, these effects are often localized in areas where herbivore density is high (Bryant & Chapin, 1986) and are most pronounced where deciduous species are relatively uncommon

(i.e. stands that are initially spruce dominated) (Feng *et al.*, 2009). Thus postfire herbivory by generalist herbivores is more likely to magnify differences in relative recruitment between spruce- and deciduous-dominated stands than to alter the nature of successional trajectory. Large scale, species-specific mortality caused by disease or insect outbreaks appear to play the greatest role in causing stands to shift from deciduous to conifer dominance (Bergeron, 2000; Schulze *et al.*, 2005). Consequently, we interpret our prefire stand data to indicate that most of the burned stands were dominated by spruce seedling recruitment after the previous fire cycle. Under the conditions of the 2004 burns, however, many of these stands have shifted to deciduous seedling dominance and will likely develop deciduous-dominated canopies.

The extreme fire year of 2004 provided an exceptional opportunity to investigate postfire recovery across a wide range of landscape and fire conditions. The results of this study advance our understanding of factors controlling postfire community recovery by providing insight into the relative roles of environmental gradients, vegetation legacies, and disturbance effects in driving forest dynamics within heterogeneous landscapes. Boosted regression tree analysis provided a flexible modeling system that produced biologically interpretable results and highlighted the role of threshold responses in driving regeneration dynamics. These models predicted observed patterns of seedling density and composition with relatively low error, indicating that our models captured the major factors determining initial tree recruitment in this system. Nevertheless, as is ultimately the case with all observational studies, our inability to independently manipulate the potential driving factors means that we must be cautious in extrapolating from these results. Landscape factors such as latitude and elevation interact with site moisture to influence patterns of both forest composition and fire conditions (e.g. Duffy *et al.*, 2007), and these interactions will influence forest responses to future changes in climate and fire. Our results build on evidence from previous studies that have highlighted the potential importance of fire severity to boreal forest regeneration (Arseneault, 2001; Johnstone & Kasischke, 2005; Greene *et al.*, 2007; Chen *et al.*, 2009) and provide a strong weight of evidence that severe fires can dramatically alter patterns of postfire succession. An important insight that emerges from this broad-scale study is that the potential for fire to drive shifts in successional trajectories is contingent on landscape factors such as site moisture. Consequently, we should expect that the resilience of black spruce forests to changing climate and fire regime will not be uniform across the landscape and that drier spruce forests may have the greatest

potential to switch to deciduous-dominated forests under future environmental change.

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