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A sensitive slope: estimating landscape patterns of forest resilience in a changing climate

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Abstract. Changes in Earth's environment are expected to stimulate changes in the composition and structure of ecosystems, but it is still unclear how the dynamics of these responses will play out over time. In long-lived forest systems, communities of established individuals may be resistant to respond to directional climate change, but may be highly sensitive to climate effects during the early life stages that follow disturbance. This study combined analyses of pre-fire and post-fire tree composition, environmental data, and tree ring analyses to examine landscape patterns of forest recovery after fire in the south-central Yukon, Canada, a climatically dry region of boreal forest where there is evidence of increasing drought stress. Pre-fire stand composition and age structures indicated that successional trajectories dominated by white spruce (*Picea glauca*) with little aspen (*Populus tremuloides*) comprised most of the study area during the last fire cycle. Although spruce seedling recruitment after the fire was highest at sites near unburned seed sources and where surface organic layers were shallow, spruce seedling densities were often insufficient to regenerate the pre-fire spruce forests. In particular, sites in the warmer topographic locations of the valley lowland and south-facing slopes typically had few spruce seedlings and instead were dominated by aspen. The opposite pattern was observed on north-facing slopes. Age reconstructions of pre-and post-fire stands indicate that future canopy composition is driven by initial post-fire recruitment and thus observed landscape differences in seedling recruitment are likely to be maintained through the next 100–200 years of succession. Observed results support the hypothesis that sites experiencing greater environmental stress show the lowest resilience to disturbance, or greatest compositional changes. Analyses of tree-ring responses to climate variables across the same landscape indicate that patterns of tree growth prior to a disturbance may be a useful predictor of landscape variations in forest resilience, allowing managers to better anticipate where future changes in forest composition are likely to occur.

Key words: age structure; dendrochronology; equivalent latitude; fire; forest regeneration; landscape ecology; seed dispersal; slope aspect; topography; Yukon.

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INTRODUCTION

Earth's climate is undergoing a period of rapid change driven by anthropogenic impacts on the composition of greenhouse gases in the atmosphere (Solomon et al. 2007). Rates of climate

change are expected to be greatest in high latitude regions, where current observations already provide evidence of substantial warming and changes in climate-driven processes (ACIA 2005, Soja et al. 2007). The distribution of ecosystem types in high latitude tundra and boreal biomes is fundamentally tied to climate (Woodward and Williams 1987) and changes in climate are expected to lead to shifts in vegetation cover types both within and across biome boundaries (Soja et al. 2007). Forest species are generally expected to shift northwards as the climate warms, with boreal forest expanding into tundra at its northern boundaries and contracting at its southern boundaries (Hansen et al. 2001). However, such shifts in the distribution of plant communities, and the biomes they define, are unlikely to occur uniformly across a landscape. Rather, we can expect changes to occur in a complex fashion, influenced by interactions between directional climate change, disturbance events, biotic interactions, dispersal behavior, and landscape heterogeneity in environmental factors (Pearson and Dawson 2003). Understanding and predicting these dynamics is a central element of forecasting the non-equilibrium responses of ecosystems to climate change over the coming century.

There is ample evidence that changes in climate influence the growth of many forest tree species (Briffa et al. 2004), but it is less clear how current changes in climate will influence the dynamics and distributions of forest types in coming decades to centuries. In the circumboreal forests of the northern hemisphere, growth records recorded in tree rings indicate that boreal conifers are already responding to regional changes in climate (Lloyd and Bunn 2007). Upland populations of white spruce (*Picea glauca*) in Alaska and Yukon have shown a consistent signal of reduced radial growth during recent warm decades (Barber et al. 2000, Hogg and Wein 2005), and many treeline forests in northwestern North America show an increasing frequency of negative growth responses to temperature (Wilmking et al. 2004, Pisaric et al. 2007). More broadly, satellite-based observations of boreal forests suggest widespread declines in productivity (Goetz et al. 2005). Portions of the boreal forest have shown increases in tree mortality that are likely associated with periods of drought (Hogg et al. 2008) or climate-driven insect outbreaks (Berg et al. 2006), patterns that are consistent with a global increase in incidences of climate-induced tree mortality (Allen et al. 2010).

Despite these signals of direct climate effects on tree growth, productivity, and mortality, large portions of the boreal forest currently show little evidence of compositional change (Masek 2001, Soja et al. 2007). Similarly, paleorecords of boreal forests and other terrestrial plant communities often show long periods of stable community composition, with ecological responses lagging behind environmental changes (e.g., Camill and Clark 2000, Arseneault and Sirois 2004). Periods of rapid compositional change in these records are frequently associated with disturbance events or changes in disturbance regime (e.g., Camill and Clark 2000, Franklin and Tolonen 2000). These dynamics are consistent with resilience theory, which predicts that internal feedbacks can maintain long periods of ecosystem stability even under changing environmental conditions (Holling 1973, Gunderson 2000). Stabilizing feedbacks are typically interrupted by a disturbance, which then triggers a period of community reorganization and adaptive change in response to altered conditions (Holling 1973, Gunderson 2000). Long periods of apparent stability in an ecosystem can mask changes in the underlying *resilience* of communities, or their ability to return to a previous compositional state following disturbance (Gunderson 2000, Folke et al. 2004). Our ability to anticipate sudden shifts in ecosystems and their long-term consequences requires an understanding of the conditions under which ecological resilience is maintained or eroded (Folke et al. 2004).

Several mechanisms help to maintain the compositional stability of boreal forests. The large resource capture networks of mature individuals can act to buffer plant responses to annual variations in climate (e.g., Arseneault and Sirois 2004). Plant effects on environmental conditions help maintain a relatively stable local environment even under conditions of regional change (Camill 2000, Chapin et al. 2004). Consequently, mature trees may be able to persist under conditions that preclude their successful recruitment under the same conditions (Hogg and Schwarz 1997, Bouchon and Arseneault

2004). Similarly, disturbances may trigger rapid changes in environmental conditions that exceed a species' tolerance limits for re-establishment (Astrom et al. 2007). In cases where future composition is strongly determined by initial patterns of community assembly, factors that influence patterns of post-disturbance recruitment play a key role in mediating between alternative stable states of community composition (Jasinski and Payette 2005, Baskett and Salomon 2010).

In the boreal forests of western North America, fire is the dominant landscape-scale disturbance and forests are subject to large, stand-replacement fires that occur at intervals of 50 to 200 years (Yarie 1981, Cumming 2001). Regeneration of the forest canopy largely occurs from seedlings that recruit within the first decade after fire when seedbeds are optimal for establishment (Gutsell and Johnson 2002, Peters et al. 2005). By monitoring patterns of seedling recruitment after fire, we can thus obtain valuable insights into the resilience of forest ecosystems to disturbance (Bruelheide and Luginbuhl 2009).

This research uses a natural experiment provided by a large wildfire to examine landscape variations in forest resilience to disturbance in an area currently experiencing rapid changes in climate (Serreze et al. 2000). Our study takes place in the dry boreal forest of south-central Yukon, where tree rings provide evidence of widespread and increased drought stress of mature white spruce populations in the region (Barber et al. 2000, Hogg and Wein 2005). We measured the post-fire recovery of white spruce forests across landscape gradients in microclimate to assess whether landscape units exposed to more severe climate conditions showed evidence of decreased resilience to fire. We also tested whether the growth patterns of mature trees could be used to predict landscape variations in the resilience of white spruce stands to fire disturbance. Our analyses provide information about how the resilience of boreal forest communities may vary across heterogeneous landscapes and identify potential tools to anticipate changes in ecological resilience under ongoing climate change.

Methods

Study area

The study area was located in south-central Yukon Territory, north of Whitehorse, in a region dominated by white spruce forests. Sampling occurred within a NE-SW oriented valley catchment that encompasses the upper drainage basins of Fox Lake and Little Fox Lake (latitude 61°18′ N, longitude 135°34′ W). Prior to the most recent fire, the valley was largely covered by forests of mature white spruce with patches of aspen (*Populus tremuloides*) woodlands and open grassland localized on steep, south-facing bluffs (Oswald and Brown 1986). In 1998, a large (45,000 ha) fire burned through much of the northern portion of the valley, causing complete or near-complete stand mortality in large patches of white spruce forest.

The south-central Yukon is one of the most arid regions of boreal forest in North America, receiving less than 300 mm of precipitation per year on average due to rain shadow effects of the nearby Coast Mountains (Hare and Hay 1974). The nearest climate station to the study area is located at Braeburn (latitude 61°28.2′ N, longitude 135°46.8′ W), approximately 15 km to the North, where average annual precipitation for 1979–2000 was 279.8 mm/year (Environment Canada 2010). Mean daily temperatures in July and January for the same period were 13.6°C and −21.2°C, respectively. The soils of the study area are largely fine-grained clay or silt loams derived from lacustrine sediments or wind-blown loess (Smith et al. 2004).

Field data

We evaluated pre-fire and post-fire forest composition by measuring dead trees and new seedlings 7–10 years after fire, when we expected that most of post-fire seedlings that comprise the future canopy would have been recruited (Gutsell and Johnson 2002, Johnstone et al. 2004, Peters et al. 2005). Topographic variation has been shown to have a large impact on microclimate conditions in mountainous areas of boreal forest (Van Cleve et al. 1991). Our sampling was stratified into three topographic classes categorized by coarse-scale aspect: a) warm, dry southwest-facing aspects, b) intermediate sites in the valley bottom, and c) relatively cool and

moist northeast-facing aspects. Because variations in seed availability can have important impacts on post-fire recruitment densities (Albani et al. 2005, Peters et al. 2005), we also structured our observations to vary in distance from potential seed sources within unburned patches of forest.

We collected field observations in June 2005 of pre-fire stand composition, post-fire seedling recruitment, and site characteristics in nested circular plots that were randomly located within a coarse-scale aspect class (Table 1). The first sample sites within an aspect class were randomly located. The locations of subsequent sites within an aspect class were determined based on a random compass orientation (within a range of 180° to prevent back-tracking) and random distance (5–150 m). All sampled plots were georeferenced in three dimensions (i.e., including elevation; mean accuracy 6 m) using handheld GPS units. Furthermore, all unburned forest edges and unburned patches of trees observed in the field that were within 500 m of a sample site were walked with a handheld GPS to georeference the dominant potential seed sources. Sampling intensity was highest in the lowland aspect class (Table 1), where the Klondike Highway provided relatively easy access to points close to and distant from unburned edges. This area represented about 30% of the burned valley catchment. Lowland areas also had highly variable microtopography caused by relic ice melt features (Smith et al. 2004), which provided a range of moisture drainage conditions.

At each sample site, we established two nested circular plots around a center point marked by a metal post. The inner plot had a minimum radius of 2.0 m (12.6 m^2) and was used for estimating the density of post-fire seedlings of white spruce and aspen. The ground area within the plot radius was carefully searched and all tree seedlings in a plot were counted and identified to species. If no seedlings were encountered, the area searched was expanded to a 4.0 m radius plot (50 m^2). For up to three spruce seedlings in a plot, we estimated seedling age by counting the number of bud scars on the main stem axis with the aid of a hand lens (10× magnification).

Pre-fire stand characteristics were measured from standing or fallen deadwood originally rooted within an outer circular plot of 4.0 m radius. Because fire rarely consumes the bark and stem of live, mature trees, we were able to identify tree species and measure the density and basal area of each species present in the pre-fire stand. White spruce and aspen comprised the only tree species regularly encountered in the pre- or post-fire stands, with occasional observations of lodgepole pine (*Pinus contorta*) and balsam poplar (*Populus balsamifera*). Black spruce (*Picea mariana*) is rare in the study area (Oswald and Brown 1986) and was not encountered.

We also measured a number of environmental variables at each sample site. Slope and aspect were measured with a clinometer and compass. The local shape of the slope (convex, concave, or flat) was noted as an index of moisture drainage at the sites. The depth of the post-fire soil organic layer was measured on extracted soil plugs at three points within each plot. Mineral soil texture was estimated by feel for the near-surface mineral soil. To characterize aspects of the post-fire substrate that may affect seedling establishment and survival, we estimated percent cover in the seedling plot for the following substrate types: coarse woody debris, mineral soil, dead moss, live moss, fibric organic material, and plant litter.

In late June 2008, we returned to the study area to collect repeat measurements on a subset of sample sites and obtain new measurements from a small number of sites to be used to validate

Table 1. Summary of the distribution of sample sites between aspect classes and sample years.

Aspect class	2005 sites used in model development	2005 sites used in model validation	2008 sites used in model validation
Valley lowland	53	53†	5
NE-facing slope	27	0	14
SW-facing slope	38	0	11
Total	118	53	30

†The 53 lowland sites from 2005 used in model development are independent of the 53 lowland sites used in model validation.

models developed from the 2005 data (Table 1). We randomly selected 17 sites (≥5 per aspect class) from 2005 to be re-measured so that we could quantify any differences in seedling establishment that had occurred between 2005 and 2008. An additional 13 new sites were randomly located and sampled at the same time. Sample procedures followed those described above. We also collected spot measurements of soil moisture over a three day interval without rain at the 17 resampled sites using a hand-held reflectometry probe (HydroSense, Campbell Scientific, Edmonton, Alberta, Canada) inserted in the mineral soil to a depth of 12 cm.

We collected tree ring samples from pre-fire white spruce trees at 23 of the 30 sites sampled in 2008. Three pre-fire trees located closest to the plot center were cored with an increment borer at breast height (1.4 m) to obtain a 5.4 mm diameter core for ring-width measurements. At one site, only two trees were sampled because rotten wood prevented us from obtaining a complete core from a third stem. All trees had a diameter at breast height of greater than 5 cm and smaller individuals were not encountered in our sample. Two cores were taken from each stem at right angles to each other. Stem cores were mounted in wooden blocks and sanded to 600 grit prior to measuring ring widths with a digital scanner system (WinDendro v.7.0, Regent Instruments, Québec City, Québec, Canada). Paired ring width series from each tree were visually matched to detect missing rings, and the paired sample ring widths were then averaged. Between-tree ring width series were aligned by visual cross-dating to match patterns of extreme maximal and minimal points between sites. These ring width series were used to assess relationships between tree stem growth and climate variables (see Data analyses, below).

We collected a limited set of stand age data to evaluate whether our expectations of a short, 7–10 year recruitment window after fire (Gutsell and Johnson 2002, Johnstone et al. 2004, Peters et al. 2005) were likely to be appropriate for this study area. We randomly selected 6 sites sampled in 2005 (2 in each aspect class) for detailed study of pre-fire stem ages. At each plot, we selected the 20 pre-fire trees with their root base closest to the plot center point, regardless of stem diameter. In all cases these trees were white spruce. We cut a basal stem disk at a height of 10–30 cm above the root collar of each tree to avoid rings distorted by root development that make cross-dating more difficult (Speer 2010). Stem sections were sanded to a fine polish using successive grades of sand paper up to 400–600 grit. Ring widths were measured under a binocular microscope using a Velmex moveable stage (Velmex Inc., Bloomfield, New York, USA) attached to a digital recorder. Ring-series from pre-fire trees were cross-dated with a living chronology developed from trees growing outside of the 1998 burn area and the accuracy of the cross-dating was assessed using the software program COFECHA (Grissino-Mayer 2001). Stand age distributions were assessed by plotting the frequency of observed ages in 5-year age classes. To assess the potential effects of aging errors in estimating the time since the previous fire, we compared observed age distributions to stem ages from a portion of the Fox Lake burn with a known time since last fire. Tree stem sections were obtained from 40 white spruce trees located on SW aspects at the northern edge of the 1998 Fox Lake burn where it overlapped with areas burned in the 1958 Braeburn fire. All stems had recruited following the 1958 fire and then were killed in the 1998 fire. Stem sections were taken from just above the root collar and processed as described above.

Data analyses

Data analyses were performed using the R statistical package (R Development Core Team 2006) unless otherwise noted. Distance to a seed source was calculated as the Euclidean straight-line distance to the nearest live stand, identified either from field GPS coordinates, when live trees were tiny tree islands visible from the plot (within approximately 500 m), or visually from a single Landsat image taken after the fire. This latter method poorly detects small islands of seed source trees and thus we combined the two datasets to obtain a more accurate assessment of most probable seed source trees. We used slope and aspect data to calculate the "equivalent latitude" of a site based on the equations in Lee (1962). This index represents the impact of slope exposure on incoming radiation to estimate an equivalent latitude if a site were in flat terrain. Consequently, flat sites in our study had equiv-

alent latitudes equal to the true latitude (~61°N), while north-facing aspects were estimated to be equivalent to higher latitudes and south-facing aspects equivalent to lower latitudes (Lee 1962).

We compared pre- and post-fire densities for spruce and aspen to assess how the relative composition of forest stands changed after fire in the different coarse-scale aspects. We tested the statistical significance of differences between means between these categorical factors using a mixed model approach in the lme4 package in R (Bates and Maechler 2009). The mixed model used tree density as the response, sample site as a random effect, and fixed effects for aspect class and "fire treatment" (pre or post-fire), with an interaction between aspect and treatment. All tree and seedling data were ln-transformed prior to analysis. Because some sites had zero seedlings observed, we added a constant equal to the smallest observed seedling density to all density values. Issues associated with this treatment of zero values are discussed below.

Recruitment model.—Our ultimate goal was to determine the factors driving seedling recruitment. To do this, we first used a general additive model (GAM) with all environmental factors entered as smoothed terms to determine which factors were associated with spruce density, and to suggest functional forms. The GAM used nonlinear terms fitted by cubic penalized regression splines, with the smoothing term chosen by generalized cross-validation (from the mgcv package in R; Wood 2000). Only sites from 2005 for which all stem density and environmental information was available (n = 118) were included when fitting recruitment models (Table 1).

Smoothed terms were removed from the model if at least two of the following criteria were met (adapted from Wood and Augustin 2002): 1) their effective degree of freedom was close to the minimum value of 1; 2) the confidence intervals included zero effects over the whole range of the variable, and 3) model fit, as measured by AIC, did not decrease following removal of the variable. Furthermore, equivalent latitude was removed from the final model since visual inspection of the data revealed that its significance as a predictor of spruce density depended on the influence of two sites with very low equivalent latitude, in which no seedlings were observed.

The final model of spruce density was fit using the non-linear least squares (NLS) function in R. Recruitment was assumed to be the product of two factors: how many seeds fell on a given site (based on distance) and the proportion of those seeds that germinated and survived until they were surveyed. The number of seeds falling on a site was fit to an exponentially declining curve, which leveled off to a background rate of seed rain at sites distant from unburned seed sources. The other factors were entered into the regression as standard linear predictors. The assumed model of seedling dynamics was:

$$G_j = (b_6 e^{b_7 d_j} + b_5) e^{\sum_{i=1}^{4} b_i x_i} \varepsilon_j,$$

where, G_j are densities of germinants in each plot j; d_j are the distances to closest seed source; x_i are model covariates representing aspect class (NE aspect, SW aspect or lowland) and linear and quadratic terms for organic depth to account for a unimodal response of spruce density to organic layer depth; ε_j represents independent, log-normally distributed error; and b_i are parameters to estimate. For categorical site factors, the reference site was lowland. To make fitting easier, we took the natural log of both sides and fit the following model:

$$\ln(G_j) = \ln(b_6 e^{b_7 d_j} + b_5) + \sum_{i=1}^{4} b_i x_i + \ln(\varepsilon_j)$$

Because aspen seed is known to be widely dispersed via air-borne seeds (Romme et al. 2005) and we found no evidence for a decline in seed availability with distance to unburned edges, the final model for aspen density was a linear model, with log-aspen density fitted as a function of organic depth and landscape unit. Model fit was assessed by AIC and visual evaluation of the distribution of residuals around the fitted values.

We tested how well our recruitment models fit new data by predicting expected density values of the sites sampled in 2008 (n = 30) and a subset of sites sampled in 2005 (n = 53). The 53 validation sites from 2005 were excluded from the original model fit because, due to a recording error, they were missing pre-fire stem density (which was tested as a candidate variable but not

used in either of the final recruitment models). These validation sites were all located in the lowland aspect class and had a spatial distribution that overlapped the 2005 lowland sites used in the original model fit (Table 1). We also validated our approach for modeling zero seedling counts (adding a small constant to all values) by comparing our model results with two alternative but less powerful methods. Alternative models were obtained using 50% quantile regression or 2-stage regression, first with presence-absence data and then on densities, using only presence data. The results from these alternative models were functionally very similar to the results we obtained with the least squares models. In particular, for the spruce data, all models confirmed the presence of non-linear distance terms, a constant level of background seed rain, uni-modal relationships with organic depth, and a significant effect of aspect on recruitment.

Tree ring width model.—We analyzed relationships between tree ring width measurements and recorded climate variables to assess whether the relationship between tree growth and climate varied between sites differing in solar exposure and therefore temperature and potential evaporation. Climate data were extracted from the Canadian National Climate Data and Information Archive for 1943–1998 for the Whitehorse A station, which had a longer time record than the Braeburn station. Data for 1996–1997 were missing from the Whitehorse A station and data for these years was taken from the Whitehorse WSO station. Precipitation imbalance was calculated using P-PET calculations based on evaporation models, after Hogg and Wein (2005).

To determine which monthly climate variables were most strongly correlated with ring width series from individual trees, we used the program DendroClim (Biondi and Waikul 2004) to find correlation and response-function values between each tree ring series and climate variables. Climate variables included monthly average temperatures and P-PET from March of the previous year to August of the year of growth. These were used to determine appropriate monthly- and seasonally-averaged climate variables to use as predictors in the model described below.

We constructed a multi-level model to examine the relationship between tree growth and the direct and interactive effects of climate and aspect (equivalent latitude; Lee 1962) using the lme4 package in R (Bates and Maechler 2009). We represented climate effects as the partial correlation of ring widths at a site with each climate variable. In this analysis, ring width series were exponentially detrended by log-transforming the data and then extracting any linear trends. Results of the analyses were qualitatively similar whether ring series were exponentially or linearly detrended, and only the exponentially detrended data are presented here. Time series of detrended ring widths and climate variables were standardized by calculating z-scores ((observed-average)/standard deviation) for each ring width and climate variable. We then fit the following multi-level model to examine the climatic influences on growth rings:

$$R_{j,t} = \sum_{i=1}^{3} (\alpha_i + \beta_i E_k + \gamma_{i,j}) C_{i,t} + \varepsilon_{j,t}$$

$$\gamma_{i,j} \sim N(0, \sigma_{\gamma,i}), for\ j = 1, ..., J$$

$$\varepsilon_{j,t} \sim N(0, \sigma)$$

where $R_{j,t}$ are the standardized ring widths for tree j at time t; J is the number of trees (68); C_i are the climate values (April temperature, June temperature, April precipitation, and fall P-PET) observed in year t; α_i, are the study-wide fixed effects; β_i are the study-wide fixed effects for the interaction between the C_i covariates and E_k, equivalent latitude at site k; $\gamma_{i,j}$ are the random effects on the slope of the regression for individual trees; the $\varepsilon_{j,t}$ are independent and identically distributed residuals; σ and $\sigma_{\gamma,i}$ are the standard deviations for the residuals and γ_i, respectively. The notation $x \sim N(0,\sigma)$ indicates that a variable, x, is distributed according to the normal distribution, with mean of 0, and standard deviation of σ. Because all variables were z-score transformed prior to analysis, the ring width series have a zero intercept by definition and no intercept term was included in the model. The formulation of the model essentially assumes that each tree has its own response function to different climatic signals, and that these individual responses are a function of tree level properties and the solar exposure of a site (Gelman and Hill 2007). This

formulation allows us to determine if the response of tree growth to various climatic variables varied systematically with solar exposure, represented by equivalent latitude as a proxy for light availability and evapotranspiration potential (Lee 1962).

Results

Environmental characteristics

Sites in the Fox Lake burn that were located on NE- and SW-facing slopes and in the valley bottom showed patterns of environmental characteristics that were consistent with hypothesized differences in microclimate and drainage among coarse-scale aspects. As expected, measured slopes were typically steeper on the NE- and SW-facing sides of the valley than in the valley bottom (Table 2). Broad differences in slope and aspect resulted in NE-facing slopes having higher equivalent latitudes than the valley bottom and SW-facing slopes, indicating cooler conditions. However, differences in the local topography at a site meant that the observed ranges of environmental variables often overlapped among the coarse-scale aspect classes. Organic layer depths were thickest on the NE-facing slopes, likely reflecting the cooler and generally moister conditions in these areas (Table 2).

Past patterns of stand regeneration estimated from stand age reconstruction

Cross-dated counts of tree rings in basal stem disks from six sites in the Fox Lake burn indicated that pre-fire trees ranged in age from 93 to 267 years, with a median of 121 years. This distribution of ages is consistent with estimates from tree cores sampled at breast height for ring width analyses, which had ring counts ranging from 37 to 246 rings with a median of 106 rings. Tree ring counts from breast-height cores are typically lower than those obtained from basal samples because of the increased time required for a tree to reach a greater sampling height (Gutsell and Johnson 2002).

Five of the six sites used in stand age reconstructions showed evidence of a concentrated peak in stem ages consistent with a short pulse of stem recruitment following a stand-replacing fire (Fig. 1). White spruce at sites located on the SW-facing slope of the valley showed a peak in stem ages at ~120 years, which likely indicates a pulse of recruitment following a fire that occurred around 1870–1880 (Fig. 1a, b). Stems sampled from one site on the opposite NE-facing slope were slightly younger and may have recruited following a fire in the same or following decade (Fig. 1c). Two sites, one in the lowland and one on the NE aspect, showed evidence of a relatively low-severity fire in the 1850s that stimulated a pulse of new recruitment (stems 140–150 years old) but also left some older trees alive in the stand (Fig. 1d, e). In contrast to these five stands, one site in the valley lowland showed a broader distribution of stem ages that was not consistent with our hypothesis of recruitment being largely constrained to the decade immediately following the last fire (Fig. 1f). At this site, most stems aged between 170–210 years, indicating that either recruitment occurred over a longer period than the other white spruce stands or that aging errors in this relatively old stand reduced our ability to detect a peak in stem recruitment (Peters et al. 2002).

Interpretation of these stand age distributions can be considered in the context of similar age

Table 2. Distribution of environmental conditions measured at sites within three coarse-scale aspect classes in the Fox Lake valley, south-central Yukon (values are mean ± standard error).

Environmental variable	Lowland	NE-facing slope	SW-facing slope
Slope (degrees)	3.1 ± 4.1 [a]	10.6 ± 11.3 [b]	8.0 ± 6.5 [b]
Equivalent latitude (degrees)	61.3 ± 4.3 [ab]	63.5 ± 10.0 [a]	58.6 ± 6.7 [b]
Organic layer depth (cm)	2.4 ± 5.3 [a]	7.3 ± 7.5 [b]	2.1 ± 4.8 [a]
Volumetric soil moisture	21.6 ± 5.0	34.4 ± 10.1	18.8 ± 1.7

Notes: Significant differences between aspect classes were tested with a one-way analysis of variance followed by multiple comparisons with Tukey's honestly significant difference test. Superscript letters not shared across aspect classes indicate significant differences in an environmental variable. Sample sizes are the same as those listed in Table 1 for the 2005 samples used in model development, except for soil moisture, where n = 5, 7, and 5 sites for the valley lowland, NE slope, and SE slope, respectively.

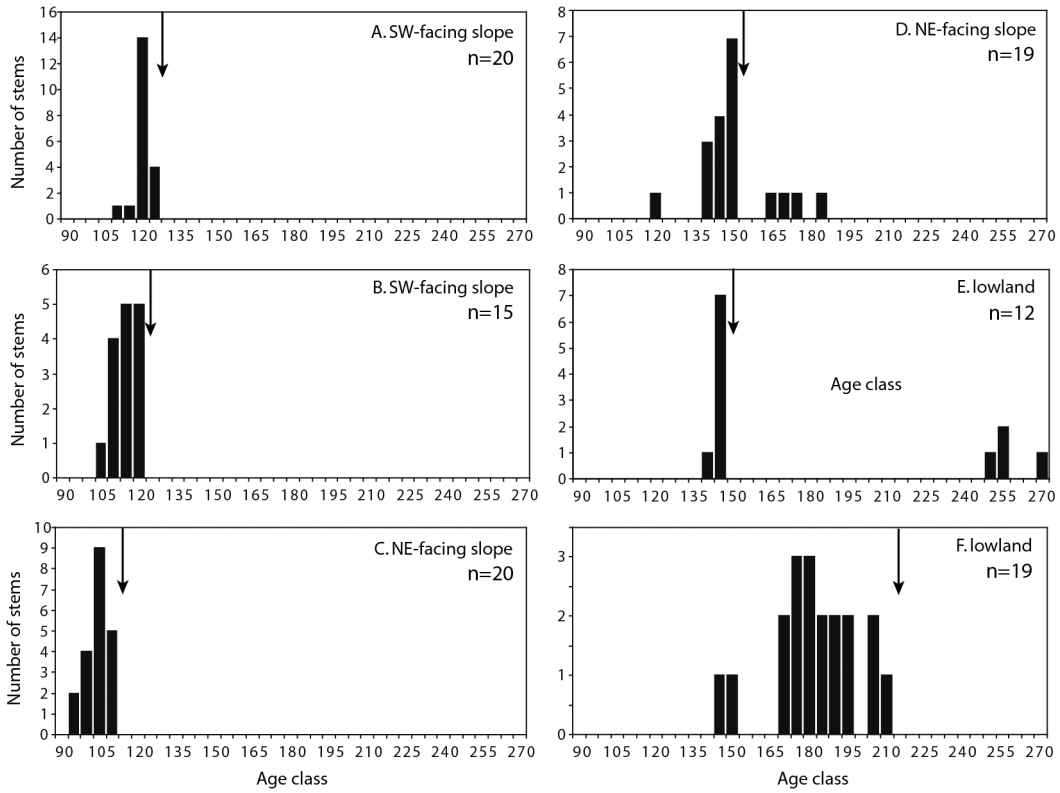

Fig. 1. Histograms of stem ages within 5-year age classes for six sites (a–f) in the Fox Lake valley. Arrows indicate the inferred time since the last stand-replacing fire. Stem ages were obtained from cross-dated ring counts of basal stem sections of mature white spruce trees that were killed in the 1998 Fox Lake fire. Two sites were sampled in each of the main aspect classes in the valley: southwest-facing slopes (a, b), northeast-facing slopes (c, d), and the valley lowland (e, f). The total number of stems sampled is given on each panel. Although 20 stems were sampled from each site, sample size varied due to internal decay in some stems.

distributions observed after a known historical fire. Stems of white spruce that regenerated after the 1958 Braeburn fire and then were killed in the 1998 Fox Lake fire showed a peak in stem ages of 34–35 years (Fig. 2), compared to a maximum possible age of 40 years. The oldest stem sampled was aged at 38 years and youngest stem at 26 years. When stem ages were summarized in a histogram of 5-year age classes, there was a clear and strong peak in stem ages that occurred at ~5 years after the fire and extended to 15 years post-fire (Fig. 2).

Age estimates of post-fire tree seedlings based on counts of bud scars indicate that 84% (168/200) of post-fire white spruce seedlings established within two years and 97% (193/200) within three years after the Fox Lake fire. No current-year or one-year old stems of white spruce were observed when sampling in 2005, and there were no significant differences in the density of white spruce seedlings between sites that were sampled both in 2005 and 2008. Although we did not examine the age structure of post-fire aspen stems, we observed an increase in stem density of aspen between samples collected in 2005 and 2008 that suggests continued recruitment of aspen stems in the post-fire stands, likely through asexual root sprouts (Hogg and Wein 2005).

Comparison of pre- and post-fire tree composition

Within the Fox Lake burn, pre-fire stem densities of white spruce were similar across all three aspect classes (Fig. 3a). Compared to the pre-fire stands, white spruce stem densities were significantly reduced in post-fire stands across all

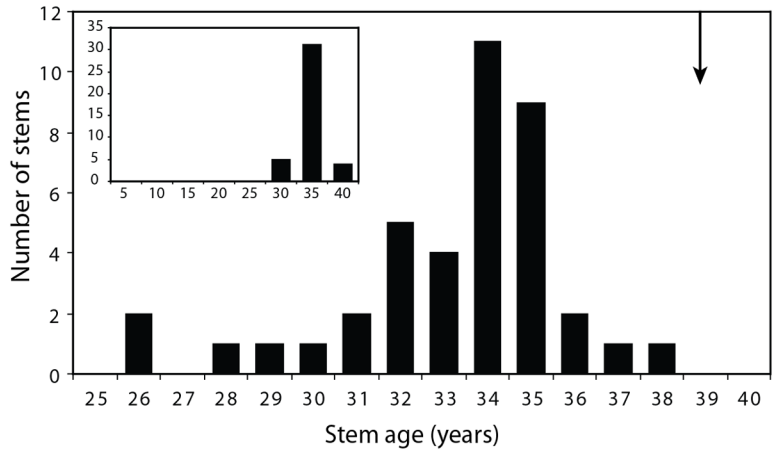

Fig. 2. Histograms of stem ages of white spruce that regenerated following the 1958 Braeburn fire and were burned in the 1998 Fox Lake fire. The arrow indicates the time since the last stand-replacing fire as inferred from tree ages. Stem ages were obtained from cross-dated ring counts of basal stem sections (n = 40). The inset shows the same data plotted as a histogram using 5-year age classes on the x-axis.

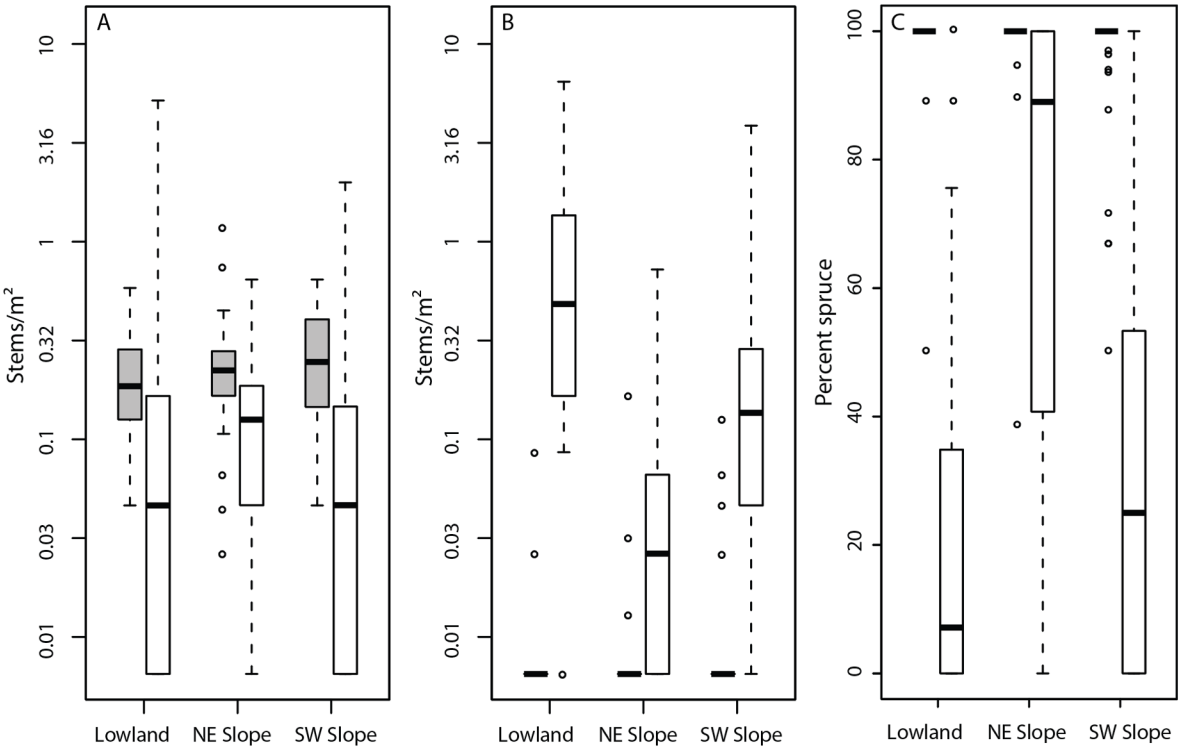

Fig. 3. Distribution of pre-fire (grey boxes) and post-fire (white boxes) stem densities of (a) white spruce and (b) aspen, along with (c) the proportion of spruce stems relative to total stems within different coarse-scale aspect classes based on slope exposures. Stem densities in A and B are plotted on a $\log_{10}$ scale. Boxes encompass the median (horizontal line) and 25–75% quantiles of the data, with whiskers extending to the 95% quantile and extreme values indicated by open circles.

Table 3. Results of mixed effects models used to test differences in ln-transformed stem density between categorical factors of pre- and post-fire stands and coarse-scale aspects.

Model coefficients	Modeled response variables	
	Spruce density, ln(stems /m^2)	Aspen density, ln(stems /m^2)
Intercept	**−1.73 ± 0.18**	**−4.96 ± 0.19**
NE-facing	0.15 ± 0.32	0.13 ± 0.32
SW-facing	0.27 ± 0.28	**0.35 ± 0.29**
Fire: Pre- vs. post-fire	**−1.33 ± 0.26**	**3.71 ± 0.25**
NE-facing × Fire	0.44 ± 0.45	**−2.58 ± 0.44**
SW-facing × Fire	−0.34 ± 0.40	**−1.22 ± 0.39**

Notes: Pre-fire and post-fire data were collected at the same sites and site was included as a random effect in the model. To fit the model, the effects of pre-fire stands and the lowland aspect class were set to zero. Values are estimated model coefficients ± SE and those significantly different from zero ($p < 0.05$) are indicated in bold font.

aspect classes (Table 3). Although all sample sites had white spruce present in the pre-fire stand, a large proportion of sites in both the lowland and SW-facing slope had few to no spruce seedlings that successfully established after the 1998 fire (Fig. 3a).

In contrast to white spruce, trembling aspen was only rarely observed in pre-fire stands at Fox Lake. Aspen stems became significantly more abundant following the 1998 fire, with the post-fire increase in aspen stem density dependent on the coarse-scale aspect (Table 3). The highest post-fire densities of aspen were observed at lowland sites, with intermediate densities at sites on the SW-facing slope of the valley, and the lowest post-fire densities on the NE-facing slope (Fig. 3b).

The trend towards lower densities of white spruce and higher densities of trembling aspen in the post-fire versus pre-fire stands led to a notable shift in stand composition following the 1998 Fox Lake fire (Fig. 3c). Prior to the fire most stands (>85%) had a tree composition that was 100% white spruce. After the fire, stands regenerated to a composition that was frequently dominated by trembling aspen rather than white spruce. The compositional dominance of white spruce observed in the pre-fire stands was maintained after fire only on the NE-facing slope, while the majority of stands in the lowland or SW aspect classes switched from spruce to aspen dominance following fire.

Modeling post-fire regeneration responses to driving variables

The initial GAM model identified coarse-scale aspect, log distance from the nearest unburned white spruce, and post-fire organic layer depth as being related to post-fire white spruce densities. These variables were then included in the final model that was fit using non-linear least squares analysis. AIC values of the GAM (187.1) and NLS (190.0) models indicated approximate equivalence. However, AIC values corrected for small sample sizes, AIC_c (Burnham and Anderson 2002), indicated far superior support for the NLS model (NLS: 231, GAM: 278) as the extra terms in the GAM were heavily penalized given the sample size. Both the GAM and NLS models were able to capture approximately 40% of the variation in post-fire spruce densities (GAM $R^2 = 0.43$, NLS $R^2 = 0.39$). The functional form of the NLS model is preferable because it captures the expected exponential decline in seedling establishment with distance from a seed source (e.g., Greene and Johnson 2000).

Post-fire white spruce densities were significantly and non-linearly related to distance to the nearest unburned stand (Fig. 4, Table 4). Observed seedling densities tended to be highest at sites located within 10–30 m of an unburned stand, and declined steadily as this distance increased up to ~100 m. At distances >100 m from an unburned edge, post-fire spruce densities were generally low and insensitive to further observed variations in distance up to >1000 m. For a given distance, the highest spruce densities observed were at sites located on NE aspects with intermediate organic layer depths (5–10 cm; Fig. 4).

The fitted GAM models provided no evidence of a significant relationship between aspen stem densities and distance from unburned stands, but did indicate effects of organic layer depth and coarse-scale aspect on aspen density. Consequently, aspen recruitment was fitted with a least squares linear model (Table 4). Both the GAM and linear models of aspen recruitment had similar AIC_c (281 for both, due to a virtually linear GAM fit) and explained approximately one third of the variation in post-fire aspen density ($R^2 = 0.35$). Sites in all aspect classes showed a pattern of declining post-fire aspen recruitment with increasing organic layer depth (Fig. 5).

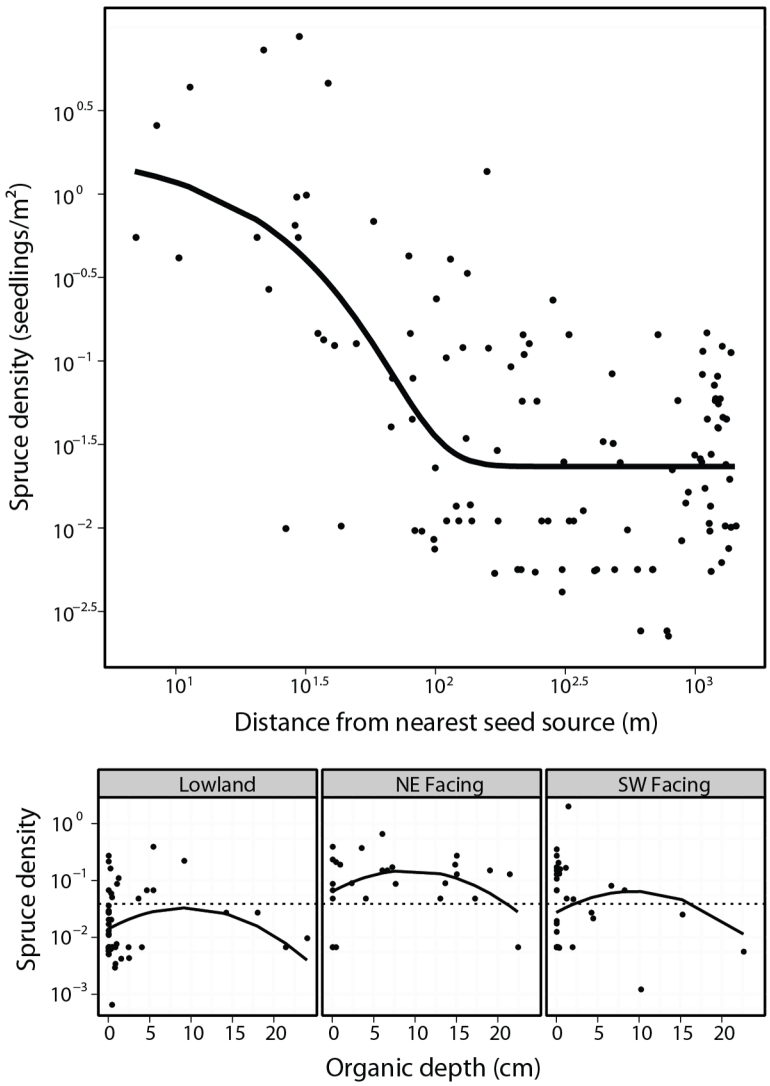

Fig. 4. Marginal spruce densities (i.e., setting all non-depicted quantitative covariates to their mean, and dummy categorical variables to zero) (points, n = 118) and fitted models (solid lines) as a function of distance based on the non-linear model (see text). The upper panel compares spruce density to distance (m, on a log-scale) from the nearest unburned seed source. The lower panel graphs show relationships between organic depth and slope exposure. The dashed line in the lower graphs indicates the overall sample mean.

Although there was a wide range of stem densities observed at sites with shallow organic layer depths, aspen densities at sites with thick organic layers (up to ~20cm) were always low. Aspen stem densities were also related to aspect, and were significantly higher at sites in the lowland and lowest on the NE-facing slopes (Fig. 5).

Model validation

Predicted patterns of spruce stem densities from the fitted spruce model provided a reasonable and relatively unbiased estimate of observed spruce stem densities in the validation data set (Fig. 6) (Pearson correlation between observed and predicted values = 0.55). The validation dataset showed a similar pattern of declining spruce densities with increased distances from an unburned seed source up to ~100 m, and a unimodal response to organic layer depths. As in the original model, spruce densities also tended

Table 4. Fitted coefficients for least squares models of continuous and categorical factors affecting post-fire spruce and aspen densities measured at Fox Lake (n = 118).

Model	Term	Coefficient estimate	95% CI (lower, upper)	P-value
Spruce recruitment	b_1 (intercept)	0.014	0.008, 0.024	0.0003
	b_2 (slope)	1.15	0.36, 4.39	0.08
	b_3 (exponential distance coefficient)	−50.8	−92.8, −25.5	0.0002
	$c_{\text{organic depth}}$	0.180	0.029, 0.34	0.02
	$c_{\text{organic depth2}}$	−0.010	−0.017, −0.002	0.01
	$c_{\text{SW facing slope}}$	0.67	0.045, 1.29	0.04
	$c_{\text{NE facing slope}}$	1.52	0.74, 2.21	0.0002
Aspen recruitment	b_1 (intercept)	−0.94	−1.42, −0.47	0.0001
	$c_{\text{organic depth}}$	−0.13	−0.18, −0.08	<0.0001
	$c_{\text{SW facing slope}}$	−0.90	−1.60, −0.19	0.01
	$c_{\text{NE facing slope}}$	−1.81	−2.64, −0.98	<0.0001

Notes: 95% confidence intervals are provided for each estimate as an upper and lower bound, along with the significance value for the null hypothesis that the coefficient is equal to zero (see methods for details on model fitting). Reported p-values are based on an assumed t-distribution and don't take into account the fact that the confidence intervals for the parameters are not symmetric. However, all p-values are confirmed by confidence intervals that do not overlap with zero.

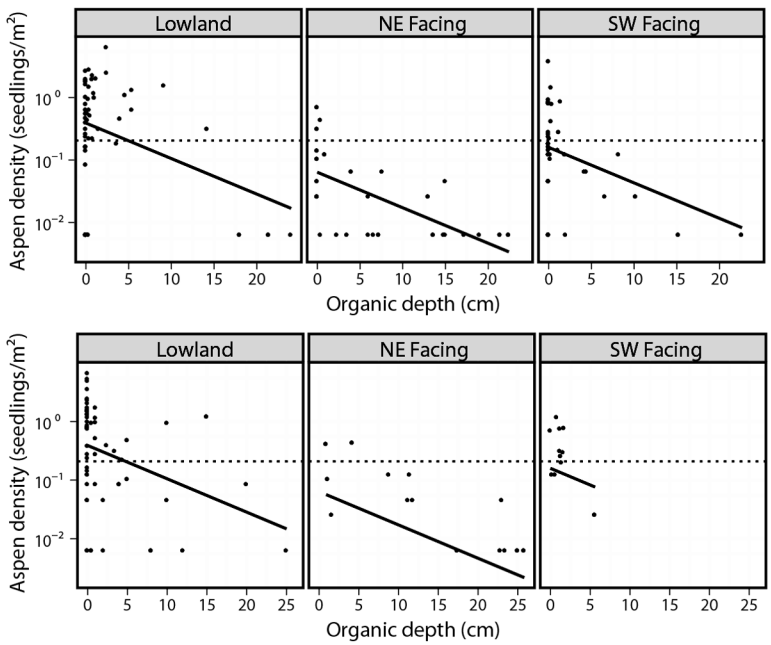

Fig. 5. Marginal aspen density (points, n = 118) and fitted models (solid lines) as a function of organic depth, by aspect class (see Fig. 4). The upper panel of graphs represents 2005 data used to fit the linear model, and the lower panel shows the fit of that model to validation data collected in 2005 and 2008. The dashed line indicates the overall mean.

to be highest on NE-facing slopes.

The fit of the aspen model to validation data was not as strong as the spruce model, as aspen densities were somewhat under-predicted for the validation data set (Fig. 5). However, this effect is at least partially due to an increase in mean aspen densities between 2005 and 2008. The original model was fit only to data collected in 2005, while the validation dataset included data from both 2005 and 2008. Furthermore, the correlation between observed and predicted data was still strong (Pearson correlation = 0.52).

Landscape patterns of tree ring sensitivity to climate in pre-fire white spruce

Tree ring widths measured from pre-fire white

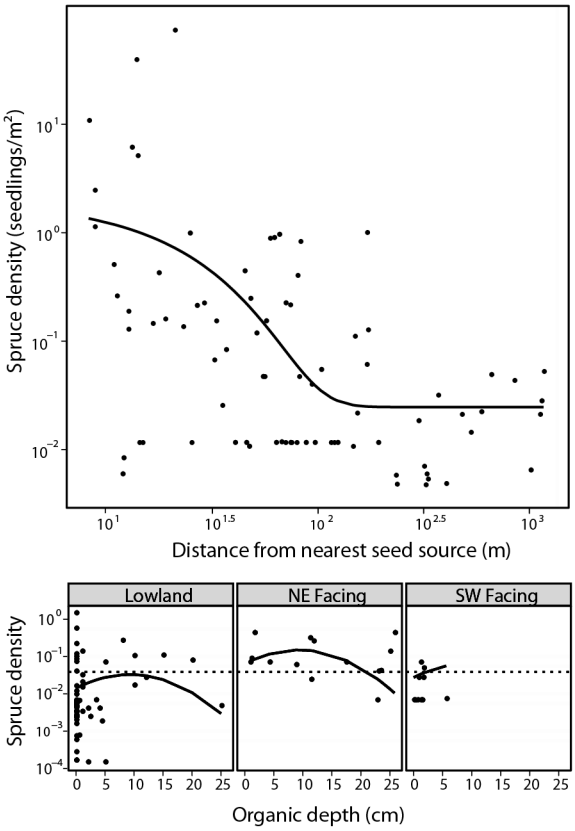

Fig. 6. Marginal spruce densities and predicted values (solid line) using validation data as a function of distance to nearest seed source (upper panel) and organic depth by aspect classes (lower panel) (see Fig. 4).

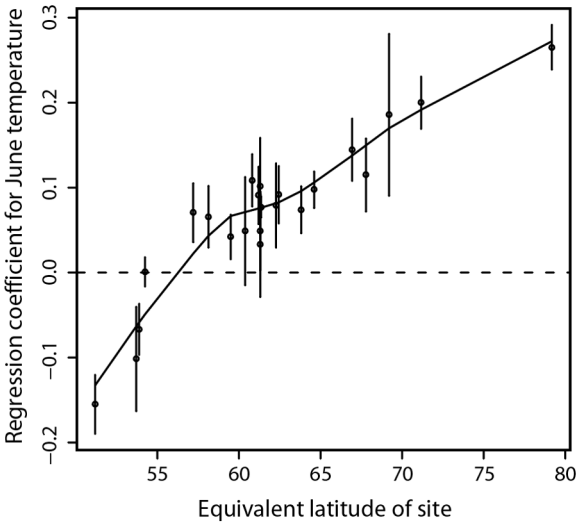

Fig. 7. Standardized regression coefficients of tree ring widths against average June temperature, showing the interaction effect of equivalent latitude and June temperature (see text for a full explanation of the multi-level model). Points represent the average regression coefficients for each site, ±1 standard deviation. The black line is a loess regression of regression coefficients on equivalent latitude.

spruce trees were most frequently correlated with June temperatures of both the current and previous years, April temperatures and precipitation in the previous and current years, and fall precipitation imbalance (PET-P) of the previous year. The strongest correlations observed were with June temperatures.

The multilevel model of tree growth responses to direct and interactive effects of climate and aspect indicated that tree ring widths were negatively associated with June temperatures at low equivalent latitudes (hot and dry sites with a southerly aspect). Ring widths became more positively associated with June temperature as equivalent latitude increased to indicate cooler, north-facing sites (Fig. 7). Once June temperatures were accounted for, none of the other climate variables were significantly related to the detrended ring widths.

Discussion

This study combined measurements of pre-fire and post-fire tree densities, environmental data, and tree ring responses to climate with the aim of deciphering how climate and disturbance may interact in driving landscape patterns of forest resilience. Our results provide evidence of shifting successional trajectories after fire in the dry boreal forests of south-central Yukon that are consistent with the environmental tolerances of the two dominant tree species, white spruce and trembling aspen (Albani et al. 2005). Although pre-fire stands were uniformly dominated by white spruce and showed no systematic differences in pre-fire stand density or composition across coarse-scale aspects, analysis of tree ring records provided evidence of temperature stress on south-facing aspects. North-facing slopes were the only portions of the landscape where pre-fire trees had ring widths that were positively associated with June temperatures, and these

areas had consistently higher densities of white spruce regenerating after fire. The homogeneity of forest composition and structure across coarse-scale aspects in the pre-fire but not post-fire stands suggests that there have been landscape-scale changes in the resilience of these forests that may be predictable from tree ring-climate relationships.

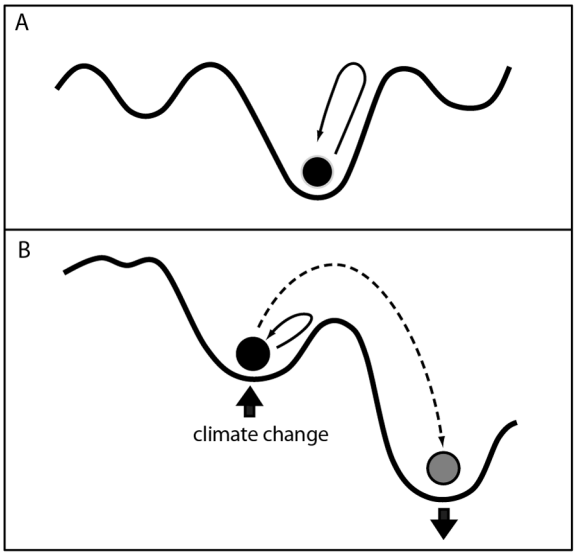

Fig. 8. A conceptual ball-and-trough diagram illustrating how underlying changes in the resilience landscape (thick solid lines) may lead to reduced ecological resilience and rapid changes in ecosystem composition following disturbance (dashed arrow). Variation in community composition is indicated along the x-axis and the current state of a community is indicated by the black ball. In panel A, a stable resilience landscape with no net slope and a deep trough in the region of current community composition illustrates a high probability of ecosystem recovery to a similar composition following disturbance. In panel B, the directional slope in the resilience landscape suggests an underlying regime shift, such as climate change (block arrows), that has altered the optimal configuration of community composition (indicated by the deepest trough) (after Folke et al. 2004). When disturbed, the likelihood of the current community (the black ball) returning to a similar composition is reduced, and this reduction in resilience is associated with a high likelihood of transformation to a new composition domain (dashed arrow leading to the grey ball). Interactions between local environmental conditions and directional environmental change may result in scenarios of both stable (A) and shifting (B) resilience landscapes occurring within the same regional landscape.

Patterns of forest response to fire disturbance in the Fox Lake valley are consistent with the conceptual model of long periods of stability and abrupt change postulated by resilience theory (Gunderson 2000). Directional changes in the environment may cause "hidden" changes in ecological resilience that are masked by the stabilizing processes that maintain ecological resistance; these processes are then disrupted by disturbances that stimulate abrupt changes in community composition (Fig. 8; Folke et al. 2004). For the purpose of ecological forecasting, it is important to recognize that changes in resilience occur within a landscape context and the impacts of environmental change on resilience will be contingent on the local conditions of an ecosystem (e.g., Peterson 2002, Danby and Hik 2007). Data from the Fox Lake burn indicate that patterns of forest resilience to fire disturbance are contingent both on topographic conditions that affect local microclimate and the effects of individual fires. Thus, even with widespread climate change in the North (Serreze et al. 2000), we can still expect substantial variation in the resilience of different landscape units and their vulnerability to change. A challenge remains to ecologists and managers to predict sets of conditions under which we expect the greatest potential for threshold changes and to adjust our management strategies accordingly (Chapin et al. 2006, Thrush et al. 2009).

Estimating patterns of forest resilience

Our interpretation of forest resilience following the Fox Lake fire is based on the assumption that patterns of early seedling regeneration accurately reflect the rate and ability of future forest stands to recover to a composition similar to the pre-fire forest. Several studies in the boreal forests in western North America have found that canopy composition in boreal forests is strongly determined by the initial composition of seedlings that establish within the first 3–7 years after fire (Gutsell and Johnson 2002, Peters et al. 2002, Johnstone et al. 2004). This short recruitment window is influenced by rapid declines in seedbed quality after fire (Charron and Greene

2002) and a high variability in white spruce seed production (Peters et al. 2005). Consequently, post-fire regeneration of white spruce may be largely attributed to seed produced in a single mast year (Peters et al. 2005). Nevertheless, patterns of forest composition established during this initial post-fire establishment phase appear to persist for at least the lifespan of the initial cohort (Johnson et al. 1994, Gutsell and Johnson 2002).

Our observations of tree recruitment in the Fox Lake valley showed clear evidence of recruitment concentrated in a short post-fire window. The vast majority of white spruce seedlings that established after the 1998 fire recruited within the first three years after fire. Similarly, white spruce stems that recruited after a known 1958 fire also showed a pulse of post-fire recruitment, with a peak in estimated stem ages that lagged approximately 5 years after the fire. Finally, five of six pre-fire stands of unknown age showed age structures that suggested stems originated synchronously during a 10–20 year recruitment period. Given that errors in accurately aging individual trees increase with tree age (Gutsell and Johnson 2002, Peters et al. 2002), we interpret all these data to indicate that most of the white spruce in both the pre-fire and post-fire stands at Fox Lake recruited within a few years after fire (Peters et al. 2002, 2005). Although delayed recruitment of white spruce can occur several decades after a fire (e.g., Fig. 1F; Peters et al. 2006), competitive interactions typically constrain later recruits to poor growth and survival in the forest understory for decades to centuries (Johnson et al. 1994, Bergeron 2000). Delayed recruitment is thus unlikely to substantively alter the landscape patterns of forest composition we observed at Fox Lake.

Although we did not age aspen trees in this study, previous work in an nearby area burned in 1958 indicated that initial aspen recruitment also occurred within a few years after fire, and may subsequently increase through asexual reproduction (Hogg and Wein 2005). Consequently, our estimates of aspen dominance in post-fire stands may be conservative if aspen densities continue to increase beyond 10 years after fire. However, we found very limited evidence of aspen in the pre-fire stands and interpret this to indicate a low abundance of aspen following the previous cycle of stand-replacing fires. Ring counts from pre-fire stands indicated most stands were approximately 100–150 years old when they burned in the 1998 fire, with a small number of trees or stands aging up to 250 years. Chronosequence and height-growth analyses suggest that boreal mixedwood stands require ~100–200 years of succession for white spruce to replace aspen in the forest canopy (Bergeron 2000, Kurkowski et al. 2008, Strong 2009). If aspen had been abundant in post-fire stands during the previous fire free interval, we would expect to have seen a large portion of our sites showing evidence of aspen in the pre-fire stands. However, aspen deadwood was absent from 85% of the sites we sampled. This suggests that post-fire forest regeneration following the last set of fires in the Fox Lake basin followed successional trajectories dominated by white spruce with relatively low densities of aspen. Pre-fire tree ages indicate that much of the white spruce forest that burned in the 1998 Fox Lake fire originated prior to the start of the 20th century. Proxy climate indicators show that the climate in the 1800s was cooler than what has been observed at the end of the 20th century (Youngblut and Luckman 2008). White spruce is found at sites that are cooler and wetter than those occupied by aspen (Thompson et al. 1999, Albani et al. 2005) and a cooler climate may have favored the recruitment of white spruce over aspen after fires in the previous fire cycle.

Taken together, these data provide evidence of a substantial shift in forest successional trajectories after fire in the Fox Lake drainage basin. Pre-fire stands appear to have followed spruce-dominated successional trajectories that were initiated after previous fires. Post-fire seedling counts suggest that spruce regeneration is insufficient at many sites to restock white spruce to a level similar to that found in the pre-fire stands. This is particularly true given the likelihood of future stem mortality and stand thinning (Kabzems and Lowster 1997, Johnstone et al. 2004). Following the 1998 Fox Lake fire, many of the formerly monotypic spruce stands have shifted to mixed-wood or deciduous successional trajectories likely to be dominated by aspen rather than white spruce over the next century. Based on our understanding of post-fire recruitment and succession processes, this appears to repre-

sent an important change in successional trajectories that will lead to a substantially greater portion of deciduous-dominated forests than occurred during the preceding fire interval. Shifts in successional trajectories from primarily conifer-dominated to primarily deciduous-dominated will influence a wide range of ecosystem processes, including wildlife habitat use (Nelson et al. 2008), land-atmosphere energy exchange (Chapin et al. 2000), and patterns of forest productivity and carbon storage (McGuire et al. 2002).

Landscape patterns of resilience

Shifts in successional trajectories at Fox Lake have not occurred uniformly across the landscape. This observation is of particular importance to predicting the dynamics of ecosystem responses to environmental change. When factors such as distance from seed source and organic layer depth were controlled for, regeneration densities of white spruce were highest at cool and moist sites found on NE-facing slopes, whereas the opposite was true for trembling aspen. This pattern was not apparent in the pre-fire forest composition, and is consistent with what would be expected for non-uniform changes in community composition under directional environmental change. Namely, we should see changes in forest composition *first* at the "margins," i.e., where species are found relatively close to their physiological tolerance limits (e.g., Lloyd and Bunn 2007). At locations on the margins of a species' limits, relatively small changes in limiting factors, such as local climate, may cause large changes in community composition (e.g., Arseneault and Sirois 2004, Landhausser et al. 2010). Likewise, in communities composed of long-lived individuals that maintain stable canopy dominance over decades to centuries (Bergeron 2000), impacts of climate change on community composition may not become apparent until a disturbance interrupts the dominance of established individuals and requires re-assembly at the seedling stage (Payette et al. 2001, Wirth et al. 2008, Landhausser et al. 2010).

Are there tools that may help us predict landscape variations in resilience? This study provides preliminary evidence that relationships between pre-fire tree-ring growth and climate variables may be useful as an indicator of the vulnerability of forest communities to rapid compositional change after disturbance. We found that trees growing on warm, SW-facing slopes showed a negative response to June temperatures, and these sites showed the greatest change in forest composition after fire. In contrast, trees on cool, NE-facing slopes showed a positive response to June temperatures and post-fire seedling communities were compositionally similar to the pre-fire stands. Negative responses of tree rings to summer temperatures has been widely interpreted as a signal of drought stress in the boreal forest (Lloyd and Bunn 2007). Drought stress signals in tree rings have been linked to periods of episodic mortality in adult trees (e.g., Hogg et al. 2008, Allen et al. 2010). However, our study is one of the first (that we are aware of) to show an association between landscape-level variations in tree-ring signals of drought stress and landscape patterns of forest resilience to disturbance. Further testing is warranted to determine if tree-ring signals can be reliably used as an indicator of forest vulnerability to compositional change after disturbance.

Our models provide insight into the patterns of fire conditions that shape the composition of white spruce forests. The spruce seedling model is consistent with previous research indicating that spruce recruitment is likely to be seed-limited at distances of ~100m from a seed source (Greene and Johnson 2000, Purdy et al. 2002). However, our data indicate that there is also a level of background seed dispersal that permits seedling establishment far from an unburned seed source (see also Wirth et al. 2008). Nevertheless, seedling establishment away from unburned edges is insufficient to create stand densities similar to those observed in the pre-fire forest at Fox Lake. Although secondary waves of regeneration may occur as fallen logs decompose and provide a suitable seedbed (Peters et al. 2006), age reconstructions from the pre-fire stands suggest that secondary recruitment has not historically played a large role in canopy development in the forests of our study area. Consequently, our data suggest that changes in environmental conditions or the spatial patterning of burns in the landscape have altered the potential for white spruce recruitment at Fox

Lake since the previous set of fires and forest renewal.

The results of this study are consistent with other studies of post-fire succession in boreal forests that indicate controlling effects of site moisture, organic layer depth, and seed availability on forest structure and composition (e.g., Greene et al. 2004, Peters et al. 2005, Johnstone et al. 2010). Although white spruce recruitment may be strongly limited by seed dispersal from unburned edges as discussed above, landscape differences in environmental conditions also strongly constrain post-fire white spruce recovery (Albani et al. 2005). Seed dispersal did not appear to act as a strong constraint on aspen recruitment, even though aspen was absent from most of the pre-fire forest and thus must have depended on recruitment from seed rather than by asexual resprouting (Romme et al. 2005, Landhausser et al. 2010). However, trembling aspen was much more sensitive than white spruce to the presence of a thick organic layer, a pattern consistent with the greater sensitivity of small vs. large-seeded species to variations in seedbed quality (Johnstone and Chapin 2006, Greene et al. 2007). Differences in species traits such as seed characteristics and physiological tolerance limits are likely to be key factors that interact with changing environmental conditions to drive new patterns of community reorganization following fire in boreal forest landscapes.

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