Regional-scale hydrologic settings buffer black spruce regeneration in the presence of post-fire droughts

by

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Abstract

Climate change is increasing the frequency of droughts and wildfires, reducing tree recruitment, and altering post-fire species composition. In Canada's western boreal forests, post-fire recruitment, particularly of drought-intolerant coniferous species like black spruce, has declined in recent decades to the benefit of early-successional species like jack pine and trembling aspen. Groundwater supplied to forests via adjacent peatlands may help to resist such reductions in recruitment and compositional shifts, particularly during droughts. The degree to which peatlands buffer adjacent forests from drought-induced regeneration failure may therefore depend on topographic position and soil texture, factors that govern groundwater connectivity. I examined how these topoedaphic factors influence upland tree regeneration from post-fire drought, defined in this study as the post-fire climate moisture deficit across sampled fires. Since higher-positioned peatlands (bogs, poor fens) are mostly fed by precipitation, they are more vulnerable to drought compared to fen-like peatlands at lower topographic positions that are fed by groundwater. I therefore hypothesized that regenerating forest density, growth, and composition at lower topographic positions would be buffered from post-fire drought by water sources from the adjacent fen across a range of soil textures. Specifically, I predicted that tree density, volume, and proportions of black spruce should decline with high topographic positions, favoring instead jack pine and aspen following post-fire drought. I tested this prediction by measuring 58 post-fire upland forest stands ranging from 5 – 20-years old that experienced wet or dry post-fire weather. Study sites spanned local (relative to adjacent peatland) and regional topographic position (relative to a regional low) gradients. I used generalized linear mixed effects models to test interactions between these local and regional topographic positions, soil texture, and post-fire climate. I found significant reductions in regenerating black spruce proportions at high regional topographic positions across fine- and coarse-textured soils with post-fire drought. Total regeneration (stem density), tree volume (basal area), and species of jack pine and aspen showed no correlations with post-fire drought. This study highlights that hydrologically well-connected areas of Alberta's boreal forest may act as refugia from drought and fire for drought-intolerant black spruce, and that more predominant upland jack pine and aspen species appeared to be resilient under the current fire regime. Larger scale ecohydrological dynamics therefore interact with forest regeneration and should be considered to identify areas that may resist altered post-fire trajectories.

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Finally, I would like to acknowledge the land on which this project was conducted. This project spanned Alberta's Treaty 6 and 8 territories. These are traditional territories of the Cree, Saulteaux, Dene, Nakota-Sioux, Anishinaabe, Niitsitapi, and Métis people who have stewarded these lands for millennia. The land on which I stand, and the land on which I conducted this

project, is special as all lands are. When the rumbling of cars on a summer evening gives way to frog, and cricket calls from the nearby pond. When coyotes silently track a jack-rabbit on freshly fallen, suburban snow. When wild blueberries provide a beach-front snack break in a sandy pine forest while adjacent lake breezes cool my body, I am grateful that this land, and the life it sustains, exists regardless of my presence.

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Glossary of terms

ABMI: Alberta Biodiversity Monitoring Institute

AICc: Akaike's information criteria, corrected for small sample sizes

CanLaBS:Canadian landsat burn severity product

CMD: Climate moisture deficit. Monthly evapotranspiration (Eref) − precipitation

DEP: Derived ecosite phase

Eref: Evapotranspiration

GLMM: Generalized linear mixed effects model

Local topographic position: The elevation of an upland plot relative to its adjacent peatland.

Post-fire drought: Cumulative climate moisture deficit over years 0 – 3 post-fire a

Regional topographic position: Elevation of an upland plot above a regional (within a variable and defined neighborhood) low point.

Introduction

Climate change is expected to directly increase the frequency of biotic and abiotic forest disturbances globally, particularly within coniferous boreal forests (Seidl et al., 2017). In the boreal plains ecozone of western Canada, a warmer and drier climate (Gauthier et al., 2015; Ireson et al., 2015; Price et al., 2013) may hinder post-fire tree recruitment (Boucher et al., 2020) following expected increases in wildfire frequency, extreme fire weather, and fire season length (Flannigan et al., 2013; Hanes et al., 2019; Kasischke and Turetsky, 2006; Wang et al., 2015). This may undermine the resilience of boreal tree species, reducing overall density, biomass, and relative abundance of species like black spruce (*Picea mariana* (Mill.) BSP) and white spruce (*Picea glauca* (Moench) Voss) along their southern climatic limit while favouring early successional post-fire species like jack pine (*Pinus banksiana* Lambert) and trembling aspen (*Populus tremuloides* Michx.) (Baltzer et al., 2021; Boulanger et al., 2017; Searle and Chen, 2017a, 2017b; Stevens-Rumann et al., 2018).

Simulations by (Stralberg et al., 2018) predicted that wildfire-mediated conversion from mixedwood to more open, deciduous western boreal forests, may occur throughout Alberta's boreal plain by 2100. Although wildfires release nutrients and create seedbeds for tree germination (Miyanishi and Johnson, 2002; Prescott et al., 2000), short fire return intervals burn young conifers before they produce sufficient cones for regeneration (Hart et al., 2019; Johnstone and Chapin, 2006) This effect can be amplified by post-fire drought, shifting post-fire dominance in favour of deciduous species (Whitman et al., 2019). Indeed, the northwestern boreal biome has already recorded a net 15% loss in evergreen forest with a corresponding net increase in deciduous forest since 1984 (Wang et al., 2019). Compositional shifts from mixed wood and coniferous to deciduous stands have also been observed following post-fire drought and were likely to occur at dry landscape positions (Hogg and Wein, 2005; Walker et al., 2017). This indicates that boreal landscape features that retain moisture may confer resilience and serve as refugia from climate change (Morelli et al., 2020; Stralberg et al., 2020).

Peatlands cover approximately 50% of Alberta's boreal plains ecozone (Tarnocai et al., 2011), maintain water levels here despite potential evapotranspiration often exceeding precipitation (Thompson and Waddington, 2013; Waddington et al., 2015), and promote fire refugia in upland forests (Kuntzemann et al., 2023). Peatlands may also promote local climate-change refugia for regenerating upland tree species (Chasmer et al., 2018), acting as seed and water sources for surrounding uplands (Goodbrand et al., 2019; Hokanson et al., 2020; Whitman et al., 2019a). Indeed, increased groundwater connectivity has shown reduced wildfire severity within peatlands (Hokanson et al., 2016; Lukenbach et al., 2017). Therefore, the degree to which peatlands may provide refugia for regenerating trees may depend on groundwater connectivity, which on the boreal plain, is governed by topographic position and soil texture (Devito et al., 2012, 2005; Hokanson et al., 2019). For example, hydrological regimes on fine-textured hummocky moraine landforms are more locally dominated, as these regionally elevated areas of low soil permeability preclude groundwater recharge to regional aquifers, resulting in peatland formation in depressions among aspen-dominated uplands, and less groundwater connectivity. Lower-relief, fine-textured, clay plains, often have larger well-connected peatlands (mainly fens). In contrast, on coarse-textured soils, regionally high upland forests, and peatland systems perched atop a confining layer, recharge regional groundwater that discharge into low-lying fens (Devito et al., 2012, 2017; Ferone and Devito, 2004; Schoeneberger and Wysocki, 2005, Figure 1).

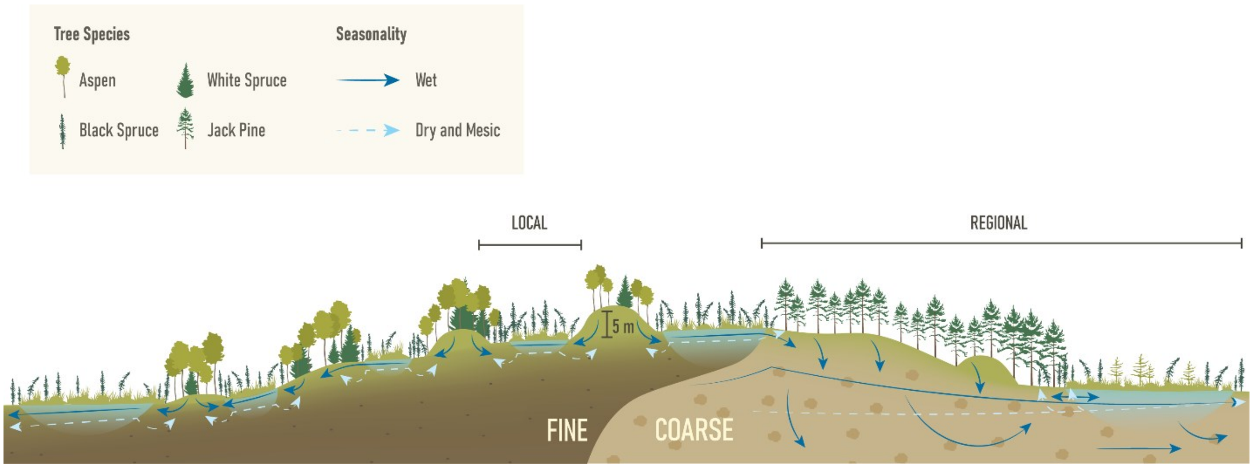

Figure 1. Conceptual model of boreal plains groundwater movement (blue) during wet (solid) as well as dry and mesic (dashed) periods across fine- and coarse-textured soils. Aspen and jack pine dominate the upland forest hummocks which recharge local (metres to 100's of metres) and regional (metres to kilometres) scale groundwater during wet periods in fine- and coarse-textured soils, respectively. During dry and mesic periods, peatlands recharge upland forests. Conceptualized by Devito et al. (2012). Informed by Bridge and Johnson (2000), Ferone and Devito (2004), Hokanson et al. (2020, 2019), Schoeneberger and Wysocki (2005), Winter (2001), and Winter et al. (2003).

Boreal forest regeneration responses to fire and post-fire climate across hydrological gradients has been studied empirically in the northwestern boreal plain region (Baltzer et al., 2021; Whitman et al., 2019) and assessed via remote sensing (Chasmer et al., 2018), but has not been addressed in field studies farther south. In this field study, I examined whether terrain and substrate features are related to the local or regional buffering of upland tree regeneration following post-fire drought. To do this, I examined the density, size (diameter), and composition of regenerating tree species along local and regional topographic position gradients in 5- to 20-year post-fire upland stands throughout Alberta's boreal forest, approximately half of which had burned and regenerated during the Canadian prairie drought period from 1999 – 2005 (Hanesiak et al., 2011). To address this question, I compared different generalized linear mixed effects models to test whether local or regional topographic position and soil texture (coarse vs. fine) affect regenerating tree density, basal area, and the proportions of predominant boreal plain tree species in response to post-fire drought. I hypothesized that forests at low topographic positions would be relatively buffered from post-fire drought, owing to sustained groundwater from this higher connectivity (Ireson et al., 2015; Winter, 2000). I predicted that drought-affected forests at high topographic positions would have lower stem density, basal area, proportions of black (more drought-intolerant post-fire species), and higher proportions of jack pine and trembling aspen (more drought-tolerant post-fire species) relative to forests at lower topographic positions. I also considered white spruce as another drought-sensitive indicator species (Hogg and Wein, 2005), although it is less common across soil textures and pre-fire stand ages than black spruce (Downing and Pettapiece, 2006). Alternatively, terrain controls on vegetation and thus pre-fire species composition (Bridge and Johnson, 2000; Day et al., 2022) may override effects of post-fire climate on recruitment. Top-down controls of post-fire climate may reduce regenerating tree biomass similarly across topographic positions as species adaptations to local site conditions may offset drought stress (Searle and Chen, 2017b). My hypotheses and predictions are summarized in more detail in Table 1.

Table 1. Hypothesized forest regeneration responses to post-fire drought (annual cumulative climate moisture deficit [CMD] for years 0 – 3 post-fire) based on soil texture and local (elevation above peatland) or regional (relative to regional low) topographic position. (+) or (-) denote hypothesized effect on response variables. * Denotes hypothesized interactions. Drought (CMD) = Sum of monthly differences in evaporation and precipitation for years 0 – 3 post-fire. Note that H_3 was only hypothesized for regenerating stem basal area.

Hypothesis	Response variable	Prediction	Reference
H_1: Topoedaphic buffering	Stem density Stem basal area Black spruce proportion	(-) Topographic position*(-) drought (CMD)	Baltzer et al. (2021) Day et al. (2020), Ireson et al. (2015), Whitman et al. (2019), Walker et al. (2017), Winter (2000)
	Jack pine proportion	(+) Topographic position*(+) drought (CMD)*(+) sand (-) clay	Baltzer et al. (2021) Day et al. (2020), Ireson et al. (2015), Whitman et al. (2019), Walker et al. (2017), Winter (2000)
	Trembling aspen proportion	(+) Topographic position*(+) drought (CMD)*(+) clay (-) sand	
	White spruce proportion	(-) Topographic position*(-) drought (CMD) (-) sand	Day et al. (2020), Hogg and Wein (2005) Ireson et al. (2015), Whitman et al. (2019), Winter (2000)
H_2: Terrain controls	Stem density Stem basal area Black spruce proportion	(-) Topographic position	Bridge and Johnson (2000), Day et al. (2022)
	Jack pine proportion	(+) Topographic position*(+) sand (-) clay	
	Trembling aspen proportion	(+) Topographic position*(+) clay (-) sand	
	White spruce proportion	(-) Topographic position (-) sand	
H_3: Climate controls	Stem basal area	(-) drought (CMD)	Searle and Chen (2017b)

Methods

Study Area and Site Selection

Study sites were in the boreal plains ecozone (BPE) of Canada (Figure 2a). At the provincial scale, study sites were located within the Central Mixedwood subregion of Alberta's Boreal Forest Natural Region except for one site, located in Alberta's Athabasca Plain subregion. The Central Mixedwood subregion has a cold, sub-humid climate with a mean annual temperature of 0.2° C, mean annual precipitation of 471 mm, and mean annual potential evapotranspiration typically exceeding precipitation (517 mm) (Downing and Pettapiece, 2006; Ecological Stratification Working Group, 1995) The physiography of the central mixedwood is generally flat with gently undulating (hummocky) topography. Surficial materials are comprised of fine-textured, glacio-lacustrine soils and clay-rich till moraines, as well as coarse-textured, glacio-fluvial and eolian deposits (Hokanson et al., 2019). Peatlands occupy approximately half of the subregion's area and are often dominated by black spruce. Upland forests on fine-textured lacustrine plains and till moraines are typically dominated by trembling aspen and paper birch in early successional stages and are succeeded by white spruce and balsam fir (*Abies balsamifera*). Upland forests on well-drained, coarse-textured sites are typically jack pine-dominated. Black spruce mixes with aspen and jack pine on coarse- and fine-textured soils, respectively, in peatland-upland transitional zones (Bridge and Johnson, 2000; Downing and Pettapiece, 2006).

I selected upland forest stands in Alberta that burned between 2001 and 2016, across a range of post-fire moisture (drought) conditions, surficial geologies, and pre-and post-fire species composition. Specifically, I sampled the 2011 Richardson Fire, the 2001 Chisholm fire, the 2016 Horse River fire, the 2011 Utikuma fire, and the 2002 House River fire. Stands within the Chisholm and House River fires burned and regenerated during the period of extreme drought from 2001 – 2002 that affected most of western Canada (Hogg et al., 2017). I ranked each fire by the cumulative climatic moisture deficit (CMD) for years 0 – 3 post-fire, averaged across study sites within each fire. The site within the Richardson fire was the driest post-fire, followed by those within the Chisholm, Horse River, Utikuma fire, then the House River Fire (Figure 2 a). Sites spanned a peatland-upland gradient (Figure 2 c), capturing local-scale nutrient and moisture gradients.

All sites spanned a peatland-to-upland transition with both uplands and peatlands having burned. No forest harvesting had occurred for any of the sites for at least 30 years before burning. Sites were located between 100 m and 1 km from the nearest road or other anthropogenic disturbance, except seismic lines, which are common in the area but small (<8 m wide). Sites were broadly classified into coarse (n = 30)- and fine (n = 28)-textured soils based on descriptions from Fenton et al. (2013). Pre- and post-fire species composition data used to select sites were from the Canadian Landsat Burn Severity (CanLaBS) and the Derived Ecosite Phase products, respectively (Government of Alberta, 2020; Guindon et al., 2021). Uplands dominated by jack pine and aspen were selected in the coarse- and fine-textured surficial geology categories, respectively (Downing and Pettapiece, 2006).

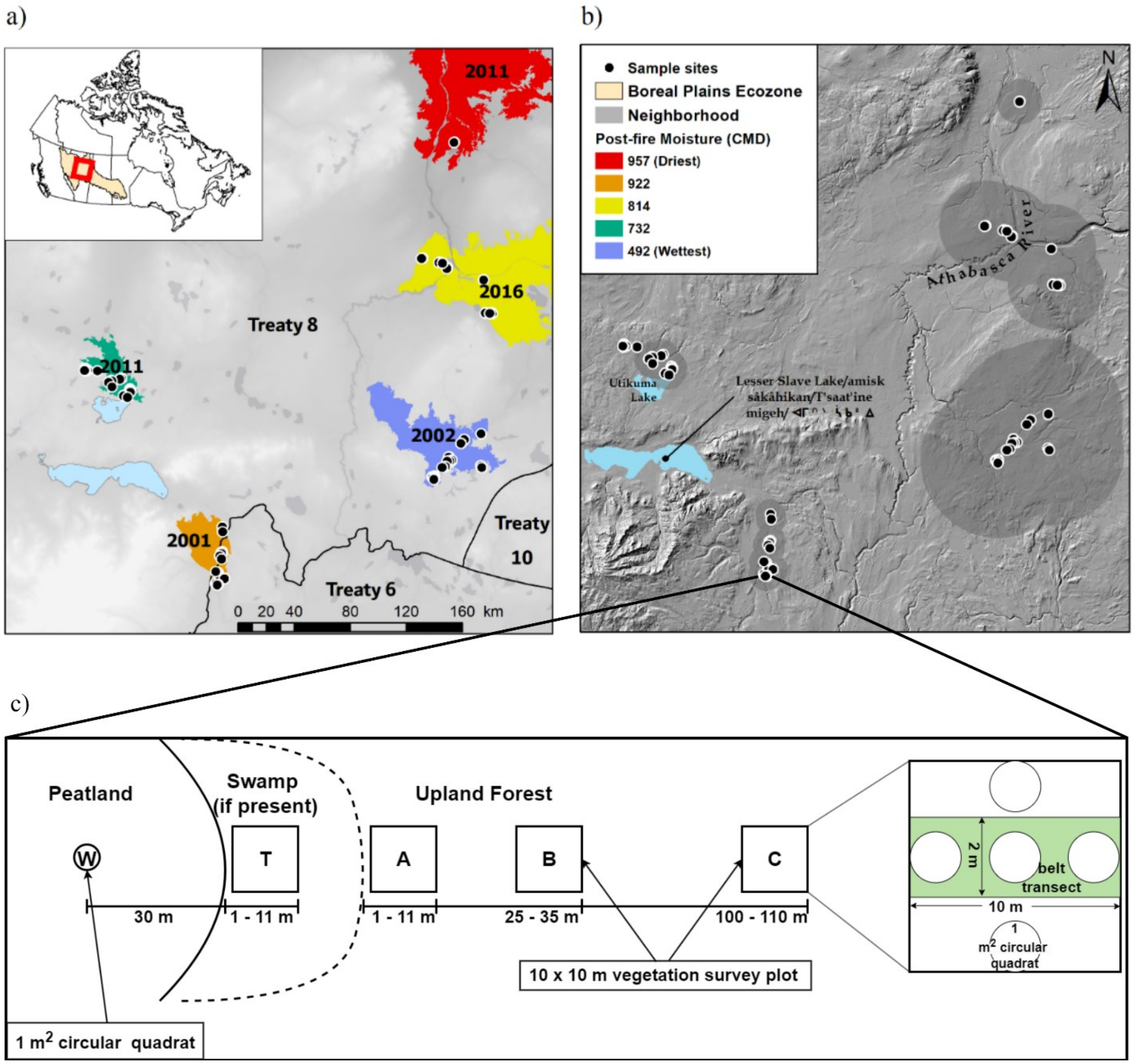

Figure 2. a) Study area map of post-fire sites sampled within the boreal plains ecozone of Canada and their post-fire moisture conditions as measured by the annual cumulative climate moisture deficit (CMD) for years 0 – 3 post-fire, averaged across sites. Sites spanned Treaty 6 and 8 territories in Alberta (Crown-Indigenous Relations and Northern Affairs Canada, 2023). CMD = climate moisture deficit, defined as the monthly difference between evapotranspiration and precipitation; b) Neighborhood sizes used to calculate the regional topographic position of each sampled plot, and c) Field sampling design of upland forest plots across the peatland-upland

gradient at each site. Where present, swamp ("T") plots were sampled at 1 – 11 m from the adjacent peatland ("W"), and the adjacent upland ("A") plots were then measured 1 – 11 m from the end of the swamp transition zone. Other upland plots were located 25 – 35 m ("B") and 100 – 110 m ("C") from the peatland or swamp edge. "C" plots were not always present. **Note**: Regeneration data were not collected in peatlands since this study was focused on adjacent upland post-fire regeneration; diagram not to scale.

Data Collection

At each site, upland overstory and understory vegetation was surveyed, and stand characteristics were measured at increasing distances from an adjoining peatland. Transects consisted of two-to-four 10 × 10 m plots in upland forest stands at 1 – 11 m, 25 – 35 m, and 100 – 110 m from adjacent peatlands (with edges defined by the presence of *Sphagnum* mosses) or swamp transition zones where present. Total transect length varied depending on the size of the upland stand and the presence of swamp transition zones. Swamp transition plots were also surveyed at 1 – 11 m from the adjacent peatland (Figure 2 c).

Transects ran on a straight bearing, perpendicular to the peatland-upland interface, capturing upland ecosite gradients (Appendix A Table 1). Diameters of overstory tree species (> 7 cm DBH) and their mortality status were surveyed in the entire 10 × 10 m plot. In the center of the 10 × 10 m plot, a 10 × 2 m belt transect ran along the transect bearing where stem counts and diameter at breast-heights of regenerating tree saplings (≥1.3 m tall, <7 cm DBH) were recorded. At the plot center and inside each plot edge, arranged orthogonally about the transect bearing, regenerating tree seedlings (<1.3 m tall) were recorded in equidistant 1 m^2 circular quadrats (Figure 2 c). Mineral soil samples to a depth of 15 cm were taken outside each of the 1 m^2 quadrats in upland plots.

Explanatory Variables

I used local and regional topographic position, post-fire drought, % sand, clay, and post-fire stand age as variables in statistical analyses. Local and regional topographic positions were calculated as the upland plot elevation relative to the adjacent peatland, and the minimum within a regional neighborhood, respectively. Neighborhood size depended on the hydrogeologic context. For most sites, major rivers were used as elevation references. Within the 2011 Utikuma fire, the Utikuma Region Study Area (URSA) provided knowledge of hydrogeological discharge areas that were used as reference elevations (Hokanson et al., 2021, 2019; Smerdon et al., 2008). In the 2001 Chisholm fire and the 2016 Horse River fire, the Athabasca and Clearwater Rivers provided reference elevations. Sites within the 2002 House River fire were between the Stoney Mountains and lowlands to the southeast and a larger (roughly 50 km radius) neighborhood was used to capture this (Figure 2 b). This neighborhood was determined by comparing preliminary terrain models of regenerating stem density with radii of 5 km, 10 km, then increasing by 10 km increments to 150 km to examine responses and rank then with AICc to select the most supported scale. % Sand, silt, and clay were measured from field samples via the hydrometer method. I used % sand as a measure of soil "coarseness", while % clay was used as the measure for fine texture (see model selection), thus leaving out the remaining collinear variable % silt. The measure of post-fire drought in this study was the annual cumulative sum of monthly evapotranspiration (E_{ref}) − precipitation , also known as climate moisture deficit (CMD, (Baltzer et al., 2021; Whitman et al., 2019, 2018), from PRISM data downscaled at 800 x 800 m resolution to local elevation from Climate NA (Wang et al., 2016). CMD values for the year of the fire, the first, second, and third years after each fire were. Post-fire age was calculated by subtracting the sampling year from the year each fire occurred to account for post-fire thinning, succession, and biomass accumulation (Table 2).

Table 2. Variables and the descriptions of why they were used in statistical analyses. All variables were continuous.

Variable	Description
Stem density (stems/ha)	Covariate in models of regenerating stem basal area
% Clay	Measure of soil fine texture
% Sand	Measure of soil coarse texture
Cumulative CMD	Measure of post-fire drought. Cumulative sum of monthly [evapotranspiration (E_{ref}) − precipitation] for years 0 − 3 post-fire (Wang et al., 2016)
Local topographic position (m)	Upland plot elevation – elevation of the adjacent peatland
Regional topographic position (m)	Upland plot elevation – minimum elevation within a neighborhood (sizes ranged from 2 km to 50 km)
Post-fire age (years)	Control for post-fire stand age

Model Selection

Model selection and statistical analyses were done in R (R Core Team, 2022). Before model construction, variables that had a Pearson's correlation coefficient > |0.7| were excluded except for % clay as it was the measure of fine-textured soils and had a lower |Pearson's R|, and therefore lower collinearity, than % silt. To evaluate which hypotheses were best supported, I used a model selection framework that compared statistical models of primary and alternative hypotheses, as well as ecologically- and statistically null outcomes for all response variables. Six candidate models were compared where the "Topoedaphic Buffering" model represented the hypothesized interactions between topographic position, post-fire drought (CMD), and soil texture (% sand and clay) (Table 1). Terrain and Climate models considered bottom-up terrain and top-down climate controls on upland tree regeneration, respectively. Time-since-fire and null (mean of the response) models were also considered. Time-since-fire terms were included in all non-null candidate models to account for post-fire stand age across soil textures. Models involving terrain also considered quadratic transformations to local and regional topographic positions (Table 3).

I used Akaike's Information Criterion, corrected for small sample sizes (AICc) within the AICc function from the AICcmodavg package in R (Mazerolle et al., 2023) to select the best-fitting models at either local or regional scales were selected within each candidate model (topoedaphic buffering, terrain, climate, time-since-fire, null). The best of these models was chosen, and stepwise variable selection eliminated terms using AICc to construct the most parsimonious final model. Model residuals were tested for uniformity, overdispersion, normality, and variance homogeneity using R's dHARMA package (Hartig, 2022). GLMMs were fit with additional dispersion models when required to satisfy these assumptions.

Table 3. Table of candidate models and their terms used to evaluate responses in regenerating tree density, basal area, jack pine, aspen, as well as black and white spruce proportions. Within each relevant candidate model, local (elevation above adjacent peatland) and regional (relative to regional low) topographic positions, as well as their quadratic transformations (2) and interactions with soil textures were considered. All variables were continuous and scaled by subtracting the mean and dividing by one standard deviation. Models contained a site-level random effect. Total stem density was used as a covariate in regenerating stem basal area models. CMD = Sum of monthly differences in evaporation and precipitation for years 0 – 3 post-fire.

Candidate Model	**Model Fixed Effect Terms**
Topoedaphic buffering	Regional topographic position(^{2})*% Sand*CMD + Regional topographic position(^{2}) *% Clay*CMD + Post-fire age*% Sand + Post-fire age*% Clay (+Regional topographic position)(^{2}) (+ Total Stem Density) Local topographic position(^{2})*% Sand*CMD + Local topographic position(^{2}) *% Clay*CMD + Post-fire age*% Sand + Post-fire age*% Clay (+Local topographic position)(^{2}) (+ Total Stem Density)
Terrain	Regional topographic position(^{2})*% Sand + Regional topographic position(^{2})*% Clay + Post-fire age*% Sand + Post-fire age*% Clay (+Topographic position)(^{2}) (+ Total Stem Density) Local topographic position(^{2})*% Sand + Local topographic position (^{2})*% Clay + Post-fire age*% Sand + Post-fire age*% Clay (+Topographic position)(^{2}) (+ Total Stem Density)
Climate	% Sand*CMD + % Clay*CMD (+ Total Stem Density)
Time since fire	Post-fire age*% Sand + Post-fire age*% Clay (+ Total Stem Density)
Null	Intercept

Statistical Analyses

I used generalized linear mixed effects models (GLMMs), fit using the glmmTMB package in R (Brooks et al., 2017) to test how local and regional topographic position, soil texture, and post-fire drought (CMD) affected total regenerating tree stem density, basal area, proportions of jack pine, aspen, black spruce, and white spruce (Table 3). Post-fire tree density was modeled to a negative binomial distribution with a log link function. Regenerating tree basal area was modeled to a generalized, exponential (Tweedie) distribution with a log link function, indicated by the check_distribution function R's performance package (Lüdecke et al., 2021). This package was used to identify an alternative distribution as the residuals of a gamma-distributed model, often used for continuous, positively skewed response variables (McCullagh and Nelder, 1989), failed to satisfy assumptions of normality and variance homogeneity. Models for species proportions were fitted to beta distributions with logit link functions. Independent variables were standardized before model fitting. All models contained a site-level random effect.

Marginal and conditional R^2 values were calculated using Nagakawa's R^2 (Nakagawa and Schielzeth, 2013) and likelihood-ratio-based pseudo-R^2 values were calculated for models fit with dispersion parameters (Magee, 1990; Nagelkerke, 1991). Random effect variances were zero for the black spruce proportion model, so the random effect was eliminated, leaving its coefficients and standard errors unchanged.

Results

Model selection found that the regional scale, the topoedaphic buffering model best predicted black spruce proportions. The time-since-fire model best predicted stem density. Regional-scale terrain models best predicted stem basal area while local-scale terrain models best predicted jack pine and aspen proportions. White spruce proportions were best explained by the null model (Appendix A Table 2 a, b, c, d, e, and f, Table 4).

Table 4. The best supported generalized linear mixed effect models, determined via AICc, and support for hypothesized responses to post-fire drought across coarse- and fine-textured soils at either local (elevation above peatland) or regional (relative to regional low) scales. (+) and (-) denote hypothesized effects on response variables. Drought (CMD) = Sum of monthly differences in evaporation and precipitation for years 0 – 3 post-fire.

Response Variable	**Prediction**	**Best model**	**Spatial Scale**	**Hypothesis Supported**
Stem density	(-) Topographic position*(-) drought (CMD)	Time since fire	NA	None
Stem basal area	(-) drought (CMD)	Terrain	Regional	**H_2**
Jack pine proportion	(+) Topographic position*(+) drought (CMD)*(+) sand (-) clay	Terrain	Local	**H_2**
Trembling aspen proportion	(+) Topographic position*(+) drought (CMD)	Terrain	Local	**H_2**
Black spruce proportion	**(-) Topographic position*(-) drought**	**Topoedaphic buffering**	**Regional**	**H_1**
White spruce proportion	(-) Topographic position*(-) drought (CMD) (-) sand	Null	NA	None

While there was no main effect of post-fire drought, it was negatively correlated with black spruce proportion at higher regional topographic positions ($\beta_{(std.)}$ = -0.84, SE = 0.43, P = 0.049) in fine- and coarse-textured soils ($\beta_{(std.)}$ = -2.77, SE = 1.02, P = 0.007; $\beta_{(std.)}$ = -4.97, SE = 1.37, P = <0.001). At both maximum sand (98%) and maximum clay (49%) values, black spruce proportions depended strongly on post-fire moisture conditions. Black spruce proportions increased with regional topographic position under wet post-fire climate conditions and did the opposite under dry and average post-fire conditions (Figure 3). Black spruce proportion also decreased non-linearly with regional topographic position at mean (60%) sand and (15%) clay values when CMD exceeded mean observed values, approaching 0.00 at around 100 and 200 m of regional topographic position. The black spruce model's likelihood ratio-based R^2 (R^2_{LR}) was

0.31 (Table 5).

Table 5. Final model results for regenerating black spruce proportions, fitted to a beta distribution with a logit link function, and a dispersion model. Standardized coefficients (β std.) are on the log-odds scale. Significant predictors are bolded. Cumulative CMD = Sum of monthly differences in evaporation and precipitation for years 0 – 3 post-fire.

	Black spruce proportion	
Predictor	***β std.* (SE)**	**P-value**
Intercept	-3.64^{***} (0.37)	**<0.001**
Regional topographic position (m)	-0.63^{*} (0.28)	**0.025**
% Sand	0.05 (0.54)	0.920
Cumulative CMD	0.29 (0.23)	0.212
% Clay	-0.95 (0.74)	0.200
Regional topographic position^2 (m)	0.80^{***} (0.19)	**<0.001**
Post-fire age (years)	-0.31 (0.34)	0.364
Regional topographic position x % Sand	-1.99^{**} (0.65)	**0.002**
Regional topographic position x % Clay	-3.16^{**} (0.92)	**0.001**
% Sand x Cumulative CMD	0.50 (0.34)	0.141
% Clay x Cumulative CMD	0.74 (0.43)	0.084
Post-fire age x % Sand	-2.75^{**} (0.87)	**0.002**
Post-fire age x % Clay	-4.49^{***} (1.12)	**<0.001**
Regional topographic position x Cumulative CMD	-0.84^{*} (0.43)	**0.049**
Regional topographic position x % Sand x Cumulative CMD	-2.77^{**} (1.02)	**0.007**
Regional topographic position x % Clay x Cumulative CMD	-4.97^{***} (1.37)	**<0.001**
Observations	144	
R^2_{LR} (likelihood ratio)	0.31	
AICc	-2107.57	

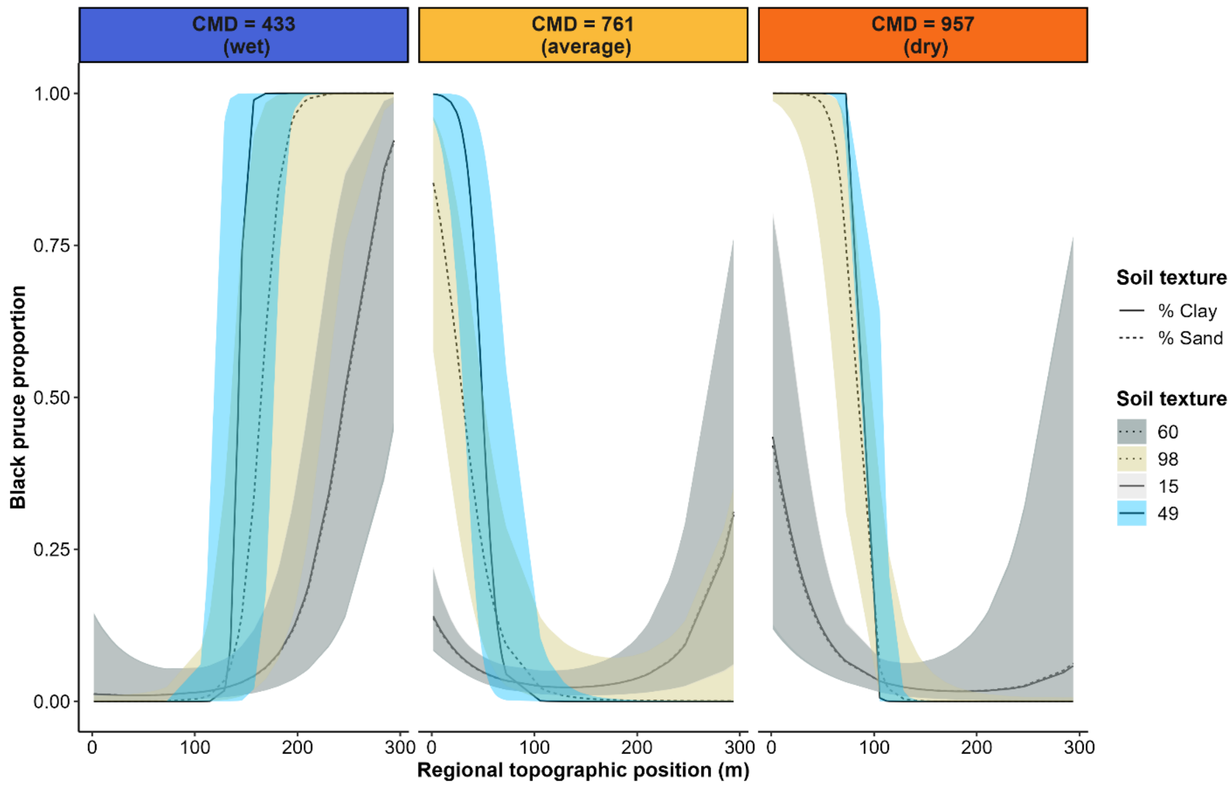

Figure 3. Interactive effects of regional topographic position, sand, clay, and drought (cumulative annual CMD of years 0 – 3 post-fire) on black spruce proportions at observed mean and maximum % sand (dotted) and clay (solid) values across minimum (wet), mean (average) and maximum (dry) CMD values. CMD = climate moisture deficit, defined as the monthly difference between evapotranspiration and precipitation. Error bars represent 95% prediction confidence intervals. **Note:** Curves for mean % sand and clay overlap each other.

Post-fire moisture was not correlated with regenerating stem density, basal area, jack pine, or aspen proportions (Appendix A Figure 1). However, local and regional site conditions were important. For example, stem density decreased with post-fire stand age on fine-textured soils ($\beta_{(std.)}$ = -0.327, SE = 0.074, P<0.01). Stem density increased roughly two-fold at minimum and mean values of % clay over 15 years (Figure 4). The stem density model's likelihood ratio-based R^2 (R^2_{LR}) was 0.25 (Appendix A Table 3). Stem basal area was positively affected by sandy soils across regional topographic positions, remaining relatively constant with regional topographic position at maximum % sand values while decreasing 17-fold and 5-fold at minimum and mean % sand values, respectively ($\beta_{(std.)}$ = 0.245, SE= 0.116, P = 0.035, Figure 5 a). Stem basal area was negatively affected by clay soils with stand age as its temporal post-fire trend went from a non-linear increase to remaining relatively constant over minimum to maximum % clay values ($\beta_{(std.)}$ = -0.257, SE = 0.088, P= 0.003, Figure 5 b). The stem basal area model's likelihood R^2_{LR} was 0.63 (Appendix A Table 4). Final model selection eliminated local topographic position from the jack pine proportion model. Jack pine proportions increased with stand age on sandy soils (β = 0.004, SE = 0.001, P = 0.001, Appendix A Figure 1) as they decreased 8.5-fold, increased by 8%, and increased roughly 3-fold at minimum, mean, and maximum values of % sand, respectively over observed post-fire ages (Appendix A Figure 2). The jack pine model's R^2_{LR} was 0.31 (Appendix A Table 5). Aspen proportions declined with stand age at 2% per year post-fire and non-linearly by three-fold over observed % sand values (β = -0.100, SE = 0.036, P = 0.006; β = -0.030, SE = 0.007, P < 0.001, respectively, Appendix A Table 8). Aspen proportions increased non-linearly with local elevation (above peatland) up until 3 – 5 m, where they attenuated, then declined by 3.5 times the maximum predicted proportion (0.6) (Appendix A Figure 3 a, b, and c). The aspen proportion model's marginal (R^2_m; fixed effects only) and conditional R^2 (R^2_c; fixed and random terms) were 0.37 and 0.96, respectively (Appendix A Table 6).

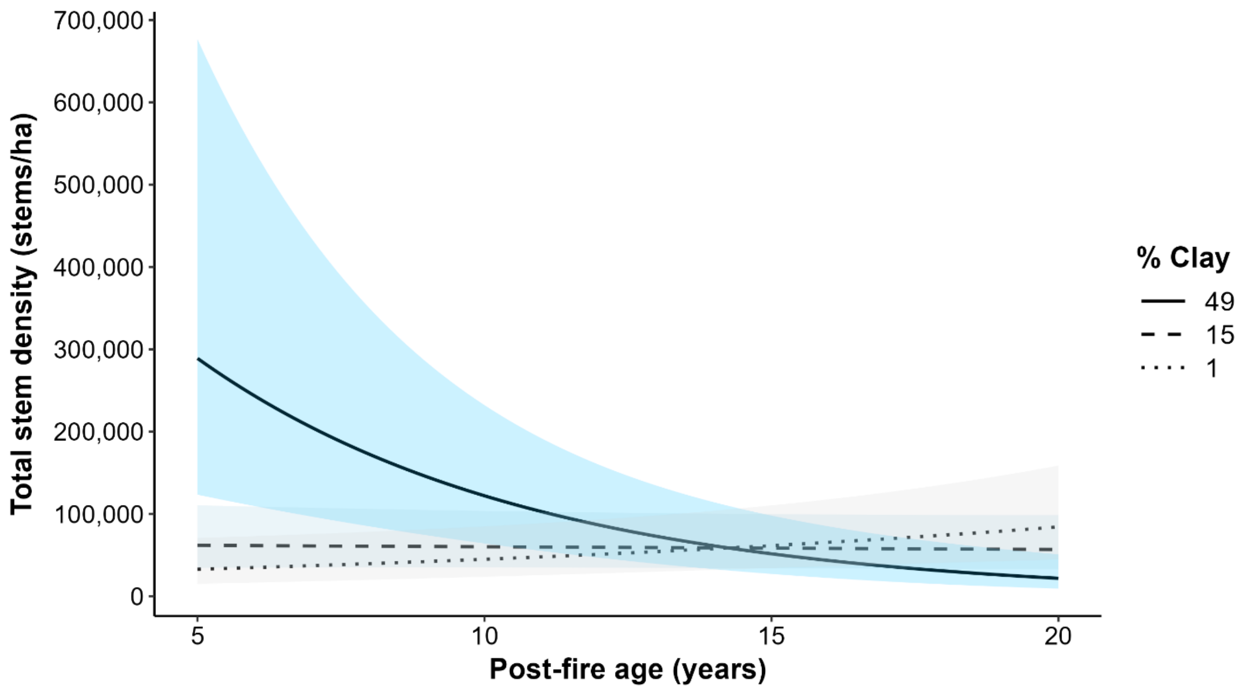

Figure 4. Effects of post-fire age on regenerating total stem density (stems/ha) at observed maximum, mean, and minimum % clay values. Error bars represent 95% prediction confidence intervals.

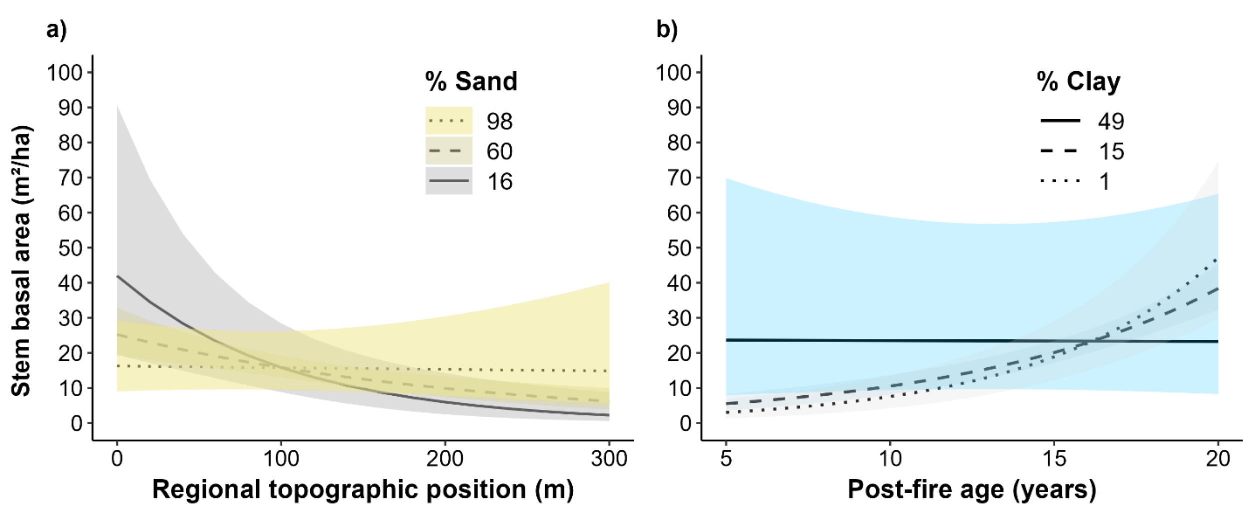

Figure 5. Effects on regenerating stem basal area (m^2/ha) of a) regional topographic position at observed maximum, mean, and minimum % sand values, and b) post-fire age at maximum,

mean, and minimum % clay values. Error bars represent 95% prediction confidence intervals.

Discussion

I found that post-fire black spruce regeneration declined in regionally high topographic positions on both coarse- and fine-textured soils following post-fire drought, while post-fire tree density, total basal area, jack pine proportion, and aspen proportion were unaffected by post-fire climate. This supported my hypothesis that tree species at low topographic positions may be buffered from post-fire drought, though only for black spruce (Table 4), suggesting the potential for additional compositional reductions in black spruce with more extreme drought and fire conditions.

Treed fens in low topographic positions may provide stable groundwater and seed sources for black spruce, buffering drought-induced declines in post-fire recruitment (Devito et al., 2012; Goodbrand et al., 2019; McLaughlin et al., 2017; Whitman et al., 2019). Local to regional-scale controls on groundwater dynamics by fine- and coarse-textured soils, respectively (Devito et al., 2005, 2017; Hokanson et al., 2019; Winter, 2001), appeared to be expressed in the recruitment of black spruce experiencing post-fire drought in this study. Baltzer et al. (2021) and Whitman et al. (2019) also observed declining black spruce regeneration with short fire return intervals and post-fire drought, while Johnstone et al. (2010) noted the importance of topoedaphic factors in maintaining resilience.

Unexpectedly, post-fire drought did not affect overall regenerating stem density, basal area in jack pine, or the proportion of stems that were aspen. Antecedent and post-fire drought conditions in this study may not have diminished the large water storage capacities of upland forests (Devito et al., 2012) enough reduce the density, growth, nor the dominance of early-successional, drought-tolerant species like jack pine and aspen (Boucher et al., 2020). Post-fire drought conditions of sufficient length and intensity necessary to inhibit regeneration are also associated with higher flammability and fire likelihood, which would further reduce regenerating tree density, basal area, and conifer dominance (Davis et al., 2019; Parks et al., 2018; Whitman et al., 2019). I also observed strong bottom-up and site controls as basal area and aspen proportions responded to regional and local topoedaphic factors, respectively. The importance of regional-scale terrain on stem basal area suggests large-scale bottom-up controls on growth, driven primarily by soil texture, rather than top-down controls of climate observed by Searle and Chen (2017b). Aspen regeneration peaked at 3-to-5 m of local elevation before declining, since plots over 5 m were in sandy, jack pine-dominated sites (Appendix A Figure 4). Black spruce decline may help explain the increase in jack pine dominance over time and consistency in basal area across sandy topographic positions as its growth dominance and growth in young (≤40 years) stands may offset drought-induced mortality (Chen et al., 2016).

None of the candidate models explained white spruce regeneration. Instead, the null model performed best, suggesting that terrain, climate, and stand age did not affect post-fire white spruce regeneration. However, pre-fire stands with white spruce represented only 17% of sites with only 53% being mature enough (>70 years pre-fire) to support self-replacement (Johnstone and Chapin, 2006), although 33% of sites had unknown pre-fire ages (Appendix A Figures 5 and 6). This reflects the relative lack of representation among mixedwood white spruce stands in the study area, particularly relative to areas recently burned as white spruce was more common at wetter ecosites post-fire. The more abundant mesic ecosites were dominated by aspen or jack pine pre-and post-fire (Appendix A Table 1, Appendix A Figure 7). Pre-fire presence and therefore seed source availability is key in predicting white spruce regeneration (Johnstone et al., 2010), while the importance of microsite characteristics may outweigh regional- or plot-scale factors (Purdy et al., 2002). White spruce may also be delayed (until 35 – 45 years post-fire) via multiple pathways (Peters et al., 2006, 2005). Capturing the intricacies in white spruce regeneration was outside the scope of this study, particularly due to the less common occurrence of these stands in the region, especially with respect to recent fires, and the short post-fire time frame (up to 20 years post-fire) that occurs before typical ingress from white spruce later in stand development.

Overall, my study demonstrated the buffering potential of low regional topographic positions on black spruce regeneration in the presence of post-fire drought. However, I found no effect of post-fire drought on the density, growth, nor any other regenerating tree species. Enlarging the study area to drier and more topographically diverse areas of Alberta's boreal plain, like the Athabasca sand plain and dry mixedwood subregions, could reveal stronger post-fire drought and potential hydrologic buffering effects on forest regeneration. Extending post-fire age to include stands older than 20 years may capture instances of delayed white spruce regeneration, a longer post-fire trajectory. More large-scale hydrological monitoring networks would also capture groundwater and shallow-surface water interactions, providing more direct measures of groundwater connectivity rather than topoedaphic proxies (like topographic position and soil texture). Regardless, it appears that beyond black spruce, most post-fire droughts in the Alberta's boreal forest have little influence on overall tree regeneration and do not require hydrological buffering, at least under drought conditions observed within the last 20 years.

Conclusion

This study highlights that regional-scale topoedaphic factors may buffer regenerating black spruce from post-fire drought, while having little effect on total regenerating density, basal area, and the regeneration of more predominant upland tree species. Due to its relative scarcity among upland tree species in western Canada's boreal plains ecozone (Downing and Pettapiece, 2006), black spruce decline would minimally impact upland forest composition, in contrast with forests farther north (Johnstone and Kasischke, 2005). However, the observed resilience of overall forest regeneration to post-fire drought may be threatened under increasing drought conditions and shortened fire return intervals, which are anticipated with climate change (Hanes et al., 2019; Wang et al., 2015; Whitman et al., 2019). Examining the influence of peatland-dominated areas on the regeneration of Alberta's more resilient tree species at short fire return intervals presents a logical next step. Nevertheless, lower regional topographic positions with large-scale groundwater connectivity may serve as refugia for black spruce, helping slow compositional loss of black spruce in western boreal forests. This knowledge can help managers identify areas that may resist altered post-fire trajectories, refining predictions of ecosystem transitions in the presence of climate change and directing management efforts where they will be most effective for vulnerable tree species. Managers should employ hydrological classification frameworks that consider surficial geology prior to topography when identifying areas of high groundwater connectivity as it determines the scale of hydrological controls in low-relief landscapes (Devito et al., 2005; Winter, 2001). For example, protecting regional upland areas and perched peatland systems that recharge lowland fens from which adjacent forests access moisture would preserve groundwater connectivity in coarse-textured soils. In fine-textured soils, preserving surface flow between the hillslope and its adjacent peatland will allow recharge of peatland groundwater during wet periods. Protecting these peatlands that locally recharge adjacent uplands (Hokanson et al., 2020) would enable adjacent upland forests to receive local groundwater during dry periods, enhancing the resilience of vulnerable tree species like black spruce to post-fire drought.

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Appendix A

Table 1. Number of upland plots sampled within each ecosite, classified at each site using the Alberta Biodiversity Monitoring Institute's (ABMI) terrestrial field protocols (Alberta Biodiversity Monitoring Institute, 2011). The number of ecosites varies as transect length, and therefore, number of survey plots varied depending on upland stand size.

Ecosite	T (1 - 11 m)	A (1 - 11 m)	B (25 - 35 m)	C (100 - 110 m)
swamp	3	0	0	0
hygric rich	0	5	0	0
hygric medium	0	11	5	2
mesic medium	0	24	30	14
mesic poor	0	14	15	4
xeric medium	0	4	6	2
xeric poor	0	0	2	3

Table 2. Model selection tables of top candidate models for: a) regenerating stem density, b) stem basal area, c) jack pine proportion, d) aspen proportion, e) white spruce proportion, and f) black spruce proportion.

a) Black spruce proportion

Model	*K*	Rank	AICc	Log Likelihood
Topoedaphic buffering	18	1	-2104.52	1073
Terrain	11	2	-2101.98	1012.98
Null	3	4	-2097.58	1002.56
Post-fire age	8	5	-2090.74	1004.42
Climate	11	6	-2084.47	1005.16

b) Stem density

Model	*K*	Rank	AICc	Log Likelihood
Post-fire age	8	1	3474.92	-1728.93
Terrain	12	2	3475.24	-1724.43
Climate	11	3	3481.01	-1728.5
Null	3	4	3482.83	-1738.33
Topoedaphic buffering	17	5	3486.13	-1723.64

c) Stem basal area

Model	*K*	Rank	AICc	Log Likelihood
Terrain	13	1	922.6	-446.88
Topoedaphic buffering	19	2	932.48	-444.12
Post-fire age	10	3	937.1	-457.71
Climate	15	4	945.84	-456.01
null	4	5	1008.98	-500.34

d) Jack pine proportion

Model	*K*	Rank	AICc	Log Likelihood
Terrain	11	1	-1668.00	846.007
Post-fire age	8	2	-1665.49	841.28
Climate	11	3	-1663.36	843.68
Topoedaphic buffering	17	4	-1656.26	847.56
Null	3	5	-1627.70	816.94

e) Aspen proportion

Model	*K*	Rank	AICc	Log Likelihood
Terrain	11	1	-780.52	403.45
Post-fire age	8	2	-775.94	396.5
Topoedaphic buffering	18	3	-774.51	407.99
Climate	11	4	-771.08	397.54
Null	3	5	-761.69	383.93

f) White spruce proportion

Model	*K*	Rank	AICc	Log Likelihood
Null	3	1	-3227.2	1616.68
Topoedaphic buffering	17	2	-3218.27	1617.67
Post-fire age	8	3	-3211.91	1617.95
Climate	11	4	-3211.64	1617.82
Terrain	11	5	-3209.34	1617.86

Table 3. Final model results for regenerating stem density, fitted to a negative binomial distribution with a log link function and a dispersion model. Coefficients (β) are on the log scale. P-values of significant predictors are bolded.

	Total Stem Density (stems/ha)		
Predictor	***β*** **(SE)**	***β std.*** **(SE)**	**P-value**
Intercept	10.013 *** (0.422)	10.986 (0.085)	**<0.001**
Post-fire age (years)	0.068 (0.026)	-0.037 (0.074)	0.616
% Clay	0.070 (0.018)	0.058 (0.068)	0.392
Post-fire age x % Clay	-0.005*** (0.001)	-0.327 (0.074)	**<0.001**
Random Effects			
σ^2	0.00		
$\tau_{00\ site}$	0.06		
ICC	1.00		
N_{site}	58		
Observations	144		
R^2_{LR} (likelihood ratio-based)	0.25		
AICc	3449.63		

Table 4. Final model results for regenerating stem basal area, fitted to a Tweedie distribution with a log link function and a dispersion model. Standardized coefficients (*β std.*) are on the log scale. P-values of significant predictors are bolded.

	Stem Basal Area (m^2/ha)	
Predictor	***β std.* (SE)**	**P-value**
Intercept	2.753 *** (0.094)	**<0.001**
Regional topographic position (m)	-0.393 *** (0.088)	**<0.001**
% Sand	0.003 (0.161)	0.985
Post-fire age	0.783 *** (0.095)	**<0.001**
% Clay	0.130 (0.151)	0.386
Total stem density	0.367 *** (0.086)	**<0.001**
Regional topographic position x % Sand	0.245 * (0.116)	**0.035**
Post-fire age x % Clay	-0.257 ** (0.088)	**0.003**
Random Effects		
σ^2	0.00	
$\tau_{00\ site\_s}$	0.00	
N_{site_s}	57	
Observations	142	
R^2_{LR} (likelihood ratio-based)	0.63	
AICc	891.53	

Table 5. Final model results for regenerating jack pine proportion, fitted to a beta distribution with a logit link function and a dispersion model. Coefficients (β) are on the log-odds scale. P-values of significant predictors are bolded.

	Jack pine proportion		
Predictor	***β*** **(SE)**	***β std.*** **(SE)**	**P-value**
Intercept	-0.604 (1.081)	-0.964 (0.155)	0.576
% Sand	-0.228** (0.084)	0.172 (0.154)	**0.007**
Post-fire age (years)	-0.012 (0.017)	1.095 (0.152)	0.473
Post-fire age x % Sand	0.004** (0.001)	0.646 (0.171)	**0.001**
Random Effects			
σ^2	0.00		
$\tau_{00\ site}$	0.41		
ICC	1.00		
N_{site}	58		
Observations	144		
Pseudo-R^2 (likelihood ratio)	0.36		
AICc	-1682.626		

Table 6. Final model results for regenerating aspen proportion, fitted to a beta distribution with a logit link function. Coefficients (β) are on the log-odds scale. P-values of significant predictors are bolded.

	Aspen proportion		
Predictor	***β*** **(SE)**	***β std.*** **(SE)**	**P-value**
Intercept	2.434^{***} (0.656)	-0.149^{***} (0.213)	**<0.001**
Local topographic position² (m)	-0.077^{**} (0.026)	-0.097^{**} (0.065)	**0.003**
Local topographic position (m)	0.587^{**} (0.186)	0.308^{**} (0.289)	**0.002**
% Sand	-0.030^{***} (0.008)	-0.697^{***} (0.207)	**<0.001**
Post-fire age (Years)	-0.100^{**} (0.036)	-0.509^{**} (0.214)	**0.006**
Random Effects			
σ^2	0.13		
$\tau_{00\ site}$	1.90		
ICC	0.94		
N_{site}	58		
Observations	144		
Marginal R^2 / Conditional R^2	0.37 / 0.96		
AICc	-782.546		

Table 7. Summary table of variables analysed. N refers to the total number of observations grouped within N_{site}. The two types of relative landscape elevation refer to elevations relative to the mean or minimum elevation within the specified neighbourhood. Note: One site's worth of stem basal area data was lost due to a technical error, resulting two fewer observations in N.

Variable	**Type**	**Mean**	**Standard Deviation**	**Range**	**N**	N_{site}
Stem density (stems/ha)	Dependent and Independent	67463	50995	0 – 240200	144	58
Stem basal area (m^2/ha)	Dependent	25.94	23.91	0 – 97.88	142	57
Aspen proportion	Dependent	0.44	0.38	0 – 1	144	58
Black spruce proportion	Dependent	0.1	0.19	0 – 1	144	58
Jack pine proportion	Dependent	0.33	0.38	0 – 1	144	58
White spruce proportion	Dependent	0.02	0.08	0 – 0.91	144	58
% Clay	Independent	15.07	10.95	1 – 48.96	144	58
% Sand	Independent	60.46	25.01	16 – 98	144	58
Climate moisture deficit (CMD)	Independent	762.06	155.76	433 – 957	144	58
Elevation above peatland (m)	Independent	1.5	1.93	-1.78 – 9.44	144	58
Regional topographic position (relative to minimum, m)	Independent	100.6	84.13	1.54 – 293.78	144	58
Post-fire age (years)	Independent	13.17	6.09	5 – 20	144	58

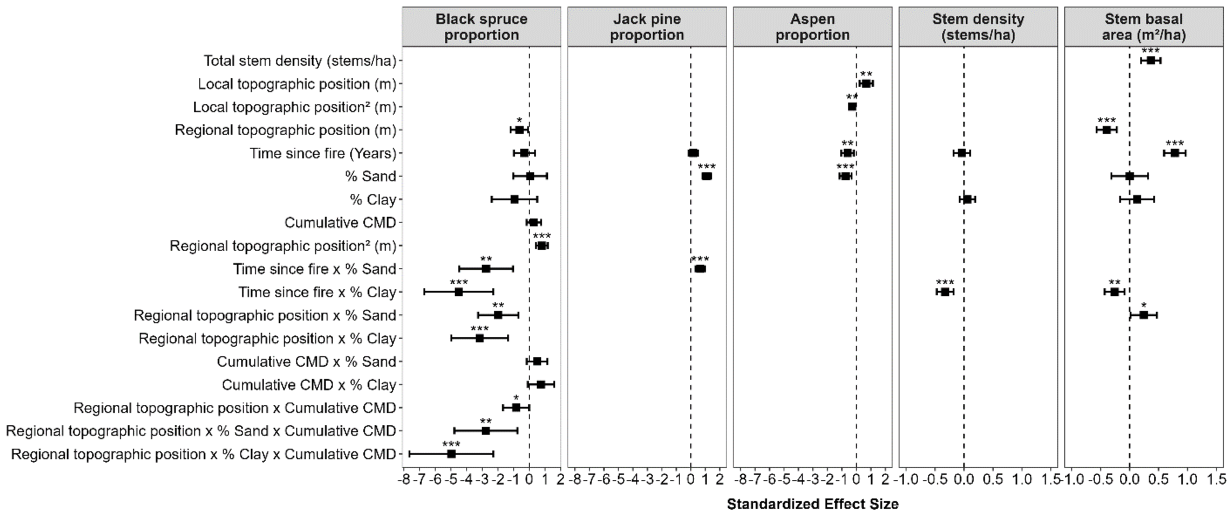

Figure 1. Standardized effect sizes for study variables from final selected models for the proportions of black spruce, jack pine, aspen, regenerating total stem density, and regenerating stem basal area. Error bars represent 95% confidence intervals. *** denote p-values <0.001, ** denote p-values <0.01, * denote p-values <0.05. **Note:** Panels for total stem density and stem basal area are on different scales than panels for tree species proportions.

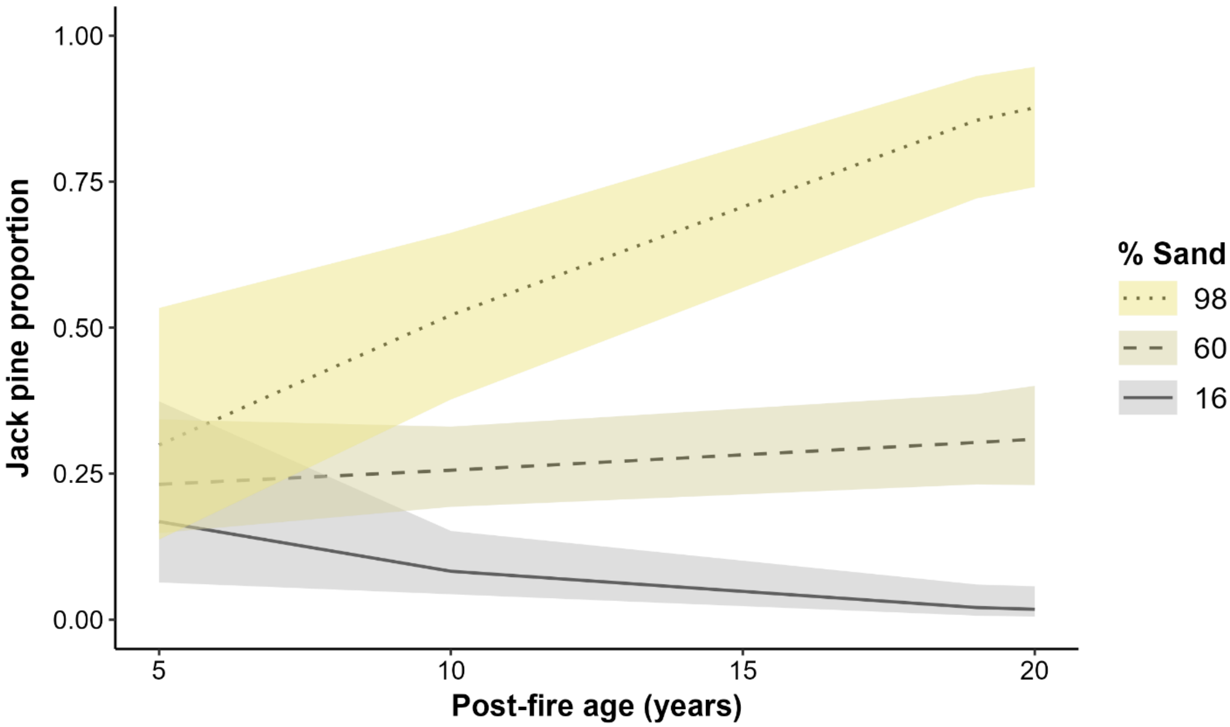

Figure 2. Effect of minimum, mean, and maximum % sand values across observed stand ages on regenerating jack pine proportions. Error bars represent 95% prediction confidence intervals.

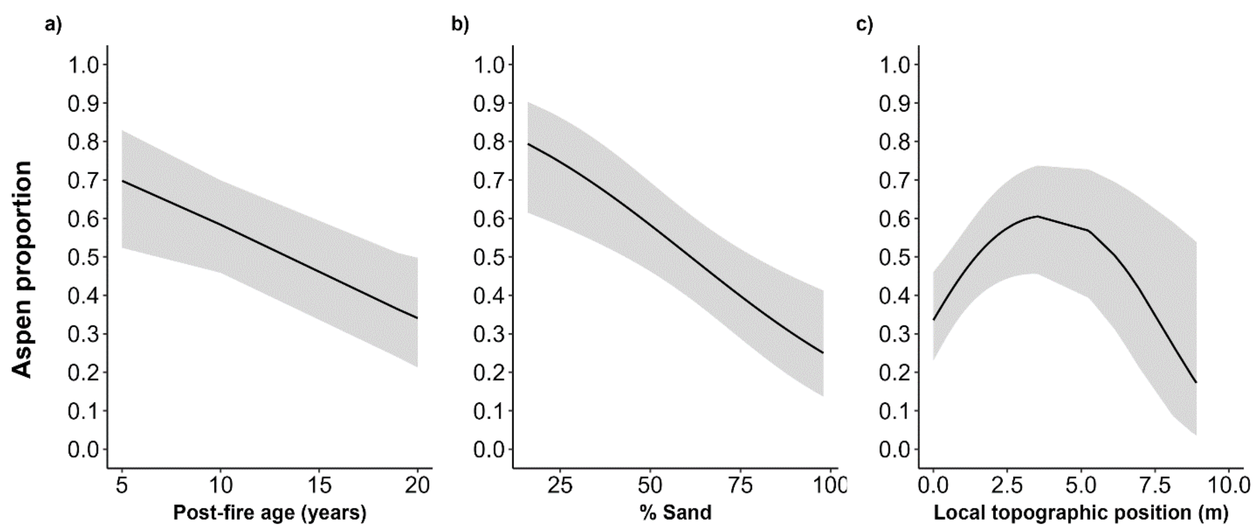

Figure 3. Predicted effects of a) stand age, b) % sand, c) local topographic position on the proportion of regenerating aspen. Error bars represent 95% prediction confidence intervals.

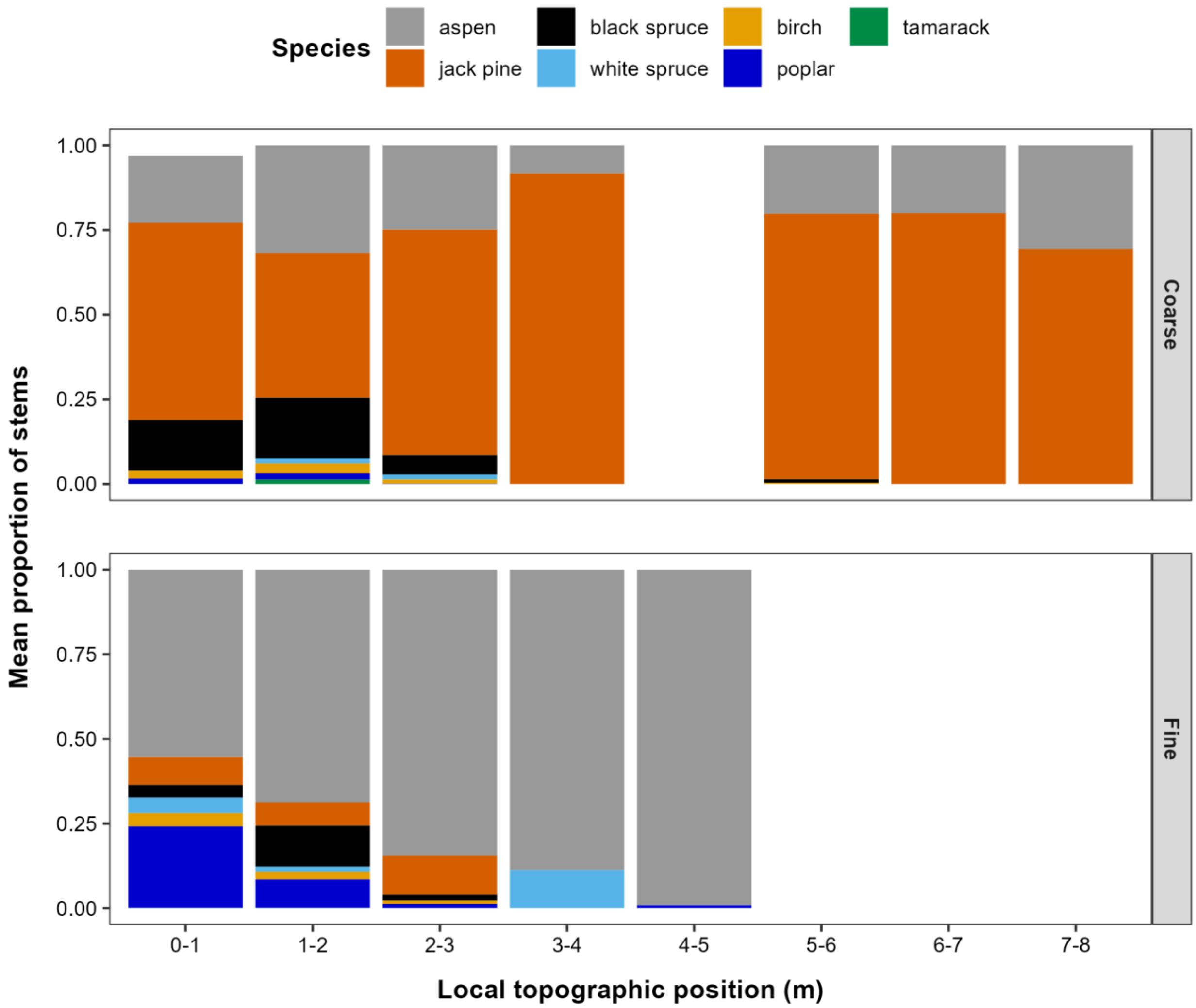

Figure 4. Average proportions of tree stems within each metre of local topographic position (plot elevation above the adjacent peatland) in coarse (n = 74) -and fine (n = 70)-textured soils based on descriptions from Fenton et al. (2013).

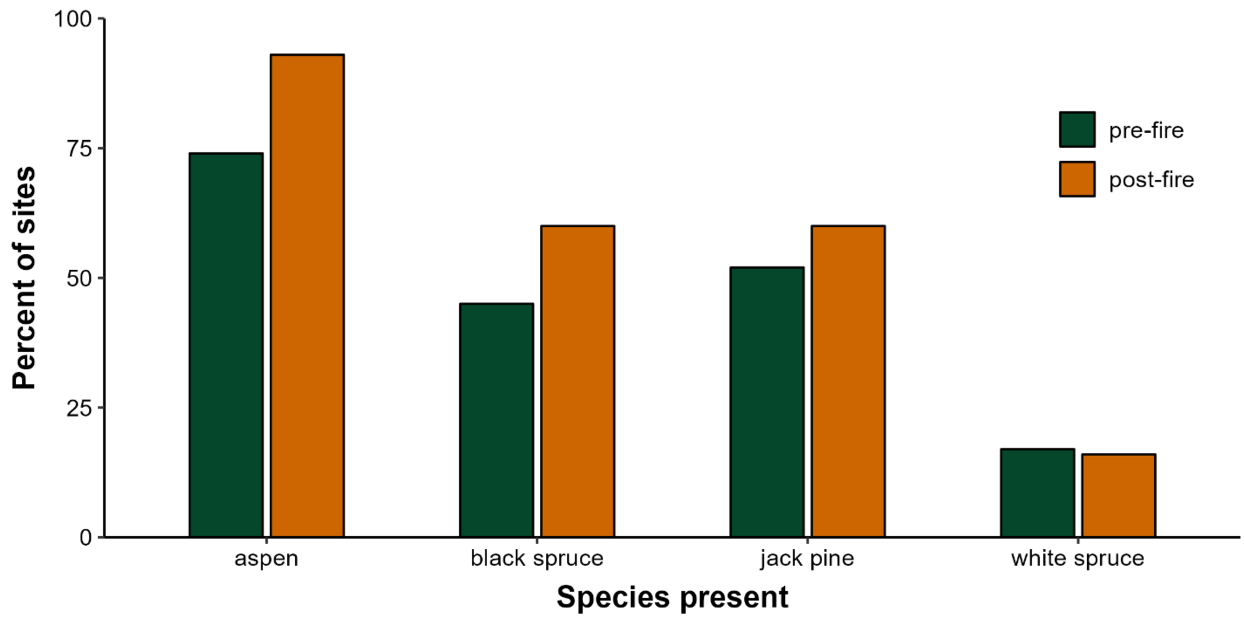

Figure 5. Pre- and post-fire percentage of sites (N= 58) where each tree species analysed was present. **Note:** Pre-fire species presence was assumed from dead standing trees at each site. Dead, fallen trees were not recorded.

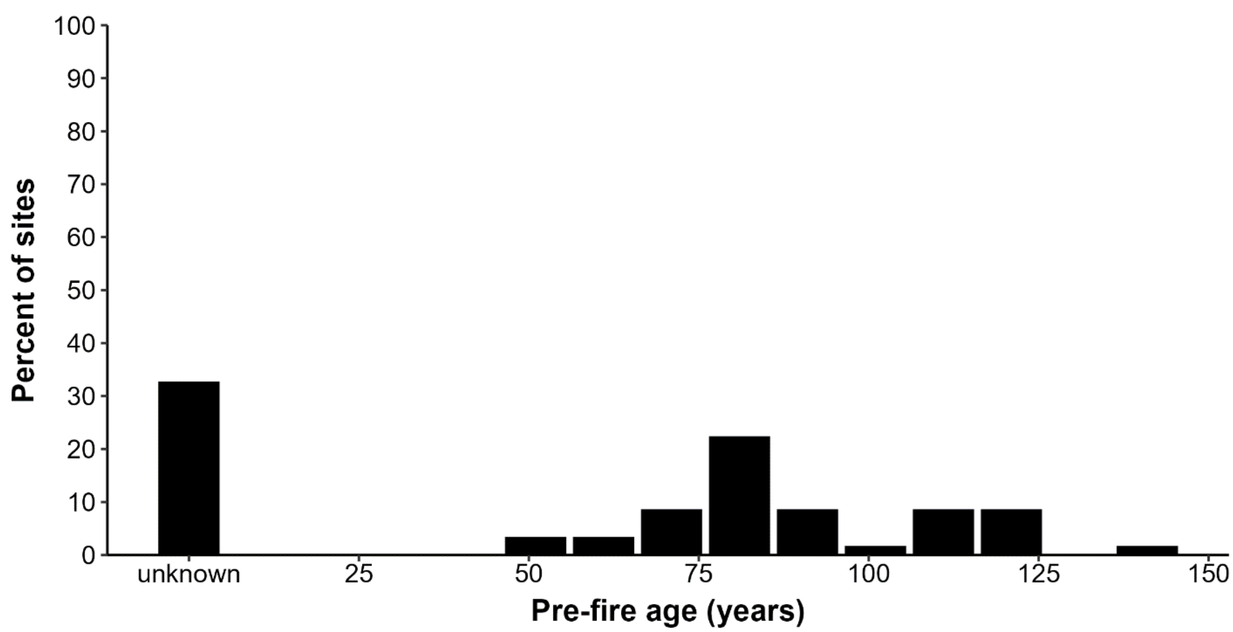

Figure 6. Percentages of pre-fire ages across study sites (N=58). Pre-fire ages for each site were collected from the Derived Ecosite Phase (DEP) product (Government of Alberta, 2020). **Note:**

Sites with either a pre-fire age of zero or the year of its respective fire were classified as unknown.

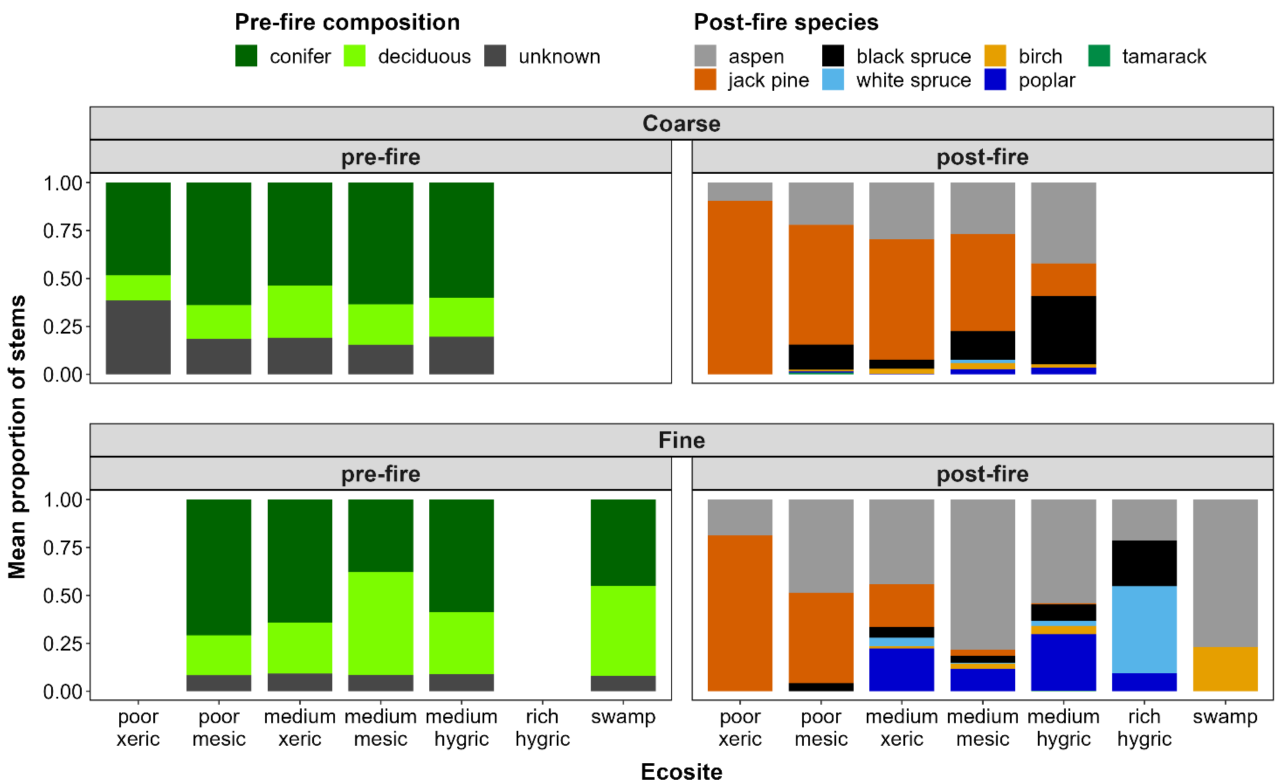

Figure 7. Mean pre- and post-fire species proportions, weighted by the number of plots, at observed ecosites across soil textures. Ecosites were classified by their nutrient and moisture regimes according to the Alberta Biodiversity Monitoring Institute's (ABMI) terrestrial ecosite protocols (Alberta Biodiversity Monitoring Institute, 2011). Pre-fire species composition data were from the Canadian Landsat Burn Severity product (CanLaBS) of Guindon et al. (2021). Missing pre-fire species composition values were omitted.