

Burn severity and fire history in the northwestern Canadian boreal forest: drivers and ecological outcomes

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Forest Biology and Management

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University of Alberta

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Abstract

Wildfire is the dominant stand-renewing disturbance in the northwestern Canadian boreal forest. Fires burn extensive areas in Canada, disturbing an average of 1.96 Mha yr^{-1} , primarily in the boreal zone. Fires generally occur every $\sim 30 - > 200$ years in this region, due in part to a lack of fuel that allows young stands to resist reburning. Boreal understory plants and trees are adapted to stand-renewing wildfire through mechanisms such as serotiny, seed banking, and resprouting from roots and rhizomes of top-killed individuals. Such adaptations confer resilience to boreal forests, and post-fire vegetation communities generally resemble the pre-fire ones, following a stand self-replacement trajectory.

Recently, the area burned, average fire size, and fire season length in northwestern Canada have increased. Severe fire weather has enabled reburning of young forests at very short intervals (sometimes ≤ 10 years between fires). Such changes in fire regime appear to be driven by anthropogenic climate change and increasingly severe fire weather. Furthermore, increasing moisture stress is implicated in simultaneous increases in fire activity, and worsening conditions for post-fire establishment of trees. Shifts in fire regime characteristics, such as burn severity and fire-free interval may lead to changes in vegetation composition following fire, thwarting stand self-replacement expectations.

The 2014 and 2015 fire seasons in the Northwest Territories (NWT) and Northern Alberta (AB) were severe, with fires burning approximately 4 Mha, including instances of short-interval reburning. Inspired by these two fire years, in this dissertation I sought to understand the drivers of burn severity and the ecological outcomes of burn severity (biomass loss) and fire intervals, and how they interact with climate in this fire-adapted ecosystem. Specifically, my objectives

were to: 1. characterize drivers and landscape patterns of burn severity, 2. describe the ecological outcomes of burn severity and fire history, and 3. examine the effects of post-fire moisture stress and fire regime on post-fire vegetation communities. These research objectives are contextualized in a methodological and ecological overview in Chapter 1.

In Chapter 2 of this thesis I used remotely sensed multispectral imagery and field observations of burn severity to map landscape patterns of burn severity in six large wildfires. Fires were dominated by moderate- and high-severity patches. These patches were extensive, adjacent to similar patches, and had large core areas. Field measurements allowed me to demonstrate that burn severity was primarily a product of pre-fire vegetation structure (fuels) and hydrology (uplands and wetlands), providing a mechanism by which the severity of disturbance experienced is limited by the vegetation communities themselves. Similarly, field measurements of post-fire vegetation communities and shifts in tree species composition (Chapter 3) were largely explained by pre-fire forest structure, hydrology, and climate normals. The landscape of the NWT and AB was altered by the extensive area burned in 2014 and 2015, however, burn severity is highly variable. Post-fire ecological outcomes from these years are likely to be variable, as well.

Although both site- and stand-level controls on burn severity and post-fire vegetation confer resilience, where fire activity and severity increase there is a possibility for forest change. I found evidence of post-fire shifts in tree species composition (Chapter 3). Black (*Picea mariana*) and white (*P. glauca*) spruce dominance declined in uplands following fire, whereas shifts in dominance of jack pine (*Pinus banksiana*) were variable, and trembling aspen (*Populus tremuloides*) dominance generally increased following fire. Where changes in tree species composition and density occurred, they were mediated by burn severity and fire frequency.

Shortening of fire-free intervals due to drought is likely to accelerate climate-driven shifts from conifer-dominated boreal forests to open woodlands and grasslands. Paired sites that reburned at short fire-free intervals had significantly lower post-fire recruitment of trees than long-interval pair members, due to decreased establishment of conifers (Chapter 4). These differences were persistent and occurred in both uplands and wetlands. Increasing temperatures and aridity are likely to increase fire activity, and to reinforce the changes to forests caused by shifts in fire regimes. Post-fire moisture stress in both short- and long-interval sites interacted with burn severity, further reducing tree seedling density. This dissertation suggests that increasing wildfire activity and severity may alter the composition and structure of northwestern Canadian boreal forests, accelerating expected ecosystem changes as northern climates warm and dry.

Preface

This thesis is the original work of Ellen Whitman. Ellen Whitman conducted the research for this dissertation as part of a collaboration between Natural Resources Canada and the government of the Northwest Territories department of Environment and Natural Resources, led by Marc-André Parisien at the Canadian Forest Service, Northern Forestry Centre. Ellen Whitman designed the field methods, and collected and processed all data. Those chapters (2 and 3) that are published works have been re-formatted for consistency, but the text has not been changed.

Chapter 2 of this thesis is published as: Whitman, E., Parisien, M.-A., Thompson, D.K., Hall, R.J., Skakun, R.S., and Flannigan, M.D. 2018. Variability and drivers of burn severity in the northwestern Canadian boreal forest. *Ecosphere*, 9(2). E02128.

<https://doi.org/10.1002/ecs2.2128>. The data analysis and manuscript composition were conducted by Ellen Whitman. M.-A. Parisien, D.K. Thompson, R.J. Hall and M.D. Flannigan contributed to manuscript edits and concept formation. R.S. Skakun assisted with data processing and manuscript edits.

Chapter 3 of this thesis is published as: Whitman, E., Parisien, M.-A., Thompson, D.K., and Flannigan, M.D. 2018. Topoedaphic and forest controls on post-fire vegetation assemblies are modified by fire history and burn severity in the northwestern Canadian boreal forest. *Forests*, 9(3). 151. <https://doi.org/10.3390/f9030151>. The data analysis and manuscript composition were conducted by Ellen Whitman. M.-A. Parisien, D.K. Thompson, and M.D. Flannigan contributed to manuscript edits and concept formation.

Chapter 4 of this thesis is submitted to an academic journal and under review as: Whitman, E., Parisien, M.-A., Thompson, D.K., and Flannigan, M.D. 2019. Short interval reburns interact with drought to alter forest structure and composition in the Canadian boreal forest. The data analysis and manuscript composition were conducted by Ellen Whitman. M.-A. Parisien, D.K. Thompson, and M.D. Flannigan provided input into earlier drafts, and contributed to concept formation.

Acknowledgements

The research included in this dissertation was funded by the Natural Sciences and Engineering Research Council of Canada (Funding Reference Number: CGSD3-471480-2015), the Government of the Northwest Territories, and the University of Alberta. Parks Canada Agency provided in-kind support during field data collection, as did the Canadian Forest Service. I acknowledge that my field research was conducted within the territory of treaties 8 and 11, and on the traditional lands of the Akaitcho, Chipewyan, Dehcho Dene, Métis, and Tlicho peoples.

I thank Mike Flannigan and Marc Parisien for their invaluable supervision, support, criticism, and guidance. I am so grateful that I had such a wonderful experience as a student, and it is largely due to the two great supervisors I got to work with. You are excellent researchers and champions of the students that work with you; I am very lucky to have had the opportunity to do so. I also thank the rest of my committee, Scott Nielsen, Jill Johnstone, and Charles Nock for their guidance and valuable feedback I received throughout the process of completing this degree, and on this written dissertation. I also thank Dan Thompson for his awesome field skills, board game skills, and patience. Thank you to Rick Olsen, Matt Coyle, Kathleen Groenewegen, and Jean Morin. Without the support of these folks and their agencies I never would have had access to the amazing places I have travelled to for my research, nor would I have had the essential perspective of those actually involved in land and fire management in this region. I thank everyone in the Northern Forestry Centre wildfire group, and other NoFC friends and colleagues who gave their time, space, equipment, and data to help me learn and apply the methods I needed for this work. I am thankful for the support, help, feedback, and friendship of the other students and post-docs in the Canadian Partnership for Wildland Fire Science labs. Thanks to all of you, and good luck in the future. Thanks also to the administrative and support staff at the University of Alberta in FGSR, ALES, Renewable Resources, and the Canadian Partnership for Wildland Fire Science, especially Christie Nohos, Karen Blouin, Wankui Zhou, and Renee Beaulac.

I am extremely grateful for the field assistance of Xinli Cai, Rodrigo Campos-Ruiz, Matt Coyle, G. Matt Davies, Derek Hall, Joshua Gauthier, Kathleen Groenewegen, Marc Parisien, Sean Parks, Mary Stephens, Scott Stephens, Dan Thompson, Xianli Wang, and Thea Whitman. Thank you all so much! I would also like to thank the families of these people for allowing and enabling

their partners, parents, and children to travel to remote areas for such long periods of time in support of my work.

Finally, I am very thankful for the support and love of my family. Alex, you are beyond supportive and encouraging and I am so grateful for your help, love, patience, and accommodation of me as I went through this process. Thank you so much. I'm so proud of you, and I love you tonnes. I hope to keep returning the favour as time goes on. Thank you to my Mum and Dad. It is wonderful to have parents who I know I can ask for help if ever I need it. Your guidance and encouragement led me to have an inquiring mind and an interest in working outside and in natural sciences. Finally, thank you to Brent, Clara, and Thea Whitman. I love you guys. Having fun with the three of you every year, playing music and games, travelling, and laughing together is so important to me. I'm proud of all of you, and I'm thankful for your friendship, both in the past and as I worked on this degree.

Dòjeh, gracias, hai, hai; mahsi; marsi; masi; merci; obrigada, thank you, and xièxiè.

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Introduction

1.1 Background

The circumpolar boreal forest makes up approximately 30 % of all forested land and contains some of the most extensive unmanaged forest area in the world. One third of the Earth's boreal forest is in North America, with 552 Mha (88 % of North American boreal forests) occurring in Canada (Brandt et al., 2013; Gauthier et al., 2015). Boreal forests are globally important, as they cover a substantial proportion of the Earth's surface, provide essential ecosystem services and habitats, and contain as much as 30 % of all global carbon stocks. They are exploited by humans for natural resources supporting rural and urban economies, and are home to communities ranging in size from settlements to cities (Gauthier et al., 2015).

At present, North American boreal forests are dominated by coniferous trees, especially *Picea* spp., due to the long cold winters and short warm summers in this northern biome. Broadleaf trees are not uncommon, and often form mixed stands with conifers or generally smaller pure broadleaf stands (Brandt et al., 2013; Ecological Stratification Working Group, 1995). In some parts of the boreal zone extensive peat-forming wetland (peatland) complexes cover vast areas, as much as 50 % of the land's surface (Tarnocai et al., 2011; Thompson et al., 2016). Boreal forests have expanded northward since the most recent glacial maximum. As glaciers retreated from North America, white (*P. glauca*) and black (*P. mariana*) spruce trees established first alongside paper birch (*Betula papyrifera*), with Jack Pine (*Pinus banksiana*) and trembling aspen (*Populus tremuloides*) establishing later. By approximately 7000 years BP boreal vegetation formed an extensive band from Alaska to Newfoundland, which has persisted in some form since that time (Brandt et al., 2013; Dyke, 2005).

Wildfires are the dominant stand-renewing disturbance in North American boreal forests, generally affecting a larger area than either defoliating insects and forest disease, or harvesting (Brandt et al., 2013; White et al., 2017). On average, wildfires affect 1.92 Mha of the Canadian landscape annually, with the majority of such events occurring in boreal forests (Hanes et al., 2018). Wildfires in boreal forests are substantially driven by both weather (day-to-day and minute-to-minute variations in atmospheric conditions) and longer-term climate (variability in

atmospheric processes and conditions over timescales longer than a fire season; Bedia et al., 2015; Flannigan & Wotton, 2001). Naturally occurring lightning ignitions, and the flammability of vegetative fuels and biomass are a result of weather-mediated fuel moisture. Furthermore, length of the fire season (the annual period during which wildfires are likely to occur) is determined by weather (Flannigan et al., 2000; Van Wagner, 1987; Weber & Flannigan, 1997).

Boreal forests co-evolved with wildfire. Their establishment was concurrent with increases in fire activity, as both area burned and the ranges of tree species responded to climate (Carcaillet et al., 2001; Hu et al., 2006; Larsen, 1996). Fire regimes (characteristics and landscape patterns of fire; Krebs et al., 2010) vary substantially across the Canadian boreal zone. In general, however, few (3.2 % of all ignitions) large fires (≥ 200 ha) are responsible for the significant majority of the area burned (96.8 %) in Canada (Hanes et al., 2018). Lightning ignites approximately half of all fires, but causes fires that burn large areas (90 % of area burned; Stocks et al., 2002). Fires in the boreal forest are often high-intensity crown fires, which burn large areas, including wetlands, and kill most overstory trees. Although crown fires are considered characteristic of the North American boreal biome, ground or surface fires, and intermittent crown fires also regularly occur, depending on fuels (stand structure and composition, and combustible biomass) and fire weather (Forestry Canada Fire Danger Group, 1992; Johnson, 1992). Fires recur in this region at intervals ranging from ~ 30 to > 1000 years, depending on climate, fuels, and weather (Boulanger et al., 2012). Young forests resist reburning for upwards of 30 years following severe wildfire, due to lack of fuel (Héon et al., 2014; Parks et al., 2018; Thompson et al., 2017).

Resilience is the ability to recover structure and function following disturbance (Holling, 1973). Boreal forests are resilient to fire, as they can tolerate severe wildfire without permanently shifting to alternative states, such as non-forest. Through adaptations and characteristics of species, such as serotiny (information legacies), forests are capable of self-replacement or ‘direct regeneration’ in the years immediately following a wildfire. This process also depends on the physical availability of in-situ or nearby propagule sources (material legacies; Buma et al., 2013; Johnstone et al., 2016). Post-fire vegetation communities often resemble those that existed prior to fire (Ilisson & Chen, 2009). Jack pine and black spruce have serotinous and semi-serotinous cones, respectively, which provide an aerial seedbank for post-fire re-establishment of seedlings, if mature trees are heated and possibly killed by fire. Trembling aspen, balsam poplar (*Populus*

balsamifera), and paper birch are capable of vegetative regeneration, and often vigorously resprout (sucker) following fire (Greene et al., 1999). Understory plants are also adapted to fire, and may resprout (e.g., willows, *Salix* spp.), vigorously seed-in on disturbed surfaces (e.g., fireweed, *Chamerion angustifolium*), or re-establish from persistent soil seedbanks (e.g., Bicknell's geranium, *Geranium bicknellii*) (Franklin, 2018; USDA Forest Service Rocky Mountain Research Station Fire Sciences Laboratory, 2018). Plants that require live seed sources, such as white spruce, may experience local extinctions following fire, and re-establishment may occur much more slowly, taking as long as 40 years (Ilisson & Chen, 2009; Peters et al., 2006). Unburned islands, or residuals, resulting from mixed fire severity (partial mortality) are another material legacy conferring resilience to forests for such species (Galipeau et al., 1997; Meddens et al., 2018).

Despite adaptations to fire in boreal plants, there is variability in post-fire vegetation establishment and community composition within and amongst boreal forest wildfires. Variable fire intensity (energy emitted) results in variable fire effects. Burn severity is the above and belowground biomass loss from fire, and is often represented with diverse field and remotely sensed metrics (synonymous with fire severity; Keeley, 2009). Burn severity influences the post-fire composition of vegetation communities by altering seed sources or availability of seed and bud banks (Arseneault, 2001; Brown & Johnstone, 2012; Splawinski, Greene, et al., 2018; Wang & Kemball, 2005; Whittle et al., 1997), affecting the availability of substrates for seedling germination (Charron & Greene, 2002; Johnstone & Kasischke, 2005; LePage et al., 2000), and killing live plants. Burn severity can have immediate (e.g., Bernhardt et al., 2011) and lasting (e.g., Gibson et al., 2016; Johnstone & Chapin III, 2006a; Pinno et al., 2013) effects on species composition and richness (e.g., Pinno & Errington, 2016) of boreal forest plant communities.

1.2 Climate change

Climate change has already caused shifts in the plant species composition of boreal forests, favouring fast-growing ‘early successional’ tree species, such as jack pine and trembling aspen, to the detriment of late-successional species (i.e., *Picea* spp.) at rates of 0.13% (broadleafs) to 0.32% (conifers) increase in relative abundance per year (Searle & Chen, 2017a). Aboveground biomass in western forests has declined in recent years due to tree mortality (Searle & Chen,

2017b, 2018), and increases in moisture stress and severe drought have been implicated in extensive die-offs and declines in growth of both coniferous and broadleaf species (Hogg et al., 2017; Michaelian et al., 2011).

In addition to direct effects of anthropogenic climate change on forest composition and structure (e.g., through tree mortality), climate change has also caused fire activity in western North America to rise, as indicated by larger fire sizes, greater annual area burned, and lengthening fire seasons (Abatzoglou & Williams, 2016; Hanes et al., 2018; Jain et al., 2017). Projections of future climate change suggest that fire weather severity (Wang et al., 2015), fire intensity (and therefore burn severity; Wotton et al., 2017), area burned (Boulanger et al., 2014; Wang et al., 2017), and fire frequency (Bergeron et al., 2004) will continue to increase in many areas as climates in the North American boreal forest become warmer and more arid (Wang et al., 2014).

Although boreal forests are resilient due to adaptations to fire amongst keystone tree species, shortening intervals between fires may result in the loss of information and material legacies and leading to vegetation state-changes (Johnstone et al., 2016; Turetsky et al., 2017). Severe fire weather has enabled short-interval reburning of young boreal forests with low propagule loads, leading to shifts in the species composition, stand structure (Johnstone, 2006; Johnstone & Chapin III, 2006b), and what amounts to vegetation state-changes in boreal forests (Brown & Johnstone, 2012; Hart et al., 2018). Furthermore, droughts and moisture stress are implicated in both the occurrence of short-interval reburning (Parks et al., 2018) and in lower stem densities and recruitment failures in post-fire tree cohorts (Harvey et al., 2016; Stevens-Rumann et al., 2018). Thus, there is potential for interactions amongst direct (moisture stress) and indirect (fire regime changes) effects of climate change on boreal forest regeneration.

1.3 Research justification

Climate change is projected to increase temperatures, aridity, and fire activity in Canada's western boreal forest (Boulanger et al., 2014; Wang et al., 2015; Wang et al., 2014), potentially leading to relatively rapid and extensive conversion of boreal forests to grasslands and open woodlands (Stralberg et al., 2018). Climate change effects on fire regimes and boreal forests are already apparent in northwestern North America. The 2014 fire season in the Northwest Territories (NWT) and the 2015 fire season in NWT and Alberta (AB) were of significant interest. Together, these two years were responsible for more than 4 Mha of area burned in NWT

and AB, which is nearly four times the Canadian *national* average for a single year (Canadian Interagency Forest Fire Centre, 2019). Furthermore, during these two fire years there were notable events of short-interval reburning. For this reason, I chose to focus my research on northern AB and the southern NWT (Fig. 1.1). In this dissertation I seek to understand the drivers of burn severity, and the ecological outcomes of burn severity and fire intervals, and to learn how they interact with climate in this fire-adapted ecosystem.

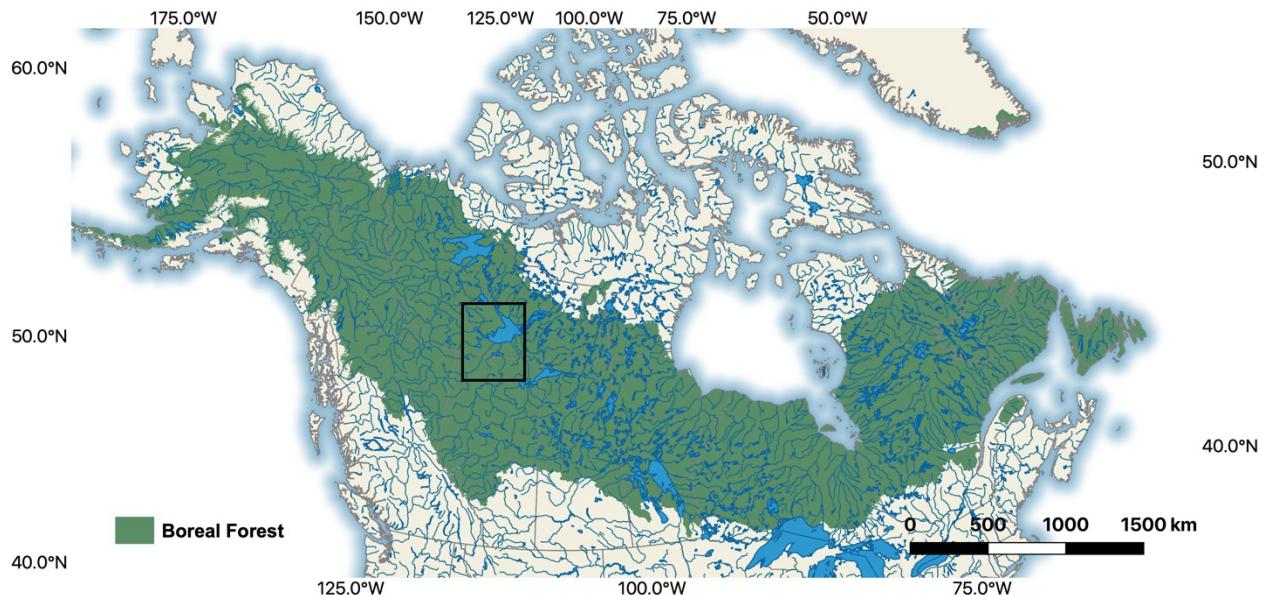


Figure 0.1 The extent of the North American boreal forest (Brandt, 2009), and the study area examined in this research (black rectangle). Lakes and rivers are shown in blue, and the non-boreal landmass is shown in beige.

1.3.1 Knowledge gaps and research questions

The applicability of multispectral remote sensing indices to describe spatial burn severity has yet to be consistently demonstrated in the northwestern boreal forest. Researchers have found relationships of varying strengths between field and remotely sensed burn severity, across fires, fire years, and regions (French et al., 2008). Those studies that have been conducted have mostly considered one field measure of burn severity, the composite burn index (CBI) (e.g., Boucher et al., 2016; Hall et al., 2008; Soverel et al., 2010). Due to the variability in burn severity and on-the-ground fire effects between regions, fires, and fire years, it has been suggested that regional models of burn severity that relate ecologically meaningful severity metrics are necessary to adequately characterize burn severity from remotely sensed spatial data (French et al., 2008; Hall et al., 2008; Morgan et al., 2014). At the time of this research, models relating field observations

of multiple burn severity metrics to remotely sensed burn severity have not been developed for this study area, limiting the conclusions that may be drawn from readily available current and historic multispectral imagery. Landscape patterns of burn severity have been extensively documented outside of Canada, and especially outside of the boreal zone, however, despite the importance of wildfire to this ecosystem spatial analyses of burn severity in this region are limited.

Although it is generally known that burn severity is related to fire intensity (which is partially explained by vegetation structure and fuels), stand-level drivers of burn severity in northwestern Canadian boreal forests are largely undescribed beyond broad vegetation classes and canopy closure (e.g., Ferster et al., 2016; Hall et al., 2008; San-Miguel et al., 2016). Detailed information about the top-down effects of fire weather, and bottom-up effects of stand structure and site moisture on burn severity would improve our ability to predict and explain burn severity, and to manage boreal forests.

At present, knowledge gaps exist about the applicability and relationship of remotely sensed burn severity metrics to field observations of burn severity in this region. Furthermore, stand-level drivers of burn severity are unknown in the northwestern Canadian boreal forest. Building relationships between field observations of burn severity, pre-fire forest characteristics, and remotely sensed severity metrics would provide new burn severity data, allowing broader characterizations of landscape patterns of burn severity relative to pre-fire vegetation controls. I developed the following research questions about characterizing burn severity in northwestern Canadian boreal forests to address these knowledge gaps, considered in Chapter 2 of this dissertation:

1. How do different overstory, understory, and stand-level field metrics of burn severity correspond to remotely sensed multispectral burn severity indices?
2. What is the landscape pattern of burn severity in an extreme fire season, and what are the drivers of burn severity?

Faced with a changing climate and fire regime, gaining an enhanced understanding of boreal forest resilience and limits to stand self-replacement is important. Although several studies about the ecological outcomes of fire-free intervals and burn severity have been conducted in the

northwestern boreal forest (e.g., Brown & Johnstone, 2012; Hart et al., 2018; Johnstone, 2006; Johnstone & Chapin III, 2006b; Shenoy et al., 2011), few of these have examined the boreal plains (but see Pinno & Errington, 2016; Pinno et al., 2013), a climatically dry region with low relief (and therefore possibly low potential for refugia from climate change; Dobrowski & Parks, 2016) and a substantial peatland component, that is regularly disturbed by large fires. The boreal plain is projected to experience substantial vegetation change in the near future (Stralberg et al., 2018). At present it is unclear whether and by what mechanisms shifts in fire regimes in this region may overwhelm topoedaphic controls on vegetation communities (Boiffin et al., 2015), and how responses to burn severity and fire-free interval may vary between upland and wetland environments. How such changes may interact with future climates in this region is also uncertain, despite evidence that post-fire moisture stress may lead to regeneration failure or delayed regeneration in other ecosystems (Harvey et al., 2016; Stevens-Rumann et al., 2018).

The relative strength of fire effects and topoedaphic controls on post-fire vegetation communities within the study area are not yet clearly documented. Although post-fire vegetation shifts within the northwestern boreal forest have been observed, it is important to elucidate the drivers of such changes, their ecological outcomes, and how they may interact with ongoing climate change. I developed the following research questions about the effects of burn severity and fire history on post-fire ecological outcomes in northwestern Canadian boreal forests to address these knowledge gaps:

1. What is the relative importance of fire, pre-fire conditions and climate, and post-fire soils to post-fire vegetation communities? (Chapter 3)
2. How do post-fire shifts in tree species composition occur in an ecosystem with in situ propagule sources? (Chapter 3)
3. How are vegetation communities affected by short-interval reburning, and are differences caused by short and long fire-free intervals persistent and detectable in both uplands and wetlands? (Chapter 4)
4. Does post-fire moisture stress influence forest structure and composition? (Chapter 4)

The main body of this dissertation is structured as three individual papers (Chapters 2 – 4). These chapters all stand alone, and can be read individually without requiring supporting details from other chapters of this document. Chapter 2 is formatted in the style of the journal *Ecosphere* and

Chapter 3 is formatted in the style of the journal *Forests*. Chapter 4 is unpublished at this time. This research builds on existing knowledge of the importance of burn severity and fire history to post-fire ecological outcomes to answer the questions above, and to refine our understanding of how fire regimes interact with post-fire climate. The major findings from this research are summarized and synthesized in Chapter 5 of this dissertation.

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2 Variability and drivers of burn severity in the northwestern Canadian boreal forest

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2.1 Abstract

Burn severity (ecological impacts of fire on vegetation and soils) influences post-fire stand structure and species composition. The spatial pattern of burn severity may compound the ecological impacts of fire through distances to seed sources and availability of bud banks and seedbeds. Land managers require spatial burn severity data to manage post-fire risks, ecosystem recovery, and assess the outcomes of fires. This research seeks to characterize and explain variability in burn severity in the northwestern boreal forest. We assessed burn severity one year post-fire in six large wildfires that burned in 2014. We measured burn severity using the Composite Burn Index, surface Burn Severity Index, Canopy Fire Severity Index, and percent overstory mortality, describing a range of surface and overstory fire effects. Burn severity was variable, ranging from unburned residuals to complete overstory mortality and intense combustion. We related field measurements to remotely sensed multispectral burn severity metrics of the differenced Normalized Burn Ratio (dNBR), the Relativized dNBR, and the Relativized Burn Ratio. Diagnostic models of burn severity using relativized metrics had lower errors and better (though not significantly so) fits to the field data. Spatial patterns of burn severity were consistent with those observed in other large fires in North America. Stand-replacing patches were large, aggregated, and covered the largest proportion of the landscape. These patterns were not consistent across the four mapped burn severity field metrics, suggesting such metrics may be viewed as related, but complementary, as they depict different aspects of severity. Prognostic models indicated burn severity was explained by pre-fire stand structure and composition, topoedaphic context, and fire weather at time of burning. Wetlands burned less severely than uplands, and open stands with high basal areas experienced lower burn severity in upland vegetation communities. This research offers an enhanced understanding of the relationship between ground observations and remotely sensed severity metrics, in conjunction

with stand-level drivers of burn severity. The diverse fuel complexes and extreme fire weather during the 2014 fire season produced the complex patterns and broad range of burn severity observed.

2.2 Introduction

The boreal forest is the largest biome in Canada, extending from west to east, and as far north as the Arctic coast. Wildfire is the primary stand-renewing disturbance in the boreal forest (Stocks et al., 2002), and such disturbances can determine forest succession and stand composition (Weber & Stocks, 1998), post-fire site productivity (Amiro et al., 2000), and may temporarily convert forested lands from carbon sinks to carbon sources, thus driving the regional carbon balance (Bond-Lamberty et al., 2007; Goodale et al., 2016). Although the fire regime of the North American boreal forest is regularly characterized as one of high-intensity, high-mortality crown fire (Johnson, 1992), there is substantial variability in burn severity (changes to vegetation and soils from fire), ranging from unburned residuals and areas of low-mortality surface fire to highly charred and combusted areas with complete above-ground mortality (Kafka et al., 2001; Stocks et al., 2001).

Land managers in the boreal forest region require information about burn severity for diverse purposes with different temporal scales, from managing long-term post-fire recovery of ecosystems to addressing more immediate hazards and outcomes resulting from wildfire. For example, locating areas of high-severity burned sites containing mortality of overstory trees from fire is relevant to salvage logging (Greene et al., 2013), whereas the severity of the consumption of the surface organic layer and presence of exposed mineral soil may be more relevant to understory vegetation community development (Wang & Kemball, 2005) and erosion risk management (Robichaud et al., 2000). Wildfire impacts to both the overstory and the surface are relevant to post-fire recruitment potential (Lentile et al., 2007) and estimating ecological effects on forest communities (Greene et al., 2004; Greene et al., 1999; Turner et al. 1999), wildlife habitat (Bond et al., 2009; Koivula & Schmiegelow, 2007), identifying fire refugia and unburned islands (Kolden et al., 2012; Krawchuk et al., 2016), and estimating combustion for carbon accounting (Kurz et al., 2009; Veraverbeke et al., 2015). Spatial burn severity data are also

applied for wildfire management uses, as they allow managers to engage in highly detailed mapping of fire perimeters (Kansas et al., 2016; Kolden et al., 2012), and to assess the role of fuel treatments and prescribed burning in reducing (Lydersen et al., 2017; Parks et al., 2014a; Prichard & Kennedy, 2014) or promoting (Harvey et al., 2016a) subsequent fire intensity and severity through altering fuel loads or post-fire stand structure. Depending on the wildfire effect of interest, managers may require information about overstory mortality, combustion, or a combination of the two. Due to the diversity of management uses for severity data, many field metrics have been developed to measure burn severity. Percent overstory mortality measures mature tree survival following fire, whereas the Composite Burn Index (CBI; Key & Benson, 2006) is a generalized measure of burn severity, mortality, and combustion across all strata of forest stands. Other metrics of burn severity aim to measure only combustion of the overstory or soil surface.

The use of multispectral remotely sensed burn severity metrics is widespread across North American forests, but the relationships of such metrics to ground observations of burn severity are variable, especially in the boreal forest (French et al., 2008). The differenced Normalized Burn Ratio (dNBR; Key & Benson, 2006) was developed to assess changes in reflectance of healthy vegetation, soils, and soil moisture due to fire. Subsequently, Miller and Thode (2007) adapted this metric to better capture change relative to pre-fire conditions, with the Relativized dNBR (RdNBR). Most recently, Parks et al. (2014a) introduced a newer relativized severity metric, the Relativized Burn Ratio (RBR), which remains unassessed in the boreal region. Researchers have primarily assessed burn severity in the boreal forest using CBI, which has demonstrated inconsistent relationships to observed severity in the boreal forest, and studies examining other burn severity metrics such as percent overstory mortality and surface burn severity are limited (French et al., 2008).

Relationships between field measurements of burn severity and remotely sensed severity metrics are used to produce maps of burn severity (Key & Benson, 2006; Morgan et al., 2014). Spatial patterns of burn severity can have long-lasting ecological effects on the composition and structure of forests that regenerate following fire (Johnstone & Chapin III, 2006). Varying overstory burn severity (ecological impacts on large trees from fire) and surface burn severity (combustion of organic soils, and ecological impacts on understory vegetation) have important

direct effects on post-fire forest recovery in the boreal biome. The relative availability and depth of seedbeds (mineral vs. organic soil), and fire intensity and overstory mortality affect seedling recruitment in a manner that can potentially lead to shifts in stand composition (Johnstone & Chapin III, 2006a; Lavoie & Sirois, 1998). The mosaic of burn severity within a fire also influences landscape heterogeneity and stand-age distributions, with implications for both species assemblies and diversity (Chipman & Johnson, 2002; Tews et al., 2004), and the flammability of post-fire landscapes due to fuel continuity (Parks et al., 2012; Turner & Romme, 1994). Quantifying the relative performance of remotely sensed burn severity metrics in describing diverse field measurements of burn severity will provide insight into the utility and application of multispectral imagery for estimating and mapping meaningful burn severity in the northwestern boreal forest and allow a broader characterization of landscape patterns of burn severity in this region.

In ecosystems dominated by tree species that require live trees for seed sources (non-serotinous), landscape patterns of overstory mortality are important to post-fire vegetation recovery due to limits of seed dispersal (Collins et al., 2017). Analyses of the landscape pattern of stand-replacing fire in such ecosystems show that large fires, like those characteristic of the boreal forest fire regime, tend to incorporate moderately high proportions burned severely (~25 %), and that stand-replacing patches are often large, simple in form with substantial core areas, and aggregated, with some variability driven by local climate and vegetation (Cansler & Mckenzie, 2014; Harvey et al., 2016b). It is therefore possible to characterize the landscape patterns of diverse overstory and understory burn severity metrics in the northwestern boreal forest, relative to documented patterns of stand-replacing fire in this (Ferster et al., 2016; Kafka et al., 2001) and other ecosystems (Cansler & Mckenzie, 2014; Collins et al., 2017; Harvey et al., 2016b). In the boreal forest, however, many tree species have adaptations that provide *in situ* budding rhizomes or seed sources following fire, regardless of tree mortality (Greene et al., 1999), suggesting that ecological characterizations of landscape patterns of burn severity in this region should address other fire effects, in addition to overstory mortality (Bergeron et al., 2014).

Climate acts as a significant top-down control on fire activity and area burned, having a direct effect on fire size. Large fires have larger areas of stand-replacing fire that are simpler in shape than smaller fires (Cansler & Mckenzie, 2014; Harvey et al., 2016b). Burn severity is also a

product of both pre-fire vegetation (Boucher et al., 2016; Collins et al., 2007) and topography (Dillon et al., 2011; Krawchuk et al., 2016), which provide bottom-up controls on wildfire. Fire weather at the time of burning influences fire behavior and combustion (Forestry Canada Fire Danger Group (FCFDG), 1992), and in west-central North America, researchers have demonstrated that extreme fire weather may overwhelm the effects of bottom-up controls on burn severity (Dillon et al., 2011; Harvey et al., 2014; Krawchuk et al., 2016). Linkages between fire weather, fuel structure, and burn severity have been identified for the forests of the western United States (Lydersen et al., 2017; Prichard & Kennedy, 2014), but they remain sparsely documented in northern forests. An enhanced understanding of top-down and detailed bottom-up controls on burn severity in the northwestern boreal forest would offer insights for fuel and fire management in this fire-prone region.

The goal of this research is to describe and explain variability in burn severity in the northwestern boreal forest. Our objectives were to (1) assess the performance of three remotely sensed burn severity metrics in characterizing field observations of burn severity from the northwestern boreal forest, (2) contextualize and describe the landscape patterns of burn severity in the sampled fires, and (3) characterize the relative importance of top-down (daily fire weather) and bottom-up (topography and vegetation structure) controls on burn severity in an extreme fire year. Hypotheses related to each objective are reported in Table 2.1.

Table 2.1 Research objectives and hypotheses, and associated supporting literature used in hypothesis development.

Objective	Hypothesis	Supporting References
1) Assess the performance of three remotely sensed burn severity metrics in characterizing field observations of burn severity from the northwestern boreal forest	H1 _a : Bivariate relationships between the four field metrics of burn severity and remotely sensed burn severity will have different forms. H1 _b : Relativized metrics of burn severity (RBR, RdNBR) will have a significantly stronger relationship to field metrics of burn severity than non-relativized metrics (dNBR).	(Miller et al., 2009) (Cansler & McKenzie, 2012; Hoy et al., 2008; Parks, Dillon, et al., 2014)
2) Contextualize and describe the landscape patterns of burn severity in the sampled fires	H2 _a : Greater than 25% of the area burned in the sampled wildfires will have burned at high severity, reflecting the large fire sizes and stand-replacing fire regime of the northwestern boreal forest. H2 _b : High-severity patches will have larger average sizes, larger core areas and less complex patch shapes than unchanged, low, and moderate severity burned patches, reflecting the large sizes of the sampled fires and stand-replacing fire regime of the northwestern boreal forest. H2 _c : Landscape patterns of burn severity will vary with the different modeled burn severity field metrics.	(Cansler & Mckenzie, 2014; Collins et al., 2017; Harvey et al., 2016b) (Cansler & Mckenzie, 2014; Collins et al., 2007; Harvey et al., 2016b) (Miller et al., 2009)
3) Characterize the relative importance of top-down (daily fire weather) and bottom up (topographical and vegetation structure) controls on burn severity in an extreme fire year.	H3 _a : Burn severity is significantly related to topoedaphic context, pre-fire vegetation, and fire weather at the time of burning in the northwestern boreal forest. H3 _b : During the extreme fire year of 2014, top-down controls of daily fire weather were of dominant importance to burn severity, due to the “overwhelming” of other drivers by extreme weather.	(Dillon et al., 2011; Harvey et al., 2016b; Prichard & Kennedy, 2014) (Dillon et al., 2011; Harvey et al., 2014; Krawchuk et al., 2016)

2.3 Methods and Data

We measured pre-fire stand structure and burn severity metrics one year post-fire and developed bivariate models of field observations and remotely sensed burn severity metrics, linking satellite

imaging of fire effects to ground observations of post-fire environments. These relationships were used to create maps of burn severity, which we analyzed with landscape patch metrics. Finally, we fit models explaining burn severity field metrics from measured stand structure, topoedaphic context, and daily fire weather at the time of burning. All analyses were performed in R (R Core Team, 2018), unless otherwise specified.

2.3.1 Study area

The six studied wildfires were very large (~14,000 to > 700,000 ha), lightning-caused fires that burned in 2014 within the Northwest Territories or Wood Buffalo National Park (Fig. 2.1). The study area experiences infrequent, stand-replacing (i.e., lethal) fires every 40–350 yr (Boulanger et al., 2012). Although fires in this region are typically small (< 200 ha), rare large fires, such as those studied here, are responsible for the vast majority of the area burned (Stocks et al., 2002). 2014 was an extreme fire year in this region, which took place during a multi-year drought (Northwest Territories Environment and Natural Resources (NWTENR), 2015). Due to the dispersed and small human population in this area, naturally occurring wildfires are generally managed following an appropriate response philosophy, with limited suppression and control efforts, where acceptable. For these reasons, the fires sampled for this study presented a rare opportunity to study burn severity in multiple concurrent, large, free-burning wildfires, in a broad range of fuel complexes.

The study area is characterized by long, cold winters and short hot summers, with mean annual temperatures between -4.3°C (in the north) and -1.8°C (in the south). It generally receives low-to-moderate annual precipitation, ranging from approximately 300 to 360 mm, primarily in the summer months (Ecological Stratification Working Group (ESWG), 1995; Wang et al., 2012). In the western part of the study area, glacial deposits have produced a flat to undulating plain. To the northeast of Great Slave Lake, bedrock lies closer to the surface, and the terrain becomes rolling granitic hills on the Canadian Shield (ESWG, 1995). Peatlands are a substantial component of the entire study area, covering roughly a third of the area, but locally as much as 75–100 % of the land's surface, with a higher cover of peatlands west and south of the Great Slave Lake (Tarnocai et al., 2011). Due to the glacial history of this region, there is minimal topography, and surficial geology and soils may contribute more meaningfully to hydraulic gradients than topography in the boreal plain (Devito et al., 2005). The study area is within the

discontinuous and sporadic permafrost zones of northern Canada (Natural Resources Canada (NRCan), 1993). No field sites had an active permafrost layer in the top 1 m of soil.

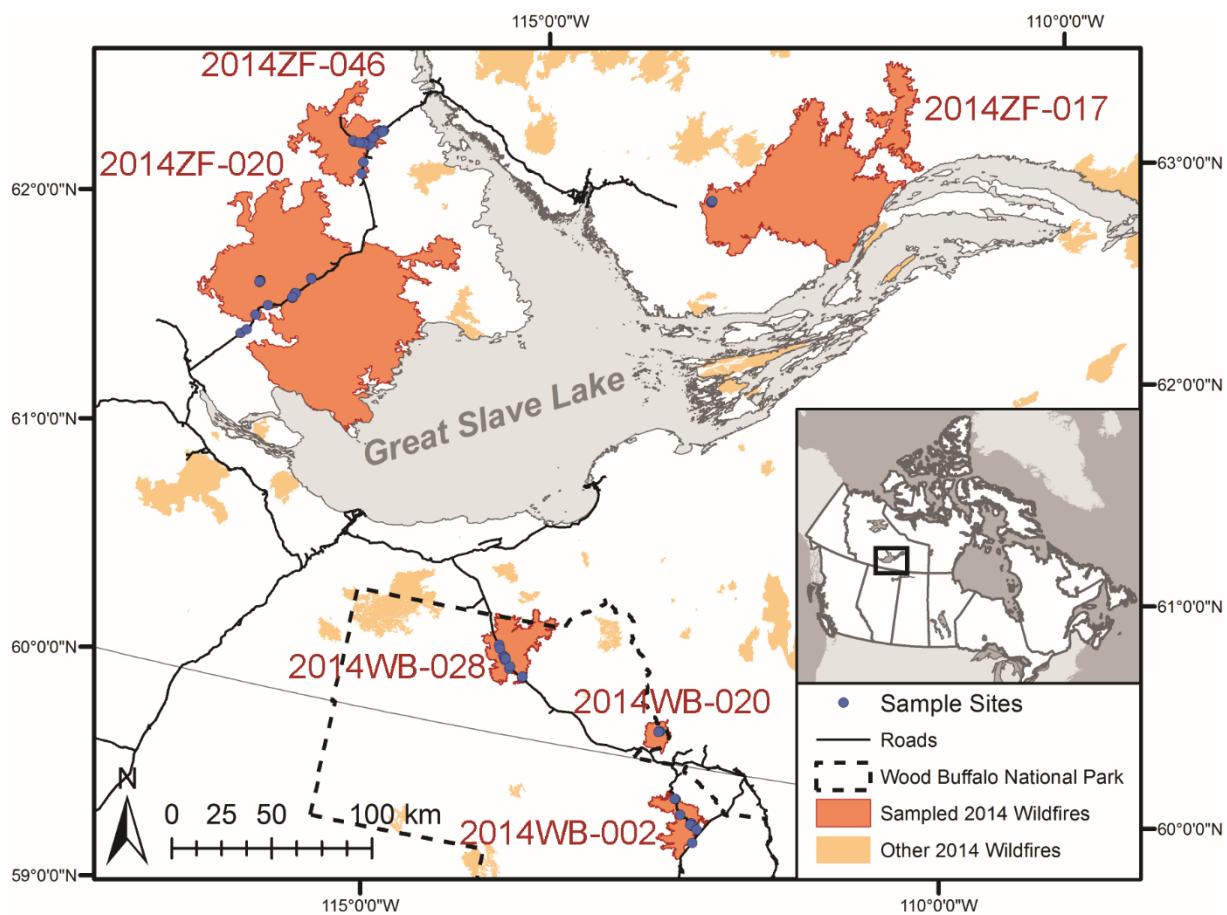


Figure 2.1 The study area (extent indicated in black on inset map), located in context within North America. Dark orange areas indicate perimeters of sampled 2014 wildfires, and lighter orange areas are other 2014 wildfires. Sampled fires are labeled in red with the fire name. The 51 burned sampled field plots and 12 unburned control points are identified with blue circles. Detailed descriptions of fires and distribution of sample plots by fire are included in Table 2.2.

The dominant tree species in this region are black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), and trembling aspen (*Populus tremuloides*). Secondary species of eastern larch (*Larix laricina*), balsam poplar (*Populus balsamifera*), and paper birch (*Betula papyrifera*) are also common. Many of these tree species are adapted to recurrent wildfires and have serotinous or semi-serotinous cones, or sucker from roots and rhizomes following fire (ESWG, 1995; Greene et al., 1999). These characteristics make distances to live seed sources following fire a less significant driver of post-fire seedling recruitment for many

species, with the exception of white spruce, which requires live trees for regeneration. Pre-fire organic soil depths range from sub-centimeter depths in xeric pine stands to meters in peatlands.

2.3.2 Field site selection and sampling

Sampling of pre-fire stand structure and post-fire burn severity took place one year post-fire. Proposed field sites were located in areas > 100 m and ≤ 2 km from roads, with a stratified random sample of burn severity, evenly distributed across low-, moderate-, and high-burn severity classes produced from initial assessment dNBR images (Key & Benson, 2006) classified using thresholds reported in Hall et al. (2008). When traveling by helicopter, additional remote field sites were selected to represent the local range of burn severity and vegetation communities accessible from the landing site. We sampled 51 burned field sites and located twelve unburned control points, which we used to identify remotely sensed burn severity and reflectance values of unburned areas. The range of vegetation communities sampled in the burned plots was represented in the sample of unburned controls. At field sites, we placed plot centers randomly within a homogenous area of burn severity, vegetation community, and topoedaphic setting (upland or wetland) that extended ≥ 60 m in any direction from the plot center. Plot locations were recorded with a differential GPS unit. Plot centers of all field sites were a minimum of 103 m apart, but were on average 170 km apart.

Field sites were 30×30 m square plots, oriented so that two 30-m transects aligned with the cardinal directions crossed at the plot center at right angles. The vegetation community and topoedaphic context (upland or wetland class) of a plot were described according to the Field Guide to Ecosites of Northern Alberta (Beckingham & Archibald, 1996). Ecosites were generalized into five functional vegetation community classes: Upland Jack Pine, Upland Black Spruce, Upland Mixedwood, Treed Wetland, and Open Wetland.

We described burn severity in each plot using percent overstory mortality, CBI with height thresholds modified for northern forests (Key & Benson, 2006; Verbyla et al., 2008), Canopy Fire Severity Index (CFSI; Kasischke et al., 2000), and Burn Severity Index (BSI; Loboda et al., 2013). Composite Burn Index values ranging from 0 (unburned) to 3 (severely burned) were estimated for each forest stratum present in the 30×30 m plot and averaged. Canopy Fire Severity Index was used to estimate the level of crown involvement in fire and intensity of overstory combustion, whereas BSI was used to assess the burn severity of the forest floor and

ground surface. We estimated the relative area of the seven CFSI classes, ranging from 0 (no tree mortality) to 6 (no primary branches remaining, pole charring occurred) in four 10×10 m subplots, at the four corners of the plot. In the same four subplots, we also estimated the relative area of five surface BSI classes described in Dyrness and Norum (1983) ranging from 0 (unburned) to 4 (organic soil ashed, mineral soil exposed). The area of each class was used to calculate weighted sums following the method described in Loboda et al. (2013), and the resulting four CFSI and BSI values per plot were averaged. Percent overstory mortality (MORT) from fire, pre-fire overstory tree species composition, stem density (stems ha^{-1}), tree basal area (BA; $\text{m}^2 \text{ha}^{-1}$), and estimated pre-fire live conifer crown base height (CBH; m) were measured for 32 trees > 3 cm in diameter at breast height with the point-centered quarter method (Cottam et al., 1953; Mitchell, 2015) at eight evenly spaced points along the two transects. Where stem density was very low (i.e., open wetlands), a variable radius circle plot with a minimum length of 15 m was taken at the plot center to measure overstory trees. Pre-fire understory stem density of seedlings and saplings was measured using 3-m radius plots at the end points of each transect. The number of understory density plots sampled ranged from one to four, depending on the density and evenness of the seedling and saplings. Understory and overstory stem density were combined for analyses. Pre-fire overstory fuel load (flammable biomass in t ha^{-1}) at each site was modeled using allometric equations (Thompson et al., 2017; Ung et al., 2008). Sections from fire-scarred trees were collected to determine stand age and fire history at each plot. If no scarred trees were identified nearby, a section of a mature dominant tree was collected.

2.3.3 Remote sensing of burn severity

Remotely sensed burn severity within the six fires was estimated using multispectral Landsat 8-OLI (Operational Land Imager) and Landsat 5-TM (Thematic Mapper) images (Landsat Level-1 imagery, courtesy of the U.S. Geological Survey). Image pairs were selected for an extended assessment of burn severity, where post-fire images were captured in the growing season after the fire (Table 2.2; Key & Benson, 2006). Images were converted to at-surface reflectance using dark-object-subtraction in QGIS with the semi-automatic classification plugin (Congedo, 2016; QGIS Development Team, 2017). Clouded and shadowed areas within fire perimeters were masked by hand in ArcGIS (Esri Inc., 2012), and permanent waterbodies (NRCan, 2008) were also masked. The Normalized Burn Ratio (NBR; Eq. 1), dNBR (Eq. 2), RdNBR (Eq. 3), and

RBR (Eq. 4) were calculated from at-surface reflectance of near-infrared (NIR) and short-wave infrared (SWIR; Landsat bands 4 and 7 [TM] or 5 and 7 [OLI]) and then multiplied by 1000. All remotely sensed burn severity metrics were calculated in R with the raster package (Hijmans, 2016). We included an offset term ($dNBR_{offset}$), normalizing dNBR values in unburned areas to 0 by subtracting the average dNBR in unburned areas to account for phenological differences between images (Eq. 2; Key, 2006; Miller & Thode, 2007). Values of the remotely sensed burn severity metrics at each field plot were estimated from the four nearest 30×30 m pixels using bilinear interpolation.

(1)

$$NBR = \frac{NIR - MIR}{NIR + MIR}$$

(2)

$$dNBR = (NBR_{prefire} - NBR_{postfire}) - dNBR_{offset}$$

(3)

$$RdNBR = \frac{dNBR}{|(NBR_{prefire})|^{0.5}}$$

(4)

$$RBR = \frac{dNBR}{(NBR_{prefire} + 1.001)}$$

Table 2.2 Pairs of Landsat 8-OLI and Landsat 5-TM images used for measurement of remotely sensed burn severity. Images are listed by the name of the fire analyzed. The size and start date of sampled wildfires are also reported, as well as the number of field plots located within the fire. Two post-fire images for fire 2014ZF-017 were mosaicked together.

Fire Name	Start Date	Fire Size (ha)	Number of field plots	Pre-Fire Sensor	Path	Row	Pre-Fire Image Date	Post-Fire Sensor	Path	Row	Post-Fire Image Date
2014ZF-020	June 17, 2014	730,855	12	Landsat 8-OLI	48	17	May 30, 2013	Landsat 8-OLI	48	17	May 20, 2015
2014ZF-017	June 16, 2014	450,207	5	Landsat 8-OLI	45	16	June 12, 2014	Landsat 8-OLI	46	16	June 23, 2015
2014ZF-017	-	-	-	-	-	-	-	Landsat 8-OLI	44	16	June 25, 2015
2014ZF-046	July 3, 2014	106,485	17	Landsat 8-OLI	48	16	May 30, 2013	Landsat 8-OLI	47	16	May 29, 2015
2014WB-028	August 1, 2014	66,673	8	Landsat 8-OLI	45	18	June 13, 2014	Landsat 8-OLI	46	18	June 23, 2015
2014WB-002	June 15, 2014	38,060	6	Landsat 5-TM	44	18	June 14, 2011	Landsat 8-OLI	44	18	June 25, 2015
2014WB-020	July 8, 2014	13,979	3	Landsat 5-TM	44	18	June 14, 2011	Landsat 8-OLI	44	18	June 25, 2015

2.3.4 Daily fire weather

To assess the potential relationship between weather and burn severity, we interpolated Moderate Resolution Imaging Spectroradiometer (MODIS; Canadian Forest Service, 2015) and Visible Infrared Imaging Radiometer Suite (VIIRS; USDA Forest Service, 2014) hotspots from the year 2014, using a weighted mean (Parks, 2014) to estimate the day of burning (DOB) for each field site. Fire weather conditions were represented using the Canadian Forest Fire Weather Index (FWI) System, which uses daily inputs of temperature, relative humidity, precipitation, and wind speed to produce three fuel moisture codes (Fine Fuel Moisture Code [FFMC], Duff Moisture Code [DMC], and Drought Code [DC]) and three indexes of fire behavior potential (Initial Spread Index [ISI], Buildup Index [BUI], and Fire Weather Index; Van Wagner 1987). Noon (Local Standard Time) weather and FWI System values on the DOB for each site were downscaled from North American Regional Reanalysis data (NARR; Jain et al., 2017; Mesinger et al., 2006) using ordinary kriging. Fire Weather Index System indexes were calculated from the interpolated temperature, precipitation, relative humidity, and wind speed using the cffdrs package (Wang, Wotton, et al., 2017), with starting values from the interpolated values of the FFMC, DMC, and DC from the previous day (Jain et al., 2017).

2.3.5 Analysis

Statistical differences in burn severity and stand structure between vegetation communities were assessed with Wilcoxon signed-rank tests, ANOVA, and post hoc least-squares means tests (lsmeans package; Lenth, 2016). We produced scatterplots and computed Spearman's rank correlation coefficients to determine the nature of the relationships between the field measures of burn severity and remotely sensed burn severity metrics. Subsequently, we used generalized linear models (GLMs) and landscape patch metrics to examine landscape patterns and drivers of burn severity in this region. Bivariate GLMs were used to develop diagnostic models describing the relationship between remotely sensed burn severity and field metrics of burn severity. All model fits were assessed using averages of root-mean-square error and R^2 (the square of the correlation between observed values and predicted values), calculated following a 10-fold cross-validation (CV) with 100 repeats in the caret package (Khun, 2017). All statistical tests in this study were conducted at the 5 % level of significance. Continuous values of the four burn severity field metrics were predicted from rasters of remotely sensed burn severity using the bivariate GLMs and subsequently classified into unchanged, low, moderate, and high severity

using breaks described in Table 2.3. The relative quality of each remotely sensed burn severity metric as a classifier of burn severity was assessed using the kappa statistic in the psych package (Revelle, 2017).

Burn severity thresholds were identified from field observations of meaningful differences in burn severity for each metric and validated with the distribution of sampled data. Generally, unchanged sites are unburned or lightly burned, where mild and patchy fire effects were intermingled with unburned areas. Low-severity burned areas had scorched or lightly charred surfaces but substantial organic matter still existed post-fire. Some overstory mortality may be evident in the stand, but any crown involvement in the fire did not consume all small branches in the overstory. Moderate-severity burned areas have charred surfaces and may have some exposed mineral soil and ash present. Overstory tree mortality was more common in these stands, with primary branches and some dead non-combusted foliage remaining on the trees despite fire crowning. High-severity burned stands have surfaces substantially composed of exposed mineral soil or ash. There was complete stand mortality, and the majority of primary branches are consumed (illustrative photographs provided in Appendix A: Table A1). Models using relativized burn severity metrics generally had lower error and higher CV R² values than models using dNBR to describe burn severity field metrics; however, all bivariate models were significant ($p \leq 0.001$) and none had statistically stronger fits to the field data (Wilcoxon signed-rank tests of model residuals $p \geq 0.44$). Furthermore, because the confidence intervals of the kappa statistic for all three remotely sensed metrics overlapped, we chose to present only RBR in subsequent analyses and visualizations.

Table 2.3 Breaks used to classify maps of modeled burn severity field metrics of Composite Burn Index (CBI), surface Burn Severity Index (BSI), Canopy Fire Severity Index (CFSI) and percent overstory mortality (MORT). Modeled values of burn severity metrics were estimated from raster maps of the remotely sensed Relativized Burn Ratio (RBR). Representative photographs of burn severity classes are included in Appendix A: Table A2.

Burn Severity Metric	Unchanged	Low	Moderate	High
CBI (0–3)	≤ 0.1	$> 0.1 - 1.5$	$> 1.5 - 2.25$	> 2.25
BSI (0–4)	≤ 0.5	$> 0.5 - 1.75$	$> 1.75 - 3$	> 3
CFSI (0–6)	≤ 0.1	$> 0.1 - 2$	$> 2 - 4$	> 4
MORT (0–100)	≤ 10	$> 10 - 50$	$> 50 - 95$	> 95

Landscape patterns of classified burn severity within fire perimeters were assessed using a selection of patch metrics calculated in FRAGSTATS (McGarigal et al., 2012). Patches were defined using the eight-neighbor rule. To limit edge effects, landscape patterns of burn severity were assessed within the core area of fire perimeters only, excluding areas ≤ 100 m from the fire edge (following Parks et al., 2014b). Single-pixel patches were removed using a majority filter in ArcGIS, also with an eight-neighbor rule. Patch metrics were selected to characterize the relative dominance, and spatial arrangement and distribution of patches of each severity class. The area-weighted mean patch size and the proportion of the landscape burned in each severity class were used to describe the relative dominance of severity classes on the landscape. Area-weighted means were used as they capture the higher relative probability of a randomly selected point falling into a large patch. The core area of a patch was defined as areas ≥ 600 m from the edge. This threshold was selected as a conservative estimate of the maximum distance for long-distance seed dispersal for white spruce (Greene & Johnson, 2000), in an ecosystem where most trees have in situ bud banks or seed sources, regardless of overstory mortality. The clumpiness index and area-weighted perimeter-to-area ratio (PARA) were selected to characterize how patches are arranged on the landscapes, capturing the relative dispersion and complexity of shape of the different severity classes. Clumpiness is the deviation in the proportion of like adjacencies (pixel edges shared with a pixel of the same class) from that expected in a random landscape. Together, these metrics were used to characterize the post-fire pattern of combustion, seedbeds, and seed sources, and the heterogeneity of the post-fire landscape mosaic.

We also fit prognostic multivariable GLMs to estimate burn severity field metrics from pre-fire stand structure, topoedaphic context, and fire weather. A complete suite of stand structure and age, and fire weather variables were considered for each model. Only those explanatory variables that were significant ($p \leq 0.05$) were retained. If explanatory variables were highly correlated ($|p| \geq 0.6$) with one another, then the variable contributing most significantly to the model was retained and the other correlated variable was removed. Upland and wetland datasets were separated and differences in model performance and in burn severity between the two groups were assessed. Finally, the three remotely sensed burn severity metrics were assessed for complementarity to the field data by adding each to the complete prognostic multivariable model and examining model fit metrics and t -values of predictor variables.

2.4 Results

2.4.1 Field measures of burn severity

The CBI, BSI, CFSI, and percent or proportion overstory mortality (MORT) field measures of burn severity were sensitive to pre-fire vegetation communities described by dominant upland tree species, and treed or open wetlands (Fig. 2.2). Of the vegetation communities, Upland Jack Pine tended to incur the higher ranges of burn severities. Burn severity was most variable in Upland Mixedwood stands, which is likely attributable to the variable proportions of conifer and deciduous species that would influence fuels and the likelihood to burn. Not unexpectedly, Open Wetlands had lower values of burn severity compared to Treed Wetlands (Fig. 2.2).

Of interest was the degree to which remotely sensed burn severity metrics were statistically correlated to the four burn severity metrics. Both dNBR and RBR were most highly correlated to CFSI, followed by CBI. Relativized dNBR was more correlated to CBI than CFSI. All three remotely sensed metrics were less correlated with BSI than CBI and CFSI, and had the weakest correlation to MORT; however, all correlations were statistically significant ($p < 0.001$; Appendix A: Table A2). These correlations were supported by the scatterplots of the data points between the remotely sensed metrics and the four field burn severity metrics. In particular, there was a distinct sigmoidal relationship between the remotely sensed severity metrics and MORT, which explains the lower correlation coefficient (Fig. 2.3).

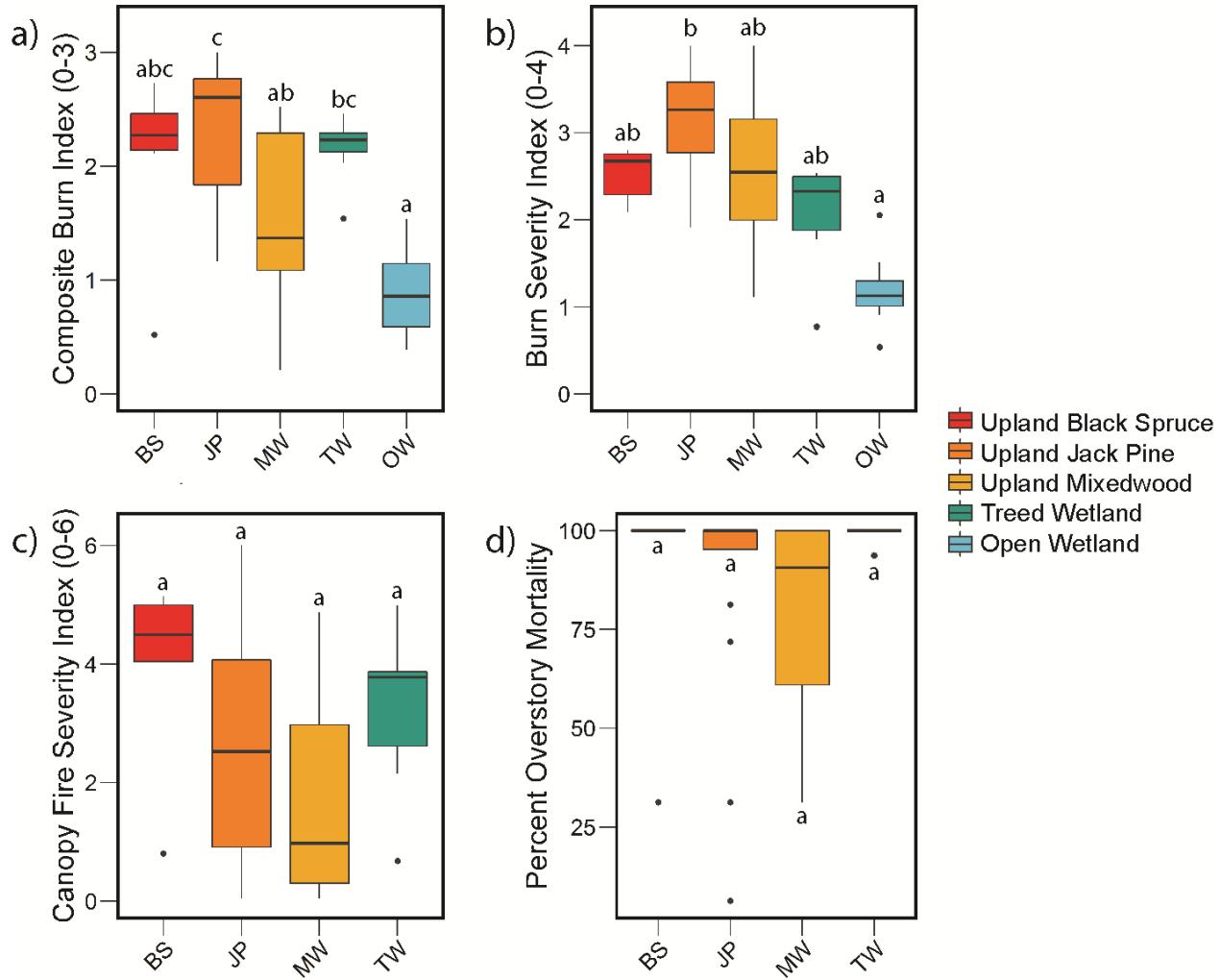


Figure 2.2 Distribution of burn severity metrics within vegetation communities of Upland Black Spruce (BS), Upland Jack Pine (JP), Upland Mixedwood (MW), Treed Wetland (TW), and Open Wetland (OW). Burn severity metrics are: a) Composite Burn Index (CBI), b) surface Burn Severity Index (BSI), c) Canopy Fire Severity Index (CFSI), and d) percent overstory mortality. CFSI and Percent overstory mortality are not reported for OWs as these are not forested systems. Letters above each boxplot indicate significant differences ($p \leq 0.05^*$) in least-squares means with a Tukey p -value adjustment.

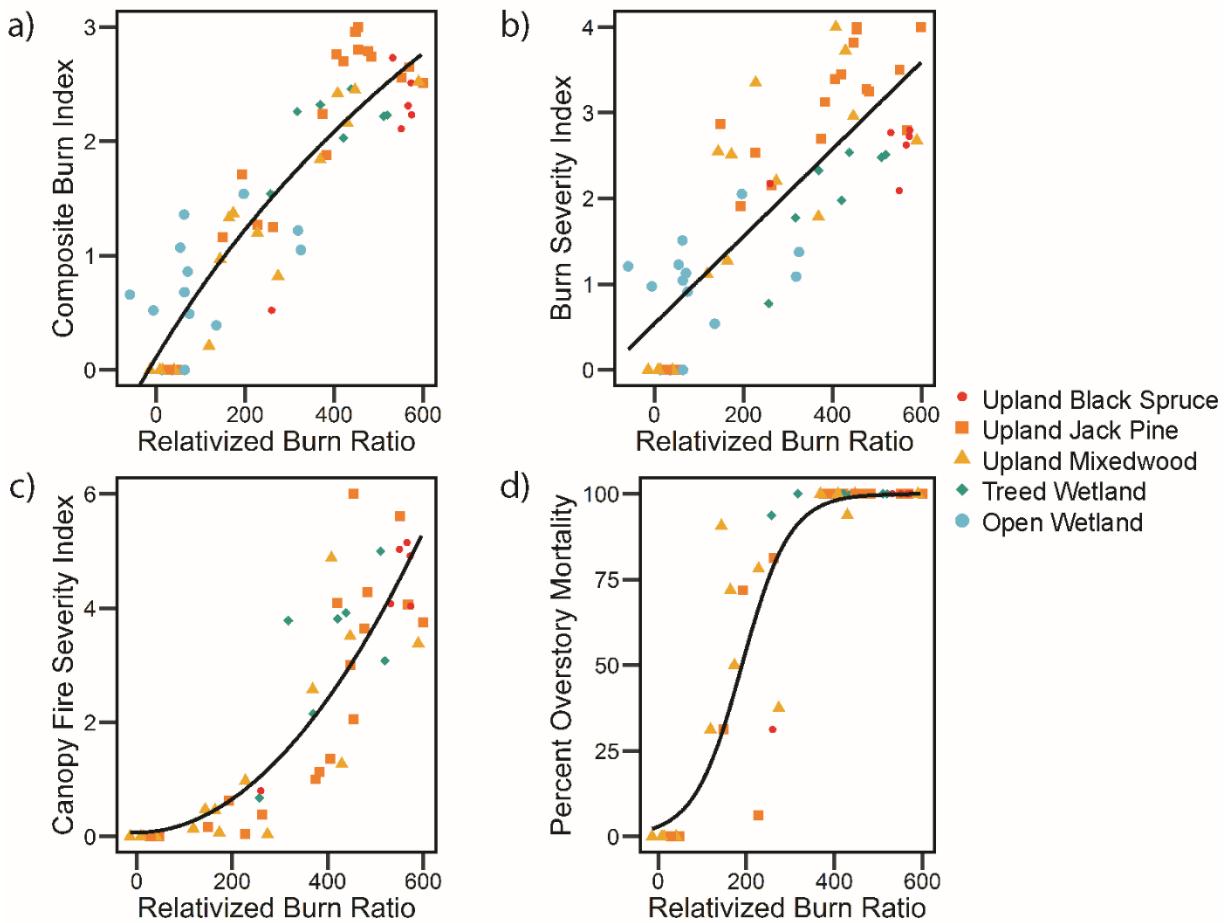


Figure 2.3 Relationships between a) Composite Burn Index (CBI), b) surface Burn Severity Index (BSI), c) Canopy Fire Severity Index (CFSI), and d) percent overstory mortality (MORT) and the Relativized Burn Ratio (RBR) across all vegetation communities (indicated by point color and shape). Open wetlands are excluded from the CFSI and MORT models as these are not forested systems. Unburned control sites are classified into the same vegetation communities, and are identifiable as points with values of zero. Model fit statistics are reported in Table 2.4, as are models of the same form with independent variables of the differenced Normalized Burn Ratio (dNBR) and Relativized dNBR (RdNBR).

2.4.2 Diagnostic models of burn severity

Burn severity was statistically lower in wetlands than in uplands (Wilcoxon signed-rank test, $p \leq 0.02$) when measured by CBI, and BSI, but not when using the overstory burn severity measures of CFSI and MORT ($p \geq 0.20$; Fig. 2.2). Composite Burn Index, CFSI, and BSI were explained by pre-fire vegetation communities (Type II ANOVA, $p < 0.003$); however, MORT was not statistically related to vegetation community ($p = 0.5$). Vegetation community classes alone explained 22.6 % (CFSI), 41.7 % (CBI), and 54.1 % (BSI) of the variance (ω^2) in field measurements of burn severity. Post hoc comparisons of least-squares means with a Tukey p -value adjustment confirmed some statistical differences in burn severity among vegetation

communities for CBI and BSI ($p \leq 0.05$; Fig. 2.2). Upland Jack pine and Open Wetlands demonstrated distinct levels of CBI and BSI. Other vegetation communities shared similar levels of severity with one or both of these two communities. The forms of the bivariate relationships between the burn severity field metrics and the remotely sensed burn severity metrics were different for each field metric (Fig. 2.3). Composite Burn Index, CFSI, and MORT were best modeled with nonlinear model forms, whereas BSI had a linear relationship to remotely sensed burn severity (Fig. 2.3).

All diagnostic bivariate models estimating field observations of burn severity from the three remotely sensed severity metrics were significant (Table 2.4; $p \leq 0.001$). Models using the relativized burn severity metrics (RdNBR and RBR) generally better described the burn severity field data and had lower error and higher CV R² values than those using dNBR. Relativized dNBR typically had the lowest error and the highest CV R²; however, RBR had the best fit for the CFSI model. Relativized dNBR had the highest accuracy and reliability (kappa statistic) in classifying burn severity metrics that considered surface burn severity (CBI and BSI), but performed the worst in classifying burn severity landscapes where only overstory impacts were measured (CFSI and MORT). Relativized Burn Ratio had the highest accuracy and reliability in classifying overstory burn severity (Table 2.4). Although there were differences in error, CV R² values, and classification accuracy of the three different remotely sensed severity metrics in describing observed burn severity, there was no statistical difference in model fits (Wilcoxon signed-rank tests of model residuals $p \geq 0.44$) and the 95% confidence intervals of kappa statistics overlapped.

Table 2.4 Diagnostic generalized linear models of Composite Burn Index (CBI), surface Burn Severity Index (BSI), Canopy Fire Severity Index (CFSI), and proportion overstory mortality (MORT) predicted from the remotely sensed burn severity metrics differenced Normalized Burn Ratio (dNBR), Relativized dNBR (RdNBR), and Relativized Burn Ratio (RBR). Model fits are described using averages of 10-fold cross-validated (CV) mean absolute error (MAE), root mean square error (RMSE), and R^2 , derived from 100 repeats. Error terms are expressed in the units of the predicted variable. P -values of models were derived from χ^2 tests of model deviance explained, relative to a null model. $P \leq 0.001^{***}$ for all models. The classification accuracy of mapped burn severity produced using each model, and Kappa statistic and associated 95 % confidence intervals (CI) are also reported.

Severity Metric	Formula	Distribution	CV MAE	CV RMSE	CV R^2	Overall Accuracy	Kappa	Kappa CI +/-
dNBR	$CBI = dNBR \times (0.1651[dNBR] + 161.8346)^{-1}$		0.38	0.45	0.83	49.21	0.31	0.16
RdNBR	$CBI = RdNBR \times (0.52379[RdNBR] + 46.13491)^{-1}$	Gaussian	0.34	0.40	0.87	57.14	0.41	0.16
RBR	$CBI = RBR \times (0.1267[RBR] + 140.1737)^{-1}$		0.36	0.43	0.85	53.97	0.36	0.16
dNBR	$BSI = 0.6178 + (dNBR \times 0.0037)$		0.71	0.80	0.66	36.51	0.12	0.15
RdNBR	$BSI = 0.484 + (RdNBR \times 0.0021)$	Gaussian	0.61	0.71	0.72	39.68	0.19	0.15
RBR	$BSI = 0.537 + (RBR \times 0.0051)$		0.66	0.75	0.70	38.10	0.16	0.15
dNBR	$CFSI^\dagger = -0.2069 + (dNBR^2 \times 0.000008)$		0.78	0.99	0.80	73.47	0.65	0.18
RdNBR	$CFSI^\dagger = 0.1324 + (RdNBR^2 \times 0.000002)$	Gaussian	0.81	1.04	0.76	57.14	0.43	0.18
RBR	$CFSI^* = -0.0714 + (RBR^2 \times 0.0001)$		0.70	0.93	0.82	73.47	0.65	0.18
dNBR	$MORT^\dagger = -3.361 + (dNBR \times 0.0134)$		0.09	0.15	0.83	59.18	0.37	0.21
RdNBR	$MORT^\dagger = -3.5882 + (RdNBR \times 0.008)$	Quasibinomial	0.08	0.14	0.86	57.14	0.33	0.21
RBR	$MORT^\dagger = -3.508 + (RBR \times 0.0185)$		0.09	0.15	0.85	59.18	0.35	0.21

[†] Subset of forested sites only, excluding data from open wetlands.

When datasets were limited to topoedaphic subsets (wetlands and uplands), dNBR generally had the best fit in wetland-only datasets, whereas models with RdNBR and RBR had stronger

relationships to the field data and lower error when fit with only upland field sites. Model significance (p) decreased slightly from the significance of the full models when fit with wetlands only, but remained < 0.05 (Appendix A: Table A3). For severity metrics that considered surface burn severity, partitioning into uplands and wetlands generally improved the model fit, but increased error in the wetland-only datasets. When the CFSI model was fitted with upland sites the error decreased and the CV R² increased; however, the MORT model fit worsened slightly, but non-significantly (Appendix A: Table A3). Models of CFSI and MORT were not significant when fitted using wetland data only due to the small sample size of forested wetlands ($n = 8$), and thus, these models are not reported in Appendix A: Table A3.

2.4.3 Landscape patterns of burn severity

Although all classified maps were derived from the same RBR rasters, the landscape pattern metrics differed, depending on the modeled burn severity metric (Fig. 2.4). When all fires were considered together, maps of CBI, BSI, and CFSI classified the majority of the burned landscape as moderate severity, and this class tended to have the largest mean patch size. MORT demonstrated a different trend, where high-severity classes were the majority of the area, and also had the largest mean patch size (Fig. 2.4; Appendix A: Table A4). Unchanged and low-severity patches tended to be more complex in form for all modeled severity metrics. Mapped CBI was an exception to this and had more complex moderate-severity patches, although unchanged patches had a similar mean PARA value to that of moderate-severity patches (Fig. 2.4; Appendix A: Table A4). Relatively few patches had significant core areas (> 600 m from the patch edge). Core area of severity classes varied from fire to fire, and with the mapped burn severity field metric. Unchanged and low-severity patches had the largest total core area when landscapes were classified by CBI, BSI, and CFSI. Once again, MORT exhibited a substantially different trend and each fire had patches with quite substantial core areas, especially within high-severity burned patches. High-severity patches were broadly the most aggregated and were substantially more likely to have like neighbors, when classified severity landscapes were derived from modeled values of CBI, BSI, or MORT. Canopy Fire Severity Index differed from this pattern, with unchanged patches being the most likely to share like adjacencies; however, this varied substantially between fires (Fig. 2.4; Appendix A: Table A4).

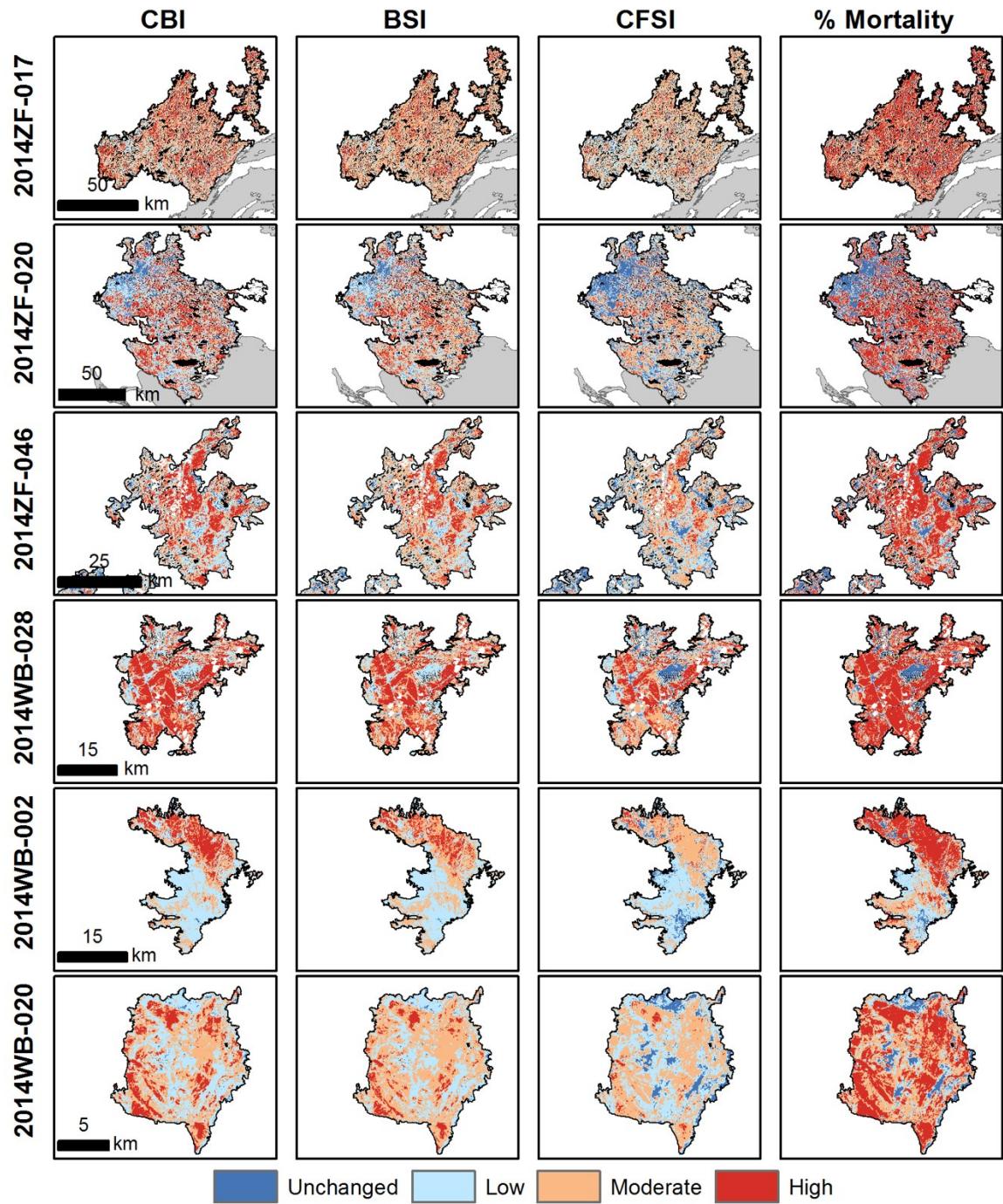


Figure 2.4 Remotely sensed burn severity maps produced by estimating Composite Burn Index (CBI), surface Burn Severity Index (BSI), Canopy Fire Severity Index (CFSI), and percent overstory mortality (% Mortality) from bivariate relationships with the Relativized Burn Ratio (RBR) within six fires: 2014ZF-020, 2014ZF-017, 2014ZF-046, 2014WB-28, 2014WB-02, 2014WB-20. Continuous burn severity values were classified using thresholds reported in Table 2.3. Clouded areas inside fires (fire perimeters outlined in black) are masked, and appear in white. Waterbodies inside fire perimeters are shown in black, and Great Slave Lake is shown in grey. Statistical summaries of landscape patterns of burn severity are reported in Appendix A: Table A4.

2.4.4 Prognostic models of burn severity

The four burn severity field metrics were significantly explained by multivariable prognostic models, with CV R² values ranging from 0.62 to 0.65 (Table 2.5). Burn severity metrics that integrated overstory impacts (CBI, CFSI, and MORT) were predominantly related to stand total BA ($\text{m}^2 \text{ ha}^{-1}$), median conifer live CBH (m), and stem density (STEMS; stems ha^{-1}). Time since last fire and time since stand origin were not significant variables ($p \geq 0.05$) in any model. Burn Severity Index was the only severity metric for which model fit improved with the inclusion of fire weather variables. Severity metrics that considered surface impacts (BSI, CBI) also included topoedaphic context (whether a site was an upland or wetland) as an important explanatory variable (Table 2.5; Appendix A: Table A5). The stand structure, composition, and pre-fire overstory fuel load variables retained in models were significantly different between sampled uplands and wetlands (Wilcoxon signed-rank test, $p \leq 0.04$). Post hoc comparisons of stand structure and fuel load using least-squares means with a Tukey p -value adjustment confirmed statistical differences between vegetation communities, primarily associated with dominant tree species and overstory density in each community (Fig. 2.5).

The explanatory power of all prognostic multivariable models could be improved with the addition of remotely sensed burn severity metrics (Appendix A: Table A6), with RBR providing the most significant improvement in model fit to field measurements of burn severity. When models were fitted using both field and remotely sensed burn severity metrics RBR was typically the most important predictor of burn severity, whereas dNBR and RdNBR were typically less important than measured pre-fire variables. For the BSI model whether the site was a wetland or not remained the most important variable after RBR was added (Appendix A: Table A7). The multivariable linear models did not represent a significant improvement in predictive power compared to the bivariate models of severity (Tables 2.4, 2.5); however, they elucidate significant relationships between pre-fire stand structure and composition, and fire weather drivers of observed severity. Models fitted with both field data and RBR had similar fits to the models using remotely sensed burn severity metrics alone (Table 2.4; Appendix A: Table A6).

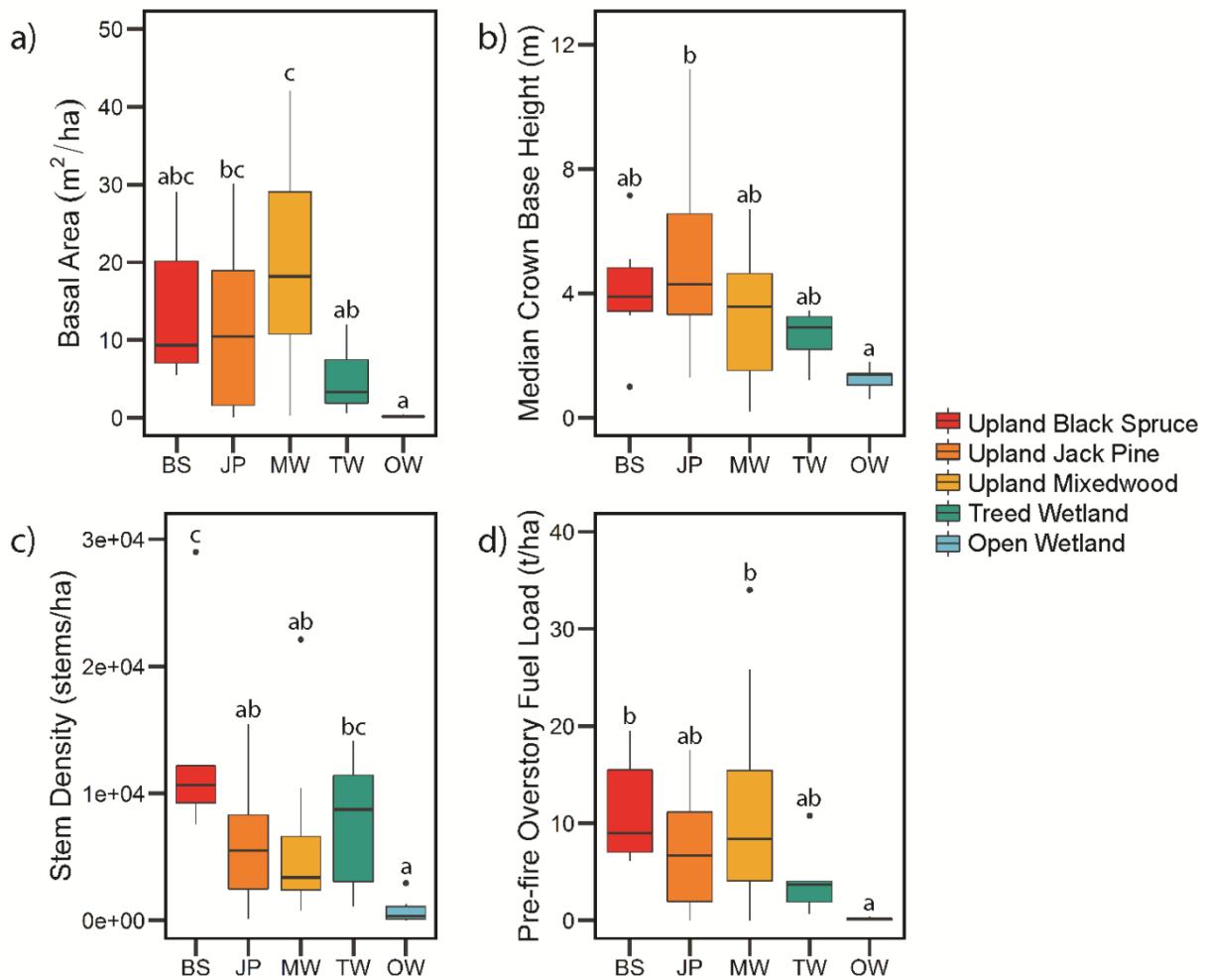


Figure 2.5 Distributions of pre-fire stand structural characteristics of a) basal area (m^2/ha), b) median live crown base height of conifers (m), c) stem density (stems/ha), and d) pre-fire overstory fuel load (t/ha) within pre-fire vegetation communities of Upland Black Spruce (BS), Upland Jack Pine (JP), Upland Mixedwood (UW), Treed Wetland (TW) and Open Wetland (OW). Detailed relationships between burn severity metrics, stand structure, and pre-fire overstory fuel load are shown in Appendix A1: Fig A1. Letters above each boxplot indicate significant differences ($p \leq 0.05^*$) in least-squares means with a Tukey p -value adjustment.

Table 2.5 Prognostic generalized linear models of Composite Burn Index (CBI), surface Burn Severity Index (BSI), Canopy Fire Severity Index (CFSI) and proportion overstory mortality (MORT) predicted from pre-fire fuel structure, topoedaphic context, and fire weather at the time of burning. Independent variables in each equation appear in order of importance (*t*-values in Appendix A: Table A5). Model fits are described using averages of 10-fold cross-validated (CV) mean absolute error (MAE), root mean square error (RMSE), and R², derived from 100 repeats. Error terms are expressed in the units of the predicted variable. *P*-values of models were derived from χ^2 tests of model deviance explained, relative to a null model.

Formula	Distribution	<i>p</i>	CV MAE	CV RMSE	CV R²
CBI = 1.883 - (BA [†] × 0.03451) + (CBH [‡] × 0.1361) - (WET [§] × 0.9656) + 0.00009(WET × STEMS ^{**}) + (STEMS × 0.000009)	Gaussian	0.004**	0.44	0.54	0.62
BSI = 0.5082 - (WET × 1.1514) - (FL ^{††} × 0.0507) + (CBH × 0.0979) + (CON ^{‡‡} × 0.0272) + (BUI ^{§§} × 0.0212) - 0.0003(CON × BUI)	Gaussian	<0.001***	0.51	0.63	0.63
CFSI [†] = 4.2193 - (BA × 0.0707) + 0.2192(CBH × log(STEMS)) - (CBH × 1.5453) - (log(STEMS) × 0.2215)	Gaussian	<0.001***	1.27	1.46	0.62
MORT [†] = 1.9986 - (BA × 0.0872) + (CBH × 0.3972)	Quasibinomial	0.019*	0.13	0.17	0.65

[†] Subset of forested sites only, excluding data from open wetlands

[†] Basal area (m²/ha)

[‡] Median live crown base height of conifer species (m)

[§] Wetland (binary factor; 1 = wetland, 0 = upland)

^{**} Stem density (understory and overstory stems/ha)

^{††} Pre-fire overstory fuel load (t/ha)

^{‡‡} Stand percent non-deciduous conifer by fraction of fuel load

^{§§} Buildup Index

2.5 Discussion

2.5.1 Selecting multispectral remotely sensed burn severity products for application in the northwestern boreal forest

Multispectral remotely sensed imagery is widely available, making it an appealing source of spatial burn severity data. The utility of such imagery for burn severity assessment in the northwestern Canadian boreal forest is supported by our results, as all four measured field metrics of burn severity can be estimated from remotely sensed burn severity. Each field metric of burn severity had a different form of relationship to the remotely sensed severity metrics, supporting hypothesis H1_a. Miller et al. (2009) identified nonlinear relationships between RdNBR and various measures of fire severity. We also found that primarily nonlinear regressions best fit the relationship between the field data and the remotely sensed severity metrics, with the exception of BSI. Burn Severity Index had a linear relationship to the remotely sensed variables, and had the worst modeled fit and classification accuracy, regardless of the remotely sensed severity metric employed.

Both of the relativized metrics had better fits to the field data, providing some support for our hypothesis H1_b. Differences in model fit as measured by residuals and the classification accuracy of the different metrics (kappa statistic) were not statistically different, leading us to reject our hypothesis that the relativized metrics have significantly stronger relationships to the field data. These findings generally match those of researchers who have examined the explanatory power and classification accuracy of dNBR and RdNBR in southwestern North America, with relativized metrics offering some improvement over dNBR for modeling and classifying burn severity (Cansler & McKenzie, 2012; Miller & Thode, 2007; Parks et al., 2014a), as well as some research in boreal Alaska (Hoy et al., 2008). When Soverel et al. (2010) compared the performance of RdNBR and dNBR in Canada, they found that dNBR was a better classifier of burn severity. Although the relativized transformations of dNBR had better fits to field data in our study, we examined more burn severity field metrics than just CBI and the geographic extent of our study was narrower than that of Soverel et al. (2010), possibly accounting for these differences. Model fits between CBI and dNBR and RdNBR were similar (in terms of R²) within the three northern boreal fires they assessed, and generally

demonstrated a higher accuracy when RdNBR was used for classification, despite their finding that dNBR best represented their complete suite of fires. We found no statistical improvement in model fits and classification accuracy when using relativized metrics, supporting the assertion that dNBR remains a useful and applicable severity metric in this region (Hall et al., 2008; Soverel et al., 2010).

We failed to consistently replicate the significant improvement in model fit when comparing RBR to RdNBR, observed by Parks et al. (Parks et al., 2014a); however, our sample size was much smaller. Of the two relativized metrics, RdNBR typically had the best fit to the field data and the lowest error, but RBR had a better or equivalent model fit and higher classification accuracy when describing overstory burn severity metrics (CFSI, MORT). Relativized Burn Ratio also had the strongest explanatory power when pre-fire forest structure, landscape, and weather variables were controlled for in models. It is possible the difference in importance when pre-fire variables are considered is due to the slightly higher correlation of RBR to pre-fire NBR and thus to the pre-fire landscape, relative to the less correlated RdNBR (Parks et al., 2014a). If they are available or easily calculated, it is likely preferable to use relativized multispectral remotely sensed burn severity metrics (RdNBR, RBR), rather than dNBR, to map burn severity in the northwestern boreal forest. When surface burn severity impacts are of interest, RdNBR may offer a slight improvement over RBR, whereas overstory burn severity impacts may be best represented by RBR.

As all four field metrics were statistically related to remotely sensed burn severity metrics, the interpretation of remotely sensed burn severity pixel values and maps can therefore vary, depending on the ground-based measurement of interest. For example, in this dataset, an RBR value of approximately 400 indicates near-complete stand mortality, yet this same value corresponds to a tree with secondary branches remaining (in terms of CFSI), and moderate scorch and charring of the soil surface (in terms of surface BSI). Therefore, multispectral estimates of burn severity can and should be interpreted relative to specific management or research interests. Although modeled relationships to CBI offer insight into general fire effects and combustion, it is also beneficial to use remotely sensed burn severity to characterize other specific ecological impacts of fire (Morgan et

al., 2014), as in this study. Whereas stand mortality and landscape patterns of stand-replacing fire are of great importance and interest in mixed-severity fire regimes (Cansler & Mckenzie, 2014; Collins et al., 2017; Dillon et al., 2011; Harvey et al., 2016b), the same maps of remotely sensed burn severity can be used to estimate post-fire seed viability due to combustion (CFSI), as well as seed bed and bud-bank availability (BSI), in an ecosystem adapted to recurrent stand-replacing fires, such as the northwestern boreal forest.

2.5.2 Landscape patterns of burn severity in the northwestern boreal forest

The 2014 northwestern boreal fire season occurred in a year of extreme drought. Fires burned for months at a time, often with limited suppression, and in a broad range of weather conditions and fuels (NWTENR, 2015). Although the landscape patterns of burn severity in these fires are the result of extreme conditions, and in some cases of dramatic fire behavior, the variable weather and fuels produced a complete range of burn severity, including unburned residual stands. The spatial burn severity patterns within these fires result from the clear predominance of crown fire in this ecosystem, but the product of such lethal fires is not a uniformly homogenous level of burn severity. By altering the local stand-age distribution and post-fire forest structure (Brassard et al., 2008) large wildfires such as these cause persistent changes in heterogeneity and spatial pattern across both landscape and local scales (Burton et al., 2008; Weir et al., 2000), affecting species richness and diversity of vegetation (Hart & Chen, 2008), animal (Smucker et al. 2005), and invertebrate (Buddle et al., 2006) community assemblies.

When considered in terms of overstory mortality, the spatial patterns of burn severity in the six studied fires were broadly consistent with those expected from a high-severity stand-replacing fire regime, providing support for hypotheses H2_a and H2_b. Stand-replacing patches in the six sampled fires were large, with substantial core areas, aggregated, and simple in form. Approximately 40 % of the burned area experienced stand-replacing fire. Others have observed that with increasing fire size the proportion burned severely also increases, as does the mean area-weighted patch size (Cansler & Mckenzie, 2014; Collins et al., 2017; Harvey et al., 2016b). The fires studied here are of a substantial size, with only six fires burning more than 1,400,000 ha in a single year, an

area equivalent to that burned by 295 fires over 26 yr in the montane study area examined by Harvey et al. (2016b), and over four times the area burned by 125 fires over 24 yr in a study of the northern Cascade Range (Cansler & Mckenzie, 2014). The proportion experiencing complete mortality was much higher than the average proportions of stand-replacing fire observed in the western United States (Cansler & Mckenzie, 2014; Collins et al., 2017; Harvey et al., 2016b); however, this proportion was smaller than the 64 % observed by Ferster et al. (2016) in the same boreal plains ecoregion. Although area burned severely increases with increasing fire size, it has also been suggested that larger fires tend to have larger residual stands and a higher proportion of unchanged patches in the boreal forest (Eberhart & Woodard, 1987; Madoui et al., 2010). A substantial proportion of the area within the fires (~15 %) was unchanged, offering live seed sources for white spruce and a large area of residual habitats for species requiring mature forests, within the fire perimeters.

We did not consistently observe the same patterns of high-severity patches dominating the landscape when the landscape patterns of burn severity were quantified using metrics other than overstory mortality, providing support for hypothesis H2_c. Serotinous and semi-serotinous tree species, such as jack pine and black spruce, respectively, have in situ seed sources, and if viable seeds are available stand mortality is not of substantial importance to post-fire seedling recruitment. More important to such species is the level of overstory combustion (Arseneault, 2001). Landscape patterns of canopy combustion, represented by CFSI, indicate that much of the area burned was of moderate severity (45 %), and it was rare for severely combusted stands ($CFSI > 4$) to be especially large, or to have core areas > 600 m from lower severity burned stands, suggesting that lower densities of recruitment of serotinous species will occur only in small patches. Patterns of seed bed availability and bud-bank persistence, as characterized by BSI, are also different from the landscape pattern of stand-replacing fire derived from the overstory mortality model. Given the importance of seedbeds to interspecific competition among seedlings in the boreal region (Johnstone & Chapin III, 2006), the presence of both substantial areas with remaining organic soils in peatlands as well as exposed mineral soils in uplands suggests a potentially less severe ecological outcome of burn severity that is relevant to conifer seedling recruitment (Kemball et al., 2006). The observed differences in

landscape patterns of burn severity depending on the modeled metric of choice will lead to different conclusions about relative levels of burn severity and potential ecological impacts from fires, and thus, it is important to select meaningful burn severity metrics for the local fire regime when modeling spatial patterns of burn severity.

2.5.3 Vegetation, topoedaphic, and weather drivers of burn severity

The patterns of burn severity within the six wildfires are largely explained by a combination of fuels, topoedaphic context (uplands and wetlands), and fire weather, leading us to accept our hypothesis H3_a. Previous studies have demonstrated the importance of land cover and forest type to fire frequency (Cumming, 2001) and burn severity both in this ecosystem and others (Boucher et al., 2016; Collins et al., 2007; Hall et al., 2008). Our results provide further insight into the importance of stand structural and fuel loading characteristics of vegetation in driving these differences. Severity increased with stem density and median conifer CBH and decreased with increasing BA of mature trees. The effect of overstory and understory stem density on burn severity observed here is consistent with that observed in studies examining burn severity following prescribed fire and fuel treatments in the western United States; however, the same effect of pre-fire BA was not observed in this region (Lydersen et al., 2017; Prichard & Kennedy, 2014). The measured differences in burn severity reflect the crowning and rate of spread potential of different fuel complexes (FCFDG, 1992), suggesting that the burn severity of fires in the northwestern boreal forest may be largely due to the direct influence of stand structure on fire behavior. As burn severity was substantially explained by vegetation communities and their associated characteristics, the role of land cover in producing landscape patterns of burn severity should be controlled for when using remote sensing to monitor landscape patterns of burn severity (Collins & Stephens, 2010), and trends in burn severity over time and across fires in the northwestern boreal forest. The inclusion of pre-fire vegetation and topographic variables in addition to remotely sensed severity metrics may improve estimates of burn severity and combustion by incorporating variability in drivers of severity (Barrett et al., 2010).

Detailed data about stand structure and topoedaphic context were necessary to produce robust predictions of severity. Others have found that topographic variables are

important, and even dominant, drivers of burn severity (Dillon et al., 2011). In this study, wetlands consistently burned at lower severities than uplands. Site moisture likely plays a role in this effect, but wetlands also had significantly lower pre-fire overstory fuel loads and BA of trees than uplands, as is common in this region (Thompson et al., 2017). The surface burn severity-limiting effect of wetlands decreased with increasing stem density, in a gradient of increasing burn severity from open to increasingly well-stocked treed wetlands. The effect of estimated pre-fire live CBH on severity was counter to that expected, given the documented role of ladder fuels in conducting surface fires into the canopy and enabling transitions from surface to crown fire (Agee & Skinner, 2005). This evidently conflated effect is explained by the wide range of vegetation communities sampled. Although lower CBHs are associated with severe fire behavior in densely stocked stands, in our dataset the lowest CBHs were in poorly stocked wetlands and mixedwood stands with suppressed, shade-tolerant coniferous understories—ecosystems that burned at lower severity.

Burn severity of a site is highly related to pre-fire, bottom-up drivers, such as fuels and topography, but weather conditions may override or shift this relationship, leading to variability in observed burn severity (Birch et al., 2015; Harvey et al., 2014; Krawchuk et al., 2016). A fire weather variable describing long-term drying and surface combustion potential (BUI; Van Wagner, 1987) tempered the importance of stand structural effects on surface burn severity under more extreme fire weather in our model of BSI, but was not important in the other prognostic burn severity models. The very severe fire weather in 2014 may explain the relatively low importance of weather in determining overstory burn severity in this study. Of the 51 sampled field sites, only six burned under weather conditions with a DC of 300 or less, whereas the majority of sites burned under weather conditions with a DC of 500 or higher, indicating extreme long-term drying in deep layers of the soil (Amiro et al., 2004). Fire weather is important to wildfire occurrence and burn severity, but the restricted range of variability in weather in this study likely reduced predictive power gained from weather variables (Krawchuk et al., 2016; Parks et al., 2015; Stocks et al., 2004). This may also reflect the potentially weather-limited nature of the boreal forest fire regime, where fire occurrence is highly weather-dependent and

episodic (Meyn et al., 2007; Podur & Martell, 2009). The lack of variability in weather conditions prevented us from observing an overwhelming effect of fire weather on bottom-up controls on fire activity, leading us to reject our hypothesis H3_b, as we were predominantly able to detect an effect of bottom-up controls on burn severity.

Although pre-fire stand structure, composition, and topoedaphic context have a role in determining burn severity in this region (Ferster et al., 2016; Hall et al., 2008), there is still substantial variability in observed severity. A typical median level of burn severity is apparent within individual vegetation communities, but measured burn severity was quite variable, with some communities capable of burning at particularly broad ranges of severity. For example, there is substantial evidence for surface and mixed-severity fire in mixedwood and mature jack pine stands; a distinct and potentially underemphasized component of the local fire regime. The observed ranges around characteristic levels of severity for each vegetation community may be a product of pre-fire variability in stand structure and composition, and the inhibiting effect of fire weather on the influence of fuels on burn severity.

Given the importance of pre-fire stand structure and composition to burn severity outcomes, levels of burn severity falling outside of those expected for a certain stand structure and changes to both spatial and temporal patterns of fire occurrence may produce unexpected and persistent ecological outcomes from wildfires (Brown & Johnstone, 2012; Freeman & Kobziar, 2011). For example, some of the measured sites experienced very short-interval high-severity reburning (10 yr between stand-replacing fires), despite the substantially reduced fuel load from the previous fire. These sites had extremely low densities of any species of seedlings, a characteristic that will likely carry forward in time (Johnstone et al., 2004), potentially causing a shift away from the dense conifer forest previously found at the site. Although time since last fire and time since stand origin did not significantly contribute to the multivariable models, they were nearly significant in some cases (e.g., $p = 0.06$ MORT model). Our results do not support a clear relationship between stand age and field measurements of burn severity, but the other variables selected in the models are partially products of stand age and may simply relate more directly to burn severity outcomes (fuel load; Thompson et al., 2017).

2.5.4 Management implications

Remotely sensed multispectral burn severity was meaningfully related to diverse field measurements of overstory and understory burn severity in the northwestern boreal study area. Managers can use existing field datasets (where available) to build region-specific models and calibrate remotely sensed severity metrics. Predicting values of diverse post-fire burn severity metrics that are tailored to specific management objectives (e.g., estimating post-fire recruitment, erosion risk, planning salvage logging, assessing prescribed burning outcomes) adds value and facility of use to these products, and recognizes the different relationships between remotely sensed burn severity metrics and overstory, understory, and mortality impacts from fire. Multispectral burn severity metrics can provide significant and rapidly available ecological information about wildfire effects in northern forests, where access for field visits is limited or expensive.

Burn severity was explained by topoedaphic context (uplands and wetlands), pre-fire stand structure and composition (vegetation communities), and fire weather. Fire managers can use this information to make rapid estimates of severity to inform management decisions about active fires where burn severity and ecological impacts are an important consideration or intended outcome, before remote sensing data are available. For example, in a vegetation community not characterized by high-severity fire, which may be a biologically relevant fire refugia, the selective burning of unburned areas for fire control (i.e., burnouts) could be avoided. Where vegetation tends to naturally burn severely, suppression efforts may be of limited effectiveness and also ecologically undesirable, and thus, suppression resources could be redirected elsewhere, if safe to do so. This understanding of the characteristic ranges of severity in different vegetation communities could also be used in combination with modeled values of burn severity field metrics to identify areas that have burned outside of expected characteristic levels of severity, and where interventions may be necessary to manage atypical ecological impacts, for example, in severely burned stands that previously experienced recurrent low-intensity surface fires or in even-aged stands reburning at very short fire return intervals.

In variable-retention forestry, it is common to intentionally leave some residual stands and trees unharvested to act as biological legacies, provide habitat, and maintain forest diversity (Gustafsson et al., 2012). In the Canadian boreal forest, this strategy often aims to replicate patterns and outcomes of wildfire, in an attempt to emulate natural disturbance (Bergeron et al., 2002; Long, 2009). In light of these results, where foresters wish to mimic natural patterns of wildfires when harvesting by leaving residual forested areas and individual trees, it is valuable to understand that partial mortality and unburned residuals within the studied natural fires were not random, but instead were associated with certain vegetation communities (Upland Jack Pine and Upland Mixedwood) and stand structures (mature, open stands, with high BAs) that enabled surface fires and low-intensity burning. Such sites may represent old-growth fire refugia, within a predominantly high-intensity stand-replacing fire regime. The landscape patterns produced by retention areas will differ from those produced by natural wildfires if they are not located and planned in a manner that considers the causes and probability of natural residuals (Dragotescu & Kneeshaw, 2012).

2.5.5 Limitations and future research

Although we were successful in producing prognostic and diagnostic models of burn severity, there are some limitations to the conclusions that can be drawn. The NARR data product used for fire weather was downscaled significantly from its original resolution. This product also integrates modeled precipitation over northern North America, rather than observed precipitation (Mesinger et al., 2006). Although these limitations may have reduced the importance of fire weather in the explanatory models of burn severity, the low weather station density in northern Canada justified this choice. A larger sample of sites, or sampling in fires that burned in other, non-drought, years may be required to better characterize the influence of fire weather on burn severity in the study area. The multispectral images used to produce remotely sensed burn severity in this study were predominantly from satellite overpasses early in the growing season. Although spring and early summer imagery may over-estimate burn severity, the lack of cloud and smoke-free images in later seasons and years necessitated the choice of these images. The multivariable explanatory models of burn severity did not directly consider topography or elevation, which are known bottom-up controls of wildfire spread and severity (Birch et

al., 2015; Krawchuk et al., 2016). The landscape of the study area is primarily composed of gently rolling plains; however, more subtle topography such as transition zones between wetlands and uplands may still have affected burn severity in ways that are not captured in these models. Finally, the pre-fire stand structural characteristics of understory stem density and live conifer CBH were measured in the year after fire. There is a possibility that understory trees and lower branches were fully consumed and thus not measured, thereby leading to underestimates of understory density and overestimates of CBH, but this type of error is likely minimal. Even in the most severe burns, we were able to distinguish remaining stems of consumed saplings, and it is generally possible to determine whether branches were alive or dead prior to a fire's arrival due to the persistence of bark and less deep charring on live wood.

Future research in the northwestern boreal forest could include explanatory spatial models of burn severity, representing the in-stand (patch- and plot-level) drivers of burn severity identified here with mapped fuels, topography, and weather, potentially improving predictive ability across the diverse boreal landscape. The inclusion of additional fires for spatial analysis of landscape patterns of burn severity in the northwestern boreal forest would provide a more robust dataset and would permit a broader characterization of typical patterns of burn severity across fire sizes and between fires in this region. In addition, future research into drivers of burn severity using structural data from paired pre-fire and post-fire sample plots could more robustly characterize these relationships than is possible with the parameters collected post-fire in this study.

2.6 Conclusion

Overstory and surface burn severity in the northwestern Canadian boreal forest was significantly explained by the multispectral remotely sensed metrics of burn severity, in an ecologically diverse sample of burned sites. Burn severity metrics that were relativized to pre-fire conditions (RdNBR, RBR) were more related to observed burn severity than non-relativized metrics (dNBR). Burn severity was adequately predicted by pre-fire

forest characteristics of stand structure, fuel load, species composition, and topoedaphic context. Although fire weather was also related to observed burn severity, this was only significant in determining surface burn severity and we did not observe an overwhelming effect of extreme fire weather on bottom-up drivers of burn severity, despite the drought-driven nature of the sampled fires. Differences in stand structure and fuel loading translated to different characteristic levels of burn severity within vegetation communities, which explains in part why there can be considerable variation in the degree of burn severity within northwestern boreal forest wildfires. This variability influenced the range and landscape patterns of burn severity observed, despite the dominance of stand-replacing crown fire in this ecosystem. High- and moderate-severity burned patches were large, simple in form, and made up the majority of area burned, whereas low-severity burned patches were small and complex. Despite these general trends, landscape patterns of burn severity differed depending on the modeled field metric of burn severity assessed, and conclusions about characteristic spatial arrangement and overall “severity” of landscapes were not transferrable between burn severity field metrics.

Differences in severity observed between uplands and wetlands and the influence of stand structure and composition on burn severity in this study highlight the importance of considering wetlands, and all major vegetation communities, when attempting to capture the range of burn severity. The strong association between land cover and post-fire burn severity should be controlled for when using remote sensing to monitor landscape patterns and trends in burn severity over time, and across multiple fires. The prognostic models built using continuous stand structural variables demonstrate that burn severity in the northwestern boreal forest is predictable and characteristic of different ecotypes. Relationships between remotely sensed burn severity and ground observations of severity in this region allow forest and fire managers to address refined management goals, such as the estimation and management of post-fire recruitment, assessment of prescribed burning outcomes, post-fire erosion control, salvage logging planning, and assessment of wildfire effects on habitat for wildlife. The influence of pre-fire variables on burn severity could also be incorporated into forest harvesting, and prescribed and active fire management by choosing to leave residuals where they may naturally occur, preserving

probable fire refugia. The relationships between burn severity, and pre-fire drivers and fire weather presented here offer potential areas for future exploration to improve spatial modeling of burn severity and the scaling of these effects from in-stand to landscape levels.

2.7 Acknowledgments

This research was funded by the Natural Sciences and Engineering Research Council of Canada (Funding Reference Number: CGSD3-471480-2015) and the Government of the Northwest Territories. Parks Canada Agency and Jean Morin provided in-kind support. We thank Xinli Cai, G. Matt Davies, Kathleen Groenewegen, Derek Hall, Koreen Millard, and Doug Stiff for assistance in the field. We also acknowledge Xianli Wang and Sean A. Parks for their assistance with fire progression mapping. Scott E. Nielsen and two anonymous reviewers provided helpful feedback and comments on earlier versions of this manuscript, and greatly improved this work.

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3 Topoedaphic and forest controls on post-fire vegetation assemblies are modified by fire history and burn severity in the northwestern Canadian boreal forest

Ellen Whitman, Marc-André Parisien, Dan K. Thompson, and Mike D. Flannigan

3.1 Abstract

Wildfires, which constitute the most extensive natural disturbance of the boreal biome, produce a broad range of ecological impacts to vegetation and soils that may influence post-fire vegetation assemblies and seedling recruitment. We inventoried post-fire understory vascular plant communities and tree seedling recruitment in the northwestern Canadian boreal forest and characterized the relative importance of fire effects and fire history, as well as non-fire drivers (i.e., the topoedaphic context and climate), to post-fire vegetation assemblies. Topoedaphic context, pre-fire forest structure and composition, and climate primarily controlled the understory plant communities and shifts in the ranked dominance of tree species (**8 % and **13 % of variance explained, respectively); however, fire and fire-affected soils were significant secondary drivers of post-fire vegetation. Wildfire had a significant indirect effect on understory vegetation communities through post-fire soil properties (**5 %), and fire history and burn severity explained the dominance shifts of tree species (*7 %). Fire-related variables were important explanatory variables in classification and regression tree models explaining the dominance shifts of four tree species ($R^2 = 0.43\text{--}0.65$). The dominance of jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) increased following fires, whereas that of black spruce (*Picea mariana* (Mill.) BSP.) and white spruce (*Picea glauca* (Moench) Voss) declined. The overriding importance of site and climate to post-fire vegetation assemblies may confer some resilience to disturbed forests; however, if projected increases in fire activity in the northwestern boreal forest are borne out, secondary pathways of burn severity, fire frequency, and fire effects on soils are likely to accelerate ongoing climate-driven shifts in species compositions.

3.2 Introduction

Wildfires are the most extensive stand-initiating disturbance in the northwestern Canadian boreal forest, typically recurring every 50–100 years (Heinselman, 1981; Weber & Stocks, 1998). When wildfires occur, they burn with varying intensities (energy release) in response to fire weather, topography, and fuel type, producing a range of burn severities. Burn severity is defined as the ecological impacts of fire on vegetation and soils (Keeley, 2009; Morgan et al., 2014). Many boreal forest plants have adapted to repeated wildfires through traits such as resprouting or suckering, seed banking, or, in the case of some tree species, serotiny. Serotinous and semi-serotinous conifer tree species have cones that may open in response to and survive some heating, and retain some viable seeds in the canopy following wildfires. Through this mechanism, serotinous species can produce extensive seed rains from aerial seedbanks immediately following fire (Weber & Stocks, 1998; Whittle et al., 1997). Wildfire burn severity has important implications for post-fire understory vegetation communities and recruitment of seedlings. Heating and combustion from wildfires kill some trees and may reduce the viability of seeds in aerial seedbanks (including those of serotinous species) beyond a threshold of fire intensity or if the duration of heating is extensive (Alexander & Cruz, 2012; Knapp & Anderson, 1980). Variable combustion of organic soils provides diverse seedbeds for plants and trees, ranging from thick remnant organic layers to exposed mineral soils, and alters the composition and exposure of post-fire soil seed banks (Greene et al., 2005; Lee, 2004). Some burning of organic soils promotes vegetative regeneration, but deep burning may damage roots and rhizomes, negatively affecting the capacity of resprouting species to regenerate following fires (Whittle et al., 1997).

In many ecosystems, burn severity is a dominant and enduring control on post-fire understory vegetation assemblies (Lentile et al., 2007; Schimmel & Granström, 1996; Turner et al., 1999) and seedling recruitment (Chambers et al., 2016; Shenoy et al., 2011; Turner et al., 1999), influencing the resulting structure and composition of forests. Although burned sites in the boreal forest generally return to a mature forested stand structure within 100 years (Bartels et al., 2016), researchers using remote sensing to examine the post-fire recovery of vegetation following wildfires have found different rates of revegetation amongst burn severity classes. Severely burned sites demonstrated

the highest decline in vegetation immediately post-fire (Epting & Verbyla, 2005; Jin et al., 2012). In the years following a wildfire, severely burned sites subsequently experienced the largest increases in vegetation, indicating either forest recovery or colonization of these sites by disturbance-favouring plants and trees (Epting & Verbyla, 2005; Jin et al., 2012). In North American boreal forests, post-fire understory vegetation communities in black spruce (*Picea mariana* (Mill.) BSP.) (Gibson et al., 2016), jack pine (*Pinus banksiana* Lamb.) (Pinno & Errington, 2016), and mixed broadleaf and coniferous stands (Wang & Kemball, 2005) are influenced by surface burn severity and depth of burn, in conjunction with the availability of seed sources and vegetative propagules. In these studies, colonizing species such as graminoids and annual forbs established themselves broadly in severely burned areas, whereas slow-growing lichens, evergreen shrubs, and higher species richness were more prominent in low severity and scorched areas (Gibson et al., 2016; Pinno et al., 2013; Wang & Kemball, 2005). Lower densities of recruitment of coniferous trees have been observed when sites burned severely and at short intervals (Arseneault, 2001; Pinno et al., 2013), and increased proportions of early-successional tree species, such as jack pine and trembling aspen (*Populus tremuloides* Michx.) are associated with high severity burning (Johnstone & Kasischke, 2005; Lavoie & Sirois, 1998). The relative dominance of different species of trees and the density of post-fire forests are lasting legacies of boreal wildfire severity (Arseneault, 2001; Johnstone et al., 2004; Johnstone & Kasischke, 2005).

When burn severity is studied at a broader landscape scale, that is, across multiple forest types and wildfires, the effects of burn severity on post-fire vegetation communities and recruitment may be challenging to detect. Burn severity is correlated to pre-fire forest type and stand structure (Collins & Stephens, 2010; Greene et al., 2005; Lydersen et al., 2017; Whitman et al., 2018), potentially obscuring or explaining observed effects of burn severity on post-fire plants and trees. Studies of burn severity that encompass multiple forest types have identified topoedaphic and pre-fire forest conditions as the primary post-fire drivers of understory plant communities and site suitability for tree species (Boiffin et al., 2015; Day et al., 2017; Fourrier et al., 2015; Gibson et al., 2016; Turner et al., 1997), leading some researchers to characterize burn severity as a secondary “filtering” effect beneath the dominant landscape and climatological controls.

Ranges of burn severity and the relatively infrequent occurrence of large wildfires (≥ 200 ha) produce a mosaic of stand ages and patterns on the landscape, in regions with mixed- and high-severity fire regimes (Erni et al., 2016; Stocks et al., 2002; Turner & Romme, 1994). Wildfires interact with past burns, as previous fires and burn severity determine current fuels. Abnormally short fire frequencies are implicated in the dominance shifts of tree species (Johnstone & Chapin III, 2006), low stocking in post-fire forests (Pinno et al., 2013), and even near-deforestation (Brown & Johnstone, 2012), with implications for forest resilience (Johnstone et al., 2016). Furthermore, burn severity interacts with fire frequency, potentially reinforcing vegetation type conversions (Coop et al., 2016). Wildfires are a weather and, therefore, climate-driven disturbance. Fires are expected to increase in size, frequency, and intensity (and therefore in severity) (Wang et al., 2017; Wotton et al., 2017; Wotton et al., 2010) in North America as the climate warms and severe fire weather increases (Wang et al., 2015). The forests of the Canadian Northwest Territories provide an interesting opportunity to study the effects of extensive free-burning wildfires in an ecosystem with multiple dominant coniferous and broadleaf tree species, across a moisture gradient ranging from hydric to xeric. Given the ecologically important role and actively changing patterns of fire in the boreal forest, studies characterizing the relative importance of fire effects and fire history, and non-fire and climate drivers in determining post-fire vegetation assemblies and species composition shifts will provide insights into the trajectories of future forests.

This study describes post-fire vegetation communities and seedling recruitment across a broad range of topoedaphic vegetation classes and levels of burn severity, to identify direct and indirect drivers of these assemblies in the northwestern Canadian boreal forest. In support of this goal, our objectives were: 1. To characterize post-fire vegetation assemblies and recruitment of seedlings across burn severity and topoedaphic gradients; 2. To assess the relative importance of climate and pre-fire forests, burn severity and fire history, and post-fire soils to understory vegetation communities and shifts in the dominance of tree species; and 3. To identify direct and indirect effects of fires on post-fire vegetation, as well as drivers of shifts in the dominance of tree species in the post-fire cohort.

3.3 Methods

3.3.1 Study area

Field sites were established in six, large, lightning-caused wildfires (14,000 to 700,000 ha) that burned in 2014 (Fig. 3.1). The year of 2014 was an extreme fire season in the northwestern Canadian boreal forest region, with drought-driven wildfires burning a total area > 3 million ha (Northwest Territories Environment and Natural Resources, 2015). The sampled fires burned in the Northwest Territories and Wood Buffalo National Park. The fire regime of this area is one of infrequent stand-initiating wildfires (Boulanger et al., 2012; Johnson, 1992). In the Canadian boreal forest, these large wildfires comprise a small fraction of the total number of fires, but they are responsible for the vast majority of the area that was burned (Stocks et al., 2002).

The study area experiences long cold winters and short hot summers. Mean annual temperatures at the field sites ranged from -4.3°C at the furthest north site to -1.8°C at the furthest south (Ecological Stratification Working Group (ESWG), 1995; Wang et al., 2012). Topography of the study area is minimal, consisting of level terrain in the southwestern part of the study area, on the boreal plain, and rolling granitic hills on the boreal shield in the northeast (Wotton et al., 2010). The forests of the study area are dominated by jack pine, black spruce, white spruce (*Picea glauca* (Moench) Voss), and trembling aspen. Important secondary tree species include eastern larch (*Larix laricina* (Du Roi) K. Koch), paper birch (*Betula papyrifera* Marsh.), and balsam poplar (*Populus balsamifera* L.) (ESWG, 1995). There is also a substantial wetland (chiefly peatlands) component to the region. Peat-forming wetlands may form extensive complexes and cover approximately a third of the total area (Tarnocai et al., 2011). Although the study area falls within the discontinuous permafrost zone of Canada (Natural Resources Canada (NRCan), 1993), no field sites had frozen active layers in the top metre of soil.

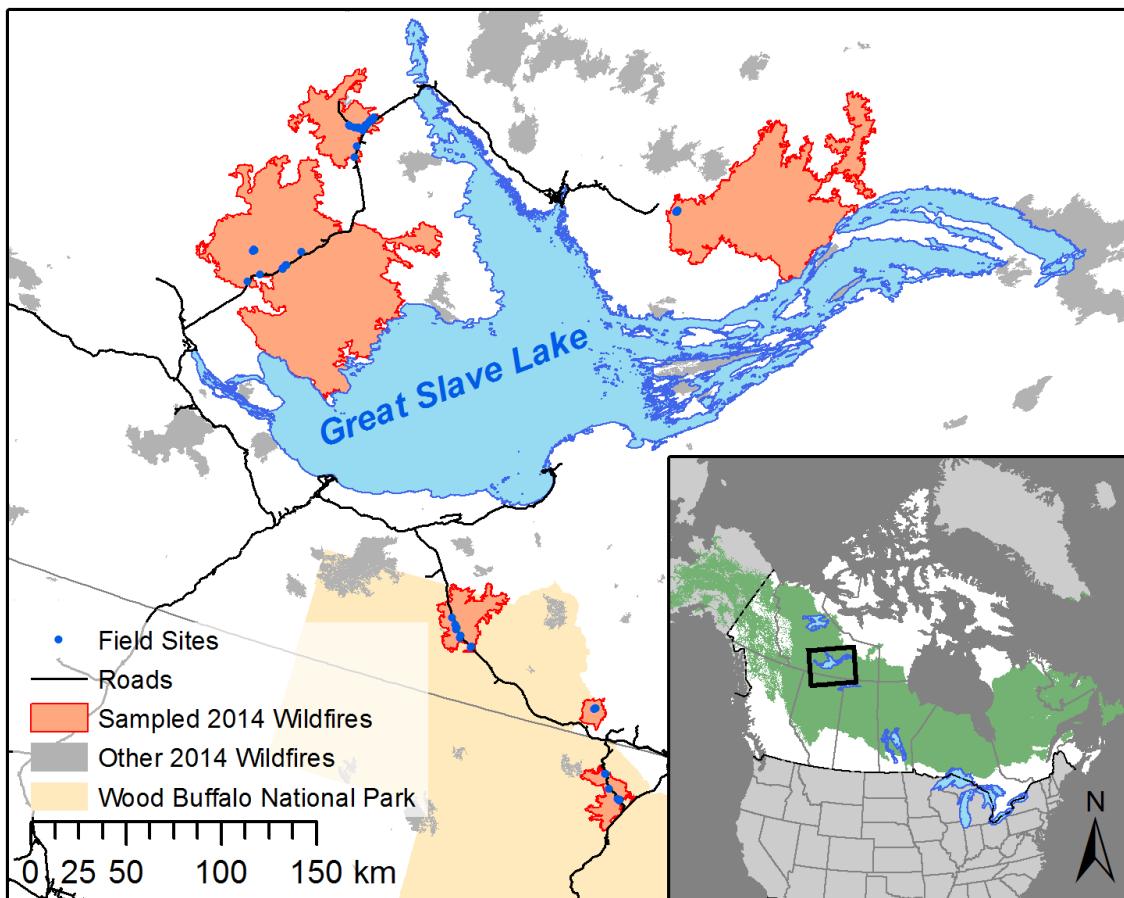


Figure 3.1 The sampled 2014 wildfires and field site locations in the Northwest Territories and Wood Buffalo National Park. The study area is indicated in black on the inset map, within the context of the North American boreal forest (shown in green) (Brandt, 2009).

3.3.2 Field methods

We sampled 51 field sites one year post-fire and resampled 30 sites three years post-fire. The sites were selected using a stratified random sample that was evenly distributed across high-, moderate-, and low-burn severity classes. The mapped burn severity was produced using an initial assessment of a differenced normalized burn ratio (dNBR) image (Key & Benson, 2006), classified with thresholds developed by Hall et al. (2008). Field sites were > 100 m and ≤ 2 km from roads. More isolated sites were also opportunistically accessed by helicopter. The field sites accessed by helicopter were located in order to capture the locally available range of burn severity and topoedaphic vegetation communities (ecosites), ensuring that each sampled site offered a distinct combination of severity and vegetation type. Field sites were positioned in an area of

homogenous burn severity, topoedaphic setting (upland or wetland), and dominant vegetation that extended ≥ 60 m in any direction. The site moisture (from hydric to xeric) and ecosite categories were classified according to Beckingham and Archibald (1996). Ecosites were generalized into the dominant topoedaphic vegetation classes of open wetland, treed wetland, upland spruce, upland mixedwood, and upland jack pine (from wettest to driest). All the sampled wetlands were peat-forming wetlands (peatlands). Plot centres were recorded with a differential GPS unit. The mean distance between the plot centres of all the field sites was 170 km, with a minimum distance of 103 m.

When sampling one year after the fire, the sample plots were 30×30 m, with two 30-m transects oriented in the cardinal directions, crossing at the plot centre. A detailed figure of the plot layouts used for field sampling is included in Appendix B: Fig. B1.

Compositions of tree species, percent overstory mortality due to fire, stem density (stems ha^{-1}), and basal area ($\text{m}^2 \text{ ha}^{-1}$) of mature trees in the pre-fire stand were measured at this time for 32 trees ≥ 3 cm diameter at breast height (DBH) using the point-centered quarter method (Cottam et al., 1953; Mitchell, 2015) at eight evenly-spaced points along the two transects. In very low stem-density areas (i.e., open wetlands), a variable-radius circle plot with a minimum radius of 15 m was used to sample overstory trees. Pre-fire understory stem densities of seedlings and saplings (stems ha^{-1}) were measured using 3-m radius plots at the endpoints of each transect. The number of understory density plots sampled ranged from one to four, depending on the density and evenness of the seedling and saplings.

We collected basal sections from fire-scarred trees to determine the time since the stand origin (TSO) and time since the last fire (TSLF) at each plot. If no scarred trees were identified nearby, a section of a mature dominant tree was sampled. Some open wetlands (fens) had no trees. Samples were sanded and digitally scanned, and annual growth rings and fire scars were dated in CooRecorder (Cybis Elektronik & Data AB, 2013).

Burn severity was measured in 10×10 m subplots at the four corners of each plot. Surface burn severity was measured using the surface Burn Severity Index (BSI; Loboda et al., 2013). BSI values range from zero (unburned) to four (ash, mineral soil exposed) using classes defined by Dyrness and Norum (1983). Overstory burn severity was

measured using the Canopy Fire Severity Index (CFSI; Kasischke et al., 2000). CFSI classes range from zero (no tree mortality) to six (no primary branches remaining, pole charring occurred). The percent cover of each BSI and CFSI severity class was estimated within the four subplots, and final values of the two severity metrics were calculated using area-weighted means of each class value, and then averaged for each field site.

We measured the post-fire organic soil depth (cm; up to a maximum of 10 cm) at the inner corners of the same subplots used for estimates of severity and seedling density. The soil cores (13.5 cm in depth, 5.5 cm in diameter) were taken one year post-fire at the plot centre and inner corners of the southwest and northeast subplots, as well as at a complementary set of neighbouring unburned control sites ($n = 12$) representing unburned examples of all sampled vegetation communities. Cores were inserted to a minimum depth of 8.5 cm and the soil samples were separated into organic and mineral horizons; the three samples from each site were pooled by the horizon. If mineral soil was not present in the top 13.5 cm of the soil profile, it was not collected. Soils were oven-dried and the physicochemical properties of both organic and mineral samples were measured in the lab. These properties were: pH, electrical conductivity (EC; mS cm^{-1}), percent total nitrogen (N), percent total carbon (C) measured by loss on ignition, calcium (Ca; mg kg^{-1}), potassium (K; mg kg^{-1}), magnesium (Mg; mg kg^{-1}), and sodium (Na; mg kg^{-1}). The percentages of sand, silt, and clay in mineral soils were also measured. Measurements from the two pooled horizons from each site were combined using sums weighted by the mean proportion of the core occupied by each horizon.

Estimates of percentage cover of understory vascular plant species were made one year post-fire in five 1×1 m plots per field site. Vegetation plots were located at the plot centre and at the inner corners of subplots. Species were identified according to Moss (1994) and Cody (2000), and the estimated percentage cover for each species was summed across the five plots and scaled to sum to 100 %. *Carex* spp. and *Salix* spp. were distinguished for counts of species richness but were not identified beyond genus for ordination or indicator species analyses (vegetation analysis explained in detail in Section 2.3).

The density of seedling recruitment was measured one year post-fire (2015), and subsequently re-measured three years post-fire (2017) in 30 forested sites (excluding open wetlands). Initial measures of seedling density were made in the 10×10 m subplots in 2015. In 2017, seedling density was re-measured using a 2-m wide 35-m long belt transect that was oriented north-south, crossing the original plot centre at 17.5 m. Belt-transect length varied by seedling and sapling size classes. Seedlings that were 0–10 cm were counted for the first 10 m of the transect (area 20 m^2) and seedlings that were 10–50 cm were counted for the first 20 m (area 40 m^2). Seedlings > 50 cm and saplings (live trees > 1.33 m with a DBH < 3 cm) were counted for the entire transect length. In cases of very uneven seedling density, transects of all size classes were extended to better represent the actual composition and density. This set of resampled sites excluded non-forested open wetlands ($n = 11$) and inaccessible sites (no helicopter or road access, $n = 7$). A further three sites were abandoned due to subsequent disturbances. The two datasets were combined and the latest available seedling density measurement for each site was used.

We calculated site climatic variables that described the average heat load and moisture stress from 30-year normals (1981–2010) of PRISM climate data (Daly et al., 2002) downscaled to local elevation (NRCan, 2016) using bilinear interpolation and elevation adjustment in ClimateWNA (Wang et al., 2012). The climatic moisture deficit (CMD; mm) was calculated as the sum of the monthly difference between Hargrave's atmospheric evaporative demand and monthly precipitation. Annual heat-to-moisture index (AHM) was calculated as the scaled ratio of mean annual temperature and mean annual precipitation (Wang et al., 2012).

3.3.3 Analysis

All statistical analyses were conducted in R (R Core Team, 2018). The variance of burn severity explained by the topoedaphic vegetation classes was assessed using a linear mixed-effects model with a random term of the fire name, fitted in the lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017) packages. We examined all model residuals and found them to be normally distributed. The statistical significance of fixed effects was estimated using an analysis of variance (ANOVA) with Type II sums of squares and

a Satterthwaite approximation of degrees of freedom (Luke, 2017). We conducted post-hoc comparisons of least-squares means with a Tukey test for multiple comparisons in the lsmeans package (Lenth, 2016). Species richness and Shannon diversity index of understory vascular plant communities of each site were calculated in the vegan package (Oksanen et al., 2017). Bray-Curtis dissimilarities between understory vegetation communities were ordinated using non-metric multidimensional scaling (NMDS). We fitted vectors of environmental variables to the NMDS axes and assessed the goodness of fit (R^2) of these relationships also using vegan (Table 3.1). Indicator species for each topoedaphic vegetation class were identified from understory vascular plant assemblies using 1000 permutations of a multi-level pattern analysis in the indicspecies package (De Caceres & Legendre, 2009). We assessed the influence of burn severity on soil properties when controlling for topoedaphic vegetation class (as a proxy for pre-fire site conditions) using an ANOVA of multivariable linear mixed-effects models with a random term of the fire name. Once again, model residuals were examined for normality. We employed Type II sums of squares where interactions between independent variables were not significant. We applied a Type III ANOVA if there were significant interactions between independent variables. The same approach was used to assess the influence of burn severity, TSLF, and topoedaphic vegetation class (pre-fire conditions) on the Shannon diversity index and seedling density. We used comparisons of least-squares means with a Tukey test for multiple comparisons to assess significant differences in species dominance shifts and seedling density between different topoedaphic vegetation classes.

Differences in the pre-fire and post-fire cohorts of trees were examined using compositional data. Overstory basal areas and total (understory and overstory) stem densities of each dominant tree species were converted to proportions relative to the absolute basal area and stem density for each site. Seedling counts were also converted to proportions by species, and these proportions, or compositions, were transformed with a centred log-ratio using the compositions package (van den Boogaart et al., 2014). We then used paired *t*-tests to identify statistical differences in the pre-fire and post-fire composition of trees, by species. We compared the natural logarithm (\log_e) of seedling density in sites that experienced very short fire return intervals to that of sites experiencing more typical fire return intervals with a Wilcoxon signed-rank test.

Significant differences in \log_e seedling density between topoedaphic vegetation classes were also tested using a Tukey test of least-squares means.

To examine shifts in the relative importance or dominance of tree species we calculated fractional ranks of pre-fire overstory tree species proportions of jack pine, white spruce, black spruce, trembling aspen, and all other tree species combined, by basal area. The most prevalent species received a rank of 1 and the least dominant (or absent) species received a rank of 5. In the case of ties, ranks were split between species, so that total rank values always summed to 15. We chose to use the pre-fire basal area rather than the number of stems as a measure of dominance as we felt that stem density did not adequately capture the potential fecundity and relative importance of less-common but large trees in mixedwood stands (e.g., white spruce). Because the basal area of trees established after fire represents only a small fraction of the pre-fire measure, post-fire tree species proportions were assigned fractional ranks by seedling stem density. The pre- and post-fire fractional rank scores of each species at each site were differenced to characterize shifts in tree species dominance in the post-fire cohort, producing a matrix of shifts in ranked dominance for each species by site. Rank shifts of near-zero indicated minimal change in the species' prevalence in the post-fire cohort, whereas negative values indicated a decrease and positive values indicated an increase in ranked dominance. Rank shift data had a theoretical range of -4 to 4. Analyses using the shift in rank dominance data were only performed for the four dominant tree species, excluding the combined "other" category. This application of fractional rank shifts characterizes the proportional change of tree species dominance relative to all tree species present in the community, rather than considering a single species at a time (as is the case with ratio data), and offers a normally distributed variable for analysis of dominance changes.

Table 3.1 Significant ($*p \leq 0.05$) explanatory environmental variables fitted to nonmetric multidimensional scaling (NMDS) of the understory vegetation community data (Fig. 3.2). Unitless variables are identified with a hyphen in the Units column.

Environmental Variable	Abbreviation	Units	Mean	Range
Basal Area	BA	$\text{m}^2 \text{ ha}^{-1}$	10.8	0.00–53.39
Burn Severity Index	BSI	-	2.39	0.54–4.00
Electrical conductivity of soil	EC	mS cm^{-1}	0.73	0.05–3.53
Organic soil depth	OSD	cm	4.7	0–10
Percentage sand in mineral soil	% Sand	%	43.9	0–95
pH	pH	-	6.29	3.21–8.12
Potassium	K	mg kg^{-1}	411.1	74.1–1148.4
Site moisture	Moisture	-	-	Xeric–Hydric
Sodium	Na	mg kg^{-1}	137.8	38.52–494.48
Time since last fire	TSLF	year^{-1}	58	9–151
Total carbon	Total C	% mass	21.9	0.61–52.8
Total nitrogen	Total N	% mass	0.81	0.18–2.66
Total stem density of overstory and understory trees	Density	stems ha^{-1}	5822	0–29,012

Subsequently, we assessed the relative importance of three groups of variables in the categories “Soils”, “Site”, and “Fire” to understory vegetation community dissimilarities and shifts in the dominance of tree species using variance partitioning. Soils were represented by post-fire soil properties, whereas Site category variables were pre-fire forests, topoedaphic context, and recent spatial climate averages. The Fire category included burn severity and fire history variables (Table 3.2). All measured and downscaled environmental variables were considered for inclusion in variance partitioning models. If the variables were highly correlated (Spearman’s $|\rho| \geq 0.7$) one explanatory variable of the pair was selected for inclusion in the model. Several highly correlated soil properties were decomposed using a principal components analysis (PCA; Table 3.2). Sites with incomplete data were removed ($n = 5$), and explanatory variables were standardized before variance partitioning. The significance ($\alpha = 0.05$) of the unique variation explained by each group of environmental drivers (Soils, Site, and Fire) was tested using distance-based redundancy analysis, also in the vegan package.

Finally, we fit explanatory classification and regression trees (CARTs) to shifts in the ranked dominance of each tree species derived from ranked proportions of the pre-fire basal area and post-fire stem density, using the tree package (Ripley, 2016). The

regression trees were constrained by requiring a minimum of five field sites per node, and a minimum within-node deviance of 0.05. We intentionally excluded pre-fire basal area and stem density of any tree species as regression tree predictor variables in order to learn about secondary climatic, soil, and burn severity effects on the dominance shifts of tree species. The same suite of environmental, burn severity and fire history, and climate variables were included as potential predictors of shifts in tree species dominance for each species' CART model (Table 3.3).

Table 3.2 Environmental variables incorporated in the explanatory variance partitioning of understory vegetation community dissimilarities and shifts in tree species dominance. Correlated soil properties collapsed with a principal components analysis for inclusion in variance partitioning are indicated with a [†]. Unitless variables are identified with a hyphen in the Units column.

Environmental Variable	Units	Mean	Range	Variance Partitioning Category
Calcium [†]	mg kg ⁻¹	13,648.6	217.1–60,815.4	Soils
Electrical conductivity [†]	mS cm ⁻¹	0.73	0.05–3.53	Soils
Magnesium [†]	mg kg ⁻¹	1461.9	22.0–5191.3	Soils
Percentage sand in mineral soil	% mass	44	0–95	Soils
Percentage silt in mineral soil	% mass	14	0–51	Soils
pH	-	6.29	3.21–8.12	Soils
Potassium [†]	mg kg ⁻¹	411.1	74.1–1148.4	Soils
Sodium [†]	mg kg ⁻¹	137.8	38.5–494.5	Soils
Total carbon [†]	% mass	21.9	0.61–52.8	Soils
Total nitrogen [†]	% mass	0.81	0.02–2.66	Soils
Absolute stem density of overstory and understory trees	stems ha ⁻¹	5822	0–29,012	Site
Annual Heat-Moisture Index	-	20.32	16.5–23.6	Site
Black spruce basal area	m ² ha ⁻¹	2.37	0–29.07	Site
Climatic Moisture Deficit	mm	191	171–214	Site
Jack pine basal area	m ² ha ⁻¹	5.61	0–51.38	Site
Site moisture	-	-	Xeric–Hydric	Site
Trembling aspen basal area	m ² ha ⁻¹	0.87	0–6.22	Site
Total overstory basal area	m ² ha ⁻¹	10.8	0–53.4	Site
White spruce basal area	m ² ha ⁻¹	1.55	0–36.53	Site
Burn Severity Index	-	2.38	0.54–4	Fire
Percentage overstory mortality	%	89	6–100	Fire
Post-fire organic soil depth	cm	4.7	0–10	Fire
Time since last fire	year ⁻¹	58	9–151	Fire
Time since stand origin	year ⁻¹	104	9–237	Fire

Table 3.3 Environmental, climate, burn severity, and fire history variables included in the classification and regression tree models of the dominance shifts of tree species. Unitless variables are identified with a hyphen in the Units column.

Variable	Units	Mean	Range
Annual Heat-Moisture Index	-	20.3	16.5–23.6
Burn Severity Index	-	2.38	0.54–4
Canopy Fire Severity Index	-	2.5	0–6
Climatic Moisture Deficit	mm	191	171–214
Electrical conductivity	mS cm^{-1}	0.73	0.05–3.53
Percentage overstory mortality	%	89	6–100
Percentage sand in mineral soil	%	44	0–95
pH	-	6.29	3.21–8.12
Post-fire organic soil depth	cm	4.7	0–10
Total nitrogen	%	0.81	0.02–2.66
Time since last fire	year^{-1}	58	9–151
Time since stand origin	year^{-1}	104	9–237
Wetland	-	-	Upland or Wetland

3.4 Results

A broad range of burn severity was represented in the field sites (Appendix B: Fig. B2). The BSI values of field sites ranged from 0.5 to 4, the CFSI values from 0 to 6, and percent overstory mortality ranged from 6.25% to 100% (Whitman et al., 2018). The surface (BSI) and overstory (CFSI) burn severity were statistically related to topoedaphic vegetation classes (ANOVA, *** $p < 0.001$ and * $p = 0.02$, respectively; Table 3.4), but overstory mortality was not. Post-hoc comparisons of least-squares means with a Tukey test confirmed some statistical differences in burn severity amongst topoedaphic vegetation classes for BSI (* $p \leq 0.05$; Appendix B: Fig. B2). Surface burn severity was lowest in open wetlands and highest in jack pine uplands. All other topoedaphic vegetation classes had BSI values that were similar to one of these two groups. The differences in least-squares means of CFSI between topoedaphic vegetation classes were not significant at $\alpha = 0.05$ (Appendix B: Fig. B2).

Table 3.4 Multivariable linear mixed-effects models describing surface Burn Severity Index (BSI), Canopy Fire Severity Index (CFSI), time since last fire (TSLF), topoedaphic vegetation classes (TVC), and ecological outcomes of seedling density and Shannon Diversity Index of understory vascular plant communities. The effect size (F) and significance (p) of terms are tested with Type II sums of squares where there are no significant interactions, and Type III sums of squares in the presence of a significant interaction (reported in column ANOVA SSQ). Significance of intendent variables is signified as follows: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$. We report model degrees of freedom (df), sums of squares (SSQ), and the ANOVA F statistic.

Multivariable Linear Mixed-Effects Model	ANOVA SSQ	df	Independent Variable	SSQ	F	p
BSI = TVC + (1 Fire Name)	II	4	TVC	20.39	14.94	*** < 0.001
CFSI = TVC + (1 Fire Name)	II	4	TVC	33.40	3.36	* 0.02
Diversity = TVC × BSI + (1 Fire Name)	III	4	TVC	2.51	3.09	* 0.03
		1	BSI	0.15	0.72	0.40
		4	TVC × BSI	2.64	3.26	* 0.02
Diversity = TVC × TSLF + (1 Fire Name)	III	4	TVC	2.08	2.52	0.06
		1	TSLF	0.00	0.01	0.91
		4	TVC × TSLF	2.89	3.51	* 0.02
Density = TVC + BSI + (1 Fire Name)	II	4	TVC	18.01	3.49	* 0.02
		1	BSI	5.62	4.35	* 0.04
Density = TVC + TSLF + (1 Fire Name)	II	4	TVC	43.94	7.84	*** < 0.001
		1	TSLF	0.59	1.14	0.29

The richness of the understory vascular plant species sampled at the field sites ranged from three to 20. Both understory vegetation community diversity and seedling density were statistically related to topoedaphic vegetation classes (Table 3.4; Appendix B: Fig. B2). Interactions between TSLF and topoedaphic vegetation classes, and BSI and topoedaphic vegetation classes significantly explained the variability in understory plant diversity (Type III ANOVA, * $p \leq 0.02$; Table 3.4). The density of seedlings was significantly explained by both topoedaphic vegetation classes and BSI (Type II ANOVA, * $p < 0.04$), but not by TSLF or CFSI, or by the interactions between topoedaphic vegetation classes and these two metrics (Table 3.4; Appendix B: Fig. B2). All sites with zero seedling establishment were open wetlands ($n = 7$). Of those sites that experienced some regeneration, seedlings ha⁻¹ ranged from 25 to $> 75,000$. The natural logarithm of the density of seedlings was significantly lower in open wetlands, treed wetlands, and upland spruce, and higher in upland jack pine and upland mixedwood

topoedaphic vegetation classes (comparison of least-squares means, with a Tukey test, $\alpha = 0.05$). The post-fire seedling density was statistically greater in sites that experienced > 17 years between fires (Wilcoxon signed-rank test, $*p = 0.02$).

The two-dimensional NMDS of understory vascular plant communities had a stress of 0.20 (Fig. 3.2). Similarity of understory species communities was primarily related to the physicochemical properties of the soil; however, pre-fire forest structural characteristics of basal area and absolute stem density of overstory and understory trees were also influential (Fig. 3.2). BSI was also statistically related to understory species community dissimilarity, and TSLF was nearly significant ($p = 0.052$, 999 permutations). Although soil properties were explained by topoedaphic vegetation classes; the organic soil depth, total nitrogen, total carbon, potassium, calcium, and magnesium were also statistically (Type II ANOVA; $\alpha = 0.05$) related to BSI when controlling for the effect of topoedaphic vegetation class. Therefore, some soil properties were affected by fire (Appendix B: Table B1). Topoedaphic vegetation classes tended to occupy characteristic areas of ordination space, but there was some overlap between the normal confidence ellipses of classes. Upland mixedwood and upland jack pine groups were especially intermingled (Fig. 3.2a), and mixedwood communities occurred in a sub-region of the broader environmental space occupied by jack pine. Similar patterns are identifiable in the post-fire understory indicator species of each topoedaphic vegetation class (Table 3.5). All topoedaphic vegetation classes had unique significant indicator species, with the exception of jack pine uplands, which shared all significant indicator species with the upland mixedwood group, and some with the upland spruce group (Table 3.5). *Potentilla palustris* (L.) Scop., *Betula glandulosa* Michx., *Epilobium palustre* L., and *Myrica gale* L. were unique indicator species of open wetlands. Treed wetlands had unique indicator species of *Rubus chamaemorus* L., *Vaccinium caespitosum* Michx., and *Vaccinium oxycoccos* L. *Viburnum edule* (Michx.) Raf. was a unique indicator species of upland mixedwood sites. Furthermore, upland mixedwood sites shared significant indicator species of *Cornus canadensis* L., *Geranium bicknellii* Britt., *Rosa acicularis* Lindl., *Linnaea borealis* L., and *Elymus innovatus* Beal with upland jack pine sites. *Vaccinium uliginosum* L. and *Geocaulon lividum* (Richards.) Fern. were unique indicator species in upland spruce communities.

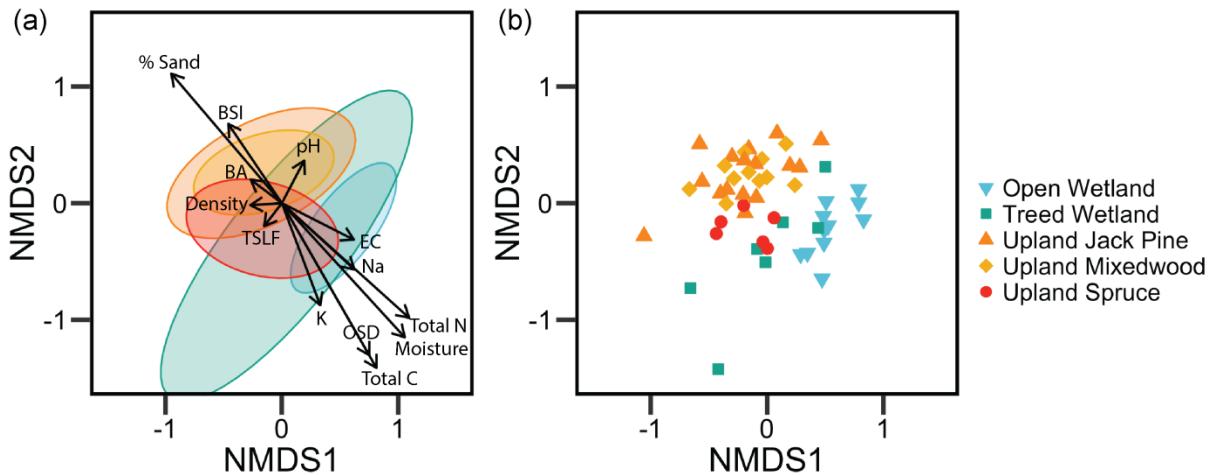


Figure 3.2 Nonmetric multidimensional scaling (NMDS) of post-fire understory vegetation community dissimilarities. Plot (a) shows normal confidence ellipses for topoedaphic vegetation classes (identified by colour) and environmental vectors derived from correlations between environmental variables and the NMDS axes, within the ordination space. Abbreviations of environmental variables are reported in Table 1. The strength of the relationship between an environmental vector and the NMDS (R^2) is indicated by the arrow length. Plot (b) shows the individual sites within the ordination space, with topoedaphic vegetation classes identified by point colour and shape.

Table 3.5 Significant (* $p \leq 0.05$) indicator species identified using multi-level pattern analysis within six topoedaphic vegetation classes. The indicator species uniquely associated with one group are indicated with a †.

Vegetation Group				
Open Wetland	Treed Wetland	Upland Mixedwood	Upland Jack Pine	Upland Spruce
<i>Potentilla palustris</i> (L.) Scop. †	<i>Rubus chamaemorus</i> L. †	<i>Viburnum edule</i> (Michx.) Raf. †	<i>Cornus canadensis</i> L.	<i>Vaccinium uliginosum</i> L. †
<i>Betula glandulosa</i> Michx. †	<i>Vaccinium caespitosum</i> Michx. †	<i>Cornus canadensis</i> L.	<i>Geranium bicknellii</i> Britt.	<i>Geocaulon lividum</i> (Richards.) Fern. †
<i>Epilobium palustre</i> L. †	<i>Vaccinium oxycoccus</i> L. †	<i>Geranium bicknellii</i> Britt.	<i>Rosa acicularis</i> Lindl.	<i>Ledum groenlandicum</i> Oeder
<i>Myrica gale</i> L. †	<i>Rubus arcticus</i> L.	<i>Rosa acicularis</i> Lindl.	<i>Linnaea borealis</i> L.	<i>Equisetum scirpoides</i> Michx.
<i>Rubus arcticus</i> L.	<i>Ledum groenlandicum</i> Oeder	<i>Linnaea borealis</i> L.	<i>Elymus innovatus</i> Beal	<i>Arctostaphylos rubra</i> (Rehder & Wils.)
<i>Carex</i> L. spp.	<i>Equisetum scirpoides</i> Michx.	<i>Elymus innovatus</i> Beal		<i>Rosa acicularis</i> Lindl.
<i>Salix</i> L. spp.	<i>Arctostaphylos rubra</i> (Rehder & Wils.) Fern.			<i>Linnaea borealis</i> L.
	<i>Carex</i> L. spp.			<i>Elymus innovatus</i> Beal
	<i>Salix</i> L. spp.			<i>Carex</i> L. spp.
				<i>Salix</i> L. spp.

The dominance of pre-fire and post-fire tree species (represented by log-ratios of compositions of basal area and stem density) were significantly different for jack pine, black spruce, and white spruce (Paired *t*-tests, Bonferroni-corrected **p* ≤ 0.04). When pre-fire dominance was characterized using total stem density (Appendix B: Fig. B3), post-fire tree species compositions were significantly different for black spruce and trembling aspen (Paired *t*-tests, Bonferroni-corrected **p* ≤ 0.02). Having confirmed significant differences between pre-fire and post-fire tree species compositions, we examined the rank shifts in dominance of tree species in order to capture directionality of species-specific changes. Jack pine both increased and decreased in dominance in the post-fire cohort, but the slim majority of sites were neutral (−0.5 to 0.5 shift in rank; 39 % of sites). Furthermore, not all plots burned with completely stand-initiating lethal wildfires (Fig. 3.3). Of the sites that experienced declines in the ranked dominance of jack pine, 41% had some surviving jack pine basal area post-fire (Fig. 3.3). Aspen dominance increased in the post-fire cohort, with 54 % of sites gaining 1 or more ranks of dominance post-fire, and no sites declining by <−0.5 of a rank (Fig. 3.3). Both varieties of spruce primarily demonstrated no change or declines, in the post-fire cohort (57 % of sites were neutral and 37 % showed a decrease for black spruce; 69 % of sites were neutral and 29 % showed a decrease for white spruce). Of those sites with declines in the dominance of black spruce, only 9 % (*n* = 2) had incomplete mortality of black spruce trees (Fig. 3.3). No sites demonstrating declines in trembling aspen or white spruce had live individuals of these species post-fire (Fig. 3.3). Declines and increases in tree species dominance were significantly related to topoedaphic vegetation classes. Increases in jack pine dominance were especially associated with wetlands and spruce uplands, whereas jack pine declines occurred in upland communities where jack pine was already established, especially mixedwood stands where the suckering of trembling aspen was prevalent (Appendix B: Fig. B4; Tukey test of least-squares means, **p* ≤ 0.05). Although increases in aspen dominance were more pronounced in uplands (Wilcoxon signed-rank test, ***p* = 0.009), there were no statistical differences in aspen dominance shifts between topoedaphic vegetation classes (Tukey test of least-squares means; Appendix B: Fig. B4). Decreases in black spruce dominance were the most pronounced in upland spruce sites, whereas black spruce dominance was largely stable in treed wetlands and other

vegetation classes (Tukey test of least-squares means, $*p \leq 0.05$). There were no significant differences in post-fire changes in white spruce dominance between topoedaphic vegetation classes (Appendix B: Fig. B4).

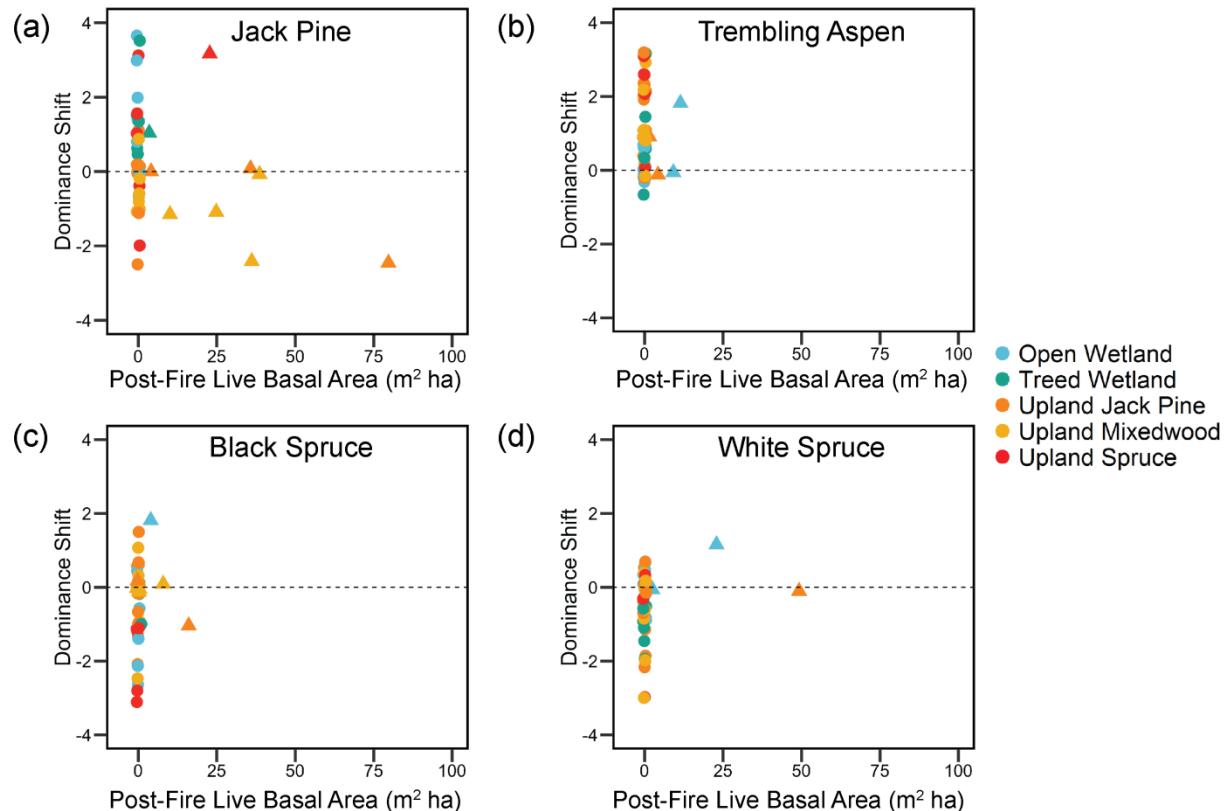


Figure 3.3 Increases and decreases in the post-fire dominance of (a) jack pine; (b) trembling aspen; (c) black spruce; and (d) white spruce, plotted against the post-fire live basal area of the same species. Points are coloured by topoedaphic vegetation classes. Circles indicate sites where the species experienced complete mortality or was absent pre-fire. Triangles indicate sites that had live residual basal areas of the species of interest following a wildfire. Points are offset (“jittered”) to reduce overlap. Dashed horizontal lines indicate no change in species dominance post-fire. Points above this line increased in dominance post-fire, and points below are those sites that experienced a decline of the species of interest in the post-fire cohort.

When representing the variance in understory vegetation and tree species dominance shifts explained by soils, we found that many soil properties were highly correlated. To address this, we decomposed the correlated soil physicochemical properties using PCA, and included only the first principal component (PC1) as an explanatory variable in the variance partitioning (Table 3.2). We chose to retain percent sand and PC1, and organic

soil depth and site moisture despite high correlations ($\rho = 0.8$) between these two pairs, as these variables characterized important elements of the three environmental driver groups. Post-fire soils (Soils); pre-fire forests, topoedaphic context, and climate (Site); and burn severity and fire history (Fire) together explained 28 % of the variance in understory vegetation communities, and 33 % of the variance in the dominance shifts of tree species (environmental variables included in model reported in Table 3.2; Fig. 3.4). There was a substantial shared variance explained between Soils, Site, and Fire. Overall, Site explained the largest portion of the variance in post-fire vegetation communities (8 %) and tree species dominance shifts (13 %; Fig. 3.4). Soils significantly explained 5 % of the variance in understory vegetation but did not significantly explain tree species dominance shifts. Conversely, Fire was of substantial importance to tree species dominance shifts (7 % of variance) but did not significantly explain post-fire vegetation communities ($p = 0.08$; Fig. 3.4).

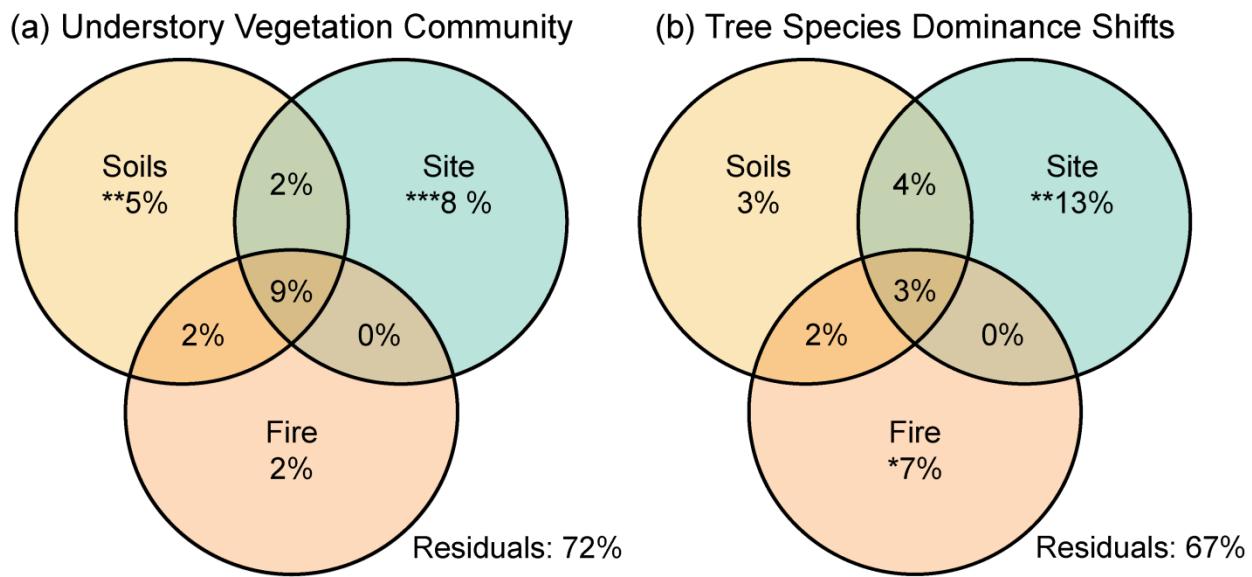


Figure 3.4 Venn diagrams showing the partitioning of variation in (a) post-fire understory vegetation community dissimilarities and (b) shifts in tree species dominance, between post-fire soils (Soils); pre-fire forests, site moisture, and climate (Site); burn severity and fire history (Fire); and unexplained residual variance. The significance of unique portions of variance explained is indicated by asterisks (* $p = 0.05$, ** $p = 0.01$, *** $p = 0.001$). The measured and interpolated environmental variables in each explanatory partition are reported in Table 3.2.

Classification and regression trees of the dominance shifts of tree species had R^2 values ranging from 0.65 to 0.43. Jack pine dominance increased in the post-fire cohort where

the total soil N was $\geq 0.48\%$ and decreased in the post-fire cohort in stands that experienced partial mortality (Fig. 3.5). These sites were typically mixedwood stands, and often had some remaining live basal area of jack pine trees, suggesting that these declines in the dominance of the post-fire cohort do not necessarily indicate persistent shifts away from jack pine dominance, although aspen suckering outpaced the establishment of pine seedlings (Appendix B: Fig. B3). Trembling aspen increased in dominance in nearly all plots, but increases were somewhat limited in lightly burned plots and plots with higher N availability, both of which tend to be characteristic of wetlands (Fig. 3.5).

Changes in black spruce dominance were neutral in young stands where black spruce was essentially absent pre-fire and in wetlands ($TSO < 80.5$). Declines in black spruce dominance were augmented in moderate aged ($TSO < 103.5$) uplands and stands experiencing severe canopy burning ($CFSI \geq 4$; Fig. 3.5). White spruce dominance increased slightly in sites with low N availability (Total N $< 0.11\%$) and lower moisture deficits ($CMD < 191.5$). White spruce dominance declined in historically drier sites, especially in those sites that experienced some canopy involvement in the fire ($CFSI \geq 2.65$; Fig. 3.5).

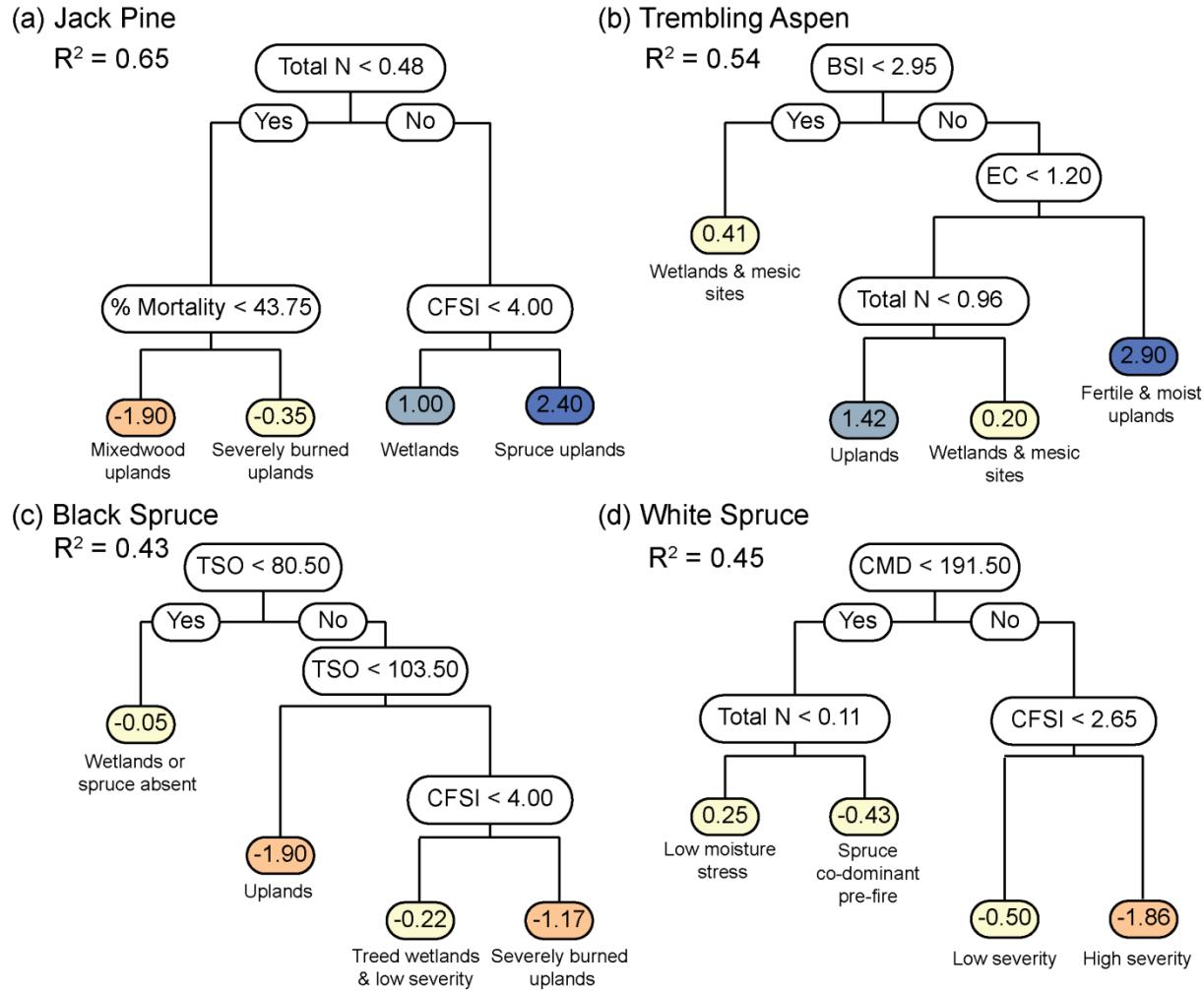


Figure 3.5 Regression trees of post-fire cohort dominance shifts for (a) jack pine; (b) trembling aspen, (c) black spruce; and (d) white spruce. Regression trees were fitted requiring a minimum of five sites per node, and a minimum within-node deviance of 0.05. Light blue terminal nodes indicate increases in dominance post-fire, and dark blue nodes indicate substantial increases in rank dominance (≥ 2). Red terminal nodes indicate decreases in dominance. Yellow nodes may be slightly negative or positive, but do not represent strong shifts (description of dominance shift metric in Section 2.3 Analysis). Descriptions of characteristic sites and drivers appear below each node. The environmental variables included in the regression tree models are reported in Table 3.3.

3.5 Discussion

3.5.1 Post-fire vegetation communities of vascular plants

Post-fire understory vegetation communities were primarily explained by site conditions, but burn severity and fire history had significant secondary effects. Topoedaphic vegetation classes occupied distinct areas of the environmental space and had

characteristic indicator species, with the exception of jack pine uplands and mixedwood stands. These indicator species were identifiable for topoedaphic vegetation classes despite recent disturbances, underscoring the importance of non-fire drivers to post-fire vascular vegetation. Understory vegetation communities of mixedwood forests appear to predominantly occur in a subset of environmental conditions that are also characterized by jack pine forests. Site moisture, climate, and pre-fire forest structure and composition, all of which were dominant drivers of understory vegetation assemblies, are independent of fire effects. Therefore, these communities may be somewhat robust to disturbance from fire, as they are primarily controlled by non-fire drivers.

Although the climate of the boreal forest is changing, changes to topography through background rates of uplift (1.3 cm year^{-1}) (Andrews, 1970) and erosion ($\sim 0.005\text{--}0.0005 \text{ cm year}^{-1}$) (Portenga & Bierman, 2011) reported in parts of the biome are slow, relative to the velocity of climate change ($\sim 1 \text{ km year}^{-1}$ in the boreal forest) (Loarie et al., 2009). Hydrological feedbacks may also reinforce the persistence of some features, such as peatlands, in the face of drying and warming (Schneider et al., 2016; Waddington et al., 2015). The persistence of these topoedaphic drivers over time, in the face of ongoing climate change, should encourage the re-establishment of understory vegetation communities following fires. As understory vegetation communities have a substantial influence on below-canopy light availability and nutrient cycling, this vegetation layer's persistence may, in turn, reinforce the similarity of post-fire communities to pre-fire conditions, with implications for seedling establishment (Messier et al., 1998; Nilsson & Wardle, 2005; Tsuyuzaki et al., 2014). Conversely, regions of the boreal forest experiencing rapid topoedaphic changes due to permafrost thaw and thermokarst formation may be more susceptible to shifts in vegetation communities as these dominant drivers undergo substantial short-term changes (Grosse et al., 2011).

Fire affects post-fire vegetation assemblies, both directly through surface burn severity and time since last fire, and indirectly via fire-mediated changes to soil properties. Despite the overarching importance of fire-independent site characteristics, burn severity and fire history were associated with understory vegetation community dissimilarity. Additionally, these variables also had significant effects on diversity, when controlling

for topoedaphic vegetation class. Furthermore, post-fire soils alone explained a substantial portion of the variance in understory vegetation communities and several soil properties that were affected by wildfire, as expected in boreal soils (Neff et al., 2005). Despite the importance of non-fire site drivers to understory vegetation communities, changes in burn severity or fire return intervals will likely translate to shifts in understory vegetation communities through these secondary pathways. Increases in burn severity, in particular, may lead to lasting, directional compositional changes in understory species assemblies (Day et al., 2017). Where understory vegetation communities exist at the boundaries of their ideal environmental space (or in areas of overlap with other topoedaphic vegetation classes), the effect of burn severity and fire history may be more apparent, and potentially override fire-independent controls.

3.5.2 Post-fire shifts in tree species dominance

Topoedaphic vegetation classes significantly explained total seedling density, but surface burn severity significantly interacted with these conditions, likely indicating an effect of seedbed availability on recruitment. Climate, pre-fire forest composition and structure, and site moisture were important variables in explaining post-fire shifts in the dominance of tree species, and in which sites such shifts occurred. Post-fire seedling density was significantly lower in wetlands and spruce-dominated sites and highest in jack pine and mixedwood uplands. Although the post-fire recruitment was lowest in open wetlands, some forested sites that reburned with very short intervals between stand-initiating fires (≤ 16 years) also experienced near-failures in the recruitment of all tree species, including those that increased in overall dominance post-fire, and had significantly lower seedling densities than all other sites. Although we observed declines in the post-fire dominance of both spruce species, black spruce maintained its dominance in treed wetlands (peatlands) and white spruce dominance was stable in sites with a lower climatic moisture stress. Furthermore, increases in the dominance of aspen in the post-fire cohort were least prevalent in wetlands. The drivers of species persistence and types of sites where spruce species retained dominance, despite the broader neutral or declining trend across sites, reflect the importance of topoedaphic and climatological drivers to post-fire tree species shifts. Local variability in site moisture may offer refugia from climate change for both of

these species, in a landscape with limited topography (Devito et al., 2005; Schneider et al., 2016).

Despite the importance of climate and pre-fire forests to seedling recruitment, burn severity and fire history had detectable and important effects on post-fire shifts in the dominance of tree species. Canopy fire severity was implicated in both positive and negative shifts in tree species dominance for all conifer species. Black spruce dominance decreased in uplands where stand-initiating wildfires occurred at a frequency of fewer than ~100 years between fires. The dominance of both spruce species was reduced in sites that experienced high-severity crown fire. Surface burn severity was the primary driver of post-fire increases in dominance of trembling aspen, and likely had further indirect effects on the post-fire dominance of white spruce, aspen, and jack pine through nutrient availability due to organic soil combustion and heating. Increases in burn severity and combustion in sites that tended to protect tree species that were susceptible to declines in dominance (i.e., peatlands) or in sites where species declines were particularly pronounced (e.g., upland spruce sites) may have important implications for future tree species compositions (Walker et al., 2018).

Jack pine and trembling aspen made substantial gains in dominance in the post-fire cohort. These two species are shade-intolerant and require canopy openings from disturbances such as fire to regenerate and are, therefore, successful post-fire species. Spruce species establish shortly after a fire, but appeared to be atypically uncommon in sampled fires from this severe drought-driven fire season, compared to previous studies of the mixedwood boreal zone (Peters et al., 2005; Peters et al., 2006) or the northern boreal forest (Johnstone & Kasischke, 2005; Lavoie & Sirois, 1998). Although spruce trees can persist as suppressed individuals, if seedlings fail to establish following fire they are unlikely to go on to become stand dominants through succession, as the cohort of seedlings established immediately post-fire ($1\text{--}20 \text{ year}^{-1}$) in boreal forests goes on to make up the future forest (Johnstone et al., 2004). In light of this, jack pine and trembling aspen appear to have gained, at the cost of longer-lived, “late-successional” spruce tree species (Greene et al., 1999; Searle & Chen, 2017). Additionally, some jack pine stems regularly remained alive post-fire, whereas this was less common for the other three tree

species—wildfires killed almost all individuals in burned patches. The successional pathways identified here suggest that increases in burn severity and fire frequency would continue to promote a growing component of jack pine and trembling aspen in northwestern boreal forests, despite topoedaphic, climate, and forest structure controls on post-fire dominance shifts.

In boreal forests, tree species adaptations to wildfire tend to promote “direct regeneration”, where post-fire stands return to pre-disturbance compositions over time. Black spruce is a semi-serotinous species that has demonstrated stand self-replacement following fires in the northern boreal forest (Bergeron et al., 2014; Ilisson & Chen, 2009). The post-fire decreases in the ranked proportional dominance of black spruce that we observed may suggest that increasing fire frequencies and severity may surpass the capacity of this species to re-establish following fires at the proportions previously expected, especially in drier uplands, if there is substantial combustion in both the overstory and understory (Johnstone et al., 2016; Lavoie & Sirois, 1998; Walker et al., 2018). Additionally, in the topoedaphic vegetation classes where the dominance of black spruce was stable (wetlands), and where spruce was previously dominant (spruce uplands), the seedling density was significantly lower than that measured in jack pine and mixedwood uplands. Declines in black spruce dominance relative to early-successional tree species, or through deforestation following severe fires, were observed in Alaska (Johnstone et al., 2010; Walker et al., 2017), the Yukon Territory (Brown & Johnstone, 2012), and in the eastern Canadian boreal forest (Lavoie & Sirois, 1998), and this research, provides additional evidence for the potential occurrence of this phenomenon in northwestern Canadian forests.

3.5.3 Implications for northwestern boreal forests

Wildfire is the stand-initiating disturbance with the largest extent in the northwestern Canadian boreal forest (White et al., 2017). Therefore, drivers of post-fire vegetation assemblies are an important determinant of future forest composition in this region. The post-fire understory vegetation communities, seedling density, and shifts in the dominance of tree species were primarily attributable to pre-fire forests, climate, and topoedaphic context, suggesting that there is substantial capacity for forests and

understory vegetation communities to regenerate post-fire. Although some variability in post-fire communities was attributed to burn severity, burn severity in this region is also associated with pre-fire forest structure and composition (Whitman et al., 2018), further reinforcing the importance of pre-fire drivers to observed vegetation assemblies.

Despite this resilience, long-term shifts in tree species compositions are ongoing in parts of the western Canadian boreal forest, with proportions of early-seral shade-intolerant species such as jack pine and trembling aspen demonstrating increasing prevalence, driven by climate change (Searle & Chen, 2017). Simultaneously, droughts appear to have caused decreases in forest productivity, altered seedling establishment and caused large-scale die-offs of mature trees in northern forests (Barber et al., 2000; Hogg & Wein, 2005; Michaelian et al., 2011). Although strong non-fire controls on understory vegetation and seedling establishment offer some resilience to change, the secondary direct and indirect effects of fire will likely serve to accelerate these ongoing changes if fire size, frequency, and severity increase as projected (Stralberg et al., 2018; Wotton et al., 2017, 2010).

An increasing broadleaf component in northwestern boreal forests, such as that observed in this study, may reduce fire severity and flammability of boreal forests (Cumming, 2001; Forestry Canada Fire Danger Group, 1992; Whitman et al., 2018) and raise the surface albedo (Euskirchen et al., 2016), potentially offering a negative feedback to shifts driven by climate change and impeding increases in fire activity (Jin et al., 2012; Terrier et al., 2013). This effect would be transient if increases of the proportion of trembling aspen in boreal forests do not persist. Increases in the frequency and severity of droughts may lead to a subsequent decline in this drought-sensitive species (Dai, 2013; Michaelian et al., 2011). Drought stress would also likely further exacerbate black spruce declines and potentially favour more drought-tolerant upland conifers such as jack pine (Darlington et al., 1997; Hogg & Bernier, 2005; Way et al., 2013). Furthermore, droughts increase the susceptibility of fuel-limited young forests to reburning (Erni et al., 2016; Parks et al., 2018), which could yet again reinforce reductions in black spruce dominance through the reduced availability of viable seeds. Observed post-fire seedling density was highly variable, substantially different from pre-fire species compositions, and several

sites experienced near regeneration-failures when severely burned at short fire frequencies. This research contributes to the growing body of literature indicating that changes to forests of this region are ongoing, despite the overarching resistance to such shifts conferred by regeneration mechanisms and topoedaphic controls (Johnstone et al., 2010; Neff et al., 2005; Walker et al., 2017).

3.5.4 Limitations and future research

Due to the opportunistic nature of this study's sampling design, we were unable to measure changes in the composition of the understory vegetation assemblies from pre-fire to post-fire communities. Although we partitioned the variance in post-fire vegetation communities to identify some role of wildfire on their determination, studies where prescribed burns are planned or existing plots are burned over in natural fires are better positioned to measure shifts in the dominance of understory vegetation species from pre-fire to post-fire conditions. Soils are important to post-fire understory vegetation communities and they are also relevant to seedling recruitment through the provision of seedbeds (Barrett et al., 2011; Greene et al., 2007, 2004). Such studies would allow researchers to measure the changes in soils as a result of fires, including changes in the organic layer depth.

We conducted our field sampling one year and three years post-fire. Studies spanning a longer time period can provide additional insights into post-fire vegetation recovery for both understory plants and trees e.g., (Collins & Stephens, 2010; Gibson et al., 2016), but this was beyond the scope of this work. An assessment of whether a forest has recovered to a state similar to pre-fire conditions would require an extensive period of time, reflecting the growing conditions at high latitudes and local disturbance regimes (e.g., stand ages at the time of burning ranged from 9 to 237 years in this study). Although the post-fire recruitment pulse for some tree species may not be complete three years post-fire, there is ample evidence that the recruitment occurring within the first few years post-fire largely determines the future species composition and structure of the stand in boreal forests (Greene et al., 2004; Johnstone et al., 2004). Just over one-third of our plots did not have repeated measures of seedling recruitment data sampled three years post-fire; however, the majority of these sites that were not revisited were non-forested wetlands

(fens), with no trees pre-fire. This data gap affected closer to a quarter of the forested sites. Spruce trees are slower to establish, and this may have biased our results; however, we did observe some spruce seedling recruitment in most plots with a pre-fire spruce presence. By converting our measurements of post-fire seedling density to compositional log-ratio data, and calculating shifts in the ranked dominance of species, we captured changes in post-fire tree species composition and normalized the highly skewed seedling density data. This method does not permit us to assess structural changes that may have occurred; for example, whether post-fire forest density increased or decreased and whether these outcomes vary by species. Although we did characterize some variability in seedling density by topoedaphic vegetation communities and fire frequencies, future research could combine ranked dominance shift data with seedling and pre-fire stem densities to directly capture regeneration failures and structural changes, in addition to the shifts in proportional dominance measured here.

At the time of burning there was an ongoing multi-year drought in the study area, which continued into 2015, and may have affected the post-fire recruitment of seedlings, as well as their growth (Hogg & Wein, 2005; Kemball et al., 2006). The drought conditions may also have affected burn severity of the fires, as fire weather is significantly related to overstory and understory combustion in boreal forests (Barrett et al., 2010; Whitman et al., 2018). The identified impacts of fire on understory vegetation and seedling recruitment may have been influenced by these pre- and post-fire environmental conditions and therefore, the observed vegetation assemblies and ecological outcomes may be most representative of severe fire years. Sampling in wildfires that occurred in different years would capture a wider range of pre- and post-fire climates.

3.6 Conclusions

In this study, the primary determinants of post-fire outcomes for boreal forest vegetation communities and shifts in tree species dominance were pre-fire forests, topoedaphic context and climate. Burn severity, fire history, and post-fire soils were significant secondary drivers. Burn severity and fire history did not significantly explain the variability in understory vegetation communities; however, post-fire soils were related to

understory vegetation community dissimilarities. Furthermore, burn severity was significantly related to understory vascular plant diversity. Severely burned vegetation communities tended to have lower understory species richness and diversity, as did very wet sites, which typically burned at low levels of severity. Post-fire shifts in tree species dominance, as characterized by differences in ranked proportional compositions, were significantly related to fire history and burn severity, but this effect was less important than pre-fire and climatological conditions. The overriding control of fire-independent drivers on post-fire vegetation may provide some resilience to forests in the face of climate change, as they are less susceptible to fire-mediated type conversions due to site moisture and pre-fire forest drivers. Despite this potential for resilience, changes to forest vegetation community compositions due to altered climates are occurring, and burn severity and fire history were important explanatory variables in our models of shifts in tree species dominance. In a forest with potentially increasing frequency, size, and severity of fires, the long-term resistance to change conferred by topographic and forest controls may be overwhelmed by the direct and indirect effects of wildfires, which offer pathways to change. Burned sites will also experience altered post-fire climates, with potential increases in moisture stress and droughts, which would exert additional pressures on initial post-fire vegetation. Ongoing shifts in the dominance of tree species are the result of both climate and fire. If these disturbances continue to increase, the observed shifts towards early-seral species such as jack pine and trembling aspen could produce large-scale changes in vegetation dominance that may lead to substantial—and perhaps unanticipated—ecological changes.

3.7 Acknowledgements

This research was funded by the Natural Sciences and Engineering Research Council of Canada (Funding Reference Number: CGSD3-471480-2015) and the Government of the Northwest Territories. Parks Canada Agency and Jean Morin provided in-kind support. We thank Xinli Cai, Matt Coyle, G. Matt Davies, Kathleen Groenewegen, Derek Hall, Koreen Millard, Sean A. Parks, and Doug Stiff for assistance in the field.

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4 Boreal forest resilience to short-interval wildfire is further impeded by drought

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4.1 Abstract

The size and frequency of large wildfires in western North America have increased in recent years, a trend likely to be exacerbated if projected changes in climate are borne out. Due to fuel limitations, recently burned forests resist burning for upwards of 30 years; however, extreme fire-conducive weather enables reburning at shorter fire-free intervals than expected. This research aims to quantify the effect of short-interval reburns in upland and wetland environments of northwestern Canadian boreal forests, and to determine whether post-fire drought alters such effects. We sampled forest structure and composition at paired sites with short (≤ 17 years) and long (≥ 30 years) fire-free intervals, from seven different fire years. Despite strong adaptations to wildfire amongst boreal plants, post-fire forests at paired short- and long-interval sites were significantly different: stem densities of recruited trees were lower following short intervals due to a decrease in conifer recruitment; the proportion of stems from broadleaf trees was higher; canopy density and residual organic layer depths were lower; and herbaceous vegetation cover was reduced. Density of broadleaf tree recruits did not increase or decrease in response to fire-free interval. Although forested wetland communities are thought to be more resilient to fire than boreal uplands, we observed the same changes at such sites. Drought reinforced changes in proportions of tree species and decreases in tree recruitment, rendering regenerating stands less resilient to short-interval reburning. Drier and warmer weather will likely increase the incidence of short-interval reburning and amplify the ecological changes such events cause, as droughts synergistically increase both wildfire activity and post-fire moisture stress. If more stands experience shortening fire-free intervals and drought this will accelerate climate-driven transitions from conifer and mixedwood forests to open woods and grasslands, with implications for habitat, forest economies, and global carbon stocks.

4.2 Introduction

The circumpolar boreal zone contains approximately 30% of forests. North American boreal forests are globally important as they provide essential ecosystem goods and services, act as carbon sinks and sources, and contain extensive areas of unmanaged land (Brandt et al., 2013; Gauthier et al., 2015; Kashian et al., 2006). Boreal forests typify the fire-adapted biome, having co-evolved with wildfire since the most recent retreat of glaciers. Large, infrequent, and high-intensity wildfires are the dominant disturbance in this region. Such fires are generally stand-replacing, as they tend to cause widespread mortality of overstory trees and understory plants (Brandt et al., 2013; Johnson, 1992). Climate change-induced alterations of fire regimes and the composition of post-fire boreal forests will have broad-reaching impacts on the global carbon balance and local ecologies and economies.

Observed fire frequencies, or fire-free intervals, in the western North American boreal forest range from hundreds of years to approximately 30 years between stand-replacing wildfires (Boulanger et al., 2012). Recently burned areas in the boreal forest generally resist reburning for upwards of 30 years after a fire (Erni et al., 2016; Hart et al., 2019; Parks et al., 2018), due to the lack of fuel necessary for supporting fire ignition and spread (Héon et al., 2014; Thompson et al., 2017). Despite such limitations to fire occurrence, extreme fire weather conditions can override these controls, allowing fires to spread in fuel-limited recently burned areas (Erni et al., 2016; Parks et al., 2018). Fuel availability and arrangement appears to limit both fire occurrence, and the resulting severity of fires that do occur. Above and belowground consumption of organic matter, (burn severity) and resulting ecological outcomes of fire are substantially the product of pre-fire vegetation and hydrology (uplands and wetlands) in the northwestern boreal forest (Walker et al., 2018; Whitman et al., 2018a). Through these mechanisms, pre-fire vegetation influences fire behaviour, severity, and frequency in the North American boreal forest.

Western Canadian boreal forests are dominated by coniferous tree species, with broadleaf tree species making up a significant but secondary component of many stands.

Adaptations to wildfire, such as vegetative regeneration (e.g., some broadleaf trees and shrubs) and seed banking in soils (e.g., some understory plants) or serotinous or semi-serotinous cones (e.g., some conifer trees), are common amongst boreal plant species and allow plants and trees to rapidly repopulate burned areas following lethal fires (Carcaillet et al., 2001; Johnson, 1992; Stocks et al., 2001). These adaptations promote the persistence of species that were present prior to the disturbance, allowing stand self-replacement or “direct regeneration”, and conferring substantial forest resilience to disturbance (Ilisson & Chen, 2009; Johnstone et al., 2010).

Although boreal forest plant species are adapted to recurrent and severe wildfires, changes to fire regimes (regional characteristics of fire behaviour, occurrence (ignitions and seasonality), extent, and effects; Krebs et al., 2010) may exceed the capacity of species to regenerate following fire as species are pushed beyond the limits of their adaptation, compromising forest resilience (Buma et al., 2013; Johnstone et al., 2016; Turetsky et al., 2017). Where disturbances occur in rapid succession relative to historical frequencies, boreal forest recovery may be severely limited by the lack of tree seed sources or bud banks (Brown & Johnstone, 2012; Greene et al., 2004), and state-changes may occur, subverting stand self-replacement expectations and shifting the balance of vegetation types on the landscape (Hart et al., 2019). Research suggests that the extent and frequency of wildfire in western North American forests has increased under modern anthropogenic climate change (Abatzoglou & Williams, 2016; Hanes et al., 2018; Kasischke & Turetsky, 2006), and will continue to do so, as the climate warms (Flannigan et al., 2005; Wang et al., 2015, 2017; Wotton et al., 2010). Increasing fire activity and extreme fire weather may in turn increase the extent and frequency of short-interval reburning events, as fuel-driven controls on landscape resistance to fire are overwhelmed (Erni et al., 2016; Parks et al., 2018). Due to the potential acceleration of this phenomenon, it is increasingly important to understand its ecological impacts to guide future land management and conservation in the boreal forest.

Complicating post-fire forest recovery, climatic conditions may be increasingly inhospitable for those viable seeds that are able to establish, due to increasing drought stress (Harvey et al., 2016; Stevens-Rumann et al., 2018; Wang et al., 2014).

Compounding the effects of drought stress, northern provenances of some boreal tree species are likely to be maladapted to altered climates, and demonstrate low resilience and adaptation to drought (Barber et al., 2000; Hogg et al., 2017; Isaac-Renton et al., 2018; Michaelian et al., 2011). Although the impacts of drought on post-fire recruitment in more south-western forests have been documented (Harvey et al., 2016; Stevens-Rumann et al., 2018), effects of drought on post-fire recruitment in North American boreal forests are largely unexplored (but see Hogg & Wein, 2005).

The occurrence of short-interval reburning and drought are inherently linked (Parks et al., 2018), and these disturbances are likely to accelerate concurrently in the future, making it important to gain an understanding of how and whether fire frequency and post-fire drought in the boreal forest may interact to alter post-fire tree recruitment. The northwestern boreal forest is a hydrologically diverse landscape, with an important wetland component (up to 50% of land area, in some regions; Tarnocai et al., 2011). It has been suggested that boreal wetlands may be resilient to fire, as forested peatlands are more resistant to shifts in tree species composition following fire than neighbouring uplands (Hart et al., 2019; Walker et al., 2017; Whitman et al., 2018a). Hydrological feedbacks that retain elevated water tables in wetland environments, and connections between wetlands and uplands may buffer drought and climate change effects in the boreal forest (McLaughlin et al., 2017; Waddington et al., 2015), but limited research on boreal post-fire recruitment exists that examines both productive uplands and wetland environments, where moisture stress may be less limiting.

Our goal was to describe and quantify differences in forest structure and composition across a biophysical and hydrological gradient of paired sites that burned with long and short fire-free intervals (FFIs), in a range of post-fire climate conditions. Specifically, we sought to determine whether the structure and composition of vegetation communities at paired short FFI and long FFI sites were significantly different, and whether these differences varied between well-drained and poorly-drained sites. Subsequently, we used generalized linear models to characterize the relative influence of pre-fire forest structure, post-fire seedbeds, and post-fire moisture stress (drought) as drivers of observed densities and compositions of trees recruited after fire. Using these methods, we are able to

quantify changes in forest structure and composition directly resulting from FFI across a range of fire histories, attribute such changes to ecological drivers, and characterize the effect of drought on post-fire recruitment in interaction with FFI, all of which represent knowledge gaps in the North American boreal forest at the time of this research.

4.3 Methods

4.3.1 Study area

The northwestern Canadian boreal forest (Fig. 4.1A) is an expansive forest biome characterized by short, warm summers, and long cold winters (Ecological Stratification Working Group (ESWG), 1995). The northwestern Canadian boreal forest is dominated by coniferous tree species, primarily black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggendb.), white spruce (*P. glauca* (Moench) Voss), and jack pine (*Pinus banksiana* Lamb.). Broadleaf tree species, largely trembling aspen (*Populus tremuloides* Michx.), often co-occur with conifers (ESWG, 1995). Large, stand-replacing wildfires are the dominant disturbance in this region (ESWG, 1995), recurring approximately every 69 (palaeoecological data; Larsen & MacDonald, 1998) to 160 years (map data; Boulanger et al., 2012; Stocks et al., 2002). The study area has a substantial wetland component, with forested peatlands covering as much as 50% of the landscape (Tarnocai et al., 2011; Thompson et al., 2016).

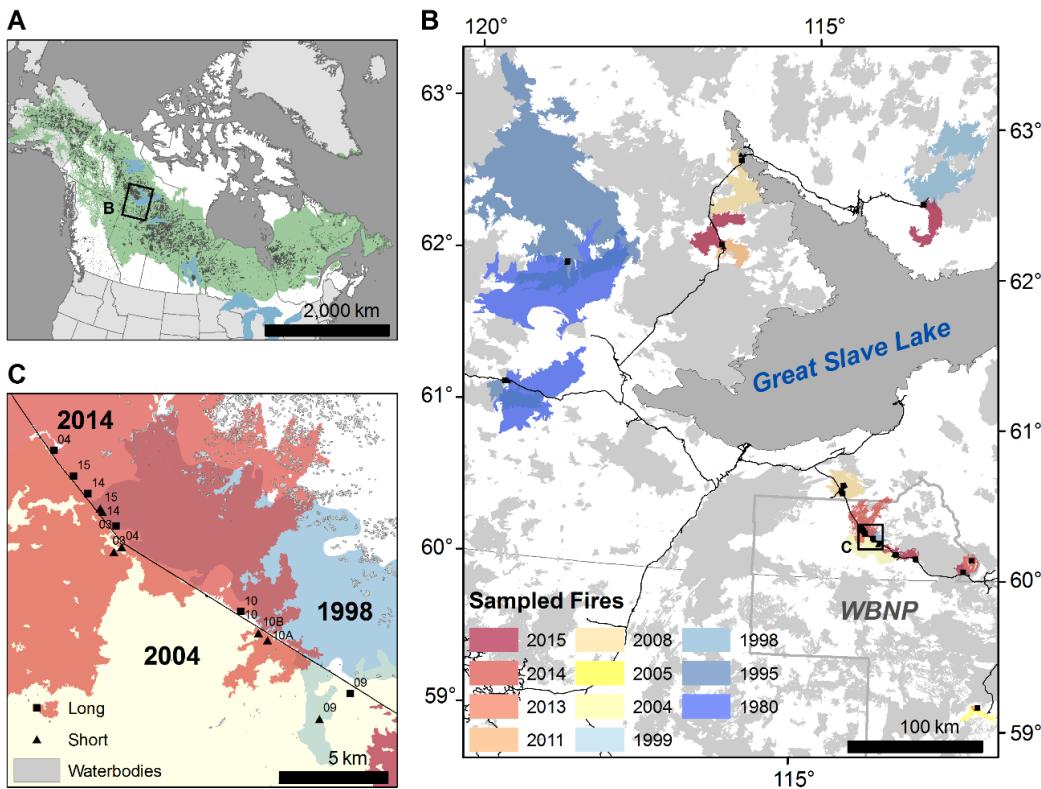


Figure 4.1 Location and fire history of the study area. (A) Recent (1984 - 2017) Canadian (Natural Resources Canada, 2018) and Alaskan (USA) (Eidenshink et al., 2007) fire perimeters (grey) in the context of the North American boreal forest (green) (Brandt, 2009). The extent of panel B is indicated with a black rectangle. (B) The distribution of sampling sites in the study area. Sites are identified as black squares. Sampled wildfires are coloured by year of occurrence and superimposed on wildfires that occurred in the recent past (1980 – 2015; grey) on the landscape at the time of sampling. Wood Buffalo National Park (WBNP) is outlined in grey, major roads are shown in black, and the extent of panel C is indicated with a black rectangle. (C) Detailed area showing an example of the sampling design of paired sites with short and long fire-free intervals. Numbered labels indicate paired sites.

4.3.2 Data collection

In 2016 we sampled 50 sites (25 pairs) around Great Slave Lake that had burned in the last 21 years, between the years of 1995 and 2015, in the Northwest Territories and Alberta, Canada (Fig. 4.1; Appendix C: Table C1). Twenty-five sites had a short recent FFI ranging from four to 17 years ($\bar{x} = 10.6$ years). These sites were paired with 25 sites with longer FFIs ranging from 30 to 112 years ($\bar{x} = 64.0$ years; Appendix C: Table C1). Of these 25 pairs, eight were wetlands and 17 were uplands. We employed a paired study design where each long FFI site was paired with a short FFI site that burned in the same

wildfire, and in the same pre-fire ecosite type (Beckingham & Archibald, 1996), but with a different stand origin, the primary difference thus being the fire history of the two sites, rather than post-fire climatological conditions. By pairing sites of the same age and ecosite in this manner we are able observe persistent differences in forest structure and composition across hydrological gradients in a large study area, and over a range of times post-fire. Site pairs were closely matched in pre-fire tree species compositions, stand structure, and biogeographic settings (pairwise correlation coefficients reported in Appendix C: Table C2). Sites were classified as short (≤ 17 years between fires) and long (≥ 30 years between fires) fire-free intervals (FFIs), with one pair-member in each group. The ≥ 30 year threshold for determining a “long” FFI was selected to represent the duration of fuel-limitation of reburning in the study area (Héon et al., 2014; Parks et al., 2018; Thompson et al., 2017), assuming that fire weather in sites experiencing short FFIs likely overwhelmed this control (Erni et al., 2016; Parks et al., 2018). We sampled sites in both uplands and wetlands with varying levels of drainage to characterize the strength of effects along a hydrological gradient. This study design also enabled us to capture a variety of post-fire climatic conditions and moisture availability, as fires originated from seven different fire seasons, and therefore experienced diverse post-fire drought conditions. Additional details of site pairing are discussed in the supplementary information.

Sites were located ≥ 100 m from roads. Some sites were accessed by helicopter. At each site we sampled live and dead mature tree (>1.33 m height, diameter at breast height (DBH) ≥ 3 cm) stem density, basal area, and species composition using the point-centered quarter method (Cottam et al., 1953; Mitchell, 2015) every 5 m along a 35-m transect oriented north-south, beginning at 0 m. On the west side of the transect at the same eight points we sampled vegetation abundance of understory species and small shrubs (≤ 0.5 m) in 1×1 m quadrats, and estimated the percent cover of exposed organic and inorganic surface substrate. We sampled the density of tall shrubs (> 0.5 m) using a 2-m wide belt transect on the east side of the transect. Percent exposed mineral soil and organic matter were averaged to produce one percent cover value for each metric, per site. We sampled tree seedling and sucker (resprouting stems from top-killed individuals) stem density, species, and status (live or dead) on the east side of the transect using a 2-m

wide belt transect with variable lengths depending on height classes with minimum transect distance increasing with tree height (< 0.1 m – 10-m transect; < 0.5 m – 20-m transect; ≤ 1.33 m – 35-m transect). Where stem density or size classes were highly uneven, we extended the length of the belt transect for smaller size classes, up to a maximum of 35 m. We measured sapling (trees > 1.3 m in height but with a DBH < 3 cm) density, species, and status for the entire 2 × 35-m transect. At 0, 17.5 and 35 m along the transect we sampled the depth of the soil organic layer and measured overstory canopy density using a densiometer. We averaged residual organic layer depth measurements for each site. We measured surface fuel and coarse woody debris (CWD) loading along the same 35-m transect and over an additional 15 m, resulting in a 50-m long transect (McRae et al., 1979).

At each site we sampled fire-scarred trees from the pre-fire cohort to verify recent FFIs suspected from fire history maps (Natural Resources Canada, 2018), and stand age at the time of the most recent fire. If multiple scarred trees were available, we sectioned up to four individuals per site. Live trees or trees killed in a known recent (< 5-year-old) stand-replacing fire were preferred; however, if no live scarred trees were available, a section of a nearby live tree of the same species was used to cross-date dead fire-scarred individuals. We sanded tree sections using a belt sander and a fine-grit sandpaper, digitally scanned each section, and counted and measured annual rings and dated fire scars on the scanned images in CooRecorder (Cybis Elektronik & Data AB, 2013).

We used ClimateWNA (Wang et al., 2016; Wang et al., 2012) to downscale PRISM historical climate data to site elevations derived from the Canadian Digital Elevation Model (Natural Resources Canada, 2016). For each site, we estimated cumulative post-fire moisture stress by summing annual anomalies in summer (JJA) climatic moisture deficit (precipitation - reference evaporative demand (mm); CMD) for the year of fire and all summers afterward, up to a maximum of three years post-fire (4 years total). Where sites had burned fewer than three years in the past at the time of sampling, we calculated cumulative anomalies using only the year of fire and intervening years (2 – 3 years total). Anomalies were the difference between the actual summer CMD of each year, and mean summer CMD for the 1961 – 1990 normals period (all sampled fires occurred after

1990). To best represent the effect of moisture stress on tree recruitment we assessed all combinations of cumulative years after fire beginning either year 0 or year 1, and ending 2, 3, and 4 years post-fire; by which time approximately half of seedling establishment has likely occurred (Johnstone et al., 2004). Possible moisture stress variables were correlated and generally had similar significance and effects in models; however, we chose 0 to 4 years as this window had the best improvement in some model fits and was significant in all models.

We pooled all coniferous tree seedlings for analyses. All broadleaf seedlings and suckers were also pooled, to characterize general trends in species composition. We described the pre-fire species composition using all live and dead dominant overstory trees measured in the point-centred quarters, as well as any dead saplings (>1.33 m height < 3 cm DBH), with the assumption that such individuals were killed in the recent fire. This method allowed us to estimate pre-fire tree species composition of regenerating cohorts in young stands that experienced short FFIs and had no or few remaining identifiable mature trees. Although live seedlings < 1.33 m in height may have originated before the fire, it is possible for broadleaf suckers and some jack pine seedlings to grow to this height within the sampling window (≤ 21 years post-fire); therefore, these individuals were not included in estimates of the pre-fire cohort.

4.3.3 Statistical analysis

All statistical analyses were conducted in R (R Core Team, 2018). We identified significant differences between short and long FFIs using statistical tests for paired data. If the difference in a variable between the short and long FFI pairs was normally distributed, we used a paired *t*-test. If the differences were non-normally distributed, we used a nonparametric paired Wilcoxon signed-rank test. Paired statistical tests were conducted for all sites pooled, and in subgroups of wetlands, and uplands. If tests for all three groups are significant, we report the significance of the total dataset. If only two tests were significant (the total dataset and a subgroup), we report only the test with the higher *p*-value. We adjusted *p*-values to account for the false discovery rate, due to our use of multiple statistical tests (Benjamini & Hochberg, 1995).

To characterize drivers and controls of post-fire seedling recruitment we fitted generalized linear models (GLMs) explaining the density of tree seedlings and propagules, and post-fire proportions of conifer stems as a function of post-fire moisture stress, fire history, soil substrates, pre-fire forest structure and composition, and stand age at the time of sampling. Total seedling and propagule density, conifer seedling density, and broadleaf propagule density (stems/m^2) were multiplied by 10 and rounded to produce integer values, approximating stem counts per 10 m^2 . We assessed the form of relationship between the independent and dependent variables and found no non-linearity and excluded collinear variables (Spearman's $\rho > 0.7$). Sites were considered individual observations in the GLMs, as opposed to pairs. Before fitting models, we standardized independent variables. To account for overdispersion in seedling and propagule count data we used negative binomial and poisson distributions for these models, whereas the conifer proportion of the post-fire cohort was represented with a binomial distribution. Models were fitted using the caret package (Khun, 2017), and model fits were assessed using pseudo R^2 , mean absolute error (MAE), and root mean square error (RMSE) from full and 10-fold cross-validated model statistics derived from 100 repeats, accounting for the small sample size and possible overfitting due to substantial outliers in seedling count data. Independent variables were retained in models only if they were significant. Significance and standard errors of independent variables was determined using White's estimator in the sandwich package (Zeileis, 2004, 2006) due to significant heteroscedasticity. Having identified the best parsimonious model for each dependent variable, we iteratively removed each independent variable to examine their relative importance (% contribution to ΔAIC).

Finally, to examine the effect of fire intervals on understory vegetation communities, we characterized understory species diversity and abundance using Hill numbers equivalents (effective numbers of equally-abundant species necessary to give the same value of a diversity measure; Chao et al., 2014; Hill, 1973) calculated in the vegetarian package with Shannon measures (Charney & Record, 2012). We identified unique indicator species (single site-groups) of short- and long-interval wetlands and uplands using multi-level pattern analysis in the indicspecies package (De Caceres & Legendre, 2009).

4.4 Results

Short-interval sites demonstrated more severe effects of fire than corresponding long-interval sites, indicated by a lower post-fire canopy density ($p = 0.006$), shallower residual organic soil ($p = 0.010$; Fig. 4.2), and less residual biomass of rotten coarse woody debris ($p = 0.009$) across all sites (Appendix C: Table C3). Upland short FFI sites had more exposed mineral soil ($p = 0.009$), and less surface cover of organic matter ($p = 0.009$; Fig. 4.2), but these effects were not detected in wetlands (Appendix C: Table C3). Post-fire soil chemistry was also significantly different between the two groups, with short-interval sites having lower mineral soil nitrogen ($p = 0.034$) across all sites. Short interval sites also likely had lower organic soil carbon ($p = 0.061$) and higher post-fire soil pH ($p = 0.052$) than sites that burned with longer FFIs, but these effects were not significant ($\alpha = 0.05$) when controlling for multiple comparisons (Appendix C: Table C3). We detected active permafrost layers ≤ 1 m depth from the surface in only two wetland pairs (four sites). Due to the small sample size we did not analyze these data; however, in both pairs the active layer thickness was greater at the short-interval pair-member site. Other research has shown that wildfire escalates rates of permafrost thaw in peatlands of this region (Gibson et al., 2018).

The density and species composition of the post-fire tree cohort was also significantly different between sites with long and short FFIs. Total post-fire stem density of seedlings and propagules was significantly lower for all tree species combined ($p = 0.007$), and for conifer seedlings, specifically ($p = 0.006$; Fig. 4.2; Appendix C: Table C4). Of those seedlings that successfully established, the proportion of conifer stems in the post-fire cohort was lower following short FFIs than in long FFIs ($p = 0.006$; Appendix C: Table C4). On average, short FFI pair-member sites had 24.2% lower total stem density of tree seedlings than the long FFI member, and conifer seedling stem density was only 51.9% of that of the long-pair member. This represents an average reduction in post-fire tree stem density of 6.18 stems/m², or a mean difference of 61782 stems ha⁻¹ due to short fire intervals. This reduction is entirely attributed to conifers; short-interval sites had an average conifer seedling deficit of 6.18 stems/m² (61818 stems ha⁻¹), relative to the

conifer stem density observed at the long-interval pair-member. 72% of short FFI sites had fewer than 50% conifer stems in the post-fire seedling and propagule cohort, whereas only 12% of long FFI sites were not dominated by conifer seedlings ($\geq 50\%$ of post-fire recruits). Broadleaf seedling and propagule density was not significantly different between short and long FFI pairs (Fig. 4.2; Appendix C: Table C4).

Density and composition of post-fire tree seedling and propagule cohorts were explained by FFI and moisture stress (drought); site hydrology, time since last fire (stand thinning, competition, and delayed regeneration), and soil surface substrates (Table 4.1). FFI was the dominant driver of total seedling and propagule density of all tree species combined (83% contribution to model fit), conifer seedling density (63% contribution), and the proportion of conifer seedlings (60% contribution), whereas seedbeds (exposed mineral soil (%MIN) 36% contribution; residual organic matter depth (RO) 29% contribution) were the most important explanatory variables in the model of post-fire broadleaf seedling density (Fig. 4.3; Table 4.1; Appendix C: Table C5). TSF was significant only in models of post-fire tree recruit stem density when stems were separated into broadleaf and conifer groups. The effect of TSF (13% contribution) indicated stem thinning occurred over time amongst broadleaf trees (Appendix C: Fig. C1), whereas in conifer seedlings (5% contribution) stem density decreased over time in uplands while it increased in wetlands (Appendix C: Fig. C1).

Post-fire moisture stress (climatic moisture deficit anomalies; MS) significantly influenced stem density of the post-fire tree seedling cohort, but was a substantially less influential driver of post-fire recruitment than FFI (0.2 – 13% contribution; Appendix C: Table C5). Often MS was only significant in models as an interaction with FFI or seedbed variables; however, such interactions were significant, improved model R^2 and reduced error, and, when considered separately from the contribution of main effects, were often important (Fig. 4.3; Appendix C: Table C6). Conifer and total stem density increased with increasing FFI, and this effect interacted with MS. Where FFIs were short and post-fire MS was high, seedling density was very low. This negative effect of MS faded with increasing FFI length (Table 4.1, Fig. 4.3). Moisture stress generally negatively affected post-fire broadleaf stem density; however, MS interacted with RO

depth. On thin residual organic layers MS led to increases in broadleaf seedling density (Fig. 4.3). This effect reversed with increasing organic layer depths. The proportion of conifer seedlings in the post-fire cohort increased with increasing FFI (Fig. 4.3). Increasing availability of mineral soil substrates (%MIN) also increased the proportion of conifer seedlings in the post-fire cohort, but this effect was dampened where moisture stress was high, favouring instead increases in the proportion of broadleaf species (Fig. 4.3).

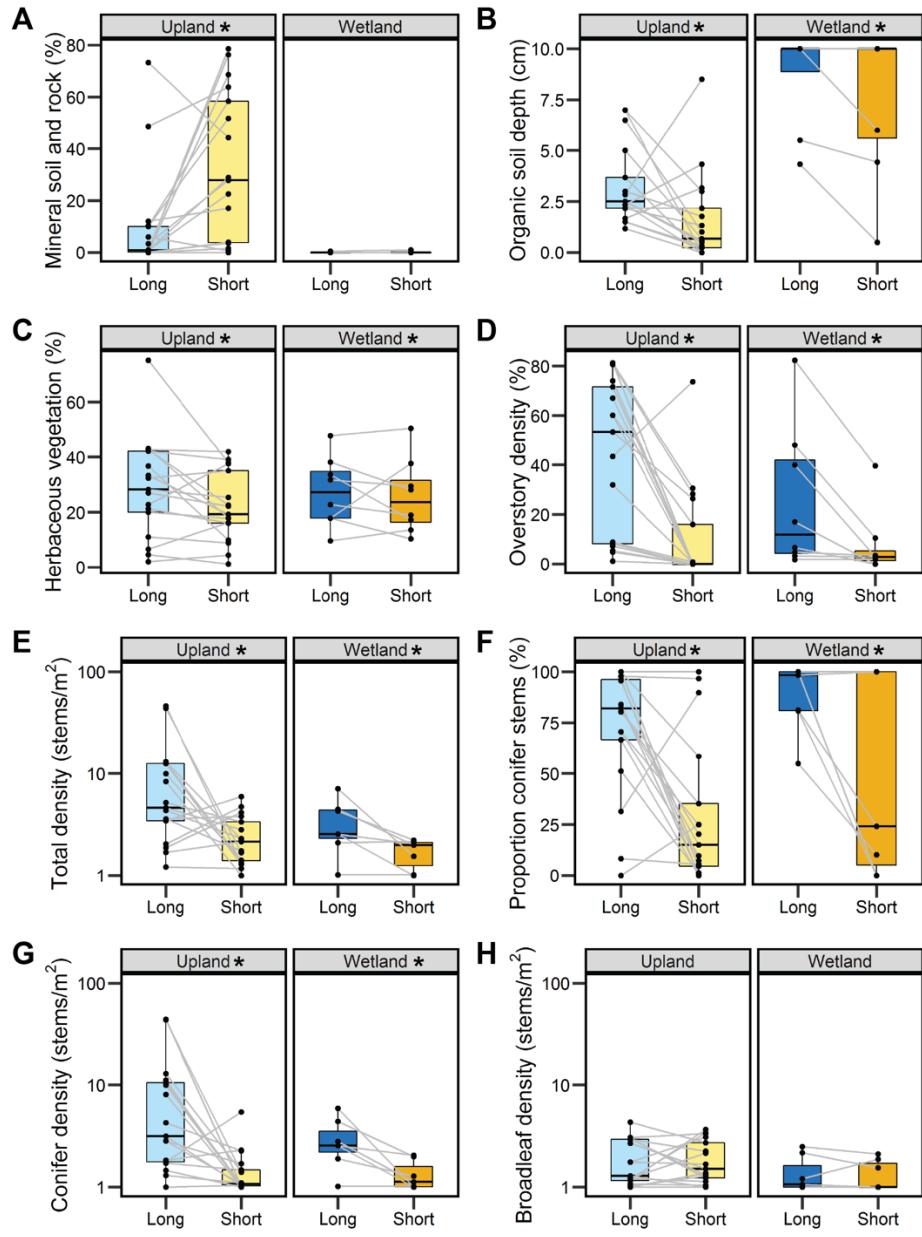


Figure 4.2 Differences between long and short fire-free interval (FFI) sites. Grey lines connect paired sites with the same elapsed time since last fire. Significance ($p \leq 0.05$) of differences between short and long pairs is indicated with an asterisk in the panel header (details of tests in Appendix C: Tables C3, C4, C7). Post-fire variables are: (A) the mean percent cover of exposed mineral soil and rock in understory vegetation abundance plots, (B) the mean depth of the residual organic soil layer, (C) the mean percent cover of herbaceous vegetation in understory vegetation abundance plots, (D) the mean post-fire canopy density, (E) the logarithm of total stem density of seedlings and propagules in the post-fire cohort, (F) the proportion of conifer stems in the post-fire cohort, (G) the logarithm of conifer seedling density in the post-fire cohort, and (H) the logarithm of broadleaf seedling and propagule density in the post-fire cohort.

Table 4.1 Generalized linear models of tree seedling and propagule density (stems/10 m²), and plot-level tree species composition. Time since fire is included in all models to account for stand thinning over time and between-fire-year differences. Significant ($p \leq 0.05$) predictor variables are bolded in equations. Model fits are described using averages of 10-fold cross-validated (CV) root-mean-square-error (RMSE), mean absolute error (MAE), and pseudo R² (pR²), derived from 100 repeats. Model degrees of freedom ($n = 49$) are reported in the column df . Model p -values were derived from χ^2 tests of model deviance explained relative to a null model.

Generalized Linear Model	Distribution	df	pR ² (CV)	RMSE (CV)	MAE (CV)	P
Total Seedling & Propagule Stems = $3.26 + (\text{FFI}^{***} \times 0.74) - (\text{MOIST}^{\dagger\dagger\dagger} \times 0.45) + 0.38(\text{FFI} \times \text{MS}^{\#\#\#}) + (\text{MS} \times 0.03)$	Negative Binomial	44	0.59 (0.44)	56.92 (58.19)	32.02 (39.13)	<0.001
Conifer Seedlings = $2.45 + (\text{FFI} \times 0.99) - (\text{TSF}^{\$\$\$} \times 0.8) + (\% \text{CON}^{****} \times 0.73) - (\text{MS} \times 0.68) + 0.58(\text{TSF} \times \text{RO}^{\dagger\dagger\dagger\dagger}) + 0.38(\text{FFI} \times \text{MS}) - (\text{RO} \times 0.2)$	Negative Binomial	41	0.61 (0.43)	54.29 (61.69)	29.21 (39.63)	<0.001
Broadleaf Seedlings & Propagules = $0.98 - 2.32(\% \text{MIN}^{\#\#\#} \times \text{BA}^{\$\$\$}) - (\% \text{MIN} \times 2.13) - (\text{BA} \times 1.4) - (\text{TSF} \times 0.78) - (\text{RO} \times 0.69) - 0.6(\text{RO} \times \text{MS}) - (\text{MS} \times 0.48)$	Poisson	41	0.45 (0.48)	6.52 (7.26)	4.64 (5.65)	<0.001
Proportion Conifer Stems = $0.60 + (\text{FFI} \times 1.18) + (\% \text{MIN} \times 1.02) + (\text{RO} \times 0.98) - 0.96(\% \text{MIN} \times \text{MS}) - (\text{MS} \times 0.4)$	Binomial	43	0.49 (0.52)	0.28 (0.3)	0.22 (0.25)	0.004

*** FFI: Fire-free interval (years)

††† MOIST: Site moisture (from subxeric to subhydric)

MS: Moisture stress (mm), as represented by site-specific cumulative anomalies of summer climatic moisture deficit (CMD) over 0 – 4 years post-fire

\$\\$\\$\\$ TSF: Time since last fire (years) at time of sampling

**** %CON: Proportion of conifer trees in the pre-fire cohort (%) calculated from basal area (m² ha⁻¹)

†††† RO: Residual organic matter depth (cm)

%MIN: Proportion of exposed mineral soil and rock (%) at the surface

\$\$\$\$ BA: Pre-fire basal area of trees (m² ha⁻¹)

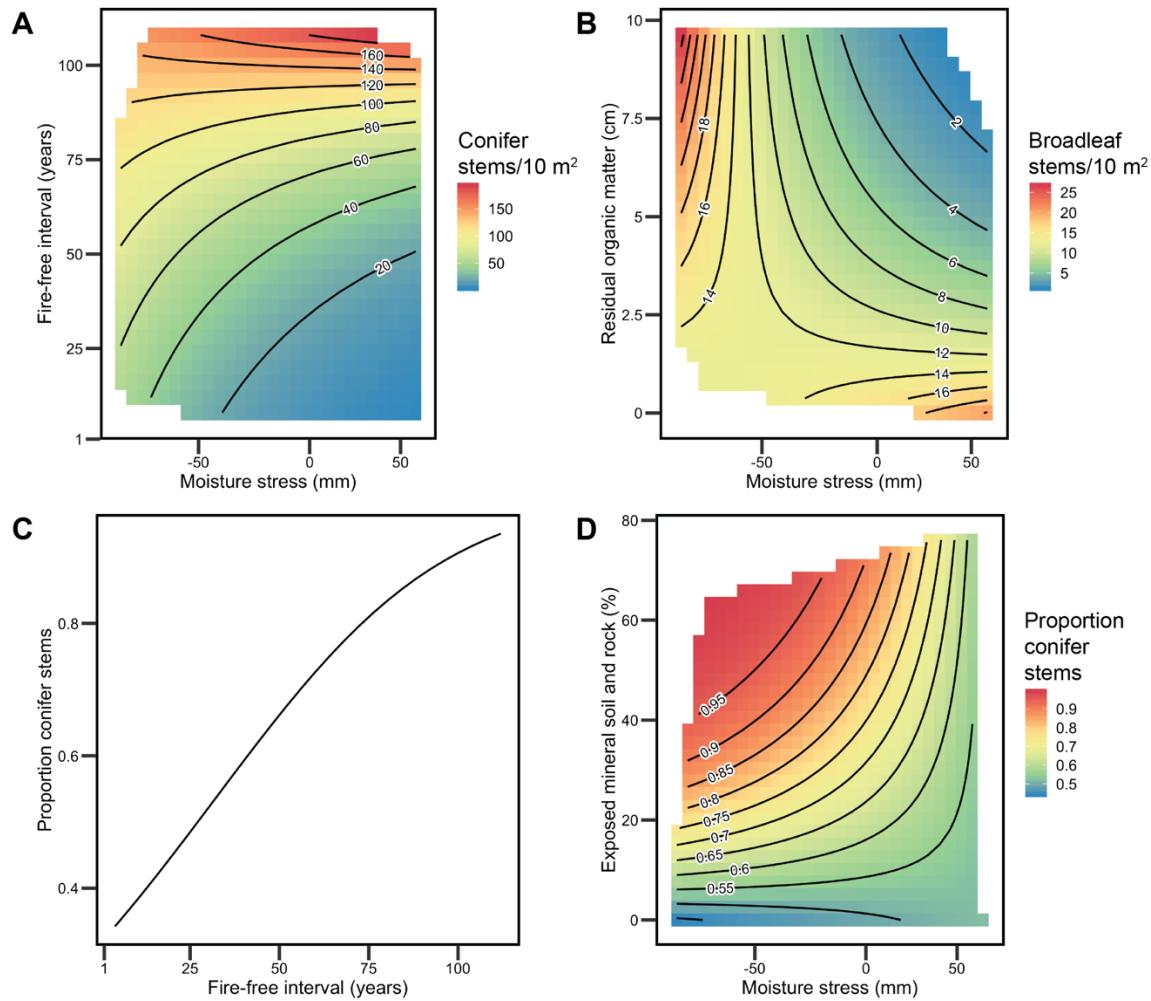


Figure 4.3 Marginal effects of fire-free interval (FFI) and moisture stress (MS) on post-fire stem density and composition of post-fire forests. Although models were fitted with standardized predictor variables, plots axes are labelled with observed values and units. (A) Effect of FFI and MS on conifer seedling density. (B) Effect of residual organic matter depth (RO) and MS on broadleaf stem density. (C) Effect of FFI on the proportion of conifer stems in the post-fire cohort. (D) Effect of percent exposed mineral soil and rock (%MIN) and MS on the proportion of conifer stems in the post-fire cohort.

Models of seedling density and composition provided some evidence for different post-fire outcomes in uplands and wetlands. Although thin residual organic layers were initially positive for conifer seedling recruitment, thinning occurred over time in upland environments (\bar{x} RO = 2.4 cm), whereas conifer seedlings continued to establish in wetlands (\bar{x} RO = 8.1 cm) over time (Appendix C: Fig. C1). Although years with low moisture stress increased broadleaf establishment in sites with deep organic layers (wetlands), higher moisture stress reduced broadleaf stem density in such environments (Fig. 4.3). Despite this interaction with moisture

stress, which promoted broadleaf establishment in some cases, the proportion of conifer stems generally increased with increasing RO depth (Appendix C: Fig. C1).

We also observed meaningful differences between short and long FFI sites in the post-fire vegetation communities of understory vascular plants and shrubs. Short FFI sites had less understory vegetation cover of herbaceous plants ($p = 0.034$; Fig. 4.2), and of forbs specifically ($p = 0.021$; Appendix C: Table C7). Stem density of tall shrubs (≥ 0.5 m) was higher in uplands following short intervals between fires than at long FFI sites, but this effect was not significant when controlling for multiple comparisons ($p = 0.077$). Graminoids made up a higher proportion of herbaceous plant cover at sites that had experienced short FFIs than in long FFIs, but this effect was not robustly confirmed ($p = 0.052$; Appendix C: Table C7).

We identified small evergreen shrubs, shallow resprouting species, and seed-banking species as indicator species in long FFI uplands, using multilevel pattern analysis (De Caceres & Legendre, 2009). The only significant indicator species identified in short FFI uplands was downy wildrye (*Leymus innovatus* (Beal) Pilg.), a grass with deep rhizomes (Appendix C: Table C8). Indicator species in long FFI wetlands were evergreen shrubs and species that resprout from shallower rhizomes, whereas indicator species in short FFI wetlands were generally fire-tolerant resprouting species (USDA Forest Service Rocky Mountain Research Station Fire Sciences Laboratory, 2018; Appendix C: Table C8).

Effective alpha diversity (Hill numbers equivalents, Shannon measures (Charney & Record, 2012)) was significantly higher by approximately one effective species in long intervals than in short intervals across all sites, and especially within uplands (Fig. 4.4). This is equivalent to an 11% decline in diversity (13% in uplands). Effective beta diversity was higher in short FFI wetlands than long FFI wetlands, and homogeneity was lower in short FFI wetlands. The same trends were present across all sites and in uplands, but differences were not significant (overlapping 95% CI; Appendix C: Fig. C2). Although all pairs of sites shared species in common, unique species were often observed in either pair member (Fig. 4.4). Some species were entirely unique to either long- or short FFI sites; however, these were rare individuals that only occurred in one or two sites.

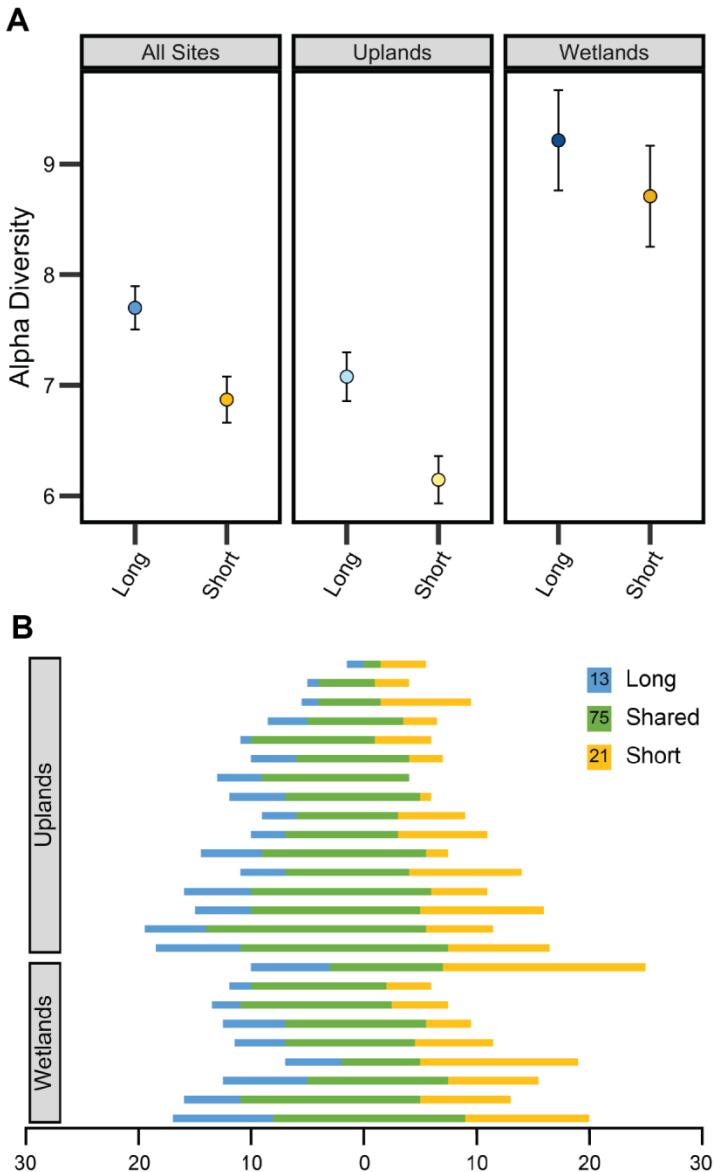


Figure 4.4 Differences in understory vegetation community diversity observed at sites with long and short fire-free intervals (FFI). (A) Differences in effective alpha diversity (Hill numbers equivalents, Shannon measures) of understory vegetation communities and bootstrapped 95% confidence intervals for the mean between long FFI (“Long”), short FFI (“Short”) sites, derived from 999 iterations. (B) Richness of shared and unique vascular plant species between paired short (blue) and long (green) FFI sites. Species shared by paired plots are represented in green. The total of unique and shared species across all sites is reported in the legend.

4.5 Discussion

Short-interval reburns in northwestern Canadian boreal forests lead to different understory vegetation communities, tree species compositions, and stem densities of trees recruited post-fire

than those observed at paired sites that burned in the same recent fire but with a longer FFI. Paired sites experienced the same post-fire climatological conditions and had the same length of time to recover and revegetate, yet differences between paired sites were persistent and significant, suggesting that they are attributable to the different fire histories of the two groups. Although FFI was the primary driver of post-fire forest composition and structure, the occurrence of drought in the years immediately post-fire further reduced forest resilience to short FFIs.

4.5.1 Differences in post-fire ecology as a result of fire history

The structure and composition of post-fire tree cohorts are significantly different between short and long FFI sites. Short FFIs led to more open forests with a reduced conifer component. Recent FFI explained the most variability in total seedling and sucker stem density, conifer stem density, and the proportion of conifer stems in the post-fire cohort. Longer FFIs had an overall positive effect on total stem density of tree recruitment, conifer seedling density, and the proportion of conifer stems. The dominant importance of FFI to post-fire stem densities of conifer seedlings, suggests that the primary mechanism for changes in conifer seedling establishment was a lack of seed sources due to mortality and subsequent combustion, as the pre-fire proportion of conifer stems and seedbeds were both less important than FFI. This likely captures interactive effects of both seed availability and seed viability due to immaturity (Brown & Johnstone, 2012; Splawinski et al., 2018), leading to the stronger influence of FFI than pre-fire conifer dominance. Seedbeds (% exposed mineral soil, residual organic layer depth) were also important drivers of recruitment (especially of broadleaf trees) and the proportion of conifer stems in the post-fire cohort. The dominant importance of seedbeds to broadleaf seedling density presumably reflects the extensive dispersal capabilities of these light-seeded species, which may not be substantially limited by seed availability (Johnstone & Kasischke, 2005; Gill et al., 2017). Compared to long FFIs, short FFI sites had substantially thinner residual organic layers and increased exposed mineral soil. As FFI directly affects soil substrate drivers (Appendix C: Table C3), this reinforces the importance of FFI as the primary determinant of post-fire recruitment across these sites.

The observed post-fire declines in the density and dominance of serotinous and semi-serotinous conifer tree species in both uplands and wetlands following fire are impressive, given the fire-

adapted nature of such species where post-fire seedling densities often exceed pre-fire conditions (Lavoie & Sirois, 1998). This is especially compelling when considered in the context of the boreal ecosystem where persistent patterns of post-fire forests are established shortly after a disturbance (Charron & Greene, 2002; Johnstone et al., 2004; Lavoie & Sirois, 1998). It is notable that shifts in abundance were due to the reduction in conifer seedling abundance, similar to trends observed in other western boreal forests (Johnstone & Chapin III, 2006b). Long-term monitoring at permanent plots has recorded ongoing biomass declines from increasing mortality of mature trees due to climate change and increasing moisture stress (Searle & Chen, 2017a). Our more limited data suggest that the post-fire establishment density of boreal trees is also likely to decline in response to both fire frequency and drought. Concurrent with ongoing biomass declines in mature forests, this reduction in the density of tree recruitment has implications for reduced biomass accumulation over time in young stands.

Research has suggested that broadleaf trees (particularly aspen) may replace conifers where they are threatened by climate change and shortened disturbance intervals, in more southerly forests (Gill et al., 2017; Kulakowski et al., 2013). Our results indicate that although the proportion of stems contributed by broadleafs was higher following short interval reburns, broadleafs did not increase in abundance in short-interval sites, leaving a gap in total stem density due to the decrease in conifers. Furthermore, stem thinning of broadleaves continued as time since fire elapsed (Appendix C: Fig. C1), leaving both forest structure and composition fundamentally altered by shortened FFIs in northwestern boreal forests. Projections of future climates in western boreal uplands suggest conditions will be too arid for aspen to persist (Stralberg et al., 2018). Furthermore, broadleaf-dominated forests resulting from short FFIs in the North may be susceptible to extensive drought-induced mortality of aspen already observed in nearby dry southwestern boreal forests (Aubin et al., 2018; Michaelian et al., 2011), raising questions about how persistent aspen-dominated short FFI forests may be.

Despite strong and plentiful adaptations to lethal wildfire amongst boreal plants, the understory vascular plant communities that established following short FFIs were effectively less species rich and had a lower abundance of herbaceous vegetation, supporting the assertions of Johnstone (2006) from northwestern boreal forests lacking pine trees and extensive wetlands. Differences in understory plants appear to be largely the result of soil heating and combustion, as indicator

species of long interval sites were fire-intolerant or tolerant only of lower-intensity fire that allowed seedbanks and vegetative propagules to persist. In uplands, indicator species at long FFI sites were forest species, whereas the only significant indicator of short FFI uplands was a grass. Such changes represent a fundamental shift in the forest understory, favouring an increasing presence of deciduous and resprouting understory species, but an overall decline of herbaceous vegetation cover.

The sampled short FFI sites experienced more severe fire effects, indicated by greater post-fire canopy openness (Johnstone, 2006) and thinner residual organic layers (Hoy et al., 2016; Brown & Johnstone, 2012; Johnstone & Kasischke, 2005). Short FFI sites also had reduced availability of coarse and downed woody debris (nurse logs; Donato et al., 2016; Johnstone, 2006), which are important for delayed regeneration of some non-serotinous boreal conifers (Peters et al., 2006). Burn severity of both recent and prior wildfires is implicated as the direct driver of differences in short and long FFI forests in our models of post-fire tree density and composition, through its influence on the availability of seed sources and bud banks, and seedbeds.

Variability in burn severity of both the most recent and prior fire is likely very important to the strength and influence of such effects on post-fire forests. Despite the dominance of large, high-mortality crown fires in the northwestern boreal forest, surface fires and intermittent crown fires also regularly occur, depending on fire weather and fuel structure (Stocks et al., 2001; Whitman et al., 2018b). Fairly frequent, low-severity surface fires are not uncommon in parts of the study area (e.g., sandy jack pine uplands) and the effects of successive low-severity short-interval events would be unlikely to lead to changes of the same magnitude and effect we report (Stevens-Rumann & Morgan, 2016; Whitman et al., 2018a). Within our sample, pairs of sites with little difference between short and long intervals may be the result of surface fires occurring at short intervals, or possibly due to severe wildfire following a long FFI (Pinno et al., 2013; Stevens-Rumann & Morgan, 2016). Paired sites that exhibited minimal differences between short- and long-interval stem densities may also relate to pre-fire differences in tree species composition not captured in our aggregated species categories (conifer and broadleaf). For example, recruitment at jack pine-dominated sites may be more robust after low-severity short-interval reburning, whereas positive responses to frequent fire, and frequent low-severity fire in

general, may be less likely in spruce forests (Hart et al., 2019; Stevens-Rumann & Morgan, 2016; Whitman et al., 2018b).

4.5.2 Upland and wetland resilience

Research suggests that wetlands burn less severely (Walker et al., 2018; Whitman et al., 2018b) and subsequently resist post-fire shifts in tree species dominance (Johnstone et al., 2010; Walker et al., 2017; Whitman et al., 2018a), indicating that they may be more resilient to disturbance from wildfire than uplands. Amongst our sites, burn severity from repeated fires was more severe in uplands and differences in short and long FFI post-fire ecology were more pronounced, suggesting that changes resulting from shortened FFIs may occur more rapidly at well-drained sites. Soil and seedbed substrates in wetland sites (deep residual organic layers) also promoted conifer dominance, and establishment of conifer trees continued in such sites over time, whereas sites with low residual organic layer depths (uplands) underwent thinning of conifer trees over time (Appendix C: Fig. C1). Despite this evidence for wetland resilience relative to uplands, we observed negative effects of short FFIs in poorly-drained sites, relative to forested wetlands that burned with long FFIs. Short-interval reburned wetlands experienced similar reductions in stem density and conifer seedling dominance to those observed in uplands, although understory vegetation changes due to short FFIs were less apparent than those detected in uplands. Such changes are consistent with a reduction in conifer seed availability and viability due to short-interval reburning (e.g., Brown & Johnstone, 2012). When rare but extreme short fire intervals occur, the relative resilience of forested wetlands to fire may be weaker than expected.

Moisture stress significantly interacted with seedbeds and RO depth in our models of seedling and propagule density and composition, suggesting that the effects of drought on tree recruitment vary across landscape positions and drainage in boreal forests. In areas with no exposed mineral soil (lightly burned uplands and wetlands) drier than average conditions slightly increased the proportion of conifer seedlings in the post-fire cohort (Fig. 4.3). Drought also reduced broadleaf stem density in the presence of thick residual organic layers, found in wetlands (Fig. 4.3). It is possible that conifer seedling establishment (and resulting competition from conifers) is more prevalent in wetlands during drought conditions. Although mature tree mortality due to drought does not appear to differ with soil drainage in this region (Searle & Chen, 2017a), it is possible that the effects of increasing drought stress on newly established seedlings may be buffered in

wetlands. Due to limitations of our study design we were unable to examine differing effects of drought between uplands and wetlands directly; however, possible differences merit further exploration, as these may provide another pathway by which boreal wetlands increase landscape resilience to fire.

Fire intervals in poorly drained boreal forests are typically longer than those observed in uplands, promoting the persistence of black spruce and reducing the likelihood of short-interval reburning (Le Goff & Sirois, 2004). This may have contributed to our difficulty in finding short-interval wetland sites, which limits the certainty of our results in the wetland group. Despite the small sample size of wetlands (n pairs = 8) their inclusion in the total dataset generally increased significance of paired statistical tests above that observed with uplands alone (n pairs = 17). It is possible that the less significant effects of short-interval reburning detected in wetlands are in part related to the relatively smaller sample size. We also grouped forested wetlands (e.g., fens and bogs) for paired statistical tests, although there are different burn rates in different wetland types (Turetsky et al., 2004). Future research with a larger sample size of wetlands would allow us to directly examine whether post-fire outcomes resulting from short-interval reburns differ between wetland types.

4.5.3 Potential climate change effects and interactions

Our sampled field sites have already experienced a substantial increase in mean annual temperature of +2.2°C, from 1915 normals (Wang et al., 2016, 2012). Much of this warming occurred in recent years, with an average temperature anomaly of +1.6°C in 2017; more than double the observed global average anomaly of +0.7 to 0.9°C (Reference period 1981 – 2010, (Blunden, Arndt, & Harfield, 2018)). In the study area, a simultaneous increase in precipitation had mitigated potential increases in moisture stress in recent years (Appendix C: Fig. C3; Larsen, 1997). If projections of future climate change in this region are borne out, increases in the volume of precipitation are expected to slow in coming decades and the proportion of precipitation occurring in the summer is expected to decrease. Increases in temperature are likely to outpace increases in precipitation, leading to an increasingly dry climate and more severe fire weather (Flannigan et al., 2016; Wang et al., 2015). Given projected increases in aridity (Appendix C: Fig. C3) and temperature in this region, there is also potential for significant

increases in regional drought in the western boreal forest (D'Orangeville et al., 2016; Hogg & Bernier, 2005; Wang et al., 2014).

Fire size, intensity, and frequency are all expected to increase in northwestern North America, under future climate change (Flannigan et al., 2005; Wang et al., 2015, 2017; Wotton et al., 2017). Others have shown that the occurrence of a drought reduces the strength of the spread-and ignition-limiting effect that young stands have on fire occurrence, and contributes to years with widespread fire (Erni et al., 2016; Héon et al., 2014; Parks et al., 2018). Furthermore, CMD anomalies are highly correlated with annual area burned in the study area (Appendix C: Fig. C4), suggesting that both the primary stand-initiating disturbance, and subsequent post-fire moisture stress are likely to increase concurrently.

Increasing frequency and severity of drought will not only make fires more frequent and more severe, overriding stand-age limitations to fire, but will also further affect the fate of forests by influencing post-fire recruitment (Harvey et al., 2016; Stevens-Rumann et al., 2018). Moisture availability is a significant, though secondary, factor affecting post-fire tree species composition and stand structure, which interacted significantly with both fire-free interval length and seedbeds in all of our models of seedling recruitment and composition. Our results suggest that moisture stress had a negative effect on both conifer and broadleaf seedling density. The negative effect of drought on conifer seedling density was particularly pronounced in sites that had experienced short-interval reburns (Fig. 4.3), indicating that drought further decreases forest resilience to short-interval reburning. Synchronous disturbance from short-interval fire and subsequent drought may substantially limit conifer seedling recruitment, eventually leading to regeneration failure.

Severely burned surfaces and exposed mineral soils are thought to provide the best substrate for seedling establishment and survival of the dominant boreal tree species (Jayen et al., 2006; Kemball et al., 2006; LePage et al., 2000). Greater abundance of mineral soil surfaces increased the proportion of conifers in the post-fire cohort in periods of low or zero moisture stress, whereas more pronounced droughts may have reduced their utility as a germination substrate, suggesting that the water-retention capacity of such soils may be limiting for conifer seedling establishment when rainfall is not readily available, or when evaporation outpaces precipitation. Furthermore, severely burned surfaces reduced the density of broadleaf stems (perhaps due to a

decrease in suckers, rather than seedlings); however, post-fire drought slightly increased their abundance in such areas (Fig. 4.3). This shift in the effect of soil burn severity on broadleaf seedling density may be due to reduced competition from conifers, which also fared poorly under drought conditions, especially where surface burn severity was high. Through these mechanisms, drought appears to reinforce the dominant fire-interval-driven changes in forest composition and structure by further reducing stand density and altering soil substrate limitations on tree recruitment, leading to an increased proportion of broadleaf species in the post-fire cohort.

It is unknown whether the rate or extent of short-interval reburning is increasing in the northwestern boreal forest, but as the duration, area burned, and frequency of fires increase in the future it is likely that active wildfires will continue to breach recently burned young forests, despite their resistance to fire (Héon et al., 2014). The role of severe drought in both the occurrence of short-interval reburning (Erni et al., 2016; Parks et al., 2018), and the post-fire outcomes for juvenile trees (Harvey et al., 2016; Kemball et al., 2006; Stevens-Rumann et al., 2018) suggests that climate change will have multiple direct negative effects on northwestern boreal forests as repeated wildfires and drought interact, although more research is needed to understand this relationship. As shifts in forest density and species composition carry forward (Johnstone et al., 2004), upland short FFI sites may come to resemble savannas, with open stands of scattered trees, and understories comprised largely of shrubs and grasses. Our results indicate that short FFI treed wetlands are also likely to be more open in structure and possibly grassier than their long FFI counterparts. Such changes may occur more gradually, due to overriding hydrological vegetation constraints and less severe fire effects (Stralberg et al., 2018; Whitman et al., 2018b).

Short-interval reburned areas may be more prone to frequent low-severity fire in the future due to the open fuel structure and slight increases in prevalence of grass, suggesting that—once established—these sites may be very persistent on the landscape, as short fire cycles maintain the altered forest structure (Archibald et al., 2013; Bond & Keeley, 2005), and potentially allow such patches to expand over time (Gartner et al., 2012; Tepley et al., 2016). The piecemeal occurrence of short-interval reburns may serve to accelerate widespread climate-driven changes in forest openness and composition, triggering transitions to grasslands and open woodland that are

projected and ongoing in much of the northwestern boreal forest (Searle & Chen, 2017b; Stralberg et al., 2018).

Short-interval reburns affected habitat and carbon stocks, though declines in rotten coarse woody debris and organic soil thickness, as well as the composition and structure of surviving and recruited trees. Shifts in boreal forests from conifer-dominated closed-canopy forests to more open woodland systems, may reduce carbon accumulation in both the overstory and the forest floor. The ecological outcomes and altered post-fire vegetation community structure and composition we observed following short-interval reburning may offer the early signs of future widespread regeneration failure anticipated in boreal forests with increasing fire activity (Splawinski et al., 2018). Furthermore, our results suggest that drought reinforces the trajectory of projected species composition shifts caused by short-interval reburning and accelerated fire frequencies in the boreal biome (Hart et al., 2019), in conjunction with decreasing establishment of trees in regenerating stands. This research contributes to mounting evidence that repeated and interacting natural disturbance events can fundamentally alter the structure and composition of boreal forests, despite widespread adaptations to fire. We also provide some evidence that wetland environments may not confer the degree of resilience to fire expected, when fire frequency is increased. Interactions with climate, mediated through drought, appear to amplify the effects of shortened fire intervals that cause species composition shifts and increase forest openness, suggesting that modelled rates of compositional change and regeneration failure driven by fire frequency (e.g., Hart et al., 2019; Splawinski et al., 2018) are potentially somewhat conservative. If the frequency and extent of short-interval reburning in the northwestern boreal forest increases with future climate change it is likely to accelerate and reinforce regeneration failures, and conversion to grasslands and woodlands due to climate maladaptation, as forests' adaptive resilience to disturbance is overwhelmed.

4.6 Acknowledgments

This research was funded by the Natural Sciences and Engineering Research Council of Canada (Funding Reference Number: CGSD3-471480-2015) and the government of the Northwest Territories. Environment and Climate Change Canada, Sam Haché, Parks Canada Agency, and Jean Morin provided in-kind support. We thank Rodrigo Campos-Ruiz, Matt Coyle, Josh

Gauthier, Kathleen Groenewegen, Mary Stephens, Scott L. Stephens, Xianli Wang, and Thea Whitman for assistance in the field.

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5 Conclusion

The landscape of the NWT and AB was substantially altered by the extensive area burned in 2014 and 2015, however, burn severity (above and belowground biomass loss) in sampled wildfires was highly variable, ranging from unburned islands to severely burned stands. This variability in burn severity reflects in part the substantial variability in forest structure and hydrology (uplands and wetlands) of this region. Generally, much of the area burned in the sampled 2014 fires was burned at high and moderate severity, regardless of the severity metric considered. As demonstrated in Chapter 2 of this dissertation, high severity burned patches were large, contiguous, had large core areas, and were very common.

Post-fire ecological outcomes from the 2014 and 2015 fire years are also likely to be variable. The post-fire density of tree seedlings and propagules, post-fire tree species dominance, understory vegetation community diversity, and understory vegetation community dissimilarity in northwestern Canadian boreal forests are all related to pre-fire topoedaphic conditions and pre-fire forest structure and composition (Chapter 3). Post-fire ecological outcomes therefore, to some extent, reflect the site capacity to support forests and species. Although burn severity has secondary effects on post-fire forest composition and structure, burn severity in this region is also substantially a product of pre-fire vegetation structure (fuels) and site hydrology (uplands and wetlands; Chapter 2), providing a mechanism by which the severity of disturbance experienced is limited by those vegetation communities themselves. The forests examined for this research are therefore expected to resist state-changes following disturbance where post-fire moisture is adequate, and seed and propagule sources are available.

Although both site- and stand-level controls on burn severity and post-fire vegetation confer resilience, where fire activity and severity increase there is a possibility for forest change. I found evidence of post-fire shifts in tree species composition and stand structure. I observed declines in black (*Picea mariana*) and white spruce (*P. glauca*) dominance in uplands following fire, whereas jack pine (*Pinus banksiana*) dominance shifts were mixed, and trembling aspen (*Populus tremuloides*) dominance generally increased following fire. Models reported in Chapter 3 of this work indicate that these changes in tree species composition were mediated by burn

severity and fire frequency; fire regime characteristics that are both expected to increase in the future.

Shortening of the interval between wildfires due to drought is likely to accelerate changes from conifer-dominated boreal forests to open woodlands and grasslands, by reducing the density of conifer recruitment due to the lack of viable seeds in such landscapes. The vegetation and forest structure of paired long- and short-interval reburned sites studied in Chapter 4 of this research are significantly different from one another, and these differences are persistent and occur in both uplands and wetlands. Short-interval reburned sites are effectively less diverse, and have a lower stem density of trees due to reduced conifer seedling recruitment. Increasing temperatures and aridity are not only likely to increase fire activity, but also to reinforce the changes to forests caused by shifts in fire regimes. In both the short- and long-interval sites sampled for this work, post-fire moisture stress interacted with burn severity and further reduced post-fire stem density of trees. As fire activity and drought both accelerate with climate change it is possible that the resilience of boreal forests to wildfire may increasingly be overwhelmed, leading to long-lasting changes to boreal forest habitats.

The results and findings of this thesis are largely drawn from one severe fire season, when fire weather conditions and post-fire moisture stress were homogenously extreme. This may have limited my ability to detect a strong effect of fire weather on burn severity. The ecological outcomes observed here (especially those reported in Chapters 3 and 4 that exclusively examine the 2014 fire season) may better reflect extreme wildfires, rather than smaller fires and those that occur under more moderate weather conditions. This could be addressed in the future by analyzing burn severity in more fires from multiple years and over a broader region, to enable a broader characterization of burn severity in this ecozone. Despite this limitation, it is likely that fire severity and activity will increase in the future, and the observations reported in this dissertation may increasingly resemble the norm. I was unable to conduct true pre- and post-fire re-measurements of the same sites due to the opportunistic nature of this study of natural wildfires. This limited my ability to directly measure and report change, especially in understory vegetation communities. I have used paired sites, variance partitioning, and detailed measurements of standing dead trees from the pre-fire cohort to enable some analysis of post-fire change.

North American boreal forest ecosystems are generally expected to resist state-changes, but shifts in forest species composition and structure due to climate change have already been detected. As the climate and fire regime of the boreal forest change it is likely that evidence of compromised forest resilience will continue to mount. The close coupling of this ecosystem's adaptation to wildfire, changing fire regimes, and unfavourable post-fire climates for forest regeneration provide multiple compounding pathways to facilitate forest change. The research presented here affirms that increasing wildfire activity and severity due to anthropogenic climate change may alter the composition and structure of northwestern Canadian boreal forests, accelerating ecosystem changes expected as northern climates warm and dry.

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Appendix A: Chapter 2 supplementary information

Variability and drivers of burn severity in the northwestern Canadian boreal forest

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Table A1. Representative photographs of surface and overstory burn severity in burn severity classes used for landscape pattern analysis of burn severity.

Burn severity	Surface burn severity	Overstory burn severity
Unchanged		
Low		
Moderate		
High		

Table A2. Spearman's ρ correlation values between burn severity field metrics and remotely sensed burn severity metrics. All correlations are significant ($p \leq 0.001^{***}$).

Burn Severity Field Metric	dNBR	RdNBR	RBR
CBI	0.87	0.88	0.88
BSI	0.78	0.82	0.81
CFSI	0.88	0.87	0.89
MORT	0.45	0.46	0.44

Table A3. Diagnostic generalized linear models of Composite Burn Index (CBI), surface Burn Severity Index (BSI), Canopy Fire Severity Index (CFSI), and proportion overstory mortality (MORT) predicted from the remotely sensed burn severity metrics Differenced Normalized Burn Ratio (dNBR), Relativized dNBR (RdNBR), and Relativized Burn Ratio (RBR). Models are produced using the complete field dataset, and subsets of upland and wetland sites. Model fits are described using 10-fold cross-validated (CV) average of mean absolute error (MAE), root mean square error (RMSE), and R^2 , derived from 100 repeats. P -values of models were derived from χ^2 tests of model deviance explained, relative to a null model.

Topoedaphic context	Formula	Distribution	p	CV MAE	CV RMSE	CV R^2
All sites	$CBI = dNBR \times (0.1651[dNBR] + 161.8346)^{-1}$		<0.001***	0.38	0.45	0.83
	$CBI = RdNBR \times (0.5238[RdNBR] + 46.1349)^{-1}$		<0.001***	0.34	0.40	0.87
	$CBI = RBR \times (0.1267[RBR] + 140.1737)^{-1}$		<0.001***	0.36	0.43	0.85
Uplands	$CBI = dNBR \times (0.1726[dNBR] + 154.9802)^{-1}$	Gaussian	<0.001***	0.35	0.42	0.87
	$CBI = RdNBR \times (0.01090[RdNBR] + 354.3011)^{-1}$		<0.001***	0.27	0.32	0.93
	$CBI = RBR \times (0.0134[RBR] + 134.7148)^{-1}$		<0.001***	0.32	0.37	0.91
Wetlands	$CBI = dNBR \times (0.1602 [dNBR] + 172.4305)^{-1}$		0.004**	0.42	0.46	0.95
	$CBI = RdNBR \times (0.7061[RdNBR] + 47.2293)^{-1}$		0.006**	0.48	0.53	0.94
	$CBI = RBR \times (0.1364[RBR] + 144.6818)^{-1}$		0.006**	0.44	0.48	0.94
All sites	$BSI = 0.6178 + (dNBR \times 0.0037)$		<0.001***	0.71	0.80	0.66
	$BSI = 1.4840 + (RdNBR \times 0.0021)$		<0.001***	0.61	0.71	0.72
	$BSI = 0.5370 + (RBR \times 0.0051)$		<0.001***	0.66	0.75	0.70
Uplands	$BSI = 0.7338 + (dNBR \times 0.0038)$	Gaussian	<0.001***	0.77	0.87	0.63
	$BSI = 1.5377 + (RdNBR \times 0.0023)$		<0.001***	0.62	0.70	0.73
	$BSI = 0.6103 + (RBR \times 0.0053)$		<0.001***	0.69	0.79	0.68
Wetlands	$BSI = 0.5941 + (dNBR \times 0.0027)$		0.003**	0.49	0.54	0.93
	$BSI = 1.5530 + (RdNBR \times 0.0014)$		0.004**	0.52	0.56	0.93
	$BSI = 0.5701 + (dNBR \times 0.0035)$		0.003**	0.50	0.54	0.93
All sites	$CFSI^\dagger = -0.6256 + (dNBR^2 \times 0.0065)$		<0.001***	0.84	0.99	0.79
	$CFSI^\dagger = -0.5809 + (RdNBR^2 \times 0.0035)$		<0.001***	0.89	1.04	0.76
	$CFSI^\dagger = -0.6813 + (RBR^2 \times 0.0087)$		<0.001***	0.84	0.98	0.80
Uplands	$CFSI^\dagger = -0.1493 + (dNBR^2 \times 0.000008)$	Gaussian	<0.001***	0.76	0.97	0.84
	$CFSI^\dagger = -0.0264 + (RdNBR \times 0.000002)$		<0.001***	0.72	0.95	0.83
	$CFSI^\dagger = -0.7274 + (RBR^2 \times 0.0087)$		<0.001***	0.66	0.88	0.87
Wetlands [‡]	-		-	-	-	-
All sites	$MORT^\ddagger = -3.361 + (dNBR \times 0.0134)$		<0.001***	0.09	0.15	0.83
	$MORT^\ddagger = -3.5882 + (RdNBR \times 0.008)$		<0.001***	0.08	0.14	0.86
	$MORT^\ddagger = -3.508 + (RBR \times 0.0185)$		<0.001***	0.09	0.15	0.85
Uplands	$MORT^\ddagger = -3.1826 + (dNBR \times 0.0124)$	Quasibinomial	<0.001***	0.11	0.16	0.82
	$MORT^\ddagger = -3.3706 + (RdNBR \times 0.0073)$		<0.001***	0.09	0.14	0.86
	$MORT^\ddagger = -3.3176 + (RBR \times 0.0170)$		<0.001***	0.10	0.15	0.84
Wetlands [‡]	-		-	-	-	-

[†]Subset of forested sites only, excluding data from open wetlands.

[‡]Not enough sites to create significant bivariate model of subgroup.

Table A4. Spatial patch statistics of burn severity patterns derived from classified remotely sensed burn severity images, in six sampled wildfires. Patch metrics were produced in FRAGSTATS from classified maps of burn severity, using the 8-neighbour rule. Orange cells contain the highest value of the landscape pattern metric, and blue cells contain the lowest value.

Fire	Burn Severity Class	Proportion of Landscape				Area-Weighted Mean Patch Size (ha)				Area-Weighted Mean Perimeter-Area Ratio				Total Core Area (>600m from edge; ha)				Clumpiness Index			
		CBI	BSI	CFSI	MORT	CBI	BSI	CFSI	MORT	CBI	BSI	CFSI	MORT	CBI	BSI	CFSI	MORT	CBI	BSI	CFSI	MORT
All Fires	Unchanged	6.49	5.76	16.16	14.74	1051.62	886.42	12748.63	10691.56	250.12	264.08	193.79	210.00	17.46	2.52	3535.65	2899.98	0.80	0.79	0.83	0.82
	Low	32.18	29.29	31.43	13.18	22360.71	22524.88	5314.48	361.11	218.82	223.30	269.27	483.85	708.30	488.88	150.66	0.00	0.76	0.76	0.71	0.58
	Moderate	36.55	48.25	45.16	28.22	31732.39	83697.17	13450.88	13877.73	257.09	177.14	167.83	340.94	0.72	4.32	684.54	0.00	0.70	0.74	0.77	0.64
	High	24.79	16.70	7.25	43.86	585.80	314.38	144.23	2819.58	169.30	196.58	257.22	129.23	350.91	92.52	0.00	3553.02	0.83	0.82	0.79	0.83
2014ZF-020	Unchanged	11.11	9.90	25.56	23.45	1156.75	971.38	15196.35	12663.73	236.05	250.73	174.09	190.12	17.46	2.52	3516.84	2881.44	0.80	0.79	0.83	0.81
	Low	38.72	36.81	30.89	16.36	34187.23	33140.08	7547.59	65.98	200.03	203.43	284.03	490.66	0.90	0.99	0.00	0.00	0.76	0.76	0.69	0.56
	Moderate	27.33	37.79	37.10	22.43	1186.52	16316.65	4175.96	162.91	314.17	211.48	178.29	416.27	0.00	0.00	28.53	0.00	0.68	0.75	0.79	0.60
	High	22.85	15.50	6.45	37.76	491.90	297.55	98.65	2149.84	165.85	193.89	264.69	128.17	63.63	0.00	0.00	1007.73	0.84	0.83	0.79	0.85
2014ZF-017	Unchanged	0.97	0.85	3.24	3.04	32.29	32.18	28.36	27.73	398.07	409.36	389.90	410.60	0.00	0.00	0.00	0.00	0.70	0.69	0.70	0.68
	Low	18.88	14.63	29.77	5.73	177.46	82.49	955.31	14.33	333.76	364.08	283.97	663.79	0.00	0.00	0.00	0.00	0.69	0.68	0.70	0.47
	Moderate	54.81	68.65	60.91	38.24	67600.54	173576.78	26910.06	2626.62	203.39	140.44	153.42	274.41	0.00	0.00	0.00	0.00	0.66	0.67	0.71	0.67
	High	25.34	15.86	6.08	52.99	247.03	98.80	28.28	3113.30	197.85	233.71	311.38	140.13	0.00	0.00	0.00	18.90	0.80	0.79	0.75	0.78
2014ZF-046	Unchanged	3.20	2.79	11.47	10.07	42.77	42.87	155.85	146.16	349.80	362.56	252.48	268.10	0.00	0.00	0.09	0.00	0.73	0.72	0.79	0.78
	Low	35.99	32.55	36.50	16.67	1390.23	997.87	6094.86	136.49	199.12	206.77	232.05	401.97	0.00	0.00	0.00	0.00	0.77	0.77	0.73	0.64
	Moderate	33.70	45.68	43.86	28.92	2100.09	14003.93	3739.42	1053.73	277.14	191.82	175.89	341.56	0.00	0.00	3.33	0.00	0.69	0.74	0.77	0.64
	High	27.11	18.98	8.17	44.34	1242.26	489.66	124.91	2770.05	148.62	174.48	262.78	122.75	0.00	0.00	0.00	409.95	0.85	0.84	0.79	0.84
2014WB-028	Unchanged	0.95	0.72	9.13	8.17	11.19	10.43	535.90	552.21	489.90	507.51	209.49	219.99	0.00	0.00	18.72	18.54	0.64	0.63	0.83	0.82
	Low	28.00	25.06	26.84	10.81	897.96	846.12	636.47	40.24	203.79	205.68	261.48	459.00	0.09	0.45	0.00	0.00	0.79	0.80	0.73	0.62
	Moderate	28.15	38.57	38.27	23.01	438.45	2584.56	1467.11	152.69	327.89	233.44	231.67	369.98	0.00	0.00	19.35	0.00	0.66	0.72	0.72	0.64
	High	42.91	35.65	25.76	58.01	1384.25	874.47	463.81	6149.73	113.46	123.91	148.01	93.27	217.98	92.52	0.00	1494.36	0.85	0.86	0.85	0.84
2014WB-002	Unchanged	0.38	0.28	8.01	5.34	10.31	5.47	132.41	86.95	402.74	447.73	247.18	276.13	0.00	0.00	0.00	0.00	0.72	0.68	0.80	0.79
	Low	48.43	44.32	49.30	27.85	8399.42	7768.65	10782.41	4899.69	90.77	96.77	117.55	188.29	707.31	487.44	150.66	0.00	0.87	0.87	0.83	0.81
	Moderate	29.85	42.37	39.70	30.76	1212.94	5515.48	7201.32	2803.51	218.98	149.54	117.18	228.55	0.00	0.00	633.33	0.00	0.77	0.81	0.86	0.76
	High	21.34	13.02	2.99	36.04	1931.05	301.79	34.08	3355.67	130.83	186.10	314.17	96.41	69.30	0.00	0.00	617.85	0.88	0.84	0.76	0.89
2014WB-020	Unchanged	0.66	0.48	8.10	6.94	3.56	3.00	90.77	55.95	455.49	481.48	204.86	227.59	0.00	0.00	0.00	0.00	0.68	0.66	0.84	0.83
	Low	36.21	31.33	41.05	14.38	2736.59	903.19	3625.62	44.81	157.77	170.86	172.56	368.45	0.00	0.00	0.00	0.00	0.82	0.82	0.79	0.68
	Moderate	46.23	59.15	48.65	39.39	3814.32	7039.16	903.49	3420.64	179.45	119.86	125.70	228.15	0.72	4.32	0.00	0.00	0.76	0.79	0.82	0.72
	High	16.89	9.04	2.20	39.29	153.55	59.03	20.57	405.82	181.71	221.09	285.42	131.42	0.00	0.00	0.00	4.23	0.84	0.83	0.80	0.84

Table A5. Importance (t) of predictor variables in prognostic multivariable generalized linear models explaining burn severity field metrics from pre-fire and fire weather drivers.

Model	Variable	Importance (t)
$CBI = 1.883 - (BA \times 0.03451) + (CBH \times 0.1361) - (WET \times 0.9656) + 0.00009(WET \times STEMS) + (STEMS \times 0.000009)$	BA	4.98
	CBH	4.21
	WET	3.58
	WET \times STEMS	2.91
	STEMS	0.59
$BSI = 0.5082 - (WET \times 1.1514) - (FL \times 0.0507) + (CBH \times 0.0979) + (CON \times 0.0272) + (BUI \times 0.0212) - 0.0003(CON \times BUI)$	WET	4.58
	FL	3.55
	CBH	2.66
	CON	2.62
	BUI	2.62
$CFSI^{\dagger} = 4.2193 - (BA \times 0.0707) + 0.2192(CBH \times \log(STEMS)) - (CBH \times 1.5453) - (\log(STEMS) \times 0.2215)$	CON \times BUI	2.58
	BA	3.81
	CBH \times log(STEMS)	2.23
	CBH	1.93
$MORT^{\dagger} = 1.9986 - (BA \times 0.0872) + (CBH \times 0.3972)$	log(STEMS)	0.53
	BA	3.44
	CBH	2.08

\dagger Subset of forested sites only, excluding data from open wetlands.

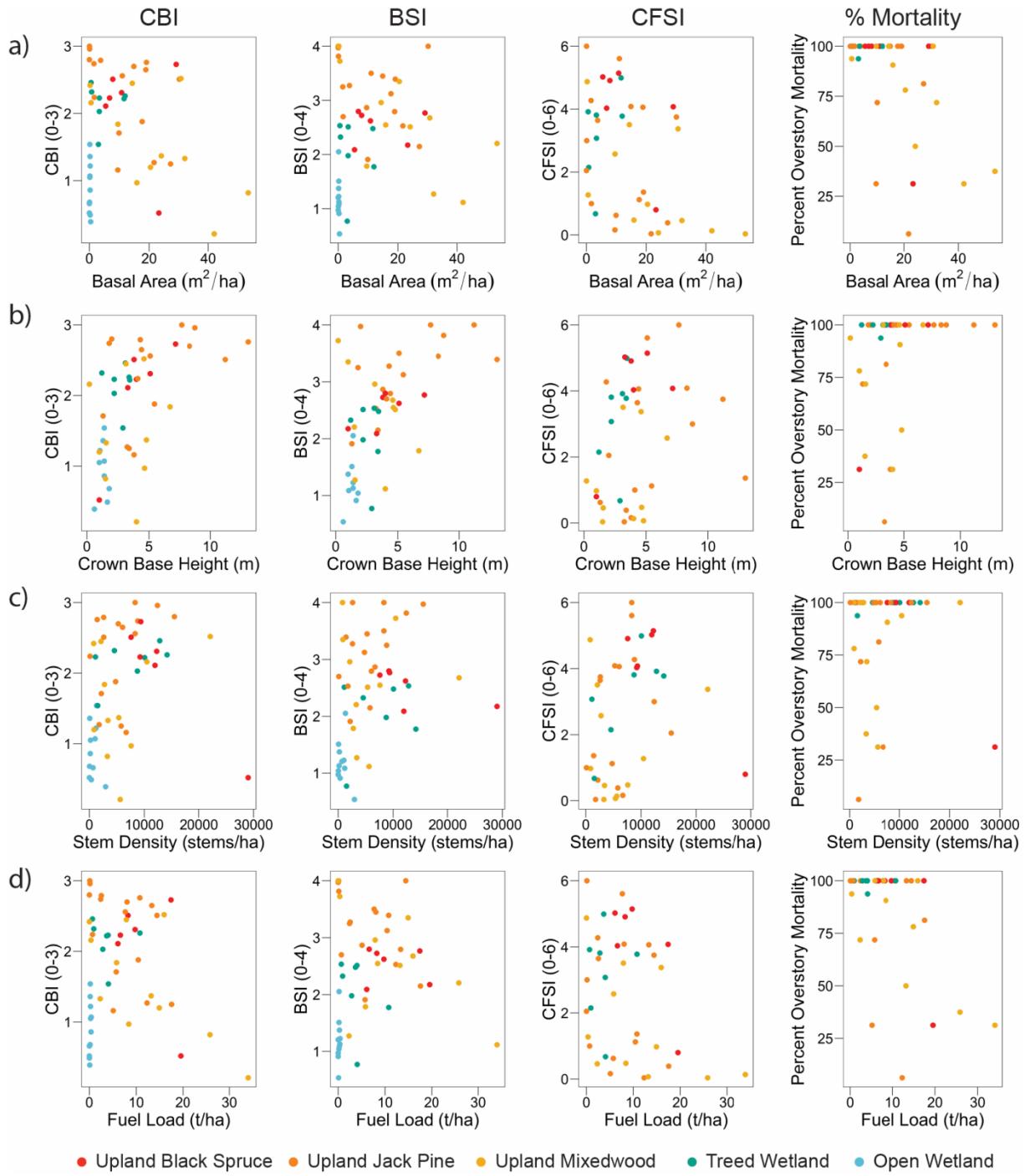


Figure A1. Relationships between burn severity metrics of Composite Burn Index (CBI), surface Burn Severity Index (BSI), Canopy Fire Severity Index (CFSI), and percent overstory mortality and a) pre-fire basal area (m^2/ha), b) median live crown base height of conifer species (m), c) stem density (stems/ha), and d) pre-fire overstory fuel load (t/ha). Observations are colored by vegetation community.

Table A6. Generalized linear models of Composite Burn Index (CBI), surface Burn Severity Index (BSI), Canopy Fire Severity Index (CFSI) and proportion overstory mortality (MORT) explained by pre-fire fuel structure, topoedaphic context, fire weather at the time of burning, and post-fire remotely sensed burn severity. dNBR, RdNBR, and RBR were added to the multivariable prognostic models to characterize the additional explanatory power gained from post-fire estimates of severity, and to allow comparisons between the importance of pre-fire and fire weather drivers, and post-fire measures in explaining observed burn severity. Model fits are described using 10-fold cross-validated (CV) average of mean absolute error (MAE), root mean square error (RMSE), and R^2 , derived from 100 repeats. P -values of models were derived from χ^2 tests of model deviance explained, relative to a null model.

Field Metric	Model	Distribution	<i>p</i>	CV MAE	CV RMSE	CV R^2
CBI	CBI ~ Field Data	Gaussian	0.004**	0.44	0.54	0.62
	CBI ~ Field Data + dNBR		0.003**	0.42	0.50	0.68
	CBI ~ Field Data + RdNBR		0.003**	0.41	0.50	0.68
	CBI ~ Field Data + RBR		<0.001***	0.31	0.36	0.85
BSI	BSI ~ Field & Wx Data	Gaussian	<0.001***	0.52	0.63	0.64
	BSI ~ Field & Wx Data + dNBR		<0.001***	0.51	0.64	0.62
	BSI ~ Field & Wx Data + RdNBR		<0.001***	0.51	0.64	0.62
	BSI ~ Field & Wx Data + RBR		<0.001***	0.47	0.57	0.69
CFSI [†]	CFSI ~ Field Data	Gaussian	<0.001***	1.27	1.46	0.62
	CFSI ~ Field Data + dNBR		<0.001***	1.17	1.41	0.65
	CFSI ~ Field Data + RdNBR		<0.001***	1.20	1.42	0.66
	CFSI ~ Field Data + RBR		<0.001***	0.81	0.96	0.81
MORT [†]	MORT ~ Field Data	Quasibinomial	0.019*	0.13	0.17	0.65
	MORT ~ Field Data + dNBR		0.029*	0.13	0.18	0.68
	MORT ~ Field Data + RdNBR		0.033*	0.13	0.19	0.66
	MORT ~ Field Data + RBR		0.004**	0.09	0.15	0.83

[†]Subset of forested sites only, excluding data from open wetlands.

Table A7. Importance (t) of predictor variables in prognostic multivariable generalized linear models explaining burn severity field metrics by pre-fire fuel structure, topoedaphic context, fire weather at the time of burning, and remotely sensed burn severity metrics.

Field Metric	Field Data		Field Data + dNBR		Field Data + RdNBR		Field Data + RBR	
	Variable	t	Variable	t	Variable	t	Variable	t
CBI	BA	4.98	CBH	5.06	CBH	5.05	RBR	7.73
	CBH	4.21	BA	4.03	BA	4.18	BA	4.76
	WET	3.58	dNBR	3.28	RdNBR	3.34	WET	2.97
	WET × STEMS	2.91	WET	2.67	WET	3.18	CBH	2.90
	STEMS	0.59	WET × STEMS	2.41	WET × STEMS	2.90	WET × STEMS	2.74
	-	-	STEMS	0.62	STEMS	0.60	STEMS	1.37
BSI	WET	4.58	WET	4.27	WET	4.37	WET	4.38
	FL	3.55	FL	3.35	FL	3.36	RBR	3.25
	CBH	2.66	CBH	2.77	CBH	2.77	FL	3.18
	CON	2.62	CON	2.40	CON	2.37	CON × BUI	2.17
	BUI	2.62	CON × BUI	2.37	CON × BUI	2.32	CON	2.16
	CON × BUI	2.58	BUI	2.33	BUI	2.29	BUI	1.92
CFSI [†]	-	-	dNBR	0.99	RdNBR	0.98	CBH	1.53
	BA	3.81	BA	2.77	BA	2.89	RBR	7.18
	CBH × log(STEMS)	2.23	dNBR	2.70	CBH × log(STEMS)	2.64	CBH × log(STEMS)	2.69
	CBH	1.93	CBH × log(STEMS)	2.60	RdNBR	2.52	CBH	2.59
	log(STEMS)	0.53	CBH	2.22	CBH	2.27	BA	2.41
	-	-	log(STEMS)	1.34	log(STEMS)	1.30	log(STEMS)	1.32
MORT [†]	BA	3.44	BA	3.02	BA	2.99	RBR	4.80
	CBH	2.08	CBH	2.36	CBH	2.30	BA	2.77
	-	-	dNBR	1.84	RdNBR	1.59	CBH	1.45

[†]Subset of forested sites only, excluding data from open wetlands.

Appendix B: Chapter 3 supplementary information

Topoedaphic and forest controls on post-fire vegetation assemblies are modified by fire history and burn severity in the northwestern Canadian boreal forest

Ellen Whitman, Marc-André Parisien, Dan K. Thompson, and Mike D. Flannigan

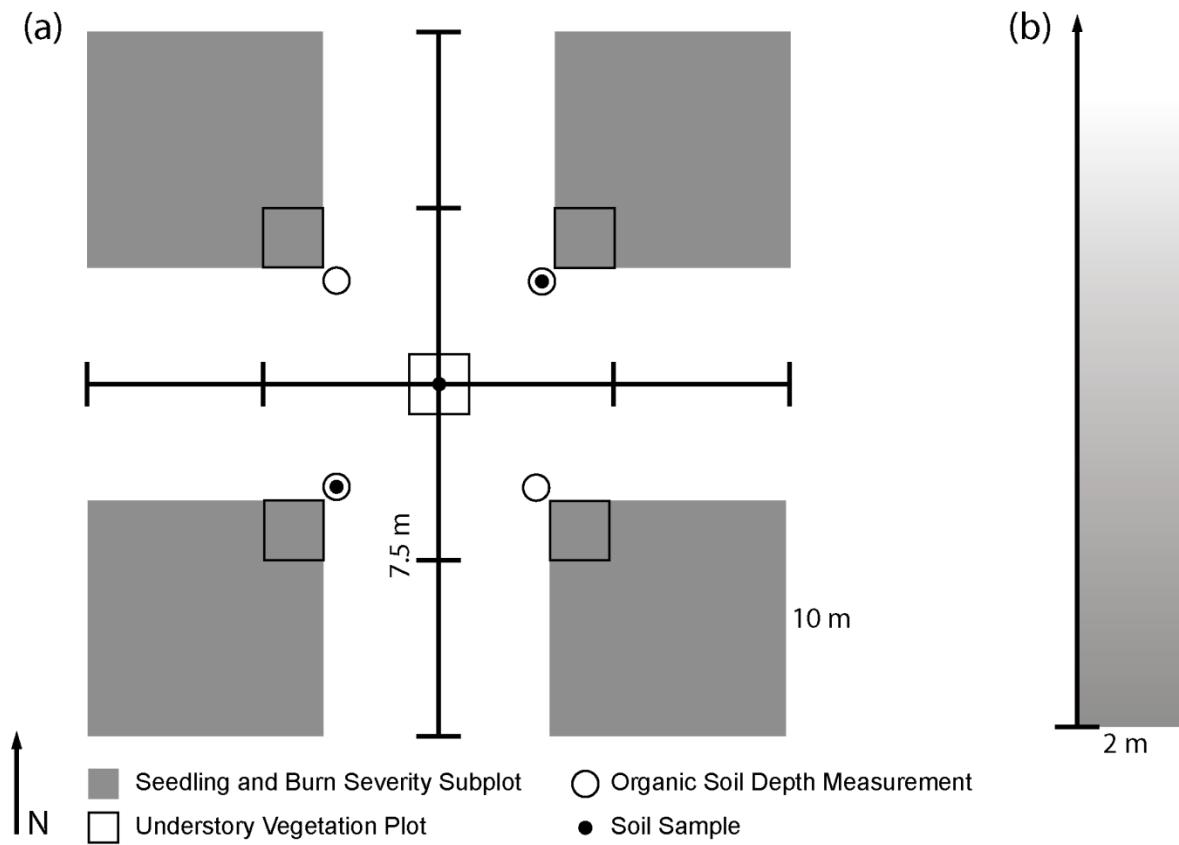


Figure B1. Plot layouts used for field sampling: (a) 30×30 m square plot one year post-fire; and (b) 35×2 m belt transect for re-measurement of seedlings three years post-fire. Plot layouts and symbols are not to scale.

Table B1. Descriptive multivariable linear mixed-effects models explaining post-fire organic soil depth and soil chemical properties as a function of topoedaphic vegetation classes (TVC) and observed surface burn severity, represented by the Burn Severity Index (BSI). The statistical significance of independent predictor variables in explaining soil properties was determined using an ANOVA considering Type II sums of squares. Significance of independent variables to soil properties is signified as follows: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$. Some interactions are nearly significant ($\alpha = 0.1$).

Soil Property	Multivariable Linear Mixed-Effects Model	Independent Variable	Degrees of Freedom	Sums of Squares	F	p
Organic Soil Depth (cm)	$OSD = TVC + BSI + (TVC \times BSI) Fire Name$	TVC	4	91.50	10.10	***<0.001
		BSI	1	30.68	13.54	***<0.001
		TVC \times BSI	4	8.80	0.97	0.43
Total Nitrogen (%)	$TN = TVC + BSI + (TVC \times BSI) Fire Name$	TVC	4	2.34	8.50	***<0.001
		BSI	1	0.81	11.77	**0.001
		TVC \times BSI	4	0.26	0.96	0.44
pH	$pH = TVC + BSI + (TVC \times BSI) Fire Name$	TVC	4	0.21	0.06	0.99
		BSI	1	0.02	0.02	0.88
		TVC \times BSI	4	0.85	0.25	0.91
Electrical Conductivity	$EC = TVC + BSI + (TVC \times BSI) Fire Name$	TVC	4	3.16	2.08	0.10
		BSI	1	0.32	0.84	0.36
		TVC \times BSI	4	0.59	0.39	0.82
Total Carbon (%)	$TC = TVC + BSI + (TVC \times BSI) Fire Name$	TVC	4	1697.20	13.20	***<0.001
		BSI	1	382.75	11.90	**0.001
		TVC \times BSI	4	91.91	0.71	0.59
Sodium	$Na = TVC + BSI + (TVC \times BSI) Fire Name$	TVC	4	121,344	6.20	***<0.001
		BSI	1	26,453	5.41	*0.02
		TVC \times BSI	4	41,222	2.11	0.09
Potassium	$K = TVC + BSI + (TVC \times BSI) Fire Name$	TVC	4	59,853	0.60	0.67
		BSI	1	35,436	1.41	0.24
		TVC \times BSI	4	226,446	2.26	0.08
Calcium †	$Ca = TVC + BSI + (TVC \times BSI) Fire Name$	TVC	4	2,000,913,013	4.00	**0.007
		BSI	1	672,020,248	5.37	*0.02
		TVC \times BSI	4	656,747,510	1.31	0.28
Magnesium	$Mg = TVC + BSI + (TVC \times BSI) Fire Name$	TVC	4	23,579,801	5.54	***0.001
		BSI	1	5,452,454	5.13	*0.03
		TVC \times BSI	4	6,042,409	1.42	0.25

† Calculated using Kenward–Roger approximation of degrees of freedom, due to the mathematical failure of Satterthwaite's approximation.

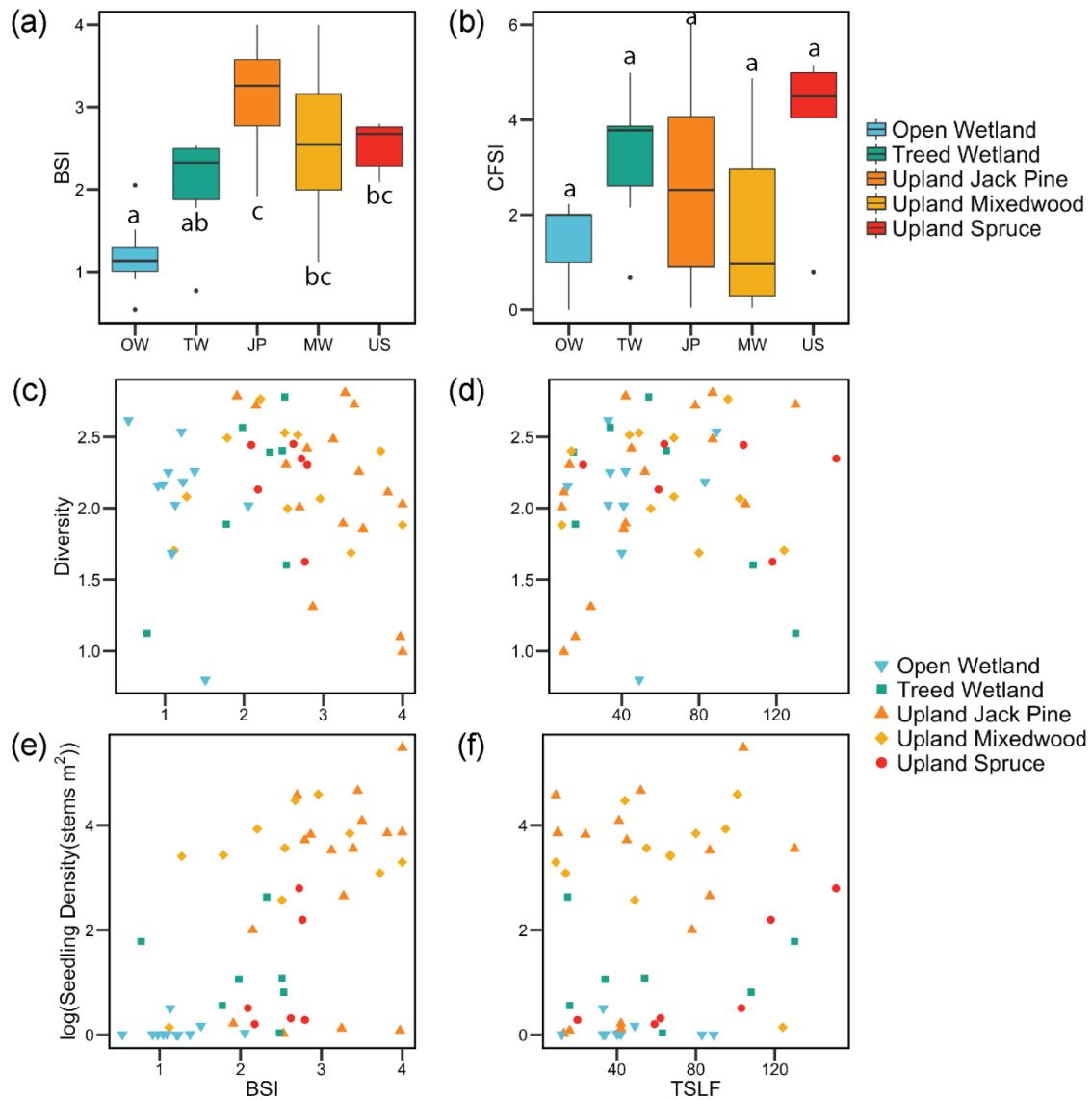


Figure B2. Descriptive plots of observed burn severity, fire history, and topoedaphic vegetation classes in relation to Shannon diversity index and seedling density within sampled plots. Patterns of burn severity within topoedaphic vegetation classes of open wetland (OW), treed wetland (TW), upland mixedwood (MW), upland jack pine (JP), and upland black or white spruce (US) are presented in (a) boxplots of surface burn severity index (BSI), and (b) boxplots of canopy fire severity index (CFSI). Letters associated with boxplots indicate significant differences ($\alpha = 0.05$) in a Tukey test of least-squares means. Shannon index is shown as a function of BSI (c) and time since last fire (TSLF; d), and the natural logarithm of stem density of seedlings is also shown as a function of BSI (e) and TSLF (f).

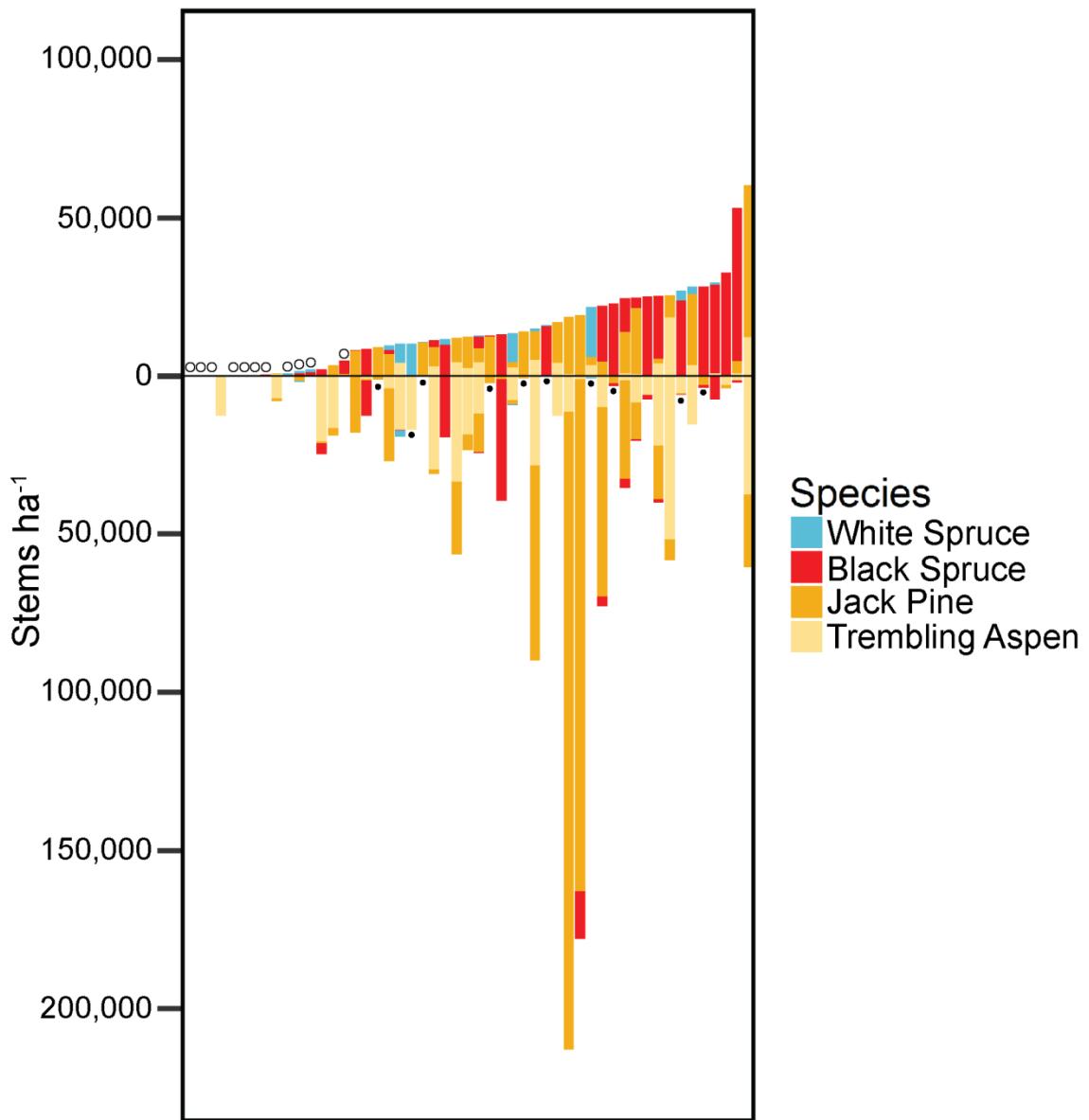


Figure B3. Pre-fire overstory (top) and post-fire (bottom) densities of trees (stems ha^{-1}) by species at 51 sampled field sites. Sites are ordered from left to right by increasing pre-fire stem density. Non-forested open wetland sites are indicated with a letter O above the pre-fire stem density. Open wetlands and all sites indicated with a black dot below the post-fire density were sampled one year post-fire only. All other sites represent seedling data from three years post-fire.

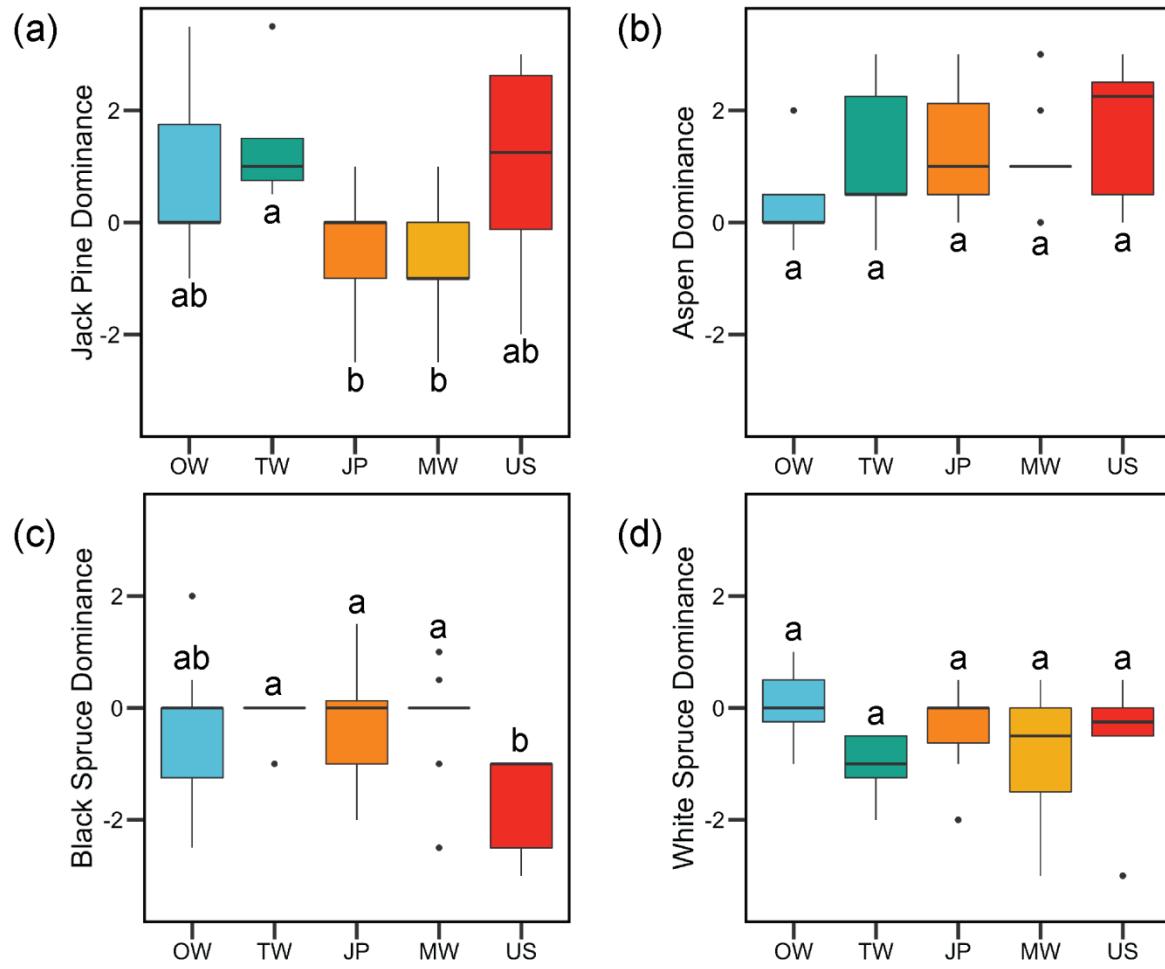


Figure B4. Increases and decreases in post-fire dominance of (a) jack pine, (b) trembling aspen, (c) black spruce, and (d) white spruce, within topoedaphic vegetation classes of open wetland (OW; blue), treed wetland (TW; green), upland mixedwood (MW; yellow), upland jack pine (JP; orange), and upland black or white spruce (US; red). Values of 0 indicate no change in dominance, whereas values greater than 0 indicate sites with an increase in dominance post-fire, and those sites that experienced a decline of the species of interest in the post-fire cohort have negative values. Letters above or below boxplots indicate significant differences in least-squares means ($\alpha = 0.05$), with a post-hoc Tukey test for multiple comparisons.

Appendix C: Chapter 4 supplementary information

Boreal forest resilience to short-interval wildfire is further impeded by drought

Ellen Whitman, Marc-André Parisien, Dan K. Thompson, Mike D. Flannigan

Field data limitations and sampling details

All sampled sites were paired with a site burned in the same wildfire and year, with the exception of one pair. The long FFI member of this pair burned in a holdover of the same fire, one year after the short member site burned. Generally, the more recently an area has burned, the lower the seedling density and vegetation cover, and the higher the observed soil burn severity. Because our results suggested that these characteristics are associated with short FFIs we were comfortable with this bias, as it did not exaggerate the effect of a short interval, but rather dampened the effect of a long one. We paired two short FFI sites with the same long FFI site, which we sampled in the same ecosite and wildfire as the short FFI pair-members. The understory tree data from one wetland site, and shrub data from two sites (one upland and one wetland) were lost due to a technical error with data collection equipment. We excluded both pair-members from paired analyses of differences between sites.

Table C1. Ecological characteristics of sampled sites, and distribution of time since last fire (TSF) and fire-free interval (FFI).

Pair name	Hydrology	Ecosite	Prior Fire Year Long (FFI)	Prior Fire Year Short (FFI)	Recent Fire Year	TSF at sample date ($\bar{x}=6.4$)
16-NT-11	Upland	C1 Labrador Tea – Jack Pine/Black Spruce	1942 (66)	1998 (10)	2008	8
16-NT-12	Wetland	F3 Horsetail – White Spruce	1973 (35)	1998 (10)	2008	8
16-NT-13	Wetland	E2 Dogwood – Jack Pine/White Spruce	1947 (61)	1998 (10)	2008	8
16-NT-16	Upland	C1 Labrador Tea – Jack Pine/Black Spruce	1901 (107)	1999 (9)	2008	8
16-NT-17	Upland	A1 Lichen- Jack Pine	1900 (108)	1999 (9)	2008	8
16-NT-18	Wetland	J1 Treed poor fen	1903 (112)	2011 (4)	2015	1
16-NT-19	Upland	A1 Lichen – Jack Pine	1976 (39)	1998 (17)	2015	1
16-NT-20	Wetland	J1 Treed poor fen	1976 (39)	1998 (17)	2015	1
16-NT-21	Upland	B1 Blueberry – Jack Pine/Aspen	1921 (74)	1980 (15)	1995	21
16-NT-22	Wetland	K1 Treed rich fen	1965 (30)	1980 (15)	1995	21
16-NT-23	Wetland	K1 Treed rich fen	1940 (55)	1980 (15)	1995	21
16-NT-24	Wetland	I1 Treed bog	1944 (51)	1980 (15)	1995	21
16-WB-01	Upland	C1 Labrador Tea – Jack Pine/Black Spruce	1980 (35)	2011 (4)	2015	1
16-WB-02	Upland	A1 Lichen – Jack Pine	1916 (97)	2005 (8)	2013	3
16-WB-03	Upland	A1 Lichen – Jack Pine	1912 (102)	2004 (10)	2014	2
16-WB-04	Upland	A1 Lichen – Jack Pine	1919 (95)	2004 (10)	2014	2
16-WB-05	Upland	D2 Low-Bush Cranberry – Aspen/White Spruce	1934 ¹⁶ (80)	2005 (9)	2014	2
16-WB-06	Upland	D2 Low-Bush Cranberry – Aspen/White Spruce	1983 (32)	2005 (9)	2014, 2015	1,2
16-WB-07	Upland	C1 Labrador Tea – Jack Pine/Black Spruce	1961 (54)	2004 (11)	2015	1
16-WB-08	Wetland	J1 Treed poor fen	1925 (90)	2004 (11)	2015	1
16-WB-09	Upland	A1 Lichen – Jack Pine	1969 (35)	1998 (6)	2004	12
16-WB-10A	Upland	B1 Blueberry – Jack Pine/Aspen	1977 (37)	2004 (10)	2014	2
16-WB-10B	Upland	B1 Blueberry – Jack Pine/Aspen	1977 (37)	2004 (10)	2014	2
16-WB-14	Upland	B1 Blueberry – Jack Pine/Aspen	1950 (64)	1998 (16)	2014	2
16-WB-15	Upland	B1 Blueberry – Jack Pine/Aspen	1950 (64)	1998 (16)	2014	2

¹⁶ Establishment date of non-serotinous tree (*Picea glauca*), not necessarily from fire origin.

Table C2. Pairwise correlation coefficients (Spearman's ρ) between short- and long-interval pairs.

Variable	ρ
Pre-fire proportion conifer stems	0.6
Pre-fire basal area (BA)	0.57
Moisture regime (subxeric to subhydric)	0.83
Summer climatic moisture deficit (CMD) (1961 – 1990 Normals)	1

Environmental Variables

Table C3. Paired statistical tests of differences in environmental variables between paired short FFI and long FFI sites. We conducted tests with all pairs for which data exists (e.g., some sites had no residual organic soil and thus are excluded from testing of effects on organic soil), and with subgroups of upland and wetland sites. Tests for which we report the *t* statistic are paired student's *t*-tests, and tests for which we report the *V* statistic are nonparametric Wilcoxon signed-rank tests. Significant results ($p \leq 0.05$) are bolded, and p -values with a false-discovery rate correction for multiple comparisons (Benjamini & Hochberg. 1995) are reported in P_{adj} . Grey cells indicate that only three sites make up this dataset, therefore we did not conduct any statistical tests.

Hypothesis and Response	All data				Uplands				Wetlands			
	N pairs	Test Statistic	P	P_{adj}	N pairs	Test Statistic	P	P_{adj}	N pairs	Test Statistic	P	P_{adj}
Canopy density (%) is lower in short FFI sites.	25	<i>V</i> = 288	< 0.001	0.006	17	<i>V</i> = 145	< 0.001	0.009	8	<i>V</i> = 28	0.01	0.015
Biomass of rotten coarse woody debris (kg/m ²) is lower in short FFI sites.	25	<i>V</i> = 249	0.002	0.007	17	<i>V</i> = 126	0.002	0.009	8	<i>V</i> = 20	0.42	0.525
Mean residual organic soil depth (cm) is shallower in short FFI sites.	25	<i>t</i> = 2.76	0.005	0.012	17	<i>t</i> = 0.34	0.02	0.04	8	<i>t</i> = 1.78	0.06	0.15
More exposed mineral soil (% cover) is present post-fire in short FFI sites.	25	<i>V</i> = 22	0.003	0.009	17	<i>V</i> = 20	0.003	0.009	8	<i>V</i> = 0	0.5	0.576
Less surface organic matter (% cover) remains post-fire in short FFI sites.	25	<i>V</i> = 230	0.04	0.052	17	<i>V</i> = 20	0.003	0.009	8	<i>V</i> = 15	0.37	0.505
Post-fire mineral soil pH is higher in short FFI sites.	20	<i>V</i> = 58	0.04	0.052	17	<i>V</i> = 46	0.08	0.105				
Post-fire mineral soil total nitrogen (% N) is lower in short FFI sites	20	<i>V</i> = 162	0.02	0.034	17	<i>V</i> = 105	0.09	0.109				
Residual organic soil total carbon (log(% C)) is lower in short FFI sites.	21	<i>t</i> = 1.73	0.05	0.061	13	<i>t</i> = 1.51	0.08	0.105	8	<i>t</i> = 0.81	0.22	0.413

Seedling recruitment

Table C4. Paired statistical tests of differences in post-fire seedling and propagule cohorts between paired short FFI and long FFI sites. We conducted tests with all pairs for which data exists, and with subsets of upland and wetland sites. Tests for which we report the *t* statistic are paired student's *t*-tests, and tests for which we report the *V* statistic are nonparametric Wilcoxon signed-rank tests. Significant results ($p \leq 0.05$) are bolded, and *p*-values with a false-discovery rate correction for multiple comparisons (Benjamini & Hochberg, 1995) are reported in P_{adj} .

Hypothesis and Response	All data				Uplands				Wetlands			
	N pairs	Test Statistic	P	P_{adj}	N pairs	Test Statistic	P	P_{adj}	N pairs	Test Statistic	P	P_{adj}
Post-fire seedling and propagule density log(stems/m ²) is lower in short FFI sites.	24	<i>V</i> = 233	0.002	0.007	17	<i>V</i> = 123	0.01	0.024	7	<i>V</i> = 20	0.03	0.112
Post-fire conifer seedling density log(stems/m ²) is lower in short FFI sites.	24	<i>V</i> = 255	<0.001	0.006	17	<i>V</i> = 138	0.001	0.008	7	<i>V</i> = 21	0.02	0.100
Post-fire broadleaf seedling and propagule density log(stems/m ²) is lower in short FFI sites.	24	<i>t</i> = -0.16	0.44	0.467	17	<i>t</i> = -0.22	0.42	0.430	7	<i>t</i> = 0.19	0.6	0.600
Post-fire broadleaf seedling and propagule density log(stems/m ²) is higher in short FFI sites.	24	<i>t</i> = -0.16	0.56	0.560	17	<i>t</i> = 0.19	0.43	0.430	7	<i>t</i> = -0.22	0.6	0.600
The proportion of conifer stems in the post-fire cohort is lower in short FFI sites.	24	<i>V</i> = 214	<0.001	0.006	17	<i>V</i> = 125	0.002	0.008	7	<i>V</i> = 14	0.05	0.15

Table C5. Percentage variable contribution of explanatory variables to linear models.

Model	Variable	AIC	ΔAIC	% Contribution
Total post-fire stem density	Full model	431.21		
	Fire-free interval (FFI)	450.07	18.86	82.86
	Site moisture (MOIST)	435.07	3.86	16.96
	Moisture stress (MS)	431.25	0.04	0.20
	Total		22.76	
Conifer post-fire seedling density	Full model	369.97		
	Fire-free interval (FFI)	384.11	14.14	63.021
	Pre-fire percent conifer (%CON)	375.47	5.5	24.51
	Residual organic matter (RO)	371.43	1.46	6.51
	Time since last fire (TSF)	371.07	1.1	4.91
	Moisture stress (MS)	370.21	0.24	1.07
Broadleaf post-fire stem density	Total		22.44	
	Full model	418.82		
	Percent exposed mineral soil and rock (%MIN)	589.15	170.33	36.16
	Residual organic matter (RO)	556.12	137.3	29.14
	Moisture stress (MS)	483.62	65.62	13.93
	Time since last fire (TSF)	480.49	61.67	13.09
Proportion conifer stems	Pre-fire basal area of trees (BA)	455.01	36.19	7.68
	Total		471.11	
	Full model	54.225		
	Fire-free interval (FFI)	66.011	11.786	59.54
	Residual organic matter (RO)	58.406	4.181	21.12
	Percent exposed mineral soil and rock (%MIN)	57.204	2.979	18.04
	Moisture stress (MS)	55.08	0.855	4.32
	Total		19.801	

Table C6. Percentage variable contribution of explanatory variables to linear models, with variance explained by interactions partitioned from main effects. Variables with negative ΔAIC values are retained to demonstrate that the variable is not significant on its own, but are not included in the total sum of ΔAIC .

Model	Variable	AIC	ΔAIC	% Contribution
Total post-fire stem density	Full model	431.21		
	Fire-free interval (FFI)	445.65	14.44	71.03
	Site moisture (MOIST)	435.07	3.86	18.99
	FFI \times MS	433.24	2.03	9.99
	Moisture stress (MS)	429.25	-1.96	0
	Total		20.33	
Conifer post-fire seedling density	Full model	369.97		
	Fire-free interval (FFI)	382.31	12.34	51.91
	Pre-fire percent conifer (%CON)	375.47	5.5	23.14
	RO \times TSF	373.03	3.06	12.87
	Residual organic matter (RO)	368.57	1.4	5.89
	Time since last fire (TSF)	370.69	0.79	3.32
	Moisture stress (MS)	370.56	0.59	2.48
	FFI \times MS	370.06	0.09	0.4
Broadleaf post-fire stem density	Total		23.77	
	Full model	418.82		
	Percent exposed mineral soil and rock (%MIN)	543.38	124.56	30.37
	Residual organic matter (RO)	502.87	84.05	20.5
	Time since last fire (TSF)	480.49	61.67	15.04
	RO \times MS	475.75	56.18	13.7
	MIN \times BA	447.42	28.6	6.97
	Moisture stress (MS)	446.9	28.08	6.85
Proportion conifer stems	Pre-fire basal area of trees (BA)	445.78	26.96	6.57
	Total		410.1	
	Full model	54.225		
	Fire-free interval (FFI)	66.011	11.786	53.82
	Residual organic matter (RO)	58.406	4.181	19.09
	Percent exposed mineral soil and rock (%MIN)	57.263	3.038	13.87
	%MIN \times MS	57.116	2.891	13.20
	Moisture stress (MS)	53.117	-1.108	0
	Total		21.898	

Supplementary plots of marginal effects in models of seedling and propagule recruitment

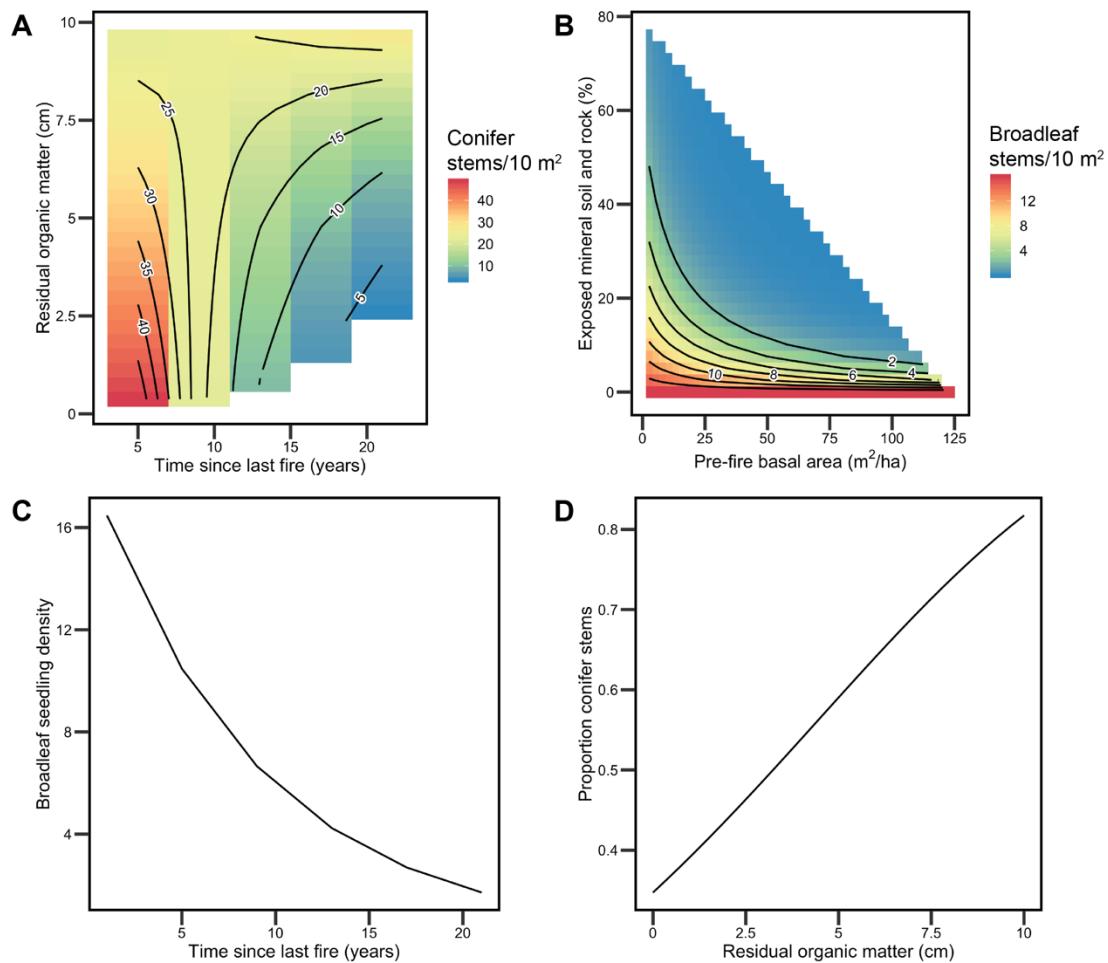


Figure C1. Marginal effects of residual organic matter depth (RO) and time since last fire (TSF) on post-fire stem density and composition of post-fire forests. Deep organic layers (≥ 8 cm) are associated with wetlands, whereas thinner organic layers were largely restricted to uplands. Although models were fitted with standardized predictor variables, plots axes are labelled with observed values and units. (A) Effect of RO and TSF on conifer seedling density. (B) Effect of RO and MS on broadleaf stem density. (C) Effect of TSF on broadleaf stem density in the post-fire cohort. (D) Effect of RO on the proportion of conifer stems in the post-fire cohort.

Understory vegetation

Table C7. Paired statistical tests of differences in post-fire understory vegetation communities between paired short FFI and long FFI sites. We conducted tests with all pairs for which data exists, and with subsets of upland and wetland sites. Tests for which we report the V statistic are nonparametric Wilcoxon signed-rank tests. Significant results ($p \leq 0.05$) are bolded, and p -values with a false-discovery rate correction for multiple comparisons (Benjamini & Hochberg, 1995) are reported in P_{adj} .

Hypothesis and Response	All data				Uplands				Wetlands			
	N pairs	Test Statistic	P	P_{adj}	N pairs	Test Statistic	P	P_{adj}	N pairs	Test Statistic	P	P_{adj}
Tall shrub density log(shrubs/m ²) is higher in short FFI sites.	23	$V = 76$	0.09	0.102	16	$V = 26$	0.05	0.077	7	$V = 11$	0.34	0.505
Cover of herbaceous plants (%) is lower in short FFI sites.	25	$V = 239$	0.02	0.034	17	$V = 120$	0.02	0.04	7	$V = 22$	0.32	0.505
Cover of forbs (%) is lower in short FFI sites.	25	$V = 247$	0.01	0.021	17	$V = 113$	0.04	0.068	7	$V = 29$	0.07	0.15
The proportion of herbaceous vegetation cover contributed by graminoids is higher in short FFI sites.	25	$V = 97$	0.04	0.052	17	$V = 57$	0.19	0.215	7	$V = 3$	0.02	0.10

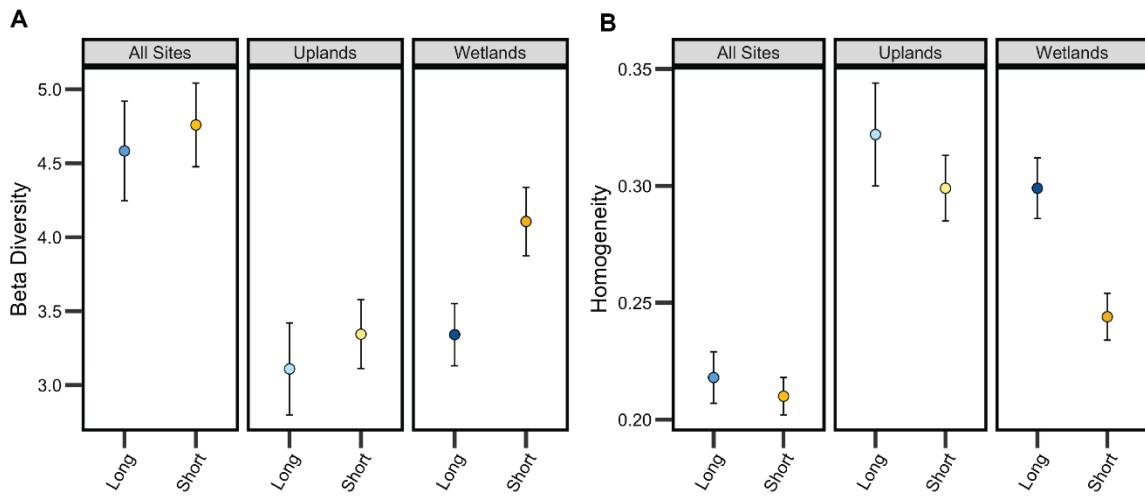


Figure C2. Hill's numbers (calculated using Shannon measures) and 95% confidence intervals for understory vegetation community data, including (A) beta diversity, and (B) homogeneity.

Table C8. Significant indicator species of short and long interval uplands and wetlands identified using multilevel pattern analysis, and their regeneration strategies and fire tolerance. Significance levels are indicated by asterisks after the species name ($p = 0.05^*$, $p = 0.01^{**}$). We identified plant species traits from the Fire Effects Information System (FEIS; <https://www.feis-crs.org/feis/>; 1).

Indicator Species	Reproduction	Post-fire regeneration strategy	Resprouting depth	Shade Tolerance	Leaf type	Fire Tolerance
Long FFI uplands (n=17)						
<i>Linnæa borealis</i> L. **	Stolons & less commonly seed	Surface rhizome & off-site seed	Surface rhizome	All light conditions	Evergreen shrub	Fire intolerant
<i>Dracocephalum parviflorum</i> Nutt. **	Soil seedbanking	Ground residual colonizer	NA	Partial shade to full light	Deciduous forb	Fire-stimulated germinant
<i>Geranium bicknellii</i> Britton *	Soil seedbanking	Ground residual colonizer	NA	Shade intolerant	Deciduous forb	Fire-stimulated germinant
<i>Arctostaphylos uva-ursi</i> (L.) Spreng. *	Stolons & shallow seedbank	Ground residual colonizer, Initial off-site colonizer	Shallow root crown	Shade intolerant	Evergreen shrub	Tolerant of moderate intensity fire, depending on rooting depth
Short FFI uplands (n=17)						
<i>Leymus innovatus</i> (Beal) Pilg. *	Rhizomes	Rhizome in soil	Deep rhizome	Partial shade to shade intolerant	Deciduous graminoid	Fire tolerant
Long FFI wetlands (n=8)						
<i>Salix</i> sp. *†	Adventitious bud, root crown	Vigorous resprouting, off-site seed	Stems, root crown, and shallow to deep rhizomes	Partial shade to full light	Deciduous shrub	Tolerant of moderate to high intensity fire and repeated fire
<i>Rhododendron groenlandicum</i> (Oeder) Kron & Judd *	Root crown, rhizome, wind-dispersed seed	Bud & root crown, on-site or off-site seed	Stems, root crown, and shallow to deep rhizomes	Partial shade to full light	Evergreen shrub	Tolerant of low to moderate intensity fire, depending on rooting depth
<i>Equisetum arvense</i> L. *	Rhizomes	Rhizome in soil, ground residual colonizer, initial off-site colonizer	Deep rhizome	All light conditions	Deciduous forb	Fire tolerant
<i>Chamaedaphne calyculata</i> (L.) Moench *	Rhizomes, seed	Rhizome at surface or in soil, off-site seed	Deep rhizome	Shade intolerant	Evergreen shrub	Fire tolerant
<i>Vaccinium uliginosum</i> L. *	Seed, layering, rhizomes	Survivor species, Rhizome or root crown, off-site seed	Shallow to deep rhizome in organic layer	Partial shade to full light	Deciduous shrub	Tolerant of moderate to high-intensity fire that does not completely consume organic layer
Short FFI wetlands (n=8)						
<i>Betula pumila</i> L. **	Layering, root crown, rhizomes, seed	Adventitious buds, rhizome or root crown, off-site colonizer	Deep root and rhizome	Shade intolerant	Deciduous shrub	Tolerant of low to moderate intensity fire
<i>Salix</i> sp *	Adventitious bud, root crown	Vigorous resprouting, off-site seed	Stems, root crown, and shallow to deep rhizomes	Partial shade to full light	Deciduous shrub	Tolerant of moderate to high intensity fire and repeated fire
<i>Epilobium palustre</i> L. *‡ (2, 3)	Stolons & slender rhizomes, seed	Rhizome, seed bank, off-site seed	Unknown	Partial shade to full light	Deciduous forb	Unknown

† *Salix* sp. Characteristics were generalized from *Salix arbusculoides*, *S. fuscescens*, *S. glauca*, *S. lucida*, *S. myrtillifolia*, *S. planifolia*, and *S. scouleriana*.

‡ Species not found in FEIS.

Historical climate and area burned

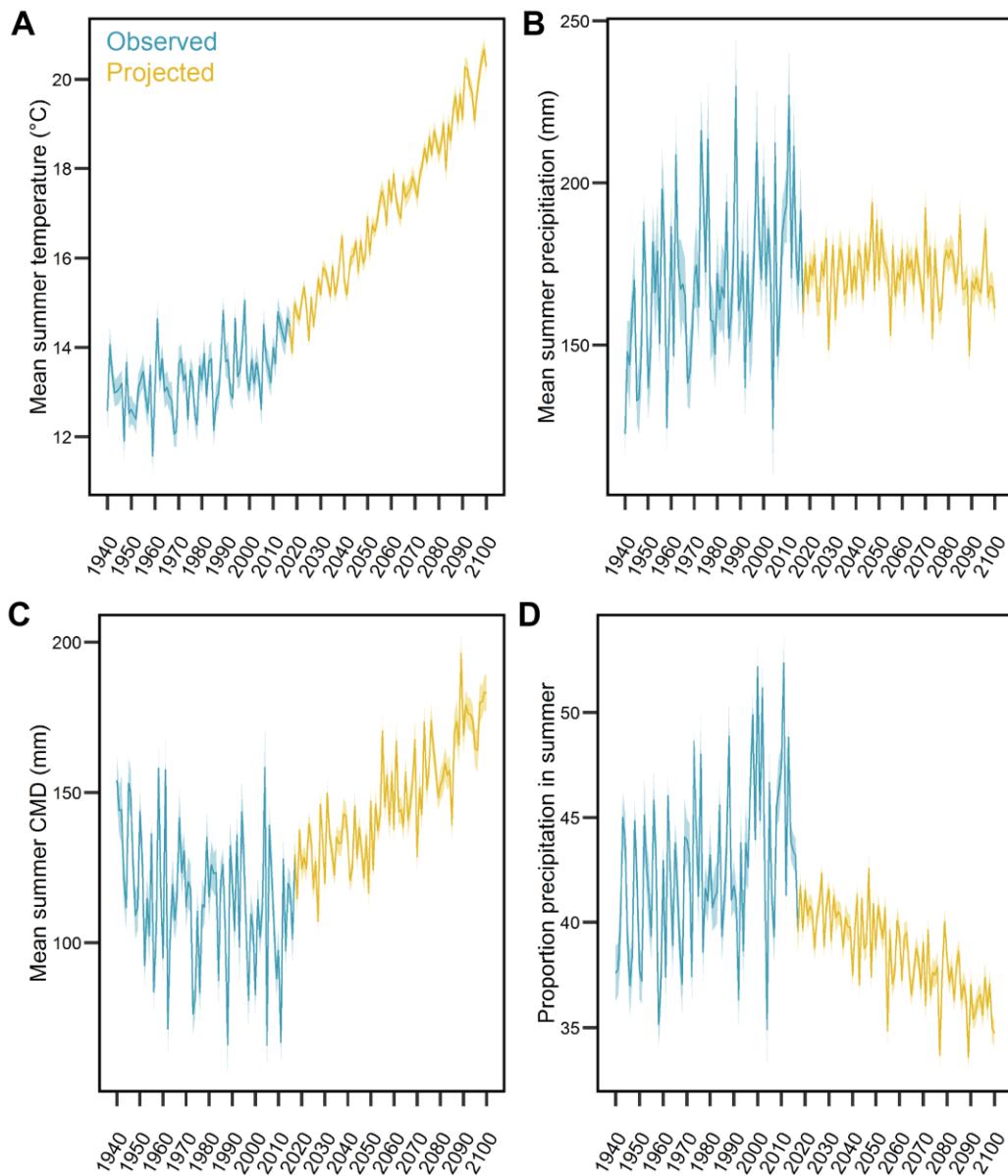


Figure C3. Observed historical summer and projected future climate (RCP 8.5) across the taiga plains and the western portion of the boreal plains ecoregion. Historical climate variables were downscaled from PRISM using ClimateWNA (4) and a digital elevation model (5). Projected climate conditions are an average of an ensemble of projections from 5 global circulation models (GCMs): ACCESS1.0, CanESM2, CNRM-CM5, CCSM4, and CSIRO Mk 3.6. Shaded areas behind darker lines represent the 95% confidence interval for the mean. Climate variables displayed are: (A) Mean summer temperature (°C), (B) Mean summer precipitation (mm), (C) Mean summer climatic moisture deficit (CMD; mm), and (D) the mean proportion of total annual precipitation occurring in the summer months.

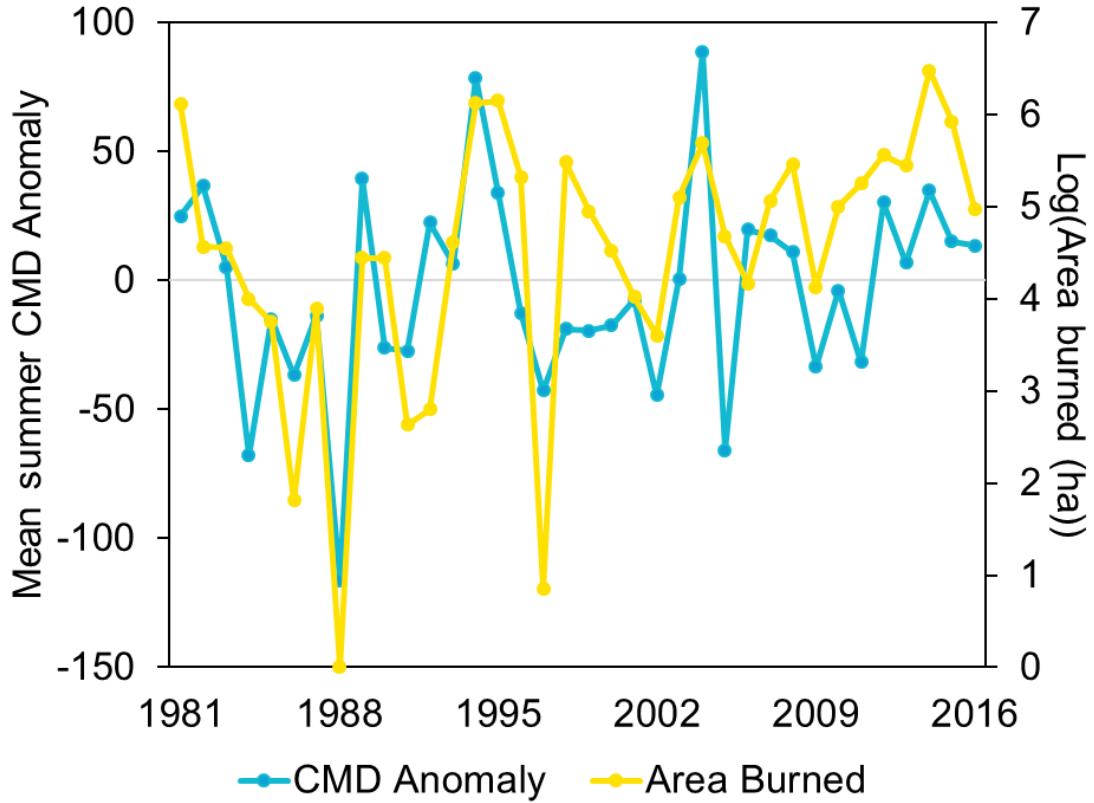


Figure C4. Temporal correlation (Spearman's $\rho = 0.6$) between annual summer climatic moisture deficit (CMD) anomaly relative to a 30-year mean of summer CMD at sampled sites, and annual area burned (ha) within 150 km distance from field sites. The reference period for each year's anomaly is the 30 years prior.

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