BEYOND BLACK SPRUCE: SHIFT IN PLANT COMMUNITIES AFTER FREQUENT FIRE IN A YUKON SUBARCTIC BOREAL FOREST

by © Carissa Wasyliw

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Abstract

Rapid warming in northern climates is altering plant successional trajectories at their northern extent. Changing fire regimes under ongoing climate change are predicted to further influence shifts in vegetation successional trajectories in boreal forests. New fire regimes impact ecosystem vegetation legacies, which dictate the regeneration success of forests and can rapidly change ecosystem states to non-forested trajectories. Two closely timed fires (1990/1, 2005) in the Eagle Plains region of northern Yukon resulted in a failure of black spruce (*Picea mariana*) regeneration. Our study characterized the alternate regeneration trajectories in the absence of black spruce regeneration and examined possible abiotic factors driving those changes. We found evidence of alternate regeneration trajectories favouring tall shrub growth in sites experiencing a shortened fire return interval. Particularly, denser tall-shrub regeneration occurred in sites with deeper active layers. Increased shrub dominance may have implications on culturally significant species such as barren-ground caribou (*Rangifer tarandus*), berry producing plants, and those that depend on these species. Increased shrub growth will impact ecological processes like carbon sequestration, nutrient cycling, and permafrost dynamics. As disturbance regimes evolve, divergent post-fire successional pathways will continue to emerge, influencing other landscape processes, and impact important species to Indigenous communities of the area.

Keywords: post-fire regeneration, fire frequency, climate change, tree regeneration, shrubs, ecological state change

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Table of Contents

List of Tables

List of Figures

List of Appendices

Co-Authorship Statement

Dr. Carissa Brown is a co-author on all chapters of the thesis. Dr. Kirsten Reid is also a co-author on Chapter 2 of the thesis. As the primary author, I have been the principal contributor across all aspects of the thesis including the literature review, project proposal, experimental design, field methods, data analysis, and preparation of the manuscript. Dr. Kirsten Reid contributed significantly to the project proposal, experimental design, field methods, and manuscript review of Chapter 2. Dr. Carissa Brown supported all aspects of the project, and greatly contributed to the experimental design, data analysis, and manuscript preparation.

Chapter 1: Introduction and thesis overview

1.1 Introduction

1.1.1 Climate change and range shifts

Global surface temperatures have increased over the last century due to climate change (IPCC, 2019), with northern climates warming at greater than twice the rate of the global average (Rantanen et al., 2022). At higher latitudes, fluctuations in temperature and precipitation beyond historical ranges are affecting present-day species and biophysical systems in ways that have not been previously observed (Box et al., 2019; IPCC, 2019). As climate warming and extreme weather patterns continue to change, impacts will be felt across the biophysical world causing numerous feedbacks to the environment and the organisms that inhabit northern ecosystems. The effects of these environmental changes are still not fully understood, but will impact the composition of species, their distributions, biomass, phenological timing, nutrient cycling, among other outcomes (Box et al., 2019, Parmesan, 2006).

As climatic conditions shift poleward, species' ranges across numerous taxonomic groups are generally predicted to follow (IPCC, 2019; Parmesan & Yohe, 2003). For instance, the northern or altitudinal limit of tree distributions known as treeline are expected to shift northward in tandem with increases in temperature and precipitation (Harsch et al., 2009). Given that forest growth experiences a common temperature threshold restricting growth among tree species at treeline (Körner & Paulsen, 2004), it is predicted that climate warming could lessen this temperature limitation thus allowing forests to expand their range northward and increase their growth (Ruckstuhl et al., 2008). However, others have observed the opposite effect, showing range contraction at both the northern and southern limits of forest ranges (Zhu et al., 2012).

Some studies have demonstrated that while many tree species would have suitability to grow in warmer climates, certain species are exhibiting limited northward range expansion (Murphy et al., 2010). While studies have shown the potential for a northern shift in forest ranges, there has not yet been any evidence supporting treeline advance over the last half century along the subarctic boreal-tundra ecotone in western North America (Timoney & Mamet, 2020). Furthermore, it is unlikely that the rate of treeline advance along the boreal-tundra ecotone will keep pace with current climate projections (Rees et al., 2020). Conflicting evidence suggests that treeline response to climate change is complex and will likely vary by species and by region (Körner & Paulsen, 2004; Timoney & Mamet, 2020; Trant & Hermanutz, 2014).

Environmental factors other than temperature, such as precipitation, may have a greater influence on tree growth than previously considered and may be responsible for regional variation in tree growth and treeline advance (Rees et al., 2020). For example, in northwestern boreal Alaska, drought stress has reduced black spruce (*Picea mariana*) radial growth (Walker et al., 2015). Drought conditions suggest an increased risk of tree species mortality and die-off due to heat stress and drought (Allen et al., 2010). Increasing unsuitability in climatic conditions and existing vegetation assemblages provides opportunities for new plant communities to thrive and may result in changes to composition and distributions of boreal-tundra ecotonal sites. It is therefore important to assess climatic conditions specific to the area in question to get an accurate interpretation on the response of species range shifts to ongoing climate change.

The link between climate change and the complexity of covarying environmental factors influencing plant growth is well-illustrated by the response of the active layer – the portion of soil that thaws during the growing season in permafrost landscapes – to ongoing global change. The depth of the active layer (ALD) plays an important role in determining which species may grow in a given location, and many physical properties are related to ALD. Air temperature, winter snow conditions, and soil moisture are some of the most important contributors to determining the thickness of the active layer (Zhang & Stamnes, 1998; Wang et al., 2020; Clayton et al., 2021). For instance, the winter insulating effect of snow depth on the soil is thought to increase ALD. Greater snow depth results in more meltwater, increased soil temperature and thermal conductivity, which melts the permafrost and results in a deeper ALD (Johannson et al., 2013; Nowinski et al., 2010). However, greater soil moisture may result in shallower ALD due to the high heat capacity of water (i.e., high latent heat of fusion), meaning that soils with high ice content would require more energy to melt permafrost (Clayton et al., 2021). Both processes may occur simultaneously but in different parts of the soil column, with thermal conductivity being more influential in the upper part of the soil (Clayton et al., 2021). This moisture at the surface of the soil interacts with the energy exchange of the atmosphere via thermal conductivity and effectively regulates the ALD (Hinkel et al., 2001).

Biotic components also exert an influence on ALD. For instance, the soil organic layer acts as a thermal insulator (Dyrness, 1982), retaining moisture, regulating the soil temperature and ultimately the active layer through thermal conductivity (O'Donnell et al., 2009). Bryophyte mats have also been shown to reduce the amplitude of soil temperature fluctuations and likeliness of freeze-thaw during the growing season (Soudzilovskaia et al., 2013). Further, tree and understory canopy covers can limit permafrost thaw, resulting in shallower ALD (Fisher et al., 2016). Therefore, not only does the active layer influence the assemblages of vegetation, but it is also affected by the numerous biotic and abiotic components of its environment and their interactions.

1.1.2 Changing fire regimes in black spruce forests

Disturbance plays an essential role in shaping ecosystems, especially in northern forest ecosystems. Disturbance regimes – a pattern of disturbance over a given time and space – alter ecological trajectories and drive heterogeneity within a given system (Turner, 2010). For instance, fire is considered the dominant process shaping the landscape within the northern boreal forest (Flannigan et al., 2003). Many plant species within this system have evolved to grow in conjunction with this regular pattern of disturbance. Fire regimes consist of spatial and temporal traits including fire frequency, intensity, and severity (Turner, 2010). Fire frequency refers to the interval of time between fires and is hereinafter referred to as fire return interval. The intensity of fire refers to the energy released by the fire (i.e., heat) in a given time and space, while the lasting effects of the fire on the landscape (e.g., the biomass that is consumed) are known as fire severity (McLauchlan et al., 2020). These characteristics of a fire regime shape species' composition, distribution, interaction, and life strategies in the boreal forest (McLauchlan et al., 2020). Plant species within this fire regime have a suite of fire adaptive characteristics that enable them to thrive in this environment (Keeley et al., 2011). In turn, the ecological community also exerts influences on fire behaviour through its traits (McLauchlan et al., 2020). This cycle enables the continued dominance and perpetuation of the same vegetation communities through time.

Features that persist after a disturbance event and affect the resulting ecosystems are important components of disturbance regimes and are known as the ecological memory of a system (Franklin et al., 2000; Johnstone et al., 2016). Ecological memory encompasses both adaptations and physical relics, or information and material legacies, respectively, that guide ecosystem regeneration (Johnstone et al., 2016). Information legacies include species traits that have evolved to recurring disturbances. An example of this can be found in conifer cones of boreal systems through a trait known as serotiny, or the storage of seeds in cone structures that require high temperatures to open and release the seeds (Beaufait, 1960; Viereck, 1983). Material legacies include the physical structures that remain post-fire, like tree seeds or biomass (Johnstone et al., 2016). Together, these legacies allow the perpetuation of the dominant disturbance regimes and drive these cycles into a predictable pattern.

Black spruce dominated forests, which comprise a large proportion of boreal forests along the northern extent, contain many legacies linking their successional trajectories and fire regime. Sites are generally low in productivity, rich in organic soils, and have an understory often covered in sphagnum mosses and reindeer lichen (Black & Bliss, 1980; Van Cleve & Viereck, 1981). Black spruce trees reproduce vegetatively through a process known as layering, where lower branches are covered by forest substrate and develop adventitious roots (Van Cleve & Viereck, 1981). This species also reproduces by seed, an important material legacy, which develop in cones that grow and persist in clusters at the tips of the trees, known as aerial seedbanks. Cones will open and disperse slowly until exposed to fire, where seeds will be largely dispersed due to their semi-serotinous nature (i.e., information legacy; Zasada et al., 1992). Black spruce trees have flammable bark, which in addition to lower branches that die as the tree ages, encourages fire to climb the tree towards the cones. The heat from the fire melts the resin that seals seeds inside the cones, dispersing seeds to the forest floor through a process known as seed rain, which tends to occur within the first few years after fire (Johnstone et al., 2009). The fire consumes some or all of the highly flammable organic layer of the forest floor, providing a flush of nutrients from the burn (Greene et al., 2007; Van Cleve & Viereck, 1981). The consumption of the organic layer also exposes and thaws some of the permafrost layer (i.e., deepens the active layer, described further below) resulting in warmer mineral soil, providing good conditions for seed germination, establishment, and initial growth in some black spruce forests (Charron & Greene, 2002). Black spruce recruitment is more complex in treeline-tundra ecotones, as suitable recruitment substrate can be limiting, and requirements may shift throughout the life cycle of the seedling (Goodwin & Brown, 2023). In such places, black spruce benefits from facilitative interactions having greater survival and growth in *Pleurozium* moss substrates where they are protected from fluctuating temperatures and predation (Wheeler et al., 2021).

Generally, there is less competition for the black spruce on the forest floor post-fire, providing an opportunity for seeds to germinate and establish. This process of post-fire regeneration enables the continued dominance of black spruce through the process known as self-perpetuation. As seedlings grow, the organic layer is built back up, the permafrost recovers, and the sites develop into low productivity black spruce sites once more (Kasischke, 2000). This suite of fire-adapted traits and structures contribute to the ecological memory of the system and ensure continued dominance of black spruce.

In subarctic ecosystems, fire also plays a key role in determining the ALD. Typically, fire will indirectly cause deeper ALD by altering site characteristics that help insulate the permafrost. For instance, typical fire behaviour of boreal ecosystems is to consume the tree canopy and some of the insulating organic layer (Viereck, 1983). A loss in tree canopy will increase the amount of solar radiation that reaches the ground, warming the soil, and will also reduce the ability of trees to transpire, increasing post-fire soil moisture (Fisher et al., 2016). This increase in both soil moisture and soil temperature will promote thawing of permafrost, deepening the ALD. As time passes in these fire adapted ecosystems, vegetation and the organic layer will build back up and gradually the permafrost will recover to a shallower ALD and can take more than 40 years after fire (Heim et al., 2021).

Other vegetation in black spruce landscapes often have fire adaptive traits that enable them to take advantage of the fire cycle. For instance, some forbs and shrubs reproduce vegetatively through their above-ground structures such as rhizomes and below-ground structures like root systems (Zasada, et al., 1992). In low severity fires, these structures are often not entirely consumed by fire, leaving material legacies on the landscape. This allows them to quickly resprout after fire and take immediate advantage of the flush of nutrients (De Groot & Wein, 2004). Other examples of adaptations to this system include information legacies such as strategies for below-ground resource allocation. In permafrost sites, more resources are allocated to fine root structures of both trees and understory plants to improve efficiencies of resource acquisition in colder environments (Noguchi et al., 2016).

While changes in the climate of northern ecosystems can profoundly alter ecological communities through direct effects (e.g., drought stress on forests), climate-induced disruptions to the natural disturbance cycles will incite more change to these systems (Harvey & Enright, 2022). Since the second half of the twentieth century, there has been a marked increase in the burned area of trees, with a decrease in the extent of live trees along the boreal subarctic (Timoney et al., 2019), and the burned area is expected to increase (Flannigan et al., 2005). Fire return interval in this region is shortening, fire seasons are lengthening due to longer growing seasons, and lightning strikes (i.e., ignition sources) are predicted to increase (Kasischke & Turetsky, 2006; Veraverbeke et al., 2017). Changes in human activity, like increased recreational activities and the alteration of fuel loads via commercial and industrial clearing, are also increasing the conditions that lead to ignitions for wildfire (Pausas & Keeley, 2021). Since black spruce seed production is already constrained by environmental conditions along its northern extent (Black & Bliss, 1980), changes to the fire regime across treeline will impose further stress on the ecological system and transform the recovery of vegetation communities. A marked decrease in tree regeneration after fire has already occurred over the last few decades (Stevens-Rumann et al., 2018), exemplifying how changing disturbance regimes could tip the equilibrium of the natural system and change recovery trajectories, including the extent of tree species' ranges.

Changes to the historic disturbance regime are also disrupting reproductive cycles and regeneration strategies of plants in boreal subarctic ecosystems. These changes are shifting information and material legacies out of sync with natural cycles, altering vegetation recovery from predictable, recurring trajectories to unexpected and altered groupings. With an increase in fire frequency and severity, the regeneration of black spruce forests in eastern Canada will be most susceptible to increased temperatures, whereas in western Canada regeneration of the species will be most influenced by drought (Boucher et al., 2020). Increased fire severity is known to reduce seedling growth via the consumption of biomass (e.g., roots, rhizomes, seeds), and increase susceptibility to pathogens to trees that survive post-fire (Hewitt et al., 2016). A shortened fire return interval would have similar effects on vegetation biomass, as compounding burns lead to greater consumption of soil organic layer prior to forest recovery. In Quebec, short interval fires are leading to a transition from spruce to pine dominance (Lavoie, 1998), and are anticipated to lead to an increase in spruce regeneration failure (Splawinski et al., 2019). Consequently, post-fire recruitment may be particularly vulnerable to a shortened fire return interval, especially as climatic effects on propagules intensify (Nolan et al., 2021). For instance, in black spruce dominated ecosystems, a shortened fire return interval has caused tree regeneration failure due to immaturity of the trees and the lack of seed production pre-fire (Brown & Johnstone, 2012; Johnstone, 2006). This lack of material legacies restricts the regeneration of black spruce post-fire and prevents a self-perpetuation cycle, demonstrating a misalignment between tree species adaptations and the disturbances. These imbalances have pushed this black spruce ecosystem outside of its safe operating space and reduced its resilience to future disturbances (Johnstone et al., 2016). In this way, ongoing climate change can enable disturbance events to cause a critical transition of vegetation recovery to a new ecosystem state (Martin, 1993; Scheffer et al., 2012).

Changes in fire regime can also create variability in seed bed conditions and cause more extremes in soil temperature and snow depth (Brehaut & Brown, 2022). The alteration of site conditions may continue to encourage unexpected successional trajectories. As such, changes to fire regime along the western subarctic are likely to drastically alter the dominant vegetation communities and lead to landscapes with unforeseen functions and characteristics. More broadly, increasing fire frequency and severity may also facilitate northward range shifts of various other vegetation species and increase overall species richness (Heim et al., 2022). These assemblages of vegetation communities can influence and change nutrient cycling, energy transfer, hydrologic cycle, and other processes, potentially altering the feedback loops and further the deviation of ecosystems from typical post-fire recovery trajectories (Johnstone et al., 2016). A shift in fire characteristics could have major direct and indirect impacts; thus, there is growing urgency to better understand how novel fire regimes may influence ecosystem function and structure.

As these conditions become more prevalent, there are still many unknowns in regard to consequences on future plant communities and ecosystems. It is important to understand how current species can withstand quickly changing site conditions (Brown, 2010). Future research is needed in understanding post-fire vegetation feedbacks and their likelihood of being susceptible to fire (Harvey & Enright, 2022). There still appears to be resilience in many North American black spruce forests but they may be approaching critical thresholds for changing ecosystem states (Baltzer et al., 2021; Nolan et al., 2021). Black spruce communities may in fact be experiencing an interval squeeze (Nolan, 2021), where decreased recruitment due to changes in climate, coupled with a shortened fire return interval, leads to reduced persistence of their population in a landscape (Enright et al., 2015). This phenomenon is likely playing a critical role into the lack of range expansion along the boreal-tundra ecotone, and likewise is creating opportunities for other ecological successional pathways.

1.1.3 Black spruce post-fire vegetation trajectories

Forest ecosystems have four primary responses to disturbances such as fire, which include the combinations of changes in their composition and structure (Seidl & Turner, 2022). The four responses include (1) resilience, where the post-disturbance vegetation structure and composition that remain resemble pre-disturbance ecosystems; (2) restructuring, where post-disturbance vegetation communities remain, but there are changes to the spatial structure (e.g., changes to densities and sizes of species); (3) reassembly, where the post-disturbance vegetation community changes but the structure is maintained; and (4) replacement, where both the post-disturbance vegetation composition and structure do not match pre-disturbance ecosystems but it still remains a forest ecosystem (Seidl & Turner, 2022). These trajectories are typical of all forest communities that exist within disturbance regimes, where a disturbance event most often does not constitute a change to the successional pathway. It is only when there are major alterations to both the structure and composition of these forests that it can be considered out of the norm, and a change in forest regime or alternate successional trajectory (Seidl & Turner, 2022). Since ecosystems within disturbance regimes are always changing, it is necessary to know their typical successional pattern to understand if an extraordinary disturbance event constitutes an alternate trajectory.

There are two principle successional pathways of black spruce forests. The first pathway consists of feathermoss as the dominant understory. Following fire, the first vegetation to re-establish are liverworts and mosses that are adapted to disturbance (e.g., *Marchantia* spp., *Ceratodon* spp.) and quick growing species like fireweed (*Chamaenerion angustifolium*; Viereck, 1983). During this first stage, which lasts about four years, black spruce seeds will germinate and establish. Eventually, this stage is replaced by the shrub stage, which is dominated by shrubs that grow from shoots and sprouts that persisted through the fire. After approximately 25 years, the tree canopy begins to form and shade out these shrubs (Viereck, 1983). Feathermosses and fruticose lichens begin to dominate the understory and the organic layer builds back up. The second pathway includes a lichen-dominated understory, where a similar set of stages occurs. The initial dominant plant community consists of pioneer moss species and can last up to 20 years (Viereck, 1983). The following stage occurs once fruticose lichens establish, along with an ericaceous shrub understory (Viereck, 1983). An open canopy forms during this period. As the stand continues to age, other *Cladina* spp. and *Stereocaulon* spp. establish. The typical fire return interval in both these forest types in the Canadian northwest boreal ecosystem is 80-150 years, allowing enough time for the ecological communities to return to a similar state that they were prior to disturbance (Larsen, 1997; Randerson et al., 2006; Viereck, 1983). Though there are changes to both the structure and composition of the forest, it is within its typical cycle and maintains its forest regime.

Across North America, changing fire patterns are influencing successional trajectories, leading them to respond in different ways. In western North America, forests are burning at younger ages resulting in shifts in stand dominance (Hart et al., 2019). For example, in some places, black spruce stands are shifting to aspen dominated stands after an increase in fire severity or frequency (Baltzer et al., 2021; Johnstone, 2006; Whitman et al., 2018). Deciduous trees have a stronger growth response to increasing temperatures than cold tolerant species like black spruce, investing more resources into their leaf biomass, and less resources into their roots (Way & Oren, 2010). This reorganization in forest composition may not lead to an alternate successional trajectory, but with continued climate warming, it may eventually result in a shift if deciduous trees experience increased growth and productivity.

Less is known about the effects of changing fire regime on post-fire successional trajectories in stands where only one tree species is abundant in the region. Tall deciduous shrubs may be well suited to become dominant in post-fire landscapes after tree regeneration failure in monospecific forests and are already known to be expanding and infilling across the circumpolar north due to increasing temperatures (Myers-Smith et al., 2011). Such a change would constitute an alternate trajectory, resulting in a loss of forest cover. Another observed trajectory to shortened fire return intervals in tundra portions of boreal-tundra ecotones includes a transition to grass-dominated ecosystems, devoid of trees (Hollingsworth et al., 2021). Knowing that dominance is determined in the first ten years post-disturbance, studying initial successional communities and the abiotic and biotic factors that may influence trajectory shifts are therefore important for anticipating future ecosystems states (Johnstone et al., 2004; Seidl & Turner, 2022).

1.1.4 Shrubs as an alternate successional trajectory

Over the last century, northern latitudes are greening due to increased growth and expansion of shrubs (Myers-Smith et al., 2011). Simultaneously, there has been a loss of trees and lichen, known as browning (Epstein et al., 2013; Orndahl et al., 2022). Range expansion in shrubs is occurring primarily with tall shrubs (e.g., species of willow, birch, and alder; Myers-Smith et al., 2011). Prostrate evergreen shrubs are also increasing in growth (Vowles & Björk, 2019), while some lower-statured shrubs (i.e., dwarf shrubs, <15cm height) have declined in abundance (Elmendorf et al., 2012b). Air temperature is the greatest contributor to this trend for tall shrubs, affecting their abundance, growth, and recruitment (Mekonnen et al., 2021; Walker et al., 2006). Some suggest that seasonality of temperature variability is also important. In Greenland, positive radial growth response of green alder (*Alnus viridis*) and grayleaf willow (*Salix glauca*) were attributed to summer temperature (Jørgensen et al., 2015). Further, in Alaska, expanding tall shrub patches were found to have a high correlation between increased summer temperature and radial stem growth, whereas stable patches did not (Tape et al., 2012). In western Greenland, positive growth of dwarf birch (*Betula nana*) related to both warmer summer and winter temperatures (Hollesen et al., 2015). However, there is still uncertainty around the response of specific shrub species to changes in climate. A dendroecology study on radial stem growth of three boreal shrubs in southwest Yukon demonstrated variability in growth response by species to fluctuating climatic conditions (Grabowski, 2015), suggesting that there is variability in species-specific growth responses.

The expansion of shrubs has also been variable across the north, with different environmental factors contributing to their ability to reproduce and expand (Elmendorf et al., 2012a). Besides air temperature, soil moisture is thought to be one of the main determinants of shrub growth (Elmendorf et al., 2012a; Myers-Smith et al., 2015); however, there is likely a threshold for when conditions are too wet for shrubs to grow (Myers-Smith et al., 2015; Van Der Kolk et al., 2016). Factors like soil temperature and ALD are also important contributors to shrub growth. Stable shrub patches have exhibited shallower active layers and cooler annual and summer soil temperatures (Tape et al., 2012). Other understudied site conditions are also likely contributing to the resulting shrub growth, such as various biotic interactions (e.g., fungal interactions), soil properties (e.g., soil stability, nutrient content, etc.), and plant-atmosphere interactions (e.g., insolation, fire, frost, etc.; Martin et al., 2017). Snowpack dynamics (e.g., snow depth, timing of snowmelt, etc.; Wipf et al., 2009) and herbivory also contribute to shrub growth (Myers-Smith et al., 2011). Thus, feedbacks between environmental factors and shrubs are nuanced and relationships may not always be direct or linear. Such variability and complexity to this system suggest that there is still a lot to learn from shrub response to changing climatic conditions in northern latitudes.

Shrubs, already increasing in productivity and numbers with rising temperatures, may proliferate even faster in response to shifts in fire regime. Fire limits existing competition and stimulates new growth of shrubs from their surviving legacies (i.e., rhizomes; De Groot & Wein, 2004). Warmer soils, increased soil nutrient availability, and deeper active layers enable fast growing species to quickly establish in post-fire sites (Martin et al., 2017; Payette, 1992). Tall shrubs hold an additional advantage to outcompeting other plants; some tall shrubs have acquired material legacies related to their physiology that increase their efficiency at transferring water throughout the plant (Nielsen et al., 2017). Furthermore, tall shrubs have developed information legacies by forming symbiotic associations with mycorrhizal fungi to absorb nutrients more efficiently with one of the results being improved competitive advantage (Deslippe & Simard, 2011). Shorter fire return intervals that reduce tree regeneration eliminate a later successional competitor that would limit light and nutrient availability for tall shrubs. This alternate successional trajectory may further deviate from typical regeneration pathways as shrubs are known to mediate site conditions by warming soils and deepening active layers, which may further perpetuate shrub growth (Sturm et al., 2005). It is therefore feasible for shrubs to follow an alternate successional trajectory in response to changes in fire regime in the subarctic.

1.1.5 Culturally significant species and climate change

Many northern Indigenous communities have long been voicing that changes to climate and the environment are underway (ACIA. 2004; Fox, 2004; Smith, 2007). Living in these ecosystems for centuries, they have formed deep connections with the land and the features that occupy these spaces. These communities have developed a deep respect for these natural systems and practices that promote the sustainability of their highly valued resources (Sherry et al., 1999). In fact, most of the world's remaining biodiversity can be attributed to Indigenous territories (Ogar et al., 2020). Many Indigenous communities have been tracking changes on the land and can confirm that environmental change is occurring on their traditional territories (Kuntz & Vuntut Gwitchin First Nation, 2018). However, many academic institutions still do not hold these knowledge systems to the same esteem as western science, requiring peer-reviewed results to validate these truths.

Despite the immense amount work still needed to decolonize academia, awareness surrounding the colonial structures of western research is slowly growing in natural sciences. Some researchers are taking steps at being more mindful and changing ways in which they do their work (Wong et al., 2020). This change is slow, it can take time for the larger research community to understand, recognize, and acknowledge that mindsets need to change in valuing different forms of knowledge and appropriate ways to engage with Indigenous communities in research. Structures still exist within academia that are prohibitive to working meaningfully with Indigenous communities. One way in which we, as researchers, can contribute towards this more inclusive form of research is to base our research on the priorities that have been set by the communities that we are working in (Wong et al., 2020). With our research, it is therefore important to focus our attention on what changes to the dominant disturbance regime and the subsequent effects on regeneration trajectories might mean for Indigenous groups that inhabit these northern ecosystems.

Though there are numerous culturally important species to these communities, in this work we focus our attentions on barren-ground caribou (*Rangifer tarandus grantii*) and berry producing plants. By considering these two central themes, we believe that we are capturing important viewpoints of these communities. Barren-ground caribou are one of the most important species to northern Indigenous groups, particularly the Gwich'in people. Historically, caribou shaped many of their practices and movements. Caribou not only provided the entire community with food, but also with spiritual, physical, and cultural well-being (Sherry et al., 1999). Hunting caribou required a deep knowledge of the animal, their movements, and the land. During migration, caribou fences were used to hunt caribou, with the involvement of all community members including men, women and children (Sherry et al., 1999). In other seasons, hunters in the community, mostly men, would hunt the caribou. Once harvested, all members of the community would assist with processing the animal and using the animal for food, clothing, medicine, among other uses (Sherry et al., 1999). Additionally, for northern Gwich'in communities, berry picking provides women with many socio-ecological health benefits ranging from medicine, individual and communal well-being, and deeper connections to the land, their culture and each other (Parlee et al., 2005; Sherry et al., 1999). These culturally important species, though important for the entire community, are managed by different groups within the community and so by focusing on both subjects will help us to understand how these impacts of climate change will impact more of the community.

Changes to the recovery trajectories of vegetation communities as a result of changes to fire regime will both directly and indirectly impact culturally important species in these northern landscapes. Traditional foods remain an important part of the diet of Yukon First Nation communities (Schuster et al., 2011). Indigenous peoples hold deep connections to the land, and this relationship will change with continued climate change. Shifting ecological community composition and timing may lead to trophic and phenological mismatches with species who have evolved to consistent pulses. Further, increasing dominance of shrub landscapes may also impact the abundance and distribution of both caribou and berries.

1.2 Thesis rationale

1.2.1 Context and background

In the western subarctic, Yukon is warming over twice as fast as the global average and precipitation is increasing but is highly variable (Perrin & Jolkowski, 2022). These conditions generally support increased tree growth and should have an impact on the geographic distribution of tree species at both their altitudinal and latitudinal extent. Over the next century, northern regions of Yukon (e.g., Taiga Cordillera ecozone) are anticipated to experience as many as three distinct changes to climate conditions and their associated vegetation communities (Rowland et al., 2016). With conditions changing at such a rapid pace, there is a large potential for misalignment between vegetation adaptations and climatic conditions in these areas. Models of plant functional groups suggest that shifts are currently underway, with coniferous and deciduous tree and shrub cover already increasing, whilst graminoids and macro lichens top covers are decreasing across northwestern North America, including Yukon (Macander et al., 2022). It is important to study these ecological communities at a regional level to better understand whether climate-vegetation mismatches are happening.

At altitudinal treeline in the boreal subarctic Yukon, white spruce (*Picea glauca*) is showing signs of increasing, infilling, and increasing in density as a result of temperature increases (Danby & Hik, 2007). Information is largely lacking about vegetation responses at latitudinal treeline of the boreal-tundra ecotone in the Taiga Cordillera ecozone, however, declines in radial growth of both black and white spruce have been observed due to drought stress (Griesbauer & Green, 2012; Walker & Johnstone, 2014). Though precipitation trends are increasing, in some areas it may not be enough to offset the accelerated rate of evapotranspiration, potentially leaving some tree species water stressed (D'Arrigo et al., 2004). Drought stress is occurring in black spruce populations of elevational treeline in Alaska as well (Walker et al., 2015). It is likely that among boreal-tundra treeline populations in the subarctic of Yukon, responses will vary by landscape position, which can contribute to drainage, and species composition (Reid et al., 2022).

In addition to the effects of drought stress, tree expansion is unlikely to occur in the boreal-tundra ecotone due to a lack of viable seed and inhospitable microhabitat conditions, which may not support tree growth (Reid et al., 2022). Previous research has demonstrated a suite of reproductive bottlenecks towards black spruce range expansion in the region suggesting the possibility of an interval squeeze. Black spruce trees exhibit a range of habitat requirements in early development and these conditions are lacking at their northern extent of the region (Goodwin & Brown, 2023). For example, subarctic black spruce trees are known to only produce high quantities of seed after 50 years of age (Viglas et al., 2013). Further, due to the variability in microsite conditions, black spruce seedling emergence is naturally low post-fire (Brehaut & Brown, 2022). As fire patterns continue to change, these bottlenecks could become more important. Though fire trends in Yukon remain highly variable, shortened fire return intervals have occurred in this region (Perrin & Jolkowski, 2022). Immature black spruce stands of only 14 years led to black spruce regeneration failure, post-fire, due to a lack of available seed following a second fire (Brown & Johnstone, 2012). It is therefore unlikely that black spruce forests will recover in areas that have experienced a shortened fire return interval, and their future ecosystem states remain unclear. Currently, it is not well known how both abiotic and biotic components of subarctic ecosystems of Yukon will react to both a changing climate and fire regime (Reid et al., 2022).

In other regions of northwestern subarctic, a shortened fire return interval in black spruce forests is shifting their ecosystem dominance towards deciduous dominated species consisting of aspen (*Populus tremuloides*) or birch (*Betula papyrifera* or *B. neoalaskana*; Day et al., 2022; Johnstone, 2006). However, while black spruce is the only stand-dominating tree species growing in this region of subarctic Yukon, a shortened fire return interval may introduce an opportunity for alternate recovery trajectories to emerge. In a review of black spruce resilience across North America, this ecozone had a higher rate of regeneration failure than other ecozones (Baltzer et al., 2022). Thus, possible changes in post-fire recovery trajectories of the boreal-tundra ecotone of Yukon may include an increase in birch (*B. neoalaskana*: the only deciduous tree present pre-disturbance) occurrence, or alternate trajectories that diverge from forest recovery. Tall shrub dominated ecosystems may emerge in the absence of tree regeneration, as has been observed elsewhere along boreal-tundra ecotone of Northwest Territories (Travers-

Smith & Lantz, 2020). While there is some understanding of ecosystem response in other regions, influence of fire on shrub establishment and expansion remains as a knowledge gap in the boreal-tundra transitional zone of subarctic Yukon (Reid et al., 2022). Thus, future research is needed in understanding post-fire vegetation feedbacks and their fire susceptibility (Harvey & Enright, 2022). Presently, there is an opportunity to study post-fire ecosystem recovery in this area to better understand community response to sudden changes in climatic conditions and natural disturbance regimes.

1.2.2 Objectives and significance

A shortened fire return interval along the boreal-tundra ecotone of subarctic Yukon has led to black spruce regeneration failure and a subsequent shift from typical boreal black spruce forest towards an alternate ecosystem state (Brown & Johnstone, 2012). Knowing that the first 10 years after fire are most important for black spruce recruitment and future dominance (Johnstone et al., 2004), the absence of the material legacy (i.e., black spruce seeds) at the time of the second fire set this ecosystem on a divergent regeneration pathway. Increasing fire frequency and severity has occurred in other parts of the northwestern boreal forest of north America, however, in many of these documented areas, there have been other tree species present and changes in fire regime have resulted in a shift towards deciduous dominance. Sites in this study are located near latitudinal treeline where black spruce is the only common tree species occupying these sites, leaving some uncertainty as to the direction of their possible regeneration pathways.

The objectives of this thesis are to characterize the regeneration of this divergent pathway by understanding vegetation recovery trajectories and their associated site conditions within and between different fire histories. In Chapter Two, we describe the plant communities regenerating in the area that experienced a shortened fire return interval and compare them to vegetation communities of the same age that are regenerating following a typical fire history, as well as with communities from a mature forest stand of the same area (collectively referred to as fire history classes in subsequent text). To do this, we (1) used non-metric multidimensional scaling (NMDS) ordination analyses and indicator species analyses to determine the similarity of the different fire history classes; (2) assessed the density and heights of shrubs and black spruce within each fire history class using analysis of variance (ANOVA) tests; (3) examined the difference in individual site parameters using ANOVAs to better understand the differences of environmental conditions of the different fire history classes; and finally, (4) used a mixed modelling approach to examine the relationships between site characteristics and the regeneration densities of tall shrubs. In Chapter Three, we discuss implications of a shortened fire return interval on culturally important species of the area. We also offer some thoughts about the direction of future research in this field. In doing so, we aim to address some of the remaining knowledge gaps in this region that may contribute towards a better understanding of how changes in fire patterns will affect forest ecosystems and future recovery trajectories. Examining drivers of vegetation change at a local scale will help inform on the complexity of these systems and contribute to a better understanding of how climate will affect future northern landscapes.

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Chapter 2: Beyond Black Spruce: Shift in plant communities after frequent fire in a Yukon subarctic boreal forest

2.1 Introduction

Increased warming caused by climate change is underway in North America with the greatest change occurring in northwestern region (Vincent et al., 2015). This trend is having sweeping ramifications on ecological communities, altering their structure and composition. Since temperature is considered to be the primary control limiting the northward expansion of forest extent (Körner & Paulsen, 2004; Harsh & Bader, 2011), tree species ranges across the boreal-tundra ecotone, herein termed treeline, are predicted to shift northwards in concert with warming (Holtmeier & Broll, 2005; Zhang et al., 2013). However, treeline advance is not universal (Harsch et al., 2009), varying by species and location. The lack of consistent response to warming suggests that treeline growth is complex and controlling factors in addition to air temperature may also be contributing to its spatial response (Holtmeier & Broll, 2005; Zhu et al., 2012).

In addition to direct effects on tree establishment and growth, warming may be indirectly impacting treeline by influencing the growth response of other plant species and affecting the dominant disturbance systems of the sub-arctic, which encompasses the boreal-tundra ecotone. For instance, a rise in temperature has led to the circumpolar expansion of tall shrub species at treeline (Tape et al., 2006; Myers-Smith et al., 2011). Changing fire regimes (i.e., more frequent, larger-size, and greater severity fires) under ongoing climate change are predicted to further affect changes in plant successional trajectories (Johnstone, 2006; Johnstone et al., 2010b; Johnstone et al., 2010c; Kasischke & Turetsky, 2006). Combined, these factors are likely interacting with tree growth and contributing to the varied response of treeline at the boreal-tundra ecotone.

New fire regimes impact the vegetation legacies (i.e., ecosystem structure and function) which dictate the regeneration success of forests and can rapidly change ecosystem states to non-forested trajectories (Johnstone et al., 2016). Altered fire regimes that impact forest recovery signify a misalignment with tree reproductive cycles (Brown & Johnstone, 2012). Black spruce (*Picea mariana*) forests in western North America, often characterized by relatively low productivity and cold soils, typically follow an 80 - 150 year fire return interval (Randerson et al., 2006; Viereck, 1983). A new, shorter fire return interval of less than 50 years has resulted in fewer tree seedlings regenerating after fire in populations in interior Alaska (Hayes & Buma, 2021), northern Alberta (Dawe et al., 2022; Whitman et al., 2019), northern Saskatchewan (Hart et al., 2019), Northwest Territories (Dawe et al., 2022; Day et al., 2022; Travers-Smith & Lantz, 2020; Whitman et al., 2019), and Yukon (Brown & Johnstone, 2012; Johnstone, 2006; Johnstone & Chapin, 2006; Viglas et al., 2013). These changing fire patterns have disrupted the historic disturbance cycle and have introduced uncertainty surrounding future ecosystem states throughout the boreal-tundra ecotone. It is possible that these populations are encountering an interval squeeze, where changes in climate coupled with a shortened fire return interval are causing a reduction in black spruce (Enright et al., 2015). In some places, this disruption has led to a transformation in both the structure and composition of the recovering plant communities towards an ecosystem state that is distinct from its initial trajectory, as well as the environmental characteristics associated with those communities (Baltzer et al., 2021; Hayes & Buma, 2021; Johnstone, 2006; Lantz et al., 2010; Seidl & Turner, 2022).

Under typical fire regimes in subarctic black spruce forests, fire consumes portions of the organic layer, which acts as an insulator of the soil and keeps soil temperatures cool and the permafrost layer intact. This reduction of the soil's protective cover leads to warming of the soil and deepening of the active layer – the portion of soil above the permafrost layer that thaws out during the growing season and is where biological processes occur (i.e., nutrient cycling) – rendering more soil moisture and nutrients available for plant uptake (Fisher et al., 2016; Schuur et al., 2008; Viereck, 1983). Moisture at the soil surface generates energy exchange between the soil and the atmosphere via thermal conductivity, promoting permafrost thaw and furthering feedbacks that deepen the active layer (Hinkel et al., 2001; Fisher et al., 2016). As post-fire recovery trajectories progress, the organic layer slowly thickens, allowing the permafrost layer to also recover and return to cooler, low productivity sites (Heim et al., 2021). With so many processes occurring simultaneously, it is still not fully understood as to whether environmental parameters and site processes are interrupted after a shortened fire return interval. Therefore, understanding the drivers shifting vegetation communities in places experiencing altered disturbance patterns will be instrumental in predicting the outcomes of these changes to northern landscapes.

In the Eagle Plains ecoregion of northern Yukon, two fires overlapped in quick succession with only 15 years apart (1990/1991 and 2005). This portion of the boreal-tundra ecotone is located in the continuous permafrost zone and is dominated by black spruce forest (Smith et al., 2004). Prior to the fires, these sites were mature black spruce forest that had not burned in over 75 years (Brown & Johnstone, 2012). Preliminary observations since the second fire revealed black spruce regeneration failure and a subsequent shift in post-fire successional trajectories to a tall shrub-dominated ecosystems (Brown & Johnstone, 2012; Reid et al., *in* *prep*). Under a typical fire regime, black spruce seedlings establish, mature, and return the ecosystem back to black spruce dominance through self-replacement. Here, because the second fire consumed the black spruce before they had matured, there was a lack of material legacies (i.e., seed) available to perpetuate post-fire regeneration. This misalignment with the typical life cycle of black spruce forests caused a dramatic shift in the regeneration of the plant communities, pushing the ecosystem towards an alternate ecological trajectory.

Fire modelling projects that an increase in annual area burned in Yukon will occur over the next century (Boulanger et al., 2014). Mismatches between fire return interval and black spruce life cycles may become more commonplace introducing more alternate trajectories to the landscape. These new trajectories will generate further changes to ecosystem processes across the boreal-tundra ecotone. Increased rates of permafrost thaw (Gibson et al., 2018; Williams et al., 2020), decreases in carbon sequestration (O'Donnell et al., 2011; Schuur et al., 2008), changes to nutrient cycling (Keuper et al., 2012; Schuur et al., 2008; Shenoy et al., 2013), and altered patterns of precipitation (Veraverbeke et al., 2017) may be observed, highlighting the importance of studying both the vegetation communities and environmental characteristics of these ecosystems. In addition to affecting the ecological components of this landscape, divergent regeneration pathways will also cause changes to species and processes that are important to Indigenous communities in the area, potentially impacting their interactions and, consequently, their relationships with the land. Documenting changes in areas such as Eagle Plains may not only provide insights to future landscape conditions under ongoing climate change, but also to how these changes may impact culturally important species and practices.

We examined how altered disturbance regimes are changing the dominant vegetation species in the overlapping burn sites of Eagle Plains and investigated the driving abiotic factors behind these changes. To do this, we characterized and compared the regeneration of vegetation communities from the overlapping burn sites (i.e., sites experiencing a shortened fire return interval) with sites that were following a typical regeneration pattern, as well as with mature forest sites of the area, collectively referred to as fire history classes. Our intention was to test explicit hypotheses of established post-fire vegetation environment relationships within each fire history class, based on previously established biotic-environment associations (Table 2.1). To meet this goal, we measured the environmental characteristics of each site to tease out the drivers behind the differences in community composition. We predicted that black spruce stem density would be highest in sites recovering from a typical fire interval and that tall shrub density would be highest in sites with overlapping burns. We expected that short interval sites would have the thinnest soil organic horizons compared to the other fire history classes and the deepest active layers. Within short interval sites, however, we also expected that sites with thicker soil organic horizons would have more available soil moisture and, consequently, denser tall-shrub communities and taller individual shrubs. Finally, we also gave some thought towards the implications for culturally important species in this area. By exploring how changes to successional communities may affect some species of significance to Indigenous groups in the area, we hope to bring relevance of the meaning of this work by using concrete examples of how this may affect those that hold deep ties to this landscape and may be most affected by these potential changes.

Table 2.1. Hypotheses of individual site characteristics for each fire history class. Long interval (LI) sites are part of the fire history class following a typical regeneration pattern, short interval (SI) sites are the overlapping burn sites that have experienced a shortened fire return interval, and unburned (UB) sites are mature forest sites that would be typical of this area prior to burning.

Parameter	**Hypothesis**	**Support**
Active layer depth (ALD)	Short interval sites will have the greatest ALDs and UB sites will have the shallowest ALDs	Fisher et al., 2016; Gibson et al., 2018; Smith et al., 2015
Canopy closure	Short interval sites will have the greatest canopy closure and UB sites will have the least	Heim et al., 2021; Myers-Smith et al., 2011
Organic layer depth (OLD)	Short interval sites will have the thinnest OLDs and UB sites will have the thickest OLDs	Holloway et al., 2020; Johnstone et al., 2010a; Nossov et al., 2013; Walker et al., 2018
Slope	Short interval sites will be on the steepest slopes and UB sites on the flattest slopes	Holloway et al., 2020; Smith et al., 2015; Walker et al., 2018
Soil moisture	Short interval sites will have the most available soil moisture and UB sites will have the least available soil moisture	Johnstone et al., 2010a; Nossov et al., 2013; Walker et al., 2018
Soil pH	Short interval sites will have most basic soil pH and UB sites will have the most acidic soil pH	Day et al., 2019; Holloway et al., 2020; Taş et al., 2014
Soil nutrients	Short interval sites will have the most soil available nutrients (including NH_4N, NO_3, PO_4, K) and UB sites will have the least soil available nutrients	Keuper et al., 2017
Soil temperature	Short interval sites will have the highest soil temperatures and UB sites will have the lowest soil temperatures	Gibson et al., 2018; Nossov et al., 2013
Total carbon	Short interval sites will have the least total carbon in the mineral soil and UB sites will have the most	O'Donnell et al., 2011; Taş et al., 2014
Total nitrogen	Short interval sites will have the least total nitrogen in the mineral soil and UB sites will have the most	Taş et al., 2014

2.2 Methods

2.2.1 Study sites

This study occurs on the traditional lands of Vuntut Gwitchin First Nation, within the Eagle Plains ecoregion of Yukon Territory (66° 22' 12" N, 136° 43' 48" W; Figure 2.1). The mean elevation for this area is 560 m and is part of the continuous permafrost zone, where permafrost can be up to 200 m thick in some places and the active layer depth (ALD) is less than 1m (Smith et al., 2004). The mean annual temperature is -5.9 °C, with a mean monthly temperature of +12.9 °C in July and -22.9 °C in January (ECCC, 2023). Mean annual precipitation is 400 mm and occurs mainly in the summer months (Smith et al., 2004). Black spruce forests dominate the upland areas of this region, and black spruce- cotton grass tussocks dominate the lowlands. Shrub tundra occurs at higher elevation areas.

Overlapping burns in this area, which had experienced a decrease in fire return interval, created an opportunity for an observational study. Fires that burned in 1990 (33,500 ha), 1991 (4,800 ha), and 2005 (69,000 ha) overlapped in road-accessible locations along the Dempster Highway approximately 20 km south of Eagle Plains. All three fires were low-moderate severity, but the fire weather index was higher in 2005 than for the other fires, resulting in a larger area burned (Brown, 2011). The regeneration in these overlapping burns has previously been studied because they provided a unique opportunity to better understand divergent regeneration pathways (Brown and Johnstone 2011, 2012; Brown et al. 2015). Brown and Johnstone (2012) focused on understanding the bottlenecks of black spruce recovery after a shortened fire return interval and the subsequent recovery trajectories. Findings demonstrated that the absence of black spruce recovery occurred due to a lack of seed availability in overlapping burn sites (Brown & Johnstone, 2012). Building on this knowledge, we revisited the same sites ten years after Brown and Johnstone to study the alternate successional patterns of the vegetation communities that had demonstrated black spruce regeneration failure.

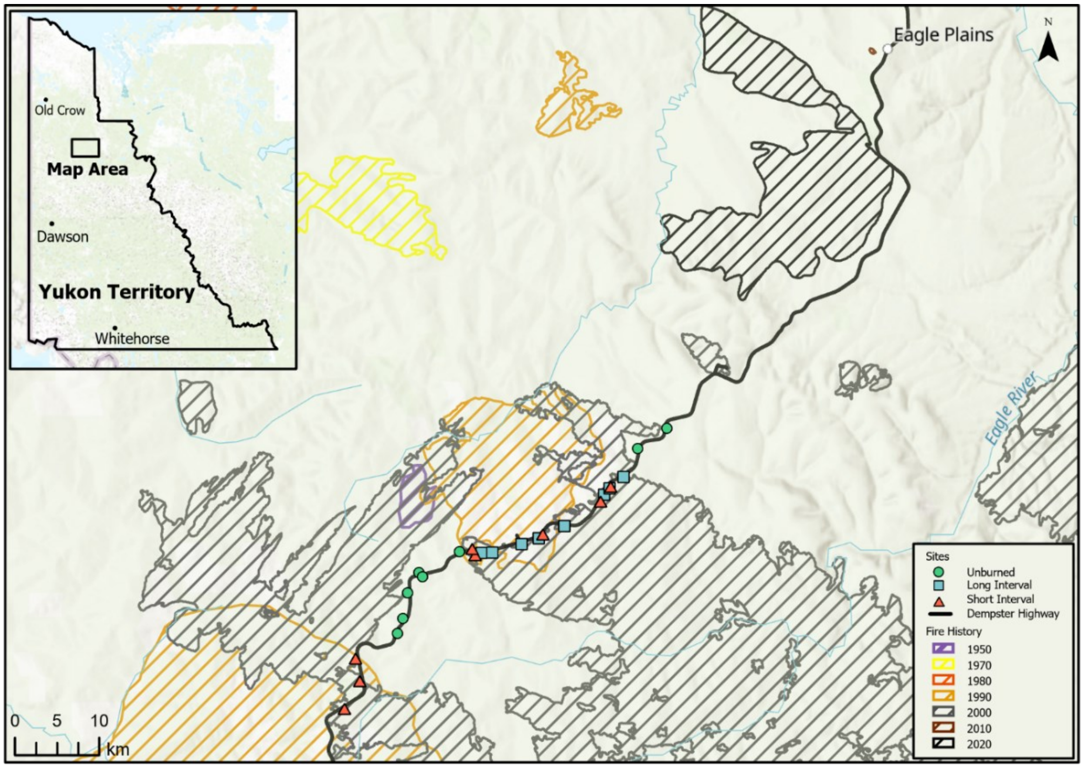


Figure 2.1. A map of the study area in the traditional territory of the Vuntut Gwitchin First Nation in Yukon, Canada. Site types are represented by different coloured shapes. Eight sites in each site type were selected for this study, for a total of 24 sites. Unburned sites consist of mature forest following a typical fire return interval of 80-150 years (green circles). Long interval sites were mature forest before they burned in 2005 and are following a typical regeneration pattern for the area (blue squares). Short interval sites were mature forests before they burned in 1990/1991 and again in 2005 (red triangles). Dashed polygons represent fire perimeters and are grouped by the decade in which they burned (Yukon Government, 2021).

2.2.2 Field methods

Twenty-four sites were established in the initial study (2007) and were comprised of three fire history classes and eight replicates of each fire history class. The fire history classes were selected to represent the range of burn scenarios on the landscape and included: long interval (LI) sites, which experienced a typical fire return interval (most recent burn 2005; mature forest prior); short interval (SI) sites which burnt twice in quick succession (burned in 1990/1991 and 2005; mature forest prior), and unburned (UB) sites which were mature forest and had not burned in approximately 100 years (Figure 2.1). All sites were a minimum of 300 m apart and at least 80 m from the highway to avoid any road effects (Auerbach et al., 1997). Each site was 30 m x 30 m in size (Figure 2.2). Two 30 m x 1 m belt transects were established North-South so as not to capture any trace effects from the previous study, where transects were established East-West. To characterize vegetation communities, four 1 m x 1 m vegetation quadrats were placed along each transect for a total of eight quadrats per site. In each quadrat, percent cover estimates were completed for vascular plants to the species level and were grouped by growth forms for lichens and mosses. Total cover was able to sum to greater than 100% because overhanging shrubs and trees counted in the totals (but were noted that they were above the ground layer). If any species were unable to be identified in the field, a sample was collected with a relevant label for further identification later using the Flora of the Yukon (Cody, 2000). Further, individual stem counts of tall shrub and tree species emerging from the ground were conducted along the belt transects. Counts were separated into three lengths (0 - 10m, 10 - 20m, 20 - 30m) of the transect. The height of the tallest stem of each tall shrub and tree species present was recorded except for the height of black spruce stems occurring in UB sites because we were only interested in the regenerating stem heights of that species.

General site characteristics including elevation (m a.s.l.), slope (degrees), and aspect were measured at the southwest corner of each site. At each vegetation quadrat, canopy closure, active layer depth (ALD), soil temperature, soil moisture, organic layer depth (OLD), and soil pH were taken. Canopy closure was measured using a spherical densiometer (Lemmon, 1956). Depth to resistance was measured using a metal probe as a proxy for ALD, and up to three attempts were taken at each quadrat. Soil moisture was recorded using a GS3 Ruggedized Soil Moisture Sensor (Decagon Devices, Inc., Pullman, USA). The depth of the soil organic layer was measured from the base of vegetation to the mineral layer of the soil. Finally, two samples of mineral soil were collected from each site. Large samples of soil were collected to ensure the minimum weight for analysis (25g, dry weight) would be met. These samples were collected from all sites over a period of three days, the quickest this could be done due to logistical constraints. In the field, samples were kept as cold as possible using coolers and ice until they were able to be air-dried to a constant mass (on average four days) post-fieldwork. After air-drying, the samples were sieved using a 2 mm sieve and sent to the University of Alberta Natural Resources Analytical Laboratory. Analyses on the soils included: available nitrogen (ammonium and nitrate), phosphorous, and potassium, soil pH, total percent carbon, and total percent nitrogen. Total carbon and total nitrogen were analyzed using dry combustion method (Horwitz & AOAC, 2000; Schumacher, 2002). Phosphorous and potassium were analyzed by inductively coupled plasma-optical emission spectroscopy method (Skoog et al., 2007). All site characteristics were taken within a span of three days to keep as close weather conditions as possible across sites. Measurements were taken as late in the field season as possible to capture the maximum ALD of the area.

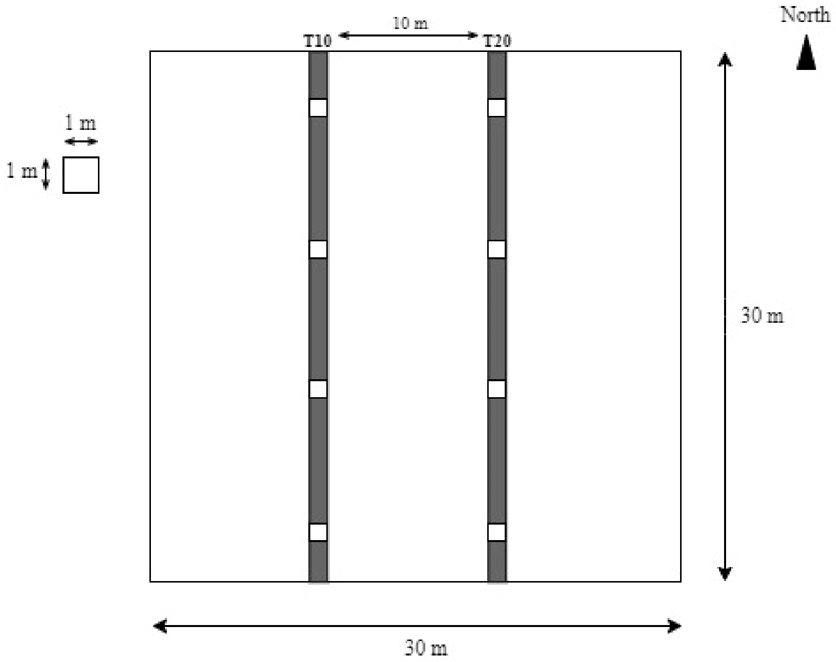


Figure 2.2. A diagram of the set up of each site. Each site was 30 m x 30 m in size with two 30 m x 1 m belt transects set north-south (T10 and T20, area of each transect is represented by the gray shading). Eight 1 m x 1 m vegetation quadrats (white squares) were placed at 3 m, 11 m, 19 m, and 27 m on the west side of each transect.

2.2.3 Data analysis

To understand the similarity of vegetation assemblages between sites, non-metric multidimensional scaling (NMDS) ordinations of Bray-Curtis distance matrices were created using vegan package version 2.5.7 (Oksanen et al., 2012) in R base version 4.0.2 (R Core Team, 2022). NMDS ordinations are well-suited to ecological data because it is a rank-based approach that represents the similarity of objects in ordination space. This means that NMDS can accommodate many forms of data including a mix of categorical and numerical data (Buttigieg & Ramette, 2014; Legendre & Legendre, 2012). We used percent cover class data of abiotic and biotic variables (e.g, species-level vegetation cover, bare soil) averaged to the site level to plot the similarities of plant communities in ordination space. The Bray-Curtis distance measure was used, between one and six dimensions were specified, and the iteration with the least stress was selected (Legendre & Legendre, 2012). Vectors of environmental characteristics were overlaid on the NMDS ordination to identify the factors influencing the placement of sites in the ordination. Hulls were used to visually represent the similarities in plant communities of sites in each fire history class. An analysis of similarities (ANOSIM) test was preformed to test our null hypothesis that there would be no significant difference between the different fire history classes. ANOSIM test uses the Bray-Curtis object distances from the NMDS, which are transformed into ranks, to analyze the similarities between sites (Legendre & Legendre, 1998).

Indicator species are useful for predicting the composition of other species within a given area as they can represent the condition of the environment in which they grow, and they can also provide insights towards changes in the environmental conditions (McGeoch, 1998). To determine which indicator species are responsible for differences in vegetation communities between fire history classes, we performed an indicator species analysis using the indicspecies package (De Cáceres et al., 2010). This method analyzes the relationship between the abundance of the species within the different fire history classes and tests the significance of these relationships with a permutation test (De Cáceres et al., 2010). A unique feature of this analysis is that it independently investigates each species from one another (De Cáceres & Legendre, 2009). This analysis examined the relationships of species with both the individual fire history classes and combinations of fire history classes. We considered a species to be an indicator of a fire history class when its probability was less than 0.05. To better visualize these results, the top three indicator species of each fire history class and the combined fire history classes were overlayed on the NMDS ordination.

To better understand the difference in shrub and black spruce stem counts and heights between fire history classes at both the species and species group level, we used one-way analysis of variance (ANOVA) tests. Tall shrub species were grouped together at the site level and included species from the *Alnus, Betula*, and *Salix* genera. We also tested our null hypotheses for each environmental parameter (that there was no difference between the fire history classes) using one-way ANOVA tests for each fire history class (Table 2.1). If test assumptions were not met, the non-parametric test Kruskal Wallace test was performed instead. Pairwise comparison Tukey tests were then completed to better understand the differences between fire history classes.

To assess the relationships between tall shrub density (count data) and the associated site conditions, we used a general linear mixed model (GLMM) with a quasi-Poisson distribution and a log link to account for the structure of count data, using the glmmTMB package in R (Brooks et al., 2017). This model included soil nutrients as possible explanatory variables as possibilities in the model selection process. Site was included as a random factor to account for natural variability between sites. To avoid overfitting the model, only variables that had a variance inflation factor of < 3 (suggesting less collinearity) were retained (Zuur et al., 2010). To determine the most suitable model, a backwards elimination stepwise approach was used and the model with the lowest AICc value was retained. To look at the influence of parameters beyond soil nutrients and avoid overfitting the model, we also ran a shrub density GLMM without including soil nutrients. The same stepwise elimination approach was used for this model.

The relationship between black spruce density (count data) and environmental characteristics was also assessed using a GLMM with a quasi-Poisson distribution and a log link. As above, site was included as a random factor, and only variables with variance inflation factor < 3 were used in the backwards elimination stepwise approach for identifying the final model. Finally, we assessed the relationship between shrub height and site characteristics using a GLMM with a Gaussian distribution and an identity link, with site as random factor, only using variables with variance inflation factors of < 3. This model followed the same backwards elimination stepwise approach to find the final model with the lowest AICc.

2.3 Results

2.3.1 Characterizing post-fire vegetation communities

Our NMDS ordination analyses show distinct differences in the plant community composition of sites with different fire history classes (Figure 2.3). The proximity of SI and LI sites in the NMDS suggests that their plant communities are more similar to each other than to the UB sites. Further, the ANOSIM test showed a statistical difference between fire history classes (R: 0.87, $p < 0.001$). The ordination in two dimensions was within the acceptable stress limit (< 0.2) at 0.08 (Clarke, 1993).

The indicator species analysis revealed the species most associated with each fire history class (Table 2.2). UB sites were characterized by caribou-forage lichen (i.e., *Cladonia rangiferina*, *Cladonia mitis, Flavocetraria* spp.; referred to as caribou lichen in subsequent text), *Peltigera* spp., sphagnum mosses, pleurocarpus mosses, black spruce, and other boreal plants. LI sites included coarse woody debris, bare soil and *Cladonia* spp. Indicator species in SI sites included *Polytrichum* spp. mosses, Bebb's willow (*Salix bebbiana*), Alaska wild rhubarb (*Polygonum alaskanum*), and Lappland reedgrass (*Calamagrostis lapponica*). Additionally, fireweed (*Chamerion angustifolium*), litter, and woodland horsetail (*Equisetum sylvaticum*) were characteristic of both LI and SI sites, whereas northern Labrador tea (*Rhododendron tomentosum*) and cloudberry (*Rubus chamaemorus*) were indicative of both UB and LI sites.

Site characteristics and indicator species data were overlaid on the NMDS to visually assess which parameters may be associated with the varying fire history classes (Figure 2.4). Several soil nutrient parameters were more associated with UB sites, including deeper soil OLDs, total carbon, total nitrogen, and ammonium (NH_4N). Further, in UB sites, soil OLD was closely aligned with occurrence of sphagnum moss, and higher caribou lichen cover was positively associated with ammonium. Deeper ALD was associated with the SI and LI sites where fireweed, litter, and woodland horsetail occurred.

Our graphical assessment of the density and height of tall shrubs and trees within the different fire history classes showed that black spruce stem count was highest in LI sites (Figure 2.5). Conversely, in SI sites, there were lower black spruce densities but higher willow and birch densities (Figure 2.5). The heights of the shrub species varied across fire history classes; Bebb's willow was taller in the SI sites than any other species across all sites (Figure 2.5). One-way ANOVAs revealed statistical differences in densities of black spruce between all fire history classes ($p = 2.81 \times 10^{-8}$; Table 2.3, Figure 2.6). Tall shrub densities were not significantly different ($p = 0.053$). Heights of regenerating black spruce were not statistically different between fire history classes (black spruce heights only collected in LI and SI sites; $p = 0.27$). Tall shrub heights in UB sites were significantly shorter than in the other fire history classes ($p = 8.82 \times 10^{-6}$).

Table 2.2. List of significant indicators ($p < 0.05$) associated with each fire history class (LI = long interval, SI = short interval, UB = unburned) based on the indicator species analysis. The statistic used for this test is a point biserial correlation coefficient (r_{pb}). Lichens are indicated as '†'.

Species	r_{pb}	**p-Value**
LI sites		
Coarse woody debris	0.734	0.0001
Bare soil	0.605	0.0008
Cladonia spp. †	0.499	0.0353
SI sites		
Polytrichum mosses	0.764	0.0005
Salix bebbiana	0.670	0.0010
Polygonum alaskanum	0.557	0.0073
Calamagrostis lapponica	0.523	0.0219
Scat	0.427	0.0435
UB sites		
Pleurocarpus mosses	0.931	0.0002
Picea mariana	0.776	0.0001
Petasites frigidus	0.729	0.0003
Vaccinium vitis-idaea	0.720	0.0002
Cladonia mitis †	0.704	0.0001
Sphagnum spp.	0.690	0.0002
Flavocetraria spp. †	0.637	0.0001
Cetraria spp. †	0.564	0.0002
Peltigera spp. †	0.525	0.0234
Acrocarpus mosses	0.504	0.0303
Cladonia rangiferina †	0.496	0.0001
Oxycoccus microcarpus	0.399	0.0202
LI and SI sites		
Chamerion angustifolium	0.790	0.0003
Litter	0.653	0.0016
Equisetum sylvaticum	0.526	0.0268
LI and UB sites		
Rhododendron tomentosum	0.837	0.0001
Rubus chamaemorus	0.626	0.0036

Table 2.3. Summary ANOVAs for tall shrub and black spruce densities and heights. Black spruce height data was only collected for LI and SI sites. When model assumptions were not met, the non-parametric Kruskal Wallace test was performed to achieve a χ^2 statistic. Bolded values are considered significant ($p < 0.05$).

Parameter	**Degrees of freedom (df)**	**F (χ^2)**	**p-Value**
Black spruce density	2, 45	34.773	**< 0.0001**
Tall shrub density	2,45	5.8807	0.05285
Black spruce height	1, 30	23.278	0.2744
Tall shrub height	2, 43	1.1946	**< 0.0001**

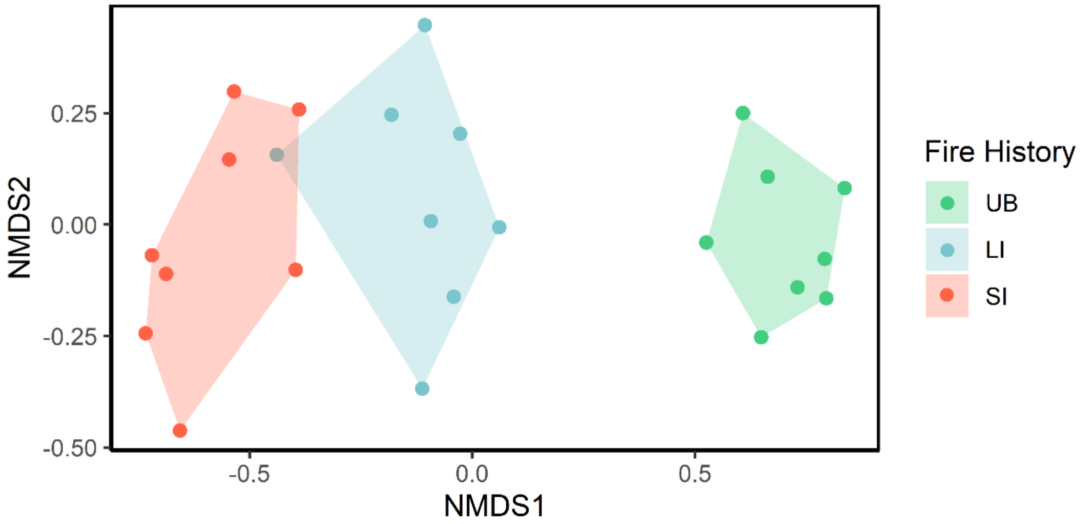


Figure 2.3. NMDS ordination of vegetation communities using species percent cover data. Individual sites are represented by points and color represents the different fire history classes (UB = unburned, LI = long interval, SI = short interval). Polygons encompass the entire range of variation of plant communities within a single fire history class.

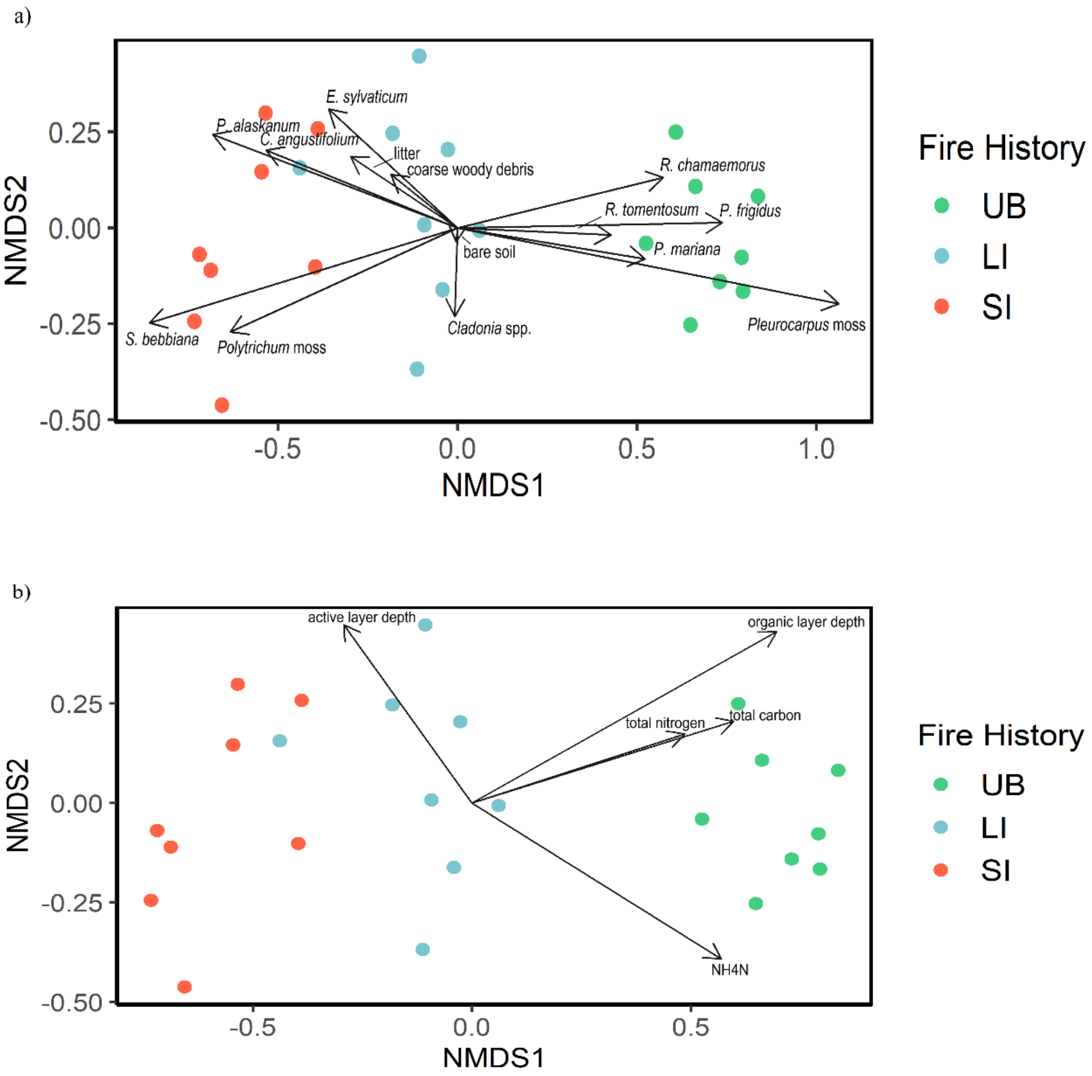


Figure 2.4. NMDS of sites in different fire history classes (coloured points; UB = unburned, LI = long interval, SI = short interval) with **(a)** overlay of the top three indicator species of each fire history class and top three indicators of the combination of fire history classes. Lines indicate the direction and magnitude of influence of the variable, the longer the line, the stronger the impact. See Appendix A for full species names. **(b)** NMDS of sites in different fire history classes with overlay of environmental characteristics. Lines indicate the direction and magnitude of influence of the variable: longer lines represent stronger influence of variables.

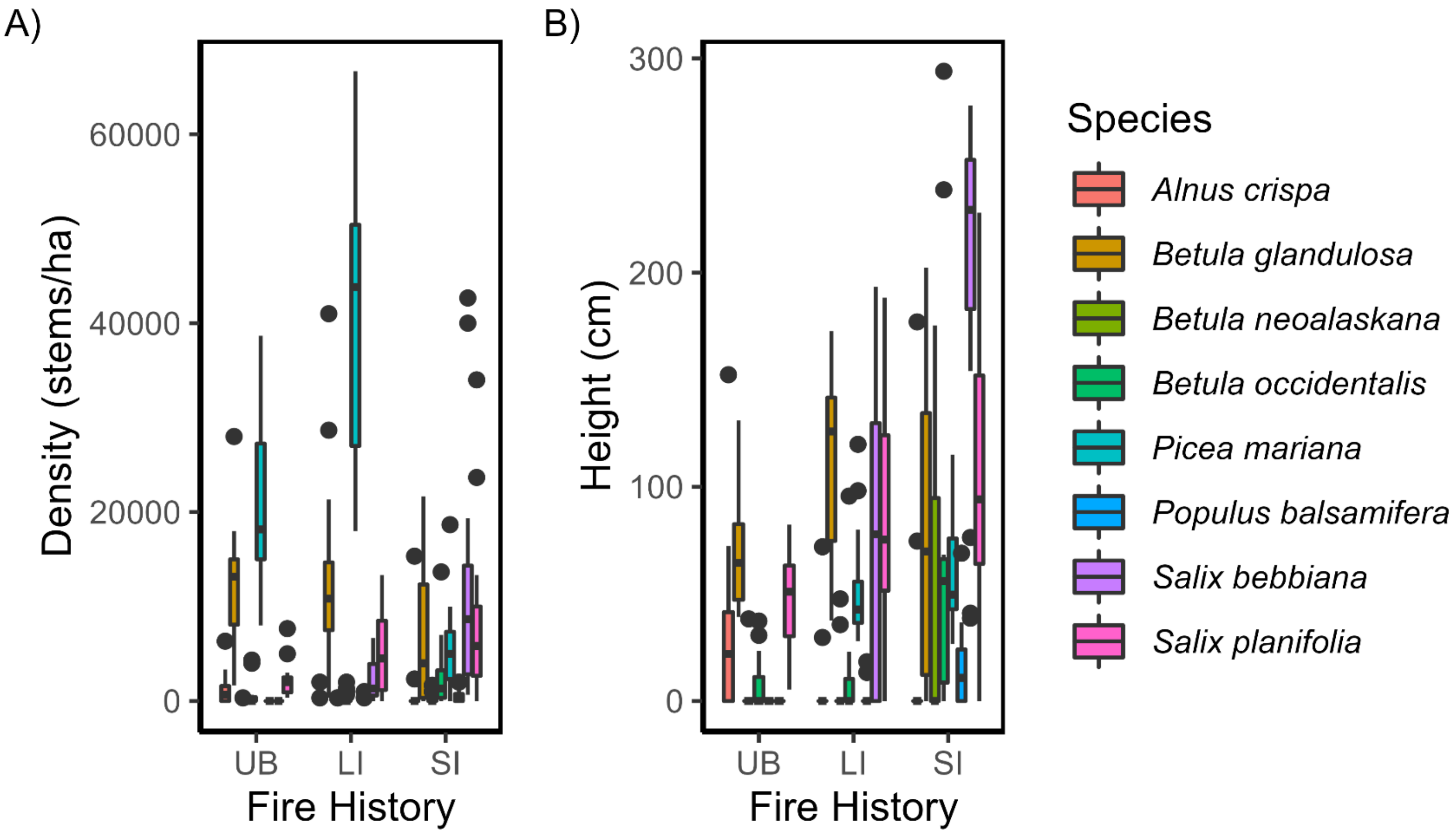


Figure 2.5. (a) Boxplot of the average tree and shrub densities grouped by species within all sites of the different fire history classes. **(b)** Boxplot of the average tree and shrub height grouped by species within all sites of the different fire history classes. No black spruce height data was collected in UB sites. The horizontal line in the boxes represents the median of the observations within each site. The boxes represent the 25-75% quartiles, while the whiskers represent the 95% quartiles. Dots beyond the whiskers represent outlier observations. Full species names can be found in Appendix A.

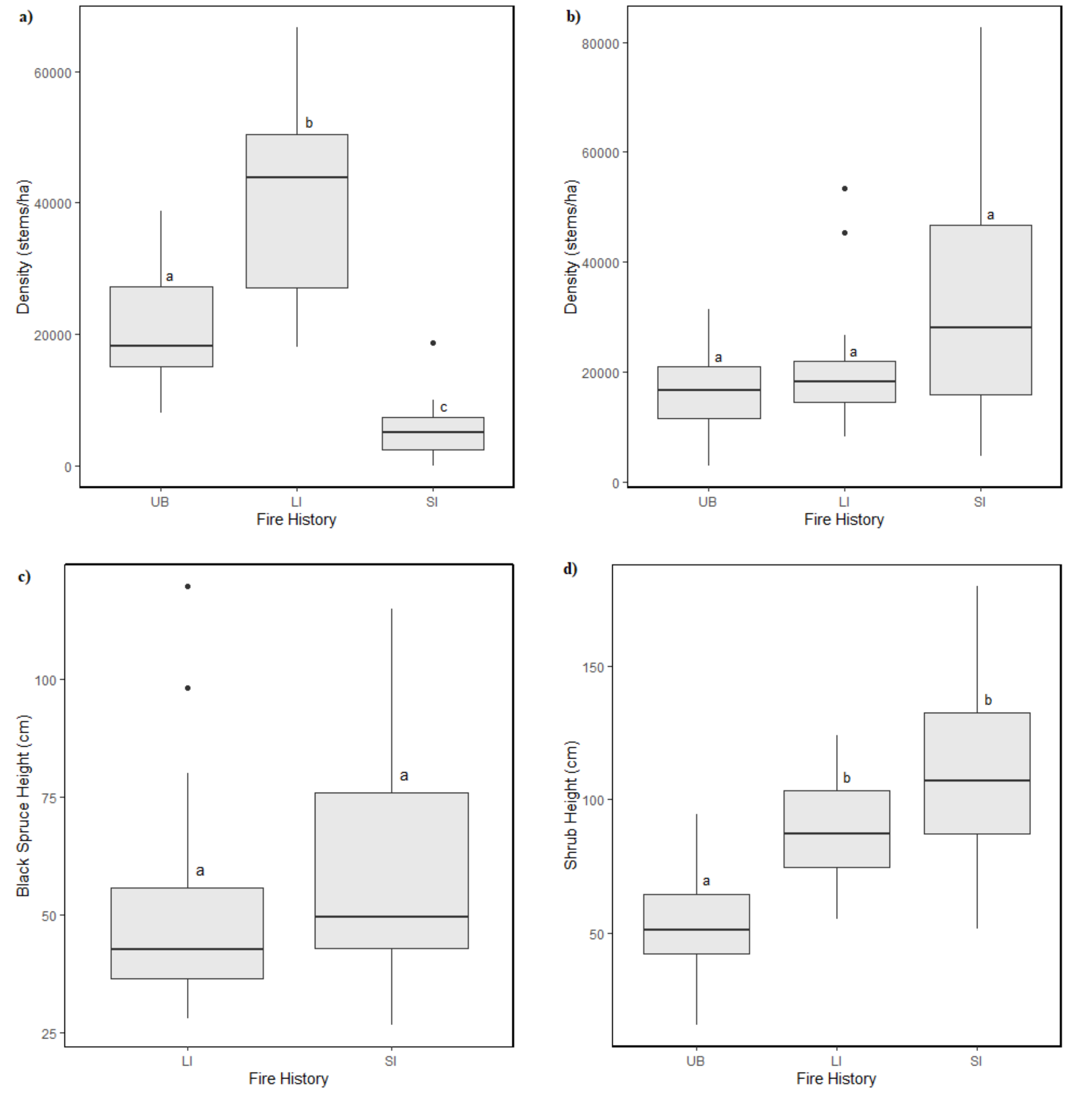


Figure 2.6. **(a)** Boxplot of black spruce densities grouped by fire history class. **(b)** Boxplot of tall shrub densities (tall shrub species were combined) grouped by fire history class. **(c)** Boxplot of average black spruce height grouped by fire history class. **(d)** Boxplot of tall shrub heights. Horizontal lines in the boxes represents the median of the observations within each site. The boxes represent the 25-75% quartiles, while the whiskers represent the 95% quartiles. Dots beyond the whiskers represent outlier observations. Letters above the boxes indicate significant differences between fire history classes obtained using the Tukey HSD test.

2.3.2 Examining post-fire site characteristics

There were significant differences between the fire history classes for ALD, canopy closure, NH_4N, OLD, slope, soil temperature and total carbon (Table 2.4, Figure 2.7). UB sites were most distinct of the fire history classes for several parameters including, the greatest OLD, the most total C, the most NH_4N, and the coolest soil temperatures. Canopy closure between UB and LI sites were also distinct. SI sites had greater slope. Each fire history class had distinct ALD, with LI having the greatest ALD and UB sites the least.

Our mixed effects models assessing the relationships between shrub and tree attributes and site characteristics revealed several significant effects between species metrics and site conditions (Tables 2.5-2.8). Sample sizes varied slightly between models (Appendix B). In our model that included soil nutrients, the final model included the following explanatory variables: fire history, slope, soil moisture, ALD, and the interactive effects of both fire and soil moisture and fire and ALD (Table 2.5). Higher shrub density was associated with SI sites with deeper active layers. Shrub density was lower in UB sites, and also on higher sloped sites. The marginal r-squared for this model was 0.56 and the conditional r-squared was 0.77, again suggesting high variability within sites of each fire history class.

When we excluded soil nutrients from our model, explanatory variables for the final model included: fire history, soil moisture, soil temperature, ALD, the interaction between fire and soil moisture, and the interaction between fire and ALD (Table 2.6). Denser shrubs occurred in SI sites with deeper active layers and in SI sites with greater soil moisture. This model had a marginal r-squared of 0.51 and a conditional r-squared of 0.74 suggesting high variability within sites of each fire history class.

The final model for the GLMM of black spruce density included: fire history class, soil temperature, and ALD as explanatory variables (Table 2.7). This model revealed black spruce density was lowest in SI sites. Marginal r-squared for this model was 0.77 and conditional-r squared was 0.87, also suggesting high variability within sites of each fire history class.

Finally, the GLMM for shrub height included fire history, slope, ALD, and the interaction between fire history class and ALD as explanatory variables (Table 2.8). This revealed that the tallest shrubs occurred in SI sites with deeper active layers. Shrub heights were tallest in SI sites and shortest in UB. Shrub height was negatively associated with both slope and ALD, meaning shrubs were tallest on flatter sites and sites with shallower active layers. Marginal r-squared for this model was 0.82 and conditional r-squared was 0.82, suggesting variability between sites within each fire history class.

Table 2.4. Summary of the one-way ANOVA results for each of the environmental characteristics that were measured. When variables did not meet the assumptions of ANOVA, a Kruskal Wallace test was performed to obtain a χ^2 statistic. Bolded values are significant ($\alpha < 0.05$).

Parameter	**df**	**F (χ^2)**	**p-Value**
ALD	2, 45	26.409	**< 0.0001**
Aspect	2, 45	1.0307	0.5973
Canopy closure	2, 45	8.611	**0.0135**
Elevation	2, 45	3.577	0.1672
NH_4N	2, 45	9.905	**0.000272**
OLD	2, 45	31.430	**< 0.0001**
pH	2, 45	4.023	0.1338
PO_4P	2, 45	5.235	0.07299
Slope	2, 45	8.939	**0.0115**
Soil moisture	2, 45	0.657	0.7199
Soil temperature	2, 45	7.316	**0.0258**
Total C	2, 45	13.281	**0.0013**
Total N	2, 45	4.574	0.1016

Table 2.5. GLMM of shrub density modeled with the following site conditions (including soil nutrients, which were dropped during the modelling procedure) using a quasi-Poisson distribution and a log link, with site as a random factor; n = 45. Bolded values are significant (α < 0.05).

Explanatory Variable	Estimate	Standard Error	z-Value	p-Value
Intercept	10.0105	0.1796	55.74	**< 0.0001**
Fire SI	0.3582	0.2248	1.59	0.1111
Fire UB	-0.9163	0.4009	-2.29	**0.0223**
Slope	-0.1849	0.0947	-1.95	0.0509
Soil moisture	0.1100	0.0987	1.11	0.2649
ALD	-0.2514	0.1918	-1.31	0.1899
Fire SI : soil moisture	0.3384	0.2064	1.64	0.1012
Fire UB : soil moisture	0.3296	0.1964	1.68	0.0933
Fire SI : ALD	0.7742	0.2428	3.19	**0.0014**
Fire UB : ALD	-0.1610	0.3803	-0.42	0.6721

Table 2.6. GLMM of shrub density modeled with the following site conditions using a quasi-Poisson distribution and a log link, with site as a random factor; n = 48. Bolded values are significant (α < 0.05).

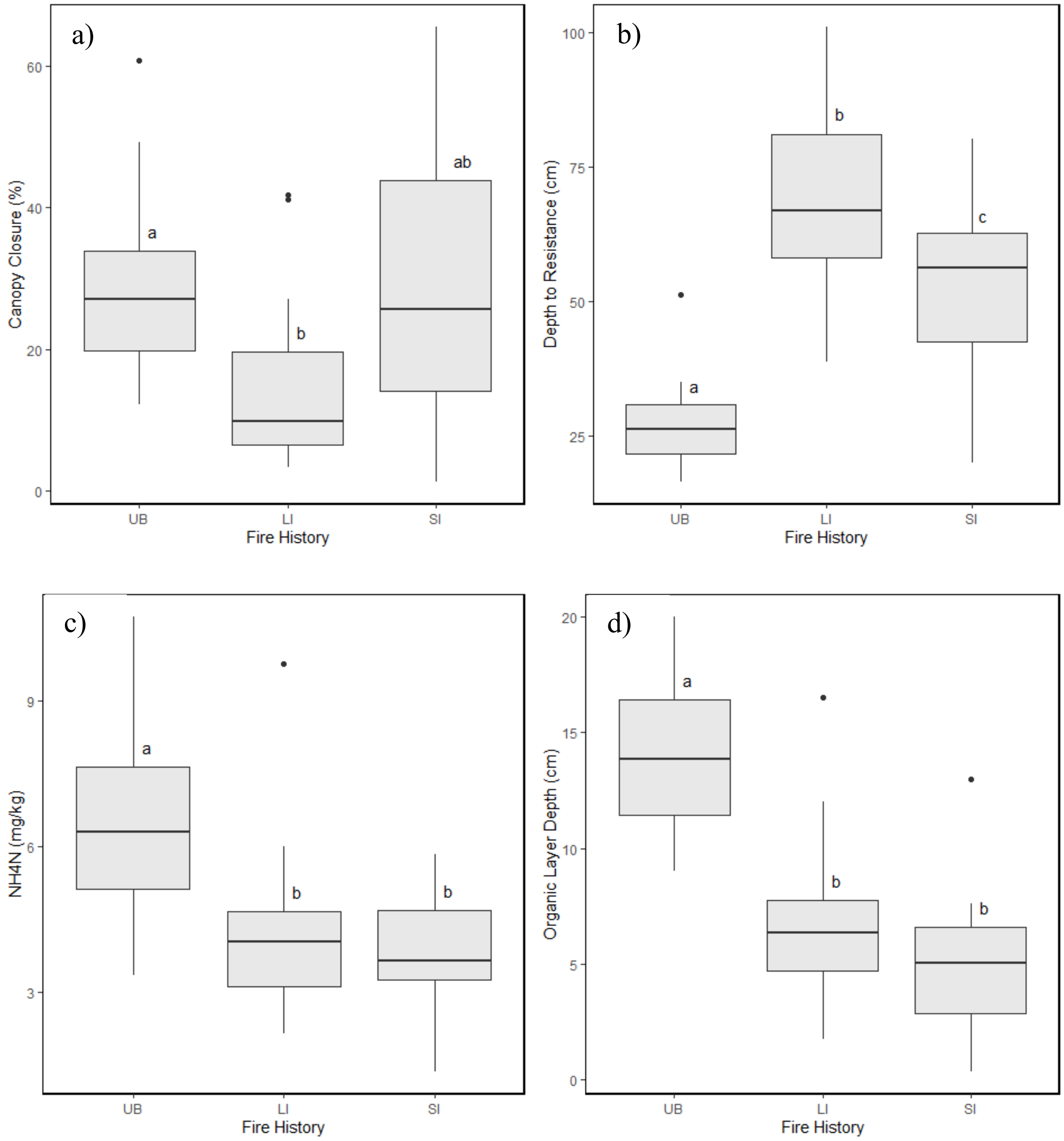
Explanatory Variable	Estimate	Standard Error	z-Value	p-Value
Intercept	9.9378	0.2039	48.75	**< 0.0001**
Fire SI	0.2489	0.2344	1.06	0.2883
Fire UB	-0.5394	0.4134	-1.30	0.1920
Soil moisture	0.0757	0.0947	0.80	0.4238
Soil temperature	0.1152	0.0955	1.21	0.2273
ALD	-0.1232	0.1931	-0.64	0.5235
Fire SI : soil moisture	0.5062	0.2138	2.37	**0.0179**
Fire UB : soil moisture	0.3100	0.1875	1.65	0.0982
Fire SI : ALD	0.7771	0.2446	3.18	**0.0015**
Fire UB : ALD	-0.2395	0.3594	-0.67	0.5052

Table 2.7. GLMM of black spruce density modeled with the following site conditions (including soil nutrients) using a quasi-Poisson distribution and a log link, with site as a random factor; n = 45. Bolded values are significant ($\alpha < 0.05$).

Explanatory Variable	**Estimate**	**Standard Error**	**z-Value**	**p-Value**
Intercept	10.4783	0.1982	52.87	**< 0.0001**
Fire SI	-2.1043	0.3052	-6.89	**< 0.0001**
Fire UB	-0.4539	0.4012	-1.13	0.258
Soil temperature	0.0422	0.1204	0.35	0.726
ALD	0.1017	0.1449	0.70	0.483

Table 2.8. GLMM of shrub height modeled with the following site conditions (including soil nutrients) using a gaussian distribution and an identity link, with site as a random factor; n = 43. Bolded values are significant ($\alpha < 0.05$).

Explanatory Variable	**Estimate**	**Standard Error**	**z-Value**	**p-Value**
Intercept	91.570	5.823	15.727	**< 0.0001**
Fire SI	30.655	7.741	3.960	**< 0.0001**
Fire UB	-74.216	13.481	-5.505	**< 0.0001**
Slope	-16.673	3.165	-5.268	**< 0.0001**
ALD	-14.429	4.993	-2.890	**0.0039**
Fire SI : ALD	37.018	7.205	5.137	**< 0.0001**
Fire UB : ALD	-7.833	12.806	-0.612	0.5408


a)
Canopy Closure (%)
0
20
40
60
a
b
ab
UB
LI
SI
Fire History
b)
Depth to Resistance (cm)
25
50
75
100
a
b
c
UB
LI
SI
Fire History
c)
NH4N (mg/kg)
3
6
9
a
b
b
UB
LI
SI
Fire History
d)
Organic Layer Depth (cm)
0
5
10
15
20
a
b
b
UB
LI
SI
Fire History

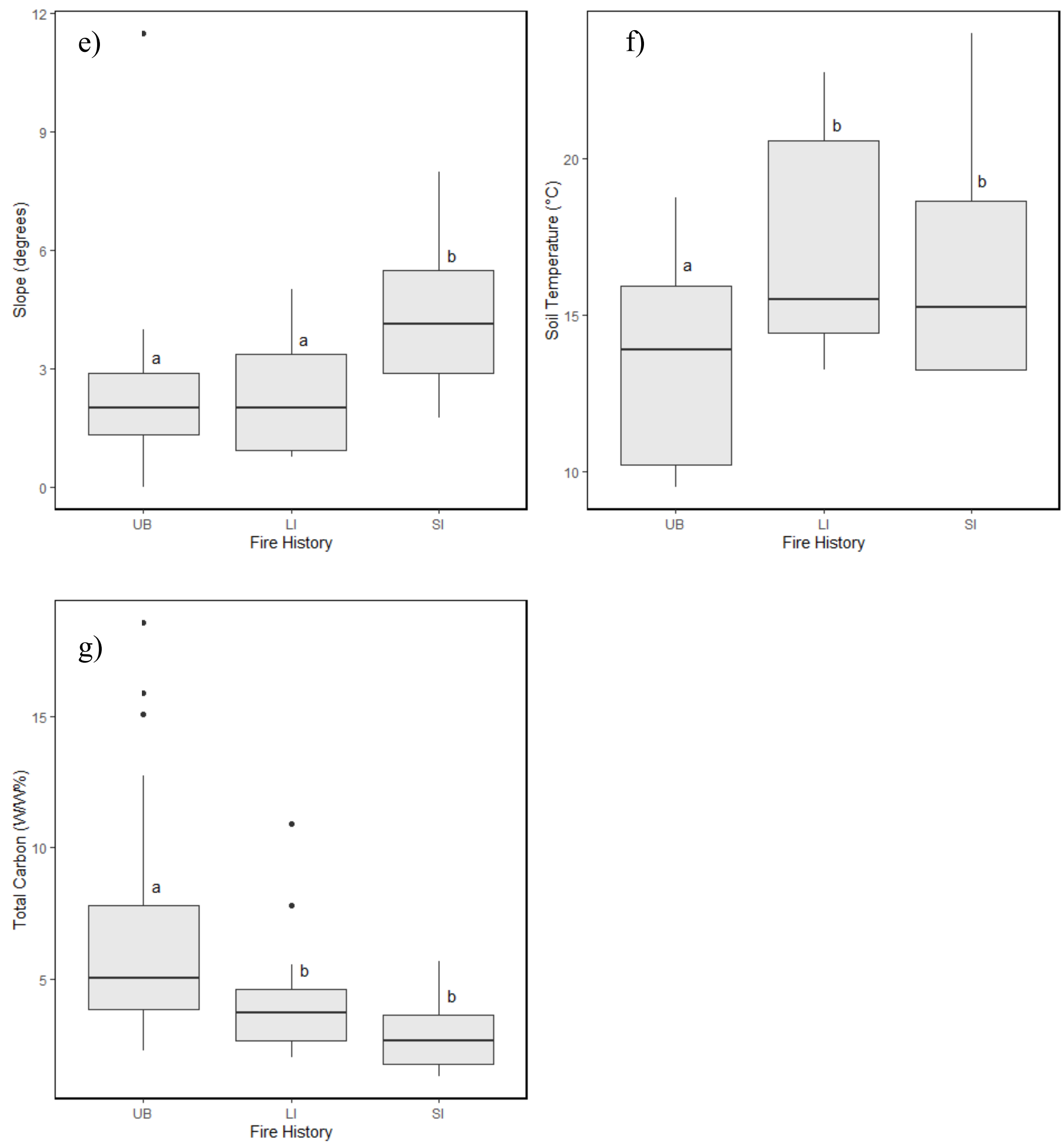


Figure 2.7. Boxplots of the significant environmental characteristics measured at all sites of the different fire history classes, including: **(a)** canopy closure (%), **(b)** ALD (cm), **(c)** ammonium (NH_4N; mg/kg), **(d)** OLD (cm), **(e)** slope (degree), **(f)** soil temperature (°C), and **(g)** total carbon (w/w%). Horizontal lines in the boxes represent the median of the observations within each site. Boxes represent the 25-75% quartiles, while whiskers represent the 95% quartiles. Dots beyond the whiskers represent outlier observations. Letters above the boxes indicate significant differences between fire history classes.

2.4 Discussion

2.4.1 Current recovery trajectories

Our findings support the idea that changes to the material legacies of black spruce have caused a misalignment between their adaptations and the disturbances. Similar to other locations in the boreal-tundra ecotone of northwest North America, our sites in northern Yukon show that a decrease in fire return interval is resulting in a divergent recovery trajectory (Johnstone & Chapin, 2006). As expected, black spruce abundance and densities were distinct between fire history classes with the lowest black spruce densities in short interval (SI) sites. In the absence of black spruce, we observed greater shrub density and heights in SI sites with deeper active layers, further distinguishing SI burned sites from those with historic fire return intervals. This deviation from a typical recovery path in the SI sites is a consequence of black-spruce forests burning a second time before becoming reproductively mature and capable of producing large quantities of seed (Brown & Johnstone, 2012). Losing this key process in the disturbance regime of black spruce forests is an example of a loss in resilience, or change in identity, feedbacks, function, and structure of the system (Walker et al., 2004). Tall shrubs have been able to take advantage of this change in disturbance regime and the favorable growing conditions (i.e., deeper active layer) devoid of competition by black spruce, which would otherwise eventually shade out the shrubs.

Loss of resilience has been demonstrated elsewhere in black spruce forests across northwestern North America after a decrease in fire interval or fire severity, however, the reorganization of the post-disturbance ecosystems does not always result in a complete regime shift (Baltzer et al., 2021; Seidl & Turner, 2022). In our SI sites, we found a distinct change in composition (i.e., loss of black spruce and increase in abundance of tall shrubs) and structure (i.e., loss of regeneration of canopy layer), thus there is evidence to support that a regime shift is underway (*sensu* Seidl & Turner, 2022). Therefore, understanding the regrowth of the ecological communities in the SI sites will help predict future trends of community response to changing disturbance regimes and the potential ripple effects on other ecosystem processes of these lesser understood trajectories. What follows is a contemplation of our findings on community regeneration in the different fire history classes, our examination of the influence of shrubs on ecosystems, and how site characteristics like active layer depth (ALD) may alter recovery trajectories. Finally, we will discuss the variability of ecological community response, and potential implications for culturally important species.

Our unburned (UB) study sites were exemplars of mature, sub-arctic black spruce forests in the area, and representative of the other fire history classes prior to their burns. These sites had the greatest organic layer depths (OLDs) and were characterized by their sphagnum and pleurocarpus moss layers, which are key components to preserving the permafrost layer and to maintaining low productivity of the site (O'Donnell et al., 2009, Soudzilovskaia et al., 2013). The potential for low productivity was also reflected in that they had the coolest soil temperatures of the fire history classes. Additionally, UB sites had the second highest density of black spruce after the long interval (LI) sites, and the lowest density and the shortest tall shrubs of all the fire history classes.

UB sites also had the highest concentrations of total carbon and ammonium (NH_4N). Our NMDS ordination revealed that these soil nutrients, as well as total nitrogen, were often associated with sphagnum moss and caribou lichens. This association is likely because these soil nutrients are in an inaccessible form for plant uptake. For instance, the thicker organic layer suggests that nitrogen may be in its organic state in the organic layer. It needs to go through the mineralization process, as in be decomposed by microbes, to become ammonium. In cold soils, this process is slow because microbes are less active (Sturm et al., 2005). Once nitrogen reaches the ammonium state, it is still a less mobile and an inaccessible form of nitrogen for vegetation (Oulehle et al., 2016). It requires further decomposition from soil microbes, known as nitrification, to become its most accessible form of nitrogen for plant uptake (Johnson et al., 2005). Further, mature boreal forest is known to be a major carbon sink, storing carbon in its organic layer (Kasischke, 2000). The association of total carbon in sites with more soil organic matter and slow growing lichens reflects this process. Thus, though the UB sites are characterized by the presence of these soil nutrients, it is because they are in inaccessible forms that make them unavailable for plant uptake.

As we expected, LI sites are experiencing typical recovery patterns of black-spruce forests in its adapted fire regime. Black spruce densities were highest in these sites, suggesting that post-fire recruitment from seed was successful. Coarse woody debris was indicative of LI sites, aligning with typical fire cycles where standing dead wood persists in post-fire landscapes into mature successional stages, whereas they would be consumed by the second fire in SI sites (Johnstone, 2006). In quadrats with deeper ALD, more litter and early colonizing species like horsetail and fireweed were growing, suggesting higher site productivity. Finally, there was less canopy closure in LI sites than UB sites, likely because the canopy layer is still recovering in these sites. This lack of a canopy allows more light to reach the soil, stimulating more productivity of the fast-growing shrub understory layer (Hart & Chen, 2006).

The SI sites, having experienced two closely timed fires, displayed little to no regeneration of black spruce, illustrating the persistent black spruce regeneration failure first identified by Brown and Johnstone (2012). Black spruce forests tend to be self-replacing, meaning that post-fire recovery of ecological communities eventually return to black spruce dominated stands (Suffling, 1995). Knowing that the first 10 years post-disturbance are crucial for the recruitment of black spruce and their subsequent dominance in later successional stages, a failure to regenerate in SI sites suggests that these sites are on an alternate regeneration trajectory (Johnstone et al., 2004). This possibility is supported by the unique community composition in SI sites, which have almost no overlap in species assemblages with LI sites. Though the ecological communities of these fire history classes are currently more similar to each other than the UB sites, it is likely that these sites will become more distinct over time as the black spruce saplings mature in the LI sites and the shrubs mature in the SI sites. With higher densities of shrubs in SI sites with deeper active layers, and SI sites with greater soil moisture, growing constraints have been lessened allowing for quick-growing species to take advantage of these conditions. Shrubs in the deeper ALD sites also tended to be taller, suggesting that there may be more soil productivity in these SI sites. In addition, SI sites also have greater slope than the other fire history classes, suggesting that better drainage may contribute to drier sites thus increasing the likelihood of the sites burning twice in quick succession.

Species densities varied between sites of each fire history class with greater densities of willow (a tall shrub) in SI sites. Dwarf birch (*Betula glandulosa*), also a tall shrub, occurred in all fire history classes but had higher densities in UB and LI sites. Shrub heights were variable with taller shrubs in LI and SI sites, and taller shrubs in SI sites with deeper ALDs. Willow species were the tallest, followed by the birch species. High variability in species response is a common occurrence at a landscape scale and underscores the importance of understanding specific site characteristics that may influence this dissimilarity across landscapes (Elmendorf et al., 2012a). However, it is still important to understand species-specific responses in shrub growth to various abiotic and biotic factors because different shrubs perform varied roles within this landscape.

Different shrub species and growth forms will differ in albedo reflection, decomposition rates, productivity, and snow capture ability (Elmendorf et al., 2012b; Grabowski, 2015; Semenchuk et al., 2015). The composition of our SI sites varies slightly from those in the existing literature on trajectories after black spruce failure in the Cordillera ecoregion. To date, birch (i.e., *Betula neoaslaskana* and *Betula papyrifera*) and aspen (*Populus tremuloides*) species have been the most common alternate regeneration state in this ecozone (Baltzer et al., 2021). Though there was some Alaskan birch (*Betula neoaslaskana*) present at our LI and SI sites, it was in low densities without much site influence at the time of our study. As such, characterizing this shrub species response to a shortened fire return interval has identified a potential divergent trajectory in this area.

2.4.2 Shrubs as an alternate trajectory in short interval sites

Across the northwest boreal region, including the ecoregion of this study, changes to post-fire successional pathways via a shift from conifer to broadleaf species is occurring (Baltzer et al., 2021). For instance, a shortened fire return interval of conifer-dominated sites in southern Yukon resulted in a shift to deciduous forest stands (Johnstone & Chapin, 2006). Similarly, in Northwest Territories and northeastern Alberta, greater fire severity has shifted conifer stands to aspen dominated forests (Dawe et al., 2022, Day et al., 2022; Whitman et al., 2019). Climatic conditions favoring greater fire activity are anticipated to persist (Coops et al., 2018; Flannigan et al., 2005; Wang et al., 2015), which will create more opportunities for distinct shifts in recovery trajectories of vegetation communities (Johnstone et al., 2010a). Understanding the varied response of ecosystems in these areas is of crucial importance to fully decipher the effect on more broadscale processes and interactions including nutrient cycling, carbon sequestration, water balances, and wildlife interactions, among others.

With shrub expansion already underway as a response to climate change (Myers-Smith et al., 2011), deciduous tall shrubs may be uniquely positioned to fill the void created by failed post-fire tree regeneration if the conditions are favourable. This alternate trajectory may especially thrive in the continuous permafrost zone where black spruce is often the only abundant tree species and uncertainty still exists surrounding sudden shifts in vegetation assemblies. Key requirements for an increase in tall shrub biomass include rising air temperatures, increased soil moisture, favourable topography like mid-slope positions, permafrost thaw, increased nutrient availability, disturbance, and a lack of herbivory (Mekonnen et al., 2021). With a shortened fire return interval, tall shrubs may be at an advantage to other vegetation communities in this region since fire is known to impact most of these abiotic and biotic factors. Our study documented denser and taller shrubs in sites with permafrost thaw (i.e., deeper active layers). Furthermore, greater soil moisture was also associated with denser SI shrub sites, aligning with the larger trends observed across northern latitudes in the last half century (Elmendorf et al., 2012a). These findings suggest that one possible trajectory of post-fire communities of shortened fire return interval in the boreal-tundra ecotone of Yukon may be a regime shift away from conifer canopies and towards shrub dominated sites. In the long term, these sites may result in higher stem densities and taller shrub communities with lower densities of black spruce when compared to normal recovery trajectories and mature forests.

A shift to shrub dominated landscapes is significant for several reasons, including changes to ecosystem structure, function, and processes. Tall shrubs act as ecosystem modifiers primarily through the winter biological processes that their physical properties facilitate (Sturm et al., 2005). In most landscapes, tall shrub canopies more effectively trap snow, insulating the soil, thereby allowing for increased winter microbial activity, breaking down nutrients and rendering them available for plant uptake (Frost et al., 2018; Myers-Smith & Hik, 2013; Sturm et al., 2005). Not only does the structure of the shrubs trap snow, but it also reduces spring albedo since tall shrubs may be above the snowpack in some places. This will lead to earlier green up, contributing to warmer air temperatures (Epstein et al., 2013), and potentially giving shrubs a competitive advantage over other plant species (Tape et al., 2012). Though denser and taller shrubs create more shade in the summer, recent modelling reinforces that winter warming in shrub environments overwhelms any summer shading effect of vertical growth (Way & LaPalme, 2021). Further, an experimental study that looked at over 100 years of data of dwarf birch (*Betula nana*) in western Greenland demonstrated that periods with greater snow depth were associated with more radial stem growth than in times with less snow depth (Hollesen et al., 2015). Though a canopy layer was already present in the typical successional trajectories of our sites, a shift to tall shrub-dominated sites with higher densities will likely cause changes to the resulting canopy layer, snow depth, and the subsequent processes that these attributes influence.

Across Canada, fewer soil freezing days have been observed over the previous 50 years and are expected to continue (Henry, 2008). In landscapes where shrubs already occur, tall shrubs are able to take advantage of these conditions and quickly expand their growth (Hallinger et al., 2010). This warming trend may also facilitate the expansion of tall shrubs into areas that currently do not have tall shrubs (Myers-Smith & Hik, 2018). Increased shrub growth from higher winter soil temperatures creates a positive feedback loop leading to warmer air temperature, warmer soil, and deeper active layers (Epstein et al., 2013). Yukon is predicted to have greater warming in the winter months compared to other seasons, perpetuating this cycle (Perrin & Jolkowski, 2022). As shrubs continue to influence change on their surroundings, the successional pathways of post-fire SI communities will further diverge from that of a typical black spruce regeneration cycle. This process will further the unlikeliness that the SI stands return to black spruce stands but carry on in their new alternate trajectory instead.

2.4.3 Influence of active layer depth on vegetation communities

Though the most obvious link between shrub expansion and climate change is air temperature, there are many other site parameters that also influence shrub growth (Tape et al., 2012, Mekonnen et al., 2021). An important abiotic component of the plant-site environment is the active layer. Not only does ALD influence the vegetation communities that grow in those areas, but it also influences ecosystem productivity (Anderson et al., 2020), and species richness of some ecosystems (Wang et al., 2012). ALD is one of the most important factors in dictating vegetative growth in northern latitudes where permafrost occurs.

As fire patterns change in subarctic ecosystems due to climate change, this will undoubtedly impact ALD and the resulting plant communities. Ecosystem post-fire recovery periods, specifically permafrost recovery, are expected to lengthen from lingering effects on ALD (Holloway et al., 2020, Jafarov et al., 2013). Fires with greater extent, frequency, and severity are expected to increase summer soil temperatures and deepen the active layer (Holloway et al., 2020, Loranty et al., 2018). Changes in fire patterns will also lengthen the active period, reducing the time in which the ground is frozen (Loranty et al., 2018). In these new fire landscapes, retention of OLD will be most influential in determining the extent of permafrost degradation caused by fire (Jafarov et al., 2013). It is inevitable that as the fire regime of the northwestern subarctic changes, several influential parameters for vegetation communities in the region will also be altered.

Deepening ALD signifies two important things for vegetative growth, additional space for plant rooting and an influx in available nutrients due to thawing permafrost. Increasing the volume available for plant rooting enables plants of some functional groups like graminoids to root into the area and take advantage of the newly available resources (Blume-Werry et al., 2019). In shallow permafrost areas of black spruce forests, cold-adapted species have developed strategies to improve their nutrient uptake. One strategy is to increase the proportion of fine roots to total root biomass, effectively maximizing surface area for nutrient uptake in the limited space available (Noguchi et al., 2016). With a deepening ALD, plants with deeper root systems will be able to expand their total root growth, with less need to focus on fine rooting. Graminoids and some forbs have shown to be capable of rooting deeper whereas dwarf shrubs of northern latitudes tend to limit rooting to higher in the soil column (Hewitt et al., 2019). Knowing that plant functional groups have different strategies to concentrate root growth in different parts of the soil column, it is likely that the functional groups with deep-rooting strategies will be able to take immediate advantage of a thickening active layer (Blume-Werry et al., 2019, Hewitt et al., 2019, Oulehle, et al., 2016).

Deeper active layers are known to have greater microbial activity and more active nutrient cycling (Webber, 1978). Nitrogen and phosphorous availability tend to increase in response to warming temperatures, a reflection of increased mineralization (Chapin et al., 2005). Unsurprisingly, this increased activity in the soil layer is sometimes reflected in the aboveground vegetation growth. Deeper ALD is positively correlated with specific leaf area of both coniferous and deciduous trees, suggesting greater photosynthetic rates and plant production (Anderson et al., 2020; Standen & Baltzer, 2021). Not only can changes to nutrient cycling affect plant productivity, but it can also lead to changes in community composition. For instance, an increased presence of graminoids and forbs and a decrease in evergreen shrubs was observed in the thawing boreal peatland (Standen & Baltzer, 2021). Some suggest that this could be a result of sustained nutrient availability over a long period of time (Gough et al., 2012). In our study, deeper ALD was more associated with woodland horsetail, fireweed, and Lappland's reedgrass in LI and SI sites. Reedgrass and horsetail both have deeper-rooting capabilities (deep rhizomes in the case of horsetail) and all three are quick growing species that also produce a lot of litter, allowing for quicker nutrient cycling and sustained warming of the soils (Beasleigh & Yarranton, 1974; Keuper et al., 2017). Given the ongoing changes to the soil environment, shifts in community composition, due to changes in fire regime, away from coniferous dominated ecosystems are likely to be observed.

Since deciduous tall shrubs can take advantage of nutrient influxes (Chapin & Shaver, 1989; Webber, 1978), they may be well suited to future climate and fire patterns that encourage thawing permafrost. A thickening of the active layer, as a result of changing fire patterns, may further encourage an increase in tall deciduous shrubs (Martin et al., 2017). Black spruce stands are failing to regenerate after greater severity fires, when most of the organic layer is consumed (Baltzer et al., 2021). This failure is exacerbated in areas where greater severity or more frequent fires are consuming material legacies, leaving sites with less seed available prior to fire (Brown & Johnstone, 2012; Day et al., 2022). Moreover, in dense conifer sites, post-fire turnover in vegetation communities is more common (Walker et al., 2021). The flush of nutrients post-fire, combined with nutrients released from thawing permafrost, may be setting the stage for deciduous tall shrubs to establish and thrive. This aligns with an Alaskan study that observed deeper active layer in areas in which willow shrubs have colonized within ten years of a burn (Racine et al., 2004). Our study demonstrated that sites with increased fire activity and deeper active layers had higher densities and heights of tall shrubs, which suggests that shrubs are taking advantage of the newly suitable post-fire habitat. One plausible outcome to increased fire activity is an increase in tall deciduous shrubs densities. This occurrence in conjunction with other fast-growing species, such as graminoids and forbs, in deeper active layer sites will lead to quicker nutrient cycling, productivity, and warming of the soil. This ultimately supports the idea that there will be further deviation from typical black spruce successional community towards a larger regime shift and non-forest trajectory.

2.4.4 Other possible alternate regeneration pathways

Though general climate trends and predictions favour shrub expansion in the north, shrub response to warming has shown regional variability (Elmendorf et al., 2012a). The many indirect and direct impacts of climate change comprise a complex system where the outcomes are not always well understood or immediately recognized. Our study found large variation between shrub densities and heights between sites of the same fire history class, suggesting that differences in the microsite environmental characteristics are driving the observed difference. Many shrub studies have demonstrated that shrub canopies alone do not have a strong impact on summer nutrient cycling, suggesting that individual abiotic factors may not have a significant effect on ecosystem dynamics as has been predicted (Kropp et al., 2021; Myers-Smith & Hik, 2013). This was true in our study where deeper ALD was found in some of the LI sites compared to SI sites, yet only a significant ALD effect in relation to shrub densities was noticed in SI sites. Furthermore, climate parameters at the regional level may mediate shrub growth (Elmendorf et al., 2012a; Myers-Smith & Hik, 2018; Semenchuk et al., 2015; Schmidt & Forchhammer, 2006). Unevenness in shrub response may also depend on the contiguity of the landscape in an area. For instance, along edges of open areas, shrubs capture more snow and result in warmer temperatures than surrounding open areas (Roy-Léveillée et al., 2014). Additionally, disturbances like fire add a layer of complexity to this already variable system. It may not be immediately apparent whether an ecosystem will become shrub-dominated and more understanding of the abiotic components of the environment may be required to accurately determine successional pathways.

With their ability to quickly access deeper, more nutrient rich environments, graminoids are poised to take advantage of sites with deeper active layers (Oulehle et al., 2016). Van der Kolk et al. (2016) have already predicted dominant functional groups of northern ecosystems under varying climate scenarios. They demonstrated that graminoids may be better suited than shrubs to establish post-disturbance in areas with sudden thawing of the permafrost layer, creating thaw ponds. Excessive water in the soil is thought to drown shrubs whereas graminoids can tolerate water-saturated soils (Van der Kolk et al., 2016), and is consistent with real-world observations (Myers-Smith et al., 2015; Tape et al., 2012). Studies have also found decreased concentrations of nutrients in above-ground biomass of deciduous shrubs in wet sites (Jasinski et al., 2022). It is predicted that shrubs will thrive along the edges of the collapsed ice wedges, suggesting that better drainage is a key component of shrub growth. However, as with all models, they may be simplified representations of the ecosystem. Not all contributing factors are able to be accounted for, and thus caution is needed when interpreting results. Therefore, there still is uncertainty in predicting the conditions in which lead to dominance in different vegetation groups.

In situ observations confirm that temperature plays a large role in shrub growth. A global review found that shrubs have been expanding in areas with warmer air temperatures, while graminoids have expanded in cooler areas (Elmendorf et al., 2012a). These observations coupled with our findings and predictions suggests that in our study area, it is likely shrubs will continue to thrive with patches of grassland intermixed in places with poor drainage. It is unlikely that the northern expansion of other tree species will occur for some time, likely due to a time lag between changing climatic conditions and species' specific responses (Svenning & Sandel, 2013). Continued monitoring of these sites will help provide valuable information into how some northern landscapes will respond to shortened fire return intervals.

2.4.5 Culturally important species

Understanding the mechanisms that drive species specific responses are important not only from an ecological perspective, but also to understand the impact on the human dimensions of northern ecosystems. The landscape holds significant value to Indigenous communities and changes to the environment and the ability for people to connect with the land may have sweeping emotional and wellness ramifications (Cunsolo Willox et al., 2013). For instance, a shift to shrub dominated sites may have future implications on culturally significant species such as barren-ground caribou (*Rangifer tarandus grantii*) and commonly harvested berry species.

An increase in shrub habitat may provide more summer forage for caribou, however, it may result in less protein availability (i.e., nitrogen) for an equivalent amount of forage compared to lichen (Thompson & Barboza, 2014). Caribou also rely largely on lichen for winter forage (Klein, 1982) and studies have shown that lichen recover slower than other vegetation post-fire (Jandt et al., 2008). A shorter fire return interval could further reduce the abundance of lichen and lead to limited winter forage availability for caribou. An increase in burned area may also impact caribou movements and their habitat use (Sharma & Côté, 2009). This could change caribou migration patterns and affect accessibility for communities to the herd.

Further, shifts in shrub composition due to frequent fire may alter the abundance of berry plants and their berry production by changing the site conditions in which berry plants are adapted to grow. Berries play an important role in the spiritual, individual, and communal well-being of Indigenous peoples (Boulanger-Lapointe et al., 2019). Changes to fire return interval may indirectly change engagement behaviors of people with the landscape (Brinkman et al., 2016). As such, monitoring of these ecosystem components should be integrated into long-term vegetation tracking efforts.

2.4.6 Conclusion

By studying vegetation communities and their associated environmental conditions in sites with misaligned fire history classes, we have identified divergent regeneration patterns away from typical black spruce regeneration. Our findings suggest that deciduous tall shrubs can take immediate advantage of these improved growing conditions and are proliferating faster than other species. Knowing that tall shrubs are able to exert positive feedbacks on their environments, it is likely that the post-fire recovery trajectories of these sites will further depart from the current LI successional pathways.

Findings from SI sites resulted from a sudden and unexpected shift in sub-arctic plant communities due to the indirect effects of climate change and its impact on the ecological memory of the dominant ecosystem. Fires are expected to become more frequent in the boreal-tundra ecotone, and more areas may experience similar shifts to their material and physical legacies, possibly leading towards an interval squeeze in black spruce forest populations. With the possibility that shortened fire return intervals may become more commonplace, studying areas that are already experiencing these changes is important to know how ecosystems will respond. Feedbacks between climate-permafrost systems are complex, making it challenging to predict changes in soil thermal properties and ecosystem processes in permafrost ecosystems (Loranty et al., 2018). There are also often multiple feedback levels occurring, operating on various spatial and temporal scales. Knowing how some ecosystems are changing may help understand possible implications for other ecological processes, and culturally important species.

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Chapter 3: Study implications and conclusions

3.1 Summary of findings

Our study in the subarctic boreal forest region of Eagle Plains, Yukon, examined the influence of fire return interval on vegetation regeneration trajectories. Our study demonstrated altered vegetation community regeneration patterns, a decade following multiple fires, due to black spruce (*Picea mariana*) regeneration failure. Vegetation communities within each of the three fire history classes were distinct from one another. Our unburned (UB) sites were the most discrete in their composition, dominated by mature black spruce and the sparsest tall shrubs, containing the shallowest active layer depths (ALDs), the greatest organic layer depths (OLDs), the coldest soils, and the greatest total carbon and ammonium. Our long interval (LI) sites had the deepest ALDs and the highest densities of black spruce and the second highest densities of tall shrubs, following typical post-fire recovery for the region. The short interval (SI) sites, or sites experiencing a shorter fire return interval, had the lowest densities of black spruce and the highest density of tall shrubs. In particular, sites in this fire history with deeper ALDs had higher tall shrub densities and overall taller shrubs on average. Furthermore, SI sites with greater soil moisture had higher densities of shrubs. Finally, regeneration failure of black spruce was obvious in the SI sites as these sites had distinctly lower densities of black spruce. With the absence of black spruce seedling regeneration in SI sites, recovery in these sites shows to be diverging further from the LI sites, likely leading away from black spruce-dominated systems in the future.

Fifteen years after the last fire, tall deciduous shrubs are the most dominant group in SI sites. Our findings suggest that a shortened fire return interval can set ecosystems on completely different growth trajectories than ones that occurred in typical, longer fire return intervals. With continued climate change, favourable conditions for sudden shifts to the dominant disturbance may become more common and lead to dramatic shifts in regeneration patterns of vegetation communities. Understanding how ecosystems may respond to these changes is critical to predict and prepare for the potential ecological and cultural consequences that may follow.

3.2 Ecological implications of a shrubbier environment

Transformations from a low productivity plant community with a tree canopy to a more productive site dominated by shrubs will result in substantial changes to the natural system. Alternate successional trajectories of vegetation communities can influence nutrient cycling, energy transfer, water cycling, and other ecological processes, potentially altering the feedback loops and furthering the deviation of ecosystems from typical post-fire communities (Myers-Smith et al., 2015). A loss of black spruce in this area will likely reduce the below-ground stores of carbon, result in more storage and emissions of above-ground carbon effectively changing carbon cycling (Walker et al., 2020). Another consideration of an increasingly shrubby environment is the potential for loss of species diversity, especially in some functional groups like bryophytes and lichens (Walker et al., 2006). Experimental studies with shrubs also found significantly less species diversity in long-term fertilization and temperature manipulated studies (DeMarco et al., 2014). These changes, coupled with shrub effects on the active layer, will result in a much different ecosystem than that of the typical black spruce system.

Additionally, a shift towards shrub-dominated ecosystems will impact wildlife habitat and their interactions with the landscape. Herbivory, predation, and habitat use of many species will be impacted by shrubbier landscapes for several reasons including, the alteration of summer and winter forage availability for wildlife (Thompson & Barboza, 2014). In Arctic Alaska, shrub expansion is thought to be the cause of the recent establishment of snowshoe hares and expansion of their predators (Tape et al., 2016). Other shrub-loving animals may also expand or shift their ranges' in response to these landscape changes and bring their predators and ecosystem-influencing abilities with them. Regular pulses in the population of small mammal herbivory have top-down effects on community composition and abundance by driving biomass fluctuations of targeted species (Olofsson et al., 2013). Additionally, herbivore browsing can limit shrub encroachment in some areas, and modify the growth forms of the shrubs that they are eating (Kaarlejärvi et al., 2015; Ravolainen et al., 2014). Individual shrub species have different palatability to herbivores due to their varying concentrations of chemical compounds, meaning that some areas will be more targeted by browsing than others, depending on species composition (Christie et al., 2015). Changes to the structural dimensions of these areas will influence breeding habitat of migratory songbirds (Boelman et al., 2015; Wauchope et al., 2017), and the movement patterns of other mammals (Zhou et al., 2020). As such, the introduction of shrubbier landscapes will greatly alter species dynamics and processes of these subarctic ecosystems.

Shrubbier ecosystems may also eventually reduce the flammability of the landscape due to a reduction of fuel (Hart et al., 2019). As fire frequency increases and more severe fires burn the available biomass, it may eventually lead to fuel limitations, especially if drought conditions persist and lead to lower productivity of vegetation (Parks et al., 2016). Further, if greater fire activity leads to burning younger forest stands of under 50 years in age, resulting in more deciduous and shrub species, once fire prone landscapes may become less affected by fire. This would be a drastic change in ecosystem processes as fire has long been considered one of the most important disturbance agents in boreal systems. Across North America, successive fires are resulting in more contiguous landscapes of immature forests that can reburn every 10-15 years

(Harvey et al., 2023). As such, shrub dominated areas may provide some heterogeneity to the larger landscape and reduce its overall susceptibility to fire.

3.3 Implications for culturally significant species

Understanding the impact of expansion of tall shrubs on culturally significant species is a documented research gap in Yukon (Reid et al., 2022). Though we were unable to offer findings that directly address this question, here we will present some possible implications of changing regeneration trajectories.

This research took place near Eagle Plains, Yukon, in the traditional territories of the Vuntut Gwitchin First Nation (VGFN). The VGFN are a part of the larger Gwich'in First Nation, with traditional lands that extend from Alaska to the Northwest Territories (Smith & Vuntut Gwitchin First Nation, 2010). The Eagle Plains region has long been used for trapping and hunting and is important winter habitat for the Porcupine Caribou herd (PCH; *Rangifer tarandus grantii*; Smith & Vuntut Gwitchin First Nation, 2010). The VGFN have long been supportive, initiated, and collaborated in numerous natural science research projects on their lands. In 2018, they commissioned a report that identified environmental changes to their lands and identified research and monitoring priorities (Kuntz & Vuntut Gwitchin First Nation, 2018). This report included several items that relate to our project. The report listed shifts in caribou habitat due to changes in vegetation, water levels, forest fires, and predation as a concern. Other priorities that were highlighted included better understanding of the connection between vegetation changes and climate, and the resulting changes to fire and important food plants like berry producing species. Findings from our study may provide some insights to these monitoring priorities.

Traditional foods are still an important component of diets of the Vuntut Gwitchin (Schuster et al., 2011). However, as environmental conditions change, so do resources required to maintain a traditional food diet. As it stands, 26% of community households reported less than ideal amounts of traditional foods (Schuster et al., 2011). This can include both harvested meat like caribou, and berries for picking. Relationships with these valued resources extend beyond being important food staples for the Vuntut Gwitchin, they are intertwined with their culture and practices that have been developed over millennia.

3.3.1 Caribou

The VGFN have long relied on caribou as an important food source and still do today (Wesche et al., 2011). The PCH have been reported as their main cultural and dietary resource (Schuster et al., 2011). However, with a potential increase in industrial activities, changes in climate patterns, available habitat, and increasing hunting pressure around the Dempster Highway (the only road to intersect the PCH range), there is a desire to understand how this may affect the herd. PCH are less productive compared to other herds and as such may be vulnerable to a decrease in numbers, making calf survival more important (Russell & Gunn, 2019). Fortunately, their population has been increasing over the last number of years (218,000 individuals recorded in 2017, a 2.5% annual increase from 2013; Russell & Gunn, 2019). The Porcupine Caribou Management Board (PCMB), an advisory board involving members from all First Nations and other pertinent government bodies, have long been monitoring the health and population of the herd, have cooperatively developed sustainable harvest management plans, and lobbied for continued protection of critical habitat for the herd. Their efforts have been successful in raising awareness of potential threats associated with the herd and the importance of ethical harvesting practices.

Disentangling the impacts of increased fire activity on caribou and their habitat is nuanced and may have both positive and negative effects for the PCH. Immediate threats to the herd are mostly linked to their spring calving grounds in Alaska, which recently faced risk of industrial development (Russell & Gunn, 2019). With respect to threats during winter months, the largest risks have been associated with the likeliness of an increase of rain-on-snow and freezing rain events, and the potential for renewing oil development projects near Eagle Plains (Foster et al., 2022; Russell & Gunn, 2019). As it stands, changes to winter food resource availability of lichens are not currently included in cumulative effects analyses, nor is it considered an imminent threat for the herd (Russell & Gunn, 2019). This is understandable as overlapping burned areas are small compared to the entire winter range of the herd. However, it is important to note that a climate-induced increase in fire frequency may result in more fires in the PCH home range. Climate models project a decrease in winter habitat for the PCH of as much as 21% by the end of the century (Gustine et al., 2014). Due to the potential effects of fire, monitoring habitat loss and change in the PCH range will be important to the overall health of the herd and their habitat. Long-term effects of vegetation change to the winter habitat of PCH are more complex, with both direct and indirect impacts on the herd.

A direct and long-term effect on the PCH is a change in their main source of winter forage. Caribou-foraged lichens (hereafter referred to as caribou lichen) are slow growing and often associated with mature black spruce forests and open tundra. These lichens are one of the most important food sources for caribou in the winter months because they are highly digestible and have the highest nutrition available during the winter period (Thomas & Hervieux, 1986). As part of their life strategy, caribou typically forage on protein rich items in summer such as deciduous shrubs, and more carbohydrate digestible foods in the winter like terrestrial lichens (Denryter et al., 2017; Klein, 1982). Mature lichen forests also have less dense snowpack, thinner snow crust, and less downed debris, allowing caribou to move unencumbered through these areas (Schaefer & Pruitt, 1991). Burned areas, in contrast, have denser snowpack, thicker and harder snow crust, and more downed woody debris (Schaefer & Pruitt, 1991). Over the last thirty years, canopy cover of deciduous shrubs in northwestern North America has increased in conjunction with climate change, while lichen cover has declined (Fraser et al., 2014; Orndahl et al., 2022). This shift, coupled with a change in fire frequency, will likely further reduce the abundance of caribou lichen and potentially shift caribou movement patterns and impact their energy budgets. For instance, caribou have been shown to avoid burned areas for up to 55 years (Anderson & Johnson, 2014; Joly et al., 2003; Joly et al., 2007; Joly et al., 2010; Palm et al., 2022), which may be linked to lack the lack of lichen in these landscapes. It can take more than 40 years for caribou lichen to re-establish post-fire and even longer for their biomass to accumulate to foraged quantities (Heim et al., 2021; Maikawa & Kershaw, 1976; Thomas et al., 1996). Caribou may also be avoiding the deeper snow in burns due to the higher demands to their energy consumption and less time foraging (Russell et al., 1993). As such, caribou may shift their movement patterns to avoid these burned areas.

At the herd level, caribou do not select burns (Joly et al., 2007), but on an individual basis some caribou have been found along edges of burns and young successional stands in the winter (Anderson & Johnson, 2014; Joly et al., 2003). When individuals select burns in the winter, they avoid more severely burned areas due to the absence of lichen cover (Palm et al., 2022). As the influence of fire severity and fire frequency is similar in terms of the loss of lichen biomass, a link may likewise be made between caribou avoidance of areas with higher fire frequencies which have low to no lichen availability. Individuals may be occupying burns because some of the vegetation in regenerating patches may be higher in protein than the other available forage, or perhaps the openness enables them to see predators from greater distances

(Fleischman, 1990; Rickbeil et al., 2016). As the proportion of burned areas within caribou home range increases, caribou are in fact selecting burns in the summertime (Palm et al., 2022). This could be because they have less of an ability to avoid burns or that they are selecting more protein-rich species in burned areas that are unobtainable in other seasons and habitats. Caribou can shift their movement behaviors, this has allowed them to survive in many different habitats spanning a wide spatial and temporal range; however, they require large intact areas to do so (Joly et al., 2021). This plasticity that caribou have demonstrated may become important as fire regimes continue to change landscape patterns, affecting caribou habitat and the requirement to alter their movement patterns based on current available habitat.

With more fire on the landscape, it is possible that caribou will not always be able to shift their movement patterns to avoid shrub landscapes and burned areas. It raises the question of whether caribou will change their winter diets to adjust to the new landscape. Though caribou have historically foraged lichen in winter, they can adjust their diets if lichen is less available (Heggberget et al., 2002). Rapid shifts in vegetation may not necessarily be detrimental to caribou but could represent an alternative stable state (van der Wal, 2006). Herds in areas with low predation (e.g., Svalbard) have been documented to forage primarily on shrubs as an alternative to lichen in winter, however this is primarily due to a reduction in lichen cover from grazing (Heggberget et al., 2002). Caribou have been known to consume large quantities of tall shrubs, primarily leaves and berries, as part of their summer diet (Denryter et al., 2017). With evidence of shrubs comprising a large proportion of caribou summer diet, in a shrubbier landscape with less available lichen, it is possible that caribou shift their winter diet to include a greater proportion of shrubs. Higher statured shrubs may also be less affected by freezing or rain-on-snow events, compared to lichen which often become inaccessible due to an ice barrier that forms during these events, making them unavailable to caribou. However, shrubs may be sub-optimal for caribou, due to the higher concentrations of structural compounds (i.e., fiber content), and secondary metabolites like phenols and tannins, and less protein and carbohydrate, meaning that digestible forage in shrubs may actually be limited (Thompson & Barboza, 2014). Though shrubs may be available for caribou to forage in winter, it is unlikely that shrubs alone would provide necessary digestible nutrients. Instead, in areas of shortened fire return intervals, caribou may abandon their winter range fidelity and follow the presence of lichen to maintain their winter diet selection.

In a shrubbier future, it will be important to consider the impacts of shrubs on other wildlife and the secondary impacts on caribou. Moose, and most other arctic herbivores are known to select willow species more than other erect shrubs (Christie et al., 2015). In tundra Alaska, moose have expanded their range as shrubs have become more abundant throughout this region due to an increase in growing season (Tape et al., 2016). Observations from Vuntut Gwitchin community members support the observation of an increase in shrubs and moose within their traditional territories (Kuntz & Vuntut Gwitchin First Nation, 2018). This northward shift in the range of moose will likely increase the density of predators, specifically wolves, in these areas. Caribou predation by wolves may increase through apparent competition, where caribou may become an alternate food source for this increased abundance of wolves in caribou range (James et al., 2004). Sustained densities of wolves in areas due to the increased presence of non-migratory prey such as moose, would also likely threaten barren-ground caribou when they are at their most vulnerable. Seasonal northward migration is a strategy employed by caribou to put physical space between themselves and wolves during the calving period as wolves are required to stay close to their dens along the forest-tundra ecotone (Hayes & Russell, 2000). This change to wolf distribution may effectively eliminate one of the evolutionary adaptation caribou have developed to avoid predation during calving season.

It is reasonable to predict that caribou will likely avoid shrubby areas when lichen is readily available. Whether or not caribou will choose alternative forage items in the absence of lichen forests is likely dependent on specific conditions for the herd, like available habitat at the local scale, their population densities, and predation rate (Mallory & Boyce, 2018). Caribou need to balance the need for consuming quality food with the need to avoid predators (Parker et al., 2009). Tall shrub habitats are an unlikely winter food source for caribou, may be more difficult to move through, and may have a higher presence of moose and their predators. Lichen forests provide highly digestible winter forage, are easier to move through and may have less predator density. However, if shrubs were to be more prevalent, it is possible that caribou may eventually be required to change their winter foraging habits. If caribou were required to change their winter diet, it could result in a lack of necessary winter nutritional and energy inputs and contribute to reduced fitness at individual and population levels in the long run.

To date, the PCH has exhibited similar mortality rates, dietary, and behavioural patterns of other migratory caribou herds. Historically, approximately one third of PCH adults were killed by wolves, a comparable rate to other packs in Alaska and NWT, with wolves' primary prey being moose (Hayes & Russell, 2000). Further, the PCH access the Eagle Plains area in years with less snow, which has significantly greater lichen cover than other wintering areas and allows them to achieve a positive winter energy budget (Russell et al., 1993). Understanding these particulars is important as it enables us to monitor changes to the herd as pressures of climate change and other stressors continue to evolve. For instance, there is still access to winter forage and lichen forests in this area, but their available habitat should be mapped and monitored in the event that future disturbances like large fires disrupt their winter habitat in a way that may influence their movements and health. In overlapping burns, we found that the composition of tall shrubs in the SI sites is predominantly willow and birch species. Willow species are known to have lower concentrations of tannins, making them palatable to most herbivores (Christie et al., 2015; Denryter et al., 2017), whereas alders are avoided due to their defense mechanisms (Christie et al., 2015). As such, overlapping burns in the Eagle Plains area, composed predominantly of willow and birch regeneration may attract more moose. Overall, it is likely that the PCH will maintain their winter foraging strategy of choosing mature lichen forests and avoid shrub-dominated areas. One tangible way changes to post-fire successional communities may influence the PCH in the future is if the protection for the calving grounds in Alaska ever change, quality winter forage may become more important to the PCH for maintaining their health. The current calving grounds in the northern section of Arctic National Wildlife Refuge in Alaska has significant nutritional advantage than areas surrounding it for quality forage during calving. If the PCH lose access to this prime forage area, or choose to avoid the area due to an increased anthropogenic footprint at this energetically demanding time, it will become very important that they have built up fat reserves over the winter and not be nutritionally deprived for calving season (Russell & Gunn, 2019). Additionally, PCH may shift calving and post-calving further west where vegetation production is expected to increase with future climate trends. This may put them in conflict with resource extraction and could also impact their migration routes (Severson et al., 2021). As time progresses and fire becomes more frequent in the wintering grounds of the PCH, potential changes to their winter habitat may eventually become an important component of the cumulative effects analyses when it is coupled with icing events, increased industrial and other anthropogenic pressures.

Beyond these effects to the PCH, changes to their wintering habitat will impact how Indigenous communities interact with the herd. Given the patchy nature of wildfire on the landscape, caribou will likely choose to avoid burned areas for other more optimal habitat. Avoiding burns may shift caribou distributions and migrations away from current communities in their range. For instance, with increases in burned areas near the Dempster Highway, it is possible that PCH may shift their movements further away from these accessible areas (Gustine et al., 2014). Migration of caribou occurs from 'collective behaviour' and memory (Joly et al., 2021), or how they adapt to variability in climate and anthropogenic activity. Changes to their winter habitat may affect their collective behaviour, shifting their migratory routes. This potential shift in their range may complicate the ability for individuals to interact with the herd. Over time this may change the relationships that these communities hold with this species.

3.3.2 Berries

Within academia, effects of climate change on berry producing plants have received less attention than other natural resources like caribou. Yet, berries have long played a central role in Indigenous communities that inhabit the north. Berry picking holds value in providing nutritional food and medicine for these communities. Beyond these uses, however, there is a more complex and deeper connection of the people to this practice. This link offers a way of knowing the land, understanding where and when to harvest, and which conditions will produce an abundant harvest year (Smith & Vuntut Gwitchin First Nation, 2010). It has also served as a social activity, family and friends will gather at peak harvest to pick together (Parlee et al., 2005; Sherry et al., 1999). Berry patches have spanned temporal and geographical scales, as some will even pick from the same patches as their grandparents (Parlee et al., 2005). At times, it can also be an opportunity for solitude, solo pickers are able to engage with this practice (Parlee et al., 2006). These relationships are complex, and deep cultural and spiritual connections have been developed surrounding these practices. It can also be viewed through a gendered lens where, historically, berry picking was completed by women in the community whereas hunting tasks were more often completed by men (Sherry et al., 1999). So, by focusing climate change discussions solely on topics such as caribou, voices of women have not always been adequately captured within current frameworks of research in the north (Desbiens, 2010). Berry picking fosters an intimacy with the land, and an understanding of how year-to-year variation may impact berry harvest. Thus, berry pickers could be seen as an undervalued voice in the climate change discussion. Changes to the supply of berries may impact the roles of women in the community as berries remain among the most harvested plants today (Boulanger-Lapointe, 2019). This practice continues to provide cultural and physical well-being and an affordable resource gathering activity, also providing economic and food sovereignty to communities (Beebe, 2012, Boulanger-Lapointe et al., 2019).

Berry picking is deeply rooted within Indigenous cultures. Gwich'in berry harvesters have developed informal rules for berry picking. This has helped ensure the long-term viability of berries and in dealing with the highly variable nature of the plants (Parlee et al., 2006). Furthermore, some cultures have stewarded their berry patches using techniques like igniting low severity burns, and weeding shoots of alder and other tall shrubs (Beebe, 2012; Thornton, 1999). Indigenous knowledge shares that blueberries are highly susceptible to willow encroachment and active management of berry patches is sometimes used to maintain berry yield (Parlee et al., 2006). Having this deep-seated knowledge in berry production could be key in developing strategies to protecting this valuable resource. By focusing on potential effects on berries, we are listening to the experience of members of northern communities that may not have already been recognized, and framing the impacts of climate change in a context that is more inclusive.

Berry production in many species is complex and highly variable from year to year. In general, it is limited by four main factors: resource availability, pollination, external events and genetics (Charlesworth, 1989; Parkinson & Mulder, 2020; Stephenson, 1981). Yield is dependent on conditions from previous years (e.g., snow depth, soil moisture) as well as from the current year (e.g., wind conditions, air temperature; Beebe, 2012; Krebs et al., 2009; Parkinson & Mulder, 2020). Those who harvest berries often understand its variable nature. For instance, members of the Vuntut Gwitchin recognize the irregularity in abundance of cultural resources of berries depending on weather and climatic factors (Schuster et al., 2011). However, recently, Vuntut Gwitchin berry harvesters are reporting less berry availability (Kuntz et al., 2018). They have highlighted the need to understand how climate change is impacting their three most commonly harvest berry-producing plants to ensure their continued availability (Kuntz et al., 2018). These species of interest include cranberries (*Vaccinium vitis-idaea*), blueberries (*Vaccinium uliginosum*), and cloudberries (*Rubus chamaemorus*). Each of these species have different growth forms, therefore, the response of each species to climate change will likely vary. It is thus necessary to understand the life strategy and growth form of each individual species.

Cranberries are a creeping, prostrate low shrub that grows along the forest floor. This species is well-adapted to colder climates, it is frost tolerant, and can retain photosynthetic capabilities under snow (Nestby et al., 2019). Cranberry also thrives in acidic soils but grows in many different habitats (Beebe, 2012; Nestby et al., 2019). It is an early successional species that grows well with the increased light from an open canopy (Hitztaler & Bergen, 2013). When it occurs in shady locations, vegetative growth via rhizomes is more common than sexual reproduction through seeds, though it is capable of reproducing both ways (Beebe, 2012; Holloway, 2006). Berry yield fares better on more acidic sites, but their reproductive tissues (e.g., flower structures) are sensitive to cooler summer temperatures (e.g., frost) and can affect resulting berry production. Therefore, low snow cover offers less flower bud protection (Beebe, 2012). Conversely, blueberry is a dwarf shrub with a more upright growth form than cranberries, however it can have both prostrate and upright growth. This species also grows in acidic and peaty soils and is more susceptible to freeze-thaw conditions than cranberry (Nestby et al., 2019). It occurs both as individual plants and as large clones in forests, proliferating by layering using above-ground shoots under the organic layer (Nestby et al., 2019). Light availability and warmer soil temperatures are the strongest predictors of fruit production in blueberry (Siegwart Collier, 2020).

Unlike the other two species, cloudberry grows sparsely throughout the forest and is sensitive to its habitat. This forb requires bog and moss communities with large amounts of moisture and low competition, and is often found in permafrost sites (Beebe, 2012). It is dioecious but will also reproduce vegetatively from rhizomes; both male and female plants will flower but only female plants will produce drupes (Beebe, 2012). It has a skewed sex ratio, with many more male plants than female plants. Limited fruit production in this species may be due in part from its scattered distribution coupled with cold temperatures, lack of pollination, low nutrient availability and slow maturity (Beebe, 2012). It produces far fewer berries than the other species and they are more delicate in nature, easily squished.

Climate change will likely create conditions that both benefit and disadvantage the growth of berry species and berry production. An Alaskan study posits that climate change may affect future quantities and quality of berry species (Kellogg et al., 2010). For example, as drought conditions may become more prevalent, blueberry production may be negatively impacted as water availability throughout the growing season is an important factor for their growth in the northern portion of their range (Boulanger-Lapointe, et al., 2019). At the same time, some resources, like available nutrients, may become less limited, and plant growth may not be as constrained. However, these conditions may also favour its vegetative proliferation strategy as opposed to sexual reproduction which, in turn, would affect berry production. For instance, adapted to boreal fire regimes, berry species like cranberry resprout quickly after fire via the rhizomes or ramets that occur along the forest floor and are often not consumed via low severity crown fires. This allows for quick regeneration post-fire once there is more sunlight penetrating the forest, less competition from other plants, and more soil nutrients readily available. Though fire does create some better growing conditions for these berry species, in many cases berry production is reduced post-fire (Holloway, 2006). More severe and frequent fires may also consume more of the organic layer and may kill or damage the rhizome and ramets of berry plants in the process (Holloway, 2006). This may interfere with their growing strategy and limit the species abundance and distribution on a more fire prone landscape.

Frequent fire may also indirectly affect the growth of berry producing species by increasing the prevalence of tall shrubs on the landscape. The expansion of tall shrubs may form a dense canopy, shading understory plants and reducing growth and fruit production of dwarf berry shrubs in the long-term (Siegwart Collier, 2020). In upland sites, dense canopy can limit sunlight and reduce berry yield of both cranberry and blueberry species, instead resulting in more energy investment in vegetative growth (Parkinson & Mulder, 2020). Warming experiments have demonstrated that prostrate berry shrubs like cranberry are more sensitive to warming and tall shrub height of competitor species than dwarf shrubs with upright growth like blueberries

(Siegwart Collier, 2020). In the short-term, improved growing conditions may favor blueberry berry production but may make blueberry more susceptible to overcrowding and interspecific competition from the tall shrubs in the long term (Siegwart Collier, 2020). This aligns with a study in Sweden which found that warming and increased nitrogen resulted in *Vaccinium myrtillus* and *Vaccinium uliginosum* being better competitors for resources than other evergreen shrubs (Koller et al., 2016). In other places, blueberry (*Vaccinium uliginosum*) production decreased as erect shrub cover increased in Nunavik (Lussier, 2017). Berry production was higher for blueberry in northern extent of range instead of forest-tundra likely due to fewer biotic constraints like light competition or other biotic interactions (Boulanger-Lapointe, et al., 2019). Additionally, increased winter temperatures, a possible outcome from an increase in shrubs, may make blueberries more susceptible to fungal pathogens (Graae et al., 2008). Further, increasing canopy cover may lead to a limitation in pollinators (Ambruster & Guinn, 1989). Both cranberry and blueberry species showed signs of being limited by pollination in lowland sites (Parkinson & Mulder, 2020). Therefore, a larger prevalence of tall shrubs will therefore likely limit berry production of cranberry and blueberries. This was observed in our study, where the percent cover of both cranberry and blueberry were lower in SI sites than in the LI sites, and highest in UB sites and the densest tall shrubs occurred in SI sites and were lowest in UB sites. Blueberry was not abundant in any sites of any fire history class. Additionally, the presence of all berries species was very sparse in all sites across fire history classes. It is likely that the material legacies (i.e., rooting structures) were consumed by the second fire and post-fire shrub communities may be outcompeting these two species.

Improved growing conditions coupled with an increase in tall shrubs will also likely result in a decline in abundance of cloudberry. One fertilization study, mimicking warming conditions, found an increase in cloudberry (Gough et al., 2014). However, cloudberry requires shaded areas with low competition and thus may not thrive if environmental constraints are lessened. This reinforces the complexity of conditions required for berry production, and that drivers at the local scale that may be influential. Berry species have adapted to areas with low competition and rely on strategies that may be disrupted with increasing tall shrub cover. As shrub cover increases temperatures, this may change the growing cycle of these species, flowering at different times. One study in Arctic Greenland has found the simultaneous shortening of flowering period with the decline pollinator flower visits with increased warming, suggesting a mismatch between pollinators and resources (Høye et al., 2013). As shifts in both growing conditions and biotic communities occur with ongoing climate change, it is likely that berry species that require specific conditions for berry production will have to invest in vegetative growth to maintain abundance in this more competitive environment. In the long run, this may have implications for growth strategies of berry producing species and their resulting yields. In our study sites, cloudberry was most prevalent in UB sites, with low percent covers in LI sites, and almost completely absent from SI sites. Again, very few berries were observed with the vast majority of the plants observed to be vegetative growth. This reinforces the idea that the cloudberry reproductive structures were likely consumed in the second fire, preventing it from proliferating in the SI sites, and being outcompeted by shrubs.

In addition to affecting the abundance and distribution of berry plants, a shrubbier landscape could change access that communities have to berry picking sites. Prior to harvesting, information is shared amongst people about how the berries are growing that year (Parlee et al., 2006) and find alternative areas where harvest may be more fruitful. Access can be difficult when patches are further afield, making it more difficult to engage with this activity if patches close to town or camps are not productive (Parlee et al., 2006). Accessibility will depend on the local effects of climate change and will likely vary spatially, reinforcing the need for pro-active regional planning.

3.4 Study limitations and considerations

Our study took advantage of the easy access to overlapping burn sites in proximity to a road and was therefore accessible by foot. The disadvantage of this approach was that it was limited to one forest type in a restricted geographic area. Further investigation is required to test and challenge our findings at a broader scale. Our study could also have benefited from having a more robust study design, with more sites and site types, and more sophisticated, finer resolution, sampling techniques. Most of our measurements were taken at single points-in-time over the summertime period. Taking more measurements of site conditions throughout the summer would be ideal for gaining a better idea of their variation and range throughout the growing season; being limited by time and resources, this was not possible for this study. Further, studies have shown that non-growing season plant nutrient uptake is a major contributor to shrub growth in northern environments (Riley et al., 2021), without this ability, they would have less of a competitive edge. Our study would therefore also have benefited by to taking measurements in all seasons.

To gain a more meaningful understanding of the impacts on culturally important species, a study design specifically targeting each species may be necessary. For instance, with different growing strategies, it would be advantageous to identify existing berry patches and compare to different fire history classes. Taking measurements throughout the growing season and of the site conditions prior to burn would be valuable. Additionally, other measurements that may be important to consider in future studies include flowers per area, pollinator visit frequency, and stem size or other measures of vegetative growth and sex ratios of plants in a pre-defined area. For lichen, having more sites in different stages of recovery would have enabled us to build recovery curves using biomass allometric equations. Instead, we were mostly restrained by extremes (i.e., recent burn and unburn), with large abundance of caribou lichen in mature forest sites with almost no lichen in the other site types.

Finally, it is important to note that this study addresses only one type of pulse disturbance. There are also many other pulse disturbances like insect outbreaks, permafrost thaw, and extreme weather events and continuous, slow acting disturbances like climate change that could further alter ecosystem trajectories (Foster et al., 2022). Creating a comprehensive study that is able to look at several disturbance features would be a better reflection of reality of these landscapes.

3.5 Recommendations for future research

Our study demonstrated that alternate trajectories are possible in this part of the boreal-tundra ecotone. To capture more of the variability within this landscape, it would be beneficial to continue with similar studies in sites of a wider variety of fire histories and landscape positions (i.e., lowland in addition to upland). Additionally, having overlapping burn sites in different stages of regeneration (i.e., different time since fire) and with different fire return intervals would provide a more comprehensive assessment of regeneration in this region. Periodically returning to these sites to continue to track the regeneration within the different fire history classes will be beneficial as there are still many unknowns regarding the effects of fire on shrubification process and the long-term consequences of shrub expansion (Mekonnen et al., 2021). Further, specific focus on long-term monitoring of the environmental parameters (e.g., ALD and ground temperature) will contribute to a better understanding of ecosystem response to disturbance (Holloway et al., 2020).

Given the complexity of these systems, more studies using multi-factorial study designs will assist in a better understanding of the indirect effects that most influence shrub growth (Mekonnen et al., 2021). While our study provides a glimpse into changing processes and successional trajectories, more information is needed to effectively understand the interactions between fire and vegetation communities within permafrost landscapes (Foster et al., 2022). For instance, if anthropogenic footprint increases within the Eagle Plains area, it may become prudent to understand how multiple disturbances influence these regeneration trajectories. Previous research near the Dempster Highway in the Peel Plateau has shown that areas adjacent to road disturbance have increased shrub growth (Cameron et al., 2016). Adding in development infrastructure for industry, coupled with an active fire regime, may further disrupt natural regeneration cycles. The cumulative effects of these multiple disturbances may play a role in future vegetation trajectories in the area (Reid et al., *in prep*).

While our study provided some insights into how this boreal-tundra ecotonal ecosystem is changing, other comprehensive analyses including additional parameters may assist in land management and planning operations. Forecasting the likeliness of regeneration failure of black spruce using reproductivity maturity as a threshold along the boreal-forest ecotone could provide a better understanding of the potential for alternate regeneration trajectories in the area because of climate change (Splawinski et al., 2019). Vulnerability mapping of black spruce has been done at the national scale using future climate parameters and knowledge of its species recruitment (Boucher et al., 2020). A finer scale resolution of this may be prudent since regional factors may influence ecosystem response. Further, despite robust records of fire in northern boreal of North America, substantial gaps in fire mapping extent still exists (Foster et al., 2022). The resolution of existing fire maps is relatively coarse and burn polygons do not accurately capture the spotty nature of fire (Foster et al., 2022). Knowing the effects of fire suppression (i.e., current and historic) would help in situations where fire suppression is deemed to be an acceptable practice to maintain desired vegetation communities or landscape features that are important for culturally important species (Foster et al., 2022). This information could be used for landscape and species management purposes, to assist with value-based fire management decisions and in future research projects.

It may be beneficial to update our knowledge and understanding relating to the effects of alternate trajectories on culturally important species like caribou. A more current analysis of the how these divergent trajectories may be impacting winter diets of the PCH may include a reexamination of their pellets to measure how their diets may have changed. A 1993 study found that 64% of their winter diet consisted of fruticose lichen, 3% graminoids, and 2% deciduous shrubs (Russell et al., 1993). If prolonged changes to their winter habitat occur, including a reduction in preferred forage, the PCH may slowly adjust their diet out of necessity. Monitoring their diets, their ongoing movement patterns, and classifying vegetation communities across their range will help understand if they change their behavior and range as site conditions change over time.

Regarding berries, significant questions related to the results of climate change remain. Will sustained changes to the environment further shift the already variable nature of berry species to the point where these well-developed systems are no longer effective at ensuring the sustainability of the resource? It is therefore important to consider berries in land-use planning, mapping existing berry patches, and documenting changes in abundance and yield over time.

This will help ensure their persistence, continued berry-production, and access to these sites as the environment changes (Boulanger-Lapointe et al., 2019). Creating berry focused studies will better inform changes and appropriate management decisions.

Finally, perhaps the most important point to make, is that researchers should be focusing on research questions that are driven by communities with generations of knowledge of the land and who are living, first-hand, the effects of climate change. Listening to and valuing the knowledge of those with centuries of lived experience in these landscapes should not be ignored. Prioritizing research questions with this at the helm should be the only way forward for research in the north. The goal should be to shift power dynamics in research relationships so that future research projects are collaborations that provide benefits to all involved (Wong et al., 2020). Co-production of knowledge can be effectively incorporated into study designs of research projects and help emphasize the value of other ways of knowing in the eyes of western scientists. To be successful in anticipating and adapting to future ecosystems where valued species hold their ground, it will be imperative that we adjust our ways of doing research. Researchers need to begin dialogues with communities early in the research process and strive to co-develop research questions with communities. Understanding whether their work is important to communities will foster more collaborations and assist in re-prioritizing knowledge systems. Researchers may also want to consider ways in which their research can provide economic benefit to these communities, like compensating people for sharing their knowledge or hiring community members. As the research project progresses, it is important to continuously check in with the community and ensure that consent and priorities have not changed. This speaks to the core values of Indigenous peoples', that of relationships, respect, and reciprocity. One example of retuning our knowledge system to incorporate all voices includes workshops joining community members, including youth and elders, as well as researchers facilitates knowledge sharing. This creates a space to listen to concerns and knowledge of the community, develop and strengthen relationships, share research and knowledge, and create lasting ties amongst generations (Cuerrier et al., 2012). It also provides cultural connection learning local names and knowledge about species, learn about changes, and leave a tangible output to remain in the community as a product of knowledge gathered and shared.

As more natural scientists begin to incorporate community participation within their research, it will be important to continuously apply a critical lens to the work. This will help ensure that it is being done in a way that furthers the decolonizing of research and values other forms of knowledge. Both Indigenous and western knowledge systems hold great potential to inform the other. Learning how to do this successfully will further our collective understanding of these changing northern systems and deepen our relationships with each other and the land. Taking a mindful approach to community engagement is the first step in achieving this reality. Finally, we believe that we will achieve successful relationships and co-production of knowledge between natural scientists and communities of the north. Conversations of change are happening among academics and better partnerships are being formed. With continued effort and reflection, we will see more positive stories emerge.

3.6 Conclusions

In this changing landscape, it can be difficult to predict future ecosystem states. Understanding changes in disturbance regime is not straightforward and there are likely cascading effects on the resulting ecological communities. Our research contributed a small piece to the larger research gap surrounding the effects of fire on shrub expansion (Mekonnen et al., 2021). To date, a shortened fire return interval appears to be raising the likelihood of non-forested trajectories with favourable growing conditions for tall shrubs in the boreal-tundra ecotonal area of Eagle Plains, Yukon. This change in fire regime is leading to a complete shift in vegetation trajectories in these sites, which will undoubtedly affect the environmental processes and biological interactions to follow. It will have profound impacts on the species that already occur in these areas, and the ones that may flourish as they potentially expand or establish where they were once absent in these future ecosystems. As changes to disturbance processes and their successional patterns continues across the subarctic, abrupt changes in ecosystem conditions will increase the likelihood of mismatches between species adaptations and current environments. Sudden disruptions have already been exemplified from the mismatch between post-fire landscapes and black spruce regeneration, possibly even creating conditions for an interval squeeze for the species in this area. However, other potential mismatches may also occur, like phenological mismatches between flowering of berry species and pollinators or the timing of green up in calving grounds of barren-ground caribou.

Increasing shrub habitat is likely at the expense of lichen dominated-ecosystems, a winter staple for barren ground caribou – a highly valued cultural resource. Additionally, shrubbier communities will likely improve moose habitat and facilitate their expansion northward (Zhou et al., 2020). Their expansion may also further change ecosystem processes by attracting more predators to the area. This may have detrimental impacts on caribou who use avoidance as a main tactic to prevent predation. However, it may also be offset by providing alternative summer forage and contribute to warmer environments and earlier green up. Moreover, tall shrubs will likely outcompete berry producing shrubs and result in fewer berries in tall shrub areas.

Changes to the dominant plant communities will also influence those who have ties to the landscape and share close connections with it. Though all the potential outcomes of these changes may still be unclear, it is essential that protective measures of valued natural resources and ecological processes are safe guarded for their continued preservation. Listening to the priorities of Indigenous peoples who hold close ties to these areas is of the utmost importance. These communities have built an ethic surrounding sustainable practices on the land and have developed methods for ensuring the longevity of the resources in which they depend. By listening to their concerns, focusing research and land management based on their priorities, we may not only work to restore some of the damage done by colonialism but also find some solutions to preserving important ecosystem processes that are at risk of being lost. Paying attention to different types of culturally significant species may help in recognizing the potential impacts on different members of the community. Though we will not always get it right every time, it is important to continue to strive for better inclusivity within our own research. Finally, by exposing the colonial frameworks in our own work, we hope to contribute to the growing awareness surrounding colonial practices in research and offer suggestions as to how we, as researchers, can consciously choose to become better collaborators.

3.7 References

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Appendices

Appendix A. Table of species abbreviations, their latin names and common names.

Latin Name	**Common Name**	**Abbreviations**
Chamaenerion angustifolium (formerly *Epiliobium angustifolium*)	fireweed	*C. angustifolium*
Equisetum sylvaticum	wood horsetail, woodland horsetail	*E. sylvaticum*
Petasites frigidus	sweet coltsfoot	*P. frigidus*
Picea mariana	black spruce	*P. mariana*
Polygonum alaskanum	knotweed	*P. alaskanum*
Rhododendron tomentosum (formerly *Ledum decumbens*)	northern Labrador-tea	*R. tomentosum*
Rubus chamaemorus	cloudberry, baked-apple	*R. chamaemorus*
Salix bebbiana	long-beaked willow, beaked willow	*S. bebbiana*

Appendix B. Table of describing sample sizes used in general linear mixed effects models.

Model	**Sample size (n =)**	**Comments**
Shrub density with soil nutrients	45	Three transects were omitted from data analyses due to errors in soil sampling.
Shrub density without soil nutrients	48	All sites and transect data were used.
Black spruce density	45	Three transects were omitted from data analyses due to errors in soil sampling.
Shrub height	43	Three transects were omitted were omitted from data analyses due to errors in soil sampling. Two additional transects were omitted because shrub heights were not recorded from one long interval site.