BIODIVERSITY IN THE YUKON: PATTERNS, DYNAMICS, AND DISTURBANCES

by
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Abstract

Northern ecosystems are in a period of significant change. Combined, global climate change and human land use are rapidly and significantly changing the structure, function, and resilience of northern ecosystems. In Yukon, Canada, air temperatures have increased by 2°C over the past 50 years with further increases of up to 3.7°C expected by the end of the century. At the same time, large-scale industrial development is ongoing throughout the Territory. Ecosystems here are faced with the amalgamation of these changes: an increasing number, intensity, and combination of pressures. In this thesis, I investigate the structure of Yukon's ecosystems, focusing on past pressures and changes as well as future changes likely to arise from both natural and anthropogenic pressures.

I review documented changes to vegetation communities throughout Yukon, assessing the vulnerability and resilience of different regions and vegetation structures and highlighting knowledge gaps that will direct future research to provide an in-depth understanding of Yukon's changing vegetation. Through a large-scale field experiment, I identify the dominant controls on biotic community composition throughout northern Yukon. Vegetation communities have increased species richness at more northern study locations, a pattern counter to global biodiversity theory. The length of the snow season plays an important role in this relationship; as winter precipitation patterns continue to change, vegetation communities and ecosystem functioning may be negatively affected. Finally, focusing on the Eagle Plains ecoregion in Northern Yukon, I synthesize the ways that natural, anthropogenic, and cumulative disturbances are significantly changing the landscape, shaping the future trajectories. An integrated approach is required to direct future land management, conservation, and use.

The results highlighted in this thesis contribute to a dynamic understanding of the current state of subarctic ecosystems, highlighting the complex and adaptive nature of Yukon's ecosystems. Yukon’s ecosystems are inherently resilient but current and future pressures are likely to challenge this resilience, potentially forcing state changes with numerous cascading effects.

General Summary

Throughout northern regions, the combined effects of climate change and human land use (e.g., mining and infrastructure) are causing significant changes to natural landscapes. In Yukon, Canada, climate change has already caused an increase in air temperature of 2°C since 1972, and further increases of up to 3.7°C are likely within the next 50 years. Industrial development is ongoing throughout Yukon and neighbouring regions, negatively affecting vegetation growth and animal habitat. As a result of these pressures and others, ecosystems throughout Yukon must adapt in order to continue functioning in these new conditions.

In this thesis I focus on understanding the current state of Yukon's ecosystems to increase our ability to predict how ecosystems will change in the future. I review how vegetation communities have been affected by climate change and document current knowledge gaps. I detail a large field study, investigating the dominant factors that control vegetation growth throughout Yukon. I highlight the role of snow in shaping vegetation communities and how this snow-vegetation relationship may change with continued climate change. Finally, I focus on Eagle Plains in northern Yukon, a region with high ecological, cultural, and industrial value. I describe the different pressures that the region faces, including increasing air temperatures, more frequent wildfires, and ongoing industrial activities. The combined influence of these pressures will dictate the ecological future of Eagle Plains.

This thesis provides a current understanding of terrestrial ecosystems in Yukon, Canada, which are representative of northern ecosystems more broadly. I highlight how interconnected and complex ecosystems are, and how changes to individual ecosystem components can have widespread consequences. Large changes to Yukon's ecosystems are likely in the immediate future. The details of current ecosystem patterns and processes that are presented here will allow

us to better understand how ecosystems may change in the future and how these changes will affect the people, plants, and animals of Yukon.

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Co-Authorship Statement

Chapter Two was co-authored with Dr. Don Reid (Wildlife Conservation Society Canada) and Dr. Carissa Brown. It has been published in Environmental Reviews and as such, formatting follows the requirement for that journal. This manuscript was conceived as part of a Mitacs Internship in 2020. All authors contributed to the study design and research questions. I completed the literature review and wrote the manuscript with input and edits from Drs. Reid and Brown.

Chapter Three was co-authored with Dr. Carissa Brown. It is in preparation for submission to Environmental Reviews: Ecology. This research idea was conceived jointly with Dr. Brown, and we contributed equally to the study design. I completed the fieldwork, data analysis, and first written draft. Dr. Brown provided feedback throughout the process.

Chapter Four was co-authored with Dr. Jeremy Brammer (Vuntut Gwitchin Government), Dr. Jill Johnstone (Yukon University Research Centre, Yukon University, Whitehorse, Yukon, and Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska), and Dr. Carissa Brown. It is in preparation for submission to Arctic Science. Dr. Brown and I conceived the study idea with subject input and expertise from Drs. Brammer and Johnstone. I completed the fieldwork for section and wrote the first drafts of the paper with input from all co-authors. Dr. Brammer and the Stewardship and Sustainability Profile at Vuntut Gwitchin First Nation (Brandon Kyikavichik, Megan Williams) contributed the cultural description of the Eagle Plains region.

Chapter 1: An introduction to ecosystem science with a focus on northern ecosystems

1.0 Ecosystem dynamics

1.1 Ecosystem states and cycling

Ecosystems are the basic units of nature on earth and are characterized by the interactions among animals, plants, and their physicochemical environment (Tansley 1935). Ecosystems have structure, perform functions, and change through time. The structure and function are controlled by a variety of factors, including spatial and temporal context (Weathers et al. 2013b). Ecosystems include both biotic or live components (e.g., vegetation and animals) and abiotic or non-living components (e.g., rocks and soil) (Weathers et al. 2013a). Primary production drives life processes throughout the ecosystem (Currie 2011). External factors, such as air temperature, function as controls on the ecosystem: fluctuations in controls can result in a change to the size or nature of any ecosystem component or flow (Currie 2011; Weathers et al. 2013a). Understanding ecosystem controls allow us to understand why ecosystems function the way they do, predict the structure and function of ecosystems in the future, and understand the consequences of human intervention or management of ecosystems.

Humans depend on ecosystems for their well-being; the values that ecosystems provide to humans, including economic value, health outcomes, and pollination are referred to as ecosystem services (Weathers et al. 2013). In turn, ecosystems have been continually and significantly modified by human societies (Walker and Salt 2006). Ecosystems are interconnected systems and the species within them support each other. It is therefore prudent to study the many species and components of an ecosystem together, rather than in isolation (Bak et al. 1988; Currie 2011). Ecosystems are inherently organized systems, and it is the role of ecologists to identify the principles and causes of these organizational structures (Gleason 1926; Odum 1953).

Energy and nutrients flow between ecosystem components and the surrounding environment (Currie 2011; Weathers and Ewing 2013). Carbon is a major component of all life forms, and, along with oxygen, is one of the most important elements in organisms (Cole 2013). Two carbon compounds, carbon dioxide (CO_2) and methane (CH_4), significantly contribute to global anthropogenic climate change and warming potential. Carbon cycling is of particular interest in northern ecosystems: boreal forest and tundra systems absorb more carbon than they emit, storing it within their soils and vegetation and making them carbon sinks (Bruhwiler et al. 2021). As global climate change continues, the carbon storage capacity of these ecosystems prevents global CO_2 and CH_4 levels from increasing to an even greater degree. While global carbon levels are not in equilibrium (human activities continue to emit more carbon than the planet can handle), carbon sequestration by northern ecosystems plays a significant role in maintaining global functioning and activity.

1.2 Ecosystem resilience and change

Through time, all ecosystems change and become more complex (Schulze et al. 2019). Ecosystems are adaptive systems: their components interact, and can also adapt, self-organize, and show emergent properties in the face of external drivers or controls (Currie 2011). Resilience is the ability of a system to persist through a disturbance and retain the same structures, functions, and feedbacks post-disturbance (Holling 1973) and is one example of the adaptive capacity of ecosystems. Resilience is a consequence of biologically derived legacies, which serve to preserve ecological memory and help to shape recovering ecosystems (Franklin et al. 2000; Johnstone et al. 2016). Biological legacies can take two forms: information or material legacies (Johnstone et al. 2016). Information legacies are the species traits that are present as a result of historical disturbance cycles and biogeography. These traits arise as adaptations to disturbance regimes and allow post-disturbance ecosystems to recover to a similar state as they were in pre-disturbance. Material legacies consist of the individuals or propagules that persist in an ecosystem after a disturbance. These legacies are determined by the characteristics of the disturbance as well as the state of the ecosystem at the time of the disturbance. Legacies serve as a way for ecological memory to be transferred from the pre-disturbance system to the post-disturbance system (Johnstone et al. 2016).

Changes to ecosystems may be gradual in their onset and long-lived in their influence, termed *press events*, or may be abrupt in their onset and termination, termed *pulse events* (Glasby and Underwood 1996). Pulse events in the form of natural disturbances are becoming increasingly frequent with climate change, largely due to the increased variability in global climate (Turner 2010). In northern ecosystems, these pulse events tend to be wildfires, permafrost thaw, and flooding. Wildfire and permafrost thaw both emit significant quantities of carbon back into the atmosphere (Schuur et al. 2015). As these disturbances become more frequent and severe, the amount of carbon emitted from northern ecosystems is likely to be significant, with large repercussions for global carbon cycling and budgets (Schuur et al. 2015; Walker et al. 2019).

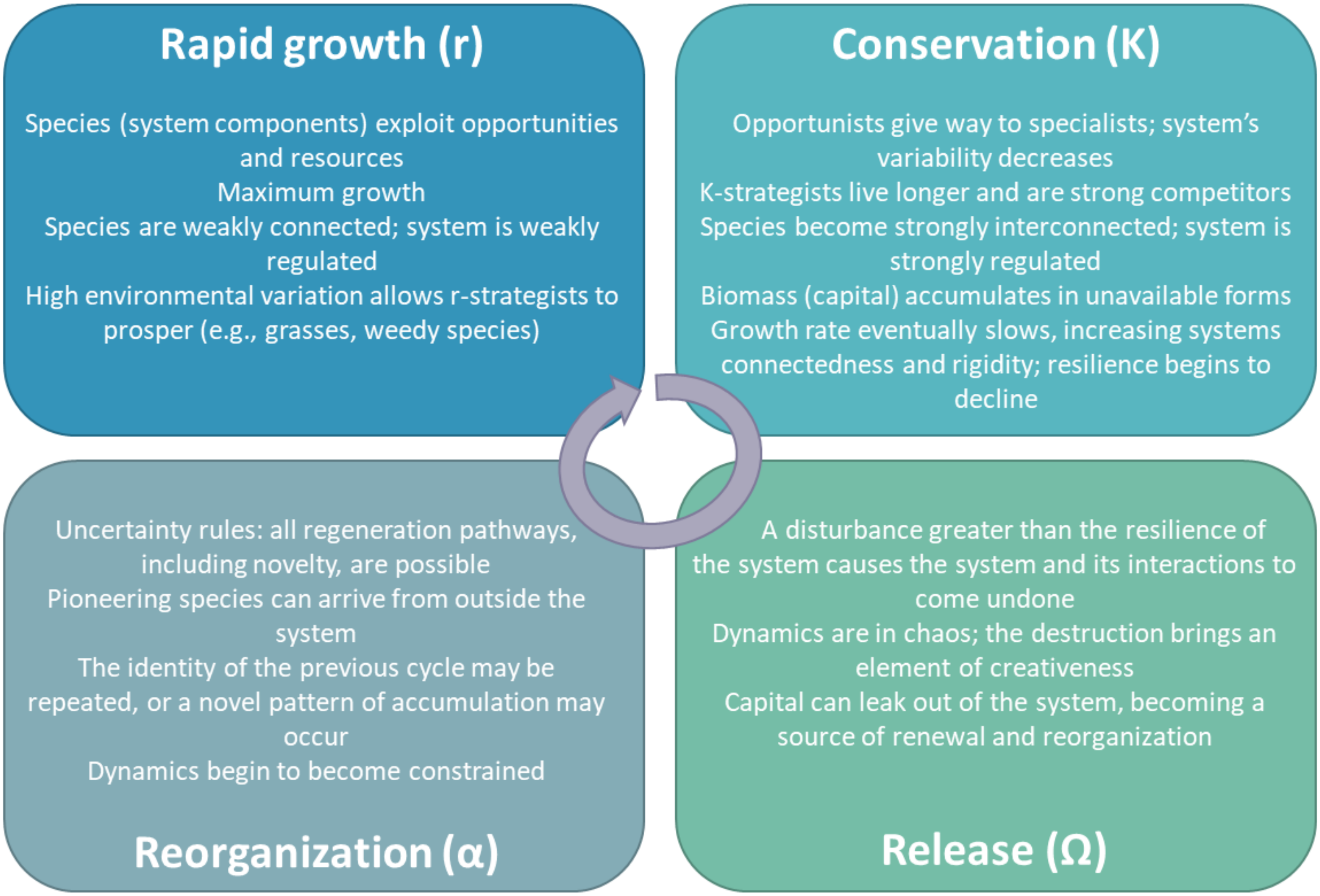
When disturbances act within the historical disturbance regime, the ecological memory carried by legacies helps to maintain the structure and composition of the community that dominated pre-disturbance. A cycle of self-replacement and ecological resilience ensues (Johnstone et al. 2016). However, as disturbance regimes change, species adaptations that confer resilience can become misaligned with individual disturbances, threatening current legacies and resilience (Turner 2010; Keeley et al. 2011). After both press and pulse disturbances, species present before the disturbance are generally favoured. However, both disturbance types may result in new species entering via seed as a result of decreased competition for resources and opening of suitable areas for germination and establishment. A resilient ecosystem will change because of the disturbance but will remain within its operational boundaries and recover over time. When a disturbance event is more frequent or intense than the ecosystem has acclimatized to, it can overcome the adaptive capacity of the ecosystem, potentially transforming the ecosystem into an alternative stable state where dominant life forms and interactions differ (Scheffer et al. 2001; Schulze et al. 2019).

Recent shifts to alternative stable states have occurred in the boreal forest of Alaska and the Yukon where severe fire years have led to shifts from forests dominated by black spruce to trembling aspen (Johnstone and Chapin 2006; Johnstone et al. 2010). Vegetation shifts as a result of a changing climate and disturbance have also occurred at the paleoecological scale. Fire frequency in interior Alaska peaked 3,000 to 6,000 years ago because black spruce invaded forests previously dominated by white spruce and deciduous species, increasing site flammability (Kelly et al. 2013). Fire severity and area burned subsequently increased, and the less flammable deciduous vegetation was favoured over the typical black spruce self-replacement patterns (Kelly et al. 2013). In the future, the nature of such shifts will be dictated in part by the available species pool. Species establishment is determined by historical filters that dictate which species will reach the site (Lambers et al. 2008). From a vegetation perspective, the outcome of a disturbance will therefore be a combination of past patterns of biogeography and the current characteristics of disturbance.

1.3 Adaptive cycles

The lifespan of an ecosystem follows an adaptive cycle, which controls how the system is organized and how it responds to change (Gunderson and Holling 2002; Walker and Salt 2006). The framework of adaptive cycles can be used for systems outside of ecology: it is commonly used in both finance and business (Gunderson and Holling 2002). Below and in Figure 1.1, I describe the four phases of adaptive cycles, focusing on ecosystems. In Chapter 5, I revisit this framework, highlighting the adaptive cycle and capacity of the northern ecosystems examined in my thesis.

Adaptive cycles are made of four phases. These phases can occur in any order, and some phases may be skipped under certain circumstances (Gunderson and Holling 2002; Walker and Salt 2006). In most cases, ecosystem adaptive cycles occur in the following order: rapid growth (r), conservation (K), release (Ω), and reorganization (α) (Figure 1.1). The rapid growth phase is a period of establishment, where many species have the opportunity (and resources) to establish. Slowly, the system will shift to the conservation phase which is characterized by the establishment of specialist species that become increasingly interconnected. Over time, the structures and processes that dominate the environment become increasingly relied on, making the system vulnerable to disturbance. The shift from the conservation phase to the release phase is marked by a disturbance that overcomes the system's resilience. If a system has a long conservation phase, only a small disturbance is needed to 'shock' the system into the release phase. The release phase is chaotic and centered on the 'creative element' of the destruction (Schumpeter 1950; Walker and Salt 2006). The capital released (information and material legacies) brings the system to a period of reorganization and renewal. The transition from the reorganization phase to the rapid growth phase is marked by the emergence of a new system identity (Gunderson and Holling 2002; Walker and Salt 2006).



Rapid growth (r)

Species (system components) exploit opportunities and resources
Maximum growth
Species are weakly connected; system is weakly regulated
High environmental variation allows r-strategists to prosper (e.g., grasses, weedy species)

Conservation (K)

Opportunists give way to specialists; system's variability decreases
K-strategists live longer and are strong competitors
Species become strongly interconnected; system is strongly regulated
Biomass (capital) accumulates in unavailable forms
Growth rate eventually slows, increasing systems connectedness and rigidity; resilience begins to decline

Uncertainty rules: all regeneration pathways, including novelty, are possible
Pioneering species can arrive from outside the system
The identity of the previous cycle may be repeated, or a novel pattern of accumulation may occur
Dynamics begin to become constrained

Reorganization (α)

A disturbance greater than the resilience of the system causes the system and its interactions to come undone
Dynamics are in chaos; the destruction brings an element of creativeness
Capital can leak out of the system, becoming a source of renewal and reorganization

Release (Ω)

Figure 1.1 Framework or adaptive cycles, modified from Gunderson and Holling (2002) and Walker and Salt (2006). The framework can be used to represent a variety of systems, including financial systems and independent businesses. Here, I summarize the components of each of the four phases for ecosystems.

1.4 Ecosystem diversity and transitions

Biodiversity is the variation in all levels of biological organization, generally considered to be composed of genetic, organismal, and ecological diversity (Gaston and Spicer 2004). The biodiversity of an area is often quantified by species richness or the number of species present. Species evenness (the uniformity of species distribution in a community) and species diversity (the number of species and their abundance) are other commonly used metrics (Gaston and Spicer 2004). Biodiversity is in constant flux: despite constantly increasing since the beginning of biological life, over 90% of species that have existed are now extinct. Notably, there has been a marked decline in global species richness throughout the late quaternary period (Gaston and Spicer 2004).

Despite having lower species richness than southern regions (see 1.4 *Biodiversity Theory*), northern ecosystems as a whole are not species-poor. There are approximately 2,100 species of vascular plants in the Arctic, and despite increased human activities and warming at northern latitudes, no Arctic-specific species have gone extinct in the past 250 years (Daniels et al. 2013). There are a further 900 species of bryophytes, most of which have circumpolar ranges (Daniels et al. 2013). Bryophytes are an important component of flora in northern ecosystems, and their ubiquitous nature contributes significantly to the species richness of many communities (Daniels et al. 2013). Globally, northern ecosystems represent 2% of mammalian diversity and 2% of avian diversity. Due to the harsh climatic conditions, bird species in northern ecosystems are often highly specialized and composed of a number of endemics. Within the northern ecosystems, waterfowl (*Anatidae*), shorebirds (*Charadriiformes*), and gulls (*Laridae*) are proportionately over-represented while songbirds (*Passeri*), the most abundant and diverse group in the rest of the world, are underrepresented (Ganter and Gaston 2013). Seabirds present an interesting anomaly to the latitudinal gradient of species richness as they are more abundant (and equally as diverse) in cold seas as in warm seas (Gaston 2004).

For terrestrial ecosystems globally, the first filter in time for species diversity is the species' regional presence (Walker 1995). In northern ecosystems, this filter plays a particularly important role as only 0.4% of the known vascular plants exist throughout northern ecosystems

(Billings 1992). Vegetation in northern ecosystems must also be freeze-tolerant, which excludes 75% of global vascular plants (Korner 1995). Subsequent filters on species diversity are biogeographical patterns (e.g., climatic gradients, geological history) and the distribution of species within a community (e.g., biological interactions, habitat diversity) (Walker 1995). Biodiversity in northern ecosystems is particularly vulnerable to changes in growing conditions such as increasing air temperatures and increased summer precipitation (Callaghan et al. 2004c). Northwestern North America has a greater concentration of rare plants and animals than other Arctic regions; therefore local changes to biodiversity may therefore be particularly pronounced there (Callaghan et al. 2004c).

Ecosystems are inherently heterogeneous systems: they differ in structure over three-dimensional space and/or time (Pickett and Cadenasso 2013). Heterogeneity can exist at different scales and both within and between ecosystems. In northern ecosystems, heterogeneity exists at both large and small spatial scales. For example, vegetation richness and diversity change over hundreds of kilometres (from productive boreal forests to sedge tundra as a result of temperature-induced growing constraints) and within <1 m (where nutrient pools vary with microtopography). Within any ecosystem, the success of an individual plant (or species) is determined by its physiological characteristics and its response to the environment. Other plant species also influence success, acting as competitive neighbours. During the germination and establishment stages, competition or facilitation with other individuals and species influences rates of germination and survival. At later life stages, the ability of an individual or species to withstand invasive species, extreme events, or management practices, contributes significantly to their ability to thrive. Particularly, following extreme events (such as pulse disturbances), resource pools can be dramatically altered (e.g., sudden loss of key nutrients or a large influx of water), determining the longevity of neighbouring species (Schulze et al. 2019).

The area between two ecosystems, where one transitions into another, is called the ecotone. Ecotones can be abrupt, identified by sudden changes in vegetation or productivity, but more often, they are indistinct, large areas of transition. Ecotones can be highly productive and species rich as species from both ecosystems often coexist in this transition zone. The boreal-tundra ecotone is one such indistinct boundary, covering over 13,000 km across the northern hemisphere (Callaghan et al. 2004b). It is typically thought to be represented by the northern limit of continuous forest, but this boundary itself is also fluid and indistinct. Instead, the boreal-tundra ecotone covers a wide latitudinal range where dense boreal forest gradually gives way to tundra. Under continued warming, vegetation in northern ecosystems is more likely to change its distributions than evolve significantly (Callaghan et al. 2004a). As the boreal forest expands northwards, species that are currently found in the northern taiga and southern tundra (hypoarctic species) will likely be the primary colonizers of the 'new' boreal forest range (Callaghan et al. 2004a). Reduction of tundra biodiversity due to a warming climate will likely have far-reaching consequences: since the tundra is relatively species-poor, the loss of an individual species will have a disproportionately large consequence on the ecosystem (Vitousek 1990; Chapin et al. 1995).

Physical characteristics of the local environment including extreme seasonality, short growing seasons, and permafrost, influence biogeography in northern ecosystems (Payer et al. 2013). Unique to northern latitudes and high elevations, permafrost is perennially frozen ground that remains at or below 0°C for at least two years (Jones et al. 2010). In northern ecosystems, the heterogeneity of vegetation and landscape forms is significantly influenced by the presence of permafrost. Permafrost is widely distributed, covering 40% of Canada's total landmass (Tarnocai and Smith 1993). In regions with underlying permafrost, poor soil drainage is common as permafrost creates a relatively impermeable barrier (Bockheim and Tarnocai 2012). The resulting microtopography influences broad patterns of vegetation establishment and soil distribution. Vegetation-microtopography relationships are not limited to simple cause-and-effect relationships. Instead, relationships are dictated by changes in soil chemical properties (Gough et al. 2000), plant functional traits (Vonlanthen et al. 2008), and life history strategies (Benscoter et al. 2015), among other influences. Vegetation is also key to maintaining the structural integrity of small-scale permafrost features. For example, after a wildfire destroys vegetation on earth hummocks, the hummocks collapse and only re-form once the vegetation begins to recover (Kokelj et al. 2007). In turn, patterned ground features are integral to the maintenance of unique and distinct vegetation communities (Kade et al. 2005). Examples of mutually reinforcing relationships like this are common throughout northern ecosystems and play a key role in maintaining the systems' ecological resilience under amplified warming. The response of permafrost regions to a warming climate presents many unknowns, potentially including increased releases of greenhouse gases (Schuur et al. 2015).

1.5 Biodiversity theory

Decreasing species diversity from the equator to the poles (the latitudinal gradient of diversity) is one of the most widely accepted patterns in biogeography (Hillebrand 2004). Globally, this pattern is dependent on a combination of historical, geographic, biotic, and abiotic forces (Schemske 2002). The latitudinal gradient of diversity is recognized at a variety of scales, from quadrats (Kaufman 1995) to hemispheres (Lees et al. 1999) and the pattern has been demonstrated in all continents and biomes (summarized by Willig et al. 2003). While the fine details vary (e.g., the slope of the relationship, location of maximum richness), the pattern has emerged across terrestrial plants (Cowling and Samways 1994), terrestrial arthropods (Lobo 2000), birds (Rahbek and Graves 2001), and mammals (Lyons and Willig 2002). Exceptions to the latitudinal gradient of diversity, demonstrated by a positive or neutral relationship between species richness and latitude, fall into four main groups: wasps (Janzen 1981), ecto- and endoparasites (Poulin 1995), aquatic plants (Bolton 1994), and secondary marine birds and mammals, including pelagic birds (as reviewed by Willig et al. 2003).

Furthermore, the degree to which this theory holds true in northern ecosystems has recently been questioned. Subarctic boreal forests in the Northwest Territories of Canada show an inverse relationship between latitude and species diversity due to reduced competition for light and nutrients at high latitudes, outweighing the proposed effects of energy availability or climatic harshness (Marshall and Baltzer 2015). It is unclear if this is a regional and vegetation-specific phenomenon or whether this inverse pattern also holds true across the broader boreal-tundra ecotone, where nutrient availability is further limited. Diverse communities are better able to withstand stresses; understanding how patterns of diversity change with latitude will provide insight into the resilience of these communities under continued climate change.

2.0 Ecological divisions of the Yukon

2.1 Geography and Ecology of the Yukon

Yukon Territory is located in northwestern Canada (Figure 1.2), bordered by Alaska (USA) to the west at 141° longitude, British Columbia to the south at 60°N, the Beaufort Sea to the north, and the Northwest Territories to the east, along the boundary between the Yukon and Mackenzie River watersheds. Yukon covers 483,450 km^2 (Smith et al. 2004) and has six major watersheds: North Slope, Porcupine, Peel, Yukon, Alsek, and Liard (Janowicz 2004). As of June

2022, Yukon was home to 43,964 people, with 79% of the population living in the Whitehorse area (Yukon Bureau of Statistics 2022). Evidence of humans on the land in Yukon dates back 24,000 years in the Bluefish Caves of northern Yukon (Gotthardt 2004).

Indigenous Knowledge about Yukon's social and ecological history has been documented in First Nations-produced publications about the vegetation and wildlife present in these regions (Andre and Fehr 2002; Andre 2006; Crewe and Johnstone 2009), as well as documentation of the climate change induced effects on these resources (Gwich'in Social & Cultural Institute 2008; Benson 2011; Inuvialuit Regional Corporation 2016; Wildlife Management Advisory Council (North Slope) and Aklavik Hunters and Trappers Committee 2018). Many floras have been published for northwestern Canada beginning with *Flora Borealis Americana* (Hooker 1840). The two most significant and detailed floras of this region are *The Flora of the Yukon Territory* (Cody 2000) and *Vascular plants of continental Northwest Territories* (Porsild and Cody 1980), both of which describe the biogeography of over 1,100 vegetation species.

Vegetation, animals, and topography vary vastly throughout Yukon: regional subunits with less variation are used to describe the ecology in detail. Current biophysical descriptions of the Yukon Territory are found in Ecoregions of the Yukon Territory (Smith et al. 2004) and Bioclimate Zones of the Yukon (Environment Yukon 2016). Previous descriptions and maps include Ecoregions of the Yukon (Oswald and Senyk 1977) and the Yukon Ecoregions report (Yukon Ecoregions Working Group, 1995). Following Ecoregions of the Yukon Territory (Smith et al. 2004) and federal land classification structure, a majority of Yukon is comprised of two ecozones, the Boreal Cordillera and the Taiga Cordillera (Figure 1.2). These ecozones are described in detail below. In addition, I highlight some areas of biological or cultural value in both ecozones.

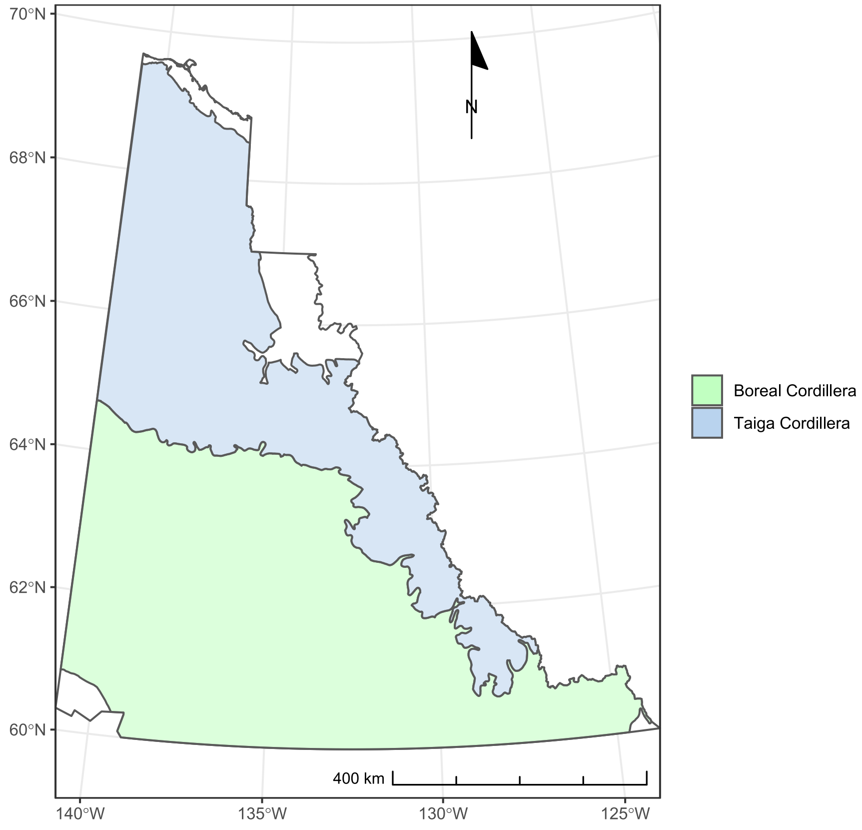


Figure 1.2 Yukon Territory, located in Northwestern Canada. The two main ecozones of Yukon are the Boreal Cordillera (green) and the Taiga Cordillera (blue).

2.2 Boreal Cordillera

The Boreal Cordillera ecozone represents a boreal zone modified by strong elevation, temperature, and precipitation gradients. Vegetation ranges from grasslands on south-facing slopes to boreal forests on north-facing slopes with dwarf shrub tundra at high elevations. Dominant tree species include black and white spruce (*Picea mariana* and *P. glauca*), trembling aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), and balsam poplar (*Populus balsamifera*). Vegetation below treeline is heavily influenced by widespread discontinuous permafrost, and stunted black spruce dominate the cold soils (Yukon Ecoregions Working Group 2004).

Within the Boreal Cordillera ecozone, the Klondike Plateau Ecoregion represents part of the habitat of the Fortymile caribou herd (*Rangifer tarandus grantii*) (Yukon Ecoregions Working Group 2004). This barren-ground herd dipped from a high of 50,000 animals in the mid-nineteenth century to ~6,500 individuals in the 1930s. This decline has been attributed to wildfires, food limitations, and overharvesting. In 2001, the herd was estimated to have recovered to a size of 40,200 (U.S. Bureau of Land Management et al. 1995; Yukon Ecoregions Working Group 2004). The Klondike Plateau is also an important area for bird migration and has two major migration corridors. The Shakwak Trench facilitates spring and fall migration of swans (*Cygnus* sp.), geese (*Anser* and *Branta* spp.), and shorebirds (Department of Natural Resources 1994). The Tintina Trench is a migration corridor for swans, geese, and sandhill cranes (*Antigone canadensis*) travelling to and from their Alaskan breeding grounds (McKelvey 1977).

The Ddhaw Ghro Habitat Protection Area is also located in the Boreal Cordillera ecozone (Yukon Ecoregions Working Group, 2004). Ddhaw Ghro means “many peaks” in the Northern Tutchone language and refers to the McArthur Mountains, where the protected area is situated. Elders say that Northern Tutchone people (Na-Cho Nyak Dun and Selkirk First Nations) have harvested game and plants in this area as part of their seasonal travels for the past 3,000 to 4,000 years. During the Last Glacial Maximum, the Protected Area was largely unglaciated, providing refuge for many plant and animal species. Vegetation in the area consists of grasslands in the alpine, largely unvegetated scree slopes and willow meadows in the subalpine, and full stands of spruce, pine, and aspen at lower elevations. The Ddhaw Ghro Habitat Protection Area is culturally significant to the Northern Tutchone people because of its rich and diverse plant and animal communities. The most unique of these communities is the Fannin Mountain sheep (*Ovis dalli fannini*) population of approximately 70 individuals which is endemic to this region. One of the main reasons for the original establishment of the protected area was to meet concerns raised about possible overhunting as a result of the Klondike Highway. A hunting ban in the sanctuary has protected the population, although numbers remain low. The population remains sensitive to future disturbances.

2.3 Taiga Cordillera

Vegetation is highly variable throughout the Taiga Cordillera ecozone. In Eagle Plains, the dense and stunted black spruce forests with thick mats of moss and lichen dominate; in the North Ogilvie Mountains Ecoregion, calcareous bedrock dominates and hosts calcium-loving plants that are rare glacial relicts. Unique species in this ecozone include the Ogilvie Mountains collared lemming (*Dicrostonyx nunatakensis*), which is the only endemic mammal in the Yukon (Yukon Ecoregions Working Group 2004). The North Yukon Planning Region (located in the traditional territory of the Vuntut Gwitchin First Nation) is home to over 600 vascular plant species and 40 mammal species. Of special interest are the grizzly bear (*Ursus arctos*) and the wolverine (*Gulo gulo*), which are both present throughout this region and are listed as Special Concern by COSEWIC (North Yukon Planning Commission 2007; COSEWIC 2012, 2014).

The Old Crow Flats Special Management Area (OCFSMA) is located in the traditional territory of the Vuntut Gwitchin. Known as “Van Tat”, this area is rich in natural resources such as lakes and wildlife. The protection status of the OCFSMA was included as part of the Vuntut Gwitchin Final Agreement. The lakes in the OCFSMA are shallow and teeming with aquatic vegetation that is important for the abundant waterfowl in the area. Lakes tend to have abundant fish populations which were traditionally used as food for both people and dog teams during travelling periods. Fish currently support the biodiversity of the area as they are an important food source for otters, bears, and ducks. The most iconic wildlife in the OCFSMA is the Porcupine caribou herd (*Rangifer tarandus granti*). The herd passes through during spring and fall migrations. Occasional late winter snow may prevent pregnant cows from reaching their traditional calving grounds in Alaska. When this happens, Elders report that calving occurs within the OCFSMA. As part of their migration route, caribou pass through the community of Old Crow; if migration routes are changed due to weather or other unsuitable conditions, the community turns to moose (*Alces alces*) as a food source (Technical Working Group 2006).

3.0 Thesis Objective and Summary

The overall goal of my thesis is to disentangle the factors that shape ecosystems in the Yukon. Within the context of a rapidly changing climate, it is important to understand the current state of ecosystems (including species diversity, species interactions, and drivers) to give us the best attempt at foreseeing future ecosystem structure and functions. My research is focused on Yukon Territory for the many ecological and social reasons explained above and in subsequent chapters. In addition, Yukon is where I make my home, furthering my commitment to preserving its environment and ecosystems for the future. Specifically, my research advances our understanding of how vegetation in Yukon ecosystems has responded to climate change over the recent past (**Chapter 2**); characterizes the distribution of biotic communities throughout central and northern Yukon and the biotic and abiotic factors that control these communities (**Chapter 3**), and uses testable hypotheses to investigate the future states of subarctic boreal forests in Eagle Plains (**Chapter 4**). Finally, I summarize my findings and integrate common themes and threads throughout my research, within the framework of adaptive cycles (**Chapter 5**). Within each chapter, I address the following research goals and questions:

Chapter 2

i) Synthesize recently (1980 - present) documented patterns of change in vegetation communities throughout Yukon and surrounding areas

ii) Highlight Yukon-specific knowledge gaps and topics for future research

Chapter 3

i) What are the relationships between latitude, species richness, environmental variables, and ecological and geographic constraints?

ii) What role do environmental and habitat variables play in species diversity and distribution patterns?

Chapter 4

i) Present five testable predictions that represent our best estimate of future trajectories of change to ecosystem states and services in the subarctic boreal forest of northwest North America.
    1. Environmental constraints on vegetation growth will change
    2. The intensification of the natural wildfire regime will reduce the resilience of subarctic boreal forests
    3. The influence of additional natural disturbances will become increasingly pronounced
    4. Industrial activity will reduce the resilience of the ecosystem
    5. The cumulative effects of climate change and industrial activity will introduce new disturbances and species interactions

In sum, my research advances our knowledge of Yukon ecosystems and the broader subarctic boreal forest. Data and results presented here will contribute significantly to our understanding of the current and future states of ecosystems in Yukon and can help direct future research and management efforts.

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Chapter 2: Patterns of vegetation change in Yukon: Recent findings and future research in dynamic subarctic ecosystems

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Abstract

In Yukon, Canada, average air temperature has increased by 2°C over the past 50 years and, by the end of the century up to 6.9°C of further warming is predicted, along with increased climate variability. As a result of these and other changes, vegetation communities are predicted to shift in space and composition. Changes to the vegetation assemblages across multiple ecological units or bioclimate zones will impact carbon and nutrient cycling, animal habitat, biodiversity levels, and other ecosystem processes. Yukon has a wide variety of vegetation communities (including Beringian relicts), and paleoecological evidence indicates that significant vegetation changes have occurred throughout the territory in the past. No documented synthesis of changes to vegetation assemblages exists, restricting predictions of their future likelihood, abundance, and influence. Here, we review the literature of documented examples of vegetation change throughout Yukon that have occurred (i) in different vegetation communities due to the persistent press of climate change and (ii) after natural disturbances. Future research into all vegetation responses under ongoing climate change are warranted. We identify critical research gaps for each vegetation community and disturbance type that should be addressed to produce a more encompassing understanding of the response of Yukon bioclimate zones and vegetation communities to future warming and disturbances.

Keywords: subarctic; climate change; vegetation change; range shift; disturbance; bioclimate zones

2.1 Background

Arctic and boreal regions are being significantly impacted by climate change. Between 1971-2017, pan-Arctic average annual air temperatures rose by 2.7°C, a change 2.4 times greater than the Northern Hemisphere's average (Box et al. 2019). Other widespread changes include increasing trends in NDVI (or greening), attributed to increases in plant growth and productivity (Arndt et al. 2019), and a reduction in snow cover by 2 - 4 days per decade (Box et al. 2019). The increase in the number of snow-free days contributes further to summer warming (Chapin et al. 2005).

Changes in dominant vegetation patterns, as well as the processes that affect vegetation, are some of the most likely outcomes of climate change in northwest North America. Well documented examples of vegetation change in the Arctic include widespread expansion of shrub communities (Tape et al. 2006) and reduced tree growth (McGuire et al. 2010) both of which are directly attributable to warming climates. Regarding processes, drought is strongly implicated in reduced tree growth (Walker et al. 2015) and boreal fires have increased in intensity (Flannigan et al. 2009) and area (Coops et al. 2018) in recent decades, with further increases in fire activity predicted by the end of the century (Balshi et al. 2009). Earlier and warmer springs are likely to contribute to extreme fire years and to increased incidence of lightning at treelines (Veraverbeke et al. 2017). Future changes to northern wildfire regimes will have a myriad of biophysical implications (e.g., carbon sequestration, range expansion in plants, successional pathways; (Veraverbeke et al. 2017) Baltzer et al. 2021).

In addition to widespread climate change typical of northwest North America (Streicker 2016), Yukon is experiencing major social and policy changes through implementation of modern-day treaties with Indigenous peoples and revision of pre-devolution legislation and policy (Natcher and Davis 2007; Staples et al. 2013). These processes are, for example, mandated to lead to regional land use planning, forest management planning, and wetland policy development (UFA 1993). Now is an ideal time to integrate a synthesis of science on the emerging effects of climate change on vegetation into these institutional processes that are re-orienting ecosystem management and biodiversity conservation (e.g., ecosystem mapping, forest harvesting, wildlife habitat management, fire management) under the treaty-mandated rubric of sustainable development (UFA 1993). These processes have yet to seriously deal with climate change, so knowledge of the patterns is crucial for good governance. Further, changes in distribution of vegetation communities directly affect peoples' mental and physical wellbeing (e.g., Dodd et al. 2018), so an appreciation of emerging changes can help with planning for and accommodating change when it occurs.

The goals of this review are to (i) synthesize recently (1980 – present) documented patterns of change in vegetation communities throughout Yukon and surrounding areas, and (ii) highlight Yukon-specific knowledge gaps and topics for future research.

2.2 Geography and Ecology of Yukon

Located in northwestern Canada, Yukon Territory has been the traditional homeland of First Nations peoples for over 10,000 years and currently supports a population of 42,000 First Nations and other peoples (Government of Yukon, 2021). Along with Alaska and northern British Columbia, Yukon forms a substantial part (~483,450 km^2) of North America's northern boreal mountains. In this sparsely populated region, many inhabitants rely on subsistence resources that are directly affected by climate-driven vegetation change.

Yukon has a subarctic continental climate, being relatively dry with temperature and precipitation patterns strongly dictated by major orographic barriers and the Pacific Ocean (Wahl

2004). Bound by the 60th parallel in the south and the Arctic Ocean to the north, annual mean temperatures vary from -2°C in southern Yukon to -10°C in coastal Arctic regions, with seasonal temperatures varying greatly from -60°C in the St. Elias Mountains to >30°C in the central interior. Annual precipitation ranges from ~250 mm in valley bottoms up to 1000 mm in parts of the St. Elias Mountains (Wahl 2004). Over the past 50 years, the average annual air temperature in Yukon has risen by 2°C (Streicker 2016); by the end of the 21st century, temperatures could rise by 3.9°C - 6.9°C compared to the 1961-1990 average (SNAP-EWHALE 2012)). In general, climate variability is predicted to increase, manifesting as increasing incidence and severity of wildfires, permafrost thaw and degradation, flooding, and forest insect infestations (Streicker 2016). Previous shifts in Yukon's climate have resulted in significant changes to vegetation communities. For example, throughout the Holocene there was conversion from balsam poplar forests to tundra (Cwynar & Spear, 1991, 1995), and in the 19th century spruce stands in southern Yukon were more abundant than they are now (Strong 2017, 2020).

Vegetation composition in Yukon ranges from closed- to open-canopy forests in plateaus and valleys; shrub-dominated communities within open canopy forests, in disturbed areas, wetlands, and at treeline; sedge and cottongrass wet tundra on poorly drained sites; alpine tundra at high elevations; and grasslands mostly on steep, south-facing slopes. The dominant tree and shrub species in Yukon are white spruce (*Picea glauca*), black spruce (*P. mariana*), lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), balsam poplar (*Populus balsamifera*), trembling aspen (*Populus tremuloides*), birches (*Betula* spp.), and willows (*Salix* spp.) (McKenna et al. 2004). Two unusual features of Yukon vegetation communities are a high number of endemic species, and grasslands. Yukon has three national hotspots of endemicity (Ogilvie Mountains, Kluane, and Central Yukon Plateau), and ranks among the top locations for number of national (n = 43) and subnational (n = 20) endemic species (n = 20; Enns et al. 2020). In Yukon, grasslands likely developed during the Holocene Thermal Maximum (~11,000 – 9,000 years ago; Strong 2018), with considerable species persistence and exchange as Beringian steppe evolved into Holocene grasslands (Vetter 2000). These grasslands provide particularly unusual habitats and act as refugia for species that would otherwise not be present in boreal regions (Sanborn 2010).

Biome shifts are projected based on future distributions of climate envelopes that have supported those communities in recent history (Rowland et al. 2016). Through to 2090, projections across Yukon include shifts from boreal forest to grasslands, Arctic tundra to shrublands and forests, and alpine tundra to forest, with the incursion of North American "prairie-type grasslands" representing a climate regime that has had no analog in recent history. In addition, many established forest types are projected to shift latitudinally and elevationally, resulting in communities that closely resemble current areas of Alberta, British Columbia, and southern Yukon (Rowland et al. 2016). As the climate continues to change at a rapid pace, vegetation composition across Yukon is likely to change. Changes to the location and composition of vegetation communities will have ecosystem-level implications and consequences, including changes in carbon cycling (Mack et al. 2004), litter decomposition (Hobbie 1996), distribution of preferred habitats (Gustine et al. 2014a; Lantz 2017), and migration patterns (Gustine et al. 2014a), among others. These ecosystem consequences affect numerous governance and stewardship decisions ranging from calculations of carbon budgets, locations of new protected areas, fire suppression regimes, translocations of threatened species, and mitigation measures in environmental impact assessments.

2.3 Approach

We conducted an integrative literature review, an in-depth non-systematic approach to assess and synthesize literature (*sensu* Torraco 2005). The causes, prevalence, and consequences of recent (1980 – present) climate- and disturbance-driven community level vegetation change throughout Yukon have not yet been synthesized. This synthesis is therefore warranted given the substantial body of new science and lack of any integration to date. We focus our review on vegetation, not other life forms, as understanding changes to vegetation communities in response to climate change will be important for key decision-making processes. These include: regional land use planning for food security based on habitat suitability for ungulates and harvestable plants; quantifying the carbon storage and sequestering capacities of ecosystems as we develop nature-based solutions to excessive atmospheric carbon; planning for fire mitigation and suppression based on deciduous vs. coniferous forests; projecting the distributions of species at risk for conservation attention.

In our review, we include peer-reviewed literature found through database searches (Scopus and Web of Science) and grey literature found via government databases and snowball reading. The review is in two sections. The first (4.1) concentrates on the persistent changes in growing conditions resulting from the chronic press of climate change (*sensu* Harris et al. 2018). The second (4.2) concentrates on the abrupt, or pulsed, changes (Harris et al. 2018) in vegetation composition that appear to emerge following disturbances and extreme events, some of which may be exacerbated by the changing climate regimes. These sections observe the following structure: standard conceptual view and general knowledge of the topic, Yukon specific studies, and other related information from the northwest boreal. Finally, we identify gaps in our knowledge that future studies will ideally fill to provide a more comprehensive picture of the emerging future (Tables 2 and 3).

Current land classification divides Yukon into nine bioclimate zones, based on regional climate, vegetation, and soil development (Figure 1; Table 1; Environment Yukon 2016). To organize a discussion of vegetation change, we used the bioclimate zone framework, rather than the National Ecosystem Framework (ESWG, 1995). The National Ecological Framework uses physiography integrated with climate to classify regions (Smith et al., 2004). Bioclimate zonation relies more directly on climate, as expressed by elevation and latitude, and a focus on vegetation composition, to classify regions. It is also the dominant scheme used for land cover classification and mapping in Yukon's land planning and management (Environment Yukon 2016). Herein we summarize studies based on the specific zones (capitalized names) where they occurred.

We focus our review mainly on field studies of woody vegetation dynamics (forests, shrublands etc.) as there is a scarcity of information about vegetation change in the Subarctic Subalpine, Arctic Tundra Low Shrub, Subarctic Alpine Tundra, and Arctic Alpine Tundra bioclimate zones (but see Section 4.1.5 for patterns of change in the Arctic Tundra Dwarf Shrub bioclimate zone). We are not discounting the inherent value of these bioclimate zones or the changes within them, but without baseline data and research, an investigation into changes in these bioclimate zones is beyond the scope of this review. Further, we do not address changes with the Pacific Maritime Glacierized bioclimate zone, which is dominated by ice and snow (Environment Yukon 2016), as we found no studies from this zone. This is an important gap in our understanding of the response of northern ecosystems to change as the St. Elias Mountains (located with the Pacific Maritime Glacierized bioclimate zone) have experienced some of the most significant environmental change in all of Yukon. We also did not specifically include remote sensing studies of vegetation change, except where they were used to support findings from field studies.

2.4 Vegetation change

2.4.1 Changing growing conditions and vegetation responses

2.4.1.1 Forests

Trees respond directly to temperature and moisture regimes, so chronic forest stress and mortality are predicted where global air temperatures rise and result in long-term and widespread drying (Boyer 1982; Allen et al. 2010). Many perennial plants, such as canopy trees and woody shrubs, have lifespans lasting into future periods with means and extremes in temperature and precipitation outside their historical experience. These plants may therefore need to make physiological adjustments to survive (Crous 2019). Forest mortality may be particularly noticeable in regions that experience cold winters because, as winter temperatures rise, physiological activity may continue after the growing season has ended (Allen et al. 2010). Together, warming and drought are already responsible for rising mortality rates of boreal trees in some parts of northwestern North America (Johnstone et al. 2010b; Porter and Pisaric 2011; Way et al., 2013), and general patterns of browning, or decreasing NDVI (Sulla-Menashe et al. 2018).

In continuous forests, white spruce showed consistent growth declines across both latitude and elevation, while other species were more variable in their responses (Miyamoto et al. 2010). Across Yukon and northern British Columbia, the response of lodgepole pine to temperature and precipitation patterns differed across latitudes (Miyamoto et al. 2010), a pattern previously been documented across North America (Wheeler and Guries 1982; Xie and Ying

1995; Miyamoto et al. 2010) In Yukon, radial growth of lodgepole pine responded positively to summer precipitation, suggesting that warm summer temperatures may induce similar moisture stress as seen in white spruce (Miyamoto et al. 2010). Lodgepole pine is also demonstrating continued northward range expansion at the current lodgepole pine - white spruce interface (Johnstone and Chapin 2003). Patterns of subalpine fir growth differed across elevations; radial growth of lower elevation populations was negatively correlated with spring temperatures, while higher elevation populations responded positively to summer temperatures (Miyamoto et al. 2010). Further north, Griesbauer and Green (2012) and Walker and Johnstone (2014a) demonstrated that, in the Subarctic Woodland, both white and black spruce experience declines in growth related to seasonal increases in temperature and drought.

There is widespread evidence of reduced white spruce growth in Yukon due to increasing air temperatures and drought conditions throughout the Boreal Low and Boreal High (Figure S1; Hogg and Wein 2005; Zalatan and Gajewski 2005; Miyamoto et al. 2010; Griesbauer and Green 2012; Chavardès et al. 2013; but see Youngblut and Luckman (2008)). These negative relationships likely result from warming exceeding a physiological threshold of water availability; this could result in widespread die-off across the north (D'Arrigo et al. 2004; Way and Oren 2010). Drought stress has been demonstrated in white spruce stands in interior Alaska; if widespread across white spruce's range, this pattern could disrupt carbon sequestration throughout boreal North America (Barber et al. 2000a). Further, long-term predictions indicate that white spruce's optimal growth conditions are likely to become increasingly rare, resulting in decreased productivity and possibly a range contraction of white spruce to cooler and moister locations (Lloyd et al. 2013). Alternatively, if warming does not induce growth limitation through drought, cold-adapted tree species can grow larger at temperatures that exceed their current realized niche (Way and Oren 2010). Northward range expansion of northern tree species may therefore be enhanced by warming if seedlings can become established under these new conditions. The resulting combination of native species and northward shifting novel competitors could produce new combinations of species (Allen et al. 2010). Should the climate become wetter, white spruce may be outcompeted by black spruce in some landscape positions; conversely widespread permafrost thaw may lead to expansion of white spruce over black spruce (Nicklen et al. 2021). Overall, there is a strong need to understand how changing temperature and precipitation patterns, and their extreme events, are interacting to affect drought risk and survival of forest trees across a range of growing conditions (Table 2).

2.4.1.2 Treeline

While widely perceived as thermally limited, the Arctic and alpine boundaries of forests at treeline show complicated responses to elevated temperatures. This treeline ecotone is the transition from continuous forest to non-forested vegetation. Treelines form due to growth limitation, seedling mortality, and dieback of trees (Bader et al. 2020), and the ecotones encompass ecologically distinct range-edge populations of trees. Since global responses of treeline to climate warming are not uniform (Harsch et al. 2009), regional assessments of treeline dynamics are warranted.

In Yukon, treeline research thus far has predominately occurred at elevational treeline in the Boreal Subalpine in the Kluane region, a transition zone between white spruce forests (Boreal High/Subalpine) and shrub tundra (Boreal Alpine Tundra). Although underrepresented in the literature, treeline also occurs throughout the Subarctic Woodland (e.g., Goodwin 2019;

Brown et al. 2019; Brehaut 2021) and Subarctic Subalpine, as both latitudinal and elevational treelines.

In the Boreal Subalpine, white spruce treelines are responding to global changes in three distinct ways, all of which are attributed to increasing air temperatures (Danby & Hik, 2007a, 2007b, 2007c). First, over the past four decades, individual trees within the treeline ecotone have significantly increased their height and cover. Given the slow growth rate of trees at this elevation and latitude, significant growth of individuals is notable (Danby & Hik, 2007a). Second, individuals are establishing beyond the previous range edge on south-facing slopes, indicating treeline advance if those individuals survive and successfully reproduce (Danby & Hik, 2007c). Third, high occurrence of successful germination within the treeline ecotone has resulted in increased density of well-established stems on north-facing slopes (Danby & Hik, 2007c).

Continued expanding distribution, increased growth, and increased density of trees in this ecotone are likely as air temperatures continue to warm, and other conditions (e.g., moisture regimes, levels of seed mortality) remain favourable for recruitment and growth (Danby & Hik, 2007c). Asynchronous treeline change within a region is expected, as treeline responses to global change differ with aspect (Danby & Hik, 2007c; Dearborn & Danby, 2020): treelines on south-facing slopes are more likely to experience upslope treeline advance (Dearborn and Danby 2020), while seedlings on north-facing slopes are more likely to experience increased growth (Danby & Hik, 2007b). Furthermore, current and future increases in air temperature may lead to drought stress in altitudinal and elevational treelines, as demonstrated in Alaska (Wilmking et al. 2004). The asynchronicity of change is likely to lead to variable biotic communities across space as other species shift in concert with or independently of trees.

Treelines throughout the circumarctic forest-tundra ecotone are often seed limited, hindering the ability of a treeline to successfully expand its range farther northward or upslope (Brown et al., 2019). In masting years, high seed production levels and dispersal may reduce reproductive constraints on treeline expansion (Kambo and Danby 2018a). Masting tends to occur the year after summer drought (Ascoli et al. 2019); mast-dependent expansion of treeline may therefore become more common if drought years increase, but only up to the point that masting becomes limited by nutrients available for tree growth and cone production.

Disturbances can act as catalysts for change when other drivers act slowly (Turner 2010a). In ecotones such as the forest-tundra treeline, where colonization and growth are slow processes (Danby & Hik, 2007a), small-scale disturbances creating microsites that are superior seedbeds may be an essential abiotic process in seedling recruitment and establishment. Still, a large number of suitable conditions (e.g., optimal soil temperature and moisture) must occur synchronously before this can happen (Kambo and Danby 2018b). Experimental fine-scale disturbance (i.e., manual scarification) at treeline contributes positively to treeline advance, serving as a proxy for natural fine-scale disturbances such as denning and digging by grizzly bears (*Ursus arctos*), burrowing by Arctic ground squirrels (*Urocitellus parryii*), trampling by caribou (Rangifer tarandus; Dufour Tremblay and Boudreau 2011), and cryoturbation (Kambo and Danby 2018b). The best understood of these disturbances is cryoturbation, which results in patches of bare mineral soil representing easy habitats for vegetation to colonize (Frost et al. 2013). However, climate change will likely reduce the frequency of cryoturbation (Aalto and Luoto 2014) and thus the presence of these optimal germination substrates. Furthermore, a gradual shift of trees towards higher latitudes would likely further reduce the prominence of cryoturbation (Hjort and Luoto 2009).

Studies outside Yukon indicate that treelines are not advancing as fast as climate conditions might allow, and that disturbance is an important catalyst in overcoming inertia. At the boreal-alpine treeline in the Kenai and Chugach Mountains in Alaska, treeline did not advance as fast as the climate envelope, but shrubs successfully colonized available upslope niche space faster than trees, suggesting that dispersal ability of propagules and competition between trees and shrubs are affecting forest advance (Dial et al. 2016). At the taiga-tundra ecotone in Northwest Territories, cold temperatures and limited dispersal ability of trees continue to limit treeline advance into the tundra, and fire appears to facilitate novel establishment of trees and shrubs (Lantz et al. 2019, Travers-Smith and Lantz 2020), likely by providing suitable microsites for germination and seedling recruitment which are generally limiting in this region (Walker et al. 2012). At the forest-tundra ecotone in southwest Alaska, abundance of white spruce seedlings, saplings and mature trees were positively correlated with temperature (Miller et al. 2017). However, further north in the Brooks Range, radial growth of mature white spruce at treeline responded positively to temperature in the west but not in the east (close to Yukon) where trees appeared to be drought stressed (Wilmking and Juday 2005).

Treelines are diverse in landscape position and species composition, so require more attention such as in the poorly studied Subarctic Woodland to Subarctic Subalpine ecotone. Substantial treeline advance at the expense of alpine tundra is unlikely to be realized at rates projected by Rowland et al. (2016). Although empirical evidence shows that some changes are happening, treeline advance may be hindered by insufficient supply of viable seeds in treeline stands (Brown et al. 2019), poor dispersal of seeds, insufficient microsites for recruitment, and competition with expanding shrub growth in the same ecotone (see *4.1.4 Shrub Ecosystems* below). Further, soil types and genesis in some landscapes currently above treeline may not support robust tree growth. Yet fire may facilitate treeline advance in some settings. We are left with many uncertainties about dominant mechanisms in different regions, and the need for more widely distributed field studies and monitoring (Table 2).

2.4.1.3 Grasslands

Worldwide, grasslands are associated with conditions unsuitable for forest growth, which may include insufficient moisture, herbivory of seedlings, frequent disturbance such as fire, or insufficient depth of soil. In northwest North America, grasslands are interspersed within boreal forests, generally in well-drained locations on south-facing slopes, having been described in both southern Yukon and Alaska (Vetter 2000). Soils in Yukon grasslands have properties akin to grasslands in more southern latitudes (i.e., chernozems in prairies; Sanborn 2010), indicating these habitats have a long paleoecological history without forests and an enhanced ability for colonization by other grassland species. Although previously proposed to be relict communities of Beringian origin (a region that was largely unglaciated during Pleistocene glacial periods; Conway & Danby 2014), differences between current and Beringian climate moisture balances suggest that this is unlikely (Strong 2018).

Yukon grasslands are edaphically limited, and therefore both climate and topographic parameters (notably the mix of aspect and temperature, both of which affect moisture availability) strongly define their presence (Sanborn 2010). Increasing temperatures and changing precipitation patterns may therefore affect the size of grassland patches as shrubs and trees in bordering communities experience changing growing conditions. At the grassland-forest ecotone in the Kluane region of southern Yukon (Boreal Low), increased establishment of aspen but not white spruce has occurred at the ecotone's leading edge. This ecotone's tree age structure, including the marked absence of older and dead individuals at the grassland edge, indicates progressive forest encroachment into the grassland, likely due to a lengthening growing season and heightened moisture availability (Conway and Danby 2014).

Grasslands likely expanded to their recent distribution during past periods of drought (Swanson 2006). Drought is projected to increase in some portions of the Boreal Low by 2050, producing growing conditions in which grasslands could occur over a much wider range of topographic circumstances than they currently cover (Rowland et al. 2016). Aspen stands currently persist in the most drought-prone growing conditions of any forest type in Yukon, often adjacent to grasslands. For grasslands to expand, aspen dieback will likely occur. Dieback is likely to be primarily driven by increasing drought levels, as documented further south (Hogg et al. 2002, 2008). Fire may play a role, including repeated anthropogenic fires started by Indigenous peoples to create good grassland conditions for grazers in northern British Columbia (Leverkus 2015), and a hypothesized role for fire in the expansion of grasslands in the aspen parkland zone of the Canadian prairies (Schwarz and Wein 1990). However, we find no documentation of wild or anthropogenic fires influencing the spatial extent of grasslands in Yukon.

Yukon grasslands' response to climate change is unlikely to be homogenous as precipitation differs by region and with longer term climate patterns such as the Pacific Decadal Oscillation and El Niño (Whitfield et al. 2010). Although in southwest Yukon (the lower elevations of the Ruby Ranges ecoregion), evidence indicates that grasslands are contracting with incursion of aspen (Conway and Danby 2014), aspen stands adjacent to grasslands near Whitehorse demonstrate considerable aspen dieback (author, pers. obs.). Projections by Rowland et al. (2016) indicate a conversion of forest to grasslands throughout considerable portions (Southern Lakes ecoregion) of the Boreal Low.

Losing grasslands to forest could result in a reduction of biodiversity, especially if rare grassland species are lost (see Vetter 2000 for detailed species information). Grassland community composition may transition into communities analogous to aspen parkland (along the prairie edge of the western boreal forest), depending on the diversity and functional traits of species currently present. Alternatively, if aspen understory species and grassland species co-exist, a novel community may emerge. Future research directions are listed in Table 2.

2.4.1.4 Shrub Ecosystems

Shrub communities across boreal and Arctic biomes have responded dramatically to new climate conditions, often with expanded cover and increased vertical growth (Mekonnen et al. 2021). Shrubs are perennial plants that range in height from <0.1 m to ~4 m and take on three distinct statures: tall multi-stemmed, erect dwarf, and prostrate dwarf (Myers-Smith et al. 2011a; Götmark et al. 2016). Globally, shrubs are important for ecosystem water balance, carbon uptake and storage, climate control, and soil stabilization, among other functions (Götmark et al. 2016). With climate change, the relative abundance and distribution of shrubs within alpine and tundra environments are predicted to shift (Myers-Smith et al. 2011a). Globally, shrubification (increases in shrub biomass, cover, and abundance) in Arctic and alpine regions occurs via three mechanisms: infilling (an increase in cover of existing individuals as well as recruitment of new individuals), increased individual growth (increased individual height or cover), and colonization beyond current/previous range limit (advancing shrubline) (Myers-Smith et al. 2011a). Plant structural changes are already occurring across circumarctic tundra ecosystems, most rapidly demonstrated by an overall increase in plant height. While shifts in dominant structural traits (e.g., plant height) will be influenced by warming, large-scale changes in these traits are not predicted to occur until novel competitors arrive from warmer, more southern environments (Bjorkman et al. 2018).

In Yukon, shrub research has mainly focused on the Boreal Subalpine, with some work occurring in the Boreal High and Arctic Tundra Low Shrub. In the Boreal Subalpine, Myers-Smith and Hik (2018a) demonstrated that infilling of tall willows results from a combination of increased recruitment rates and reduced mortality rates. Patterns of shrub advance were uniform across site conditions such as slope and aspect, suggesting that a regional factor such as climate warming, rather than site-specific factors, was the primary factor responsible for observed changes (Myers-Smith and Hik 2018a). Continued favourable conditions for shrub expansion in the Boreal Subalpine could result in continued advance of shrubline into alpine tundra, increasing cover by upwards of 20% (Myers-Smith and Hik 2018a). The influence of shrubs' shifting distribution on the wider biotic community will depend on the spatial coverage that shrubs attain. When shrubs are sparse, their influence on abiotic processes (e.g., shading and snow trapping) is negligible. As cover reaches ~50% of the landscape, shrub canopies can increase soil temperature in the winter and decrease it in the summer (Myers-Smith and Hik 2013a). Abiotic changes such as soil temperature may lead to changes in ecosystem functions such as nutrient cycling, decomposition, and plant growth (Myers-Smith and Hik 2013; Livensperger et al. 2016; Sullivan et al. 2020). In the Boreal Subalpine, research has been limited to willows. We lack information on other prominent species, notably birch shrubs. Studies from neighbouring regions may indicate how we expect other species to respond in the Boreal Subalpine (Lantz et al. 2010; Rinas et al. 2017; Brodie et al. 2019). Detailed understanding of responses to warming of all major shrub species is required because the most prominent effects of climate change (e.g., changes in snow accumulation and albedo, soil temperatures, and community floristics) are driven by the full shrub community.

In the Ruby Range (Boreal Subalpine to the Boreal Alpine Tundra ecotone), Weijers et al. (2018) found consistent climate sensitivity for two structurally different shrub species: *Cassiope tetragona* (an evergreen dwarf shrub often found in depressions with long-lasting snow cover), and *Salix pulchra* (a tall deciduous shrub widespread through the subalpine). Found on the same mountain slopes but in different habitats, similar responses in annual growth variability to early summer temperatures by both species suggest that climatic influences on plant growth are remarkably consistent across species (Weijers et al. 2018). Growth patterns of willow in the same region support these findings (Dearborn and Danby 2018).

Greening via shrubification is generally ascribed to tall, deciduous shrubs colonizing beyond their current limit (Elmendorf et al. 2012a, 2012b). However, greening may also occur via colonization by evergreen shrubs: the positive growth response of *C. tetragona* to early summer temperatures suggests that it may be able to expand its range and/or cover within the Boreal Alpine Tundra with continued warming temperatures (Weijers et al. 2018). Dense mats formed by *C. tetragona* may prevent other shrubs from expanding in these locations (Weijers et al. 2018). The ecological consequences of expanding evergreen (compared to deciduous) shrubs will likely differ due to the evergreens' slower decomposition and lower nutrient mineralization rates, relationships with different mycorrhizal fungi, and reduced influence on snow cover and soil temperature as a result of their lower stature (Vowles and Björk 2019).

Shrub communities in the forested Boreal High are often extensive, effectively forming the vegetation canopy. They often have multiple species with similar structure in the same stands (e.g., *Betula glandulosa* and *Salix glauca*). In the Kluane region (Boreal High), relationships between growth and climate variables differ by species: radial growth was negatively correlated with summer air temperatures in *B. glandulosa*, but positively correlated with summer drought and negatively correlated with precipitation in *Shepherdia canadensis*. This suggests that species-specific projections of climate responses over time are warranted (Grabowski 2015). The degree to which understory shrubs are shaded by canopy trees is likely to be a strong influence on shrub growth. Canopy trees are more climate and nutrient-sensitive than understory shrubs, suggesting that where they co-exist (e.g., Boreal High and especially Boreal Low), trees in the canopy may provide a buffering effect to shrubs in the understory, protecting them from environmental fluctuations (Grabowski 2015).

Studies from the Arctic Tundra Dwarf Shrub (Herschel Island) demonstrate increased canopy cover and height of willow but no corresponding increase in radial growth (Myers-Smith et al. 2011b). Willows were also demonstrated to preferentially establish on bare ground rather than vegetated ground (Angers-Blondin et al. 2018). The pattern and rate of change of willow growth were not determined (i.e. whether pulsed or continuous), meaning that the future growth trajectory cannot be confidently predicted (Myers-Smith et al. 2011b). Recruitment of willow was impeded chemically and/or physically by the community *in situ* (Angers-Blondin et al. 2018), suggesting that successful range expansion of willow will depend on overcoming the inherent inertia of the tundra community.

Alaskan studies may provide insight into responses of shrub communities in Yukon. For example, long-term monitoring in the western Brooks Range suggests that the successful establishment and dominance of tall shrubs beyond their historical range may be an ephemeral process in the absence of any form of disturbance (Terskaia et al. 2020). Further, at upper elevations in the Chugach–St. Elias Mountains ecoregion, where montane forests (including black and white spruce, paper birch, trembling aspen, and balsam poplar) and tall shrubs (green alder (*Alnus viridis*) and willow) co-exist, only tall shrubs were able to expand their range to higher elevations (Dial et al. 2016). Competitive range expansion by both shrubs and trees has not yet been explored in Yukon, although the presence of shrubs has been demonstrated to facilitate tree seedling establishment and growth in the Boreal Subalpine (Kambo and Danby 2018c).

The shrub component of ecosystems is clearly changing in response to climate, especially at ecotones, and unlikely in concert with all other members of plant communities (Angers-Blondin et al. 2018), suggesting a variety of future research directions (Table 2).

2.4.1.5 Arctic tundra

Yukon's Arctic tundra communities are diverse, ranging from drier prostrate shrub – herb landscapes, through various graminoids, to erect shrub types (Smith et al. 2004), yet they have not been well studied. In the Arctic Tundra Dwarf Shrub bioclimate zone, an early study (Kennedy et al. 2001) documented shifting abundances of non-shrub species, correlated with warming, in upland tundra on Herschel Island – Qikiqtaruk. The cover of polargrass (*Arctagrostis latifolia*) and Arctic lupine (*Lupinus arcticus*) increased over a 13-year period, mainly by expanding into cryogenic frost-boils and mud hummocks. The opportunity for this expansion is attributed to drying of the active layer of frozen ground, and consequent reduction in cryogenic disturbance (Kennedy et al. 2001). This work complements both the documented expansion of dwarf and willow shrubs (4.1.4 above) and the changes driven by permafrost thaw slumping also at this site (4.2.2 below). Becher et al. (2018) proposed reduced cryogenic soil disturbance as a general pathway for vegetation in-filling on Arctic tundra. More recent vegetation monitoring on Herschel Island has revealed continuation of some of these patterns in upland tundra, with a decadal doubling of shrub (especially deciduous) and graminoid abundance, coupled with substantial decreases in extent of bare ground. All functional groups, except lichens, showed increased cover (Myers-Smith et al. 2019). Factors driving these and other changes, such as increased shrub height, appeared to be increased length of the growing season and warmer autumn temperatures, with resultant increases in depth of the active layer (Myers-Smith et al. 2019).

Patterns in neighbouring regions highlight the propensity for these communities to change. For example, over three decades in the Tuktoyaktuk Coastlands (Northwest Territories), shrubs proliferated at the expense of other terrain types (mainly tussock tundra and polygonal terrain) as a result of increased temperature and precipitation (Moffat 2016). In Alaska, rapid climate change has reduced the fitness of *Eriophorum vaginatum* tussocks range-wide, thereby reducing their competitive success (Souther et al. 2014; Parker et al. 2017). The ongoing and diverse influences of climate warming on growing season length, temperature regimes, soil moisture, and active layer depth (among others) warrant further investigation in conjunction with studies of tundra vegetation response (Table 2).

2.4.2 Disturbance-induced changes to vegetation patterns

Large-scale disturbances, discrete events that alter community and population structures as well as substrates, resources, and the physical environment (Pickett and White 1985), take place over a relatively short period of time (e.g., hours to days) but have large influences on ecological heterogeneity. Disturbances can be biotic (pests or pathogens), abiotic (permafrost thaw and subsidence), or a combination of both (e.g., wildfire, which requires biotic components such as fuel in combination with suitable abiotic conditions, such as weather). The characteristics of disturbances (e.g., size, frequency, and severity) over an extended period of time are referred to as a disturbance regime (Turner 2010a). Since many disturbances have a strong and significant climate forcing, disturbance regimes are likely to change with climate change. Understanding the ecosystem consequences from these changes is critical for future research (Turner 2010a).

2.4.2.1 Fire

Climate induced changes to the wildfire regime are significantly altering the distribution and composition of northern forests (Baltzer et al. 2021). Wildfire is the dominant disturbance throughout the boreal forest of North America and influences characteristics such as forest structure and carbon cycling (Bond-Lamberty et al. 2007; Beck et al. 2011; Walker et al. 2019). Three components of wildfire control post-disturbance regeneration, and all three are likely to be amplified with further warming. Fire frequency, the mean time between consecutive fires, varies across the dominant ecozones of Yukon (Boreal and Taiga Cordillera) from 439 years to 709 years, respectively (Coops et al. 2018; Figure 2A). There is further variation in fire risk within ecozones and therefore the demonstrated fire return interval varies from these means (Figure 2A). Fire severity, the amount of aboveground and surface organic matter consumed by wildfire (Bonan and Shugart 1989a), influences the quantity (or availability) of reproductive plant stages (seed and regenerative roots) available for regeneration and the seedbed quality. Fire intensity, the amount of energy (heat) released from fire (Bonan and Shugart 1989a), influences the amount of viable seed available for reproduction when embryos within seeds cannot survive the heat from a fire.

A majority of post-fire establishment occurs within 3-10 years after fire (Johnstone et al. 2004). Boreal forests have tended to experience cycles of self-replacement and, therefore, have been considered resilient to regular wildfires (Johnstone et al. 2010a). When fires are not severe enough to consume the entire organic soil layer, deciduous seeds from local trees demonstrate low recruitment (Johnstone and Chapin 2006a). In contrast, relatively large-seeded conifers can successfully recruit (Hesketh et al. 2009). However, the severity of fires throughout the Canadian boreal forest is predicted to increase throughout the 21st century (Wotton et al. 2017a), a phenomenon already observed across northwestern North America, including Yukon (Kasischke and Turetsky 2006). Such changes to fire severity are likely to have significant regeneration implications.

As air temperatures in Yukon continue to rise, the number of lightning-ignited fires and the annual area burned are likely to continue to rise; in central Yukon, the number of fires per year may increase by up to 60% by 2039 (McCoy and Burn 2005). Further, landscapes where fire has been suppressed by humans are increasingly susceptible to wildfire risk (Prince et al. 2018). Weather has exerted significant control over the amount of fuel (i.e., organic material) burned in the past, and future warming, especially extreme heating events, is predicted to increase risk, leading to shorter intervals of time between fires.

A majority of fire-vegetation research in Yukon has focused on the post-fire regeneration patterns of black spruce, a semi-serotinous conifer that releases most of its seeds after extreme heat, usually from wildfire. Black spruce is a dominant conifer through considerable portions of Yukon and is present in many different ecosystem types (McKenna et al. 2004). In Eagle Plains (Subarctic Woodland), fires that burned 14-15 years after the previous fire resulted in reduced recruitment of black spruce seedlings compared to fires that burned after longer time intervals;

the parent trees were not reproductively mature when they burned the second time, severely depleting the seed bank (Brown and Johnstone 2012). Also in Eagle Plains, black spruce had a 50% chance of producing cones at 30 years old, increasing to 90% at 100 years (Viglas et al. 2013a). Johnstone and Chapin (2006b) demonstrated similar patterns of low black spruce regeneration in young burned stands near Watson Lake (Boreal Low). Reduced recruitment, and possibly regeneration failure, leave opportunities for other species to colonize. Near Pelly Crossing (Boreal Low), black spruce stands that burned at a young age differed in their post-fire understory community from stands that burned when mature (Johnstone 2006). Aspen regeneration was not affected by altered fire return intervals, suggesting that where conifers struggle to regenerate, aspen may successfully achieve dominance given sufficient survival or ingress of propagules such as roots and seeds (Johnstone and Chapin 2006b). In areas where alternate tree species, like aspen, are absent, regeneration failure of black spruce stands may result in post-fire grass- or shrub-dominated communities (Brown and Johnstone 2012). The ecological repercussions of this magnitude of community shift are unknown yet are likely to have wide-reaching influence across different patterns and processes.

White spruce is also a dominant conifer through much of Yukon but, unlike black spruce, it has pulses of recruitment after masting events, which vary in local intensity (Lamontagne and Boutin 2007). After a fire, white spruce relies on dispersal of seeds from adjacent, unburned stands as its dominant regeneration strategy. When a masting seeder such as white spruce co-occurs with fire-adapted species such as black spruce and lodgepole pine, the masting species only experiences reproductive success if dispersal occurs within a short time frame after the fire, before the burned forest floor becomes too competitive for seedling establishment (as reviewed by Ascoli et al. 2019).

After an extensive fire in the Fox Lake area of the Boreal Low, a majority of sites switched from white spruce to aspen dominance. This shift was notable since, pre-fire, aspen was only present in ~15% of stands and before this most recent fire, stands experienced cycles of white spruce self-replacement after disturbance (Johnstone et al. 2010c). Regeneration data from across the boreal forest indicate that at the time of this Fox Lake study (7-10 years after fire), a large majority of successful recruitment would have already taken place (Charron and Greene 2002; Gutsell and Johnson 2002; Johnstone et al. 2004; Lavoie and Sirois 1998), meaning species present at the time of the study were those expected to continue to dominate in the next succession cycle. The shift towards aspen dominance and a new vegetation community suggests the system's resilience threshold had been exceeded (Johnstone et al. 2010c).

Increased fire severity in the Boreal Low has reduced recruitment constraints in white spruce stands (i.e., thick layers of ground cover and organic soil), thereby increasing the number of potential establishment outcomes. Specifically, after high combustion, small-seeded deciduous species (e.g., aspen) have successfully established in high numbers (Johnstone and Chapin 2006a). Like black spruce stands, white spruce stands in the Boreal Low regenerate with different understories after short (40 years) and long (80-250 year) fire-free intervals. Instances of short fire return intervals tend to be dominated by woody shrub species whose regeneration strategy relies on re-sprouting from roots in mineral soil (e.g., aspen and willow). Conversely, sites with long fire return intervals are dominated by black spruce as well as species (e.g., *Ribes hudsonianum*, *Chamerion angustifolium*), that regenerate via roots in the organic soil and those found in mesic site conditions (e.g., *Ceratodon*-type moss), both of which are more typical of late succession stands (Johnstone 2006).

Throughout the Holocene, wildfire facilitated the expansion of lodgepole pine, a fully serotinous species, into existing spruce forests in eastern Yukon (Edwards et al. 2015; McKenna et al. 2004). At its current northern distributional limit, the proportion of lodgepole pine consistently increased, demonstrating strong evidence of non-equilibrium succession dynamics and a continuation of the species' early Holocene range expansion (Johnstone and Chapin 2003). Expansion of lodgepole pine into regions previously dominated by black or white spruce will likely alter understory community composition. Even in low abundance, the shadows cast by white spruce play a dominant role in creating understory heterogeneity. Loss of these trees (to fire, increased dominance of lodgepole pine, or some other disturbance) will decrease understory heterogeneity (Strong 2011).

The potential future distributions of Yukon vegetation communities projected by Rowland et al. (2016) would entail shifts in forest canopy composition and structure within regions currently forested. Projected shifts included expansion of mixed boreal forests and aspen parklands from limited distributions in the south to cover the majority of southern and central Yukon, conversion of subarctic woodland to a variety of more closed-canopy boreal forests, and conversion of higher elevation forests in the south to closed canopy boreal forests with more southerly affinities (Rowland et al. 2016). To occur, such changes will require significant range expansion of lodgepole pine (and to a lesser extent, aspen and white spruce), plus shifts in the relative dominance of canopy species. Their likelihood would seem to depend on disturbances, particularly fires, because these provide the particular conditions for colonization (e.g., germination beds) and the opportunities for shifts in species dominance through succession. Substantial terrain variability in the Yukon and the variation of fire behaviour at a landscape scale (e.g., with respect to aspect, and local winds) will add a further level of complexity to these patterns. The integrated effects of warming and higher precipitation (i.e. drought risk), plus extreme events, will affect the relative recruitment of tree species to the canopy through succession.

Fire significantly influences the composition of vegetation communities, and, with global warming, can drive substantive changes in the distribution of those communities, so further investigation is needed (Table 3).

2.4.2.2 Permafrost Thaw

Increasing rates of permafrost thaw events throughout the arctic play a significant role in the establishment and successional trajectories of vegetation communities. Permafrost (perennially frozen ground that remains at or below 0°C for >2 years) underlies 10-50% of land in southern Yukon and 90-100% of land in northern Yukon (Smith et al. 2004a). Globally, continued air temperature increases are predicted to lead to permafrost warming and thaw (Biskaborn et al. 2019), that may lead to large-scale collapses of ice-rich land surfaces (thermokarsts) with influences on both above- and below-surface processes. For example, in interior Alaska, widespread thawing of permafrost is predicted to lead to a range expansion of white spruce into landscape positions typically dominated by black spruce (Nicklen et al. 2021). Permafrost-elevation relations in Yukon are non-linear and are significantly impacted by continentality: in areas with a strong maritime climate influence, the probability of permafrost increases with elevation, while in areas with continental climate influence, permafrost is commonly found in valley bottoms but less frequently at higher elevations (Bonnaventure et al. 2012).

In Yukon, studies of permafrost-vegetation relationships are uncommon (but see Price 1971). However, permafrost distribution, thermal patterns, and degradation are generally well explored through much of the territory, including: ice-wedge polygon development, coastal erosion, and thaw slumping in the Arctic Tundra Low Shrub (Lantuit and Pollard 2008; Lantuit et al. 2012; Fritz et al. 2016); permafrost vulnerability in thermokarst lakes and the influence of ground-ice on lake shores in the Subarctic Woodland (Roy-Léveillée and Burn 2010, 2017); the influence of fire on permafrost degradation in the Boreal Low (Burn 1998); and permafrost mapping in the Boreal High and Boreal Subalpine (Lewkowicz and Ednie 2004) and regionally in southern Yukon (Bonnaventure et al. 2012).

In the Arctic Tundra Low Shrub, permafrost thaw occurs on a continuum of scales from 0.4 m^2 (Wolter et al. 2016) to 24,400 m^2 (Cray and Pollard, 2015). At smaller scales, elongated ice wedges often delimit polygons on the tundra surface, called ice wedge polygons (IWPs). Widespread degradation of IWPs has occurred in recent decades, with vegetation changes (e.g., reduction in lichen and moss cover, and changes in the distribution of species) often the first sign of degradation. Intensified summer warming may promote ice-wedge degradation more rapidly than background-level climate change (Liljedahl et al. 2016). In the Arctic Tundra Low Shrub, draining IWPs may transition the vegetation towards greater shrub dominance with reduced vascular plant diversity, tipping the landscape's equilibrium from circumneutral graminoids to acidic shrub tundra with possible effects for land surface properties (Wolter et al. 2016). Shifts in community composition rather than a decrease in overall community diversity are likely as different microhabitats and microtopographies still exist once these features drain (Wolter et al. 2016).

At larger scales on Arctic tundra, thaw characteristically results in retrogressive thaw slumps, where water-laden upper layers of soil slide downhill exposing bare mineral soil (Cray and Pollard 2015). These exposures are ideal microhabitats for germination of many functional groups. Willows and grasses rapidly establish, likely as they both produce high quantities of seed with high dispersal potential that can germinate on post-disturbance substrates and can survive with fluctuating soil moisture. In addition, willows can survive as a ‘vegetation island’ of pre-existing tundra, moving from the slump headwall downslope as an intact vegetation unit (Cray and Pollard 2015). Differences between disturbed and undisturbed substrates as well as their associated vegetation communities likely remain for ~250 years (Cray and Pollard 2015). As environmental conditions (e.g., ground thermal regime, slope, soil acidity, etc.) also continue to change, restructuring of vegetation communities and trajectories may be irreversible (Cray and Pollard 2015).

In the Subarctic Woodland, Lantz (2017) observed that catastrophic drainages of thermokarst lakes led to two distinct regeneration trajectories, dictated by moisture conditions. In wet areas, the vegetation became dominated by sedges, while in drier areas (which composed a majority of the drainage basin), tall willow shrubs dominated, reaching upwards of two times the size of willows in undisturbed control sites, and often competitively excluding other species. Based on vegetation communities in older drained basins, the willow's overpowering dominance is probably a seral stage that will later transition to communities of similar composition as those in older drained basins (e.g., dwarf shrub and tussock tundra). Transitioning to a community that is more representative of the current climate in the region (i.e. warmer than historical average) is also possible; however, it is not clear what that community would look like (Lantz, 2017).

After retrogressive thaw slumps in the Boreal Low, vegetation propagules and surficial soil moisture are the two main determinants of community composition. Burn and Friele (1989) identified two distinct vegetation communities post-disturbance, separated based on their distance from the slump headwall and, therefore, meltwater supply. Closer to the headwall and in areas of higher soil moisture, willows and horsetails (*Equisetum* spp.) dominated. In drier areas further away from the headwall, the pre-disturbance forest community started to establish with fast-growing and wind-dispersed herbs establishing first, followed by tree saplings 10-15 years post-disturbance; re-establishment of the original community was predicted to begin 35-50 years after disturbance (Burn and Friele 1989). Similarly, Bartleman et al. (2001) predicted that the transition from shrub birch to spruce forests would occur once the surface began to dry out (i.e. with increasing time since disturbance). Longer-term monitoring of sites such as these would be valuable for a detailed understanding of the recovery trajectories.

Under continued climate change, permafrost becomes increasingly vulnerable to degradation by fire; thermal changes initiated by fire can cause surface subsidence and the development of thermokarst features in boreal and tundra landscapes (as reviewed by Holloway et al. 2020)). In the last century, permafrost demonstrated resilience to fire, recovering after several decades in most situations. However, a combination of year-round warming and more frequent and severe fires will likely cause slower or no recovery of permafrost to its pre-fire state (Holloway et al. 2020). At its southern extent, permafrost tends to be thermally protected by forest cover. In these regions, fires that cause shifts in the dominant vegetation patterns (such as shifts from conifer to deciduous dominated forests) act as a destabilizing influence, and the permafrost is likely to degrade entirely (Jafarov et al. 2013; Holloway et al. 2020). For example, discontinuous permafrost in the Boreal Low maintained its integrity under unburned white spruce forest but started an ongoing process of progressive degradation in the burned areas, which were regenerating primarily as deciduous species (Burn 1998). Modelling efforts from Alaska suggest that when the post-fire organic layer is <30 cm thick, permafrost is increasingly vulnerable to disturbance (Jafarov et al. 2013). When combined with the trend towards more severe wildfires completely combusting the organic layer, this suggests there could be widespread degradation of boreal forest permafrost. The frequency of permafrost failures triggered by fire (e.g., active layer detachments and permafrost-related landslides) is predicted to increase over time in central Yukon (Boreal Low; Lipovsky and Huscroft 2006).

The currently increasing rates of permafrost thaw in the boreal and Arctic are unprecedented and leave many unanswered questions as to how vegetation communities will respond and develop after colonization (Table 3).

2.4.2.3 Insects & Pathogens

Insects and pathogens that consume trees in the forest canopy (or other characterizing forest components) can change forest composition and structure over large areas (Forest Management Branch 2020). In this regard, they can be thought of as agents of natural disturbance, much like wildfire. While insects and pathogens are currently limited in their spatial influence in Yukon, and thus poorly studied, the declining vigour of trees in many landscapes may increase the possibility that they become more significant agents of change. Consequently, we do not review all insects and pathogens present; here, we focus on the bark beetles (*Dendroctonus* spp.) because they have, or could have, by way of their outbreak dynamics, the most widespread influence on Yukon's forests and the trajectories of future vegetation communities. In our recommendations for future work, we suggest locations where some of the other insects require attention because they also could be prominent agents of change in vegetation.

Spruce bark beetle (*Dendroctonus rufipennis*) is perhaps the most studied forest insect in Yukon, having killed over 400,000 ha of white spruce in southwest Yukon since an outbreak that began in 1990. Spruce bark beetle is present throughout the range of white spruce and generally occurs at low densities killing individual trees sporadically. As a result of drought stress, trees emit specific chemical(s), beetles respond to the chemical cues and attack the stressed trees, and the stressed trees have limited resources with which to attack the beetle, causing most trees to be killed, including healthy, seed-bearing trees (Garbutt et al. 2006). The beetle attacks semi-mature to mature trees, with a preference for larger individuals that can least defend themselves. Cold winter temperatures limit over-winter beetle survival, and beetle densities can increase rapidly and irrupt following unusually warm winters. These irruptions or outbreaks are responsible for the most intensive changes to mature spruce forests of any insect in Yukon (Government of Yukon 2019; Forest Management Branch 2020).

Spruce bark beetle outbreaks have been detected in Yukon since the 1930s, generally in years of above-average temperatures (Forest Management Branch 2020). Compared to infestations in Alaska (the Kenai Peninsula), Kluane does not have a long history of spruce bark beetle infestations, likely due to its lower winter temperatures and different wildfire regime (Berg et al. 2006). In the late 1980s, warm temperatures in the Boreal Low, Boreal High, and Boreal Subalpine (mostly within the Ruby Range ecoregion) caused drought stress in white spruce stands and increased overwinter survival of beetles (Garbutt et al. 2006; Forest Management Branch 2020). Following this, a 12-year beetle outbreak occurred between 1994-2006 (unprecedented in its spatial scale). In the Boreal Subalpine, larger trees and trees at relatively lower elevations were more susceptible to attack (Mazzocato 2015). Larger trees were also selected for by beetles in lower elevation bioclimate zones (Boreal High, Boreal Low; Garbutt et al. 2006). In Yukon, infestations have only been actively studied in association with the 1990s Kluane region outbreak (Berg et al. 2006; Garbutt et al. 2006; Randall et al. 2011; Chavardés et al. 2012; Hawkes et al. 2014; Mazzocato 2015; Paudel et al. 2015; Campbell et al. 2019).

White spruce continues to be the dominant tree in the post-beetle outbreak forest, albeit with a different age class distribution. In most cases, the growth trajectory of saplings establishing after the disturbance determines forest recovery (Campbell et al. 2019). In some landscapes (notably in the Boreal High), young trees survived the outbreak and quickly became dominant within the canopy. Repeated site surveys show that most white spruce seedlings/saplings established 6-14 years after the outbreak started (Hawkes et al. 2014). Patterns of increasing summer and winter temperatures already well established in Yukon (Streicker 2016) will probably increase the likelihood of drought stress to spruce and the overwinter survival of spruce bark beetles, possibly leading to more frequent and widespread outbreaks (Forest Management Branch 2020).

Mountain Pine Beetle (*Dendroctonus ponderosae*) is currently not present in Yukon, but is found in the Liard Basin of British Columbia, within 20 km of the Yukon border. (Forest Management Branch 2020). Mountain Pine Beetle is considered the most extensive forest health concern in western Canada and can turn forests from carbon sinks to large carbon sources (Kurz et al. 2008; Forest Management Branch 2020). Northward migration of the mountain pine beetle from BC (likely the Rocky Mountain Trench) into Yukon (likely the Liard Basin (Boreal Low)) is possible (Forest Management Branch 2020). Mountain pine beetles attack and kill mature and old stands of lodgepole pine, and so place at risk ecosystem values associated with these old-growth stands, notably caribou winter range (Cichowski and Williston 2005). However, depending on the species composition and disturbance history of stands before beetle outbreak (i.e. fire and/or fire-suppression impacts), stands can have divergent post-beetle recovery trajectories (Axelson et al. 2009), which might include novel forest types in particular landscapes.

The Yukon Forest Management Branch maintains an annual monitoring regime for forest health, with a priority focus on mapping the stand and landscape-scale distributions of (i) eight insects or groups of insects that consume canopy trees, (ii) a rust-induced disease, and (iii) aspen dieback due to drought (Forest Management Branch 2020). In addition to monitoring initiated by the Forest Management Branch, we recommend future monitoring and research of a variety of pests across bioclimate zones (Table 3).

2.5. Major Findings

Despite dramatic projected changes in climate envelopes and the forest and vegetation types they support, there is relatively little published evidence of changes so far, reflecting: (i) too little on-the-ground attention towards ecosystem changes; and (ii) the strong inertia of many forests in the face of the chronic press of incremental change until a disturbance event can induce a relatively abrupt shift in existing or emerging canopies. Trends in some climate parameters are prominent, but there is high variability between years and within bioclimate zones. Further, changes in vegetation assemblages in response to climatic trends and disturbances vary sub-regionally. Findings synthesized here are likely relevant to similar communities in the Northwest Territories and interior Alaska.

We have identified knowledge gaps in the response of different vegetation assemblages to persistent trends in climate parameters and to disturbances influenced by climate parameters (Table 2 and 3). Most documented changes have taken place in the Boreal Low bioclimate zone (Table 1), suggesting it needs ongoing attention. However, the Subarctic Subalpine and Arctic Tundra Dwarf Shrub zones have received little or no attention, suggesting another set of priorities. Ongoing research in Yukon is beginning to address these questions.

Two monitoring approaches – interpretation of remotely sensed imagery and permanent ground plots sampling stand composition – would ideally be systematically expanded and implemented to start to fill many knowledge gaps. These approaches work best in combination, with on-the-ground field plots providing training data, and validation data, in the development of interpretative and projection models that rely on remotely-sensed inputs. Ideally, they would be designed to test hypothesized changes, and will require hypothesis-specific protocols and analyses that can be automated and replicated (in time and space).

Early investigation into changing ecological communities throughout Yukon will enable more pro-active management and conservation policies and practices. It is our hope that the research gaps identified in this paper can help guide future research within Yukon and elsewhere in the North as rapid climate change threatens to change ecosystems, habitats, and subsistence lifestyles. Identifying these research gaps is timely as northern science and conservation are in a period of change. For example, the newly created Yukon University, Canada's first northern university, emphasizes northern science and resource management in the context of equitable partnerships with First Nations; and the Yukon Government Science Strategy is planned for re-evaluation by 2025, with goals of establishing long-term science capacity and approach throughout Yukon and supporting evidence-based decision making through gathering and storing scientific and Indigenous Knowledge (Qatalyst Research Group 2020).

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Tables and Figures

Table 2. 1 Yukon bioclimate zones with documented historical and natural changes in structure and composition of dominant vegetation communities. Bioclimate zones follow the framework laid out by Environment Yukon (2016). Two bioclimate zones are excluded: i) Pacific Maritime Glacierized (vegetation is sparse; rock, snow, and ice dominate ground cover; no published research on vegetation dynamics or changes); ii) Subarctic Subalpine (no documented vegetation changes were reviewed in this paper). References for documented vegetation changes can be found in the Supplementary Information.

Bioclimate Zone and Areal Extent	Description	Documented historic and natural vegetation changes
Boreal Low 6.47×10^6 ha	- Low to mid-elevations - Near continuous forest in all mountain valleys and plateau regions; wetlands and edaphic grasslands common - Forests with single species and mixed-species canopies, often closed (lodgepole pine, white spruce, aspen); moderately developed understory	- Warming and drought are responsible for mortality rates amongst white spruce[1,2,3,4,5,6] but there are some examples of different patterns[7] - Radial growth of lodgepole pine is positively related to summer precipitation[4] - Subalpine fir radial growth differs with relative elevation[4] - Increased establishment rates of aspen (but not white spruce) at forest-grassland edge[8] - Reduced recruitment in young burned black spruce stands[9] - Extensive fire converts white spruce forests to aspen dominance[3] - After high combustion, small-seeded species (e.g., aspen) can successfully establish in high quantities[10] - Understory community composition differs in white spruce stands after different fire return intervals[11] - Pre-disturbance community is more likely to re-establish farther away from permafrost slump headwall, where it is drier; re-establishment occurs 35-50 years after disturbance[12] - Permafrost under coniferous trees remained unaffected by fire, but in previously burned areas that are currently dominated by aspen, it degrades[13] - After a 12-year spruce bark beetle outbreak, white spruce stands showed compositional resilience[14]

		- Understory community differs between young- and mature-burned black spruce stands[11]
Boreal High 1.68x10⁷ ha	- Mid- to upper elevations - Near continuous forests in all mountain valley and plateau regions - Forests with single and mixed species canopies (white spruce, lodgepole pine, subalpine fir). Canopies more open than Boreal Low; tall shrubs dominate canopy gaps	- Warming and drought are responsible for mortality rates amongst white spruce[1,2,3,4,5,6] - The response of tall shrub growth to warming is species-specific[15] - Young white spruce trees can survive spruce bark beetle outbreaks and achieve canopy dominance[16]
Boreal Subalpine 7.18x10⁶ ha	- Moderate to high elevations - Transitional zone between Boreal Low/ High and higher, non-treed alpine - Trees sparse (<10%) (subalpine fir, white spruce); tall to medium shrubs dominate	- Increased height and cover of trees within treeline[17] - Successful tree establishment beyond range edge on south-facing slopes[18] - Increased density of trees at treelines[18] - Ground scarification increases germination outcomes[19] - Increasing cover of tall willow shrubs[20] - Larger trees and trees at (relatively) lower elevations are most susceptible to attack by spruce bark beetle[21]
Subarctic Woodland 1.02x10⁷ ha	- Valley bottoms, lower slopes of mountain valleys, plateaus, and plains - Open canopy forests of single and mixed species canopies (black spruce, white spruce, aspen); tall shrubs frequent in canopy gaps	- Fires that burned when black spruce trees were ~14 years old had reduced recruitment due to immature seed sources[22] - Two vegetation recovery trajectories dominate after catastrophic lake drainage: a wetter trajectory dominated by sedges and a drier (more common) trajectory dominated by willows, up to double the size of undisturbed willows. Willow dominance is likely a seral stage[23] - Black and white spruce radial growth declines with increasing temperature and drought[5,24]
Arctic Tundra Dwarf Shrub and Low Shrub 2.88x10⁶ ha	- Sea level to 500m - Low to moderate shrubs (>40cm tall) dominate; dwarf shrub-willow tundra and sedge tussock tundra are common	- Increased height and canopy cover of willows[25,26] - Infilling of cryogenic boils and hummocks by grass and vetch[30] - Greater shrub dominance and reduced vascular plant diversity after draining of microtopographic permafrost features[27]

		- Long-term (~250 years) differences remain between vegetation assemblages in disturbed (retrogressive thaw slump) vs. undisturbed conditions[28]
Alpine Tundra 4.51×10^6 ha	- Boreal, subarctic, and Arctic bioclimate regions - Boreal: high elevations above the Boreal Subalpine (above altitudinal treeline) - Subarctic: mid to high elevations, above the Subarctic Subalpine - Arctic: High elevations (>950m), above the Arctic Tundra Dwarf Shrub - Vegetation dominated by dwarf and low shrubs, cryptograms, and herbs	- In the boreal alpine tundra, consistent climate sensitivity amongst structurally unique shrubs[29]

Table 2. 2 Priority knowledge gaps for further investigation summarized for each of the vegetation structures in the text, by bioclimate zones and associated landscapes.

	Research goal or question	Location
Forests	Investigate which forest types are greening, remaining relatively unaffected, or browning as a result of changing growing conditions. Widespread dendrochronological surveys of mature stands of the major forest canopy species would be required; growing conditions that present a range of drought risk should be sampled.	Given the Alaskan evidence, white spruce may be the highest priority species, and lower elevation growing conditions (Boreal Low) with warmer temperature regimes would be the priority sites.
	Given the prominence of drought as a risk factor for forest change in the boreal forest, assess historical climate data for each bioclimate zone using a drought index (e.g., The Palmer Drought Severity Index;(Guttman 1998)).	Most weather data are collected at low elevations (i.e., Boreal Low), which would be suitable for this analysis.
Treeline	Assess whether patterns demonstrated at treeline in the Boreal are present in other bioclimate zones and whether there are species-specific responses to warming.	Subarctic Woodland and Subarctic Subalpine
	Investigate the compounding effects of climate change and disturbances (e.g., wildfire, beetle, or pathogen outbreak) on treeline dynamics to understand future abiotic and biotic interactions within this ecotone.	Boreal High, Boreal Subalpine, Subarctic Woodland, Subarctic Subalpine
	Understand the role of abiotic constraints on continued upslope advancement. In the Rocky Mountains, upslope advancement of Engelmann spruce (*Picea engelmannii*), a regionally dominant conifer, is limited by soils' physical and chemical properties, even when climate conditions are favourable (Davis et al. 2018). A Yukon-specific understanding of these interactions will contribute to future predictions concerning treeline communities.	Boreal High, Boreal Subalpine, Subarctic Woodland, Subarctic Subalpine
	Use remotely sensed imagery to monitor change in treeline and in the distribution of subalpine shrubs. Quantify rates of change in alpine tundra communities.	Boreal Subalpine, Subarctic Woodland, Subarctic Subalpine, Subarctic Alpine Tundra; Boreal Alpine Tundra
Grasslands	Determine the extent to which historical temperature and precipitation regimes have correlated with periods of more intense or less intense drought (e.g., Palmer Drought Severity Index; Guttman 1998). How are these patterns related to documented changes in grassland extent?	Boreal Low where most grasslands currently occur.
	Quantify the drought levels that can be tolerated by aspen forests currently growing in southern Yukon. Assess how these relate to projected levels of drought and consequently the relative risk of aspen dieback subregionally and across different toposequences.	Boreal Low
	Understand the role of "natural" disturbances (notably fire and infestations of large aspen tortrix moth	Boreal Low in southern Yukon where aspen and grasslands co-occur.

	(*Choristoneura conflictana*)) in affecting the viability of aspen stands close to grasslands.	
	Where forests have been encroaching on grasslands, quantify how persistent this process is over time. To what extent is it threatening loss of grassland sites where endemic plant and insect species, some of which are listed species, are currently found, thereby exacerbating their level of risk? (e.g., Yukon Draba (*Draba yukonensis),* Yukon grasshopper (*Bruneria yukonensis*)),	Boreal Low (Ruby Ranges ecoregion)
Shrub Ecosystems	Where and under what parameters are shrub species changing in concert vs. individually? Grabowski (2015) suggests that they respond individually, while Weijers et al. (2018) indicate that they respond similarly.	Yukon-wide
	Further understanding of critical filters (other than plant-plant interactions and suitable microsites) that are important for tall shrub recruitment across many bioclimate zones	Yukon-wide
	Determine feedback mechanisms between changing shrub height and/or location and other drivers of shrub change (e.g., soil temperature).	Yukon-wide
	Understand competition between the expanding niches of shrubs and trees where both functional groups are present. Understanding this relationship is essential for understanding future treeline advance as well as shrub community dynamics.	Yukon-wide (with specific focus on Boreal Subalpine)
	Continued monitoring of shrub-dominated landscapes to understand whether, in the absence of disturbance, the successful establishment and dominance of tall shrubs beyond their historical range is ephemeral or permanent.	Yukon-wide
	Conclusions from Grabowski (2015), the only known work on boreal shrub understory in Yukon, suggest that future studies of boreal shrub understory focus on the following; we support investigation of these knowledge gaps as essential areas for future study. Non-climatic factors that influence boreal shrub establishment and growth (e.g., herbivory, fires of differing severity). The role of canopy cover and nutrient availability, and their interactions, in open-canopy forests. The spatial extent of boreal shrubification. The interaction between understory shrubs and canopy trees in forested zones. We	Yukon-wide (with specific focus on Boreal Subalpine)
	Predict the extent to which tundra-dependent species are at increasing risk from expansion of the erect shrubs into the tundra biome. These could include species at risk (e.g., Yukon Podistera (*Podistera*	Boreal Subalpine; Boreal Alpine Tundra; Subarctic Subalpine; Subarctic Alpine Tundra

	yukonensis)), keystone species (e.g., Arctic ground squirrel (*Urocitellus parryii*)), tundra obligates (e.g., collared lemming (*Dicrostonyx groenlandicus*)), and bioculturally valuable species (e.g., thinhorn sheep (*Ovis dalli*) and barren-ground caribou (*Rangifer tarandus*))	
Arctic tundra	Monitoring of fixed plots aimed at quantifying changing vegetative composition over time.	Arctic Tundra Low Shrub; Arctic Tundra Dwarf Shrub
	Understand the role of shrub expansion within tussock and polygonal terrains.	Arctic Tundra Low Shrub; Arctic Tundra Dwarf Shrub
	Document the fitness of *Eriophorum vaginatum* and other dominant species to understand how they may be outcompeted in the near future.	Arctic Tundra Low Shrub; Arctic Tundra Dwarf Shrub
	Document the ongoing and diverse influences of climate warming on growing season length, temperature regimes, soil moisture, and active layer depth (among others) and understand how in turn, these influence plant community composition.	Arctic Tundra Low Shrub; Arctic Tundra Dwarf Shrub

Table 2.3 Priority knowledge gaps for further investigation summarized for each of the natural 'pulse' disturbances in the text, by bioclimate zones and associated landscapes.

	Research goal	*Location*
Fire	Investigate the relationship between high severity fires (and high degree of cone combustion) and post-fire seed rain that has been demonstrated in Alaska and Northwest Territories (Johnstone et al., 2009; Reid et al., in review).	Yukon-wide, for forested zones
	Simulation experiments from Alaska show that if forests transition to deciduous dominance post-fire, the resulting communities are resilient to a wide variety of warming, fire return intervals, browsing, and disturbance scenarios (Hansen et al. 2020). Shifts to deciduous dominance are projected to be commonplace throughout the northwestern North American boreal forest, including in Yukon. Monitor for shifts to deciduous dominance and associated disturbance patterns.	Yukon-wide
	The incidence of tundra fires in Yukon has been low, and they have therefore not received any attention. In Alaska, regeneration after tundra fires is usually led by rapidly growing pioneer species and the proliferation of shrubs (Rocha et al. 2012). Investigate regeneration trajectories after tundra fires via remotely sensed imagery and field studies.	Arctic tundra
Permafrost Thaw	Determine if vegetation assemblages that colonize ground exposed by permafrost degradation (e.g., thaw slumps and thermokarst lake drainages) are transitional (temporary) or successional (part of longer succession). What are the various trajectories of vegetation establishment in different bioclimate zones and degradation scenarios?	Yukon-wide
	Slope failures in forested zones are sources of sedimentation into streams and rivers (Lipovsky and Huscroft, 2006) with negative consequences for fish. How quickly can revegetation stabilize slope failures and reduce and stop the downslope movement of sediments?	Yukon-wide
	After fires, permafrost degradation frequently occurs, with or without any landslides, and often appears irreversible. Is this degradation irreversible no matter the dominant vegetation (conifer vs. deciduous) and duration of the successional trajectory after the fire?	Yukon-wide
	Greater permafrost thaw and nutrient release post-fire may relax establishment constraints, resulting in a post-fire successional trajectory that differs from the pre-fire composition (Bret-Harte et al. 2013). To what extent does the thaw itself create soil conditions that influence the successional trajectory?	Yukon-wide
Insects and Pathogens	Continued monitoring of the locations and intensity of spruce bark beetle outbreaks due to summer drought and warmer winter temperatures. Monitoring must also	Boreal Low (where drought is projected to be most prevalent; Rowland et al., 2016).

	follow the successional trajectories of beetle-killed stands to determine whether spruce forests will regenerate or shift to aspen dominance as has happened following at least one fire (Johnstone et al. 2010b).	
	Large areas of dead trees from beetle outbreaks may create substantial fire hazards if other factors increasing fire risk are in place (Garbutt et al. 2006). Investigate the various potential interactions (synergism, neutrality, dampening) of a beetle outbreak with subsequent risk and severity of fire (see Turner 2010) .	Boreal Low
	Establish a network of forest plots in the Liard Basin in anticipation of mountain pine beetle's range expansion into Yukon and assess pre- and post-beetle forest stand composition and quantify changes to forest dynamics and caribou winter ranges.	Boreal Low (Liard Basin)
	Drought and warming temperatures may influence the sources of recruitment and the survival of regenerating seedlings following outbreaks of insects, as has been seen following fire. In addition to spruce bark beetle, shifts in biome or forest type could conceivably occur in the following insect and geographic combinations, each of which needs monitoring: i) Aspen tortrix moth (*Choristoneura conflictana*) contributing to shifts in aspen stands to grassland. ii) Aspen serpentine leaf miner (*Phyllocnistis populiella*) contributing to shifts in aspen stands to grassland. iii) Western balsam bark beetle (*Dryocoetus confusus*) contributing to shifts in subalpine fir stands to subalpine shrubs.	Boreal Low (Southern Lakes ecoregion) Boreal Low (Southern Lakes ecoregion) Boreal Subalpine (Yukon-Stikine Highlands, Southern Lakes, Pelly Mountains, and Hyland Highland ecoregions).

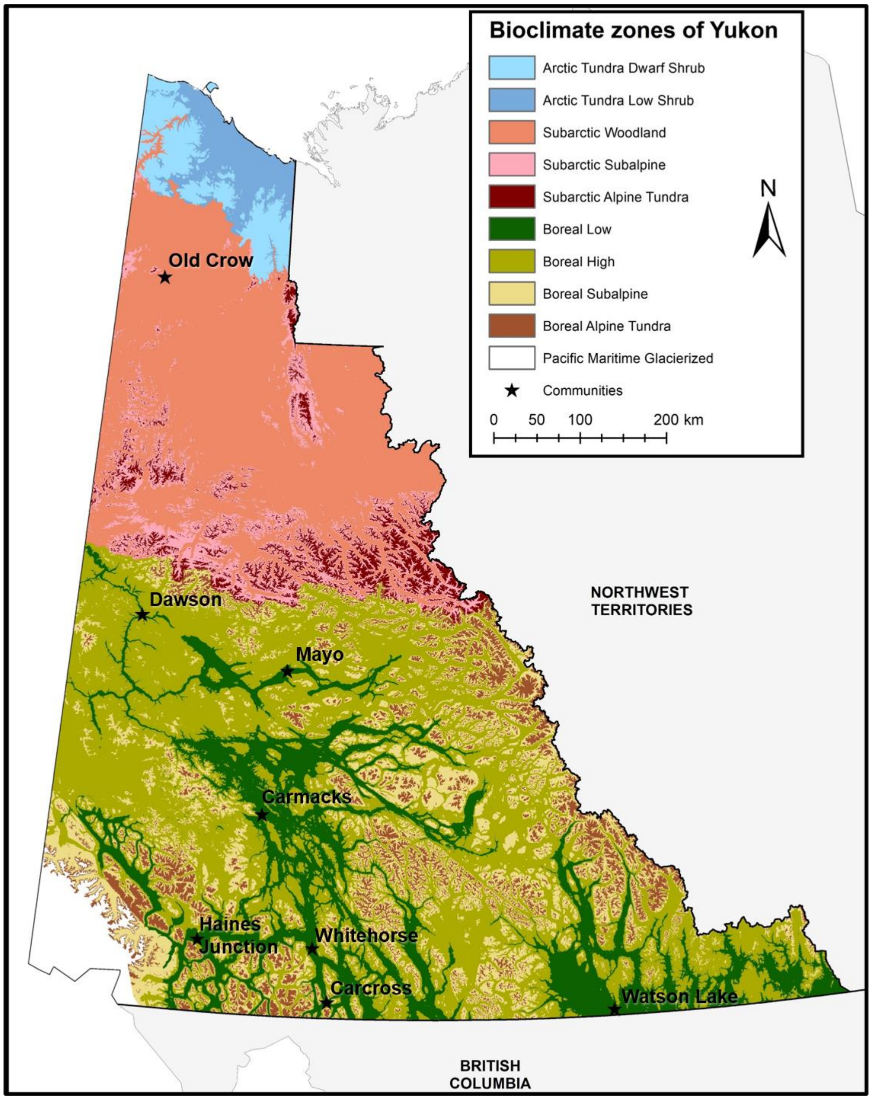

Figure 2. 1 The distribution of bioclimate zones in Yukon. Bioclimate zones map regional differences in vegetation structure attributable to latitude and elevation - two of the prominent drivers of climate. Within zones, climate norms can still vary substantially from place to place, best represented by ecoregions (Smith et al. 2004). Map data source: Bioclimate zones (Environment Yukon 2021). This data source is more detailed than the previous summary (Environment Yukon 2016) and differentiates between the Subarctic and Boreal Alpine Tundra bioclimate zones.

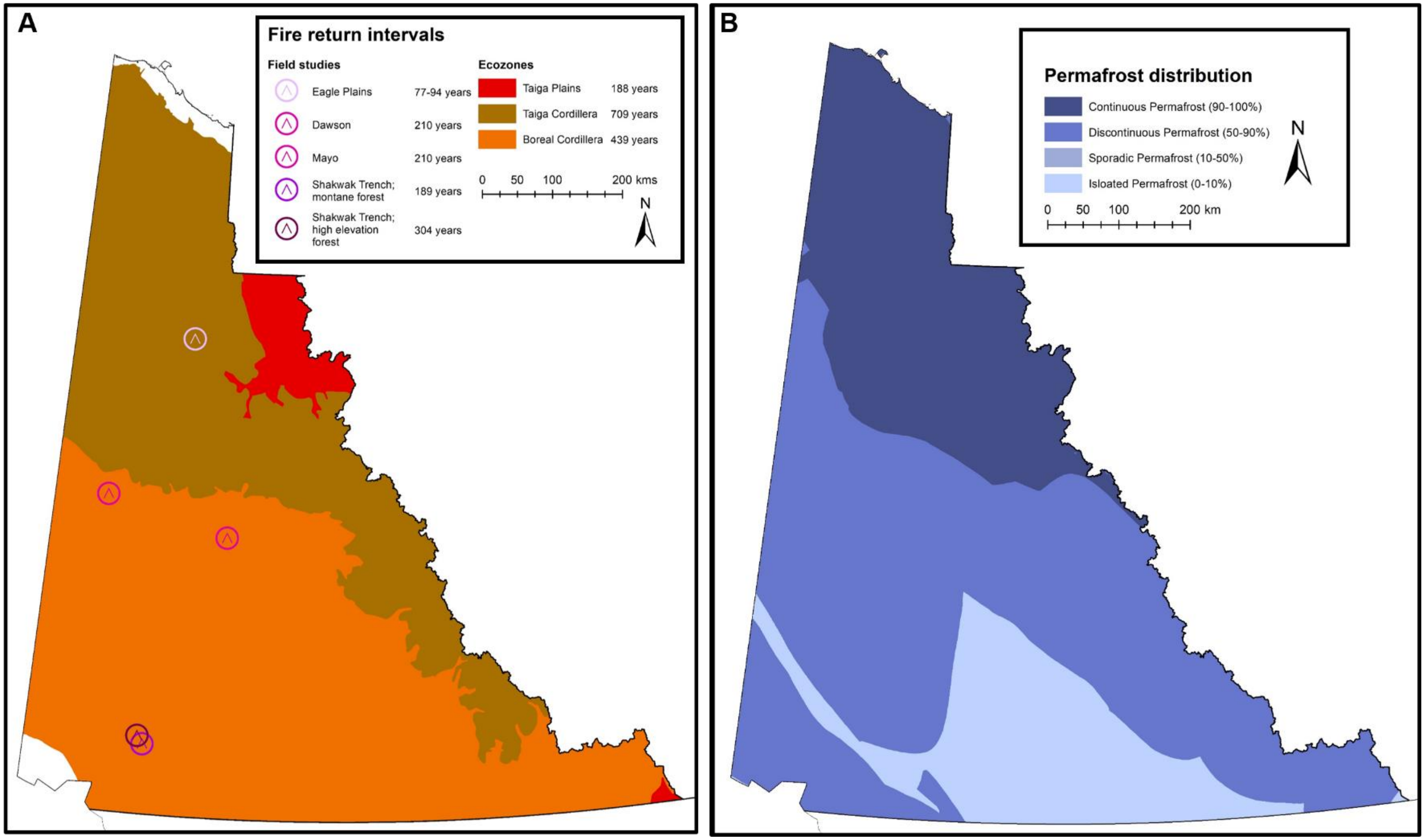

Figure 2. 2 Distribution of fire activity and permafrost throughout Yukon. A) Fire return intervals measured via remote sensing by ecozone (Coops et al. 2018) and by field studies. In Central Yukon (Dawson and Mayo), the current fire return interval is ~210 years (McCoy and Burn 2005); in Shakwak Trench in southwest Yukon, the fire return interval differs between montane forests (~189 years, frequent small-scale disturbances lead to relatively even-aged stands) and high elevation forests (~304 years, infrequent and large disturbance events; Francis, 1996); in Eagle Plains, mature forests were ~77 and ~94 years old when burned (Brown & Johnstone, 2011). B) Permafrost distribution throughout Yukon. Map data sources: Ecozones (Government of Canada 2013); Permafrost distribution (Brown et al. 1998).

Supplementary Information

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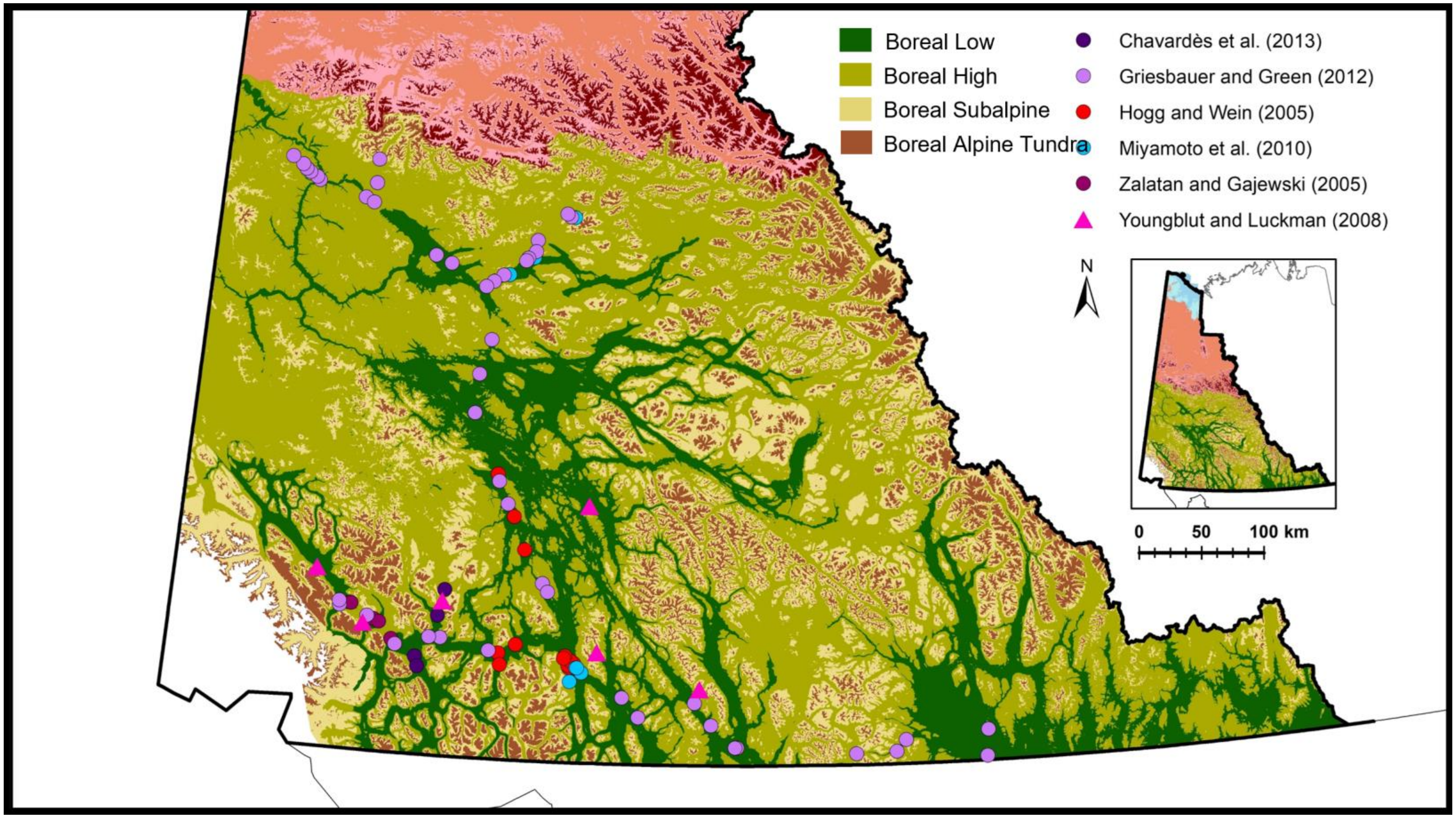

Figure S2. 1 Studies of white spruce response to warming and drought in the Boreal Low and Boreal High bioclimate zones in southern Yukon. Circles represent research sites from studies that demonstrated decreased growth of white spruce under warming conditions. Triangles represent research sites in Youngblut and Luckman (2008) that showed variable response of white spruce to warming and drought. Bioclimate zones follow the framework laid out by Environment Yukon (2016). Map data source: Bioclimate zones (Environment Yukon 2021).

Chapter 3: Species richness increases with latitude in subarctic Canada

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In preparation for submission to Environmental Reviews: Ecology

Abstract

In northwestern Canada, previous evidence suggests that species richness of understory vegetation and spider communities increase with latitude, counter to global patterns. A clear understanding of the a/biotic factors that control species richness in this region will help with predictions of the location and functioning of communities under future climate scenarios as communities respond to new and continued pressures. Here, we investigate the role of latitude in shaping understory vegetation and spider communities throughout central and northern Yukon and examine the direct gradients that latitude is acting as a proxy for. We found that species richness increased with latitude and that this was associated with negative gradients of air temperature and insolation (cold temperatures and low insolation in northern sites) and a positive gradient of snow cover duration (longer snow cover in northern sites). At northern sites, a combination of sparser tree canopies, longer duration of insulating snow, and reduced competition for light and nutrients maintain a more heterogeneous community of understory vegetation. In high-latitude regions, continued global change is predicted to manifest as increasing air temperatures and reduced snow cover. These new conditions could dramatically alter the existing vegetation communities with ecosystem-wide consequences possible.

3.1 Introduction

The latitudinal gradient of diversity is one of the most widely accepted patterns in biogeography. It suggests that globally, species richness decreases from the tropics to the poles (Willig et al. 2003; Hillebrand 2004), though some exceptions exist across biomes and taxa (reviewed by Willig et al. 2003). Under scenarios of global change, latitude itself will not be affected; yet, latitude is often used as a proxy for environmental gradients (Willig et al. 2003). Understanding which underlying variables that latitude is 'masking' is therefore important to make accurate predictions about future drivers of species diversity and distribution patterns. While high-latitude regions are relatively species-poor compared to lower latitudes, they remain highly complex and interconnected systems with abrupt environmental gradients (Figure 3.1), confounding their response to environmental changes (Taylor et al. 2020).

In subarctic regions of northwestern Canada, recent observational evidence suggests that the latitudinal gradient of diversity pattern is outweighed by other constraints on species diversity and distribution. Marshall and Baltzer (2015) demonstrated a positive relationship between vascular plant species richness and latitude (60-68°N) in 134 permanent sample plots in the Northwest Territories. They determined that reduced competition (biotic interactions) was responsible for increased species richness with latitude. Historical biogeography and soil conditions did not significantly influence this pattern. In the Tombstone, Ogilvie, and Richardson Mountain ranges of northern Yukon, Bowden and Buddle (2010b) demonstrated a neutral relationship between spider community richness and latitude (64-67°N), concluding that community assemblage was more strongly influenced by site type and elevation. In both studies, local characteristics outweighed global richness-latitude patterns.

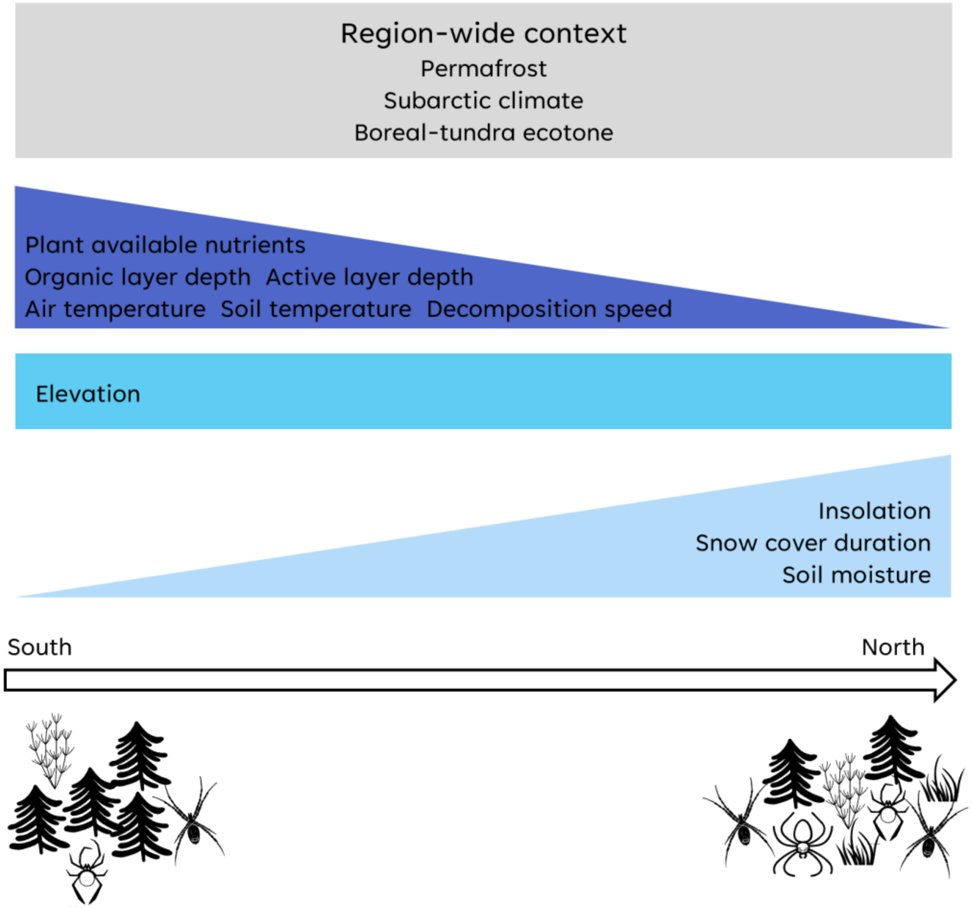


Figure 3. 1 Conceptual view of the environmental gradients throughout subarctic Canada. In addition to changing biotic conditions throughout the region, species diversity of plants and spiders are predicted to increase with latitude, as per results from Bowden and Buddle (2010a, 2010b) and Marshall and Baltzer (2015).

Compounding these species diversity-latitude relationships is anthropogenic climate change, which is likely to introduce new stressors and competitors. Climate change is occurring at unprecedented rates in polar regions (Box et al. 2019; IPCC 2022), and biotic communities are responding to this environmental stress by altering life history traits such as growth patterns and distributions (Walther et al. 2002). In arctic and subarctic regions, stress responses have been documented at various scales. For example, improved recruitment and growth conditions have facilitated the upslope movement of shrub communities in high-latitude alpine tundra in southwestern Yukon (Myers-Smith and Hik 2018b); drier climates and more severe fire conditions have reduced the resilience of black spruce forests throughout North America (Baltzer et al. 2021); and a previously undocumented range overlap of three North American bear species has occurred in northern Manitoba, potentially leading to novel interspecific interactions (Clark et al. 2019).

Biotic changes throughout the arctic lag behind rising air temperatures (Huang et al. 2017) and are spatially heterogeneous (Myers-Smith and Hik 2018b; Bjorkman et al. 2020; Taylor et al. 2020). This heterogeneity necessitates regional-specific understanding of biotic community responses to environmental pressures and the influences these pressures have on community assembly. Understanding the underlying drivers of species occurrence in the subarctic will help improve predictions of when and where species will shift their distributions under ongoing climate change, potentially pinpointing regions of community decoupling or conservation concern.

We wanted to further investigate the latitudinal gradient of diversity in the subarctic by looking across a large geographic area in Yukon (63.2-66.6°N). We examined the distribution and drivers of species richness throughout central and northern Yukon for understory vegetation and spiders. We chose to look at these specific communities because understory vegetation diversity typically follows the global latitudinal diversity gradient (Hillebrand 2004), with reverse patterns detected in the subarctic (Marshall and Baltzer 2015), and spider communities and their drivers are well documented in arctic and subarctic Canada (e.g., Buddle et al. 2000; Bowden and Buddle 2010a, 2010b; Loboda and Buddle 2018). Additionally, vegetation forms habitat for spiders, and the structural and life history characteristics of those plants characterize that habitat. Spiders respond readily to small changes in habitat and temperature (Downie et al. 1995; DeVito et al. 2004; Bowden and Buddle 2010a,b), and are considered a model taxon for investigating species assemblages at large (200-4000 km) scales (Waide et al. 1999). By looking at vegetation and spiders together, and specifically spiders in plant habitat, we can begin to tease apart large-scale climatic and latitudinal drivers of species richness, from small-scale habitat drivers.

We asked **1)** What are the relationships between latitude, species richness, and environmental drivers? And **2)** What role do environmental and habitat variables play in species diversity and distribution patterns? We predicted species richness would increase with latitude (Figure 1) as seen in other studies at smaller scales and that environmental drivers strongly correlated with latitude (e.g., air temperature) would be the strongest determinants of species richness. We hypothesized that the following environmental drivers may influence vegetation species richness (Q1) and diversity and distribution (Q2): decomposition rate, organic layer depth, depth to resistance (active layer depth), soil available nutrients, soil moisture, soil temperature, air temperature, insolation, snow cover duration, latitude, and elevation. Similarly, we hypothesized that the following environmental drivers may influence spider species richness (Q1) and diversity and distribution (Q2): organic layer depth, soil available nutrients (used as a proxy for site productivity), air temperature, snow cover duration, latitude, elevation, and dominant ground cover (habitat). We explicitly tested the role of habitat type in influencing spider richness and diversity as Bowden and Buddle (2010a, 2010b) identified this as a strong driver of community composition in the region. Predicted relationships and mechanistic rationale for each driver are listed in Table 3.1.

Table 3. 1 Predicted direction (+/-) of the relationship and mechanistic control on species richness and diversity for vegetation and spiders.

	Vegetation	Spiders
Site location and characteristics		
Elevation (m a.s.l)	**(-)** Higher elevation increases environmental harshness, reducing species richness and diversity (Stevens 1992)	**(-)** Habitats at higher elevations are likely to be less favourable (based on results from Bowden and Buddle, 2010b)
Insolation (W/m^2)	**(+)** Increased insolation means more energy for metabolic activity supporting more individuals and species (Clarke and Gaston 2006)	NA
Air temperature (°C)	**(+)** More individuals and species will persist as air temperature is within the physiological requirement of more species (Clarke and Gaston 2006)	**(+)** More individuals and species will persist as constraints on air temperature are relaxed
Access to resources		
Organic layer depth (cm)	**(-)** Thicker organic layers reduce plant access to nutrients (Van Cleve et al. 1983)	**(+)** Thicker organic layers will increase the amount and types of habitats available
Soil temperature (°C)	**(+)** In warmer soils there will be increased nutrient availability and greater physiological activity in vegetation (Van Cleve et al. 1983)	NA
Soil moisture (m^3 H_2O/m^3 soil)	**(+)** Wetter soils will increase plant growth, until the point of saturation where growth will be limited (due to slower nutrient turnover and low oxygen) (Van Cleve et al. 1983)	NA
Soil available nutrients (µmol/10 cm^2/length of burial)	**(+)** Increased available nutrients will increase plant growth (Turkington et al. 1998)	**(+)** High available nutrients is used as proxy to indicate a productive site
Decomposition rate	**(+)** Faster decomposition rate indicates greater nutrient turnover and greater availability of nutrients to plants (Turkington et al. 1998)	NA
Depth to resistance (cm; active layer depth)	**(+)** Increased depth to resistance provides deeper rooting depth for plants and higher access to nutrients (Van Cleve et al. 1983)	NA
Snow cover duration (days)	**(-)** Longer snow cover duration indicates less growth time and therefore reduced recruitment and establishment (Wipf and Rixen 2010)	**(-)** If longer snow cover duration indicates reduced recruitment and establishment of vegetation, spider habitat diversity (and therefore spider diversity) will be reduced

3.2 Methods

3.2.1 Site establishment

We established field sites throughout central and northern Yukon in 2018 in the Traditional Territories of the Nacho Nyäk Dun, Vuntut Gwitchin, and Tr’ondëk Hwëch’in First Nations, with permission. We completed fieldwork in 2018, 2019, and 2021: fieldwork was not possible in 2020 due to COVID-19 travel restrictions. To select sites, we generated a cluster of random points every 90-110 km along the Klondike and Dempster Highways, with the goal of establishing one site every ~100 km. We visited random points in numerical order and assessed them with the following criteria: i) 100 m to 1 km from a safe highway access point, ii) no fire within past 80 years (determined using fire maps from Wildland Fire Management (2018)), iii) no obvious signs of human or natural disturbance (e.g., logging, slumping, animal denning), iv) representative of the local (~15 km) vegetation, topography, etc., and, iv) encompassing a 50 m x 50 m area that was relatively homogenous (vegetation, microtopography, etc.). We avoided wetlands and steep slopes controlled for forest structure and composition. After we identified a suitable site within a cluster, we did not visit additional random points. We reviewed all sites prior to commencing site instrumentation etc. to ensure that they were all similar in their forest composition and structure and landscape position. Ultimately, we established seven sites along the Dempster and Klondike Highways (Table A3.1; Figure 3.2).

As a direct result of COVID-19 related travel restrictions, study sites were unevenly distributed between subarctic boreal forests (n = 5) and dwarf shrub tundra (n = 2). Originally, we had four additional sites in the Northwest Territories (two in each the forest and tundra), but these were inaccessible for most of the study period due to border closures. We recognize that any assumptions about spatial patterns are therefore more limited than the original intention of this study. Due to the smaller sample size, we separated all analyses by i) all sites and ii) forested sites.

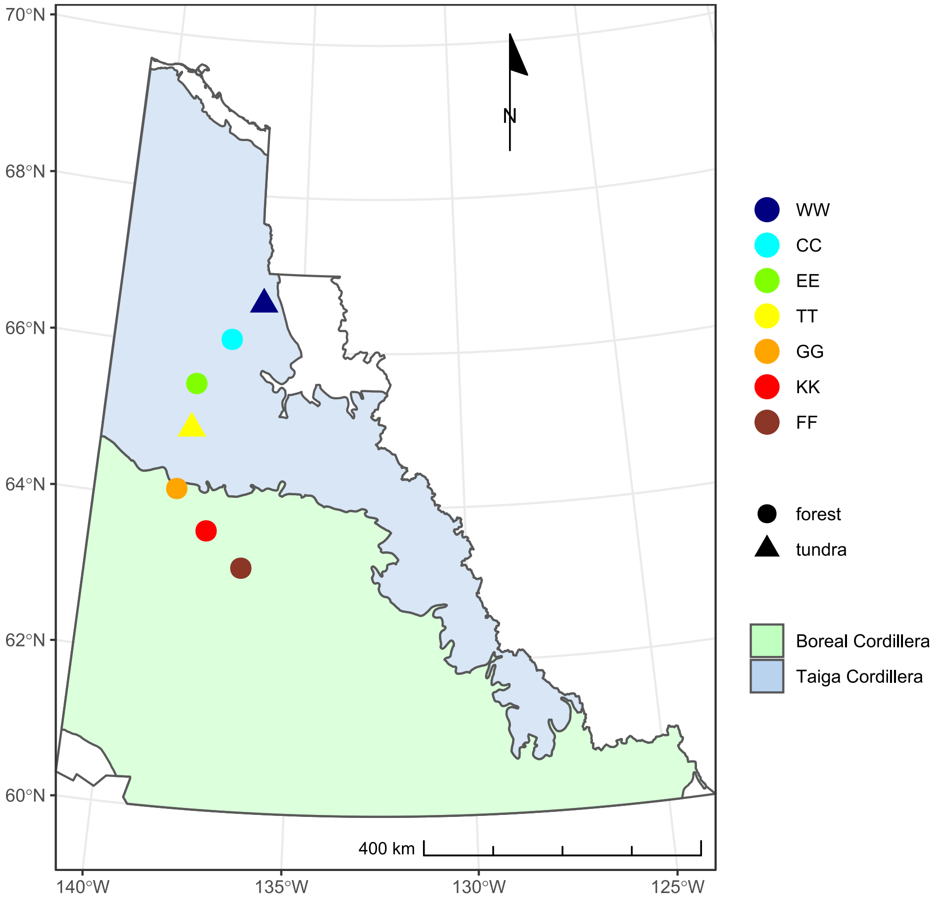


Figure 3. 2 Study sites in central and northern Yukon. Sites are colour coded here and in all subsequent figures to help with visual analysis; colder colours representing northern sites and warmer colours represent southern sites. Two sites are in tundra environments (denoted by triangles) and the remainder are in forests (circles). Sites are in the Boreal Cordillera and Taiga Cordillera ecozones (green and blue polygons, respectively). Details on site characteristics (by 2-letter code name) can be found in Tables 3.2 and A1.

3.2.2 Biotic communities and predicted drivers

To quantify understory vegetation community, we identified and visually estimated percent cover of understory vegetation (vascular and nonvascular) in ten 1 m x 1 m quadrats; one quadrat was placed at the centre of the site and the others were haphazardly distributed. We identified all vegetation to species except for the following groups: pleurocarpous, acrocarpous, *Polytrichum* spp., and *Sphagnum* spp. mosses, *Peltigera* spp., *Cladonia* spp., and *Cetraria* spp. lichens, and sedges and grasses (note: *Calamagrostis lapponica* was identified to species and not included in this group). Wasyliw et al. *(in prep*) independently assessed understory vegetation at eight sites in the Eagle Plains ecoregion, where CC is located. Since we had a relatively small sample size (one site every ~0.5° of latitude), we used data from Wasyliw et al. to place our results in the context of the regional species pool and to indicate whether we had captured a significant proportion of the regional variation by only assessing one site.

Using data from our vegetation analysis above, we categorized each vegetation species into one of six functional categories (moss, lichen, graminoids/herbs, deciduous shrubs, evergreen shrubs, prostrate shrubs) and calculated the percent cover of each of these categories (Table A3.2). We used these functional categories to qualify spider habitat; this analysis approach also allows us to assess direct links between the two taxonomic groups.

We quantified the spider community using pitfall traps, a common method for assessing arthropod biodiversity at large scales which has previously been used within this study region (Bowden and Buddle 2010a, 2010b). We dug holes so that the top of the trap was flush with the ground surface; we placed one trap at the centre of each site and four paired randomly with vegetation quadrats. At the end of each collection period (n = 2; June-August 2018 and 2019), we emptied the traps, and all invertebrates were transferred to clean containers with ethanol. In our pitfall traps we collected more invertebrates than just spiders; however, we chose to focus exclusively on spider diversity due to the breadth of spider knowledge that exists for the region. All other specimens remain preserved, but identification and analyses of additional communities is outside the scope of this study. In the lab, we separated spiders from other individuals and identified them to species. Nomenclature followed the World Spider Catalog (2021) and voucher specimens were donated to the Royal BC Museum (Victoria, British Columbia).

We measured the following drivers of species diversity and distribution at each site, detailed in Tables 3.2 and A3.3: elevation, average annual air temperature, average annual soil temperature, soil moisture, snow cover duration, organic layer depth, active layer depth, plant-available nutrients, insolation, and decomposition rate. We also measured site basal area at all forested sites to facilitate comparison with results from Marshall and Baltzer (2015).

Table 3. 2 Summary of the environmental predictor variables. [a] Variable averaged over multiple measurements across the site; [b] Annual average; [c] Nutrient gradient is a multidimensional variable, originating from a Principal Components Analysis; [d] Spider collections were pooled at the site level due to destroyed pitfall traps.

Site	Elevation (m a.s.l)	Organic layer depth (cm)[a]	Nutrient gradient[a, c]	Snow cover duration [b,c]	Insolation	Air temperature (°C)[b]	Decomposition rate[a,b]	Active layer depth (cm)[a]	Soil temperature (°C)[b]	Soil moisture (m^3 H$_2$O/m^3 soil)[b]	Understory plant species richness (mean ± sd)	Spider species richness[d]
WW	696	3.95	0.486	237	208	-4.19	0.002	40.5	-3.85	0.22	16 (13.9 ± 0.876)	16
CC	604	4.5	-0.178	229	210	-5.22	0.004	52	-1.60	0.20	16 (12.8 ±1.69	11
EE	547	44.1	0.123	219	213	-3.63	0.004	44.5	-1.09	0.20	18 (12.5 ±1.65)	9
TT	937	60	0.376	219	215	-4.05	0.003	55.5	-2.39	0.34	9 (6.9 ±1.91)	12
GG	749	7.05	-0.179	215	218	-2.85	0.002	67	1.22	0.12	16 (9.7 ±1.77)	7
KK	467	7.4	-0.274	190	221	-1.61	0.003	55.8	1.89	0.23	10 (5.1 ±1.29	12
FF	749	5.1	-0.354	192	223	-0.80	0.004	64	-0.87	0.19	12 (9.4 ±1.26)	9

3.2.3 Statistical analyses

All statistical analyses were done in R version 4.1.2 (R Core Team 2021). To test relationships between latitude, species richness, and environmental variables, we used simple linear models with variables pooled/averaged at the site level and compared the multiple R^2 values (R Core Team 2021). To test the role of environmental and habitat variables in species diversity and distribution, we used nonmetric multidimensional scaling (NMDS) in the package vegan version 2.5-7 (Oskanen et al. 2020). We used the predictor variables that we hypothesized would be important for each community and fit matrices of continuous environmental (or habitat) variables to each set of community data to demonstrate the direction of environmental gradients. For understory vegetation, data were analyzed at the quadrat level (n = 10 per site) to gain an understanding of within site variability. The coloured polygons that represent each site encompass all the variation within that site. For spiders, we pooled samples across the five traps per site but left data separate for the two years to account for interannual variation; each NMDS plot therefore has two symbols to represent each site, one for each 2018 and 2019.

We intended to assess the role of environmental variables in driving community composition using a mixed effects modelling approach. However, due to the loss of sites resulting from COVID-19 travel restrictions, we were only able to look at bivariate relationships. Our regressions are only across seven data points (five when excluding tundra sites), and we recognize that our ability to extrapolate or make strong inferences about underlying patterns is therefore limited.

3.3 Results

Vegetation

We identified a total of 27 vascular species and 11 non-vascular understory species. At forested sites, we identified 22 vascular species and 11 non-vascular species; at tundra sites we identified 15 vascular species and nine non-vascular species. Comparing our results to Wasyliw et al.'s data suggests that we captured 80% of the richness in the ecoregion (Figure A3.1). This suggests that our data encompasses a high amount of the regional variation. We assume that we had the same sampling bias for other sites and for spiders.

Spiders

We collected 969 adult individuals in 30 species. The Lycosidae family (wolf spiders) was the most abundant, representing 82% of the collection (802/969 individuals). Three species in this family represented 63% of the collection: *Pardosa moesta* (n = 215/969), *P. uintana* (n = 211/969), and *P. sodalis* (n = 186/969). All three of these species have previously been identified in this study region (Bowden and Buddle 2010a, 2010b; Loboda and Buddle 2018); Bowden and Buddle (2010b) also found notably high abundance of *P. uintana.* In total, forest sites accounted for 46% of the total number of spiders collection; these comprised 20 species. *P. uintana* was the most abundant species in these samples (n = 211/445 individuals), followed by *Alopecosa aculeata* (n = 65/445 individuals), and *P. moesta* (n = 35/445 individuals). *A. aculeata* and *P. moesta* have also both been previously described in the region (Bowden and Buddle 2010a, 2010b; Loboda and Buddle 2018) and were of noticeably high abundance (Bowden and Buddle 2010b).

What are the linear relationships between latitude, species richness, and environmental variables?

Understory species richness increased with increasing latitude (Figure 3.3). The relationship was slightly stronger when only forested sites were considered ($R^2 = 0.574$ for all sites; $R^2 = 0.620$ for forested sites). Spider species richness increased with latitude at forested sites ($R^2 = 0.310$; Figure 3.3). When tundra sites were removed from the analysis there was no relationship ($R^2 = 0.018$).

Latitude was negatively correlated with soil temperature ($R^2 = 0.540$), active layer depth ($R^2 = 0.671$), insolation ($R^2 = 0.999$), and air temperature ($R^2 = 0.828$; Figure 3.4). Latitude was positively correlated with snow cover duration ($R^2 = 0.892$), and did not correlate with elevation, soil moisture, and decomposition rate (Figure 3.4). When tundra sites were removed, most relationships remained constant or became marginally weaker. However, the relationship with air temperature and decomposition rate became stronger ($R^2 = 0.944$ and $R^2 = 0.336$ respectively; Figure A3.2).

As expected, species richness for both communities was correlated with many of the factors that were correlated with latitude (Figure A3.3). For understory vegetation, relationships tended to become stronger once tundra sites were removed. There were no strong relationships between elevation and species richness except for spiders in the forest where a strong negative relationship was present. Two outliers strongly influenced organic layer depth (one forested and one tundra); when the tundra sites were removed the direction of the relationship changed but was still influenced by the forest outlier. Overall, this relationship was weak (for both understory vegetation and spiders). The nutrient gradient had high variation, but nutrient availability was generally highest in tundra and northern forest sites. As predicted, the nutrient gradient did not have a strong influence on spider communities. We also explored the relationship between species richness and basal area at all forested sites to compare our results to those of Marshall and Baltzer (2015). Relationships were weak and negative; $R^2 = 0.355$ and $R^2 = 0.007$ for both understory vegetation and spiders respectively (Figure A3.3).

Variables that had strong, negative relationships with latitude (air temperature, soil temperature, insolation) had weakly negative influences on plant species richness. Relationships were slightly stronger when only forested sites were included (Figure A3.3: air temperature all sites, $R^2 = 0.007$; forested sites, $R^2= 0.125$; soil temperature all sites, $R^2 = 0.001$; forested sites, $R^2 = 0.389$; insolation all sites, $R^2 = 0.016$; forested sites, $R^2 = 0.297$). Snow cover duration, which was positively related to latitude, was a positive predictor for both understory species richness ($R^2= 0.169$) and spiders ($R^2= 0.568$).

What role do environmental variables play in species diversity and distribution?

Our multivariate analyses identified environmental gradients underlying the latitudinal patterns observed with the linear models above. For understory vegetation (all sites; Figure 3.5), sites at lower latitudes clustered together on the right side of the NMDS plot, while higher latitude sites clustered on the left. The NMDS revealed that low latitude communities were associated with high soil and air temperatures, deeper active layers, and high insolation. Conversely, high latitude sites were associated with longer snow cover duration. High latitude forest sites (teal and green) were associated with higher decomposition rates, lower soil moisture, and shallower organic layer relative to the other sites. The tundra sites were associated with higher nutrient availability.

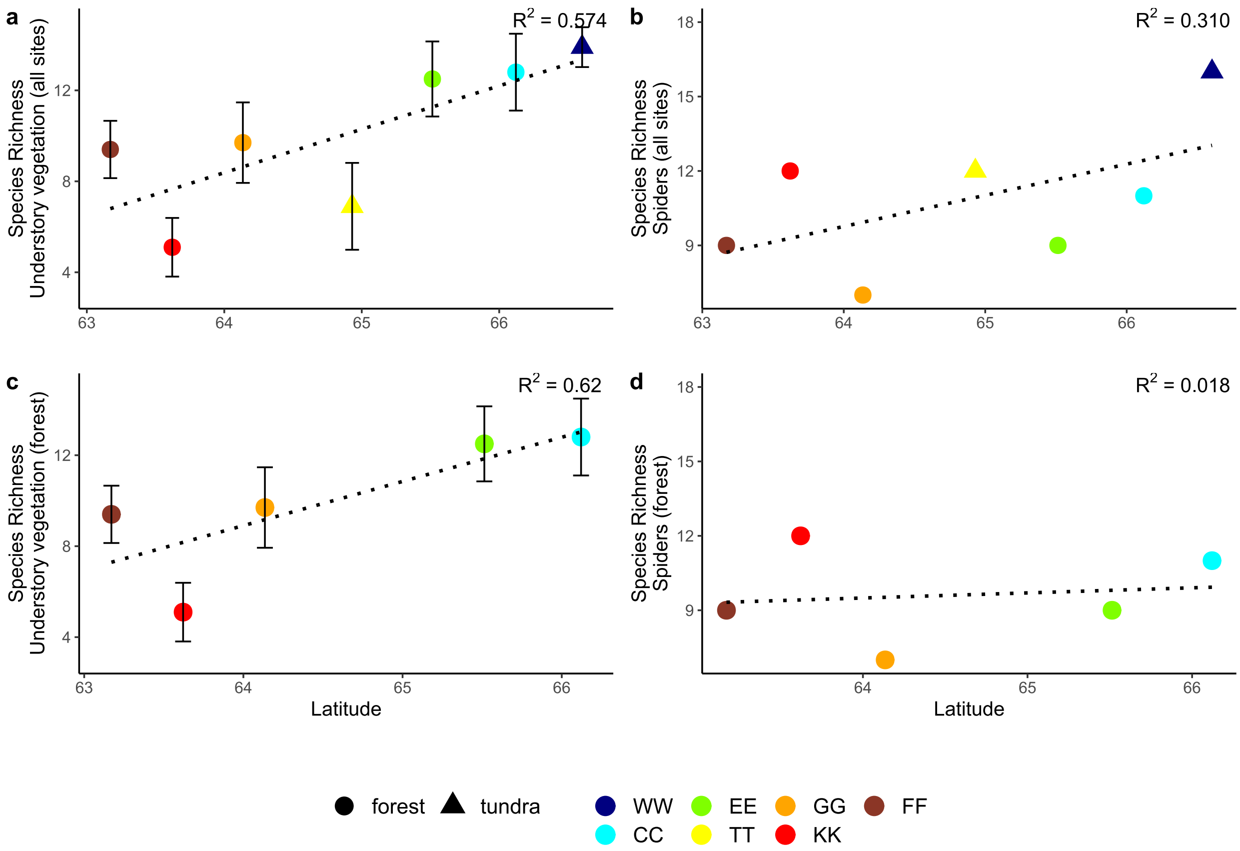


Figure 3.3 Relationship between latitude (x-axis) and species richness (y-axis). Plots A and C show average understory vegetation species richness for at all sites (A) and forested sites (C); error bars represent the standard error within quadrats at each site. Plots B and D show spider species richness for all sites (B) and forested sites (D). R^2 value represents the multiple R^2 of the linear model. Colours correspond to sites in Figure 3.2. Sites represented by triangles in plots A and B are tundra sites, sites represented by circles are forested sites.

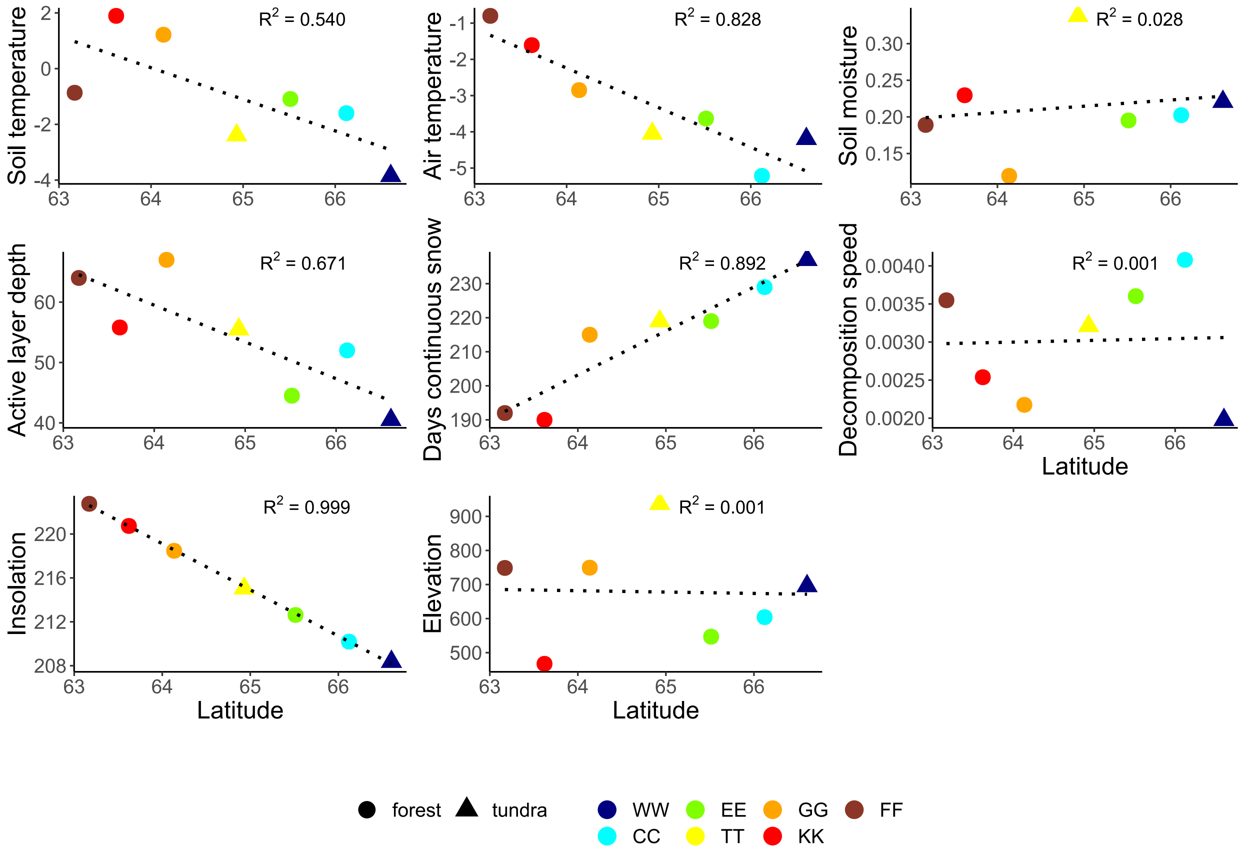


Figure 3. 4 Relationships between latitude (x) and all measured environmental predictor variables (y). R^2 values presented are the multiple R^2 of the linear models. Data are shown for all seven sites; plots without tundra sites generally show the same relationships and are presented in Figure A2. Colours correspond to sites in Figure 3.2.

When tundra sites were removed from the NMDS analysis (Figure 3.6), there was greater separation of the low latitude sites (right side of NMDS1) and the high latitude forest sites (left). As before, higher latitude sites were associated with faster decomposition rate and longer snow cover duration, while lower latitude sites were associated with increased air temperature, insolation, and active layer depth. Community composition of understory vegetation at low latitude communities was more similar than high latitude communities, evidenced by their spatial clustering on the NMDS plot. The size of each site's polygon indicates that within site variation was approximately the same at all sites apart from FF, the lowest latitude site, which had low variation as indicated by the small area of the representative polygon.

Spider community analyses include data separated for the two study years. Figure 3.7, therefore, shows each symbol repeated; the small distances between the repeated symbols indicate low interannual variation within a site. We found that the variation between sites (the spatial separation of sites) is greater than the within site (temporal) variation. Spider communities at all sites were clearly separated by latitude, representing gradients of high air temperature and insolation in the south to extended periods of continuous snow in the north (Figure 3.7a). When tundra sites were removed, the gradient became less pronounced, and communities did not separate by latitude as clearly (Figure 3.7b). Our NMDS analysis overlaid by habitat variables, which allowed us to examine links between our taxonomic groups, indicated there was a gradient of moss dominance in the south and prostrate shrub dominance in the north, with tundra sites associated with graminoids and herbs (Figure 3.7c). When tundra sites were removed (Figure 3.7d), a gradient from moss to lichen dominance separated sites from south to north. The two highest latitude forest sites were separated by evergreen/prostrate shrubs (EE) and deciduous shrubs (CC).

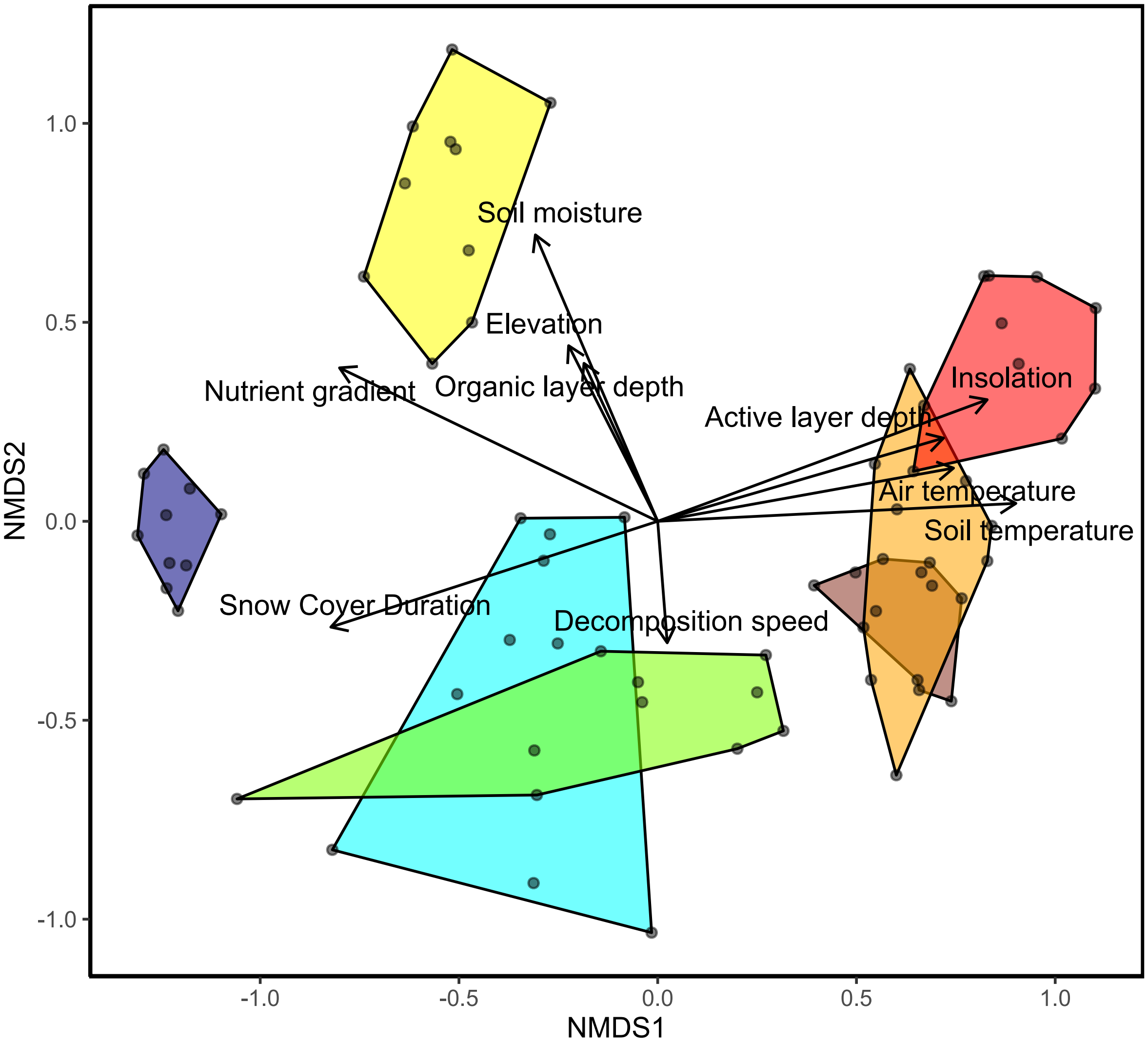


Figure 3. 5 Distribution of understory plant communities at all sites in multivariate space (non-metric multidimensional scaling; NMDS). Each point represents a 1 m x 1 m quadrat within a site (10 quadrats) and the polygons around each set of points captures all the variation within a site; larger polygons represent more variation within a site than smaller polygons. Sites (and points) closer together in multidimensional space are more similar than sites (or points) that are farther from each other. Overlaid vectors represent the environmental variables associated with each community or community type. Polygon colours correspond to sites in Figure 3.2.

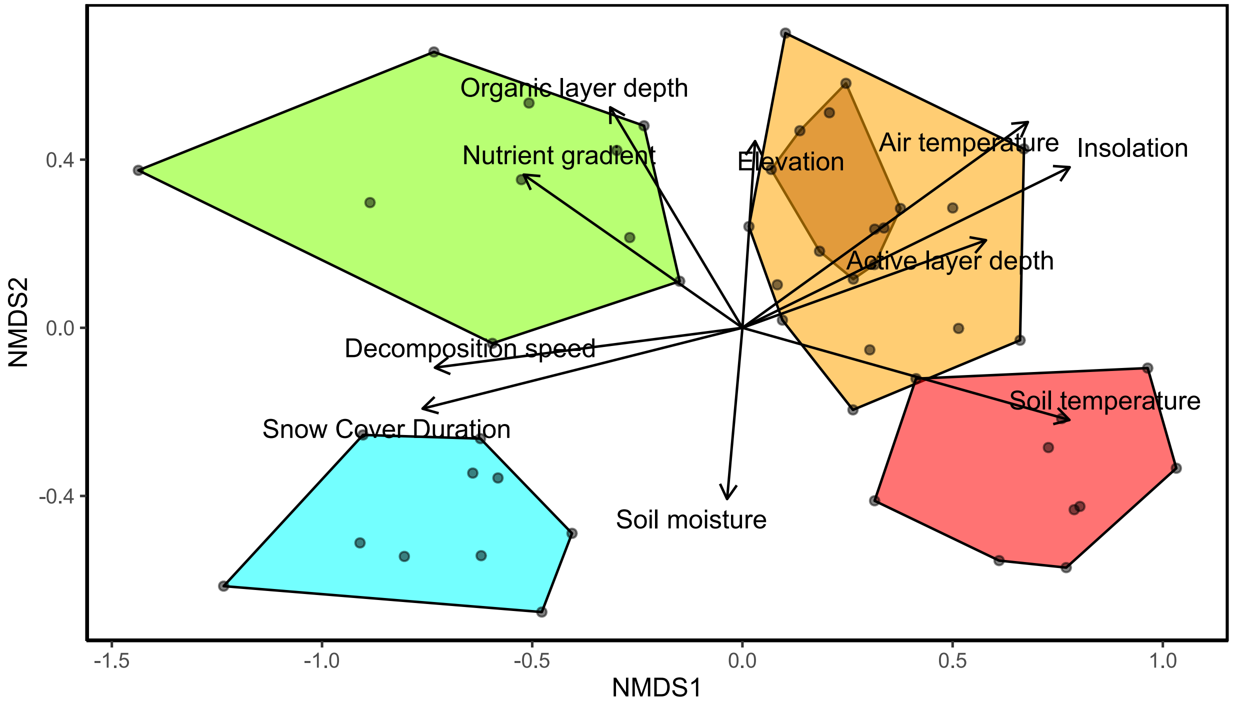


Figure 3. 6 Distribution of understory plant communities at forested sites in multivariate space (non-metric multidimensional scaling; NMDS). Each point represents a 1 m x 1 m quadrat within a site (10 sites) and the polygons around each set of points captures all the variation within a site; larger polygons represent more variation within a site than smaller polygons. Sites (and points) closer together in multidimensional space are more similar than sites (or points) that are farther from each other. Overlaid vectors represent the environmental variables associated with each community or community type. Polygon colours refer to sites in Figure 3.2.

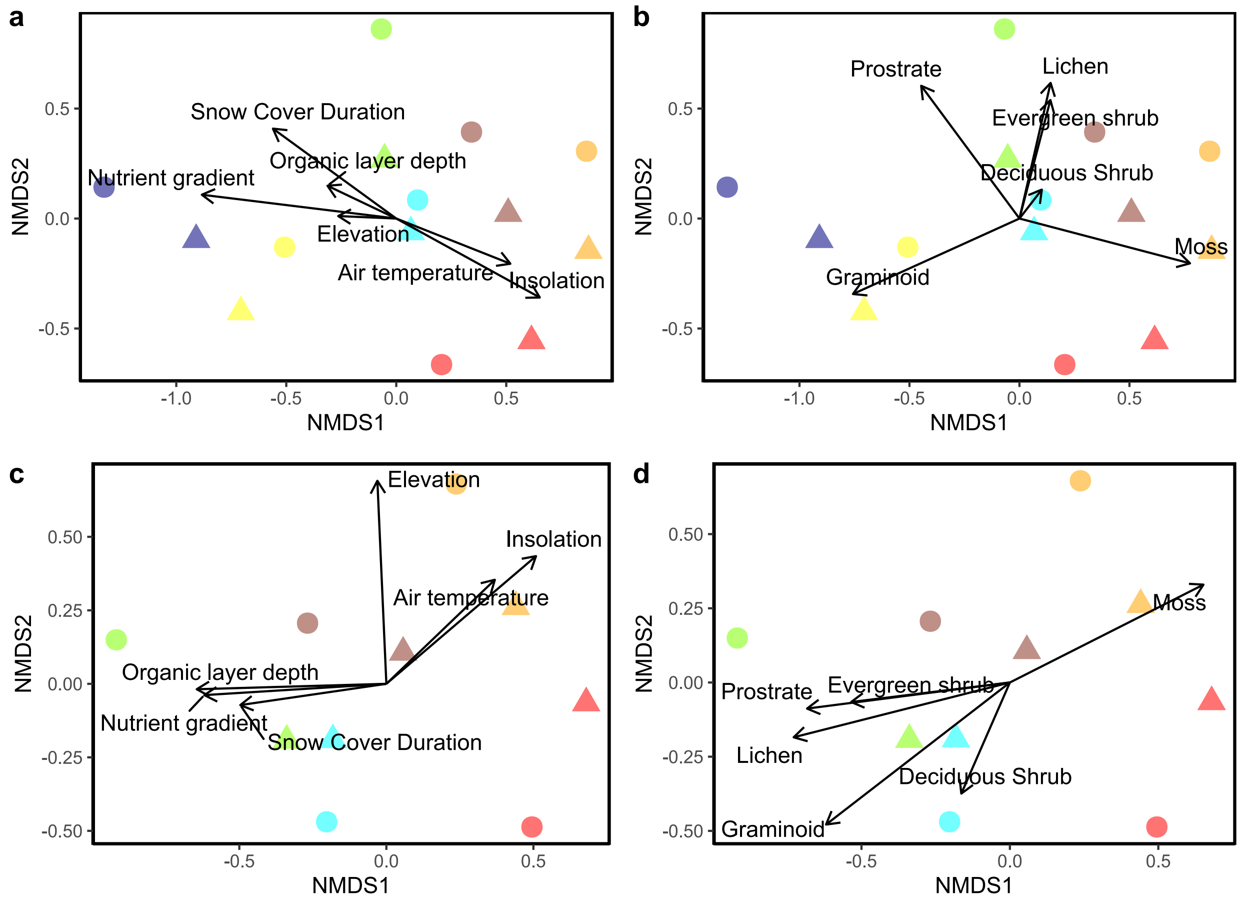


Figure 3. 7 Distribution of spider communities in multivariate space (non-metric multidimensional scaling; NMDS). a: spider communities at all sites, overlaid by environmental variables; b: spider communities at forested sites, overlaid by environmental variables; c: spider communities at all sites, overlaid by habitat variables; d: spider communities at forested sites, overlaid by habitat variables. Each point represents a site and colours correspond to sites in Figure 3.2. Species richness measurements were repeated for two years; circles represent 2018 and triangles represent 2019. Sites closer together in multidimensional space are more similar than sites that are farther from each other. Overlaid vectors represent the variables associated with each community or community type.

3.4 Discussion

Our results suggest that biotic communities in the western Canadian subarctic are responding differently than we would predict based on global patterns of biodiversity. Using a series of sites in northwestern Canada, we demonstrated that species richness increases with latitude for understory vegetation and spider communities. This pattern is contrary to global hypotheses of species richness (Willig et al. 2003; Hillebrand 2004) but expands on other findings in the region (Bowden and Buddle 2010a, 2010b; Marshall and Baltzer 2015). Our data indicate that the latitudinal gradient is representative of environmental gradients of air temperature, insolation, and snow cover. Predictions of species' future responses to ongoing climate warming must integrate these gradients into their predictive and theoretical frameworks.

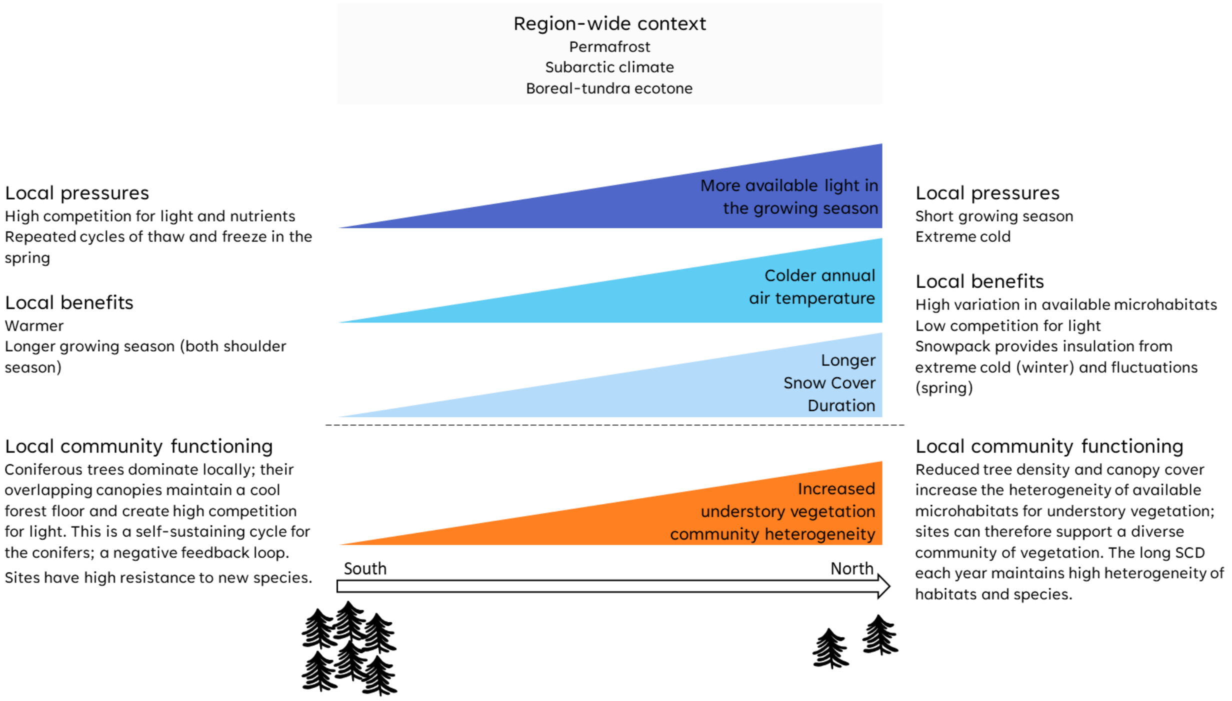
One of the goals at the outset of this study was to identify whether preliminary indications of species richness patterns from other regional studies were representative of a more widespread pattern, and to disentangle the underlying processes that shape these communities. Our results expand findings from Marshall and Baltzer (2015), with understory species richness increasing with latitude in both studies. Marshall and Baltzer (2015) attribute this pattern to lower air temperatures in northern locations. Low temperatures reduce tree growth and survival and thus reduce tree biomass, which in turn lowers competition for light and other limiting resources. We also found a negative relationship between understory vegetation species richness and basal area (Figure A3.4), which corresponded negatively with latitude (i.e., higher latitude sites had higher understory vegetation species richness and lower basal area).

Our findings also add to evidence presented by Bowden and Buddle (2010a, 2010b) that regional spider communities are more strongly associated with habitat type than any climate variables. This pattern suggests that habitat differences are important at different scales: local, within-mountain range (Bowden and Buddle 2010a, 2010b) and regional, cross-latitude and cross-elevation (present study). Bowden and Buddle (2010b) found that community differences between mountain ranges were larger than within mountain ranges. We did not study community differences within latitudinal regions (or mountain ranges) but, based on Bowden and Buddle (2010b) we assume that we did not miss a significant portion of the community. Bowden and Buddle (2010a) found that large-scale climate variables explain limited variation within spider communities and suggested that microclimate variables would be more influential. We measured microclimate variables and still found that, apart from air temperature, spider diversity and distribution was more clearly associated with gradients in habitat variables in our NMDS analyses. As vegetation communities change with climate, spider species occurrence and community composition throughout this region could therefore be affected.

3.4.1 What does latitude mean?

In ordination space, we found that vegetation communities separated strongly by latitude. The short growing season in northern sites places a strong selective pressure on the vegetation that can establish and survive there. Our greatest difference in snow cover duration from south to north was 39 days between forested sites (sites KK vs. CC) and 47 days when including the most northern tundra site (sites KK vs. WW). Species that do not have a short life history and cannot tolerate the truncated growing season may be able to survive in southern sites where those pressures are relaxed. However, competition for light and nutrients will be higher there (Figure 3.8).

Results from the ordinations highlight that the latitudinal gradient represents measurable gradients of high air temperature and insolation in the south and high snow cover duration in the north. Combined with the understory vegetation-species richness-basal area-latitude relationship described above, we interpret the importance of snow cover duration to be as follows (Figure 3.9). From south to north, we observed a gradient of decreasing stand basal area (Figure A3.5). Thinner and sparser canopies in northern forested sites promote greater variation in the characteristics of microsites; some microhabitats are shaded and cold (and have higher soil moisture) whereas others receive constant sunlight during the growing season. Combined, those provide more heterogenous microsites for species with a broader range of niche requirements to occupy. Canopy shade has a strong influence on the composition of the understory vegetation community (Strong 2011b). The constant light in the summer coupled with fewer tall trees or shrubs means that competition for light in northern sites is lower than in the south. In forested stands, trees can also influence spatial distribution of snow (Rasmus et al. 2011). Thus, the presence and density of trees likely influences the vegetation community in both the summer and winter. Canopy openness may also account for the change in spider community across latitude as different species specialize in open versus closed habitats and communities have been demonstrated to change with forest succession (Buddle et al. 2000).



Region-wide context
Permafrost
Subarctic climate
Boreal-tundra ecotone

Local pressures
High competition for light and nutrients
Repeated cycles of thaw and freeze in the spring

Local benefits
Warmer
Longer growing season (both shoulder season)

Local community functioning
Coniferous trees dominate locally; their overlapping canopies maintain a cool forest floor and create high competition for light. This is a self-sustaining cycle for the conifers; a negative feedback loop.
Sites have high resistance to new species.

Local pressures
Short growing season
Extreme cold

Local benefits
High variation in available microhabitats
Low competition for light
Snowpack provides insulation from extreme cold (winter) and fluctuations (spring)

Local community functioning
Reduced tree density and canopy cover increase the heterogeneity of available microhabitats for understory vegetation; sites can therefore support a diverse community of vegetation. The long SCD each year maintains high heterogeneity of habitats and species.

Figure 3. 8 Conceptual diagram detailing the hypothesized selective pressures at northern and southern sites.

The high diversity of understory communities at northern sites occurs because the longer snow cover duration protects the heterogeneity of microhabitats. If microhabitat heterogeneity were high but snow cover duration was low, we would predict short bursts of vegetation productivity in the summer that would not necessarily recover in following years. We hypothesize that longer snow cover duration provides an insulating effect for all vegetation in the northern sites, protecting them from spring freeze (Pomeroy and Brun 2001; Walker et al. 2001; Wheeler et al. 2014). The extra ~6 weeks of insulation under snow at northern sites means that when those vegetation communities emerge from the snowpack, it is usually during a warmer period (Wahren et al. 2005). In contrast, earlier snowmelt at more southerly sites could mean a greater risk of exposure to spring freeze-thaw cycles (Brehaut and Brown 2022). In the coastal arctic tundra, vegetation productivity was more strongly influenced by the environmental conditions after snowmelt rather than the timing of the snowmelt event (Humphreys and Lafleur

2011; Gamon et al. 2013). Further investigation into the growing conditions in the days or weeks immediately after snowmelt throughout this region may help to tease apart other factors controlling understory community diversity that are facilitated by longer snow cover duration.

Winter conditions play an important role in tree seedling emergence and establishment at the treeline in the boreal-tundra ecotone (Renard et al. 2016; Maher et al. 2020; Brehaut and Brown 2022) and the influence of snow cover on vegetation has been well studied in the tundra (e.g., Sturm et al. 2001; Myers-Smith and Hik 2013b). However, the role of snow depth and snow cover duration in shaping understory communities in the boreal forest have not been well studied, presenting a major gap in our understanding of the largest forested biome in the world and one where winter conditions prevail for at least half the year. As ongoing climate change continues to present new challenges throughout the boreal forest and other high latitude ecosystems, a detailed understanding of the role of snow in shaping and maintaining vegetation communities is required.

Selective pressures at these study sites may be further amplified by their relative location within the boreal-tundra ecotone. Our entire study region could be considered part of the larger boreal-tundra ecotone, with sites from GG northward irrefutably being within this ecotone. This ecotone is a relatively indistinct boundary that covers over 1.6 million km^2 of land throughout North America and Greenland and is highly variable in its forest structure (Hofgaard et al. 2012; Montesano et al. 2020). Species richness in ecotones is generally higher than that of the adjacent biomes or environments although these patterns are variable (as reviewed by Kark and van Rensburg 2006). However, whether unique ecotonal species exist (Odum 1953) or whether species within ecotones benefit from increased heterogeneity of discrete habitats (Nekola and White 1999) remains unclear (Kark and van Rensburg 2006). Here, we suggest that at the northern extent of our study region, within the true boreal-tundra ecotone, the shift between biomes overrides any constraints that are usually dictated by latitude. Indeed, the large variety of microsites afforded by the ecotone at large invites the possibility of high biodiversity at a landscape scale (Hofgaard et al. 2012; Goodwin and Brown 2022). While we are limited in extrapolation power from our small number of study sites, we note that our northernmost and tundra sites each have one or more unique species (species which are not found other places in the study gradient).

3.4.2 The role of global change

Air temperature and snow cover duration, two of the main drivers of community composition highlighted here, are both likely to experience significant changes with current and future global change. Air temperatures throughout western North America are rising at 2.4 times the global average (Box et al. 2019) and regional precipitation patterns are predicted to trend towards being dominated by rain (Vincent et al. 2015). Over the next few decades, snow cover duration is predicted to decrease, especially in the shoulder seasons (Thackeray et al. 2016). Together, these trends could have wide-ranging implications for the vegetation communities throughout this study region. While the exact impacts on the vegetation communities are too many to list, a change in the snowpack in northern sites may reduce the heterogeneity of vegetation across microsites at these sites. In the tundra, snowpack has been proposed to mediate the effects of other a/biotic factors on plant functional traits (Niittynen et al. 2020). A change in tundra snowpack may drive a change in tundra plant functional traits, changing the functionality of the whole ecosystem (Niittynen et al. 2020). A change in growing conditions at the northern sites may also lead to local extirpation of some species, when no additional habitat occurs beyond their current latitudinal or altitudinal limit (e.g., Kruse and Herzschuh 2022; Lyu and Alexander 2022).

3.4.3 Future directions

In addition to the variables that dominate the gradients discussed above, other variables emerged as important in the ordinations. For example, we found a gradient from deep organic layers with dry below-surface soil moisture to thinner soil organic layers with high below-surface soil moisture in forest plant communities (Figure 3.6). We predict that some of these variables are likely associated with more biologically relevant variables to plant diversity and distribution, for example soil microbial community which varies significantly with soil moisture (Ma et al. 2015; Li et al. 2017). Although we did not assess them here, soil microbial communities throughout the region warrant investigation; arctic microbial communities are not markedly different from those in other biomes (Tedersoo et al. 2014) but they are strongly driven by environmental factors (e.g., Chu et al. 2010; Siles and Margesin 2016; Kotas et al. 2018) and community composition is not predicted to shift in response to rapidly warming climate (Ballhausen et al. 2020).

Biotic interactions beyond our measured habitat variables likely have a significant controlling effect on communities. Similarly, deeper, but not necessarily longer, tundra snowpacks increase nitrogen mineralization in the soil, influencing the amount and timing of plant available nitrogen (Schimel et al. 2004). Our evaluation of plant-available nutrients demonstrated higher plant available nutrients in northern sites (Figures 3.5 and 3.6) and higher levels of NO_3^- in northern sites; levels of NH_4 were variable throughout sites (data not shown). As above, this pattern likely indicates an underlying and unexplored biotic interaction that would benefit from further study. In the subarctic, complex multitrophic interactions such as those between nutrients-microbes-vegetation-animals are often poorly understood. Our study sheds light on the need for deeper understanding of ecosystem processes and interactions that shape patterns of multitrophic interactions. Baseline studies that monitor environmental conditions and species distribution in subarctic regions are integral for assessing future consequences of local and regional climate warming (Post et al. 2009). The permanent sites initiated here will contribute to these ongoing efforts.

3.5 Conclusion

In combination with other studies, our results indicate that species richness increases with latitude throughout northwestern Canada. Here, latitude is representative of gradients of air temperature, insolation, and snow cover duration. In northern forested sites, sparser canopies increase the heterogeneity of available microsites for understory vegetation; diversity of understory species is maintained by a long-lasting snowpack, allowing vegetation to germinate when daily air temperatures are higher. As climate change dramatically alters the air temperature and precipitation patterns throughout the north, this regional pattern stands to be strongly impacted. Specific changes to the regional species pool remain unseen but potentially could be significant enough to alter the functioning of the region.

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Appendix

Table A3. 1 Details of the seven (7) study sites. All sites were located <500 m from the Klondike or Dempster Highways.

Site	Latitude	Longitude	Elevation (m a.s.l.)	Dominant vegetation structure	Yukon Ecoregion	Ecozone
WW	66.60	-136.29	695	Tundra	British Richardson Mountains	Tundra Cordillera
CC	66.12	-137.24	604	Forest	Eagle Plains	Taiga Cordillera
EE	65.51	-138.24	546	Forest	North Ogilvie Mountains	Taiga Cordillera
TT	64.93	-138.27	936	Tundra	North Ogilvie Mountains	Taiga Cordillera
GG	64.14	-138.56	749	Forest	McQuesten Highlands	Boreal Cordillera
KK	63.62	-137.59	467	Forest	McQuesten Highlands	Boreal Cordillera
FF	63.17	-136.50	748	Forest	Yukon Plateau-North	Boreal Cordillera

Table A3. 2 Measured drivers of species diversity and distribution.

Driver	Field measurement	Data manipulation
Elevation (m a.s.l)	Recorded in June 2018 once at the centre of each site Garmin GPSMAP 64 (Garmin, USA)	
Air temperature (°C)	Recorded every 4 hours between July 2018 – August 2021 at the centre of the site Onset Computer Corporation, Cape Cod, MA, USA; HOBO Pendant® UA-002-64)	Data averaged to annual average air temperature
Soil temperature (°C)	Recorded every 4 hours between July 2018 – August 2021 at the centre of the site Maxim Integrated; iButton Thermochron, DS1921G	Data averaged to annual average soil temperature
Soil moisture (m^3 H_2O/m^3 soil)	Recorded every hour between July 2018 – August 2021 at the centre of the site Onset Computer Corporation, Cape Cod, MA, USA; 10HS Soil Moisture Smart Sensor, S-SMD-M005	Data averaged to annual average volumetric soil moisture
Snow cover duration (days)	One camera (Bushnell Trophy Cam HD and Reconyx Hyperfire 2) recorded an image twice daily (11 a.m. and 3 p.m. PDT) of a plastic stake with delineations at 10 cm increments at the centre of the site.	Images were processed manually, and the depth of the daily snowpack was recorded. The length of the continuous snow period each winter was calculated and averaged across years with full data.
Organic layer depth (cm)	At the centre of the site and four additional vegetation quadrats, a soil knife and tape measure were used to measure the depth from the top of the organic soil layer to the underlying layer (mineral soil, ice, or rock; cm).	Data averaged to average site organic layer depth
Active layer depth (cm)	a metal rod with increment markings was used to measure the depth from the ground surface to resistance (ice or rock) at each vegetation quadrat (n = 10) in August 2021	Data were averaged across the ten measurements
Plant available nutrients (µmol/10 cm^2/length of burial)	At the centre of the site and at two vegetation quadrats, we buried Plant Root Simulator™ ion exchange probes (Western Ag Innovation Inc., Saskatoon, Saskatchewan, Canada). The anion and cation exchange resin probes were buried vertically at 10 cm depths for the 2018 and 2019 growing seasons (June – August). When probes were removed, they were cleaned with deionized water and sent to Western Ag for nutrient analysis.	Using Principal Coordinates Analysis, we reduced the resulting data to a single axis that represents a gradient of high to low nutrient availability.
Insolation (W/m^2)		Using the daily average sunlight in 2021, the annual average insolation (sunlight received at the top of the atmosphere) was calculated

		(Goddard Institute for Space Studies 2021)
Decomposition rate	Following methods from Keuskamp et al. (2013), we buried pairs of Lipton Rooibos and green tea bags at approximately 8 cm deep (Lipton, Unilever, Dublin, Ireland). Each pair was buried for one of three periods: - Growing season (June - August 2018) - Full year *minus* growing season (August 2018 - May 2019) Full year (June 2018 - May 2019)	The per cent mass loss was calculated which was then used to calculate a decomposition rate (k) and stabilization value (S). We used the decomposition rate (k) averaged across the three burial periods.
Basal Area (BA/m^2)	Diameter of each tree was measured at 1.37 m where possible.	Basal area of each tree per site was calculated (BA= π (DBH/2)^2) and then values were converted to units of BA/m^2.

Table A3. 3 Summary percent cover of vegetation communities used as the 'habitat' variables for spider analyses. Each vegetation species was assigned to one of the six functional categories and the percent area covered by 10 quadrats at each site was summed.

Site	Moss	Lichen	Graminoid/ herb	Deciduous shrubs	Evergreen shrubs	Prostrate shrubs
WW	0.26	0.07	0.51	0.06	0.03	0.07
CC	0.31	0.20	0.11	0.23	0.15	0.00
EE	0.52	0.15	0.11	0.05	0.10	0.07
TT	0.18	0.02	0.75	0.04	0.01	0.00
GG	0.71	0.07	0.06	0.07	0.09	0.00
KK	0.87	0.03	0.05	0.04	0.00	0.01
FF	0.66	0.18	0.05	0.07	0.03	0.01

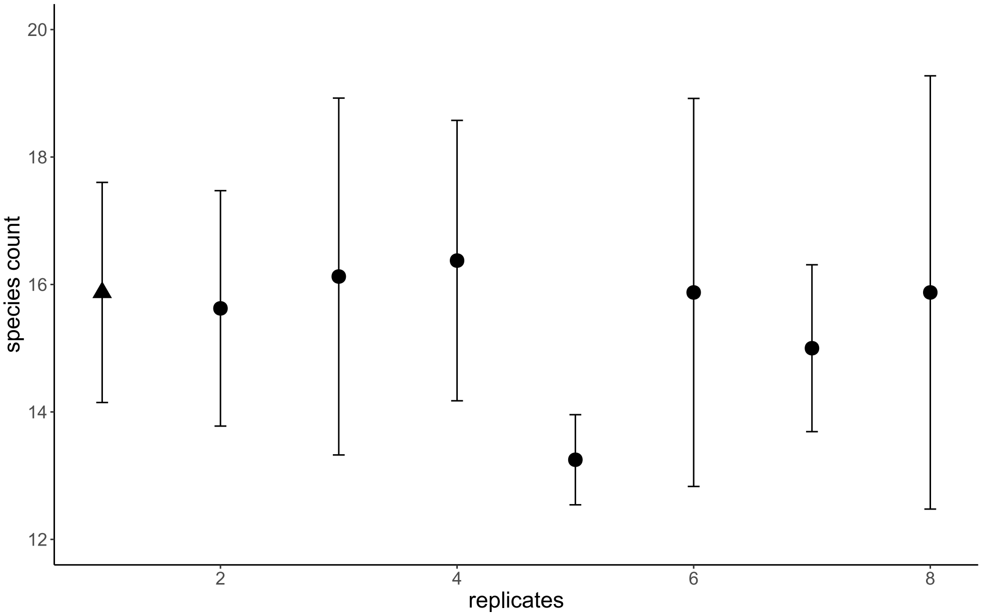

Figure A3. 1 Data from Wasyliw (*in prep*) who measured understory species richness throughout the Eagle Plains Ecoregion, including at our study site, CC. Wasyliw et al. measured understory species richness at 8 quadrats per site at 8 sites (x-axis) including at CC (replicate 1; represented by a triangle). Error bars represent the standard error between quadrats at each site (replicate). Understory species richness at CC represented 28 out of the 35 species (80%) found in all sites; we assume that we had the same sampling bias at all sites.

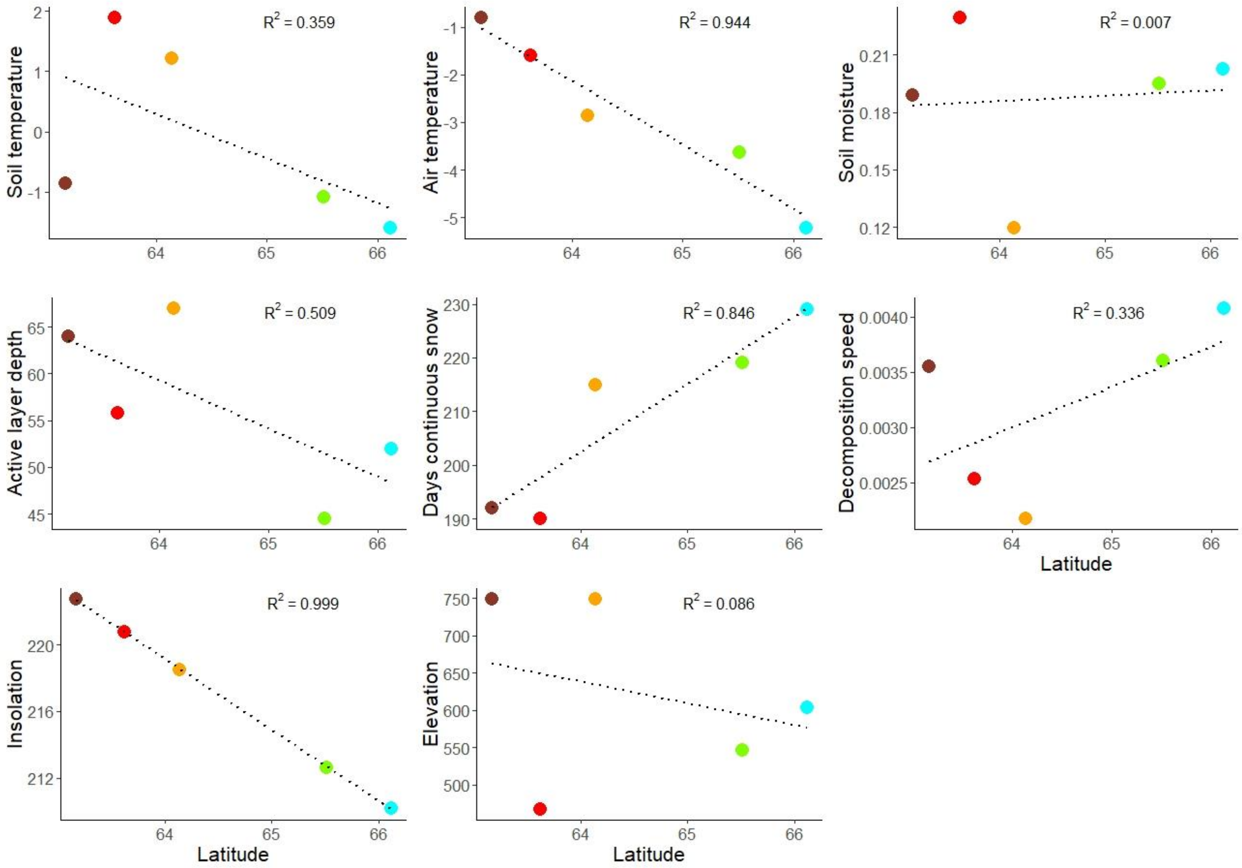

Figure A3. 2 Relationships between latitude (x-axis) and measured drivers of species richness (y-axis) for forest sites only. Colours correspond to sites in Figure 2. R^2 value represents the multiple R^2 of the linear model.

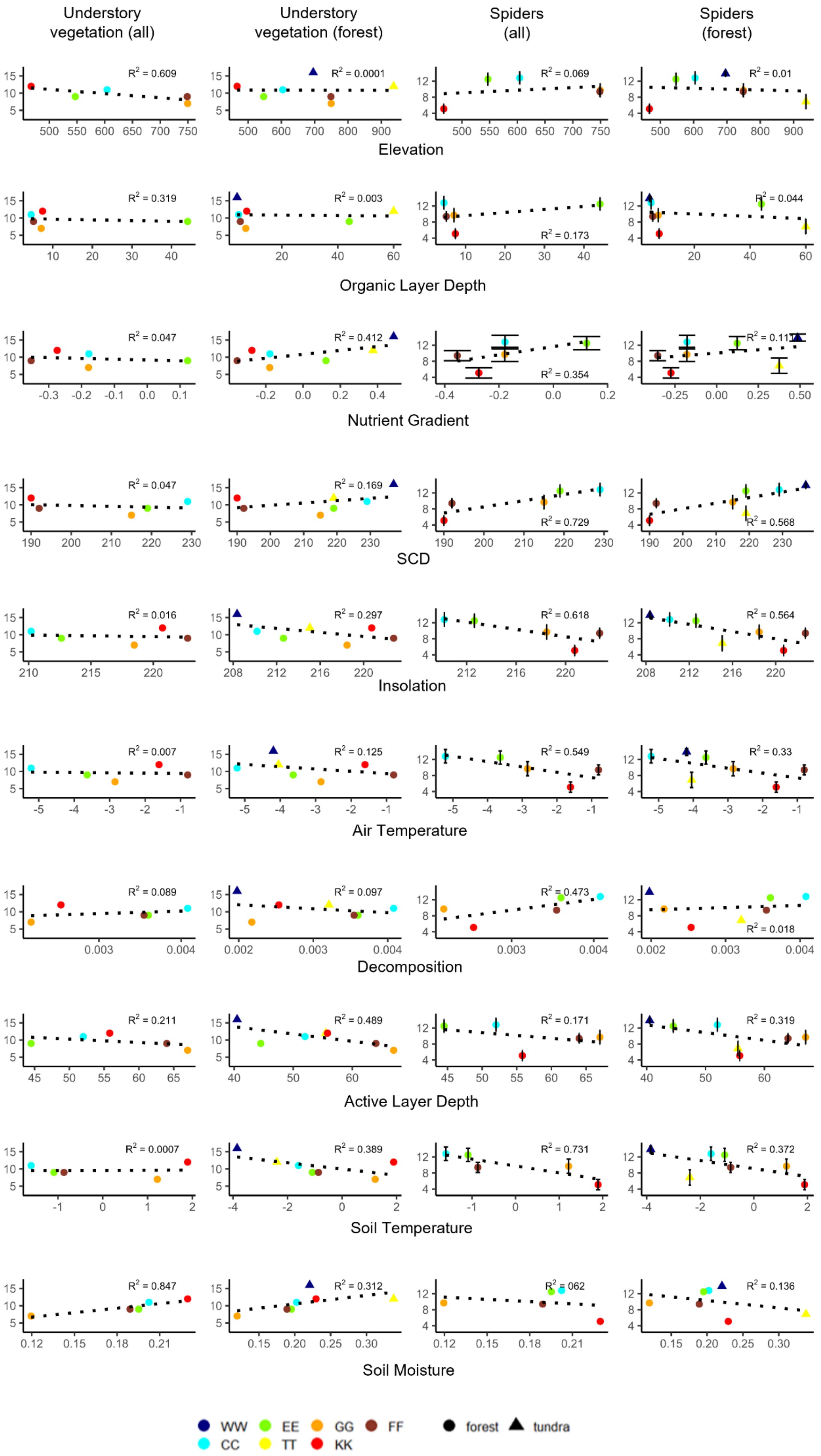
Understory vegetation (all)
Understory vegetation (forest)
Spiders (all)
Spiders (forest)
R² = 0.609
R² = 0.0001
R² = 0.069
R² = 0.01
Elevation
R² = 0.319
R² = 0.003
R² = 0.173
R² = 0.044
Organic Layer Depth
R² = 0.047
R² = 0.412
R² = 0.354
R² = 0.111
Nutrient Gradient
R² = 0.047
R² = 0.169
R² = 0.729
R² = 0.568
SCD
R² = 0.016
R² = 0.297
R² = 0.618
R² = 0.564
Insolation
R² = 0.007
R² = 0.125
R² = 0.549
R² = 0.33
Air Temperature
R² = 0.089
R² = 0.097
R² = 0.473
R² = 0.018
Decomposition
R² = 0.211
R² = 0.489
R² = 0.171
R² = 0.319
Active Layer Depth
R² = 0.0007
R² = 0.389
R² = 0.731
R² = 0.372
Soil Temperature
R² = 0.847
R² = 0.312
R² = 062
R² = 0.136
Soil Moisture
WW
EE
GG
FF
CC
TT
KK
forest
tundra

Figure A3. 3 Relationships between species richness (y) and environmental variables (x). Different representations of species richness are shown in each of the four columns. 1 Understory plant species richness at all sites; 2 Understory plant species richness at forested sites; 3 Spider species richness at all sites; 4 Spider species richness at forested sites. Understory plant species richness (columns 1 and 2) display the mean species richness from 10 replicates; error bars show the standard deviation. Two plots do not have error bars (decomposition rate and soil moisture) because the variation was so high that the error bars obscured the plot. See Figure A2 for plots that include the error bars. Colours correspond to sites in Figure 2.

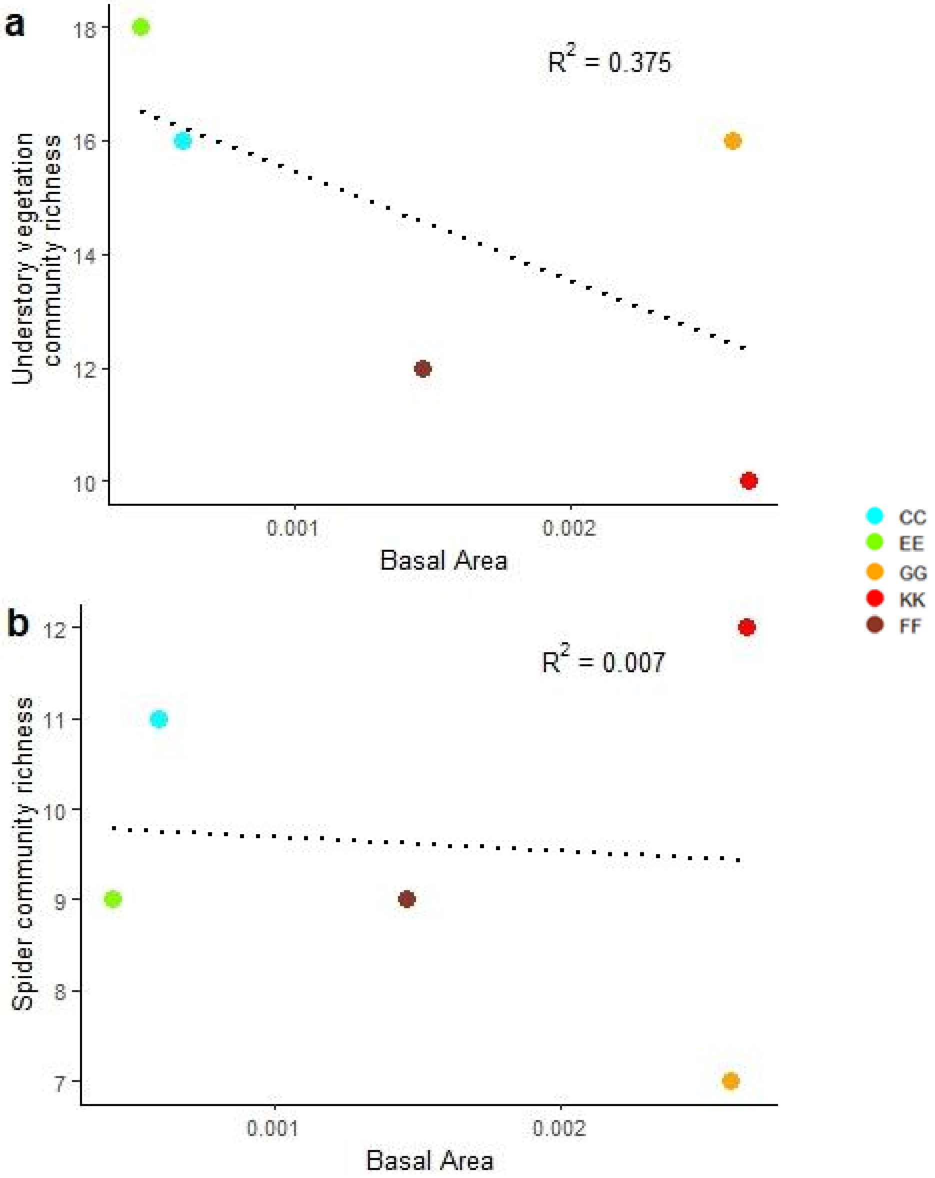

Figure A3. 4 Modelled relationships between site level basal area (x-axis) and understory vegetation community richness (a) and spider community richness (b). Data is shown for forested sites only; basal area could not be measured at tundra sites. R^2 value on each plot is the multiple R^2. Colours correspond to sites in Figure 2.

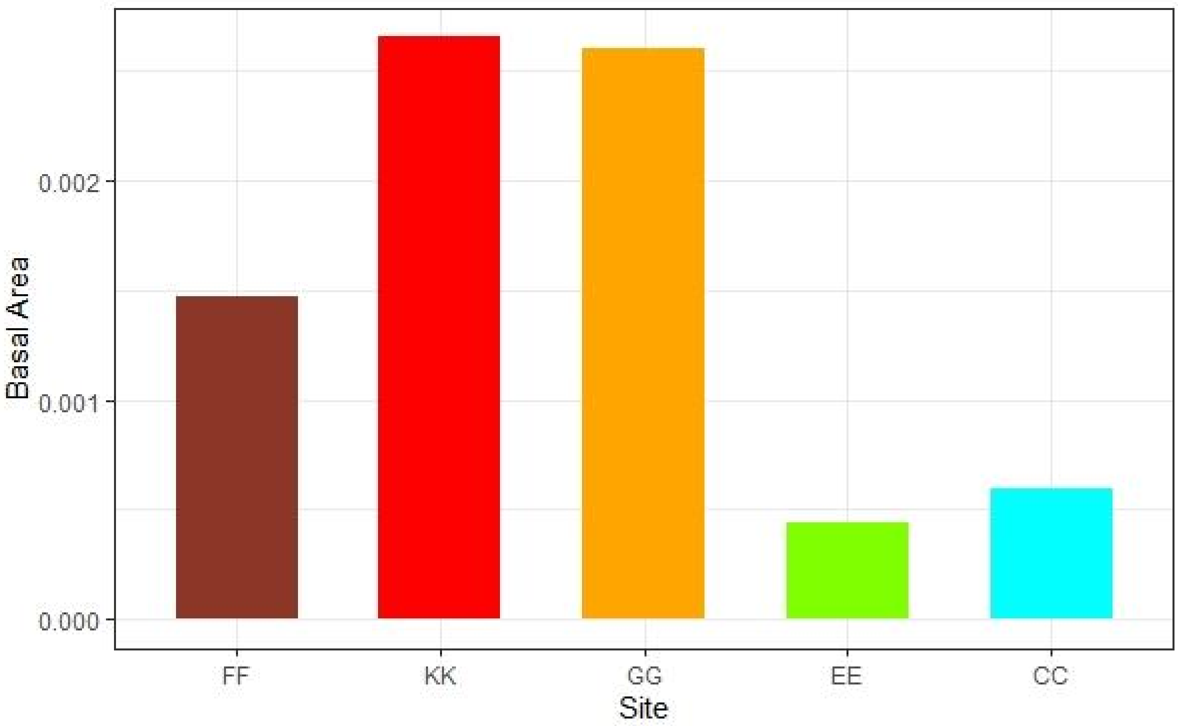

Figure A3. 5 Basal area ($\pi r^2/m^2$) of each site from south (left, FF) to north (right, CC). Colours correspond with sites in Figure 2.

Chapter 4: Responses of subarctic boreal ecosystems to climate change and cumulative disturbances: Applications to Eagle Plains, Yukon, Canada

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Abstract

The response of ecosystems to the combined pressures of climate change and human land use and development is complex, and impacted by a variety of factors, including land use intensity, dominant vegetation species, and the type and severity of natural disturbance regimes. Under scenarios of ongoing climate change and increased industrial development, boreal and subarctic ecosystems are increasingly vulnerable to changes that can reduce their ecological integrity, altering future trajectories of the ecosystem state. Here, we investigate five testable predictions that represent our best estimate of the future pressures and states of subarctic boreal forests in northwest North America. Specifically, we focus on Eagle Plains in northern Yukon, an ecoregion with significant cultural, ecological, and industrial value. Over the next several decades, landscape-scale changes will become increasingly prevalent throughout subarctic boreal forests. The effects of disturbances (wildfire and industrial development) will likely overshadow the effects of direct climate change and will have a greater influence on the future trajectories of the ecosystem. Integrated approaches, such as the one presented here, allow researchers, land managers, and land users to incorporate the effects of cumulative stressors, directing future land management and conservation.

Introduction

Ecosystem-disrupting natural disturbances are not generally considered catastrophic due to the innate resilience of ecosystems (Holling 1973); yet, the interaction between natural disturbances and human development and land use may produce catastrophic results, particularly under the press of ongoing climate change (Turner 2010b). Projecting the future dynamics and states of ecosystems requires consideration of land-use legacies, which are the abiotic or biotic site conditions that have resulted from past and present land use (Foster et al. 2003; Perring et al. 2016). Land-use legacies affect the state of the current ecosystem and the influence of cumulative environmental changes on the future trajectory of the ecosystem (Perring et al. 2016). When multiple disturbances (natural or human-caused) occur sequentially, the cumulative, synergistic or attenuated effects of the disturbances are varied and complex to predict (Darling and Côté 2008; Turner 2010b).

The interactions between ecosystems and climate change are also complex. While they are vulnerable to climate change, ecosystems can also support climate change adaptation and mitigation (Malhi et al. 2020). Adaptive ecosystem research identifies species-specific, ecosystem-specific, and interspecific interactions that may occur with ongoing and future environmental change. Adaptive ecosystem management requires new modelling and monitoring frameworks to prepare for and adjust to future environmental changes (Malhi et al. 2020). In the past, the boreal forest has demonstrated significant resilience to anthropogenic climate change (Chapin et al. 2010). However, under scenarios of future change, the historical resilience of this system is likely to be challenged as the scale of future ecological change will dwarf past changes (Walther et al. 2002). As cold regions such as the boreal forest warm, the potential for greater species richness exists either from increased regional carrying capacity or because more species can tolerate those conditions (Harrison 2020).

In the Taiga Cordillera ecozone in the western Canadian subarctic annual mean minimum and maximum temperatures are projected to rise by 5.5°C and 4.5°C, respectively (Price et al. 2013). These changes will be particularly apparent in the winter when minimum temperatures are predicted to rise by up to 8°C versus 4°C in the summer (Price et al. 2013). Also in the Taiga Cordillera, annual precipitation is predicted to increase by 11% by the 2050s and 25% by 2100 (Price et al. 2013); across the wider boreal forest, interannual variation in precipitation is predicted to increase, especially in the shoulder seasons (Price et al. 2011). Differential responses by biotic communities to new temperature and precipitation regimes will have cascading effects across trophic levels (Ernakovich et al. 2014), demonstrated by changes such as altered life and reproductive cycles for mammals (Bronson 2009), no-analogue communities (Urban et al. 2012b), and a new hierarchy of processes which control vegetation growth (Sturm et al. 2005).

Approach & Goals

In the following sections, we present five testable predictions that represent our best estimate of future trajectories of change to ecosystem states and services within the subarctic boreal forest of northwest North America. These predictions were formed following two lines of inquiry: i) broader literature of global change impacts in subarctic boreal forests, and ii) regionally specific considerations of drivers of ecosystem change in subarctic Yukon. Towards ii), we specifically searched for peer-reviewed studies, government reports, and First Nations-produced publications, as well as local knowledge of the region via one author's role with the Vuntut Gwitchin Government. This was not a systematic literature review, but rather a diverse means of bringing together all sources of information we could access on this region. These predictions can be applied regionally, and here we illustrate them using Eagle Plains, an ecoregion in northern Yukon. We use a combination of local and regional knowledge to summarize and synthesize our understanding of ecosystem changes, responses, and potential consequences. We also highlight gaps in our understanding of the future trajectories of subarctic boreal forests in northwestern North America and Eagle Plains specifically.

Eagle Plains

Eagle Plains is a boreal forest-dominated ecoregion (20,400 km^2) in northern Yukon, in the Traditional Territory of the Vuntut Gwitchin First Nation (Figure 4.1). Located in the Taiga Cordillera ecozone, between the Richardson and Northern Ogilvie Mountains, Eagle Plains is underlain by continuous permafrost (Oswald and Senyk 1977; Smith et al. 2004b) and is mainly low-relief terrain (~300-600 m asl). Mean annual air temperature is -7.5°C, with average January temperature varying from -31°C at low elevations to -25°C at higher elevations; mean July temperature is 13°C. Annual precipitation averages 400 mm (Smith et al. 2004b); average snow depth in March (1984-2016) is 74.5 cm (Environment Yukon 2022). Black spruce (*Picea mariana*) woodlands dominate the ecoregion, with shrub tundra (*Betula* and *Salix* spp.) and white spruce (*P. glauca)* present in upper elevations and well-drained areas, respectively (Smith et al. 2004b).

The uniform habitat contributes to Eagle Plains having one of the lowest counts of mammal diversity within the broader Taiga Cordillera Ecozone (Smith et al. 2004b). Throughout the winter, much of Eagle Plains is part of winter range for the Porcupine Caribou Herd, one of the largest migratory ungulate herds in the world (Sherry and Vuntut Gwitchin First Nation 1999; Burch 2012). Migrating annually from their summer calving grounds along the Arctic coast to their wintering grounds distributed between the Dalton Highway and Eagle Plains, Porcupine Caribou have inhabited this region for ~27,000 years and have been an integral part of Van Tat Gwich'in culture for generations (see cultural description below; Russell et al. 1993; Burch 2012).While their use of the Coastal Plain has remained relatively consistent since at least the 1960s (Miller et al. 2021), climate change could be leading to more unpredictable migration patterns (Vuntut Gwitchin Government and Smith 2017) and a shift to a more westward calving location (Severson et al. 2021). Like other herds throughout North America, industrial development threatens the quality of the Porcupine Caribou winter habitat (Francis and Hamm 2011).

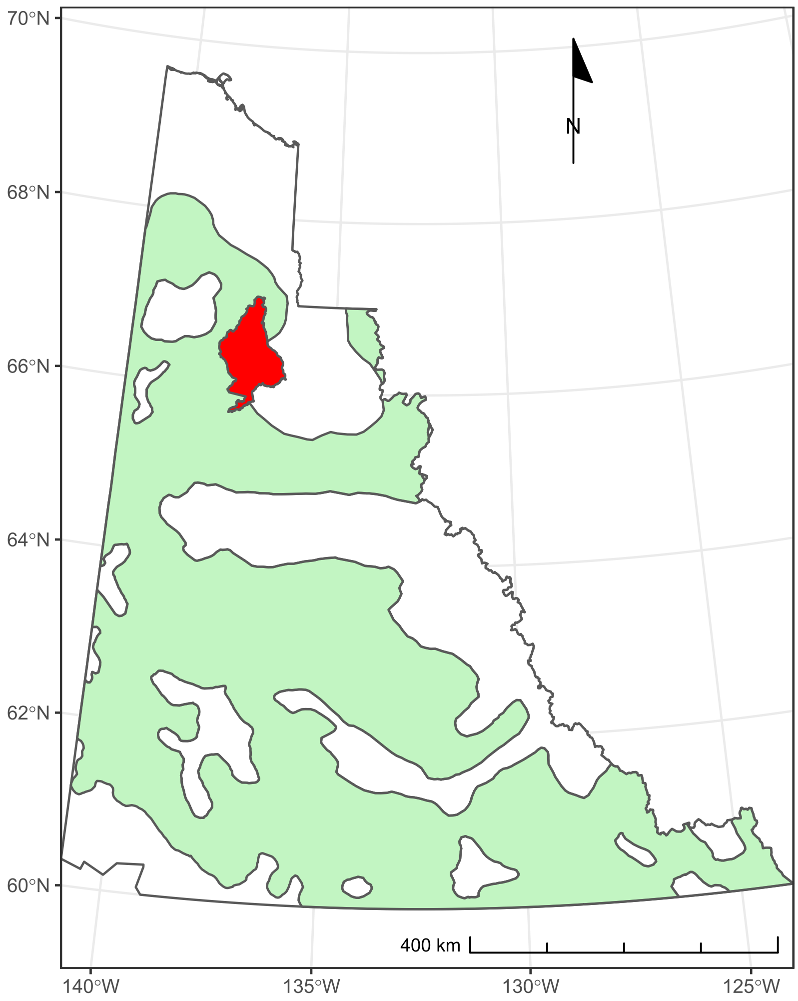


Figure 4. 1 Eagle Plains (highlighted in red) is a 20,400 km^2 ecoregion and land management unit in northern Yukon. Eagle Plains is within the Van Tat Gwich'in, the Tr'ondëk Hwëch'in, and the Ehdiitat and Teetl'it Gwich'in traditional territories. The distribution of black spruce throughout Yukon is outlined in green.

Eagle Plains has some of the largest untouched oil and gas reserves in Yukon; between 1957 and 2004, 35 exploration wells were drilled within or adjacent to the basin, with an accompanying ~10,000 km of seismic lines. Within Eagle Plains, there is an estimated 96.7 x 10^9 m^3 of in-place gas and 52.2 x 10^6 m^3 of in-place oil which could generate up to $1.2 billion/year and $30 million/year for natural gas and oil revenues, respectively (Francis and Hamm 2009; Hannigan 2014). Although large by Yukon standards, these reserves are small compared to deposits in the Alaskan North Slope or the Mackenzie Delta. Extraction from Eagle Plains alone is therefore unlikely; regional extraction would be contingent on the completion of the Alaska Highway Pipeline or the Mackenzie Valley Pipeline, as well as the creation of a lateral pipeline(s) from Eagle Plains to one of these pipelines (Fekete Associates and Vector Research 2005).

As part of the Umbrella Final Agreement (UFA 1993), Eagle Plains is managed by the North Yukon Land Use Plan. The plan focuses on the intensity of use that an area can handle rather than the specific type of disturbance (North Yukon Planning Commission 2009). All land uses (e.g., oil and gas exploration, human and wildlife travel, conservation areas) are permissible, provided they do not surpass specified disturbance intensity criteria. Eagle Plains (Land Management Unit 9) has a listed management intent of 'high development', the highest level within the plan (North Yukon Planning Commission 2009). This designation results from its 'low ecological and cultural value…within a moderately sensitive biophysical setting'. The degree of land use and acceptable level of change (to the landscape) are both described as high, with the risk of significant impact being low (North Yukon Planning Commission 2009).

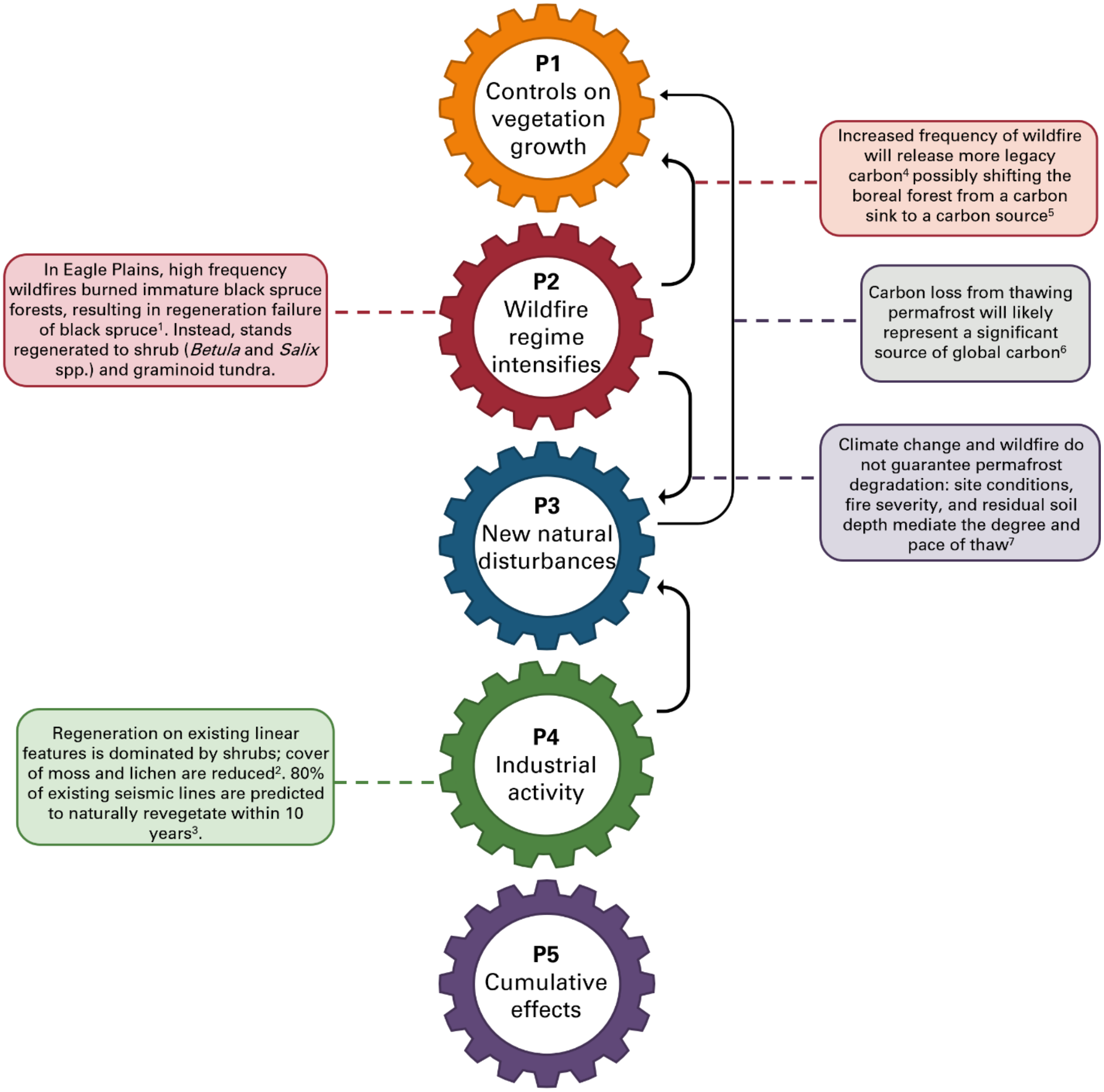
The Eagle Plains region is at the intersection of several traditional territories, including the Van Tat Gwich'in, the Tr'ondëk Hwëch'in, and the Ehdiitat and Teetl'it Gwich'in. Historically the headwaters of the Porcupine watershed, which include Eagle Plains, were the homelands of the Dagoo Gwich'in. The Dagoo, alongside their Gwich'in neighbours, were all part of a larger Gwich'in Nation that was very flexible in its definition of groups and boundaries, and its approach to mixing and sharing. The Dagoo specifically occupied the headwaters that include the Richardson and Ogilvie Mountains, and so were known at the "Over the Mountain People", in contrast to the Van Tat Gwich'in who were known as the "People of the Lakes".

While the headwaters were the homelands of the Dagoo, Teetl'it, Ehdiitat, and Van Tat Gwich'in would not have been uncommon in the region as well. The Dagoo lived off of caribou (*Rangifer tarandus*), moose (*Alces americanus*), various species of fish, beaver (*Castor canadensis*), waterfowl, and species of smaller game like ptarmigan (*Lagopus spp.*), snowshoe hares (*Lepus americanus*), and Arctic ground squirrels (*Urocitellus parryii*). As time passed, the Dagoo settled in various communities including Old Crow and Dawson, YT, and Fort McPherson, NT. As such, Dagoo families are members of various land claims, including the Vuntut Gwitchin First Nation Final Agreement, the Gwich'in Comprehensive Land Claim Agreement, and the Tr'ondëk Hwëch'in Final Agreement. Today, the Eagle Plains region is used by Van Tat, Dagoo, Teetl'it, Gwichya, Ehdiitat Gwich'in, and Inuvialuit harvesters, most frequently to harvest Porcupine caribou. The region is also crossed by the Dempster Highway, which provides a transportation corridor for industrial activities and recreational use by other residents of Yukon and beyond.

Prediction 1: Environmental constraints on vegetation growth will change

Climate change will interact with local environmental conditions to alter patterns of vegetation growth and recovery from disturbance (Figure 4.2). Moderate increases in atmospheric CO_2 concentration and air temperature resulting from climate change provide the potential for boreal tree species to experience positive growth and physiological changes (Bronson et al. 2009; Stinziano and Way 2014). Rising atmospheric CO_2 levels increase rates of photosynthesis and enhance overall vegetation productivity, a process termed the CO_2 fertilization effect. Since the 2000s, the CO_2 fertilization effect has accounted for 44% of the increase in gross primary productivity globally (Chen et al. 2022). The CO_2 fertilization effect can have both biogeophysical effects (e.g., changing vegetation distribution, water use efficiency) and biogeochemical effects (e.g., ameliorating CO_2 effects via carbon sequestration; Kolby Smith et al. 2016) and allows ecosystems to become greater carbon sinks (Medlyn et al. 2002).

In high latitude regions where the growing season length is predicted to extend proportionally longer, the CO_2 fertilization effect was predicted to have a significant positive effect on photosynthesis rates (Rustad et al. 2001; Morales et al. 2007). However, recent global trends indicate a reduced response of global primary productivity to rising atmospheric CO_2 levels (Wang et al. 2020). Photosynthesis levels are therefore not predicted to increase as much as previously estimated which will likely reduce land-based climate change mitigation efforts, potentially accelerating global warming (Wang et al. 2020). As trends of growing carbon sinks are slowing, we are likely to shift from a period of vegetation growth positively influenced by CO_2 fertilization to a period where nutrient, photoperiod, and moisture deficits constrain vegetation growth (Stinziano and Way 2014; Peñuelas et al. 2017). These multifaceted constraints may limit growth in ways that modelled results (versus field studies) do not account for (Stinziano and Way 2014).



Increased frequency of wildfire will release more legacy carbon[4] possibly shifting the boreal forest from a carbon sink to a carbon source[5]

In Eagle Plains, high frequency wildfires burned immature black spruce forests, resulting in regeneration failure of black spruce[1]. Instead, stands regenerated to shrub (*Betula* and *Salix* spp.) and graminoid tundra.

Carbon loss from thawing permafrost will likely represent a significant source of global carbon[6]

Climate change and wildfire do not guarantee permafrost degradation: site conditions, fire severity, and residual soil depth mediate the degree and pace of thaw[7]

Regeneration on existing linear features is dominated by shrubs; cover of moss and lichen are reduced[2]. 80% of existing seismic lines are predicted to naturally revegetate within 10 years[3].

Figure 4. 2 The five predictions that represent our best estimate of future trajectories of change to subarctic boreal ecosystems. Arrows represent how some of the predictions feedback into each other. Bubbles represent documented examples of the predictions or feedbacks in Eagle Plains or the subarctic boreal forest. References: 1 = Brown & Johnstone (2012); 2 = Simpson (2013); 3 = Francis & Hamm (2009); 4 = Walker et al. (2019); 5 = Bond Lamberty et al. (2007); 6 = Schuur et al. (2008); 7 = Holloway & Lewkowicz (2019).

Precipitation throughout Arctic regions is predicted to increase, dominated by increases in rain; through the 21st century, rainfall is predicted to increase by 422% (Bintanja 2018; McCrystall et al. 2021). In the Taiga Cordillera, annual precipitation is predicted to increase by 11% by the 2050s and 25% by 2100, compared to the 1961 - 1990 average (Price et al. 2011, 2013) and rain will compose approximately two thirds of the additional precipitation (Price et al. 2011). Across the wider boreal forest, interannual variation in precipitation is predicted to increase, especially in the shoulder seasons (Price et al. 2011). However, increases in precipitation will not necessarily be reflected by increases in soil moisture and plant available water because associated warming will inevitably lead to changes in evapotranspiration demand (Price et al. 2011; Beck et al. 2011b). In Alaska, years of high precipitation (snow) delayed the onset of sap flow which supports photosynthesis, subjecting trees to moisture stress (Walker et al. 2015). Drought can restrict the carbon uptake of the boreal forest; if widespread, the future capacity of boreal forests to sequester carbon may be diminished (Barber et al. 2000b).

Widespread sensitivity of dominant vegetation species to moisture limitation suggests that few species-location combinations will be resistant to drought, and landscape-wide declines in productivity are therefore likely (Beck et al. 2011b; Walker et al. 2015). In Eagle Plains and interior Alaska, landscape position was a consistently poor predictor of black spruce growth response. Instead, forests responded negatively to fall and winter precipitation in Eagle Plains, likely due to delayed onset of growth after heavy snow fall (Vaganov et al. 1999; Walker and Johnstone 2014). Negative growth responses to temperature were common; future warming may therefore negatively influence black spruce radial growth across this broad region due to temperature induced moisture stress (Barber et al. 2000b; Walker and Johnstone 2014b). Since Eagle Plains is dominated by this single tree species, the effects of drought could be significant and further investigation to understand the past and current growth patterns of black spruce in Eagle Plains are warranted.

Combined, increased winter precipitation and constraints on the capacity of boreal forests to sequester carbon are likely to significantly impact growth of subarctic vegetation and contribute to the boreal forest shifting from its role as a carbon sink to a carbon source. This shift will be exacerbated by wildfire (Prediction 2) and permafrost thaw (Prediction 3), which both release ecosystem stored carbon. In Eagle Plains, shortened fire return intervals in black spruce forests resulted in a net loss of locally stored carbon (Brown and Johnstone 2011), a pattern supported by work in other subarctic boreal forests (Walker et al. 2018, 2019). Future increases in fire frequency will have significant negative impacts on legacy carbon in the boreal forest and will be important in shifting the ecosystem from a carbon sink to a carbon source (Walker et al. 2019).

Prediction 2: Intensification of the natural wildfire regime will reduce the resilience of subarctic boreal forests

Natural wildfire is the dominant disturbance process throughout the boreal forest, playing a key role in forest dynamics and structure (Beck et al. 2011a). Typically, fires burn in predictable intervals, burning mature, conifer-dominated forests and facilitating an ecological reset. As a result of this disturbance cycle, vegetation in the boreal forest has adapted to reproduce with these cycles, conferring their ecological resilience (Johnstone et al. 2010a). Specifically, most black spruce recruitment and regeneration occurs after the heat from wildfires and death of trees stimulates the opening of semi-serotinous cones and releases seeds onto the wildfire-primed substrates (Charron and Greene 2002b; Keeley 2009).

Crucial components of this repeated cycle of fire and regeneration are likely to be impacted by climate change, leading to different ecological outcomes. Continued climate change in boreal forests is predicted to increase both fire severity, the quantity of organic material lost during the fire, and fire intensity, the quantity of heat released during the fire (Wotton et al. 2017b). Changes in these factors will influence the quantity and quality of reproductive plant structures and the quality of the seedbed for post-fire regeneration (Bonan and Shugart 1989b; Arseneault 2001; Johnstone et al. 2009). When fire severity increases, significant portions of the organic soil layer burn, and the moister mineral soil that remains is more hospitable on which a variety of species can recruit (Johnstone and Chapin 2006c). Small seeded, fast-growing species such as trembling aspen are at an advantage in these conditions, and in some cases, aspen dominance has resulted (Johnstone and Chapin 2006d; Johnstone et al. 2010b). This shift from coniferous to deciduous dominance can have many implications, including a shift in the resilience of permafrost (Stuenzi et al. 2021) and reduced lichen abundance, which is a critical component of caribou winter diet (Joly et al. 2010). Deciduous forests have a greater capacity to store carbon than the previously dominant black spruce. If deciduous dominance prevails, boreal forests may remain a carbon sink, possibly mitigating further climate warming (Mack et al. 2021).

In this self-sustaining pattern of wildfire and black spruce dominance, forests must be reproductively mature when they burn so that the released seeds have regeneration potential, which does not occur until ~50 years of age in northern stands (Viglas et al. 2013b). As crown fires become frequent throughout the 21st century (Wotton et al. 2017b), the risk increases that immature forests will burn. Early understanding of the consequences of this change in wildfire regime comes from Eagle Plains where repeat wildfires provided a natural field experiment to test the role of increased wildfire frequency on black spruce ecosystem regeneration (Brown and Johnstone 2012). This knowledge contributes significantly to our understanding of forest resilience throughout subarctic boreal forests. Natural wildfires burned in 1990/1991 and 2005, with portions of the 2005 fires overlapping the earlier fires. The result is three distinct areas of fire history on the landscape: mature forests (>90 years old), which represent late-stage successional processes; long-interval forests that were mature in 1990/1991 when they burned; and short-interval forests that were mature when they burned in 1990/1991 but were not mature when they burned again in 2005.

Approximately four years after the 2005 wildfires, short-interval forests had close to no black spruce regeneration (Brown and Johnstone 2012b). Since most black spruce regeneration occurs in a pulse within the first few years post-fire (Charron and Greene 2002b; Greene et al. 2013), regeneration failure had likely occurred in these short-interval forests as a result of burning immature trees (Brown and Johnstone 2012b). We revisited these sites in 2019 and 2021 (see SI for methods) and confirmed the persistence of significantly reduced black spruce regeneration at these sites (Figure 4.3). Stem counts from short-interval forests 14 years after the second wildfire confirm predictions by Brown and Johnstone (2012b) that regeneration failure occurs after an increased frequency of natural wildfires.

Results of this wildfire case study indicate three general patterns. 1) In the absence of disturbance, black spruce forests are resilient to background climate change (demonstrated by the insignificant change in stem density in mature forests). 2) When a mature forest burns, a period of self-thinning follows a pulse of black spruce recruitment. After ~15 years, these sites have higher diversity in the canopy and sub-canopy than unburned sites due to high shrub abundance (Figure 4.4). However, black spruce dominates the forest composition, and when the stand reaches full maturity, we predict that black spruce density will mirror that of the mature forests. 3) After two closely timed fires, regeneration failure by black spruce shifts the dominant vegetation functional type from coniferous trees to deciduous shrubs.

It is likely that ungulates will change their land use patterns in response to changes in vegetation dominance. The response of Porcupine Caribou to fire in the area has not been documented but predictions indicate significant declines in winter habitat are likely under future climate projections (Gustine et al. 2014b). Elsewhere in Canadian boreal forests, recently burned forests have been used as calving ground for caribou (Silva et al. 2020) however the slow post-fire accumulation of lichen may negatively impact caribou's use of burned areas for many decades until lichens recover (Russell and Johnson 2019; Greuel et al. 2021). Furthermore, the deciduous vegetation now dominant in many parts of Eagle Plains represents high quality moose browse. Increased deciduous dominance may in turn alter the presence and distribution of moose throughout the region.

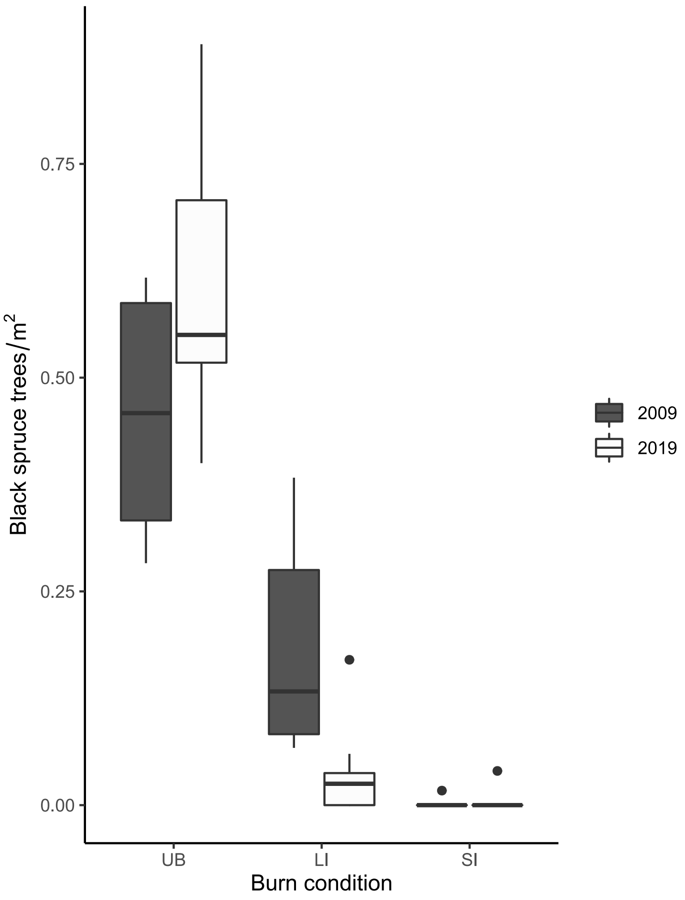


Figure 4. 3 Densities of live black spruce in three forest conditions (UB = unburned, LI = long interval, SI = short interval). Darker boxes represent measurements in 2009 (Brown and Johnstone 2012); lighter boxes represent measurements in 2019. Boxes themselves encompass the 25 – 75% quartiles with the horizontal line representing the median of 8 samples. Whiskers extending beyond boxes represent the 95% quartiles and black points denote extreme outliers. Trees in the UB sites were predominantly mature trees, while those counted in the LI and SI sites were seedlings and saplings that regenerated after the 2007 fire.

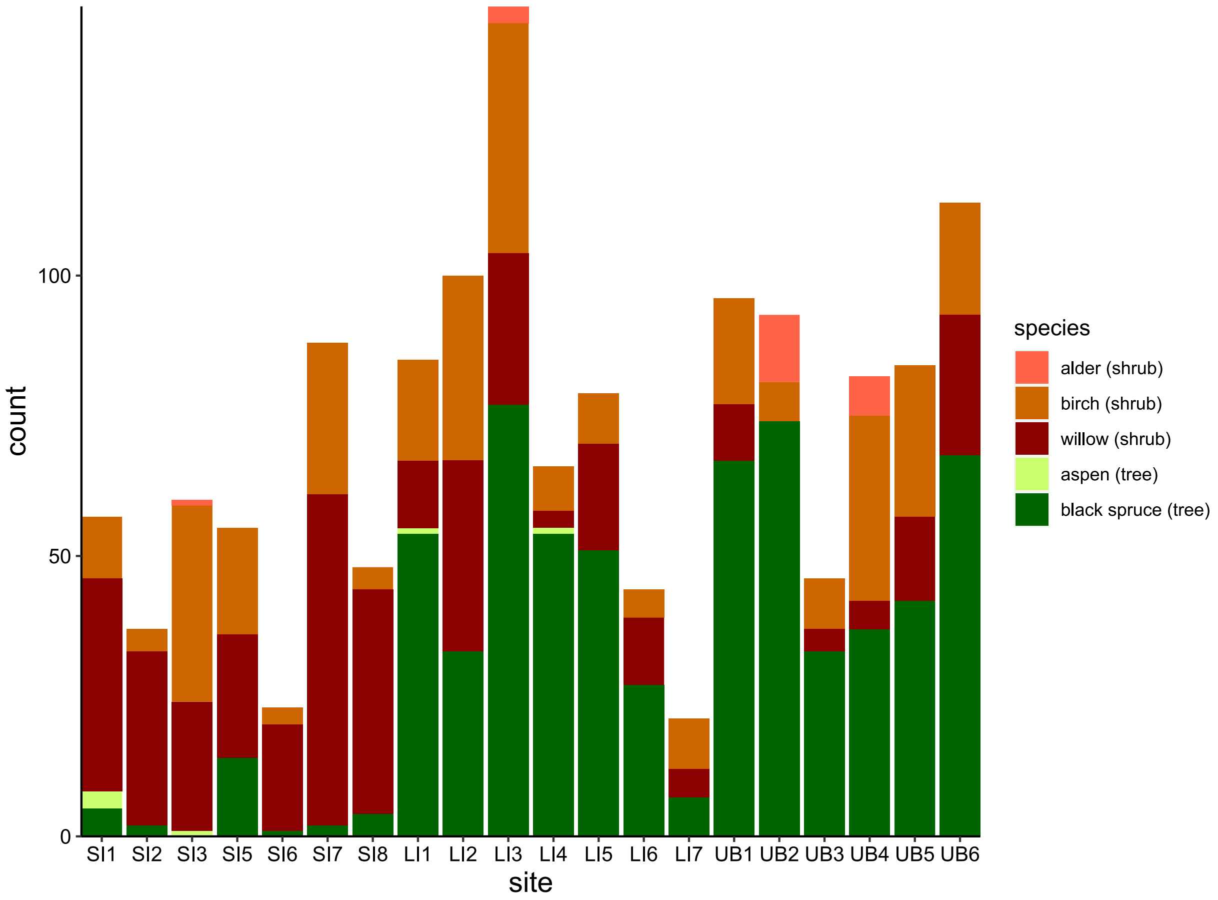


Figure 4. 4 Stem count for all woody shrubs and trees at each site in the burned study area at Eagle Plains. All individuals in a 50 m x 50 cm belt transect were recorded and occurrences were summed. Site labels (x-axis) represent three categories of fire: SI1-SI8 = short-interval sites where repeat fires burned in 1990/1991 and 2005; LI1-LI8 = long-interval sites where fires burned in 1990/1991; and UB1-UB8 = unburned sites where fires have not occurred for the past ~90 years.

Prediction 3: The influence of other natural disturbances in addition to fire will become increasingly pronounced

While wildfire is the dominant natural disturbance in the boreal forest of Eagle Plains, other natural disturbances such as permafrost thaw, forest pests, and invasive species may play an increasingly prominent role in shaping future boreal communities.

Permafrost thaw

Seventy percent of Canada's boreal forest is underlain by permafrost, ground that is at or below 0°C for two or more years (Jones et al. 2010). Much of the permafrost throughout the boreal forest lags the current climate; that is, it only exists because it is 'protected' by the ecosystem and insulated from increasing air temperatures (Vitt et al. 2000; Shur and Jorgenson 2007). Warmer air temperatures thaw permafrost, leading to surface instability and gas emissions. Continued warming threatens the integrity and persistence of permafrost. Disturbances to the surface such as wildfires or industrial activity, create networks of permafrost-free terrain which may leave the landscape permanently altered (Quinton et al. 2009; Williams et al. 2013; Price et al. 2013). Thickening active layers (from permafrost thaw) cause water limitation in the rooting zone of trees (Quinton and Baltzer 2013), leading to negative temperature-growth trends (Sniderhan and Baltzer 2016). The distribution of future black spruce forests is strongly tied to the current and future distribution of permafrost (Quinton et al. 2011). Where black spruce does not regenerate after permafrost subsidence, ecosystems may shift to sparsely treed or unforested wetlands (Baltzer et al. 2014) or become dominated by more competitive species such as deciduous trees (aspen) or shrubs (birch, willow, alder) or white spruce (Lantz et al. 2009; Chapin et al. 2010). To our knowledge, the study of the relationship between permafrost and the black spruce ecosystems of Eagle Plains has not occurred, leaving us to extrapolate from other regions such as northwestern Northwest Territories (e.g., Baltzer et al. 2014; Sniderhan and Baltzer 2016; Dearborn et al. 2021).

The effects of thawing permafrost extend beyond the ecological implications and exert a strong influence on infrastructure throughout northern regions. Ninety percent of the Dempster Highway, a major transportation corridor that bisects Eagle Plains, was built on continuous permafrost (Idrees et al. 2015). Constructed between 1959 and 1978 to support oil and gas development in the Eagle Plains area, the highway now connects the Beaufort Delta (Northwest Territories) to Yukon and southern Canada (Gates 2015). This all-season road is a 1.4 m deep gravel bed overlaying the ground and is an important mainstay for northern residents and a seasonal attraction for global tourists (Gates 2015). Most of the Dempster Highway is considered highly sensitive to disturbance via warming and surface modification (Burn et al. 2015) but the Eagle Plains section of the highway is considered to be relatively free from permafrost hazards due to its shallow soils and general lack of water courses (Burn et al. 2015). However, thermokarst lakes are developing adjacent to the highway in Eagle Plains, likely due to ice-rich ground (Camels et al. 2018).

Carbon release via permafrost thaw represents significant carbon loss from the ecosystem and greatly overwhelms the carbon uptake possible from CO_2 fertilization (Schuur et al. 2008, 2009). In an increasingly warmer world, permafrost carbon could become a significant biospheric source of carbon (Schuur et al. 2009). In the Northwest Territories, permafrost in certain environments (e.g., under thick organic layers and in colder places) appeared resilient to fire over a five-year period (Holloway 2020). Climate change (warming) and wildfire do not guarantee permafrost degradation; the degree and pace of thaw depend on site conditions, fire severity, and residual organic layer depth (Holloway and Lewkowicz 2019).

Forest pests and pathogens

Without environmental stressors, the conditions for forest diseases to persist and spread exist in a dynamic equilibrium, maintaining a healthy forest. As ecological conditions become warmer and drier, host plants become stressed, weakening their defences, and increasing their susceptibility to pests and pathogens (Price et al. 2013 and references within). Pathogen activity is predicted to increase in frequency and magnitude throughout the boreal forest and pathogens are likely to be able to adapt quickly to new environmental conditions and locations. Both climate and host plants are likely to become more favourable to insect populations which may lead to insect populations becoming a significant agent of change in the future (Price et al. 2013). Most invasive insects in North American boreal forests are defoliators of European origin (Sanderson et al. 2012), which reduce leaf productivity, weakening the tree (Digweed et al. 2009). Extreme defoliation can lead to widespread species-specific death and a shift to alternate dominant species (Jardon et al. 1994; Werner et al. 2006). Spruce budworm, spruce bark beetle, forest tent caterpillar, and mountain pine beetle are some of the most common insects influencing Canadian forests (Price et al. 2013) and all except mountain pine beetle have been observed in Yukon forests (Government of Yukon 2021). In general, forest pests and pathogens have limited spatial extent in Yukon and thus have received limited attention (Reid et al. 2022). To date, there has only been one documented study of forest pests in the Eagle Plains region (insect cone granivory; Brehaut et al. Accepted). Further investigation into the role of forest pests in this region would indicate whether pests such as spruce bark beetle and spruce budworm are absent or insufficiently monitored. In particular, the black spruce monoculture within Eagle Plains greatly increases the risk associated with pests and pathogens that attack black spruce.

Invasive species

Other pressures will continue to arise or gain prominence, possibly requiring management efforts, as the climate and land use continue to change. For example, further climate warming will increase the rates and densities of invasive forest pests (Langor et al. 2014). Already, exotic earthworms and slugs have gained prominence in southern boreal regions as air and soil temperatures have increased (reviewed by Sanderson et al. 2012). Should a large-scale shift to deciduous dominance occur as a result of fire (P2), permafrost thaw (P3), industrial activity (P4), or a combination of these processes, forest pests of emerging concern such as the aspen leaf miner (*Phyllocnistis populiella* Cham.), may pose an increasingly large risk. This pest is already listed as one of the biggest threats to forests in the Yukon with several outbreaks over the past several decades (Government of Yukon 2021). In Alaska, negative effects of this pest on aspen productivity superseded the effect of moisture limitation (Boyd et al. 2019, 2021).

Non-native vegetation species in the boreal forest are generally limited to opportunistic weedy species that, so far, have not been demonstrated to be particularly problematic for the ecosystem (Sanderson et al. 2012). Throughout Alaska, over 60 non-native plant species have been documented (Carlson and Shephard 2007; Carlson et al. 2008) with some specifically establishing within clear cuts (e.g., *Trifolium pratense* and *Senecio jacbaea*; Carlson et al. 2008), and many introduced via revegetation efforts (reviewed by Sanderson et al. 2012). In Eagle Plains, non-native grasses were introduced in reclamation efforts in the 1970s (see P4; Simpson 2013). Survey efforts in Tombstone Territorial Park (~250 km south of Eagle Plains) in 2018 found that only 0.8% of all documented species were introduced or non-native (eight species: two beetles, one bird, five vascular plants) (Bennet 2019). These results represent an increase from previous surveys which found only two non-native species in the park (*Taraxacum* *officinale* and *Plantago major*; Bennet 2019). In Yukon, these surveys represent the northernmost documented study of invasive species.

Prediction 4: Industrial activity will reduce the resilience of the ecosystem

Boreal forests are rich in natural resources. Consequently, there is significant vested interest in resource exploration and extraction; approximately 8% of Canadian boreal forest bears the footprint of industrial activity (not including forest harvest; Anielski and Wilson 2009). Studies of ecological responses of subarctic boreal systems to industrial pressures are limited, requiring extrapolation to Eagle Plains from either (i) low latitude boreal systems (e.g., concentrated industrial exploration in Alberta and Saskatchewan); or (ii) high latitude tundra systems (e.g., the response of tundra vegetation communities to seismic lines and roads in Alaska and Northwest Territories). The presence of permafrost in all high-latitude ecosystems further increases the complexity of predicting the responses and interactions amongst vegetation, soil, topography, and climate.

Landscape disturbance and recovery

Vegetation regeneration on linear features (including roads, cutlines, seismic lines is dependent on many factors including stand type, disturbance history, and terrain features (Lee and Boutin 2006). In permafrost regions, alteration of soil temperature regimes and thawing of ground ice can initiate hydrological changes that alter vegetation communities for decades, centuries, or even millennia. For example, recovery in lowland black spruce forests is slower than in white spruce or trembling aspen forests (Lee and Boutin 2006) and regeneration outcomes are overall higher on narrower seismic lines (van Rensen et al. 2015) though delayed regeneration is a concern regardless of width (Kansas et al. 2015). In tundra ecosystems, winter vehicle travel negatively impacts vegetation cover and permafrost conditions and increases the presence of bare ground (Kemper and Macdonald 2009; Jorgenson et al. 2010). In the Mackenzie Delta, on 30-year-old abandoned drilling sumps, the cover of regenerated vegetation was similar in quantity to surrounding undisturbed areas, but the community composition was unique with tall deciduous shrubs and grasses dominating disturbed substrates and sedges dominating the surrounding undisturbed substrates (Johnstone and Kokelj 2008). Sump caps are associated with relatively higher microtopography; distinct vegetation communities are therefore predicted to remain for as long as the differences in microtopography persist (Johnstone and Kokelj 2008; Kearns et al. 2015).

Once recovered, seismic lines and adjacent forest edges show reduced cover and diversity of nonvascular and herbaceous plants, with edge effects persisting up to 5 m into the forest (Dabros et al. 2017). In general, the edge effects of seismic lines remain poorly understood and warrant further investigation especially since the footprint of influence of the seismic may be much greater than is visible (Dabros et al. 2018). In Eagle Plains, recovery of vegetation on seismic lines has been dominated by deciduous shrubs (attributed to short-term increases in nutrient availability after the disturbance) with overall reduced cover of moss and lichens (Simpson 2013). As this trajectory follows that of post-fire regeneration, seismic lines are predicted to recover to pre-disturbance site characteristics (Simpson 2013). Seismic lines further from road experience higher regeneration, likely attributed to lower use by off-road vehicles (van Rensen et al. 2015). Seismic lines in Eagle Plains may therefore likely have increased regeneration potential as recreational vehicle use is likely to be low. However, the potential cumulative effects of regeneration and continued recreational (or industrial) use of seismic lines in Eagle Plains has not been addressed.

In Eagle Plains landscape disturbance associated with past industrial exploration is estimated at a linear density of 0.14km/km^2; future exploration is likely to increase the density by 5 to 9.3 times (Francis and Hamm 2009). Current linear densities already surpass the cautionary threshold outlined by North Yukon Land Use Plan and are approaching the critical threshold (Francis and Hamm 2009; North Yukon Planning Commission 2009). Future increases in linear density will almost certainly cross these thresholds. Francis and Hamm (2009) estimate that 80% of existing landscape disturbances will naturally revegetate within 10 years and that 60-100% of future features would revegetate within 100 years. However, these estimates do not match measured responses in Alberta where over 60% of seismic lines were still present on the landscape 35 years after initial disturbance and it was estimated that it would take > 110 years for a seismic line network to completely recover (Lee and Boutin 2006). Given the overall slower growth rates in subarctic forests, regeneration on seismic lines in Eagle Plains is likely to be as slow or slower than that of forests in Alberta.

During industrial exploration, ground cover is often compacted, leading to increased soil moisture and ponding which is evident a decade later (Emers et al. 1995). This compaction can present a significant barrier to vegetation reestablishment. As part of regeneration or reclamation efforts, manual recreation of microtopography (mounding) is a common practice. This practice can lead to higher rates of natural tree regeneration than non-mounded features (Filicetti et al. 2019) but can also contribute to increased carbon loss from the system via enhanced organic matter decomposition (Davidson et al. 2020). Further, mounding alters the composition of the understory community composition including a reduction in overall bryophyte community (low impact seismic lines only; Echiverri et al. 2020). Mounding may be an option to assist in recovery after future disturbances in Eagle Plains.

Reclamation

In Eagle Plains, early revegetation efforts involved seeding Kentucky bluegrass (*Poa pratensis*), a non-native grass, in the 1970s (Simpson 2013). In the Ogilvie Mountains south of Eagle Plains, live staking of willow and backfilling with local material have been successfully employed after repeated trail use by heavy machinery (Laberge Environmental Services 2010). Willow staking (planting live branches or trunks) has also occurred with reasonable success in parts of southern Yukon (Yukon Fish and Game Association et al. 2013). To date, we are unaware of any follow-up studies in Eagle Plains, but we would encourage studies indicating whether the existing features have in fact recovered. This knowledge would facilitate a more accurate understanding of recovery trajectories in Eagle Plains.

If active reclamation is desired in Eagle Plains for either existing landscape disturbances or as a condition of future industrial activities, clear reclamation goals are required. The reclamation process could have a variety of end goals, including reclamation to the pre-industrial landscape (i.e., dominated by black spruce). Since Eagle Plains does not have broad variation in plant community assemblages, there are limited possibilities of local vegetation combinations that we could seek to match. Reclamation goals may therefore be chosen to focus on the dominance of vegetation species that will fare better in a new, warmer subarctic, or dominance by vegetation species that will be good habitat and food source for mammals which dominate the region or may dominate in the future. If manual reseeding or revegetation (via nursery germinated plugs) occurs, using native species from local populations is the best practice;

however, local and prepared material is recognized as a barrier in the Yukon, mainly due to insufficient supply and limited nursery availability (Vogt and Janin 2017). Efforts should be taken to avoid the use of non-native species such as the grass previously used in Eagle Plains restoration efforts.

Given the existing land-use legacies in Eagle Plains, the creation of new landscape disturbances resulting from future industrial activity should be viewed with caution. The footprint of existing disturbances is not small and complete vegetation recovery has likely not yet occurred (although this has not been recently assessed). The potential for new industrial activity in Eagle Plains is large. If they proceed, extreme caution should be taken to ensure that critical landscape thresholds are not surpassed and that all disturbances have ongoing, regionally appropriate reclamation plans from the outset.

Prediction 5: The cumulative effects of climate change and industrial activity will introduce new disturbances and species interactions

The cumulative effects of anthropogenic climate change and industrial disturbances are likely to have significant impacts across subarctic boreal forests. Industrial land use often involves multiple stressors (Chapman and Maher 2014) and stresses from multiple land uses accumulate (Smith and Spaling 1995). Most land use changes (both industrial and natural) reduce ecosystems' carbon sink potential (Peñuelas et al. 2017). Targeted investigations into these effects are rare but including them in future decision-making processes is integral to promoting future healthy and productive ecosystems. In the Yukon in particular, there is no official framework for assessing cumulative effects although they are considered in part in many decision-making processes (Staples 2022).

Where their ranges overlap, interactions between caribou and wolves are typically avoided since they occupy distinct habitat types (Latham et al. 2011b). Yet in southern boreal forests, increased rates of industrialization have resulted in more frequent negative encounters between the two species as newly created linear features (such as seismic lines) permit wolves to travel further and faster and increase their visual and olfactory senses (Latham 2009; Dickie et al. 2017). In northern Alberta, wolves have been identified as being proximately responsible for declining caribou populations (Latham et al. 2011a, 2011b; Filicetti et al. 2019). Adding to these complex relationships, increasing land use may lead to spread of deer range throughout the northern boreal forests (Dawe and Boutin 2016). Indeed, in Alberta, a complex multi-species and habitat interaction has evolved, involving moose, deer, wolves, beavers, and caribou. High deer densities have led to increased wolf populations and higher incidental predation on caribou (Latham et al. 2011a, 2011b). Burgeoning populations of moose and deer owing to increased availability of early seral vegetation from wildfire and/or industrial activities (P2 and P4) may further increase wolf populations, further exacerbating negative wolf-caribou interactions (Latham et al. 2011a, 2011b). In southern boreal forests, other animals have demonstrated altered behaviours or densities in response to linear features including black bears (Tigner et al. 2014), bees (Nelson et al. 2021), and butterflies (Riva et al. 2018). Seismic lines did not significantly alter songbird communities in boreal NWT (Machtans 2006) but atypical burning scenarios in Eagle Plains (P2) has increased songbird activity as a result of higher shrub densities (Davol et al. *in prep*).

While these patterns have not yet been demonstrated in Eagle Plains, the possibility remains for them to occur in the future, with negative implications for caribou populations. Mule and white-tailed deer (*Odocoileus hemionus and O. virginianus*) are both present in southern

Yukon (Hoefs 2001) although their distribution patterns are not well documented. The potential exists for these species to continue their northward range expansion, changing the ecosystem dynamics in Eagle Plains. The Porcupine Caribou herd, while generally considered stable in its population, faces threats in different parts of its range. Eagle Plains represents the southern extent of their range, whereas the 1002 lands in the Arctic National Wildlife Refuge, Alaska represent the northern edge. Significant oil and gas development plans have been proposed for the 1002 lands and the herd are vulnerable to these developments (Russell and Gunn, 2019).

To reduce the impact of linear features on vegetation and wildlife communities, future exploration in Eagle Plains (and other subarctic boreal regions) should i) when possible, avoid permafrost terrain and use pre-existing features; ii) prevent compaction to reduce the disturbance to soil and vegetation; and iii) keep new linear features (where required) as narrow as possible, removing trees only when necessary (Williams et al. 2013). In Eagle Plains, reduced development of current and future linear features is required to maintained desirable Porcupine caribou winter habitat (Francis and Hamm 2011).

Towards adaptive ecosystem management

Forecasting the future of Eagle Plains is a combination of knowing what is happening locally (e.g., Brown and Johnstone 2012b) versus extrapolating from patterns in other subarctic boreal forests. Here, we present five predictions with the intention that they be useful tools for adaptive ecosystem management, both for our case study of Eagle Plains, and more broadly across subarctic boreal forests, which continue to face similar pressures of global change. A combination of climate change and increasing industrial pressures means that landscape wide changes will become increasingly prevalent over the next few decades. Natural and industrial disturbances effects will likely dwarf the direct effects of climate change alone in terms of shaping trajectories of ecosystem change. As an example, our case study of natural recovery after fire in Eagle Plains indicates that disturbances can trigger persistent changes in vegetation that will substantially alter direct responses to ongoing climate change. For Eagle Plains and other subarctic regions, an integrated approach focused on understanding the effects of cumulative stressors is required to properly conserve, manage, and use this landscape.

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Supplementary Information

Wildfire field studies

In 2019 and 2021, we resurveyed the sites that Brown and Johnstone (2012b) established in 2007-2009. Fieldwork was not possible in 2020 due to COVID-19 related travel restrictions. For detailed methods of the original survey, see Brown and Johnstone (2011, 2012b). In the resurvey, we established a 2 m x 50 m belt transect at each site. We recorded the species, and diameters at breast height (1.37 m) and stem base for all live trees within the belt. To facilitate a comparison, data for both the original survey and the resurvey were converted to units of trees/m^2. On-the-ground observations indicated that woody shrubs dominated in many of the burned sites. Standard measures of tree density (above) did not accurately capture the density of shrubs present. To account for this, we recorded the presence of all woody shrubs within a 50 cm x 50 m belt transect at each site. This metric provided a comparison of the range of shrub densities found across all sites.

Chapter 5: Discussion

5.1 Summary of thesis findings

My research has culminated in three broad findings relevant to northern ecosystems and future biodiversity. Vegetation communities in Yukon ecosystems are generally resilient to background warming; large disturbances can overcome the adaptive capacity of the ecosystem, forcing the system into an alternative stable state (Chapter 2). In subarctic Yukon, richness of biotic communities increases with latitude which corresponds to environmental gradients of air temperature and duration of snow cover (Chapter 3). In subarctic boreal ecosystems, the cumulative effects of climate change and natural and industrial pressures can force systems into a variety of ecological trajectories, many of which remain understudied. As rates of change throughout the boreal forest increase, landscape wide changes are likely (Chapter 4). Here, I place those findings back into the framework of adaptive cycles introduced in Chapter 1, connect to the concept of novel ecosystems, and discuss future research directions.

5.2 Adaptive cycles

Ecosystems are adaptive cycles, generally moving sequentially through four phases: rapid growth, conservation, release, and reorganization (Figures 1.1 and 5.1; Gunderson and Holling 2002; Walker and Salt 2006). Within each phase, the structure and function of the ecosystem changes drastically as new species dominate, new interactions occur, and the system is regulated by new constraints. Ecosystems are not static systems. They are constantly cycling within and between these four phases. The transition between phases can be subtle and protracted (e.g., from the rapid-growth phase to the conservation phase) or can be marked by a sudden and discrete event (e.g., from the conservation phase to the release phase). Importantly, ecosystems do not need to move through each phase sequentially or even at all: the common depiction of the cycle represents the most generic pathway of ecosystems. In the preceding three chapters, I have detailed the dynamics of multiple ecosystems throughout Yukon, Canada. Here, I will discuss the findings from each pattern in the context of the adaptive cycle framework (Figure 5.2).

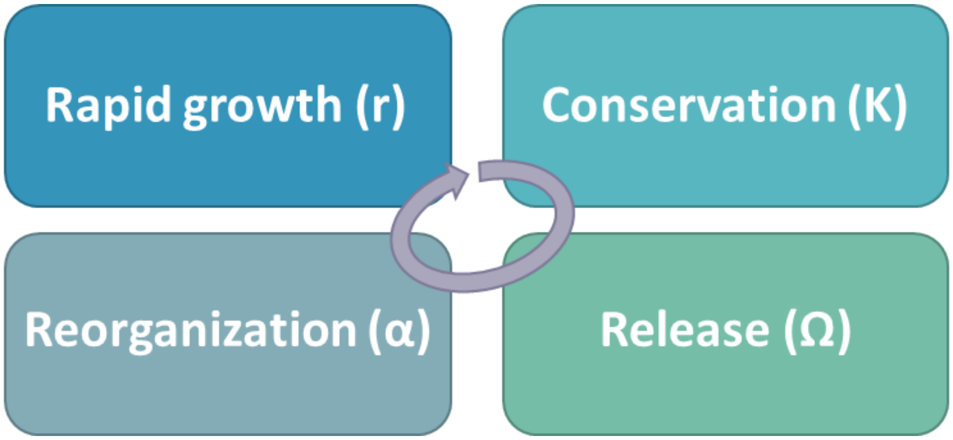
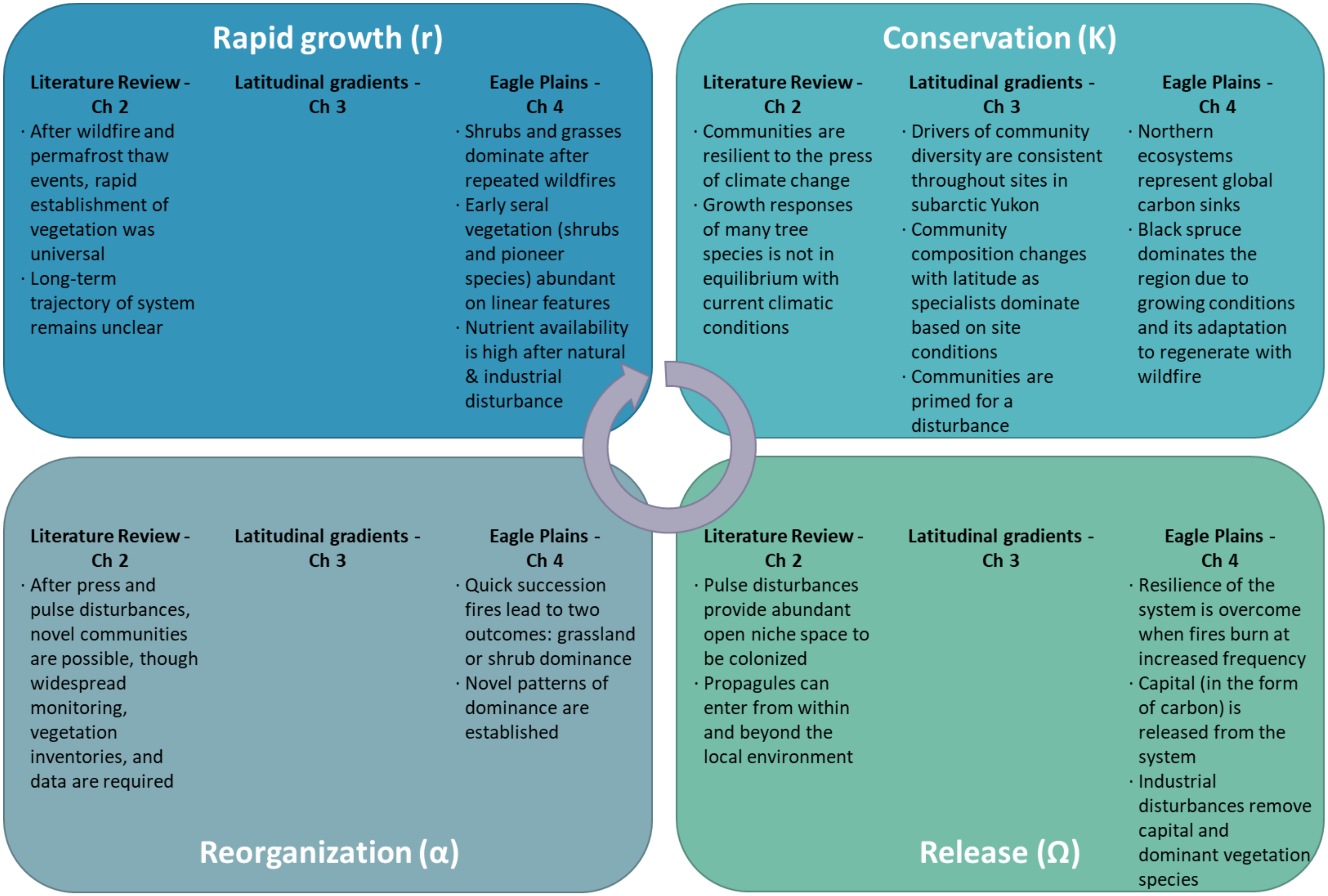


Figure 5.1 Overview of the four phases of the adaptive cycle framework, modified from Gunderson and Holling (2002) and Walker and Salt (2006). For a more detailed explanation of the cycle and its phases, see Chapter 1 and Figure 1.1.

In Chapter 2, I reviewed the existing literature for examples of vegetation changes that have already occurred throughout Yukon as a result of either the chronic press of climate change (background warming, changes to precipitation patterns) or from pulse disturbances (wildfire, permafrost thaw, insects and pathogens). Most available literature was about communities in the conservation phase. In general, vegetation in late successional communities is not in equilibrium with current climate conditions, suggesting that only a small disturbance will be required to overcome the system's resilience (Figure 5.2). Where communities were documented in their release phase, a variety of propagules were available, increasing the number of trajectories that the system may take. Unless an exceptionally large disturbance occurred (some documented wildfire examples), most communities showed evidence of returning to their previous state as the reorganization phase led to the rapid growth phase. Cycles for some communities still present unknowns. For example, after large-scale permafrost thaw events, many types of vegetation including coniferous trees, deciduous shrubs, and grasses, established on the newly available substrate (reorganization and rapid growth phases). However, the transition from the rapid growth to the conservation phase is a slow process and, at the time of the studies, had not finalized. The final composition of these communities is therefore uncertain. The community type that dominates throughout the conservation phase will dictate species interactions, how the system is regulated, and how resilient the system is to disturbance and future change.

In Chapter 3 (Latitudinal Gradients Study), all study sites were in the conservation phase. Sites were purposefully selected this way so that the vegetation present was most likely to represent specialists adapted to that sites conditions rather than opportunists establishing after disturbance. It is only by studying the established site specialists that we can understand system controls and regulations. Species within these sites were strongly connected, with clear controls on composition for both vegetation and spider communities. These sites are primed for disturbance; as late conservation-phase sites, the connections within and between species and the inherent reliance on established processes is gradually increasing the systems' rigidity. Small- to medium-sized disturbances are likely to have the ability to shift these sites into the release phase. Characteristics of these sites in the release, reorganization, and rapid growth phases of the adaptive cycle are unknown. In the event of disturbances at these sites in the near future, investigation into the dynamics and outcomes of these three phases would be beneficial and fill gaps in the general understanding of subarctic ecosystem dynamics. After future disturbances, the uncertainty within each site will be high and the system dynamics will be in chaos (Figure 1.1). Based on results from Chapter 4, which overlapped sites from Chapter 3 in space, multiple regeneration pathways are possible for each site after a disturbance and sites will not necessarily return to their previous composition.

Chapter 4 (Disturbances in Eagle Plains) represents the most complete effort at following one system or location through this complete cycle, thanks in large part to long-term monitoring. In Eagle Plains, systems in the conservation phase (unburned, mature forests) represent significant carbon sinks. The dominant species, black spruce, is a specialist, adapted to the cold and wet soils of the region and able to regenerate with the natural wildfire of the region. Multiple instances of wildfires in the region allow us to follow different pathways of the cycle. First, in long-interval forests where fires burned in 1991 after approximately 90 years without a wildfire, the system released its seeds on to ground that was primed for regeneration. Although other species were able to establish (Brown and Johnstone 2012), black spruce dominated the reorganization phase, and the identity of the previous cycle (black spruce dominance) was repeated in the rapid growth phase. The system is currently in a transition between the rapid growth and conservation phase. In the second wildfire scenario, short-interval wildfires burned the forest first in 1991 and then again in 2005. After the system burned in 1991 (release phase), it moved to the reorganization and rapid growth phases where black spruce was starting to gain dominance. The second wildfire occurred during the rapid growth phase, moving the system straight to the release phase, a rare occurrence of a phase being skipped altogether (Figure 5.3). In this instance, there was very little capital (black spruce seed) to be released which limited the renewal capacity of the system (Figure 5.2). As the reorganization phase began, uncertainty dominated, and multiple pioneer species established. Locally novel patterns of dominance established as some areas transitioned to shrub-dominated systems while grassed dominated others (Wasyliw et al., in prep.).



Rapid growth (r)

Literature Review - Ch 2	Latitudinal gradients - Ch 3	Eagle Plains - Ch 4
· After wildfire and permafrost thaw events, rapid establishment of vegetation was universal · Long-term trajectory of system remains unclear		· Shrubs and grasses dominate after repeated wildfires · Early seral vegetation (shrubs and pioneer species) abundant on linear features · Nutrient availability is high after natural & industrial disturbance

Conservation (K)

Literature Review - Ch 2	Latitudinal gradients - Ch 3	Eagle Plains - Ch 4
· Communities are resilient to the press of climate change · Growth responses of many tree species is not in equilibrium with current climatic conditions	· Drivers of community diversity are consistent throughout sites in subarctic Yukon · Community composition changes with latitude as specialists dominate based on site conditions · Communities are primed for a disturbance	· Northern ecosystems represent global carbon sinks · Black spruce dominates the region due to growing conditions and its adaptation to regenerate with wildfire

Reorganization (α)

Literature Review - Ch 2	Latitudinal gradients - Ch 3	Eagle Plains - Ch 4
· After press and pulse disturbances, novel communities are possible, though widespread monitoring, vegetation inventories, and data are required		· Quick succession fires lead to two outcomes: grassland or shrub dominance · Novel patterns of dominance are established

Release (Ω)

Literature Review - Ch 2	Latitudinal gradients - Ch 3	Eagle Plains - Ch 4
· Pulse disturbances provide abundant open niche space to be colonized · Propagules can enter from within and beyond the local environment		· Resilience of the system is overcome when fires burn at increased frequency · Capital (in the form of carbon) is released from the system · Industrial disturbances remove capital and dominant vegetation species

Figure 5.2 Summary of the adaptive cycles in Yukon ecosystems explored in this thesis. The adaptive cycle is composed of four phases which can occur in any order (or be skipped entirely). The flow of phases presented here represents the most common cycle that occurs in ecosystems. Examples from the preceding three chapters are included for each of the four phases where possible.

In sum, research presented throughout this thesis contributes to a growing understanding of the adaptive capacity of ecosystems. In some systems (e.g., Eagle Plains Ecoregion) we have high spatial and temporal data resolution, providing detail for all four phases of the adaptive capacity model (Figure 5.1) and also showing the pathway of alternative trajectories (Figure 5.3). In other systems (e.g., systems studied over a brief period of time during their conservation phase, Chapter 4), we lack a nuanced understanding of many of the phases. Continued, site-specific, long-term monitoring is required to fully realize the details of the full adaptive capacity cycle throughout these systems. In northern ecosystems, a complete understanding is particularly important as the opportunities for novel systems to dominate are high and have already been demonstrated locally in Eagle Plains.

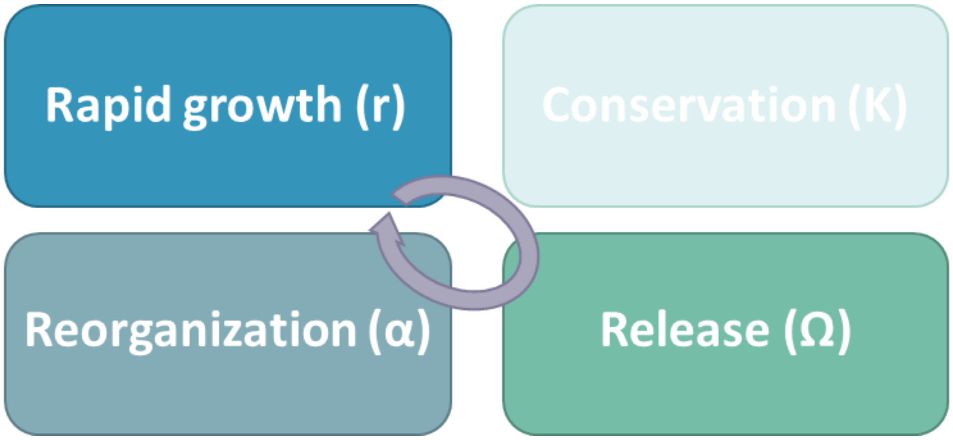


Figure 5.3 Visual representation of the adaptive capacity of Eagle Plains (Chapter 4) after wildfires occurred during the rapid growth (r) phase. The conservation (K) phase was skipped, and the system moved straight to the release phase. Because the system was not able to mature throughout the conservation phase, there was limited capital in the form of seeds for the system to release in the release (Ω) phase. In the reorganization phase, the system followed two separate pathways, both of which were unique from the previous system that dominated.

5.3 Ecological novelty: The communities of the future

With ongoing climate change, species' ranges and interspecific interactions are likely to change, resulting in species assemblages dictated by new constraints (Urban et al. 2012a). These new species assemblages necessarily go through various demographic, trophic, and adaptive processes as species interact to survive. They can emerge as novel ecosystems, unable to return to previous historical conditions given the ongoing influence of anthropogenic climate change (Mascaro et al. 2013). The formation of novel communities is more likely to occur in certain geographical circumstances, including unique or isolated systems (Ewel et al. 2013), ecotonal communities (Trant and Hermanutz 2014), or those facing multiple and often compounding threats (cumulative effects). Northern ecosystems, including those within Yukon, are therefore a likely location for novelty to arise in the near future.

Novel plant assemblages themselves are not unique to the 21st century but, due to global change at unprecedented scales, are predicted to arise at a uniquely rapid pace (Jackson 2013). A detailed understanding of novel communities' functioning and their wider ecosystem implications will help meet global conservation and climate change adaptation goals (Jackson 2013). Novel communities can persist without the need for continued human intervention or maintenance (Mascaro et al. 2013). However, management may be desirable in specific instances to conserve target species or overall biodiversity, restore or maintain ecosystem functions or services, or manage unique community assemblages (Hulvey et al. 2013).

Novel ecosystems have the potential to significantly change the structure and function of northern ecosystems. Novel ecosystems coupled with dramatic changes to experienced climate will alter interspecific interactions, with cascading consequences across trophic levels, for human-animal interactions, and for landscape management. In novel scenarios, it will be important to employ an adaptive management framework to accurately understand and respond to the novel adaptive systems most accurately (Angeler and Allen 2016).

5.4 Limitations and Future Directions

Many aspects of this research have changed as a result of COVID-19 travel restrictions. For my research, the main impact was the reduction in the number of study sites. Originally, I had 14 sites throughout Yukon and Northwest Territories but due to border closures, the Northwest Territories sites were unreachable for multiple years. Consequently, Chapter 3 focuses on a smaller geographic area and, while caution should be used when scaling up results, patterns highlighted (increasing species diversity with latitude) compliment other research in the region. This finding suggests that these results are not a function of a smaller than intended study region.

My thesis has set the stage for future work in many different areas. Notably, in Chapter 2, I have highlighted 30 research gaps specific to our understanding of Yukon vegetation communities. I hope that some, if not all, of these gaps are addressed soon by the larger research community to assist with management, conservation, and understanding of Yukon's ecosystems. During this time of rapid environmental and industrial change, having a thorough understanding of the baseline conditions and functions of ecosystems is key prior to predicting how or when ecosystems may change.

In Chapter 3, I showed how vegetation and spider communities change with latitude and environmental variables. Two key future directions of research are as follows. 1) How do communities change to altered environmental conditions? For example, snow depth is predicted to decrease throughout subarctic regions, and a large scale (i.e., multi-site) snow depth manipulation experiment could indicate where plant communities are most vulnerable to changes in snow cover, and how these changes may affect the larger plant community. 2) Do all biotic communities follow the same patterns with latitude and environmental variables? Understanding multi-trophic responses to different environmental variables is key to understanding how future ecosystems will function. The distribution of avian, microbial, and soil-dwelling insects and worms throughout this region remains understudied and could contribute to a multi-faceted understanding of northern ecosystems.

Finally, in Chapter 4, many states and trajectories remain unknown in the Eagle Plains area. While much information can be extrapolated from other regions, understanding patterns and processes specifically in subarctic boreal ecosystems is important for managers, conservationists, and land users going forward.

5.5 Conclusion

This thesis contributes to a broad understanding of how northern ecosystems function and how they are structured. Much is known about the adaptive cycles of northern ecosystems, including their rapid growth and conservation phases and how their release and reorganization phases unfold after disturbances that do not overcome the systems resilience. However, knowing that disturbance cycles are changing and that the numbers of pressures on ecosystems is steadily increasing, practitioners, land managers, and northerners alike must be proactive in preparing for and responding to the inevitable changes that will occur throughout northern ecosystems.

In this thesis, I have highlighted research questions to be addressed. These are wide-ranging in both their geographic range and vegetation communities considered. Filling these knowledge gaps is crucial for understanding how northern ecosystems will function and be structured in the future. The systems studied in this thesis are resilient. But the stage is set for rapid change. The fact that specific systems have not already experienced change, does not exclude them from the possibility of changes in the future. Appropriate and effective management actions can help to maintain the resilience these systems. In sum, we can help to ensure and maintain resilience of northern ecosystems if we: 1) further our understanding of northern ecosystem structure, functions, interactions, and adaptive cycles; and 2) better plan for and manage natural and anthropogenic changes.

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