

LITTLE PLANTS, BIG CHANGES: DISTURBANCES FACILITATE SHRUB  
SEEDLING ESTABLISHMENT IN THE ARCTIC

by

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## THESIS ABSTRACT

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Title: Little Plants, Big Changes: Disturbances Facilitate Shrub Seedling Establishment in the Arctic

Currently warming at more than twice the rate of the global average, the Arctic is rapidly changing with global consequences. Climate change enables arctic shrub expansion, which alters ecosystem structure and contributes to permafrost degradation. This research demonstrates that landscape disturbances (such as fire and thermokarst) enhance shrub expansion by facilitating shrub seedling establishment. Through a manipulative seed-addition experiment, this research shows that disturbances result in over a four-fold increase in the number of seedlings surviving the 2<sup>nd</sup> growing season, a critical bottleneck for seedling establishment. Mortality is higher in undisturbed areas, where 4% of seedlings survived their first year of growth (compared to approximately 20% in disturbed areas). Seedling survival is controlled by seedbed quality and microsite suitability, which are altered by landscape disturbance. As disturbance regimes are increasing in frequency and severity, shrub expansion is expected to increase at a greater rate than is predicted from warming alone.

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For the youth of the world and the communities of the Arctic,  
may this work add to the chorus of voices speaking up for a better future.

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# CHAPTER I

## INTRODUCTION

The story of the Arctic is one of extremes. For much of the year, this land is cast in darkness, a frozen, treeless landscape illuminated only by the dancing lights of the aurora borealis and stars overhead. For other parts of the year, it is a soft carpet of moss, lichen, wildflowers, grasses, and sedges springing up underneath the constant sunlight of summer. Some of these wildflowers, like the Arctic poppy (*Papaver radicum* Rottb.), follow the sun in a dance as it circles around the sky. Through this process of heliotropism they are able to warm their inflorescences by as much as 10°C over the surrounding air, an adaptation that helps their seeds to mature before the short growing season comes to an end (Huryn and Hobbie 2013). Woody shrubs, which in some parts of the world grow to heights of 10 meters, are often no taller than one's knees in the far north, however climate change is allowing them to grow to new heights (Allaby 2019). These changes are most prevalent within the Boreal-Arctic Transition Zone, the area where tall shrubs grow but trees do not.

In the landscape of the Arctic, dichotomies prevail. While extended periods of darkness and light characterize the winter and summer months, change happens quickly in the fall and spring. In these periods of transition, daylight grows or shortens by 15-minute increments from one day to the next. Just as the rate of change in daylight shifts dramatically depending on the time of year, throughout earth's history arctic ecosystems have experienced long periods of continuity punctuated by periods of abrupt change. For millennia, the Arctic has been a carbon sink, as long winters of frigid temperatures have

prevented decomposition of the plant matter that is produced during the short summers. Most of the Arctic is underlain by carbon-rich permafrost, perennially frozen ground, containing centuries of plant growth essentially locked away by icy temperatures from the soil microbes that would decompose it if given the chance. Permafrost soils currently store more than twice as much carbon as is in the atmosphere, a reserve that has built up through the simple act of photosynthesis carried out over millennia (Schuur and Bockheim 2008). However, the future of the Arctic's carbon balance and these carbon reserves is uncertain. The arrival of spring warmth brings rapid snowmelt and the emergence of plants during the quick transition from the long, frozen winter. In this same way, climate change is rapidly warming the long-frozen Arctic, thawing permafrost soils, releasing ancient carbon reserves, and accelerating plant growth.

Anthropogenic climate change has been increasing global average temperatures since the beginning of the industrial revolution, and the mean temperature has already warmed by 1°C in comparison to the late 1800's (Pachauri and Meyer 2015). As humans release ancient carbon from the ground to the atmosphere through the combustion of fossil fuels (like oil, coal and natural gas); we change the earth's carbon balance. By emitting carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), nitrous oxide (N<sub>2</sub>O), and other greenhouse gases through industrial and agricultural activities we directly contribute to the warming of our planet. While climate science has shown us the direct link between fossil fuel emissions and global warming, it also demonstrates that climate change does not affect the planet equally (Edenhofer et al. 2014). Both the processes and consequences of climate change disproportionately affect certain areas of the globe. As such, climate risks are borne more heavily by certain regions than others. The Arctic has

already experienced and will continue to experience rapid change as a direct result of these disparities. The Arctic is warming at more than twice the rate of the global average. As a result, mean temperatures in the Arctic are projected to increase by 2.2°C (RCP 2.6) to 8.3°C (RCP 8.6) by 2100 (as compared to the 1986-2005 reference period, RCP = representative concentration pathway) (Edenhofer et al. 2014).

As temperatures increase in the Arctic, permafrost thaw increases. Earlier snowmelt and later freeze-up extend the season during which soils thaw, while deeper snowpack and warmer winter temperature reduce refreezing. As a result, soil microbes have more access to the ancient carbon underneath the Arctic. Just as we exhale carbon dioxide produced through our conversion of food into energy, microbes decompose soil carbon and release carbon dioxide or methane to the atmosphere, the same greenhouse gases that drive anthropogenic climate change. As the Arctic warms, this process is expected to accelerate due to increased permafrost thaw, adding greenhouse gases to the atmosphere and leading to more warming. The positive feedback cycle of permafrost carbon emissions is the result of many small changes occurring throughout the Arctic, which together lead to big changes that affect the whole globe. While this process may seem intangible, it is common to see methane bubbles trapped underneath the ice of ponds in the fall, subtle clues revealing the unseen changes occurring within the permafrost. In this way, what happens in the Arctic does not just stay in the Arctic.

Walking through tundra wetlands in the middle of summer, small bubbles of methane rise from underneath one's footsteps. The soft gurgling sounds mark the release of trapped gas dislodged by the simple act of walking, ancient carbon on its new journey from permafrost to atmosphere. This phenomenon, the literal manifestation of humanity's



carbon footprint, is a sight to behold. Underpinning arctic change is the continual release of greenhouse gases by fossil fuel combustion. While the positive feedbacks of arctic climate change will contribute to additional warming of the earth's atmosphere, these changes can only be mitigated through global action to reduce greenhouse gas emissions. The consequences of arctic warming are global, their severity will depend on the willingness of the world to address climate change.

Arctic change is already manifesting itself on the landscape. Wildfire, which is typically quite rare in the tundra, is becoming more common (Hu et al. 2015; Euskirchen et al. 2016a; Schuur and Mack 2018). In areas where permafrost has thawed, the ground is collapsing causing damage to homes, roads, and oil pipelines. In reaction to the changing physical environment, plants are flowering earlier, growing taller in stature, and moving into new habitats. In the Boreal-Arctic Transition Zone, the northern latitude treeline, an ecotone shaped by climate and topography, marks the transition from tundra in the north and boreal forest in the south. This boundary zone typically exists where mean July temperatures are 10°C (Huryn and Hobbie 2013). All over the globe, tree lines are moving up in elevation and latitude. Warming has already been implicated in half of these cases (Myers-Smith and Hik 2018). In the subarctic, these rates range from 10 – 100 m per year (Rees et al. 2020). North of treeline, there exists another climatically-driven threshold, the environmental limits of tall shrubs. While shrublines have been understudied in comparison to treelines, studies have detected a mean July temperature threshold of 11.0-11.8°C for feltleaf willow, *Salix alaxensis* (Andersson) Colville, in the Alaskan Arctic (Swanson 2015; Zhou et al. 2020). As the climate continues to warm throughout the Arctic, both trees and shrubs are expected to expand northward. However,

these advances will be shaped by limitations on seed production and seedling establishment.

This thesis examines the factors controlling shrub expansion within the Boreal-Arctic Transition Zone, the area where tall shrubs grow but trees do not. This region is of critical research importance because it provides the opportunity to understand the way in which the rest of the Arctic ecosystem will respond to climate and landscape changes in the future. The effects of climate change within this region are expected to be a combination of small shifts punctuated by rapid changes. This thesis investigates the way in which landscape disturbances (wildfire and permafrost collapse) can accelerate slower rates of change (temperature limitations on shrub expansion), potentially leading to rapid ecosystem change. Chapter 2 introduces climate change in the Arctic with a focus on biophysical processes, biogeochemical consequences, and terrestrial ecosystem impacts. Chapter 3 investigates the link between warming-induced landscape disturbances and shrub expansion through an *in-situ* seed addition experiment. Chapter 4 places shrub expansion and disturbance interactions into a broader context of climate-vegetation feedbacks. Tundra ecosystems are shaped by climate change and in turn, shape the global climate. Landscape disturbance regimes and vegetation dynamics are a critical control on these processes.

## CHAPTER II

### THE CHANGING ARCTIC

Changing climate conditions are amplified in polar regions, and the Arctic is warming at more than twice the rate of the global average (Edenhofer et al. 2014). These modifications result in ecosystem interactions and feedbacks that can either augment or mitigate climatic changes. Vegetation dynamics will play a pivotal role in shaping whether the Arctic remains a carbon sink, as it has been for thousands of years, or becomes a carbon source, further exacerbating the effects of global climate change (Webb et al. 2016).

Arctic amplification, the ocean-ice-albedo feedback cycle which causes the Arctic to warm more rapidly than other parts of the world, accelerates permafrost degradation. As a result of increased thawing of frozen soils, microbial decomposition increases, releasing the Arctic's vast quantities of soil carbon to the atmosphere in the form of greenhouse gases (Lawrence and Swenson 2011; Myers-Smith and Hik 2018). The ramifications of increased permafrost thaw are of global concern, as arctic soils contain the largest pool of soil carbon worldwide, an estimated 1672 petagrams (1 Pg = 1 billion tons), approximately twice as much carbon as is currently within the atmosphere (Schuur et al. 2008; Narita et al. 2015). Ultimately, biogeochemical feedbacks in the Arctic region (which are primarily driven by increased decomposition rates as permafrost thaws) are expected to contribute 0.13-0.27°C of additional warming by 2100 and up to 0.42°C by 2300, amplifying anthropogenic warming on the global scale (Schuur et al. 2015). As

global climate mitigation targets attempt to limit warming to 1.5-2°C, the fate of the Arctic will shape the efficacy of these efforts (Hoegh-Guldberg et al. 2018).

### *1. Processes and Impacts of Arctic Climate Change*

In agreement with earth system model projections of future climate scenarios, the Arctic is warming at more twice the rate of the global average. In the years since 1900, the global mean temperature has risen by approximately 0.8°C. However, over that same period the Arctic has warmed by approximately 2-3°C (Overland et al. 2014; Post et al. 2019). The phenomenon responsible for this increased rate of change is known as “arctic amplification” (Hoegh-Guldberg et al. 2018; Natali et al. 2019). There are multiple processes that have been hypothesized to contribute to this mechanism (such as increased cloud cover or the poleward transfer of heat by atmosphere and ocean circulation). However, reductions in the cover and duration of both sea-ice and snow are thought to be the primary driver. Both sea-ice and snow are highly reflective substances with correspondingly high albedo (the percentage of incident solar radiation that is reflected). As snow and ice extent is reduced, the exposed ocean and land surfaces absorb more heat, contributing to additional warming of the region (Letterly et al. 2018). Arctic amplification has the greatest impact during the cold season due to both a delayed freeze-up of sea-ice and advection of moisture (with associated increases in latent heat flux) into the region (Box et al. 2019). The sea-ice-albedo feedback, in combination with atmospheric moisture and heat feedbacks, contribute to a positive warming cycle that amplifies the magnitude of climate change across the Arctic (Pithan and Mauritsen 2014).

Global climate change has already, and is expected to continue to, alter multiple climate parameters throughout the Arctic. While year-round temperatures are expected to

increase, fall and winter temperatures are expected to increase most significantly, rising by more than four times the global average during these seasons (Edenhofer et al. 2014; Hoegh-Guldberg et al. 2018). As a result of stronger arctic amplification effects during the winter months, the Arctic could emit 41% more carbon each winter by 2100 (Natali et al. 2019). For the period 1971-2017, warming throughout the region averaged 2.7°C overall (with 3.1°C warming during the October-May cold season and 1.8°C warming during the June-September warm season) (Box et al. 2019). This seasonal warming coincides with a marked shift in the duration and timing of the snow-free period. Earlier snowmelt and later freeze-up dates are extending the duration of the snow-free period (Letterly et al. 2018). Less warming occurs in summer than winter because excess heat energy is absorbed through the process of ice melt or by the open Arctic Ocean during these months (Pachauri and Meyer 2015). Additionally, humidity and precipitation are increasing along with concurrent temperature changes (Box et al. 2019). These precipitation increases primarily occur during the cold season. As a result, hydrologic cycle is intensifying (as a consequence of increased winter precipitation combining with a longer snow-free period), ultimately yielding a longer period of summer drying. As a direct consequence of increasing soil temperatures stemming from longer snow-free periods, the active layer (the portion of the upper soil profile that thaws out seasonally and refreezes during winter) is deepening and soil temperatures are increasing (Grosse et al. 2016).

The changes occurring throughout the Arctic region are of global consequence as these processes shape the global climate budget. While the Arctic has been a carbon sink for millennia due to slow rates of decomposition, this is not expected to be the case in the

future (Webb et al. 2016). Under current warming projections, the Arctic is expected to become a carbon source, as increasing trace gas fluxes exceed the rate of carbon assimilation (carbon uptake by plants). Approximately  $1,035 \pm 150$  Pg (mean  $\pm$  95% confidence interval) of Arctic soil carbon is contained within the permafrost surface layers (within the top 0-3 m) and are vulnerable to thaw (Schuur et al. 2015). Deepening active layer depth, rising soil temperatures, and a longer thaw period combine to increase microbial decomposition of this organic carbon (Schuur et al. 2008). As a consequence, rates of heterotrophic respiration, methanogenesis (anaerobic conditions), and methane oxidation (aerobic conditions) increase. These microbial processes mobilize this ancient carbon pool to the atmosphere emission of carbon dioxide and methane (Schuur et al. 2015).

Whether the Arctic will continue in its role as a carbon sink or becomes a carbon source largely depends upon the productivity of vegetation throughout the region. If increasing rates of carbon assimilation are sufficient to keep pace with soil efflux, then the Arctic will continue to be a carbon sink. However, given the pace of Arctic warming, it is expected to shift to a carbon source. For example, while earth system model (ESM) projections estimate that increased vegetation growth will increase carbon storage by  $17 \pm 8$  Pg (mean  $\pm$  standard error) of carbon by 2100, however RCP 8.5 model scenarios project permafrost carbon release ranging from 37-174 Pg (with an average of  $92 \pm 17$  Pg) for that same period (Schuur et al. 2015). Other model projections indicate that the Arctic could remain a carbon sink until the end of the century as a result of increased shrub growth and increased shading of soil during summer months. However, even these estimates indicate that by 2100 the balance would shift to be a carbon source (Mekonnen

et al. 2018). Within the active layer, biogeochemical cycles are accelerated as microbial decomposition of soil organic matter increases, yielding increased rates of heterotrophic respiration. While rates of nitrogen mineralization by soil microbes are also expected to increase throughout the region, this process will not be sufficient to remove terrestrial ecosystem nutrient limitations (Bouskill 2014). As such, increased plant productivity is not expected to keep pace with mobilization of the ancient soil carbon pool despite warmer conditions. The coupling of biophysical and biogeochemical processes throughout the region will shape the degree by which the Arctic will exacerbate climate warming worldwide.

## ***2. Vegetation as a Driver and Mediator of Change in the Arctic***

As plant growth is limited by low temperatures and short growing seasons, increasing average temperatures in the Arctic increase the rate of autotrophic carbon assimilation. This results in increased vegetation productivity and biomass. This trend has been observed through a “greening” of the Arctic captured by remotely-sensed NDVI (Normalized Difference Vegetation Index) observations since the beginning of the satellite record in 1982 (Box et al. 2019). While there have been some portions of the Arctic that have exhibited recent browning trends, these are anomalies are hypothesized to occur due decreased soil moisture availability because of localized drying and increased evapotranspiration. Increases in plant biomass in response to warming have also been shown through experimental studies and observations along climate gradients, however the magnitude to which plant growth can track increasing temperatures is not well-defined because of nutrient limitation dynamics (Bouskill et al. 2014; Berner et al. 2018). As a result of the coupling between plant productivity and warming, vegetation

can mediate climatic changes through enhanced carbon assimilation. However, the degree to which plant growth can offset carbon release from permafrost is unknown.

As the Arctic warms, large shifts are projected to occur throughout the Boreal-Arctic Transition Zone as tall-statured woody vegetation advances northward within tundra ecosystems. These ecosystem changes are the result of warmer, longer summer growing seasons, deeper snowpack (which protects vegetation from freeze-damage and is a result of increased precipitation), and increased nutrient mineralization (Myers-Smith et al. 2011; Berner et al. 2018). While the northward migration of treeline advance has been well-studied, the dynamics of shrubline advance have been relatively understudied in spite of the more rapid advancement of shrubs (Lorantý et al. 2016; Myers-Smith and Hik 2018). The onset of shrub expansion has been documented through historical imagery, remote sensing, field observations, experimental manipulations, and placed in context with paleoecological data (Anderson et al. 1994; Chapin III et al. 1995; Bret-Harte et al. 2001; Silapaswan et al. 2001). “Shrubification” of tundra ecosystems manifests through advancing shrub line, increasing density, and growth of individuals (Myers-Smith et al. 2011).

Shrubs have a complex biophysical and biogeochemical relationship with the Arctic ecosystem. While there are mediating impacts of their presence and expansion throughout the region, they also exacerbate warming-induced feedbacks (Table 1). For example: while shrubs increase the rate of carbon assimilation by tundra vegetation, they also reduce albedo; representing both positive and negative climate feedbacks (Myers-Smith et al. 2011). The complex canopy structure of these plants allows for shading of soils which reduce summer warming effects, but there are additional processes that



increase soil warming. As a result of the tall stature of shrubby vegetation, wind-blown snow is trapped creating deep snowpack which promotes warmer soil temperatures in the winter (by insulating the soil from cold air temperatures) (Paradis et al. 2016). Shrub cover is associated with a reduction of moss biomass, decreasing ground insulation and impacting soil moisture (Bueno et al. 2016). While these processes act as both positive and negative feedbacks, they are expected to exacerbate permafrost thaw (Lawrence and Swenson 2011; Myers-Smith and Hik 2018).

<b>Positive feedbacks</b>	<b>Negative feedbacks</b>	<b>Landscape changes</b>
<ul style="list-style-type: none"> <li>• Permafrost thaw due to trapping of snow</li> <li>• Decreased surface albedo</li> <li>• Increased evapotranspiration</li> <li>• Increased nitrogen mineralization</li> <li>• Increased fire frequency and intensity</li> </ul>	<ul style="list-style-type: none"> <li>• Reduced summer soil temperature due to shading</li> <li>• Increased biomass</li> </ul>	<ul style="list-style-type: none"> <li>• Amplified species turnover</li> <li>• Lichen declines</li> <li>• Migration of boreal species (such as moose and beaver)</li> </ul>

*Table 1: A brief summary of climate-vegetation interactions associated with shrub expansion in the Arctic. Summarized from: Myers-Smith et al. (2011); Lawrence and Swenson (2011); Lorant and Goetz (2012); Chapin III et al. (2005); Swann et al. (2010); Weintraub and Schimel (2005); Mack et al. (2011); Mod and Luoto (2016).*

Additional consequences of shrub expansion link hydrologic and nutrient cycling dynamics to vegetation change processes. For example, shrubification is expected to increase rates of evapotranspiration leading to increased latent heat flux (Pearson et al. 2013). Tall-stature arctic shrubs are deciduous and impact microbial decomposition by simultaneously increasing litter quantity and decreasing quality (due to higher carbon-

nitrogen ratios of woody debris) in comparison to low-stature tundra vegetation (Weintraub and Schimel 2005). Conversely, shrub-induced soil warming has the potential to increase nitrogen mineralization, an important process in the nitrogen-limited tundra ecosystem. Increasing populations of nitrogen-fixing symbiont shrubs have the potential to further alter the nutrient balance of locations where they occur (Salmon et al. 2019). The net impact of changing litter inputs on microbial processes in the Arctic needs is complex and currently undefined (Myers-Smith et al. 2011). However, nutrient cycles are expected to shape the ability of vegetation to track climate warming within the Arctic.

### **3. Summary**

Global climate change is significantly impacting arctic ecosystems. Warming at the Earth's poles is happening at more than twice the rate of the global average. Arctic amplification is caused by positive biophysical warming feedbacks induced by decreased reflection of incoming solar radiation (albedo) which is a consequence of diminishing sea-ice and snow cover (Box et al. 2019). As a result of arctic amplification, the region is warming at a rate of more than twice the global average. The Arctic, which has acted as a carbon sink for millennia and contains the largest pool of soil organic carbon worldwide, is expected to become a carbon source as a result of anthropogenic climate change (Webb et al. 2016). While plant growth is increasing, it is not expected to keep pace with the increased release of greenhouse gases from soil microbial respiration, which is accelerating because warming soil temperatures and permafrost thaw (Schuur et al. 2015).

Vegetation change will play an important role in determining the magnitude of warming caused by Arctic change (Euskirchen et al. 2016b; Lorantý et al. 2016).

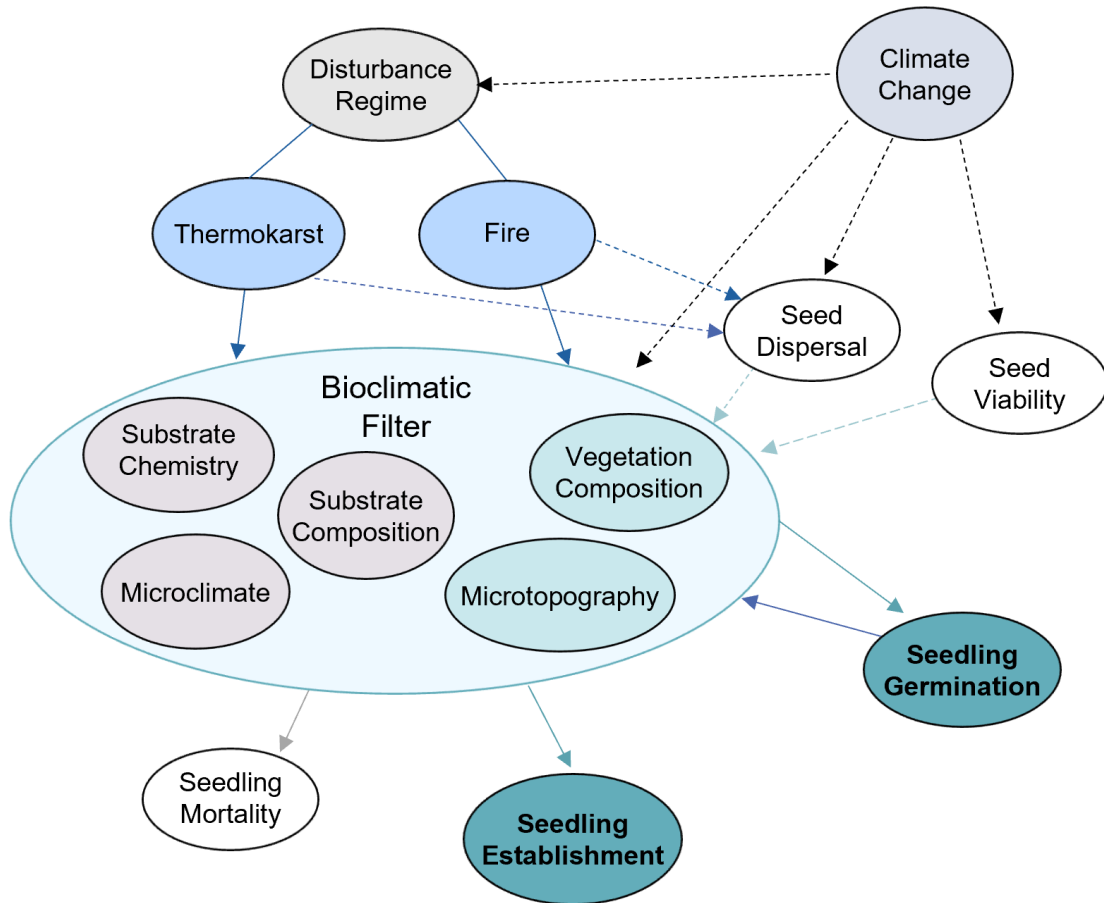
Increasing vegetation productivity, characterized by a greening of the Arctic, demonstrates that plants will assimilate more carbon in a warmer Arctic (Box et al. 2019). Woody shrubs are expanding into and within tundra ecosystems. Taller plants store more carbon in their biomass but cause localized warming and permafrost thaw. For example, tall shrubs decrease tundra albedo and increase winter soil temperatures through trapping of snow. However, they also cool summer soil temperatures by shading the surface (Myers-Smith et al. 2011). Ultimately, vegetation acts both as an important mediator of and driver for Arctic climate change. The rate of vegetation change controls the degree to which the Arctic will become a carbon source in a warmer world.

## CHAPTER III

# LANDSCAPE DISTURBANCE FACILITATES SHRUB SEEDLING ESTABLISHMENT

### *1. Background*

Shrub expansion is currently occurring throughout the Arctic biome. This northward shift of shrubline and infilling of shrub populations is controlled by seedling recruitment (Myers-Smith and Hik 2018). Past shrub expansion research has focused on the controls of shrub height and impact of shrubification on Arctic carbon and energy balances (Myers-Smith et al. 2011). Consequently, the processes that control the recruitment of new shrubs are often overlooked. However, in order to model changing tundra shrub and ecosystem dynamics, it is necessary to understand the conditions that promote or limit seedling establishment (Swanson 2015). While environmental conditions in the Arctic are changing in ways that promote shrub growth, observations of shrub expansion are typically derived from adult individuals. However, seedlings have both a limited capacity to survive suboptimal conditions and a constrained bioclimatic envelope (which can differ from that of adults) (Büntgen et al. 2015; Milbau et al. 2017). As a result, seedlings are a critical component of shrub expansion processes. In this thesis, I examine the bioclimatic controls on the germination and establishment bottleneck for shrub seedlings, an essential component of Arctic shrubification (Figure 1).



*Figure 1: A conceptual framework for climate and landscape disturbance controls on shrub seedling establishment.*

Climate change is increasing annual temperatures, lengthening the growing season, and altering the hydrologic cycle of the Arctic, facilitating shrub expansion (Graae et al. 2011; Martin et al. 2017). Shrubification causes cascading ecosystem effects which further alter tundra ecosystem structure and function. By increasing winter soil temperatures (via increased snowpack insulation), buffering summer soil temperatures through shading, reducing albedo, and altering nutrient cycles the proliferation of shrubs fundamentally alters tundra ecosystems. The Boreal-Arctic Transition Zone, the area beyond treeline where tall shrubs currently intermix with graminoid tundra, is expected to

rapidly change significantly with warming and provides a window into the future for northern tundra ecosystems.

Warming temperatures can increase the rate of shrub recruitment from seed by increasing both the quantity and viability of seed produced by adults, as well as creating favorable conditions for germination (Figure 1) (Douhovnikoff et al. 2010). Seedlings are rare in tundra ecosystems as a result of seed viability and germination limitations. The prevalence of asexual reproduction (through clonal propagation) in Arctic plants in combination with limited sexual reproduction has led them to be characterized as dispersal-limited (Gough 2006). However, it has been suggested that tundra plants could be limited by seedling establishment rather than dispersal, since adults produce abundant seed but bioclimatic conditions limit seedling germination and survival (Milbau et al. 2017). Seed addition studies have indicated that germination rates would increase if suitable substrate and environmental conditions are available (Gough et al. 2015). Bioclimatic conditions in the first couple of growing seasons are a critical control on shrub recruitment as seedlings are particularly vulnerable to environmental stresses (such as desiccation and frost damage) and must acquire sufficient carbon reserves in order to survive prolonged snow-cover during winter (Büntgen et al. 2015; Milbau et al. 2017). Longer growing seasons and warming are expected to ameliorate conditions for seedlings in tundra ecosystems, increasing seedling establishment rates. As a result, warming-induced changes in the Arctic are expected to modify both dispersal and establishment controls on shrub recruitment.

In addition to changing vegetation composition, warming also increases the frequency and magnitude of landscape disturbances throughout the Arctic (Pizano et al.

2014; Schuur and Mack 2018). The two dominant Arctic disturbance regimes are wildfire and thermokarst, ground subsidence that occurs as a result of permafrost thaw. Both types of disturbance are facilitated by warming, and the area burned in the Alaskan Arctic is expected to double before the end of the century (Hu et al. 2015; Euskirchen et al. 2016b). These disturbances alter landscape conditions by removing vegetation, reducing soil organic matter, exposing mineral soil, increasing permafrost thaw, warming soil temperatures, and altering hydrologic conditions (Schuur and Mack 2018). The interaction of landscape disturbances on warming-induced vegetation change will shape the future of the Arctic (Hoegh-Guldberg et al. 2018). Higher cover and abundance of shrubs in the decades following disturbance events has been noted in multiple observational studies, suggesting a mechanism for facilitation of shrub expansion (Racine et al. 2009; Myers-Smith et al. 2011; Bret-Harte et al. 2013).

Landscape disturbances have the potential to increase shrubification rates beyond warming-induced expansion (Myers-Smith et al. 2011; Schuur and Mack 2018). In addition to warming, fire and thermokarst potentially increase seedling establishment rates by reducing competition and improving seedbed quality (Figure 1) (Lloyd et al. 2002; Narita et al. 2015). In the Boreal-Arctic Transition Zone, where much of the soil surface is covered by thick moss, lichen, and organic matter layers; disturbances which alter the surface organic layer or expose the mineral soil surface could facilitate seedling establishment if they provide higher quality substrates for plant growth (Schuur and Mack 2018; Frost et al. 2020). Within boreal forests this process has been linked to facilitation of tree seedlings and altered successional trajectories following high-severity fires (Johnstone et al. 2005). While fire severity is typically lower in tundra, combustion

of soil organic matter could promote shrub establishment through substrate modification as well, and anecdotal observations suggest that fire events can double the rate of seedling establishment in tundra ecosystems (Myers-Smith et al. 2011). Observational surveys in the Alaskan Arctic show that soils exposed by thermokarst action can serve as shrub seedling nurseries by creating areas of exposed ground that have higher soil temperatures and increased nitrogen content (Huebner and Bret-Harte 2019). As a result, both fire and thermokarst may facilitate seedling establishment through alteration of bioclimatic conditions and substrate modification (Figure 1). Disturbance-driven seedbed quality improvements may increase seedling establishment to a greater degree than climate-driven bioclimate alterations. For example, at treeline, experimental moss removal has been shown to facilitate tree seedling establishment more than warming of 1°C while moss competition exerted more control than soil moisture (Lett et al. 2020).

Through a manipulative field experiment, I test the controls shaping this critical phase of shrub expansion, seedling recruitment and establishment. In addition to quantifying the effect of disturbance on seedling success, I examine the environmental parameters that define conditions for establishment. I investigate whether shrub seedling establishment is facilitated by landscape disturbance, and if so, which processes underpin such control. I hypothesize that the establishment of shrub seedlings with the Boreal-Arctic Transition Zone is limited by a lack of suitable substrate and increases following disturbance due to improvements in seedbed quality. This hypothesis incorporates the theory that seedling establishment represents a two-phase filtering process that controls the establishment bottleneck and is mediated by landscape disturbances (Figure 1). The first phase consists of requisite conditions for seedling germination, while the second



phase regulates seedling survival. I hypothesize that substrate quality is a key component of this bioclimatic filter, exerting control over both recruitment and establishment rates.

## ***2. Materials and Methods***

### ***2.1 Study Site***

My study is located within the Boreal-Arctic Transition Zone, on the Seward Peninsula in northwestern Alaska. This region is characterized by vulnerable discontinuous permafrost, relatively frequent tundra fires, and recent shrub expansion (Racine et al. 2004; Swanson 2015; Busey et al. 2008). While shrub expansion is a circumpolar process, areas within this low Arctic transition zone are expected to demonstrate warming-induced vegetation responses most quickly – making the region a model area for studying shrub expansion (Myers-Smith et al. 2011). The Seward Peninsula can be viewed as a proxy for a warmer Arctic as it features tussock tundra, expanding shrubs, and transitional permafrost (Busey et al. 2008). Additionally, throughout the historical period this area has experienced a higher fire frequency in comparison to other tundra areas and is expected to experience to increased fire activity with climate warming (Hu et al. 2015; French et al. 2015; Hoegh-Guldberg et al. 2018). An estimated 15% of the region has experienced multiple fire events in recent history, an atypically high proportion for tundra regions under current conditions (Figure 2) (Rocha et al. 2012). Given these characteristics, the Seward Peninsula provides a proxy for projections of intensified fire regimes throughout the Arctic (Liljedahl et al. 2007; Bret-Harte et al. 2013).

The Seward Peninsula is included within the Beringian Arctic floristic sector (Walker et al. 2018). It was a part of the Bering Land Bridge, which remained

unglaciaded during the Last Glacial Maximum (28-15 thousand years before present) and was a cryptic refugium for trees, shrubs, and herbaceous tundra species during this time (Brubaker et al. 2005). Currently it is classified within subzone E of the Circumpolar Arctic Vegetation Map. Subzone E the warmest subzone, with mean July temperatures of 10-12°C (Walker et al. 2018). Unburned vegetation within subzone E is typically dominated by sedges, shrubs (mainly <80 cm in height), lichen, and moss (which forms a layer 5-10 cm thick) (Walker et al. 2018; Frost et al. 2020). The southeastern portion of the Seward Peninsula marks the westernmost limit of white spruce, *Picea glauca* (Moench) Voss, and treeline advance has been observed within this region (Lloyd et al. 2002).

My study is focused upon two landscape disturbance regimes, tundra fire and thermokarst, both of which are paired with reference undisturbed tundra sites (Figure 2). In the fire treatment (site name: Quartz Creek, 65°26'N, 164°37'W), plots are distributed across a tundra fire complex where there have been multiple overlapping fires in the past 50 years (AICC 2020). Experimental plots are located within areas that have burned three times during this period; in 2015, 2002, and 1971. During the 2015 “Mingyk Lake” fire, 61% of the 21,136 acre fire was characterized as low severity, 27% moderate severity and 0% high severity (Eidenshink et al. 2007). Fire severity data is unavailable for earlier fires. There were additional fires on this complex in 1997 and 2019, although they did not overlap the experimental plots. The thermokarst treatment is located within close proximity to the *P. glauca* treeline at the boreal-tundra ecotone. At this site, the landscape features carbon-rich soils currently undergoing subsidence due to thermal degradation of permafrost (site name: Council, 64°51'N, 163°42'W). Both sites are characterized by

lichen-rich tussock tundra (primarily dominated by the tussock-forming sedge *Eriophorum vaginatum* L.), however a mixture of moist acidic tundra and dwarf shrub tundra communities also co-occur.

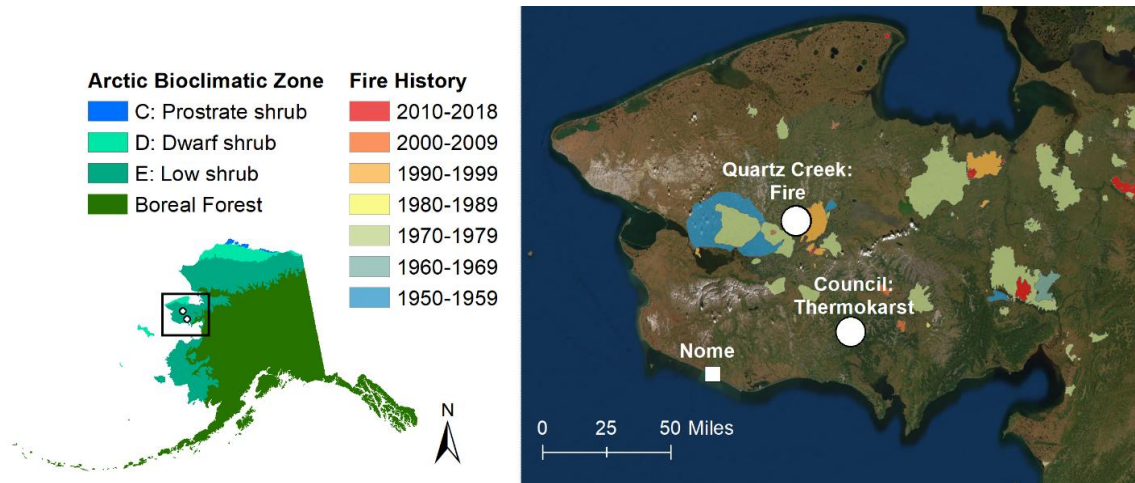


Figure 2: Study site locations on the Seward Peninsula (northwestern Alaska) in relation to current bioclimatic zones and fire history (CAVM Team 2003; AICC 2020).

## 2.2 Focal Species

My study focuses on five erect deciduous shrub species currently growing throughout the Seward Peninsula. Two families, Betulaceae and Salicaceae, are represented within this species assemblage, consisting of birch, willow, and alder genera (*Betula*, *Salix*, and *Alnus* respectively). *Betula nana* L. is a frequent low-growing, dwarf shrub component of tussock tundra. In contrast, *Betula glandulosa* Michx., *Salix pulchra* Cham., *Salix glauca* L., and *Alnus viridis* subsp. *fruticosa* (Rupr.) Nyman are taller in stature and typical components of the dwarf shrub-lichen tundra assemblages that are dispersed throughout subzone E. *B. nana* has been documented to grow larger (both in

cover and taller in stature) with increased warming and nitrogen-addition (Bret-Harte et al. 2001; Mack et al. 2004). Both *Betula* species form ectomycorrhizal relationships with fungal symbionts, which can facilitate increased growth under future warming scenarios (Treseder et al. 2004; Deslippe et al. 2011). *A. viridis* forms symbiont relationships with the nitrogen-fixing bacteria actinomycete *Frankia*, which increases nutrient availability in an otherwise typically nitrogen-limited system (Salmon et al. 2019). *Betula* and *Alnus* seeds are produced in small cone-like structures, which typically mature during the fall and are wind-dispersed during the winter months (Viereck and Little 2007). *Salix* seeds form in capsules, mature in mid-summer and are wind-dispersed during the late summer and early fall (Viereck and Little 2007). *Salix* seeds are known for their limited longevity and ease of decay, with many seeds only remaining viable for a couple of weeks (Huryñ and Hobbie 2013; Huebner and Bret-Harte 2019).

### 2.3 Sampling and Experimental Design

#### Seed Addition Experiment

In the beginning of the 2018 growing season I established a manipulative experiment to examine the process by which landscape disturbance influences shrub seedling recruitment and establishment. I used a factorial design to compare two site-level disturbance treatments with reference undisturbed sites (Figure 3). The disturbance treatment was combined with a split-plot scraping treatment (scraped, unscraped) with 5 replicate blocks per disturbance treatment. Each block consisted of pair of 0.75 x 1.5m plots separated by less than 2m. I used historical fire perimeters confirmed through observations of charcoal and tussock morphology to evaluate fire history (AICC 2020). I collected seeds of five shrub species from sites throughout the Seward Peninsula in the

fall of 2017 and cold stratified them at -20°C for 8 months (late October – May). In June 2018, I broadcast seeded each plot with 100 seeds each of *A. viridis* subsp. *fruticosa*, *B. glandulosa*, *B. nana*, and 50 seeds of *S. pulchra* and *S. glauca*.

To determine the effect of seed bed preparation by disturbance upon seedling establishment, one plot from each pair was scraped to remove bryophytes (mosses and lichens) in a surface manipulation treatment (Figure 4). This treatment mimics the substrate modifications and increased access to mineral soil that occurs as a result of disturbances events (via combustion during fire or subsidence during thermokarst). This form of novel disturbance was done using a hand cultivator in accordance with the protocol utilized by the Global Treeline Experiment (Brown et al. 2013). All removed material was collected, dried, and weighed for biomass quantification. Each plot was divided into 50 subplots (15 x 15cm) and seed was sown 16 randomly selected subplots at a rate of 25 seeds per subplot. The subplot method was chosen to ensure efficacy of seedling census efforts by restricting search area and to isolate seeds by species (since germinants of the same family can be difficult to identify at species-level prior to development of true leaves). Overall, 16,000 seeds were broadcast during experiment establishment.

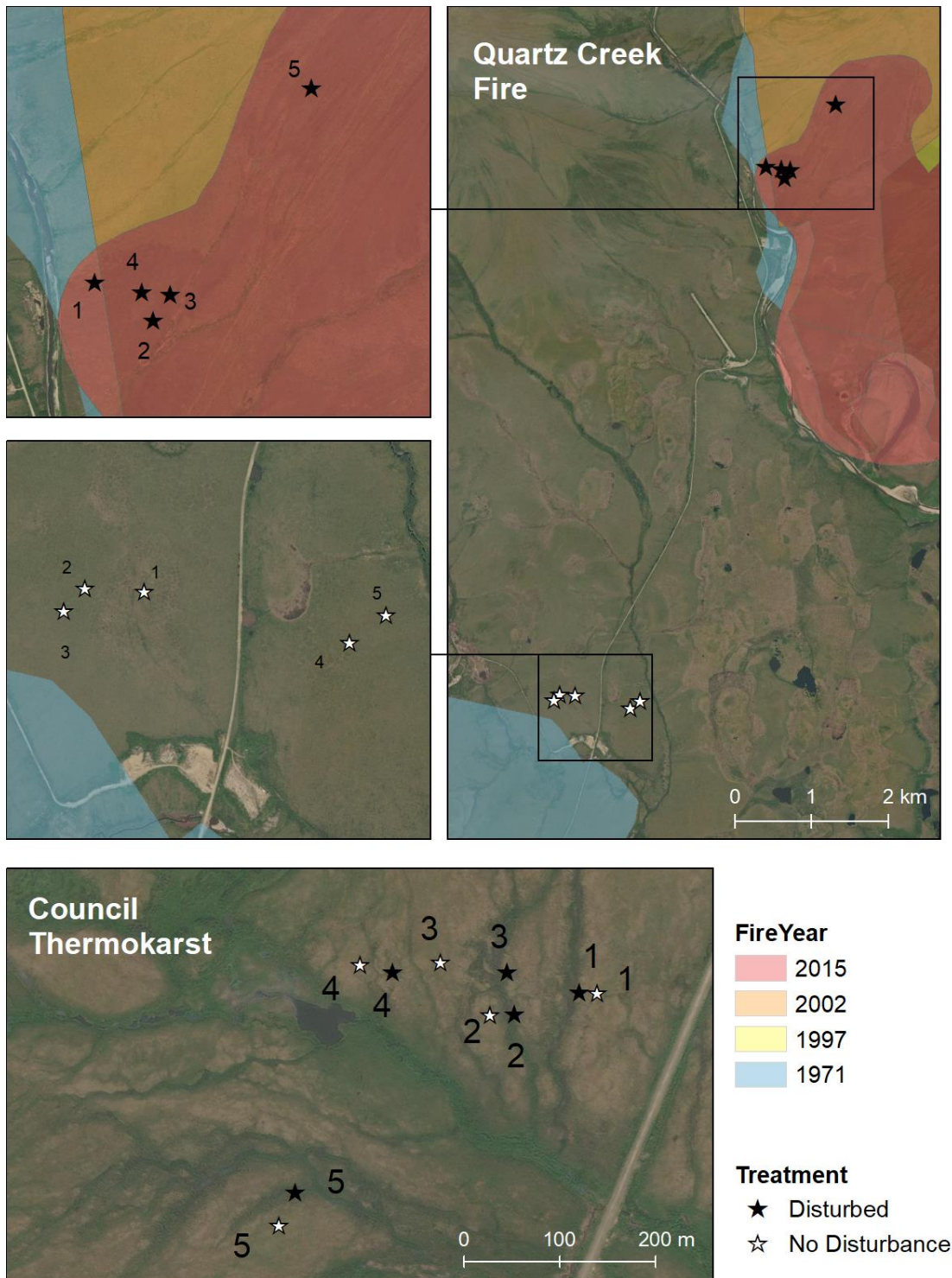
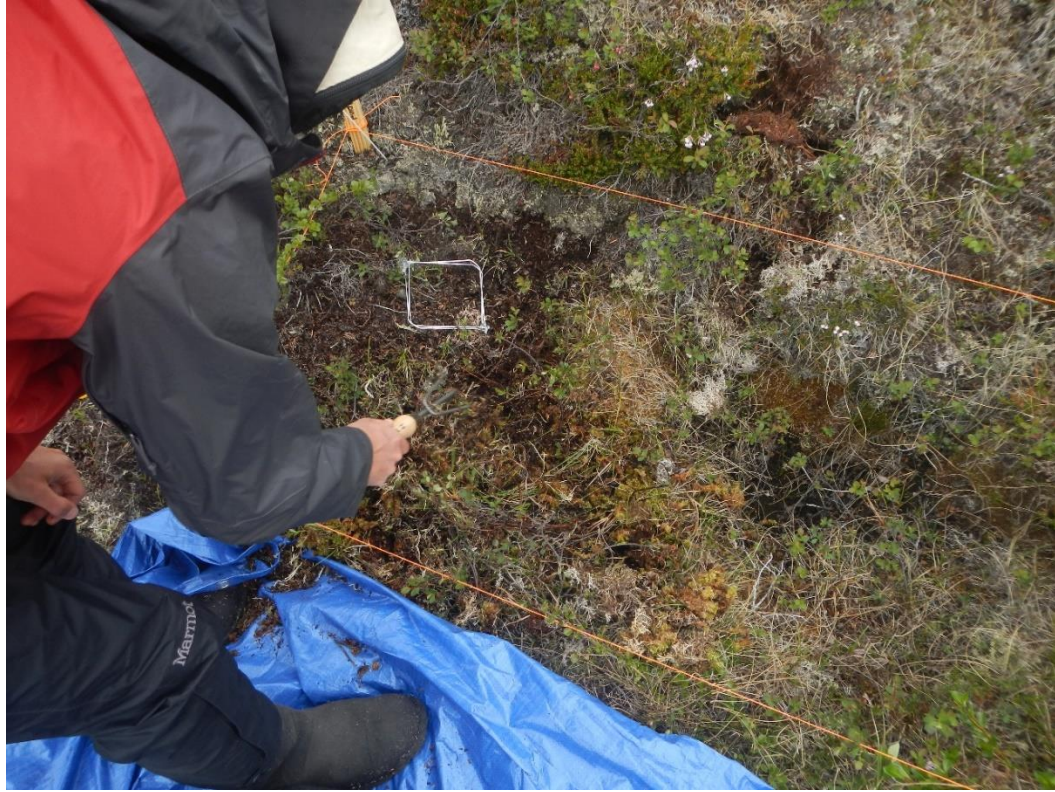


Figure 3: Seed addition experimental design. Two disturbance types were tested in comparison to undisturbed tundra, with 5 replicates per treatment. Each replicate consists of a pair of plots (scraped and unscraped) testing the effect of lichen and moss removal on seedling establishment.





*Figure 4: Photograph of the "scraping" surface disturbance treatment methodology. Left-hand portion of the plot has been partially scraped, revealing soil surface (organic horizon) while the central area contains loosened moss (*Sphagnum* sp.) and lichens (*Cladonia* sp.). The right-hand portion of the plot contains unmanipulated bryophytes. The plot is located within a thermokarst area at the Council site. A 15x15 cm wire frame is in the upper left corner for scale.*

#### Seedling Recruitment and Establishment

After sowing seeds in June 2018, I conducted population-level censuses at the end of the first growing season (August 2018) and second growing season (August 2019).

During each census I quantified seedling abundance and mortality. Seedling "emergence" consists of individuals that germinated and survived in the first growing season. Seedling "establishment" consists of seedlings that survived through second growing season.

Delayed germination of seedlings was observed during a census conducted at the beginning of the second growing season (June 2019). As a result, seedling establishment

counts include both seedlings that germinated during the first season in addition to those which emerged during the second season.

#### Microsite Bioclimatic Characteristics

Within each plot I measured multiple abiotic and biotic parameters to characterize environmental conditions controlling seedling success. In order to characterize microsite variability, I measured each of these parameters in three subplots per plot, with each of the parameter measurements co-located. In each of the three census periods I monitored the depth of soil thaw using a tile probe marked with centimeter increments. August measurements represent approximate active layer depth (depth of maximum thaw). Soil temperature during each sample period. In 2018 the measurements were made at a 20 cm depth using a Traceable® long-stem digital thermometer, while in 2019 they were located at 15 cm using an Aquatuff 35200-K thermocouple. Soil temperature and thaw depth measurements were each averaged over the two sample periods in order to characterize microsite thermal regimes. In 2019, average percent moisture for the top 0-20 cm of the soil profile was measured using Time Domain Reflectometry with a MiniTrase (Soil Moisture Incorporated). I measured seedbed substrate thickness (the distance between the top surface of the moss or lichen layer to the O<sub>i</sub> soil horizon). I sampled micro-scale topography (which is the depth from vegetative surface to the seedbed substrate).

Within each I estimated plot vascular and non-vascular absolute percent cover by plant functional type (erect dwarf shrub, deciduous prostrate shrub, evergreen prostrate shrub, graminoid, forb, live moss, lichen, liverwort) and as well as substrate (bare, dead moss, litter). I quantified the Normalized Difference Vegetation Index ( $NDVI = (NIR -$



Red)/(NIR+Red)) at each plot in August 2019 using a portable SpectroSense2 (Skye Instruments). I also measured canopy height in August 2018.

### Soil Biogeochemistry

I collected two sets of soil cores for laboratory analysis from locations adjacent to each plot. In August 2018, cores were collected from the organic horizon surface to a depth of 10 cm (the rooting zone substrate) using a sharpened 2.5 cm diameter core liner. In August 2019, cores were collected from the entirety of the active layer (thawed soil) and the depth of sample was noted. These samples were extracted using a 2.5 cm diameter AMS soil corer and the sample was transferred to a sealed plastic bag. All cores were frozen after collection and stored at -20°C until processing. In the laboratory, samples were thawed, oven-dried at 105°C for 48 hours, ground using a mortar and pestle, and sieved in preparation for analysis. As samples were taken from outside of the plot boundaries and thus were not affected by the scraping treatment, samples were analyzed at the replicate level as opposed to per plot.

After sample preparation, I measured carbon and nitrogen composition (% total C and % total N) using a Costech ECS 410 elemental analyzer. I quantified soil organic matter concentration was quantified loss on ignition via combustion in a 550°C furnace. I measured bulk density in order to convert soil stoichiometry to stocks. I measured soil pH was measured for the 10 cm depth soils only using a weight-based 7:1 deionized water to soil ratio in order to account for the large organic component of these samples.

## 2.4 Data Analysis

### Microsite Bioclimatic Characteristics

I tested for significant differences in soil physical properties (thaw depth, temperature, moisture, and substrate thickness), microsite properties (microtopography), vegetative productivity (canopy height, NDVI), and vegetation composition across plot- and site-level treatments using two-way analysis of variance (ANOVA). Additionally, I tested for differences in soil biogeochemical properties (percent total carbon, percent total nitrogen, C:N ratio, pH, bulk density) across site-level treatments using one-way ANOVA. For statistically significant differences ( $p < 0.05$ ), I then performed post hoc multiple comparisons using Tukey's honestly significant difference tests (Tukey's HSD) to identify significance (adjusted  $p < 0.05$ ) by treatment. Mean values per plot were used for analyses that had multiple observations per plot to prevent pseudo-replication.

### Seedling Emergence and Establishment

I tested the responses of seedling emergence and survival to disturbance and scraping using a generalized linear mixed model (GLMM) with a negative binomial distribution. The models included survey year, disturbance treatment, scraping, with their two-way and three-way interactions as fixed effects. Plot, replicate, and site were included as nested random effects crossed with species. A Tukey HSD test was used to compare differences in seedling emergence and survival between treatments. All generalized linear mixed model and post hoc analyses were conducted using the "lme4" and "emmeans" packages in R (Bates et al. 2020; Lenth et al. 2020; R Core Team 2020). To ease interpretation, all seedling count values have been converted to proportion of

seeds sown prior to plotting, uncertainty estimates are indicated with 95% confidence intervals (CI), unless otherwise noted.

I conducted separate analyses for seedling mortality and survivorship estimates. In order to account for delayed germination of seedlings within mortality estimates, I utilized survey data from seeded subplots that did not have an increase in seedling density from 2018 to 2019 (the “initial germinant subset”). Survival rates were calculated as the proportion of seedlings that survived through 2019 using this same subset. I then tested the responses of seedling mortality and survival rates to disturbance and scraping treatments using GLMMs drawn from the binomial distribution with the same random effects structure as above and conducted post hoc Tukey HSD tests to compare groups.

#### Bioclimatic Controls on Seedling Establishment

I used piecewise structural equation models to evaluate the way that disturbance and scraping treatments affect seedling establishment through proximal controls on tundra bioclimatic conditions. Using the “piecewiseSem” package, I tested linear mixed models for the control of disturbance and scraping treatments on microsite bioclimatic characteristics, and GLMMs for the control of these characteristics on seedling emergence and establishment (Lefcheck et al. 2019). In order to evaluate controls on seedling survivorship rates, I constructed a separate model using the same framework, but with the initial germinant data subset and a GLMM drawn from the binomial distribution. Structural equation model goodness of fit was evaluated using a chi-squared test of Fisher’s C with a criterion of  $p > 0.05$ .

### **3. Results**

#### **3.1 Seedling Emergence and Establishment**

Seedling emergence during the first growing season did not vary significantly between disturbed and undisturbed plots. However, seedling establishment through the second growing season was greater in disturbed areas than undisturbed (Figure 5). Scraped plots did not significantly differ from unscraped plots, except for a marginal increase in undisturbed tundra ( $p = 0.12$ ). Seedling counts were significantly lower in undisturbed plots at the end of the growing season, indicating high mortality within undisturbed tundra. In contrast, seedling counts in disturbed plots did not vary significantly between the seasons, indicating increased establishment within disturbed areas. Approximately four times as many seedlings established in disturbed plots than undisturbed (Table 2).

Mortality was a significant factor across all treatments, however both disturbance and scraping positively affected survivorship (Figure 6). Estimated median survivorship was 4% in undisturbed-unscraped plots. In comparison, disturbed-unscraped plots had median survivorship of 18%, while in undisturbed-scraped it was 11%, and in disturbed-scraped it was 16%. The distribution of seedling survival rates varied across treatments, with greater variance in disturbed and scraped plots (Figure 7). In undisturbed-unscraped plots, seedling survival rates ranged from 3-13%. In contrast survival rates ranged from 8-50% in undisturbed-scraped, 11-34% in disturbed-unscraped, and 10-37% in disturbed-scraped.

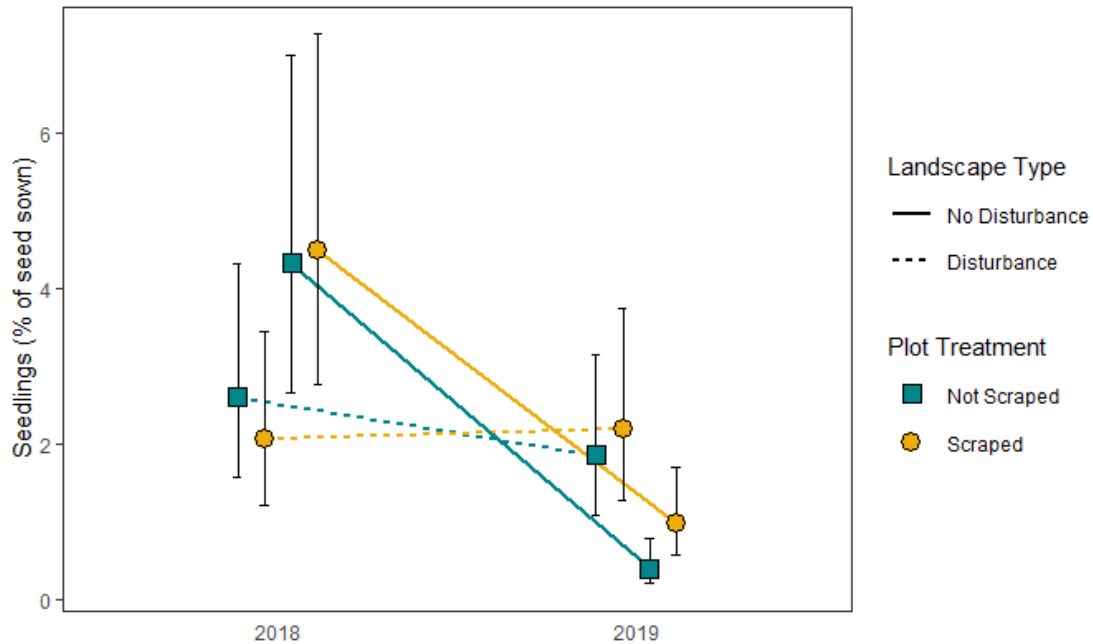


Figure 5: Effect of disturbance on shrub seedling recruitment and establishment. Number of seedlings as a percentage of seed sown at the end of the 1st and 2nd growing seasons (estimated marginal mean  $\pm$  95% confidence interval). Initial seedling emergence did not consistently vary across disturbance treatments (2018). Seedling survival was low in undisturbed areas (solid lines) and high in disturbed sites (dashed lines). In undisturbed areas seedling establishment was higher in scraped plots (yellow circles) than unscraped (green squares).

Treatment		2018	2019
Undisturbed	Not scraped	4.39% ( $\pm$ 1.05)	0.44% ( $\pm$ 0.14)
Undisturbed	Scraped	5.32% ( $\pm$ 1.26)	1.01% ( $\pm$ 0.28)
Disturbed	Not scraped	2.59% ( $\pm$ 0.65)	1.93% ( $\pm$ 0.51)
Disturbed	Scraped	2.28% ( $\pm$ 0.58)	2.33% ( $\pm$ 0.62)

Table 2: Estimated mean number of seedlings by treatment ( $\pm$  standard error). Values are the proportion of seedlings as percent of seed sown.

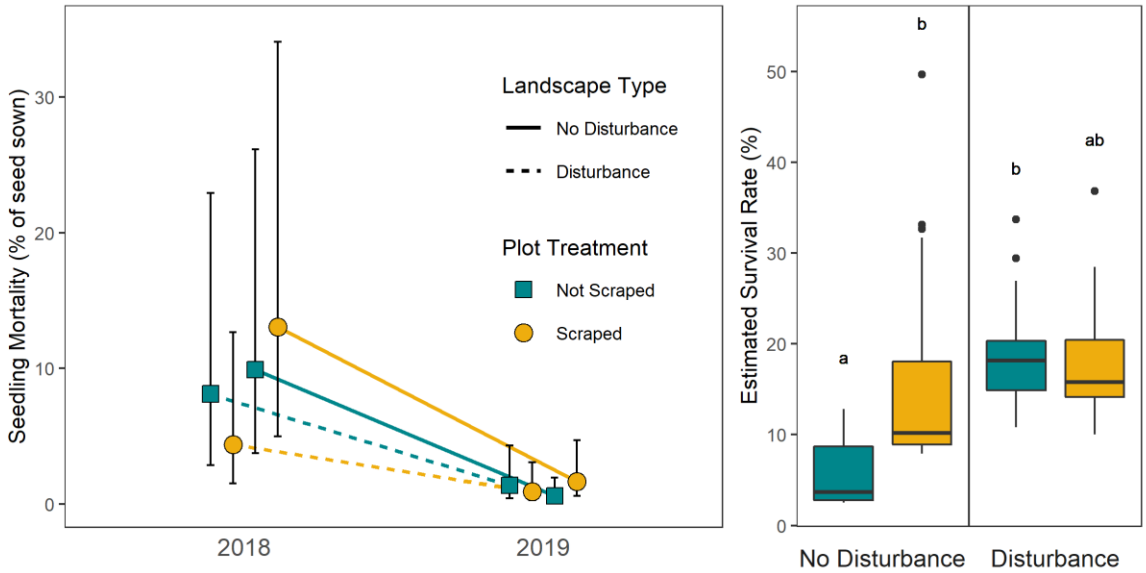


Figure 6: Estimated effect of disturbance on shrub seedling mortality (left) and survival rates (right) for seedlings that germinated during the first season. Estimated marginal means with 95% confidence intervals, lower case letters indicate significant differences between groups in post hoc tests.

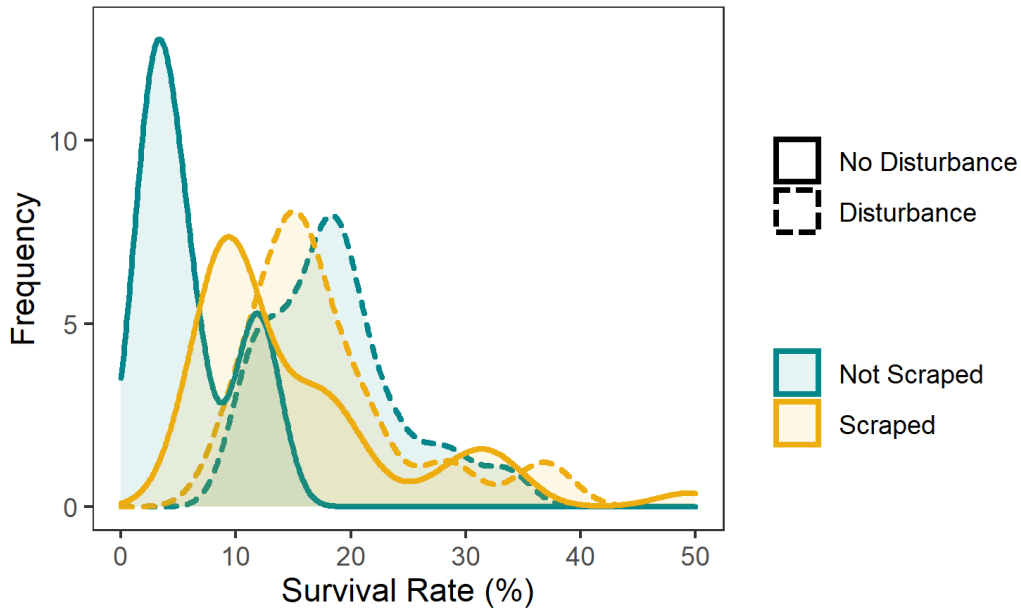
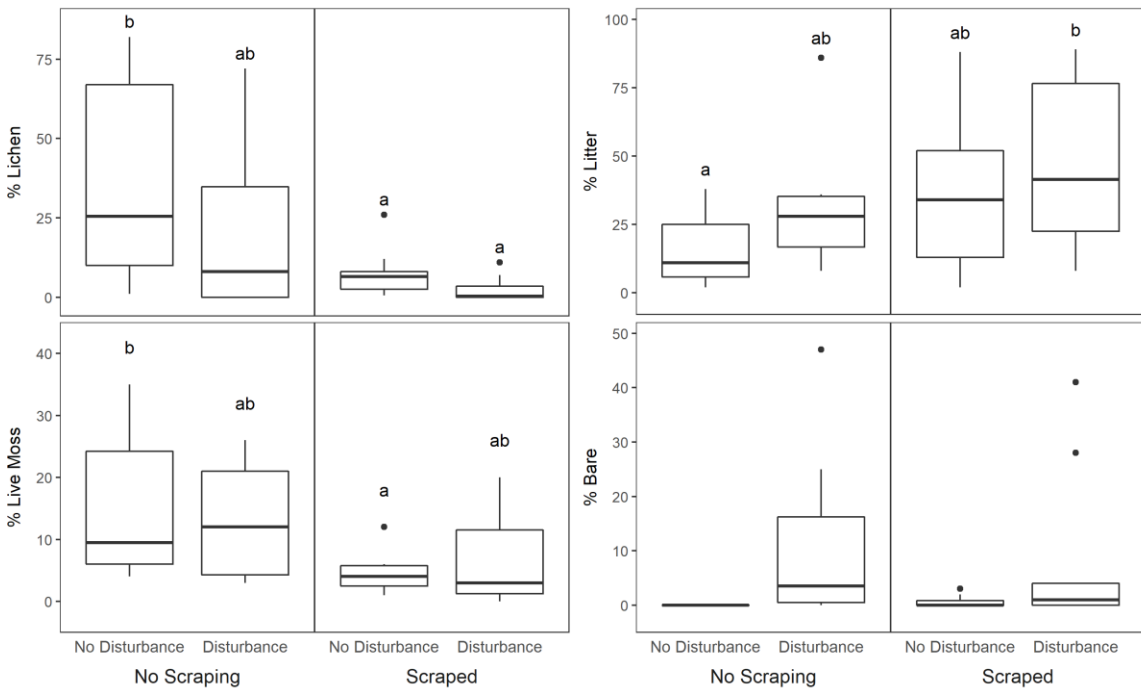


Figure 7: Density plot showing the distribution of seedling survival rates for seedlings that germinated in the first season. Seedlings within unscraped, undisturbed plots had lower survivorship (as indicated by the high frequency of low survival rates), while disturbed and scraped plots had higher survivorship (as indicated by the greater frequency of higher survival rates).

### 3.2 Substrate Quality and Bioclimatic Conditions

Both scraping and landscape disturbance affected seedbed substrate composition. Scraping significantly decreased lichen and live moss abundance, while disturbance increased litter cover (Figure 8). The dry mass of lichens and mosses removed varied between 2.3 and 1,216.8 g/m<sup>2</sup>, with significant differences between sites but not disturbance treatment (medians: Council: 830 g/m<sup>2</sup>, Quartz Creek: 196 g/m<sup>2</sup>) (Figure 9, bottom-right). Seedbed substrate thickness ranged from 0.5-20 cm and was thinner in disturbed areas but did not vary with scraping.



*Figure 8: Effect of landscape disturbance and scraping treatments on seedbed substrate composition. Lower case letters denote significant differences between groups in post hoc tests, the absence of lowercase letters indicate no difference between treatments.*

Landscape disturbance alters edaphic conditions, resulting in increased soil thaw (active layer depth) and surface soil temperatures (Figure 9). Across all plots, thaw depth ranged from 28-91 cm, with deeper thaw in disturbed areas (median 68 cm) and shallower in undisturbed (56 cm). Surface soil chemistry varied with disturbance, dependent on site and disturbance type. Carbon concentration and the C:N ratio were higher within undisturbed areas at Council while pH was lower (Figure 9). Tundra fire had a variable effect on bulk density, decreasing bulk density at the soil surface (top 10 cm) while increasing it over the full thawed soil profile. However, there was no significant effect of disturbance on the total carbon and nitrogen stocks with surface substrate or active layer (see Appendix, Table 3).

Ecosystem structure, as reflected in canopy height and microtopography measurements, varied by site but not disturbance history (Figure 9). At Quartz Creek, NDVI was higher within burned areas than unburned, which were higher than Council (Figure 9). The cover of lichen and graminoid species varied by site, but not disturbance (Figure 10). The two PFTs were inversely correlated, with higher lichen abundance at Council and graminoid dominance at Quartz Creek. The proportion of bare ground, litter, and evergreen prostrate shrubs were affected by disturbance.



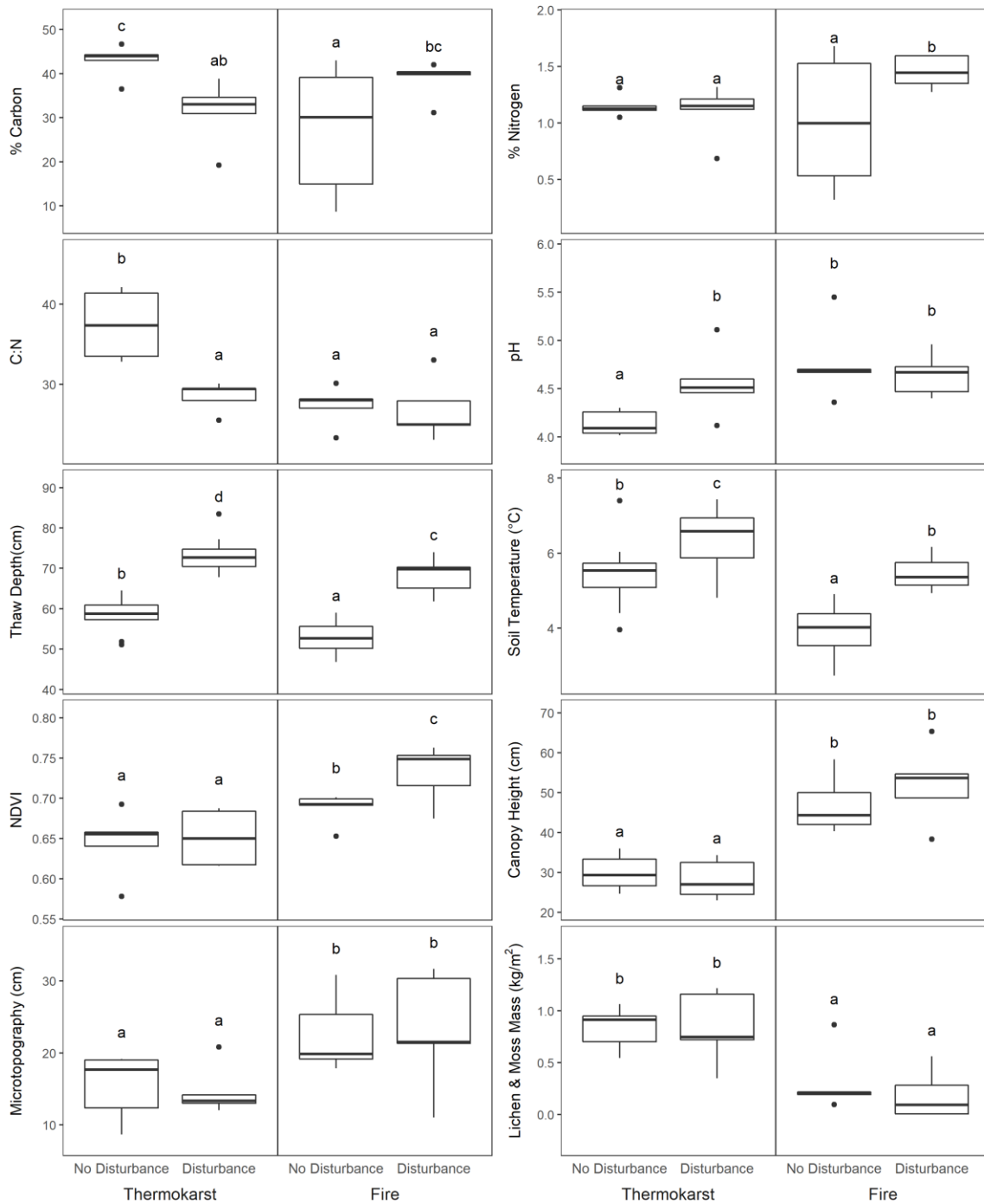


Figure 9: Effect of landscape disturbance on bioclimatic parameters, grouped by site (Thermokarst = Council, Fire= Quartz Creek). Lowercase letters indicate significant difference between groups in post hoc tests.

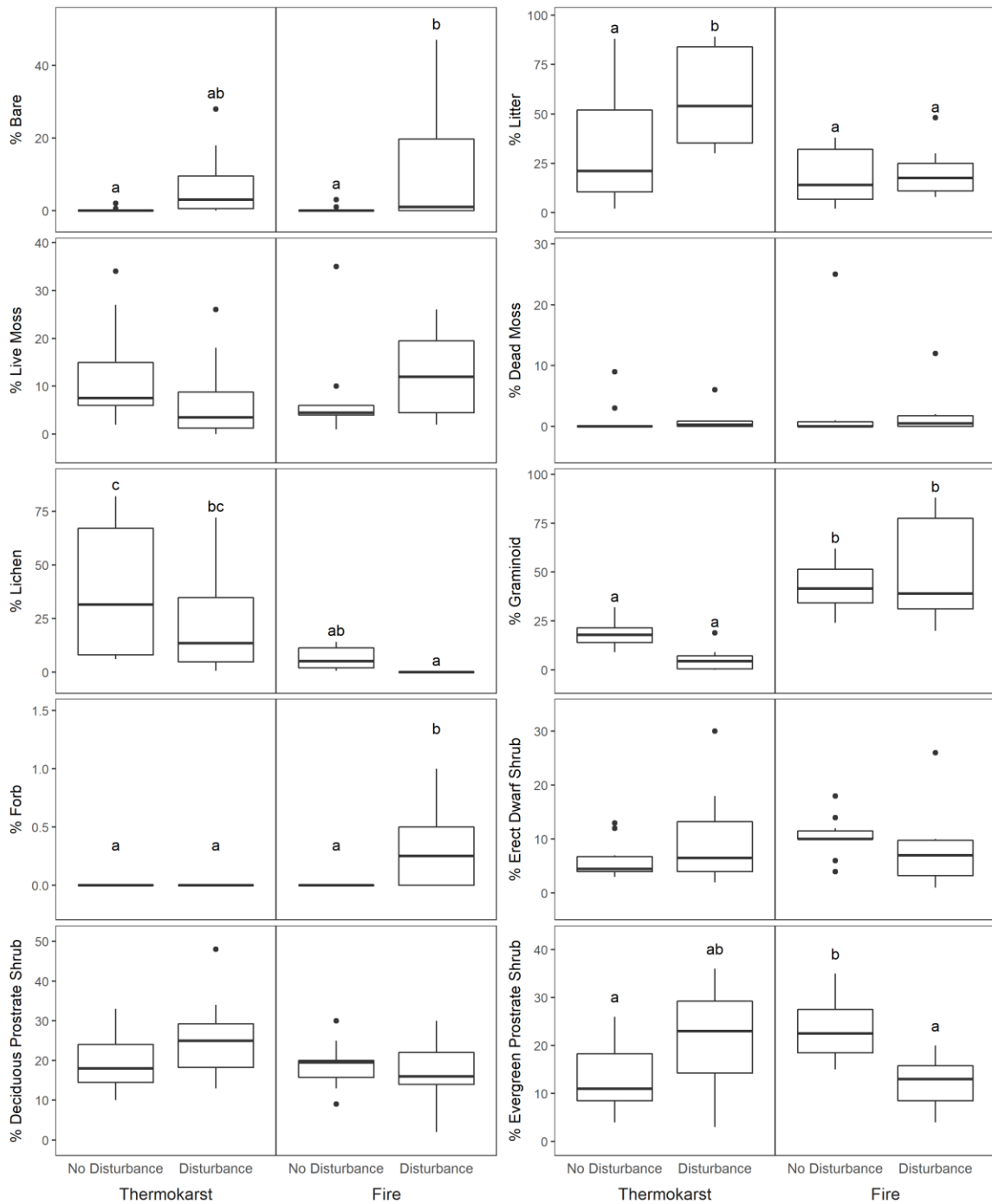


Figure 10: Effect of landscape disturbance on vegetation composition (absolute percent cover), grouped by site (Thermokarst=Council, Fire=Quartz Creek). Lowercase letters indicate significant difference between groups in post hoc tests, the absence of letters denote no difference between treatments.

### 3.3 Bioclimatic Conditions for Seedling Establishment

Disturbance and scraping indirectly controlled seedling emergence ( $R^2=0.24$ ) and seedling establishment ( $R^2=0.23$ ) through alteration of soil, substrate, and vegetation properties (Figure 11). While disturbance controlled both seedling emergence and establishment, scraping only influenced seedling establishment. Seedling survival was controlled by disturbance and establishment treatments ( $R^2=0.19$ ) through modification of microsite bioclimatic conditions (Figure 12). Seedling survival was primarily controlled by substrate quality and microclimate conditions, but not by vegetation structure. Survival was positively associated with substrate structure, soil temperature, and soil moisture. In contrast, survival was negatively correlated with substrate composition (a combination of substrate thickness and lichen abundance). Disturbances increased soil temperature and decreased substrate composition. Scraping increased soil moisture and vegetation structure, while decreasing vegetation composition, as well as substrate structure, composition, and temperature. Disturbance and scraping indirectly control seedling survival through modification of the bioclimatic conditions.

## **4. Discussion**

### 4.1 Bioclimatic Controls on Establishment

The seedling establishment bottleneck is shaped by bioclimatic filtering. Whereas seedling emergence happens equally in disturbed and undisturbed areas, survival differs. I found that seedling survival and establishment were higher with disturbed areas than undisturbed. While lichen and bryophyte removal (scraping) increased seedling survival in undisturbed plots, it did not fully account for the increased rates of seedling establishment within disturbed areas. This demonstrates that the controls on

establishment are a dynamic combination of limits on both seedling germination and survival. While substrate quality is an important control, vegetation structure also shapes seedling success through constraints of light availability and degree of exposure to abiotic extremes.

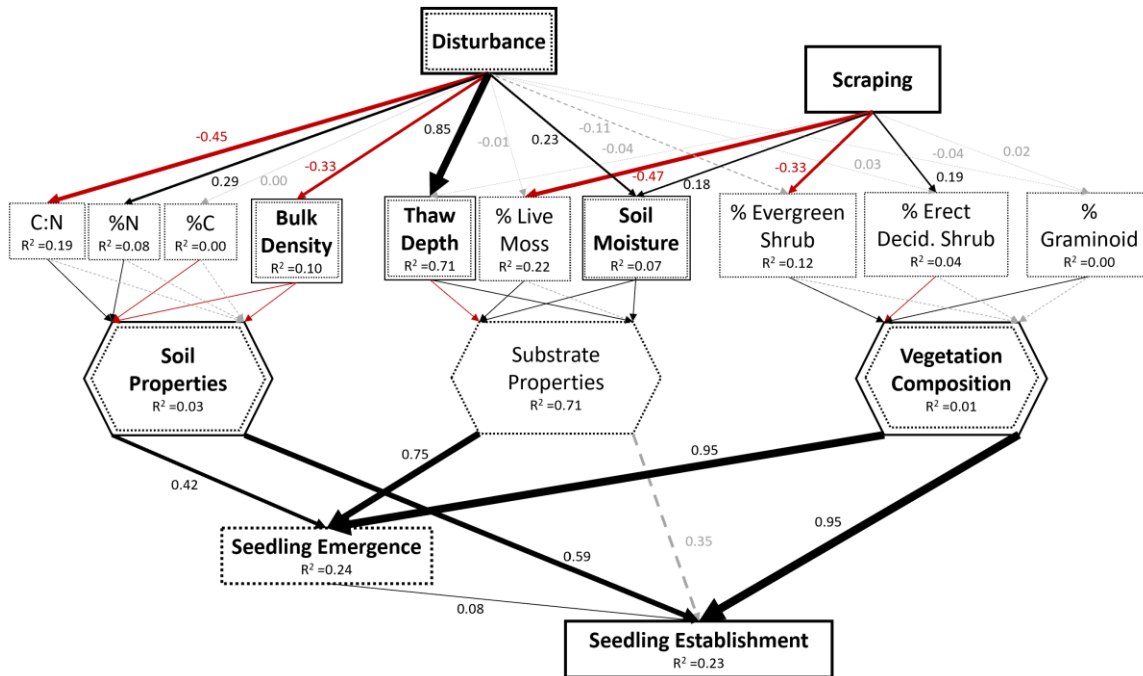


Figure 11: Results from piecewise structural equation model of disturbance and scraping effects on bioclimatic conditions, and their influence on seedling emergence and establishment. Black lines are positive correlations and red are negative, nonsignificant correlations ( $p > 0.05$ ) are in gray. Numbers adjacent to arrows are the standardized path coefficients and arrow thickness corresponds to these values.  $R^2$  values inside each box reflect relationship strength between that variable and the disturbance and scraping treatments. Variables significantly correlated with seedling emergence have dotted borders, while solid borders are correlated with seedling establishment. Variables with both solid and dotted borders are significantly correlated with both seedling stages.

Arrows extending from bioclimatic parameters into the top left of each composite hexagon show the relationship between that variable and seedling emergence. Conversely, arrows going into the top right of the hexagon are the relationship with seedling establishment.

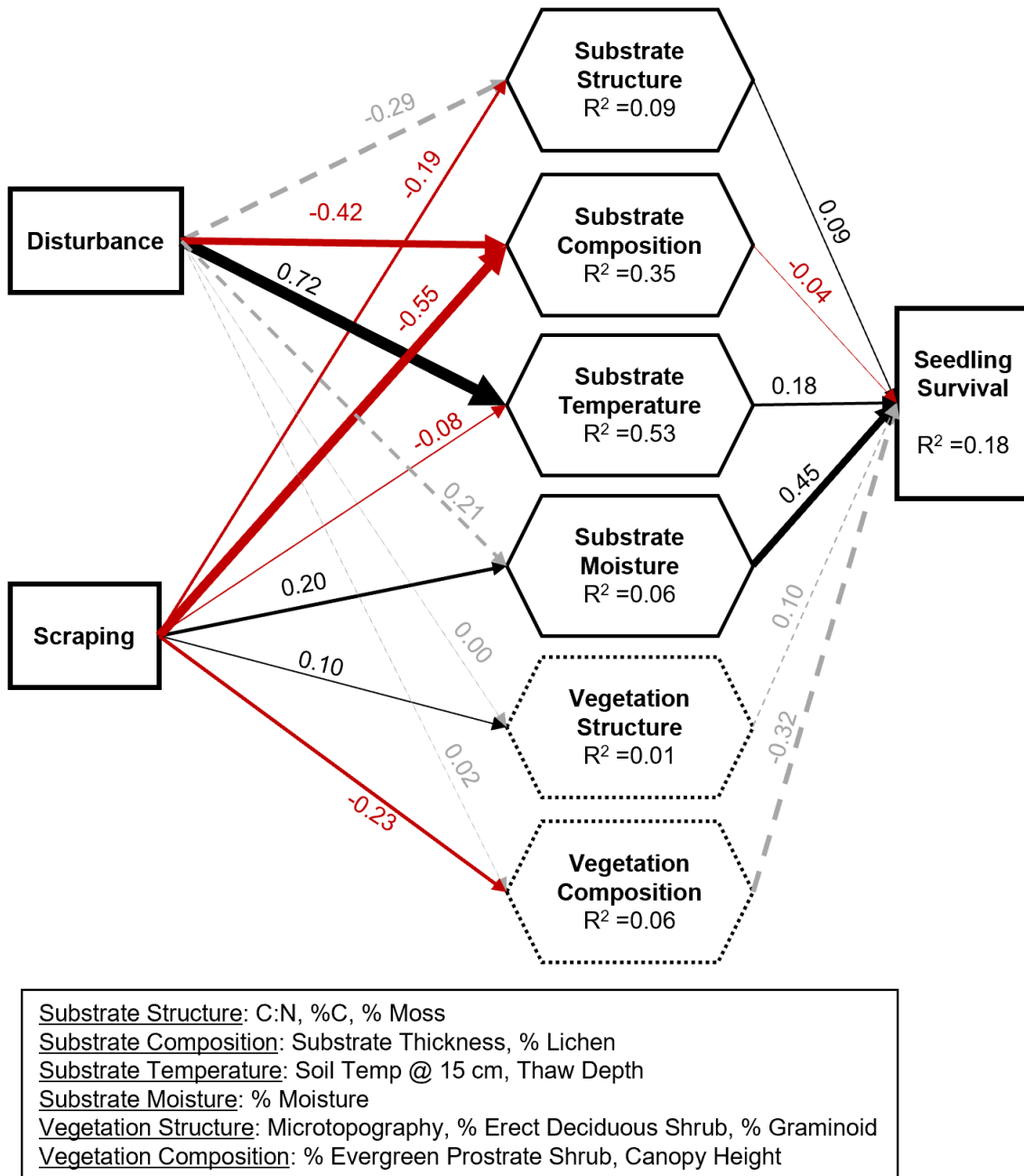


Figure 12: Results from piecewise structural equation model of disturbance and scraping effects on bioclimatic conditions, and their influence on seedling survival. Black lines are positive correlations and red are negative, nonsignificant correlations ( $p > 0.05$ ) are in gray. Numbers adjacent to arrows are the standardized path coefficients and arrow thickness corresponds to these values.  $R^2$  values inside each box reflect relationship strength between that variable and the disturbance and scraping treatments. Variables with solid borders are significantly correlated with seedling survival, while those with dotted borders are not. Bioclimatic components of each composite variable are listed in bottom left.

I found that a combination of substrate parameters influence seedling survival, suggesting that substrate quality is an important component for germination and establishment. While substrate physical and chemical properties strongly influence seedling emergence, vegetation structure also influences these patterns by affecting seedling exposure and light availability. In contrast, seedling establishment is more affected by vegetation structure than substrate properties, indicating a shift in controls during the establishment phase. While initial emergence is strongly influenced by substrate suitability, microsite properties such as exposure to abiotic extremes, light availability, and competition affect establishment success. In this way, tundra ecosystem structure exerts control on seedling establishment through modification of bioclimatic conditions. Changes in plant community structure and composition also result in differences in substrate surface composition, which directly affect seedling establishment conditions.

#### 4.2 Disturbance Facilitates Establishment

The results of my study indicate that landscape disturbance events can facilitate shrub expansion in the Arctic by increasing rates of seedling establishment. While seedling emergence occurs equally within disturbed and undisturbed areas, the establishment bottleneck does not. Estimated survival rates were five times greater in disturbed areas than undisturbed and three times greater in scraped plots than unscraped. In disturbed areas, the number of seedlings did not significantly change between the first and second growing season. In contrast, seedling counts significantly decreased within undisturbed plots. This filtering resulted in an average of four times more seedlings establishing in disturbed areas than undisturbed. These results support observational

surveys that I conducted at Quartz Creek prior to implementing this experiment, which show that shrub seedling density may be over 10 times higher in burned areas than unburned (unpublished data). These results show that disturbances cause fundamental differences in ecosystem structure which modify seedbed quality and microsite suitability.

I found that while substrate quality affects establishment, it is intrinsically with overall bioclimatic conditions experienced by seedlings. Disturbance facilitated seedling establishment even though there was little to no exposed mineral soil within experimental plots, indicating that seedling establishment is facilitated even by low severity disturbances. Tundra fires typically set the stage for secondary succession unless they are overly severe, and may not expose mineral soils in areas with thick organic layers (Frost et al. 2020). Additionally, many tundra species can resprout from underground biomass following fire, and so vegetation tends to return relatively quickly (except for slower growing species such as lichen or moss) (Bret-Harte et al. 2013). However, this research demonstrates that mineral soil exposure is not a requisite for establishment and shrub recruitment is facilitated by these low-severity disturbances, increasing the potential for altered successional trajectories. The reduction in bryophyte and lichen abundance, coupled with a reduction in soil organic layer thickness act together to facilitate shrub seedling recruitment and can amplify rates of shrub expansion.

As this study was limited in geographic extent, caution must be exercised when extrapolating these results to the circumpolar region. However, these findings support other studies that examine the interaction between landscape disturbance and shrub seedling recruitment in the Arctic. Research from the western Canadian Arctic has shown

a positive association between *A. viridis* subsp. *fruticosa* recruitment and disturbances such as fire and permafrost degradation (Lantz et al. 2009, 2010, 2013). Similarly, research from northeastern Alaska has shown increased seedling recruitment in thermokarst areas (Huebner and Bret-Harte 2019). My research also supports work from the Scandinavian alpine treeline which showed that seedling establishment was higher in areas of reduced moss competition than in warming and precipitation treatments (Lett et al. 2020). These studies indicate that disturbance events alter ecosystem structure in a manner that facilitates shrub recruitment through alteration of the establishment bottleneck.

#### 4.3 Establishment controls shrub expansion

The observed patterns of seedling emergence and mortality indicate that that shrub seedlings are limited by bioclimatic conditions during establishment. Approximately 4% of seedlings survived in unburned tundra, compared with 20% in disturbed. This supports a reframing of the traditional dispersal-limitation paradigm for arctic plants, emphasizing importance of controls on recruitment (Milbau et al. 2017). While this study only tracks seedling survival over the first two growing seasons, it demonstrates the bioclimatic filtering that occurs during the critical bottleneck phase for seedling establishment. During this period, seedlings must successfully acquire enough resources to survive prolonged snow-cover as well as resist desiccation (Gough 2006). Until seedlings have developed sufficient root systems they are particularly vulnerable to frost damage and drought stress, with mortality likely after just a few hours of unfavorable conditions (Büntgen et al. 2015). By altering substrate physical and chemical properties, disturbances improve conditions for seedling survival.



Increased rates of seedling establishment following disturbance events are layered on top of warming-induced changes to the establishment bottleneck. As a result, it can be expected that changing climate conditions will facilitate shrub recruitment within the Arctic and that disturbance events will further increase the rate of shrubification. Furthermore, these disturbances increase soil temperatures and promote permafrost thaw, further altering ecosystem structure and amplifying the effects of climate warming (Schuur and Mack 2018). This research suggests that the interaction between disturbance events, seedbed quality, and seedling establishment must be addressed when modelling shrub expansion rates in the Arctic. The area burned in the Alaskan Arctic is expected to double by 2100 and warming increases the frequency of thermokarst events (Hu et al. 2015; Schuur and Mack 2018). Consequentially, shrub expansion rates can be expected to substantially increase as disturbance regimes intensify. This is especially important as coupled vegetation-fire model projections indicate that 14-24% (31,300-54,500 km<sup>2</sup>) of the Alaskan Arctic could transition from graminoid- to shrub-dominated tundra with warming and fire, however many earth system models do not account for fire-induced facilitation of shrub expansion (Euskirchen et al. 2016b). As my research demonstrates that these disturbances can produce a four-fold increase in seedling establishment rates, models that do not account for fire-induced facilitation of shrub expansion may substantially underestimate shrub expansion rates, with significant consequences for projections of Arctic change.

#### 4.4 Synopsis

My research demonstrates that ecosystem structure and disturbance are closely linked. I found that disturbances facilitate shrub seedling establishment through

modification of bioclimatic conditions and substrate quality. As fire and thermokarst disturbance regimes are increasing in frequency and magnitude throughout the Arctic region, shrub expansion rates are likely to increase at a greater rate than is expected from climate warming alone. Shrub expansion is a critical component of Arctic change which alters permafrost thaw, nutrient cycling, and tundra energy balance (Myers-Smith et al. 2011; Euskirchen et al. 2016b; Mekonnen et al. 2018). As a consequence of warming and disturbance-driven shrub expansion, climate feedback cycles driven by shrubification are expected to strengthen with substantial consequences for the Arctic carbon budget (Mack et al. 2011; Myers-Smith et al. 2011; Hoegh-Guldberg et al. 2018). Seedling establishment rates are a critical control on shrub expansion and are expected to increase as a result of disturbance facilitation.

## CHAPTER IV

### CONCLUSION

While climate is a control on ecosystem structure and function, vegetation also exerts control on climatic conditions. Changes to the soil-plant-atmosphere continuum can cause largescale alteration to regional carbon and energy balances. Shrubification is one such change within the Arctic; however, these linkages occur throughout the globe. Two prominent examples of these processes are warming driven by tropical deforestation and warming associated with treeline expansion in boreal forests (Bonan 2008). Over the course of Earth's history, rapid shifts between warm and cool climatic conditions have been driven by positive feedback cycles. These processes can act in to either cool the climate (through increased rates of photosynthesis) or warm it (through changes in albedo driven by sea-ice loss) (Ruddiman 2014). These feedbacks provide evidence for the critical linkages between ecosystems and the climate. As shrubification is associated with multiple positive and negative feedback cycles, the future of the Arctic and the Earth's climate will depend upon factors controlling the rates of vegetation change (Euskirchen et al. 2016b). Shrub growth will lead to increased rates of carbon assimilation; however, it is the cumulative biophysical and geochemical feedbacks that will shape to what extent these changes enhance warming driven by anthropogenic climate change (Hoegh-Guldberg et al. 2018; Schuur and Mack 2018).

This research demonstrates that disturbance events facilitate shrub seedling establishment in arctic tundra. As a result, disturbances are likely to facilitate shrub expansion at greater rates than is to be expected from warming alone. These findings

highlight the potential for alternative successional trajectories following wildfire and thermokarst events, which are expected to increase in frequency and severity (Hoegh-Guldberg et al. 2018; Schuur and Mack 2018). Paleoecological evidence links domination of shrubs in the tundra with more frequent and severe fires, providing a glimpse into the window of the future through Earth's past (Higuera et al. 2008). Given that the area burned in the Alaska Arctic is projected to double by 2100, the effects of disturbance on ecosystem trajectory are of critical importance (Hu et al. 2015). While limitations on shrub recruitment have been relatively understudied, they will shape the response of arctic ecosystems to anthropogenic climate change (Myers-Smith et al. 2011). In this way, the factors controlling the fate of small seedlings in the far north have large global consequences.

The rapid rate of change in the Arctic has strong linkages to climate feedbacks, ecosystem services, and human well-being. The trajectory of environmental change in the Arctic has significant consequences for the region's indigenous communities. Climate risks are disproportionately borne by Arctic residents, many of whom have close relationships with sea-ice, marine, and tundra ecosystems (Hoegh-Guldberg et al. 2018). The rapid pace of change throughout this region directly impacts community health and safety. Entire communities are faced with relocation in order to adapt to coastal erosion caused by the loss of sea-ice (Ford et al. 2014). Throughout the region, traditional resources are becoming more difficult to access and changing in availability as a consequence of warming (Brinkman et al. 2016). Shrub expansion is expected to alter the distribution of wildlife populations, with consequences for subsistence hunting. For example, increased shrub populations and fire activity decrease lichen abundance, a

critical food source for caribou (Fauchald et al. 2017). Shrub expansion is already facilitating the expansion of beavers, moose, and other boreal species into tundra regions affecting ecosystem function and impacting arctic species (Tape et al. 2018; Zhou et al. 2020). The risks to arctic ecosystem structure and permafrost stability are very high under climate change scenarios of 2.0°C warming and above, in order to limit these risks it is necessary to limit anthropogenic warming to 1.5°C (Hoegh-Guldberg et al. 2018).

The extent to which arctic warming and shrubification will amplify global climate change is still unwritten. Increased rates of carbon sequestration within woody shrub biomass are expected to be greatly outweighed by warming-induced losses of irrecoverable permafrost carbon. However, the magnitude of this change will depend on global climate conditions (Euskirchen et al. 2016b; Mekonnen et al. 2018).

Anthropogenic climate change is projected to transform the Arctic from a carbon sink to a carbon source, but the quantity of permafrost that degrades is directly tied to the magnitude of warming (Webb et al. 2016). The ecosystem changes and associated climate feedbacks discussed in this thesis will be difficult to mitigate within the Arctic region (Schuur and Mack 2018). As such, the primary way to limit their severity is to slow the rate of anthropogenic climate change by focusing on reducing greenhouse gas emissions worldwide and increasing carbon sequestration through implementation of natural climate solutions (Fargione et al. 2018; Hoegh-Guldberg et al. 2018).

## APPENDIX: SOIL PHYSICAL AND CHEMICAL PROPERTIES

	Council				Quartz Creek			
	Undisturbed		Disturbed (Thermokarst)		Undisturbed		Disturbed (Fire)	
	Substrate	Soil	Substrate	Soil	Substrate	Soil	Substrate	Soil
<b>Carbon (kg/m<sup>2</sup>)</b>	8.57 ±0.75	14.66 ±3.23	7.36 ±1.06	18.66 ±3.61	9.02 ±1.29	11.91 ±1.53	8.01 ±1.19	20.56 ±2.60
<b>Nitrogen (kg/m<sup>2</sup>)</b>	0.23 ±0.03	0.48 ±0.15	0.26 ±0.03	0.62 ±0.10	0.33 ±0.05	0.48 ±0.15	0.31 ±0.05	0.60 ±0.07
<b>Sample Depth (cm)</b>	10	21 ±1	10	28 ±5	10	23 ±2	10	35 ±2
<b>Bulk Density (g/cm<sup>3</sup>)</b>	<b>0.20</b> ±0.02	<b>0.18</b> ±0.03	<b>0.23</b> ±0.02	<b>0.34</b> ±0.08	<b>0.40</b> ±0.08	<b>0.28</b> ±0.10	<b>0.21</b> ±0.04	<b>0.56</b> ±0.03
<b>% SOM</b>	87.40 ±4.48	<b>79.83</b> ±7.04	73.30 ±7.45	<b>49.80</b> ±10.29	58.22 ±13.82	<b>54.19</b> ±10.73	81.70 ±4.29	<b>22.85</b> ±3.95
<b>% C</b>	<b>42.89</b> ±1.71	<b>38.60</b> ±2.91	<b>31.33</b> ±3.30	<b>22.94</b> ±4.48	<b>27.16</b> ±6.70	<b>23.99</b> ±4.92	<b>38.68</b> ±1.92	<b>10.70</b> ±1.82
<b>% N</b>	1.15 ±0.04	<b>1.12</b> ±1.77	1.10 ±0.11	<b>0.82</b> ±0.17	1.01 ±0.27	<b>0.73</b> ±0.17	1.45 ±0.07	<b>0.31</b> ±0.05
<b>C:N</b>	<b>37.43</b> ±1.93	39.57 ±9.80	<b>28.49</b> ±0.82	29.28 ±2.19	<b>27.32</b> ±1.12	34.61 ±2.91	<b>26.78</b> ±1.75	34.51 ±0.92
<b>pH</b>	<b>4.14</b> ±0.06	-	<b>4.56</b> ±0.16	-	<b>4.78</b> ±0.18	-	<b>4.65</b> ±0.10	-

Table 3: Effect of disturbance on soil physical and chemical properties (mean ± SE). Significant differences between groups are in bold ( $p < 0.05$ ).

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