THE ECOLOGY OF DECAYING ICE WEDGES

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A thesis submitted to McGill University in partial fulfillment of the requirements
of the degree of doctorate

For my grandparents

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ABSTRACT

The Canadian high Arctic is experiencing one of greatest increases of atmospheric temperatures on the planet due to climate change. Permafrost, ground that remains at or below 0°C for at least two consecutive years, is a cryospheric phenomenon with a thermal balance that fluctuates in accordance with changes in atmospheric temperatures and geophysical conditions. As such, the seasonal depth of thaw, the active layer, is predicted to increase substantially over the next century. Within the permafrost are large bodies of ice called ice wedges – ubiquitous periglacial features that exist nearly everywhere within the continuous permafrost region. Ice wedges occupy up to 50% of the ground near-surface and grow or decay based on changes in active layer depth. Due to their mass, abundance, and susceptibility to temperature changes, ice wedges will likely be a catalyst for significant landscape change across the entire high Arctic region. What form the polar desert landscape will take in the near future will depend on the balance of competing forces – increased ice wedge thermokarst verses the stabilizing effect of increased vegetation cover, both of which are predicted as a consequence of warming.

My dissertation examines the geomorphic, ecologic, and edaphic changes instigated as a result of ice wedge melt (thermokarst). First, I assess a site of climate-induced thermokarst located on the polar desert of the Fosheim Peninsula, Ellesmere Island, Nunavut, Canada. I found that thermokarst produced a suite of changes to local surface hydrology, vegetation biodiversity and abundance, and soil chemistry. Interestingly, I also observed that thermokarst areas had decreased active layer thickness, likely due to the stabilizing feedback of amplified vegetation growth. Next, I examined this stabilization process in greater detail by constructing and testing a path-analysis model of the direct and indirect dampening effects of vegetation on active layer depth. I found that, contrary to other studies, thermokarst is unlikely to be self-reinforcing, and in some situations thermokarst-induced vegetation growth may attenuate a significant proportion of future permafrost warming. Finally, I quantify the long-term environmental impacts of anthropogenic disturbance to the ice wedge/vegetation system at an abandoned tundra runway. I found that in addition to altering vegetation biodiversity and soil surface characteristics, the landscape preserves a significant thermal legacy from human disturbance that likely has induced an alternative stable-state of the landscape.

My results show that ice wedge thermokarst, whether naturally or anthropogenically induced, has significant consequences for the polar desert biome. The changes I quantified locally will likely affect the polar desert regionally, given the rate of current warming and the prevalence of ground ice. Contrary to much of the current climate-change literature, my thesis emphasizes the often overlooked stabilizing ecosystem feedbacks on geomorphic change.

RÉSUMÉ

En raison du changement climatique, le haut Arctique canadien connaît une des plus fortes augmentations de températures atmosphériques de la planète. Le pergélisol, sol qui demeure égale ou inférieure à 0 ° C pendant au moins deux années consécutives, est un phénomène cryospheric dont l'équilibre thermique fluctue en fonction des changements de températures atmosphériques et des conditions géophysiques. De ce fait, la profondeur de dégel saisonnier, c'est à dire la couche active, est prévue d'augmenter sensiblement au cours du prochain siècle. Dans le pergélisol se trouvent de grandes étendues de glace appelées coins de glace - caractéristiques périglaciaires omniprésentes qui existent un peu partout dans la région continue du pergélisol. Ces coins de glace occupent jusqu'à 50% de la couche proche de la surface et grandissent ou diminuent selon les changements de la couche active profonde. En raison de leur masse, de leur abondance ainsi que de leur sensibilité aux changements de température, les coins de glace seront probablement un catalyseur de changements significatifs du paysage dans toute la région du haut Arctique. La forme que le paysage du désert polaire aura dans un proche avenir dépendra de l'équilibre de forces concurrentes – l'augmentation de la fonte des coins de glace (thermokarst) versus l'effet de stabilisation de l'augmentation de la couverture végétale, qui sont tout deux prédits comme étant des conséquences du réchauffement climatique.

Ma thèse examine les changements géomorphologiques, écologiques, et édaphiques résultant de la fonte de coins de glace thermokarstique. Tout d'abord, j'ai évalué un site thermokarstique impacté par le climat et situé dans le désert polaire de la péninsule de Fosheim sur l'île d'Ellesmere au Nunavut, Canada. J'ai découvert que le thermokarst produit une série de changements locaux à l'hydrologie de surface, sur la biodiversité et l'abondance de végétation

ainsi que sur la chimie du sol. Fait intéressant, j'ai aussi trouvé que les zones de thermokarst avaient diminué l'épaisseur de la couche active, probablement en raison de la réaction de stabilisation à croissance amplifiée de la végétation. J'ai ensuite examiné ce processus plus en détail par la construction et l'essai d'un modèle de cheminement analytique des effets modérateurs directs et indirects de la végétation sur la profondeur de la couche active. J'ai trouvé que, contrairement à d'autres études, il est peu probable que le thermokarst puisse s'auto-renforcer, et que dans certaines situations la croissance végétal induite par le thermokarst peut atténuer de façon importante le réchauffement du pergélisol. Enfin, j'ai quantifié les impacts environnementaux à long terme des perturbations anthropiques du système coins de glace / végétation sur une piste abandonnée de la toundra. J'ai découvert qu'en plus de modifier la biodiversité de la végétation et de la chimie du sol, le paysage conserve un héritage thermique importante de toute perturbation humaine qui a probablement provoqué un état alternatif stable du paysage.

Mes résultats montrent que les coins de glace thermokarstiques, naturels ou anthropiques, ont des conséquences importantes sur le biome du désert polaire. Étant donné le taux de réchauffement actuel et la prévalence de la glace de sol, les changements que j'ai chiffrés localement affecteront probablement le désert polaire au niveau régional. Contrairement à une grande partie de la littérature actuelle sur le changement climatique, ma thèse met l'accent sur la stabilisation réactive de l'écosystème aux changements géomorphiques, trop souvent négligée.

ACKNOWLEDGMENTS

A heartfelt thanks goes out to the **entire** staff of Eureka, Nunavut where I was based for much of my fieldwork. A particular thanks to Al Gaudet and André Bouchard for hosting this beaker, Jay Roberts and Kevin Sheppard for the late night company, Daryl Mclaughin for being the nicest and most generous cook on the face of the planet, and Bill MacInnis for simultaneously saving my life and nearly killing me that one time.

I'd like to thank my supervisor Wayne Pollard for offering me a total blank slate within which to design and carry out my own research interests – this is an opportunity and freedom most students would only dream of. Thank you to my committee Andy Gonzalez, George Wenzel, Jeanine Rhemtulla, and a particular thanks to Jonathan Davies for treating me like one of his own students – your guidance has been invaluable.

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I've been quite fortunate to spend the last year of my PhD writing up at the Center for Macroecology, Evolution, and Climate at the University of Copenhagen. I'd like to thank Carsten Rahbek for hosting me at his inspirational center, and Nate Sanders and Aimee Classen for helping an American understand Danish culture.

Thank you to Jeff DelVisco from the New York Times and Patrick Evans at the BBC for taking a chance on an unknown kid and giving me a leg up in the cutthroat world of media and science communication. Your editorial help and guidance is immensely appreciated.

I'd like to thank a number of people for their friendship as well as scientific discussions: my close friends Eric Pederson and Patrick Thompson, Sylvia Wood and Mike Angelopoulos (as model students in the Geography Department), and Antoine Paccard, Rowan Barrett, Hans Larsson, and Andrew Hendry for the beer and climbing.

I owe my parents and brother for their love and incredible patience at housing a very distracted son during the holidays. My father for teaching me everything to survive outdoors and my mother for showing me the dedication it takes to follow through.

And finally, Chelsea. Thank you for your love, support, adventures, and brilliant mind. You will make one hell of a scientist.

PREFACE

i. Thesis Format

This thesis was written in manuscript format according to the guidelines stipulated by the Graduate and Postdoctoral Studies Office (GPSO) and the Department of Geography at McGill. This thesis contains three research/analytic chapters that have either been submitted for publication or are in preparation to be submitted. Connecting statements are provided to link the manuscripts into a coherent thesis. Since these chapters were derived from the same geographic region in the Arctic, there is some similarity in the methods across all manuscripts as they have been written to stand-alone. To save on space and avoid repetition, all references for the chapters and manuscripts have been moved to a cumulative bibliography section at the end of the thesis. The introduction of each of these analytic chapters (three to five) provides a specific literature review according to the manuscript. As such, I have provided an overall research outline and a general review of relevant subject literature to provide the necessary background. This thesis concludes with an overarching summary for the entire body of work and highlights how each manuscript addresses specific questions in my overarching framework.

ii. Authors Contributions

For all of my chapters, I was responsible for conceptualization, planning, execution of fieldwork, data analysis, and lead writing. My advisor, Wayne Pollard, is a coauthor on all chapters as he provided input on planning, idea formation, editorial feedback, and funding.

My chapter "Ground Ice Melt in the High Arctic Leads to Greater Ecological Heterogeneity" is largely influenced by my participation with Jonathan Davies' lab in the Department of Biology. His focus on phylogenetic relationships and biodiversity helped hone my ideas and shape the form of that manuscript. Jonathan Davies provided conceptual advice as well as significant manuscript revision. Wayne Pollard provided feedback and conceptual background. I conducted the fieldwork, analyses, and primary manuscript writing.

My chapter “Climate-induced Vegetation Growth Will Buffer High Arctic Permafrost Change” originated from an observation I had over several fieldwork seasons across different sites in the Arctic. I collected the data, ran the analyses, and wrote the manuscript with substantial discussion and editorial advice from Wayne Pollard.

The idea for my final analytic chapter “60 Year Legacy of Human Impacts on a High Arctic Environment” was derived from conversations with Wayne Pollard during one of my first field seasons. His study site suggestion as well as guidance in fieldwork execution proved invaluable for the creation of this manuscript, to which he also provided editorial advice. I conceptualized the project, conducted the fieldwork, ran the analyses, and wrote the manuscript.

iii. Statement of Originality

This thesis contributes to unanswered questions as predicting changes in high Arctic biodiversity, changes in soil nutrient balances, and geomorphic stability of permafrost in light of a warming climate. Thermokarst caused through either natural or anthropogenic means may cause rapid landscape change in a way that remains unclear. This study creates a novel conceptual model of the ice wedge/vegetation system in an effort to address scientific and practical conservation questions for the Arctic. The data and analyses of this study can be used to enhance predictions of landscape change. Additionally, this study provides critical information for government and industry partners that wish to minimize their impacts on fragile arctic ecosystems. This thesis makes the following contributions to the advancement of the field:

Contributions from “Ground Ice Melt in the High Arctic Leads to Greater Ecological Heterogeneity”

- By conducting in-depth field assessments, I quantify the comprehensive geophysical and ecological effects of ice wedge thermokarst in the high Arctic. These two fields are generally approached independently, and my work represents an attempt to bridge the two.
- I demonstrate the large influence and changes that thermokarst induces on vegetation biodiversity patterns and soil chemistry. I show that thermokarst increases ecosystem

microsite heterogeneity locally, and I discuss what the regional repercussions will be in light of expected temperature increases due to climate change.

Contributions from "Climate-induced Vegetation Growth Will Buffer High Arctic Permafrost Change"

- Building on the thermokarst-induced vegetation growth from the previous chapter, I use a path-analysis modeling approach to outline and quantify the major stabilizing feedback mechanism of high Arctic vegetation on seasonal active layer depth.
- I demonstrate that a select subset of variables can explain the majority of microsite active layer variability.
- Contrary to trends in permafrost literature, I discuss how such a strong, stabilizing mechanism of vegetation growth can attenuate some of the near future permafrost thaw. Due to the strong effect size this likely affects regional projections of permafrost thaw as well as estimates of carbon emissions from warming soils.

Contributions from "60 Year Legacy of Human Impacts on a High Arctic Environment"

- By examining one of the oldest sites of anthropogenic disturbance in the high Arctic I show that land surface impacts are wide-ranging in type of effect and extraordinarily long-lived.
- I show that the landscape preserves a thermal and biotic legacy from the disturbance, but that there is great range in terrain response according to type of microtopography disturbed.
- This area of the Arctic has been identified as having one of the world's largest undeveloped coal seams, and there is renewed industry interest in development. Using my results, I generate a series of management and development guidelines for mitigating impact and improving recovery.

CHAPTER 1 – Overview

1.1 General Introduction

The Canadian high Arctic is one of the most remote landscapes on Earth and is home to the polar desert– perhaps the harshest terrestrial biome in the northern hemisphere. Despite the isolated location, this place is not beyond the reach of the impacts of southerly carbon emissions. This extreme end of the North American continent is warming faster than most of the planet, with recent reports projecting that the Arctic will be warming much more rapidly than the rest of the globe, with warming far greater on the land than the ocean (IPCC 2013). It is a particularly sensitive land, with very little vegetation cover (Wein & Rencz 1976) to protect permafrost from rising atmospheric temperatures. Despite the extraordinarily low mean annual air temperature, dearth of precipitation, and extreme seasonality of solar input, a section of Ellesmere Island called the Fosheim Peninsula supports a relatively diverse array of vascular vegetation that belies its high latitude location (Edlund, Woo & Young 1990). This "Garden Spot of the Arctic" creates a unique opportunity to study how melting ice-rich permafrost (thermokarst) will affect high Arctic biodiversity, and in turn, how changing vegetation patterns will affect the geomorphic development of a very exposed landscape.

Through the course of this dissertation I will discuss how both indirect (climate) and direct (anthropogenic disturbance) drivers of thermokarst affect the balance of permafrost, ground ice, and ecosystems of the polar desert. The polar desert differs greatly from the perhaps more familiar conditions of the lower Arctic. This region is characterized by its extreme dryness (relative lack of snow fall) and its extreme cold (Edlund & Alt 1989). The lack of significant precipitation limits primary productivity (Hudson & Henry 2009), and therefore restricts the capacity of the landscape to support large abundances of higher trophic levels (i.e. reduced numbers of herbivores, and in turn less predators). Due to the extreme cold, the polar desert is underlain by an immensely thick (up to 500m) permafrost layer – ground that remains at or below 0°C for at least two consecutive years (Taylor 1991).

The extreme cold of the ground surface generates one of the region's most characteristic features – ice wedge polygon systems (Couture & Pollard 1998). These patterned ground shapes are ice wedge polygon systems (Mackay 1972), and their processes I discuss in greater detail in the Chapter 2 literature review. Much of the high Arctic landscape is comparatively new (2000 – 9000 years before present) as it is currently emerging from the sea through isostatic rebound due to glacial retreat from the last ice-age maxima (Taylor 1991). Land-surface processes such as thermal-contraction cracking during the harsh winter months transform the landscape into an array of polygonal shapes – rectangles, hexagons, octagons, etc. that introduce microtopographical heterogeneity into an otherwise featureless barren ground (Zona *et al.* 2011). Under each of these cracks that delimit the shape of the polygons lays a large body of ground ice known as an ice wedge. These vertical bodies of ice extend downwards for 3-4m below the subsurface, exist nearly everywhere within the continuous permafrost region, and can take up to 50% of the ground subsurface (Pollard & French 1980; French 2007). These bodies of ice sit in a fine equilibrium with the thickness of the seasonal depth of thaw – the active layer. As the active layer increases or decreases, the ice wedge decays or grows, respectively (Mackay 1972). As the region is currently warming, and projected to warm further, the active layer stands to increase significantly with the potential to create enormous changes to the Arctic landscape through ice wedge thermokarst.

While thermokarst is often part of the polar environment's natural evolution, it is the increase in frequency, severity, and distribution of this disturbance process that could greatly affect ground surface subsidence (through the volumetric loss of ice). Changing the ground surface alters surface hydrology through changing snowpack depths, promoting the collection of surface melt runoff during spring, and in general the redistribution of scare water resources (Rydén 1977), thereby shifting the patterns of high Arctic vegetation. Already there are signs of increased plant biomass in the high Arctic and changing diversity patterns when just considering atmospheric temperature rises alone (Hudson & Henry 2009) and simulated warming chambers across the region predict a broad array of plant community changes (Elmendorf *et al.* 2012a).

However, despite research predicting vegetation changes across the Arctic, and research projecting geomorphic changes through increased thermokarst, there has been little overlap between the two fields even though the two are inexorably interlinked (Hjort & Luoto 2009; Hupp & Osterkamp 2013). This examination of processes separately from one another leaves a significant gap in knowledge and understanding of how a complex system can be expected to change in light of a warming climate. Not all work has neglected these interactions (Billings &

Peterson 1980; Mackay & Burn 2002), but historically the fields have been split, I believe to the detriment of both.

Given the evidence for the interaction of vegetation development concurrent with polygon development reviewed further in Chapter 2, any study of changes to the ice wedge system in the high Arctic should examine both geomorphic and biologic processes in concert. There has been a current attempt to bridge the different fields of geomorphology and ecology to better describe the complex abiotic/biotic interactions for the purposes of anticipating the effects of climate change (Hupp & Osterkamp 2013). Additionally, as most of the high Arctic is a relatively young landscape (Hodgson, St-Onge & Edlund 1991a), the Canadian high Arctic may reflect less complex interactions between abiotic and biotic development than would be present elsewhere in the world (i.e. within the discontinuous permafrost or low Arctic regions). This makes the region a premiere area to study the biogeomorphological processes of landscape evolution. Additionally, as climate change is projected to influence the Canadian high Arctic proportionately more than other areas of the world, a significant change will perturb the system. The question is not whether there will be an effect, but rather what the strength of the effect will be. Given the recent age of the landscape, relatively low diversity, slow biogeochemical processes, the polar desert represents the perhaps the best ecosystem to understand how fundamental abiotic/biotic interactions respond to perturbations such as climate change.

In this dissertation I focus my efforts on broadening our understanding of the interactions of permafrost and vegetation in light of a changing climate's direct and indirect effects. As I show in Chapter 3, thermokarst, by altering surface hydrology, induces significant changes in vegetation diversity, alters soil chemistry, and importantly fuels an abundant increase in vegetation cover. Paradoxically, this stimulated vegetation growth then begins to stabilize the ground from further thermal change and may offset some of the near future permafrost thaw, as I demonstrate in Chapter 4. The powerful stabilizing effect of the ecosystem on ice wedge thaw, and the ability of the system to mitigate thermal disturbance is discussed in Chapter 5, through the analysis of long-term repercussions from a direct anthropogenic disturbance to the landscape.

1.2 Research Objectives

My research aims to link geomorphic and ecosystem processes to better understand how ice wedge thermokarst in high Arctic polar deserts shapes landscape morphology, vegetation biodiversity and soil chemistry. Specifically, landscape and ecosystem processes have traditionally been examined in a unidirectional manner, whereas I propose it is more likely that the two are reciprocally linked. The analytic chapters of this dissertation involve data collected over three field seasons (2012 – 2014) near Eureka, Ellesmere Island, Nunavut. Previous studies, discussed in the Chapter 2 literature review, have focused on either the permafrost dynamics of the landscape or the ecological characteristics of vegetation communities, but few have examined both as a coupled system.

To accomplish this I have developed a number of field sites across the Fosheim Peninsula, as discussed in further detail below. One site I developed is south of Slidre Fiord; it is a section of climate-induced thermokarst occurring within a broader region undergoing thermokarst. My second site is north of Slidre Fiord, and is the old abandoned Eureka runway used for the initial development of the station in 1947 – 1951. At both sites a comprehensive set of geomorphic, geocryologic, edaphic, and vegetation measurements were collected, in an effort to truly capture as much data about thermokarst effects as possible.

This project will bridge the geomorphology/ecology gap in the literature by using a biogeomorphological framework in examining how the ice wedge/vegetation system responds to both natural and anthropogenic disturbances. The consequences of an initial thermokarst perturbation and the resulting ecosystem response are examined using a space-for-time approach within the landscape, with local changes also interpreted in a regional context to assess how the polar desert will respond at a broader level. This approach will be used to address the following research themes, with precise hypotheses discussed in their respective chapters:

> *(1) What are the local microtopographic, vegetation biodiversity, and edaphic repercussions of climate-induced thermokarst on a high Arctic ecosystem? What are the implications of this regionally and in light of projected increases of atmospheric temperature?*
>
> *(2) How does thermokarst-stimulated vegetation growth influence the stabilization of the active layer from further thermal change? What are the implications of this for estimates of northern permafrost thaw and biogeochemical cycles?*
>
> *(3) What are the long-term consequences of anthropogenic disturbance to high Arctic*

polar deserts? Can this ecosystem recover from ground disturbance, and if not, what form does it take? What does this imply for management practices regarding potential large-scale mineral or industrial development in the far north.

Each question is addressed individually and in order in Chapters 3 to 5.

1.3 Study Sites

My study sites are in an area of the Fosheim Peninsula near Eureka, Ellesmere Island, Nunavut (see Figures 1.1 and 1.2). This region was selected for my scientific work due to the nearby logistical hub of the Eureka Weather Station (whereby I received significant logistic support throughout my PhD), my supervisor's 25+ years of experience in this region, and the relatively high scientific history of this area when compared to other polar deserts. The Fosheim has been called the "Garden Spot of the Arctic" due to the diversity of vegetation that exists here, that while atypical for its geographical location it is not atypical for its thermal regime (Edlund, 1988). Precipitation records cannot account for the high vegetation abundance and diversity of this region, as the evaporative effect of the polar desert greatly exceeds that of rain or snowfall. This initially led to the question of what is supplying the alternate moisture sufficient to sustain this diversity. Edlund et al.'s (1990) study of the Fosheim peninsula suggested that this alternate water source is most likely the melting of ground ice, ice wedges in particular as their troughs often delimit many of the damp areas. Indeed, during initial site aerial reconnaissance in 2011, the Peninsula was identified as having key processes already occurring that would allow for the study of my questions of interest. It was during this initial flight where I accompanied Wayne on his own research that the genesis of my major thesis questions began to take form, and I cannot stress strongly enough what a huge benefit this "pre-season" exploration was to the development of my ideas.

For this area of the high Arctic, there are several regional characteristics that make geocryologic and ecosystem processes easier to study than other areas. The first is that the region is underlain by deep, continuous permafrost of over 500m in depth, with shallow active layers in the range of 0.3 – 0.5m (Couture & Pollard 1998). The largely flat topography has, in geologic timescales, recently risen from the sea due to isostatic rebound from around 2000 – 9000 years before present depending on elevation (Hodgson 1985; Bell 1996). The benefit of a flat, new, young topography is that it acts somewhat like a large control – most differences in terrain or biology can be inferred to come from recent processes, and the background landscape acts similar to a control in the space-for-time approach. The resulting landforms are comparatively new, and we can infer that there have been relatively minor effects from biological processes given the slow rate of community succession in cold environments (Edlund *et al.* 1990). In the Fosheim Peninsula, there is an estimated 1456.8km^2 of ground ice, of which ~700km^2 is comprised as wedge ice (Couture & Pollard 1998), giving the region an abundance of polygonal systems to study.

Throughout the area there is a severe seasonality of the solar regime, with 24-hour light and 24-hour darkness in the polar summer and winter, respectively. The 24-hour light in the summer months provides for continual solar input for plants, however the intensity of light is not as strong as in more temperate latitudes due to the angle of the sun. 24-hour light means a decreased difference between 'daytime' and 'nighttime' temperatures, which has the additional effect of preventing dew-condensation on plant life – another deprivation of water in an already water-scarce environment. Soils are nutrient poor, with nitrogen and phosphorus generally the limiting agents (Edlund & Alt 1989; Hodgson, St-Onge & Edlund 1991b; Young, Woo & Edlund 1997). Spring, summer, and autumn are condensed into a 4-month period, with a long, harsh winter characterizing the other 8 months. The main input of liquid water occurs during the spring thaw period, where the winter snowpack runs off and the water is retained in low-relief areas, typically ice wedge troughs (Rydén 1977). The brief summer (roughly from end of June to beginning of August) sees the thawing of the active layer and the release of ground water stores. Evaporation greatly exceeds precipitation during the summer months, qualifying the area as a polar desert from a precipitation perspective. Autumn sees the refreezing of the active layer and the beginning development of the winter snowpack. Winter is largely biologically inactive for plant life, but very active for permafrost as this is when ice wedge cracking occurs (more details in Chapter 2). All of these characteristics make life in the high Arctic particularly harsh, but a stalwart 140 vascular plants species still call this region home (Edlund *et al.* 1990).

For Chapter 3, data collection occurred at a site of naturally occurring thermokarst that I developed south of the Slidre Fiord. This area was chosen for the naturally induced thermokarst chapter because of its representativeness of both periglacial and biotic polar desert conditions found across the high Arctic, the accessibility of nearby logistical support (within helicopter flight distance of Eureka), and the resources that the landscape provided for fieldwork operations (primarily a regular freshwater drinking source – something quite difficult to find in polar deserts). To select this study site, I first examined remote sensing data for the region (coarse-resolution Google Earth imagery) based on my pre-fieldwork 2011 location scouting, and identified 14 sites across the area for aerial survey. During the aerial survey, I scouted half on the ground with visual assessment, taking photographs, active layer depth measurements, and determined which site would be both representative of processes of interest as well as provided the basics for logistical operation. The study site (79.84574°N, 85.37028°W), a 200m x 100m area containing both polar desert and thermokarst plant communities, was representative of the broader area and processes occurring across the Fosheim. There were no major landscape features in the immediately area, indicating that the site was not a drainage for regional snowmelt or rainfall catchment. Because of the *lack* of surrounding features that could influence landscape shape, geomorphic differences at the site represent *localized* thermokarst processes affecting the ice wedge/vegetation system. At 101m elevation, the area lies below the Holocene marine limit (Hodgson 1985; Bell 1996) and soils consist of fine-grained marine clay sediments.

For Chapter 4, the path analysis model was informed by data gathered at the site used for Chapter 3.

For Chapter 5 the research location was the old tundra airstrip near Eureka, Ellesmere Island, Nunavut (80.0175°N, 85.7340°W). The airstrip was constructed in 1947 by the grading and removal of vegetation, and the infilling of uneven ground into a flat, compacted 1.6 km x 60m tundra runway. While primarily used as an ice-runway for winter transport, the yearly removal of vegetation continued from 1947 until its abandonment in 1951. Since 1951 the airstrip has had no further development, but vegetation and geomorphic differences between the disturbed and undisturbed areas are still readily visible. A 400m x 400m subsection of the area was selected and a network of transects were overlain on the site of disturbance, with a significant border area of undisturbed, control terrain on the east and west sides of the runway. This section of the Fosheim has similar regional characteristics to those described for the site from Chapter 3. Given the very distinct nature of the grating disturbance, easy visualization of location, and discrete time frame of occurrence, data interpretation has the added benefit of daily historical records written by early Eureka staff that catalogued when and what kind of landscape alteration was conducted (Department of Transport – Canada & Department of Commerce – US

1951). It was during a particularly dull June in 2012 that I was trapped at Eureka for several weeks unable to reach my site due to a very late spring snowmelt that created impassable mud. I read the entire first year (from 1947) of daily logs of the station and it is better than most fictional novels – the first crew endured months of poor rations, no mail delivery, and the plane taking the crew back home (after a year in the field) crashed in the mountains of Labrador. Incredibly everyone survived. Interestingly, the record keeper went blind midway through the first season due to a chemical explosion in camp. At that point, daily records become short, but the keeper continues to write by feeling out the shape of the typewriter keys. Gradually his eyesight returns, logs get longer, and he peppers in details of his experience of regaining eyesight while illustrating the growing tension between US military personnel and Canadian scientists in camp.

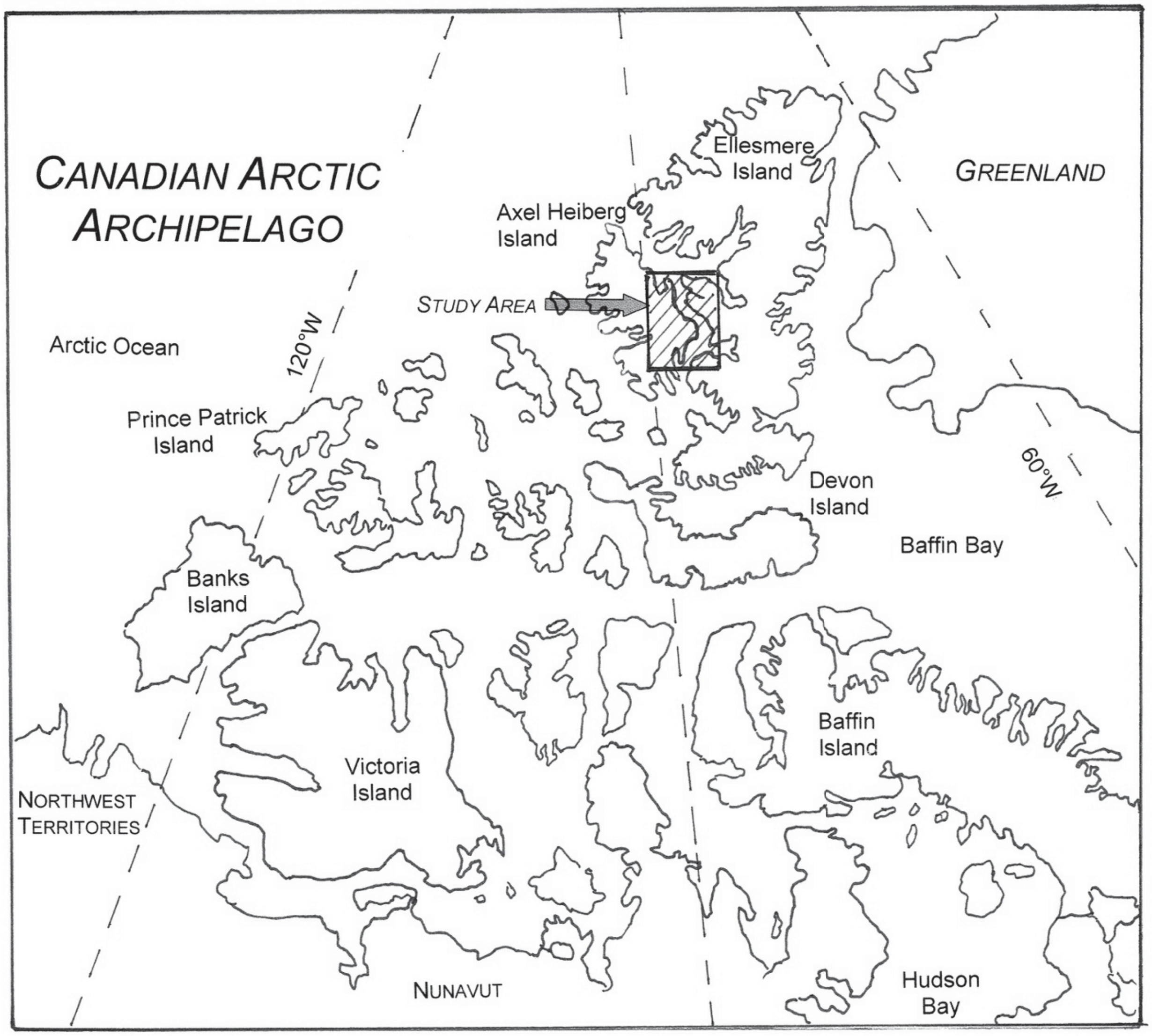

Figure 1.1: Map of the Canadian high Arctic Archipelago. Study sites were located on the Fosheim Peninsula on Ellesmere Island within the shaded region, with a more detailed map provided in Figure 1.2.

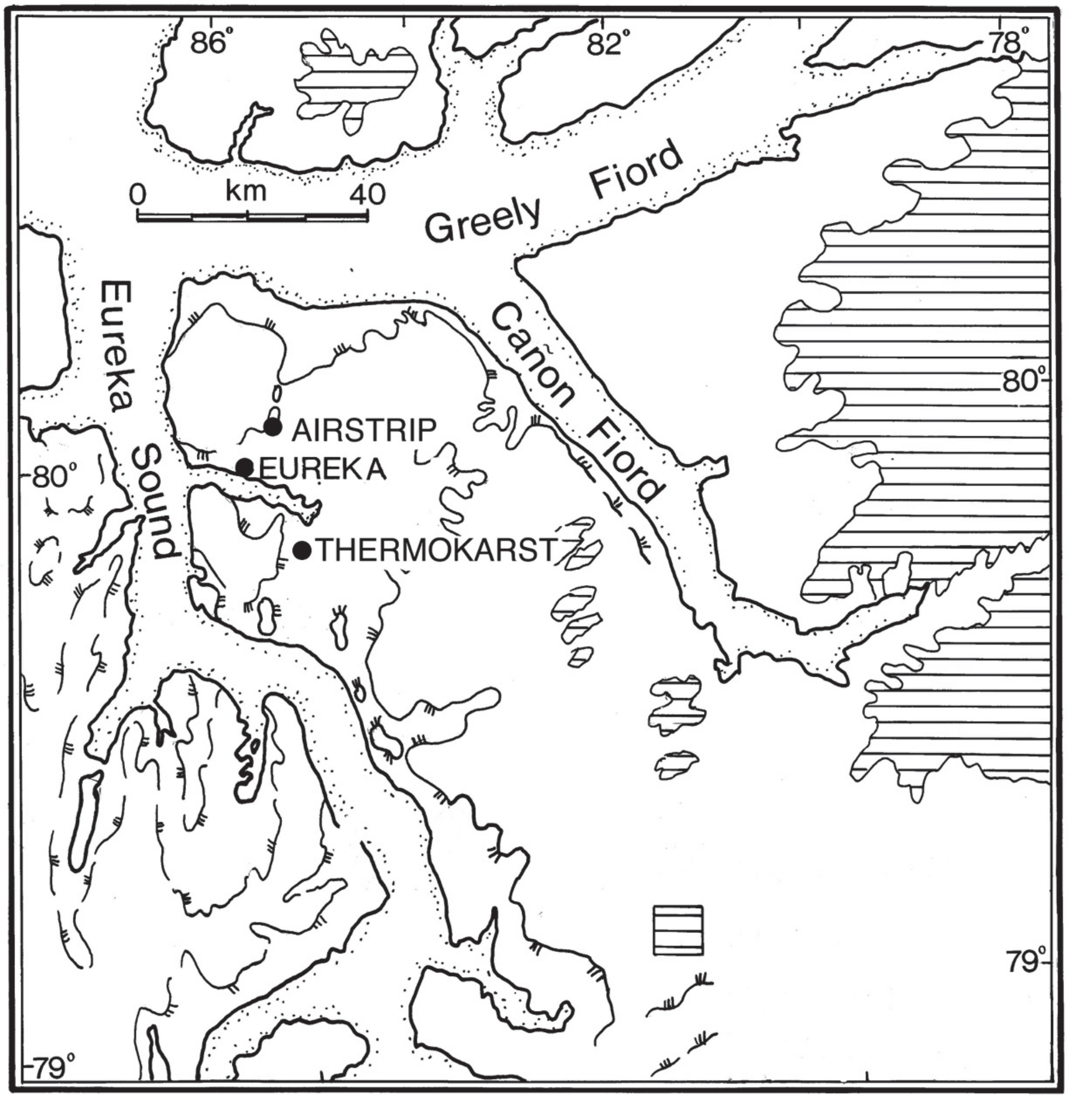

Figure 1.2: The Fosheim Peninsula of Ellesmere Island. Study sites were located near the logistical hub of the Eureka Weather Station. Data for chapters three and four originate from the site designated as “Thermokarst” above. Data for chapter five originates from the site designated “Airstrip” above, and refers to the old Eureka runway.

CHAPTER 2 – Literature Review

The role of ice wedges in shaping arctic ecosystems has been largely overlooked despite their near omnipresence and significant mass throughout the continuous permafrost region. The Canadian high Arctic is currently experiencing significant atmospheric temperature increases, with the depth of the permafrost active layer projected to increase substantially. Due to the widespread distribution and abundance of ice wedges, changes in active layer depth should result in significant alteration of the geomorphic and vegetation landscape due to thermokarst and the volumetric loss of ground ice. What form the polar landscape will take in the near future will depend on the balance of competing forces - increased ice wedge thermokarst versus the stabilizing effect of increasing vegetation cover in high latitudes, both of which are predicted by climate change (Hinzman *et al.* 2005). This balance remains unclear as analyses of biotic and abiotic interactions are generally missing from most geomorphic literature (Hjort & Luoto 2009). My research examines the processes of the ice wedge/vegetation system and determines how thermokarst in high Arctic polar deserts changes the geomorphic and ecologic characteristics of the landscape. Here, I present a background literature review that provides a backbone to the more specific literature reviews that comprise the introductions of the analytical chapters.

2.1 Ice wedges: distribution, processes, geomorphology

The periglacial environment covers approximately 25% of Earth's surface, of which an additional 20-25% experienced it in the past (French 2007). Several cryogenic processes and features are unique to this cold environment: permafrost, thermal contraction cracks, the formation of wedge ice within the permafrost, and the thawing of this ice-rich permafrost (thermokarst). Permafrost is a term coined by Simon Muller (1943) for the previously labeled "permanently frozen ground" used by Leffingwell (1919) to describe ground that underlies almost the entire terrestrial part of the Arctic. The current usage of the term pertains to ground that remains at or below 0°C for at least two consecutive years (French 2007). The distribution of permafrost is governed by the interactions of climate, mean annual air temperature (MAAT), ground temperature, and local microclimatic conditions and can be divided into zones of continuous and discontinuous coverage. The southern limit of the continuous permafrost zone correlates roughly with the -6 to -8°C MAAT isotherm. Within the continuous zone, permafrost generally occurs everywhere except beneath large bodies of water. The southern limit of the discontinuous zone is roughly around the -1ºC MAAT isotherm (French 2007).

Ice wedges are one of the defining features of the periglacial environment as they are found nearly everywhere within the continuous permafrost region (see Figure 2.1). Within the Northern Hemisphere, ice wedges may underlie a million square miles (2,600,000km^2) of tundra and boreal forest (Mackay 1972), and in extensive areas, as much as 50% of the upper 3m of the ground is occupied by wedge ice (Brown 1966; Pollard & French 1980). These ice wedges may be classified as active or inactive depending on their dynamic state – i.e. is cracking occurring or not. The range of active ice wedges roughly coincides within the zone of continuous permafrost in North America while the ice wedges within the zone of discontinuous permafrost are generally inactive (Péwé 1973).

The general *qualitative* idea of thermal contraction cracks leading to ice wedge growth was first described by Leffingwell (1915). This principle was generally accepted in the literature, but it was not until the first examination of this process from a physics standpoint by Lachenbruch (1962) that the mechanical theory was laid out in detail. This theory posited that as the ground surface cools it contracts if it is not constrained. Since it is constrained, horizontal tensions are generated, although generally without observable horizontal strain. This tension increases until the tensile strength of the ground material is exceeded, resulting in a vertical thermal contraction crack to relieve some of the accumulated tension. Mackay (1974) found that average cracks on Garry Island, Northwest Territories were 1cm wide at the ice wedge surface and extended downwards for over 5m, and other studies report maximum crack depths of around 5.5m (Mackay 1986; Fortier & Allard 2004). These cracks form as a result of the winter cooling of the frozen active layer and top of permafrost, with a rapid drop in temperature being the trigger mechanism required for cracking. However, a variety of site-specific factors such as snow cover, vegetation cover, ground temperature gradient, or soil moisture content can result in non-homogenous cracking rates in environments of similar atmospheric variables. The site-specificity of cracking growth rates makes it nearly impossible to estimate the age of an ice wedge by its width (Mackay 1986).

After the winter crack is formed, spring snowmelt seeps into the crack and the freezing of this water results in the growth of the ice wedge. Mackay (1989) notes that an ice wedge's growth rate does not correspond with the size of the newly opened crack as this crack can widen, narrow, or close before it becomes infilled with water, and that most cracks may narrow in late March/early April as the surrounding ground expands due to warming air temperatures. Actual ice wedge growth rate measurements are few: Black (1974) found growth rates of 2mm/year in old wedges in Barrow, Alaska; Mackay (1974) noted ice veinlet growth rate of 1-3mm/year at Garry Island, NWT; and Mackay & Burn (2002) recorded a larger veinlet growth rate of 1-3 cm/year in Illisarvik, NWT. As the annual cycle of winter cracking, spring infilling and refreezing repeats this results in the growth and expansion of the ice wedge.

This continued development of an ice wedge does not occur in isolation, as vegetation cover often develops concurrently with the ice wedge and influences wedge development (Mackay & Burn 2002). This vegetation cover alters albedo, moisture retention rates, but importantly increases snow trapping - resulting in the insulation of the ice from harsh winter temperatures and potentially decreased thermal cracking. The decrease and eventual ending of cracking and ice wedge growth can result from increased vegetation growth, snow entrapment, or an increase in winter ground temperatures as a result of changing climate.

The growth and shape of an ice wedge are thus controlled by the local ground dynamics of where they occur. Ice wedges themselves are classified by the geomorphic process of their origin, which is primarily influenced by the local ground surface dynamics. Three distinct morphotypes exist: epigenetic, syngenetic, and anti-syngenetic (Mackay 1990).

Epigenetic wedges develop in the pre-existing permafrost, and they grow wider rather than higher or deeper (Mackay 1974) since the ice wedges tend to crack near the center were v-shaped ice veinlets grow. The age of the ice increases from the center outwards but changes little from top to bottom and these wedges grow in stable areas that experience little or no fluctuations in ground surface material volume. *Syngenetic wedges* develop as sedimentation occurs, and grow both higher and wider as material is deposited and the permafrost aggrades (Mackay 1990). As the ground surface rises due to the addition of material (through processes such as peat growth, mass wasting, etc.), the permafrost table rises and results in the upward growth of the ice wedge. *Anti-syngenetic wedges* go through downward vertical growth in a process opposite to syngenetic growth. They occur on slopes where surface erosion removes surficial material, and growth progresses in a downward direction normal to the slope (Mackay 1990).

Leffingwell (1915; 1919) demonstrated that ice wedges underlie the troughs of the large polygonal patterned ground networks in the Arctic. One of the most recognizable Arctic features is the extensive network of polygonal patterned ground. During thermal contraction cracking, only a slight relief of tension is released in the direction parallel to the new crack in the ground surface, resulting in large horizontal stress differences (Lachenbruch 1962). Cracking will continue to occur to try to relieve this tension, and the second crack will generally be perpendicular to the direction of greatest tension, resulting in a second crack that intersects the first one at a right angle (Mackay & Burn 2002). This series of right angle cracking leads to "orthogonal systems of polygons" that can be further classified as "random" or "oriented". Random systems have no preferred orientation, whereas oriented systems are generally oriented by gradually receding large bodies of water (such as lakes or rivers) which results in one set of cracks parallel to the receding water and another set perpendicular to it. The local sediment has an effect on polygon diameter, and in general drier sediment develops less thermal stress and theoretically forms wider polygons (Lachenbruch 1962).

Importantly, these polygon networks of connected ice wedge troughs link to form erosional tunnels and channels during the spring snowmelt period. During this time the active layer is generally still frozen, inhibiting the snowmelt runoff from percolating through the ground. Because of this, runoff becomes concentrated in the troughs of polygons and through processes of thermal and mechanical erosion tunnels can form through ice wedge troughs (see Figure 2.2). Runoff through these well-developed trough systems can initiate large hydrologic and geomorphologic terrain modifications at a local scale (Fortier, Allard & Shur 2007).

Ice wedges and their polygon systems have large influences on the local hydrology and micro-relief topography. The cascading effects of these processes are found in varying soil moisture regimes, nutrient profiles, and differing vegetation patterns. Due to the permafrost's resistance to water drainage, the polygon system's micro-relief greatly influences the distribution of both organic and mineral material. High-centered polygon tops may have well-drained upper surfaces, while their troughs may contain standing water and the differences in these moisture regimes are reflected in their differing composition of corresponding plant communities (Drew & Tedrow 1962). Soil conditions and vegetation characteristics are highly variable at a local scale of decimeters to meters but quite homogenous at the regional scale when examining whole polygonal networks (Kutzbach, Wagner & Pfeiffer 2004). These networks support a diverse array of plant species and vegetative ecosystems and are responsible for the creation of microhabitats within an otherwise very homogenous environment (Billings & Peterson 1980).

The different physical pressures and characteristics between ice wedge troughs and polygon centers are reflected in their respective vegetation communities. Generally speaking, taxa differ in their water requirements and will have greater or less success in colonizing different types of polygons and different microsites on a polygon depending on the soil moisture regime of the site (Ehleringer & Miller 1975; Shaver, Chapin & Billings 1979; Grulke & Bliss 1988). As noted, that polygon development does not generally occur in isolation from the development of its overlying vegetation community. Pioneer species are present throughout the entire cycle of polygonal development, however the relative dominance of species turns over as polygons grow, stabilize, or undergo thermokarst processes (Billings & Peterson 1980).

Ice wedges and their polygon networks are a dynamic geomorphic and ecologic system that both affect the landscape and are affected by changes in the thermal regime at the regional and local level. Questions remain about the reciprocal biogeomorphic interaction of vegetation communities and ice wedge polygon system, which I address in this thesis. As climate change continues to affect the Arctic, these dynamic systems stand to be affected in a way that is not currently understood due to the general separation of geomorphic and ecologic literature. Given the large expanse of ice wedges worldwide, no picture of northern climate change would be complete without the careful consideration of this quintessential periglacial feature.

2.2 High Arctic Ecology: vegetation, soils, biogeography

The predominant biome of Ellesmere Island is the polar desert, characterized by nutrient poor soils, low precipitation, high evaporation, high winds, low ground temperatures, and an extreme seasonality of solar input. The macroclimate of the Arctic Archipelago is one of a ‘continental landmass’ for much of the year. Even though the islands are surrounded by ocean, the water is frozen for about 10 months of the year and provides little moisture to the general precipitation pattern (Young *et al.* 1997). This both drives down winter temperatures as well as keeps summer temperatures mild when the breakup of sea ice exposes the ocean and cools the region. Eureka, on the Fosheim Peninsula, has the coldest recorded MAAT in North America, roughly -18.8°C. Little snowfall occurs, and what does has a very low water-equivalent (Rydén 1977), and the area receives extraordinarily low rainfall during summer months. Strong winter storms occur, blowing ice-crystals that damage exposed and upright vegetation, and the growing season typically lasts only from end of June to beginning of August (Edlund *et al.* 1990).

Despite these incredible constraints, low-level topography such as ice wedge troughs modifies surface hydrology in a manner that can support relatively lush and diverse vegetation in an otherwise harsh polar desert (see Figure 2.3). The presence of ice wedge polygon systems leads to major heterogeneity within the Arctic landscape, with many environmental characteristics varying significantly over the meter or decimeter scale (Zona *et al.* 2011). Small differences in elevation (less than 10 cm) can lead to significant variations in pH, dissolved CO_2, nutrients, and soil moisture. The presence of permafrost inhibits nutrient release of the soils by depressing ground temperatures and restricting drainage and vertical water movement. For low-lying areas this favors anaerobic soils, denitrification of nitrates, and a lack of oxygen necessary for decomposition. Additionally, winter ground temperatures can be higher in troughs where snow accumulates in greater depth compared to windblown polygon centers. The net effect of these factors results in different types of vegetation communities selectively colonizing different microsites within each polygon. This patchwork mosaic of minor differences in elevation, moisture status, and substrate material results in significant changes in environmental and nutrient regime for vegetation. Indeed, the spatial transfers involved in nutrient cycling within the microtopography of Arctic systems are done largely through hydrologic and vegetation processes (Babb & Whitfield 1977).

The spatial patterns of Arctic plant communities reflect the microtopographic environmental gradients caused be geomorphic, cryologic, and hydrologic processes. Frost cracking, frost heaving, and ice wedge activity in the winter; runoff and flow dynamics during the spring freshet; depth of summer thaw; and activities such as wind erosion and sediment deposition are the primary processes influencing vegetation development. Permafrost, precipitation, and solar regime transform microtopographic features such as polygon tops and troughs into steep environmental gradients along which vegetation communities turnover quickly (Bliss, Svoboda & Bliss 1984; Engstrom *et al.* 2008; Huemmrich *et al.* 2010).

Vegetation communities can also have influential effects on microtopographical patterns. This contrasts with the general assumption in older literature that vegetation cover is a passive reflection of local hydrological conditions that are determined by microtopography, with key community types reflecting local moisture regimes (Bliss *et al.* 1984; Chapin & Körner 1995). This linear progression of process has been re-examined in recent years and the reciprocal feedback effects of vegetation cover on permafrost processes have gained wider attention (Euskirchen *et al.* 2009; Swann *et al.* 2010; Cutler 2011).

Vegetation is both a result of the environment it colonizes, as well as a reinforcing driver of the conditions that favour growth. These effects vary along the Arctic climate gradient and have an increasingly important role where greater vegetation densities are found. The stabilizing effect of these communities serves to modify frost heave and frost cracking (Walker *et al.* 2008) thereby counteracting geocryological processes. By altering the energy balance and gas exchange with the ecosystem, landscape, and atmosphere, vegetation distribution can have great effects on geomorphological dynamics through feedbacks involving the surface energy balance (Gamon *et al.* 2012). For instance, the strength of vegetation influence on ground thermal conditions can be large enough to challenge assumptions of permafrost dynamics based on latitude alone. Walker et al. (2008) found comparable mean depths of thaw in areas of vegetated pattern ground within sites of both the highest and lowest soil surface temperatures (36 cm at 69°N and 31 cm at 78°N latitude respectively). Importantly, vegetation does not always have to be a counteracting (stabilizing) feedback on environmental processes. Recent work examining the northward march of the shrub line showed that areas of Subarctic tundra undergoing this ecosystem shift resulted in a 69-75% increase in absorbed solar radiation during the snow cover period (Sturm *et al.* 2005). These results show that consequences of ecologic change across the Arctic are much more variable due to microclimate conditions than is generally discussed.

Some believe that the current rate and magnitude of warming may be too great for species to migrate to new suitable habitats (Rice & Emery 2003; Aitken *et al.* 2008). During the Quaternary period, species were able to successfully migrate to higher latitudes in response to climate warming, but with the result of extinctions and distribution changes in local populations (Davis & Shaw 2001; Petit *et al.* 2003). While successful species migrations have occurred in recent decades (Parmesan & Yohe 2003; Bertin 2008), recent population extinctions in places like the Mediterranean are likely driven by warming trends that exceed the tolerance range of native species (Penuelas & Boada 2003; Lavergne *et al.* 2005).

Indeed, most evidence from the post-glacial period suggests that plant species respond to a warming climate by migrating, however the record shows that some species stay in the same locality through an evolved adaptive capacity (Bradshaw & McNeilly 1991). This adaptive capacity is termed phenotypic plasticity – the ability of an organism to express a range of morphological characteristics without undergoing genetic change. In the Arctic, it may be possible that a significant level of phenotypic plasticity would be able to soften selection pressures sufficiently to allow a local population to persist within a changing climate. Phenotypic plasticity can allow for plant survival and development in varying environments (Pigliucci, Murren & Schlichting 2006), and with sufficient adaptive capacity they may persist in their local environment despite changing pressures (Lindner *et al.* 2010). Additionally, short-term plasticity can allow for plants to compensate for rapid change (Pigliucci *et al.* 2006; Ghalambor *et al.* 2007).

Despite low rates of sexual reproduction (Bauert 1996), there is a large range of ecotypic differentiation within Arctic specialists, and it may be this diversity of ecotypes that allows native high Arctic vascular plants to locally persist within the regional warming. The high Arctic zone has a large diversity of microsite climates, each of which harbors unique habitats with their own set of selective pressures. This microsite heterogeneity has produced *relatively* high genetic diversity even within clonal plant populations through diversifying selection (Ellstrand & Roose 1987). Given that climate change will affect microclimate conditions, and some Arctic species are good generalists due to ecotypic plasticity while others are not, serious questions remain as to what the effects of habitat change on vegetation biodiversity and community composition will be.

2.3 Climate Change Context

The effects of climate change are global, but nowhere are the effects of warming projected to be more pronounced than in the Arctic. The region is warming at double the rate of any other region (Johannessen *et al.* 2004; IPCC 2013), which has led to warmer ground surface temperatures (Allison *et al.* 2011), shifts in surface hydrology (Smith *et al.* 2005), increases in active layer thaw depth (Åkerman & Johansson 2008; Schuur *et al.* 2008), and changes in vegetation cover (Elmendorf et al. 2012a). The general prediction of ecosystem shifts in the

Arctic is that boreal tree and shrub cover will continue to expand northward into the tundra zone (Gamon *et al.* 2012). However, not all Arctic landscapes show the same pace or degree of change (Callaghan *et al.* 2011), indicating that there are different balances of positive and negative feedbacks at the local level – showing that some areas that may be resistant to change and some may be particularly susceptible. There is a predicted northward shift of vegetation zonal boundaries in response to warmer temperatures and deeper snowpack, but local vegetation may not necessarily shift in parallel with climate. The re-zoning and redistribution of arctic vegetation is not likely to be uniform, as microtopographical heterogeneity results in non-uniform environmental gradients. Areas of high cryoturbation and thermokarst disturbance may change more quickly than areas with stable plant communities that insulate the thermal properties of the soil surface (Lantz *et al.* 2009). It is unclear how high Arctic patterned ground systems will respond to warmer and moister climates, as any vegetation change is dependent on water availability and nutrients in an area traditionally poor in both. Because of this, some have suggested that the overall response of the high Arctic may be slower than in warmer low Arctic environments (Walker *et al.* 2008). I posit that *certain* aspects of the high Arctic, such as thermokarst initiation, are more likely to change faster due to the relative scarcity of vegetation and the increased exposure that bare ground has on subsurface temperatures.

The general consensus is that climate warming will have significant effects on plant community composition, biomass, and productivity both through direct changes of increased soil and air temperatures, and indirect changes of soil moisture and nutrient availability (Elmendorf et al. 2012a; Elmendorf et al. 2012b). These factors are difficult to simulate collectively in an experimental approach (i.e. the International Tundra Experiment – ITEX), particularly those of permafrost thaw and ground subsidence. Shuur et al. (2007) took the approach of examining a natural gradient of permafrost thaw and subsidence across sites of different degradation stages. They found that biomass shifted from graminoid-dominated tundra in the youngest disturbed site to shrub-dominated in the oldest disturbed site. While this specific pattern cannot be generalized given the heterogeneity of Arctic landscapes, the theme that warming climates will change the governing permafrost, microtopography, and vegetation dynamics is a common one (Jonasson, Michelsen & Schmidt 1999; Shaver *et al.* 2001; Van Wijk *et al.* 2003; Walker *et al.* 2006). Indeed, in the high Arctic the first signs of the effects of global warming on vegetation communities are becoming evident (Hill & Henry 2011). Interestingly, their findings are contrary to the hypothesis that infertile high Arctic grasslands are resistant to climate change (Grime *et al.* 2008).

One of the indirect impacts of climate change on Arctic ecosystems is the expected increase of industrial development at high latitudes (Forbes, Ebersole, & Strandberg, 2001). The last decade saw a record minimum of Arctic sea ice cover, with shipping across the Northwest Passage becoming increasingly viable. Shipping routes allow for larger scale development of the Arctic's mineral wealth and fuel reserves, many of which would require significant terrestrial infrastructure support. The range of these land-based impacts are difficult to predict ahead of time, particularly due to a relative lack of long-term impact studies in this region (Forbes, 1993). The high Arctic biome will be under considerable pressure with one of the slowest community recovery rates of any ecosystem (Edlund & Alt 1989), exacerbated by a high susceptibility to any change in permafrost thermal balance. It is predicted that with increased anthropogenic activity in the far north, we should see an increasingly patchy mosaic of ecosystem types due to disturbance (Forbes et al., 2001).

2.4 Summary

My thesis will draw upon these bodies of knowledge, in addition to the more specific literature reviews I layout at the beginning of each analytic chapter. As the full range of high Arctic climate effects on ground ice and vegetation community is difficult to simulate *in situ,* I examined a site of naturally occurring thermokarst in Chapter 3. I identify which of these ecosystem factors are most susceptible to change and quantify their response in an area of locally induced thermokarst. Through my results, I identify that in addition to large changes in biodiversity, edaphic conditions, and surface hydrology, vegetation growth is concurrent with decreased active layer depth. I expand on this in Chapter 4, where I model that the stimulated vegetation growth through altered surface hydrology should be able to dampen and inhibit a significant proportion of subsurface thermal change in the near future. Lastly, in Chapter 5 I examine a site of historical anthropogenic disturbance to quantify the long-term consequences of disturbance to high Arctic ground surfaces, and what this may mean for the recovery trajectory of the ecosystem. Together these results give an indication of how the most ubiquitous and widespread periglacial feature – ice wedge polygon systems – can be expected to change as a result of direct and indirect disturbances in the near future.

Figure 2.1: An ice wedge as seen in cross section. This photo is of a natural exposure of an ice wedge as caused by thaw slump thermokarst on the Fosheim Peninsula, Ellesmere Island in 1992 (modified from (Couture & Pollard 2007)).

Figure 2.2: An ice wedge trough caused by the subsidence and volumetric loss of wedge ice. As the active layer deepens, wedge ice is melted and this loss in volume causes the ground above it to subside resulting in the increased expression of polygon troughs. These troughs form drainage networks that collect surface water runoff.

Figure 2.3: The region of the Fosheim Peninsula from which the site for chapter three and four was chosen. This aerial shot south of Slidre Fiord shows the polygonal networks created by repeated thermal contraction cracking and the expression of polygon troughs and tops. As easily visible here, ice wedge troughs show distinct vegetation patterns from tops and the area overall appears to be undergoing climate-induced thermokarst.

CHAPTER 3 - Ground ice melt in the high Arctic leads to greater ecological heterogeneity

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3.1 Abstract

The polar desert biome of the Canadian high Arctic Archipelago is currently experiencing some of the greatest mean annual air temperature increases on the planet, threatening the stability of ecosystems residing above temperature-sensitive permafrost. Ice wedges are the most widespread form of ground ice, occurring in up to 25% of the world's terrestrial near-surface, and their melting (thermokarst) may catalyze a suite of biotic and ecological changes, facilitating major ecosystem shifts. These unknown ecosystem shifts raise serious questions as to how permafrost stability, vegetation diversity, and edaphic conditions will change with a warming high Arctic. Using in-depth, comprehensive field observations and space-for-time approach, we investigate the highly structured landscape that has emerged due to the thermokarst-induced partitioning of microhabitats. We examine differences in vegetation diversity, community composition, and soil conditions on the Fosheim Peninsula, Ellesmere Island, Nunavut. We hypothesize that (1) greater ice wedge subsidence results in increased vegetation cover due to elevated soil moisture, thereby decreasing the seasonal depth of thaw and restricting groundwater outflow. (2) Thermokarst processes result in altered vegetation richness, turnover, and dispersion, with greater microhabitat diversity at the landscape scale. (3) Shifts in hydrology and plant community structure alter soil chemistry. We found that the disturbance caused by melting ice wedges catalyzes a suite of environmental and biotic effects: topographical changes, a new hydrological balance, significant species richness and turnover changes, and distinct soil chemistries. Thermokarst areas favor a subset of species unique from the polar desert and are characterized by greater species turnover (β-diversity) across the landscape. Our findings suggest that projected increases of thermokarst in the polar desert will lead to the increased partitioning of microhabitats, creating a more heterogeneous high Arctic landscape through diverging vegetation communities and edaphic conditions, resulting in a wetland-like biome in the high Arctic that could replace much of the ice-rich polar desert.

3.2 Introduction

The high Arctic biome is warming at double the rate of any other region (Johannessen *et al.* 2004; IPCC 2013), which has led to warmer ground surface temperatures (Allison *et al.* 2011), shifts in surface hydrology (Smith *et al.* 2005), increases in active layer depth (Åkerman &

Johansson 2008; Schuur *et al.* 2008), and changes in vegetation cover (Sturm *et al.* 2005). Indeed, in the high Arctic the first effects of warming air temperatures on plant communities are becoming evident (Hill & Henry 2011), and a warming climate has been linked to changes in the dynamics of permafrost, microtopography, and vegetation (Jonasson *et al.* 1999; Shaver *et al.* 2001; Van Wijk *et al.* 2003; Walker *et al.* 2006). Not as well understood is how the potential of melting ground ice, currently contained within permafrost and particularly sensitive to a warming climate, may directly and indirectly catalyze ecological changes across the high Arctic.

Permafrost underlies more than 25% of the Earth's land surface (Zhang *et al.* 1999) and one particularly common type of ground ice, known as ice wedges, occurs wherever continuous permafrost exists (French 2007) and in places may constitute over 50% of the volume of the top 3m of ground (Pollard & French 1980). An ice wedge is a v-shaped body of ice that extends downwards for three to four meters and is formed by repeated thermal contraction cracking of the ground during winter months that is subsequently filled by surface water during the spring melt period. Ice wedges in the polar desert create a network of high-centered polygons, surrounded by low-relief polygon troughs under which the ice wedges lay. Given their ubiquitous nature, large mass, and sensitivity to warming temperatures, the melting of ice wedges plays an important role in changing moisture regimes throughout this water-scarce region (Edlund *et al.* 1990), as high Arctic polar deserts receive 80% of their annual precipitation in the form of low density snow, with little liquid precipitation during summer months (Rydén 1977).

Thermokarst is the climate or disturbance induced process of ice-rich permafrost melt and its effects resonate through the geomorphology, ecology, and biota of the Arctic (Billings & Peterson 1980). Two primary effects of thermokarst are the groundwater contributions made by melting ground ice during hot years (Edlund *et al.* 1990), and changes in local relief. Changes in landscape topography (subsidence) occur due to the volumetric loss of excess ice during melt, causing linear depressions in the ground known as troughs. These troughs are localized low points that promote the collection and transmission of water either directly from greater snow accumulation during winter months or from surface runoff during the snowmelt period. The enlargement of troughs through continued thermokarst-induced subsidence (and mechanical erosion due to run off) increases snowpack and surface runoff collection and should amplify local accumulation of water.

The presence of ice wedge polygon systems also creates biotic heterogeneity within the Arctic landscape, as many environmental characteristics vary significantly over the meter or decimeter scale (Zona *et al.* 2011). Small differences in elevation (less than 10 cm) can lead to significant variations in pH, soil nutrients, and soil moisture. The net effect is a highly structured landscape with microsite variation in vegetation cover and composition within the ice wedge polygon system. The general climate features of permafrost, precipitation, and solar regime transform these microtopographic differentiations into steep environmental gradients along which vegetation communities change dramatically (Billings & Peterson 1980; Bliss *et al.* 1984; Engstrom *et al.* 2008; Huemmrich *et al.* 2010). Thermokarst, which amplifies differences in microtopography, is thus predicted to further increase biotic heterogeneity.

The harsh conditions of dry polar deserts have left the high Arctic with a relatively homogenous vegetation cover of low diversity (Edlund & Alt 1989). However, we suggest that the amplification of microtopographic differences through thermokarst likely results in greater environmental heterogeneity and thus greater community composition change among thermokarst areas compared to the surrounding polar desert. Further, these changing community patterns and abundances are likely to alter soil chemistry of thermokarst areas through increased plant growth and associated microbial activity. While microbial nitrogen fixation – a process that requires sufficient soil moisture (Mengel *et al.* 2001) is likely to increase in thermokarst areas, increased plant growth may deplete soil nitrogen, phosphorus, and potassium, and decrease soil pH (through selective ion uptake at their roots) while increasing organic matter build-up through the deposition of dead material.

With the breadth of possible ecosystem and landscape alterations due to thermokarst it is surprising that ecosystem and landscape changes have been researched relatively independent of one another. Climate change is predicted to be the largest driver of Arctic biodiversity loss (Sala *et al.* 2000), yet significant gaps remain in our understanding of the underlying landscape processes that structure Arctic biodiversity. Changes in thermokarst rate and magnitude may resonate through the ecosystem at all levels – potentially intensifying predicted and documented changes to edaphic conditions (Lang *et al.* 2012), vegetation primary productivity (Elmendorf *et al.* 2012b), and carbon sink/source dynamics (Abnizova *et al.* 2012) that may be expressed regionally and globally. A clear need exists to examine ecosystem and geomorphic processes as a coupled system in light of a warming climate.

Using a space-for-time approach, we examined the ecological effects of thermokarst in the Fosheim Peninsula, Ellesmere Island, Nunavut within the Canadian high Arctic. This region is characteristic of a polar desert environment with little precipitation, nutrient poor soils, an extremely short growing season, and a homogenous vegetation cover comprised primarily of dry dwarf-shrub tundra with pockets of sedge communities (Edlund *et al.* 1990). Within a hypothesis validation framework, we evaluate whether: (1) greater ice wedge subsidence results in increased vegetation cover due to elevated soil moisture, thereby decreasing the seasonal depth of thaw (active layer) and restricting groundwater outflow. (2) Thermokarst processes result in altered vegetation richness (alpha-diversity, Shannon's H), turnover (beta-diversity), and dispersion (NRI, NTI), and whether amplified differences in relief between polygon tops and troughs drives greater microhabitat diversity at the landscape scale. (3) Shifts in plant community structure alter soil chemistry, elevating organic matter, NH_4+, and NO_3-, and decreasing P, K, and soil pH.

3.3 Methods

Study Site

Data were collected from a thermokarst site within a flat plateau region of the Fosheim Peninsula near Eureka, Ellesmere Island, Nunavut, Canada. This area was chosen for our study because it is representative of both periglacial and biotic polar desert conditions found across the high Arctic, the accessibility of nearby logistical support, the relatively lengthy (for the region) historical record of previous environmental study, and the authors' field experience within the region. Permafrost in the area exceeds 500m thickness (Taylor 1991) with a relatively thin average active layer thickness of 57cm that varies considerably depending on microclimatic conditions (Couture & Pollard 1998). The largely flat topography has, in geologic timescales, recently risen from the sea due to isostatic rebound (2000 – 9000 years before present depending on elevation - Hodgson, 1985; Bell, 1996). The resulting landforms are comparatively new, with relatively minor effects from biological processes given the slow rate of community succession in cold environments. In the Fosheim peninsula alone, there is an estimated 1456.8km^2 of ground ice, of which ~700km^2 is probably wedge ice (Couture & Pollard 1998).

To select our study site, we first examined remote sensing data for the region (coarse-resolution Google Earth imagery), and identified 14 sites across the Fosheim peninsula for aerial survey. During the survey, half were scouted with on the ground visual assessment, and the site selected for intensive fieldwork needed to be both representative of processes of interest and able to provide the basics for logistical operation. The study site (79.84574°N, 85.37028°W), a 200m x 100m area containing both polar desert and thermokarst plant communities, is representative of the broader area. There are no major landscape features in the surrounding area and the site is not a drainage corridor for regional snowmelt or rainfall catchment (see Fig. 3.1). Thus, geomorphic differences at this site represent localized thermokarst processes affecting the ice wedge/vegetation system. At 101m elevation, the area lies below the Holocene marine limit (Hodgson 1985; Bell 1996) and soils consist of mainly fine-grained marine clay sediments.

Data Collection

All data was collected during June and July 2013. Plant community composition was measured by visually estimating percent cover within 0.5m^2 quadrats placed at alternating polygon tops and troughs (between 5-10m apart) along five transects running 200m east to west, spaced 25m apart north to south. We followed a stratified random sampling approach, recording compositional data within 80 quadrats with 20 samples in each of the following microtopography subunits: polar desert (control) tops, polar desert (control) troughs, thermokarst tops, and thermokarst troughs. Five thermokarst trough quadrats were excluded due to standing water that remained throughout the study season. All vascular vegetation was identified to the species level, with vouchers submitted to the Marie-Victorin Herbarium in Montreal, QC (see Table S3.1 in Supporting Information). Vascular plant nomenclature in this paper follows Saarela *et al.* (2013). Percent cover of moss, lichen, leaf litter, and bare ground were also noted.

Microtopographical subunits were initially classified by visual inspection of the dominant plant community and later verified using ground penetrating radar (GPR). Assigning the category of polygon top or trough is straightforward as troughs delineate the edges of tops. The GPR was used to create a near-surface hydrological map along each transect, and thermokarst/polar desert quadrats were easily separated by their distinct hydrological conditions. GPR data was collected using a Sensors & Software GPR unit with 500MHz range sensors with a 0.25m step-size (Annan 2004). A detailed digital elevation model (DEM) of the site was created in ArcGIS (ESRI 2011) using 2000 elevation points collected by a Trimble 5800 dGPS system throughout the site and at each quadrat. GPR survey transects were corrected for relief using interpolated dGPS elevation points from the DEM in EKKO View Deluxe software

(Sensors & Software Inc. 2003). Polygon trough subsidence was calculated by taking the difference between trough elevation and the average elevation of immediately neighboring polygons tops.

Phylogeny Reconstruction

A molecular phylogeny of vascular plants was reconstructed using GenBank sequences for *rbcL* and *matK* from Saarela *et al.* (2013)(see Table S3.1). These two genes have by far the best taxonomic coverage for species in the region. For one species, *Papaver radicatum var. radicatum*, there was no exact match in GenBank. In this instance we used *Papaver dahlianum* as a placeholder as this most likely represents the closest taxonomic relative in the region. No other representatives from the *Papaver* genus were present at our site.

Sequences were aligned with MAFFT version 7 (Katoh & Standley 2013) and checked manually in MacClade (Maddison & Maddison 2005). The modelTest function from the *phangorn* R package (Schliep & Paradis 2014) was used to determine the best fit evolutionary model for each gene region (for *rbcL* this was the HKY + G + I, and for *matK* the GTR + G model was selected). A partitioned analysis was then run in MrBayes 3.2 (Ronquist *et al.* 2012) for 4 million generations, which was sufficient for model convergence, defined as average standard deviation of chain split frequencies of 0.01. The phylogeny was dated using the *chronopl* function from the *ape* package (Paradis, Claude & Strimmer 2004) with the following calibration points: Monilophytes 354mya (Bateman 1991), Eudicots 124mya (Hughes & McDougall 1990), and Saxifragales 91mya (Hermsen *et al.* 2003), and rooted using *Equisetum arvense* as an outgroup.

Soils

At each quadrat we collected data on soil chemistry and physical properties. Active layer depth was measured using a permafrost probe that was pushed into the ground at the four corners of the quadrat and calculating the average depth of penetration. Ground temperature was taken at 12cm soil depth, which general corresponds to the maximum rooting depth. Soil samples were collected by taking 12cm deep slices from the four corners of the quadrat. Samples were homogenized, air dried for several days, and then pulverized. Wet/dry weight ratios were taken in the field for moisture content (%H_2O).

Soil chemistry was analyzed as follows: pH using a 1:2 soil-to-solution ratio using H_2O then measured by pH meter (Hendershot, Lalande & Duquette 1993). Extractable NO_3- and NH_4+ were obtained using a 2 M KCl extraction ratio of 1:10 soil-to-solution and shaken for 1 hour. The filtrate was analysed by colorimetry for the determination of N on a multi-channel Lachat Quikchem auto-analyser (Lachat Methods 13-107-06-1-A, 10-107-06-2-C, 13-107-06-2-B; Maynard & Kalra, 1993). Available P and K were determined by a multi-element extraction using Mehlich III solution and then measured by flow injection analysis (Lachat Instruments; Tran & Simard 1993). Percent organic matter was measured by loss on ignition of a (previously heated to 105 ^{o}C for 24 hours) sample burned at 360 $^{\circ}$C for 4 hours. The difference in weight between the two steps is attributed to loss of organic matter expressed as a percent (Schulte, Kaufmann & Peter 1991).

Statistical Analysis of Vegetation and Soil Data

First, spatial structure in vegetation abundance and soil moisture were evaluated using Moran's I, for which positive values indicate positive spatial autocorrelation and negative values indicate negative autocorrelation. Values around zero signify spatially independent data. Computed distances were binned into distance classes to smooth out stochastic effects. Significance was assessed by randomizations (n = 1000). Second, we evaluated spatial structure in the residuals from a linear regression run on total plot vegetation abundance explained by soil moisture.

We examined plant community differences of the four microtopographies by ordinating each plot's species composition and abundance using non-metric multidimensional scaling (NMDS) of a Bray-Curtis distance matrix calculated from percent cover in the r-library *vegan* (Oksanen *et al.* 2013). Differences among groups were calculated using a permutational multivariate analysis of variance (PERMANOVA) on a Bray-Curtis distance matrix and 1000 randomizations. Species richness (alpha diversity) was measured as number of species per plot and evenness was measured using the Shannon diversity index H´. Phylogenetic structure in plant community composition was assessed using two metrics, the net-relatedness index (NRI) and mean nearest taxon index (NTI) in the r-library *picante* (Kembel *et al.* 2010), weighting by abundance to take into account the relative dominance of each species within a given quadrat. These metrics quantify the phylogenetic clustering of taxa relative to a null expectation that species composition is a random draw from the regional species pool (999 randomizations).

Positive NRI and NTI values point towards phylogenetic clustering (closely related species tend to co-occur) whereas negative values indicate phylogenetic over-dispersion (closely related species tend not to co-occur).

Means testing for richness, percent cover, evenness, NRI, and NTI were assessed using two-way, type III ANOVAs for imbalanced designs to account for the unequal number of samples (due to 5 plots being dropped from thermokarst troughs because of standing water) followed by Tukey tests for post-hoc significance testing. The explanatory variables were location (control or thermokarst) and type (top or trough). We used type III ANOVAs as they are less dependent (than type I) on the ordering of explanatory variables and more accurate for analyses with unequal sample sizes. Finally, the turnover of plant species composition among plots (β-diversity) was quantified using the *raup-crick* function from Chase *et al.* (2011). β-diversity values of -1 indicate plots are more similar to each other than expected by random chance and values of 1 indicate dissimilarity. Differences in β-diversity distributions between groups were tested using a two-tailed Kolmogorov-Smirnov test.

For means-testing soil chemistries between microtopographies, two-way, type III ANOVAs for imbalanced designs were run followed by Tukey tests for post-hoc analysis. All analyses were conducted in R version 3.0.2 (R Core Team 2014).

3.4 Results

Microtopography

The dGPS and GPR surveys detected differences in soil moisture and provided the basis for a subsurface hydrological map of the site that clearly delineated thermokarst (see Fig. S3.1 and Fig. S3.2) that was ground-truthed with soil moisture analyses. Strong contact reflections (representing the boundary between different subsurface materials) were detected at the current depth of thaw within the thermokarst area where soil moisture content was high (confirmed by soil moisture analysis in Fig. 3.2) and showed a much weaker signal in control plots where the gradation into permafrost was less abrupt (see Fig. S3.2). Subsidence of troughs within the thermokarst area (31cm) was significantly greater than in non-thermokarst areas (18cm) ($F_{1,33} = 25.17$, $p < 0.001$). Further, it is likely that mean thermokarst trough subsidence was even greater, as troughs that had standing water (and thus lower relief) were excluded from analysis.

Thermokarst plots had significantly shallower active layer depths ($F_{1,71} = 79.83$, $p < 0.001$) than control plots (see Fig. 3.2) with troughs significantly shallower than tops ($F_{1,71} = 51.20$, $p < 0.001$), with a significant interaction effect ($F_{1,71} = 13.88$, $p < 0.001$) indicating that thermokarst effects (thaw consolidation) were greater in troughs. Ground temperature at 12cm depth (measured at 4pm) within thermokarst plots was markedly colder ($F_{1,71} = 41.38$, $p < 0.001$) than control plots with troughs significantly colder than tops ($F_{1,71} = 29.61$, $p < 0.001$), with a non-significant interaction effect. Post hoc tests were all significant ($p < 0.001$).

Plant community composition

The study site included 22 vascular plant species (see Table S3.1) out of the estimated 140 species indigenous to the Fosheim Peninsula (Edlund *et al.* 1990), with control and thermokarst zones both having a gamma diversity (pooled species richness) of 17. The polar desert top and trough included 16 and 17 species, respectively, with *Salix arctica* and *Poa pratensis* dominating. *Pedicularis hirsuta* was found in tops but not troughs. Five species, *Cerastium arcticum*, *Saxifraga tricuspidata*, *P. radicatum*, *P. hirsuta*, and *D. integrifolia*, were found in polar desert but were completely absent from thermokarst.

Thermokarst top had the smallest species pool (13 species), and was dominated by *S. arctica* and *Dupontia fisheri*. Thermokarst trough contained 16 species and was the only microhabitat not dominated by *S. arctica*, instead being dominated by *D. fisheri* and *C. aquatilis*. Five species, *D. fisheri*, *C. aquatilis*, *S. cernua*, *E. triste*, *E. scheuchzeri* were unique to thermokarst areas, being absent from the surrounding polar desert.

Vegetation cover shows strong spatial autocorrelation (see Fig. S3.3), shifting from positive to negative autocorrelation as distance increases up to a distance of 100m, and with plots >150m apart again appear more similar. However, the residuals extracted from a linear regression of abundance explained by %H_2O show no significant spatial autocorrelation.

A best-solution NMDS ordination of plot community composition was reached after 18 runs with a resulting stress of 0.14, indicating a good fit in 2D space (see Fig. 3.3). Tops and troughs overlapped within each of polar desert and thermokarst, however there was little overlap between polar desert and thermokarst. Additionally, thermokarst had a greater spread in ordination space indicating greater variance in species composition and abundance. PERMANOVA results show that thermokarst communities are significantly distinct from control

($p < 0.001$); however, tops do not differ significantly from troughs. Importantly, the significant interaction ($p = 0.02$) of location (control or thermokarst) and type (top or trough) indicates a differing response in community composition change depending on whether thermokarst occurs to a polygon top or trough (see Table S3.2).

Richness, Turnover, and Dispersion

Thermokarst plots had significantly lower species richness ($F_{1,71} = 37.82$ $p < 0.001$) than control plots, but there were no significant differences between tops and troughs (see Fig. 3.4). Percent cover was significantly greater in thermokarst plots than control plots ($F_{1,71} = 47.21$ $p < 0.001$), with troughs having significantly greater percent cover than tops ($F_{1,71} = 10.43$ $p < 0.01$); interaction effects were non-significant. Evenness results showed similar patterns to species richness, with thermokarst plots significantly less even than control plots ($F_{1,71} = 27.79$ $p < 0.001$), with no significant differences between tops and troughs. We note that contrast in richness and percent cover should, however, be interpreted cautiously as plots do not represent fully independent sampling units.

The distribution of β-diversity values between thermokarst and polar desert was significantly different for both tops ($D = 0.1785$, $p = 0.005$ from Kolmogorov-Smirnov test) and troughs ($D = 0.1682$, $p = 0.01$ from Kolmogorov-Smirnov test). For polar desert tops and troughs there is a distinct leftward skew of β-diversity, indicating greater relatedness of species composition within microtopographic classifications (see Fig. 3.5). In contrast, for thermokarst tops and troughs the distribution of β-diversity values shifts right, indicating a greater dissimilarity of vegetation within thermokarst. For both tops and troughs, thermokarst plots are significantly more dissimilar in their community composition than polar desert.

There were no significant differences in NRI or NTI between thermokarst and control plots, or between tops and troughs (see Fig. S3.4).

Soil chemistry

Soil chemistry differed significantly between thermokarst and control plots. P, K, and pH values were lower in thermokarst for both tops and troughs, with K and pH significantly lower in thermokarst troughs than thermokarst tops (see Fig. 3.6). Organic matter content was significantly higher in thermokarst consistent with the deposition and accumulation of plant material in thermokarst soils, but there was no discernable difference for NO_3-, and most results were below laboratory detection limit. However, there was a trend for higher NH_4+ in thermokarst, significantly so for thermokarst tops.

3.5 Discussion

A suite of biotic and abiotic differences are apparent in the area of thermokarst-induced subsidence of ice wedges. Most notably, subsidence alters surface hydrology (Edlund *et al.* 1990) such that plant growth is promoted, giving rise to new, wetland-like plant communities in the high Arctic. Thermokarst plant communities are distinct in species composition, have altered microtopographical soil chemistries and result in an increased microhabitat divergence of tops and troughs in ice wedge polygon systems (Zona *et al.* 2011). As a consequence of these changes, a highly structured landscape has emerged that is distinct from polar desert. Due to the abundance of ice wedges in this environment, we predict local ecosystem heterogeneity to generally increase across the high Arctic with further climate warming. A key question is whether such changes will exacerbate or ameliorate current warming trends. Our results suggest that increased graminoid/sedge vegetation growth insulates the ground from further thermal change, likely through increased albedo (Blok *et al.* 2011) and retention of soil moisture (Pearson *et al.* 2013), thereby initially reducing active layer depth and promoting system resiliency.

Microtopography

We show that ground penetrating radar (GPR), ground-truthed with soil moisture data, accurately maps thermokarst subsurface moisture conditions, and may be able to identify areas sensitive to thermokarst but that do not yet show ground surface evidence. The tops and troughs of thermokarst represent the same top and trough features found in non-thermokarst sites (i.e. the ice wedges occur in both areas) – but the relief change (subsidence) caused by thermokarst amplifies the expression of these features and induces a change in subsurface hydrologic conditions. Importantly, our results reveal that thermokarst areas tend to have *shallower* active layers, meaning that the seasonal depth of thaw does not penetrate as deeply. This finding may appear counter-intuitive, however, we suggest that vegetation growth, stimulated by increased water collection, over time provides an insulating layer that reduces active layer depth (Shur &

Jorgenson 2007), and thereby limits further groundwater seepage. We further suggest that thermokarst may induce a negative feedback cycle that stabilizes the ground to thermal change from high Arctic warming, as noted in long-term remote observation analysis (Jorgenson, Shur & Pullman 2006). The link between stabilizing vegetation growth and permafrost thaw is of great importance globally and needs further examination as potential negative feedbacks would greatly alter projections of permafrost thaw extent.

Novel plant communities

The altered hydrology within thermokarst plots results in novel plant communities distinct from the vegetation of the polar desert. For example, thermokarst troughs were the only microtopographic feature not dominated by *Salix arctica* (see Fig. S3.5). This willow species, which dominates across the other three microtopographies (while still being fairly low in percent cover), appears to be an ecological generalist capable of tolerating a broad range of hydrological conditions (Dawson & Bliss 1989). However, the waterlogged soils in thermokarst troughs appear to fall outside its natural tolerance (Dawson & Bliss 1989), and this microtopography may reflect a tipping point of abiotic change – where thermokarst has pushed the community from polar desert into wetland conditions. Indeed, we show that spatial structure in vegetation cover is almost entirely explained by soil moisture, demonstrating the large effect of altered hydrological patterns on plant growth.

With the exception of thermokarst troughs, dominant species were similar among microtopographies, likely reflecting the broad water tolerance of these species (Ehleringer & Miller 1975; Shaver *et al.* 1979; Grulke & Bliss 1988). However, five species were unique to polar desert and five different species were unique to thermokarst areas, indicating that community composition shifts occur primarily with subdominant species. Distinct vegetation succession patterns of polygonal tundra vary greatly as thermokarst features evolve through time (Billings & Peterson 1980), and as a thermokarst feature stabilizes, so should its resident vegetation. The broader implication of diverging communities is that with increasing thermokarst, and over time, we should expect to see polar desert communities transition to wetland communities with distinct assemblages.

Novel soil chemistry

Mirroring the patterns we observed for plant communities, we also found a significant divergence in soil chemistry between thermokarst and polar desert. Most striking was the increase in soil moisture content within thermokarst, likely through the collection of melt runoff and increased snow accumulation as a consequence of altered microtopography through subsidence (Edlund *et al.* 1990). Wetter soil moisture conditions in trough locations are sustained later in the thaw season through melting ground ice in both the lower part of the active layer and from the underlying ground ice. While we might have expected leaching to elevate soil nutrient content in thermokarst troughs, we found that P and K values were lower in thermokarst than in the surrounding polar desert. P and K are depositional and would have been laid down when this area was still sea floor. We therefore suggest their depletion in thermokarst reflects consumption of these resources through increased plant growth. Increased plant activity also explains the lower soil pH values in thermokarst, as acidification of soil occurs through selective ion uptake at the roots (Mengel *et al.* 2001). Elevated plant growth also increases the organic matter content of thermokarst soils, resulting in soils that are significantly more carbon-rich than surrounding polar desert. As the area has only relatively recently (in geologic timescales) emerged from the sea (2000-9000 years before present) and northern ecosystem processes are notoriously slow, the development of carbon-rich thermokarst soils should be regarded as a new feature resulting from biotic development (Edlund & Alt 1989). However, whether thermokarst areas will function as carbon sinks will ultimately depend on rates of microbial soil respiration relative to rates of carbon sequestration through vegetative growth (Soegaard & Nordstroem 1999).

In contrast to P and K, soil nitrogen is not depositional; instead it accumulates through the conversion of atmospheric N_2 to ammonium and nitrate mediated by aerobic bacterial action. We find a weak but significant trend for higher ammonia accumulation in thermokarst soils, but no matching trend for soil nitrate. Low soil nitrate is not entirely surprising for two reasons. First, the second step in the oxidation reaction, the conversion of ammonia to nitrate, is slowed down by cold temperature and waterlogged soils. Second, plants in this area may be nitrogen deprived such that they take up NH_4+ as soon as it becomes available in the soil, leaving less available for the second oxidation stage.

Our results suggest that thermokarst soils may be N limited, rather than P limited (Haag 1974). However, we predict this to change over time, as nitrogen can be replenished through continual, slow microbial input, whereas there is little depositional input of phosphorus (Gordon, Wynn & Woodin 2002). Thus, with increased moisture and microbial-plant associations to facilitate nitrogen fixation in thermokarst areas, we may see a gradual shift from a nitrogen- to phosphorus-limited system. The consequences of such a shift on arctic vegetation are not yet clear, but our analysis already shows that thermokarst soils are increasingly divergent from the soils of the polar desert.

Increasing ecological heterogeneity

We initially predicted that thermokarst processes would induce changes to richness, turnover, and dispersion amongst plant communities. Thermokarst was found to have lower alpha-diversity at the plot-level, but the species pool (gamma-diversity) of thermokarst was equally as rich as the non-thermokarst control. We propose that as thermokarst changes microhabitat conditions, polygon top and trough differences are amplified, creating new hydrological niche space for colonization. Incoming (wetland) species dominate this niche, as indicated by decreased species evenness, resulting in lower species richness per plot but increased turnover between plots.

However, we found the lack of difference in phylogenetic dispersion between plant communities between control and thermokarst areas surprising given the strongly divergent soil conditions, particularly the strong soil moisture gradient. It is possible that after initial colonization of thermokarst, competitive interactions dominate for later-successional species (Cargill & Chapin 1987), removing any signal of phylogenetic clustering. Alternatively, water tolerance might demonstrate only weak phylogenetic conservatism. A wide range of water tolerance has been documented within many different arctic species, often through ecotypic differentiation (Teeri 1973; Shaver *et al.* 1979; Grulke & Bliss 1988). In this landscape, hydrologic conditions vary from water-saturated conditions of the spring snowmelt to desert conditions during dry summers. It might therefore be unsurprising if water tolerance is an evolutionary labile trait that is not strongly structured on the phylogeny. Such evolutionary plasticity would explain how it is possible for vegetation communities to differentiate significantly between microtopographies, yet demonstrate little phylogenetic structure (see Fig. S3.5).

Importantly, not only does the composition of vegetation of thermokarst diverge from that of the polar desert, there is also greater ecological heterogeneity at the site scale. Thus, while plot-level alpha diversity and evenness are lowered, there is greater compositional turnover in thermokarst communities across the site, particularly within troughs. This shift is driven by changes in the dominant species within thermokarst, and is mirrored by shifts in soil nutrients. We posit that the greater relief change between tops and troughs promotes the creation of microhabitats, resulting in a greater diversity of habitats. While we observe heterogeneity increasing locally, we suggest that due to the large spatial coverage of polygons across the high Arctic that this is likely repeated across the region. However, regional heterogeneity may not necessarily increase, since other locales may increase heterogeneity in a similar way. Given that ice wedges are ubiquitous across the continuous permafrost region, and they occupy enormous ground volume across the arctic zones of North America, Europe, and Asia, we believe they will be a catalyst for widespread ecosystem change in light of warming Arctic.

Summary

Climate change is predicted to be the largest driver of future biodiversity loss in the Arctic (Sala *et al.* 2000). Our study suggests that in the near future it is likely that further geomorphic partitioning of habitats due to thermokarst will facilitate community restructuring drawn from local species pools. This restructuring may lead to an increasing shift of polar desert towards a more heterogeneous landscape comprised of a mosaic of different habitat types. Contrary to studies suggesting loss of biodiversity with climate change, our results indicate that ecosystem changes in the High Artic might result in a wider range of habitat types supporting a greater diversity of plant species. In addition, increasing Arctic primary productivity (Elmendorf *et al.* 2012b) may provide greater nesting habitats for migratory birds, richer foraging for ungulates, and in general better support the needs of higher trophic levels. However, increased thermokarst and ponding of water may lead to elevated permafrost carbon emission. Polygonal tundra thermokarst ponds release carbon at an order of magnitude higher than dry polar desert (Abnizova *et al.* 2012), and the expansion of thaw lakes in neighboring Siberia has been linked to a 54% increase in methane emissions (Walter *et al.* 2006). The shrinking of polar desert therefore represents the gradual loss of one of Earth's most extreme biomes and disadvantageous carbon dynamics, whilst favoring the expansion of a novel and perhaps more biotically diverse wetland system.

3.6 Acknowledgements

We would like to thank Chelsea Chisholm and Jared Simpson for their assistance on data collection and valuable input during fieldwork. We would also like to thank members of the Davies lab at McGill University for feedback and manuscript revision. A particularly large appreciation goes to the staff of Eureka Weather Station, Nunavut for their logistical assistance and company on Ellesmere Island. This study was supported through a doctoral research scholarship from Fonds de Recherche du Québec: Nature et Technologie (FRQNT) (M.S.B.), a Research Support Opportunity from ACUNS and Environment Canada (M.S.B.), NSERC Discovery grant (W.H.P.), and ArcticNet funding (W.H.P.).

3.7 Figures

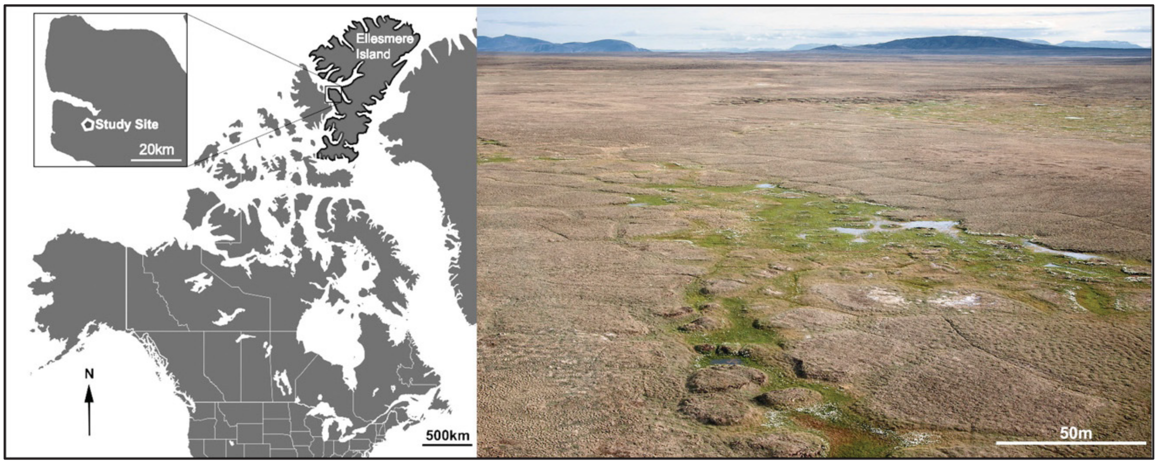

Figure 3.1: Thermokarst study site on the Fosheim Peninsula, Ellesmere Island, Canada (79.84574°N, 85.37028°W). The area is an exceptionally flat plateau of marine sediments having recently (~9000 years ago) been exposed from the sea through isostatic rebound. The thermokarst zone is clearly visible with bright green vegetation and marked subsidence and geomorphic expression of ice wedge troughs. (Map created from Geocommons).

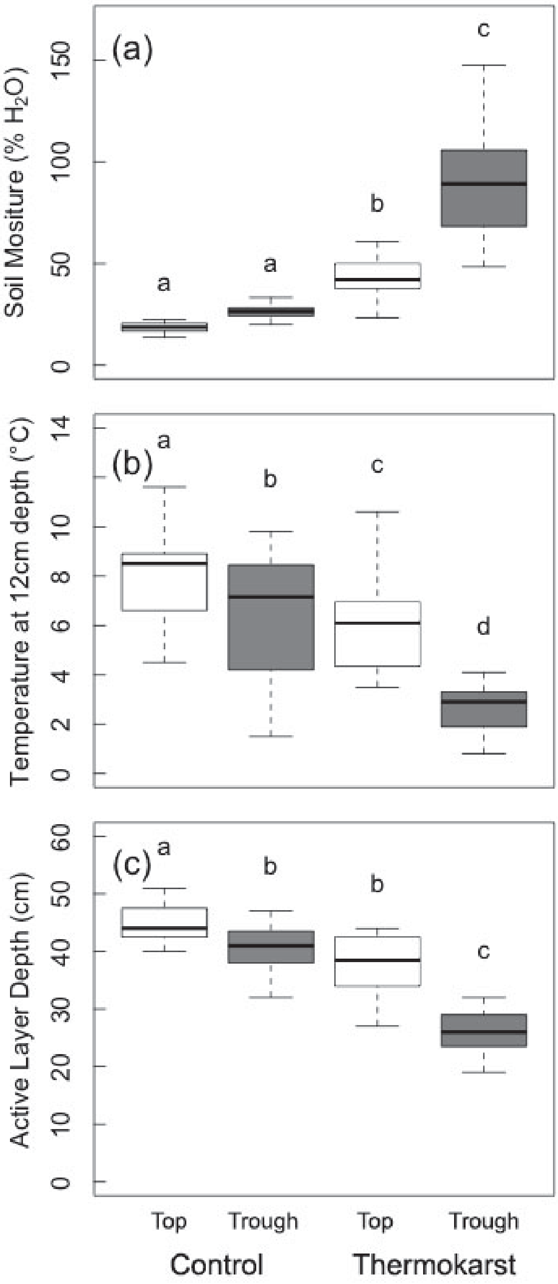

Figure 3.2: Soil abiotic variables measured at the four different microtopographies. Box whiskers represent 1.5 interquartile range (IQR) boundaries. Letters above boxes represent significantly different values ($p < 0.01$, ANOVA and Tukey post-hoc test).

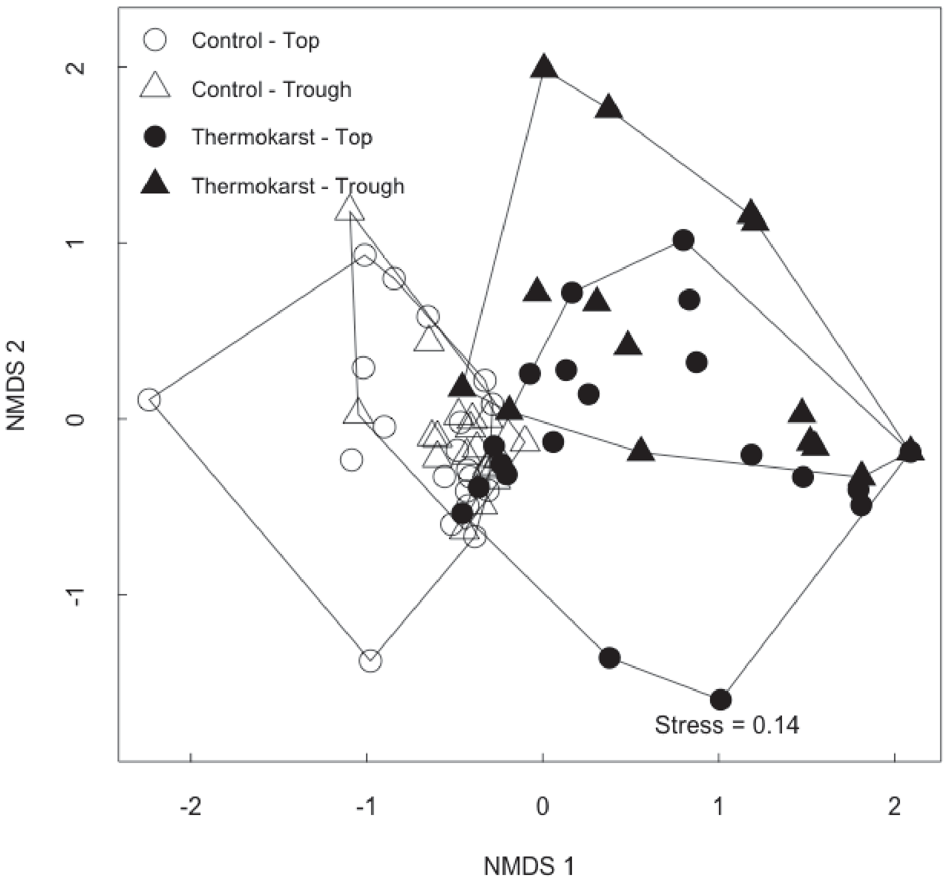

Figure 3.3: NMDS ordination using a Bray-Curtis dissimilarity matrix generated from plant community composition. Hulls connect the outermost points of each microtopography to show spread of the data. The control and thermokarst groups show clear separation from one another, but top and trough compositions do not significantly differ. Thermokarst microtopographies also show more variance in community structure than control groups.

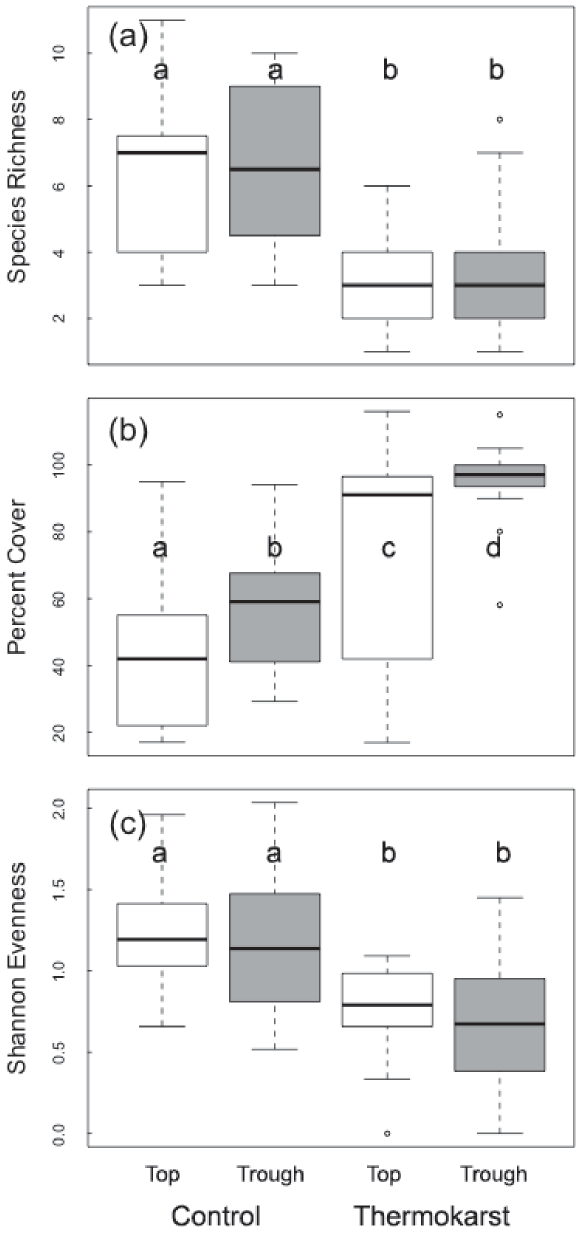

Figure 3.4: Measures of plant species richness (alpha-diversity) (a), percent cover (b), and evenness (c) of the four microtopographies. Box whiskers represent 1.5 interquartile range (IQR) boundaries. Letters above boxes represent significantly different values ($p < 0.01$, ANOVA and Tukey post-hoc test).

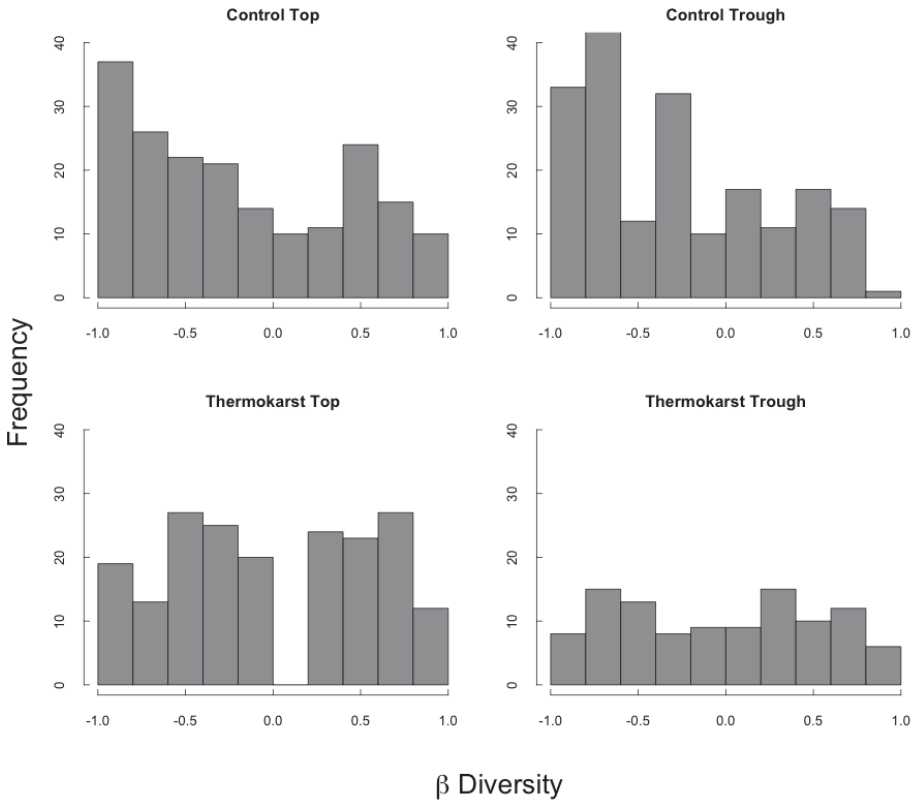

Figure 3.5: β-diversity of plots within each of the four microtopographies. This calculation used a modification (Chase *et al.*, 2011) of the Raup-Crick metric of β-diversity (Raup & Crick 1979). It calculates all pair-wise comparisons of sites to see if local communities are more dissimilar (approaching +1), as dissimilar (approaching 0), or less dissimilar (approaching -1), than expected by random chance. By splitting the calculation into the different microtopographies we can see how the relatedness of plots within each group changes. Control areas are distinctly left-skewed – they tend to be less dissimilar (more similar) than expected by chance, whereas both thermokarst groups are more evenly distributed. Therefore as a region of tops and troughs experience thermokarst they become less similar to one another in species composition. Frequencies in thermokarst trough group are lower overall because there were less plots to compare than the other three groups (15 as opposed to 20).

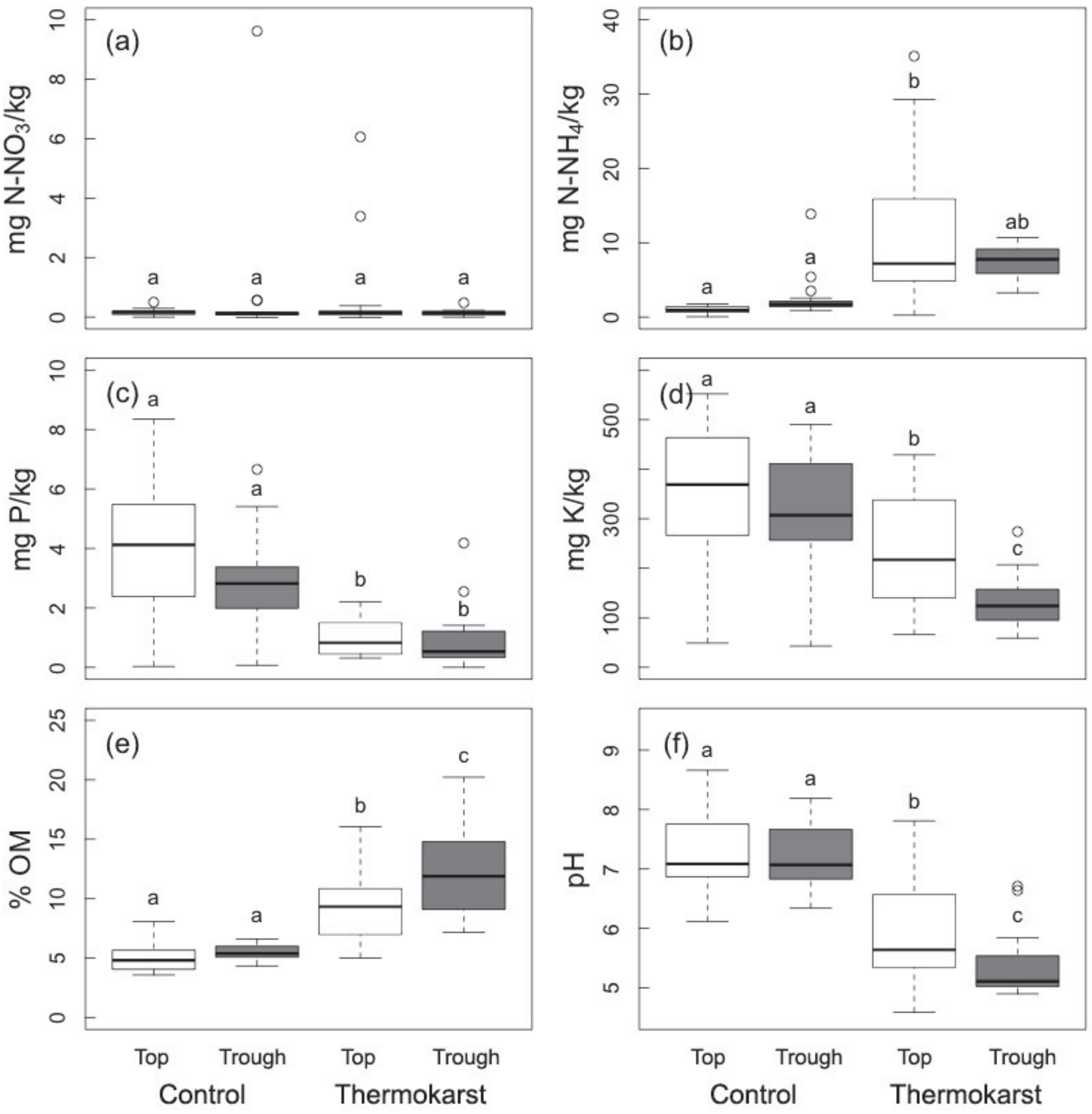

Figure 3.6: Soil chemistry variables measured at plots on control tops, control troughs, thermokarst tops, and thermokarst troughs: (a) plant available nitrate, (b) plant available ammonium, (c) phosphorus, (d) potassium, (e) percent organic matter of loss on ignition, and (f) pH. Box whiskers represent 1.5 interquartile range (IQR) boundaries; dots are outliers beyond the 1.5 IQR. Letters above boxes represent significantly different values ($p < 0.01$, ANOVA and Tukey post-hoc test).

3.8 Supplemental

Table S3.1: Species list with family names and sequence information used for phylogenetic analysis. Ascension number refers to this paper's voucher collection submitted to the Marie-Victorin Herbarium in Montreal, QC. The ascension numbers for *rbcL* and *matK* refer to the gene sequences from Saarela *et al*., 2013 submitted to GenBank.

Species Name	**Family**	**Ascension Number**	***rbcL* (553 bp)**	***matK* (791 bp)**
Alopecurus magellanicus	Poaceae	187791	KC481897	KC473974
Arctagrostis latifolia subsp. *latifolia*	Poaceae	187815	KC481989	KC474059
Carex aquatilis var. *minor*	Cyperaceae	187792	KC482227	KC474286
Carex rupestris	Cyperaceae	187808	KC482345	KC474381
Cerastium arcticum	Caryophyllaceae	187793	KC482409	KC474436
Draba arctica	Brassicaceae	187795	KC482546	KC474554
Dryas integrifolia	Rosaceae	187801	KC482650	KC474660
Dupontia fisheri	Poaceae	187817	KC482670	KC474676
Elymus alaskanus	Poaceae	187819	KC482675	KC474680
Equisetum arvense var. *alpestre*	Equisetaceae		KC482714	
Eriophorum triste	Cyperaceae	187803	KC482830	KC474771
Eriophorum scheuchzeri	Cyperaceae	187804	KC482811	KC474756
Festuca brachyphylla var. *brachyphylla*	Poaceae	187818	KC482878	KC474811
Luzula confusa	Juncaceae	187809	KC483109	
Papaver radicatum var. *radicatum*	Papaveraceae	187798	KC483282	KC475113
Pedicularis hirsuta	Orobanchaceae	187812	KC483368	KC475206
Poa pratensis subsp. *alpigena*	Poaceae	187820	KC483576	KC475415
Potentilla arenosa	Rosaceae	187797	KC483603	KC475442
Salix arctica	Salicaceae	187802	KC483913	KC475719
Saxifraga cernua	Saxifragaceae	187816	KC484018	KC475823
Saxifraga tricuspidata	Saxifragaceae	187821	KC484081	KC475864
Silene involucrata subsp. *involucrata*	Caryophyllaceae	187794	KC484106	KC475887
Stellaria longipes subsp. *longipes*	Caryophyllaceae	187811	KC484154	KC475931

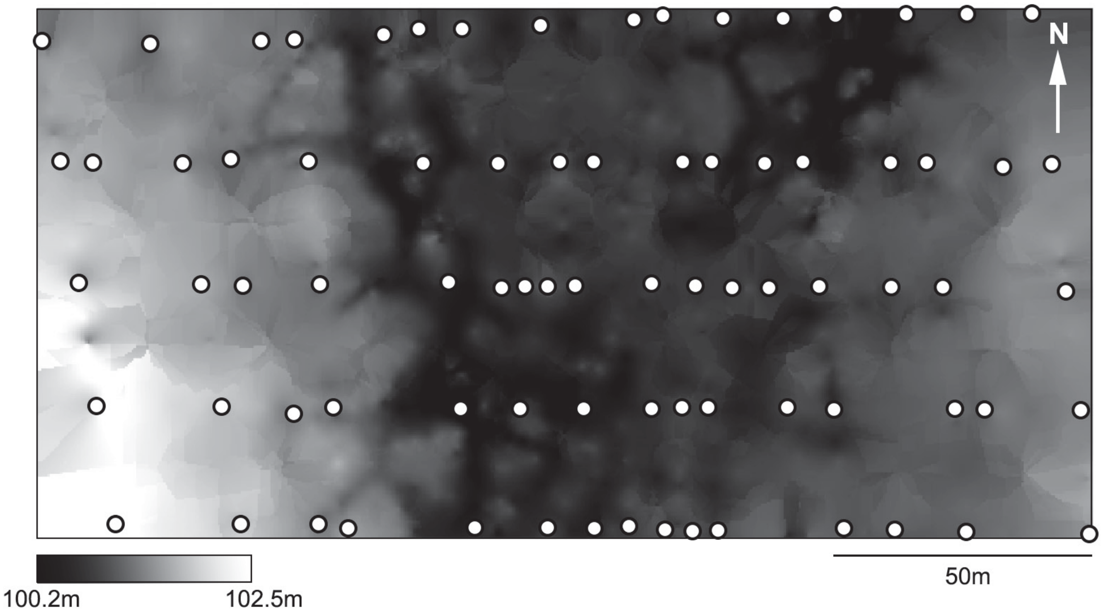

Figure S3.1: The Digital Elevation Model (DEM) of our site. Darker tones show subsided areas, with overall site elevation differences of 2m. White dots represent the location of plots within transects that ran from west to east. The thermokarst zone is in the center of the DEM and its borders coincide largely with the dark, heavily subsided trough systems. Also noticeable within the thermokarst area are small “island” polygon tops that rise above the subsidized troughs.

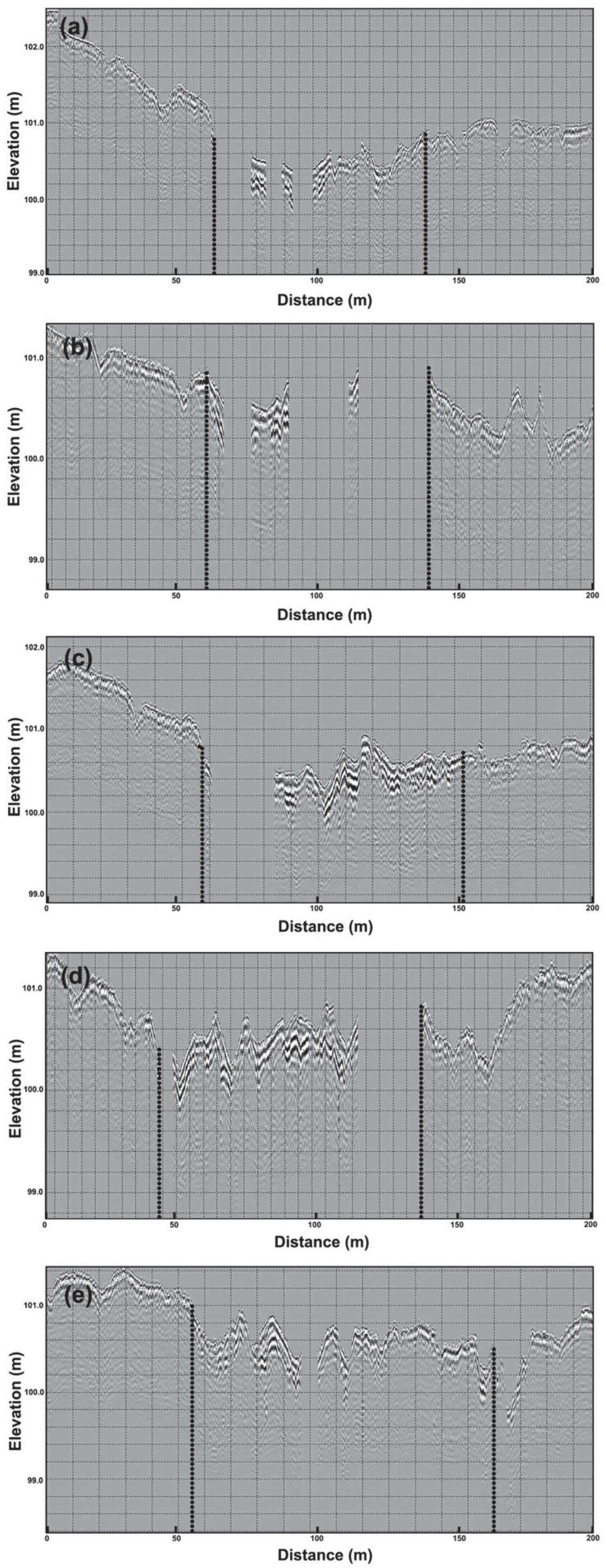
(a)
Elevation (m)
102.0
101.0
100.0
99.0
0
50
100
150
200
Distance (m)
(b)
Elevation (m)
101.0
100.0
99.0
0
50
100
150
200
Distance (m)
(c)
Elevation (m)
102.0
101.0
100.0
99.0
0
50
100
150
200
Distance (m)
(d)
Elevation (m)
101.0
100.0
99.0
0
50
100
150
200
Distance (m)
(e)
Elevation (m)
101.0
100.0
99.0
0
50
100
150
200
Distance (m)

Figure S3.2: 500 MHz GPR surveys collected at the site. This image is of five cross-profile west-to-east transects collected at 25m apart throughout the site. Distance 0 m is west and 200 m is east. Elevation refers to the corrected GPR profile incorporating dGPS elevation points analyzed from our DEM. The surface of the GPR profile has been corrected for topographical features such as polygon troughs and tops. Depth estimates of features are based on a signal velocity of 0.065 m/ns. Dotted lines delimit the central thermokarst area bordered by control areas on both sides. Within the thermokarst zone, a strong signal is detected where moisture-saturated soils in the active layer are in contact with frozen surfaces. Active layer signal is less strong in control areas due to drier soil conditions. The breaks in data are due to standing water in which the GPR cannot operate.

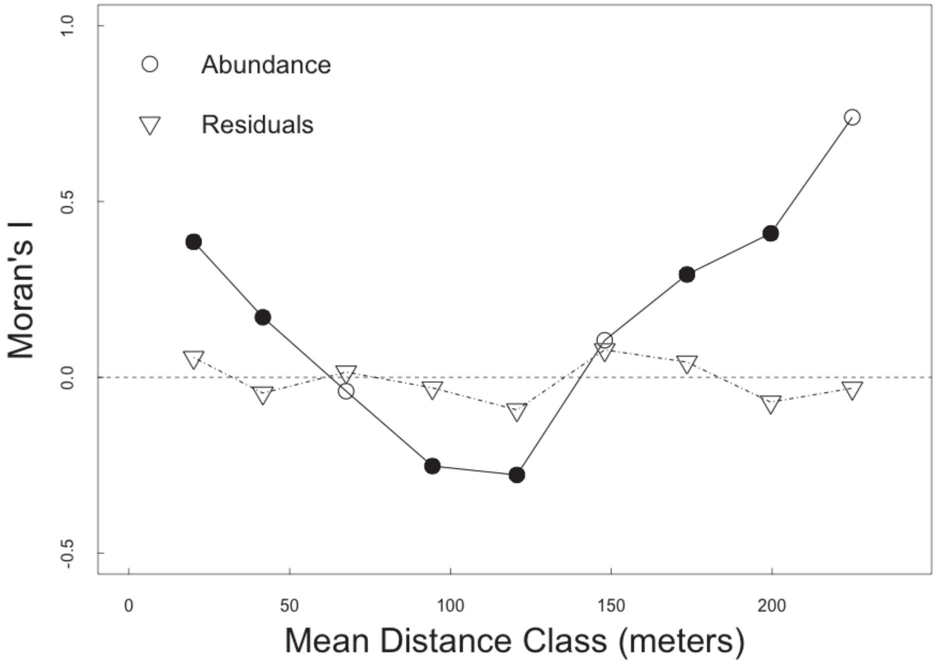

Figure S3.3: Values of Moran's I range from -1 (strong negative spatial autocorrelation) to +1 (strong spatial autocorrelation). Values around zero signify spatially independent data. The filled points indicate values of Moran's I ($p < 0.05$) that are significantly autocorrelated. The circle line is vegetation abundance and shows a clear spatial pattern across the site, with significant spatial autocorrelation in most distance classes. The triangle line is the residuals from a linear regression of abundance explained by H_2O % content of soil. Here, we show that once soil moisture is taken into account the spatial pattern of vegetation abundance disappears.

Table S3.2: PERMANOVA results testing difference in community structure of different microhabitats. Thermokarst communities are significantly distinct from control communities (called “location”), however tops do not differ significantly from troughs (called “type”). The significant interaction of location and type likely indicates a differing response in community composition change depending on whether thermokarst occurs to a polygon top or trough.

Term	**Df**	**Sum Of Sqs**	**MeanSqs**	**F**	**r^2**	**P**
location	1	3.95	3.95	17.9958	0.19248	0.001
type	1	0.4045	0.4045	1.8426	0.01971	0.072
location:type	1	0.5835	0.5835	2.6583	0.02843	0.021
Residuals	71	15.5844	0.2195		0.75939	
Total	74	20.5224			1	

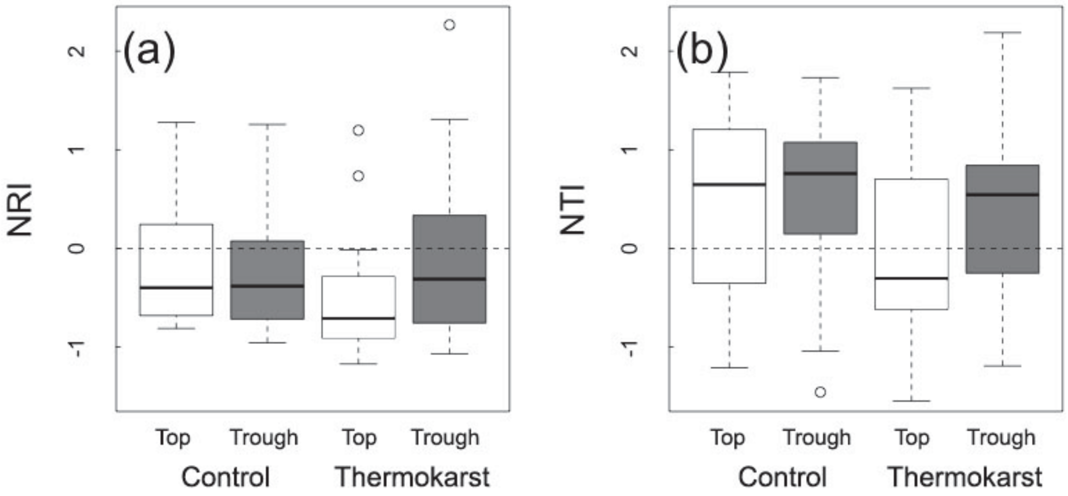

Figure S3.4: Two common metrics used to quantify phylogenetic dispersion of species assemblages. Both measures are used to see whether the phylogenetic diversity of a community is greater or less than expected given a community's species composition. Both relatedness calculations here are weighted by abundance of each species. NRI (a) examines whether the species in a plot are more closely related than chance, whereas NTI (b) focuses on whether the most *closely related* co-occurring species is more or less closely related than chance. Negative NRI and NTI values indicate higher than expected phylogenetic diversity (overdispersion), whereas positive NRI and NTI values indicate less than expected phylogenetic diversity (clustering). NRI and NTI values less than ±1.96 are non-significant as they fail to pass $\alpha < 0.05$. The majority of our data points do not meet this criterion, and we therefore see a lack of significant overdispersion/clustering in either NRI or NTI. We also see no significant differences between any of the microtopographies.

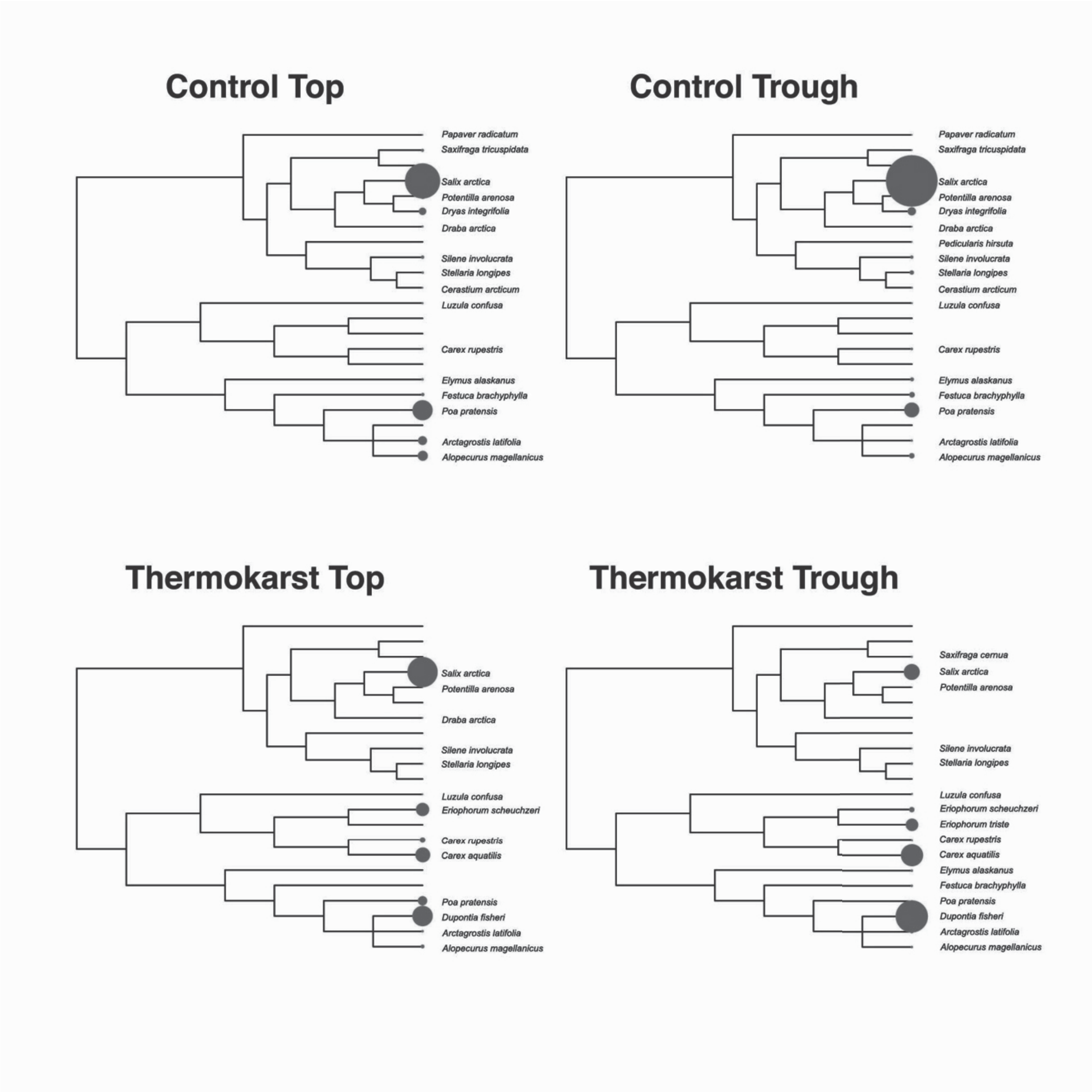

Figure S3.5: Averaged phylogenetic trees of the four microtopography types, weighted by abundance. For each microtopography, the plots' vegetation abundances were averaged together to generate the grey circles (i.e. greater abundance equals larger dots). The species names listed are those that are present in any abundance at a given microtopography. Absence of a species indicates that it was not found in that microtopography.

CONNECTING STATEMENT: From Ecological Change to Stabilization

In chapter three I show how climate-induced thermokarst has altered the local hydrology, vegetation, and soil characteristics of a site in the polar desert. Of the multitude of environmental changes that occur, perhaps the single most significant effect is the amplified vegetation growth in the form of highly dense, clonal plant species. This dense vegetation cover begins the stabilizing feedback mechanism that then goes on to limit further thermokarst by decreasing active layer depth. And yet, the stabilization of subsidence by vegetation growth is a process that has attracted relatively little attention in the literature. In chapter four I outline the pathways through which thermokarst-stimulated vegetation growth decreases active layer depth. Additionally, I examine the implications of including this stabilization mechanism in permafrost models and their projections of permafrost thaw.

CHAPTER 4 - Climate-induced vegetation growth will buffer high Arctic permafrost change

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4.1 Abstract

The thaw of sensitive, ice-rich permafrost and melting ground ice (thermokarst) in high Arctic polar deserts is predicted to increase with a warming climate, causing widespread land-surface changes, release of soil carbon stores, and shifting vegetation patterns. In an attempt to forecast these changes researchers have created permafrost models that incorporate the relationship between permafrost and vegetation, however most have done this as a linear feedback – either through permafrost's direct effect on vegetation (Wolf *et al*. 2008; Wania, Ross & Prentice 2009; Swenson, Lawrence & Lee 2012) or vegetation's effect on permafrost (Sazonova & Romanovsky 2003; Hollesen, Elberling & Jansson 2011; Jiang, Zhuang & O'Donnell 2012; Zhang *et al*. 2012; Zhou *et al*. 2013; Deng *et al*. 2014). These unidirectional approaches generally ignore the amplified vegetation growth induced by warming permafrost, thereby overlooking the stabilizing effects of this new vegetation growth on geophysical processes (Shur & Jorgenson 2007). We posit that the lack of a stabilizing vegetation mechanism in dynamic feedback models may overestimate projections of permafrost thaw. Here, we use a path analysis approach to quantify both the direct and indirect dampening effects of vegetation on the active layer. We found that vegetation cover had the greatest total effect on stabilizing active layer depth and the model was able to explain 69% of active layer variance. Our results contradict other findings that argue that thermokarst leads to positive feedback warming (Nauta *et al*. 2014), and we demonstrate the powerful stabilizing mechanism missing from many permafrost models. We suggest that thermokarst-induced vegetation growth in the high Arctic may attenuate a significant proportion of future permafrost warming.

4.2 Introduction

The high Arctic is experiencing the greatest atmospheric warming of any region due to climate change with significant effects predicted on the vegetation, soils, and geomorphology of the region (IPCC 2013). Permafrost, ground that remains at or below 0°C for at least two consecutive years, is a high latitude geologic phenomena that affects all of these landscape properties, and its depth and distribution is projected to diminish with warming temperatures (Zhang, Chen & Riseborough 2008). The diminishing cover of permafrost poses a threat to arctic vegetation (Swenson *et al*. 2012), adversely affects carbon cycling (MacDougall, Avis & Weaver

2012), and damages human infrastructure (Nelson 2003), with thermokarst a catalyst for large-scale landscape change in temperature-sensitive polar regions (Jorgenson *et al*. 2006).

The interactions of permafrost and vegetation affect the thermal regime of the active layer (French 2007). Generally, vegetation cover stabilizes the activity of periglacial processes by dampening the impact of warming on ground thermal regime through insulation (Shur & Jorgenson 2007), increased albedo and moisture retention (Blok *et al*. 2011) when compared to bare ground. Despite the importance of vegetation, most permafrost models do not incorporate how vegetation feedbacks change based on growth/decay in response to abiotic factors. However, some authors have noted that a dynamic model of vegetation is a major goal in the forecasting of permafrost changes (Lawrence *et al*. 2008; Hollesen *et al*. 2011; Jafarov, Marchenko & Romanovsky 2012; Nyland *et al*. 2012).

Incorporating the influence of vegetation change is especially important in high Arctic polar deserts that traditionally have very little vegetation cover while containing very ice-rich permafrost (Couture & Pollard 1998). Areas abundant in ground ice will initially experience significant ground subsidence with increased active layer depths due to the volumetric loss of ground ice. However, this change in local relief alters microsite hydrology, redistributing water into thermokarst terrain that stimulates vegetation growth and buffers the ground from thermal change (Jorgenson *et al*. 2006). This terrain change eventually experiences a degree of self-stabilization due to the dampening effects of vegetation. As climate change is predicted to both increase high Arctic vegetation cover (Elmendorf *et al*. 2012b) as well as increase ground temperature, the balance of these developmental forces on active layer dynamics remains unclear without a fully developed dynamic ecosystem-permafrost model.

The first step of formulating the stabilizing mechanism of vegetation growth requires conceptualizing the primary model structure, which we have outlined in Figure 4.1. The next step requires testing a causal model of the system and the quantification of vegetation stabilization effect sizes, which we have done using a path analysis approach (Fig. 4.2). The advantage of path analysis is that it allows for the use of correlational data to unravel the various causal processes underlying the system of interest (Grace 2006). As an extension of multiple regression it allows for the estimation the effect sizes within the model system. Additionally, it can be used to test the fit between two or more causal models, which we have done to illustrate that only our conceptualization of pathways adequately fits the data structure (see Supplemental Data).

It is important to note that as thaw only occurs during the summer months and multiyear vegetation records are not available, that non-recursive (feedback – see Fig. S4.1) path modeling was not methodologically appropriate (Grace 2006), and therefore we conducted our analysis using a recursive path model that shows causality in only one direction, i.e. the stabilizing effect of vegetation. We feel this is appropriate for two reasons: first is that all vegetation types present in our site are perennials – their growth is continuous over several years, meaning that their cover is not the result of current abiotic conditions. Additionally, the development of a seasonal active layer is dependent primarily on past vegetation growth. This means that explaining the variance of a single year's active layer fits better with a recursive approach. Second, this recursive approach allows for the quantification of the primary stabilizing feedback of vegetation, which we feel is the effect missing from most permafrost models.

4.3 Methods

Site data collection

We examined the thawing of ice-rich permafrost (thermokarst) within a region of the Canadian high Arctic on Ellesmere Island, Nunavut. Observations of the relationship of decreased active layer thickness under thick vegetation cover was noted during several field seasons on other scientific projects across the high Arctic Archipelago on Cornwallis Island, east and west Axel Heiberg Island, and Ellesmere Island. The Fosheim Peninsula was finally selected for in-depth study as it best represented the thermokarst processes of interests and provided the basics for logistical operation. Prior to field deployment, an examination of available remote sensing data for the region was conducted (LANDSAT and Google Earth), and a set of 14 sites were selected for aerial assessment. During aerial reconnaissance half of the sites were investigated on the ground, and the final site was selected on the basis of the thermokarst and vegetation processes at work.

The study site (79.84574°N, 85.37028°W) is an area containing both undisturbed and thermokarst-affected geomorphic features and is representative of the broader area. The Fosheim is categorized as polar desert climate (Edlund *et al.* 1990), with permafrost depth exceeding 500m thickness (Taylor 1991), and a relatively thin mean active layer of 35-57cm known to vary considerably due to microsite conditions (Couture & Pollard 1998). The site, at an elevation of 101m, lies below the Holocene marine limit (Hodgson 1985; Bell 1996) and soils consist of fine-grained marine clay sediments.

Data were collected during June and July 2013. We conducted a stratified random sampling approach, recording elevation, vegetation cover, soil moisture, and active layer depth within 75, 0.5m^2 quadrats across the study site. 2000 elevation points were collected by Trimble dGPS throughout the site and at each quadrat. Mean site elevation using all values was calculated, and then plot difference from mean was used to compute relative relief values for analysis. Both vascular and non-vascular vegetation percent-cover were visually estimated, and totaled into total percent cover to calculate the cumulative effect of the *entire* vegetation community. Soil moisture values were collected by taking a set of four, 12cm deep slices from the four corners of a plot, homogenizing, air-drying, pulverizing, and then calculating wet/dry weight rations for %H_2O. Active layer depth for each plot was determined by inserting a permafrost probe in the four quadrat corners and averaging the depth of penetration.

Data Analysis

The direct and indirect effects of vegetation on active layer were assessed by path analysis techniques using the *lavaan* library (Rosseel 2012) in R version 3.0.2 (R Core Team 2014). Prior to path analyses, all data were examined for distribution properties and relationship linearity. Endogenous variables were Box-Cox transformed to meet normality distribution assumptions (Grace 2006), and multicolinearity of all variables was examined using Variance Inflation Factors (VIFs). All variables were standardized so that effect sizes could be compared, regardless of unit of measurement.

Our model was constructed to examine the direct effects of vegetation percent cover and elevation on soil moisture, the direct effects of soil moisture and vegetation percent cover on active layer depth, and the indirect effect of vegetation (through soil moisture) on active layer depth (Fig. 4.2). Three alternate models were constructed that: reverse the directionality of soil moisture effect on active layer, remove direct effect of vegetation on active layer, and remove the indirect effect of vegetation (see Fig. S4.2). Each model was fitted using maximum likelihood measures and model fits were assessed using the χ^2 statistic (Grace 2006). Chi-square values with an associated P-value > 0.05 indicated good model fit. Models were compared using

AIC values (Burnham & Anderson 2002), with the lowest AIC being deemed the most parsimonious.

The significance of individual pathways within models were tested using *Z*-statistics, where a *P*-value of < 0.05 indicated a significant pathway. The magnitude of direct and indirect effects was quantified using rules for path coefficients as outlined in Grace (2006). Direct effects of variables were quantified as their standardized path coefficients, while indirect effects were calculated by multiplying the path coefficients along the indirect pathways. Total effect of vegetation on active layer depth was calculated by summing direct and indirect effects.

4.4 Results

Our model (Fig. 4.2) of vegetation's direct and indirect effects on active layer depth was found to be structurally sound and sufficiently passed the model test ($\chi^2 > 0.64$, $p > 0.42$) (see Table 4.1). It successfully quantified the relative interaction strengths between all the variables, and all pathways within our model were assessed as significant ($p < 0.01$, see Table 4.1), meaning that all connections and directionality we proposed between the variables were deemed statistically valid.

The weighted arrows on Figure 4.2 reflect the relative effect sizes of standardized path coefficients. Vegetation was found to have the single largest negative effect on active layer depth when considering both direct and indirect pathways (Table S4.1). The standardized effects of vegetation on active layer depth were: -0.287 direct effect, -0.335 indirect, for a total effect of -0.622, greater than either the direct effect of soil moisture (-0.591) or the indirect effect of relief (0.230). It is worthwhile to note that while soil moisture had the greatest direct negative effect on active layer variance, it was vegetation's positive effect on soil moisture that amplified vegetation's powerful negative influence on active layer depth.

The two exogenous variables elevation and vegetation percent cover (variables not 'caused' by something else within the model), had an unanalyzed covariance of -0.49. This was not deemed to sufficiently violate multicolinearity assumptions (VIF < 3.0). Overall, our model was able to explain a significant amount of variance of the endogenous variables of soil moisture and active layer ($r^2 = 0.689$ and $r^2 = 0.692$ respectively).

None of the other models based on alternative theory passed the χ^2 test (all *p*-values < 0.05, see Table S4.2 – S4.5), and therefore these models failed to adequately represent the structure of our data. This means that the only causal structure that sufficiently explains our field data is the stabilizing feedback model we proposed in Figure 4.2. Additionally, all alternative models had higher AIC values, indicating that our proposed model would have been the most parsimonious even in the event of other models passing the χ^2 test (Table S4.2) (Burnham & Anderson 2002).

4.5 Discussion

It is clear from our results that the stabilizing effect of vegetation is strong – and given the strength of the mechanism it is particularly surprising that it is not incorporated more broadly in projections of permafrost thaw. The only causal structure we tested that appropriately explains our data is one that incorporates both direct and indirect effects of vegetation. With climate projections in the high Arctic predicting both greater soil moisture (Zhang *et al*. 2013) and greater vegetation cover, in particular the graminoid- and sedge-dominated tundra types found in our region (Elmendorf *et al*. 2012b), this mechanism of stabilizing vegetation cover must be fully incorporated prior to finalizing projections of permafrost thaw. Indeed, the exclusion of this effect may lead to exaggerated predictions from permafrost and land surface models ranging from active layer depth increases (Harden *et al*. 2012), decreasing permafrost cover distribution (Burn & Nelson 2006), and carbon mobilization through thawing carbon stores (Burke, Hartley & Jones 2012), particularly within ice-rich areas of the continuous permafrost region. In contrast to previous research where thermokarst led to positive feedback warming (Nauta *et al*. 2014), we show that areas that have stabilized through stimulated plant growth that aids the retention of water should contribute to the greater ice-content of their soils, which due to latent and sensible heat fluxes should initially attenuate much of the warming of permafrost. This attenuation happens for two reasons: a larger amount of heat is required to melt ice within the active layer due to latent heat fluxes during phase changes, and the seasonally differing thermal conductivities of thawed/frozen organic layers, which are good insulators in the summer but in the winter frozen vegetation allows less resistance to the cooling of underlying soil (Osterkamp & Romanovsky 1997).

In the interpretation of our analyses it is worth noting the great heterogeneity of arctic soil types and vegetation cover (Elmendorf *et al*. 2012b) – i.e. we do not suggest our results are general to the entire Arctic. Specifically, the variance of edaphic conditions across the region means that the path coefficients we have calculated are not absolute across all Arctic locations. Rather, the structure of the model should serve as a guide to explaining localized active layer variance, and most importantly, form the basis of stabilizing feedback mechanisms. Dynamic models of permafrost thaw should incorporate direct and indirect effects of vegetation but also consider the heterogeneity of landscape response in terms of vegetation heterogeneity – i.e. increasing shrub cover may amplify subsurface warming rather than decrease it. But for high Arctic deserts that have minimal vegetation cover to begin with and large tracts of bare ground, the predominant influence on ground temperature will be stimulated graminoid/sedge vegetation growth and this increased insulation and albedo.

The stabilization predicted by our mechanism of vegetation growth is mirrored in long-term observations. Jorgenson et al. (2006) found that the expansion of thermokarst terrain over 6 decades was due primarily to the initiation of new thermokarst, rather than the expansion of old. Indeed, over this entire period, the stabilizing, older thermokarst showed only gradual change, and they estimate that advanced stabilization, through vegetation growth, can be achieved within 20-30 years. Predicted increases of graminoid/sedge cover over bare ground in the high Arctic (Elmendorf *et al*. 2012b) could potentially have a net cooling effect on the region through increased albedo and moisture retention, thereby reducing active layer depth and thus promoting system resiliency.

Given the strength of our model, we feel that a re-examination of projected permafrost thaw as it applies to the high Arctic is necessary and should incorporate the redistribution of surface water through thermokarst, the thermal stabilizing effects of increasing vegetation cover, and the interaction of vegetation and soil moisture. Due to the ubiquitous nature of ground ice across the high Arctic (French 2007), our analyses have an incredibly widespread application across the continuous permafrost. While in some cases other forms of catastrophic thermokarst occur such as mass wasting (active layer detachments) and thaw slumps, they influence a relatively small percent of the total area when compared to ground ice thaw. This thaw and subsequent erosion is a natural part of Arctic landscape evolution. Widespread scaring of the ground surface due to both natural and human induced disturbance reflects how readily these landscapes adjust to change, and vegetation is an essential part of this adjustment. Given the strength of the mechanism we have described, we feel that permafrost forecast models that lack a stabilization mechanism will grossly overestimate thaw in the high Arctic biome.

4.6 Acknowledgements

We would like to thank members of the Sanders and Classen labs at University of Copenhagen for feedback and manuscript revision, and Bill Shipley at University of Sherbrooke for his methodological assistance. This study was supported through a doctoral research scholarship from Fonds de Recherche du Québec: Nature et Technologie (FRQNT) (M.S.B), a Research Support Opportunity from ACUNS and Environment Canada (M.S.B), NSERC Discovery grant (W.H.P.), and ArcticNet funding (W.H.P.)

4.7 Figures

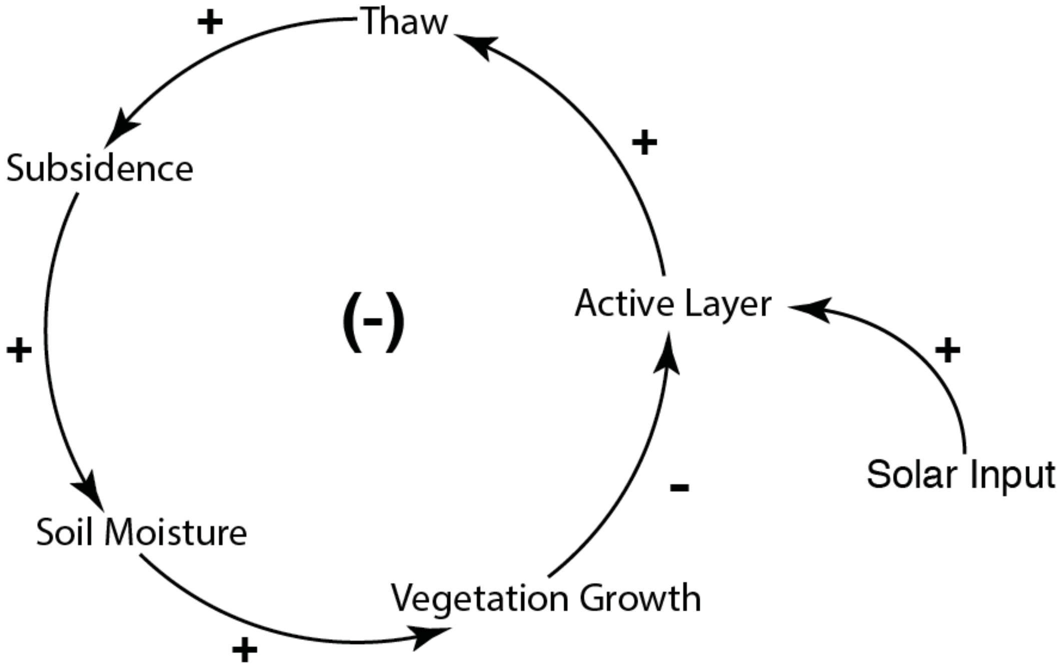

Figure 4.1: Our conceptual model of the primary stabilizing feedback mechanism. Increased air temperatures (designated as solar input) cause an increase in the active layer, which thaws ground ice, causing ground subsidence that promotes the collection of surface water that stimulates vegetation growth. This vegetation growth then decreases the active layer, limiting further thaw. Plus signs indicate that there is a positive relationship between two variables; negative signs indicate an inverse relationship. Whether a model is overall self-reinforcing or stabilizing is based on whether the individual arrow signs multiply to positive (self-reinforcing) or negative (stabilizing).

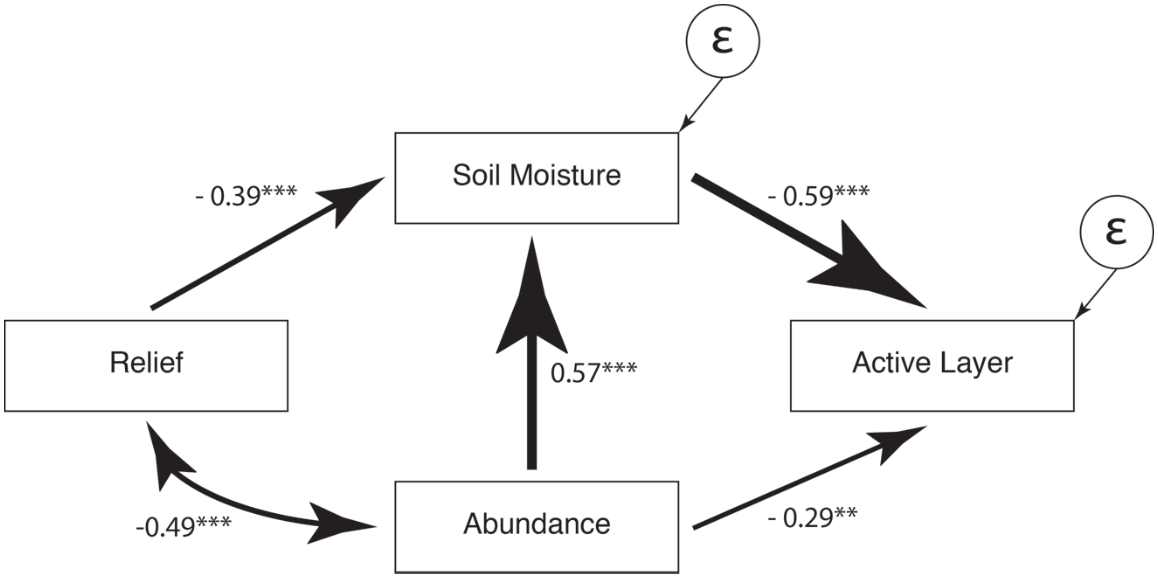

Figure 4.2: The results of our path analysis of vegetation's effect on active layer thickness. Weighted arrows reflect the relative strength of variable interactions (path coefficients). Path coefficients have been standardized in order to compare effect sizes across different units. Abundance has a direct effect of -0.29 on active layer, as well as an indirect effect (0.57 x -0.59) of -0.34, combing for a total effect of -0.62. Model has an overall *P*-value = 0.421, sufficiently passing > 0.05 criterion for acceptance. Signs of soil moisture are correct but inversed (to correct for data transformation) to the data from those reported on Table 1, to illustrate true effect relationships. Double-headed arrow represents unanalyzed covariance between exogenous variables. No sign indicates that there is a positive relationship between two variables; negative signs indicate an inverse relationship.

Table 4.1: Output from *lavaan* analysis of our proposed model. Regressions are designated as the arrows in Figure 4.1. Covariance is the double-headed arrow on Figure 4.1. Unexplained variance is the amount of variation of the endogenous variables not explained in the model. Elevation and abundance have high unexplained variance due to the fact they are exogenous variables – there is no statistical attempt to explain them. Active layer and soil moisture on the other hand have nearly 70% of the variance explained, showing the high power of our model.

	Path Coefficients	**Standard Error**	**Z-Value**	**P**
Regressions				
Soil Moisture ~ Elevation	-0.390	0.074	5.268	0.000
Soil Moisture ~ Abundance	0.566	0.074	-7.653	0.000
Active Layer ~ Soil Moisture	-0.591	0.099	5.964	0.000
Active Layer ~ Abundance	-0.287	0.099	-2.894	0.004
Covariances				
Elevation ~~ Abundance	-0.491	0.127	-3.859	0.000
Unexplained Variances				
Soil Moisture	0.304	0.050		
Active Layer	0.307	0.050		
Elevation	0.987	0.161		
Abundance	0.987	0.161		
Explained Variance (r2)				
Active Layer	0.689			
Soil Moisture	0.692			

4.8 Supplemental

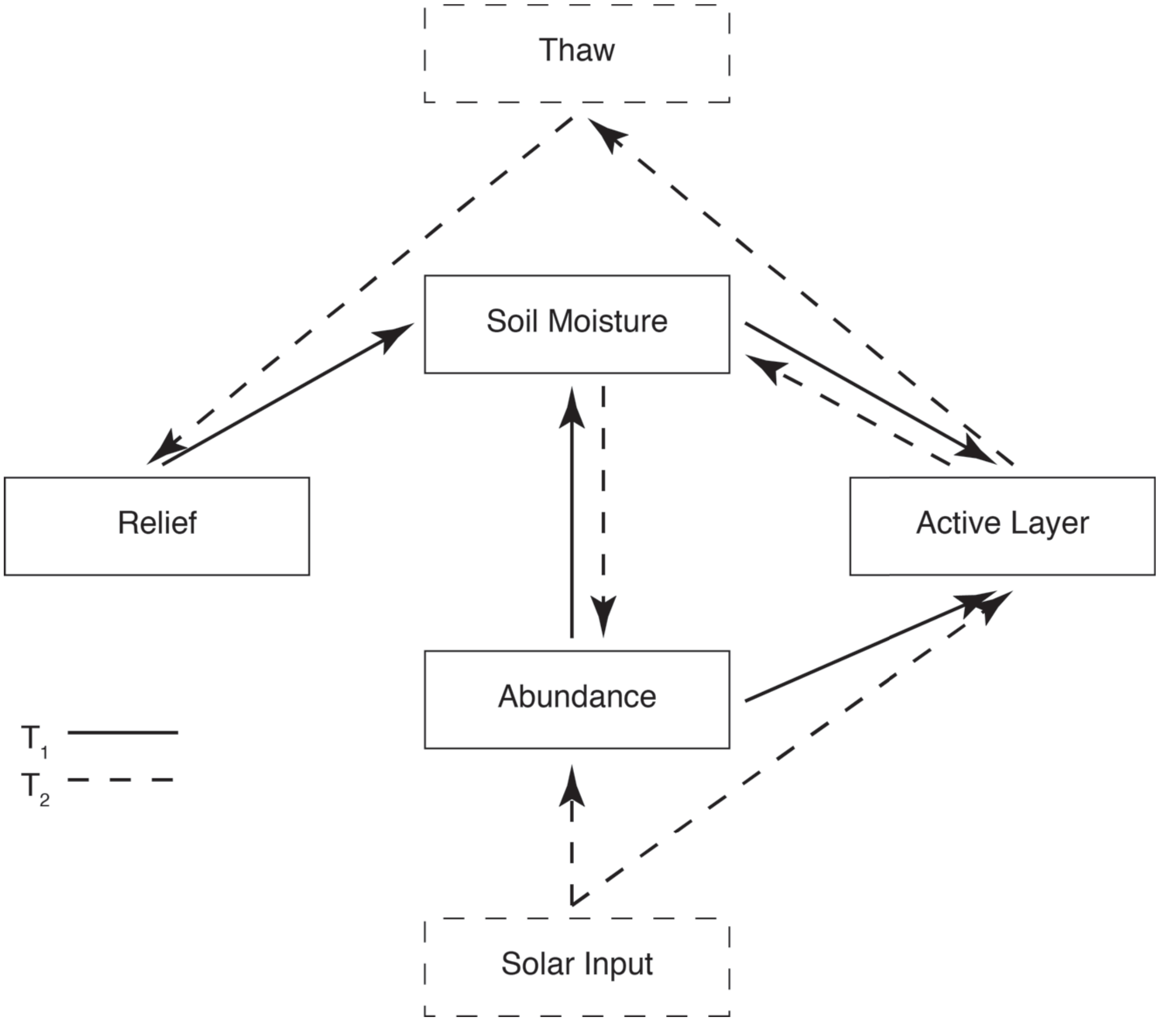

Figure S4.1: The non-recursive path model of our system involving multi-year feedbacks. The solid arrows are at Time 1 (year 1 for all intents and purposes). Time 2 (dashed lines) represents the carryover of effects from year 1 into year 2. In this way, the model cycles and stabilizes from year to year. Data was not appropriate to analyze in this manner according to reasons described in the introduction.

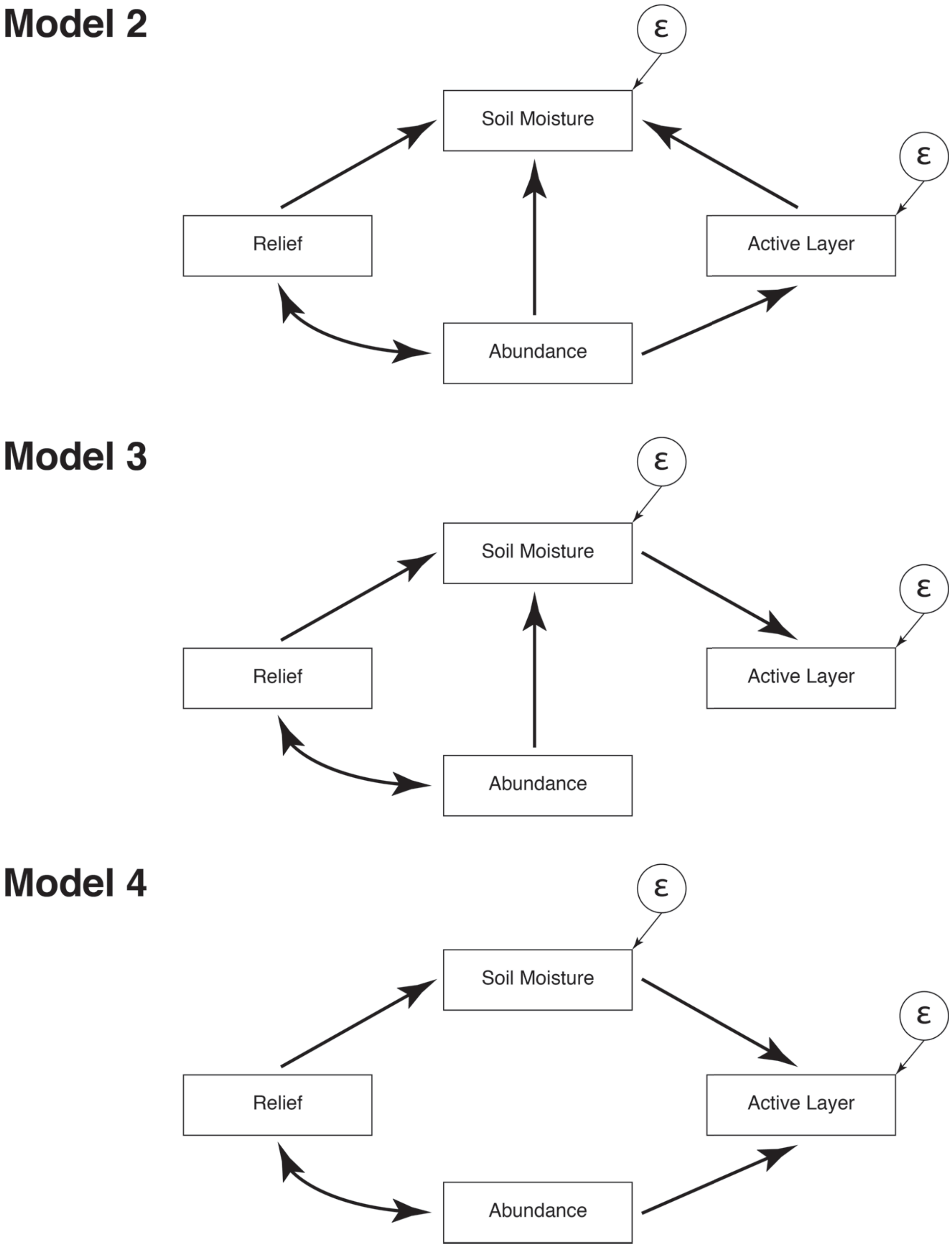

Figure S4.2: Alternate models tested. In Model 2, the arrow between active layer and soil moisture was reversed to test whether active layer was causal of soil moisture. In Model 3, the direct effect of vegetation on active layer was removed. In Model 4, the direct effect of vegetation on soil moisture (and therefore indirect effect on active layer) was removed.

Table S4.1: Variables' direct, indirect, and total effects on active layer depth. Vegetation percent cover (abundance) had the greatest total negative effect on active layer depth.

Variable	Direct Association	Indirect Association	Total Effect
Abundance	-0.287	-0.335	-0.622
Soil Moisture	-0.591		-0.591
Elevation		0.230	0.230

Table S4.2: Output of *lavaan* analysis of our proposed model (1) compared to the three other models (2 - 4) described in Table S4.2. Our model was the only one to pass the criteria of P > 0.05, showing that the other three models do not adequately fit the data. AIC was tabulated in the event other models would pass. Model 2 was the closest to passing the χ2 test, but would still have not been the most parsimonious.

#	Model	AIC	χ2	d.f.	P
1	Soil Moisture ~ Elevation + Abundance Active Layer ~ Soil Moisture + Abundance	668.213	0.647	1	0.421
2	Soil Moisture ~ Elevation + Abundance + Active Layer Active Layer ~ Abundance	671.625	4.060	1	0.044
3	Soil Moisture ~ Elevation + Abundance Active Layer ~ Soil Moisture	674.155	8.589	2	0.014
4	Soil Moisture ~ Elevation Active Layer ~ Soil Moisture + Abundance	709.502	43.936	2	0.000

Table S4.3: Out from *lavaan* testing model 2, where the relationship between active layer and soil moisture was reversed to test whether active layer was causal of soil moisture. This was tested as in the literature active layer does influence soil moisture by restricting groundwater flow, however this model does not fit the data as it fails the χ2 test. While there is truth in the theory, our data show that is more likely that the strongest pathway between the two variables is where soil moisture influences the depth of the active layer – as stated in our first model.

	Path Coefficients	**Standard Error**	**Z-Value**	**P**
Regressions				
Soil Moisture ~ Elevation	-0.308	0.062	4.947	0.000
Soil Moisture ~ Abundance	0.273	0.086	-3.184	0.001
Soil Moisture ~ Active Layer	-0.454	0.080	5.688	0.000
Active Layer ~ Abundance	-0.736	0.078	-9.408	0.000
Covariances				
Elevation ~~ Abundance	-0.491	0.127	-3.859	0.000
Unexplained Variances				
Soil Moisture	0.216	0.035		
Active Layer	0.453	0.074		
Elevation	0.987	0.161		
Abundance	0.987	0.161		
Explained Variance (r2)				
Active Layer	0.541			
Soil Moisture	0.772			

Table S4.4: The *lavaan* output from testing model 3, where the direct effect of vegetation on active layer was removed. This was tested as many studies do not consider the effect of vegetation on active layer, thus we wanted to assess model behavior with this absence. As shown in Table S4.2, this model failed the χ2 test, likely do to the fact that there is a strong and significant influence of vegetation on active layer depth as shown in our model 1.

	Path Coefficients	**Standard Error**	**Z-Value**	**P**
Regressions				
Soil Moisture ~ Elevation	-0.390	0.074	5.268	0.000
Soil Moisture ~ Abundance	0.566	0.074	-7.653	0.000
Active Layer ~ Soil Moisture	-0.809	0.068	11.910	0.000
Covariances				
Elevation ~~ Abundance	-0.491	0.127	-3.859	0.000
Unexplained Variances				
Soil Moisture	0.304	0.050		
Active Layer	0.341	0.056		
Elevation	0.987	0.161		
Abundance	0.987	0.161		
Explained Variance (r2)				
Active Layer	0.654			
Soil Moisture	0.692			

Table S4.5: The output of *lavaan* in assessing model 4, where the direct effect of vegetation on soil moisture (and therefore indirect effect on active layer) was removed. This was tested to show that a model must consider vegetation's indirect influence through soil moisture in addition to direct effects. As shown in Table S4.2, this model also failed the χ2 test.

	Path Coefficients	**Standard Error**	**Z-Value**	**P**
Regressions				
Soil Moisture ~ Elevation	-0.671	0.086	7.843	0.000
Active Layer ~ Soil Moisture	-0.591	0.068	8.647	0.000
Active Layer ~ Abundance	-0.287	0.068	-4.196	0.000
Covariances				
Elevation ~~ Abundance	-0.491	0.127	-3.859	0.000
Unexplained Variances				
Soil Moisture	0.542	0.089		
Active Layer	0.307	0.050		
Elevation	0.987	0.161		
Abundance	0.987	0.161		
Explained Variance (r2)				
Active Layer	0.636			
Soil Moisture	0.451			

CONNECTING STATEMENT: From Natural to Anthropogenic Thermokarst

In chapter four I outline and quantify the mechanism by which vegetation growth can stabilize and reduce active layer depth. This theory stemmed from observations made at a site of natural, climate-induced thermokarst in chapter three, but it is likely that this stabilizing mechanism holds for many cases of permafrost thaw – regardless of origin. In chapter five I examine a site of historical anthropogenic disturbance, where thermokarst occurred in ice-rich permafrost due to the stripping of vegetation to make a tundra runway. While the site was abandoned over 60 years ago, the landscape has not recovered to pre-disturbance conditions – instead it appears to have reached an alternative stable-state ecosystem. The ecological effects of anthropogenic disturbance in chapter five bear remarkable similarity to those of climate-induced thermokarst in chapter three, and it is likely that the landscape responds to different disturbance types through the mechanism described in chapter four.

CHAPTER 5 – 60 Year Legacy of Human Impacts on a High Arctic Ecosystem

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5.1 Abstract

The high Arctic is the world's fasting warming biome, allowing access to sections of previously inaccessible land for resource extraction. Starting in 2011, exploration of one of the Earth's largest undeveloped coal seams was initiated in a relatively pristine, polar desert environment. However, due to the relative lack of historic anthropogenic disturbance, significant gaps in knowledge exist on how the landscape will be impacted by development. Using a disturbance case–control approach, we evaluate the long-term ecological consequences of high Arctic infrastructure disturbance on sensitive ice-rich permafrost. We quantify: (1) long-term anthropogenic effects on vegetation diversity, community patterns, and soil nutrients; (2) the alteration of ground abiotic conditions and subsurface thermal changes. We found that in over 60 years since abandonment, the disturbed landscape has not recovered to initial conditions but instead reflects a disturbance-initiated succession towards a different stable-state community. Additionally, the type of microtopography disturbed greatly influences recovery patterns in the landscape. The terrain overlaying buried ice (ice wedge polygon troughs) is the most sensitive to disturbance, and show a novel species composition, decreased plot-level species richness, significant increase in vegetation cover, and a drastically reduced seasonal fluctuation in subsurface temperatures. Alternatively, disturbed polygon tops show resiliency in vegetation recovery, yet bear remarkable increases of seasonal depth of thaw (active layer). Our results indicate that disturbance effects differ depending on microtopographic feature, leading to an increased patchiness of the landscape as found at other disturbance sites elsewhere in the Arctic. Managers who wish to lessen their impact on high Arctic environments should avoid areas of sensitive, ice-rich permafrost, constrain the geographic scale of near-surface ground disturbance, limit vegetation removal where possible and reseed disturbed areas with native species.

5.2 Introduction

The high Arctic is warming, allowing access to large sections of previously inaccessible or logistically unfeasible land for development (IPCC 2013). Much of the Arctic is considered a "storehouse of resources" (ADHR 2004), while at the same time governments of circumpolar nations have introduced new regulatory changes and policies to encourage further exploration and increased land use (Haley *et al.* 2011). Arctic Canada, a resource frontier region, has recently expanded the development of mining in their far north (Prowse *et al.* 2009), despite significant industry concerns over the perceived threat of and lack of adaptation plans to future climate change (Ford *et al.* 2010; Pearce *et al.* 2011). Starting in 2011, exploration of one of the largest undeveloped coal seams in the world was initiated on the Fosheim Peninsula of Ellesmere Island, Canada (O'Donnell 2012). The region is a relatively pristine, polar desert environment that lies within the high Arctic Archipelago, and significant gaps in knowledge exist on how this landscape will respond to an increase in mining pressures.

High Arctic environments are thought to be particularly sensitive to anthropogenic disturbance, given the slow rate of vegetation community growth as well as the presence of large amounts of thermally-sensitive ice-rich permafrost (Reynolds & Tenhunen 1996; Forbes *et al.* 2001). In particular, the coal-rich Fosheim Peninsula is estimated to have 1456.8km^2 of ground ice within the permafrost (Couture & Pollard 1998), with roughly 700km^2 of it composed as ice wedges that make up the ubiquitous Arctic patterned-ground polygon systems. These bodies of ice are especially prone to disturbance, as any increase in the seasonal depth of thaw (active layer) results in topographic subsidence and the collapse of the ground surface (Edlund *et al.* 1990). This change in surface relief due to melting ground ice (thermokarst) is known in natural environments to substantially alter vegetation biodiversity and near surface soil characteristics (Becker, Davies & Pollard 2015).

Given the broad swath of possible Arctic mining impacts on coastal marine biota (Larsen *et al.* 2001), freshwater ecosystems (Laperrière *et al.* 2008), permafrost thaw/thermokarst (Sharkhuu 2003; Weaver & Kulas 2003), soil contamination (Elberling *et al.* 2007; Yakovlev *et al.* 2008), and plant community composition (Forbes 1997; Forbes *et al.* 2001) it is important to assess the range of potential landscape impacts prior to large-scale operations (ACIA 2004). One such way to mitigate and minimize impacts of future high Arctic industrial development is to assess outcomes of historical anthropogenic disturbance. Due to the remote location and relatively recent occurrence of human activity in the high Arctic, examples of historic disturbance are generally small scale, with most non-industrial anthropogenic activities creating disturbances in the range of 100m^2 – 1km^2 (Forbes, 1993;Walker & Walker, 1991). However, one of the oldest records of human disturbance in the region comes from the joint US – Canadian partnership established in the 1940's and 1950's to create a network of high Arctic weather stations (Department of Transport – Canada & Department of Commerce – US, 1951). These stations required the development of several forms of infrastructure – tundra airstrips, buildings, and seashore loading zones – all essential to future industrial work. One such station, the Eureka Weather Station, is situated on the Fosheim Peninsula directly adjacent to the area of mining interest.

Eureka was established in 1947 through a joint US – Canadian partnership. Initial delivery of goods for the station setup arrived via icebreaker, nonetheless the crew quickly developed an area of flat tundra to create a winter ice-runway for more regular delivery of supplies and personnel. The runway was created by the grading and removal of vegetation, and the infilling of uneven polygonal ground to create a smooth surface for a compacted winter runway. Used from 1947 – 1951, the runway was then abandoned to create a year-round airstrip closer to the base (3km away). Since its abandonment the area has been without human activity, aside from a few scientific observational studies (Department of Transport – Canada & Department of Commerce – US, 1951), and the landscape has been allowed to 'recover' along its own trajectory.

The old Eureka runway provides a unique opportunity to examine the long-term effects of a form of infrastructure essential to future mining development. Over the last several decades, research has qualitatively described both the vegetation changes and geomorphic disturbances to arise from this historic anthropogenic impact (Beschel 1963; Couture & Pollard 2007). Similar ecosystem impacts that are visible today were noted as little as two years after the disturbance stopped in 1951 by Bruggemann, P.C (Beschel 1963). This suggests that colonizing communities rapidly filled available niches and show marked stability over time, reflective of other Arctic locations where disturbance-induced community composition changes demonstrated consistency and resiliency (Forbes, 1993; Jorgenson, Ver Hoef, & Jorgenson, 2010).

However, limitations of previous high Arctic disturbance studies have been in the examination of vegetation and permafrost effects separately, whereas it is more likely that the two are parts of a coupled system (Becker *et al.* 2015) and the recovery of one may affect the outcome of the other. We address these gaps by evaluating the following hypotheses: (1) anthropogenic disturbance to the high Arctic environment creates long-term changes to vegetation biodiversity, community composition, and soil nutrients; (2) the alteration of the ground surface and removal of vegetation results in long-term abiotic ground conditions changes and subsurface thermal changes. By examining these effects of impact, we wish to highlight which aspects of the ecosystem are most susceptible to disturbance and to provide managers and industry professionals with clear ways of minimizing and mitigating long-term disturbances to high Arctic landscapes.

5.3 Methods

Study Site

The abandoned tundra airstrip near Eureka, is located at 80.0175°N, 85.7340°W approximately 3 km from the current runway (see Fig. S5.1). The airstrip was constructed in 1947 by the grading and removal of vegetation, and the infilling of uneven ground into a flat, compacted 1.6 km long x 60m wide tundra runway. While primarily used as an ice-runway for winter transport, the yearly removal of vegetation continued from 1947 until its abandonment in 1951. Since 1951 the airstrip has had no further development, but vegetation and geomorphic differences between the disturbed and undisturbed areas are still readily visible (Fig. 5.1). The region overall is characteristic of a polar desert environment, with scarce annual precipitation, low water-equivalent snow, and intense seasonal fluctuations of 24-hour daylight during summer and 24-hour darkness during winter (Edlund *et al.* 1990). Soils consist of nitrogen-poor, fine-grained marine clay sediments, typical of the region (Hodgson *et al.* 1991b). Given the very distinct nature of the grating disturbance, easy visualization of location, and discrete time frame of occurrence, data interpretation has the added benefit of daily historical records written by early Eureka staff that catalogued when and what kind of landscape alteration was conducted (Department of Transport – Canada & Department of Commerce – US 1951). A 400m x 400m subsection of the area was selected and a network of transects were overlain on the site of disturbance, with a significant border area of undisturbed, control terrain on the east and west sides of the runway.

Data Collection

Plot level vegetation, soil, and abiotic data were collected during June and July 2012. Vegetation percent cover and community composition were visually estimated within 0.5m^2 quadrats placed at alternating polygon tops and troughs along five transects running 400m east to west, as well as one additional transect running north to south along the airstrip. We conducted a stratified random sampling approach, recording compositional data within 80 quadrats divided into the following microtopographical groups: 22 control tops, 23 control troughs, 18 disturbed tops, and 17 disturbed troughs. Microtopographical groups were assigned as disturbed or control based on whether they fell within the airstrip-grating zone, and the category of polygon top or trough was clear as troughs delineate the edges of tops. Plot locations were marked by handheld GPS and coloured stakes for ease of identification for follow-up data collection and retrieval of data loggers.

Vascular vegetation was identified to the species level, and specimen vouchers were submitted to the Marie-Victorin Herbarium in Montreal, QC (see Table S5.1). Vascular plant nomenclature follows Saarela *et al.* (2013), phylogenetic tree construction follows the same procedure as Becker *et al.* (2015), and additional measures of percent moss cover, leaf litter, and bare ground were taken. Elevation measurements of the 400m x 400m site were conducted by taking 471 surveying measurements using a laser surveying level, with individual plot elevations recorded as well. Active layer depth was taken using a permafrost probe inserted into the four corners of the vegetation quadrat and calculating the average depth of penetration. Snowpack measurements were taken on June 5, 2013 prior to the spring melt period. This measure best represents the maximum total accumulated snow for the winter season, and therefore a good general measure of the bulk of annual water input for the system (Rydén 1977) as well as an idea of the snow insulation layer influencing soil temperate data.

Plot level soil temperature data was collected for a period of one year from June 20, 2013 to June 18, 2014. iButton data loggers were buried at 12cm depth (maximum rooting depth) at the locations of all quadrat plots and set to record ground temperature data every four hours. 13 data loggers, all at disturbed trough locations, were unable to be buried on June 20, 2013 as the ground at these locations was still frozen. Instead, these sites were revisited a month later on July 23, 2013 and all successfully buried. 74 of the 80 data loggers were recovered on June 19, 2014 and none malfunctioned.

Soil Chemistry

At each plot, soil samples were collected by taking 12cm deep slices from the four corners of the quadrat, homogenizing, air-drying for several days, and then pulverizing. Wet/dry weight ratios were taken in the field for soil moisture content (%H_2O).

Laboratory soil chemistry was conducted as follows: pH using a 1:2 soil-to-solution ratio using H_2O then measured by pH meter (Hendershot *et al.* 1993). Extractable NO_3- and NH_4+ were obtained using a 2 M KCl extraction ratio of 1:10 soil-to-solution and shaken for 1 hour. The filtrate was analysed by colorimetry for the determination of N on a multi-channel Lachat Quikchem auto-analyser (Lachat Methods 13-107-06-1-A, 10-107-06-2-C, 13-107-06-2-B; Maynard & Kalra, 1993). Available P and K were determined by a multi-element extraction using Mehlich III solution and then measured by flow injection analysis (Lachat Instruments; Tran & Simard 1993). Percent organic matter was measured by loss on ignition and the difference in weight is attributed to loss of organic matter (Schulte *et al.* 1991).

Statistical Analysis of Vegetation, Soil, and Temperature Data

Vegetation differences among the four microtopographies were analyzed using the following techniques: community differences were examined by ordinating plot composition and abundance using non-metric multidimensional scaling (NMDS) of a Bray-Curtis distance matrix calculated from percent cover in the r-library *vegan* (Oksanen *et al.* 2013), and quantified using a permutational multivariate analysis of variance (PERMANOVA) set for 1000 randomizations. Mean plot species percent cover (of vascular vegetation), richness (alpha-diversity), and evenness (Shannon's H) were compared between microtopographies using two-way, type III ANOVAs for imbalanced designs to account for the unequal number of sample sizes, followed by Tukey tests for post-hoc significance testing. Soil chemistries were tested in a similar fashion, using two-way, type III ANOVAs for imbalanced designs followed by Tukey tests for post-hoc analysis.

Temperature analysis was divided into two measures: thawing degree days (TDD) and freezing degree days (FDD). TDD and FDD are measures of the magnitude of annual warming above 0°C or freezing below 0°C, respectively. For TDD, each plot had its daily mean temperature calculated, and then mean temperatures for all days greater than 0°C were summed. For FDD, all mean temperatures for days less than 0°C were summed. For group means testing of TDD, all data from before July 23, 2013 were removed as a large portion of the thermokarst troughs loggers were not yet buried. Therefore the TDD metric should be viewed as the *relative* TDD differences between microtopographies for the yearly period, rather than the absolute TDD for the summer period. Since all loggers were successfully buried for the winter season, FDD represents the true values experienced through the 2013 – 2014 winter season.

All analyses were done in in R version 3.0.2 (R Core Team 2014).

5.4 Results

Diversity

The vegetation patterns of disturbed troughs have followed a distinct trajectory similar compared to other microtopographies. The NMDS ordination of communities (Fig. 5.2) shows that disturbed troughs have a vegetation composition dissimilar from the other three microtopographies, with PERMANOVA results indicating this is highly likely ($p < 0.001$) (see Table S5.2). Examining averaged phylogenetic trees of the four microtopographies demonstrates a similar picture, as a clear shift from willow-dominated communities in the other three microtopographies has changed into a wet-sedge-dominated community of disturbed troughs (Fig. 5.3).

The study site included 23 species out of the estimated 140 species indigenous to the Fosheim Peninsula (Edlund *et al.* 1990), with control and disturbed zones having a gamma diversity (pooled species richness) of 18 and 17, respectively. The control top and trough included 12 and 15 species, respectively, with *Salix arctica* dominating and *Poa glauca* and *Dryas integrifolia* the next greatest in cover. Five species, *Saxifraga oppositifolia*, *Pedicularis hirsuta*, *Cerastium arcticum*, *Bistorta vivipara*, and *Poa pratensis* were unique to control terrain and completely absent from disturbed. *Saxifraga tricuspidata* was also found within control terrain but was not present in any plots.

Disturbed tops had a species pool of 13, and were dominated by *S. arctica*, with *P. glauca* and *Deschampsia brevifolia* the next most dominant. Disturbed troughs had a species pool of 14 and were the only microhabitat not dominated by *S. arctica*, instead being dominated by *Alopecurus magellanicus*, with secondary dominance split between *Eriophorum scheuchzeri* and *S. arctica*. However, it is worth noting that when *E.scheuchzeri* was present, it tended to entirely cover plots, and these soils had the greatest moisture content. Four species were unique to disturbed plots: *Juncus arcticus*, *Pleuropogon sabinei*, *Elymus alaskanus,* and *Dupontia fisheri.*

Despite pronounced compositional changes, disturbance effects on species richness and evenness appear more minor (Fig. 5.4). Disturbed plots had significantly less species richness than control plots ($F_{1,76}$ = 7.23 $p < 0.01$). Control tops and disturbed tops did not differ significantly, however, disturbed troughs had significantly less species richness than control troughs ($p < 0.001$). This difference in response of tops and troughs is likely driven by a significant interaction effect between disturbance and microtopography ($F_{1,76}$ = 4.98 $p < 0.05$). Evenness values follow a similar trend with disturbed plots having significantly lower evenness than control plots ($F_{1,76}$ = 5.04 $p < 0.05$). Disturbed tops again did not significantly differ from control tops, but disturbed troughs had significantly lower evenness than control troughs ($p < 0.01$) likely driven by the significant interaction of disturbance and microtopography ($F_{1,76}$ = 6.57 $p < 0.01$).

Soils

Despite pronounced changes in species composition and abundance, soil analysis showed less prominent differences (see Fig. S5.2). NH_4 values were extraordinarily low across the entire site. Disturbed plots had significant greater NH_4 content than control plots ($F_{1,76}$ = 5.55 $p < 0.05$) with troughs significantly greater than tops ($F_{1,76}$ = 10.73 $p < 0.01$). The interaction effect was significant ($F_{1,76}$ = 5.94 $p < 0.05$) indicating that the effect of disturbance was greater on troughs than tops, since disturbed troughs had significantly greater NH_4 than control troughs ($p < 0.01$). NO_3 values were near detection limit for most samples and did not significantly differ. Disturbed plots showed decreased levels of K compared to controls ($F_{1,76}$ = 11.03 $p < 0.01$), with troughs having significantly less K than tops ($F_{1,76}$ = 18.02 $p < 0.001$). A significant interaction was present ($F_{1,76}$ = 8.58 $p < 0.01$) since disturbed tops did not differ significantly from control tops, but disturbed troughs had significantly less K than control troughs ($p < 0.001$). Levels of P were significantly less in disturbed plots than control plots ($F_{1,76}$ = 7.82 $p < 0.01$) but did not differ significantly between tops and troughs, with no significant interaction effect. Organic matter content did not differ significantly between disturbed and control plots, but tops and troughs differed significantly within their respective groups ($F_{1,76}$ = 18.88 $p < 0.001$). pH showed significant differences between control and disturbed plots ($F_{1,76}$ = 14.13 $p < 0.001$) and between tops and troughs ($F_{1,76}$ = 14.79 $p < 0.001$), but this is likely driven by a significant interaction effect ($F_{1,76} = 6.55$ $p < 0.05$) with the effect of disturbance more pronounced for disturbed troughs when compared to control troughs ($p < 0.001$).

Abiotic

The most prominent effect of disturbance to abiotic soil conditions was the marked increase in soil moisture of disturbed troughs (Fig. 5.5). Disturbed plots had greater moisture than control plots ($F_{1,76} = 22.85$ $p < 0.001$), and troughs had greater moisture than their respective tops ($F_{1,76} = 77.15$ $p < 0.001$). A significant interaction effect ($F_{1,76} = 18.45$ $p < 0.001$) indicates that the effect of disturbance on soil moisture was far more pronounced for troughs than tops. This comes despite no significant difference between troughs for the depth of winter snowpack – the largest annual input of moisture to the system. However, we find that vegetation percent cover in the disturbed plots was significantly greater than control plots ($F_{1,76} = 28.90$ $p < 0.001$) with troughs having significantly greater percent cover than tops ($F_{1,76} = 45.52$ $p < 0.001$), mirroring effects found with soil moisture. Disturbance effects on percent cover were influenced by a strong interaction effect ($F_{1,76} = 26.50$ $p < 0.001$) since control tops and disturbed tops did not differ significantly. Importantly, disturbed plots had greater active layer depth than controls ($F_{1,76} = 46.90$ $p < 0.001$), with tops having a deeper active layer than troughs ($F_{1,76} = 19.71$ $p < 0.001$), however this was driven by a significant interaction effect ($F_{1,76} = 19.17$ $p < 0.001$) whereby disturbance only increased the active layer of tops.

We also found significant annual differences in soil temperatures between the disturbed and control microtopographies. When examining the plot of mean daily temperatures over the year (Fig. 5.6), two things become abundantly clear: disturbed troughs have lower summer soil temperatures and warmer winter soil temperatures, and there are decreased seasonal fluctuations in temperature. These differences are reflected in the significantly less TDD experienced by disturbed plots compared to control plots ($F_{1,70} = 18.23$ $p < 0.001$), with troughs significantly lower than tops in their respective groups ($F_{1,70} = 47.46$ $p < 0.001$). A significant interaction effect was present ($F_{1,70} = 20.63$ $p < 0.001$), showing that disturbance affected troughs more greatly than tops, as troughs were significantly difference ($p < 0.001$) while tops were not (Fig. 5.7). FDD also significantly differed between disturbed plots and control plots ($F_{1,70} = 7.32$ $p < 0.01$) as well as between tops and troughs ($F_{1,70} = 108.77$ $p < 0.001$). However, disturbed tops did not differ significantly from control tops, and the significant interaction effect indicates ($F_{1,70}$

= 11.55 $p < 0.001$) that the effect of disturbance was primarily on troughs as disturbed troughs had significantly fewer FDD than control troughs ($p < 0.001$).

5.5 Discussion

In over 60 years after abandonment, the disturbed landscape has not recovered to a state comparable to surrounding undisturbed terrain. Most importantly, the disturbed ground does not appear to be on a recovery trajectory towards the control conditions, but instead reflects a disturbance-initiated succession towards a different stable-state community (Forbes *et al.* 2001; Kemper & Macdonald 2009). The terrain overlaying ice wedges within the polygon networks are the most sensitive to disturbance, with divergent species compositions as well as the largest impact on abiotic soil conditions and subsurface temperatures. Disturbed tops also preserve a thermal legacy of impact with the largest active layer depth changes, despite having re-vegetation patterns that appear to have returned to normal. These results indicate that both types of microtopography can bear the hallmarks of disturbance long after human activity has stopped and geomorphic effects have subsided. These effects differ depending on microtopographic feature, leading to an increased patchiness of the landscape as found elsewhere in the Arctic (Forbes et al., 2001). Managers who wish to lessen their impact on high Arctic environments would do well to avoid areas of sensitive, ice-rich permafrost, constrain the geographic scale of near-surface disturbance, and limit vegetation removal where possible.

Diversity

The vegetation community's response to anthropogenic disturbance differs greatly depending on microtopography. Disturbed polygon troughs, underlain by ice wedges, have followed a unique trajectory when compared to their disturbed top counterparts and the surrounding control conditions. Rather than follow a vegetation recovery pattern like tops, the troughs appear to have stabilized into a different wetland stable state – a wetland that bears extraordinarily similar patterns to naturally-induced thermokarst (Becker *et al.* 2015). Most notable is that the dominant type of vegetation has changed from willow to wet-sedge, and troughs show a plot-level decrease in species richness and evenness. This decreased species richness, but near 100% cover, likely results from the incoming, rapidly growing clonal species that leave very little niche space for new colonization, also making it unlikely for further diversity to spread into the plots (Forbes, 1996). Recruitment to disturbed sites generally comes from local soil seed bank stores rather than freshly dispersed seeds or vegetative runners (Cooper *et al.* 2004), and plot-level species richness may be kept low by both a dearth of microsite space availability and a limited number of efficient colonizers in the Arctic (Forbes, 1996). In contrast to studies where diversity was lowered for the entire disturbance area (Forbes et al., 2001), we find it interesting that plot-level species richness has remained unchanged for disturbed tops. This points to a relative resiliency for polygon tops to recover from vegetation removal. Indeed, pooled species richness for tops has not changed significantly due to disturbance, as gamma diversity is essentially the same in disturbed and control conditions.

The effects of differential and increased vegetation growth in disturbed troughs are mirrored in the impacts on soil nutrients, primarily the consumption of K and the increase of pH and OM through increased plant activity. Low nitrogen concentrations are typical for high Arctic ecosystems (McKane *et al.* 2002). However, the increased NH_4 concentrations in disturbed troughs may act as localized nutrient pools that could increase over time from greater microbial fixation due to more favourable (increased moisture) soil conditions (Mengel *et al.* 2001). While soil nutrient conditions do not yet greatly differ for disturbed locations, it is likely that over time the altered vegetation communities will produce increasingly divergent soil conditions (Edlund & Alt 1989).

Abiotic

While vegetation diversity of disturbed troughs has decreased, one of the impacts of increased vegetation cover has been the alteration of abiotic soil conditions – primarily the drastically higher soil moisture content. Given that troughs in both control and disturbed locations are receiving roughly the same amount of water input (i.e. no significant difference in snowpack), we believe the increased plant over in disturbed troughs is helping to retain moisture when compared to bare ground (Blok *et al.* 2011). Wet-sedge species rely on higher water content but also need this greater water content to successfully colonize. Edlund et al. (1990) speculated that in hot years, melting ice wedges provided increased soil moisture. In our case, we posit that the removal of vegetation decreased the insulation of the ground (Shur & Jorgenson 2007), increased the seasonal depth of thaw, resulting in melted ground ice that contributed the essential moisture needed for sedge colonization. As sedge growth continued, further moisture was retained, and successive years reinforced this wet-sedge ecosystem.

This wet-sedge ecosystem has also significantly dampened annual ground temperature fluctuations. The marked decrease in TDD and FDD of disturbed troughs demonstrates that these plots are colder in the summer, and warmer in the winter, due to the insulating effects of a greatly increased vegetation cover (Shur & Jorgenson 2007). We doubt that the decrease in FDD plays much of a role in the annual development of the active layer – yet – as the mean annual air temperature of the region is so cold that the active layer completely refreezes by mid-winter. However, the significantly less TDD experienced during the summer means that active layer depth is reduced, and it is possible that the disturbed troughs are now more resistant to further thermal change (i.e. from climate change) when compared to control plots. Thus, while the vegetation biotic composition has shifted completely for disturbed troughs, the greater biomass of clonal species is a stabilizing feedback that may help with the overall resistance to further change of the underlying permafrost.

Recommendations for Management:

Given the divergent trajectories for disturbed polygon tops and troughs, we would like to emphasize the following points for decreasing the physical and biotic anthropogenic impacts of development on high Arctic environments:

- Avoid areas of ice-rich soils: as we found that disturbed ice wedges showed the most pronounced diversity and compositional changes, it is likely that any operations that affect the ground surface will cause thermal changes to underlying wedge ice with long-term biotic effects. Additionally, the dominant recovery growth in the form of thick, clonal wet-sedge cover insulates the ground to further change, it is recommended that if disturbance occurs, to facilitate colonization as quickly as possible. Stripping ice-rich permafrost of vegetation cover and not promoting recovery growth would likely leave these areas extraordinarily susceptible to further melt and disturbance (Shur & Jorgenson 2007).
- Keep impacts spatially confined: the disturbance we measured appears to be confined explicitly to the area of the airstrip, with very little adjacent effects. Other areas of high

Arctic ground disturbance show highly constrained impacts (Forbes *et al.* 2001), likely limiting chance of disturbance "runoff" beyond the immediate area.

- Remove as little vegetation as possible: given the aforementioned thermal and abiotic changes and the creation of niche space, there is also a potential danger of species contamination. As the disturbance opens up a new ecological niche (particularly over ice wedges) there is the potential for the introduction of non-native species from dirt attached to industrial machinery that is transported from the south. While our site survey did not detect any non-native species, we recommend thorough cleaning of incoming machinery, as the establishment and persistence of non-native seeded species may act as further dispersal points in cases of neighbouring disturbance (Kearns *et al.* 2015). Additionally, we recommend industry-assisted revegetation using native varieties of *Eriophorum* and *Carex* species as they have been shown to be successful colonizers (Chapin & Chapin 1980), there is likely additional seed bank of *E.scheuzeri* (Forbes 1993) already present, and success rates of revegetation in wet areas is relatively high (Forbes & Jefferies 1999). Furthermore, Chapin & Chapin (1980) showed that fertilization of adjacent, existing patches of vegetation next to the disturbance site could provide a local seed bank at a cost-effective level. While it is likely that there is already sufficient resident seed bank for colonization, recolonizers are unlikely to be the original *Salix* community (Cooper *et al.* 2004). Thus, while "recovered" areas will not resemble the original vegetation community, they could at least be natively derived species and help to prevent further thermal damage to the subsurface.

In the Arctic, it appears that early recolonizing communities of disturbed terrain are self-perpetuating and relatively stable over time (Forbes 1993, 1996; Forbes *et al.* 2001). The distinct patches that have been created through landscape disturbance may represent alternative, wetland stable states in the high Arctic environment with novel biotic and abiotic feedbacks that persist over a long timescale. Thus, both small and large-scale disturbances arising from increased anthropogenic activity in the Arctic should be planned with great caution and foresight, keeping in mind the legacy we impart on the environment long after we have left.

5.6 Acknowledgements

A particularly large appreciation goes to the staff of Eureka Weather Station, Nunavut for their logistical assistance and company on Ellesmere Island. This study was supported through a doctoral research scholarship from Fonds de Recherche du Québec: Nature et Technologie (FRQNT) (M.S.B.), a Research Support Opportunity from ACUNS and Environment Canada (M.S.B.), NSERC Discovery grant (W.H.P.), and ArcticNet funding (W.H.P.).

5.7 Figures

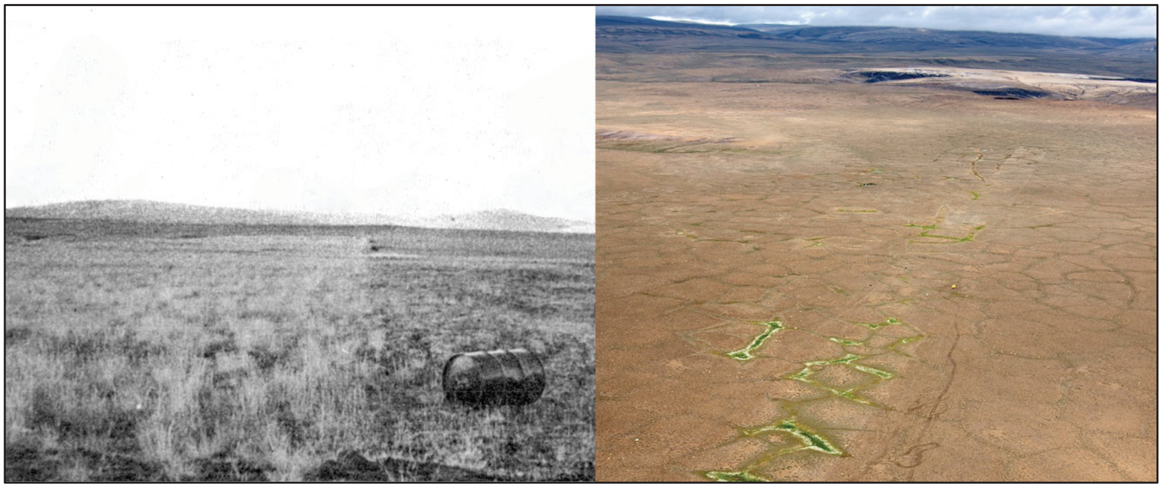

Figure 5.1: Images of the old Eureka tundra airstrip on Ellesmere Island, Nunavut, Canada. The image on the left was taken in 1960 (modified from Beschel (1963)) and the left half shows the marked line of newly-colonized disturbance vegetation. The aerial image on the right was taken in 2012. Clear differences in vegetation remain, as well as more greatly expressed polygon features within the disturbance zone.

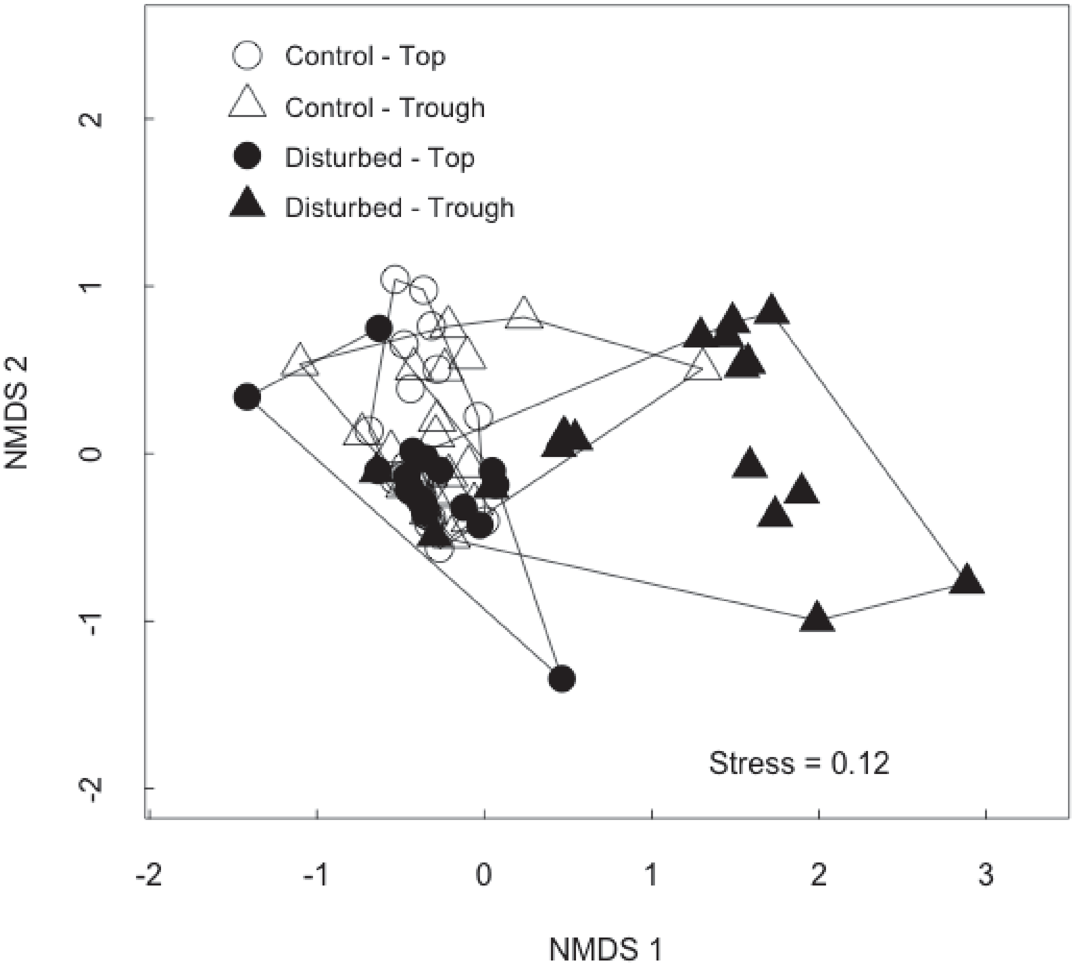

Figure 5.2: NMDS ordination using a Bray-Curtis dissimilarity matrix generated from plant community composition. Hulls connect the outermost points of each microtopography to show spread of the data. Only the disturbed troughs show clear separation from the other microtopographies, reflected in the strong interaction effect shown in PERMANOVA results (see Table S5.2).

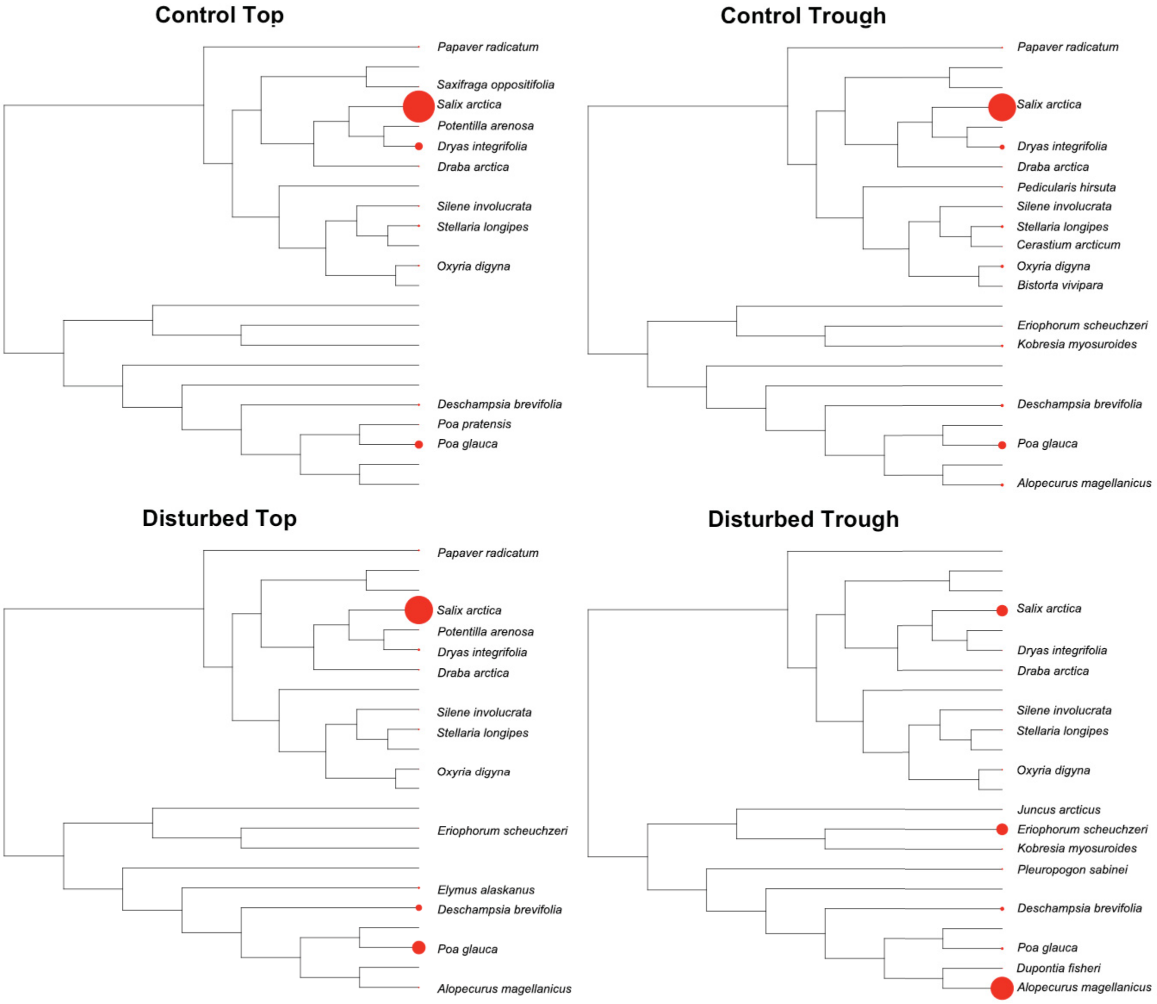

Figure 5.3: Averaged phylogenetic trees of the four microtopography types, weighted by abundance. For each microtopography, the plots' vegetation abundances were averaged together to generate the red circles (i.e. greater abundance equals larger circles). The species names listed are those that are present in any abundance at a given microtopography. Absence of a species indicates that it was not found in that microtopography.

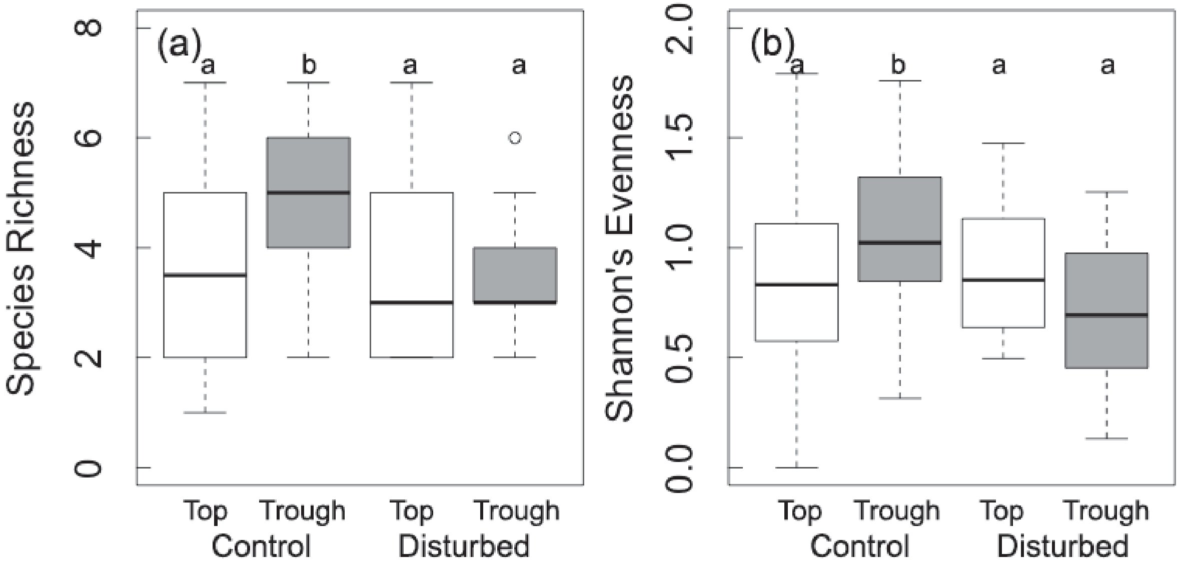

Figure 5.4: Measures of plant species richness (alpha-diversity) (a), and evenness (b) of the four microtopographies. Box whiskers represent 1.5 interquartile range (IQR) boundaries. Letters above boxes represent significantly different values ($p < 0.01$, ANOVA and Tukey post-hoc test).

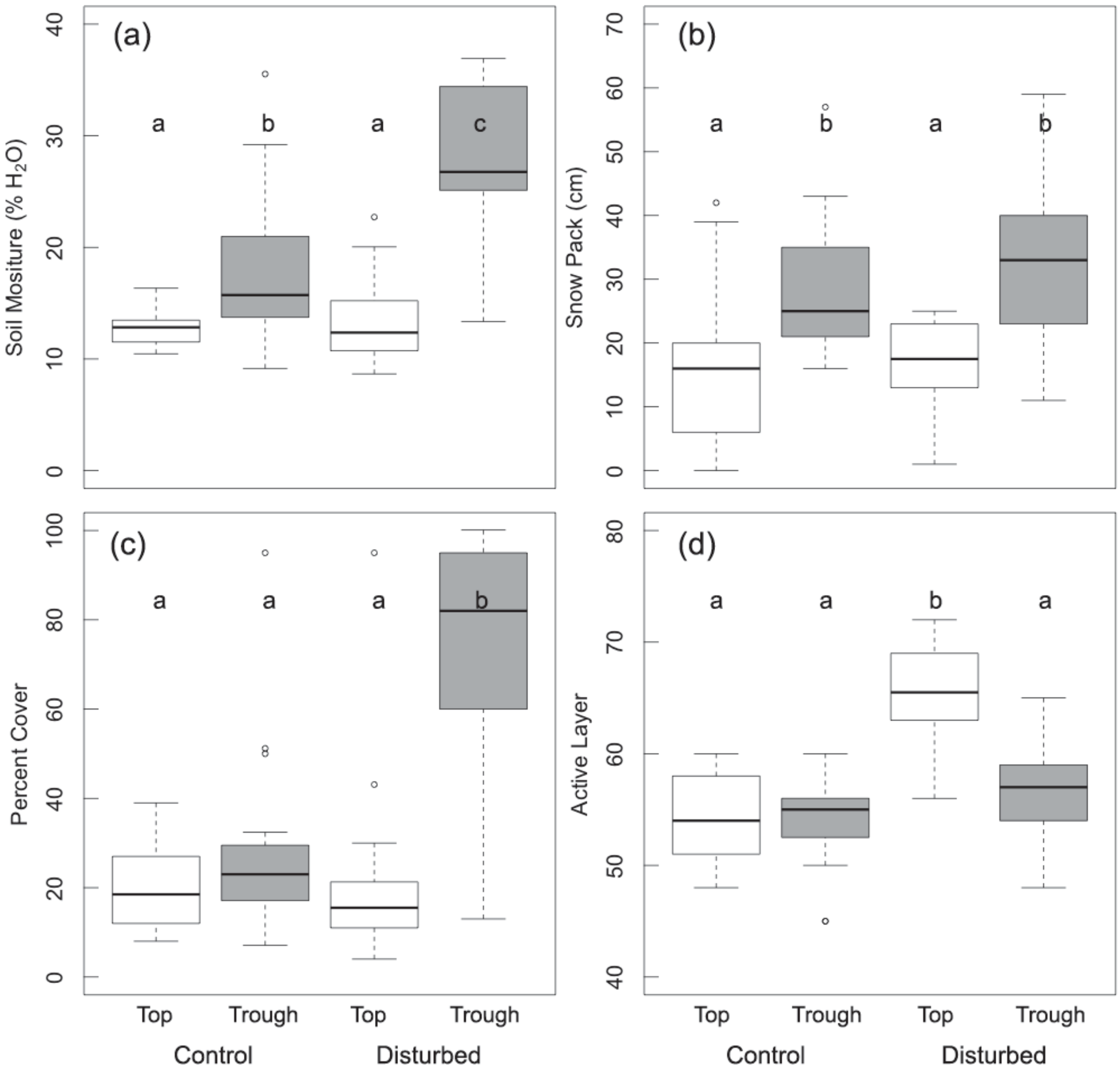

Figure 5.5: Measures of soil moisture (a), snowpack depth (b), vegetation percent cover (c), and active layer depth (d) of the four microtopographies. Box whiskers represent 1.5 interquartile range (IQR) boundaries. Letters above boxes represent significantly different values ($p < 0.01$, ANOVA and Tukey post-hoc test).

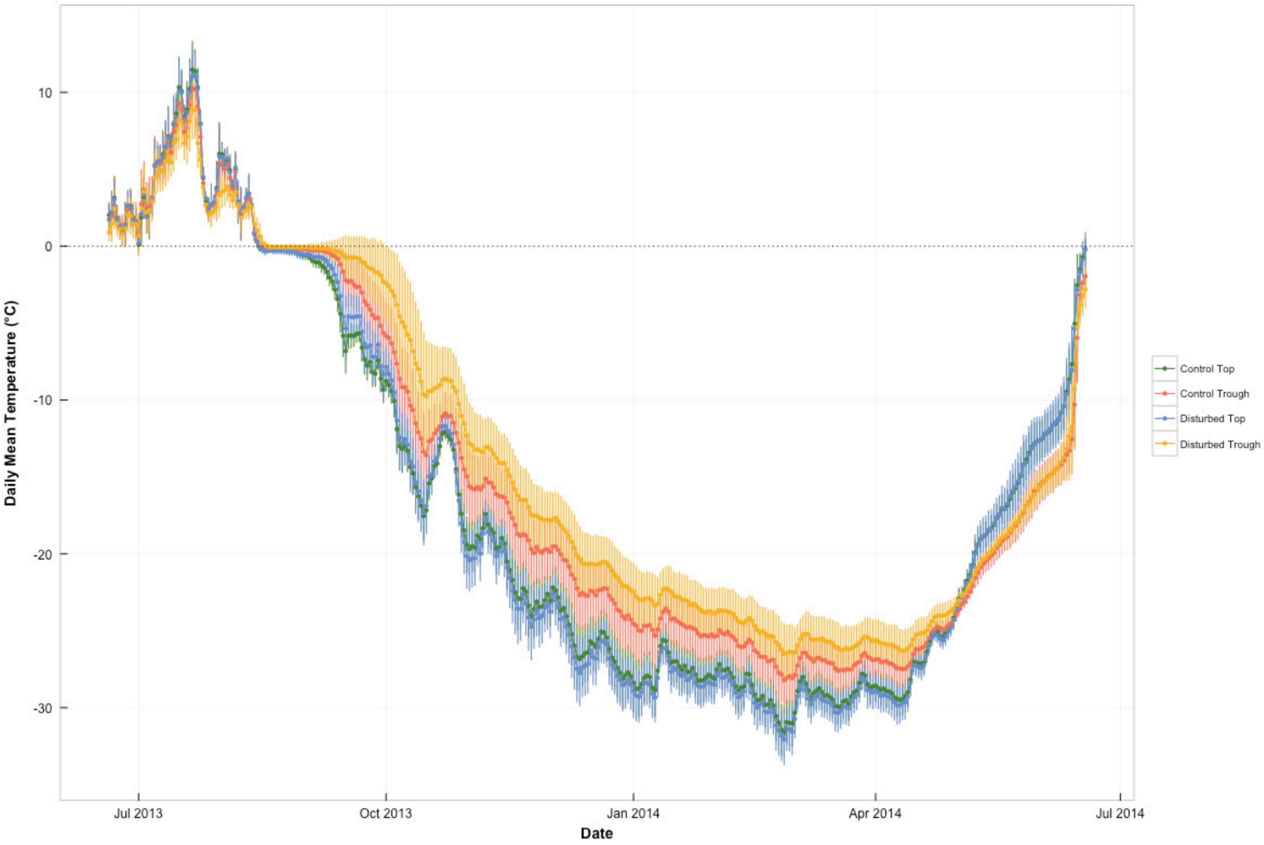

Figure 5.6: Averaged daily soil temperatures at 12cm depth, bars denoted standard deviation. Disturbed troughs clearly demonstrate lowest summer temperatures and warmest winter temperatures, with reduced fluctuations throughout the year.

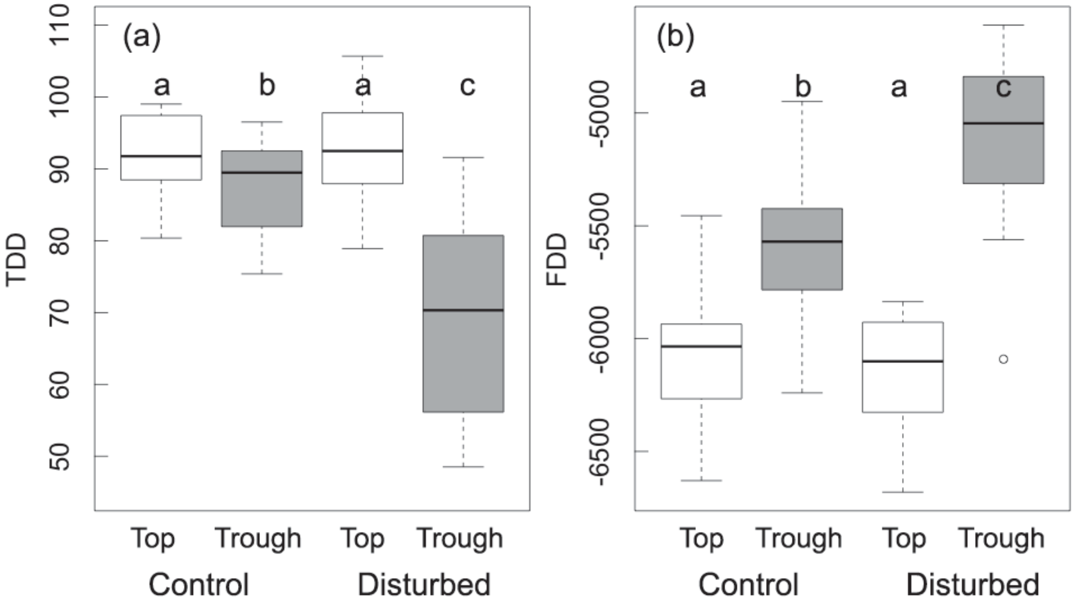

Figure 5.7: Measures of Thawing Degree Days (a), and Freezing Degree Days (b) of the four microtopographies. Box whiskers represent 1.5 interquartile range (IQR) boundaries. Letters above boxes represent significantly different values ($p < 0.01$, ANOVA and Tukey post-hoc test).

5.8 Supplemental

Figure S5.1: Map of study site and geographical region. The old Eureka airstrip is located ~7km inland from the Slidre Fiord on the Fosheim Peninsula, Ellesmere Island, Nunavut, Canada (80.0175°N, 85.7340°W).

Table S5.1: Species list with family names and sequence information used for phylogenetic trees. Ascension number refers to this paper's voucher collection submitted to the Marie-Victorin Herbarium in Montreal, QC. The ascension numbers for *rbcL* and *matK* refer to the gene sequences from Saarela *et al*., 2013 submitted to GenBank.

Species Name	**Family**	**Ascension Number**	***rbcL* (553 bp)**	***matK* (791 bp)**
Alopecurus magellanicus	Poaceae	187791	KC481897	KC473974
Bistorta vivipara	Polygonaceae	187828	KC482107	KC474182
Cerastium arcticum	Caryophyllaceae	187793	KC482409	KC474436
Deschampsia brevifolia	Poaceae	187827	KC482483	KC474495
Draba arctica	Brassicaceae	187795	KC482546	KC474554
Dryas integrifolia	Rosaceae	187801	KC482650	KC474660
Dupontia fisheri	Poaceae	187817	KC482670	KC474676
Elymus alaskanus	Poaceae	187819	KC482675	KC474680
Equisetum arvense var. *alpestre*	Equisetaceae		KC482714	
Eriophorum scheuchzeri	Cyperaceae	187804	KC482811	KC474756
Juncus arcticus var. *alaskanus*	Juncaceae	187860	KC483009	
Kobresia myosuroides	Cyperaceae	187824	KC483056	KC474928
Oxyria digyna	Polygonaceae	187810	KC483221	KC475051
Papaver radicatum var. *radicatum*	Papaveraceae	187798	KC483282	KC475113
Pedicularis hirsuta	Orobanchaceae	187812	KC483368	KC475206
Pleuropogon sabinei	Poaceae	187858	KC483465	KC475302
Poa glauca var. *glauca*	Poaceae	187838	KC483534	KC475370
Poa pratensis subsp. *alpigena*	Poaceae	187820	KC483576	KC475415
Potentilla arenosa	Rosaceae	187797	KC483603	KC475442
Salix arctica	Salicaceae	187802	KC483913	KC475719
Saxifraga oppositifolia var. *oppositifolia*	Saxifragaceae	187806	KC484066	KC475857
Saxifraga tricuspidata	Saxifragaceae	187821	KC484081	KC475864
Silene involucrata subsp. *involucrata*	Caryophyllaceae	187794	KC484106	KC475887
Stellaria longipes subsp. *longipes*	Caryophyllaceae	187811	KC484154	KC475931

Table S5.2: PERMANOVA results testing differences in community structure of different microhabitats. Disturbed communities are significantly distinct from control communities (called "location"), and tops differ significantly from troughs (called "type"). However, a significant interaction effect is present, and as seen in the NMDS results it is likely that significant changes in composition are driven by disturbance's greater effect on troughs than tops.

Term	**Df**	**Sum Of Sqs**	**MeanSqs**	**F**	**r^2**	**P**
location	1	1.7108	1.71081	12.164	0.10943	0.001
type	1	1.7669	1.76692	12.563	0.11302	0.001
location:type	1	1.4666	1.46658	10.428	0.09381	0.001
Residuals	76	10.6889	0.14064		0.68373	
Total	79	15.6332			1	

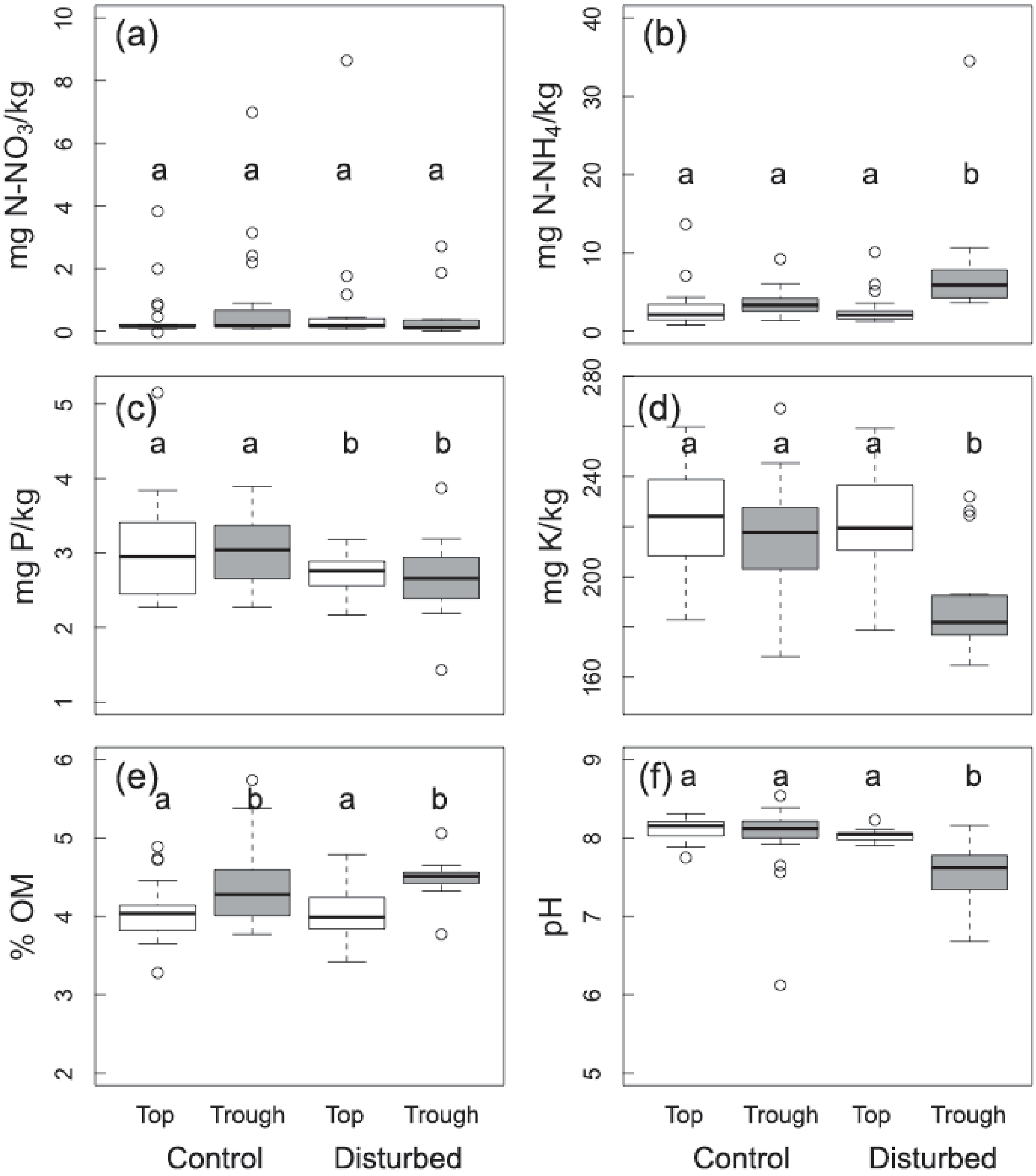

Figure S5.2: Soil chemistry variables measured at the four different microtopographies: (a) plant available nitrate, (b) plant available ammonium, (c) phosphorus, (d) potassium, (e) percent organic matter of loss on ignition, and (f) pH. Box whiskers represent 1.5 interquartile range (IQR) boundaries; dots are outliers beyond the 1.5 IQR. Letters above boxes represent significantly different values ($p < 0.01$, ANOVA and Tukey post-hoc test).

SUMMARY AND CONCLUSIONS

6.1 General Summary

Melting ice wedges are a catalyst for extensive ecosystem change in high Arctic polar deserts. This often overlooked feature in the ecological and climate change literature is capable of initiating a wide range of effects whether a disturbance is of climatic or anthropogenic in origin. Climate change is predicted to be the largest driver of biodiversity loss in the Arctic (Sala *et al.* 2000). However, in chapter three I show that the thermokarst-induced partitioning of microtopography and habitats facilitates greater local diversity within ice wedge polygon systems, resulting in community restructuring rather than species loss. I predict that this restructuring will lead to a more heterogeneous landscape comprised of a mosaic of different habitat types, quite contrary to studies suggesting a loss of biodiversity with climate change. In chapter four, I show that the significant vegetation growth stimulated by thermokarst has a sizeable dampening effect on ground temperatures, with the ability to substantially decrease active layer depth. As this stabilizing mechanism is often not included in permafrost modeling, I provide a structure for including the direct and indirect vegetation effects on the active layer. In chapter five, I quantify the long-term biotic and abiotic repercussions of direct anthropogenic disturbance to the high Arctic ground surface. I show that the recovery trajectory of this disturbed area has likely proceeded to a wetland alternative stable state – a state that greatly resembles the vegetation and soil conditions of the naturally induced thermokarst in chapter three. I posit that the stabilization reached in the anthropogenic-disturbed site follows a similar mechanism to one I laid out in chapter four. Together, this thesis provides a comprehensive assessment of the ecologic and geomorphic processes that work in unison to shape the Arctic's most ubiquitous landscape feature.

6.2 Conclusions

Each manuscript within this thesis makes their own individual contributions to the scientific literature, and taken together they give a broader idea of biogeomorphic landscape processes within the high Arctic. In each manuscript, a number of significant conclusions have been reached:

The first goal of this thesis was to assess the microtopographic, vegetation diversity, and edaphic repercussions of climate-induced ice wedge thermokarst. I found that the local subsidence of ice wedges instigated a suite of biotic and abiotic changes, and that these changes may result in a high Arctic with a wider range of habitat types that can support a greater diversity of vegetation. This greater diversity of vegetation also coincides with a much greater percent cover, mirroring findings of increasing primary productivity across the Arctic with climate change (Elmendorf *et al.* 2012b). It is likely that this change of polar desert conditions into those that more closely resemble the wetlands of the low Arctic will support greater abundances of high trophic levels. Anecdotally, I noticed that my site was disproportionately grazed by muskoxen and hares (more to the point – I had to repeatedly chase them off my site in order to conduct my work), and this area supported a much greater number and diversity of nesting birds compared to the surrounding desert conditions. However, while increased primary productivity and herbivore abundance may be a boon to high Arctic ecosystems that are traditionally low in both, the increased ponding of water within these thermokarst areas may lead to disadvantageous carbon cycling dynamics. Indeed, wet polygonal tundra releases carbon (through soil respiration, methanogenesis, etc) at an order of magnitude higher than dry polar desert (Abnizova *et al.* 2012). Thus it appears that ice wedge thermokarst is a double-edged sword: climate warming will lead to the shrinking of the polar desert, the gradual loss of one of Earth's most extreme biomes, and disadvantageous carbon dynamics. However, it facilitates the expansion of a novel and perhaps more biotically diverse wetland system.

Within chapter three a number of specific conclusions were reached. Subsidence altered surface hydrology such that plant growth is amplified, giving rise to wetland-like plant communities within a dry high Arctic environment. These communities were distinct in species composition, yet the species pool was not reduced, indicating that vegetation restructuring will be the primary effect of increasing temperatures. Through increased vegetation growth and activity the soil conditions have been greatly altered, depleting macronutrients while increasing stored organic matter content. As a consequence of these effects, a highly structure landscape has emerged from the relatively homogenous polar desert, and thermokarst will result in the increasing divergence of polygon top and trough microhabitats.

The results of chapter three led largely to the questions I addressed in chapter four – can thermokarst-stimulated vegetation growth stabilize the active layer from further thermal change? And importantly, what are the implications of this for estimates of northern permafrost thaw and biogeochemical cycles? My results from chapter three suggested that increased graminoid/sedge vegetation growth insulates the ground from further thermal change, likely through increased albedo (Blok *et al.* 2011) and retention of soil moisture (Pearson *et al.* 2013). Using my site data, I constructed a path analysis model of active layer depth based on this idea. Using relatively few explanatory variables, it was capable of explaining a very large proportion of active layer depth variance. The strength of the model resides in its intuitive causal pathways and the clear quantification of the vegetation stabilization mechanism – a mechanism that may prove key in the goal of developing dynamic models of permafrost thaw (Lawrence *et al*. 2008; Hollesen *et al*. 2011; Jafarov *et al*. 2012; Nyland *et al*. 2012).

Furthermore, the implication of chapter four's results can be seen in long-term observations, though this stabilization aspect is not widely publicized. Primarily, the findings of Jorgenson et al. (2006) show that during the most recent six decades of atmospheric warming, the landscape change that occurred was due primarily to the initiation of new thermokarst, rather than the expansion of old. During this timeframe, the older thermokarst showed only gradual change due to prior stabilization achieved through vegetation growth – a growth achieved within 20-30 years from first disturbance. Combined with predicted increases of graminoid/sedge cover (Elmendorf et al., 2012) I find that a re-examination of projected high Arctic permafrost thaw is warranted. The implications are significant – if vegetation provides such a strong stabilizing force, it may decrease depth of thaw and limit the release of high Arctic carbon stores. The sink/source dynamics of permafrost carbon are one of the major challenges facing science today given the radiative forcing of further carbon in the atmosphere. The conceptualization of the problem requires careful consideration and inclusion of all feedbacks, to which I hope chapter four contributes.

One of the significant indirect effects of climate change on the Arctic is the increasing accessibility of the area for industrial development, which I address in chapter five. My study area on the Fosheim Peninsula is located on one of the richest undeveloped coalmines in the world. True to point, the group planning to develop the region has marked a number of my field sites as drilling test sites for the near future. However, given that even naturally induced thermokarst instigated a number of ecosystem changes that were unknown (until my research as outlined in chapter three), how can we expect direct anthropogenic disturbance to affect the landscape? The best way to predict this is to examine the long-term repercussions at a site of historical anthropogenic disturbance, as I did in chapter five.

I found that in over 60 years since abandonment, the disturbed landscape from the tundra runway had not recovered to a state resembling the surrounding undisturbed terrain. Rather, I found that the old runway likely reflects a succession towards different wetland stable-state community, initiated by the disturbance. Similar to chapter three, I also found that the disturbance led to an increased patchiness and heterogeneity of the ecosystem, as the response of the landscape greatly depends on the type of microtopography affected. Ice wedges were the most sensitive to disturbance and, like chapter three, resulted in a novel species composition, decreased plot-level richness but large increases in cover. As explained in chapter four, this vegetation growth is likely what is responsible for stabilizing these disturbed ice wedges from further change, as shown through the drastically reduced seasonal fluctuation in soil temperatures. However, the polygon tops bear the hallmark of disturbance with greatly increased depths of thaw, despite having a remarkably resilient vegetation cover. My results show that if development is allowed to expand in the high Arctic, industry should avoid areas of sensitive ice-rich permafrost, as this is the most vulnerable terrain feature. If these areas do become affected, they should limit vegetation removal where possible and reseed disturbed areas with native species, as it is likely to have success in recolonization.

Taken together, my work has reexamined thermokarst processes in light of its effects on biodiversity and landscape structure to better understand how the high Arctic will respond to the increasing likelihood of wide-scale disturbance.

6.3 Future directions

We face a number of questions, concerns, and challenges about the fate of the Arctic environment in the near future. How will this area change as a result of the climate warming that has already occurred, and what will happen if the current projections of further temperature rise hold true? We can continue to chip away at these larger questions by expanding on the research of this thesis.

There are many serious spatial scale and heterogeneity implications from the research in chapter three. While the study was intensive and comprehensive, it is performed at one study site. There is much to benefit from a large dataset from a single site, but replication is important. While I have done as much as possible to select an area I believe to represent the broader region, it would be advisable to replicate this work at a number of other sites within the Canadian high Arctic Archipelago. International collaborations with high Arctic sites in Zachenberg, Greenland and Svalbard, Norway would allow us to test whether the generalization of increasing local heterogeneity holds true across the circumpolar region. It would be extraordinarily interesting to see if thermokarst also increases regional diversity – i.e. landscapes have differing responses to this perturbation. A diversity of terrain responses would make it even more difficult to create generalizable rules of Arctic warming response.

The next step for the mechanism of vegetation stabilization from chapter four is integration into a dynamic, forecasting permafrost model. Increasing the predictive power of permafrost models would allow us to generate more accurate sink/source carbon dynamics. There is very little we can do to mitigate the release of carbon stores in permafrost soils, but increasing our knowledge of its radiative forcing potential would help us generate more accurate global temperature predictions. Stabilization to disturbance would also help us predict widespread land-cover change, and create more refined predictions of albedo and surface hydrology changes.

It is a decent goal to quantify the effects of anthropogenic disturbance as I have done in chapter five, but it is a much greater achievement to fix them. If industry were to be expanded in the Canadian high Arctic (as it indeed appears to already have), it would be advisable to have a comprehensive landscape recovery toolkit of procedures and policies for minimizing our impact. Future work could involve small, replicated, controlled vegetation disturbance removals at high Arctic sites, and test a number of prescribed treatments. Some of this recovery work has been attempted piecemeal in more southerly sites (Chapin & Chapin, 1980; Forbes, 1993), but controlled and replicated experiments would allow us to develop the best response framework for mitigating Arctic landscape disturbance.

Given that ice wedges are ubiquitous across the continuous permafrost region and they occupy enormous ground volume across the arctic zones of North America, Europe, and Asia, we believe they will be a catalyst for widespread ecosystem change in light of warming Arctic.

The sheer scale of their potential effects should be enough to renew interest in a cryologic phenomenon that has languished on the backburner of research since the 1980’s.

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