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International Polar Year (IPY) Back To The Future (BTF): Changes In Arctic Ecosystem Structure Over Decadal Times Scales

Sandra Villarreal

University of Texas at El Paso, svillarreal3@miners.utep.edu

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INTERNATIONAL POLAR YEAR (IPY) BACK TO THE FUTURE (BTF):
CHANGES IN ARCTIC ECOSYSTEM STRUCTURE OVER DECADAL
TIMES SCALES

SANDRA VILLARREAL
Department of Biological Sciences

APPROVED:

Craig E. Tweedie, Ph.D., Chair

Thomas E. Gill, Ph.D.

Vanessa L. Lougheed, Ph.D.

Elizabeth Walsh, Ph.D.

Benjamin C. Flores, Ph.D.
Dean of the Graduate School

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INTERNATIONAL POLAR YEAR (IPY) BACK TO THE FUTURE (BTF):
CHANGES IN ARCTIC ECOSYSTEM STRUCTURE OVER DECADAL
TIMES SCALES

by

SANDRA VILLARREAL, B.Sc.

DISSERTATION

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Abstract

Arctic vegetation communities are responding to climate warming through shifts in species composition and diversity but most observations have been made over relatively short time frames, and/or in association with experimental manipulations. Because vegetation plays a key role in regulating ecosystem productivity, nutrient cycling, surface energy budgets, and trophic interactions in the Arctic, there is a need to better understand shifts in tundra vegetation communities over decadal time scales. Understanding these shifts and their impact on ecosystem structure and function in the Arctic has important implications for predicting the future state of both the Arctic and the Earth System. Long term monitoring, and/or rediscovering, rescuing, securing, and resampling historic research sites to ascertain past and future trajectories of decadal time scale change are among the few approaches for advancing knowledge of how Arctic terrestrial ecosystem properties and processes are likely to change decadal time scales.

The primary objective of this International Polar Year (IPY) dissertation project was to determine how key structural characteristics of high-latitude arctic terrestrial ecosystems have changed over the past three to five decades at three different historic research locations spanning the high and low Arctic. Historic sites were established by Dr Patrick J. Webber early in his career using the same methodology and include (1) the International Biological Program (IBP) research sites established in 1972 near Barrow, Alaska, (2) the Research on Arctic Tundra Environments (RATE) research sites established in 1975 near Atkasuk, Alaska, and (3) his dissertation research sites established in 1964 in North-Central Baffin Island, Nunavut, Canada. Historic IBP sites established in alpine tundra on Niwot Ridge, Colorado were also used in a synthesis that compared change across all locations and tundra vegetation types. All sites measured 1 m x 10 m and consisted of ten contiguous 1 m² plots that were resampled during summer field seasons when sites were snow free between 2008 and 2010. Percent cover for vascular, non-vascular, and lichen species were estimated at all three sites.

The following key questions were addressed by resampling these historic sites:

- I. *Is there evidence of vegetation community change?*
- II. *Which vegetation communities are changing most/least and is there evidence of a shift in the rate of change over time?*
- III. *Are changes in specific vegetation functional groups driving community change?*
- IV. *Are diversity, richness and individual species changing?*
- V. *Along which environmental gradients are changes occurring and what are the likely biophysical factors driving change?*
- VI. *Have patterns of primary succession following deglaciation changed over time at Baffin Island, Canada?*
- VII. *Do herbivores mask or facilitate decade time-scale vegetation community change at Barrow, Alaska?*
- VIII. *How have vegetation communities, species richness, evenness, and diversity changed across the tundra, and how does this change differ between long-term and short-term sampling intervals?*

Vegetation community change varied by location and vegetation community type, and within a particular site. At Baffin Island, Canada species richness did not change but diversity increased over a 45-year period. All vegetation communities shifted in a similar direction, and indicated landscape drying. Young successional sites show that changepoints for vegetation cover, species richness, and Shannon Index of diversity are earlier for 2009 sites less than 200 years of age, suggesting that rates of succession are accelerating. In Barrow, Alaska species richness and diversity increased over the 38 year sampling period, wet vegetation communities changed more than dry communities, and the response of vegetation to lemming population cycles were found to mask long-term changes in vegetation change. In Atqasuk, Alaska species richness and diversity did not change, but evenness increased significantly. Vegetation communities changed little over the 34-year sampling period, however, the change documented for many communities indicated a shift towards a wetter state. Vegetation community change was also found to be accelerating over the last decade for sites near Atqasuk, and that the rate of change in diversity is accelerating.

These findings demonstrate that the response of arctic vegetation communities to global change, which includes climate change, is spatiotemporally complex. Considering the importance of vegetation community assemblage and ecosystem structure to ecosystem function and the potential for arctic terrestrial ecosystem change to impact other components of the Arctic and Earth System, it is important to continue to monitor change in tundra landscapes over decadal time scales. The Back to the Future approach has demonstrated new capacities for achieving such knowledge and has the potential to be scaled across the Arctic and other disciplines to advance systems understanding and response to global change.

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Chapter 1: Introduction

1.1 Rationale for this Dissertation

There is growing evidence that anthropogenically induced climate warming, which is amplified in the Arctic (Serreze et al. 2011), is affecting arctic ecosystems (ACIA 2004, IPCC 2007). Shifts in hydrologic regimes (Hinzman et al. 2005), permafrost thaw (Romanovsky et al. 2012), disappearance of summertime sea ice (Maslanik et al. 2011, Tschudi et al. 2010), longer growing seasons (Zeng et al. 2011), and vegetation shifts (Elmendorf et al. 2012) are all examples of changes affecting tundra ecosystems. The terrestrial landscape of the Arctic is vulnerable to such changes since these ecosystems are strongly constrained by temperature (Billings & Mooney, 1968).

Recent studies suggest that there has been an increase in the photosynthetic capacity of tundra plants (i.e. “greening”, Epstein et al. 2012, Frost et al. 2013, Jia et al. 2009), especially in tundra landscapes where summer warming and extensive sea ice loss have also been more pronounced (Bhatt et al. 2010). Changes in tundra landscapes have significant implications for global processes since land-atmosphere interactions are significant in the Arctic due to a close coupling between the terrestrial and atmospheric systems (Myers-Smith et al. 2011, Pearson et al. 2013). If the substantial soil organic carbon pool in the Arctic were to be released to the atmosphere in the form of greenhouse gases, regional to global-scale warming could be enhanced by this positive feedback (Schaphoff et al. 2013, Schuur et al. 2013). Recent studies documenting vegetation community shifts in tundra landscapes suggest these changes are potentially lowering surface albedo causing increases in net radiation and atmospheric heating (Chapin et al. 2005, Pearson et al. 2013), which can increase rates of decomposition in permafrost soils and subsequently enhance carbon release to the atmosphere. In contrast, increased vegetation photosynthetic capacity also has the potential to reduce warming through enhanced carbon sequestration (i.e. increased primary production, McGuire et al. 2009). Thus, the Arctic contributes to global processes through land and atmospheric feedbacks and any changes within this biome have the potential to alter the Earth System.

Vegetation is one of the main structural components of tundra landscapes and detecting change in vegetation community assemblage has significant implications for understanding how ecosystem

function may be responding to arctic change. Different vegetation communities have different ecosystem functional properties (Lara 2012, Lin et al. 2012, Street et al. 2013), and there is strong evidence that shifts in the relative cover of individual species can dramatically alter ecosystem function (Heskel et al. 2013, Lara 2012). Shifts in species abundance and diversity in tundra vegetation communities not only have the potential to alter photosynthesis and respiration rates (Marushchak et al. 2013), but also nutrient cycling (Sundqvist et al. 2011), energy budget (Chapin et al. 2005), and trophic interactions (Tveraa et al. 2013). Thus, a change in the extent of different vegetation communities, and even the abundances of individual species, could alter regional to landscape fluxes of carbon and surface energy budgets (Marushchak et al. 2013, Sturtevant and Oechel 2013).

Arctic tundra has significant spatial variation in vegetation community composition, and landscape level vegetation community composition in different arctic regions can be broadly classified as wetland, desert, barren, and/or characterized by dominant functional groups such as bryophytes or graminoids (Walker et al. 2005). Topography often determines community composition by controlling environmental factors such as soil moisture, nutrient availability, wind speed, and snow cover (Webber 1971, 1978). Dry tundra is usually characterized by caespitose graminoids, shrubs, and lichens. Moist regimes are dominated by bryophytes and other graminoids where shrubs and forbs can be relatively common. Wet areas are usually characterized by homogeneous distributions of graminoids, mosses and some forbs (Walker et al. 2005). Shifts in vegetation species abundance are now well documented by a gamut of experimental warming and some observational studies (Callaghan et al. 2011a, Hudson and Henry 2010, Villarreal et al. 2012). Synthesis studies documenting changes in the abundance of functional types have also been produced (Elmendorf et al. 2012, Walker et al. 2006), and many of these studies have linked greening of the Arctic to shifts in species and functional groups, especially increases in shrub abundance (Myers-Smith et al. 2011, Epstein et al. 2013).

Most studies focused on documenting changes in arctic vegetation communities have centered on manipulative experiments such as the International Tundra Experiment (ITEX), however, their historical data does not usually span more than two decades. Recent studies have highlighted discrepancies between experimental and observational data (Morin et al. 2010, Wolkovich et al. 2012), and without

long-term (decadal time scale) observational studies, we lack the capacity to detect change in ecosystems and validate results from manipulative experiments. This is especially the case in the Arctic, which is forecast to undergo rapid climate change over the next century (IPCC 2007). Rediscovering, revisiting, and resampling old research sites provides a window back in time that allows for the long-term assessment of vegetation change, and enables the potential to model and predict future change trajectories. Thus, this project bridges a fundamental gap in our knowledge of how arctic vegetation communities have changed over decadal time scales.

1.1.1 Arctic Tundra Ecosystems

The Arctic includes a mostly ice-covered ocean and terrestrial landmasses that include parts of North America, Europe, and Asia. Historically, the Arctic has been defined in many ways, but the most common definition used in literature defines it as the region above the Arctic Circle (66° 32' N). A mean daily summer temperature that does not exceed 10°C and the northern tree line are also commonly used descriptors for the Arctic. Arctic climate is characterized by long snow-covered winters and short snow-free summers, with the shoulder seasons between winter and summer commonly being referred to as the “fall freeze-up” and “warm-up” seasons (Pielou, 1994). Arctic weather and climate have considerable regional and temporal variability (Elmendorf et al. 2011, Epstein et al. 2004). Mean annual precipitation can be as low as 10 cm, which is comparable to arid biomes (ACIA 2005). The North Atlantic Oscillation (Hurrell, 1995) plays a crucial role in controlling winter climate in Greenland and Central Asia, and the Pacific Decadal Oscillation plays a similar role in the North Pacific and Beringia region. Various types of terrain are found in the Arctic, ranging from flat plains and rolling hills, to vast mountain complexes that include thousands of glaciers among the largest non-Antarctic ice caps on Earth. The surface hydrology of the Arctic is complex and shows key linkages between the terrestrial, cryospheric, oceanic, and atmospheric components of the Arctic System (Vörösmarty et al. 2002). A key component of Arctic terrestrial ecosystems is permafrost. Importantly, it is estimated that the Arctic and its permafrost soils comprise approximately 16% of the global land area, and contain almost one half of the global soil organic carbon pool (Tarnocai et al. 2009). The prevalence of freezing and thawing cycles, the type of permafrost (continuous or discontinuous), and allogenic processes are among the

primary factors determining the structure and function of tundra vegetation through their influence on microtopography and soil moisture (Peterson and Billings 1980, Pielou 1994, Webber et al. 1980). In many low-land tundra landscapes, polygonized tundra can be prevalent. Tundra polygons are features formed by ice wedges created by open cracks in the landscape in which water enters and expands during freezing events (Pielou 1994). These polygons generate microtopographic features and fine scale heterogeneity in surface microclimates and habitat that varies on the scale from centimeters to several meters. As a result, very distinct vegetation communities can arise to result in landscapes with spatially heterogeneous land cover (Figure 1).

Arctic tundra has been classified into many vegetation types (Figure 4, Walker et al. 2005). Oosting (1953) described the tundra as being composed of 0% trees, 61% graminoids, 23% shrubs, 15% cryptophytes, and < 1% annuals. Arctic flora is diverse with approximately 1500 extant species (Murray 1995). Although much of the evolutionary history of arctic flora has yet to be described (Abbott and Brochmann 2003), the flora probably originated in the Miocene and Pliocene from earlier alpine, marsh, and bog floras (Matthews and Ovenden 1990). Deglaciation has played a key role in the development and radiation of arctic flora, and extant species are likely descendants of species that survived in arctic *refugia* (Pielou 1994).

Tundra plants have developed an array of adaptations to survive in cold climates. For the most part, tundra plants are slow-growing, long-lived perennials or semi-evergreens/evergreens that allocate relatively little resources to sexual reproduction (Molau 1993) and in many cases reproduce asexually (Billings 1974). Flower buds are produced up to several years before bloom (Sørensen 1941) and plants rely on carbon and nutrient stores from the previous year to be productive at the beginning of the snow-free season (Berendse and Jonasson 1992). The greatest limiting factor to tundra vegetation productivity is the length of growing season, since some tundra plants are as productive during snow-free periods as vegetation from temperate regions (Hollister 2003, Webber 1978). Individuals have short statures in order to maximize tissue temperatures by reducing exposure to wind and cold weather, and some retain dead leaves which insulate and protect plants against harsh conditions (Billings 1974, Pielou 1994).

These adaptations are, however, difficult to isolate to single adaptive mechanisms since many have multiple functions (Hollister 2003).

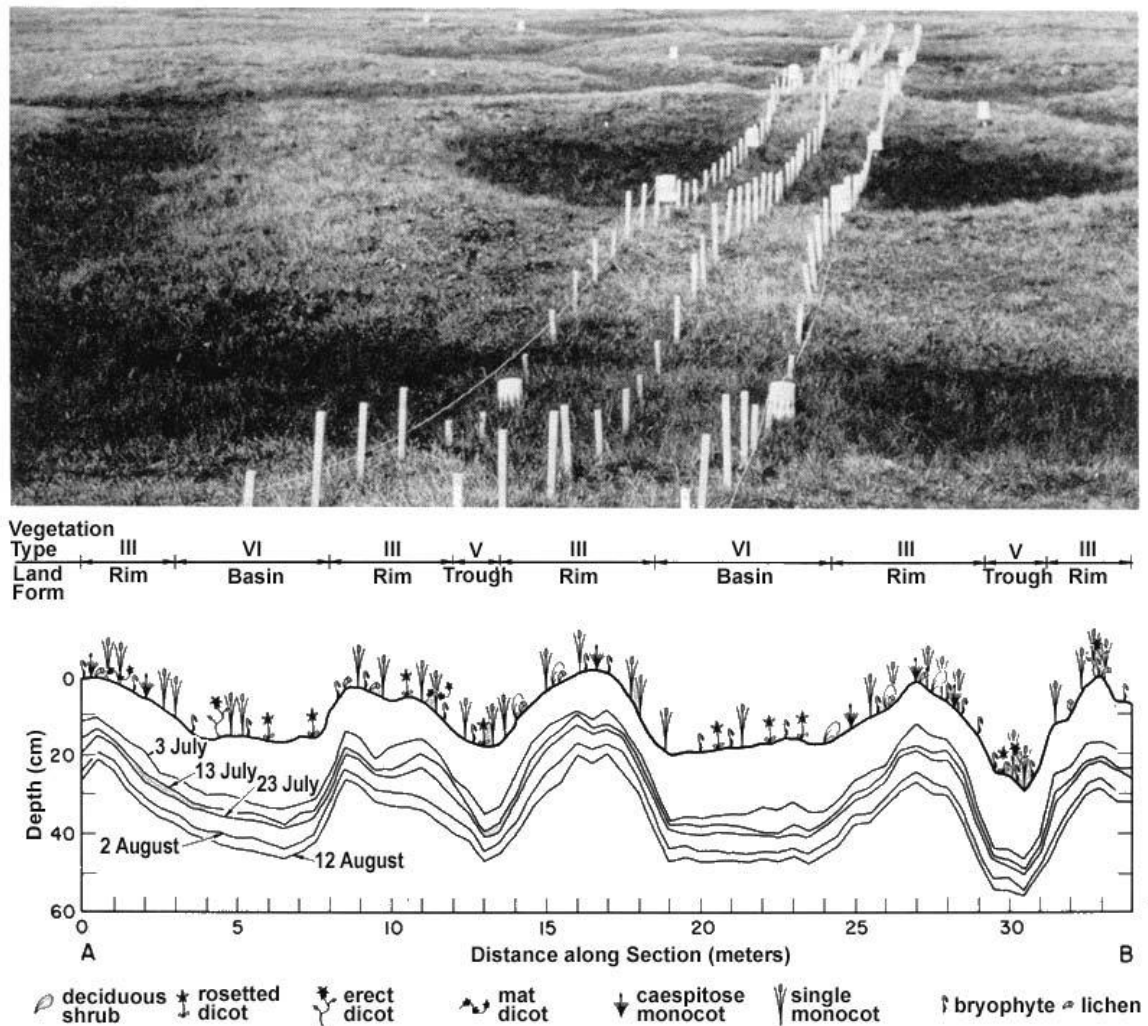


Figure 1. Photograph of the International Biological Program (IBP) microtopography grid situated in polygonized tundra near Barrow, Alaska (top) 1971. A profile drawing of a section of the IPB microtopographic grid showing land form classifications, depth of thaw, and three vegetation types (bottom). The vegetation types are III – *Carex-Poa* meadow, V – *Dupontia* meadow, and VI – *Carex-Eriophorum* meadow (from Webber et al. 1980).

1.1.2 Recent Changes in Tundra Ecosystem Structure

The Arctic is dynamic with rapid shifts in vegetation that have been demonstrated repeatedly in the paleoclimate record (Overpeck et al. 1997). Mounting evidence suggests that although there is in some cases substantial spatial variability, drastic changes are occurring in high latitudes in response to

recent changes in climate. This includes sea ice retreat and thinning (Maslanik et al. 2007), permafrost warming and thaw (Romanovsky et al. 2012), glacial retreat (Sharp et al. 2012), and decreased snow cover (Derksen and Brown 2012), and these changes have been linked to recent increases in temperature (ACIA 2005, IPCC 2007, Kaufman et al. 2009). In the most recent Intergovernmental Panel on Climate Change assessment (IPCC 2007), models indicate that the Arctic was warming 1.9 times faster than the global average, which has given rise to the concept of arctic amplification – the concept that trends in surface air temperature tend to be greater in the Arctic than any other region in the Northern Hemisphere or globe as a whole (Serreze et al. 2011). Warming is undoubtedly anthropogenically driven and related to the doubling of the carbon dioxide concentration in the atmosphere since the onset of the industrial revolution (Winton 2006, IPCC 2007). The potential for carbon dioxide concentrations in the atmosphere to alter global temperatures, especially in Polar Regions, was first described in the late 1800's (Arrhenius, 1896). This hypothesis has held true and warming in the Arctic has been recorded at a rate of $1.36^{\circ}\text{C century}^{-1}$, with an accelerated rate occurring in the last decade (Bekryaev et al. 2010).

The important role climate plays in controlling ecosystem structure and function has been recognized for a long period of time. Whittaker (1975), for example classified biomes of the world in a chart based on temperature and precipitation gradients (see Figure 3). However, recent changes in temperature have caused terrestrial systems in northern latitudes to undergo dramatic changes. Vegetation can respond in numerous ways to changes in climate. Individual species respond to alterations in their environment by adapting, shifting in distribution, or becoming extinct (Holt 1990). Additionally, the mechanisms by which species respond to climate change can vary in time. Immediate responses trigger changes in physiology, short-term responses alter reproduction rates (Bellard et al. 2012), mid-term responses impact growth, and in the long-term, shifts in vegetation community composition are likely, as better adapted species outcompete other less adept species to changing conditions. Extinction could result for species that cannot acclimate (short term) or adapt (longer term) to the rate of change. A recent survey of European alpine flora found a link between increased temperatures and a decrease in the prevalence of cold-adapted species as a result of increases in warm-adapted species in just five years (Gottfried et al. 2012).

However, these shifts are difficult to predict (Doak et al. 2008) and a large effort in the global change sciences has focused on improving capacities to model future system by parameterizing models with species responses (e.g. phenology, range, physiology) at community, ecosystem, and global scales (Bellard et al. 2012, Harley 2011). A large-scale experimental warming study (Walker et al. 2006) documented decreases in diversity with short-term warming (seven years), but this may not accurately assess long-term change since a similar study found differences between short-term and long-term vegetation change to experimental warming (Hollister et al. 2005b).

In the Arctic, plot-scale observational and experimental studies have shown that tundra systems have been responding to warming at different rates and some locations show little or no change at all (Daniëls et al. 2010, Elmendorf et al. 2011, Hudson and Henry 2010). Experimental (Walker et al. 2006) and observed (Elmendorf et al. 2012b, Myers-Smith et al. 2011, Sturm et al. 2001) biome-wide studies have shown both increases in the numbers and densities of shrubs throughout the arctic over the past decades. Graminoids have also been documented to increase in abundance with experimental warming in large-scale studies, and Klady et al. (2011) attributed these trends to stimulation of reproductive effort and success.

Landscape to regional satellite remote sensing studies are also detecting vegetation shifts and report widespread greening since 1981 (Bhatt et al. 2010, Fraser et al. 2012, Jia et al. 2003, Olthof et al. 2008, Pouliot 2009). These greening trends derived from remote sensing are thought to indicate a myriad of ecosystem responses including increased biomass, proliferation of shrubs at some locations, and increased productivity (Forbes et al. 2010, Jia et al. 2003, Myers-Smith et al. 2011). This trend has a considerable range of impacts on tundra ecosystem structure and function (Figure 2), including altered surface energy and carbon balance and patterns of nutrient cycling, changes in species diversity, and changes in snow cover and surface hydrology.

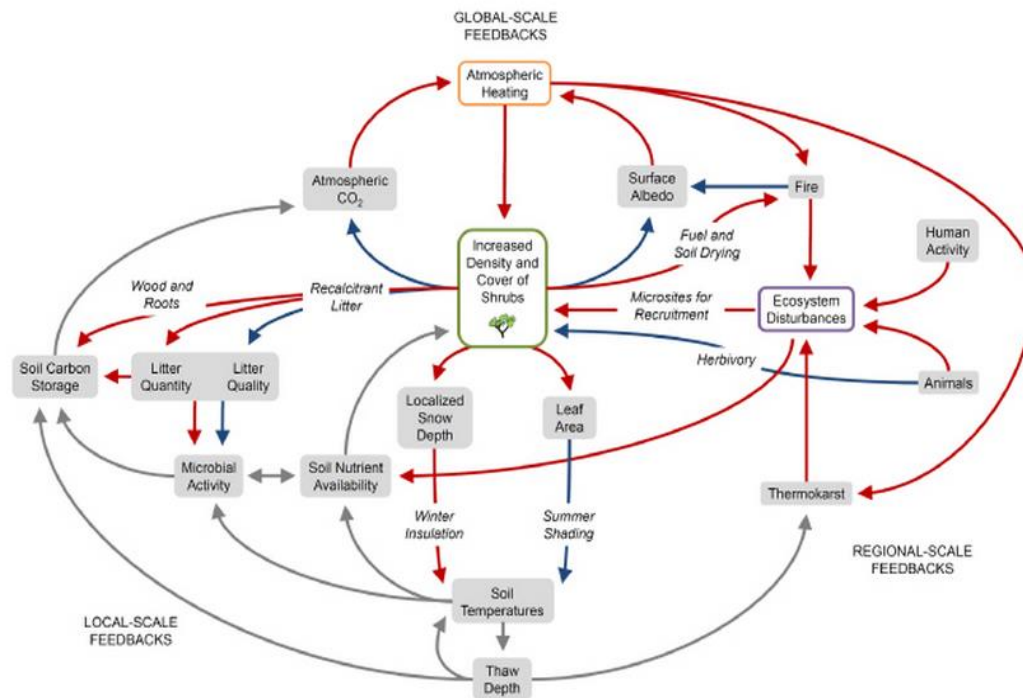


Figure 2. Potential feedbacks from increased shrub abundance to ecosystems structure and function. Red arrows indicate positive relationships, and blue arrows indicate negative feedbacks. Gray arrows indicate undetermined relationships (from Myers-Smith et al. 2011).

These responses to change are just beginning to be understood in a manner that is suitable for parameterizing complex models (McGuire et al. 2009). Consequently, many of the processes and consequences associated with environmental change in the Arctic remain under investigation. One such challenge is to understand how warming affects ecological succession. Additionally, it is poorly understood how the relationship between tundra vegetation and herbivores may be altered in future arctic ecosystem states (Ims et al. 2011). These two topics are discussed in the following sections of text.

1.1.3 Patterns of Succession

A fundamental knowledge of the complex and interacting ecological processes that control vegetation community composition is crucial in order to comprehend how species assemblages are distributed through space and time and control ecosystem structure (Shipley 2010). There are numerous theories, analyses, and models that focus on vegetation succession, which is an ecological concept with a complicated and extensive history (Johnson 1979, McCook 1994). Some of the earliest theories of succession described succession as a linear process with an ultimate climax state (Clements, 1928,

McCook et al. 1994). Such theories were derived by suggesting that as species become more dominant, they make their environment less favorable for themselves and more favorable to new species, thereby allowing invading species to dominate. As fewer species invade, the closer the community gets to a climax stage. However, later reviews generally found consensus in that vegetation succession overarchingly presents “a bewildering variety of patterns” (Horn, 1976) that clearly differs among ecosystems and in response to different successional scenarios, such as those following fire, colonization of invasive species, or deglaciation. To effectively understand patterns of vegetation succession in a given ecosystem, marked plots should be established as close as possible to the time at which the surface is suitable for colonization but before colonization initiates. Repeat sampling of plots should occur at regular and appropriate time intervals following establishment to sample critical data on changes in vegetation cover and diversity. In most instances in the Arctic, this approach is extremely difficult to execute and most researchers utilize a space for time substitution and describe successional trends by comparing land surfaces of different ages and stages of vegetation colonization and succession (Cutler 2010, Johnson and Miyanishi 2008, Walker et al. 2010).

Northern landscapes are generally regarded as relatively young surfaces and many offer a relatively unique opportunity examine successional dynamics, especially primary succession following deglaciation. Northern land masses retain remnants of the last Ice Age, and it is estimated that approximately 400,000 km² of the Arctic currently consists of terrestrial ice (i.e. glaciers, and ice caps, Sharp et al. 2012). Vegetation studies that initially focused on deglaciated surfaces at Glacier Bay, Alaska suggested that primary succession was facilitated by nitrogen-fixing early colonizing species (Bormann and Sidle, 1990), a mechanism generally believed to drive primary succession in extreme environments (Connell and Slatyer 1977) such as desert soils and Antarctic terrestrial landscapes (Garcia-Pichel and Belnap 2008, Wynn-Williams 1994). However, Chapin et al. (1994), using multiple sites at different stages of succession at Glacier Bay, Alaska later documented that no single factor controls primary succession, and that initial site conditions, facilitation, and/or competition all influence patterns of succession. Other biological drivers, such as competition, the prevalence of mycorrhizae, seed rain (Jones and Henry 2003), and a range of abiotic drivers (e.g. environment, and initial site

conditions, Chapin et al. 1994), play key roles in determining successional pathways in deglaciated environments. Studies in similar tundra landscapes have determined that micro-scale substrate topography is also an important determinant of vegetation (Cutler et al. 2008, Garibotti et al. 2011), highlighting the importance of cryo-geomorphic processes in these environments.

Due to warming, arctic glaciers are melting rapidly (Gardner et al. 2011). Studies reporting on the sustained monitoring of arctic glaciers have documented extremely high rates of loss in glacial ice mass in Alaska, Arctic Canada, Iceland, Svalbard, Norway and Sweden, with some glaciers losing as much as 3800 km² per year (World Glacier Monitoring Service, 2012). In many cases, deglaciation exposes bare surfaces suitable for primary colonization. Understanding how patterns of succession in these deglaciated environments will be affected by climate change remains a topic of investigation, although one study documented that community succession is less predictable with climate disturbances in coastal dunes (Miller et al. 2010). In recently vegetated lava flows in Iceland, Cutler (2011) found that vegetation succession had a positive relationship with soil temperature. Patterns of succession provide a useful means of determining the future state of ecosystems, provided long-term data are considered (Johnson and Miyanishi 2008).

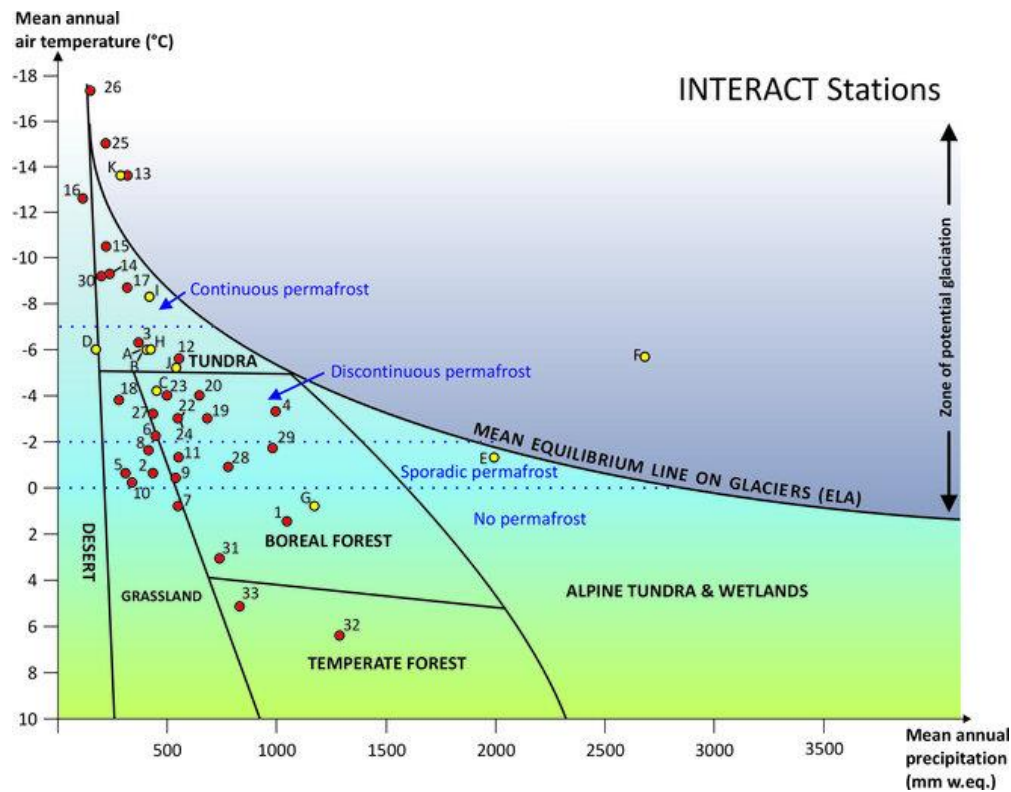


Figure 3. Location of various arctic research stations in environmental space defined along gradients for mean annual temperature and mean annual precipitation (from Elger et al. 2012).

1.1.4 Tundra Vegetation and Herbivores

Herbivores are important in tundra ecosystems for their role in trophic structures and may either directly (e.g. selective grazing, harvesting of nest structures, or trampling) or indirectly (e.g. soil disturbance or nutrient cycling) affect vegetation composition (van der Waal et al. 2011). In ecological studies, the relationship between herbivores and plants is usually considered to be either top-down (herbivores controlling vegetation) and/or bottom-up (vegetation controlling herbivores). Traditionally, the main drivers of vegetation composition and abundance in arctic tundra have been considered to be physical and thus herbivores have rarely been acknowledged as an important component of vegetation studies (Archer and Tieszen 1980). With herbivore dynamics being highly spatiotemporally variable in most tundra ecosystems (Batzli 1980), it has also been difficult to study. However, recent effects of climate change on vegetation structure (see section 1.1.2) and animal populations (Ims et al. 2011, Vors and Boyce 2009) have highlighted the need to further understand vegetation-herbivore interactions. A common methodology is the use of exclosures to separate the effects of herbivores from other

biophysical processes in tundra environments. Tundra herbivores exert varied grazing pressures, and the composition of herbivore diet can largely depend on the composition of the vegetation community within their home range (Soininen et al. 2013). In tundra ecosystems, where lemmings are prevalent, resampling of herbivore exclosure plots and inter-comparisons with control plots found that lemming exclusion reduced overall vegetation biomass and increased lichens and bryophytes while decreasing graminoids, and the absence of lemmings in these plots also affected wet graminoid tundra more so than moist or dry tundra vegetation (Johnson et al. 2012; Lara 2012). Functionally, exclosure plots had lower albedo, and reduced depth of thaw, NDVI, methane flux, and increased loss of carbon dioxide into the atmosphere (Lara 2012). In Norway, exclusion of rodents and caribou caused significant shifts in species composition after only one growing season (Ravolainen et al. 2011), but a minimum of ten years was needed for caribou exclusions to alter vegetation near the Brooks Range, Alaska (Gough et al. 2008).

Nearly all of these studies emphasize the substantial variation in herbivore-vegetation interactions in tundra ecosystems. Furthermore, studies have highlighted that herbivory can directly alter climate-driven vegetation shifts. Zamin and Grogan (2013) found that after five years of reindeer exclusion shrubs and nitrogen pools increased significantly in the Canadian low Arctic, and Olofsson et al. (2009) found that shrub abundance was controlled by an interaction between herbivores and climate and that caribou presence inhibits shrub growth in northern Fennoscandia. A bottom-up approach determined that increased vegetation density (greening) and early an advanced phenology had positive effects on caribou calf body masses (Tveraa et al. 2013). Although our understanding of tundra vegetation-herbivore interactions has improved, recent evidence suggests an urgent need to not only understand the relative importance of biophysical processes controlling the abundance of herbivores and plants, but to incorporate these in models to explore how these interactions and feedbacks with other components of the Arctic may change in the future.

1.2 Current Research Challenges

Addressing the consequences of increased temperatures in the Arctic is of high importance because this region is warming faster than any other on Earth, and thus it will be the first to respond and

offer insight into future ecosystem states elsewhere on the planet (Luo et al. 2011). Currently, assessing change in many arctic ecosystems is limited by the paucity of decadal-time scale monitoring. Several recent studies have highlighted the urgency to establish such efforts (Callaghan et al. 2011b, Luo et al. 2011), and in doing so, an improved capacity to understand ecosystem variability, to ground-truth satellite-based observations, to integrate ground and remotely sensed observations, and to predict future change will be gained.

Since responses to global change can be slow and are generally governed by processes that are long-term relative to human generation times and funding cycles for research (Rastetter, 1996) and have a great deal of inter-annual variability, the value of historic datasets cannot be overstated (Callaghan et al. 2011b). Additionally, it is well-documented that arctic tundra is spatiotemporally heterogeneous and dynamic (Elmendorf et al. 2011, Epstein et al. 2004, Helbig et al. 2013, Villarreal et al. 2012), and adequately accounting for this variability has been an enduring challenge (Elmendorf et al. 2011, Stoy et al. 2009), especially with ongoing impacts of warming. Microtopographic features are a major factor in tundra heterogeneity and on the structure of vegetation (see section 1.1.1), and recent evidence also suggests that these features may favor proliferation of shrubs (Frost et al. 2013). These features are further complicated by the fact that vegetation responses are also dependent on the dispersal potential of certain species (Lenoir et al. 2011) and thus predicting shifts in species is akin to “chasing a moving target” (Garcia-Valdés et al. 2013). Documenting temporal heterogeneity involves many factors. Community succession (Johnson and Miyanishi 2008) and species nutrient cycling and turnover (Chapin and Shaver 1996) are generally considered long-term processes that may be facilitated by warming (Bellard et al. 2012), however, evidence in the Arctic suggests that communities can also respond to experimental warming after just a few growing seasons (Walker et al. 2006). The role of temporal climate variability is complex, but has direct impacts on vegetation and can be aggravated by climate change, which makes these studies extremely important with the effects of anthropogenically driven global change (Hinzman et al. 2005, Xu et al. 2013).

Satellite-remote sensing has proven to be useful in capturing long-term changes in high-latitude ecosystems (see section 1.1.2). However, several limitations involving these non-*in situ* studies have

recently come to light. First, these studies may incorporate various ecosystem processes, which are difficult to isolate, into a single index (Goswami et al. 2011, Stow et al. 2004). Remote sensing observations that have adequately captured tundra greening, however, may not potentially capture changes in species composition and other factors that otherwise explain how the greening occurred (Bhatt et al. 2010, Callaghan et al. 2011b). There is also evidence that Normalized Difference Vegetation Index (NDVI), which has wide-spread use in ecological studies, can reach a point of “saturation”, and be affected by atmospheric noise and soil properties (Liu et al. 2012). Thus, our understanding of change in arctic systems is currently hindered by a lack of ground-based studies that complement the duration and spatial coverage of satellite-derived measures (Callaghan et al. 2005, Lin et al. 2012).

Predicting the future state of any ecosystem is difficult without long-term data, which are useful for parameterizing, verifying, and validating models. Recently, some models have proven to output poor predictions (Kapfer et al. 2012), and sometimes fail to incorporate important factors, such as vegetation feedbacks (Schapoff et al. 2013). Thus, there is a pressing need to improve models with not just short-term experiments, but also historical data and paleo-ecological research. Limitations considered, modeling remains an important research tool that tests and advances our understanding of ecosystem function and change, establishes hypotheses of future change scenarios, and connects monitoring and research with both management, policy, and other disciplinary activities (IPCC 2007, McGuire et al. 2012). Integrating models with long-term data could provide the most effective approach to study the future of ecosystems.

1.3.1 Goals and objectives

This study is part of the Back to the Future (BTF) project, an endorsed International Polar Year (IPY #512) project that rescues and resamples historic research sites to assess how arctic ecosystem structure and function has changed over decadal time scales. The project addresses the following overarching question:

How has arctic ecosystem structure changed over the last few decades?

This study explicitly resampled historic sites at three locations near Barrow, Alaska, Atkasuk, Alaska, and North-central Baffin Island, Canada (Section 1.3). Dr. Patrick Webber established comparable sites at each research location during the early 1960's and 1970's, and sites were resampled at least once. In all cases, the historic research sites were initiated to study the assemblages and spatial patterns of tundra vegetation communities. Thus, all sites were originally selected to best represent the local vegetation communities in a general location. Except for sites on Baffin Island, where detailed site maps and/or historic photographs were taken, sites were marked using wooden stakes. All sites measured 1m x 10m with the exception of 10 sites at Barrow, which were aligned to allow for integration with other studies being conducted in the area. Sites were relocated using a range of approaches (e.g. coordinates, photographs, historic site maps, historic field notes). For each of the study locations, the following five questions were addressed:

- I. Is there evidence of vegetation community change?*
- II. Which vegetation communities are changing most/least and is there evidence of a shift in the rate of change over time?*
- III. Are changes in specific vegetation functional groups driving community change?*
- IV. Are diversity, richness and individual species changing?*
- V. Along which environmental gradients are changes occurring and what are the likely biophysical factors driving change?*

An additional key question was addressed at two of the research locations (Baffin Island, Canada and Barrow, Alaska, Chapters 2 and 3) and one questions was addressed (as detailed in Chapter 5) at an alpine tundra location (Niwt Ridge, Colorado), which was added in order to derive a tundra biome-wide analysis:

- VI. Have patterns of primary succession following deglaciation changed over time at Baffin Island, Canada?*
- VII. Do herbivores mask or facilitate decade time-scale vegetation community change at Barrow, Alaska?*

VIII. How have vegetation communities, species richness, evenness, and diversity changed across the tundra, and how does this change differ between long-term and short-term sampling intervals?

1.3 Study Areas

A map showing the three primary study site locations and their respective Circumarctic Vegetation Map (CAVM) vegetation units is shown in Figure 4. A summary of all of the study locations is presented in Table 1.

Table 1. Description of physical parameters, vegetation map classification, and BTF summary of the four study locations.

Physical Parameters	Location			
	Baffin Island, CAN	Barrow, AK	Atqasuk, AK	Niwot, CO
Location	70°25'N, 74°40'W	71°18'N 156°40'W	70°29' N, -157°27' W	40°3'N 105°36'W
Elevation (m ASL)	600	3	30	3000
Mean Annual Temperature °C	-12.8	-12.6	-11.9	-3.7
Mean July Temperature °C	2.9	3	7.2	8.2
Mean Annual Precipitation (cm)	23	124		93
Average maximum Thaw Depth (cm)	n/a	35-39	36-71	n/a
Soil pH	Circumneutral/Acidic	Acidic	Acidic	Acidic
Substrate	Sand, gravel, silt	Sand, gravel, silt	Aeolian sand and Sand, silt	Sand, silt
Succession Pattern	Deglaciation	Thaw-Lake Cycle	Thaw-Lake Cycle	Alpine/Treeline
Circumarctic Vegetation Map Classification				
Bioclimate Subzone	C	C	D	n/a
Community	B2: Cryptogam barren complex	W1: Sedge/grass, moss wetland	W2: Sedge, moss, dwarf-shrub wetland	n/a
Back to the Future Summary				
Historic study	Webber Dissertation	IBP	RATE	IBP
Historic publication	Webber, 1971	Webber, 1980	Komárková and Webber 1980	Ebert-May 1973
Year of Site Establishment	1964	1972	1975	1971
Resampling Dates	2009	1999, 2008, 2010	2000, 2009	1991, 2001, 2011
Number of Original Sites	82	43	60	30
Number of Resampled Sites	79	33	31	30
Number of Species	117	81	213	128
Type sampled	Vascular and non-vascular	Vascular and lichens only	Vascular and non-vascular	Vascular only

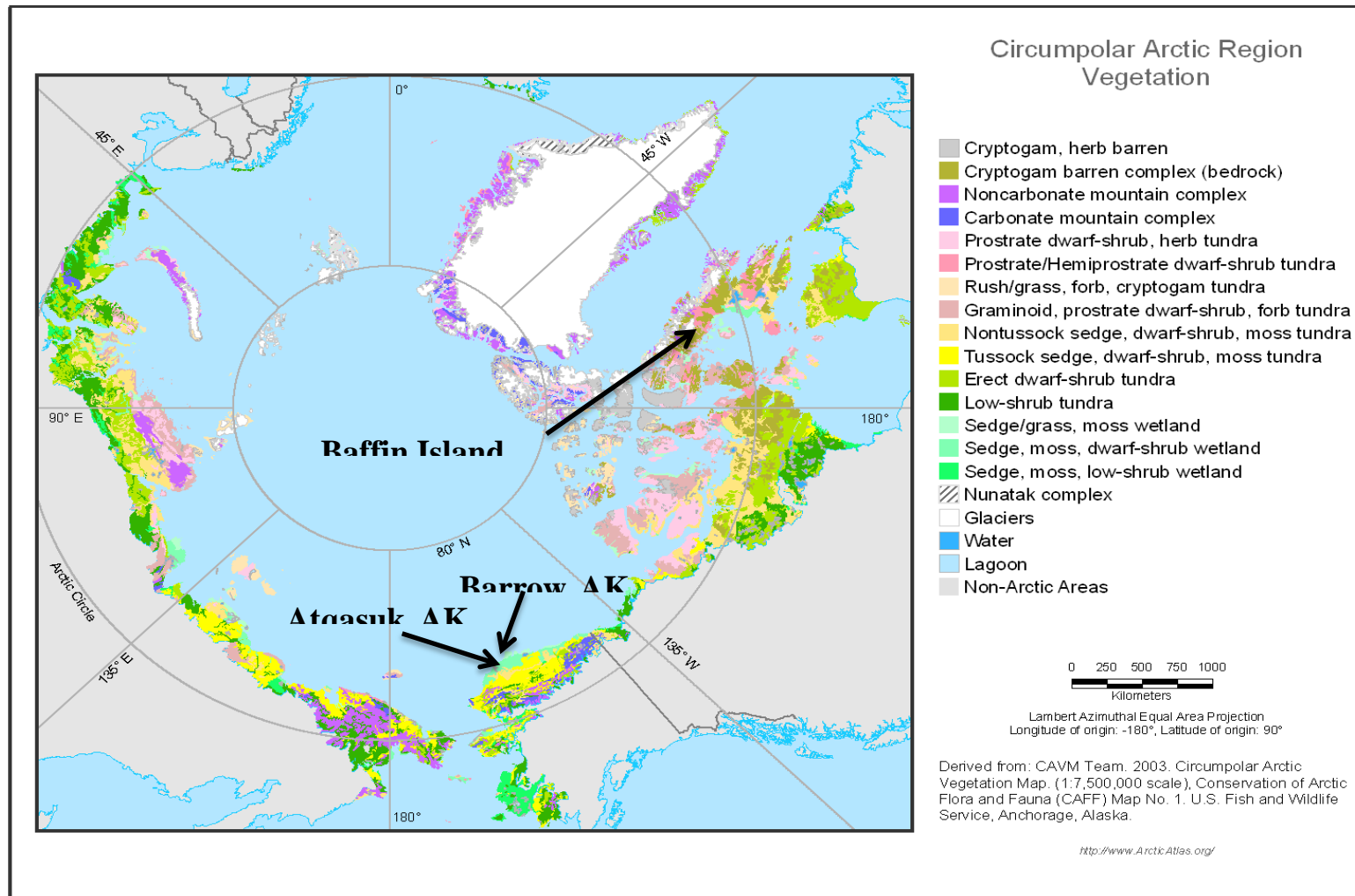


Figure 4. The Circumpolar Arctic Vegetation Map (CAVM) displaying major arctic tundra vegetation units and the three main research locations where historic sites were resampled for this dissertation. The vegetation types for each location are: Barrow, Alaska - Sedge/grass moss wetland, Atqasuk, Alaska – sedge, moss, dwarf-shrub wetland, Baffin Island, Canada – Cryptogam barren complex (modified from CAVM 2003).

1.4 Structure of this Dissertation

This dissertation is composed of six chapters, four of which are data chapters prepared for submission to peer-review journals (chapters 2-5). A brief description and current publication status of each dissertation chapter is given in Table 2. A brief introduction to the Arctic and the research challenges addressed by this dissertation is offered in Chapter 1, and a more site-specific review of literature is included in each data chapter. The author of this dissertation has also contributed to the following publications, which have drawn data and other information from dissertation-related activities:

1. A recent Nature Climate Change article that synthesized results from the International Tundra Experiment (ITEX) (Elmendorf et al. 2012);
2. A synthesis for the Back to the Future (BTF) project published in AMBIO (Callaghan et al. 2011b);
3. A companion paper to Chapter 3 by Lara (2012) published in Environmental Research Letters

Table 2: Publication status of chapters presented in this dissertation

Chapter	
1	Introduction S. Villarreal No submission intended
2	Vegetation change in a deglaciaded high-arctic landscape between 1964 and 2009 Authorship: S. Villarreal, P.J. Webber , D.R. Johnson, M.J. Lara, J.D. Jacobs, D. Witt, and C.E. Tweedie Target journal: Global Change Biology Estimated date of submission: : Fall 2013
3	Tundra vegetation change near Barrow, Alaska (1972-2010) S. Villarreal, R.D. Hollister, D.R. Johnson, M.J. Lara, P.J. Webber, and C.E. Tweedie Published in 2012: <i>Environmental Research Letters</i> , 7(1), 015508. doi:10.1088/1748-9326/7/1/015508
4	Little evidence of decade time-scale change in vegetation communities at a low-arctic site near Atkasuk, Alaska S. Villarreal, M.J. Lara, D.R. Johnson, P.J. Webber, and C.E. Tweedie <i>Arctic, Antarctic and Alpine Research</i> Approximate submission date: Fall 2013

- 5 **Decadal changes in North American tundra vegetation communities**
S. Villarreal, D.R. Johnson, R.D. Hollister, D. Ebert-May, P.J. Webber, C.E. Tweedie
Ecology Letters
Approximate submission date: Fall 2013
- 6 General Discussion
S. Villarreal
No submission intended

Chapter 2: Vegetation Change in a Deglaciaded High-Arctic Landscape between 1964 and 2009

2.1 Abstract

The high Arctic is expected to undergo rapid terrestrial deglaciation in the coming decades. Since a considerable land area of the Arctic is composed of terrestrial ice, studying ecosystem structure in regions undergoing recent deglaciation is of high importance since these changing landscapes present new sites for vegetation colonization. Additionally, although tundra vegetation is known to respond rapidly to experimental warming, long-term observations of vegetation change in the high Arctic are relatively scant. During the summer of 2009, 79 of 82 sites established in 1964 for vegetation community ecology studies near the margin of the Barnes Ice Cap, North-Central Baffin Island, Nunavut, Canada were revisited and resampled. Here we assess i.) how vegetation communities have changed in the study area and what biophysical factors appeared to be most strongly associated with vegetation community change, ii.) how the relative cover of vegetation functional types, and species richness, evenness, and diversity have changed, and iii.) how the dynamics of primary succession have changed. The study area has experienced sustained increased July temperatures and summer warming index (SWI) since the mid-1970s. We found evidence of warming in various analyses. Repeat photography showed a reduction in snowbanks and the height and extent of the Barnes Ice Cap, and overall landscape greening. Within ordination space, trajectories of change for all nine vegetation communities identified from 1964 vegetation community data were similar, with the exception of *Cassiope* snowbeds, cryptogamic crusts, and successional meadows, which had the greatest magnitude of change. We report increases in shrubs, graminoids, forbs, lichens, and species diversity across all sites. Early successional change points for vegetation cover, species richness, and Shannon Index of diversity were 40-60 years sooner in 2009 than in 1964, suggesting that warming may be accelerating successional trajectories. Thus, vegetation change in this high-arctic landscape not only demonstrates a capacity for relatively dramatic decadal time-scale change in vegetation communities, but also a capacity to be even more dynamic given the documented acceleration of vegetation succession on newly exposed surfaces.

2.2 Introduction

Northern high latitudes are warming faster than most other regions on earth (ACIA 2005, Serreze 2010). Within the Arctic, warming has been linked to shifts in hydrological regimes, permafrost thaw, longer snow-free periods, (Callaghan et al. 2011b, Epstein et al. 2013, Post et al. 2009, Romanovsky et al. 2012), shifts in vegetation functional groups, and an increase in the density of vegetation or “greening” of the Arctic (Bhatt et al. 2010, Elmendorf et al. 2012 Myers-Smith et al. 2011, Walker et al. 2006). Additionally, much of the Arctic is forecast to continue undergo rapid deglaciation over the next few decades (Radić and Hock 2011). With approximately 400,000 km² of the Arctic currently consisting of terrestrial ice in the form of glaciers and ice caps (Sharp et al. 2012), there is a large potential for vegetation to colonize and for vegetation to expand as new surfaces are exposed. Relative to other regions of the Arctic, studies examining the response of vegetation communities to decade time scale environmental change have been scant. Nonetheless, they are crucial for advancing our knowledge of not only the response of vegetation diversity to environmental change, but also how tundra ecosystems function and interact with regional to global energy balance and biogeochemical cycles.

Understanding vegetation community change in the Canadian high Arctic is especially important because many locations within this region have undergone warming and recent and rapid deglaciation (Gardner et al. 2011). As such, and documenting changes in vegetation structure in this region has the capacity to offer unique insight into how patterns of vegetation primary succession are influenced by warming. Additionally, landscape greening is well documented for this region (Frasier et al. 2011, Jia et al. 2009, Pouliot et al. 2009), with the highest magnitude of greening across the Arctic occurring in the Canadian high Arctic (Bhatt et al. 2011). For the assessment of decade time scale change in Canadian high arctic ecosystem properties and processes, north-central Baffin Island, Nunavut, Canada is particularly well-suited. A relatively large collection of historic photographs are available and some of the oldest vegetation community and plot-level studies conducted in the high arctic have been executed in this area. The glacial history of the area is also well known (Andrews 1979, Jacobs et al. 1993, Webber 1971). Repeat photography has been used extensively in many fields and is well recognized for its capacity to enhance historical reconstruction and process recognition (Cerney 2010). In the Arctic, some of the most convincing and extensive accounts of shrub expansion were detected through repeat

photography (Sturm et al. 2001, Tape et al. 2006). Analysis of vegetation community data derived from repeat sampling of marked plots are essential, however, for quantifying shifts in species associations. Such studies have proven useful for validating remotely sensed products capturing arctic greening (Bhatt et al. 2010). Decade time scale time series data are necessary to maximize the detection of change and adequately parameterize models for predicting future ecosystem states (Callaghan et al. 2011b), and Johnson and Kiyoko (2008) stress the importance of decadal data in understanding patterns of ecological succession.

Very few studies have examined how warming may impact vegetation successional dynamics and vegetation community structure and composition in the Arctic (*sensu* Elmendorf et al. 2012, Hill and Henry 2010, Hudson and Henry 2009). In one exception, Cutler (2011) found that vegetation succession on recently colonized lava flows in Iceland proceeded more rapidly on plots that were warmer with more sheltered microclimates. Outside of the Arctic it has been shown that successional trajectories for vegetation communities can be largely forced away from deterministic pathways by stochastic climatic events (e.g. Miller et al. 2010). Thus, it remains largely unknown how vegetation succession on recently deglaciated surfaces will change with warming in the high arctic.

There are many studies documenting vegetation community changes at vast scales (Walker et al. 2006, Elmendorf et al. 2012). More specifically, increases in shrubs have been observed at both plot-level measurements across the Arctic (Elmendorf et al. 2012), and using repeat photography in the Alaskan low Arctic (Sturm et al. 2001). But more localized long-term experimental warming studies in the Canadian Arctic have found that although some of these high- arctic communities were not very sensitive to change after 15 years of warming (Hudson and Henry 2010), biomass increased over time after 25 and 27 years of experimental and non-experimental measurements (Hill and Henry 2011, Hudson and Henry 2009). Diversity was not found to change, while the cover of the most abundant species, such as *Salix arctica*, did respond to induced warming. Moss cover increased in both short-term experimental warming (Hudson and Henry 2010), and long-term non-experimental warming (Hudson and Henry 2009), while other functional types showed inconsistent patterns of change or no response.

This study reports on repeat photography and the 2009 relocation and resampling of 79 sites established in North-central Baffin Island, Canada in 1964 during a study that examined the relationship between vegetation communities, a range of biophysical factors and time since deglaciation or lake drainage (Webber 1971). The study area spans a relatively young deglaciated landscape that has been colonized by plants spanning the past 1200 years (Andrews and Webber 1964, 1969). Specifically, for these 45-year old sites, we assess how: i.) vegetation communities have changed in the study area and what biophysical factors appear to be most strongly associated with these changes, ii.) how the relative cover of vegetation functional types, species richness, evenness, and diversity have changed, and iii.) how the dynamics of primary succession have changed. A companion study by Lara (2012) documents the implications of these ecosystem structural changes on ecosystem function (i.e. peak season ecosystem CO₂ exchange, surface albedo, reflectance, and several other biophysical properties). This study is a contribution to the International Polar Year – Back to The Future (IPY-BTF) project (IPY #512), which aims to determine the impacts of arctic vegetation community change on ecosystem structure and function over decadal time scales by revisiting and resampling historic research sites more than 25 years in age (Callaghan et al. 2011).

2.3 Methods

2.3.1 Study Area

This study was conducted within a 200 km² landscape characteristic of high-arctic tundra (Walker et al. 2005) in north-central Baffin Island, northwest of the Barnes Ice Cap and near the Lewis Glacier (70°25'N, 74°40'W, (Figure 5). Precipitation averages 25-37cm per year and the mean annual temperature is -10°C (Andrews and Barnett 1979, Andrews and Webber, 1969). The Barnes Ice Cap has mostly retreated throughout the Holocene, which in combination with four periods of re-advancement, has resulted in a mostly barren and boulder-strewn landscape with vast uplands and broad valleys. Cross-valley moraines are common, as are the shorelines of historic glacial lakes. Perennial snowbeds were relatively common during the 1960's (Andrews & Barnett, 1979, Webber 1971) but have largely vanished (see Figures 7a, 7b, 7e and 7f). Snowmelt streams are common on hillsides and the Isotoq, Striding, and glacial-fed Lewis Rivers dominate local valley floors. Flitaway Lake is the only substantial

lake in the study area and is situated adjacent to the Barnes Ice Cap in the northeast section of the study area. Ponds and wetlands are relatively rare. Soils include silts, clays, sands, and gravels, and most surfaces have been deglaciated for 50-1300 years (Figure 5). Humans have been generally absent from the study area since the early 1960's, with the exception of a Canadian Geographic Survey team who conducted research in the area during the 1989 summer in order to place a weather station and continue reconnaissance surveys (Jacobs et al. 1993).

The Circumpolar Arctic Vegetation Map classifies the study area as a “cryptogamic barren complex” with many areas of exposed rock covered with lichens and sparse vegetation (Walker et al. 2005). Nine vegetation communities were identified in the current study (Table 6) and 78 vascular plant species were documented in the surveyed sites. Approximately 15% of the vegetation cover is composed of vascular plant species. Herbivory appears to be minimal, but caribou, arctic hare and lemmings have been observed infrequently in the area. Waterfowl appear to be uncommon in ponds and wetlands (Webber 1971).

2.3.2 Site Relocation

The 79 sites resampled in this study in 2009 are a subset of 82 sites established in 1964 by Webber (Webber 1971). The original sites were established to characterize vegetation communities found in the study area and determine how these were influenced by various biophysical and successional properties and processes. Although site markers were not situated at site establishment, Webber located each site with a pin hole on aerial photographs and described each site location with detailed notes and hand drawn maps. For some sites, black and white color photographs were taken at the time of establishment in 1964. These detailed notes and site aerial photographs were used for site relocation in this study to maximize the comparative potential between the 1964 and 2009 sampling efforts.

In preparation for the 2009 resampling effort, the 1961 aerial photographs marked with site locations were digitized and georeferenced to a Landsat image in ArcMap 9.3 (ESRI 2011). The approximate locations of each 1961 site were then digitized to allow for the extraction of Global Positioning System (GPS) coordinates. This approach generally allowed for navigation to within 200 m

of the historic site location. Site location was then narrowed using Webber's detailed site notes that included the description of explicit geographic features, spatial relatedness to other sites and adjacent vegetation communities and small-scale geographic features such as streams, rock outcrops, or large isolated boulders. The exact location of a given site was made using the culmination of resources described above. To avoid the potential bias of placing a site in a vegetation community similar to that described for 1964, a greater degree of confidence was placed in historic physiographic site notes and field-drawn site maps than historic vegetation community data. Where the relative vegetation cover and abundance data were used to aid site relocation, a greater emphasis was given to species that are generally known for being long lived or relatively slow-growing (e.g. *Salix* spp and some lichen species). The presence of rare species, especially if they were long-lived or slow-growing, also proved to be useful for explicit site relocation. A descriptive justification for the final site relocation was compiled and a subjective confidence value (1 = least confident – 10 most confident) was assigned to each relocated site to indicate the perceived geobotanical relocation accuracy of the site. Future site relocation will benefit from each site being permanently marked, thoroughly photographed, and site coordinates recorded. Three of the 82 sites were not sampled due to logistic constraints and poor weather encountered during the 2009 resampling period.

2.3.3 Vegetation Sampling

Each site was established in 1964 within a physiognomically homogenous vegetation community and consisted of ten contiguous 1 m² plots that were sampled individually. All sampling was conducted close to peak growing season between mid-July and early August. Site resampling utilized the same methodology employed by Webber in 1964 and was conducted as close as logistically possible to the calendar day of the original sampling. The presence of all vascular plant, bryophyte, and lichen species, was recorded in each plot and percent cover was estimated within a 10 cm x 100 cm strip along one edge of each plot. All historic sampling was conducted by Webber, while Villarreal and Johnson completed the resampling. Our experience in the resampling and analysis of similar sites established by Webber in other locations (Johnson et al. 2011, Villarreal et al. 2012) suggests that there is a low likelihood of

observer error. Ecosystem functional measurements were made in close proximity to study sites and are reported by Lara (2012).













Included within the 79 resampled vegetation sites, were six sites established in 1964 close to the Flitaway Lake shoreline (Figure 5), which were classified as successional sites by Webber due to their location on newly exposed surface resulting from lake drainage. During the 2009 resampling effort, five new sites were established in the Flitaway region below the 1964 Flitaway Lake shoreline. Three of these sites (sites 83, 84, and 85) were placed along a down-slope gradient away from the 1964 Flitaway beach to the present location of the Flitaway Lake shoreline, and two sites (sites 86 and 87) were situated to represent more distinct pioneer vegetation communities on mostly bare ground near the extant Flitaway Lake shoreline close to the Barnes Ice Cap. Sampling of vegetation within 1 m² plots followed the method described above, however, the new successional sites were only 5m (i.e. 1 x 5 m²) in length due to time constraints imposed on the 2009 field team.

2.3.4 Estimation of Surface Age

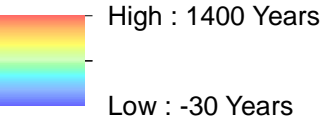
To improve the accuracy of spatiotemporal estimates of surface age (time since glaciations or lake coverage), previous surface age estimates determined by Andrews and Webber (1964) were revisited. During 2009, lichen measurement stations established in 1963 were revisited and the width and breadth of non-coalescing crustose rock lichens were re-measured using the method described by Andrews and Webber (1969). Measurements were used to update lichen growth curves and, using the landscape history established by Andrews and Webber (1969), an updated isochrone map of surface age contours was produced. This map was scanned and georeferenced to a 2002 Landsat satellite image using ArcMap 10 (ESRI 2011). To build a raster data coverage of surface age, a 500 m grid was overlaid and points of ‘known’ surface ages were established wherever this grid transected isochrone contour lines. Various spatial interpolation analyses (kriging, spline, inverse distance weighted, and natural neighbor) were run using these point values. Bivariate regression analyses comparing surface age at points of known age with surface ages derived for an independent point cloud showed that an exponential semivariogram model using 4 radial input points offered an optimal solution for spatially

extrapolating surface ages between isochrones lines. Surface ages for each of the 79 resampled sites were then extracted from the extrapolated surface age raster coverage (Figure 5).

Legend

-  Sites
-  Flitaway Lake 2002
-  Flitaway Lake 1964
-  Glacier Forelands
-  River/River Beds
-  Stable surface(-300 Years)
-  Stable surface (+300 Years)
-  Lewis Glacier 1964
-  Lewis_Glacier 2002
-  Drained Lake 766 Years Old
-  Drained Lake 1009 Years Old
-  Drained Lake 1281 Years Old

Surface Age



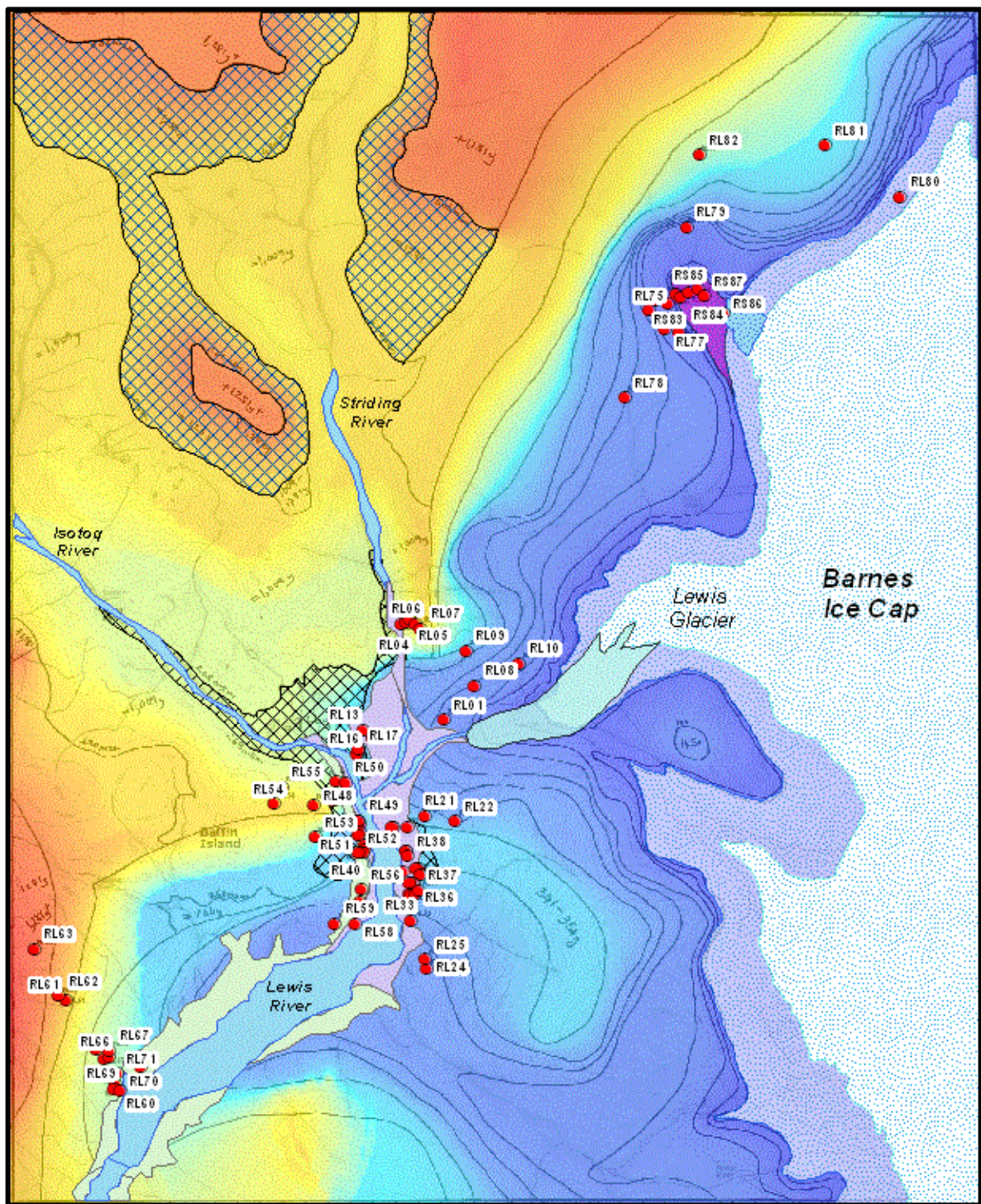


Figure 5. Map display of the 79 resampled sites, Webber isochrone lines, important landscape features, the Lewis Glacier, the Barnes Ice Cap, and colored kriging display of landscape surface age.

2.3.6 Climate Reconstruction

The following describes the method used by our colleague Dr. John Jacobs from the Department of Geography at Memorial University, Canada, who completed a climate reconstruction for the study area. Data from temporary weather stations established at the study site during two time periods (1963-1965 and 1989-1995) were used with data from the two closest permanent weather stations at Dewar Lake and Clyde River (68°39'N, 71°10'W and 70°29'N, 68°31'W, respectively) to reconstruct the July temperature climate of the study area for the period between 1958-2010. Data from Dewar Lakes and Clyde River were obtained from the Meteorological Service of Canada Historic Climate Data Archive. In order to temporally extrapolate from the two periods of observations at the study site (1960s and 1990s), multiple linear regression was applied to mean July temperatures from Dewar Lakes and Clyde River for the two periods when temporary automatic weather stations were operated in the study area. Data from both weather stations (Dewar Lake and Clyde River) were used in the model. The multiple regression models were determined not to be biased by autocorrelation (Durbin-Watson statistic). Summer warming index (SWI) was derived using multiple linear regression for field data from the two weather stations between 1958 and 2010.

2.3.7 Data Analysis

Relative cover for each species was calculated by multiplying the sum of cover estimates for each species in the 10 cm x 1 m sampling area by 100 and dividing this by the total cover of all species in the given site. Relative presence was calculated by multiplying the sum of all species present in a 1m² plot by 100 and dividing by the total species richness of each site. We then summed relative cover and relative presence and divided this by two to obtain a species index for each species at every site (*sensu* Villarreal et al. 2012, Webber, 1971). The same method was repeated for estimates of index values for vegetation functional types. Species index values (n = 117 species) were used to classify the original sites sampled in 1964 (n = 82 sites) into discrete vegetation communities using a Sørensen's similarity coefficient with a flexible beta linkage method ($\beta = -0.25$) to minimize chaining (McCune and Grace 2002), as described in Villarreal et al. (2012). Indicator species analysis was also performed on the 1964

dataset using species index values in PC-ORD (*sensu* Villarreal et al. 2012) and the three species with the highest indicator value in each vegetation community are reported in Table 3.

To assess the effectiveness of the 2009 sampling, non-relativized cover data were used to generate species area curves for each vegetation community and for the entire dataset. These were calculated in PC-ORD 4.10 (MjM Software Design Gleneden Beach, Oregon, USA) using Sørensen (Bray-Curtis) similarity coefficient to calculate a species mean and distance metric for each site sampled. A cumulative mean distances between sites were used to determine the species area accumulation curves.

We used species index values to run a Non-Metric Multidimensional Scaling (NMS) ordination of all sites for all sampling years in PC-ORD using a Sørensen (Bray-Curtis) similarity coefficient, a random starting configuration, and 250 runs with randomized and real data. Dimensionality and stress were determined by PC-ORD and to aid visualization, axes scores for each site in a given vegetation community (derived from the classification of 1964 data), were averaged (Figure 8). The vector lengths between 1964 and 2009 site axis scores were calculated and normalized by the number of years (45 years) and averaged for each vegetation community. To determine the gradients of change underpinning change vectors between 1964 and 2009, regression trees (recursive partitioning) was performed in JMP 9.0 (SAS Institute Cary, North Carolina, USA) using multiple biophysical variables: surface age, elevation, slope, soil wetness, soil type, pH, conductivity, organic matter (loss on ignition), as well as site relocation confidence (see section 2.3.2). Initial analysis showed site relocation confidence did not explain the variability among change vectors, suggesting site relocation accuracy explains less of the vegetation community change than the other environmental variables included in the analysis, thus relocation confidence was removed from subsequent analysis and is not reported in results hereafter.

Changes in the relative cover of vegetation functional types (*sensu* Chapin et al. 1996) and relative cover of individual species were also assessed as described in Villarreal et al. (2012). To determine if species richness, evenness, and Simpson's and Shannon's indices of diversity varied between sampling years and among vegetation communities through time, we used Multivariate Analysis of Variance (MANOVA) for repeated measures in JMP 9.0 with vegetation community as the

within subject factor. If the multivariate F statistic for time, or time by vegetation community interaction resulted in a probability less than 0.05, differences for each community between sampling years were tested using a least significant difference (LSD) test of the univariate analysis of variance (ANOVA) within the repeated measures.

To test the likelihood for a shift in the change point for succession patterns following deglaciation or lake recession over the past 45 years, sites younger than 200 years in both 1964 and 2009 were identified and mean vegetation cover, species richness, and diversity (Shannon Index) were analyzed using one point regression trees in JMP 9.0 following a similar method described by Lougheed et al. (2007). Vegetation cover and species richness data were arcsine transformed and diversity data were log transformed to meet the assumptions of normality. Sites that were less than 200 years of age in 1964 but over 200 years in 2009 were excluded in the 2009 analysis and the new succession sites that were placed in 2009 were included.

2.4 Results

2.4.1 Evidence of change derived from repeat photography

Repeat photography (Figures 6a-f) showed a reduction in the height and extent of the Barnes Ice Cap (Figure 6b), overall greening of the landscape throughout the study area (6b), loss of snow banks (Figure 6b, 6d, 6f), and a spread of the shrub *Cassiope tetragona* (figure 6d). Relocation confidence values did not explain any of the variation in regression trees. Consequently, site relocation was considered sound and confidence values were not included in the following analysis.

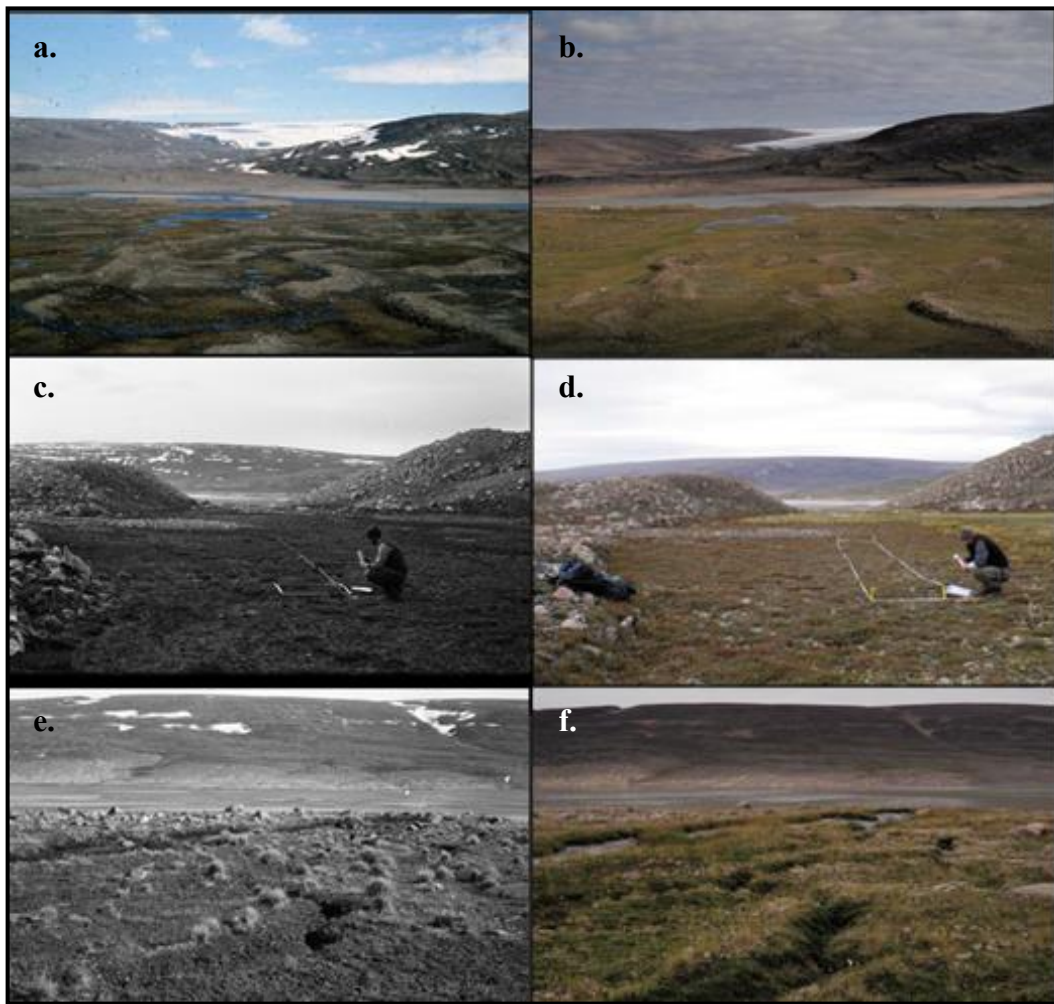


Figure 6a-f. Repeat photographs of three locations near the Barnes Ice Cap, Baffin Island, Nunavut, Canada. Figures a, c, and e were taken in 1964, and figures b, d, and f are corresponding locations in 2009. All photos were taken during peak season and the repeat photographs were taken within a few calendar days of the 1964 photographs. Photo credit: Patrick J. Webber (1964) and Craig E. Tweedie (2009).

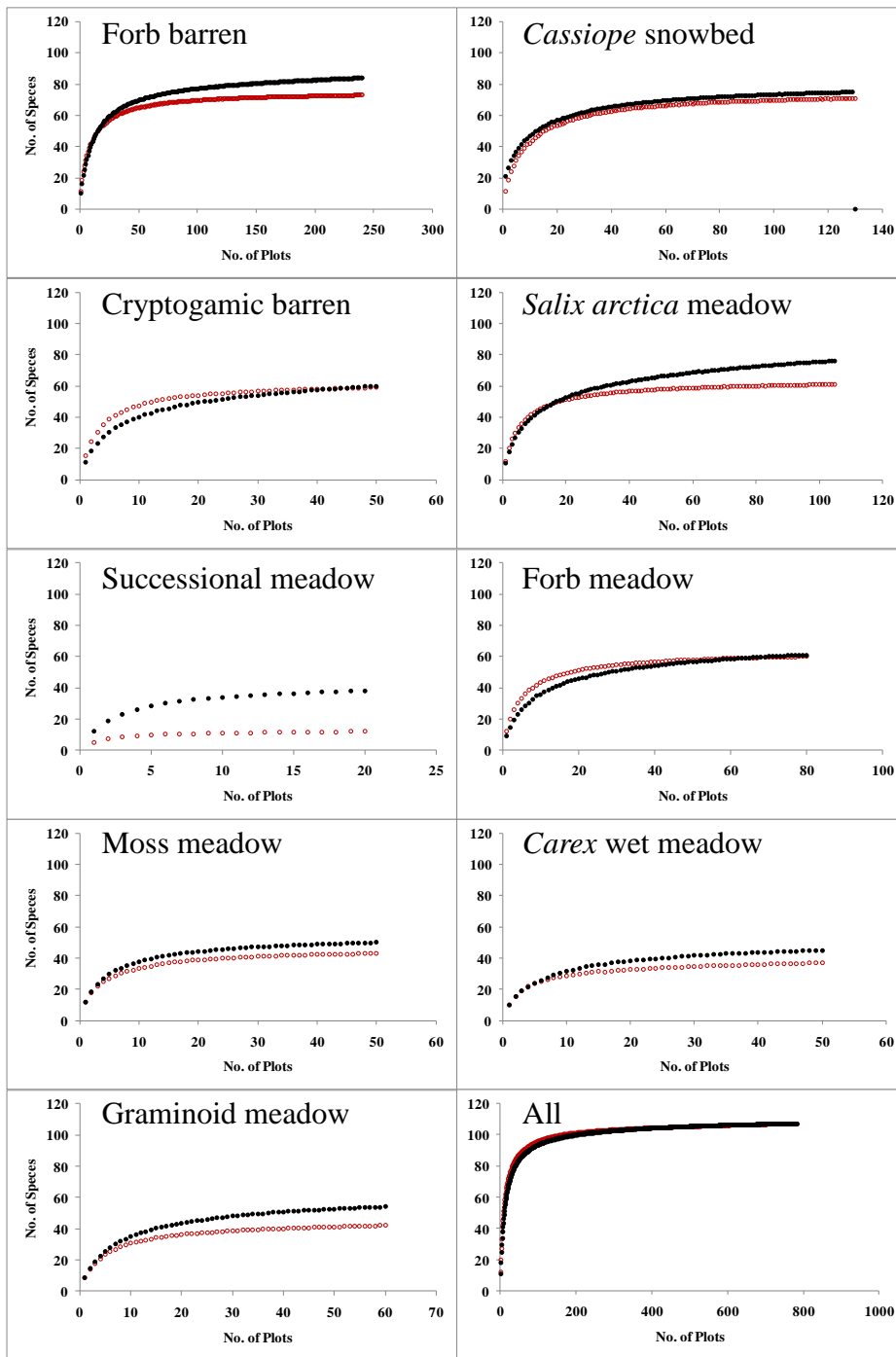


Figure 7. Species area curves for each vegetation community, and for the entire dataset (All). Red circles represent 1964 sampling, and black circles represent the 2009 sampling.

2.4.2 Vegetation community change

Eight species that were recorded in the 1964 sampling (*Arabis arenicola*, *Cardamine bellidifolia*, *Deschampsia pumila*, *Mnium affine*, *Oncophorus whalenbergii*, *Poa abbreviata*, and *Saxifraga hyperborean*) were not found in 2009, while *Alectoria* spp, *Dactylina arctica*, *Ochrolechia frigida*, *Salix richardsonii*, *Thamnolia* spp, and *Vaccinium uliginosum* were recorded for the first time in the study area in 2009. Species area curves showed similar sampling patterns between years throughout all sites and for each community (Figure 6). Classification of the 82 sites sampled by Webber in 1964 yielded nine vegetation communities. Species area curves for successional communities and *Salix arctica* meadows for 2009 deviated from those for 1964 more than any other vegetation community type. Overall, species and indicator species were different between communities (Table 3).

Table 3. Vegetation community names and descriptions for vegetation communities sampled on Baffin Island. Each vegetation community is a distinct cluster of similar species composition. Each vegetation community, with the exception of the successional community, is arranged in a sequence according to the average site moisture from dry to wet along the mesotopographic gradient. The communities correspond to the nodal concept presented by Webber (1971, 1978). Leading strategic growth forms (modified from Webber, 1978) are given with corresponding species index (SI). For each community characteristic, species are listed in two categories. These categories are Dominant (D), Frequent (F), and/or Indicator (I). Dominants are the three species with the highest SI. Numbers of sampled sites, total number of species and average percentage cover are given for each vegetation community.

Common Name	Moisture index	Mean vegetation cover	Landform	Characteristic Species	Species Richness	Sites resampled
<i>Poa-Papaver</i> barren	2.1	42	Dry exposed slopes	<i>D. Stealp, Cladon</i> <i>F. Rhacan, Salarc</i> <i>I. Poagla, Paprad</i>	91	24
<i>Saxifraga oppositifolia</i> cryptogamic crust	3.0	85	Moist stony surfaces	<i>D. Ceparc,</i> <i>Cladon, Salarc</i> <i>F. Saxopp,</i> <i>Luzcon</i> <i>I. Antjur, Carmar</i>	70	5
<i>Cassiope- Sphenolobus</i> snowbed	2.6	88	Well drained sheltered patches	<i>D. Castet,</i> <i>Ceparc, Stealp</i> <i>F. Salher, Salarc</i> <i>I. Sphmin, Lycsel</i>	89	12
<i>Salix arctica- Alopecurus</i> meadow	3.0	66	Moist sandy river terraces	<i>D. Salarc,</i> <i>Ceparc, Cladon</i> <i>F. Stealp, Aloalp</i> <i>I. Rhacan, Pedhir</i>	77	14
<i>Luzula confusa</i> - forb meadow	3.2	51	Moist sandy streamsides and slopes	<i>D. Luzcon,</i> <i>Poaarc, Epilat</i> <i>F. Paprad,</i> <i>Stellar,</i> <i>I. Carbel, Ceralp</i>	63	5
<i>Campylium-Aulacomnium</i> meadow	4.0	91	Flat early summer-wet lowlands	<i>D. Camste,</i> <i>Salarc, Aloalp</i> <i>F. Aultur, Brypse</i> <i>I. Junbig, Fesbra</i>	47	5
<i>Carex stans</i> wet meadow	4.2	74	Wet level sites and pond margins	<i>D. Carsta,</i> <i>SalArc, Calsar</i> <i>F. Aultur, Juncas</i>	47	5

<i>Eriophorum-Pleuropogon</i> wetland	4.3	92	Pond margins	I. Polviv, Saxcer D. Calsar, Eriang, Aultur F. Salarc, Aloalp I. Ricpin, Plesab	51	7
Pioneer lacustrine sedimentSuccessional meadows	3.0	60	Moist recent lacustrine silts and sands with moderate	D. Phialg, Stemon, Erisch F. Sagint, Saxcer I. Cocoff, Ranhyp	34	5
All sites	3.3	72			62	-

The initial NMS of 1964 and 2009 data showed a split of data between years. Further analysis of species index value data showed that close to an 18% difference in species common to both years. Site samplers and site relocators revised species nomenclature and derived categories defining reasons for inconsistencies in species presence between 1964 and 2009. The categories and the number of species found in each category included the following:

Category	Description	Number of Species
1	Species found in both years and no problem perceived for this species	99
2	Species ID sound and found only in 1964 and likely to have been missed or not there in 2009	2
3	Species ID sound and found only in 2009 and likely to have been missed or not there in 1964	3
4	Species documented in 2009 or 1964 only because of likely site relocation issues	1
5	Species likely to have been unknown to 2009 sampling personnel	10

A two-dimensional solution was recommended for the NMS ordination, which included all sites and sample times and had a final stress of 18.94 (Figure 8). Although this stress is high, it is not unusual for a dataset of this size (McCune and Grace, 2002). Instability was 0.00010 after 500 iterations and the proportion of the variance explained by the ordination represented 76.4% of the cumulative variance with axis one and two representing 49.2% and 27.2% respectively. With the exception of the two communities that shifted the least in ordination space (*Cassiope* snowbeds and cryptogam barrens), all communities shifted along a similar vector within the ordination. The greatest community change was detected in the early successional community (mean vector length = 0.04, figure 13). Recursive partitioning explained 47.8% of the variability in ordination vector lengths. A large portion of this variability was best explained by site age, which accounted for 20.1% of the cumulative variation in the regression tree. Additionally, slope and organic matter were also important variables determining the

variability at sites that have been deglaciated for more than 280 years, (3.5% and 4.4%, of vector length variation, respectively). In sites younger than 281.7 years, pH and the presence of gravel explained the greatest variation in vector length (6.7% and 2.5%, respectively).

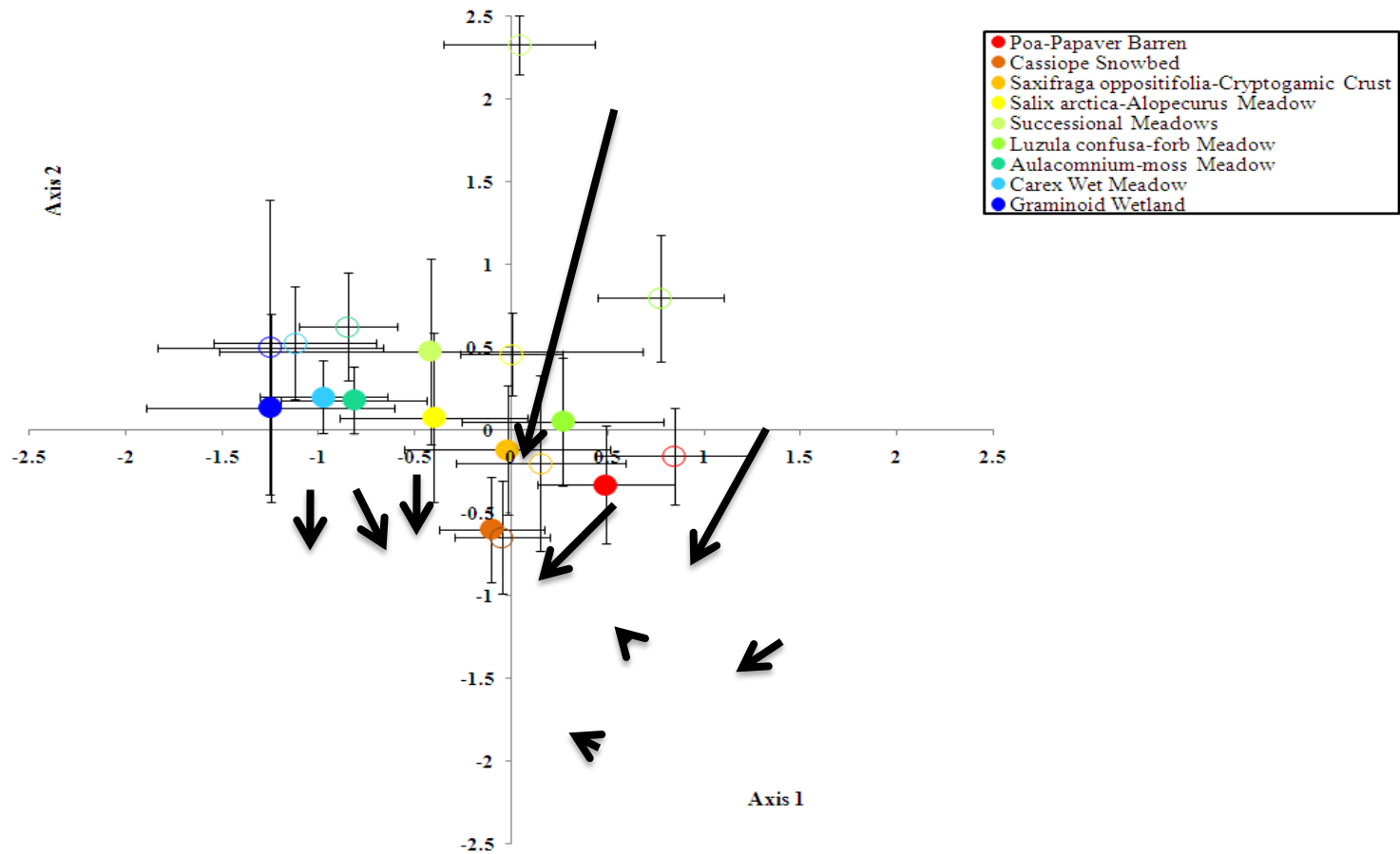


Figure 8. Non-metric Multidimensional Scaling ordination of all vegetation communities for 1964 (open circles) and 2009 (closed circles). Points represent mean NMS axis scores for all sites classified in a given vegetation community for each year. Vegetation communities are arranged along a moisture gradient in the legend, and standard deviations are shown for each axis for each community. Arrows represent average trajectories of change for each community.

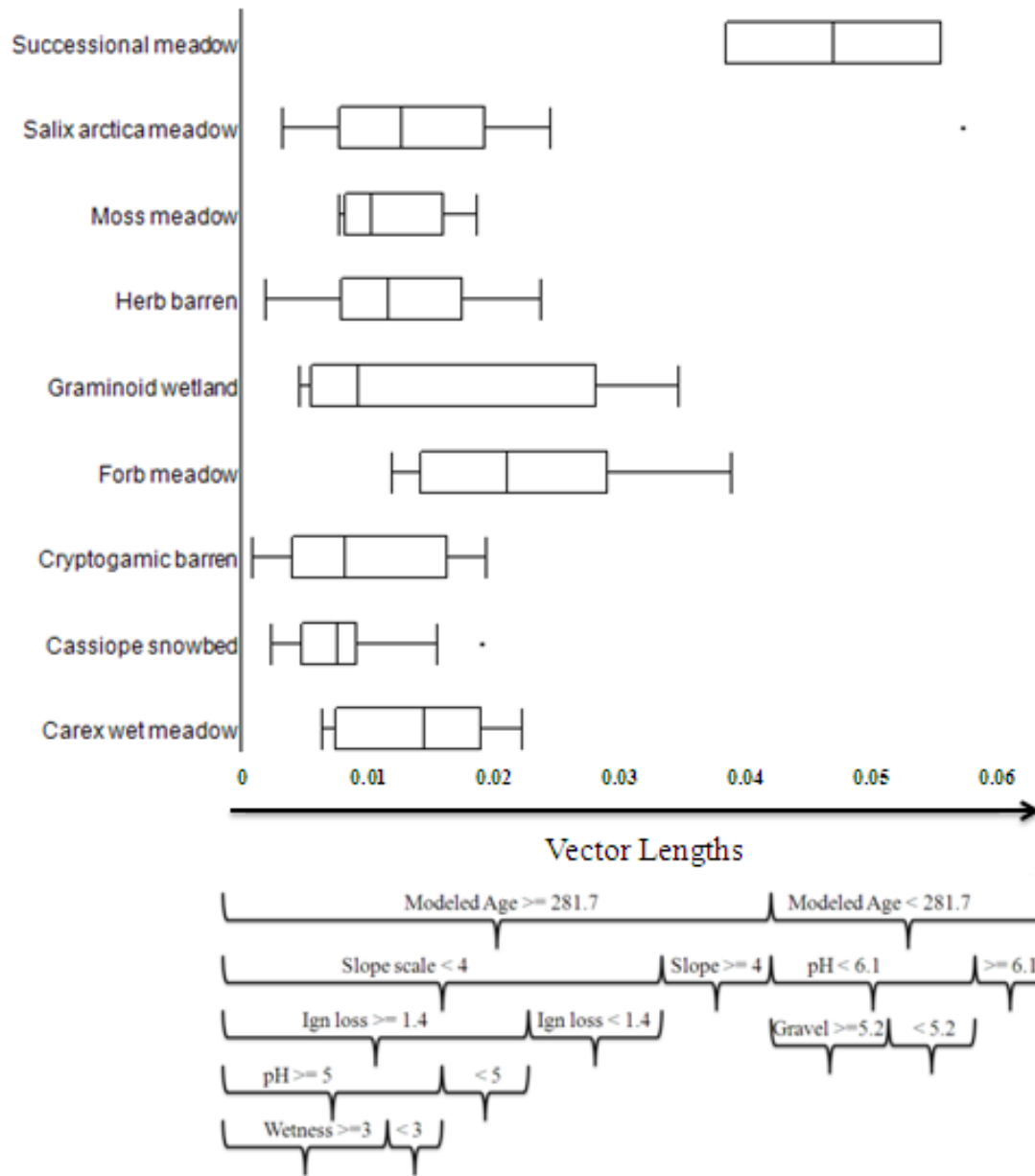


Figure 9. Box and whisker plots for site-based vector lengths calculated from NMS axis scores between 1964 and 2009 for each vegetation community. Edges of boxes represent minimums and maximums, lines within box represent means, and whiskers represent standard deviations. Results of a regression tree analysis below the x-axis illustrate changepoints for factors explaining the variability in vector lengths (cumulative $r^2 = 47.8\%$).

2.4.3 Change in vegetation functional groups

The relative cover of vegetation functional types within the entire dataset was significantly different between 1964 and 2009 for all functional groups except mosses (MANOVA, $p < 0.05$,

numerator df = 1, denominator df = 1,580). Shrubs showed the greatest change in relative cover with an increase of 6.23% ($P < 0.05$, Figure 14 All). Graminoids, forbs and lichens also increased between 1964 and 2009 by 0.2%, 1.3%, and 3.2% respectively. Liverworts decreased by 1.0% ($P=0.055$), and the relative cover of mosses and cryptogamic crust did not change. In herb barren communities, the cover of shrubs increased (+0.9%). In *Cassiope* snowbed communities the cover of shrubs increased by +0.9%. *Salix arctica* meadows showed cover increases for graminoids, shrubs, and forbs (+2.2, 2.0 and 0.3%, respectively), while that for mosses decreased (-4.0%). Cover for graminoids, forbs and shrubs increased in successional communities (+0.6, 0.8, and 0.7%, respectively). Forb meadows had large increases in shrub cover (+1.9%), and decreases in graminoid cover (-1.0%). In *Carex* wet meadows the cover of forbs (+0.7%) and shrubs (+1.0%) increased. Finally, graminoid wetlands experienced an increase in shrub cover (+0.9%). Although these are small changes in relative cover, especially for forbs, lichens, and liverworts, their relatively low abundance in this landscape indicates that even changes of less than one percent are significant. For example, although liverworts had a 1.0% change in relative cover, this value is significant because they comprise only about 1.8% of the relative cover for all functional groups, thus their cover increased by slightly more than 50%.

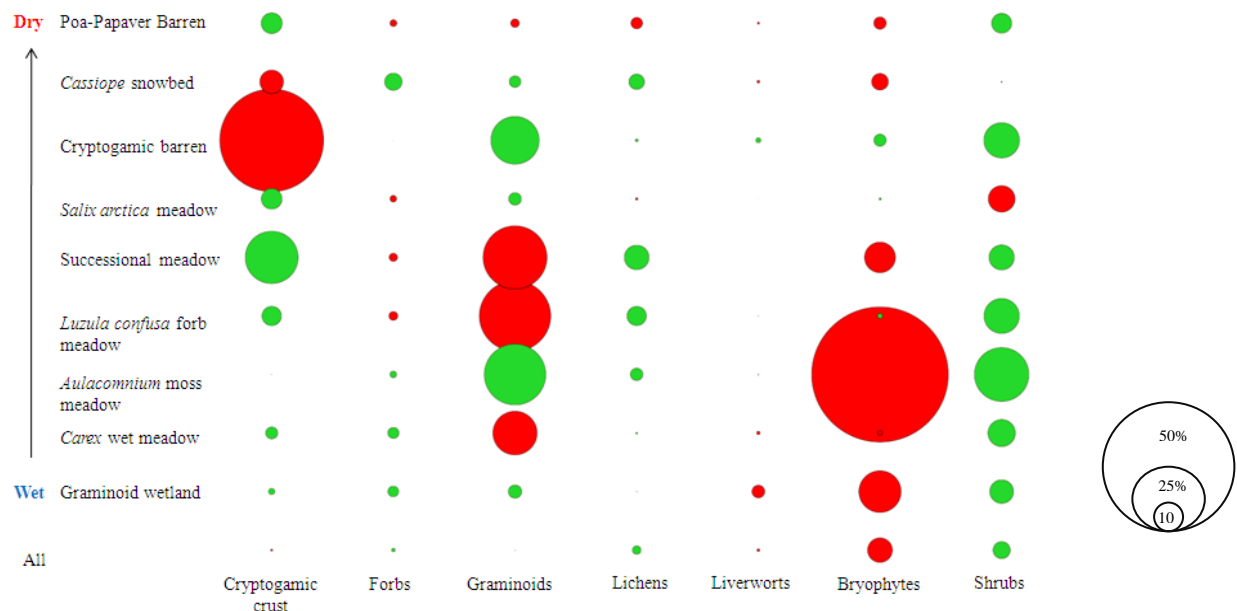


Figure 10. Differences in relative cover of vegetation functional groups for each vegetation community between 1964 and 2009. Green represents an increase in percent cover, red represents a decrease. Size of circle represents percent change in relative cover (see legend).

Table 4. Difference in the mean species richness, evenness, and Shannon Index of diversity for each vegetation community between 1964 and 2009 (* significant increase or decrease, ANOVA, $p < 0.05$).

Community	Richness	Evenness	Simpsons Index	Shannon Index
<i>Poa-Papaver</i> barren	-0.38	0.01	0.03	0.01
<i>Cassiope-Sphenolobus</i> snowbed	-4.23	0.04*	0.03	0.02
<i>Saxifraga oppositifolia</i> -cryptogamic crust	-1.00	0.06*	0.20	0.06*
<i>Salix arctica-Alopecurus</i> meadow	-0.64	0.02	0.05	0.02
Successional meadow	14.50*	0.15*	-1.05*	0.20*
<i>Luzula confusa</i> -forb meadow	1.13	0.03	0.12	0.03
<i>Campylium-Aulacomnium</i> meadow	0.40	0.06*	0.21	0.05*
<i>Carex</i> wet meadow	2.40	-0.03	-0.21	-0.04
<i>Eriophorum-Pleuropogon</i> wetland	1.00	0.05*	0.24	0.05*
All sites	-0.23	0.03*	0.12*	0.03*

2.4.4 Diversity, evenness, richness and species changes

Despite no overall significant change in species richness between 1964 and 2009, evenness, and both Shannon's and Simpson's indices of diversity increased overall (Table 4). This was also true for five of the nine vegetation communities. Successional communities showed significant increases in richness, evenness, and Shannon Index of diversity, however, Simpson's Index of diversity decreased. Based on relative cover, the five species with the greatest increases across all sites were *Salix arctica*, *Polytrichum* spp, *Stereocaulon alpinum*, *Aulacomnium turgidum*, and *Festuca hyperborea*. The following five species underwent the greatest decrease in relative cover: *Luzula confusa*, *Pogonatum*

capillare, *Calliergon sarmentosum*, *Cladonia* spp, and *Campylium stellatum* (Table 5). Within communities, various shifts in species abundances were also recorded.

Table 5. Mean difference between 1964 and 2009 for species relative cover over all sites resampled. Bold values represent statistical significance ($\dagger < 0.1$, $* < 0.05$, $** < 0.01$, $*** < 0.001$) from a general linear model assuming a Poisson distribution is represented by different symbols. Changes in functional groups are also shown (Lich-lichen, Gram-graminoid, Bryoph-bryophyte, Crypt-cryptogamic crust).

Species	Functional Type	Forb barren	<i>Cassiope</i> snowbed	Cryptogamic barren	<i>S. arctica</i> meadow	Successional meadow	Forb meadow	Moss meadow	<i>Carex</i> meadow	Graminoid wetland	All Sites
<i>Alectoria nigricans</i>	Lich	3.5	0.7	0.5	0.0		0.0			0.0	4.6
<i>Alectoria ochroleuca</i>	Lich	21.41*	2.6	1.4	0.0		0.1				25.5†
<i>Alopecurus alpinus</i>	Gram	18.97*	4.54*	3.0†	5.48*	2.8†	-11.1*	-2.8*	0.3	-5.0*	16.24*
<i>Anthelia juratzkana</i>	Liverw	-10.0**	6.9†	3.9	0.8		1.4	2.0	0.5	-32.1**	-26.6†
<i>Arabis arenicola</i>	Forb	0.0					-0.7				-0.7
<i>Arenaria rubella</i>	Forb	-2.8†	0.0	2.2	-0.2	1.5	0.8	0.0			1.4†
<i>Aulacomnium palustre</i>	Bryoph		0.5	-2.5*	1.6		1.3	0.0		2.6	3.6†
<i>Aulacomnium turgidum</i>	Bryoph	11.5**	34.0†	18.9*	43.5**		2.8	21.5†	-10.3**	-47.5*	74.28*
<i>Bartramia ithyphylla</i>	Bryoph	-2.6†	8.5**		-0.9		3.0†	-1.1	0.0	0.0	6.9
<i>Blepharostoma trichophyllum</i>	Bryoph		0.0	-1.1							-1.1
<i>Bryum inclinatum</i>	Bryoph	2.2		0.0	4.9	0.1	-0.8			0.0	6.5
<i>Bryum obtusifolium</i>	Bryoph	1.3	-1.0	0.0	-0.4	-0.1		-0.5	-0.5	-22.6**	-23.8†
<i>Bryum pseudotriquetrum</i>	Bryoph	-2.8	0.1	0.0	1.4	-48.3	1.3	-15.5*	-3.1	-40.8*	-107.7†
<i>Calliergon sarmentosum</i>	Bryoph	2.5	1.9		-4.0*	7.3*	3.9†	5.7*	-40.2**	-171.9*	-194.7*
<i>Campylium stellatum</i>	Bryoph	2.3	-12.4*	1.2	36.7†	8.9*	6.4†	-260.2*	38.9*	44.8***	-133.4*
<i>Candelariella placodizans</i>	Bryoph	-1.6	0.8	0.0	0.0		-0.1				-0.9
<i>Cardamine bellidifolia</i>	Forb	-0.2	0.0	-0.1	-0.1		-0.2				-0.7
<i>Carex bigelowii</i>	Gram		-17.1***	2.6	0.6			24.9***	0.0	8.1*	19.2*
<i>Carex capillaris</i>	Gram	0.0	48.3**	3.5*			7.5*		9.9*		69.2*
<i>Carex maritima</i>	Gram	-14.6**	0.9	2.0†	-19.2*	0.0	-94.2*	1.1	0.0	0.7	-123.2†
<i>Carex nardina</i>	Gram	8.7*			0.4		-55.9***				-46.8†
<i>Carex stans</i>	Gram			0.2	0.6			56.0***	-143.7**	107.8**	20.9*
<i>Cassiope tetragona</i>	Shrub	6.3*	-9.6†	1.8	1.0			0.0	0.0	0.4	-0.1†
<i>Cephaloziella spp</i>	Crypt	171.5*	-108.7*	-195.2*	71.5*	30.0*	67.9*	0.1*	21.4**	3.2*	61.7*
<i>Cerastium alpinum</i>	Forb	-0.6	0.0	2.9†	-18.0***	2.1	-3.3	0.0	-0.1		-16.9†

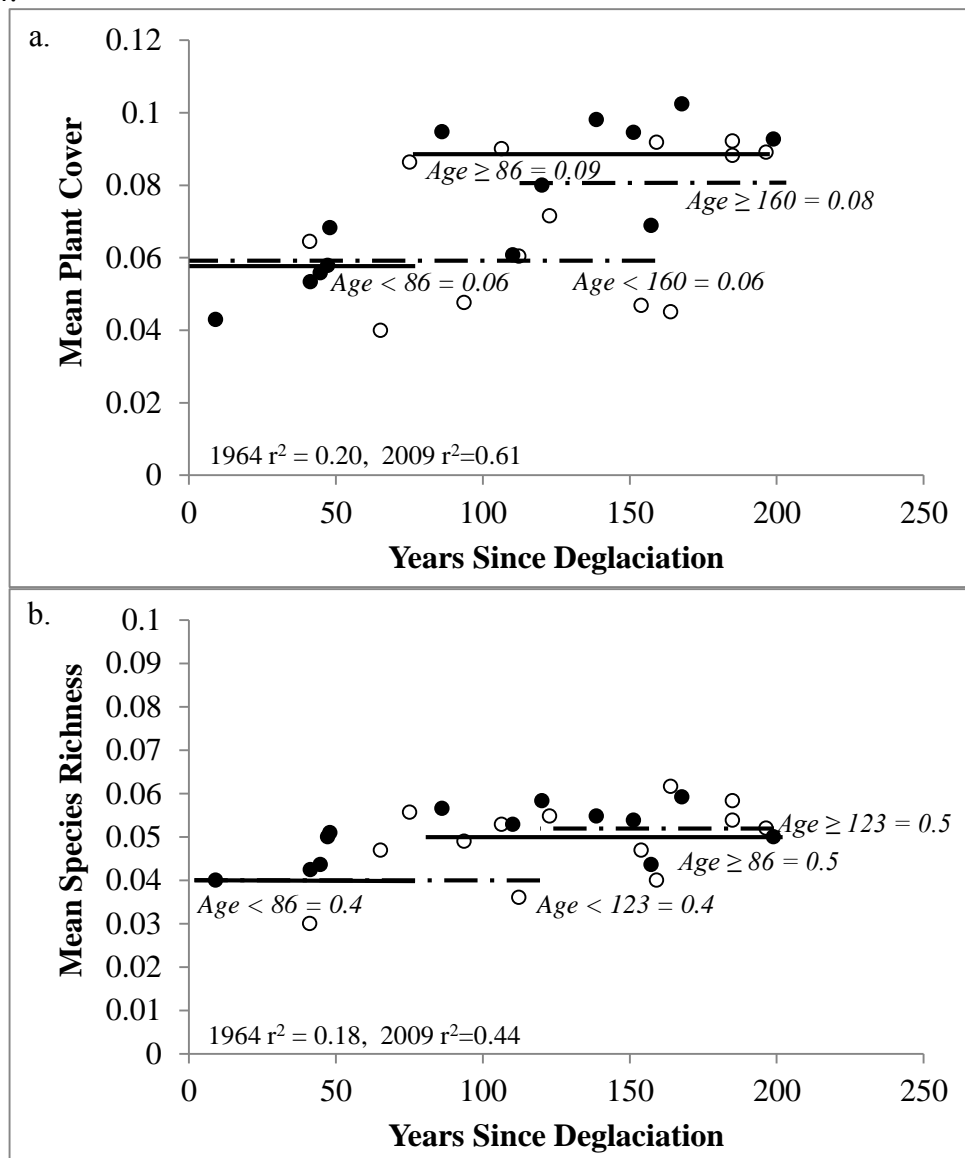
<i>Ceratodon purpureus</i>	Bryoph	-3.9	-6.1*	-0.9							-10.9†
<i>Cetraria crispa</i>	Lich	20.9*	18.8*	0.0	0.0		0.0			-0.1	39.6†
<i>Cetraria cucullata</i>	Lich	2.8	4.5		1.2		0.2			0.0	8.7†
<i>Cetraria nivalis</i>	Lich	4.3†	4.0†	0.0	0.7		0.0	0.4			9.4†
<i>Cladonia</i> spp	Lich	-63.5†	-19.4*	-15.5*	-42.6*	2.8*	1.5	0.4	0.0	0.6	-135.6†
<i>Cochlearia officinalis</i>	Forb	1.1		-0.1		-2.4	-5.9*				-7.2†
<i>Constomium tetragonum</i>	Bryoph	5.9	-24.6**	4.2	0.6		0.8	0.0		42.9***	29.8*
<i>Cornicularia divergens</i>	Lich	1.7	5.3*								7.0†
<i>Dactylina</i> spp	Lich	4.9*	1.7	0.0							6.7†
<i>Deschampsia pumila</i>	Gram								-9.2**		-9.2
<i>Dicranum elongatum</i>	Bryoph	0.0	10.3*	2.2	-1.1	0.1	0.5		0.2	0.0	12.2†
<i>Didymodon recurvirostris</i>	Bryoph	-7.7†	-1.4	-5.4	-3.7		-1.2	-2.6			-22.0*
<i>Distichium capillaceum</i>	Bryoph	0.8	-11.8**	-5.8†	0.1	-0.1	-5.6†	-11.0†	0.0	0.7	-32.7*
<i>Ditrichum flexicaule</i>	Bryoph	-2.2	8.3**	0.0	-2.8†		0.0			0.3	3.6
<i>Draba</i> spp	Forb	13.2†	0.9	0.9	-0.3	1.0	-2.1†			0.0	13.6†
<i>Drepanocladus brevifolius</i>	Bryoph		2.9*					-22.8***			-19.9
<i>Drepanocladus revolvens</i>	Bryoph	3.2	0.9	0.5	11.5*				8.7†	27.1*	51.8*
<i>Drepanocladus uncinatus</i>	Bryoph	0.1	18.7†	-0.6	25.2†	0.0		11.3	11.1*	7.5**	73.3*
<i>Dryas integrifolia</i>	Shrub	25.3†	-25.3**	31.3**	2.7		12.3*	0.9	3.0	0.2	50.4**
<i>Encalypta brevicolla</i>	Bryoph	1.6	0.0		-11.7		-12.7**			0.0	-22.8
<i>Encalypta rhabdocarpa</i>	Bryoph	-13.3	-0.1†	-0.3	-3.7		-0.1	0.0			-17.5†
<i>Epilobium arcticum</i>	Forb								2.6	0.0	2.6
<i>Epilobium latifolium</i>	Forb	8.3†	1.8	-0.7	-3.3†		13.1†		0.0	0.0	19.1†
<i>Eriophorum angustifolium</i>	Gram			3.1	7.3†			20.9**	37.3**	-80.7**	-12.0**
<i>Eriophorum scheuchzeri</i>	Gram				1.6	-55.0**	0.0	-4.1†	0.0	6.0†	-51.5
<i>Eriophorum vaginatum</i>	Gram		0.0					0.0		0.8	0.8
<i>Festuca hyperborea</i>	Gram	16.1*	1.7†	24.7*	9.8†	3.6	-0.3*	8.2†	12.6*	3.9	80.3*
<i>Fissidens bryoides</i>	Bryoph	0.4	0.1		0.0		0.6				1.2
<i>Gymnomitrium coralloides</i>	Bryoph	-46.6†	-3.0	-3.2†							-52.8†
<i>Hierochloe alpina</i>	Gram	-1.2†	3.1		17.0**						18.8†
<i>Juncus biglumis</i>	Gram	-0.1*	0.9	3.2	12.8**	-8.5*	0.5	0.5	-0.6	10.8**	19.4*
<i>Juncus castaneus</i>	Gram	2.2	1.1	2.3	0.8	30.7**	6.8†	-5.7*	-0.9*	-7.5*	29.8*

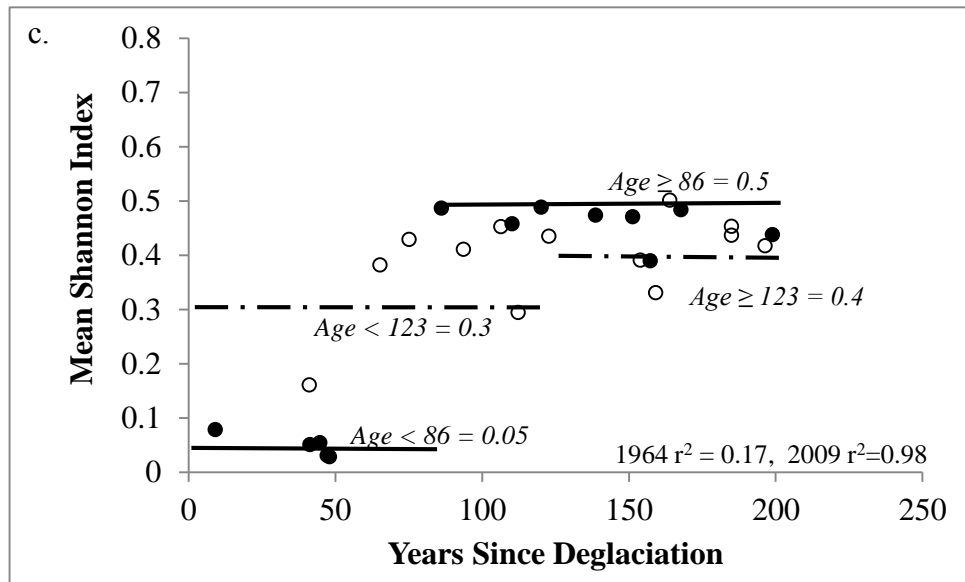
<i>Luzula confusa</i>	Gram	-165.9*	5.8	5.0	3.1	9.2**	-95.7*	0.1	1.1	0.6	-236.7*
<i>Luzula nivalis</i>	Gram	14.1†	0.0†	12.9†	1.8	1.3	2.9	-0.1	0.4	0.2	33.5*
<i>Lycopodium selago</i>	Bryoph	0.5	6.1†	1.4			0.0		0.0	0.0	8.0†
<i>Melandrium affine</i>	Forb	0.7	0.0	0.0	0.0		-0.1				0.6
<i>Mnium affine</i>	Bryoph				0.0		0.0				0.0
<i>Myurella julacea</i>	Bryoph	9.7†	4.5	0.8	32.6*		6.2	7.7	-2.1**	1.1	60.5**
<i>Ochrolechia frigida</i>	Lich	13.4**	0.5		0.4		0.0				14.3†
<i>Oncophorus wahlenbergii</i>	Bryoph	-4.8*	-0.3					0.0		-1.4	-6.5†
<i>Orthotrichum speciosum</i>	Bryoph	0.0	0.2			0.1	0.0				0.3
<i>Oxyria digyna</i>	Forb	6.0	2.1	0.0	-3.8*	2.9†	-0.2				6.9†
<i>Papaver radicum</i>	Forb	-3.4	0.4	0.1	-0.1	0.3	-15.7**				-18.3†
<i>Parmelia physodes</i>	Lich	2.2	1.1	0.0	0.6						3.9†
<i>Pedicularis hirsuta</i>	Forb	1.0	-0.1	0.3	8.2†		1.0	0.9	2.7	0.7	14.7*
<i>Peltigera aphthosa</i>	Lich	7.7*	9.9	-0.1	17.3**	0.0	3.3	7.0	0.4	-0.7†	44.7**
<i>Peltigera canina rufescens</i>	Lich	-6.0*	2.2†	6.1*	-21.4*	1.7	1.9	2.4	0.0	0.2	-13.0*
<i>Philonotis fontana</i>	Bryoph	6.9*	0.8	0.8	1.7	-127.6*	-1.2	0.9	1.3	0.8	-115.6†
<i>Phippsia algida</i>	Gram	2.1	-0.1	-4.9**	7.5†	3.0†	4.4*	16.7†	-9.9*	5.9*	24.5*
<i>Physcia muscigena</i>	Lich	-2.5†	1.7	0.0	0.3						-0.5
<i>Pleuropogon sabinei</i>	Gram					1.9			0.7	-23.7***	-21.1
<i>Poa abbreviata</i>	Gram	0.0					0.0				0.0
<i>Poa arctica</i>	Gram	-69.2*	4.1	4.3	23.0*	6.3*	-27.1*	5.2*	0.0	-3.8*	-57.1*
<i>Poa caespitosa</i>	Gram	2.2			-0.2						2.1
<i>Poa glauca</i>	Gram	-60.9*	-0.1	29.6***	-4.8*		24.8*				-11.6†
<i>Pogonatum alpinatum</i>	Bryoph			1.8				-0.1			1.7
<i>Pogonatum capillare</i>	Bryoph	-	-18.2*		-3.0		-10.9†	-1.6		0.2	-225.8**
		192.3***									
<i>Pohlia cruda</i>	Bryoph	-7.1*	-3.8*	3.6†	3.7†	5.6*	16.7*	-5.5**	0.0		13.3†
<i>Pohlia filiformis</i>	Bryoph		3.3†		-92.7*		7.8†	-0.9	3.6†	2.3	-76.7†
<i>Pohlia nutans</i>	Bryoph	9.4*	-15.3**				0.3	0.2	-0.2	0.7	-4.8
<i>Polygonum viviparum</i>	Forb	1.8†	24.3*	-1.6	0.8		5.4†	11.2†	15.3	14.5*	71.8**
<i>Polytrichum spp</i>	Bryoph	149.6*	-52.1*	0.3*	16.2†	6.8*	-11.4*	12.2*	17.5**	-1.4*	137.7*
<i>Potentilla hypartica</i>	Forb	-3.6†	11.6**	0.4	0.3		0.1				8.9†
<i>Psoroma hypnorum</i>	Lich		1.9	6.1*	-0.3	1.6	2.9	0.8			9.5*

		-3.4*									
<i>Ranunculus hyperboreus</i>	Forb					-19.2		0.0	0.0	5.4†	-13.7
<i>Racomitrium canescens</i>	Bryoph	-9.3*	12.3†	10.6*	-20.6*	0.6	56.8*	4.5*		0.0	54.7*
<i>Riccardia pinguis</i>	Liverw		0.4	0.2			0.3	0.0	-3.4	-2.8	-5.4
<i>Sagina intermedia</i>	Forb	6.1*	-0.1	-0.2	0.4	-0.3	7.3†	0.0	-0.2	0.7	13.8†
<i>Salix arctica</i>	Shrub	90.6*	17.4*	28.8†	-154.7*	21.1*	93.3*	87.8*	30.4*	6.1*	220.8*
<i>Salix herbacea</i>	Shrub	27.9†	14.2*	0.5	1.0	2.7	4.8	2.6	0.7	19.3†	73.7*
<i>Salix richardsonii</i>	Shrub	1.8			42.7**			2.7		13.0*	60.2*
<i>Saxifraga caespitosa</i>	Forb	-2.3		-3.2†	0.0	2.0	1.0				-2.5
<i>Saxifraga cernua</i>	Forb	1.3	0.4	0.0	-0.5	-1.6	-0.8	0.0	-0.6	-0.2	-2.0†
<i>Saxifraga foliolosa</i>	Forb	0.2	0.3	-0.1	0.0	0.7	0.3	0.5	0.6	0.7	3.1†
<i>Saxifraga hyperborea</i>	Forb					-0.1					-0.1
<i>Saxifraga nivalis</i>	Forb	0.1	-0.1	-0.4	-0.5	2.1†	-3.1†	0.0	0.0	0.0	-1.8
<i>Saxifraga oppositifolia</i>	Forb	-29.2**	0.0	-13.6*	-6.9		2.0†		0.0	0.0	-47.6†
<i>Saxifraga tricuspidata</i>	Forb	-52.5†	0.0	0.1			0.4				-52.0
<i>Solorina bispora</i>	Lich	0.3	-0.3	-0.8	0.5	0.1					-0.2
<i>Solorina crocea</i>	Lich	-1.8	-0.2	0.0	19.7**	0.0		0.0			17.6
<i>Sphaerophorus globosus</i>	Lich	0.1	0.0								0.1
<i>Sphenolobus minutus</i>	Bryoph		-48.3***	-5.0†	0.0					0.0	-53.3*
<i>Stereocaulon alpinum</i>	Lich	-8.6*	28.2*	10.6	15.4*	7.5†	63.4**	10.0*	2.6	0.7	129.9*
<i>Stellaria</i> spp	Forb	-18.3*	33.8*	20.3*	6.8†	-5.3*	-77.2*	0.7	0.2	0.5	-38.4*
<i>Thamnolia subuliformis</i>	Lich	0.0	0.1								0.1
<i>vermicularis</i>											
<i>Tortella fragilis</i>	Bryoph	-0.4	-2.2	-0.2	-50.0***						-52.9†
<i>Tortella ruralis</i>	Bryoph	-10.3†	0.2		8.4*		-8.3**	0.3	0.0	0.6	-9.1
<i>Tristeum spicatum</i>	Gram	1.6	0.9		-0.5		5.9*	6.0*	0.8	-0.3	14.5*
<i>Vaccinium uliginosum</i>	Shrub			0.3					0.0		0.3

2.4.5 Succession

The majority of the sites were located along the Isortoq River (Figure 5). Thirteen historic sites were determined to be younger than 200 years of age in 1964 following the spatial extrapolation of surface ages derived from isochrone lines and were located close to the Barnes Ice Cap. Regression tree analysis found that changepoints in mean plant cover, species richness, and Shannon Index of diversity occurred earlier at sites with a younger surface age in 2009 than in 1964. All three variables had changepoints at 86 years since deglaciation in 2009, whereas changepoints occurred at 160 years since deglaciation for plant cover and at 123 years since deglaciation for species richness and Shannon Index in 1964.





Figures 11a-c. Regression tree analyses showing relationships between site age (years since deglaciation) and mean plant cover (a), mean species richness (b), and mean Shannon Index of diversity (c) for sites less than 200 years of age near Flitaway Lake ($n=13$ for 1964 and $n=13$ for 2009). Open circles represent sites sampled in 1964 and closed circles represent sites sampled in 2009. Dashed lines represent 1964 mean cover, richness, and diversity values for both sides of the median changepoint value of the regression tree, and solid lines represent the same values for 2009. R^2 values for each 1964 and 2009 regression tree analysis shown on each figure.

2.5 Discussion

Studies to date detecting arctic greening have extensively used remote sensing methods using NDVI (Bhatt et al. 2010, Pouliot et al. 2009), however, plot-level studies with collected data providing the potential to explain the ecological mechanisms underpinning greening are still somewhat lacking. This study presents evidence of greening at the landscape and plot-level using vegetation data supported by repeat photography, and is one of the first to assess decade time scale vegetation change in a recently deglaciated high-arctic landscape. We found increases in diversity and the cover of individual species, more notably shrub species, which are well-known contributors to arctic greening (Forbes et al. 2010, Myers-Smith et al. 2011). Additionally, dramatic changes in sites close to the Barnes Ice Cap suggest that plant community succession (vegetation cover and species richness) has accelerated over the past half century.

A student's t-test to determine change in the total cover of bare ground throughout all of the sites sampled in the study area determined that the extent of bare ground decreased significantly ($P < 0.05$) between 1964 and 2009. Evidence of warming and landscape drying trends in the study area is apparent in repeat photography and from plant community changes observed in the study area. In 2009, prominent snowbanks and surface water evident in 1964 have mostly disappeared and plant community change has been greater in moist and wet sites than dry sites. For most plant community types sampled, increased plant cover was also documented and repeat photography suggests the biomass of several plant communities, especially graminoid wetlands, has increased dramatically. These observations are similar to recent ground-based observations of landscape greening and drying reported by studies in the Canadian High-Arctic (Hudson and Henry 2009), Greenland (Daniëls and Molenaar 2011), and northern Alaska (Lin et al. 2012, Villarreal et al. 2012). Increased plant cover has been widely documented in experimental warming studies in the high Arctic and elsewhere in tundra landscapes (Cadieux et al. 2008, Hudson and Henry, 2009, Hill and Henry 2011). Such ground-based observations of increased plant biomass appear to be consistent with satellite-derived observations of increased vegetation cover/plant biomass for the region (Bhatt et al. 2010), *Salix arctica* increased in relative abundance overall more than any other species and this change may serve as an indicator of warming and precipitation changes since Sharp et al. (2013) found that *S. arctica* increased in abundance and leaf area when both low-level and high-level warming were combined with added precipitation. Additionally, the increase in diversity, especially the addition of two new shrubs (*Salix richardsonii* and *Vaccinium uliginosum*), may also indicate warming since diversity is typically greater in warmer low-arctic regions.

2.5.2 Succession

Plant successional dynamics following deglaciation or lake retreat did not follow a linear trend, which is similar to findings of several other studies (Johnson and Miyanishi, 2008). Primary succession through increases in vegetation cover, species richness, and Shannon Index of diversity of sites less than 200 years in age appears to be accelerating. This seems to be among the first studies to report a temporal acceleration of vegetation successional dynamics for a deglaciated arctic tundra landscape using decadal time scale retrogressive vegetation change analysis. Traditionally, plant succession in high arctic

ecosystems has been considered to be relatively slow process (Svoboda and Henry 1987) and the findings from this study suggest that although still slow compared to other ecosystems, plant succession in the high arctic might become more similar to rates experienced at lower latitudes.

We report a younger changepoint for species richness in 2009 than that for 1964, which could be explained by various factors. First, the drying trend in the area could be allowing species adapted to drier conditions to colonize the area and thus make these sites richer, as our dry sites tended to have a higher species richness overall. Additionally, the abundance of cryptogamic crust in sites less than 200 years in 2009 was considerably greater than reported for 1964. Cryptogamic crusts are recognized for capacity to enhance nitrogen fixation (Dickson et al. 2012) and also stabilize the soil surface (Belnap et al. 2001), which alleviates sand abrasion and needle ice formation around seedlings. The dramatic increase of *S. arctica* in these sites also indicates that warming may be having an effect on young vegetation since experimental warming has repeatedly been shown to accelerate growth and the timing of reproduction in certain arctic willows (Jones et al. 2003).

Accelerated successional pathways on newly exposed surfaces has the potential to lead to new or alternate ecosystem states in this landscape, which makes predicting future changes trends more difficult. Additional resampling over the coming decades will be needed to test such a hypothesis, and will also need to isolate short-term variability from long-term change (Elmendorf et al. 2011, Epstein et al. 2004, Villarreal et al. 2012). Initial colonization after deglaciation in polar deserts occurs through newly recruited individuals, which are limited by nutrients, competition, and seed survival. Shevtsova et al. (2009) found that seedling germinability and establishment was decreased with induced warming causing bottlenecks, which varied in its severity between species. Our results do not agree with these findings likely because of the high abundance of the facilitator *Cephaloziella* spp. and the considerable productivity observed at the successional sites (Lara 2012) allows for high levels of recruitment and plant growth.

2.5.3 Community change

Similar directional movement between communities in ordination space suggests plant communities are changing along a common gradient of change. Regression tree analysis showed that the greatest variability in the magnitude of change for our vegetation communities was explained by surface age. *Salix arctica* meadows, herb meadows, and successional meadows were the communities that had the longest vector lengths and thus experienced the greatest magnitude of change over the past half century. Additionally, these three communities had similar slopes indicating they were mostly on horizontal surfaces. These surfaces tend to accumulate more nutrients (Webber 1980) and they are likely to have experienced a greater change in surface hydrology compared to sloping terrain. Our community data shows wet communities shifting along axis two of the ordination, towards dry sites. This agrees with a similar study in nearby Greenland that found that species changes indicated increasingly drier surface conditions (Daniëls et al. 2011).

2.5.4 Diversity and capacities for change in trophic interactions

The increase in plant diversity in the study area and in four out of the nine plant communities examined, and for all sites, agrees with findings of other studies that have assessed changes in plant diversity around the Arctic (Walker et al. 2006, Villarreal et al. 2011). However, one study in northern Alaska reported a decrease in diversity due to increases in shrub abundance (Hollister et al. 2005a). Here we report an increase in both. Although it has been noted that shrubs outcompete other species through light interception and nutrient adsorption (Myers-Smith et al. 2011), *Salix arctica* is a prostrate shrub and is found in a broad range of plant communities in our study area. Such an increase in the abundance of *S. arctica* has huge implications on forecasting high-arctic vegetation response to change, since low-arctic shrubs tend to grow upwards whereas high-arctic shrubs spread laterally (Walker et al. 2006). Although *S. arctica* increased the most in relative cover, this appears to have not been detrimental to overall species diversity. The higher vegetation cover found in 2009 could potentially alter the overall barren nature of the landscape in North-central Baffin Island. This can promote more grazing and introduce a greater number of herbivores, which are generally scarce in the study area. Potential

increases to the terrestrial trophic web could also promote alternate future ecosystem states and make predicting change more difficult.

Based on the interpretation of the observed vegetation change, mainly the acceleration of successional dynamics, the increased vegetation cover noted in the repeat photography, and the similarity of change trajectories shown by different plant communities, we conclude that the documented climate warming in association with plant succession are the main drivers of vegetation change at Baffin Island, Canada. This analysis appears to be among the first to provide ground-based evidence that validates greening trends documented using satellite remote sensing methods and also provides among the first evidence of accelerated successional trends on newly exposed surfaces in the high Arctic.

Chapter 3: Tundra Vegetation Change near Barrow, Alaska (1972-2010)

3.1 Abstract

Knowledge of how arctic vegetation communities will respond to change has been largely derived from plot level experimental manipulation, not from trends of decade-time scale environmental observations. This study documents vegetation community change in 330 marked plots at 33 sites established during the International Biological Program near Barrow, Alaska in 1972. Plots were resampled in 1999, 2008, and 2010 for species cover and presence. Cluster analysis identified nine vegetation communities in 1972. Non-metric multidimensional scaling (NMS) indicates vegetation communities have changed in different ways, and that wet communities have changed more than dry communities. The relative cover of lichens increased over time, while the response of other vegetation functional groups varied. Species richness and diversity also increased over time. The most dramatic changes in the cover of bryophytes, graminoids and bare ground coincided with a lemming high in 2008.

3.2 Introduction

Climate warming is more pronounced at high northern latitudes (ACIA 2005, Serreze 2010). Time series analysis of satellite remote sensing between 1982 and 2008 suggests that there has been a greening of arctic landscapes with the most evident changes occurring where there has been summer warming of coastal tundra adjacent to regions of high sea ice loss (Bhatt et al. 2010). Changes in ecosystem properties underpinning this greening trend remain poorly quantified (Callaghan et al. 2011b). Although some observational studies document vegetation change commensurate with warming, such as shrub expansion (Tape et al. 2006) and treeline advancement (Lloyd 2005, Danby and Hik 2007), there is a general scarcity of ground-based studies that examine vegetation change in the arctic over decade time scales. Experimental studies, however, suggest that some vegetation species respond to warming physiologically (Hobbie and Chapin 1998, Hudson et al. 2011), and phenologically (Arft et al. 1999, Klady et al. 2011), and that these responses may manifest to vegetation community changes (Walker et al. 2006).

Tundra landscapes have high levels of spatial heterogeneity and temporal variability (Epstein et al. 2004), making the evaluation of long-term vegetation change difficult to detect. In part, this is a

result of the fine scale heterogeneity of tundra landscapes - soil moisture, nutrient availability, and seasonal permafrost thaw, for example, often vary spatially over short distances (< 1 m) and are important controls of vegetation community structure and diversity (Webber 1978). Interannual variability in climate and herbivory can also affect vegetation productivity and reproduction (Johnson et al. 2011, Chapin et al. 1987, Walker et al. 1995). In particular, lemmings can remove or destroy as much as 90% of above ground vegetation during winter seasons (Stenseth and Ims 1993). Like other factors controlling vegetation and ecosystem structure and function in the Arctic, the role lemmings play in controlling vegetation structure and function over decadal time scales is poorly resolved due to a lack of a sufficient time-series of data collected at all phases of a population lemming cycle (Ims and Fuglei 2005, Pitelka and Batzli 2007).

Detecting change in the structure of arctic tundra also has significant implications for understanding ecosystem functional responses to arctic change. Different vegetation communities have different ecosystem functional properties (e.g. carbon balance and surface energy budget, Oberbauer et al. 2007, Shaver and Chapin 1991, Chapin et al. 2005), and a change in the spatial extent of different vegetation communities or changes in vegetation species composition and morphology could alter landscape to regional scale fluxes of carbon and surface energy budgets (Strom and Christensen 2007, Sullivan et al. 2008). Of primary concern is a scenario that could lead to the substantial soil organic carbon pool in the Arctic (Tarnocai et al. 2009) being mobilized to a greenhouse active state in the atmosphere or a change in vegetation structure, such as an increase in shrub density, which could alter surface energy balance (Chapin et al. 2005). Both scenarios appear to have the capacity to alter regional to global carbon balance and radiative forcing potential (Schuur et al. 2008).

Remotely detected changes in the normalized difference vegetation index (NDVI) of the Arctic Coastal Plain near Barrow, Alaska appear to be among the most dramatic recorded for much of the Arctic (Bhatt et al. 2010). Factors such as air temperature, soil moisture and snow cover, which control vegetation species composition vegetation community distribution in the Barrow area (Webber et al. 1980), are changing (Stone et al. 2002, Hinzman et al. 2005), but evidence of vegetation change supporting widespread greening in the Barrow area has not been reported. Experimental warming

studies associated with the International Tundra Experiment (ITEX) near Barrow suggest vegetation phenology and vegetation community composition, structure, and biomass respond to moderate warming of surface air (Hollister et al. 2005a, Hollister et al. 2005b, Hollister and Flaherty 2010). Species diversity has also declined in response to experimental warming, which is similar to trends reported in other manipulative warming studies throughout the Arctic (Chapin et al. 1995, Molau and Alatalo 1998, Walker et al. 2006). Although Hollister et al. (2005b) documented changes in species diversity within ITEX control plots between 1994 and 2000, few other studies have reported findings that could otherwise explain the dramatic greening trends documented from satellite imagery for the northern Arctic Coastal Plain in Alaska (Bhatt et al. 2010).

This study documents the rescue and resampling of 33 sites originally established in 1971 near Barrow as part of the International Biological Program (IBP). These sites were originally used with 10 other sites that have since been disturbed or lost to describe vegetation community composition and distribution in the Barrow area (Webber 1978). Specifically, we compare vegetation community composition data collected in 1972 with data from resampling efforts that took place in 1999, 2008 and 2010 to determine how vegetation has changed over time by assessing: i) the direction and magnitude of vegetation change and how this varies for different vegetation communities, ii) how changes in different vegetation functional groups are underpinning vegetation community change, iii) how vegetation species richness and diversity have changed over time, and iv) how the abundance of individual species has changed. A companion study (Lara 2012) reports on the consequences of vegetation community changes documented in this study on ecosystem function. This study is a contribution to the International Polar Year – Back to The Future (IPY-BTF) project (IPY #512), which aimed to determine the impacts of arctic vegetation community change on ecosystem function over decadal time scales by revisiting and resampling historic research sites more than 25 years in age (Callaghan et al. 2011b).

3.3 Methods

3.3.1 Study Area Description

The IBP study area was active between 1970 and 1973, and focused on a study area near Barrow, Alaska at the northernmost point on the Alaskan Coastal Plain (71°18'N 156°40'W) in close proximity to both the Chukchi and Beaufort Seas. The landscape is characterized by ponds, vegetated drained lake basins, low-gradient streams, hummock slopes, high and low-centered polygonal tundra, and meadows (Webber et al. 1980). Floristic diversity near Barrow (ca. 120 species, Murray and Murray 1978) is low relative to the 574 vascular vegetation species recorded on the North Slope of Alaska (Webber 1978). As a contribution to the IBP, Webber (1978) described eight vegetation communities comprised of similar dominant species that differed in their abundance between communities. The distribution of vegetation communities near Barrow is primarily controlled by soil moisture, soil anaerobicity, soil phosphate, and snow cover (Webber et al. 1980). Soils are poorly drained throughout the snow free period (June through September) and active layer depth rarely exceeds 40cm (Hinkel and Nelson 2003). Various forms of natural and anthropogenic disturbance are active in the region. The most abundant herbivore is the brown lemming, which has population outbreaks exceeding 200 ha⁻¹ approximately every 3 to 5 years (Batzli et al. 1980). Other vertebrate herbivores are largely absent from the IBP area, likely due to the close proximity to the City of Barrow. The urban fringe of Barrow has developed toward the study site and now two gravel roads transect the IBP where there is also evidence of occasional off road vehicle use. The study area is likely to have undergone subtle but sustained drying with the increased hydraulic gradient caused by the draining of Middle Salt Lagoon and Footprint and Dry Lakes in 1950 and the gradual headward erosion of Footprint Creek since this time (Brown 1980).

3.3.2 Vegetation Sampling

Forty three vegetation sites (hereafter called historic sites) in the IBP study area were established in 1971 after being chosen for their characteristic representation of the vegetation in the Barrow area. The sites were first sampled in 1972 and then relocated in 1998. Thirty-three sites were found to be intact and were resampled in 1999, 2008, and 2010 using the same method Webber employed at the first sampling in 1972. Most sites measured 1 m x 10 m and consisted of ten contiguous 1 m² plots (330

total). The exception to this are 15 irregularly shaped sites with ten randomly chosen non-contiguous 1 m² plots in sites where ecosystem functional studies were performed prior to Webber's 1972 vegetation community study. We estimated percent cover for all vascular and lichen species within a 10 cm x 100 cm strip along one edge of each 1 m² plot (bryophytes were lumped as a single record for all bryophytes within a plot). Species that occurred outside the strip but within a plot were recorded as present. Plots were sampled close to peak growing season between mid-July and early August. A range of ecosystem functional data were collected in close proximity to these study plots and are reported by Lara (2012).

3.3.3 Data Analysis

We calculated relative cover for each species and non-biological category (e.g. bare ground, litter) in every 1 m² plot by multiplying cover estimates by 100 and dividing by the total cover of all species and non-biological categories in the plot. Relative presence was calculated by multiplying presence by 100 and dividing by the total species richness of each plot. We then summed relative cover and relative presence and divided this by 2 to obtain a cover index for each species and category in every plot (*sensu* Webber, 1978). Hereafter, this index is referred to as a species index. Species index values ($n = 75$ species) were used to classify the original plots sampled in 1972 ($n = 430$ plots) into vegetation discrete communities using Hierarchical Cluster Analysis in PC-ORD 5.10 (MjM Software Design Gleneden Beach, Oregon, USA). A Sørensen's similarity coefficient was used with a flexible beta linkage method ($\beta = -0.25$) to minimize chaining (McCune and Grace 2002). A cutoff of less than 50 percent similarity was used to match our vegetation community classification with a regional supervised land cover classification produced by Tweedie et al. (Submitted). Sub-communities were created where a group not identified by the regional land cover classification clustered within the percent cutoff range. Acronyms were assigned for each community as described in Table 6. Indicator species analysis was performed using PC-ORD following Dufrene and Legendre (1997) with a randomized approach to test for significance. The five species with the highest indicator value in each vegetation community are reported in Table 6.

We used non-metric Multidimensional Scaling (NMS) to ordinate all plots for all sampling years in PC-ORD using a Sørensen (Bray-Curtis) similarity coefficient and a random starting configuration,

and 250 runs with randomized and real data. Dimensionality and stress were determined by PC-ORD and to aid visualization, axes scores for each plot were averaged by vegetation community derived from the cluster analysis (Figure 12). An index of net change for each vegetation community was determined by summing the absolute differences in axis scores between the three inter-sampling periods (1972-1999, 1999-2008, and 2008-2010). The magnitude of vegetation community change over time was assessed by running an additional NMS ordination of all data in PC-ORD with plot data arranged chronologically by year and with standardized plot names for each sampling year. The successional vector representing change through time for each plot was calculated using trigonometry to compute the hypotenuse length between successive axis scores in the ordination. Hypotenuse lengths were normalized by the number of years within a given sampling interval, and then averaged for each vegetation community and log-transformed. After reviewing preliminary results, dramatic changes in vegetation communities appeared to correspond to lemming population outbreaks. In order to ascertain the likely impact of herbivory on vegetation community change, we plotted the mean vector lengths against sampling intervals relative to a lemming population outbreak. Sampling in 2008 was the only sampling year that coincided with a lemming population high and the sampling in 1972 and 2010 were one and two years following lemming population outbreaks. Long-term vegetation community change was assessed by determining trajectories of change over the 1972-2010 sampling interval.

Relative cover of bare ground, litter and vegetation functional groups, following Chapin et al. (1996), were calculated following and analyzed using a multivariate analysis of variance (MANOVA) in JMP 9.0 (SAS Institute Cary, North Carolina, USA) to test differences in the relative cover of functional groups in each community at a given sampling year. Wilk's λ was used to determine if each functional group varied between sampling years and among vegetation communities at different sampling years (sampling year*vegetation community). Species richness and the Shannon's Index of diversity were calculated in PC-ORD for each plot for each sampling year using species cover values averaged by vegetation community. To determine how species richness and Shannon's Index of diversity varied among vegetation communities through time, we used a repeated measure ANOVA in JMP 9.0 with vegetation community as the within subject factor. If the Wilk's λ statistic for either time, or time by

vegetation community interaction resulted in a probability less than 0.05, differences between communities and sampling dates were tested using least significant difference (LSD) tests of the univariate analysis of variance (ANOVA) within the repeated measures.

To determine how the relative abundance of these species differed between sampling years, we assumed the data fit a Poisson distribution and performed a general linear model in JMP 9.0 with a log-link function using a Firth Adjusted Maximum Likelihood to estimate parameters. This approach was chosen due to the lack of uniformity for all species among vegetation communities that resulted in strongly non-normal datasets for individual species. We applied a separate general linear model for each species using vegetation community and sample data as factors, and determined significance for that species and vegetation community if the probability of the resulting X^2 for the vegetation community*sample data interaction was below 0.1. We also determined if the cover of each species was different between sampling dates across all plots if the probability of the X^2 for sample date was less than 0.1.

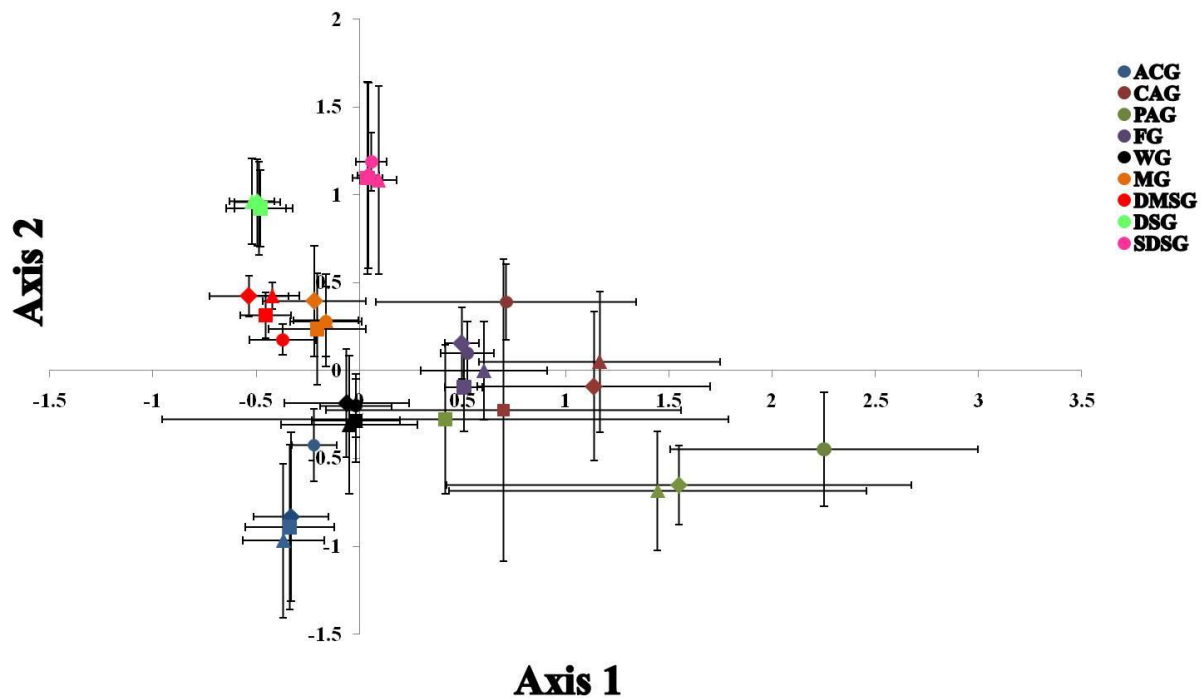


Figure 12. Non-Metric Multidimensional Scaling ordination of all vegetation communities for all years sampled (1972, 1999, 2008, 2010) in the coastal tundra near Barrow, Alaska. Points represent the mean NMS axis scores for all plots classified in a given vegetation community in a given sampling year. Sampling years are represented by different shapes (1972-circle, 1999-diamond, 2008-square, 2010-triangle). Axis one was most strongly correlated with thaw depth ($r^2 = 0.326$), and axis two was most strongly correlated with soil moisture ($r^2 = 0.839$).

Table 6. List of vegetation communities identified from the cluster analysis of the 1972 plot sampling in the coastal tundra near Barrow, Alaska. The number of plots sampled, dominant land form and vascular species, and indicator species are provided for each vegetation community. The vascular indicator was determined by indicator species analysis (* indicates $P < 0.05$) Note that only two species were present in PAG tundra in 1972.

Map Class	1972 No. Plots	No. Plots Resampled	Name	Dominant Land Form	Vascular Indicator Species	Dominant Vascular Species
ACG	53	53	Aquatic <i>Carex</i> graminoid tundra (ACG)	Low-center polygons, pond margins, ponds, polygon troughs	<i>Hierochloe pauciflora</i> * <i>Juncus biglumis</i> <i>Eriophorum russeolum</i> , <i>Carex aquatilis</i>	<i>Carex aquatilis</i> <i>Eriophorum angustifolium</i> <i>Hierochloe pauciflora</i> <i>Eriophorum russeolum</i> <i>Cardamine pratensis</i>
CAG	20	20	Creek <i>Arctophila</i> graminoid tundra (CAG)	Creek banks, creek beds	<i>Phippsia algida</i> * <i>Stellaria humifusa</i> * <i>Saxifraga rivularis</i> <i>Ranunculus pygmaeus</i> <i>Cochlearia officinalis</i>	<i>Arctophila fulva</i> <i>Arctagrostis latifolia</i> <i>Stellaria humifusa</i> <i>Dupontia fisheri</i> <i>Phippsia algida</i>
PAG	10	10	Pond <i>Arctophila</i> graminoid tundra (PAG)	Ponds	<i>Ranunculus pallasii</i> <i>Arctophila fulva</i>	<i>Ranunculus pallasii</i> <i>Carex aquatilis</i> <i>Arctophila fulva</i>
FG	60	40	Seasonally-flooded graminoid tundra (FG)	Wet meadows, pond margins	<i>Ranunculus gmelinii</i> * <i>Caltha palustris</i> * <i>Cardamine pratensis</i> <i>Cerastium jenisejense</i> <i>Eriophorum angustifolium</i>	<i>Dupontia fisheri</i> <i>Eriophorum angustifolium</i> <i>Carex aquatilis</i> <i>Arctophila fulva</i> <i>Saxifraga cernua</i>
WG	107	86	Wet graminoid tundra (WG)	Moist meadows, low-center polygons, polygon troughs	<i>Eriophorum scheuchzeri</i> <i>Carex aquatilis</i> <i>Saxifraga hieracifolia</i> <i>Saxifraga foliolosa</i> <i>Ranunculus nivalis</i>	<i>Carex aquatilis</i> <i>Eriophorum scheuchzeri</i> <i>Eriophorum angustifolium</i> <i>Dupontia fischeri</i> <i>Eriophorum russeolum</i>
MG	69	60	Moist graminoid tundra (MG)	high-center polygons, meadows, and rims of low-center polygons	<i>Cerastium jenisejense</i> * <i>Cochlearia officinalis</i> * <i>Diapensia lapponica</i> * <i>Saxifraga punctata</i> * <i>Calamagrostis homlii</i>	<i>Calamagrostis holmii</i> <i>Salix rotundifolia</i> <i>Carex aquatilis</i> <i>Poa arctica</i> <i>Eriophorum angustifolium</i>
DMSG	40	20	Dry-moist dwarf shrub-graminoid tundra (DMSG)	High-center polygons, dry meadows, and slopes	<i>Chrysosplenium tetandrum</i> * <i>Papaver macounii</i> * <i>Salix pulchra</i> * <i>Senecio atropurpureus</i> * <i>Salix rotundifolia</i>	<i>Salix pulchra</i> <i>Carex aquatilis</i> <i>Salix rotundifolia</i> <i>Eriophorum russeolum</i> <i>Poa arctica</i>
DSG	50	30	Dry dwarf shrub-graminoid tundra (DSG)	Dry meadows and hummocks	<i>Cassiope tetragona</i> * <i>Draba spp</i> * <i>Dryas integrifolia</i> * <i>Eutrema edwardsii</i> * <i>Rumex arcticus</i> * <i>Sagina intermedia</i> * <i>Salix phlebophylla</i> *	<i>Salix rotundifolia</i> <i>Dryas integrifolia</i> <i>Cassiope tetragona</i> <i>Eriophorum angustifolium</i> <i>Arctagrostis latifolia</i>

SDSG	21	11	Successional-dry dwarf shrub- graminoid tundra (SDSG)	High-center polygons, creek banks	<i>Vaccinium vitis-idaea</i> * <i>Potentilla hyparctica</i> <i>Luzula confusa</i> <i>Petasites frigidus</i> <i>Papaver hultenii</i>	<i>Salix rotundifolia</i> <i>Petasites frigidus</i> <i>Luzula confusa</i> <i>Potentilla hyparctica</i> <i>Poa arctica</i>
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3.4 Results

3.4.1 Vegetation Community Change

Cluster analysis of the original 430 plots sampled by Webber in 1972 yielded nine vegetation communities (Table 6). Wet graminoid and MG tundra had the highest number of plots, while PAG and SDSG tundra had the lowest with only one site located in each vegetation community (10 plots each). The NMS ordination of all plots and sample times recommended a two-dimensional solution and had a final stress of 23.43 that is typical for large datasets (McCune and Grace, 2002). Instability was 0.00367 after 500 iterations and the proportion of the variance explained by the ordination represented 79% of the cumulative variance with axis one and two representing 30.6% and 48.4% respectively. Axis one correlated most strongly with thaw depth ($r^2 = 0.326$), while axis two correlated with soil moisture ($r^2 = 0.839$). Generally, wet and aquatic communities were more dynamic between sampling years than dry and moist community types (Figure 12). Plots associated with each of the classified vegetation communities showed no sustained change trajectory along either axis. Mean axis scores for each vegetation community were within one standard deviation of each other at each sampling year. The greatest community change was detected after a two year period following a lemming outbreak (2008-2010, average vector length = 0.20, Figure 13), while the least change was detected over the long term 1972-2010 change trajectory (0.01).

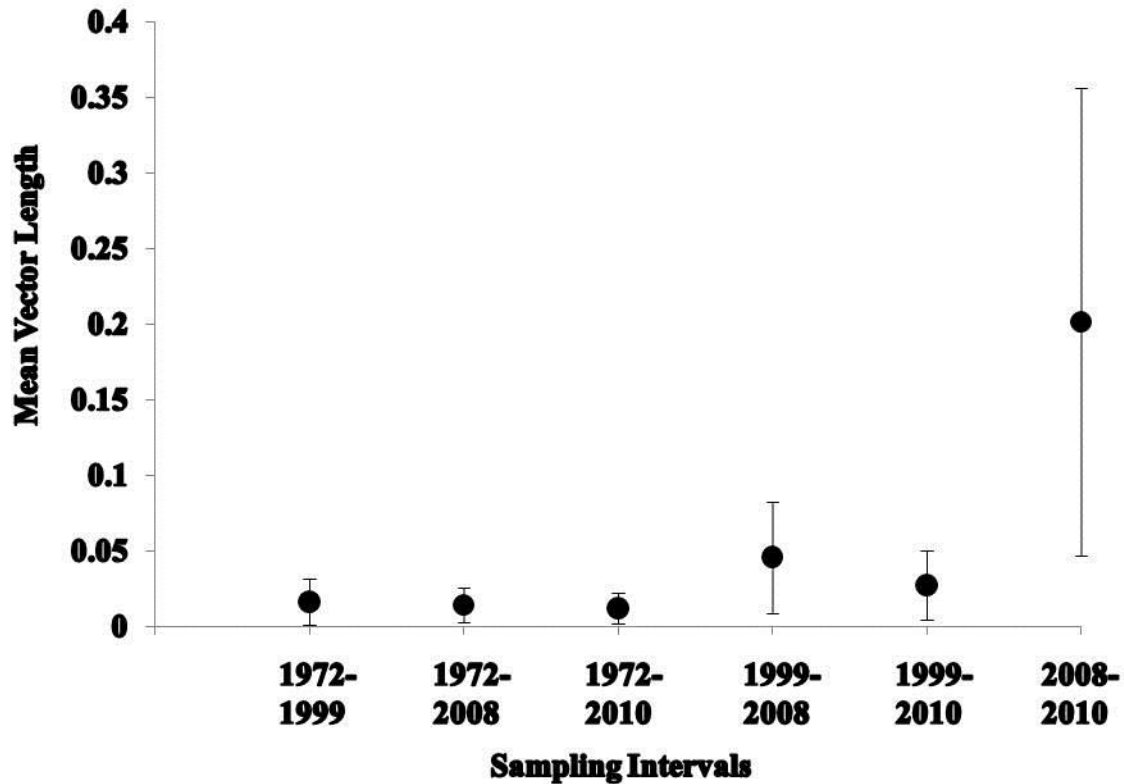


Figure 13. Plot showing mean (circle symbol) and standard deviation for vector lengths between NMS scores for the six different sampling intervals (1972-1999, 1972-2008, 1972-2010, 1999-2008, 1999-2010, 2008-2010) for communities in the coastal tundra near Barrow, Alaska. Sampling in 2008 coincided with a lemming high, and the sampling in 1972 and 2010 were one and two years following lemming population outbreaks respectively.

3.4.2 Changes in Vegetation Functional Groups

The relative cover of vegetation functional groups for all years was significantly different (MANOVA, $p < 0.05$, Wilk's $\lambda = 0.27$) between sampling years with the exception of shrubs (numerator $df = 5$, denominator $df = 1312$), and significantly different among vegetation communities at different sampling years with the exception of forbs, lichens, and shrubs (numerator $df = 15$, Denominator $df = 1312$). Shrub cover showed no noticeable change over time (Figure 14), while cover for litter, graminoids, and bryophytes appeared to vary considerably between sampling years. The relative cover of bryophytes was highest in 1972 (26.5%, Figure 14All), while lichen and shrub cover was lowest (5.2% and 4.2%, respectively). Graminoid cover was greatest (39.8%) and forbs lowest (6.5%) in 1999. Bare ground, litter, and shrub cover were highest (5.4%, 28.1% and 5.3% respectively) and graminoid

and bryophyte cover the lowest (22.5% and 19.3% respectively) in 2008. In 2010, forb and lichen cover were highest (13.3% and 13.3% respectively), while the cover of bare ground and litter was lowest (0.3% and 16.5% respectively). Lichen cover appears to have steadily increased over time (5.2-13.3%), and forb cover shows a similar trend since 1999 (6.5-13.3%).

Change in the relative cover of vegetation functional groups differed for each vegetation community (Figure 14). The relative cover of bare ground, graminoids, litter, and bryophytes in ACG tundra, FG tundra (Figure 14FG), and WG tundra fluctuated considerably. Shrub cover increased slightly in CAG tundra (CAG, Fig. 2, 0-3.7%), but showed no change in other vegetation communities. In PAG tundra, forbs and litter decreased (63.4-26.4% and 32.0-5.5%, respectively), while graminoids increased (4.5-67.8%). In MG tundra forbs and lichen cover increased over time (2.7-9.6% and 9.4-25.9%, respectively) and no change was observed for other functional groups. In DMSG tundra, the cover of forbs and lichens increased (1.3-6.5% and 1.7-27.8%, respectively), while that of graminoids, litter, and bryophytes fluctuated. In DSG tundra cover of forbs and lichens increased (10.7-19.5% and 15.9-29.4%, respectively), while the cover of bryophytes (22.6-14.5%) and shrubs (35.1-16.8%) decreased. In SDSG tundra the cover of most functional groups varied between sampling year with the exception of shrubs, which increased slightly (0-2.6%). Repeat photos (Figure 15) show a time series of aquatic (CAG tundra), wet-moist (WG tundra), and dry (DSG tundra) community change in 1972, 2000, 2008 and 2010. The most dramatic change in this photo series is for PAG, where there has been a consistent increase in the cover of *Dupontia fisheri* and a reduction in the cover of *Arctophila fulva* over time. There appears to be little obvious change in WG and DSG tundra over time. However, overall vegetation cover appeared to be lowest in 2008, particularly in PAG tundra.

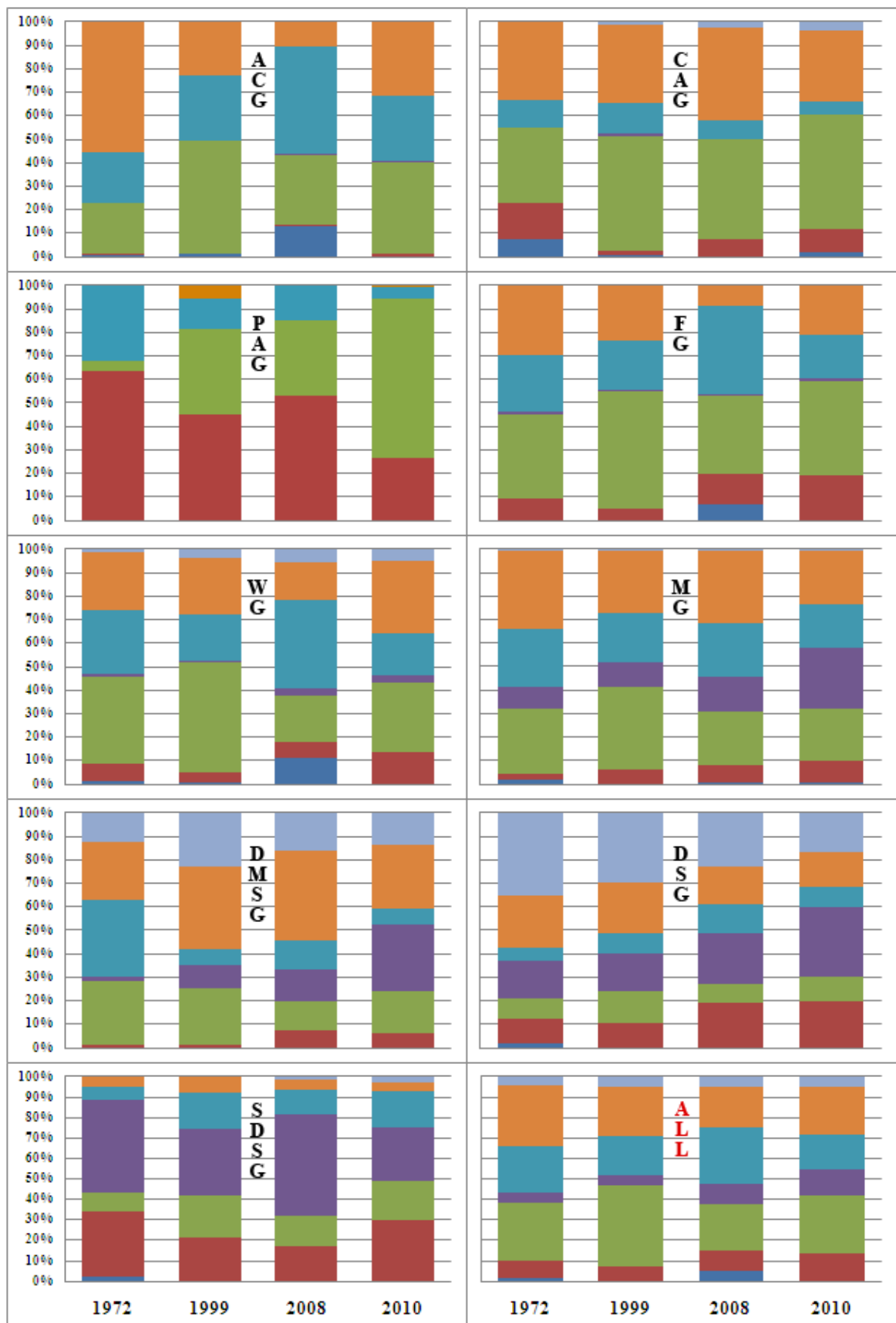


Figure 14. Relative cover of vegetation functional groups and non-biological categories for each vegetation community and sampling year (1972, 1999, 2008, 2010) in the coastal tundra near Barrow, Alaska, and for all plots in each sampling year (bare ground -dark blue, forbs -red, graminoids -green, lichen -purple, litter -aqua, bryophytes -orange, and shrubs -light blue).

3.4.3 Changes in Vegetation Diversity and Individual Species

Diversity, as measured by both richness and Shannon's Index was higher in 2010 than any other sampling date for specific vegetation communities. In general, vegetation communities with low soil moisture (e.g. DSG and SDSG) were the most diverse, while communities with higher soil moisture (e.g. ACG, CAG and PAG) were the least diverse. For most vegetation communities, the greatest increase in richness was between 1999 and 2010, and the largest increase in Shannon Index was between 1972 and 2010 (Table 7). Between 1972 and 2010, MG, FG and DSG tundra had significant increases in both richness and Shannon Index values. For CAG, richness was higher in 2010 than in 1972 but Shannon's Index was not, while SDSG and PAG had higher Shannon's Index values in 2010 but richness did not differ. Shannon's Index values for ACG and WG tundra were significantly lower in 2010 than 1972, but richness did not differ, and the diversity of DSMG tundra showed no long-term difference in either diversity metric.

Table 7. Change in mean species richness and Shannon Index of diversity between each sampling interval for each vegetation community (* significant increase or decrease, $p < 0.05$). Communities were sampled in 1972, 1999, 2008, 2010 near Barrow, Alaska.

	Species Richness					
	1972-1999	1972-2008	1972-2010	1999-2008	1999-2010	2008-2010
ACG	-1.64*	-1.55*	-0.94	0.09	0.70	0.60
CAG	1.80	1.75	2.30*	-0.05	0.50	0.55
PAG	1.60	1.20	1.40	-0.40	-0.20	0.20
FG	-1.88*	1.40	2.68*	3.28*	4.55*	1.28*
WG	-2.43*	-1.56*	-0.38	0.87	2.05*	1.17*
MG	-0.45	0.87	3.08*	1.32	3.53*	2.22*
DSMG	-1.65	-0.45	0.45	1.20	2.10	0.90
DSG	-0.03	0.53	4.40*	0.57	4.43*	3.87*
SDSG	1.73	2.18	4.27*	0.45	2.55	2.09
All	-1.09*	-0.09	1.38*	1.00*	2.48*	1.48*
	Shannon Index					
	1972-1999	1972-2008	1972-2010	1999-2008	1999-2010	2008-2010
ACG	-0.20	-0.34*	-0.23*	-0.14	-0.03	0.11
CAG	-0.08	0.03	0.12	0.12	0.20	0.09

PAG	0.54*	0.34*	0.39*	-0.20	-0.15	0.05
FG	-0.13	0.15*	0.23*	0.28	0.36	0.08
WG	-0.19*	-0.21*	-0.10*	-0.02	0.09	0.11*
MG	0.02	0.08	0.28*	0.06	0.27*	0.21*
DMSG	-0.04	0.00	0.14	0.04	0.18	0.14
DSG	0.04	0.09	0.31*	0.05	0.27*	0.22*
SDSG	0.07	0.04	0.23	-0.02	0.16	0.19
All	-0.08*	-0.06*	0.08*	0.03	0.16*	0.13*

Of the 19 species that comprised >80% of the overall cover (Table 8), five were higher in 2010 than 1972 (*Arctophila fulva*, *Cetraria islandica*, *Dupontia fisheri*, *Luzula arctica*, and *Salix pulchra*), and two were lower (*Salix rotundifolia* and *Saxifraga cernua*). Other changes were detected in the more rare species with long-term increases in *Cardamine pratensis*, *Saxifraga foliolosa*, *Stellaria edwardsii*, *Luzula confusa*, *Alectoria nigricans*, *Bryocaulon divergens*, *Cladonia* spp, and *Thamnolia* spp, and decreases in *Calamagrostis holmii* and *Pseudevernia consocians* (Table 9). Species changes were generally most significant in vegetation communities where they were most common (Table 8 and 9).

Table 8. Mean difference in the relative cover of nineteen species that comprise >80% cover in the sites sampled for all sampling years (1972, 1999, 2008, 2010) in the coastal tundra near Barrow, Alaska. Bold values represent significant differences between 1972 and 2010 ($\dagger < 0.1$, $* < 0.05$, $** < 0.01$, $*** < 0.001$) from a general linear model assuming a Poisson distribution. Functional groups (FG) include: graminoid (G), evergreen shrub (ES), lichen (L), forb (F), and deciduous shrubs (DS). *Total* describes differences in cover found in all plots.

Vegetation Community											
Species	FG	SDSG	DSG	DMSG	MG	WG	FG	CAG	ACG	PAG	Total
<i>Salix pulchra</i>	DS		2.8\dagger			4.2***			0.1		1.4\dagger
<i>Salix rotundifolia</i>	DS		-14.0***	-0.8	-0.8	0.9	0.0	3.3*			-1.0*
<i>Cassiope tetragona</i>	ES		-6.5***								-0.6
<i>Petasites frigidus</i>	F	-6.3**	0.1	0.4	4.7***	2.8**	2.9	0.7			1.8
<i>Ranunculus pallasii</i>	F						-0.1	0.6		-60.3***	-1.8
<i>Saxifraga cernua</i>	F	0.4	-0.3	-1.3	-1.3	-2.0**	-1.4	-0.2	0.0		-1.0*
<i>Arctagrostis latifolia</i>	G	13.7***	3.0**	1.5	-0.1			-8.2***			0.3
<i>Arctophila fulva</i>	G							20.9***		24.5***	2.0*
<i>Carex aquatilis</i>	G	1.4	1.2	-17.3***	-2.6\dagger	-6.0*			34.1***	5.5	2.7
<i>Dupontia fisheri</i>	G	1.6		-1.1	0.9	-1.7\dagger	4.5	18.1***	0.3	23.0***	2.1***
<i>Eriophorum angustifolium</i>	G	0.3	-1.0	-1.1	-1.4	-2.2*	-8.2**	0.3	1.8**		-1.7
<i>Eriophorum russeolum</i>	G	1.8	0.0		0.2	-3.0***	-1.7*	0.6	3.0**	6.9*	-0.2
<i>Eriophorum scheuchzeri</i>	G						-0.1				0.0
<i>Hierochloa pauciflora</i>	G								0.1		0.0
<i>Luzula arctica</i>	G		1.3	0.9	5.2***	0.0	0.5		0.0		1.2**
<i>Poa arctica</i>	G	-3.4	0.5	-1.8	-5.2***	1.1	11.8***		0.2		0.6
<i>Cetraria cucullata</i>	L	1.1	0.9	0.6	1.1**	0.0					0.3
<i>Cetraria islandica</i>	L	-0.4	4.1*	4.3*	6.0***	0.6*	0.0		0.0		1.9***
<i>Dactylina arctica</i>	L	-4.1**	1.1	3.5**	2.2*	0.2	0.1				0.6

Table 9. The mean difference in relative cover of species not reported in Table 8 for all sampling years (1972, 1999, 2008, 2010) found in vegetation communities of the coastal tundra near Barrow, Alaska). Bold values represent significant differences ($\dagger < 0.1$, $* < 0.05$, $** < 0.01$, $*** < 0.001$) from a general linear model assuming a Poisson distribution. Functional groups (FG) include classes for: graminoids (G), evergreen shrubs (ES), lichens (L), forbs (F), and deciduous shrubs (DS). The *Total* column describes changes in all communities (entire dataset).

Species	FG	Vegetation Community									Total
		SDS G	DSG	DMSG	MG	WG	FG	CAG	ACG	PAG	
<i>Diapensia lapponica</i>	ES				0.0						0.0
<i>Vaccinium vitis-idaea</i>	ES	3.9**									0.1
<i>Caltha palustris</i>	F						0.1	2.3**			0.2
<i>Cardamine pratensis</i>	F					1.4***	0.9	0.8	0.0		0.5*
<i>Cerastium jenisejense</i>	F					0.0	1.2†	1.2			0.2
<i>Chrysosplenium tetrandrum</i>	F					0.0	0.7†	0.1			0.1
<i>Cochlearia officinalis</i>	F	0.7					0.2	-1.5*			-0.1
<i>Draba spp</i>	F		0.3								0.0
<i>Eutrema edwardsii</i>	F		0.3								0.0
<i>Papaver hultenii</i>	F		-0.8			0.0					-0.1
<i>Papaver macounii</i>	F		-0.6								-0.1
<i>Pedicularis kanei</i>	F		1.7*	0.1	0.0			0.6	0.2		0.2
<i>Polygonum viviparum</i>	F		2.1**			0.2					0.2
<i>Potentilla hyparctica</i>	F	4.1**	0.4					0.1			0.2
<i>Ranunculus nivalis</i>	F		0.1	0.0	0.5	-0.5†	0.5	0.3			0.1
<i>Ranunculus pygmaeus</i>	F	1.0						-0.2			0.0
<i>Rumex arcticus</i>	F		0.1								0.0
<i>Saxifraga foliolosa</i>	F	-0.2			0.3	0.2	3.1***		0.2		0.5*
<i>Saxifraga hieracifolia</i>	F		-0.1			0.1	0.4	0.1			0.1
<i>Saxifraga punctata</i>	F		2.6**		0.0	0.1		0.1			0.3
<i>Saxifraga rivularis</i>	F							-0.9			-0.1
<i>Senecio atropurpureus</i>	F		0.2	2.6**	0.1						0.2
<i>Stellaria edwardsii</i>	F	-0.3	0.6	0.1	1.0**	0.1	1.5†	0.4			0.5*
<i>Stellaria humifusa</i>	F					0.0	0.6*	-16.3***			-0.9
<i>Stellaria laeta</i>	F			0.9		-0.3*	-0.3				-0.1
<i>Alopecurus alpinus</i>	G		0.4	0.1		-0.4	0.3	0.5			0.0
<i>Calamagrostis holmii</i>	G	-1.2		0.4	-4.7***	0.2	-2.9*		0.1		-1.2*

<i>Eriophorum vaginatum</i>	G				0.1					0.0
<i>Juncus biglumis</i>	G		0.2			-1.0*	-0.1	0.2	-0.1	-0.3
<i>Luzula confusa</i>	G	4.6*	-0.6	1.1†	0.7	0.0	0.2	0.2		0.3†
<i>Phippsia algida</i>	G							-5.0***		-0.3
<i>Alectoria nigricans</i>	L	4.0	1.0	0.1	2.7***	0.0				0.7**
<i>Bryocaulon divergens</i>	L	1.9	3.4**		1.9***					0.7**
<i>Cladonia spp.</i>	L	-0.4†	1.2	2.8†	3.9***	0.2			0.2	1.1***
<i>Flavocetraria nivalis</i>	L	0.9	0.1		0.1					0.1
<i>Lobaria linita</i>	L			1.7*		0.0			0.0	0.1
<i>Masonhalea richardsonii</i>	L		0.3		0.1					0.0
<i>Ochrolechia frigida</i>	L	0.1								0.0
<i>Peltigera spp.</i>	L		-1.0	0.8	0.0	-0.5	-1.1		0.0	-0.3
<i>Pseudevernia consocians</i>	L	-19.7***								-0.7*
<i>Psoroma hypnorum</i>	L	0.2	0.2	0.1	0.0					0.0
<i>Solorina crocea</i>	L	0.4								0.0
<i>Sphaerophorus globosus</i>	L	2.2	0.3	0.1	0.5					0.2
<i>Stereocaulon tomentosum</i>	L		-0.4					0.0		0.0
<i>Thamnolia spp.</i>	L	1.6	1.4	2.1†	2.3***					0.7***

3.5 Discussion

Because of the potential impact of climate change on biodiversity and the mobilization the large stocks of soil organic carbon to the atmosphere (Finzi et al. 2011), understanding how arctic vegetation communities have changed over decadal time scales in response to climatic and other change is imperative. While greening of the Arctic has been documented from satellite remote sensing (Bhatt et al. 2010), and change in ecosystem structure and function has been modeled (Epstein et al. 2004, Euskirchen et al. 2009) and appears to have occurred in response to experimental warming (Hudson et al. 2011) and nutrient addition (Chapin et al. 1995), relatively few studies have examined change in arctic tundra systems over decadal time scales. Two dominant themes have emerged from this study affirming that vegetation community change in Barrow is occurring. The first is that short term community responses to herbivory can be greater than and indeed mask longer-term changes depending on when sites are sampled. The second theme is that no consistent and overarching change is occurring among all vegetation communities in the Barrow landscape. Instead, most vegetation communities appear to be responding differently over time.

3.5.1 Vegetation community responses to herbivory mask long-term change

While the interannual variability of species phenology and cover can be substantial for many arctic vegetation communities (Knorre et al. 2006), interannual differences in the structure of communities that support large fluctuating populations of lemming such as those near Barrow (Pitelka and Batzli 2007) can be even greater. The large change in vector lengths between 2008 and 2010, relative to other sampling year comparisons suggests that periodic lemming disturbance can mask long-term vegetation change. The fluctuations in the relative cover of species in communities that are key lemming habitat, such as MG, FG and WG tundra between sampling years is partially explained by lemming herbivory. Lemmings in Barrow typically graze moist vegetation communities in late summer (Batzli et al. 1980), which likely explains why ACG, FG, and WG tundra showed a low cover of graminoids in 2008. The cover of shrubs and lichens (with the exception of shrubs in DMSG tundra) are likely to have not fluctuated due to the absence of these functional groups in the diets of lemmings, and

also because caribou, which graze on lichens (White and Trudell 1980), are rarely encountered in the study area.

Much of the variability in species cover and vegetation community change between sampling dates appears to be explained by the time since the last lemming population outbreak, which agrees with the notion that communities respond differently to intense herbivore disturbance (Johnson 2011, Speed et al. 2010). Studies have recorded negative impacts on moss abundance primarily as a result of trampling (Moen et al. 1993, van der Wal et al. 2006, Virtanen 2000). Our data suggest similar results, with low abundance of moss in 2008 during the lemming high. Outbreaks of lemming populations clearly influence vegetation community structure in the Barrow area (see also Johnson et al. 2011), highlighting the importance of considering the timing of resampling relative to lemming population cycles, particularly since climate warming is expected to decrease the frequency, and amplitude of lemming outbreaks in tundra ecosystems in the future (Ims et al. 2011).

3.5.2 Dynamics of vegetation community change differ between communities

The nine classified vegetation communities are similar to the eight communities reported by Webber (1978). The additional class is likely a result of both the use of more modern statistical software as well as the division of 43 historic sites, classified by Webber, into 430 individual plots. We feel our analysis correctly identified distinctive vegetation community characteristic of the coastal tundra near Barrow. Sustained directional change among all vegetation communities was not observed. The only exception to this was an overall increase in vegetation diversity, which contradicts results of passive experimental warming and some observational studies (Walker et al. 2006), but supports other observational studies (Wilson and Nilsson 2009). The mean annual air temperature near Barrow is increasing, although maritime influences may have lessened the magnitude of warming (Bhatt et al. 2010, Stone et al. 2002). However, substantial non-directional movement in ordination space between sampling periods for certain communities, as well as changes in the abundance of species and functional groups, suggests changes are occurring, although the link between climate, hydrologic, succession and other change drivers is unclear and a clear cut attribution of change is not possible at this time.

Change was greatest along NMS axis two, which correlated with soil moisture and the wettest communities appear to be the most dynamic over the study period (1972-2010). ACG tundra demonstrated a linear pattern of change through time, decreased diversity, and increases in graminoid cover, particularly *Carex aquatalis* to the detriment of bryophytes. Creek *Arctophila* graminoid and PAG tundra also fluctuated through time, but graminoids and overall diversity increased. Flooded graminoid and WG tundra didn't fluctuate as much in ordination space, but forbs and graminoids increased. Alternatively, drier communities appear to have changed little over the study period. Moist graminoid, DSMG, and DSG tundra all varied little in ordination space, although diversity increased but was largely associated with increases in lichens. In ordination space SDSG tundra also varied little and had lower lichen abundance in 2010 compared to 1972. Combined, these results suggests a slight drying of the overall coastal tundra landscape, which could be related to regional warming, historic draining of nearby lakes in 1950 (Brown et al. 1980), or other factors. Interestingly, Lin et al. (2012), using multitemporal classification of aerial and satellite imagery, suggest that a tundra landscape several kilometers from the study has generally dried over the past 60 years with the extent of dry and moist tundra increasing and that of wet tundra decreasing over time, which corroborates findings from this study. Our results for changes in shrub cover are not consistent with other long-term observations and experimental studies (Myers-Smith et al. 2011, Tape et al. 2006, Walker et al. 2006, Sturm et al. 2001). The prostrate evergreen shrub *Cassiope tetragona* and deciduous shrub *Salix rotundifolia* decreased while the more erect deciduous shrub *Salix pulchra* increased. This highlights importance of individual species responses to warming that may be masked and mask detection of functional group change when lumped into well recognized functional groups as we did in this study.

3.6 Conclusion

Resampling of vegetation communities in historic research plots suggest that vegetation community, functional groups, and species change can be dynamic and different for different vegetation communities. The short-term response of vegetation to lemming population outbreaks can mask long-term change. Graminoids and bryophytes decrease in abundance during outbreak years while litter and bare ground increase. Over the 38-year study period, Diversity increased for most vegetation

communities, and wetter communities changed more than dry and moist vegetation communities. A slight drying trend appears to be occurring at the study site but the climatic factors and hydrologic processes related to this are unclear. The continued effort to conclusively understand how tundra landscapes are responding to warming is important considering the potential consequences of feedbacks from these landscapes to the global system and the variability and complexity associated with temporal change dynamics in arctic tundra systems.

Chapter 4: Little Evidence of Decade Time-Scale Change in Vegetation Communities at a Low-Arctic Site near Atqasuk, Alaska

4.1 Abstract

As a consequence of warming in high latitudes, there have been a plethora of multifarious and widespread changes in vegetation reported for arctic tundra. These changes have been recorded from the plot level to the biome level using primarily experimental, observational, and satellite remote sensing approaches. However, a small group of studies have also documented a resistance to change in experimental warming and observation studies. To date there has been little attention paid to why some locations are prone to change while others are not under similar degrees of experimental warming and/or patterns of climate change. In order to address this overarching challenge, improved identification of hotspots of vegetation change and locations that appear to be resistant to change and improved understanding of how tundra ecosystems have changed over decadal time scales are needed. We resampled vegetation sites established near Atqasuk, Alaska in 1975 and determined i) the direction and magnitude of vegetation community change and how this varies among communities, ii) whether there is change at both the vegetation functional type and species level, and iii) whether vegetation diversity has changed over time in these communities. We report small shifts in communities in ordination space, and that the variation in the magnitude of change for all communities appears to have been controlled by soil moisture. Of the repeat cover measurements on 140 species, significant increases or decreases were documented for 47 species. No changes in vegetation functional groups between 1975 and 2009 were found. Species evenness increased across all sites but the rate of increase was lower between 1975 and 2009 than between 2000 and 2009, suggesting accelerated change and homogenization of vegetation communities in this landscape. Relative to other studies, the changes we report for vegetation communities near Atqasuk is small and several hypotheses are presented to explain this phenomenon.

4.2 Introduction

Recent changes in global climate are more pronounced in the Arctic (Kaufman et al. 2009), and there is increasing evidence that these changes, especially warming, are causing dramatic effects on arctic ecosystems (ACIA 2005, Callaghan et al. 2011b, Epstein et al. 2013). On the North Slope of

Alaska, changes in vegetation cover have been documented since 1981 using satellite derived normalized vegetation index (NDVI), which suggests a widespread greening trend has been occurring (Jia et al. 2003). This greening trend appears to be correlated with sea ice loss (Bhatt et al 2010). In Alaska, warming is impacting terrestrial landscapes as evidenced by hydrological shifts (Hinzman et al. 2005, Lin et al. 2012), and the enhanced prevalence of thermokarst (Rowland et al. 2010), tundra fires (Racine et al. 2004), and shrub expansion (Myers-Smith et al. 2011, Sturm et al. 2000). More subtle changes in ecosystem structure and function have also been reported (Hollister et al. 2005a, Hollister et al. 2005b, Lara 2012, Villarreal et al. 2012). However, decade time-scale studies suitable for assessing the impacts of multi-decade change in ecosystem structure and function in the Arctic are lacking (Callaghan et al. 2011b).

Much of our understanding of the current state of the Arctic System has been derived from studies documenting significant changes (Elmendorf et al. 2012), or from remote sensing observations (Bhatt et al. 2010). Relatively little information has been published about regions where little or no change has been detected. It is well known that tundra vegetation is responsive to experimental manipulation including canopy temperature (Walker et al. 2006), nutrient availability (Shaver and Chapin 1986), and grazing (Johnson et al. 2012), and can be spatiotemporally variable (Elmendorf et al. 2011, Epstein et al. 2004). In some cases, however, it may take from one to two decades for tundra vegetation to respond to experimental manipulations or present detectable change from observational studies (Epstein et al. 2004, Gough et al. 2008). This variability can occur due to natural factors, and in some cases arctic tundra has shown to be strongly resilient to natural perturbations such as lemming population outbreaks (Villarreal et al. 2012). However, Hudson and Henry (2010) found that after 15 years of experimental manipulation, evergreen shrub communities were resistant to passive warming. In sub-arctic tundra, Milbau et al. (2012) found that some communities dominated by *Empetrum* shrubs were resistant to species invasions. The mechanisms that control change or resistance to change are poorly understood and discerning why some tundra landscapes appear to be changing while others are not under the same climate change regime (Lin et al. 2012, Callaghan et al. 2011b) remains a central challenge.

The structure of tundra vegetation affects the response of ecosystem processes from the plot (Lara 2012) to the landscape level (Euskirchen et al. 2009). It is also well established that changes in vegetation biodiversity, functional groups, and even single species can alter ecosystem properties such as energy balance and land-atmosphere exchange of greenhouse gases (Christensen et al. 2003, Hooper et al 2005, Myers-Smith et al. 2011). Additionally, since the soils of northern tundra landscapes are predominated with permafrost and store a large amount of soil organic carbon (Schuur et al. 2013), many studies have tried to determine whether the future state of arctic tundra will transition from a carbon sink to a carbon source. However, very few studies have looked at the effects of vegetation feedbacks in model outputs and how these can alter land-atmosphere exchange of greenhouse gases (Schaphoff et al. 2013). The expansion of shrubs is one of the most recognized shifts in vegetation that can affect ecosystem processes in tundra. Satellite derived increases in productivity have been largely linked to increases in the prevalence of shrubs (Jia et al 2003, Myers-Smith et al. 2011). Increases in the abundance of shrubs can decrease surface albedo causing a positive feedback to radiative forcing and local to regional warming (Beringer et al. 2005, Chapin et al. 2005). Low-arctic systems are predicted to have the greatest increases in shrubs (Myers-Smith et al. 2011), and if some arctic vegetation communities demonstrate resistance to climate warming, it is also important to understand if and how ecosystem function is being affected in these regions.

Both flora and fauna are more diverse in the low Arctic. There is evidence that hydrological shifts are occurring near Barrow, Alaska (Lin et al. 2012), and shrub encroachment has been documented at the foothills of the Brooks Range to the South (Sturm et al. 2001, Tape et al. 2012). Thus Atqasuk, Alaska offers a unique opportunity to study ecosystem changes because it lies between these two regions where considerable changes to tundra systems have been documented. Satellite-derived greening has also been detected in the vicinity of Atqasuk (Bhatt et al. 2010, Raynolds et al. 2013). Additionally, there is a wealth of historical data, including an International Tundra Experiment (ITEX) research site near Atqasuk that has undergone experimental warming since 1996 (Hollister 2003). Atqasuk is also the location of historic vegetation sites established by Webber in 1975 as a contribution to the Research on Arctic Tundra Environments (RATE) program, a National Science Foundation

project initiated to improve knowledge of the Alaskan Arctic (Batzli 1980). The design of these RATE sites is identical to those established in Barrow, Alaska in 1971 as part of the International Biological Program (IBP) study (Webber 1978), those established in North-central Baffin Island as part of Webber's dissertation study (Webber 1971), and sites established at Niwot Ridge, Colorado also as part of another IBP study (Ebert-May 1973). Determining vegetation structural changes at Atqasuk is important in order to allow for comparison with not only other study sites established by Webber, but also with the local ITEX study where sustained experimental warming appears to have caused no significant effect on species richness or diversity, and where evergreen shrub cover at dry sites increased while the cover of bryophytes at wet sites decreased (Hollister et al. 2005b). Additionally, a remote sensing study by Lin et al. (2012) found that the cover of wet land cover types increased between 1955 and 2008 near Atqasuk and that vegetation is unlikely to undergo substantial change over the next 100 years based on trajectories of change over the past 50 years.

In order to better understand what role the Arctic will play in the future state of the Earth System, there is a need to comprehend why the response of vegetation communities to change is so variable in the Arctic, and how ecosystem function consequently responds. This study resampled vegetation sites established near Atqasuk in 1975 as Webber's contribution to the RATE program (Komárková and Webber 1980), and describes long-term changes in vegetation communities and ecosystem function. Specifically, we aim to determine i) the direction and magnitude of vegetation community change and how this varies among communities, ii) whether there is change at both the vegetation functional type and species level iii) whether vegetation diversity has changed over time in these communities, and lastly iv) how ecosystem function has likely changed over time. This study is a contribution to the International Polar Year – Back to The Future (IPY-BTF) project (IPY #512), which aimed to determine the impacts of arctic vegetation community change on ecosystem function over decadal time scales by relocating and resampling historical vegetation sites (Callaghan et al. 2011b).

4.3 Methods

4.3.1 Study Area

Atqasuk (70.41°N, -157.41°W) is located on the Arctic Coastal Plain in northern Alaska. The study area is comprised of polygons, drained lake basins, ponds, lakes, meandering streams and the Meade River is in close proximity. The presence of the river has resulted in the formation of low relief bluffs along the river, and dunes and small hills (ancient dunes) have formed where sand has been deposited over time (Komárková and Webber 1980). The soils near Atqasuk are generally acidic and are comprised of primarily loamy sands (Everett 1980). Mean summertime air temperature ranges from 3.7°-9.0° (Oberbauer et al. 2007). There are currently no reports of changes in regional climate for Atqasuk and there is no evidence of significant warming trends near these sites (Slider, personal comm.). Mean active layer depth ranges from 36-70cm (Hinkel and Nelson 2003) and can sometimes be deeper than 100cm on ridges with sandy soils (Komárková and Webber 1980). The vegetation is classified as low-arctic and species composition appears to be mostly controlled by microtopography and its influence on soil moisture and permafrost (Hinkel and Nelson 2003, Peterson and Billings 1980).

There are approximately 250 vegetation species recorded in the vicinity of Atqasuk (Komárková and Webber 1977) 235 of which were found in Webber's RATE vegetation sites in 1975. Identification of the vascular flora followed Hultén (1968), and lichens and bryophytes were determined using prior species lists from the region and those used in the local ITEX study (Hollister et al. 2005). Disturbance from the Atqasuk village is minimal, the study location is in close proximity to several off-road all-terrain vehicle trails used irregularly by subsistence hunters. Grazers include caribou, ground squirrels, lemmings and voles (Jung and Batzli 1980, White and Trudell 1980). Caribou and ground squirrels appear to have the most substantial impact on vegetation in Atqasuk through grazing, trampling, and burrowing. Ground squirrels are recognized for creating unique vegetation communities near their dens and for affecting the geomorphology of sites where denning areas occur, mainly in bluff margins and dunes (Peterson and Billings 1980). In the alpine environments of the Yukon Territory, arctic ground squirrel disturbance is known to remove as much as 320 lbs of soil per year (Price 1971), and affect the movement of soils in general (Zaitlin and Hayashi 2012).

4.3.2 Vegetation Sampling

Thirty one of the original 60 RATE sites established in 1975 were relocated in 1999 and 2000, and resampled in 2000, and in 2009 for vascular and lichen flora and in 2010 for bryophytes only. All sites measured 1 m x 10 m and consisted of ten contiguous 1 m² plots. We estimated percent cover for all vascular and lichen species in the summer of 2009 in early July, close to peak growing season. The sampling methodology is consistent with the one used during site establishment by Webber in 1975 and reported by Villarreal et al. (2012) for similar historic sites located near Barrow, Alaska. A revision of species synonymy was conducted for all sample times to ensure congruity between measurements. When the presence of a species was recorded for the first time, species identification was verified among field members between sampling years and when species identification was determined to be questionable, species were either lumped to genus or to a general group (e.g. unknown lichen).

Raw data from 1975 were not available, and only summary data of site-level species index values for each species within each site were able to be rescued. These same index values were also calculated for 2000 and 2009 data (*sensu* Webber, 1978, Villarreal et al. 2012). Since many genera of species were lumped for 1975 data, and species index values were calculated using the sum of all species within a site, relative cover could not be readily determined. Therefore, site-level species relative cover for 1975 was obtained by conservatively subtracting the mean relative presence of each species in 2000 and 2009 from the 1975 species index value. To confirm that species presence did not change considerably between 1975 and 2000, we performed a test using a similar data set derived from historic sites in Barrow, Alaska and found that for 85% of all species at each site, the difference in relative presence was less than 15% between sampling years. This was also found to be true for the relative presence of each species at each site in the Atkasuk data between 2000 and 2009 where species relative cover was derived from raw data collected in the field.

4.3.3 Data Analysis

A site-level vegetation community classification was performed using species index values (n = 212 species after species list revision) following the same method described by Villarreal et al. (2012) using data for all sites sampled in 1975 (n=60). Results of this classification are given in Table 10. In

order to determine how vegetation communities changed over time, we ran a Non-Metric Multidimensional Scaling (NMS) ordination in PC-ORD 4.10 (MjM Software Design Gleneden Beach, Oregon, USA) using a Sørensen (Bray-Curtis) similarity coefficient and species index values from all sites for all sampling years. A random starting configuration and 250 runs with randomized and real data were used, after which tests for dimensionality and stress were run. Species indicator analysis was also performed in PC-ORD using species index values. Significant results for indicator species analysis are reported in Table 10. We used environmental data along with NMS axes scores in order to determine (1) what environmental factors most strongly explained variability in NMS axis scores, and (2) what environmental factors best explain the magnitude of change along different axes in the NMS. To determine what environmental gradients best aligned with each ordination axis, Pearson's correlations, assuming a linear relationship, were used between axes scores and the following environmental variables measured in 1975 were transformed to meet assumptions of normality where necessary: site slope (°), soil pH, soil air dry moisture (%), soil carbon content estimated from soil mass lost on ignition (%), soil moisture holding capacity (%), field soil moisture content (%), wilting point (%), soil available water (%), soil mean bulk density, (%) sand, (%) silt, (%) clay, depth to permafrost (cm), winter snow accumulation scale (1-10), snow depth (cm), aluminum (Al+++), hydrogen (H+), magnesium (Mg++), and soil base saturation (%). The magnitude of change between sampling years for each site was calculated as ordination vector lengths between axis scores of the same site measured at different time intervals. Regression tree analysis was performed using vector lengths (*sensu* Villarreal et al. 2012, Chapters 2, and 3) and the above environmental variables in JMP 10.0 following the same methods outlined in Chapter 2.

Change in the relative cover of vegetation functional types (*sensu* Chapin et al. 1996, Figure 2) was assessed using a multivariate analysis of variance (MANOVA) in JMP 10.0. This tested for the difference in the relative cover of functional types in each community between sampling years. Wilk's λ was used to determine if each functional type was different between sampling years and among vegetation communities at different sampling years (sampling year*vegetation community). When Wilk's λ demonstrated no significant change, a MANOVA using an identity response to test each

functional type separately was used in order to confirm there was no change in relative cover. To determine how species richness, evenness, and Shannon's and Simpson's indices of diversity varied between sampling years and among vegetation communities through time, we used a MANOVA. If the multivariate F statistic for time, or time by vegetation community interaction resulted in a probability less than 0.05, differences between communities and sampling dates were tested using Tukey's honestly significant difference (HSD) test for all pairs using a univariate analysis of variance (ANOVA). Results for the Simpson's Index of diversity did not differ from those of the Shannon Index, thus they are not reported. Changes in the relative cover of individual species were analyzed using repeated measures ANOVA as described by Villarreal et al. (2012).

4.4 Results

4.4.1 Classification and Community Change

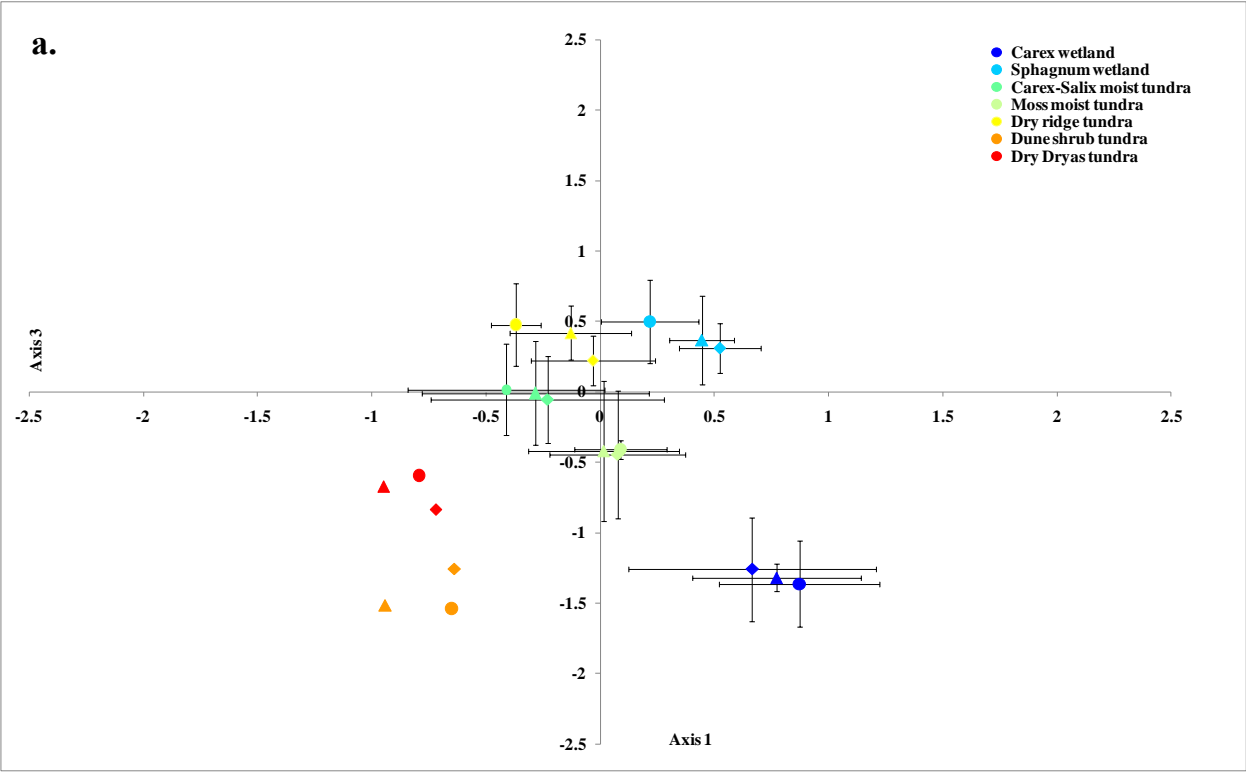
Table 10. List of vegetation communities identified from hierarchical cluster analysis of 1975 site data for species index values. The assigned moisture class number ranges from wet (1) to dry (9), number of sites established in each community in 1975, the number of sites resampled in 2000 and 2009, community name, dominant land form, indicator species (* indicates $P < 0.05$ from Indicator Species Analysis), and the five most dominant species are provided for each vegetation community.

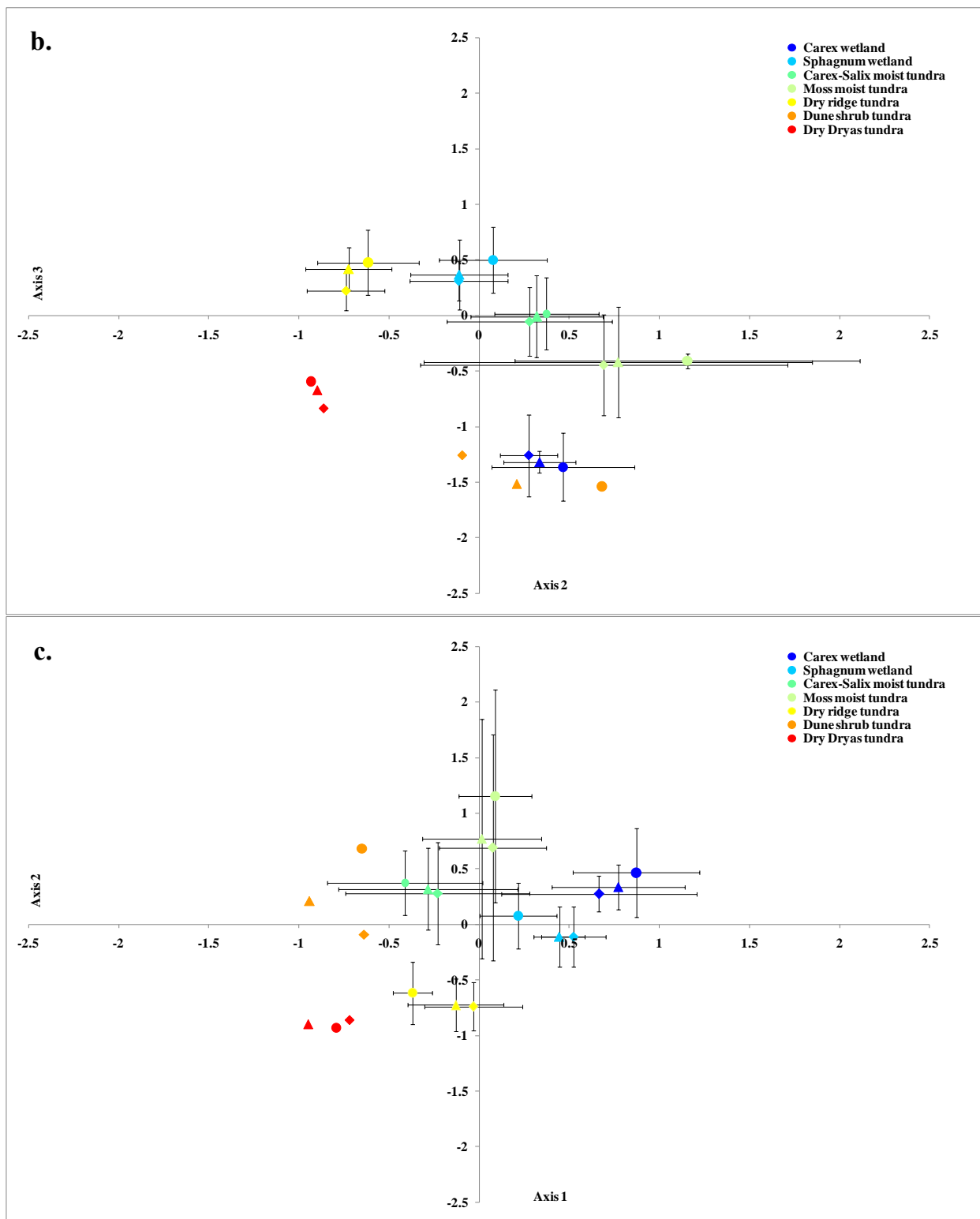
Mois ture Class	1975 No. Sites	2000/2009 No. Sites	Community Name	Dominant Land Form	Indicator Species	Dominant Species
1	1	0	<i>Arctophila</i> wetland	Ponds	<i>Arctophila fulva</i>	<i>Arctophila fulva</i>
2	7	2	<i>Carex</i> wetland	Bog, shallow pond, lake margin, wet meadow	<i>Carex membranacea</i> * <i>Chrysosplenium tetrandrum</i> * <i>Ranunculus gmelinii</i> * <i>Ranunculus pallasii</i> * <i>Potentilla palustris</i>	<i>Carex aquatilis</i> <i>Sphagnum</i> spp <i>Drepanocladus</i> spp <i>Calliergon</i> spp <i>Dupontia fischeri</i>
3	13	10	<i>Sphagnum</i> moist tundra	Moist and upland tundra	<i>Andromeda polifolia</i> * <i>Pedicularis lapponica</i> * <i>Siphula ceratites</i> * <i>Eriophorum vaginatum</i> <i>Rubus chamaemorus</i>	<i>Sphagnum</i> spp <i>Eriophorum vaginatum</i> <i>Dicranum</i> spp <i>Ledum palustre</i> <i>Betula nana</i>
4	15	7	<i>Carex-Salix</i> moist tundra	Moist lake margins, meadows and snowpatch tundra	<i>Cerastium beeringianum</i> * <i>Kobresia sibirica</i> * <i>Lophozia</i> spp* <i>Psoroma hypnorum</i> * <i>Pyrola grandiflora</i>	<i>Carex aquatilis</i> <i>Salix pulchra</i> <i>Hylocomium splendens</i> <i>Tomentypnum nitens</i> <i>Sphagnum</i> spp
5	3	3	Moss moist tundra	Moist meadows and snowpatch	<i>Arctagrostis latifolia</i> * <i>Carex lachenalii</i> * <i>Carex rariflora</i> * <i>Dicranum</i> spp* <i>Drepanocladus</i> spp*	<i>Drepanocladus</i> spp <i>Carex chordorrhiza</i> <i>Campylium stellatum</i> <i>Drepanocladus</i> spp <i>Aulacomnium</i> spp
6	8	7	Dry ridge tundra	Dry ridge and lichen tundra	<i>Carex scirpoidea</i> * <i>Lycopodium</i> spp* <i>Diapensia lapponica</i> <i>Racomitrium lanuginosum</i> <i>Salix phlebophylla</i>	<i>Dicranum</i> spp <i>Flavocetraria cucullata</i> <i>Bryoria nitidula</i> <i>Polytrichum</i> spp <i>Salix phlebophylla</i>

7	4	1	Dune shrub tundra	Streamside and sand dune shrub tundra	<i>Aster sibiricus*</i> <i>Epilobium latifolium*</i> <i>Festuca rubra*</i> <i>Gentianella propinqua*</i> <i>Hedysarum alpinum</i>	<i>Salix glauca</i> <i>Salix lanata</i> <i>Salix alaxensis</i> <i>Equisetum spp</i> <i>Juncus arcticus</i>
8	2	0	Snowpatch tundra	Snowpatch tundra	<i>Boykinia richardsonii*</i> <i>Parrya nudicaulis*</i> <i>Ranunculus pygmaeus*</i> <i>Salix rotundifolia</i> <i>Oxyria digyna</i>	<i>Salix rotundifolia</i> <i>Drepanocladus spp</i> <i>Warnstorfia exannulata</i> <i>Cassiope tetragona</i> <i>Polytrichum spp</i>
9	7	1	Dry <i>Dryas</i> tundra	Dry bank edge, stabilized dune, dry ridge tundra	<i>Achillea lanulosa*</i> <i>Armeria maritime*</i> <i>Bupleurum triradiatum*</i> <i>Carex nardina*</i> <i>Erigeron eriocephalus*</i> <i>Melandrium apetalum*</i>	<i>Dryas integrifolia</i> <i>Carex obtusata</i> <i>Stereocaulon tomentosum</i> <i>Polytrichum spp</i> <i>Elymus arenarius</i>

The hierarchical cluster analysis using all of the sampled sites from 1975 (n=60) determined that there were nine distinct vegetation communities (Table 10). Two communities (*Arctophila* graminoid wetland and snowbank tundra) were represented by only one and two sites, respectively, and these sites were not relocated in the 1999/2000 site relocation and resampling effort. Dune shrub tundra and dry *Dryas* tundra are each represented by one site in this analysis, and *Sphagnum* moist tundra represented the greatest number of sites (ten sites) for a single vegetation type among the resampled sites. The NMS ordination of all resampled sites at all sample times (n=93, 1975, 2000 and 2009/10) recommended a three-dimensional solution and had a final stress of 12.05. Instability of the NMS was 0.00010 after 500 iterations and the proportion of the variance explained by the ordination represented 83.6% of the cumulative variance with axis one, two, and three representing 20.2%, 39.1%, and 24.3% respectively. Axis one and two best correlated with mean soil bulk density ($r^2=62.15\%$ and 44.07% , respectively, table 11), and axis three best correlated with soil pH. Vegetation communities showed little change along any of the ordination axes (Figure 15a-c). Dune shrub tundra changed the most in ordination space, however, this community was only represented by one site. Regression tree analysis accounted for 51.4% of the variability in NMS vector length between axis one and two (i.e. magnitude of change), 62.3% of the vector length between axis one and three, and 49% of the vector length between axis two and three. A large portion of the variation in vector lengths between axis one and two and between axis two and three were best explained by soil carbon content determined from loss on ignition, which accounted for 33.1% and 27.5% of the cumulative variations in the regression trees respectively (Figures

16, and 18). Soil moisture (%) in 1975 explained the most variation for vector lengths between axis one and three (34.8%, Figure 17).





Figures 15a-c. Non-metric Multidimensional Scaling 3-dimensional ordination of all vegetation communities for 1975 (circle), 2000(triangle) and 2009 (diamond) sampling years. Points represent the mean NMS axis scores for all sites classified in a given vegetation community for each year. Vegetation communities are arranged along a moisture gradient in the legend, with blue depicting the wettest vegetation communities and red depicting the vegetation communities with the lowest soil moisture contents. Standard deviations are shown for each axis for each community.

Table 11. Pairwise correlation coefficients between axes scores from all three axes and environmental data (see methods). The two highest correlation coefficients for each environmental variable and NMS axis appear in bold (* P<0.05).

	Axis 1	Axis 2	Axis 3
Slope (°)	-0.43	-0.08	-0.25
pH	-0.51	0.27	-0.56*
Air Dry Moisture (%)	0.53	0.03	0.14
Loss on ignition (%)	0.56	0.02	0.12
Moisture Capacity (%)	0.43	0.02	0.02
Field Capacity (%)	0.46	-0.02	0.05
Wilting Point (%)	0.42	-0.01	0.05
Available Water (%)	0.54	-0.01	0.03
Mean Bulk Density (%)	-0.69*	-0.44*	-0.06
Sand (%)	-0.48	0.14	-0.28
Silt (%)	0.42	-0.16	0.32
Clay (%)	0.58	-0.10	0.18
Thaw Depth (cm)	-0.62*	-0.18	-0.42*
Aluminum (Al+++)	0.52	0.06	-0.02
Hydrogen (H+)	0.32	-0.27*	0.30
Base Saturation (%)	-0.49	0.16	-0.13

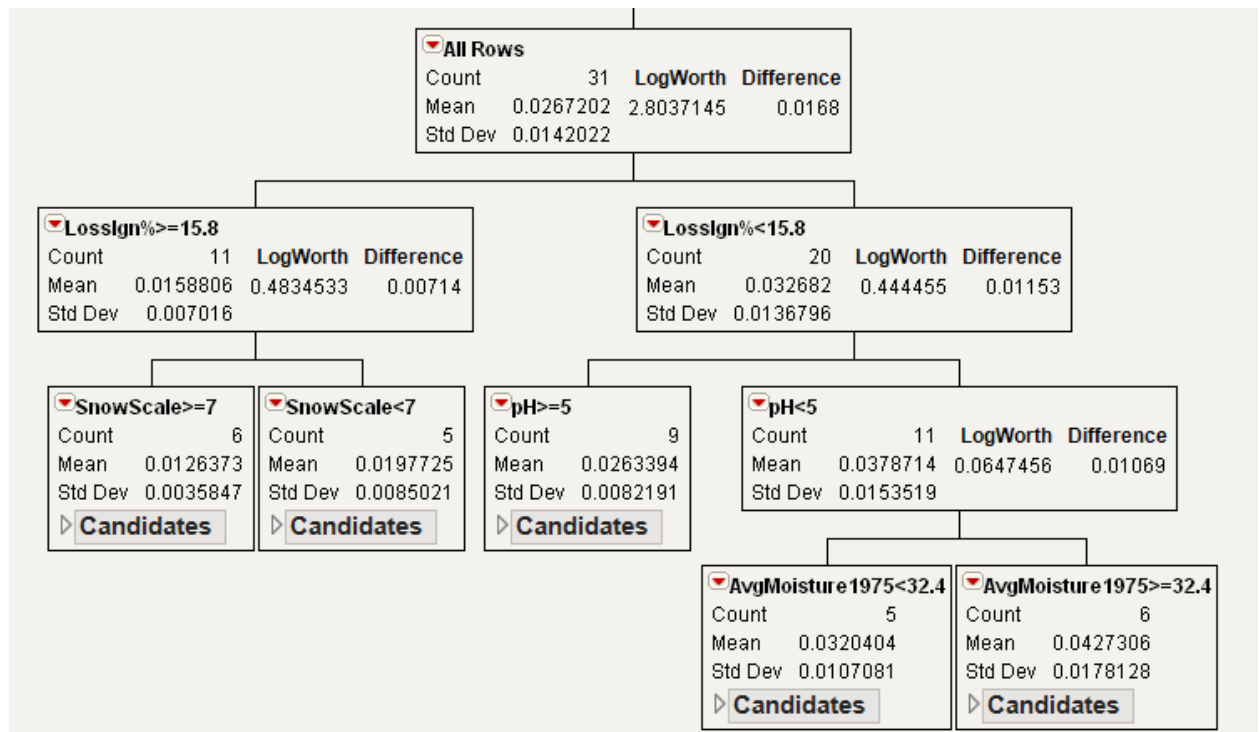


Figure 16. Regression tree showing the four variables that best explain the variation in mean vector lengths for axis one and two ($r^2 = 0.51$).

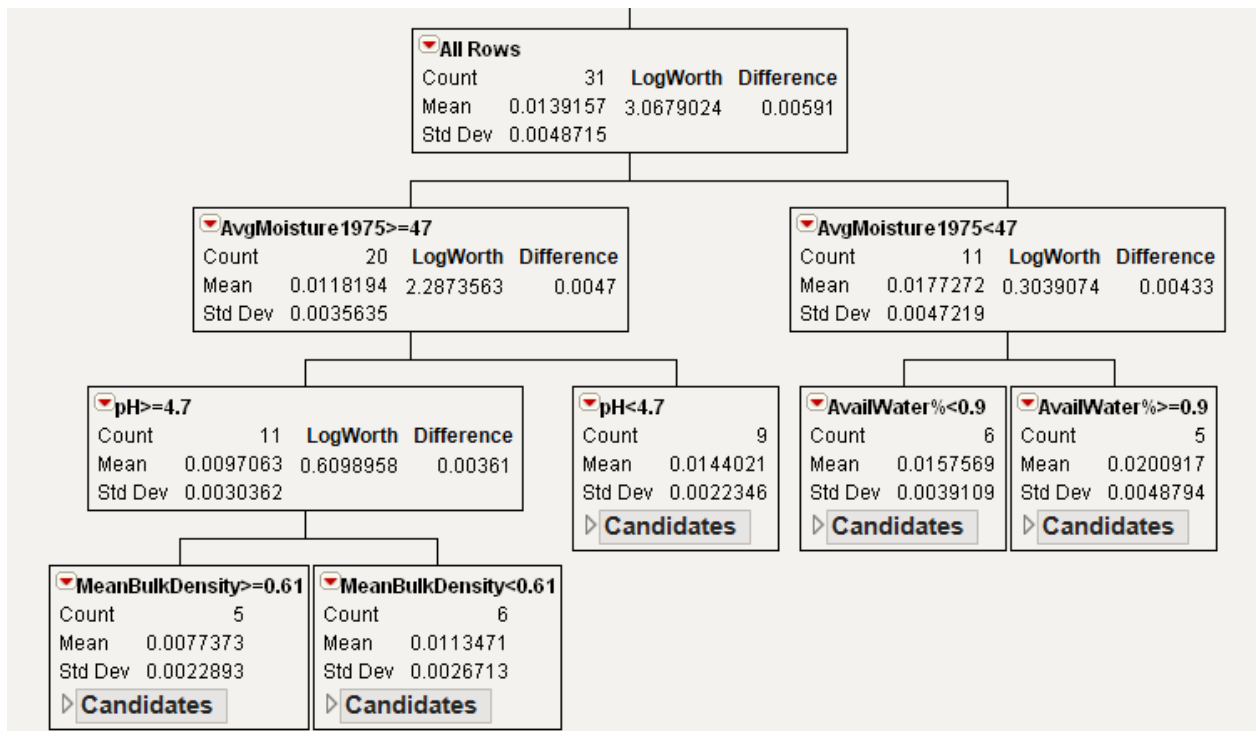


Figure 17. Regression tree showing the four variables that best explain the variation in mean vector lengths for axis one and three ($r^2 = 0.62$).

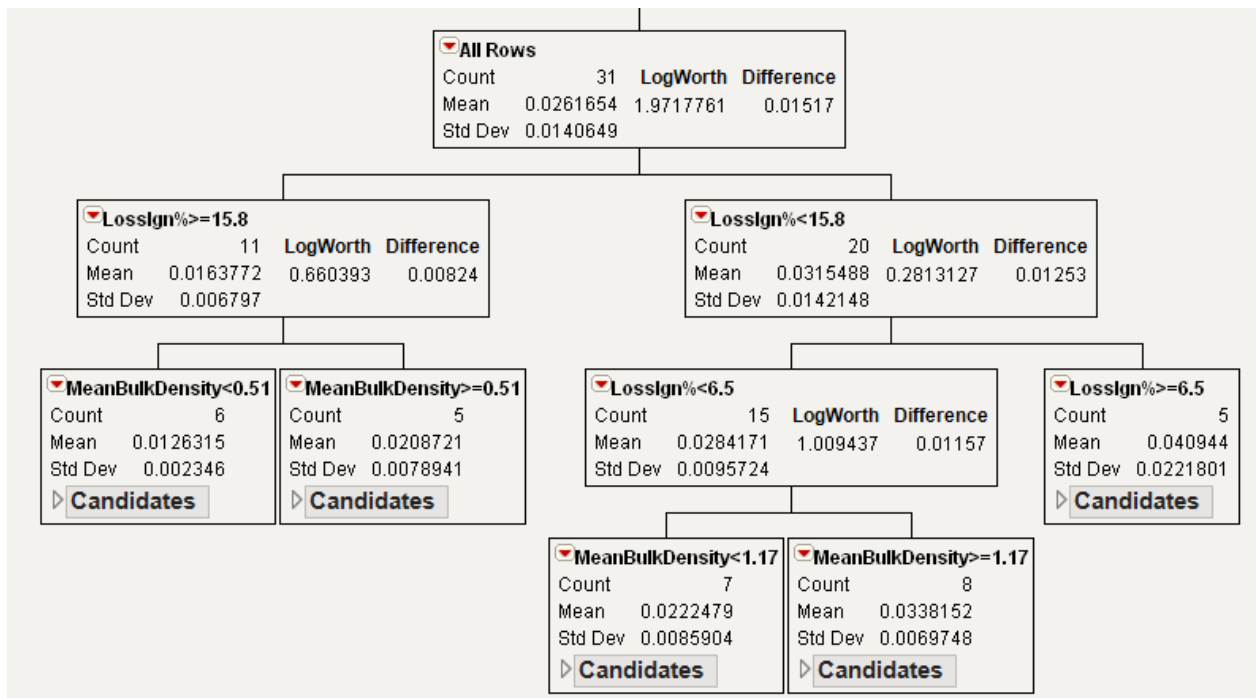


Figure 18. Regression tree showing the four variables that best explain the variation in mean vector lengths for axis two and three ($r^2 = 0.49$).

4.4.2 Vegetation Functional Types and Species Change

No significant changes in the relative cover of functional types were found between sampling efforts (Wilk's $\lambda=0.34$, $p > 0.05$ numerator df =2, denominator df=406), and further MANOVA identity response measures confirmed these results (Figure 19h). The change in relative cover after a 34 year period (1975-2009) was minimal for all functional types, but there were slight differences in the relative cover of functional types in 2000 when compared to the other sampling years. The relative cover of evergreen shrubs gradually increased over time (9.6%-13.9%), although not significantly, while the relative cover of deciduous shrubs, forb, graminoid, lichen, and liverwort cover varied slightly by sampling year. Mosses were the dominant functional type in 1975 and 2009 (35.9% and 36.5%, respectively), and graminoids were the second-most dominant type (21.9% and 18.2%, respectively). Graminoids were the most dominant type in 2000 (27.2%), while mosses had a relative cover of 26.3%.

There was also no significant change in functional type relative cover among vegetation communities between sampling years (*Arctophila* graminoid wetland and snowbank tundra were not analyzed due to low sample size, Wilk's $\lambda = 0.23$, $p > 0.05$, numerator df= 140, denominator df=6793.7). Not all functional types were present in all communities (e.g. *Carex* wetlands were comprised of forbs, graminoids, and mosses only), and thus the composition of functional types differs by community. The small differences in percent cover of functional types for 2000 was apparent for most communities.

Changes in the relative cover of individual species from 1975-2009 was apparent in many communities and across all sites (Table 13). Significant changes in relative cover were observed for 47 of the 140 species between 1975 and 2009. Two evergreen shrubs (*Vaccinium vitis-idaea* and *Empetrum nigrum*) increased in cover while the two deciduous shrubs decreased in cover but presented the greatest overall change documented for any species (*Salix lanata* increased and *S. pulchra* decreased). Among forbs, the cover of *Rubus chamaemorus* decreased the most, while the cover of *Equisetum* species increased the most. *Carex aquatilis* showed the largest decrease while *Hierochloe alpina* underwent the most considerable increase in abundance of all graminoids between 1975 and 2009. There were considerable increases in the relative cover of the lichen *Alectoria* spp, and considerable decreases in the

cover of *Cetraria cucullata*. There were many species of moss that had significant changes, however, *Dicranum* species had large losses while *Sphagnum* species had large gains in relative cover.

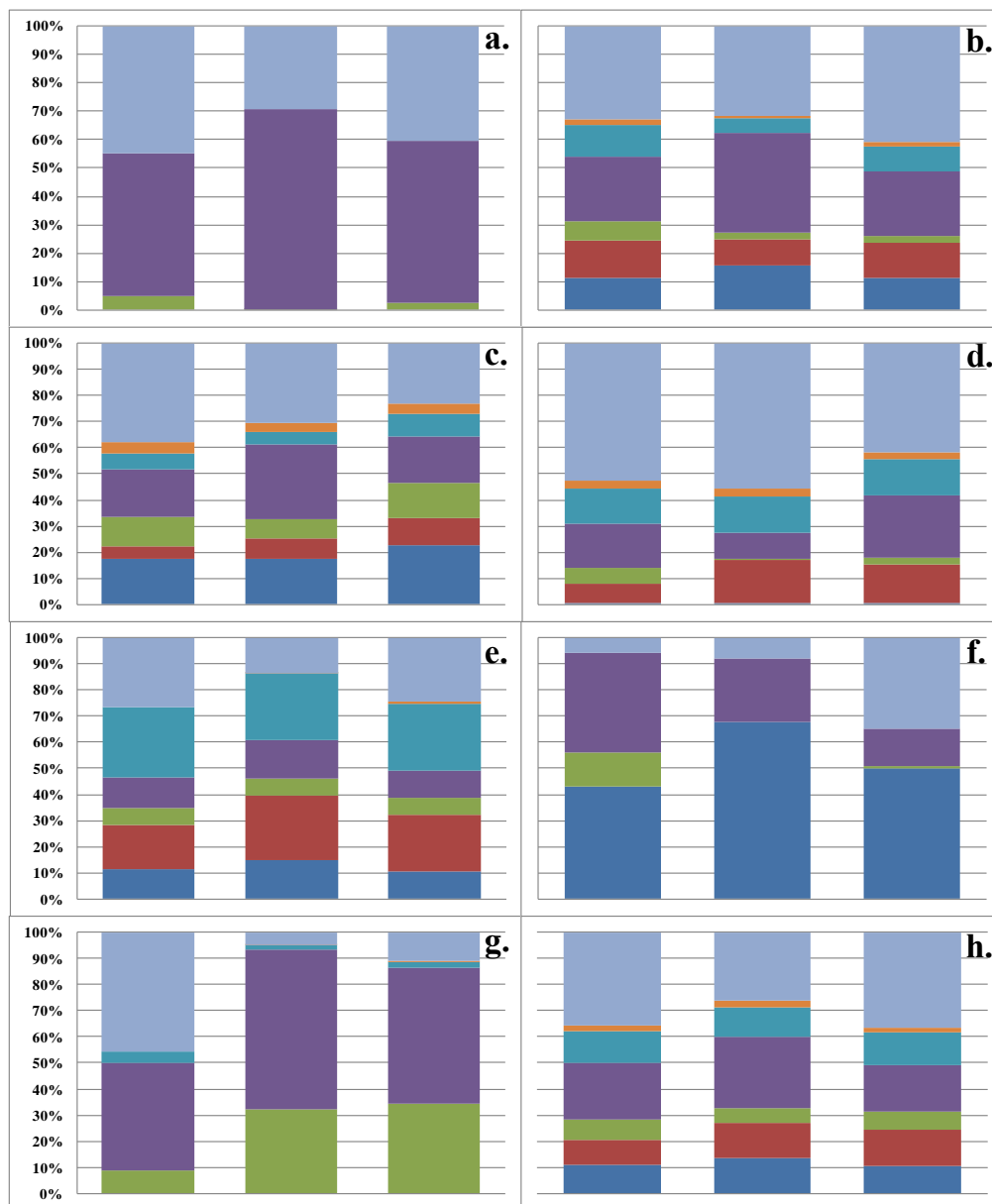


Figure 19a-h. Relative cover of vegetation functional types for each vegetation community and sampling year, and all sites combined in each sampling year (deciduous shrubs-dark blue, evergreen shrubs-red, forbs-green, graminoids-purple, lichens -aqua, liverworts -orange, and mosses -light blue). a – *Carex* wetland, b-*Sphagnum* moist tundra, c-*Carex-Salix* moist tundra, d-Moss moist tundra, e-Dry ridge tundra, f-Dune shrub tundra, g-Dry *Dryas* tundra, h-All.

4.4.3 Species Richness, Evenness, and Diversity

Evenness did not change significantly for the 1975-2000 sampling interval, but increased between the 1975-2009 and 2000-2009 sampling intervals. Shannon's diversity index decreased slightly for the 1975-2000 sampling interval, but increased for the 1975-2009 and 2000-2009 sampling intervals but changes were not significant. There were no significant changes in diversity indices at the community level, with the exception of dry ridge tundra which had significantly higher evenness between 1975 and 2009, and *Carex* wetland which had significantly higher Shannon index values between 1975 and 2009 sampling interval.

Table 12. Difference in mean species richness, evenness, and Shannon Index of diversity between each sampling interval for each vegetation community and for the entire dataset (* $P < 0.05$). A negative value indicates a decrease in richness or index of diversity.

	1975- 2000	1975-2009	2000- 2009
Species Richness			
<i>Carex</i> wetland	2.00	5.00	3.00
<i>Sphagnum</i> moist tundra	-2.22	-2.89	-0.67
<i>Carex-Salix</i> moist tundra	-3.50	-5.25	-1.75
Moss moist tundra	-9.67	-8.33	1.33
Dry ridge tundra	-4.14	-4.00	0.14
Dune shrub tundra	-3.00	-11.00	-8.00
Dry <i>Dryas</i> tundra	-7.00	-19.00	-12.00
All	-3.61	-4.55	-0.94
Evenness			
<i>Carex</i> wetland	0.01	0.05	0.04
<i>Sphagnum</i> moist tundra	0.00	0.02	0.02
<i>Carex-Salix</i> moist tundra	-0.02	0.02	0.03
Moss moist tundra	-0.02	-0.01	0.01
Dry ridge tundra	0.01	0.05*	0.04
Dune shrub tundra	0.03	0.03	0.00
Dry <i>Dryas</i> tundra	0.01	0.04	0.03
All	0.00	0.03*	0.03*
Shannon			
<i>Carex</i> wetland	0.12	0.38*	0.25
<i>Sphagnum</i> moist tundra	-0.07	0.00	0.07
<i>Carex-Salix</i> moist tundra	-0.13	-0.04	0.10
Moss moist tundra	-0.22	-0.16	0.06
Dry ridge tundra	-0.04	0.12	0.16
Dune shrub tundra	0.04	-0.16	-0.21
Dry <i>Dryas</i> tundra	-0.09	-0.22	-0.14
All	0.08	0.01	0.09

Table 13. Mean difference in species relative cover between 1975 and 2009. Bold values represent significant differences ($\dagger < 0.1$, $* < 0.05$, $** < 0.01$, $*** < 0.001$) from a general linear model assuming a Poisson distribution. Functional groups include classes for: graminoids (G), evergreen shrubs (ES), lichens (L), forbs (F), and deciduous shrubs (DS). Total column describes changes in all communities (entire dataset).

Species Name	Functional Group	<i>Carex</i> wetland	<i>Sphagnum</i> moist tundra	<i>Carex</i> - <i>Salix</i> moist tundra	Moss moist tundra	Dry ridge tundra	Dune shrub tundra	Dry <i>Dryas</i> tundra	All
<i>Arctostaphylos rubra</i>	DS			17.5***					17.5**
<i>Betula nana</i>	DS		-14.7***	1.9		8.4***			-4.3
<i>Salix alaxensis</i>	DS			-3.2***		2.2			-1.0
<i>Salix arctica</i>	DS		0.3	0.6	2.4**				3.3
<i>Salix lanata</i>	DS			-0.1***			22.5***		22.4**
<i>Salix niphoclada</i>	DS			3.3			1.0***		4.3
<i>Salix ovalifolia</i>	DS		0.7						0.7
<i>Salix phlebophylla.</i>	DS			-0.3	-0.5	-0.7			-1.5
<i>Salix pulchra</i>	DS		-3.8***	-10.0***	5.5†	0.9			-7.5
<i>Salix reticulata</i>	DS			-3.4***					-3.4
<i>Salix rotundifolia</i>	DS			-0.8***					-0.8
<i>Cassiope tetragona</i>	DS		-10.6***	16.5***	11.5***	-13.9***			3.5
<i>Diapensia lapponica</i>	DS		0.3			-0.5***			-0.2
<i>Empetrum nigrum</i>	DS		0.0	6.8***		0.1			7.0*
<i>Ledum palustre</i>	DS		-16.8***			8.2***			-8.6
<i>Vaccinium uliginosum</i>	DS		0.3						0.3
<i>Vaccinium vitis-idaea</i>	DS		76.3***	33.8***		60.4***			170.4***
<i>Achillea lanulosa</i>	Forb							4.2***	4.2*
<i>Androsace septentrionalis</i>	Forb							-1.3**	-1.3
<i>Anemone parviflora</i>	Forb			0.6					0.6
<i>Antennaria friesiana</i>	Forb					1.0			1.0
<i>Artemisia</i> spp	Forb			-0.3	1.8	-1.7			-0.2
<i>Astragalus alpinus</i>	Forb			-0.7					-0.7
<i>Bupleurum triradiatum</i>	Forb							1.1***	1.1

<i>Caltha palustris</i>	Forb	0.4			-0.9**			-0.6
<i>Cardamine pratensis</i>	Forb	-6.3***						-6.3†
<i>Cochlearia officinalis</i>	Forb		0.4					0.4
<i>Draba spp</i>	Forb						0.1	0.1
<i>Dryas integrifolia</i>	Forb			1.2***	0.4	7.6***		9.2
<i>Equisetum arvense</i>	Forb	0.5		4.6	0.5	7.7***	11.1***	24.5***
<i>Erigeron eriocephalus</i>	Forb						1.6*	1.6
<i>Lupinus arcticus</i>	Forb			-5.4***				-5.4
<i>Minuartia arctica</i>	Forb					1.3†	1.4†	3.7***
<i>Pedicularis capitata</i>	Forb			0.9		-0.7		0.2
<i>Pedicularis kanei</i>	Forb		0.5					0.5
<i>Pedicularis lapponica</i>	Forb		-0.5					-0.5
<i>Pedicularis sudetica</i>	Forb		0.9	-1.4	-1.2			-1.7
<i>Petasites frigidus</i>	Forb		-3.9	3.5		-0.8		-1.3
<i>Polygonum bistorta</i>	Forb		-0.1	2.6*	-1.3	1.4***	0.1	2.8
<i>Polygonum viviparum</i>	Forb		0.1	-3.8	-0.7	-1.1	-1.6†	-7.2*
<i>Potentilla hookeriana</i>	Forb						2.4***	2.4
<i>Potentilla hyparctica</i>	Forb							
<i>Potentilla palustris</i>	Forb				0.5			0.5
<i>Pyrola grandiflora</i>	Forb		-0.2	13.3***		1.0		14.1†
<i>Ranunculus pallasii</i>	Forb							
<i>Rubus chamaemorus</i>	Forb		-31.5***			0.5		-31.0***
<i>Rumex arcticus</i>	Forb				-0.3			-0.3
<i>Saussurea angustifolia</i>	Forb			1.0		-0.5		0.5
<i>Saxifraga cernua</i>	Forb	3.4***			0.1			3.5†
<i>Saxifraga foliolosa</i>	Forb	-2.6**			-3.5***			-6.1†
<i>Saxifraga hieracifolia</i>	Forb			-0.5				-0.5
<i>Saxifraga hirculus</i>	Forb			0.6	1.1			1.7
<i>Saxifraga punctata</i>	Forb			-5.9***	-0.9	-0.5		-7.3†
<i>Silene acaulis</i>	Forb			-0.2				-0.2
<i>Stellaria spp</i>	Forb	3.9*		-4.8†	-0.7	2.1	-1.1†	0.1
<i>Arctagrostis latifolia</i>	Graminoid		-1.7	-4.3*		-0.2	0.9	7.2***

<i>Bromus pumpellianus</i>	Graminoid					3.6***	-2.8***	0.8
<i>Calamagrostis holmii</i>	Graminoid			-18.2***	1.6			-16.6***
<i>Carex aquatilis</i>	Graminoid	-25.3***	-2.3***	-20.2***	4.1	0.6***		-43.0*
<i>Carex bigelowii</i>	Graminoid	0.0	-6.0***	18.6***	0.1	-6.0***		6.7
<i>Carex chordorrhiza</i>	Graminoid				7.3***			7.3
<i>Carex maritima</i>	Graminoid			-0.8		5.0***		4.2
<i>Carex obtusata</i>	Graminoid			0.5			3.7***	4.2
<i>Carex rariflora</i>	Graminoid				1.3			1.3
<i>Carex scirpoidea</i>	Graminoid					0.9		0.9
<i>Dupontia fischeri</i>	Graminoid	-12.0***			1.2			-10.8*
<i>Elymus arenarius</i>	Graminoid						4.3***	4.3
<i>Eriophorum angustifolium</i>	Graminoid	6.7***	1.3	6.0	2.0			15.9***
<i>Eriophorum scheuchzeri</i>	Graminoid		2.5**		0.4			2.9
<i>Eriophorum vaginatum</i>	Graminoid		-29.1***	0.2		-2.5		-31.4*
<i>Festuca brachyphylla</i>	Graminoid			0.4		0.6	0.9	1.8***
<i>Hierochloa alpina</i>	Graminoid			4.8	0.4***	14.0***		19.2**
<i>Hierochloa pauciflora</i>	Graminoid				1.5			1.5
<i>Juncus biglumis</i>	Graminoid				-2.2**			-2.2
<i>Juncus triglumis</i>	Graminoid				-0.9***			-0.9
<i>Koeleria asiatica</i>	Graminoid						-2.3***	-2.3
<i>Luzula arctica</i>	Graminoid		-2.5	-1.8		-4.8***		-9.1*
<i>Luzula confusa</i>	Graminoid		4.3	-2.3	-0.3	2.0***	-2.5***	1.1
<i>Luzula multiflora</i>	Graminoid			-2.7		0.3		-2.5
<i>Luzula wahlenbergii</i>	Graminoid	0.1	0.5	1.2	2.0			3.7†
<i>Poa arctica</i>	Graminoid	3.7*	-1.5	1.4*	-0.4	0.5	5.9***	9.5*
<i>Poa lanata</i>	Graminoid					0.7	2.3**	3.0†
<i>Tofieldia coccinea</i>	Graminoid			0.4				0.4
<i>Tofieldia pusilla</i>	Graminoid				-0.6			-0.6
<i>Alectoria</i> spp	Lichen		9.4†	1.2	2.7	42.9***		56.2***
<i>Asahinea chrysantha</i>	Lichen					1.5		1.5
<i>Bryocaulon divergens</i>	Lichen		0.4	0.3	0.1	5.5	1.8*	8.1**
<i>Bryoria nitidula</i>	Lichen			0.4		1.1		1.4

<i>Cetraria islandica</i>	Lichen		-9.2*	9.6**	2.9***	-7.1***		-3.8	
<i>Cladonia</i> spp	Lichen		16.3***	4.4	1.3	9.6*		31.6***	
<i>Dactylina arctica</i>	Lichen		-5.4***	6.6*	-1.7*	-2.0**		-2.6	
<i>Cetraria cucullata</i>	Lichen		-12.0***	-6.7*	-5.5***	-31.3***		-55.6***	
<i>Flavocetraria nivalis</i>	Lichen		0.2	0.2	-0.8	2.8***	-1.1	1.3	
<i>Masonhalea richardsonii</i>	Lichen		-2.0	-0.2	3.0***	0.5		1.3	
<i>Ochrolechia frigida</i>	Lichen					-16.1***		-16.1***	
<i>Parmelia omphalodes</i>	Lichen					-0.5***	-0.5*	-0.9	
<i>Peltigera</i> spp	Lichen		-1.0	28.8***	-2.7*	0.6	0.2	26.0***	
<i>Pertusaria</i> spp	Lichen					1.1		1.1	
<i>Psoroma hypnorum</i>	Lichen								
<i>Sphaerophorus globosus</i>	Lichen		-0.8		0.1	3.3***		2.6	
<i>Stereocaulon tomentosum</i>	Lichen		-0.8	-2.6**	-0.6	4.1**		0.1	
<i>Thamnolia</i> spp	Lichen		-4.9***	4.0	0.1	10.5***	-0.9	8.7	
<i>Anastrophyllum</i> spp	Liverwort		1.3	-11.5***				-10.2**	
<i>Ptilidium ciliare</i>	Liverwort	11.3***	2.7	-0.2***	-1.6***			12.2	
<i>Scapania</i> spp	Liverwort			0.7				0.7	
<i>Abietinella abietina</i>	Moss						-10.3***	-10.3***	
<i>Aulacomnium</i> spp	Moss		-3.3***	1.3***	-8.2***	-1.3†	0.5	-11.1	
<i>Brachythecium</i> spp	Moss			-2.3				-2.3	
<i>Bryum ambylodon</i>	Moss								
<i>Bryum</i> spp	Moss			0.7			22.3***	0.6	23.5***
<i>Calliergon</i> spp	Moss	-14.5***		-0.9	-2.2			-17.7***	
<i>Campylium stellatum</i>	Moss	0.2		1.3	-16.7***			-15.2***	
<i>Cinclidium</i> spp	Moss		0.3	3.4	-10.8***			-7.1	
<i>Climacium dendroides</i>	Moss			0.2				0.2	
<i>Conostomum tetragonum</i>	Moss					1.8		1.8	
<i>Dicranum</i> spp	Moss		-43.2***	-18.1**	-8.4*	-34.8***	-1.0	-105.5***	
<i>Distichium capillaceum</i>	Moss		0.2	0.9	1.1	4.4†		6.5**	
<i>Ditrichum flexicaule</i>	Moss		11.3***	0.9		1.1		13.3***	
<i>Drepanocladus exannulatus</i>	Moss	-5.4***	0.7					-4.7*	
<i>Drepanocladus</i> spp	Moss	-11.0	-3.5	0.6	43.5			29.6	

<i>Encalypta alpina</i>	Moss					0.1		0.1
<i>Hylocomium splendens</i>	Moss		-22.3***	-47.2***	-1.8	-1.5	0.3	-72.4***
<i>Mnium</i> spp	Moss	-0.1***				0.1	-1.5**	-1.5
<i>Myurella julacea</i>	Moss			0.1		0.2		0.3
<i>Oncophorus</i> spp	Moss		-0.4***	-16.5***	0.2			-16.8**
<i>Orthothecium</i> spp	Moss				0.1			0.1
<i>Philonotis fontana</i>	Moss			-6.6**				-6.6**
<i>Pleurozium schreberi</i>	Moss		3.9	1.0				4.9*
<i>Pohlia cruda</i>	Moss		-2.5	0.8	0.1	-0.1†		-1.7
<i>Polytrichum</i> spp	Moss	11.3***	2.7	-11.3	-8.2*	19.3†	2.3	-10.9***
<i>Racomitrium lanuginosum</i>	Moss		-1.6		-0.8	-45.4***		-47.8***
<i>Rhytidium rugosum</i>	Moss			-3.6*	-4.5*	0.4	-7.8***	-15.5**
<i>Sarmentypnum sarmentosum</i>	Moss		0.4					0.4
<i>Sphagnum</i> spp	Moss	-10.3***	88.4***	-1.2		3.0		79.9***
<i>Tetraplodon mnioides</i>	Moss							
<i>Timmia norvegica</i>	Moss			-0.7		-0.8		-1.5
<i>Tomentypnum nitens</i>	Moss		-7.2*	-19.7***	5.5**	-1.6		-23.0*
<i>Tortula ruralis</i>	Moss							
<i>Warnstorfia exannulata</i>	Moss	-5.4***	0.7					-4.7

4.5 Discussion

In consequence of recent arctic warming, studies suggest that low-arctic tundra especially has experienced drastic changes and is expected to continue to change due to its high abundance of shrubs (Myers-Smith et al. 2011, Schuur et al. 2013, Sturm et al. 2001). Following resampling of historic marked sites in tundra vegetation near Atqasuk on the North Slope of Alaska, we report only relatively small changes in vegetation communities and the abundance of vegetation functional types and species. Vegetation communities did not appear to change markedly over time, however, some individual species did change in their overall abundance. Species evenness also appears to have increased between both 1975 and 2009 and 2000 and 2009, suggesting the relative abundance of vegetation species has become more homogenous over time.

4.5.1 Classification and Community Change

Since some sites were unable to be relocated in 2000, two communities were not able to be resampled in 2000 and 2009 due to the loss of representative sites in vegetation communities since 1975 (dry *Dryas* tundra, dune shrub tundra, and *Carex* wetland, see Table 10). The historical markers at these sites were likely buried by windblown sand, broken off, have become immersed and difficult to locate under water or vegetation. Overall, there was very little evidence of vegetation community change detected in the NMS ordination for the other seven vegetation communities identified from 1975 that were resampled. This is among the first field-based studies to validate the geospatial analysis of land cover change and model output from Lin et al. (2012) who hypothesized, based on historic trajectories of change, that the landscape near Atqasuk will change little over the next 100 years. Peterson and Billings (1980) also note that some vegetation communities appear to have remained unchanged for thousands of years near Atqasuk.

Ordination axes scores correlated best with soil bulk density, a measure of soil moisture and porosity where soils with a high bulk density have low porosity and restricted water movement. Regression tree analysis suggests mean soil bulk density and moisture were also a control of the magnitude of vegetation community change along each of the ordination axes. Peterson and Billings (1980) determined that vegetation community composition is primarily controlled by soil moisture, and

results of this study not only agree with this statement (correlations with axes scores), but also suggest that three decades of community change within our ordination may have also been driven by changes in soil moisture.

Sphagnum wetlands, *Carex-Salix* moist tundra, moss moist tundra, and dry ridge tundra appear to be gradually shifting towards wetter vegetation community types, while the wettest vegetation community (*Carex* wetland) analyzed seems to be shifting toward drier vegetation community types. These findings suggest that the majority of this landscape is increasing in soil moisture status, which supports the retrospective land cover change assessment reported by Lin et al. (2012) for the Atqasuk area. Except for *Carex* wetland, this trend is, however, different to the general drying trends documented elsewhere in the Arctic (Bhatt et al. 2010, Smol et al. 2007, see Chapter 2). *Carex* wetland was the only vegetation community that shifted towards a drier status in the ordination, which may suggest drier trends in inundated vegetation communities, which commonly appear in the form of bogs or shallow areas at pond margins. These movements within the ordination suggest that the surface hydrology of the Atqasuk landscape may be changing.

4.5.2 Changes in Vegetation Functional Types and Species

The cover of vegetation functional types did not change after 34 years, however, there were slight fluctuations in the relative cover of moss, graminoid, and deciduous shrubs in 2000, which may be due to temporal variation (Epstein et al. 2004), differences in observers (Gotfryd and Hansell 1985), and/or herbivory (Villarreal et al. 2012). Our results on evergreen shrub abundances do not agree findings from Hollister et al. (2005), which documented significant increases in evergreen shrub cover following sustained summertime warming in Atqasuk. The decrease in relative cover documented for graminoids is also similar to the trends documented in dry tundra near Atqasuk (Hollister et al. 2005b), but are dissimilar to trends documented throughout the Arctic in general (Elmendorf et al. 2012, Walker et al. 2006). The relative cover of moss and graminoids was the most dynamic between sampling years, and deciduous shrubs displayed no overall change.

Species varied in their degree of change over the observational period. The relative cover of most shrub species did not change with the exception of *Vaccinium vitis-idaea*, which increased. This

disagrees with Hollister et al. (2005a) findings that reproduction of *Vaccinium vitis-idaea* was negatively impacted after five years of passive summertime warming, and highlights the importance of detailed observations and the need for sustained monitoring of important species, especially dwarf shrubs such as *V. vitis-idaea*. For species that are found at both Atqasuk and Barrow, very few similarities in species-level change were found (Villarreal et al. 2012). Lichens from the genus *Cladonia* were the only species complex that showed consistent and significant increase in cover at both locations, while the graminoid *Calamagrostis holmii* was the only species that decreased in cover at both locations. Results of vegetation community change from the ITEX site near Atqasuk (Hollister et al. 2005b) suggest that *Cladonia* spp and *C. holmii* also increased in cover.

4.5.3 Richness, Evenness, and Diversity

Species richness was not significant for all communities or for the entire dataset. This agrees with results from the nearby ITEX study (Hollister et al. 2005b) where, in response to experimental warming, changes in species richness were not observed. Evenness was higher for both 1975-2009 and 2000-2009 but not for 1975-2000, suggesting that vegetation communities are becoming more homogenous, and that this may be accelerating. Although the mechanisms explaining causes of biological homogenization are beyond the scope of this project, biological factors such as facilitation and resource use have been suggested (Zhang et al. 2012). Another hypothesis may be that if canopy height has increased as it has in experimental warming studies (Wahren et al. 2005), visual estimates may favor large species prone to increased canopy height (e.g. *Salix lanata*) and representation of smaller species may be reduced. The increase in evenness is also causing vegetation diversity to increase, is overriding the decrease in species richness. The homogenization of tundra landscapes in the future may be of concern because heterogeneity may act as a buffer against climate change (Post et al. 2009). Additionally, a global analysis of the effects of species evenness on forest productivity using regression tree analysis has found a positive relationship, and that evenness is the primary diversity parameter explaining forest polycultures (Zhang et al. 2012). Thus, although not a lot of focus has been placed on studying species evenness in the Arctic studies, it may be an important factor in determining carbon balance and other important ecosystem functional traits.

4.5.4 Implications for Trophic Interactions

One of the future research priorities outlined by Post et al. (2009) focused on furthering understanding of how trophic interactions will be altered with climate warming in the Arctic since these interactions directly affect how ecosystems are both structured and how they function. Top down interactions between herbivores and vegetation are well-documented for tundra landscapes. For instance, shrub growth in the Arctic is indirectly affected by herbivores through nutrient limitation (Chapin et al. 1995, Hobbie 1992), and directly affected through grazing (Billings and Peterson, 1980). Additionally, other studies have determined that herbivores have historically controlled tundra vegetation community composition (Zimov et al. 1995), and that they may facilitate the expansion of some vegetation functional types such as graminoids (van der Wal and Brooker 2004) and a reduction in mosses and lichens (Johnson et al. 2012). It's not known if the resistance to change in vegetation communities near Atkasuk is a result of a top-down effect of herbivory. Grazing pressure by rodents near Atkasuk is less severe than at Barrow, likely due to a greater richness in microtine rodents in Atkasuk (Batzli and Jung 1980, Villarreal et al. 2012). Furthermore, caribou near Atkasuk graze on lichen in winter and switch to shrubs and lichen in the summer (White and Trudell 1980) and could be a source of herbivore competition to rodents in the Atkasuk area. In the foothills of the Alaskan North Slope, Gough et al. (2008) found that after ten years of caribou exclusion, there was no change in vegetation at Toolik Lake, Alaska, while another study found that herbivores stimulated vegetation productivity and shrub abundances (Gough et al. 2012). Another study in the Canadian low Arctic found that *V. vitis-idaea* increased dramatically in abundance when caribou were excluded for five years (Zamin and Grogan, 2013). Monitoring evergreen shrub abundances in this region may be important, since many of the microtine herbivores dislike extracts by these plants (Batzli and Sobask 1980, Jung and Batzli 1980). Thus, although there was no overall community change, it may be important to closely monitor herbivores in the region of Atkasuk and in other regions of the Arctic, since their impact on arctic greening is still poorly understood (Oloffson et al. 2009), but a higher diversity of grazers may help maintain stable vegetation communities.

Chapter 5: Decadal Changes in North-American Tundra Vegetation Communities

5.1 Abstract

Understanding how tundra systems may respond to global change is imperative because of the likely changes to the Earth System. The decade time-scale observational data needed to advance such understanding help tease apart the many factors controlling spatial and temporal variation of tundra ecosystem structure and function are scant. Several recent efforts, however, have helped rescue, secure and resample old research sites (Tweedie and Callaghan 2013). This study synthesizes the rescue and resampling of vegetation study sites at three arctic tundra locations (Baffin Island, Canada, Barrow, Alaska, and Atqasuk, Alaska), and one alpine tundra location (Niwot Ridge, Colorado). A meta-analysis of community composition change at the four locations and three broad vegetation communities classified by soil moisture status (dry, moist, and wet), revealed that over decade time-scales, all locations and all three tundra community types changed in composition significantly in the long-term period, and only Barrow and moist communities changed in the short-term period. Changes in richness, evenness, and diversity were detected for all community types in our long-term data, while Baffin Island was the only location to show any change with an increase in diversity. Species richness at dry and moist tundra changed in the short-term interval, and Atqasuk and moist tundra showed accelerated decrease in evenness. These results highlight the importance of ongoing monitoring effort to study the heterogeneity of vegetation change at multiple spatiotemporal scales in tundra ecosystems.

5.2 Introduction

The need to enhance our knowledge of how climate change will impact tundra ecosystems is urgent (Olsen et al. 2011, Post et al. 2009, Schuur et al. 2009). Changes occurring in these ecosystems are being recorded from the plot scale (Elmendorf et al. 2012) to the landscape (Lin et al. 2012) and regional level (Bhatt et al. 2010,) for both biotic (Walker et al. 2006) and abiotic (Olsen et al. 2011) properties and processes. Responses appear to be spatiotemporally variable (Hollister et al. 2005), and in some areas, resistance to change has been documented (Hudson and Henry 2010). However, due to a lack of sustained monitoring over decadal time scales and at numerous locations in the Arctic

(Callaghan et al. 2011b), the advancement of understanding regional to global scale impacts of tundra ecosystem change remains challenging.

Increases in the density of vegetation, especially shrubs, can negatively impact species richness by limiting light availability to other species (Myers-Smith et al. 2011, Pajunen et al. 2011). A reduction in species richness can shift trophic interactions and ecosystem goods and services. For example, caribou depend on lichen for forage, and lichen biomass is predicted to decrease with warming (Elmendorf et al. 2012), which may then negatively impact caribou forage and thus the native communities that depend on their harvest for subsistence. The species richness of avifauna has also been determined to be controlled by vegetation structure in low-arctic ecosystems (Henden et al. 2013). Additionally, changes in vegetation composition in arctic tundra can affect traditional human travel routes, harvesting of berries, and the harvest of other wildlife species such as birds (Myers-Smith et al. 2011). Since the relationships between biodiversity and ecosystem services are complex and relatively poorly understood for tundra ecosystems (Mace et al. 2012), it makes shifts in tundra species composition difficult to examine. Furthermore, recent studies have also shed light on the differences in the responses to warming by different tundra regions. In a study that looked at multiple tundra locations, including Barrow, Alaska and Atkasuk, Alaska, Eurasian sites changed differently than Alaskan sites, and based on change trends over recent decades, shrub tundra was hypothesized to become more abundant in Eurasian tundra in the future (Lin et al. 2012). Bi et al. (2013), using remote sensing NDVI analysis, found that tundra in North America has shown lower rates of greening compared to Eurasian tundra under the same warming conditions. Goetz et al. (2007) found differences in the response of tundra communities between localized tundra fires at both North American and Eurasian tundra, with North American resulting in higher regrowth of deciduous shrubs.

Tundra has historically been a challenging biome for environmental studies due to the harsh conditions and logistic challenges working in these regions. Consequently, there is a general lack of sustained observations and historical time series data. Although valuable information has been obtained from traditional ecological knowledge (Huntington 2011), these data are limited and difficult to compare with recent studies. Modeling has proven useful for providing insight on ecosystem change, especially

when complimented with field based resampling efforts (e.g. Johnson et al. 2011). Satellite-based studies drawing from image archives have the capacity to provide insightful windows to how tundra ecosystems were structured and how they functioned in the past, however, these have a variety of limitations and can be problematic (Stow et al. 2004). Although Bhatt et al. (2010) report dramatic increases in NDVI throughout the Arctic, especially in northern Alaska, two recent studies using plot scale data suggest that little change has been occurring at some locations in this region for the last half-century (Lin et al. 2012, also see Chapter 4).

In the absence of sustained monitoring of tundra vegetation, we lack the capacity to understand the dynamic and coupled nature of tundra-climate interactions and future trajectories of change. This study synthesizes changes in vegetation species abundance data in tundra ecosystems from three locations in the Arctic and one alpine location in the Rocky Mountains. The temporal duration of these studies spans 34 or more years and includes some of the oldest and most robust vegetation datasets of their type. Importantly, sites at all locations were established by Dr. Patrick J. Webber and his former lab as either a component of his dissertation studies (Baffin Island, Canada), part of the International Biological Program (IBP, Barrow, Alaska and Niwot Ridge, Colorado), or as part of the Research on Arctic Tundra Environments (RATE) study near Atkasuk, Alaska. These sites provide a rare opportunity to resample a large vegetation dataset that spans multiple terrains and latitudes using a consistent methodology. At all locations, an almost identical resampling approach was adopted (*sensu* Villarreal et al. 2012). This study is a contribution to the Back to the Future project, an International Polar Year (IPY #512) endorsed study that focuses on rescuing historic data and resampling historic sites to provide an effective means of assessing decade time-scale patterns of change and extrapolating these into the future to produce hypotheses of future vegetation change. In this synthesis, we aim to determine i.) the trajectories of community change at the four locations, ii.) the magnitude of change at these locations for three vegetation communities (dry, moist, wet), iii.) if these changes have accelerated over the last decade, and iv.) how species richness, diversity and evenness have changed by location and vegetation community and if these patterns have accelerated over time.

5.3 Methods

5.3.1 Research Locations, Site Layout, and Vegetation Sampling

A description for each research location is given in Table 14. All sites at each location were established and sampled using the same method reported by Villarreal et al. (2012).

Table 14. Summary of the four locations included in this study.

Location				
Physical Parameters	Baffin Island, CAN	Barrow, AK	Atkasuk, AK	Niwot, CO
Location	70°25'N, 74°40'W	71°18'N 156°40'W	70°29' N, -157°27' W	40°3'N 105°36'W
Elevation (m ASL)	600	3	30	3000
Mean Annual Temperature °C	-12.8	-12.6	-11.9	-3.7
Mean July Temperature °C	2.9	3	7.2	8.2
Mean Annual Precipitation (cm)	23	124		93
Average maximum Thaw Depth (cm)	n/a	35-39	36-71	n/a
Soil pH	Circumneutral/Acidic	Acidic	Acidic	Acidic
Substrate	Sand, gravel, silt	Sand, gravel, silt	Aeolian sand and Sand, silt	Sand, silt
Succession Pattern	Deglaciation	Thaw-Lake Cycle	Thaw-Lake Cycle	Alpine/Treeline
Circumarctic Vegetation Map Classification				
Bioclimate Subzone	C	C	D	n/a
Community	B2: Cryptogam barren complex	W1: Sedge/grass, moss wetland	W2: Sedge, moss, dwarf-shrub wetland	n/a
Back to the Future Summary				
Historic Study	Webber Dissertation	IBP	RATE	IBP
Historic Publication	Webber, 1971	Webber, 1980	Komárková and Webber 1980	Ebert-May 1973
Year of Site Establishment	1964	1972	1975	1971
Resampling Dates	2009	1999, 2008, 2010	2000, 2009	1991, 2001, 2011
Number of Original Sites	82	43	60	30
Number of Resampled Sites	79	33	31	30
Number of Species	117	81	213	128
Type Sampled	Vascular and non-vascular	Vascular and lichens only	Vascular and non-vascular	Vascular only

5.3.2 Analysis of Community Change

Since bryophyte and lichen species were lumped into functional groups for the Niwot Ridge sampling, lumping of bryophytes and lichens was repeated for the other locations. Species index values were calculated following Villarreal et al. (2012) for each species at every site and location and were consolidated into a master relational database along with site data for location, year sampled, species, functional group, and community. Because tundra vegetation structure is highly linked to soil moisture (Lara 2012, Webber et al. 1980), sites were assigned to dry, moist, and wet classes using the site moisture regime given by the historic studies (see Table 14). Due to the large number of species in the master database (258 species), these data were crosstabulated using R Statistical Software (R Development Core Team, 2008). A Nonmetric Multidimensional Scaling ordination was then performed for all historic and resampled sites from all locations in R with the statistical package Vegan (Jari et al. 2013) using 500 iterations and a Bray-Curtis dissimilarity contingency table for index values between sites and species. Vector lengths for differences in site-level NMS axis scores between sampling years were calculated and longer vector lengths were assumed to represent a large degree of vegetation community change between sampling years (see section 3.3.3).

5.3.3 Meta-Analysis

To assess biome-wide change in diversity, we first calculated species richness, evenness, and diversity for all sites at all four locations using site by species index values and contingency tables in PC-ORD 4.10 (MjM Software Design Gleneden Beach, Oregon, USA). The percent change in the three diversity parameters between long-term (between 1964, 1971, 1972, 1975 and 2009, 2009, 2010, 2011, see Table 14) and short-term (between 1999, 2000, 2001 and 2009, 2009, 2010, 2011) sampling periods was then normalized by the number of years between samplings. Barrow 2008 data were omitted due to the timing of sampling coinciding with a lemming outbreak (see Villarreal et al. 2012), and Niwot Ridge data for 1991 were omitted due to the lack of comparable resampling data from each of the three arctic locations. Change values were then averaged by location and community (dry, moist, wet) after which means and standard deviations were adjusted for sample size and used as input for meta-analysis in MetaWin 2.10 (Rosenberg et al. 2007). Means and standard deviations for each location and community

representing different “studies” were used to calculate effect sizes (hedge’s D). A series of separate summary meta-analyses were run using a categorical fixed effects model of the effect sizes and variances for each study. Bootstrapping and randomization tests using 999 iterations were used due to our low sample size. If the probability of the X^2 of total heterogeneity (Q_T) for the summary meta-analysis was below 0.05, heterogeneity within each category was determined. A significant change in diversity occurred when the probability of the X^2 of category heterogeneity (Q_{Wj}) was less than 0.05.

5.4 Results

5.4.1 Community Change

The NMS ordination of all sites and sample times had a final stress of 11.05 after 500 iterations that derived a 2-dimensional solution (Figures 15a-b). These stress values are relatively low for an NMS of this type (McCune and Grace, 2002) and indicate a good representation of site-based data. Sites near Barrow and Atqasuk clustered close to each other (Figure 15a) whereas sites from Baffin Island and Niwot Ridge clustered away from the Barrow and Atqasuk sites as well as each other in ordination space. Niwot Ridge sites showed the greatest variation between sampling years. Vegetation communities at Atqasuk did not shift markedly or consistently along ordination axes (Figure 15b), whereas vegetation communities at Barrow for 2010, Baffin Island, Niwot Ridge showed the greatest change, especially along axis one. Vegetation communities at Baffin Island and Niwot Ridge also moved away from the Alaskan sites (Barrow and Atqasuk), suggesting vegetation communities at the different locations are responding differently to environmental change. Shifts in vegetation communities at Barrow and Atqasuk were not overly apparent, however, the 2010 sampling for dry, moist, and wet communities at Barrow did shift positively along axis one, and wet Barrow vegetation communities showed greater variation than sites in dry vegetation communities. Analysis of vector lengths (Table 15) showed that all locations and communities changed in ordination space over the long-term sampling interval, with the exception of Atqasuk. Vector lengths for Barrow and moist communities changed for the short-term sampling interval.

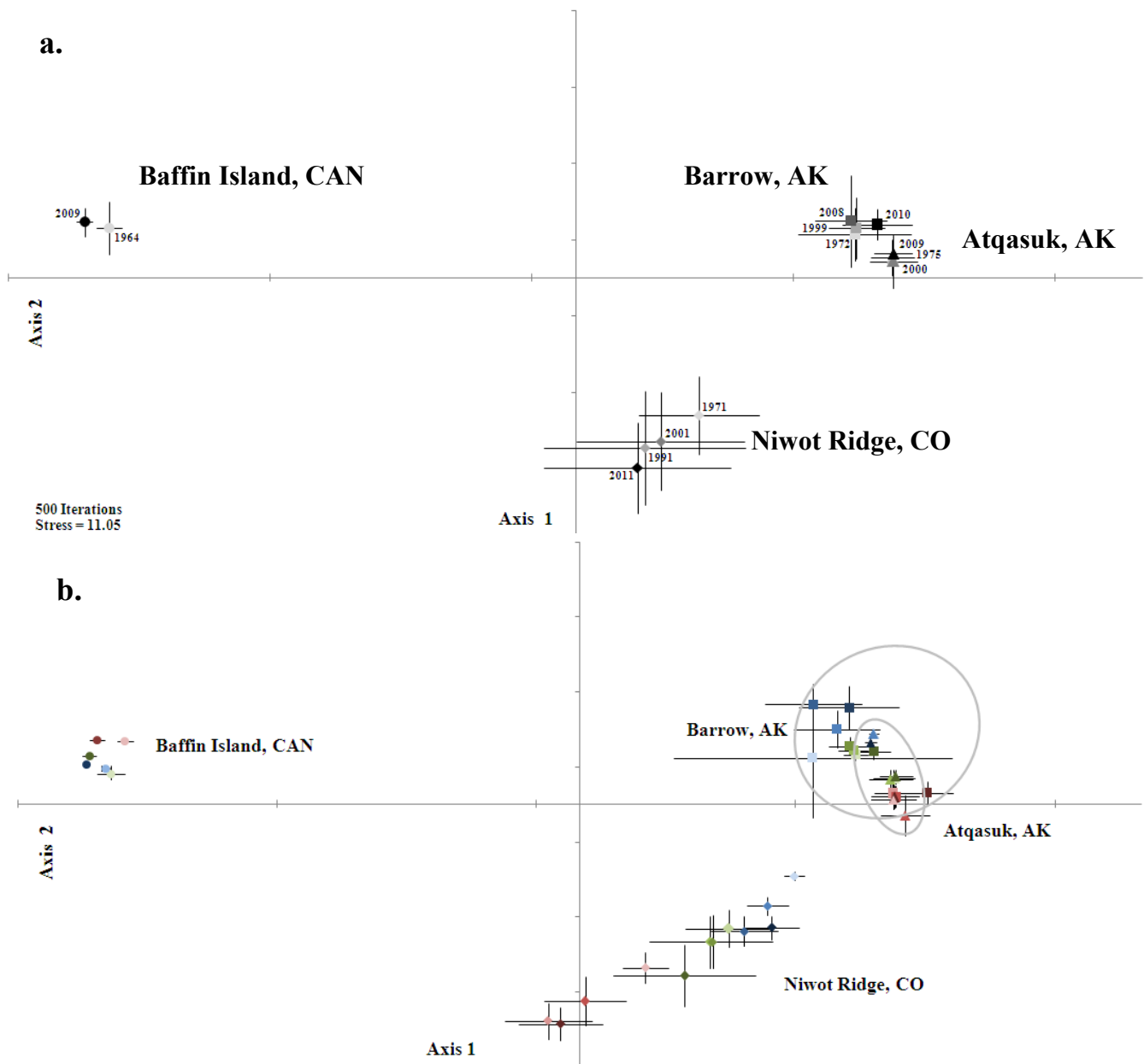


Figure 20a-b. Non-metric Multidimensional Scaling ordination of all sampling years by location (20a), and vegetation community at each location (20b). Points represent mean axis scores and standard deviations are represented as error bars (Niwot, CO – diamonds, Barrow, AK – squares, Atqasuk, AK – triangles, Baffin Island, CAN – circles) and within a community (dry – red shades, moist – green shades, wet – blue shades) at a given location. Lighter shades of color represent earlier sampling years, while darker shades represent older sampling years.

Table 15. Summary of meta-analyses for long-term and short-term changes in vector lengths at each location and for each vegetation community. N represents the number of studies in each analysis. Mean effect size (E+) is given in bold if both the total and the categorical heterogeneity probability of $X^2 < 0.05$. Degrees of freedom (df), lower and upper 95% bootstrap confidence intervals are also shown (-CI and +CI, respectively).

Vector Length Long Term							
	N	E+	df	-CI	+CI	Q _w	Prob(X^2)
Atqasuk	3	1.70	2	1.60	2.00	0.21	0.90
Baffin Island	3	2.41	2	1.15	3.47	25.07	0.00
Barrow	3	2.58	2	1.14	9.77	18.66	0.00
Niwot Ridge	3	1.95	2	1.47	4.13	5.66	0.06
Dry	4	3.06	3	2.06	3.80	13.08	0.00
Moist	4	1.71	3	1.25	2.79	16.54	0.00
Wet	4	2.23	3	1.27	3.35	8.32	0.04
Vector Length Short Term							
Atqasuk	3	1.85	2	1.65	1.95	0.20	0.90
Baffin Island	-	-	-	-	-	-	-
Barrow	3	2.62	2	1.30	3.86	9.62	0.01
Niwot Ridge	3	1.40	2	1.13	2.07	1.51	0.47
Dry	3	1.92	2	1.65	3.86	2.94	0.23
Moist	3	1.97	2	1.13	3.43	14.26	0.00
Wet	3	1.53	2	1.30	2.07	0.52	0.77

5.4.2 Richness, Evenness, and Diversity

Summary meta-analysis of change in diversity parameters at each location and each community for long-term and short-term sampling intervals revealed a variety of responses (Table 17). Species richness decreased in dry and moist vegetation communities for both long-term and short-term sampling intervals (prob $X^2 < 0.05$). Evenness increased at Niwot Ridge (prob $X^2 < 0.10$) and Atqasuk and in dry, moist, and wet communities in the long term. Evenness decreased in moist communities for both short-term and long-term sampling intervals. For the long-term sampling interval, diversity increased at Baffin Island (prob $X^2 < 0.1$) and in dry communities (prob $X^2 < 0.05$), and decreased in moist and wet communities (prob $X^2 < 0.05$).

Table 16. Summary of meta-analyses for long-term and short-term changes in diversity (richness, evenness, and Shannon's index) at each location and for each vegetation community. N represents the number of studies in each analysis. Mean effect size (E+) is in bold if both the total and the categorical heterogeneity probability of $X^2 < 0.05$, and italic if the probability of $X^2 < 0.10$. Degrees of freedom (df), lower and upper 95% bootstrap confidence intervals are also shown (-CI and +CI, respectively).

Richness Long term							
	N	E+	df	-CI	+CI	Q _w	Prob(X^2)
Atqasuk, AK	3	-0.53	2.00	-1.21	0.78	3.57	0.17
Baffin Island, CAN	3	-0.03	2.00	-0.16	0.34	1.45	0.48
Barrow, AK	3	0.68	2.00	0.15	0.88	1.50	0.47
Niwot Ridge, CO	3	-1.20	2.00	-1.50	-1.15	0.12	0.94
Dry	4	-0.37	3.00	-1.18	0.03	9.05	0.03
Moist	4	-0.11	3.00	-0.80	0.56	17.99	0.00
Wet	4	0.16	3.00	-0.62	0.41	3.85	0.28
Richness Short term							
Atqasuk	3	-0.40	2.00	-1.01	0.21	2.23	0.33
Baffin Island	-	-	-	-	-	-	-
Barrow	3	1.04	2.00	0.79	2.68	3.11	0.21
Niwot Ridge	3	-0.75	2.00	-0.94	-0.45	0.73	0.69
Dry	3	-0.34	2.00	-1.01	2.68	11.44	0.00
Moist	3	0.00	2.00	-0.94	0.96	15.83	0.00
Wet	3	0.34	2.00	-0.78	0.79	2.52	0.28
Evenness Long term							
Atqasuk	3	0.29	2.00	-0.25	1.80	9.55	0.01
Baffin Island	3	0.74	2.00	0.57	1.25	2.19	0.33
Barrow	3	-0.04	2.00	-0.34	0.50	2.66	0.26
Niwot Ridge	3	<i>-1.08</i>	2.00	-2.17	-0.65	5.20	<i>0.07</i>
Dry	4	0.46	3.00	-1.16	1.31	28.30	0.00
Moist	4	-0.12	3.00	-0.52	0.34	7.61	0.05
Wet	4	0.67	3.00	-0.75	1.13	7.42	0.06
Evenness Short term							
Atqasuk	3	0.24	2.00	-0.04	0.75	1.54	0.46
Baffin Island	-	-	-	-	-	-	-
Barrow	3	-0.35	2.00	-0.55	0.06	1.11	0.58
Niwot Ridge	3	0.50	2.00	0.11	1.35	1.77	0.41
Dry	3	0.29	2.00	-0.21	0.75	1.56	0.46
Moist	3	-0.01	2.00	-0.55	0.62	6.14	0.05
Wet	3	0.30	2.00	-0.04	1.35	1.69	0.43
Shannon's Diversity Long term							
Atqasuk	3	-0.11	2.00	-0.38	0.46	1.87	0.39
Baffin Island	3	<i>0.47</i>	2.00	0.25	1.25	4.96	<i>0.08</i>
Barrow	3	0.35	2.00	0.27	0.68	0.25	0.88
Niwot Ridge	3	-1.38	2.00	-2.31	-1.01	3.65	0.16

Dry	4	0.09	3.00	-1.44	0.44	19.44	0.00
Moist	4	-0.14	3.00	-0.74	0.28	9.93	0.02
Wet	4	0.64	3.00	-1.00	1.15	8.06	0.04
Shannon's Diversity Short-term							
Atqasuk	3	-0.04	2.00	-0.06	0.05	0.01	0.99
Baffin Island	-	-	-	-	-	-	-
Barrow	3	0.71	2.00	0.35	0.83	0.45	0.80
Niwot Ridge	3	-0.20	2.00	-0.38	-0.08	0.22	0.89
Dry	3	-0.13	2.00	-0.38	0.35	0.78	0.68
Moist	3	0.24	2.00	-0.13	0.83	5.30	0.07
Wet	3	0.35	2.00	-0.08	0.59	0.59	0.74

* Note, short-term change analysis could not be completed for Baffin Island due to just the 1964 and 2009 sampling years.

5.5 Discussion

The need for long-term observations of tundra vegetation change has been emphasized in numerous studies (Callaghan et al. 2011b, Elmendorf et al. 2012 Epstein et al. 2004). This study analyzed decade time-scale responses of vegetation communities in different tundra landscapes using repeat sampling of sites established and sampled/resampled decades ago using the same methods at all locations. Shifts in vegetation communities were detected using NMS at three of the four locations studied. Notably, vegetation community change appears to be occurring at a more rapid rate at Barrow and in moist tundra communities. Diversity changed for all communities at all locations, but was greatest in moist tundra. Inter-comparison of long and short-term analyses suggests that the decrease in species evenness and richness may be accelerating at moist and dry tundra at all sites. This study appears to be among the first to document an acceleration of community and diversity changes in North American tundra using decade-time scale datasets.

5.5.1 Vegetation community change

There was no overarching directional change in the ordination that was common to all locations or vegetation communities studied, suggesting that trajectories of change vary by location and vegetation community type. All sampling years within a respective location fell within one standard deviation of each other suggesting that an overarching step-change in vegetation communities has not occurred, with the exception of the 1964 and 2009 sampling years at Baffin Island. The relatively small

change documented for sites near Atqasuk agrees well with findings from Chapter 4 and a landscape level study conducted by Lin et al. (2012) that suggest a wetter landscape. The most recent Barrow and Atqasuk samplings (2009 and 2010, respectively) moved towards each other in ordination space, which may indicate that the vegetation at these two Northern Alaskan locations is becoming more similar. The Barrow 2008 sampling year coincided with a high lemming year that resulted in low productivity (See Chapter 3, Lara 2012). Within ordination space, site means moved in a negative direction along axis one, and away from the Atqasuk data. However, by 2010 Barrow vegetation appears to have recovered, and transitioned towards NMS axis scores reported for Atqasuk site data.

Alpine and high-arctic tundra clustered very differently from the Alaskan and Baffin Island sites in ordination space as a result of different species assemblages. Barrow and Atqasuk share similar species that can be abundant at both locations (e.g. *Aulacomnium* spp, *Cassiope tetragona*, *Carex aquatilis*, *Cetraria cucullata*, *Saxifraga cernua*). In contrast, it might be difficult to make comparisons between arctic and alpine tundra, and high-arctic and mid/low-arctic tundra because of the lack of species overlap, and caution should be taken when making biome-wide predictions on future change because the morphological plasticity of vegetation populations and between species interactions can differ markedly between arctic and alpine types (Mooney and Billings 1961). Furthermore, assessing drivers of change between these tundra types is a challenge. While warming is a considerable disturbance at both alpine and arctic tundra, changes in alpine vegetation are underpinned by range shifts in species and large-scale up and down-slope transitions of species have been reported (Britton et al. 2009, Gottfried et al. 2012). Several studies report shifts in species composition as a result of increases in vegetation density and shrub abundances in the Arctic (Myers-Smith et al. 2011, Sturm et al. 2011). Thus, the biotic mechanisms that underlie changes in vegetation community composition are likely to differ between arctic and alpine tundra.

We report that in our long-term assessment, all locations, with the exception of Atqasuk, and all communities changed significantly in ordination space. In our location-based analysis, Barrow and Baffin Island had the greatest magnitudes of change in effect size. These changes may be further evidence of widespread greening that has been detected in northern Alaska and Canada (Bhatt et al.

2010), however, an assessment of changes in the cover of functional groups at these communities and locations would be needed to affirm this. In addition, we report an acceleration of change in the ordination at Barrow and moist communities. The changes at Barrow may be accelerating due to its close proximity to the ocean. Bhatt et al. (2010) linked tundra greening to a decline in sea ice.

5.5.2 Richness, Evenness, and Diversity

Long-term changes in vegetation species richness, evenness, and diversity have occurred at the study locations investigated and support location-specific studies that have been undertaken (see Chapter 2, 3, and 4, Johnson et al. in prep). Increases in evenness at Niwot Ridge and Atqasuk, and the increase in diversity at Baffin Island agree particularly well. This study appears to be among the first to document increases in tundra vegetation species evenness over decade time-scales at multiple locations. An important implication of increased evenness may be that if tundra landscapes are becoming more homogenous, they may become more vulnerable since Post et al. (2009) discussed the importance of ecosystem heterogeneity as a climate change buffer. An increase in diversity had been predicted for tundra regions undergoing warming because diversity is generally greater in lower latitude landscapes that are also warmer (Walker et al. 1995), however, a meta-analysis of 11 locations by Walker et al. (2006) found an overall decrease in richness and diversity following six years of passive warming of the vegetation canopy. Our meta-analysis reports an observed increase in diversity at Baffin Island after 45 years, which agrees well with changes hypothesized but not those from experimental studies (Walker et al. 2006). One explanation could be that canopy height for most of the high-arctic tundra at Baffin Island has not increased much. Decreases in diversity have been documented where the increased height of the canopy of certain species, namely shrubs, outcompetes smaller species such as lichens for light (Myers-Smith et al. 2011), which results in a lower number of overall species. In addition, the vegetation communities at Baffin Island have the longest sampling period (45 years), and evidence from Chapter 1 suggests this region has undergone recent warming, which is likely to have enhanced vegetation change. Wet communities changed the most in the long term and underwent increases in diversity, which suggest they may be drying since diversity is greater at dry tundra (Hollister et al. 2005b, Chapter, 2, 3 and 4).

Additionally, we found that both Barrow and Niwot wet communities shifted along our NMS ordination towards the position of dry communities within the same location, further supporting this theory.

We found numerous changes in species diversity for vegetation communities at all locations. The most substantial changes were documented for moist tundra, where long-term species richness, evenness, and diversity decreased, and short-term richness and evenness increased. Walker et al. (2006) also found the greatest change in moist tundra and reported higher canopy heights and particularly large changes for shrubs and graminoids. The decrease in diversity documented in this study for dry and moist vegetation communities may be caused by increases in canopy cover, which can cause competition for light and a loss of short statured shade-intolerant species such as bryophytes and lichens.

Several other meta-analyses that have been conducted at the ecosystem and biome-level for vegetation response to warming in arctic and alpine tundra suggest that smaller-scale changes are occurring. In older studies, Both Dormann and Woodin (2002) and van Wijk et al. (2004) found no significant changes in overall biomass with experimental warming, although relatively small-scale measurements on individual plants (Arft et al. 1999), some species (van Wijk et al. 2004) and vegetation physiology (Dormann and Woodin, 2002) did respond. In this study, we not only found large-scale changes in vegetation, but evidence that communities and locations are changing differently, some more than others, and that these changes may be accelerating. Therefore, modeling studies such as those used to determine carbon outputs from permafrost thaw, should not only consider vegetation feedbacks to carbon dynamics (Schapoff et al. 2013), but the apparent accelerated response shown for vegetation change in this study. Additionally, tundra greening trends appear to be higher in Eurasian tundra (Bi et al. 2013), which was not studied here. However, assuming this pattern is true for the four tundra locations in this study, we may expect the acceleration trends found in this study to be higher in Eurasian tundra. Therefore, further studies using long-term observation in Eurasian tundra are recommended.

Chapter 6: General Discussion

Land-atmosphere processes are closely coupled in the Arctic and changes to tundra vegetation have the potential to impact regional to global processes through complex biophysical feedbacks with other components of the Earth System (Chapin et al. 2005, Myers-Smith et al. 2011, Schaphoff et al. 2013). In particular, increases in shrub abundance and vegetation greening have raised concerns that land-atmosphere carbon and energy exchange in the Arctic have been altered (Raynolds et al. 2012), and biodiversity has been impacted (Hansell et al. 1998). A primary challenge for assessing change and predicting future environmental states in the Arctic is the lack of time series environmental observations that span decadal time scales (Callaghan et al. 2011b, Tweedie and Callaghan 2013).

With continued anthropogenic processes affecting global change and an improved awareness that arctic change can have global-scale consequences, research on high latitude ecosystems has drawn increased attention that was enhanced by the International Polar Year (2007-2009). However, because there is a general lack of decadal data for the relatively slow-growing biological systems in the Arctic, a reliance on short-term studies to parameterize predictive models has become relatively common practice. The overarching goal of the International Polar Year Back to the Future (IPY-BTF) study, to which this study contributed, is to rescue historic research data and sites, secure, and resample these to assess how arctic terrestrial ecosystems have changed over time, and use this knowledge to improve capacities for predicting future states of arctic terrestrial ecosystems (Callaghan et al. 2011b).

This BTF study assessed ecosystem structural changes at decadal time scales for three different locations in the Arctic. This study rescued and resampled historic research sites (>35 years in age) at three locations in the Arctic and consisted of a total of 503 vegetation sites and 5030 m² plots where vegetation species cover and abundance have been measured multiple times. The research challenges presented in Chapter 1 (Section 1.2) review relevant literature and highlight the difficulties caused by the lack of decade time scale observations of change. We assessed long-term observational change at both the community and ecosystem level (Chapters 2-4) and at the biome level (Chapter 5) for vegetation by synthesizing vegetation community-based studies in different tundra ecosystems. Below,

the overarching objectives of this dissertation are revisited and addressed based on the findings presented thus far. Priorities for future research building off this study are also presented.

6.1 Recapitulation of Objectives

6.1.1 Is there evidence of vegetation community change, and spatiotemporally, which vegetation communities are changing the most/least?

Vegetation did not have the same change trajectories among sampling locations (Figure 20a-b, Chapter 5). Similar results were found for site-specific vegetation community analyses at Niwot Ridge, and at Barrow, where there was no overarching trajectory of vegetation community change common to all vegetation communities. At Barrow, herbivory associated with a natural lemming population high demonstrated the important influence herbivory can have on tundra systems (see Chapter 3, section 3.5). For resampling efforts at Baffin Island, a different pattern emerged and there was a common trajectory of change between sampling years for nearly all vegetation communities present. However, change trajectories derived from ordination space for vegetation communities near Atqasuk were minimal, which agrees well with Lin et al.'s (2012) findings associated with a low degree of future land cover change. Change appeared to be more apparent for Baffin vegetation communities, which changed in a similar direction in ordination space with the exception of *Cassiope* snowbeds and *S. oppositifolia* cryptogamic crust communities that moved opposite from the rest of communities in ordination space. Additionally, alpine tundra and high-arctic tundra clearly clustered separately from wetland and low-arctic tundra, which clustered close to each other in ordination space (Figure 20a-b, Chapter 5). These results agree with similar findings, especially from large-scale ITEX studies, which have found that community change with warming can vary substantially spatiotemporally (Elmendorf et al. 2011, Epstein et al. 2004, Hudson and Henry, 2010).

6.1.2 How are changes in vegetation functional groups driving vegetation community change?

Vegetation functional groups have proven to be a useful metric for detecting ecosystem change in tundra landscapes (Chapin et. al 2009) and have become widely used by several influential and recent synthesis studies for tundra environments (Elmendorf et al. 2011, Elmendorf et al. 2012, Walker et al. 2006). At the regional level, changes in vegetation functional groups were not always consistent

between locations. Near Barrow, changes in vegetation functional types showed variation between sampling years for the entire dataset, and this pattern was also apparent for many of the individual communities at Barrow. The relative cover of litter, graminoids, and bryophytes were unstable between sampling years, while the relative cover of shrubs did not change and that of lichens gradually increased. Near Atqasuk, some variability in relative cover was shown for the 2000 sampling year, however, between 1975 and 2009 the relative cover of all vegetation functional groups remained unchanged, a pattern that was also evident in each of the vegetation communities at this location. Baffin Island had significant differences between 1964 and 2009 for all vegetation functional types except for bryophytes, with the most noticeable changes detected for the relative cover of shrubs (+6.23%). Graminoid, forb, and lichen relative cover also increased, while that for bryophytes and liverworts decreased. One of the most robust and recent syntheses analyzing the response of vegetation functional groups to warming found that shrubs, graminoids, and forbs are likely to continue to increase in cover in the future, while the cover of mosses and lichens will decrease (Elmendorf et al. 2012). Although vegetation functional types did not change at sites resampled near Atqasuk, our results from Baffin agree with findings for all functional groups from Elmendorf et al. (2012) with the exception of lichens.

6.1.3 How are diversity, evenness, richness and individual species changing?

Patterns of vegetation composition and variation in biodiversity are important to monitor because they can show a strong association with a range of ecosystem processes (e.g. carbon exchange, Hooper et al. 2005, Oberbauer et al. 2007, Sistla et al. 2013). A large effort has focused on documenting hotspots for diversity change in the Arctic and identifying the patterns and distributions of species that underpin diversity changes (Elmendorf et al. 2011, Walker et al. 2006). A meta-analysis determined that vegetation communities at Niwot Ridge and Atqasuk increased in evenness, and Baffin Island increased in diversity. Diversity parameters also changed within communities (dry, moist, and wet), and these also suggest that rates of change are accelerating. This analysis appears to be among the first to report biome-wide increases in evenness and accelerating rates of change in diversity.

Both vegetation species richness and diversity increased significantly at Baffin Island and Barrow (1972-2010), however, these parameters initially decreased at Barrow between 1972 and 1999

(Table 7, Chapter 3), suggesting that differences between initial and long-term responses are similar to those documented in an experimental warming experiment presented by Hollister et al. (2005b). Evenness increased significantly at Baffin Island and Atqasuk (1975-2009), and results from Atqasuk suggest that the rate of change is accelerating since evenness did not change between 1975 and 2000, but did between 2000 and 2009. Diversity at Atqasuk did not change after 34 years. The largest ITEX syntheses the examined vegetation community response to warming reported decreases in diversity and richness (Walker et al. 2006), however, an eventual increase in diversity is expected in northern latitude regions due to warming (Walker et al. 1995). Increases in diversity were found in this study for two of our three locations (Baffin Island, Chapter 2 and Barrow, Chapter 3), while Niwot Ridge decreased in diversity.

6.1.4 Along what gradients is change occurring and what are the likely biophysical factors driving change?

In addition to detecting vegetation change, shifts in community composition in ordination space can be explained along environmental gradients. Sala et al. (2000), for example, reported that the most likely drivers for changes in arctic biodiversity are climatic and atmospheric carbon dioxide abundance. For Barrow, correlations between environmental data and ordination scores revealed that soil moisture and thaw depth correlated strongly, which agreed with initial studies that documented strong links between soil moisture and community composition in the 1970's (Webber 1978). For Atqasuk and Baffin Island, regression trees were used to assess how the magnitude of change in the ordination was explained by environmental variables. Soil moisture (mean bulk density) and pH best explained the variability in the magnitude of change of sites in the ordination near Atqasuk, which agree with original findings that soil moisture is a leading control of vegetation composition in this region (Peterson and Billings 1980). Site surface age since deglaciation and slope angle explained the greatest degree of variability of vegetation community change at Baffin Island, which agrees with Webber's original assessment that vegetation communities were strongly influenced by terrain characteristics (Webber, 1971).

6.1.5 How have patterns of primary succession following deglaciation changed over time at Baffin Island, Canada?

Rapid deglaciation of terrestrial ice sheets is occurring in the Arctic (Sharp et al. 2012), which exposes new terrain for colonization by tundra vegetation. These newly-exposed surfaces are also useful for studying primary succession, and few studies have explicitly examined how vegetation succession is being altered in these landscapes as a result of warming. A recent review on the assessment methods of ecological succession highlighted the need for long-term data (Johnson and Miyanishi, 2008). This study found that primary succession at a recently deglaciated area at Baffin Island did not occur linearly, and that succession patterns (vegetation cover, species richness, and species diversity) are accelerating (Figure 11a-c, Chapter 2). Sites less than 200 years in 2009 appear to be colonizing and stabilizing faster and have greater vegetation cover and number of species than similarly aged sites in 1964. This may be one of the first studies to report an increased rate of vegetation successional dynamics for recently deglaciated high-arctic tundra landscapes. Findings from this study also highlight the high Arctic as a dynamic landscape that may be more responsive to climate change impacts than previously thought.

6.1.6 Do herbivores mask or facilitate decade time-scale vegetation community change at Barrow, Alaska?

The clear temporal variation in vegetation functional group cover for the Barrow study suggested that forage and trampling by the brown lemming play a key role in controlling vegetation cover. An exclusion study near Barrow has recently shown that graminoids, mosses, and litter cover are strongly influenced by the brown lemming (Johnson et al. 2012), and that these groups were the most variable between sampling years in this study. Shrubs and lichens are largely ignored by lemmings in the Barrow area, which may explain why these vegetation functional types remained relatively stable over time. This highlights the importance of not only the timing of vegetation sampling, but also consistently monitoring vegetation-animal interactions in tundra landscapes, especially since recent studies have shown that the population dynamics of lemmings in both space and time are being affected by warming (Ims et al. 2011). Although lemmings affect vegetation cover near Barrow, it is also important to assess bottom-up interactions between plants and animals in tundra regions. For example, a large-scale study

by Hendren et al. (2013) found that avian diversity is highly dependent on vegetation structure and that climate-driven vegetation changes (shrub encroachment) can enrich bird diversity.

6.1.7 How have vegetation communities, species richness, evenness, and diversity changed across the tundra, and how does this change differ between long-term and short-term sampling intervals?

The largest biome-wide study in the Arctic that documented change in species diversity found an overall decrease in species richness and diversity (Shannon's index) in experimental warming plots (Walker et al. 2006), which was attributed to the increased canopy height of shrubs and graminoids leading to light limitation to subcanopy shade intolerant species. In contrast, we recorded an increase in diversity at Baffin Island. Consistent with Walker et al.'s (2006) documentation of increased diversity with experimental warming, however, we found that species richness did decrease at dry and moist tundra over 45 years, while diversity decreased in moist tundra and increased in dry tundra over the same time frame. Species richness (at dry and moist tundra) and evenness (in moist tundra) decreased over 45 years. Thus, this study is among the first to report long-term observational increases in evenness, and an acceleration of changes in species diversity over recent decades.

6.2 Summary of Dissertation

Understanding how the structure of tundra ecosystems has changed over the past few decades is crucial in order to improve assessments and models predicting the future state of the Arctic and Earth Systems as they continue to respond to global change. This study contributed to the International Polar Year Back to the Future project and its primary objectives. Through the re-discovery, resampling, and analysis of vegetation sites established more than three decades ago, this study has provided the arctic science community with a new and long-term dataset that provides the necessary basis to identify vegetation change dynamics, validate remote-sensing studies and models, and explore the mechanisms that may change trends in such studies. This study is also relatively unique because all locations and sites used an identical methodology, and observers were all "student descendants" of Dr. Patrick Webber, who established sites at the different locales and trained almost all of the observers associated with this study which is likely to have reduced the potential for observer error.

An important challenge facing the arctic science community is how warming of tundra vegetation will drive feedbacks with other components of the Arctic and Earth Systems. Identifying hotspots of vegetation change, therefore, is crucial to meeting this challenge. This study found that changes in vegetation are rarely consistent across different locations and tundra ecosystems. Trophic interactions, particularly the top-down effects of lemming herbivory, challenge how we detect these changes and how observing programs need to be designed in order to accommodate such environmental stochasticity. Furthermore, while some regions in the Arctic have not changed over the last few decades, the mechanisms by which vegetation changes occur, (e.g. succession), may be changing as a result of warming, as was reported for Baffin Island. Finally, we report that community composition is changing across all locations studied, and that some locations are changing more than others. This finding was also apparent for all vegetation communities (dry, moist, and wet), and these trends seem to be accelerating at Barrow, Alaska and for the moist tundra community. Although some metrics of vegetation change may take more than four decades to change (e.g. diversity), others (e.g. richness and evenness) may be changing faster, and may provide further evidence of warming-induced changes ongoing in tundra landscapes.

6.3 Future Research Priorities

This study has helped answer several key questions focused on vegetation change in the Arctic over decadal time scales. Until recently, such findings were scant due to the lack of robust, long-term historical data and sustained monitoring focused on addressing these questions. Consequently, several concerns and ideas for future research arose during the data collection and analyses of these Back to the Future datasets, and these are described below with reference to future research and monitoring priorities as a result of this study.

6.3.1 Continued monitoring efforts

Just as the International Tundra experiment (ITEX) is an ongoing international monitoring effort that aims to monitor experimentally warmed and control plots, there are many reasons why Back to the Future sites should be preserved and monitored to further our understanding of decadal time scale change and inter-annual variability. Lemming outbreaks occur every 3 to 5 years (Batzli et al. 1980),

and infrequent vegetation sampling, especially during lemming outbreaks, may lead to misleading results. If the sites near Barrow continue to be monitored, this would lead to one of the most comprehensive datasets on vegetation community change dynamics to be compiled for multiple phases of lemming population cycles (Ims and Fuglei 2005, Pitelka and Batzli 2007). In addition, the dataset for Baffin Island represents one of the oldest and robust datasets focused on vegetation community change in the high Arctic, made possible because of the dedicated effort by Dr. Webber nearly five decades ago. The Baffin Island sites not only span nine different communities, but several sites have served to assess changes in successional trends on recently deglaciated surfaces, a study that appears to be among the first of its kind using such long-term observational data. The Baffin Island sites are even more interesting due to recent studies reporting the ‘reawakening’ of 500 year-old bryophytes in the high Canadian Arctic following deglaciation (La Farge et al. 2013). A resampling effort every ten years is recommended for the Baffin Island sites, as interannual variability is likely to not be as high at this site as it is in Barrow due to lack of human disturbance and large herbivore populations. Additionally, a much greater logistic endeavor is needed for site based activities on Baffin Island due to the remoteness of the location and difficult terrain to navigate once there. Atqasuk, however, is a much more accessible location and resampling is recommended for sites near Atqasuk every five to ten years. Although change is not predicted to be high for Atqasuk, its different soil types, different geomorphology, greater diversity of vegetation, higher abundance of shrubs, and higher diversity of herbivores could lead to better insight between species interactions. Atqasuk also provides an important baseline to assist with understanding the heterogeneity of responses to global change in different tundra ecosystems. Through several years of resampling, successful documentation of ecosystem variability, model validation, and true evaluation of change can continue to be obtained and it is likely the scientific community will continue to seek access to such datasets to further understand the dynamics of tundra ecosystem responses to global change.

6.3.2 Preservation of historical sites and data

Twenty seven of the original 43 sites near Barrow have been lost due to encroachment of urban dwellings and other infrastructure in the City of Barrow, and continue to be disturbed by local off road

vehicle activity (Figure 21). Although this study successfully captured all of the original communities from Webber's initial assessment (Webber, 1978), the loss of these sites has greatly reduced the representation of some vegetation communities. Similarly, twenty nine sites were unable to be relocated near Atqasuk, and although disturbance was not a primary concern for this location, our capacity to detect change in three communities has been minimized due to very low sample size (see Table 10, Chapter 4). Three of the original 82 sites at Baffin were not resampled due to logistical constraints, however, a very detailed effort went into determining site relocation using a variety of data. Resampling these sites was a success because Dr. Webber thoroughly detailed each site with notes and measurements, which highlights the importance of high-quality site documentation (e.g. photography, coordinates, descriptions, markers). Storing these data carefully is also warranted in order to avoid data loss. The loss of the raw 1975 Atqasuk data led to challenges and limitations in the analysis, and serves as a poignant reminder that long term preservation of data is important.



Figure 21. Moist site (#1315) near Barrow, Alaska showing old off-road vehicle disturbance transecting two different sites within the site. These disturbances can last many years and at this site; the deciduous shrub *S. rotundifolia* was found to only be growing within the area of the disturbance.

In addition to preserving the sites and data included in this study, we also recognize the important need to maintain a strong cross-generational lineage of observers. A large amount of observer error was likely reduced in this study because observers are prior students of Dr. Webber, and thus have all received similar training. Although observer error has been a concern for the collection of visual estimates in other studies, especially when performed by different observers (Gotfryd and Hansell 1985), impacts of differing observers have been found to be minimal in other studies similar to here (Kennedy and Addison 1987), thereby reinforcing the power of visual estimates to successfully and rapidly sampling large areas of vegetation over decadal time scales spanning the working life of multiple investigators.

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Biographical Sketch

Sandra Villarreal

Ecology and Evolutionary Biology

Sandra Villarreal earned her Bachelor of Science degree in Environmental Science Biology concentration from the University of Texas at El Paso (UTEP) in May of 2008. She began her doctorate at UTEP in the Fall of 2008. Dr. Villarreal has been the recipient of various awards, including: a National Science Foundation (NSF) GK-12 fellowship and travel funding from the UTEP Biology Department, the Society for the Advancement of Chicanos and Native Americans in Science (SACNAS), the Association of Early Polar Career Scientists (APECS), and the Research Council of Norway.

Dr. Villarreal has presented at the following national and international conferences: the International Polar Year (IPY) Montréal conference “From knowledge to action” in 2012, the Ecological Society of America (ESA) Conference in 2011, the International Polar Year (IPY) Oslo Science Conference in 2010, the State of the Arctic Conference (SOA) in 2010, the Back to the Future (BTF) International meeting in 2009, and the Society for the Advancement of Chicanos and Native Americans in Science (SACNAS) from 2007-2009.

This dissertation was supervised by Dr. Craig E. Tweedie and publications produced from this dissertation are as follows:

Villarreal S, Johnson DR, Lara MJ, Hollister RD, Webber PJ, Tweedie CE. 2012. Tundra Vegetation change near Barrow, Alaska (1972-2010). *Environmental Research Letters*. **7**:015508, doi:10.1088/1748-9326/7/1/015508.

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Dr. Villarreal has accepted a post-doctoral position under Dr. Tweedie starting September of 2013 and plans to pursue ecological research.