University of Alberta

Entombed Little Ice Age Bryophytes: Ecology and Regeneration

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science
in
Ecology

Department of Biological Sciences

Fall 2013
Edmonton, Alberta

Abstract

Subglacial bryophytes, entombed during the Little Ice Age (LIA, 150-580 years BP) beneath the polythermal Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut, Canada, were examined. The diversity, paleoecological significance, and regeneration capacity of these bryophyte assemblages are the focus of this study. A comparison of LIA and extant assemblages from the granitic, southern slope of Sverdrup Pass, form the basis of Chapter II. The results suggest that species richness and diversity are similar in bryophyte assemblages of pre and post LIA glacier expansion and retreat and indicate diverse microhabitats. Chapter III examines the regeneration of bryophytes from a subglacial ecosystem and indicates viable tissue resumed growth after fragmentation *in vitro*. In contrast to vascular plants, bryophytes are poikilohydric, and desiccation and freezing tolerant and their tissue (stems, leaves, diaspores) consists of totipotent cells, which facilitates dormancy in subglacial ecosystems.

Acknowledgments

I would like to extend my sincere appreciation to the people whose guidance, advice, and support made this task possible. In particular, thanks to my co-supervisors, Catherine La Farge and David Hik. Dave always made time for helpful discussions, guidance, and advice. I am especially indebted to Catherine for introducing me to the brilliant bryological world. Her enthusiasm for bryophytes was contagious and her expertise is invaluable. Her comments and patience through numerous drafts of this work are immensely appreciated. She and John England made my time on Banks Island especially memorable and their passion for the Arctic inspired my own.

Polar Continental Shelf Program, NRCan, Ottawa provided logistical support for fieldwork. NSERC Discovery Grant (G121211007) provided funding to Catherine La Farge and NSERC Northern Research Chair to John England. The Canadian Circumpolar Institute, University of Alberta, Edmonton provided additional support. Thanks to D. Wilkie for assistance in the field. Staff in the Department of Biological Sciences provided professional assistance, which was greatly appreciated. Charlene Nielsen's help was indispensable with creating essential figures, and Karen Romanyk loaned materials and expertise, and offered encouragement whenever she could.

Many thanks are also due to Richard Caners for providing vital statistical advice, as well as to Kesia Miyashita for countless enlightening discussions on everything thesis-related. She was always willing to review my work and continuously provided valuable feedback. Thank you as well to my close friends, Paul Donovan, Geoff Clarke, Darrell Hepburn, Randy Schneider, and Tyler and Stephanie Watson, who helped to keep me on an even keel, and who now know more about moss than they ever imagined they would.

I owe a special thanks to all of my wonderful family and particularly to my Mom, Sharon Marshall. She instilled confidence in me by providing sensible advice, encouragement, and constancy. Without her, this project would not have been possible. Finally, words cannot express my appreciation to my husband, Adrian Szeligowski, whose reassurance, and unending patience throughout my program enabled my success.

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Chapter I: Bryophytes in High Arctic Ecosystems

The Canadian Arctic Archipelago (CAA) is the northernmost portion of North America extending east to west from Baffin Island to Banks Island, north to south from Mansel Island and Akpatok Island to the coast of northern Ellesmere Island. The Queen Elizabeth Islands form a natural topographic and phytogeographic region including Axel Heiberg, Devon, and Ellesmere Islands. The barren lowlands are often described as polar deserts due to the presence of cryosols (thin soils with continuous permafrost) and daily freezing temperatures (Svoboda and Freedman 1994). Although the CAA is mostly ice-free in the summer, permafrost exists nearly everywhere, and varies in thickness along an air temperature and latitudinal gradient (Rouse et al. 1997). The active layer (annual thaw at the surface) varies with substrate texture and water content and patterned ground (polygonal patterns caused by frost action and ice wedges on poorly drained peatlands) is common. This permanently frozen ground influences plant growth by cooling the soil and acting as a barrier to water movement. The bedrock geology consists of metamorphic Precambrian bedrock composed of granite and gneiss and Paleozoic sedimentary rock composed of calcium carbonate complexes (Dyke 1984, Edlund and Alt 1989).

Ellesmere Island, Nunavut is the largest and most northern of the Queen Elizabeth Islands in the CAA (Figure 1.1). Maxwell (1981) defines the alpine region of Ellesmere Island as a rugged mountain terrain where the exposed slopes receive 200 mm of precipitation. These mountains serve as a barrier that shelter intermontane regions from the arctic climate, and consequently receive <100 mm of precipitation annually (Maxwell 1981). Minimal cloud cover and high temperatures (3-5°C mean daily temperature; Maxwell 1981) result in relatively dense and diverse vegetation (Edlund and Alt 1989).

Glacial History

The Quaternary glacial history of Ellesmere Island has been extensively investigated (Blake 1970, England 1999, England et al. 2006, Dyke et al. 1996, 2002). During the Pleistocene (1.8 – 0.01 mya), the northern hemisphere experienced several major glaciations and the Arctic was repeatedly covered by ice. On Ellesmere Island, geological evidence, such as erratics and roches moutonnées, indicates the extent of the latest major glaciation: the Wisconsin (110-10 k years BP). It is characterized by the coalescence of the Greenland Ice Sheet and the Innuitian Ice Sheet (England 1999, Dyke et al. 2002), with the center of glaciation thought to be the northern Ellesmere ice cap (Smith 1961). Remains of the last ice age are seen in ice caps and glaciers, usually confined to the valleys. This glacial and climatic history has created a range of erosional and depositional landscape features, such as valleys and moraines overlain by glacial deposits, subglacial streams, and meltwater channels.

Ellesmere Island was subject to a Neoglacial climatic cooling, often referred to as the Little Ice Age (LIA) approximately 150 - 580 years BP. (Gribbin and Lamb 1978, Overpeck et al. 1997, Miller et al. 2010). Cooling temperatures were a consequence of decreased summer insolation initiated in response to increased volcanism and decreased solar luminosity. This was amplified by positive feedbacks such as expanded Arctic Ocean sea ice and terrestrial snow cover (Miller et al. 2010). A compilation of paleoclimate data from marine sediments, tree rings, ice cores and annually laminated lake sediments provide proxies for temperature reconstruction during the last 500 years (Overpeck et al. 1997, Rayback and Henry 2006, Cook et al. 2009). Unlike the Pleistocene glaciation, much of the Arctic remained ice-free. Instead, glaciers, ice caps, and permanent snow banks expanded reaching their Neoglacial maximum (Miller et al. 2010).

In addition to paleoclimate proxies, vegetation trimlines have been used as LIA indicators. These light-toned zones of poorly vegetated terrain often mark

former glacial advances and record snow and ice expansion during the LIA rather than seasonal persistence of recent snow cover (Beschel 1961, Wolken et al. 2005). Satellite imagery and air photos can be used to reconstruct ice volumes and equilibrium line altitudes (ELA). ELAs indicate where the accumulation and ablation of a glacier are equal (Matthews 1992) and relate to glacier advance or retreat. Patterns of ELA fluctuation have been used to make inferences about the regional scale climate change associated with Neoglacial cooling. Trimlines indicate that between the end of the LIA and 1960, terrestrial ice in the Queen Elizabeth Islands decreased by 37% (Wolken et al. 2008). During the LIA, Ellesmere Island was covered in 122,933 km^2 ice, but by 1960, only 79,317 km^2 of ice remained (Wolken et al. 2008).

Similar to geologic paleoclimatic proxies, detailed studies on preserved arctic vegetation have shown interannual variations in growth can be used to estimate LIA temperatures as well. *Cassiope tetragona* (L.) D. Don., a circumarctic ericaceous dwarf-shrub that grows on tundra soils, has xeromorphic leaves and annual growth rings that make it a model species for studying climate-related plant growth (Callaghan 1973, Havström et al. 1993). The LIA subglacial shoots (411 ± 70 radiocarbon years old) from Ellesmere Island showed that the mean July temperatures immediately preceding glaciation were 0-7°C lower than today (Havström et al. 1995).

Arctic Vegetation Zones

The tundra vegetation is dependent on climate, microclimate, drainage, nutrients, soil type, and snow cover (Aiken et al. 2007). Bryophytes, represented by mosses (Bryophyta) and liverworts (Marchantiophyta), constitute a major component of this plant diversity. Several arctic vegetation classification schemes have been developed from Russia (Alexandrova 1988, Yurtsev 1994, Matveyeva 1998), Fennoscandia (Tuhkanen 1984, Elvebakk 1999), Greenland (Daniels 1994), and North America (Porsild 1957, 1964, Hulten 1968, Edlund and Alt 1989, Bliss

1997, Walker et al. 2005), which have emphasized vascular plants and largely overlooked the bryophyte component. Longton (1988) provides a rare and comprehensive treatment of polar ecosystems, focusing on cryptogams (bryophytes, lichens and fungi) and three polar vegetation zones are outlined. His classification is based on vegetation types, which are closely related to mean summer temperatures, rather than broad ecological features, such as fauna, soils, or climate. Longton (1988) defined 1) mild-arctic region characterized by extensive grass and dwarf shrub heaths and wetlands, with highest mean monthly temperature of 6-12°C; 2) cool-arctic region dominated by dry meadows and other angiosperm communities, with the highest mean monthly temperature 3-7° C; and 3) cold-arctic region characterized with mean monthly temperatures of 0-2° C characterized by closed stands of bryophytes, lichen or algae (Figure 1.1).

Recent technology has developed a photo-interpretative approach using Advanced Very High Resolution Radiometer (AVHRR) to remotely assess and classify circumpolar arctic vegetation (Walker et al. 2005). Five bioclimatic subzones and their vegetation components have been defined (Walker et al. 2005). Their results showed that 26% of vegetated areas are shrubland, 18% are peaty graminoid (grasses, sedges and rushes) tundra, 13% are mountain complexes, 12% are classified as barren (which consists of mostly cryptogams), 11% are mineral graminoid tundra, 11% are prostrate shrub tundra, and 7% are wetlands. Descriptions of these bioclimatic subzones of the arctic include percent cover and net annual production (Walker et al. 2005). Three subzones are classified as High Arctic, two of which are dominated by 40 – 60% cover by cryptogams with net annual production ranging from 0.3 – 2.9 t ha^{-1} yr^{-1}. In addition, vegetation types, plant biomass, and net primary production patterns in the Canadian Arctic have been examined in detail and summarized in Gould et al. (2003).

North America and Greenland are often treated as the same phytogeographic region (High Arctic), which has been well documented bryologically. The most extensively studied areas include Greenland (Jensen 1910,

Holmen 1955, 1956, 1960), Alaska (Persson 1946, 1949, 1952), and Ellesmere Island (Holmen 1953, Powell 1967, Schofield 1969, Schuster et al. 1959, Brassard 1971a, 1971b, 1976, La Farge-England 1989, La Farge-England et al. 1991, Maas et al. 1994). The bryoflora of the CAA consists of largely circumpolar taxa with nearly 400 mosses (Ireland et al. 1987). This is compared to 350 vascular plants (Aiken et al. 2007).

Longton's (1988) cool-arctic region (Figure 1.1) encompasses the majority of the CAA including Ellesmere Island. Early bryological research from Ellesmere Island has focused on floristics and descriptive ecology (Schuster et al. 1959, Powell 1967, Brassard 1971a, 1971b, 1976, La Farge-England 1985, Hedderson and Brassard 1992, Maas et al. 1994) whereas later studies used quantitative ecological methods to examine contemporary assemblages (La Farge-England 1989, Bliss et al. 1994), fossil assemblages (Bergsma et al. 1984, La Farge-England et al. 1991, Ovenden 1993), and plant succession (Lévesque and Svoboda 1999, Jones 1997, Jones and Henry 2003, Hudson and Henry 2009).

Bryophyte Biology

Bryophyta (mosses) represents a distinct lineage of embryophytes, which have evolved biological and physiological solutions to succeed in polar environments. They are generally considered primitive plants and research indicates they share a common ancestor with green algae (Mishler and Churchill 1985, Shaw et al. 2011). In contrast to tracheophytes (vascular plants), bryophytes (mosses, liverworts, and hornworts) have a haplontic life cycle where the sporophyte remains attached and is dependent on the dominant gametophyte generation for its nutrition. Mosses and liverworts represent embryophytes that have leaves (typically one cell thick) developed on the gametophyte. As well, they lack roots that have complex conducting xylem and phloem vascular tissues, instead producing filamentous rhizoids that function in anchorage and water and nutrient absorption (Schofield 1985, Smith 1982, Ligrone et al. 2012).

Bryophytes are adapted to and occupy a wide range of microhabitats that have evolved from a diverse range of reproductive strategies. More than 60% of arctic mosses are dioicous (separate male and female gametophytes) and this, coupled with environmental constraints, result in the rarity of sporophyte production (Brassard 1971a, Schofield 1972). Monoicous taxa (both sexes potentially on one gametophyte) are capable of self-fertilization where the fusion of egg and sperm produced mitotically from a single gametophyte constitute a form of asexual reproduction since all spores will be genetically identical (Mishler 1988, Shaw 2000). While gametes (egg and sperm cells) represent sexual reproduction, diaspores (any structure by which a plant reproduces itself) represent asexual reproduction and include spores, specialized propagules (gemmae, bulbils, deciduous branches, caducous leaf tips), or unspecialized fragments (Longton and Schuster 1983, Pressel et al. 2007). Often formed when suboptimal conditions exist, specialized asexual propagules have critical roles in establishing and maintaining populations (Newton and Mishler 1994), and can differ in dispersal and germination capacity (Kimmerer and Young 1996). Diaspore banks, a potential source of reproductive propagules, are a means of temporal dispersal where taxa can outlast unsuitable conditions and germinate when the highest chances for successful establishment occurs (Thompson and Grime 1979).

Given the rarity of sporophyte production (Brassard 1971a), asexual reproduction by fragmentation allows for survival in cold and dry environments (Rowntree et al. 2007). In the Arctic, wind-dispersed gametophyte fragments develop into new new plants from secondary protonema (one of the initial filamentous stages of the moss life cycle) (Correns 1899, During and van Tooren 1990, Frey and Kürschner 2011). The cells of secondary protonema posses a range of developmental possibilities where the determination of an apical cell with two cutting faces (sporophytic) or three cutting faces (gametophytic) is controlled by external (e.g. sucrose) and internal (e.g. kinetin) factors (Menon and Lal 1974). Fragments play an essential role in dispersal ecology and clonal taxa can dominate vegetation communities (Pfeiffer 2007). In nearly all bryophytes, gametophytic cells

have the ability for re-growth due to their totipotency (ability to regenerate a whole plants from a single cell; Lal 1984). This enables fragments (typically gametophytic) to regenerate new plants initiated from dedifferentiated cells.

Ecological Role of Bryophytes

Bryophytes are an important part of tundra ecosystems and often form the dominant vegetation (Vitt and Pakarinen 1977). They have an essential role in ecosystem function including high productivity, biomass accumulation, nitrogen fixation, nutrient cycling, colonization and establishment and facilitation of vascular plants (Tuba et al. 2011). Extensive moss cover can affect temperature regimes, influencing soil thaw depth, decomposition rates and soil moisture capacity which ultimately affects successional vascular plant establishment (Jägerbrand et al. 2011).

Bryophytes grow close to their substrate in the boundary layer (the small interface between the atmosphere and the ground). They take advantage of this moist and insulated microenvironment where the air is still and the temperature is warm (Kimmerer and Young 1996). Terrestrial bryophytes are strongly affected by local, small-scale restrictions (Vitt and Belland 1997) and edaphic variability provides an assortment of microhabitats. The habitat patches in which individual moss populations exists ranges from millimeters to centimeters (Vitt and Belland 1997) but can extend up to two meters on stable moss banks (Longton 1988). Their ecological niches are determined by the longevity of the substratum (During 1992), its chemical properties, and its water holding capacity (Bates 2008). Some bryophytes grow on a wide range of natural substrates where as others are restricted to a particular soil type, based on texture, pH, nutrients, and organic content (Slack 1990). Bryophytes can be substrate specialists and are reliable indicators for microhabitat conditions (e.g. *Splachnaceae* on dung/carcasses; Smith 1982). Microclimate is one critical component of microhabitat and establishment, growth and distribution of bryophytes are primarily controlled by it. Microclimate of a

given niche is determined by small-scale topographic variation, aspect, moisture availability, and substrate properties (Matthews 1992).

Bryophytes, often exhibiting a colonial growth form in which individual shoots can provide protection for their immediate neighbours, allow for increased moisture retention and survival under desiccation (Sollows et al. 2001). In contrast to vascular plants, competition for habitat space is insufficient to explain moss community structure (Slack 1977, Kimmerer and Young 1996). Competition tolerance among bryophytes is especially influential for opportunistic species in areas of disturbance since the substrate may disappear before competition has a significant impact on community structure (During and van Tooren 1987, 1990, Slack 1990). Bryophytes can promote the facilitation of other species establishment and growth and are most likely to have facilitative effects when plant growth is limited by moisture (Pedersen et al. 2001). In tundra ecosystems, these facilitative interactions increase the water holding capacity and organic matter content. A high species diversity of nitrogen-fixing cyanobacteria on the leaves and stems of mosses (Ziekle et al. 2002, 2005) or symbiotic colonies in liverworts (Meeks 1998) play an important role in ecosystem nutrient dynamics, particularly in the High Arctic where competition from higher plants is absent (Bates and Bakken 1998).

Polar bryophytes are subject to long seasonal freezing, desiccation and freeze-thaw cycles. Although lacking the root systems and well-developed cuticle found in vascular plants, bryophytes have evolved varying levels of desiccation tolerance. Poikilohydry occurs when there is rapid and direct equilibration of cell water content with the surrounding environment and contribute to the success of bryophytes in extreme environments (Longton 1988). This is a primitive feature, lost in the evolution of most vascular plants (Proctor et al. 2007), allowing bryophytes the ability to lose almost all intracellular water in dry conditions and then recover normal function upon rehydration. Mosses utilize mechanisms that initiate and establish cellular protective measures as well as complex processes that activate cellular repair (Bewley 1979, Mishler and Churchill 1985, Oliver et al.

2005 for review). This enables mosses to persist in water-stressed habitats where more derived plants cannot endure. If moisture is present and photosynthesis can occur, mosses have evolved ways to hold on to moisture to prolong this window of opportunity (drought avoidance). When inevitable drought arrives, they embrace desiccation and shut down metabolic activity. Adaptation to cold soils may also explain why bryophytes may equal or surpass vascular plants in terms of species richness, cover, and net production in the Arctic (Vitt and Pakarinen 1977). *In situ* survival and regeneration capacities of biota have received recent attention as glaciers continue to retreat exposing *in situ* LIA entombed subglacial flora and fauna. Physiological adaptations of bryophytes to severe arctic conditions, such as totipotency, dominance of clonal reproduction, and desiccation and freezing tolerance make them likely candidates for subglacial survival.

Paleoecological Reconstruction

There are several different approaches to community reconstruction including the use of modern analogues from known environments for comparison with fossil assemblages. In addition, quantitatively interpreting patterns in fossil data and using information from abiotic components enables inferences about past communities (Birks and Birks 1980). Bryophyte macrofossils, in particular, are a useful tool for paleoecological research (Hedenäs 1994, Zazula et al. 2006). In addition to temperature reconstruction, plant macrofossils provide a detailed record of the species composition and structure. This, subsequently, can provide information on microhabitats of past ecosystems at a single place in time.

Preserved and intact LIA plant communities have been observed at the margin of the rapidly retreating Teardrop Glacier, Ellesmere Island, Nunavut. This newly exposed deglaciated terrain has provided unique opportunities for examining primary plant succession (Matthews 1992, Chapin et al. 1994, Jones and Henry

2003, Breen and Lévesque 2008) and is key for understanding soil regimes (Stewart et al. 2011, Brummell et al. 2012) and the role of biological soil crusts (Breen and Lévesque 2006). Paleoecological reconstruction based on the *in situ* bryophyte component may reveal significant details of terrestrial ecosystems prior to the LIA Teardrop Glacier advance. The goal here is to analyze the subglacial material in order to infer the bryophyte assemblage dynamics prior to the LIA glacial advance. The presence of species of known tolerances will provide information about this past environment, which has implications for community processes.

Objectives

In synthesis, few studies have examined subglacial, *in situ* plant assemblages in the Arctic (but see Smith 1961, Blake 1981, Bergsma et al. 1984, Jones and Henry 2003, Breen and Lévesque 2006, Breen and Lévesque 2008) and fewer have examined bryophytes in detail. The objective of Chapter II is to quantitatively examine the LIA subglacial bryophytes from the Teardrop Glacier, Ellesmere Island and utilize analogous extant assemblages to discern how bryophyte species composition is related to microhabitat.

Chapter III addresses the dormancy potential of LIA *in situ* preserved bryophytes to regenerate either by fragmentation or diaspores previously presumed dead. Experimental results will be reviewed and the hypothetical implication of these results for subglacial survival and regeneration of bryophytes will be discussed.

Chapter IV provides a summary overview of this study and discusses the implications of these findings.

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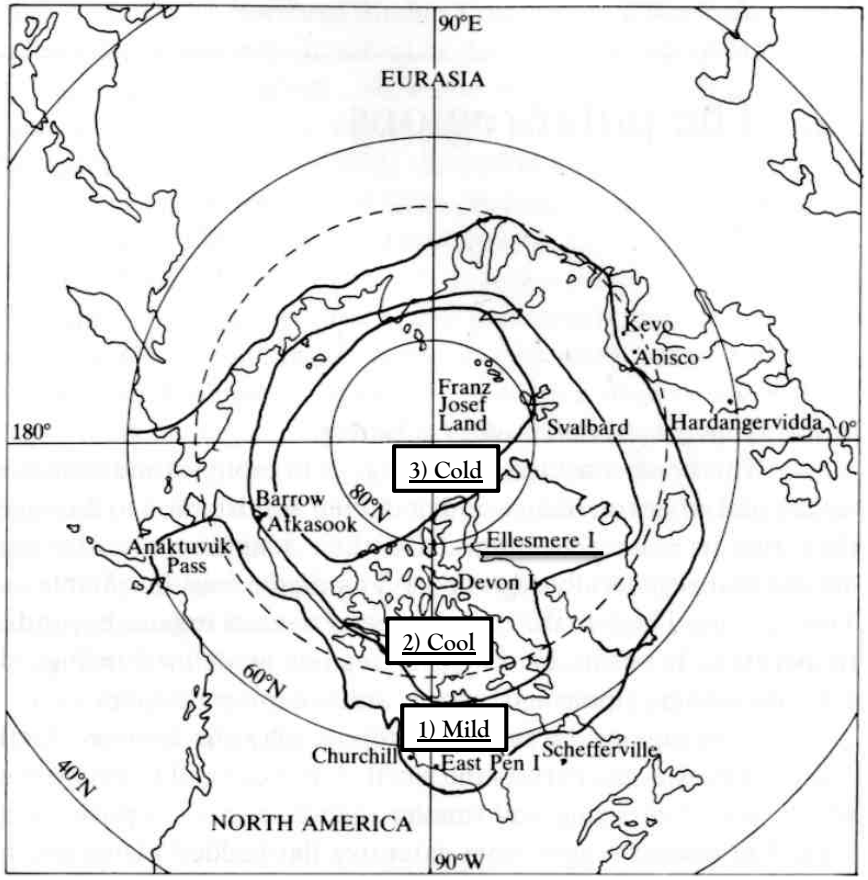

Figure 1.1 Arctic vegetation zones and the principal localities. Boundaries outlined include 1) mild-arctic, 2) cool-arctic including Ellesmere Island (underlined) and 3) cold-arctic. Based on vegetation and mean summer temperatures. Modified from Longton 1988.

Chapter II: Exhumed Little Ice Age bryophyte assemblages: diversity and species composition, Teardrop Glacier, Sverdrup Pass, Ellesmere Island (79° N), Nunavut, Canada.

Introduction

In the Arctic, mosses (Bryophyta) and liverworts (Marchantiophyta) represent the dominant lineages of bryophytes. The distribution of different bryophyte assemblages reflects specialized niches and microtopographic variations of physical factors, such as light, nutrients, and moisture availability (Longton 1988a, La Farge-England 1989, Slack 1990). Several Arctic studies have examined the significance of bryophyte macrofossils in terrestrial ecosystems for paleoecological reconstruction, glacial chronology, and paleophytogeography (Kuc and Hills 1971, LaFarge-England et al. 1991, Hedenäs 1994, Oswald et al. 1999, Miller et al. 1999, Zazula et al. 2006, Birks et al. 2012). Intact plants, once buried and preserved under ice, can provide well-preserved and identifiable macrofossils for paleoecological reconstruction.

The Little Ice Age (LIA; 150-580 years BP) represents the most recent climatic cooling in the High Arctic (Gribbin and Lamb 1978, Grove 1988, Overpeck et al. 1997, Miller et al. 2010). With its onset, glaciers and permanent snow banks expanded in polar regions and buried plant communities. A number of studies have reported preserved, intact LIA plant communities on Ellesmere Island adjacent to melting glaciers (Smith 1961, Blake 1981, Bergsma et al. 1984, Jones and Henry 2003, Breen and Lévesque 2006, 2008). However, no studies have focused primarily on the bryophyte component. In addition to insight into LIA bryophyte communities, these distinctive and undisturbed populations, exhumed from beneath melting glaciers, provide evidence for portions of polar glaciers being frozen to their substrate (Bergsma et al. 1984). Temperate glaciers, in contrast, produce significant subglacial erosion due to basal sliding. It is widely accepted that

portions of glaciers of the arctic are cold-based and advance by internal deformation (Matthews 1992, Benn and Evans 1998). Yet, it is notable that some erosion and deposition has been observed under a cold-based glacier in the Arctic (Skidmore et al. 2005) and Antarctica (Atkins et al. 2002). Cold-based ice is typical of the accumulation zone and along the glacial margin where the ice is thin, whereas erosional warm-based ice typifies the ablation zone (Copland and Sharp 2001).

These remarkably well-preserved, subglacial populations provide a unique opportunity to gain a temporal perspective on bryophyte assemblages to evaluate and effectively monitor microhabitats and site-specific environmental change. Paleoecological techniques that use *in situ* macrofossils provide precise ecological data spatially and temporally (Birks and Birks 1980). Reconstruction of the well-preserved, *in situ* LIA subglacial bryophyte assemblages from Ellesmere Island, Nunavut forms the focus of this study.

LIA bryophyte assemblages along the Teardrop Glacier margin, Sverdrup Pass, Ellesmere Island, Nunavut are analyzed and compared to contemporary assemblages at the same site. This provides a 400-600 year perspective on the evolution of High Arctic bryophyte communities during Neoglacial climate fluctuations. The objectives are to 1) determine LIA subglacial bryophyte species richness and diversity; 2) quantitatively analyze the dominant subglacial and equivalent extant bryophyte assemblages to determine patterns in species composition both temporally and spatially; and 3) to consider paleoenvironmental implications of these patterns.

Materials and Methods

Study Area: Sverdrup Pass, Ellesmere Island

Ellesmere Island is the largest and most northern of the Queen Elizabeth Islands in the Canadian Arctic Archipelago (Figure 2.1). The extensive icefields of central Ellesmere Island are separated by a narrow, deglaciated drainage divide called Sverdrup Pass (79°10'N, 79°45'W; Figure 2.1). This corridor is 75-80 km

long, 2-5 km wide and connects Flager Bay in the east and Irene Bay in the west. It is bound on the north side by the Agassiz Icefield and on the south side by the Prince of Wales Icefield. The central pass has an elevation of 250 m a.s.l. and rises up to 1350 m at the level of the icefields.

The tectonically created valley bottom is extensively covered by glaciofluvial outwash and other subglacial and erosional landforms (Blake 1981, England 1987). On the south side of Sverdrup Pass, faulted Paleozoic strata overlie Precambrian gneiss and granite. In contrast, the north side is formed by Cambrian and Lower Ordovician beds consisting of limestone and dolomite (Christie 1967). As a result, the localized topography, with diverse soil types, pH, and drainage, controls the distribution and diversity of plant and algal communities (Bergeron 1988, Elster et al. 1999).

The central portion of Ellesmere Island is classified within the Axel Heiberg and Ellesmere Island Highland subregion in the Northwestern Arctic Climate Zone (Maxwell 1981). This is characterized by mean January and July temperatures of < -28°C and 3-5°C respectively. The annual precipitation is <150 mm. Although nearly at sea level and influenced by its coastal location, the closest regional climate records are to the east in Eureka (79° 59'N, 85° 56' W elev. 10 m). The 1971-2000 Canadian Climate Normals (National Climate Data and Information Archive 2012) indicate a July daily maximum at 8.8°C and an average of 12.5 mm of precipitation. However, during the 2007 (July 14 – 25) and 2009 (June 29 – July 14) summer field season, the morning temperatures at Sverdrup Pass averaged 12°C and 6°C and reached a maximum of 18°C and 15 °C, respectively.

The High Arctic environment is characterized by relatively low temperatures and precipitation, short growing seasons and nutrient-poor soils (Edlund and Alt 1989). Vegetation is typically sparse and High Arctic environments are often categorized as polar desert (< 5% total plant cover) or polar semi-deserts (5-20% vascular plants, 20-80% lichens and bryophytes) (Bliss et al. 1973, 1984, Bliss and Svoboda 1984). Polar oases (>50% plant cover) such as Sverdrup Pass are rare representing only 1-3 % of the Queen Elizabeth Islands (Babb and Bliss 1974,

Freedman et al. 1982, Henry et al. 1986, Bergeron 1988, Raillard and Svoboda 2000). Sverdrup Pass plant communities have been described as diverse, referring especially to the rich wet meadows in the central and eastern portion. Local topography provides protection from the harsh and windswept upland climate, resulting in greater accumulation of snow, warmer climate, and a longer growing season (Freedman et al. 1982, Lévesque and Svoboda 1999). The valley flora supports high species diversity and productivity when compared to the depauperate polar desert flora typical of most the uplands in the Queen Elizabeth Islands (Bliss et al. 1984, Bliss and Svoboda 1984, Lévesque and Svoboda 1999). Even at this high latitude, Sverdrup Pass supports intense grazing from herbivores, including a high density of muskoxen (averaging 6.4 animals km^{-2}) and results in 48% of available vascular plant vegetation grazed (Raillard and Svoboda 2000).

Water availability is a limiting factor in almost any polar environment. In Sverdrup Pass, portions of the valley are deep allowing for increased snow deposition blown in from surrounding plateaus. Meltwater from eleven glaciers descend into the valley and areas of snow accumulation provide a continuous water supply during the growing season. Furthermore, the permafrost table impedes drainage and retains water in the upper soil layers, increasing available soil moisture and providing advantageous growing conditions (Bergeron 1988, Svoboda 1988). In addition to water availability, increased solar radiation in Sverdrup Pass, due to reduced regional cloud cover and reflection of the light from the north and south foothills and cliffs, contribute to favourable thermal conditions (Freedman et al. 1983).

Study Site: Teardrop Glacier and vicinity, Sverdrup Pass

The study site was located in the foreland of the Teardrop Glacier (Figure 2.2), a north-facing outflow glacier of the Prince of Wales Icefield. The study focused on the samples at the Teardrop Glacier margin and within the foreland, but included extant samples from the south side of Sverdrup Pass encompassing an

18 km^2 area (Figure 2.2). On this south slope, the 2009 GPS measurements of Teardrop Glacier snout spans approximately 1.2 km from the east (79° 07.929 N, 79° 44.175 W elev. 331 m a.s.l.) to the west (79° 07.758 N, 79° 46.795 W elev. 335m a.s.l.). A granite-gneiss boulder-strewn foreland demarcates the most recent glacial advance. The end of the foreland marks the maximum LIA advance that measured approximately 190 m from the glacier terminus in 2004 (Breen and Lévesque 2006). Additional field measurements in 2007 and 2009 totaled a distance of 208 m (pers. comm. C. La Farge 2012).

The foreland is a mosaic of glacial features and substrates including erratics, gravel and sand, push moraines, several meltwater streams, and proglacial lakes. Some portions of the foreland indicate little glacial erosion or deposition where LIA plant communities were preserved. Other portions with disturbed substrates lack intact subglacial vegetation. Soil development in the foreland indicates a range of coarse glaciofluvial sediment to dense, enriched biological soil crusts, as well as 'paleo-material' described as dead plant and organic soil matter (Breen and Lévesque 2008). Vegetation studies of Teardrop Glacier foreland indicates relatively well developed flora compared to other recently deglaciated terrain on Ellesmere Island (Breen and Lévesque 2006, Jones and Henry 2003). This is attributed to consistent meltwater supply and the development of rich biological soil crusts, which facilitate the development of plant communities (Elster et al. 1999, Breen and Lévesque 2008).

Ecological studies on the Teardrop Glacier foreland have previously focused on diversity and abundance of soil algae (Elster et al. 1999), the role and formation of biological soil crusts (Breen and Lévesque 2006, Breen and Lévesque 2008) and primary plant succession (Jones and Henry 2003). Even for this High Arctic environment, Sverdrup Pass has high species diversity with 136 terrestrial algal and cyanobacteria taxa (Elster et al. 1999), 115 lichens (Maycock and Fahselt 1992), 75 vascular species (Bergeron 1988), and 39 species when restricted to colonizing taxa in the Teardrop Glacier foreland (Jones and Henry 2003). Primary plant succession indicates four distinct zones and stages of dominance. Directional species

replacement occurs with black algal communities ca. 15 m from the glacial margin, a pioneering community of mosses and vascular plants ca. 20 – 30 m away, and intermediate and later stages predominantly comprised of vascular plants (beyond 60 – 80 m) (Jones and Henry 2003). Previous studies have not focused on the bryoflora of Sverdrup Pass or the subglacial or contemporary bryophyte component of the Teardrop Glacier foreland. This is surprising given that bryophytes typically comprise a key component of High Arctic floristic diversity (Longton 1988a).

Specimen Collection

In July of 2007 and 2009, 140 subglacial specimens were collected from the Teardrop Glacier foreland within ca. 10 m of the glacial margin (collected by Dr. C. La Farge). At the time of collection, dry samples were placed in 2lb paper bags whereas the saturated subglacial samples were placed in plastic Nasco Whirl-pak bags (Fisher Scientific) and stored in a cooler, out of light exposure, until the end of the field season. The subglacial samples were frozen at Polar Continental Shelf Program (PCSP), Resolute Bay, Nunavut, transported and stored frozen at the Department of Biological Sciences, University of Alberta, Edmonton. The samples were kept frozen until subsampling for analysis. Extensive collections (> 800 specimens) were made in 2007/2009-field season to document the extant bryoflora focusing on those bryophyte communities within the vicinity of the Teardrop Glacier. These samples form the basis for the non-quantitative portion of this study.

Non-quantitative sampling methods maximize rare taxa and minimize excessive duplication of abundant taxa. For bryophytes, whose distribution is controlled by microhabitat on a small-scale landscape, it can be the only effective way to locate rare species (Stohlgren 2007). In addition, floristic habitat sampling is more efficient for quantifying overall species diversity and is an excellent way to record a comprehensive list of species (La Farge-England 1989, Newmaster et al. 2005). The extant collections were divided into two groups (based on substrate pH; calcareous north-slope and acidic south-slope). Those from the south side of the valley (348 specimens) were examined to compare with Teardrop Glacier subglacial

specimens (140). Samples with dominant taxa (>25%/taxon) were chosen from the extant (71) and subglacial (84) as the quantitative focus for this study. Sample sizes were limited when restricted to assemblages containing >25% of a given taxon. Therefore, analyses of species assemblages with less than seven subglacial assemblages, limited by sample size and showing no discernable pattern, were not analyzed. For the purpose of this study, the term dominant is used to refer to any species in an assemblage occurring >25%. This resulted in seven major species assemblages. These samples, which formed the major component of the quantitative temporal assemblage analysis, were examined for specific species abundance. Selection of the extant specimens was based on presence of the same dominant (>25%) species analogous to subglacial assemblage dominated by the same species. If two (of the seven dominants) taxa co-dominated a specimen (*SBG 14, 19* and *36),* it was used in both assemblage analyses.

Water chemistry readings were conducted with the YSI Professional Plus pH meter (Hanna Instruments) from meltwater streams and small ponds within Sverdrup Pass and in the foreland of the Teardrop Glacier. The pH responsive electrode was calibrated between site measurements using buffer solutions (pH 4, 7, and 10). At three sites on the north slope and 12 sites on the south slope, pH, temperature (°C), specific (sp.) conductivity (millisiemens/centimeter), and total dissolved solids (TDS; milligrams/litre) measurements were taken.

Species Identification

For frozen subglacial samples, multiple subsamples were removed, thawed, and floated in petri dishes with distilled water. As many distinct taxa were subsampled as possible to maximize species richness for the sample using the dissecting microscope. Both dissecting and compound microscopes were used for taxon determination. Photographs were taken of fragments representing each taxon and subsequently dried and placed in small plastic vials as vouchers and deposited in the University of Alberta Cryptogamic Herbarium (ALTA), Department of Biological Science, University of Alberta. For dried samples (mostly extant), no

subsampling was necessary and all stems and fragments were identified and deposited in ALTA. The majority of the extant specimens were equal in size (20 cm x 15 cm) containing an assemblage of species. In most cases, the subsamples of the subglacial specimens, when compiled, were equal is size to extant dried specimens.

Floristic treatments used for the taxonomic determination on the following groups included: Mniaceae (Koponen 1974), Encalyptaceae (Horton 1981), Bryaceae (Spence 2007), Grimmiaceae (Hastings and Ochyra 2007), Marchantiophyta (Schofield 2002), as well as Nyholm (1954 - 1969), Schuster (1969), Vitt (1975) and Blom (1995). Nomenclature is based on the Checklist of Mosses (Crosby et al. 1999) except for the following: Bryaceae (Spence 2007) and Grimmiaceae (Hastings and Ochyra 2007), and Marchantiophyta (Stotler and Crandall-Stotler 1977).

Radiocarbon dating

Radiocarbon dates (^{14}C) were measured on three samples by the W.M. Keck Carbon Cycle Accelerator Mass Spectrometry (AMS) Laboratory. The three AMS ^{14}C dates were determined on stem apices (to ensure the youngest material was measured) of two subglacial moss species (*Aulacomnium turgidum* and *Bartramia ithyphylla*) and one woody *Salix arctica*, all calibrated using CALIB 6.0 (Stuvier et al. 2010).

Species richness and diversity

In ecological studies, species richness (number of species) and diversity (proportional abundance) can traditionally be calculated three ways (alpha, beta and gamma). In this study, alpha and gamma were calculated, where alpha was defined on a local scale and includes either the subglacial or extant assemblages in the Teardrop Glacier foreland and vicinity (Velland 2001). Gamma richness is usually described as the total number of species on a broad scope with landscape or regional implications (Whittaker 1972). For the purpose of this study, gamma richness is defined as the number of bryophyte species from the south side of

Sverdrup Pass, representing those taxa with similar substrate chemistry to the subglacial assemblages, which is a significant controlling factor for bryophyte distribution (Vitt et al. 1995). Species gamma richness for extant assemblages was calculated using the presence-absence survey data from specimens from the south side of Sverdrup Pass. Number of occurrences for each species in the subglacial and extant data sets was tallied as an indication of rarity. Following Pakarinen and Vitt (1974), arctic taxa are considered rare when occurrences are fewer than five on a regional or global scale. This is not to be confused with common species with low abundance.

Traditional measures of species diversity use indices, such as Shannon-Weiner or Simpson Index (Hill 1973). These indices have no units and are not readily comparable between studies. Jost (2006) proposed a measure of species diversity, termed true diversity. True diversity should only be used to refer to the effective number of species (Jost 2006, 2007). If all actual species are equally abundant, then there are as many effective species as actual species. Otherwise, there are fewer effective species than actual species (Tuomisto 2010). Effective number of species has an advantage when comparing diversity differences between studies (Tuomisto 2010). Based on the exponent form of Shannon-Weiner Index, the effective number of species for the subglacial and extant assemblages was calculated (equation 1) where H' is effective number of species and p_i is the proportional abundance of each species out of the total number of individuals (Jost 2006).

$$H' = \exp(-\Sigma p_i \ln(p_i)) \qquad (1)$$

Percent cover was estimated for each species within a specimen and assigned to a 5-class ordinal classification as a measure of relative abundance for data analysis (Table 2.1). Again, any given taxon was considered dominant if its ordinal class was

three (>25%) or more (Table 2.1). Alpha diversity was calculated for the seven most frequent subglacial and comparable extant assemblages. Two-sample T-tests (SPSS Inc. 2010) were used for testing differences in the mean true diversity between subglacial LIA and analogous contemporary assemblages. Statistical power depends on significance criteria (α), sample size, and effect size (Cohen 1992). A post hoc consideration of observed power (SPSS Inc. 2010) using true diversity index values indicated that specimens dominated by a given taxon for quantitative analysis were limited (Table 2.3). Therefore, with a limited samples size, interpretation of statistical significance should be taken with caution.

Microhabitat data for each moss species from all extant samples was qualitatively analyzed. The microhabitat conditions were categorized as follows: 1) amongst rocks; 2) between boulders; 3) around a boulder (protected); 4) rock hovel (protected & moist); 5) pond margin; 6) wet seep; 7) stream bank; 8) submerged in pond; and 9) submerged in stream. These were arranged along a moisture gradient ranging from xeric (1) to hydric (9). Substrate data for each species was categorized as: 1) muskox dung/carcass; 2) humus; 3) peat; 4) rock; 5) gravel/sand; and 6) soil.

Statistical Analysis

A species area curve was constructed to ensure adequate numbers of samples were analyzed (Gleason 1922, McCune and Mefford PCORD 6.0). A comparison of species richness and diversity between the extant and subglacial assemblages was possible, despite slight differences in sampling intensity (Krebs 1999).

Most biological data is log-normally distributed (Kenkel 2006), requiring data for continuous variables to be transformed to a log scale (Mead 1988). Based on the results of Whittaker plots of species abundance (Krebs 1999, McCune and Mefford PCORD 6.0), the data were natural log transformed to linearize the species-abundance relationships. Without log-transformation, analyses are potentially dominated by a few abundant species (Kenkel 2006).

Multivariate ordination and tests for significance were performed to analyze species distribution and composition within and between subglacial and extant assemblages (McCune and Grace 2002). Two main components were analyzed to quantitatively summarize the bryophyte assemblages: 1) temporal differences in species composition between LIA subglacial and extant assemblages; and 2) species composition differences between the seven dominant assemblages to illustrate the variety of small-scale microhabitat preferences.

Analyses were conducted using PC-ORD 6.0 (McCune and Mefford 2011). Principle coordinates analysis (PCoA) was chosen given its statistical power and robustness to moderate deviations from underlying assumptions (Hirst and Jackson 2007). PCoA permits the user to choose a suitable distance measure (Gotelli and Ellison 2004) and has an advantage over the more commonly used non-metric multidimensional scaling (NMS) for it gives consistent results with multiple analyses and percent variance is explained for each axis (Hirst and Jackson 2007). The variance explained for PCoA is the ratio of eigenvalues (importance measure of an ordination axis) to total variance (McCune and Grace 2002). PCoA was used to compare assemblage differences using species data that were log transformed with Bray-Curtis dissimilarity coefficient. Bray-Curtis ensures rare species add little to the coefficient by ignoring cases where certain species are absent in both assemblage samples (Krebs 1999).

Multi-response Permutation Procedures (MRPP) using a Bray-Curtis dissimilarity coefficient was conducted (PC-ORD 6.0; McCune and Mefford 2011) to test for multivariate significant differences in species composition between assemblages. Data were natural log transformed and tested for significance using 9,999 permutations. MRPP has the advantage of not needing assumptions, such as normality, which are rarely met with ecological data. It is important to note that for small sample size (such as species assemblage comparisons), a large effect is needed

for statistical significance (McCune and Grace 2002). Pairwise comparisons of the seven most frequent assemblages were conducted using 9,999 permutations to test for significance in species composition between the various assemblages.

Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997) was performed to detect if species were significantly affiliated with a particular assemblage (PC-ORD 6.0; McCune and Grace 2002). Indicator values combine a given species' abundance and occurrence in a group (subglacial or extant) and are calculated from 0 (no indication) to 100 (perfect indication) (McCune and Mefford 2011).

Results

Water Chemistry

Within Sverdrup Pass, 15 water samples were analyzed in the field in 2009 for pH, temperature, sp. conductivity, and TDS. At the glacial margin, the pH from the relatively acidic proglacial streams and ponds ranged from 5.20 to 5.95. Temperature ranged from 4 to 7.6°C, sp. conductivity 1.3 to 8.7 ms/cm, and TDS 1.3 to 9.6 mg/L. Further from the glacial margin, the foreland and wet meadow pH ranged from 6.00 to 7.70. Temperature ranged from 5.8 to 7.5°C, sp. conductivity 49.1 to 137.3 ms/cm, and TDS 52.0 to 133.9 mg/L/ In contrast, the calcareous north slope of Sverdrup Pass with sedimentary bedrock ranged from 6.91 to 8.31. Temperature ranged from 4.5 to 7.0°C, sp. conductivity 27.9 to 222.5 ms/cm, and TDS 22.1 to 237.3 mg/L.

Preservation

The excellent preservation of the subglacial assemblages facilitated species identification for the majority of taxa. Samples were collected as intact cushions, tufts, or mats with undamaged stems and leaves. Bryophyte stems retained their

diagnostic characters, such as leaf habit, surface ornamentation, border or margin characteristics, gametangia, and asexual propagules. Sporophytic tissues (capsules, setae, and operculae) or the associated calyptra was rare. Hyaline basal windows of *Syntrichia ruralis* and *Encalypta* spp. were generally not well preserved, but identification was possible as papillae and hair points remain intact. *Pohlia* spp., *Distichium* spp. and *Ptychostomum* spp. were abundant in the subglacial assemblages often lacking key sporophytic features for determination to species. Other specimens (*SBG 18* and *CLF 13012*) were degraded or fragmented and prevented taxon (*Pohlia* sp. and *Schistidium* sp.) identification. Several species of liverworts were preserved. These most commonly included single strands of *Lophozia* spp., *Cephaloziella arctica* and one specimen (*SBG 33*) dominated by *Gymnomitrium corallioides*. Marchantiophyta are taxonomically difficult and known for the poor preservation (Miller 1980, Janssens 1983) and many were only identified to genus. *Salix arctica* and *Cassiope tetragona* were the most abundant and best-preserved vascular plant species, but *Saxifraga oppositifolia, S. tricuspidata* and *Luzula spp.* were also observed.

Radiocarbon Dating

The 14^C AMS ages obtained utilize a two σ range, from which a median value was calculated. The mean radiocarbon dates (2σ) on three subglacial samples ranged from 404.5 to 614.5 calibrated years before present (La Farge et al. 2013).

Floristics: Species richness and diversity

The contemporary bryophyte assemblages contained 122 taxa (113mosses and 8 hepatics) based on 348 specimens from the south side of Sverdrup Pass (gamma richness) (Table 2.2). Of these taxa, 110 mosses and 5 hepatics were identified to species, (Table 2.4). From 140 subglacial specimens, the subsamples enumerated 73 taxa (66 mosses and 8 hepatics) (Table 2.2), including 59 mosses and 5 hepatics determined to species (Table 2.4). For the selected 84 subglacial

samples used for quantitative analysis, 63 (58 mosses and 5 hepatics) taxa were recorded with 57 mosses identified to species. Based on 71 analogous extant assemblages (with the same dominant taxa), 62 taxa (54 mosses and 8 hepatics) were determined (Table 2.2). The samples ranged from pure specimens containing a single taxon to heterogeneous assemblages with up to 14 species. The subglacial specimens had an average of 5.5 species/sample, where as the extant specimens had an average of 4.5 species/sample. Given the similar species richness (63 subglacial and 62 extant taxa) of all seven dominant subglacial (84) and extant (71) specimens, species composition has considerable overlap (47 species) (Table 2.4).

The subglacial taxa with the highest frequency (number of samples recorded with its occurrence: dominant or single stems) were *Polytrichastrum alpinum* (52), *Hypnum revolutum* (40), *Ditrichum flexicaule* (36), and *Bartramia ithyphylla* (32) out of 140 specimens examined. In comparison, from the 348 extant samples, the most frequent taxa included *Orthothecium chryseum* (52), *Philonotis fontana* var. *pumila* (48), *Ditrichum flexicaule* (42) and *Cinclidium arcticum* (36).

For the quantitative analysis based on the seven major assemblages with dominant (>25%) species within an assemblage, a minimum of seven subglacial samples was required. Assemblages dominated by a single taxon, but occurred in less than four samples were not temporally compared. The seven subglacial and analogous extant assemblages for quantitative analysis were *Hypnum revolutum, Aulacomnium turgidum, Bartramia ithyphylla, Niphotrichum panschii, Polytrichastrum alpinum, Hygrohypnum polare,* and *Ditrichum flexicaule.* Average alpha true diversity within each of the seven dominant assemblages were temporally comparable between subglacial and extant assemblages, but ranged spatially from as low as 2.2 effective species in *Hygrohypnum polare* assemblages to as high as 7.1 effective species in *Ditrichum flexicaule* assemblages (Table 2.3). The t-tests showed that true alpha diversity did not differ significantly between subglacial LIA and analogous contemporary assemblages (Table 2.3). Based on presence/absence data per sample,

both subglacial and extant taxa were evaluated for rarity (<5 records). The results showed similar values for subglacial (60.3%) and extant (63.4%) taxa.

Ordination

The PCoA ordination results are presented in two dimensions as the third dimension showed relatively low % variance explained and impeded interpretation. An analysis of all 140 subglacial and 348 extant specimen data showed no significant patterns, except for a cluster of extant taxa not present in the subglacial richness (Figure 2.A1.). Analysis restricted to the seven dominant subglacial (and analogous extant) assemblages showed significant results.

Spatial Assemblage Comparison: Seven Dominant Assemblages

The comparison of the seven dominant subglacial assemblages showed separation in the ordination space (Figure 2.4a). The pair-wise comparison (MRPP analysis) showed a significant difference between all assemblages (Table 2.A1). Any A value > 0.3 is high, given that when A = 1, all groups are identical. As well, comparison of the seven dominant extant species assemblages showed separation in the ordination space into 3 distinct clusters (Figure 2.4b).

For all seven of the dominant subglacial and extant assemblages analyzed, the indicator species for each dominant species assemblage was the same species (*Hypnum revolutum, Aulacomnium turgidum, Bartramia ithyphylla, Niphotrichum panschii, Polytrichastrum alpinum, Hygrohypnum polare* and *Ditrichum flexicaule*). Dominant assemblages were analyzed based on species abundance, thus the most abundant species would be expected to be the indicator for that assemblage. For two of the dominant subglacial assemblages, an additional species was determined

as an indicator: 1) *Syntrichia ruralis* as an additional indicator for both subglacial and extant *Hypnum revolutum* assemblages and (IV = 27.6, p = 0.00); 2) *Campylium arcticum* as an indicator for subglacial *Hygrohypnum polare* assemblages (IV = 16.8, p = 0.04). For extant assemblages, additional indicator species included: 1) *Niphotrichum canescens* var. *latifolium* for *N. panschii a*ssemblages (32.0, p = 0.012), 2) *Lophozia* spp. and *Ptychostomum cyclophyllum* for *B. ithyphylla* assemblages (IV = 33.1, p = 0.02 and IV = 42.9, p = 0.01 respectively), and 3) *Cinclidium arcticum* for *D. flexicaule a*ssemblages (IV = 47.5, p = 0.004). Therefore, the only indicator in common between subglacial and extant assemblages (besides the dominant species) was *Syntrichia ruralis* for *Hypnum revolutum* assemblages.

Temporal Assemblage Comparison: Subglacial versus Extant

Out of all samples in which *Hypnum revolutum* occurred, 50% of the subglacial and 58% of the extant specimens contained >25% (dominant) *H. revolutum* (Figure 2.3). The ordinations show significant overlap and the MRPP indicated no significant difference between the subglacial and extant *H. revolutum* assemblages (T = -0.491, A = 0.0004, p = 0.413) (Figure 2.5a). The indicator species analysis provided no statistically significant indicators.

When present, *Aulacomnium turgidum* formed the dominant species 70% in the subglacial specimens and 68% in extant specimens (Figure 2.3). The temporal comparison showed no significant difference (Figure 2.5b) (T = -1.753, A = 0.0114, p = 0.057) but the p-value is close to the significance level and may indicate variations on species composition. Although the MRPP was not statistically significant, some differences occurred best shown by the ISA. Significant indicator species for the subglacial included *Pogonatum dentatum* (IV = 21.4, p = 0.047), *Bartramia ithyphylla* (IV = 28.6, p = 0.0017), and *Hygrohypnum polare* (IV = 21.4, p = 0.052). The one extant indicator species was *Orthothecium chryseum* (IV = 33.2, p = 0.054).

In all samples in which *Bartramia ithyphylla* occurred, it dominated 38% of its subglacial specimens and 33% of its extant specimens (Figure 2.3). The MRPP indicated a temporal significant difference (T = -1.924, A = 0.0336, p = 0.039) in species composition but no significant indicator species (Figure 2.5c). However, the results should be interpreted with caution due to the small number of samples and the discrepancy in specimen numbers (12 subglacial and 4 extant).

In all samples where *Niphotrichum panschii* occurred, it dominated 78% of subglacial and 73% of extant specimens (Figure 2.3). When compared, there was a significant difference in species composition of extant and subglacial assemblages (Figure 2.5d) (T = -3.572, A = 0.0597, p = 0.0029). *Niphotrichum canescens* var. *latifolium* was an indicator for extant assemblages (IV = 50.0, p = 0.0177). Subglacial *N. panschii* assemblages were more commonly associated with *Polytrichastrum alpinum* (IV = 63.6, p = 0.0110).

In all samples where *Polytrichastrum alpinum* occurred, it dominated 21% of the subglacial and 44% of the extant specimens (Figure 2.3). The PCoA (Figure 2.5e) and MRPP indicated a significant temporal difference (T = -1.851, A = 0.021, p = 0.049). *Aulacomnium turgidum* was the only indicator species for extant *P. alpinum* assemblages (IV = 45.2, p = 0.0407). *Hypnum revolutum* was the indicator species for subglacial assemblages (IV = 39.6, p = 0.052), which decreased on axis 1.

When present, *Hygrohypnum polare* dominated 60% of its subglacial assemblages and 54% of its extant assemblages (Figure 2.3). The MRPP and ISA suggested no significant difference in species composition between subglacial and extant (T = -1.983, A = 0.023, p = 0.138) (Figure 2.5f).

In all samples where *Ditrichum flexicaule* occurred, it dominated 19% of the subglacial and 17% of the extant specimens (Figure 2.3). There were no significant temporal differences (T = -0.828, A = 0.021, p = 0.191) (Figure 2.3, Figure 2.5g). No taxa were identified as significant indicator species in the ISA.

Discussion

Analysis of 348 extant specimens from the predominantly acidic, granite-gneiss dominated southern slope of Sverdrup Pass enumerated 113 moss and 8 hepatic taxa. The high species richness of this study is comparable to other High Arctic polar oases where the bryophyte flora has been extensively examined, such as Piper Pass, northern Ellesmere Island (114 species; La Farge-England 1989), Lake Hazen, northern Ellesmere Island (114 species; Brassard 1971, 1976) and Truelove Lowland, Devon Island (133 species; Vitt 1975). Only 28.3% of the extant specimens were found fruiting (Table 2.4). Some taxa (*Ditrichum flexicaule, Hypnum revolutum* and *Syntrichia ruralis)* are especially frequent and abundant yet were not found fruiting and are not known to produce sporophytes at high latitudes (Brassard 1971). The subglacial moss record (73 taxa) represents 60% of the south slope extant flora. This subglacial representation is substantial given the restricted diversity of microhabitats in the glacial foreland within 10 m from the margin. The species composition highlighted differences in substrate preferences (xeric bedrock to aquatic). On a temporal scale, the analyses of subglacial and extant assemblages indicate that no major ecological change in assemblage composition has occurred. However, despite the restricted foreland of the Teardrop Glacier, the diverse assemblages represent a broad range of ecological preferences (xeric to hydric) and life strategies.

Using the most comprehensive study on northern Ellesmere mosses (Brassard 1971), the floristic analysis of the subglacial and extant mosses in the Teardrop Glacier vicinity indicate that 34.8% are considered widespread, 30.4% are restricted and 33.7% are considered rare (twenty-one species not treated by Brassard 1971). However, the comparable northern lowlands of Devon Island indicate that some of these taxa are common (*Meesia triquetra*), rare (*Pogonatum dentatum*), restricted to specific habitats (*Blindia acuta*), or very rare with only one record (*Campylium stellatum*; Vitt 1975).

The qualitative analysis of microhabitat data for extant species demonstrates a range of preferences and demonstrates which species have a wide or narrow tolerance of microhabitat conditions. Patterns emerged showing moisture primarily driving species occurrences (Table 2.A3). Species restricted to one or two microhabitat types include *Hypnum revolutum* and *Syntrichia ruralis* (mesic-xeric sites between boulders). *Cytromnium hymenophyllum* and *C. hymenophylloides* as well as *Distichium capillaceum* occur mostly in protected and moist rock hovels include. *Aulacomnium turgidum, Cirriphyllum cirrosum, Calliergon giganteum, Cinclidium arcticum,* and *Ptychostomum cryophilum* showed a strong preference along moist stream banks. *Drepanocladus revolvens* and *Hygrohypnum polare* occurred most commonly growing submerged in a stream in contrast to *Pseudocalliergon brevifolium* and *Warnstorfia sarmentosa* typically found submerged in a pond. On the other hand, some species show a wide tolerance and occur in multiple microhabitat categories. For example, *Ditrichum flexicaule* and *Timmia austriaca* commonly occurred between boulders, in rock hovels, and along stream banks. *Orthothecium chryseum* occurred in almost all microhabitat categories but was most common along stream banks (Table 2.A3).

Qualitative substrate patterns suggested most species occur predominantly on soil (Table 2.A3). However, some species indicate a substrate preference, such as members of the Splachnaceae (*Tetraplodon mnoides, Tetraplodon pallidus, Aplodon wormskjoldii,* and *Voitia hyperborea*) occurring nearly exclusively on muskox dung/carcasses. *Psilopilum cavifolium* and *Funaria arctica* occurs almost entirely on peat. Species restricted to growing exclusively on rock include *Schistidium alpicola* var. *rivulare, Hypnum bambergii, Blindia acuta* and *Kiaeria blytii.* Showing a strong preference for, but not restricted to rock, include *Hygrohypnum polare* (submerged in stream) and *Schistidium grandirete* (xeric). In contrast, species that occur on all substrate categories include *Orthothecium chryseum, Philonotis fontana* var. *pumila* (except dung and rock) (Table 2.A3).

Spatial Assemblage Comparison: Seven Dominant Assemblages

The analyses of both the subglacial and extant specimens (representing modern day analogues) indicates that species composition of seven dominant assemblages is relatively distinctive (Figure 2.4). Fine scale microhabitat differences, as well as opportunistic colonization events of species can have significant impact on species composition of bryophyte assemblages, which are largely controlled by water availability (hydric vs. xeric assemblages). The ordination shows three distinct clusters of the assemblages (Figure 2.4) and is further supported by the pair-wise comparison where the MRPP and ISA results show statistically significant differences between the seven major assemblages (Table 2.A1). Especially pronounced in the extant specimens (Figure 2.4b), mesic-hydric species (*Aulacomnium turgidum, Polytrichastrum alpinum* and *Bartramia ithyphylla)* cluster together compared to mesic-xeric assemblages (*Hypnum revolutum, Ditrichum flexicaule* and *Niphotrichum panschii*) and hydric assemblages (*Hygrohypnum polare*). *Hypnum revolutum, Aulacomnium turgidum, Niphotrichum panschii,* and *Hygrohypnum polare* were similar in that they commonly (>50% of the time) formed the major taxon in their assemblages. In contrast, *Bartramia ithyphylla, Polytrichastrum alpinum*, and *Ditrichum flexicaule*, when present, comprised the major species < 40% of the time, typically occurring as intermixed assemblages.

Paleoecological Reconstruction and Temporal Assemblage Comparison: Subglacial versus Extant

Modern day analogues of subglacial moss assemblages provide a basis for paleoenvironmental reconstruction of species composition, microhabitat data, and specific environmental and physical factors (ie: exposure, slope, pH, substrate) (Birks and Birks 1980, Smith 1982). This study is designed to reconstruct past (LIA) *in situ* bryophyte assemblages by using extant assemblages from the same site.

The temporal analysis of the seven selected species assemblages from Sverdrup Pass follows.

i) Hypnum revolutum

The analyses indicated that there was no significant difference between the subglacial and extant *Hypnum revolutum* assemblages showing species associated with *H. revolutum* assemblages are similar between LIA and extant samples. *Hypnum revolutum* is a widespread arctic-alpine species with wide ecological ranges and high abundance in several moss communities (Schuster et al. 1959, Holmen 1955-1960, Steere 1978). There were 26 extant Sverdrup Pass samples examined containing *H. revolutum* for site and microhabitat observations. When dominant, the majority of the extant specimens were collected on the dry, exposed rocky slopes both east and west of the Teardrop Glacier. Regarding substrate, the contemporary *H. revolutum* assemblages were found growing on accumulated soil between bedrock boulders (Table 2.A3). The ISA (Table 2.A2) found *Syntrichia ruralis* was a strong indicator for both contemporary and LIA *H. revolutum* assemblages. Where *H. revolutum* was present, but occurring <25%, the assemblages were typically collected in protected soil hovels or depressions and on peaty soil in the glacier foreland. They were associated with dominants such as truly xeric *Orthotrichum speciosum,* and mesic-xeric *Racomitrium lanuginosum, Niphotrichum panschii* and *Niphotrichum canescens* subsp. *latifolium.* These associated species typical of bare, dry exposed rocks (Holmen 1955-1960, Brassard 1971, La Farge-England 1989).

Brassard (1971) describes a *Bryum argenteum* community where *H. revolutum* is dominant along with *Syntrichia (Tortula) ruralis* and *B. argenteum.* Similar to Sverdrup Pass observations, Brassard (1971) describes this community as developing around rocks and often surrounded by barren gravel habitats. In the quantitative analysis of bryophyte communities at Piper Pass, *H. revolutum* was classified within a xeric restricted species group (La Farge-England 1989).

Habitat information from other arctic localities show *H. revolutum* has broad pH ranges (Schofield 2006), is a drier habitat species, and indicates mineral-rich conditions (Hedenäs 1994). Poikilohydric water relations (Oliver et al. 2005, Proctor et al. 2007) and the ability for moss cytoplasm to survive with low water content (Longton 1988b) allow *H. revolutum* to inhabit dry, exposed boulders. The lack of any statistically significant temporal difference between the extant and LIA assemblages of *H. revolutum* and its commonly associated species indicates a dry, exposed microhabitat with wide ecological preferences both prior and after glaciation.

ii) Aulacomnium turgidum

Aulacomnium turgidum is a common arctic-alpine species who, when dominant, typically formed large tufts along wet seeps and along the margins of streambeds. These dominant *A. turgidum* assemblages were collected both in the wet meadow of Sverdrup Pass, as well as along meltwater streams within the boulder strewn foreland (Table 2.A3).

The analyses showed no significant difference in species composition between subglacial and extant assemblages, but the ISA indicates that different species with significant indicator values are present in the subglacial versus extant specimens. This included *Pogonatum dentatum, Bartramia ithyphylla,* and *Hygrohypnum polare* for the subglacial assemblages, whereas, *Orthothecium chryseum* was an indicator species for the extant *A. turgidum* assemblages (Table 2.A2). All four of these indicator species (subglacial or extant) prefer moist to wet habitat (soils) and it is unlikely that moisture is driving the difference between the two temporal assemblages. *Bartramia ithyphylla* prefers moist, often calcareous and silty substrates and can occur in exposed places over rock crevices. *Hygrohypnum polare* often grows on rocks in flowing streams and *Pogonatum dentatum* is tolerant to a wide range of substrate types (ie: gravel, sandy soils). *Orthothecium chryseum,* the extant indicator species, typically grows on wet organic soils. The differences in indicator species between the subglacial and extant assemblages is likely due to differences in

substrate type. *Pogonatum dentatum* and *Bartramia ithyphylla*'s preference for sandy or silty substrates illustrates the *A. turgidum* subglacial substrate. In contrast, *Orthothecium chryseum,* an indicator for the extant assemblages, prefers organic humus or soils demonstrating the extant substrate preferences.

Brassard (1971) describes an *Aulacomnium-Abietinella* community growing in mesic conditions on and between hummocks of vascular species often co-dominating with *Cassiope tetragona*. This is similar to the subglacial assemblages from the Teardrop Glacier margin where *C. tetragona* was an abundant vascular plant growing with *A. turgidum*.

Examination of polar semi-desert plant communities from various localities of the Western Queen Elizabeth Islands found lichens and bryophytes comprised 20-80% of plant cover (Bliss and Svoboda 1984). Of the bryophytes, *Aulacomnium turgidum* was one of the bryophyte species characterizing moss-graminoid wet meadows and plays a significant role in establishment and maintenance of polar semi-desert plant communities with high species richness and high net annual plant production (Bliss and Svoboda 1984). This indicates overlap between polar semi-deserts and polar oases, where *A. turgidum* is dominant and plays an important role in the formation and continuation of wet meadow communities with high net annual production.

iii) Bartramia ithyphylla

Bartramia ithyphylla is an arctic-alpine species that is not common, but can be locally abundant (Brassard 1971). This was the case at the Teardrop Glacier before entombment. As a dominant subglacial species (>25%), it occurred in 12 samples but was rarely found within the study site on the south slope of Sverdrup Pass with only four extant dominant assemblages found. Although the MRPP indicated significant temporal differences in species composition, the small and unequal sample sizes likely exaggerated these differences.

Six extant assemblages containing *B. ithyphylla* were examined for microhabitat data (four dominants; two of which were fruiting). It was found growing along glacial stream melt-water seeps and stream/pond margins on sandy substrates (Table 2.A3). Samples with less than 25% abundance of *B. ithyphylla*, showed it associated with *Niphotrichum panschii* or *Hypnum revolutum* in mesic, protected microsites. Habitat information from other high arctic localities is similar to contemporary Sverdrup Pass assemblages, preferring mesic growing conditions (Schuster et al. 1959, Holmen 1951-960, Steere 1978). On Devon Island (Truelove Lowland) and Pearyland, Greenland, it is described as most common in moist, shady habitats, such as depressions and rock crevices (Holmen 1960, Vitt 1975). However, other High Artic microhabitat information, especially for Ellesmere Island is sparse and information from other localities can be conflicting. In Alaska, it was observed in exposed habitats and very rarely in rock crevices (Steere 1978). *Bartramia ithyphylla* may have a wide range of microhabitat preferences with a restricted distribution (Brassard 1971). However, additional contemporary assemblages of *B. ithyphylla* need to be examined for a complete consideration of its exposure preferences for northern Ellesmere Island.

iv) Niphotrichum panschii

The ordination and MRPP analysis showed significant temporal differences between LIA and contemporary *Niphotrichum panschii* assemblages. The ISA showed that the subglacial assemblages were often found with *Polytrichastrum alpinum,* whereas extant *N. panschii* assemblages were often found with the closely related *Niphotrichum canescens* var. *latifolium*. The examination of extant assemblages (11 specimens) shows that *N. panschii* was never found fruiting and is cited as sterile in North America (Hastings and Ochyra 2007). The microhabitat information from Sverdrup Pass extant specimens shows a preference for sites between boulders and rocks. Assemblages were collected in dry sites on soil and sand showing the ability for colonizing unstable substrates. *Niphotrichum panschii* was also collected in wet

sites, along the banks of glacial meltwater streams showing a wide tolerance for moisture levels (Table 2.A3). For North America, this species is cited as growing in dry, exposed sites in moist or wet sites, but with a tendency to grow in acidic conditions (Hastings and Ochyra 2007), similar to conditions on the south slope of Sverdrup Pass. The unstable environment and a wide tolerance of moisture conditions are the likely reasons for the temporal difference in species composition found.

v) Polytrichastrum alpinum

There was no significant difference between the subglacial and extant *Polytrichastrum alpinum* dominated assemblages indicating comparable species composition. However, *Aulacomnium turgidum* was an indicator species for the extant assemblages representing an increased presence of this 'wetland' taxon in contemporary *P. alpinum* assemblages compared to LIA. *Hypnum revolutum* was the indicator for the subglacial *P. alpinum* assemblages, representing drier habitat range. Twenty-seven extant assemblages were examined containing *P. alpinum* to determine microhabitat preferences. When *P. alpinum* was dominant (17 samples), a variety of substrates were present including sand and gravel as well as soil. It was consistently collected in hydric sites along streambed margins and wet seeps (Table 2.A3).

Sverdrup Pass assemblages have similar microhabitat preferences when compared to other High Arctic localities. Brassard (1971) describes a *Polytrichastrum (Pogonatum) alpinum* communities occurring mainly at high latitudes where snow melts more slowly and moisture is present throughout the summer. At Piper Pass, *P. alpinum* was most prominent in a mesic widespread species group and dominated its assemblages along with *Timmia austriaca, Philonotis fontana* var. *pumila,* and *Bryum pseudotriquetrum* (La Farge-England 1989).

Teardrop Glacier assemblages of *P. alpinum* were typically found in nearly pure tufts co-dominating with *Hypnum revolutum* and less commonly as strands intermixed with other mosses. Interestingly, similar to Sverdrup Pass, it was also

found in pure tufts only in 'special conditions' in Pearyland, Greenland (Holmen 1960). On the Devon Island Plateau, (a polar desert; Bliss et al. 1994), *P. alpinum* was one of the only bryophytes to establish and maintain populations. In comparison to polar semi-deserts (Bliss and Svoboda 1984), assemblages with *Polytrichastrum* spp., and *Aulacomnium turgidum* dominated moss-graminoid wet meadows. Primary plant succession studies (Fahselt et al. 1988, Breen and Levesque 2006, 2008 show that *Polytrichastrum/Pogonatum* spp. dominate the first successional stages 20-30 m from the Teardrop Glacier margin (Jones and Henry 2003), able to colonize unstable substrates.

vi) Hygrohypnum polare

Hygrohypnum polare is an arctic-alpine species (Schuster et al. 1959, Holmen 1956, Steere 1978) and an examination of 11 extant assemblages containing *H. polare* (6 dominants) indicate a strong preferences for rheophytic habitats, seasonally growing on rocks submerged in streambeds (Table 2.A3). No significant temporal differences were found, and it is presumed that before the LIA, *H. polare* assemblages grew in similar habitats as today. In aquatic bryophyte assemblages, pH, specific conductivity, water transparency and temperature can be some of the physical parameters best explaining occurrences of hydric species (Karttunen and Toivonen 1995, Vanderpoorten et al. 1999).

In the Teardrop Glacier extant assemblages, *H. polare* was most commonly found as a co-dominant with *Aulacomnium turgidum*. *Hygrohypnum polare* grew in relatively pure populations where the effective number of species was the lowest of all the seven subfossil dominant assemblages (3.1 for the subfossil and 2.2 for extant) and, when present, was dominant 55-60% of the time. The *Hygrohypnum* community from northern Ellesmere is described as extremely rare growing on rocks in streams with *Cirriphyllum cirrosum, Hygrohypnum luridum* and *Seligeria polaris* (Brassard 1971), but the Teardrop Glacier assemblages did not occur with any of the above-mentioned species. *Hygrohypnum polare* is also rare (Truelove Lowlands;

Vitt 1975) or restricted (Piper Pass; La Farge-England 1989) in other localities and is typically found growing on granitic boulders.

vii) Ditrichum flexicaule

Ditrichum flexicaule has one of the highest frequencies of occurrences in both the subglacial (36) and extant (42) communities. However, when present, it infrequently formed the dominant species (10%-19%). *Ditrichum flexicaule* assemblages did not differ significantly between subglacial and extant. The microhabitat data from the extant assemblages indicated that, when dominant, its substrate ranged from organic soil to sand and gravel. It was found among boulders in mesic and xeric sites as well as hydric conditions along stream banks and hummocks (Table 2.A3).

None of the contemporary *D. flexicaule* assemblages were found fruiting. For northern Ellesmere, it is noted that *D. flexicaule* does not produce sporophytes at high latitudes (Brassard 1971) but is one of the most common and abundant of all mosses occurring in almost all habitats (Vitt 1975). *Ditrichum flexicaule* is abundant in arctic and subarctic regions (Schuster et al. 1959, Holmen 1956, Steere 1978) and has been described as a weedy species tolerant to a broad range of environmental conditions including exposure, moisture and pH range (Seppelt 2007). *Ditrichum flexicaule* assemblages from Teardrop Glacier are comparable to quantitative data from Piper Pass that shows that *D. flexicaule* is present in all species groups that represent a xeric-hydric gradient, with its highest prominence value in the xeric-mesic group (La Farge-England 1989).

Life Strategies: Dominant Moss Taxa

The subglacial assemblages examined containing the principal species are classified as perennials (*Hypnum revolutum, Aulacomnium turgidum, Niphotrichum*

panschii and *Hygrohypnum polare*), or colonist and shuttle species (*Polytrichastrum alpinum, Bartramia ithyphylla* and *Ditrichum flexicaule*) (During 1979, 1992, 2001). Perennials are characterized by long life spans and have moderate to low reproductive effort (During 1979, 1992). All of the dominant perennials lacked sporophytic material. Many polar bryophytes exhibit this more primitive life strategy (Longton and Schuster 1983) and gametangia and sporophyte production of these arctic mosses is limited (Brassard 1971, Longton 1988a).

The perennial life strategy is indicative of stable environments (During 1979, 1992). Paleoenvironmental reconstruction of the *in situ* subglacial populations suggests that, before entombment, areas containing mature populations of these perennial stayers must have been relatively stable to support species where reproduction was not required for colony maintenance. This is in contrast to the other foreland species that have life strategies adapted to more unstable microhabitats. Colonist or shuttle species have a short life span of only a few years and grow on habitats with short longevity (During 1979, 1992), such as exposed patches in recently deglaciated terrain. The various moss species with different life strategies reflects the mosaic of microhabitats in the Teardrop Glacier foreland.

Conclusion

The well-preserved, intact bryophyte assemblages released from under the Teardrop Glacier are LIA assemblages. The results suggest that bryophyte assemblages in terms of species richness and diversity are similar in pre and post LIA glacier expansion and retreat. However, species composition of LIA and contemporary bryophytes assemblages indicates diverse microhabitats. Species abundance variation and significant differences between seven dominant assemblages illustrated a broad range of habitat preferences. Comparison to contemporary assemblages showed the majority of the subglacial taxa were mesic and widespread. Some mesic–hydric, as well as mesic–xeric, microhabitats were also inferred from indicator species. Species found under the Teardrop Glacier indicate

a variety of microhabitat conditions with various preferences for moisture and substrates.

Bryophytes have attained unique physiological adaptations to thriving in harsh arctic environments. Compared to angiosperms, their survival in these conditions is thought to be from features such as lower internal water content when turgid in addition to the considerable desiccation tolerance of many species (Longton 1988a). Factors driving richness and diversity include physical parameters (substrate, protection from wind erosion and water availability), the most important being moisture availability.

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Table 2.1. Ordinal Classes assigned to measure percent cover.

Class	Percent Cover (%)
1	<5
2	5-24
3	25-49
4	50-74
5	75-100

Table 2.2. Number of specimens (from the 2007/2009 field season) and bryophyte taxa for Little Ice Age subglacial Teardrop Glacier assemblages and extant Sverdrup Pass, Ellesmere Island. Non-quantitative extant specimens restricted to the Teardrop Glacier vicinity and the south side of the pass. Subglacial specimens selected for quantitative analysis chosen based on the dominant taxa present (>25%/taxon). Selection of extant specimens for quantitative analysis based on presence of dominant (>25%/taxon) species analogous to subglacial assemblages.

	Total number of specimens collected	Non-Quantitative Analysis		Quantitative Analysis	
		# of specimens	# of taxa	# of specimens	# taxa
Subglacial	140	113	73 taxa (65 mosses and 8 hepatics)	84	63 taxa (58 mosses and 5 hepatics)
Extant	>800	348	122 taxa (114 mosses and 8 hepatics)	71	62 taxa (54 mosses and 8 hepatics)

Table 2.3. Average alpha species richness, true diversity, t-test, and post hoc power analysis for seven major assemblages. Average alpha true diversity calculated as Shannon-Weiner effective number of species. T-test, and post hoc observed power results determined using SPSS Inc. (2010). Number of specimens reflect number of subglacial samples where taxon was dominant (>25%) and the selected equivalent extant specimen chosen to represent the same dominance as the subglacial samples. Analyses considered significant at $\alpha = 0.05$.

	Number of specimens		Average alpha richness / sample		Average alpha true diversity (Effective Species)					
Dominants in Assemblages	Subglacial (n)	Extant (n)	Subglacial	Extant	Subglacial	Extant	Observed Power	Test statistic for true alpha diversity	Degrees of Freedom	P-value
Hypnum revolutum	20	15	5.55	4.2	5.3	4.1	0.062	1.34	33	0.19
Aulacomnium turgidum	14	22	5.86	5.23	5.6	4.9	0.056	0.78	34	0.44
Bartramia ithyphylla	12	4	5.92	6.00	5.6	5.6	0.138	0.04	14	0.97
Niphotrichum panschii	11	8	3.82	3.88	3.6	3.7	0.09	0.12	17	0.91
Polytrichastrum alpinum	11	12	6.45	3.92	6.2	3.7	0.140	2.15	21	0.06
Hygrohypnum polare	9	6	3.22	2.33	3.1	2.2	0.071	0.88	13	0.39
Ditrichum flexicaule	7	4	7.43	4.75	7.1	4.6	0.062	1.42	9	0.19

Table 2.4. Bryophyte subglacial (Teardrop Glacier) and extant species list from southern slope of Sverdrup Pass, Ellesmere Island. Species abbreviations (Abbrev.) and authorities given along with the number of temporal occurrences based on 140 subglacial (SBG) and 348 extant (E) specimens. Taxa not identified to species excluded (3 extant moss and 3 hepatic taxa; 7 subglacial moss and 3 hepatic taxa).

Bryophyte Species	**Number of occurrences in SBG flora**	**Number of occurrences in Extant flora**	**Abbreviation**	**Found with sporophytes**	**SBG Frozen Voucher (*dried sample)**	**Extant Voucher (CLF dried samples)**
113	**59**	**110**		**26**		
Amphidium lapponicum (Hedwig) W.P. Schimper	0	8	Amphlap	*		13171
Aplodon wormskjoldii (Hornemann in Oeder) R. Brown	0	10	Aplwor	*		13067
Aulacomnium acuminatum (Lindberg & H. Arnell) Kindberg	0	8	Aacum			12982
Aulacomnium palustre (Hedwig) Schwägrichen	0	5	Apal			13788
Aulacomnium turgidum (Wahlenberg) Schwägrichen	20	33	Aturg	*	44	13107
Bartramia ithyphylla Bridel	32	6	Bartith	*	15	13121
Blindia acuta (Hedwig) Bruch & W. P. Schimper in B.S.G.	0	1	Bliacu			13348
Brachythecium turgidum (C. J. Hartman) Kindberg	1	5	Brachturg		4	13339
Bryoerythrophyllum recurvirostrum (Hedwig) Chen Pan-chieh	13	7	Bryrec		13005*	13472
Bryum argenteum Hedwig	0	4	Bryarg			13504
Calliergon giganteum (W. P. Schimper) Kindberg	0	9	Calgig	*		13314
Campylium arcticum (R.S. Williams) Brotherus	2	9	Camarc	*	13147*	12881
Campylium stellatum (Hedwig) C. E. O. Jensen	1	9	Camste		9	13555
Catascopium nigritum (Hedwig) Bridel	4	4	Catnig	*	49	12985
Ceratodon purpureus (Hedwig) Bridel	0	1	Cerpur			13583
Cinclidium arcticum W. P. Schimper	3	36	Cincarc		5	12881
Cinclidium latifolium Lindberg	0	6	Cinlat			12880
Cirriphyllum cirrosum (Schwägrichen in Schultes) Grout	0	6	Cirrcirr			12880
Conostomum tetragonum (Hedwig) Lindberg	4	0	Contet		13002*	
Cratoneuron arcticum Steere	0	1	Cratarc			13540
Cyrtomnium hymenophlloides (Hübener) T. Koponen	3	5	Cyrdes		54	13511
Cyrtomnium hymenophyllum (Bruch & W. P. Schimper in B.S.G.) Holmen	2	12	Cyrum		24	13539
cf. *Dicranella crispa* (Hedwig) Schimper	0	1	Diccris			13444
Dicranum elongatum Schleicher ex Schwägrichen	1	2	Dicelo		11	13100
Didymodon asperifolius (Mitten) H. Crum, Steere & L. E. Anderson	2	6	Didasp		17	13358

Bryophyte Species	Number of occurrences in SBG flora	Number of occurrences in Extant flora	Abbreviation	Found with sporophytes	SBG Frozen Voucher (*dried sample)	Extant Voucher (CLF dried samples)
Didymodon rigidulus var. *icamdophilus* (*Barbula icmadophila*) (Schimp. ex Müll. Hal.) R.H. Zander	1	2	Baricm		8	13361
Distichium capillaceum (Hedwig) Bruch & W. P. Schimper in B.S.G.	10	13	Distcap		8	13515
Ditrichum flexicaule (Schwägrichen) Hampe	36	42	Dflex		8	13350
Drepanocladus revolvens (Swartz) Warnstorff	0	15	Drev			13333
Encalypta alpina Smith	5	9	Ealp	*	13005*	13177
Encalypta rhaptocarpa Schwägrichen	12	4	Erha	*	8	13472
Encalypta procera Bruch	3	2	Epro		13145*	13507
Fissidens bryiodes Hedwig	0	1	Fissbry			13500
Funaria arctica (Berggren) Kindberg	0	13	Funarc	*		13433
Hennediella hemeii var. *arctica* (Hedwig) Zander	0	1	Henhem	*		13105
Hygrohypnum alpestre (Swartz ex Hedwig) Loeske	0	1	Hygroalp			13535
Hygrohypnum polare (Lindberg) Loeske	15	11	Hygpol		24	13537
Hylocomium splendens (Hedwig) W. P. Schimper in B.S.G.	2	1	Hylspl		2	13101
Hymenostylium recurvirostre (Hedwig) Dixon	1	1	Hymrec		13007*	13516
Hypnum bambergii W. P. Schimper	0	1	Hypbamb			13491
Hypnum cupressiforme Hedwig	0	1	Hypcup			13493
Hypnum plicatum (Lindberg) Jaeger	0	1	Hyppli			13178
Hypnum procerrimum Molendo	0	1	Hyppro			13179
Hypnum revolutum (Mitten) Lindberg	40	26	Hyprev		37	13492
Hypnum vaucheri Lesquereux	4	2	Hypvau		13011*	12992
Imbribryum muehlenbeckii (Bruch & Schimper) Pedersen	4	0	Imue		21	
Isopterygiopsis pulchella (Hedwig) Iwatsuki	5	10	Isopul		6	13537
Kiaeria blytii (Bruch & W. P. Schimper in B.S.G.) Brotherus	0	1	Kiably			13509
Leptobryum pyriforme (Hedwig) Wilson	6	5	Leppyr	*	19	13101
Meesia triquetra (H. Richter) Ångström	0	2	Meetri			13740
Meesia uliginosa Hedwig	0	1	Meeuli			13580
Mnium marginatum (Dickson ex Withering) Palisot de Beauvois	5	7	Mnmarg		23	13515
Mnium thomsonii W. P. Schimper	2	2	Mntho		8	13506
Myurella julacea (Schwägrichen in Schultes) W. P. Schimper in B.S.G.	14	8	Myujul		8	13324
Myurella tenerrima (Bridel) Lindberg	6	12	Myuten		13005*	13511
Niphotrichum canescens subsp. *latifolium* (C.E.O. Jensen) Frisvoll	3	8	Nipcanlat		25	12991

Bryophyte Species	Number of occurrences in SBG flora	Number of occurrences in Extant flora	Abbreviation	Found with sporophytes	SBG Frozen Voucher (*dried sample)	Extant Voucher (CLF dried samples)
Niphotrichum panschii (Müller Hal.) Bednarek-Ochyra in R. Ochyra et al.	14	11	Nippan		27	13064
Oncophorus wahlenbergii Bridel	0	3	Oncwah			13743
Orthothecium chryseum (Schwägrichen in Schultes) W. P. Schimper in B.S.G.	14	52	Ochrys		8	13333
Orthothecium strictum Lorentz	6	7	Ostric		13145*	13370
Orthotrichum speciosum Nees in J. W. Sturm	4	2	Ospec	*	13011*	13490
Philonotis fontana var. *pumila* (Turner) Bridel	12	48	Philfont	*	13009*	13451
Plagiopus oederianus (Swartz) H. Crum & L. E. Anderson	0	2	Plagoe			12985
Platydictya jungermannioides (Bridel) H. Crum	1	4	Platjun		4	13539
Pogonatum dentatum (Menzies ex Bridel) Bridel	19	3	Pogdent	*	44	13446
Pohlia cf. *filum* (W. P. Schimper) Mårtensson	5	6	Pfil		13016*	13115
Pohlia cf. *wahlenbergii* (Weber & D. Mohr) Andrews in Grout	0	1	Pohwah			13460
Pohlia cruda (Hedwig) Lindberg	25	29	Pcru	*	13007*	13515
Pohlia nutans (Hedwig) Lindberg	29	8	Pnut		2	13122
Pohlia proligera (Kindberg) Brotherus	0	3	Ppro			13437
Polytrichastrum alpinum (Hedwig) G. L. Smith	52	27	Polyalp	*	34	13123
Polytrichum hyperboreum R. Brown	0	1	Polyhyp			13434
Polytrichum juniperium Hedwig	2	3	Polyjun		4	13122
Pseudocalliergon brevifolium (Lindberg) Hedenäs	0	24	Psebrev			13376
Psilopilum cavifolium (Wilson in Seemann) I. Hagen	6	10	Psilcav	*	13058*	13583
Ptychostomum bimum (Schreber) J.R. Spence	0	1	Ptybim	*		13447
Ptychostomum calophyllum (R. Brown) J. R. Spence	4	0	Pcal		54	
Ptychostomum cf. *creberrimum* (Taylor) J. R. Spence & H.P. Ramsay	0	3	Ptycre			13442
Ptychostomum cf. *pendulum* Hornschuch	0	4	Ptypend			13452
Ptychostomum cf. *wrightii* (Sullivant & Lesquereux) J. R. Spence	0	1	Ptywri			13441
Ptychostomum cryophilum (Mårtensson) J. R. Spence	1	7	Pcry		38	13635
Ptychostomum cyclophyllum (Schwägrichen) J. R. Spence	2	3	Pcyc		14	13121
Ptychostomum neodamense (Itzigsohn in Müller Hal.) J. R. Spence	0	1	Pneo			13635
Ptychostomum ovatum (Hedwig) J. R. Spence	1	1	Pova		13015*	13328
Ptychostomum pallens (Swartz) J. R. Spence	9	4	Ppall	*	13264*	13099

Bryophyte Species	Number of occurrences in SBG flora	Number of occurrences in Extant flora	Abbreviation	Found with sporophytes	SBG Frozen Voucher (*dried sample)	Extant Voucher (CLF dried samples)
Ptychostomum pallescens (Schleicher ex Schwägrichen) J. R. Spence	0	1	Ptypal			12877
Ptychostomum pseudotriqutreum (Hedwig) J. R. Spence & H. P. Ramsay ex D. T. Holyoak & N. Pedersen	0	9	Ppseu			13118
Ptychostomum rutilans (Bridel) J. R. Spence	3	2	Prut		37	13164
Ptychostomum weigelii (Sprengel) J. R. Spence	1	2	Pwei		49	13089
Ptychostumum cf. *knowltonii* (Barnes) J. R. Spence	0	1	Ptykno			12879
Racomitrium lanuginosum (Hedwig) Bridel	0	4	Raclan	*		13063
Rosulabryum capillare (Hedwig) J.R. Spence	0	6	Rcap	*		13099
Schistidium alpicola var. *rivulare* (Bridel) Podpěra	0	1	Schalp			13300
Schistidium grandirete H. Blom	0	4	Schgra			13467
Schistidium papillosum Culm.	0	1	Schpap			12889
Scorpidium revolvens (Swartz) Rubers in Touw & Rubers	0	3	Scorrev			13043
Pseudocalliergon turgescens (T. Jensen) Loeske	0	1	Scortur			13068
Sanionia uncinata (Drepanocladus uncintatus) (J. Hedwig) L. Loeske	4	4	Dunc		2	13099
Splachnum vasculosum Hedwig	0	3	Splvas	*		12974
Stegonia latifolia (Schwägrichen in Schultes) Venturi ex Brotherus	0	1	Steglat			13362
Syntrichia ruralis (Hedwig) Weber & D. Mohr	12	13	Syrur		13148*	12991
Tetraplodon mnioides (Swartz ex Hedwig) Bruch & W. P. Schimper in B.S.G.	0	10	Tetramni	*		13178
Tetraplodon pallidus I. Hagen	0	2	Tetrapal	*		13040
Thuidium abietinum (Hedwig) Schimper	0	1	Thuiabi			13180
Timmia austriaca Hedwig	19	26	Taus		7	13174
Timmia megapolitana var. *bavarica* (Hessler) Brassard	0	2	Tmegbav			13372
Timmia norvegica J. E. Zetterstedt	0	3	Tnorv			13329
Timmia sibirica Lindberg & H. Arnell	0	1	Timsib			13364
Tomenthypnum nitens (Hedwig) Loeske	3	9	Tomnit		31	13164
Tortella tortuosa var. *arctica* (Arnold) Brotherus in B.A. Fedtschenko	1	12	Ttortarc		13162*	13467
Tortula mucronifolia Schwägrichen	0	1	Tortmucro			13514
Voitia hyperborea Greville & Arnott	0	8	Voithyp	*		12965
Warnstorfia sarmentosa (Wahlenberg) Hedenäs	2	3	Warsar		34	13087
Hepatics						
8	**5**	**5**				

Bryophyte Species	Number of occurrences in SBG flora	Number of occurrences in Extant flora	Abbreviation	Found with sporophytes	SBG Frozen Voucher (*dried sample)	Extant Voucher (CLF dried samples)
Aneura pinguis (L.) Dumort	0	1	Anepin			13305
Arnellia fennica (Gottsche & Rabenh.) Lindb.	1	0	Afen		13150*	13785
Blepharostoma trichophyllum (L.) Dumort	2	9	Bleptri		13005*	13795
Cephaloziella arctica Bryhn & Douin	12	9	Ceparc		13055*	13110
Gymnomitrium corallioides Nees	1	0	Gymcor		52	
Lophozia (Barbilophozia) atlantica (Kaal.) K. Müller	2	0	Baratl		5	
Marchantia polymorpha L.	0	1	Marchpoly			13303
Preissia quadrata (Scop.) Nees	0	4	Preiq			13360

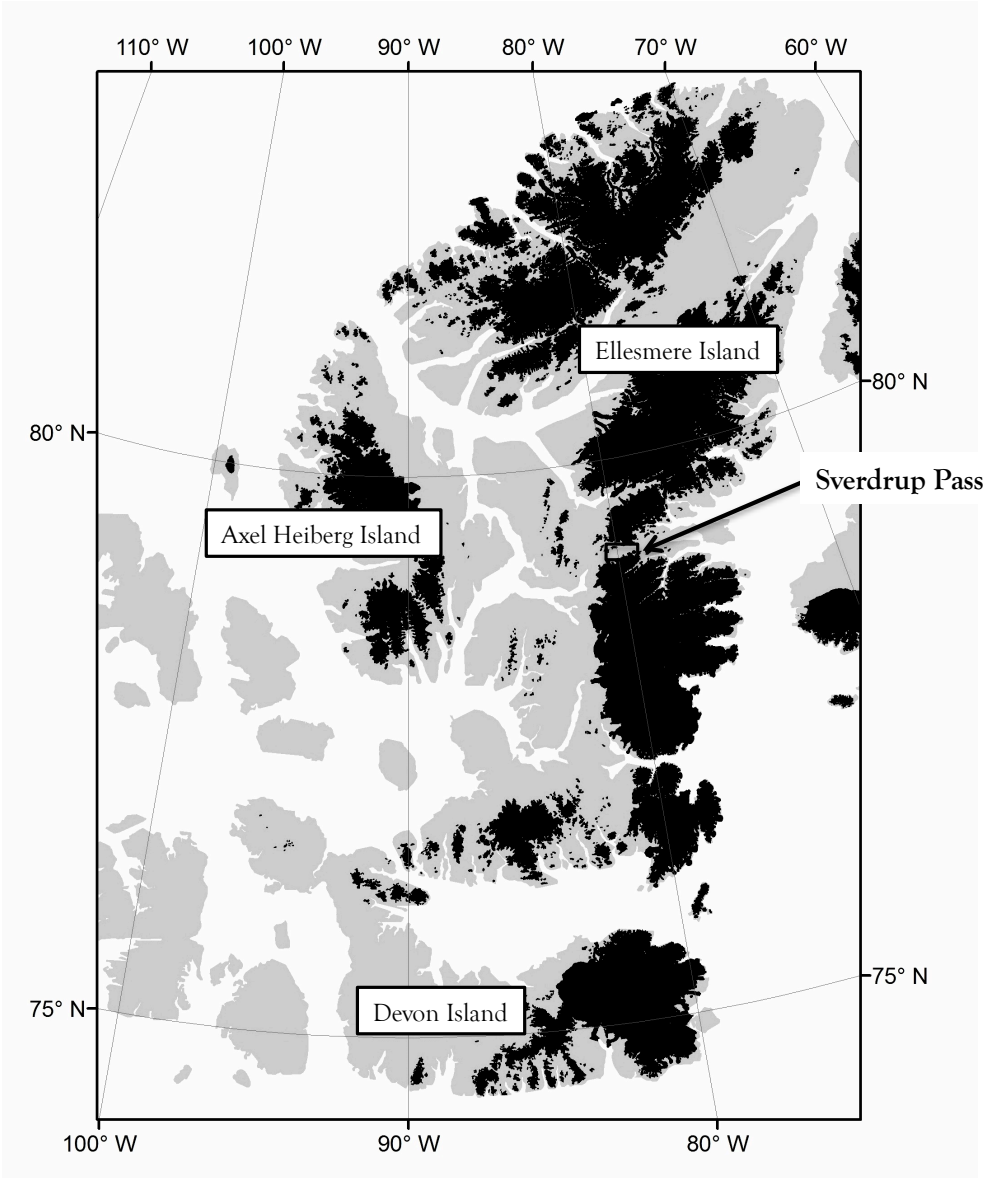


Figure 2.1. Northern Canadian Arctic Archipelago. Current (2009) ice cover (black) and location of study area (indicated by box), Sverdrup Pass, Ellesmere Island, Nunavut, Canada. (79° 10' N 79° 45' W; elev. 250 m a.sl. to 1350 m a.sl.; 75-80 km long and 2-5 km wide). Flager Bay in the east and Irene Bay in the west. It is bound on the north side by the Agasiz Icefield and on the south side by the Prince of Wales Icefield. Modified from Gardner et al. 2011.

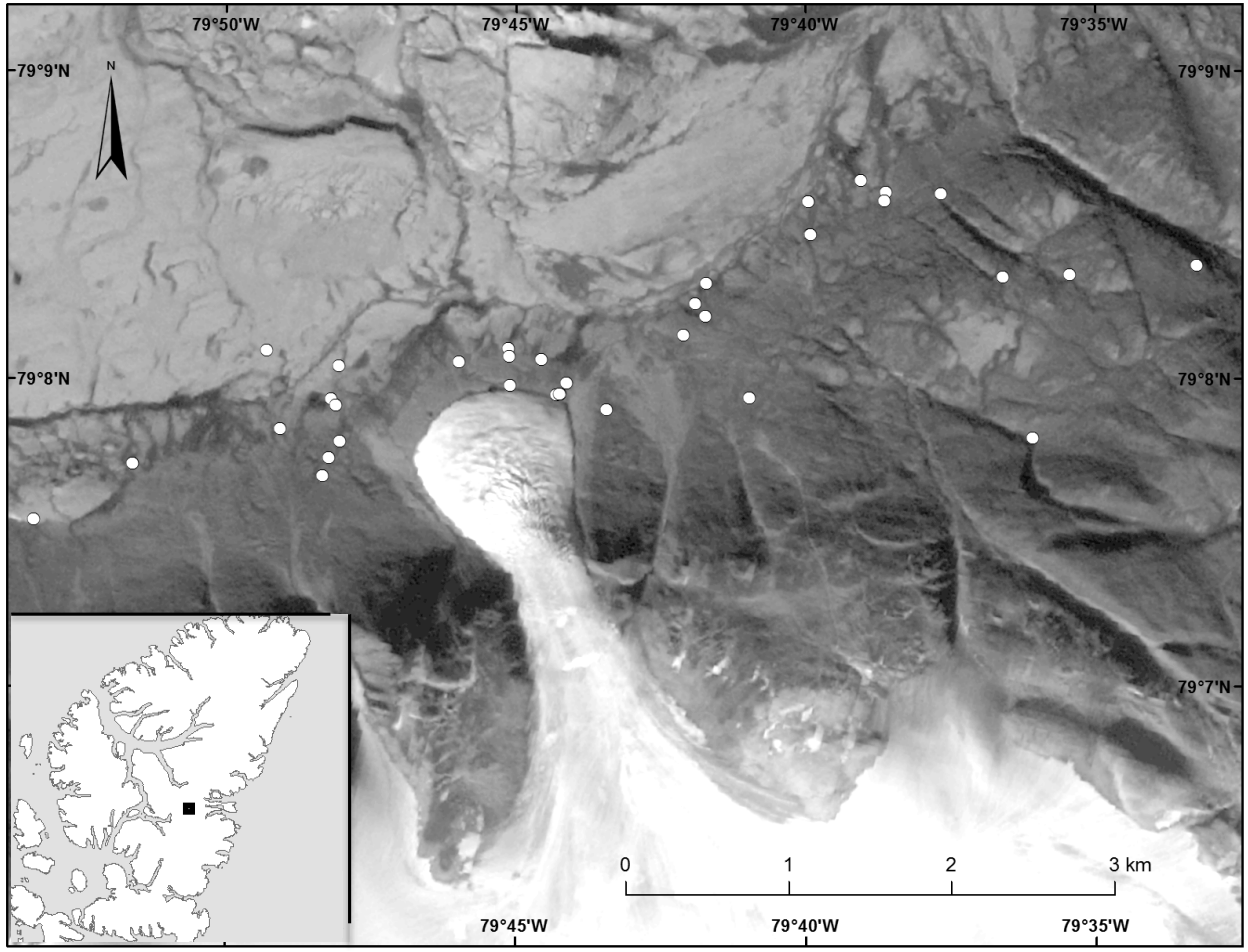


Figure 2.2. Map of Teardrop Glacier, Sverdrup Pass. (79° 07.758 N, 79° 44.175 W to 79° 087.758 N, 79° 46.795W elev. 335 m a.sl. Field study area (2007 and 2009) with extant sampling sites on the south side of Sverdrup Pass shown, Ellesmere Island, Nunavut. Inset: Map of Axel Heiberg and Ellesmere Island showing location of Sverdrup Pass.

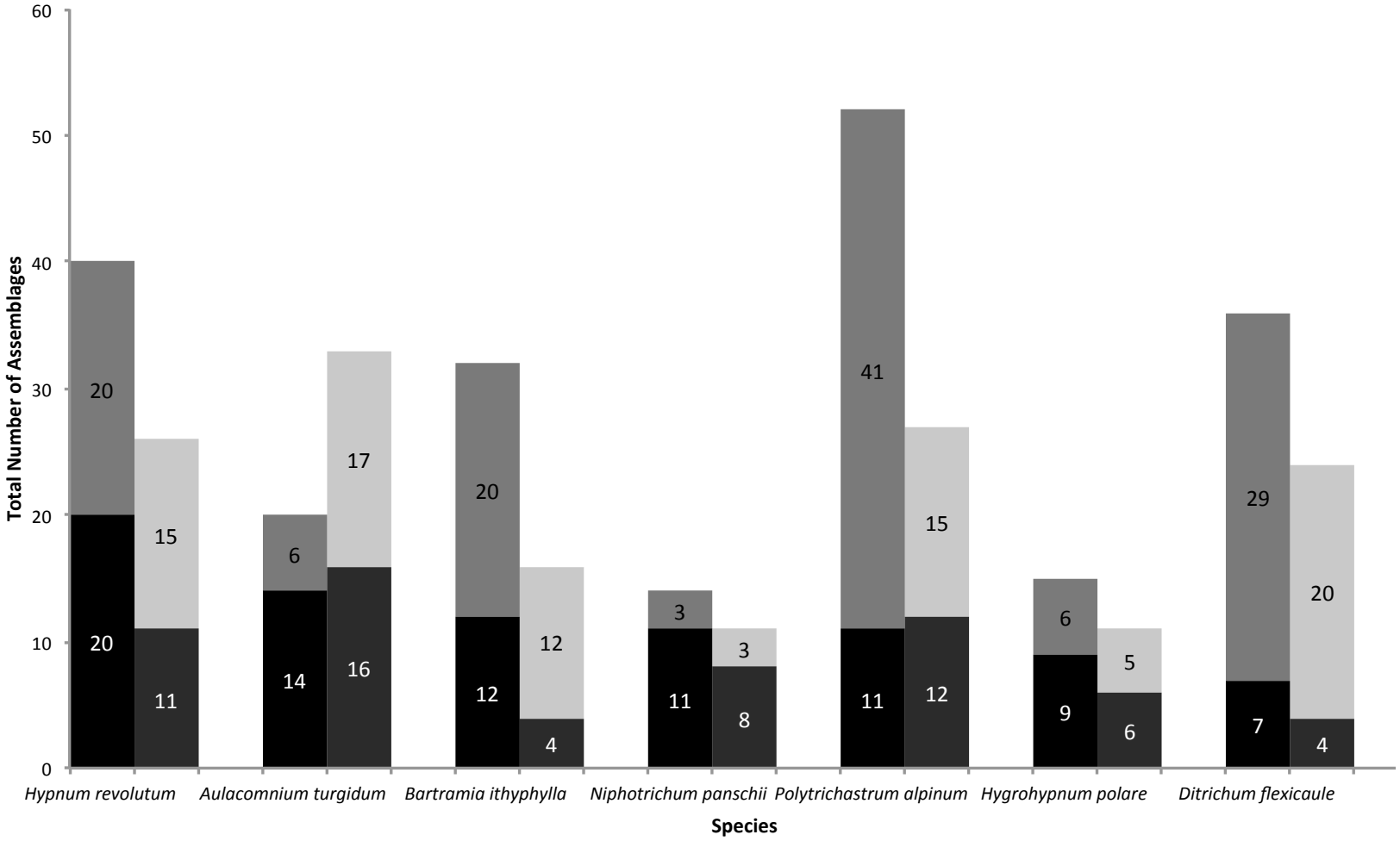


Figure 2.3. Subglacial (Teardrop Glacier foreland) and Extant (Teardrop Glacier foreland and South side of Sverdrup Pass, Nunavut) bryophyte species comprising the most common assemblages. Total number of subglacial ■; and number of subglacial when dominant (>25%) ■; Total number of extant ■ ; and number of extant when dominant (>25%) ■.

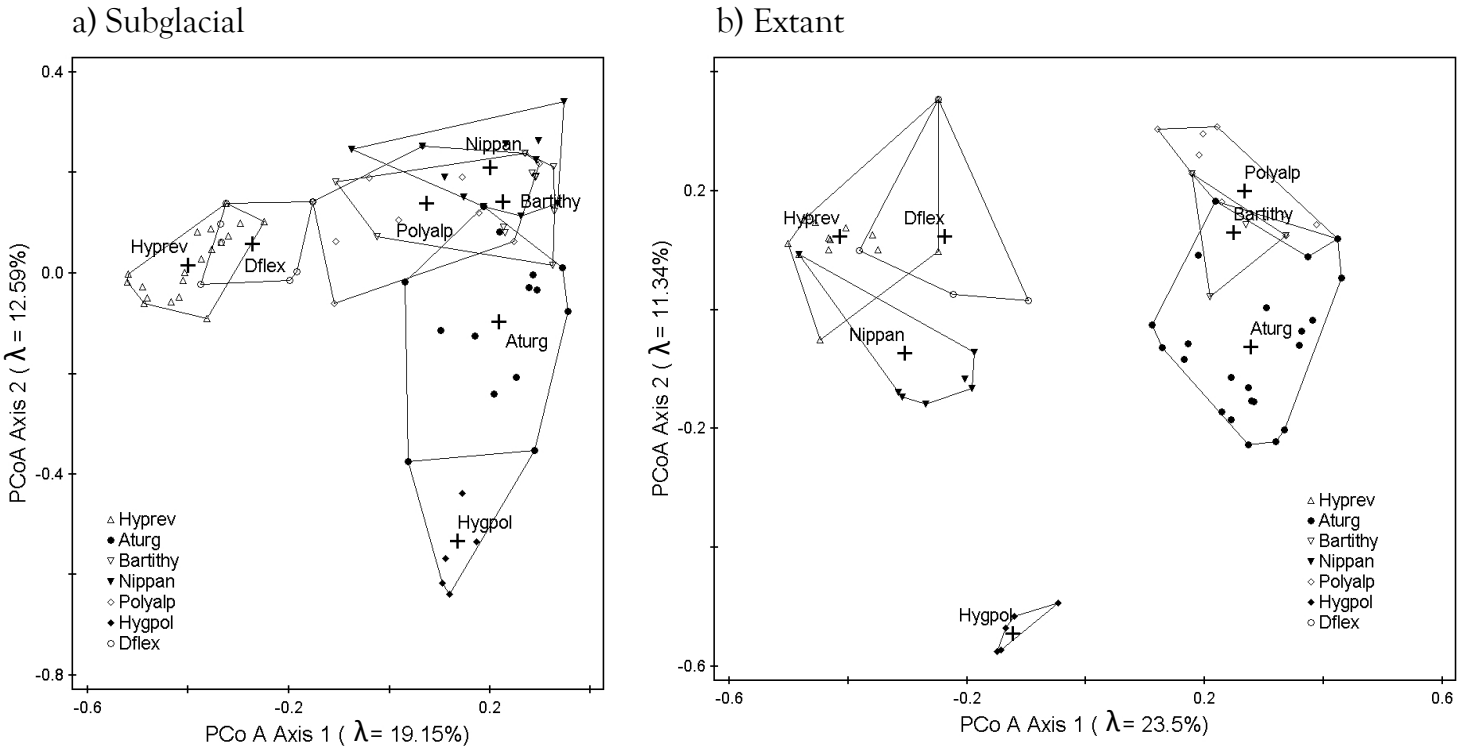
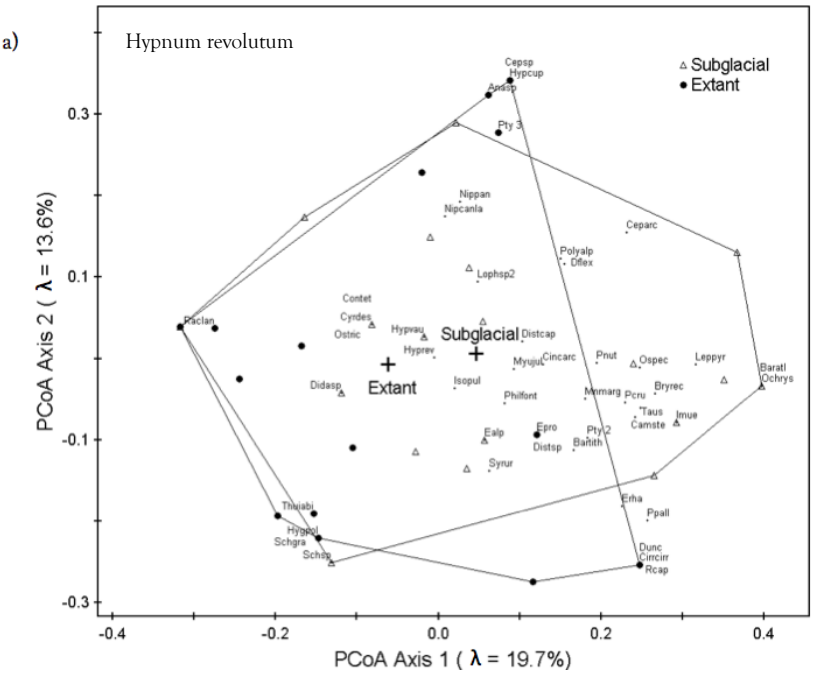
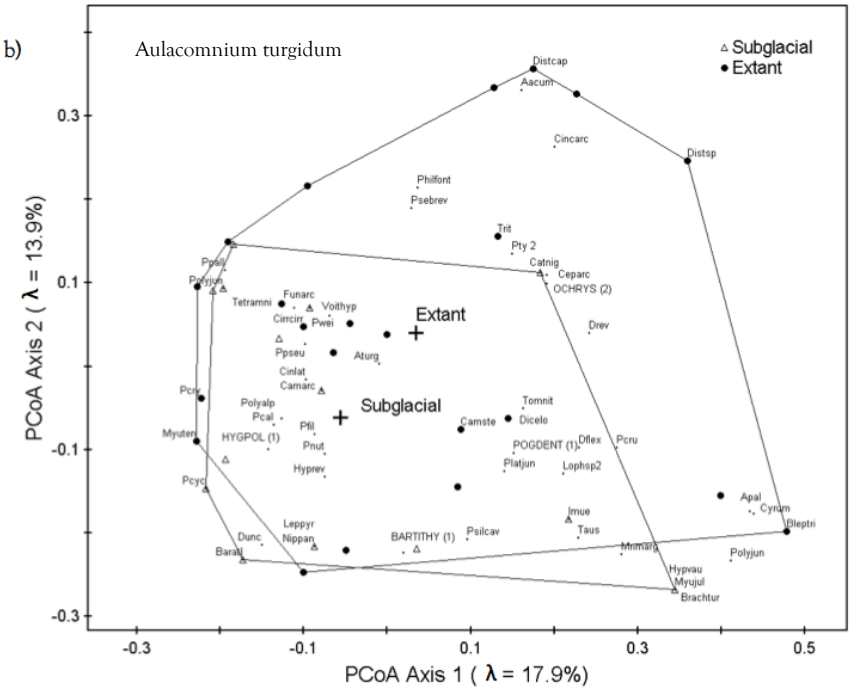


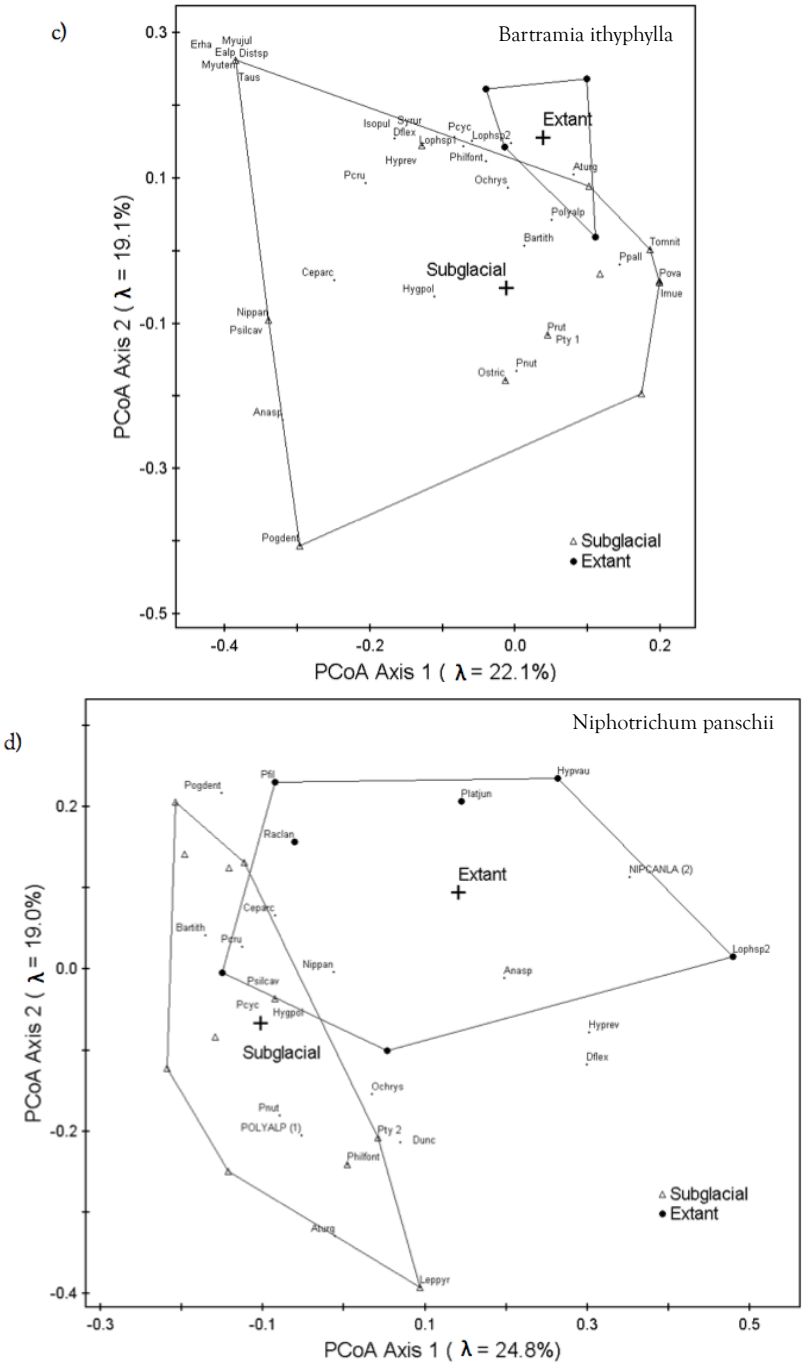
Figure 2.4. Results of PCoA ordination analysis in two dimensions of a) seven **subglacial** dominant assemblages (84 specimens) b) seven **extant** dominant assemblages (71 specimens) using Bray-Curtis dissimilarity for spatial comparison. Convex hulls enclosing plot of stands and coded by dominant species in each assemblage. Assemblage centroids showing multi-dimensional average. See Appendix 2.1 for taxon abbreviation.

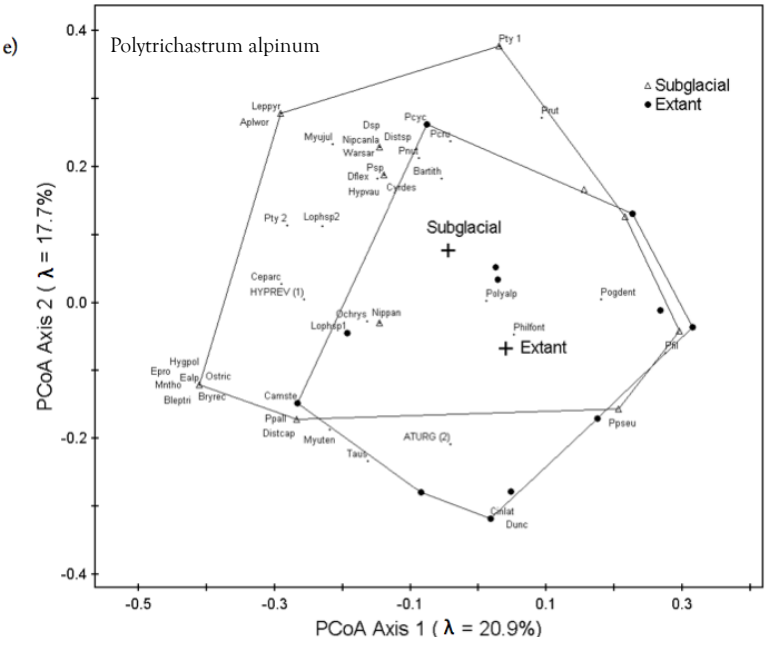
a)

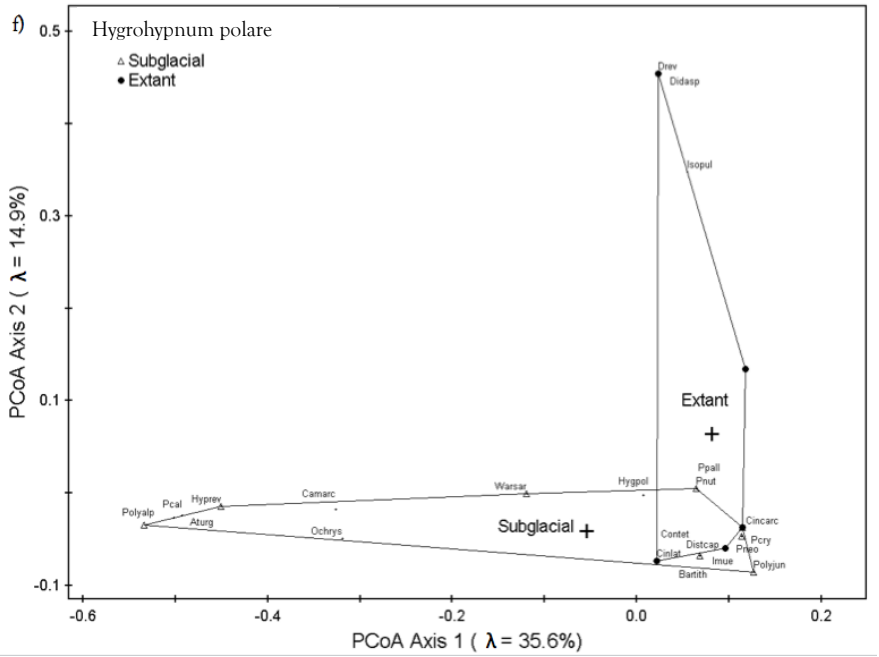

Hypnum revolutum
Subglacial
Extant
Subglacial
Extant
PCoA Axis 2 (λ = 13.6%)
PCoA Axis 1 (λ = 19.7%)
0.3
0.1
-0.1
-0.3
-0.4
-0.2
0.0
0.2
0.4
Cepsp
Hypcup
Pty 3
Nippan
Nipcanla
Ceparc
Polyalp
Dflex
Lophsp2
Contet
Cyrdes
Ostric
Hypvau
Distcap
Hyprev
Myujul
Cincarc
Pnut
Ospec
Leppyr
Baratl
Ochrys
Didasp
Isopul
Philfont
Mnmarg
Pcru
Bryrec
Taus
Camste
Imue
Ealp
Epro
Distsp
Pty 2
Barbith
Syrur
Erha
Ppall
Thuiabi
Hygpol
Schgra
Schsp
Dunc
Circirr
Rcap
Raclan

b)


Aulacomnium turgidum
Subglacial
Extant
Subglacial
Extant
PCoA Axis 2 (λ = 13.9%)
PCoA Axis 1 (λ = 17.9%)
0.3
0.1
-0.1
-0.3
-0.3
-0.1
0.1
0.3
0.5
Distcap
Aacum
Cincarc
Distsp
Philfont
Psebrev
Trit
Pty 2
Catnig
Ceparc
OCHRYS (2)
Drev
Ppseu
Polyjun
Tetramni
Funarc
Voithyp
Circirr
Pwei
Aturg
Cinlat
Camarc
Pcru
Polyalp
Pcal
Pfil
Pnut
Hyprev
Myuten
HYGPOL (1)
Pcyc
Tomnit
Dicelo
Camste
POGDENT (1)
Dflex
Pcru
Platjun
Lophsp2
Imue
Taus
Mnmarg
Apal
Cynum
Bleptri
Polyjun
Leppyr
Nippan
Dunc
Baratl
BARTITHY (1)
Psilcav
Hypvau
Myujul
Brachtur


c)
Bartramia ithyphylla
Extant
Subglacial
Subglacial
Extant
PCoA Axis 2 (λ = 19.1%)
PCoA Axis 1 (λ = 22.1%)
d)
Niphotrichum panschii
Extant
Subglacial
Subglacial
Extant
PCoA Axis 2 (λ = 19.0%)
PCoA Axis 1 (λ = 24.8%)


e)
Polytrichastrum alpinum
Subglacial
Extant
Pty 1
Leppyr
Aplwor
Pcyc
Pnut
Dsp
Myujul
Nipcanla
Distsp
Pcrs
Warsar
Pnut
Psp
Dflex
Bartith
Hypvau
Cyedes
Pty 2
Lophsp2
Subglacial
Ceparc
HYPREV (1)
Polyalp
Pogdent
Ochrys
Nippan
Lophsp1
Philfont
Extant
Phil
Hygpol
Epro
Ealp
Ostric
Mntho
Bryrec
Bleptri
Camste
Ppall
Distcap
Myuten
Taus
ATURG (2)
Ppseu
Cinlat
Dunc
PCoA Axis 2 (λ = 17.7%)
PCoA Axis 1 (λ = 20.9%)
0.4
0.2
0.0
-0.2
-0.4
-0.5
-0.3
-0.1
0.1
0.3


f)
Hygrohypnum polare
Subglacial
Extant
Drev
Didasp
Isopul
Extant
Ppall
Pnut
Hygpol
Warsar
Camarc
Hyprev
Pcal
Polyalp
Aturg
Ochrys
Subglacial
Cincarc
Contet
Distcap
Pcry
Phero
Cinlat
Imue
Polyjun
Bartith
PCoA Axis 2 (λ = 14.9%)
PCoA Axis 1 (λ = 35.6%)
0.5
0.3
0.1
-0.1
-0.6
-0.4
-0.2
0.0
0.2

g)

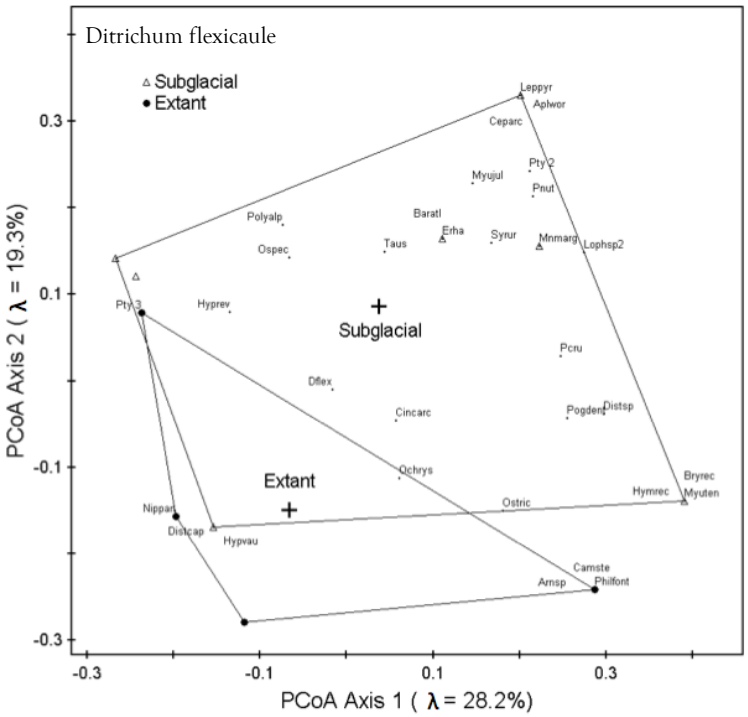


Figure 2.5. Results of PCoA ordination analysis in 2 dimensions of dominant subglacial and extant using Bray-Curtis dissimilarity for temporal comparison. Convex hulls enclosing plot of stands and coded by temporal assemblages (subglacial or extant). Group centroids showing multi-dimensional average. Bolded species indicate indicator species for subglacial (1) or extant (2) assemblages a) *Hypnum revolutum* with 35 assemblages and 50 species b) *Aulacomnium turgidum* with 36 assemblages and 56 species c) *Bartramia ithyphylla* with 16 assemblages and 33 species d) *Niphotrichum panschii* with 19 assemblages and 25 species e) *Polytrichastrum alpinum* with 23 assemblages and 44 species f) *Hygrohypnum polare* with 15 assemblages and 22 species g) *Ditrichum flexicaule* with 11 assemblages and 32 species. See Appendix 2.1 for taxon abbreviation.

Table 2.A1. Spatial comparison of seven dominant species assemblages (subglacial and extant). Multi-response permutation procedure (MRPP) accompanying each PCoA for analyses using abundance data. T = test statistic for MRPP; A = chance-corrected within-group agreement, a measure of within-group homogeneity. Only significant indicator species are included from the Indicator Species Analysis (ISA).

Dominant in Assemblage	MRPP				Seven dominant Subglacial Indicator Species Analysis			Seven dominant Extant Indicator Species Analysis		
	Assemblage compared	Subglacial T statistic (extant)	Subglacial A statistic (extant)	Subglacial p-value (extant)	Indicator Species (Indicator Value)	Indicator Value (IV)	p-value	Indicator Species (Indicator Value)	Indicator Value (IV)	p-value
Hypnum revolutum	*Aulacomnium turgidum*	-19.235	0.209	0.000 (0.000)	*Hypnum revolutum*	49.3	0.00	*Hypnum revolutum*	57.8	0.0001
	Bartramia ithyphylla	-17.557	0.21	0.000 (0.000)	***Syntrichia ruralis***	**27.6**	**0.00**	***Syntrichia ruralis***	**46.7**	**0.004**
	Niphotrichum panschii	-17.38	0.235	0.000 (0.000)						
	Polytrichastrum alpinum	-13.791	0.136	0.000 (0.000)						
	Hygrohypnum polare	-16.736	0.257	0.000 (0.000)						
	Ditrichum flexicaule	-3.973	0.0429	0.003 (0.003)						
Aulacomnium turgidum	*Bartramia ithyphylla*	-12.78	0.166	0.000 (0.000)	*Aulacomnium turgidum*	69.2	0.0001	*Aulacomnium turgidum*	57	0.0001
	Niphotrichum panschii	-11.784	0.205	0.000 (0.000)						
	Polytrichastrum alpinum	-10.376	0.12	0.000 (0.000)						
	Hygrohypnum polare	-10.37	0.218	0.000 (0.000)						
	Ditrichum flexicaule	-9.911	0.161	0.000 (0.000)						
Bartramia ithyphylla	*Niphotrichum panschii*	-10.71	0.196	0.000 (0.000)	*Bartramia ithyphylla*	58.2	0.0001	*Bartramia ithyphylla*	88.6	0.0001
	Polytrichastrum alpinum	-7.486	0.0918	0.000 (0.000)				***Lophozia spp.***	**33.1**	**0.02**
	Hygrohypnum polare	-11.655	0.279	0.000 (0.000)				***Ptychostomum cyclophyllum***	**42.9**	**0.01**
	Ditrichum flexicaule	-9.128	0.176	0.000 (0.000)						
Niphotrichum				0.000	*Niphotrichum*			*Niphotrichum*		

	Hygrohypnum polare	-11.296	0.339	0.000 (0.000)				**Niphotrichum canescens var. latifolium**	**32.0**	**0.012**
	Ditrichum flexicaule	-9.273	0.229	0.000 (0.000)						
Polytrichastrum alpinum	*Hygrohypnum polare*	-10.764	0.259	0.000 (0.000)	*Polytrichastrum alpinum*	34.1	0.0001	*Polytrichastrum alpinum*	45.7	0.0001
	Ditrichum flexicaule	-5.58	0.09	0.000 (0.000)						
Hygrohypnum polare	*Ditrichum flexicaule*	-8.702	0.286	0.000 (0.000)	*Hygrohypnum polare*	76.7	0.0001	*Hygrohypnum polare*	97.4	0.0001
					Campylium arcticum	**16.8**	**0.041**			
Ditrichum flexicaule					*Ditrichum flexicaule*	57.2	0.0001	*Ditrichum flexicaule*	62.4	0.0001
								Cinclidium arcticum	**47.5**	**0.004**

Table 2.A2. Temporal (LIA subglacial versus extant) comparison of seven dominant species assemblages. Multi-response permutation procedure (MRPP) accompanying each PCoA for analyses using abundance data. T = test statistic for MRPP; A = chance-corrected within-group agreement, a measure of within-group heterogeneity. Only significant indicator species are included from the Indicator Species Analysis (ISA). Max group 1 = Subglacial; 2 = Extant.

Assemblage	ISA				MRPP		
	Indicator Species	**Max Group**	**Indicator Value (IV)**	**p-value**	**T statistic**	**A**	**p-value**
Hypnum revolutum	no temporal indicator species				-0.491	0.0004	0.413
Aulacomnium turgidum					-1.753	0.0114	0.057
	Orthothecium chryseum	2	33.2	0.054			
	Bartramia ithyphylla	1	28.6	0.017			
	Pogonatum dentatum	1	21.4	0.047			
	Hygrohypnum polare	1	21.4	0.052			
Bartramia ithyphylla	no temporal Indicator species				-1.92385	0.0336	0.039
Niphotrichum panschii					-3.572	0.0596	0.0029
	Niphotrichum canescens var. latifolium	2	50	0.0177			
	Polytrichastrum alpinum	1	63.6	0.011			
Polytrichastrum alpinum					-1.851	0.0214	0.049
	Aulacomnium turgidum	2	45.2	0.0407			
	Hypnum revolutum	1	39.6	0.052			
Hygrohypnum polare	no temporal indicator species				-1.083	0.023097	0.1379
Ditrichum flexicaule	no temporal indicator species				-0.828	0.02068	0.1905

Table 2.A3. Distribution of 110 mosses within Teardrop Glacier vicinity, Sverdrup Pass. Categorized based on qualitative microhabitat descrption and substrate type.

Species	Microhabitat									Substrate					
	1: amoungst rocks	2: between boulders	3: around boulder	4: rock hovel	5: pond margin	6: wet seep	7: stream bank	8: submerged in pond	9: submerged in stream	1: muskox dung	2: humus	3: peat	4: rock	5: gravel/sand	6: soil
Amphidium lapponicum	0	2	0	0	0	2	0	0	0	0	0	0	3	0	1
Aplodon wormskjoldii	0	2	0	0	1	0	1	0	0	4	0	0	0	2	1
Aulacomnium acuminatum	0	0	0	0	0	0	3	0	0	0	0	0	0	0	4
Aulacomnium palustre	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3
Aulacomnium turgidum	0	0	0	1	0	3	13	0	0	1	5	1	0	4	8
Bartramia ithyphylla	0	1	0	0	1	1	1	0	0	0	0	0	0	4	0
Blindia acuta	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
Brachythecium turgidum	0	0	0	0	0	0	1	1	0	0	0	0	0	0	3
Bryoerythrophyllum recurvirostre	0	1	1	0	0	0	3	0	0	0	0	0	0	0	1
Bryum argenteum	0	1	1	2	0	0	0	0	0	0	0	0	0	0	3
Calliergon giganteum	0	0	1	0	0	0	6	1	1	0	0	0	0	1	3
Campylium arcticum	0	0	1	1	0	0	2	0	0	0	0	0	0	2	4
Campylium stellatum	0	0	0	2	0	0	7	0	0	0	0	0	0	0	4
Catascopium nigritum	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2
Ceratodon purpureus	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Cinclidium arcticum	0	3	1	2	0	1	17	0	0	1	2	1	0	0	8
Cinclidium latifolium	0	1	0	0	0	0	1	0	1	0	0	0	1	0	2
Cirriphyllum cirrosum	0	1	0	0	0	0	3	0	0	0	0	0	0	0	3
Conostomum tetragonum	0	0	0	0	1	1	1	0	0	0	0	0	0	1	2
Cratoneuron arcticum	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Cyrtomnium hymenophlloides	1	0	0	3	0	0	1	0	0	0	0	0	0	0	3
Cyrtomnium hymenophyllum	1	0	1	3	0	0	2	0	1	0	2	0	2	1	3
Dicranella crispa	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Dicranum elongatum	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2
Didymodon asperifolius	1	2	0	0	0	0	0	0	1	0	0	0	0	2	2
Didymodon rigidulus var. icamdophilus	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2

Species	Microhabitat									Substrate					
	1: amoungst rocks	2: between boulders	3: around boulder	4: rock hovel	5: pond margin	6: wet seep	7: stream bank	8: submerged in pond	9: submerged in stream	1: muskox dung	2: humus	3: peat	4: rock	5: gravel/sand	6: soil
Distichium capillaceum	1	2	0	3	0	0	2	0	0	0	1	1	0	3	2
Ditrichum flexicaule	2	9	0	4	0	0	7	0	0	1	2	0	2	2	13
Sanionia uncinatus	0	1	0	2	0	0	3	0	4	0	0	0	0	0	1
Drepanocladus revolvens	0	2	0	2	0	0	3	0	0	1	0	0	0	1	3
Encalypta alpina	0	2	0	1	0	0	0	0	0	0	0	0	0	0	3
Encalypta cf. rhaptocarpa	0	1	0	1	0	0	0	0	0	0	0	0	0	0	3
Encalypta procera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Funaria arctica	0	0	0	0	0	0	0	0	0	0	0	8	0	0	1
Hennediella heimii	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hygrohypnum alpestre	1	1	0	1	0	0	2	0	5	0	0	0	0	0	0
Hygrohypnum polare	0	0	0	0	0	0	0	0	0	0	0	0	4	1	3
Hylocomium splendens	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Hymenostylium recurvirostre	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hypnum bambergii	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Hypnum cupressiforme	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Hypnum plicatum	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Hypnum procerrimum	1	8	1	2	0	0	2	0	0	0	0	0	0	1	0
Hypnum revolutum	0	1	0	0	0	0	0	0	0	0	0	1	1	0	4
Hypnum vaucheri	1	2	0	0	1	0	2	0	2	0	0	1	0	0	0
Isopterygiopsis pulchella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Kiaeria blytii	0	0	0	0	0	0	3	0	0	0	0	0	1	0	0
Leptobryum pyriforme	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Meesia triquetra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Meesia uliginosa	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
Mnium marginatum	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Mnium thomsonii	0	0	0	1	0	0	2	0	0	0	0	0	0	0	2
Myurella julacea	0	3	1	2	0	0	4	0	0	0	0	0	0	0	1
Myurella tenerrima	0	2	0	0	0	0	1	0	0	0	0	0	0	0	1
Niphotrichum canescens subsp. latifolium	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1

Species	Microhabitat									Substrate					
	1: amoungst rocks	2: between boulders	3: around boulder	4: rock hovel	5: pond margin	6: wet seep	7: stream bank	8: submerged in pond	9: submerged in stream	1: muskox dung	2: humus	3: peat	4: rock	5: gravel/sand	6: soil
Niphotrichum panschii	0	6	0	0	0	1	1	0	0	0	0	0	0	2	1
Oncophorus wahlenbergii	1	5	1	4	1	0	15	1	1	0	0	0	0	0	0
Orthothecium chryseum	2	0	0	3	0	0	0	0	0	1	2	1	1	1	5
Orthothecium strictum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Orthotrichum speciosum	1	4	1	4	0	0	18	0	1	0	0	0	1	0	1
Philonotis fontana var. pumila	0	0	0	1	0	0	0	0	0	0	2	1	0	4	5
Plagiopus oederianus	0	1	0	2	0	1	0	0	0	0	0	1	0	0	0
Platydictya jungermannioides	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Pogonatum dentatum	0	1	0	0	0	0	3	0	0	0	0	0	0	2	0
Pohlia cf. filum	0	0	0	0	0	0	0	0	1	0	0	0	0	2	2
Pohlia cf. wahlenbergii	0	8	1	6	1	1	1	0	0	0	0	0	0	0	0
Pohlia cruda	0	1	0	1	0	1	4	0	0	0	0	1	0	0	5
Pohlia nutans	0	1	0	1	0	1	4	0	0	0	0	0	0	0	1
Pohlia proligera	0	6	0	1	1	1	11	0	0	0	0	1	0	0	0
Polytrichastrum alpinum	0	0	0	0	0	4	2	0	0	0	0	1	0	1	2
Polytrichum juniperium	0	3	0	1	1	1	9	5	0	0	0	0	0	0	1
Pseudocalliergon brevifolium	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1
Psilopilum cavifolium	0	0	1	0	0	0	0	0	0	0	0	5	0	1	0
Ptychostomum bimum	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Ptychostomum cf. creberrimum	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0
Ptychostomum cf. pendulum	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ptychostomum cf. wrightii	0	0	1	0	0	0	4	0	1	0	0	1	0	0	0
Ptychostomum cryophilum	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
Ptychostomum cyclophyllum	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
Ptychostomum neodamense	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Ptychostomum ovatum	0	1	0	0	0	0	3	0	0	0	0	0	0	0	0
Ptychostomum pallens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ptychostomum pallescens	0	1	0	2	0	0	1	0	0	0	0	0	0	0	0
Ptychostomum pseudotriqutreum	0	0	0	0	0	0	0	0	1	0	0	1	0	0	3

Species	Microhabitat									Substrate					
	1: amoungst rocks	2: between boulders	3: around boulder	4: rock hovel	5: pond margin	6: wet seep	7: stream bank	8: submerged in pond	9: submerged in stream	1: muskox dung	2: humus	3: peat	4: rock	5: gravel/sand	6: soil
Ptychostomum rutilans	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Ptychostomum weigelii	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ptychostumum cf. knowltonii	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Racomitrium lanuginosum	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Rosulabryum capillare	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0
Sanionia uncinatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Schistidium alpicola var. rivulare	0	2	0	0	0	0	0	0	0	0	0	0	3	0	0
Schistidium grandirete	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1
Schistidium papillosum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Scorpidium revolvens	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Scorpidium turgescens	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Splachnum vasculosum	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0
Stegonia latifolia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Syntrichia ruralis	0	5	0	1	0	0	1	0	0	0	0	0	1	0	2
Tetraplodon mnioides	0	1	0	0	0	1	3	0	0	5	0	0	0	0	1
Tetraplodon pallidus	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Thuidium abietinum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Timmia austriaca	0	6	1	6	0	1	3	0	0	0	0	0	0	1	5
Timmia megapolitana var. bavarica	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Timmia norvegica	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Timmia sibirica	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Tomenthypnum nitens	0	0	0	0	0	0	4	0	0	0	1	0	0	1	0
Tortella tortuosa var. arctica	0	3	0	1	0	0	1	0	0	0	0	1	0	0	2
Tortula mucronifolia	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Voitia hyperborea	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Warnstorfia sarmentosa	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0

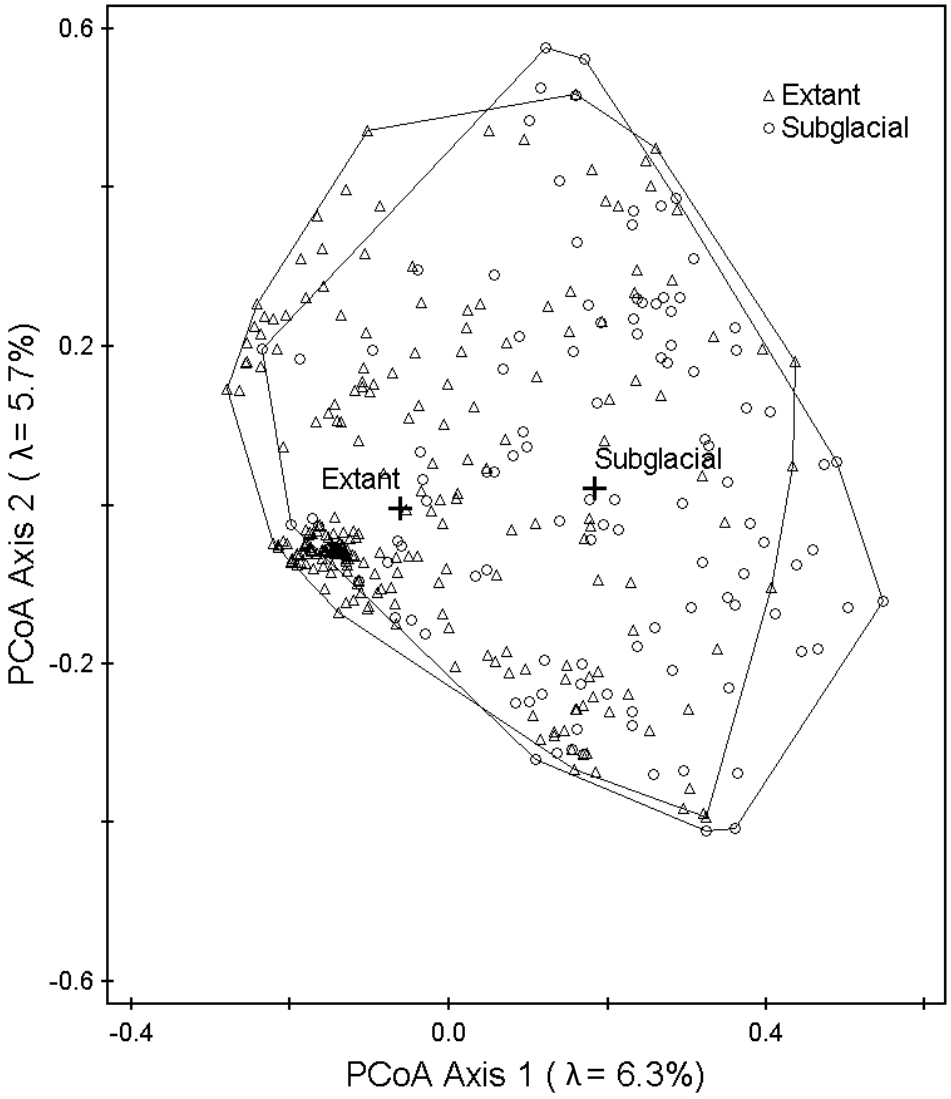


Figure 2.A1. Results of PCoA ordination analysis in 2 dimensions of all subglacial (140) and analugous extant (348) using Bray-Curtis dissimilarity for temporal comparison. Convex hulls enclosing plot of stands and coded by temporal assemblages (subglacial or extant). Group centroids showing multi-dimensional average.

Chapter III: Little Ice Age Subglacial Entombed Bryophyte Regeneration.

Introduction

High latitude glaciers and climate dynamics have a prominent role in Arctic research. Glacial retreat is the result of climate change and contributes critical data as the High Arctic atmosphere-ice-ocean system changes (ACIA 2005). In the Canadian High Arctic, most glaciers have been rapidly retreating since the end of the Little Ice Age (LIA), ca. 1850 AD (Gribbin and Lamb 1978, Grove 1988, Miller et al. 2010). Newly exposed deglaciated terrain has provided unique opportunities for examining primary plant succession (Matthews 1992, Chapin et al. 1994, Jones and Henry 2003, Breen and Lévesque 2008) and is key for understanding soil regimes (Stewart et al. 2011, Brummell et al. 2012) and the role of biological soil crusts (Breen and Lévesque 2006). However, these localities may also shed insight into the dormancy capacity of entombed biota and the regeneration potential of recently exhumed, subglacial flora.

There has been growing interest in glaciers as biotic ecosystems and glacial environments have been examined as refuges with viable biological material (see Hodson et al. 2008 for review). Glacial ecosystems are composed of three major units: supraglacial - surface of the glacier, subglacial at the ice-bed interface and englacial - within the ice. En- and subglacial ecosystems were previously considered to be devoid of life, functioning as abiotic systems, and comprised only of sediment, water, and ice (Hubbard and Nienow 1997). However, recent evidence shows various entombed, nutrient rich habitats with distinct microbial communities consisting of bacteria, cyanobacteria, diatom algae, yeasts, and filamentous fungi. They characterize en- and subglacial ecosystems in Antarctic Lake Ice (Abyzov 1993, Priscu et al. 1998, 1999, Price 2007, D'Elia et al. 2009), subglacial ice in Switzerland (Sharp et al. 1999) and in Norway along with *in situ* soil and vegetation

(Humlum et al. 2005, Sonjak et al. 2007). Also, the supra-, sub- and proglacial lake ecosystems of the John Evans Glacier, Nunavut, Canada (Lanoil et al. 2001, Bhatia et al. 2006).

Restricted mostly to examination of microbes, the dormancy of land plants (embryophytes) in sub- and englacial ecosystems has not been considered. Colonization by mosses on glaciers is unusual but has been previously documented (Benninghoff 1955, Powell 1967, Brassard 1971a) typically found growing directly on the ice with a thin film of sediment (Heusser 1972). Fickert et al. (2007) proposed that debris-covered glaciers served as Pleistocene refugia for plants after finding pioneer moss species from neighbouring communities were able to establish populations on glaciers. Therefore, it seems that glacial ecosystems provide viable habitats for land plants in supraglacial conditions but sub- and englacial ecosystems are currently restricted to microbial biota and any entombed land plant vegetation has been presumed dead (Jones and Henry 2003, Anderson et al. 2008, Breen and Lévesque 2006, 2008, Barker et al. 2009). Cold-based glaciers of the High Arctic lack evidence of glacial abrasion on bedrock and the landscape is devoid of deposits typical of warm-based ice (Dyke 1993). The presence of well-preserved soil layers and *in situ* vegetation have also demonstrated that portions of polythermal glaciers are cold-based, frozen to the substrate, and little subglacial erosion occurs (Bergsma et al. 1984, Humlum et al. 2005, Bhatia et al. 2006, Hodson et al. 2008). In High Arctic ecosystems, bryophytes often attain dominance (Longton 1988) and constitute a major component of subglacial *in situ* vegetation (Chapter II).

Bryophyta (mosses) represents a distinct lineage of embryophytes whose unique adaptations make them likely candidates for surviving severe glacial environments. Without vascular conducting tissues, mosses shut down metabolically in unfavourable conditions, then revive in favourable (poikilohydric water relations: internal water content varies passively with atmospheric humidity and water supply) (Proctor et al. 2007). Retaining their leaves, they must pass readily in and out of dormancy and their successful adaptation to land is attributed

to resistance to desiccation stress (Oliver et al. 2005). Almost all bryophytes exhibit the primitive trait of desiccation tolerance (DT), which is rare in vascular plants (tracheophytes). In polar regions especially, bryophyte survival is dependent on the ability to avoid and tolerate desiccation (Longton 1988). Mosses can maintain photosynthesis to temperatures as low as -9°C and respiration as low as -14°C, and often low temperatures are optimal growth conditions for high latitude taxa (Longton 1980). A correlation exists between freezing tolerance and DT, where xeric species are less affected by freezing and can survive extremely low temperatures (Proctor 2000). Physiological mechanisms, such as an abscisic acid (stress hormone) independent cold-signaling pathway (Minami et al. 2005), allow mosses exposed to freezing temperatures and high solar radiation levels (Lovelock et al. 1995) to freeze/desiccate without tissue damage and Antarctic mosses have shown resumed growth after being frozen for 3-5 years (Horikawa and Ando 1967, Longton and Holdgate 1967). DT allows bryophytes to successfully establish and maintain populations in extreme habitats and may positively influence their potential for freezing tolerance, dormancy, and regeneration in subglacial ecosystems.

Dormancy in plants is either enforced (no germination due to unfavourable temperature and moisture conditions; Stark 1997), or induced (no germination without a specific stimulus), and is an adaptation to temporally or spatially variable environments (Harper 1977). Bryophytes are able to rapidly decrease their water potential and suspend metabolic activity (Proctor 2000). They easily enter dormancy (Schofield 1985) but latency of diaspores (any bryophyte dispersal unit) is poorly known (Knoop 1984, Hock et al. 2004). The investigation of dormant gemmae, a type of asexual diaspore, show there is an increased frequency of gemmae entering dormancy towards the end of the growing season (Laaka-Lindberg and Heino 2001).

The culturing and regeneration of bryophytes has been investigated for cryopreservation purposes (Duckett et al. 2004, Segreto et al. 2010, Rowntree et al. 2011). Bryophytes are characterized by totipotent cells, which can be reprogrammed from living tissue to regenerate new plants (Menon and Lal 1981). The ability to

dedifferentiate living cells to a meristematic state makes the totipotent cells of bryophytes equivalent to stem cells (Ishikawa et al. 2011) and demonstrates biological resilience in polar environments. In nearly all bryophytes, gametophytic cells have the ability for re-growth even from detached fragments and typically, new plants are formed from protonema (the earliest, filamentous stage of a bryophyte life cycle) (Correns 1899, Menon and Lal 1981, During 1990, Frey and Kürschner 2011).

Bryophytes have advantages as experimental organisms due to their ease of manipulation and growth. They have been increasingly used as model systems for investigating cellular and molecular components of plant development (Cove et al. 1997, 2006 for reviews). However, the majority of research using bryophytes as model organisms is confined to three species, *Ceratodon purureus* (Hedw.) Bridel, *Funaria hygrometrica* Hedw. and *Physcomitriella patens* (Hedw.) Bruch & Schimp (Duckett et al. 2004). More recently *in vitro* cultivation of bryophytes has been recognized as an essential part of cellular, developmental, and molecular research as well as reproductive biology (Reski 1998, Duckett et al. 2004 for reviews). In addition, culture experiments have been utilized to examine systematics (Newton et al. 2000), as well as bryophyte-fungal and bacterial interactions (Davey and Currah 2006, Pressel et al. 2010). Bryophytes, in particular, respond well to *in vitro* techniques, which have been used for conservation of rare taxa (Christianson 1998, Pence 1999, Burch and Wilkinson 2002, Burch 2003, Pressel and Duckett 2010, Rowntree et al. 2011), and extraterrestrial trials of life in space (Kern et al. 2005). Cultures can be initiated by spores, propagules, or vegetative fragments and can be grown in petri dishes on their own substrates or commercial substrates including potting soil (Shaw 1986) or culture media (Duckett et al. 2004). Fragmentation of gametophyte tissue and dispersal on potting soil has been shown to be an effective propagation method (Shaw 1986), since bryophytes, *in vivo,* are predominantly clonal organisms relying on asexual modes of reproduction (Mishler and Budd 1990, Shaw 2000b).

Bryophytes reproduce sexually through the development of sporophytes and asexually through the dispersal of specialized diaspores (spores, gemmae, bulbils) or unspecialized fragmentation of gametophyte material (leaves, stems, protonema, rhizoids, tomentum). Protonemata (composed of chloronemata and caulonemata) produces leafy gametophyte shoots (Crundwell 1979) from spores, rhizoids, (nonchlorophyllose filaments that anchor the gametophyte to the substratum and act as moisture wicks; Schofield 1985) and specialized asexual propagules. These specialized propagules can include gemmae (chloronemal in origin with a differentiated abscission mechanism and starch reserves), tubers (rhizoidal in origin without an abscission mechanism and with lipid reserves), and bulbils (with inherent polarity and reduced leaf primordia around an apical meristem) (Duckett and Pressel 2003). In no other embryophyte group is asexual reproduction as important as in bryophytes. They rely on it to enable rapid colonization and effective persistence in a habitat (Longton and Schuster 1983, Frey and Kürschner 2011). In the arctic, wind-dispersed gametophytic fragments in blizzards or summer storm conditions facilitate bryophyte fragment dispersal. Previous laboratory *in vitro* culture experiments have shown that fragment samples are viable and produce protonemal growth, new shoots and rhizoids (Miller and Ambrose 1976).

Spores are diaspores most capable of long distance dispersal (LDD), where as larger and heavier asexual propagules are short distance dispersal agents for population maintenance (Kimmerer and Young 1995). Belowground diaspore banks, consisting of spores, vegetative fragments, rhizoids and asexual propagules, are a long-term, potential source of dormant, but viable, bryophyte tissue (During 2001). The arrays of diaspores produced by bryophytes (Laaka-Lindberg and Heino 2001) have a range of dispersal and germination potential (Kimmerer 1996) and assorted ecological and evolutionary roles (Newton and Mishler 1994). Under suboptimal conditions (drought and cold), sporophytes are often lacking, requiring population maintenance to be dependent on fragmentation and asexual diaspore production. The diaspore bank allows bryophytes to avoid unsuitable conditions allowing for accumulation of genetic material and temporal dispersal (Thompson

and Grime 1979, Bsiang 1996, Laaka-Lindberg et al. 2003, Hock et al. 2008, Caners et al. 2009).

The Little Ice Age (150-580 years BP) represents the most recent climatic cooling (Gribbin and Lamb 1978, Grove 1988, Miller et al. 2010). With its onset, glaciers and permanent snow banks expanded in polar regions and buried High Arctic bryophyte communities. However, since the end of the LIA, warming and melting of most glaciers of the Canadian High Arctic have exposed the subglacial terrain (Overpeck et al. 1997, Wolken et al. 2005, 2008, Miller et al. 2010). On Ellesmere Island, Nunavut, a number of studies have reported preserved LIA plant communities near melting glaciers (Smith 1961, Falconer 1966 (Baffin Island), Blake 1981, Bergsma et al. 1984, Jones and Henry 2003, Breen and Lévesque 2006, 2008). However, no studies have focused primarily on the bryophyte component or their regeneration potential.

Subglacial bryophyte assemblages released from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut provide a unique opportunity to test the viability of intact LIA bryophytes. Given their innate biology (totipotency, desiccation tolerance, cryopreservation capacity and dominance of clonal reproduction) in arctic environments, the exhumed, species-rich populations (see Chapter II) from beneath the Teardrop Glacier were investigated. Field collections indicated regrowth of exhumed bryophyte populations (*in vivo*), which stimulated trials of *in vitro* cultures. The objective of the current study was to examine the potential of intact, LIA subglacial bryophytes to regenerate *in vitro* from exhumed material given a diverse range of taxa with distinct microhabitat preferences and a range of preservation.

Materials and Methods

Description of Study Area: Sverdrup Pass, Ellesmere Island

Ellesmere Island is the largest and most northern of the Queen Elizabeth Islands in the Canadian Arctic Archipelago (Figure 3.1). The expansive icefields of central Ellesmere Island are separated by Sverdrup Pass, a narrow, deglaciated drainage divide (79°10'N, 79°45'W) (Figure 3.1). This corridor is 75-80 km long, 2-5 km wide and connects Flager Bay in the east to Irene Bay in the west. It is bound on the north side by the Agassiz Icefield and on the south side by the Prince of Wales Icefield. The central pass has an elevation of 250 m a.s.l. and rises to 1350 m at the icefields.

The tectonically created valley bottom is extensively covered by glaciofluvial outwash and other subglacial and erosional landforms (Blake 1981, England 1987). On the south side of Sverdrup Pass, faulted Paleozoic strata overlie Precambrian gneiss and granite. In contrast, the north side is formed by Cambrian and Lower Ordovician beds consisting of limestone and dolomite (Christie 1967). As a result, the localized topography, with diverse soil types, pH, and drainage, controls the distribution and diversity of plant and algal communities (Bergeron 1988, Elster et al. 1999).

The central portion of Ellesmere Island is classified within the Axel Heiberg and Ellesmere Island Highland subregion in the Northwestern Arctic Climate Zone (Maxwell 1981). This subregion is characterized by mean January and July temperatures of < -28°C and 3-5°C respectively, with annual precipitation <150 mm. Although differing by being nearly at sea level and influenced by its coastal location, the closest regional climate records are to the east in Eureka (79° 59'N, 85° 56' W, elev. 10 m). The 1971-2000 Canadian Climate Normals (National Climate Data and Information Archive 2012) indicate a July daily maximum at 8.8°C with an average of 12.5 mm of precipitation. However, 2007 and 2009 field season data from Sverdrup Pass recorded morning temperatures averaged 12°C and 6°C reaching a maximum of 18°C and 15 °C, respectively.

Sverdrup Pass is classified as a polar oasis (Bergeron 1988, Freedman et al. 1982, Lévesque and Svoboda 1999). The local topography provides protection from the harsh upland climate resulting in greater accumulation of snow, warmer climate, and a longer growing season. Therefore, the valley supports a flora with high species diversity and productivity when compared to the depauperate flora of polar deserts found on most of the uplands in the Queen Elizabeth Islands (Bliss et al. 1973, Bliss and Svoboda 1984, Lévesque and Svoboda 1999). Even for this High Arctic environment, Sverdrup Pass has high species diversity with 136 terrestrial algal and cyanobacteria taxa (Elster et al. 1999), 115 lichens (Maycock and Fahselt 1992), and 75 vascular species (Bergeron 1988). Ecological studies from the Teardrop Glacier foreland have previously focused on diversity and abundance of soil algae (Elster et al. 1999), influence of biological soil crusts (Breen and Lévesque 2006, 2008) and primary plant succession (Jones and Henry 2003), largely overlooking the bryophyte component.

Study Site: Teardrop Glacier, Sverdrup Pass

The study site was located on the foreland of the Teardrop Glacier (Figure 3.1). It is a north-facing outflow glacier of the Prince of Wales Icefield. On the south side of Sverdrup Pass, the width of the Teardrop Glacier extends approximately 1.2 km from east (79° 07.929 N, 79° 44.175 W elev. 331 m a.s.l.) to west (79° 07.758 N, 79° 46.795 W elev. 335 m a.s.l.).

The foreland is a mosaic of glacial features and substrates including erratic's, gravel and sand, push moraines, several meltwater streams, and proglacial ponds. Some portions of the foreland indicate little glacial erosion or deposition where LIA vegetation communities were preserved intact. Other portions with disturbed substrates have no subglacial vegetation preserved. The foreland substrates include sands, gravels, and coarse glaciofluvial sediment (boulders and rocks) and organic substrates of relict plant material.

The recently exhumed subglacial bryophytes examined from along the Teardrop Glacier margin and within the first 10 m of the foreland have exceptional preservation. Median radiocarbon dates from three subglacial samples ranged from 404.5 to 614.5 calibrated years BP (La Farge et al. 2013). These bryophyte assemblages, as well as extant bryophyte richness within the study area, have been enumerated. The contemporary bryophyte species richness of the granitic (south) side of Sverdrup Pass determined to date is 110 moss and 5 hepatic species. The subglacial, LIA assemblages contained 73 (66 mosses and 8 hepatics) taxa with 59 mosses identified to species. They represent 60% of the extant flora of the south side of Sverdrup Pass. This LIA representation is substantial given the diversity of microhabitat availability of the contemporary assemblages (xeric bedrock to aquatic) highlighted by differences in species composition (Chapter II).

Glacier Retreat

The most recent glacial advance is demarcated by the granite-gneiss boulders strewn foreland. The end of the foreland marks the maximum LIA advance that measured approximately 190 m from the glacier terminus in 2004 (Breen and Lévesque 2006) and additional field measurements in 2007 and 2009 totaled a distance of 208 m (pers. comm. C. La Farge 2012; Figure 3.A1)

Specimen Collection

In July of 2007 and 2009, Dr. C. La Farge collected 140 LIA subglacial specimens along the glacial margin (GLM) of the Teardrop Glacier and in the first 10 m of the foreland to ensure unequivocal determination of LIA versus colonizing extant species. The majority of the samples were collected along the central and eastern portions because large push moraines and proglacial ponds inhibited access to sites along of the western edge of the glacier. For each sample, date, elevation, and distance from the current GLM were recorded. The sample size ranged from 5 cm by 7 cm to 10 cm by 15 cm. At the time of collection, wet or frozen samples

were placed in polyethylene Nasco Whirl-pak bags (Fisher scientific) and stored in a cooler, out of exposure, until the end of the field season. Additional dry specimens were collected in standard 2lb Standard Kraft paper bags. The samples were frozen at Polar Continental Shelf Program (PCSP), Resolute Bay, Nunavut, and maintained frozen in transport until storage at the Department of Biological Sciences, University of Alberta, Edmonton until subsequent analysis.

Germination / Propagation Experiment

Twenty-four subglacial specimens were selected for culture trials; 20 of these were frozen and four were from dried material (Table 3.1). These specimens were chosen based on taxon, distance from the glacier, and preservation. Additional extant specimens were subsampled and cultured to test for species substrate and moisture preferences, as well as to test the success of germinating diaspores or fragmented gametophytic material. Each specimen (if frozen) was partially thawed and a portion of the original was subsampled. Given the nature of frozen samples, complete dissection of the original sample was not done. A subsample was removed and the remainder has been archived in a frozen state. Thawing the entire specimen could have compromised the ability to regenerate as freeze/thaw procedures can cause extensive cellular damage (Duckett et al. 2004). The subsamples included: 1) preferentially selected stems of *Aulacomnium turgidum, Distichium capillaceum, Bryoerythrophyllum recurvirostrum, Bartramia ithyphylla* and *Niphotrichum panschii* representing a range of habitat preferences; 2) biodiversity samples containing an intermixed assemblage of up to 13 species; and 3) specialized asexual propagules from leaf axils of *Encalypta procera* (Table 3.1). When the samples were collected, the substrate (mud, sand, soil) is often removed with the plant. Depending on the availability, this excess substrate was also subsampled and sown with the gametophytic tissue (Table 3.1). LIA specimens with evident extant weedy, colonizing species growing on its surface were not used. A sterilized coffee grinder and/or mortar and pestle were used to grind the sample into small fragments and

powder (Shaw 1986). The coffee grinder was surface sterilized with household 6% $NaOCL_3$ bleach and rinsed with sterilized distilled water between samples and the mortar and pestle was autoclaved. Preliminary experiments found that fine grinding techniques obtain better regeneration results than intact plants for numerous taxa.

Two culture protocols were used for the fragmented gametophytic material distribution: 1) a combination of soil or soil/sand substrates in petri dishes (60 dishes) and 2) nutrient media in sealed jars (13 samples). Trial runs indicated that regeneration of gametophytic material was maximized in petri dishes in contrast to sealed jars with growth media. In general, *in vitro* morphology and reproduction mimics natural conditions better on soil than artificial sterile nutrient medium (Shaw 1986, Duckett et al. 2004). Given that the growing conditions of the jars were sterile (autoclaved jars, media and sealed lids), parallel cultures to the subsamples sown on soil were run to test for sample contamination. Culture initiation dates are recorded for each sample (Table 3.1). The experiment was carried out from July 2011 to July 2012.

1. *Petri Dishes*

Sixty sterile polystyrene petri dishes (100 mm x 15 mm and 60 mm x 15 mm) were approximately 50% filled (7 mm depth) with sterile CIL Gro weed-free, premium-potting soil containing a blend of peat moss, humus, compost, and perlite. Fourteen petri dishes were half filled with ½ potting soil, ½ sand, and used for taxa based on their substrate preference (Table 3.1). Enough subglacial gametophytic material was sampled to thinly cover (2 – 5 mm) the surface of the soil in the petri dish.

Encalypta procera was identified in two dried subglacial specimens (*CLF 13005, 13145)* with axillary brood bodies still preserved in the leaf axils. The propagule-bearing stems were lightly ground by mortar and pestle (to remove the propagules from the leaf axils) and preferentially sown onto a sandy substrate in five petri dishes.

To maximize regeneration potential and nutrient availability, the initial dishes contained un-autoclaved potting soil. Autoclaving of organic matter can be problematic and often results in the production of toxic breakdown products (especially in peaty soils) (Duckett et al. 2004). However, in order to decrease potential occurrences of algae, fungi, bacteria, or 'weedy' bryophytes, subsequent trails also included the use of sterilized substrates (Table 3.1). Substrates (potting soil, sand) were autoclaved for 30 minutes at 78°C and the nutrient media were autoclaved for 20 minutes at 121°C to ensure sterile culture conditions. Distilled milliQ water used for misting the samples was also sterilized.

2. *Jars*

Duplicates from nine subglacial samples (*SBG 2, 3b, 4, 21, 25, 27, 37, 44, 50*) were sown on White's sterile nutrient medium and sealed in a jar (Table 3.1). Growth media was prepared as follows: 0.45 g of White's Basal Salt mixture (Sigma, St. Louis, MO) was dissolved in 500 mL of double distilled milliQ water and solidified with 7.5 g of Phytagel (Sigma, St. Louis, MO). The media was autoclaved for 20 minutes at 121°C and approximately 40 mL poured into sterile 100 mL jars with a vented Magenta B-cap closures (Sigma, St. Louis, MO) lid and sealed with parafilm M (Bemis Flexible Packaging, Menasha, WI).

3. *Controls*

Controls were initiated at three separate times with four different substrates. In July and August of 2011, three petri dishes with un-autoclaved potting soil and one sealed jar with White's nutrient medium were placed in the growth chamber. In January 2011 an additional four petri dishes with un-autoclaved potting soil, three dishes with autoclaved soil and six dishes with autoclaved ½ potting soil and ½ sand were also placed in the growth chamber as controls. Examination of controls was observed every 2-3 weeks.

4. Growth Chamber Conditions

Cultures were grown under controlled optimal growing conditions for taxa from cooler climates (Duckett et al. 2004) with a mean light intensity of 74 ± 9.3 μmol s^{-1} m^{-2}, simulating 16 hours of daylight and 8 hours of darkness with 215 W cool white fluorescent bulbs and temperatures maintained at 15°C. All samples were placed in shallow trays and repositioned every 30 days to reduce effects of light intensity variations within the chamber. Samples were misted manually with a spray bottle every 2-3 days during of 12 months in the growth chamber.

Examination of emerging bryophyte taxa or its associated protonema was conducted approximately every 2-3 weeks or less and after the 12 month growing period. Cultures were transferred to larger, glass sterile petri dish when the dishes became full.

Species Identification

The level of taxonomic determination of each cultured species was dependent on maturity of the gametophore/gametophyte and, if available, the presence of male and/or female gametangia. Juvenile leaves often did not yet exhibit diagnostic characters such as papillae, thickened cross-walls, and hair points. As well, the development of sporophytic material in culture was rare and most often remained as 'spears' and did not reach maturity. For example, to accurately determine species of *Ptychostomum*, capsules with mature peristome teeth are required. The development of any specialized asexual propagules was also noted.

A common taxon in culture was *Distichium*, which has three species that occur on northern Ellesmere: *D. capillaceum, D. inclinatum,* and *D. hagenii* (Brassard 1971a). Distinctive distichous leaves arranged in two rows along the stem characterize them (Nyholm 1954 – 1969, Vitt 1975). *Distichium capillaceum* has widely spreading leaves; whereas the less common species, *D. inclinatum* and *D. hagenii,* have more closely set leaves and are differentiated from each other by sporophytic characters. Cultures of *Distichium* with spreading leaves were identified

as *D. capillaceum*, whereas juvenile or young stems were difficult to identify to species. The autecology of all three species is similar. *Distichium capillaceum* is widespread with broad habitat specificity on northern Ellesmere and is the most common *Distichium* species of the three (Brassard 1971a) and *Distichium* spp. will be discussed herein as *D. capillaceum*.

Floristic treatments used for the taxonomic determination on the following groups included: Mniaceae (Koponen 1974), Encalyptaceae (Horton 1981), Bryaceae (Spence 2007), Grimmiaceae (Hastings and Ochyra 2007), Marchantiophyta (Schofield 2002), as well as Nyholm (1954 - 1969), Schuster (1969), Vitt (1975) and Blom (1995). Nomenclature for Bryophyta is based on the Checklist of Mosses (Crosby et al. 1999) except for the following: Bryaceae (Spence 2007) and Grimmiaceae (Hastings and Ochyra 2007), and for Marchantiophyta (Stotler and Crandall-Stotler 1977). For each representative taxon, photographs were taken and permanent vouchers were frozen and deposited in the University of Alberta Cryptogamic Herbarium (ALTA).

Results

Subglacial richness

Moss protonema, rhizoids, and gametophores/gametophytes were observed in 58% (34) of the dishes and 54% (7) of the jars. Twenty taxa were recorded representing nine different families. Seventy-one percent (17) subglacial specimens produced bryophytes. Dishes with no bryophyte germination (*SBG 3b, 6, 21, 38, 40, 50* and *CLF 13005*) contained abundant black and green algae and fungal hyphae only. The culture results can be categorized as three distinct regeneration patterns based on the presence/absence of parent material in the original SBG specimen: 1) taxa that regenerated from parent material: *Aulacomnium turgidum, Encalypta procera, Syntrichia ruralis* and *Ptychostomum* sp. (B); 2) taxa cultured from sample without identification in original sample in addition to regenerating from parent material: *Distichium capillaceum*, *Pohlia cruda, Leptobryum pyriforme* and *Psilopilum cavifolium*; 3)

taxa cultured that were not determined in the original specimen: *Encalypta rhaptocarpa, Funaria arctica, Hennediella hemeii* var. *arctica, Tortula hoppeana, Tortula leucostoma, Pogonatum urnigerum, Pohlia* cf. *filum, Ptychostomum* spp. (A,C) (Figure 3.A4), *Rosulabryum* cf. *capillare, Tetraplodon* sp. and *Pohlia annotina.*

No liverworts germinated *in vitro*. This may be due to unsuitable growing conditions, lack of material given the small nature of most liverworts (often a minor component and present as single strands) or absence of viable cells for regeneration.

1. Petri Dishes

Aulacomnium turgidum was cultured from three subglacial specimens, all of which contained original gametophyte material of *A. turgidum* (*SBG 2, 27* and 44). It was observed growing in 7 dishes all on potting soil (*SBG 2* – 4 replicates; *SBG 27* – 1; *SBG 44* – 2) (Figure 3.2; Figure 3.A2). The three subglacial specimens that successfully germinated *A. turgidum* contained nearly pure, robust tufts of mature blackened stems (Figure 3.3). Four petri dishes were sown with subglacial material from the dried 2007 *SBG 2a* & *2b*. None of the species determined in the original sample germinated. Instead, *Leptobryum pyriforme* as well as black and green algae developed.

Encalypta procera gametophores were produced in one dish on sandy substrate from one dried specimen (*CLF 13145*) where the axillary gemmae were preferentially sown (Figure 3.4d). These stems produced normal axillary gemmae, as well as copious amount of filamentous gemmae that spread to cover the substrate (Figure 3.5).

Syntrichia ruralis was cultured in two dishes (out of four replicates) on the sandy substrate from the parent material in the original sample (*SBG 37*). An additional subglacial specimen (*SBG 23*) containing parent material of *S. ruralis* failed to germinate in culture.

Distichium capillaceum was observed growing in one petri dish from regenerated parent material present from *SBG 8* where it was preferentially sown.

Distichium capillaceum was also observed in eight other petri dishes from four subglacial samples (*SBG 2, 27, 29* and *37*), all collected within 5 m (< 2 years exposure) from the GLM (Table 3.1). It germinated on both potting soil and soil/sand mixture. *SBG 8* (0 cm from the GLM) contained 8 species and four replicates (*D27, D28, D29, D30*) and produced diverse results; two of which only had green algae, one had *Tortula leucostoma* and one had *Distichium capillaceum* (Table 3.1).

Pohlia cruda was observed in three dishes from two LIA subglacial samples (*SBG 2* and *36*) that contained *P. cruda*. It grew in dishes with both the potting soil as well as the potting soil/sand mixture. It was also observed in 12 dishes in which it was not recorded in the original SBG sample. There were three distinct *Ptychostomum* spp. (Figure 3.A4) cultured, but identification to species without sporophytes was not possible. *Ptychostomum* sp. B was observed in three dishes from two subglacial samples (*SBG 2* and *25*). These two subglacial samples contained 10-25% of a single *Ptychostomum* sp. whose mature gametophyte matches those cultured.

Psilopilum cavifolium was observed in three dishes on sandy substrate from one subglacial sample (*SBG 37*) containing *P. cavifolium*. It also occurred in three other dishes where it was not recorded in the original sample.

Leptobryum pyriforme occurred in ten dishes from five different subglacial specimens (*SBG 9, 23, 37, 2a, 2b*). No *L. pyriforme* occurred any of the original subglacial specimens except *SBG 9*, which was sown onto 2 dishes (both which produced *L. pyriforme*).

Nine species were cultured *in vitro* that were not recorded from the original subglacial specimen. All of these taxa were recorded in other LIA samples or from extant collections from Sverdrup Pass, except *Hennediella hemeii* var. *arctica*, which was recorded only from the contemporary samples (not LIA). An additional species, *Pogonatum urnigerum*, was not recorded from the study area (Chapter II).

The growth experiment results indicate that even under consistent conditions (15°C and 16 hours of daylight), initial gametophore development

ranged from 6 to 10 weeks. It is important to note that, after one year, some dishes were filled with moss (consisting of pure or intermixed populations) while others remained sparse demonstrating the heterogeneity of culture results.

In vitro cultures rarely produce gametangia (Duckett et al. 2004). However, five i*n vitro* cultures (*D4, D6, D7, D20, D42*) developed gametangia resulting in sporophyte (immature) development. These taxa included *Pohlia cruda, Leptobryum pyriforme,* and *Ptychostomum* spp.

Terrestrial algal colonies (green and black) developed in all dishes where moss germination was evident. Algae appeared in an additional 21 dishes, indicating that 90% of the dishes contained some form of algae. Fungal hyphae were the only biota to grow in all dishes.

2. Jars

Mature gametophytes of five species were observed in the sealed jars growing on nutrient media. *Aulacomnium turgidum* occurred in one jar from *SBG 2* (which contained abundant LIA *A. turgidum* and also showed regeneration in three petri dishes). *Distichium capillaceum* occurred in one jar sown from *SBG 2*; however, it was not recorded from this subglacial specimen. Noteworthy, *SBG 2* was subsampled (7 times) and sown onto five dishes and two jars. Four of these subsamples (3 dishes, 1 jar) germinated *D. capillaceum*. *Pohlia cruda* and *P. annotina* occurred in two separate jars, both from *SBG 25*. *Ptychostomum* sp. (A) occurred in one jar from *SBG 2*. In addition to mature gametophytes, moss protonema/rhizoids and protonemal gemmae was observed in three jars after four months. Algae appeared in one jar whereas fungal hyphae occurred in most jars.

3. Controls

The un-autoclaved controls and experimental dishes showed high occurrecnes of *Leptobryum pyriforme* (25% and 19% respectively) (Table 3.1). The presence of *L. pyriforme* in the cultures must be interpreted with caution. This species commonly colonizes disturbed, exposed sandy or clayey soils in the study

area (Chapter II) and occurs in the LIA assemblages. It is also a common greenhouse contaminant and produces rhizoidal tubers that are difficult to detect. In addition, algae, fungal hyphae, and bacteria were observed in nearly all the control dishes.

4. Extant Cultures

Five extant specimens were cultured to determine species preferences for substrate and moisture and to test the success rate of germinating spores. A single culture of extant populations of *Ptychostomum cyclophyllum* gemmae produced gametophytes in one dish on potting soil. Ground gametophytic material of *Niphotrichum panschii* regenerated in four dishes (out of four) with ½ potting soil and ½ sand.

Extant *Psilopilum cavifolium* and *Funaria arctica* spores successfully germinated in one jar and one dish, respectively. *Pohlia cruda* spores did not produce any gametophores, rhizoids, or protonema in any of the three jars used for cultures.

Discussion

This novel study demonstrates that LIA bryophytes entombed under polythermal glaciers can be regenerated *in vitro*. The potential sources of viable tissue are the primary arguments in support of LIA moss dormancy and subsequent regeneration. Although the *in vitro* cultures were small subsamples of the original specimen, a large number of species germinated representing a broad range of life-history strategies and microhabitat preferences. The significance of these findings has critical implications for the evolution of arctic environments. The possible dormancy of bryophytes preserved in subglacial ecosystems and their regeneration potential has not been previously considered. Noteworthy is Bergsma et al. (1984) who reported on the chlorophyll content of subglacial vegetation exposed by a retreating glacier at Alexander Fjord, Ellesmere Island. *Niphotrichum (Racomitrium) lanuginosum* had the best chlorophyll preservation after 500 years BP, measuring

55% of its present day values (Bergsma et al. 1984). Not limited to bryophytes, the regeneration of vascular plants has received recent attention. For example, Late Pleistocene (35,000 years BP) seed tissue (sporophytic) of *Silene stenophylla* Ledeb. was regenerated via fruit recovered from a Siberian squirrel burrow. This required using *in vitro* tissue culture and clonal micropropagtion techniques (Yashina et al. 2012). In contrast, the regeneration of subglacial bryophytes was accomplished by simple fragmentation (grinding) of gametophytic material sown onto potting soil/sand or growth media.

Once released from the ice, these relict assemblages may become fragmented, undergo clonal reproduction and re-establish themselves in post-glaciation landscapes. In the arctic, these wind-dispersed gametophytic fragments facilitate short-distance dispersal (Miller and Ambrose 1976) and are agents for population maintenance (Kimmerer and Young 1995).

Provenance

Preservation, glacial retreat and exposure

On a regional scale, growing season is determined by climate and elevation, and in Sverdrup Pass is estimated to be a minimum 2-month period from approximately June to August. However, localized snow melt varies depending on small-scale variations in exposure, spring precipitation, ice formation, as well as the amount and compactness of the snow deposited in the winter (Cooper et al. 2011). The snow cover is well developed in winter and low summer temperatures and short growing season are the most important factors determining polar cryptogamic vegetation (Longton 1988). Given established glacial retreat rates for the 2007-2009 interval, any 2009 specimen collected within 460 cm from the GLM represents less than one year of exposure or growing season potential. The maximum distance from the GLM that LIA samples were collected was 900 cm and this distance is within a 3-year growing season exposure. Given an estimated 16-24 week growing season in a 2-year interval, newly established populations would be predictably

restricted in size and diversity, especially long-lived, mature populations of perennials. Therefore, a specimen collected close to the glacier margin indicates a shorter time exposed, and becomes increasingly doubtful that extant spores, asexual propagules, or wind-blown fragments have landed on the recently exposed subglacial material.

Two specimens (*SBG 7, 8*) collected at the ice margin (0 cm) and were chipped out from the ice, successfully produced growth. Cultures from these samples produced three bryophyte species, (*Tortula hoppeana, Distichium capillaceum* and *Tortula leucostoma*). Given the proximity to the ice margin, these taxa are not the result of wind-blown contemporary diaspores (spores, asexual propagules or fragments). *SBG 8*, containing approximately 25 % *D. capillaceum,* produced *D. capillaceum* in one of the four cultured subsamples. This species was separated and preferentially seeded as a single species. Found with abundant black algae, it was the only bryophyte species discovered growing in that dish (Figure 3.4a; Table 3.1). The diversity of results from *SBG 8* indicates the variability of results one can get from cultures (2 dishes – green algae only, 1 – *Tortula leucostoma,* 1 – *Distichium capillaceum*).

Sampling

Often bryophyte assemblages include scattered species (such as *Ptychostomum* spp., *Pohlia* spp. and *Distichium* spp.) that have a higher probability of being overlooked. Given that subsamples were used for culturing, not all species recorded for that SBG specimen were necessarily cultured. The subsamples did not produce consistent results, indicating a constraint factor of the study (Table 3.1.). Due to the methodology, differences in the subsamples occurred and resulted in varying species composition, differences in the viability of bryophyte tissue, and differences in the preserved diaspores. For example, *Distichium capillaceum* regenerated in one dish where it was preferentially seeded from the original frozen sample (*SBG 8*; Figure 3.4a). However, it was found in six other petri dishes and one jar from four different subglacial samples, none of which recorded the presence of *D. capillaceum*.

Distichium capillaceum was most commonly scattered stems in the SBG samples and rarely as pure populations. This increased the likelihood that its identification was missed in the original specimen or the subsample.

Tissue Resilience and Viability

The viability and regeneration of gametophyte material is related to desiccation tolerance (DT), dormancy capacity, and the resilience of totipotent cells in bryophytes. *Syntrichia ruralis* is found in mesic to xeric microhabitats in Sverdrup Pass (Chapter II), and regenerated in two replicate dishes from *SBG 37*. Most species of the Pottiaceae, including *S. ruralis,* are xerophytes and colonizers of dry and exposed substrates (Zander 1993). Consequently, *S. ruralis* has been used as a model organism for studying DT in bryophytes for physiological, cytological, and ecological studies (Bewley 1973, Schonbeck and Bewley 1981, Oliver 1991, Oliver et al. 2000, 2004, Pressel and Duckett 2010). The majority of bryophytes exhibit DT, which has involved the evolution of cellular protection and recovery mechanisms upon rehydration with the employment of LEA (Late Embryogenesis Abundant) proteins (Oliver et al. 2005, Proctor et al. 2007). Survival of poikilohydric plants is well understood as a repair-based mechanism with a change in translational control (Oliver 1991) where slower dehydration results in increased recovery upon rehydration (Schonbeck and Bewley 1981). Interestingly, Bewley (1973) found that *Syntrichia (Tortula) ruralis* recovered to normal functioning after slow cooling to -196°C in liquid nitrogen. His results co-oberate the regeneration of *S. ruralis* in this study indicating that extreme freezing does not adversely affect *S. ruralis*. Additionally, recent *in vivo* and *in vitro* cryopreservation protocols were tested using various moss taxa with different moisture and light regimes (Segreto et al. 2010). The results suggest that untreated, cryopreserved gametophytic material (-80°C for 24 hours) of naturally, cold-adapted populations readily regenerated suggesting a positive correlation with desiccation/frost tolerance and cryopreservation (Segreto et al. 2010). With bryophyte gametophytes highly

regenerative nature, natural stress tolerant species are likely to have a high regeneration capacity.

Other DT species, belonging to the Encalyptaceae (*Encalypta rhaptocarpa, E. procera*) and Pottiaceae (*Tortula hoppeana, T. leucostoma, Hennediella hemeii* var. *arctica*) cultured exhibiting preservation of viable cells.

Spores: Production and Life Strategies

Dependent on the taxa, sporophyte production can vary from rare (perennials) to frequent (colonists). In the arctic, *Aulacomnium turgidum* is seldom found with sporophytes (Brassard 1971b) and only two specimens (out of 33; *CLF 12999 & 13790*) were found fruiting in the extant collections from Sverdrup Pass. *Aulacomnium turgidum* is perennial and dioicous (separate male and female plants), which reduces fertilization potential. As a result, dispersal of this taxon is more dependent on asexual reproduction by fragmentation. *Syntrichia ruralis,* although widespread and common either as pure or intermixed populations, is not known to produce sporophytes in Sverdrup Pass (Chapter II) nor at high latitudes (Brassard 1971a, Vitt 1975). Also lacking specialized asexual propagules, these taxa must rely solely on clonal reproduction through fragmentation.

Several colonizing/fugitive taxa, often producing prolific sporophytes, were cultured including *Funaria arctica, Psilopilum cavifolium, Leptobryum pyriforme* and *Ptychostomum* spp. Shuttle (annual or short-lived) species typically have short life spans and a high reproductive effort (During 1979, 1992). *Psilopilum cavifolium* is a weedy colonist (annual-shuttle) species that produces abundant sporophytes. It occurs in the study area on gravel-sand substrates and was a common colonizer in the first successional stage (10 m) of the foreland (Jones and Henry 2003) on the exhumed LIA bryophytes. Extant populations are easily discernable by green gametophyte and sporophyte production. Along with other weedy species (*Ptychostomum* spp., *Leptobryum pyriforme* and *Funaria arctica),* a conservative interpretation of the regeneration of LIA material is taken with these taxa. Their

origin may be due to LIA gametophyte regeneration, diaspore bank development, or germination of extant spores.

Unspecialized asexual propagation

Given rarity of sporophyte production, High Arctic bryophytes must rely on asexual reproduction where vegetative fragments play an essential role in dispersal ecology (Pfeiffer 2007). The totipotent capacity (Menon and Lal 1981) of wind-dispersed gametophyte fragments, such as stems, leaves, and rhizoids, allows for survival and dominance in High Arctic communities. Rhizoids have been found to be highly DT and endure extreme environmental conditions (Rowntree et al. 2007). *Aulacomnium turgidum* has stem tomentum (a dense, wooly covering of rhizoids), whose growth is regulated by hormones such as auxin, cytokinins, and other growth substances (Menon and Lal 1981) for ectohydric, capillary water uptake (Kürshcner and Parolly 2005). The abundance of desiccation tolerant rhizoids and stem tomentum likely increase the amount of viable gametophyte material for regeneration.

Given that *Pogonatum* cf. *urnigerum* and *Hennediella heimii* var. *arctica* were not determined in the original LIA samples, the most plausible explanation is that they germinated from the diaspore bank (During 1979, 1992). The diaspore bank frozen beneath the overriding glacier contained preserved gametophytic tissue (leaves, rhizoids, stems) or spores that were deposited in the substrate prior to glacier advance and remained viable in the diaspore bank during the LIA. It is possible that *P. urnigerum* was present in the subglacial material and was missed completely or misidentified as *P. alpinum* as intermixed stems can be easily misidentified (Merrill 2007). Both families (Polytrichaceae and Pottiaceae) have rhizoidal ropes or wicks (Duckett et al. 2004, Frey and Kürschner 2011). These are comprised of a central broad rhizoid filament and narrower branch filaments that coil around the central rhizoid (Wigglesworth 1947). These can develop abundant erect clonal shoots (daughter ramets) from subterranean strands providing rapid colonization (Longton and Schuster 1983). Rhizoidal ropes, similar to simple

rhizoids, can function as asexual diaspores due to their ability to survive underground conditions. Unspecialized fragmentation of vegetative gametophyte fragments plays a prominent role in the regeneration success of these species.

Specialized Asexual Propagation

Ecologically, specialized diaspores (functioning as spores) play a pivotal role in dispersal, colonization and community development, and maintenance. *Pohlia filum* and *P. annotina* both are known to produce axillary gemmae and both were cultured from SBG specimens with no parent material present. In the Bryales, species within these two genera (*Ptychostomum* and *Pohlia)* are taxonomically difficult to distinguish. They are globally distributed, well adapted to disturbed sites and tend to be weedy taxa. Given the role of diaspore banks in bryophyte ecosystems, the plausible explanation is that the taxa were regenerated from gemmae or non-specialized gametophytic tissue in the substrate. Both taxa are found in the Sverdrup Pass extant flora and exhibit an array of asexual propagules (Longton and Schuster 1983). Generally, gemmae are defined as propagules, originating from chloronemata (the first stage of protonemata development), with a clear lysigenic differentiation mechanism along abscission (tmema) cells (Duckett and Pressel 2003). Mature gametophores of *P. annotina* produced abundant axillary gemmae in culture (Figure 3.4c). This development of gemmae *in vitro* also demonstrates the rapid life cycle of disturbed habitat taxa and their ability to regenerate and develop propagules for rapid colonization.

Given unfavourable arctic conditions, specialized asexual diaspores are critical in providing survival strategies for a species re-establishment. For mosses, 50% of asexual propagules fall within 1 cm from the parent colony (Kimmerer 1991). Through somatic mutations, these clonal reproductive modes can accumulate genetic variation, which may help maintain the genetic diversity of aboveground populations (Hock et al. 2008). Given that >60% of the northern Ellesmere moss flora is dioicous with 28% regular sporophyte production (Brassard 1971a), asexual reproduction is required for local maintenance. This is compared

to 31% sporophyte production for Pearyland, Greenland (Holmen 1960), 30-40% for the British Isles, and 80-90% for New Zealand (Longton 1988).

Leptobryum pyriforme is a weedy and widespread taxon with a colonist life strategy (prolific sporophyte production) that was found in ten cultures of LIA material. This species, along with several species of *Ptychostomum*, produce rhizoidal tubers (Spence 2007, Imura et al. 1992). Rhizoidal tubers are thick-walled, spherical, and comprised of 10 - 100 cells that develop on rhizoids underground. Most importantly, they are long-lived and able to survive drought and cold conditions and remain viable for a long time (Frey and Kürschner 2011). Although not detected in the substrate of the subglacial subsamples, rhizoidal tubers and spores may account for the development of *L. pyriforme* and *Ptychostomum* spp. in the cultures. The alternative hypothesis for their presence is the development, dispersal, and germination of spores from extant populations. Thus, for weedy colonist species (*Leptobryum pyriforme, Psilopilum cavifolium, Pohlia* spp., *Ptychostomum* spp.), their development in culture is interpreted with caution.

Protonemal Gemmae

Encalypta procera axillary gemmae were selectively seeded along with a few fragmented leaves. These DT asexual propagules were able to regenerate *in vitro* and developed new gametophores. The cultures of LIA *E. procera* gemmae produced both gametophores with axillary gemmae and protonemal gemmae that noticeably spread over the sandy substrate in the petri dish within four months (Figure 3.5). Protonemal gemmae have not been recorded for this species before and increased its regeneration potential. *Ptychostomum* spp. also exhibited protonemal gemmae development in culture.

Protonemal gemmae were first described and illustrated by Correns (1899), but received little or no attention until Whitehouse (1987) followed by Pressel et al. (2007), who began to systematically document and assess them. Protonemata can develop initially from a germinating diaspore and often forms an extensive filamentous network, whereas secondary protonemata can also develop from de-

differentiated cells from almost any living tissue of a moss (Figure 3.A3) (Menon and Lal 1981). Given the ephemeral and vulnerable nature of protonemata, protonemal gemmae are an important life strategy, since they increase the potential for initial establishment and the longevity of the species through dispersal of diaspores. When compared to other asexual propagules, such as rhizoidal tubers, they are presumed to have a lower tolerance for desiccation and are shorter-lived (Pressel et al. 2007). Studies on the occurrence of gemmiferous protonema produced in nature have focused solely on the genus *Ptychostomum (Bryum)* (Pressel et al. 2007, 2008).

Morphological variation of protonemata in the several dishes from various species was observed (Figure 3.A3) ranging from un-branched, single filamentous strands to highly branched and clustered forms. Though further examination is required, these results suggest that protonemata morphology may present a new character set for species determination. This could be especially advantageous in bryophyte culture experiments where identification of gametophores in a juvenile stage inhibits species identification.

Diaspore Bank

Several cultured species observed were not recorded in the original subglacial sample. These included prolific sporophyte producer *Funaria arctica* (colonizing populations present with 10 m of GLM) as well as *Pogonatum urnigerum, Encalypta rhaptocarpa, Tortula hoppeana, Tortula leucostoma, Hennediella hemeii* var. *arctica, Tetraplodon* sp. and *Ptychostomum* spp. Given that the subsamples for culture were not rinsed or sterilized, the substrate was not separated from the plant material and, when available, was deliberately included and subsequently seeded with the bryophyte material. Therefore, diaspores from the substrate may be the source for these regenerated taxa. It is impossible to rule out extant spores or fragments as a potential source for these culture results, but short exposure time decreases the likelihood. However, it is possible to rule out that the source is contaminants from the potting soil or sand as no bryophyte species (besides

Leptobryum pyriforme) were observed in any of the 16 controls. Many of the subsamples used for culturing, if available, included the natural substrate, which contains the diaspore bank. Those that produce abundant spores may have germinated from spores or asexual propagules in the diaspore bank. Two species that germinated were unknown from the subglacial assemblages (*Hennediella hemeii* var. *arctica*), or the study area (*Pogonatum urnigerum*) (Chapter II). These may have been from LIA dispersed spores, propagules or gametophytic fragments transported over long distances which remained viable in the diaspore bank and these LIA diaspores had been missed in the subglacial analysis. *Pogonatum urnigerum*, however, has been recorded from the extant and LIA subglacial flora from under the Twin Glacier, Alexendra Fjord, Ellesmere Island (Jones 1997) and likely occurs in Sverdrup Pass.

Substrate/Microhabitat Preferences and Culture Conditions

Bryophyte distribution is controlled by various substrate properties (texture, chemistry, nutrients; Slack 1990) and the results show that germination success is dependent on the substrate type used. Germination of Pottiales, Polytrichales and Encalyptales were restricted to sandy substrates (Table 3.1). In contrast, members of the Bryales showed a wide substrate tolerance and germinated on nutrient media, pure potting soil, and sand/soil mixtures. *Pohlia annotina* (which produces prolific axillary gemmae) was restricted to germination on the White's media in a jar. The broad range of species that produced successful cultures was unexpected, given the closed, moist (mesic-hydric) environment of the petri dishes. They represent taxa adapted to xeric (Pottiaceae), mesic (Bryales), and hydric (*Aulacomnium turgidum*) conditions.

Aulacomnium turgidum was a key taxon demonstrating regrowth *in vitro*. It germinated on potting soil (petri dish) or on sterile White's culture media (jar) that remained sealed for the entirety of the growth experiment (Figure 3.2b). Common in wet meadow communities, this arctic-alpine species (Brassard 1971a, Chapter II) shows a preference for moist habitats. Similarities between habitat preferences of *A.*

turgidum and growth chamber conditions facilitated regeneration of LIA samples. In the growth culture experiments, the use of potting soil, high frequency of watering, cool temperatures, high light regime and closed petri dishes all contributed to optimal growing condition for *A. turgidum*, and its *in vitro* culture success. The primary questions that these results stimulate is whether LIA populations of *A. turgidum* could and do reestablish themselves in Sverdrup Pass *in vivo*. Certainly, the green lateral branches, distinctly different in size and colour from the older LIA base material indicate regeneration of apical and lateral initials (Figure 3.2a). Culture results demonstrate that LIA material can regenerate, but exhumed subglacial material must be exposed and receive required moisture conditions with substrate and light conditions a given in order to regrow. Fragmentation and dispersal of the paleomaterial by wind or vector could enable reestablishment at a different microhabitat in the foreland.

Bryophyte culture techniques often apply a sterilization (bleach, alcohol and/or chloroform) method to reduce fungal or algal growth (contamination) (Duckett et al. 2004). This was not carried out in the culture methods in order to permit the natural soil/substrate constituents to interact for establishment. Almost all (except five) of the dishes showed growth of various species of algae, fungi, and bacteria. Therefore, the presence of algae, fungi, and bacteria likely contribute to bryophyte establishment as they do in nature.

In Sverdrup Pass, a variable and high diversity of cyanobacteria (52 species) and eukaryotic algae (84 species) has been observed with the greatest diversity on the south, granitic side of the valley (Elster et al. 1999). At the Teardrop Glacier, Breen and Lévesque (2006, 2008) stated that biological soil crusts facilitate plant establishment in early and mid-succession, but also have a greater overall positive effect on community structure. Biological soil crusts in the foreland are composed primarily of cyanobacteria-dominated crusts, particularly in the early stages of succession (Breen and Lévesque 2006).

In many arctic ecosystems, despite the relatively low temperatures, the soil contains a diverse micro flora and fauna including cyanobacteria, fungi, yeasts,

bacteria, and algae. A high species diversity of nitrogen-fixing cyanobacteria on the leaves and stems of mosses (Ziekle et al. 2002, 2005) or symbiotic colonies in liverworts (Meeks 1998) play an important role in ecosystem nutrient dynamics. *In vivo* observations have provided insight into bryophyte-fungus interactions (Davey and Currah 2006, Pressel et al. 2010). Mycorrhizal fungi have not been detected to form functional, nutrient-exchanging interfaces with mosses; instead, functioning as saprobes.

Conclusion

The regeneration of subglacial LIA bryophytes demonstrates the potential of cryopreserved, vegetative material from subglacial ecosystems. The capacity of bryophytes to regenerate is greater than previously presumed. Four taxa (*Aulacomnium turgidum, Encalypta procera, Ptychostomum* sp. B, and *Syntrichia ruralis*) were conclusively cultured from parent material in the original SBG sample. These species do not produce sporophytes (*Syntrichia ruralis*) at high latitudes or production is rare (*Aulacomnium turgidum, Encalypta procera, Pohlia cruda*). Therefore, the likelihood of extant or pre-glaciation spores lying dormant in the subglacial communities or in the diaspore bank are highly improbable.

The interpretation of cultured weedy species (*Leptobryum pyriforme, Psilopilum cavifolium* and *Funaria arctica*) is considered with caution due to prolific sporophyte production in the extant flora. This abundant reproduction increases the probability of extant spores embedded in the subglacial specimens. However, specimens chipped from the ice that regenerated (*Distichium capillaceum, Tortula leucostoma,* and *Tortula hoppeana*) are interpreted as unequivocal LIA regeneration. The remainder of species, especially those not recorded in the subglacial specimens or found in the extant flora of Sverdrup Pass (*Hennediella hemeii* var. *arctica* and *Pogonatum urnigerum*) have likely germinated from the diaspore bank. Inevitably, specialized asexual diaspores (axillary brood bodies, rhizoidal tubers, protonemal gemmae etc.) are designed to tolerate harsh conditions and desiccation and the results suggest that they have a significant role in LIA regeneration.

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Table 3.1. Cultures of subglacial specimens and regenerated taxa. Substrates: *sterilized; D = potting soil only; DS = sandy potting soil; Taxa: ** preferentially seeded. Bolded taxa are those cultured from material identified in the original subglacial specimen.

SBG Sample	Original Taxa	Dish (D) Jar (J)	Cultured Taxa	Distance from glacial margin (cm)	Culture Duration (day-month-year)
2	*Hylocomium splendens* *Sanionia uncinata* *Pohlia nutans* ***Pohlia cruda*** ***Aulacomnium turgidum***** ***Ptychostomum sp. 2***	**D 4**	***Aulacomnium turgidum*** *Ptychostomum sp. A* ***Ptychostomum sp. B*** *Distichium capillaceum* *Pohlia cf filum*	180 (< 1 year exposed)	14-Jul-11 to 25-Jul-12
		D 5	***Aulacomnium turgidum*** *Distichium capillaceum*		14-Jul-11 to 25-Jul-12
		D 20	***Aulacomnium turgidum*** *Ptychostomum sp. A*		19-Aug-11 to 25-Jul-12
		D 23	Black algae		14-Sep-11 to 25-Jul-12
		D 24	***Pohlia cruda*** *Distichium capillaceum*		14-Sep-11 to 25-Jul-12
		J 8*	*Ptychostomum sp. A* *Distichium capillaceum*		14-Jul-11 to 25-Jul-12
		J 9*	***Aulacomnium turgidum***		14-Jul-11 to 25-Jul-12
3b	*Hylocomium splendens* *Pohlia cruda* *Bryoerythrophyllum recurvirostrum*** *Timmia austriaca* *Aulacomnium turgidum* *Leptobryum pyriforme* *Lophpzia sp.* *Polytrichastrum alpinum*	**D 9**	Black algae	180 (< 1 year exposed)	19-Jul-11 to 01-May012
		J 10*	nothing		19-Jul-11 to 06-Feb-12
4	*Aulacomnium turgidum* ** *Timmia austriaca* *Tomenthypnum nitens* *Bartramia ithyphylla* *Pohlia cruda*	**D17**	*Hennediella hemii* var. *arctica*	< 100 (< 1 year exposed)	19-Aug-11 to 25-Jul-12

SBG Sample	Original Taxa	Dish (D) Jar (J)	Cultured Taxa	Distance from glacial margin (cm)	Culture Duration (day-month-year)
	Ditrichum flexicaule *Drepancoladus revolvens* *Plagiomnium sp.* *Myurella julacea* *Brachythecium turgidum* *Platydictya jungermannnoides* *Hypnum vaucheri* *Lophozia sp.*	**D18**	Black algae		19-Aug-11 to 25-Jul-12
		J 14*	Black and Green algae		19-Aug-11 to 25-Jul-12
6	*Hypnum revolutum* *Pohlia cruda* *Ptychostomum sp. 2* *Encalypta alpina* *Distichium sp.* *Isopterygium pulchellum*	**D 25**	Black and Green algae	0 (within ice)	15-Sep-11 to 01-May-12
		D 26	Black and Green algae		15-Sep-11 to 01-May-12
7	*Timmia austriaca* *Pohlia cruda* *Niphotrichum panschii* *Hypnum revolutum* *Lophozia sp.*	**D 54***	Black and Green algae	0	07-Jan-12 to 25-Jul-12
		D 55*	Black and Green algae		07-Jan-12 to 25-Jul-12
		DS 56*	*Tortula hoppeana (Desmatodon latifolius)*		07-Jan-12 to 25-Jul-12
8	***Distichium capillaceum*** ****** *Myurella julacea* *Orthothecium chryseum* *Encalypta rhaptocarpa* *Timmia austriaca* *Mnium marginatum* *Didymodon rigidulus var. icmadophila* *Ptychostomum* sp. *2*	**D 27**	Green algae	0 (chipped out from under the ice)	14-Sep-11 to 25-Jul-12
		D 28	Green algae		14-Sep-11 to 25-Jul-12
		D 29	*Tortula leucostoma (Desmatodon leucostoma)*		14-Sep-11 to 25-Jul-12
		D 30	***Distichium capillaceum***		14-Sep-11 to 25-Jul-12
9	*Hypnum revolutum* *Pohlia cruda* *Ditrichum flexicalue* *Distichium capillaceum*	**D 36**	***Leptobryum pyriforme***	100 (< 1 year exposed)	13-Oct-11 to 25-Jul-12

SBG Sample	Original Taxa	Dish (D) Jar (J)	Cultured Taxa	Distance from glacial margin (cm)	Culture Duration (day-month-year)
	Timmia austriaca *Campylium stellatum* ***Leptobryum pyriforme*** *Cephaloziella arctica* *Ptychostomum* sp. *2*	**D 37**	*Rosulabryum cf. capillare* ***Leptobryum pyriforme***		13-Oct-11 to 25-Jul-12
21	*Ditrichum flexicaule* **	**J 11***	Fungal hyphae	0	20-Jul-11 to 06-Feb-12
23	*Hypnum revolutum* *Ditrichum flexicaule* *Syntrichia ruralis* *Timmia austriaca* *Distichium* sp. *Distichium capillaceum* *Mnium marginatum* *Bryoerythrophyllum recurvirostrum* *Cephaloziella arctica*	**D 38**	*Pohlia cruda* *Leptobryum pyriforme*	0	13-Oct-11 to 01-May-12
		D 39	*Leptobryum pyriforme*		13-Oct-11 to 01-May-12
25	*Niphotrichum panshcii* ** *Polytrichastrum alpinum* *Hypnum revolutum* ***Ptychostomum* sp. *2***	**D 2**	***Ptychostomum sp. B*** *Pohlia cruda* *Leptobryum pyriforme*	900 (< 2 years exposed)	04-Jul-11 to 01-May-12
		D 3	***Ptychostomum sp. B*** *Pohlia cruda*		04-Jul-11 to 25-Jul-12
		J 4*	*Pohlia annotina*		04-Jul-11 to 06-Feb-12
		J 5*	*Pohlia cruda*		04-Jul-11 to 06-Feb-12
		J 6*	*Protonemal gemmae*		04-Jul-11 to 06-Feb-12
27	***Aulacomnium turgidum*** ** *Pohlia nutans* *Polytrichastrum alpinum* *Philinotis fontana* var. *pumila*	**D 6**	*Pohlia cruda* *Ptychostomum sp. A*	570 (< 2 years exposed)	30-Jul-11 to 25-Jul-12
		D 7	***Aulacomnium turgidum*** *Ptychostomum sp. C* *Distichium capillaceum*		30-Jul-11 to 25-Jul-12
		D 11	nothing		30-Jul-11 to 01-May-12

SBG Sample	Original Taxa	Dish (D) Jar (J)	Cultured Taxa	Distance from glacial margin (cm)	Culture Duration (day-month-year)
		J 2*	moss rhizoids		30-Jul-11 to 02-Mar-12
		J 3*	moss rhizoids		30-Jul-11 to 06-Feb-12
28	*Aulacomnium turgidum* ** *Niphotrichum panschii* *Polytrichastrum alpinum* *Ditrichum flexicaule* *Pohlia nutans* *Leptobryum pyriforme*	D 14	*Funaria arctica*	570 (< 2 years exposed)	19-Aug-11 to 25-Jul-12
		D 15	Black algae		19-Aug-11 to 25-Jul-12
		D 16	*Ptychostomum* A (w/ protonemal gemmae)		19-Aug-11 to 25-Jul-12
29	*Niphotrichum panschii***	DS 44*	*Psilopilum cavifolium* *Pohlia cruda* *Distichium capillaceum*	190 (< 1 year exposed)	29-Dec-11 to 25-Jul-12
		DS 45*	*Pohlia cruda* *Ptychostomum sp. A*		29-Dec-11 to 25-Jul-12
		DS 50*	*Pohlia cruda* *Distichium capillaceum* *Ptychostomum sp. A*		29-Dec-11 to 25-Jul-12
36	*Niphotrichum panschii*** ***Pohlia cruda***	DS 46*	***Pohlia cruda*** *Pogonatum cf. urnigerum* *Psilopilum cavifolium*	420 (< 1 year exposed)	29-Dec-11 to 25-Jul-12
		DS 47*	***Pohlia cruda*** *Psilopilum cavifolium*		29-Dec-11 to 25-Jul-12
		DS 51*	*Encalypta rhaptocarpa*		29-Dec-11 to 25-Jul-12
37	*Nipotrichum panschii* *Polytrichastrum alpinum* ***Psilopilum cavifolium*** *Hypnum revolutum*	D 40*	*Ptychostomum sp. A* ***Pohlia cruda*** *Leptobryum pyriforme*	420 (< 1 year exposed)	11-Dec-11 to 01-May-12

SBG Sample	Original Taxa	Dish (D) Jar (J)	Cultured Taxa	Distance from glacial margin (cm)	Culture Duration (day-month-year)
	Pohlia nutans ***Pohlia cruda*** *Aulacomium turgidum* *Ptychostomum rutilans (w/ axillary gemmae)* ***Syntrichia ruralis***	**D 41***	*Ptychostomum sp. A* ***Pohlia cruda*** *Leptobryum pyriforme* ***Psilopilum cavifolium***		11-Dec-11 to 01-May-12
		D 42*	*Ptychostomum A* ***Pohlia cruda*** *Leptobryum pyriforme* ***Psilopilum cavifolium*** *Distichium capillaceum* ***Syntrichia ruralis***		11-Dec-11 to 01-May-12
		D 43*	*Ptychostomum A* ***Pohlia cruda*** ***Psilopilum cavifolium*** ***Syntrichia ruralis***		11-Dec-11 to 01-May-12
		J 7*	Fungal hyphae		11-Dec-11 to 06-Feb-12
38	*Pogonatum dentatum* *Pohlia nutans* *Ptychostomum cryophilum*	**D 57***	Black and Green algae	0	07-Jan-12 to 01-May-12
		D 58*	Black and Green algae		07-Jan-12 to 01-May-12
		D 59*	Green algae and fungal hyphae		07-Jan-12 to 01-May-12
39	*Polytrichastrum alpinum* *Bartramia ithyphylla* *Pohlia nutans* *Pohlia cruda* *Ptychostomum rutilans (w/ gemmae)* *Ptychostomum sp. 1*	**DS 60***	*Rosulabryum sp. A*	0	07-Jan-12 to 01-May-12
40	*Aulacomnium turgidum* *Pogonatum dentatum* *Bartramia ithyphylla* *Ptychostomum rutilans*	**D 61***	Green algae	0	07-Jan-12 to 01-May-12
		D 62*	Green algae		07-Jan-12 to 01-May-12
		DS 63*	Green algae		07-Jan-12 to 01-May-12

SBG Sample	Original Taxa	Dish (D) Jar (J)	Cultured Taxa	Distance from glacial margin (cm)	Culture Duration (day-month-year)
44	*Psilopilum cavifolium* ***Aulacomnium turgidum*** ** *Pogonatum cf. urnigerum* *Ditrichum flexicaule* *Bartramia ithyphylla* *Polytrichastrum alpinum*	**D 10**	***Aulacomnium turgidum***	< 200 (< 1 year exposed)	05-Jul-11 to 25-Jul-12
		D 12	***Aulacomnium turgidum***		05-Jul-11 to 25-Jul-12
		D 13	Green algae		05-Jul-11 to 01-May-12
		J 1*	Fungal hyphae		05-Jul-11 to 06-Feb-12
50	*Bartramia ithyphylla* **	**D 8**	Black algae	122 (< 1 year exposed)	09-Aug-12 to 01-May-12
		J 13*	Fungal hyphae		09-Aug-12 to 01-May-12
2a	*Aulacomnium turgidum* *Hypnum revolutum* *Orthothecium chryseum* *Ptychostomum calophyllum* *Polytrichastrum alpinum*	**D 31**	Black algae	30 (< 1 year exposed)	23-Sep-11 to 01-May-12
		D 32	*Leptobryum pyriforme*		23-Sep-11 to 01-May-12
		D 33	*Leptobryum pyriforme*		23-Sep-11 to 01-May-12
2b	*Aulacomnium turgidum* *Cinclidium arcticum* *Ptychostomum calophyllum* *Orthothecium chryseum*	**D 34**	Black and Green algae	30 (< 1 year exposed)	23-Sep-11 to 01-May-12
		D 35	*Leptobryum pyriforme*		23-Sep-11 to 01-May-12
13005	***Encalypta procera*** (w/ brood bodies)**	**DS 65***	nothing	45 (< 1 year exposed)	08-Mar-12 to 25-Jul-12
		DS 66*	nothing		08-Mar-12 to 25-Jul-12
		DS 67*	nothing		08-Mar-12 to 25-Jul-12
		DS 68*	nothing		08-Mar-12 to 25-Jul-12

SBG Sample	Original Taxa	Dish (D) Jar (J)	Cultured Taxa	Distance from glacial margin (cm)	Culture Duration (day-month-year)
13145	*Encalypta procera* (w/ brood bodies)**	DS 69*	***Encalypta procera*** (w/ abundant brood bodies or protnemal gemmae)	152 (< 1 year exposed)	08-Mar-12 to 25-Jul-12
Controls	7 dishes with un-autoclaved potting soil	Controls (16 dishes and 1 jar)	*Leptobryum pyriforme* (4 dishes)	n/a	14-Jul-11, 19-Aug-11, and 07-Jan-12 to 25-Jul-12
	3 dishes with autocalved soil		Black and green algae and fungal hyphae (2 dishes)		
	6 dishes with autoclaved 1/2 potting soil and 1/2 sand		Black and green algae and fungal hyphae (2 dishes)		
	1 sealed jar with White's nutrient media		nothing		

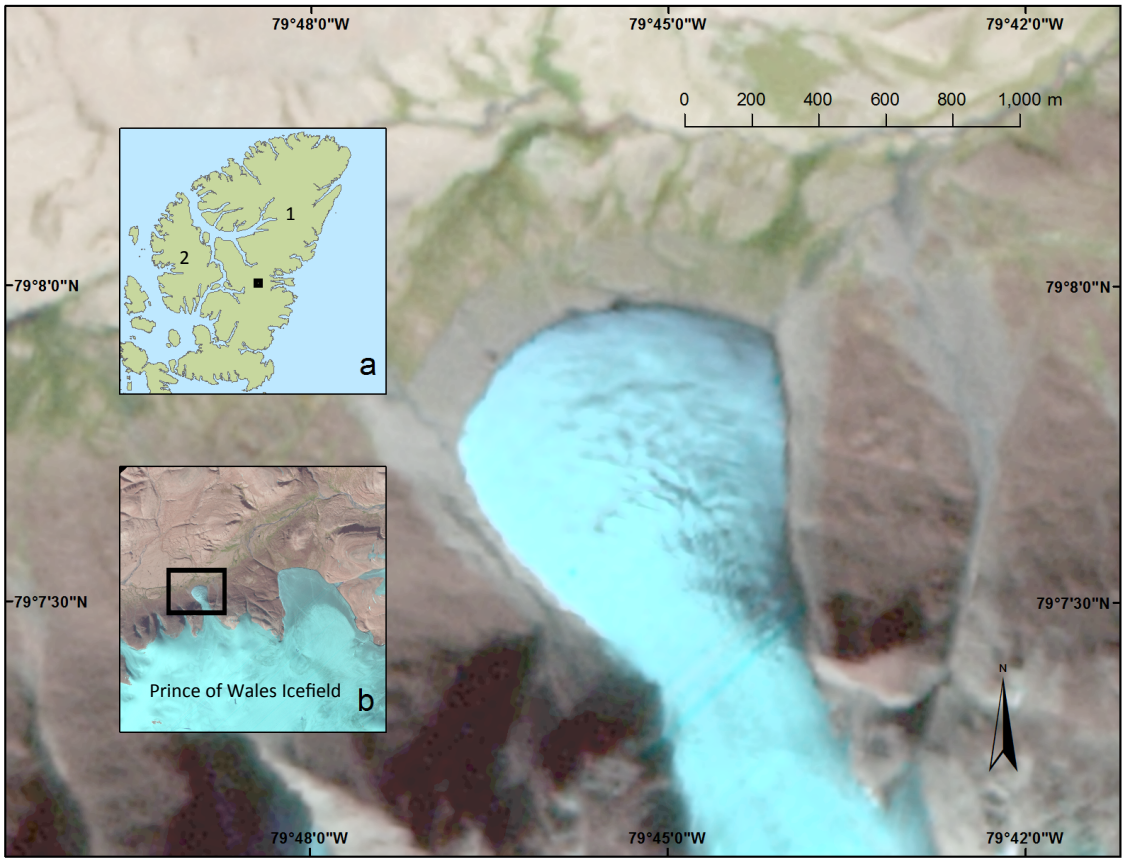

Figure 3.1. Location of study area: a) insert showing the locality of the study area in the northern Arctic Archipelago: Ellesmere Island (1) and Axel Heiberg Island (2), Nunavut, Canada. b) insert showing Sverdrup Pass, black box indicates study area: Teardrop Glacier foreland and vicintiy.

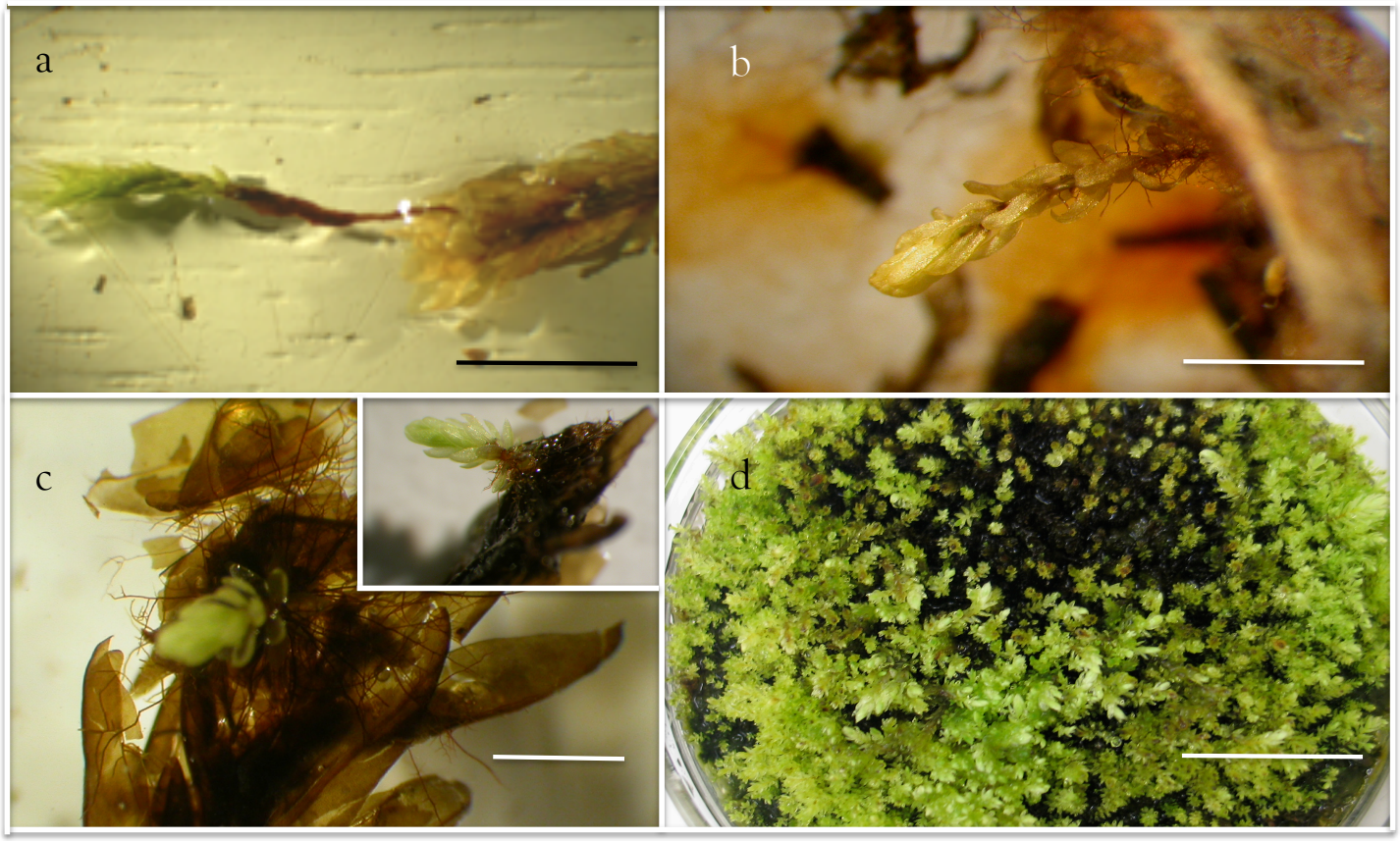

Figure 3.2. *Aulacomnium turgidum* samples showing regeneration: a) LIA field samples (*CLF 13131*) showing apparent *in vivo* regrowth b) *SBG 2* growth in J9 c) *SBG 27* (*D7*) showing regerated gametophyte on LIA parent material d) *SBG 44* growth (*D12*). Scale bars: a and b = 2.5 mm; c = 15 mm; d = 25 mm.

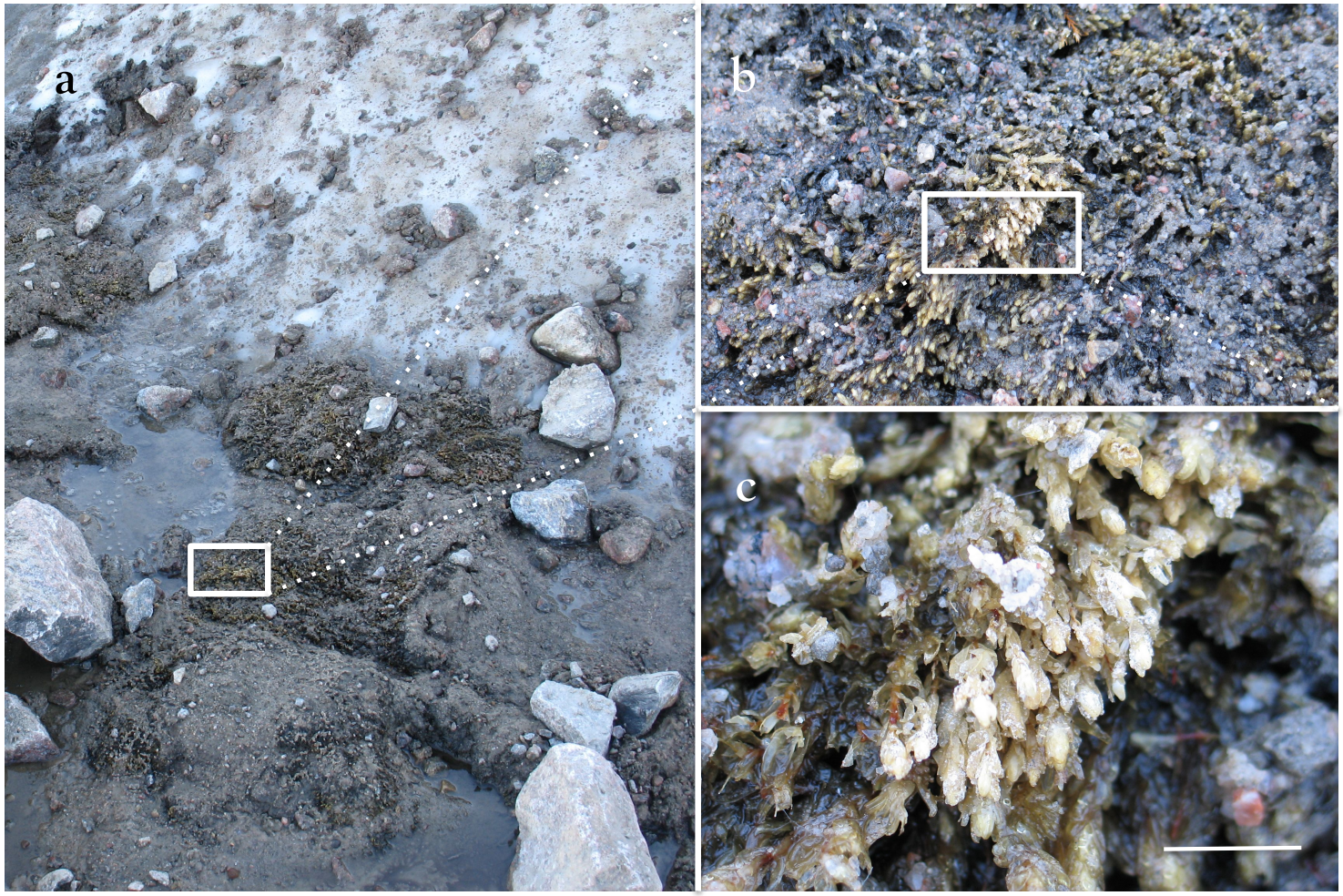

Figure 3.3. a) Exhumed, *in situ*, *Aulacomnium turgidum* subglacial specimens collected at the margin of the Teardrop Glacier, Ellesmere Island. Populations collected <1 meter from GLM. b) & c) corresponding detail of same population showing intact stems and leaves. Scale bar: c = 2.5 cm

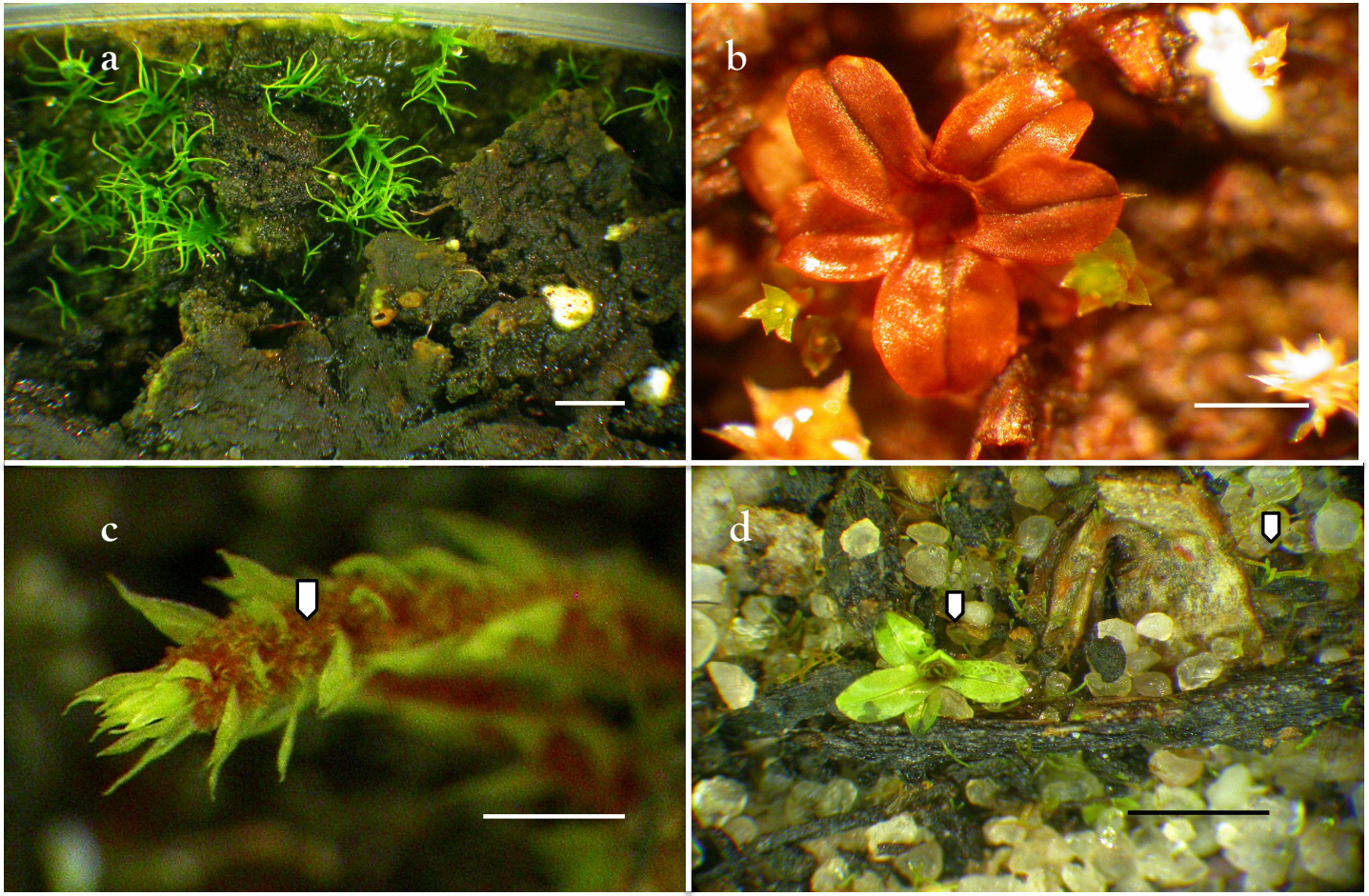

Figure 3.4. Additional regenerated subglacial moss species: a) *Distichium capillaceum* from *SBG 8 (D30)*. b) *Syntrichia ruralis* from *SBG 37 (D42)*. c) *Pohlia annotina* from *SBG 25 (J4)* with axillary gemmae d) *Encalypta procera* from 2009 dried specimen *13145 (D69)* showing gametophore and protonema. Scale bars: a and b and c = 1 mm; d = 2.5 mm.

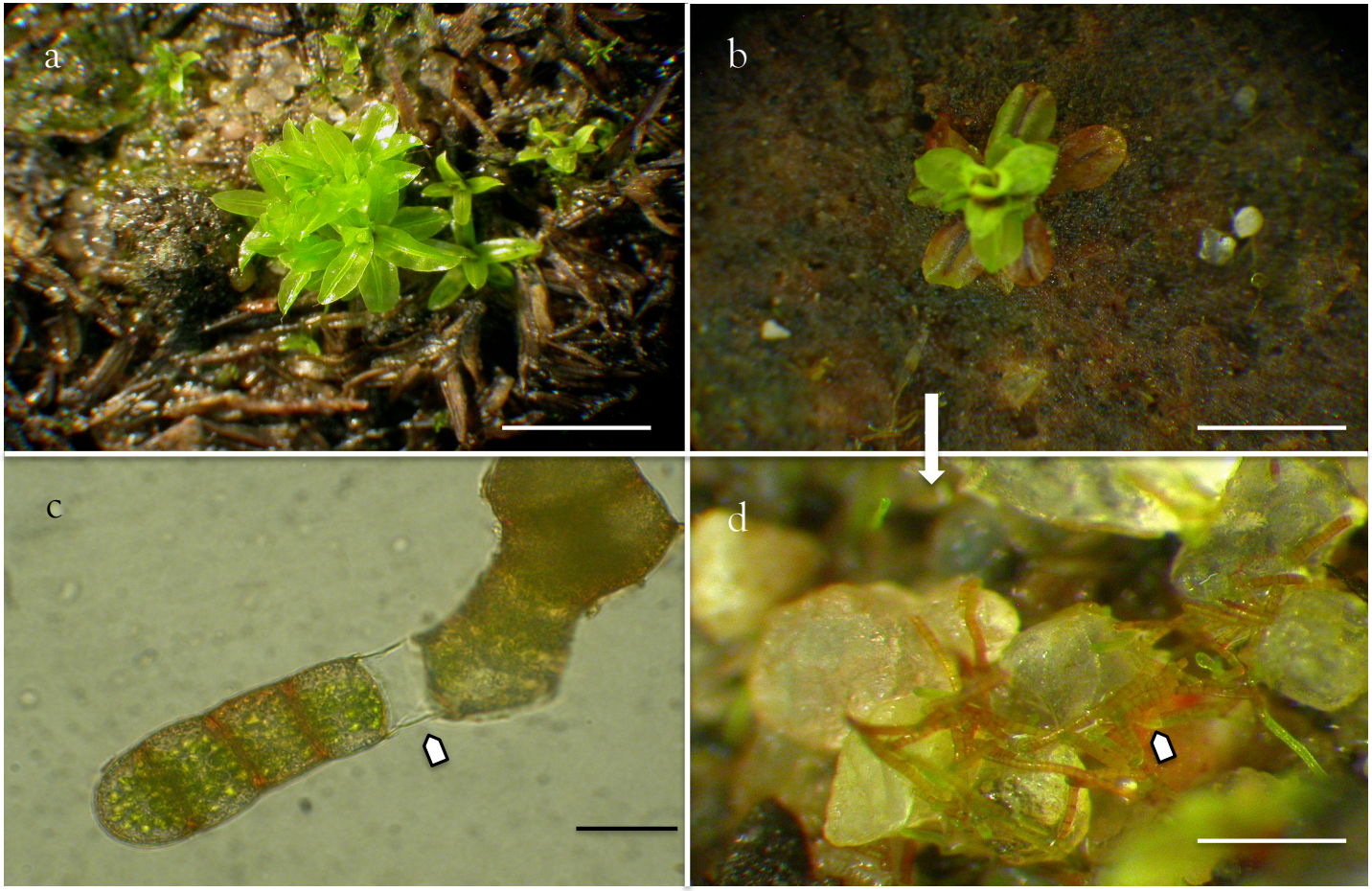

Figure 3.5. Encalyptaceae regenerated species and associated protonemal gemmae. a) *Encalypyta rhaptocarpa* gametophyte from *SBG 36 (D51)*. b) *Encalypta procera* gametophyte from dried *13005 (D69)* showing mat of protonemal gemmae on substrate. c) *Encalypta procera* detail of chloronema showing tmema cell *(D69)*. d) *Encalypta procera* brood bodies serving as protnemal gemmae *(D69)*. Scale bars: a and b = 2.5 mm; c = 50 um; d = 0.5 mm.

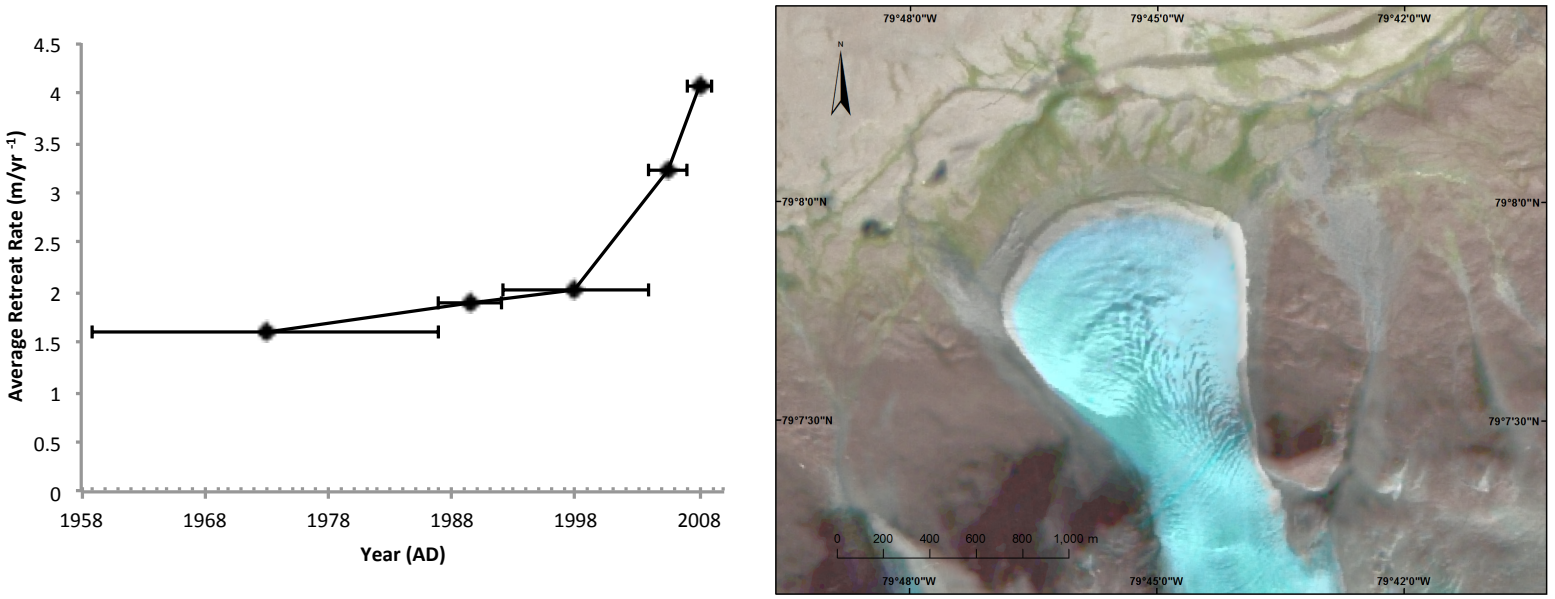

Figure 3.A1. Retreat rates of Teardrop Glacier, Sverdrup Pass, Ellesmere Island. a) Average retreat rates (m/year^{-1}) with initial rates determined for 1959 – 1986 (Fahselt et al. 1988), 1986 – 1992 (Elster et al. 1999), 1992 – 2004 (Breen and Levesque 2006), 2004 – 2007, and 2007 – 2009 (La Farge et al. 2013). b) Satellite imagery of Teadrdrop Glacier. White portion of TD Glacier: 1959 air photo (National Air Photo Library, Ottawa) superimposed on blue 2010 satellite image.

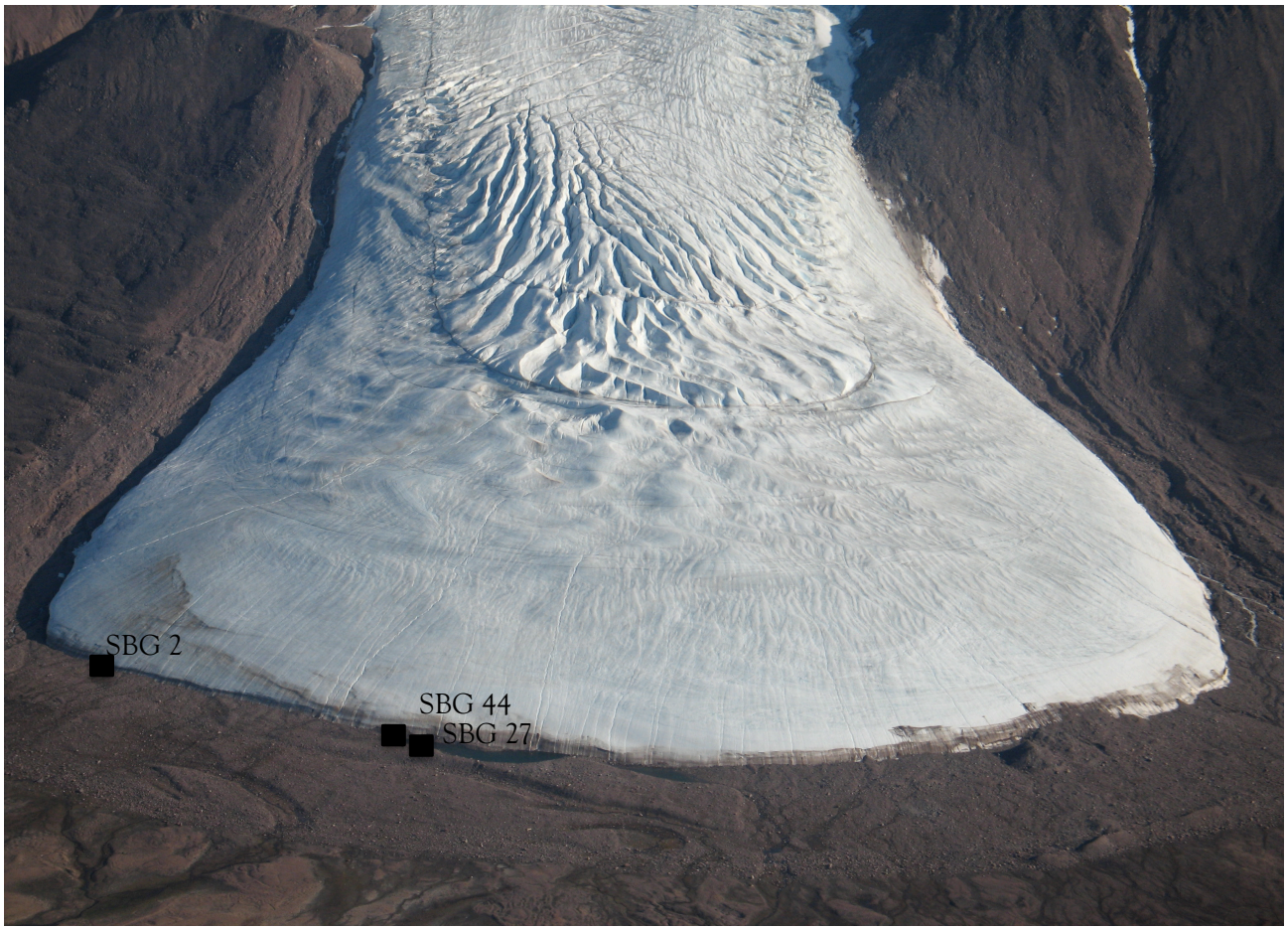

Figure 3.A2. Regenerated subglacial specimen sites of *Aulacomnium turgidum*. Collected along the margin of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island. *SBG 2*: 79° 07.934 N, 79° 44.195 W elev. 341 m a.s.l. (180 cm from GLM); *SBG 27*: 79° 07.976 N, 79° 44.961 W elev. 332 m a.s.l. (570 cm from GLM); *SBG 44*: 79° 07.978 N, 79° 44.145 W elev. 331 m a.s.l. (< 200 cm from GLM).

Figure 3.A3. Morphological variation of protonema of regenerated moss species. a) *Psilopilum cavifolium* protonema from regenerated *SBG 37 (D43)*; magnified in insert. b) *Distichium capillaceum* protonema from regenerated *SBG 29 (D50)*. c) *Aulacomnium turgidum* protonema from regenerated *SBG 44 (D12)*. d) *Pohlia cruda* protonema from regenerated *SBG 2 (D20)* showing thin film of green algae over substrate, protonema (arrow) and small gametophore (arrow). Scale bars: a = 3 mm; b = 0.5 mm; c and d = 2 mm.

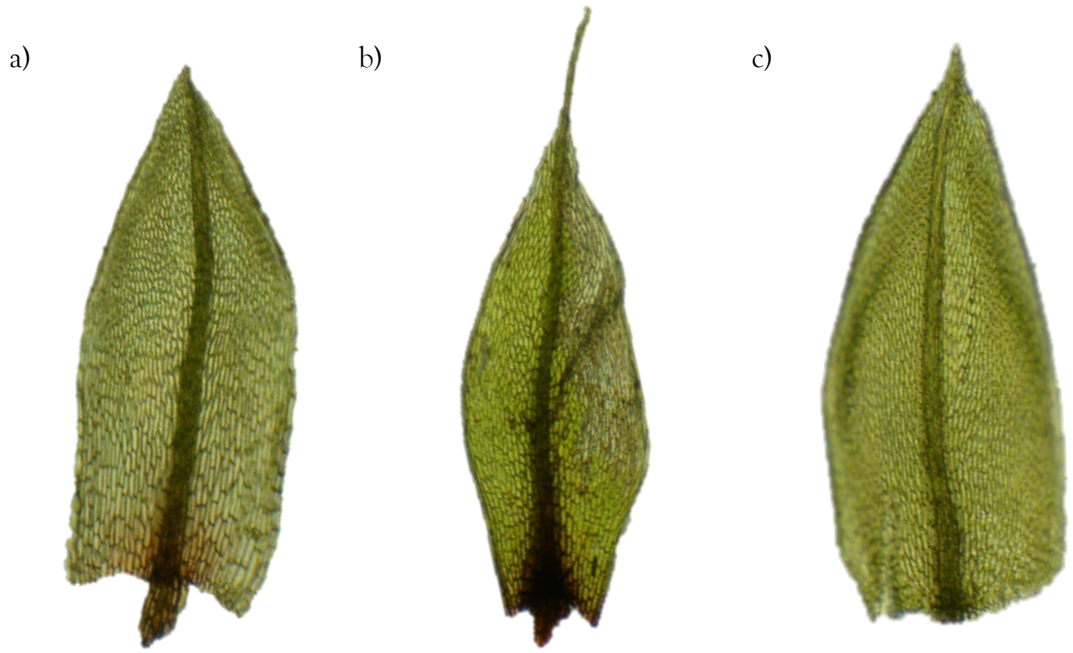

Figure 3.A4. Cultured species of *Ptychostomum*. a) *Ptychostomum* sp. A (*D4, D20, D6, D16, D45, D50, D40, D41, D42, D43 J8*). b) *Ptychostomum* sp. B (*D2,D3,D4*). c) *Ptychostomum* sp. C (D7).

Chapter IV: Summary and Implications

Bryophytes constitute a major component of tundra vegetation and play an essential role in ecosystem function (Tuba 2011). Extensive bryophyte (moss and liverwort) cover can affect temperature regimes, influencing soil thaw depth, decomposition rates, and soil moisture capacity ultimately affecting vascular plant establishment (Jägerbrand et al. 2011). Exhumed, subglacial bryophytes once entombed under the Teardrop Glacier form the basis of this thesis. The glacier margin is approximately 1.2 km wide and, due to its polythermal nature, portions of the subglacial environment indicate minimal subglacial erosion or deposition, where intact pre-Little Ice Age (LIA) plant communities are well preserved. Examination of 400-600 year old bryophyte assemblages provides a temporal continuity between pre-Little Ice Age (LIA) and the contemporary communities. Both LIA and contemporary bryophyte assemblages have been investigated for species composition and their microhabitat preferences. The key result of this study is the regeneration of LIA bryophytes from subglacial ecosystems, which is uniquely demonstrated by *in vitro* culture experiments.

Chapter II established that subglacial bryophyte assemblages form a rich species diversity that represents 60% of the extant bryoflora from the southern slopes of Sverdrup Pass. The high species richness of the extant flora of the south side of Sverdrup Pass (122 bryophyte taxa) with a total enumeration to date of Sverdrup Pass of 144 bryophyte species (La Farge et al. 2013) represents a diverse record that is only constrained by the lack of a detailed analysis of the liverworts to date. This unique polar oasis has the highest moss richness (133 species) for a single locality on Ellesmere Island to date: Alexandra Fjord (82 species; Maas et al. 1994), Lake Hazen (114 species; Brassard 1971b, 1976), Piper Pass (114 species; La Farge-

England 1989), Tanquary Fjord (125 species; Brassard 1971a, 1971b, 1976), and Alert (113 species; Brassard 1976). The species composition of the subglacial and extant assemblages indicates a broad range of moisture preferences (xeric to hydric) and substrate preferences (i.e., bedrock, soil, humus, coprophilous substrates). These diverse assemblages also represented a broad range of life strategies from perennial stayers to colonist and shuttle taxa (During 2001). Temporally, quantitative analyses of the assemblages with >25%/sample of a given taxon indicated similar LIA and contemporary species composition. As well, results demonstrate that both species richness and diversity are similar in pre and post LIA glacier expansion and retreat. These results support the expectation that bryophyte assemblages in High Arctic communities have undergone little to no change from LIA to present.

Vegetation assemblage ecology searches for repeated patterns by examining the relationship between plant distributions and the surrounding environment as well as interactions between species (e.g. competition, facilitation; Diamond 1975). It has been established that environmental factors influencing the distribution of bryophytes, specifically in the High Arctic, include substrate chemistry, water relations (Chapter II), temperature, wind, and snow (Longton 1988). Other determinates of community patterns also include reproductive biology and the availability of propagules as bryophytes show a diversity sporophyte production, spore size, and colony life expectancy (During 1979).

In addition to the physical environment, interactions between plant species determine patterns of assemblage composition. This includes competition (struggle between plants for limiting resources; Callaway 1998) and facilitation (interactions between plants that aid in the uptake of limiting resources; Matthews 1992). Plant competition research has two traditional approaches (van Andel 2005). One examines competition using an assessment of community structure and maintenance of diversity (Wilson 1999, Zobel 1992). The other examines

mechanisms of competition by focusing on acquisition and use of resources and traits that determine competitive ability. Competitive ability is based on morphology and growth rate (Grime 1979) as well as resource depletion (Tilman 1982). Stress (abiotic conditions affecting plant species and communities; Grime 1977) is also commonly investigated for predicting plant interactions to estimate the relative importance of various physical factors. The stress-gradient hypothesis (SGH) predicts that the importance of competition and facilitation vary inversely along gradients of environmental stress (Bertness and Callaway 1994). Given communities developing under high physical stress, the opportunities and importance of facilitation increase. In low stress environments, positive interactions are rare and competitive interactions are the dominant influential forces (Bertness and Callaway 1994).

SGH for vascular plants is well supported in the literature (see Maestre et al. 2009 for review), but the prevalence of these interactions is not universal among all plant communities and rarely examined for bryophytes. The High Arctic is considered a high stress and unproductive terrestrial ecosystem. Bryophytes are often dominant components due to efficient retention and utilization of resources, rather than superior competitive ability (Longton 1988). It is important to note that competitive advantage for resources is different than the capacity for dominance (Grime et al. 1990).

Grime (1979) formulated the C-S-R triangular theory of life history strategies. These strategies correspond to resource supply and include ruderals (temporary resource supply), competitors (continuously abundant resources), and stress-tolerators (continuously scarce resources). Originally established for vascular plants, patterns of ecological specialization in bryophytes parallel recognized patterns in vascular plants. Bryophyte strategies, defined by During (1979), were primarily based on reproductive biology, but have similar characteristics to Grime's C-S-R- strategies (Longton 1988). Perennials are characterized by long life spans and

low reproductive effort (During 1979, 1992). This is equivalent to stress-tolerators, typical of environments with high stress, low competition, and low disturbance. Colonist or shuttle species have a short life span of only a few years and grow on habitats with short longevity (During 1979, 1992). These are equivalent to Grime's (1979) ruderals, typical of high stress and high disturbance environments. The last strategy defined by Grime (1979) was competitors typical of low stress and low disturbance environments. Bryophytes do not achieve this competitor strategy and limit their capacity to monopolize resource capture (Longton 1988, Grime et al.1990). Hypotheses concerning assemblage ecology and the SGH are often used to explain patterns of vascular plants, but competition is insufficient to explain moss community structure (Slack 1977, Kimmerer and Young 1996). Competition tolerance among bryophytes is especially influential for opportunistic species in areas of disturbance, since the substrate may disappear before competition has a significant impact on community structure (During and van Tooren 1987, 1990, Slack 1990). However, especially in tundra ecosystems, facilitative interactions do play a significant role in assemblage ecology. Bryophytes increase the water holding capacity, as well as organic matter content and play an important role in ecosystem nutrient dynamics, particularly in the High Arctic where competition from vascular plants is absent (Bates and Bakken 1998).

Chapter III focused on the regeneration of LIA bryophytes from a subglacial ecosystem and established that viable cells resumed growth after fragmentation under optimal *in vitro* growing conditions. In contrast to vascular plants, the totipotent cells, poikilohydry, and desiccation and freezing tolerance of bryophytes facilitate the capacity for 400-600 year dormancy in subglacial ecosystems. Sources of viable tissue included fragmented gametophytes (unspecialized asexual propagation) and axillary gemmae (specialized asexual propagation). These data confirm the field and specimen observations of regrowth of *in situ* LIA populations. Given the time constraint of this study, a limited number of samples were assayed for regrowth. Further cultures of subglacial substrate examining the diaspore bank

regeneration potential would expand the data on the regeneration of LIA bryophytes.

The results of this study show that subglacial bryophytes provide a potential source for *in situ* recolonization, when portions of the glacial ice are cold-based and non-erosive. It has been proposed and debated that parts of the Canadian High Arctic have been refugia for biota during past glaciations. Botanical evidence from Ellesmere Island has been used to support *in situ* glacial survival (i.e., Brassard 1971a, La Farge and Vitt 1985, Hedderson and Brassard 1992, Eidesen et al. 2007). Further, it has long been debated to what extent bryophytes' contemporary distribution reflects past, post-glacial dispersal (Shaw 2001). Warming trends in alpine and polar regions (IPCC 2007, Gardner et al. 2011) increase the potential for dormant bryophyte assemblages to contribute to the recolonization of deglaciated terrain.

Directional succession with species replacement characterizes the Teardrop Glacier foreland (Jones and Henry 2003) where biological soil crusts facilitate plant establishment in early and mid stages (Breen and Lévesque 2006, 2008) and vascular plants persist after 20 m from the glacial margin (Jones and Henry 2003). Colonists from the surrounding populations include mosses (*Ptychostomum* spp., *Psilopilum cavifolium* and *Funaria arctica*) and lichens (*Xanthoria elegans, Lecanora crenulata* and *Umbilicaria virignis*; Fahselt et al. 1988). However, bryophyte gametophytes and diaspores from the LIA paleomaterial are an overlooked source of diaspores for succession. In addition to providing viable tissue for the germination of new plant material, the paleomaterial also provides an organic substrate for pioneer taxa including vascular plants (seeds), cyanobacteria, algae, fungi and bryophytes. The Teardrop Glacier foreland provides exceptional paleomaterial of pre-LIA communities that is used as the colonizing substrate, which facilitates recolonization.

Ultimately, this thesis provides new perspectives on several topics that relate to High Arctic LIA bryophytes. The results suggest that bryophyte assemblages in a polar oasis have high species richness and diversity in both pre and post LIA glacier expansion and retreat. Fragmentation and subsequent regeneration of subglacial LIA bryophytes demonstrate that not all subglacial plant assemblages are dead. In fact, some bryophytes survive and dormant tissue can regenerate new populations under the right conditions. The temporal span of bryophyte dormancy and their ability to renew growth are greater than previously presumed. This capacity for an expanded temporal dormancy and regeneration of bryophytes needs to be considered when examining post-glacial recolonization.

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