Yukon Ice Patches: Role of Ice-entombed Bryophytes in Alpine Environments

By

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Abstract

In Southwestern Yukon, alpine ice patches are rapidly retreating with climate warming. Ice patch forelands form unique alpine wetlands, creating critical habitats for diverse flora and fauna over millennia. A major component of the ice patch flora are bryophytes, which are critical to alpine ecosystems. This study will focus on the biological relevance of the Yukon ice patches as reservoirs of cryopreserved bryophyte diversity and for contribution of emergent vegetation on deglaciated ice patch forelands.

The relation of emergent subfossil assemblages to the extant vegetation and the successional pattern following ice retreat of the Mount Granger ice patch were determined in Chapter II. Plants were sampled within 40m of the ice margin to document the extant diversity, and the plant succession with ice margin retreat. Non-metric multidimensional scaling (NMDS) showed a three stage succession pattern that has similar diversity to the subfossil species composition.

Bryophytes have the capacity regenerate from any viable cell (totipotency), allowing them to persist through extreme conditions. Chapter III assayed regrowth of emergent ice margin samples from the Mount Granger, Gladstone, and Little Gladstone ice patches. Subfossil samples showed remarkable regrowth of bryophyte diaspores up to 4815 years old (BP cal) with 73% indicating potential regenerationl, emphasizing the viability of ancient ice patch vegetation. The results of each study reveal a cyclical role of bryophytes from exhumed assemblages that contribute to the establishment, revegetation, and maintenance of diversity in alpine ice patch ecosystems.

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Chapter I: Introduction

Bryophyte biology

Bryophytes form the three basal lineages (non-vascularized) of land plants (embryophytes), consisting of mosses (Bryophyta), liverworts (Marchantiophyta), and hornworts (Anthocerophyta; Shaw et al. 2011). The dominant life stage of a bryophyte is the haploid (n) photosynthetic gametophyte, which supports the development of the dependent sporophyte (2n) formed after fertilization. In contrast, vascular plants (tracheophytes) have an independent sporophyte (2n), forming the dominant life stage. Lacking vascularized tissue, bryophytes form small plants. They do not possess true leaves with complex anatomy (i.e. mesophyll of vascular plants), but often have unistratose laminae, consisting of blades one cell thick (Goffinet and Shaw 2008). They also do not produce true root system, but form rhizoids that facilitate nutrient absorption and anchorage (Schofield 1981, Netwon et al. 2000, Ligrone et al. 2012), allowing them to colonize hard substrates such as rock and wood, unlike vascular plants. These rhizoidal systems are uniseriate, often branched filaments that develop from stem, leaf or thalloid tissue as well as developing diaspores.

The scale and unique biology of bryophytes allow them to occupy diverse microhabitats, colonizing extreme terrain such as in high alpine and arctic environments (Longton 1997) that often limits vascular plant establishment. Bryophytes are poikilohydric, lacking structural anatomy (i.e., complex vascular tissue as in vascular plants) to maintain and regulate water content, acheiving homeostasis with their environment. This is coupled with desiccation tolerance, allowing bryophytes to survive periods of dry conditions. They undergo cryptobiosis, reducing metabolic activity until rehydration (Proctor 2000, Proctor and Tuba 2002). Cold adapted arctic and alpine bryophytes utilize their poikilohydric nature and rapid desiccation process to mitigate damaging effects of environmental freezing. During the freezing process, H_2O moves from the living cells to extracellular freezing sites, therefore lowering intracellular water potential of the bryophyte tissue, which facilitates desiccation and minimizes the formation of intracellular ice (Lenne et al. 2010). Desiccation has also been shown to protect polar bryophytes (e.g., *Ceratodon purpureus* and *Ptycostomum pseudotriquetrum*) from UVB damage by minimizing cyclobutane pyrimidine dimer formation (Turnbull et al. 2009).

Bryophytes possess several molecular mechanism to mitigate cytorrhysis (or cellular damage) caused by diurnal free thaw cycles of summer growing seasons. They constantly express dehydrins, late embryogenesis abundant (LEA) proteins regulated by abscisic acid (ABA) hormones, which are typically upregulated in during freezing and desiccation (Bopp and Werner 1993, Agarwal et al. 2017). Dehydrins protect membrane structure and enzyme integrity (Bewley et al. 1993, Graether and Boddington 2014), and sequester sucrose for cytoplasm vitrification to preserve cell viability (Buitink et al. 2002). Freeze-thaw cycles induce photoinhibition to downregulate and minimize damage to photosystem II of the photosynthetic pathway (Lovelock et al. 1995). To protect against reactive oxidative species (ROS) produced by photosynthesis inhibition, glutathione (GSH) antioxidants levels are expressed at high levels (Proctor et al. 2007). In cryopreservation experiments, bryophytes that possess this suite of cold-adaptive traits are able to survive and regenerate after extended periods of induced freezing without the aid of cryoprotectants (Burch 2003).

Prolonged periods of desiccation depletes carbon reserves, reducing the capacity of bryophytes to regenerate following rehydration (Proctor et al. 2007). If bryophytes endure cytorrhysis from dessication induced by long-term freezing, they retain viability through totipotency, with virtually any viable cell being able to dedifferentiate and develop an entirely new gametophyte (stem cells; Ishikawa et al. 2011). When faced with injury or detachment (fragmentation), normal apical dominance is lost and cells are induced to meristematic state. In the model bryophyte organism, *Phsycomitrella patens*, the loss of apical dominance in excised tissue stimulates expression of cyclin –dependent kinase A (CDKA) for cell cycle reactivation and cellular dedifferentiation (Ishikawa et al. 2011). Kofuji and Hasebe (2014) studied *Physcomitrella patens* and identified eight tissues capable of forming meristematic cells: seven within the gametophyte (e.g., rhizoids, leaves, gametangia (archegonia and antheridia etc.) and one within the sporophyte apex. Wilkinson et al. (2003) have shown that vascular plants are able to regenerate following cellular damage induced by freeze/thaw cycles where apical meristematic cells remained viable. Extended temporal limits of totipotency in bryophytes have been shown by both *in situ* and *in vitro* regeneration of populations previously entombed for 400 years (BP cal) years within the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut (La Farge et al. 2013), and gametophytes >1500 years (BP cal) from of permafrost cores collected at Signy Island, Antarctic (Roads et al. 2014). The limits of bryophyte survival has also been shown by Zobel and Antos (1992), where bryophyte material buried in tephra for eight growing seasons remained viable and were able to reestablish on disturbed terrain following emergence.

Reproduction of bryophytes in northern environments is mainly attributed to asexual propagation, opposed to sexual fertilization ultimately resulting in spore production (Longton 1988). Asexual propagulae refer to any material genetically identical (clonal) to the parent material, including gametophyte fragments, gemmae, bulbils, caducous leaf tips, deciduous branches (Pressel et al. 2007). Specialized propagulae (i.e., gemmae, tubers) have morphologies that maintain desiccation and freezing tolerant mechanisms (Proctor et al. 2007). Asexual propagulae are commonly formed under stress conditions and contribute to the establishment and maintenance of bryophyte populations (Newton and Mishler 1994, During 1997, Frey and Kürschner 2011). Disseminated propagules can remain dormant for extended periods, forming soil diaspore banks, expanding their temporal longevity to environmental conditions that stimulate germination, and facilitate the greatest chance of prolific growth (Thompson and Grime 1979, During 2001, Hock et al. 2008). Vegetative diaspores also function as effective dispersal vectors, expanding bryophyte colonization to more distant environments (van Zanten 1978, Frahm 2008). Sexual reproduction requires water and close proximity of the gametangia for motile sperm to fertilize archegonia. With over half of northern bryophyte species being dioicious (separate male and female plants) and desiccation constraining sporophyte development (Stark 2001), only 28% of high arctic species regularly develop sporophytes (Schofield 1972, Brassard 1971). In addition to vegetative propagulae, produced spores will function as diaspores, extending the temporal longevity of the plant.

Ecological role of bryophytes in Northern Environments

Plants of northern environments are highly adapted to harsh growing conditions indicative of high latitude regions. Low temperatures result in slow soil decomposition, limiting nutrient availability and overall plant productivity (Gaius et al. 1992, Brooker and Van Der Wal 2003). The cold, dry environmental regime selects for stress tolerant species that can complete metabolic processes in short growing seasons (Savile 1972, Cannone et al. 2008). Due to their resiliency, bryophyte species are the dominant component of northern vegetation, comprising the highest amount of richness and biomass (Vitt and Pakarinen 1977, Royles and Griffiths 2015).

Bryophytes are diminutive plants that grow close to the terrain, minimizing exposure to harsh conditions through the insulative properties of the soil boundary layer (thin layer of stagnant air between the soil-air interface; Proctor & Tuba 2002). Confining growth to within the boundary layer increases and stabilizes soil temperature, decreasing transpiration (water loss) thereby retaining moisture (Beringer et al. 2001, Gornall et al. 2007). Bryophytes develop vast carpets of gregarious species including bacteria, cyanobacteria, algae, fungi, and lichens, they collectively forming biological soil crusts (Belnap and Lange 2001) that create greenhouse effects necessary to facilitate germination of higher plants (Bliss and Gold 1999, Breen and Levesque 2006, Ciccazzo et al. 2016). In additional to retaining surface moisture, crust biota augment soil nitrogen content, a critical nutrient for plant development otherwise limited in northern systems (Bliss and Gold 1999, Pedersen et al. 2001, Tuba et al. 2011). Although overall biomass of crusts are lower than vascular plants, bryophyte-cyanobacteria associations have been shown to significantly influence nitrogen and carbon cycling and partitioning (Turetsky 2003, Lindo et al. 2013, Street et al. 2013). Bryophytes have been shown to retain up to 70% of accumulated carbon, creating net carbon sinks, whereas grass species retain only 40% (Woodin et al. 2009).

Bryophytes have a significant role in succession following deglaciation. The last century has shown rapid thinning and recession of ice margins in Arctic Canada (Miller et al. 2013). In 2004 – 2009 alone, 61 +/- gigatonnes per year of glacial ice were lost (Gardner et al. 2001). The de-glaciated terrain provides substrate for primary succession of vegetation, often with initial stages of development characterized by pioneer crust biota (Jones and Henry 2003, Breen and Levesque 2006, Garibotti et al. 2011, Favero-Longo et al. 2012). Bryophytes form critical associations with symbiotic N_2 fixing cyanobacteria (Lindo et al. 2013), which have been shown to contribute a high level of net primary productivity (Yoshitake et al. 2010). Bryophyte-cyanobacteria colonization augments soil nitrogen (Turetsky 2003), allowing establishment of vascular plants (Tamm 1991, Arróniz-Cespo et al. 2014).

In addition to colonization from surrounding populations, exhumed diaspores (e.g., propagules, gemmae, spores) may also contribute to successional success following deglaciation. Cyanobacteria are prolific within ice in arctic and alpine ecosystems, maintaining viability in harsh conditions (Quesada and Vincent 2012). Input of cyanobacteria from melting ice and cryoconite habitats (glacial surface) have facilitated the establishment on deglaciated terrain as early as 4 weeks following ice retreat (Schmidt et al. 2008). Cooper et al. (2004) also found that vascular plant seedling establishment on proglacial terrain was reliant on successful germination from seed banks. Exhumed bryophyte populations following deglaciation of the

Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut, have been observed regrowing *in situ*, directly colonizing the deglaciated foreland (La Farge et al. 2013).

Establishment and succession on deglaciated forelands is generally limited by nutrient availability and abiotic edaphic properties (Svoboda and Henry 1987, Chapin et al. 1994, Yoshitake et al. 2007). Soil enriched with nitrogen and phosphorus significantly accelerates microbial richness, with soils exposed for three years resembling soil exposed for 85 years after fertilization (Knelman et al. 20014). Melt water influx from rapidly retreating ice margins has also been shown to accelerate plant colonization (Burga et al. 2010), augment pioneer crust biota development (Kaštovská et al. 2005, Moreau et al. 2008), and increase edaphic nutrient content (Breen and Levesque 2008). Additional abiotic factors such as pH and ammonia (NH_4) have been correlated with cyanobacteria establishment and composition (Pushkareva et al. 2015), and overall pattern of succession (Chapin et al. 1994, Boy et al. 2016). Deposition of wind-blown organic material augmenting nutrient limited terrain may be influential in crust establishment (Hodkinson et al. 2003).

Yukon ice patches

In the southwest Yukon, a systematic aerial survey of the alpine has identified 72 ice patches that have been the subject of varied research (Bowyer et al., 1999; Kuzyk et al., 1999; Farnell et al., 2004; Hare et al., 2004, 2012; Dove et al., 2005). Over 200 artefacts have been found associated with these ice patches with the oldest dating to 9000 cal yr BP (Hare et al. 2012). With rapid and accelerated climate warming, these ice patches are under threat with some having disappeared altogether (Hare, personal communication).

The Yukon ice patches developed as snow accumulations compressed into ice over decades and millennia, many of which are remnants of former glaciers with internal flow lines or indicted associated end moraines (John England, personal communication). These ice patches range in size from 100m -1km wide (Farnell et al. 2004), and are characterized by accumulations of dung (predominantly caribou; *Rangifer tarandus*) and organic debris, creating a unique stratigraphy throughout the ice. They form on north facing mountain slopes, ranging from 1550m -2705m asl, in incipient cirques (Washburn 1979) throughout the Yukon-Stikine Highlands, Ruby Range, and Southern Lakes ecoregion (Smith et al. 2004). Analogous to cold based glaciers that have limited basal flow (Paterson 1981), ice patches lack sufficient mass to flow, and therefore buried substrate is preserved at the terrain-ice interface. The small size of these ice patches has made them vulnerable to climate fluctuations (Mount Granger ice patch in 1995 was 6% its Little Ice Age (LIA) maximum determined by the lichen free zone (LFZ); Farnell et al. 2004). This rapid retreat has exhumed accumulated dung, bones, hunting artefacts, and buried plant populations (Kuzyk et al. 1999, Farnell et al. 2004, Hare et al. 2004).

Sixty-five ice patches have been surveyed for archeological material, with 43 containing diverse artefacts up to 9000 cal yr BP from early First Nations hunters (Hare et al. 2004, 2012). The ice patches function as summer refuge for large alpine fauna, most frequented by Caribou (*R. tarandu*), Dall sheep (*Ovis dalli*), and moose (*Alces alces*; Hare et al. 2012) protecting them from insect attack (Anderson and Nilssen 1998). This is recorded in the mass amount of dung accumulated within the ice patch strata and in the forelands. Summer refuges for the local fauna made them ideal hunting grounds for First Nations people (Hare et al. 2004). Previous research on these ice patches records the rich data from 207 artefacts and 1700 faunal remains from >16 species (Hare et al. 2012).

Paleobotantical research on these relict ice patches provides novel opportunity to reconstruct the environmental history of northern regions. Macrofossils from unglaciated regions of the Yukon Klondike have demonstrated the use of diverse vascular plants and bryophytes to provide a detailed reconstruction of paleo-ecosystems (Zazula et al. 2006). A recent study on glacial retreat on Ellesmere Island, Nunavut has indicated that exhumed bryophyte populations contribute to the recolonization of deglacial forelands, expanding the concept of refugia to a novel level (La Farge et al. 2013). Paleo reconstruction of the Yukon ice patches is currently limited to vascular plant pollen analysis from the Friday Creek and Mount Granger ice patches (Bowyer et al. 1999). Bowyer and Schweger (2001) showed temporal shifts in plant diversity, with pine pollen accumulating 1900 years ago (cal BP), consistent with pine invasion within this region (MacDonald and Cwynar 1999). Ice samples and dung also showed a rich diversity of vascular plant pollen (i.e., *Picea, Betula*, *Salix*, sedges, *Equisetum*, and *Artemisia*), reflecting summer diets of the alpine fauna or anemochory deposition that accumulated over periods of thaw. The emergent subfossil assemblages of have not been studied nor the succession of the deglaciated foreland. Bryophytes have been noted as the dominant taxon within the Granger foreland (i.e., *Polytrichum juniperinum* Hedw.; V. Bowyer unpublished data). Preliminary samples from the LIA margin of the Mount granger ice patch collected by Greg Hare (2014) indicated potential *in situ* regrowth, showing prolific germination of *Pohlia drummondii* (Müll. Hal.) A.L. Andrews from ancient caribou dung (Catherine La Farge, personal communication 2014). The alpine ice patch ecosystem represents a unique temporal record through millennia of high altitude faunal and botanical interdependence. The current study will address both the subfossil and extant flora associated with this unique ecosystem.

Shifts in northern vegetation

Northern regions have experienced warming at rates exceeding global average (IPCC 2013). Surface air temperatures have increased 0.4 ^{o}C per decade, approximately double what is observed at lower latitudes (Elmendorf et al. 2012b). This sustained warming has the potential to cause large-scale shifts in plant biodiversity (Henry and Molau 1997). To determine the patterns of plant community response, several long term simulated climate warming experiments (up to decades) have been conducted throughout diverse northern environments (Elmendorf et al. 2012a).

A climate warming study conducted in a sub-arctic Tundra near *Toolik Lake, Alaska* (Chapin et al. 1995) over nine years showed increased in shrub abundance, whereas all other plant groups decreased in biomass. Moss and lichen species were particularly effected with drastic declines in community presence. Henry and Hudson (2010) conducted a similar experiment over 15 years on Alexandra Fiord, Ellesmere, Nunavut. Influx of snow melt maintains soil moisture at level comparable to the tundra meadows from the previous two studies. Vascular plants and bryophytes slightly increased in abundance, due to the influx of snow melt, whereas lichen species generally decreased. In southwest Yukon, slopes within the Ruby Range surveyed for plant richness over a 42 year span showed overall increase in diversity, particularly graminoid species (Danby et al. 2011).

Regional and local variation of environmental factors such as snow cover, pH, precipitation regime, and herbivory may affect vegetative response to climate warming (Epstein et al. 2004). As such, long term warming experiments yield inconsistent results. To elucidate an estimate of overall vegetation response, Elmendorf et al. (2012a) compiled analysis from 61 long term warming experiments from the past twenty years across tundra sites worldwide. Predictive consensus showed that vascular plants will collectively increase, whereas lichens and bryophyte diversity will decline. The detrimental effects to bryophytes is attributed to shifts in optimal temperature for photosynthesis, decreasing metabolic activity, and through intensifying desiccation frequency beyond bryophyte survival capacity, which will particularly affect high bryophyte diversity areas such as alpine biomes and high latitude regions (He et al. 2016). Loss of bryophytes and symbiotic nitrogen fixing bacteria has severe implications for below ground carbon storage and nitrogen fixation in the north (Lindo et al. 2013). With the detrimental environmental affects to bryophytes, bryophyte diversity has become increasingly necessary to protect and monitor (Hallingback and Tan 2010). A detailed study on the Yukon ice patch alpine ecosystem provides a temporal examination of the resilience of the upland alpine tundra. Simulated climate change experiments conducted on the subalpine tundra of Wolf Creek, Yukon, showed that vascular plants with high reproductive effort maintained high levels of variability that allowed them to rapidly adapt to temperature variations (Pieper et al. 2011). The successful regeneration and establishment of exhumed plants from the Yukon ice patches represent a potential increase of diversity and stabilization of plant communities.

Objectives

The objective of this study is to determine the significance of Yukon ice patches to the maintenance and resilience of alpine environments. The ice patch paleoenvironment and extant ecosystems will be addressed.

Chapter II will assess the primary succession of the deglaciated foreland (≤40m from the ice margin) of the Mount Granger and evaluate potential factors that influence the observed pattern (i.e., soil moisture, volumetric water content, pH). Plant diversity within the vicinity of Mount Granger (≤1km from the ice patch), and assessment of emergent subfossil assemblages will be determined and compared to the foreland diversity illuminating whether succession relies on external input (surrounding vegetation; Bullock et al. 2002; Kirmer et al. 2008, Prach and Řehounková 2006; Jones and del Moral 2009) or is self-generating from emergent subglacial communities (Breen and Levesque 2006, 2008; La Farge et al. 2013). This will provide insights to the plant communities the ice patch supports, and if it has persisted over millennia.

Chapter III will assess the age (^{14}C) and regeneration potential of the exhumed bryophyte assemblages, to evaluate the limits of totipotency. A comparison between Mount Granger, Mount Gladstone and Little Gladstone subglacial assemblages will determine the capacity of ice patches to function as biological reservoirs. This has implications for contributing biodiversity to Yukon alpine systems predicted to experience detrimental effects of climate warming.

Chapter IV will summarize the most significant conclusions of this study, implications for the Yukon alpine environment, and future directions of this research such as population genetic studies between subfossil and extant populations of bryophytes.

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Chapter II: Yukon Ice Patches: Primary succession following ice patch retreat indicates temporal preservation of community plant structure

Introduction

Rapid glacial retreat observed in arctic and alpine regions (WGMS 2016), has been triggered by climate warming (IPCC 2013). Particularly within the Canadian Arctic, massive ice loss has been recorded with a 64 ± 14 Gt yr^{-1} per 1 K increase in ice loss from 2004–2006 to 2007–2009 alone (Gardner et al. 2011). De-glaciated terrain has provided a forefront in understanding the mechanisms of primary succession. Interdisciplinary research has elucidated temporal shifts in vegetative composition (Matthews 1992, Chapin et al. 1994, Fastie 1995, Klaar et al. 2015), characterized the role of early colonizer soil microbes (Schmidt et al. 2008, Hodson et al. 2008, Ciccazzo et al. 2016), and determined the suite of abiotic factors that influence successional patterns (Wietrzyk et al. 2016). Successional studies provide insights to the biological plasticity and stability of perturbed northern alpine environments.

Throughout Southern Yukon, Canada, there are small alpine glacial formations referred to as ice patches (Hare et al. 2004). The ice patches are relatively small ice accumulations on north facing mountain slopes, ranging from 100 m to 1 km wide (Farnell et al. 2004). They are characterized by stratified layers of accumulated prehistoric Caribou dung (*Rangifer tarandus*) mixed with wind-blown sediment and show evidence of ice margin temporal fluctuation following climatic variation (Farnell et al 2004). They provide summer refuge for alpine fauna over millennia, making them traditional ancestral hunting grounds for generations of First Nations people. Since 1997, the ice patches have been surveyed and investigated for archeological (Kuzyk et al. 1999, Hare et al. 2004, 2012), palynological, and glacial geomorphological data (Farnell et al. 2004). Effects of global warming have led to substantial retreat of ice margins and the disappearance of smaller, vulnerable ice patches (Hare et al. 2012). These ice patches sustain specialized hydric alpine plant communities, but remain unstudied despite their significance to Yukon fauna and hydrological enrichment to upland vegetation.

The Mount Granger ice patch was the first site of archeological discovery, and has been one of most productive (highest recorded amount of biological and archeology remains). Previous radiocarbon dating of subglacial vegetation indicates initial formation of the Granger Ice patch at 7990+/-70 years BP uncalibrated (Farnell et al. 2004). Relative to the expansive archeological and geomorphological research done at Mount Granger, the emergent subfossil vegetative composition and primary succession remains undocumented. The glacial foreland supports a rich plant community that follows a progressive successional pattern following ice patch retreat. Given the rich plant community within the foreland, accessibility, and radiocarbon dated vegetation, this site will provide the best insight on ice patch ecosystem dynamics. The presence of emergent subfossil vegetation also provides the opportunity to explore the temporal evolution of the ice patch ecosystem.

Plant establishment following deglaciation has been shown to be strongly influenced by the surrounding vegetation (Bullock et al. 2002; Kirmer et al. 2008, Prach and Řehounková 2006; Jones and del Moral 2009). As well, emergent subglacial assemblages have been shown to have a critical impact on the diversity and richness of foreland ecosystems (Breen and Levesque 2006, 2008; La Farge et al. 2013). The persistence of ice entombed plant assemblages provides a basis to compare if succession follows a pattern strictly controlled by the extant floral composition, or if it more closely resembles preburial assemblages. The specific objectives of this study are to: 1) determine the pattern of primary succession within the foreland of the Mount Granger ice patch, 2) determine the role of emergent subfossil assemblages in the succession of the extant Mount Granger vegetation, and 3) determine if the successional vegetation composition is more similar to the subfossil or the extant assemblages. Subfossil samples were collected at the Granger ice margin following maximum summer retreat (exposure of oldest material), and transects were established within the glacial foreland to determine succession. Surrounding communities (referred to as biodiversity sites surveys) with similar hydrological conditions (hydric-mesic) to the glacial foreland (along ice patch melt water channels), were selected for comparative richness analysis.

Arctic and alpine tundra is predominately composed of cryptogamic species (moss, liverworts, lichens; Longton 1988), making them an integral part of northern ecosystems. Their habitat plasticity and resiliency allow them to flourish in areas many other plants cannot. Bryophytes are one of the first plant functional groups to thrive within early successional stages (Breen and Levesque 2006). Their initial establishment can provide a critical component that facilitates the establishment of vascular plants (Taylor 1920, Svoboda and Henry 1987, Bliss and Gold 1999, Gornall et al. 2007). Classic primary succession studies commonly underestimate the significance of bryophyte diversity by excluding them in analysis or compiling them into a single group (Whittaker 1993, Chapin 1994, Cannone et al. 2008, Burga et al. 2010). This study will emphasize bryophytes as individual biological components that facilitate resilence and maintenance of alpine ecosystems following ice patch retreat and succession.

Methods

Study area

Mount Granger is approximately 20 km SW of Whitehorse, Yukon located within the intermontane belt of the boreal cordillera ecozone, in the southern-lakes ecoregion (Smith et al. 2004). This region is characterized as semi-arid, with a mean annual temperature of -1 to -2^{o}C, being five degrees warmer in high alpine areas due to inversion affects. Annual precipitation is limited, from 200-235 mm, with snow cover from October to April. The low precipitation and strong winds limit vegetative cover. Surface deposits are from the Cordilleran glaciation, covering this regions 26 000-10 000 years ago, consisting of metamorphic and granitic rocks, mafic volcanic rocks, limestone reefs and clastic sediments. The soils in this regions are characterized by these glacial deposits and discontinuous areas of permafrost (Smith et al. 2004).

The study site was at the Mount Granger ice patch (N 60.538975°, W 135.256047°, 1875m asl) in the alpine tundra (Fig. 1, Fig. 2). The Granger Ice Patch has formed on the N-facing slope of Mount Granger in a shallow bedrock bowl resembling and incipient cirque. Felsenmeer (frost shattered bedrock) forms the dominant substrate with accumulated fines over flat terrain, forming an alpine tundra wetland with melt water channels that supports 100% cover, composed of predominantly of bryophytes, lichens and graminoid species.

Between melt water channels, xeric rock stripes formed dense *Umbilicaria* spp. and *Cladina* spp. lichen populations.

The 2015 basal ice margin (IM) was 135m wide (Fig. 1), with each shoulder defined by large felsenmeer bedrock boulders and minimal soil well into the foreland (exceeding 40m). The central portion of the ice patch bowl foreland (50m wide section) was enriched by accumulated caribou dung and fine sediment saturated with melt water run-off.

Experimental Design

Vegetative succession was quantitatively analyzed within the Granger Ice Patch foreland from August 3-12, 2015 to maximize seasonal ice retreat. GPS measurements were taken approximately every 10m to determine the ice margin width and to estimate the perimeter of the ice patch (Fig. 2). In the central 50m (width) of the ice patch containing the most saturated plant growth, six transects 10m apart that extended 40m from the ice margin (IM) were staked (Fig. 1). Five zones were established at distance intervals from the IM (Z1: @ IM; Z2: 0-10m, Z3: 10-20m, Z4: 20-30m, Z5: 30-40m) following observed vegetation shifts. Zone 1 was restricted to emergent subfossil vegetation at the ice margin (maximum 20cm from the IM), recording paleo-assemblages. Two plots ($0.5m^2$) per zone (Z 2-5) were placed randomly along each of the six transects, for a total of 48 plots surveyed. Within each plot, taxon sampling and percent cover was recorded for each species. For each plot, environmental data including volumetric water content (VWC), soil moisture (SM), and pH were recorded on the same day.

In the surrounding alpine tundra of Mount Granger, eight additional mesosites were sampled for non-quantitative species richness, at a minimum of 1km from the ice patch

(Biodiversity sites, BD 1-8, Fig. 2). Sites were selected based on comparable soil moisture conditions, being in proximity to ice patch melt water channels or ‘rivulettes’ and presence of dominant foreland taxa *Pohlia* spp.(*Pohlia nutans* or *Pohlia drummondii*) and *Polytrichum* spp. (*Polytrichum juniperinum* or *Polytrichum hyperboreum*). Samples were collected outward from a selected point until no additional species were observed. These hydric-mesic sites were chosen to represent the biodiversity capacity of Mount Granger to compare to the ice patch foreland diversity.

All subfossil material (Z1 and Z2) was collected in whirl-pak bags then stored in a cooler for preservation. Extant samples were collected in paper bags and air dried on site. All samples were transported to the La Farge lab at the University of Alberta. Subfossil material was frozen and stored at -20^{o}C. Determination and nomenclature followed Flora of North America Editorial Committee, eds. 1993+ (vol. 27 2007, vol. 28 2014- Bryophytes), Damsholt (2009- Liverworts), Brodo et al. (2001- Lichens), Cody (1996- Vascular plants), and Arora (1986- Fungi). Vouchers of all taxa are deposited in the Cryptogamic or Vascular plant herbarium (ALTA), Department of Biological Sciences, University of Alberta.

Subfossil Radiocarbon Dates

Three subfossil bryophyte samples were submitted for radiocarbon dating (^{14}C) at A.E. Lalonde AMS (Accelerator Mass Spectrometry) Laboratory, University of Ottawa and four to W. M. KECK Laboratory, University of California, Irvine, to determine the age range of subfossil material (Table 5). Each sample was analyzed for species composition and washed in double-distilled H_20 to remove any plant debris (fungal hyphae, moss rhizoids, algae) prior to submission. Calibrated dates for A.E. Lalonde AMS submitted samples were calculated from conventional ^{14}C yr BP values and dates for KECK submitted samples were calculated from modern carbon fraction values through IntCal13 bomb calibration (Reimer et al. 2013).

Seasonal Growth Period

Seasonal snow melt signaling summer growth period was estimated using eight Thermochron iButton data loggers, placed ~5 cm into the soil every 10m along the center of the Granger ice margin on August 12, 2015: (5) at each transect, (1) 10m E of transect 1, (2) 10 and 20m W of transect 5 (Fig. 1). Data loggers were set to record temperatures every 240 minutes, overwriting the oldest data once maximum memory capacity was met ('rollover' was activated), capturing the 2016 growing season: September 4 2015-July 28 2016 when they were collected. Thermochon iButton data loggers were analyzed using 1-Wire®/iButton® viewer (Maxim Integrated).

Statistical Analyses

Quantitative analysis using species percent cover estimates from foreland zones 2-5, were utilized to calculate richness and diversity indices (Shannon and Simpson; Morris et al. 2014) in R 3.3.2 using the BiodiversityR package (Kindt and Coe 2005). Vegetation succession and similarity between zones (2-5Z; n=48; 12/Z) was assessed with non-metric multidimensional scaling (NMDS; Legendre and Legendre 1998, McCune and Grace 2002) under a Bray-Curtis distance metric (Clarke and Warwick 2001) in PC-ORD 6.19 (McCune and Mefford 2011). NMDS illustrates the spatial auto-correlation of objects where more similar groups (zones) will appear closer (De'ath 1999). This method is most appropriate due to the high level of double zero data and rare taxa and provides the best spatial representation of zone relationships with the lowest possible stress (higher reliability). With the prevalence of zero's within the data matrix, transformations would fail to normalize and therefore were not necessary prior to statistical analysis (Bolker et al. 2008).

NMDS analyses included quantitative variables from each zone data matrix with 55 attributes: 46 plants species with estimated percent cover of each taxon (vascular plants, bryophytes, lichens, and fungi), subfossil tissue percent cover, biodiversity values (richness, Shannon, Simpson), and all environmental measurements (pH, VWC, SM). Joint plots overlays of quantitative variables with high correlations to ordinal axes ($r>0.2$) were included to indicate the factors contributing most to the spatial organization of each zone. Significant differences between zones were tested using multi-response permutation procedure (MRPP; McCune and Grace 2002) with a Bray-Curtis distance metric in PC-ORD 6.19 (McCune and Mefford 2011). MRPP provides an effect size value (A) and test statistic (T) where similar groups will have less negative T-values and A-values closer to 1 (McCune and Grace 2002). Rejection criteria for zone similarity due to chance was corrected for multiple comparisons ($p<0.003$). Indicator Species Analysis (ISA; Dufrêne and Legendre 1997) was conducted in PC-ORD 6.19 (McCune and Mefford 2011) with 9999 permutations for Monte Carlo analysis of indicator value significance. ISA values identify specific taxa significantly associated with a respective successional zone. MRPP values coupled with ISA data will determine the pattern of succession within the ice patch foreland.

The foreland vegetation zones were analyzed using NMDS to compare their affinity with the emergent subfossil populations (Z1; n=19) versus the surrounding Mount Granger vicinity biodiversity sites (BD sites, n=8) at various altitudes. Percent cover was not applicable to biodiversity site (BD) and subfossil (Z1) sampling, resulting in quantitative data based on presence/absence being used to evaluate relationships. The NMDS was run with only bryophyte taxa (moss and liverworts) using a Jaccard distance metric (most appropriate for presence/absence data; Legendre and Legendre 1998). Bryophyte richness and composition does not significantly change along altitudinal gradients (Sun et al. 2013), whereas vascular plant richness decreases (Bruun et al. 2006). Limiting analysis to bryophytes eliminates the vascular plant basis and will develop relationships that are not influenced by altitude change.

Results

Seasonal Growth Period

Granger ice margin soil temperatures were above 0 ^{O}C from approximately July 13 to September 9 2015, indicating a minimum seasonal growth period of two months. Data loggers placed along the 2015 IM indicate soil temperatures above 0 ^{O}C from July 13-24 2016. Seven data logger recorded approximately 1900 soil temperature reads, one failed to be recovered due to snow cover (data logger E of transect 1; Fig. 1). Within the measured growing season (July 13- collection of data loggers on July 28 2016) soil temperatures ranged from 0.5 ^{O}C - 6.2 ^{O}C, with an overall average of 3.7 ^{O}C. Complete snow cover of the Granger ice patch and surrounding vicinity was observed on September 9, 2015 (M. Svoboda, personal communication) ending seasonal growth period.

Succession Pattern

NMDS analysis of 46 species (Table 1) and six variables (environmental factors and diversity indices) indicated a successional pattern of vegetation following ice patch retreat (Fig. 6a). Axis 2 represented more than half of the variation (r^2= 0.567) and had the highest correlation with the VWC gradient (r^2=0.487). On average, VWC was higher in zone 2 (30.7%) and decreased into zone 5 (24.5%; Table 2). Axis 2 was correlated with *Pohlia nutans*, *Marsupella emarginata,* and *Cephalophzia bicuspidata* (r^2≥0.2). These species showed strong associations due to their shared high percent cover ($\leq$ 40%) and presence in ≥ 3 zones. Axis 1 was highly correlated with subfossil tissue (r^2=0.86), distance from the IM (r^2=0.818), Shannon diversity (r^2=0.790), richness (r^2=0.748), and Simpson diversity (r^2=0.553). Of the factors measured, zone 2 showed subfossil tissue had the highest composition (negatively correlation), whereas moving towards zone 5 (positive correlation), richness and diversity increased. *Polytrichum hyperboreum* showed positive correlation with axis 1, which can be attributed to high frequency within zones 4 and 5 (83% of plots, Table 1), and high percent cover (up to 95%). Substrate pH (6.71-1) and soil moisture (0.96-2.46) were relatively consistent throughout the foreland, and did not contribute to the successional pattern (Table 2).

Zones 2-5 varied more significantly than expected by chance (A= 0.154, p<0.000). Zone 2 was most distinct with strong dissociation with all others zones: zone 5 (T= -12.793, A=0.268, p<0.008), zone 4 (T= -8.382, A=0.181, p<0.008), and zone 3 (T=-6.918, A=0.141, p<0.008). These relationships are visualized within the ordinal analysis where the boundary of zone 2 has minimal to no overlap with other zones (Fig. 6a). This is attributed to high abundance of subfossil tissue within zone 2 (Table 1, Fig. 4) and presence of only four bryophyte species

(*Pohlia drummondii*, *Pohlia nutans*, *Polytrichum piliferum*, and *Dicranum elongatum*). All zone 2 taxa were found throughout the surveyed foreland, with the exception of *Dicranum elongatum* which was restricted to this zone. Extant populations of vascular plants, liverworts and lichens were observed in zones 3-5, extending beyond the measured zones in ice patch foreland, and were not able to establish within zone 2 (Fig. 3).

Zones 3 and 5 were also distinct, exhibiting minimal spatial overlap (T=-5.334, A=0.0630, p<0.008). Zone 3 was characterized by ruderal (primary disturbed site colonizer) taxa (*Ceratodon purpureus*, *Leptobryum pyriforme*, *Pohlia nutans*; Table 1) and contained several unique taxa (*Aulacomnium palustre*, *Leptobryum pyriforme*, and *Dryas octopetalus*). Zone 5 contained a more speciose composition of liverworts, lichen and graminoids (Fig. 3). Zones 3 and 5 were found to be statistically analogous to zone 4 (p=0.042 and p=0.5, respectively). Each of these zones formed a unique composition, but shared several taxa, contributing to that overlap within the NMDS output (Fig. 6a). The most frequently occurring taxa that contributed to zone similarities were *Pohlia nutans* (65%), *Polytrichum hyperboreum* (52%), *Ceratodon purpureus (44%)*, *Pohlia drummondii* (42%), *Poa alpinum* (39%), *Polytrichum piliferum* (33%), *Marsupella emarginata* (23%), *Lophozia ventricosa* (23%), *Polytrichum juniperinum* (19%), and *Imbribryum alpinum* (19%). These ten species formed the dominant ice patch foreland composition, with average percent cover that fluctuated between zones but was overall high (Fig. 6a). Although Polytrichales taxa were frequent within all succession zones, *Pogonatum urnigerum, Polytrichastrum alpinum*, *Polytrichum commune*, and *Polytrichum piliferum* were indicative of zone 4 (Table 1). Indicator analysis found that only the subfossil tissue and four species were statistically significant (Table 1), due to their greater abundance across the entire foreland, whereas other taxa were infrequent or restricted to their indicative zone (Dufrêne and Legendre 1997).

The first stage of succession (0-10m; zone 2) was sparsely vegetated relative to subsequent stages, but contained early colonizer species such as *Pohlia nutans* (1-25% cover), and *Pohlia drummondii* (1-6%). These ruderal species exhibit a wide range of habitat compatibility, thriving typically in mesic conditions. *Dicranum elongatum* and *Polytrichum piliferum* were observed, but each only contributed to <1% of plot cover in 1/12 surveyed plots. Subfossil assemblages were abundant within this zone, forming 100-10% cover (Fig. 4).

The second stage (10-20m; zone 3) had over three times the species richness, and over seven times the diversity compared to the first stage (Fig. 3). Percent cover of colonizing taxa increased, ranging from 7-90%, whereas subfossil material was present, but less abundant (1-80%; Fig. 4). Pioneer species such as *Ceratodon purpureus* (25% cover) were prolific with an increased abundance of the *Pohlia nutans* (1-20% cover) and *Pohlia drummondii* (2-40%) observed from zone 2. Polytrichales taxa such as *Polytrichum hyperboreum* (35% cover) and *Polytrichum juniperinum* (20% cover) were first observed within this zone. Four species of liverworts were able to colonize this zone with overall 36% cover. Vascular plants and lichen species were also able to colonize, but with limited abundance and richness (3 species with overall 2% cover, and 4 species with overall 3 % cover, respectively).

The third successional stage (30-40m; zone 5) contained almost twice as many plant species as the second stage, and 10 times the species of first stage (Fig. 5). Species diversity compared to the second stage was comparable, only about 1.14 times greater (Table 2). This stage contained the highest percent cover, ranging from 12- over 100% cover (gregariously growing species). Total moss abundance and richness increased, *Polytrichum hyperboreum* had up to 95% cover and *Polytrichum juniperinum* up to 70% cover of plots. Lichen richness was three times higher, but percent cover was comparable (0-5%). This zone had four times the amount of liverwort species of stage three, and 100% frequency (present in 100% of plots) which were growing gregariously within *Polytrichum* colonies, forming dense soil crusts. Vascular plant richness did not substantially increase, with only one additional taxa (*Dryas integrifolia*), but species were able to better colonize the terrain (3-31% cover; Fig. 4). The highest cover included common alpine tundra graminoids: *Poa alpina* (up to 20%) and *Carex eleusinoides* (up to 35%).

The progressive development of species within the Granger foreland indicates that zone 4 does not represent an distinct successional stage, but represents a transition between zones 3 & 5 ($p>0.008$), with higher similar to zone 5 ($A=-0.002$). It was characterized mostly by Polytrichales and liverworts, and did not contain any taxa exclusive from zones 3 or 5.

Influence of subfossil material and surrounding biodiversity

The species composition of successional zones were more closely related to the emergent subfossil assemblages than to the equivalent biodiversity sites surrounding the Granger ice patch. NMDS analysis of all sites including zone 1 (emergent subfossil populations) and BD sites show more extensive overlap between ice patch foreland sites, and no overlap with BD sites (Fig. 6b). Axis 2 represented the majority of the observed variation ($r^2=0.546$) and was correlated with richness ($r^2=0.446$) and Shannon diversity ($r^2=0.449$). Axis 1 explained less variation (r^2=0.727), but was more strongly correlated with richness (r^2=0.617) and Shannon diversity (r^2=0.542). Species highly correlated to each axis ($r^2 \geq 0.2$) occurred frequently across plots and resulted in strong influence of zone spatial auto-correlation.

Zones were overall significantly distinct (A= 0.138, p<0.000). The most significant differences were seen in pairwise comparisons of each successional zone to the biodiversity sites (Table 4). Zone 5 and 1 were also relatively dissimilar (T=-9.455, A=0.122, p<0.003). Zone 3 composition was still considered similar to zones 4 and 5 (p>0.003), and zone 2 was found similar to zones 1 and 3 (p>0.003). The differences observed are a result of the variation in richness and diversity. Bryophyte richness values were generally similar within the successional zones, but were over 3 fold higher in the biodiversity sites of the surrounding alpine tundra (Fig. 5). Liverwort and lichen richness were more comparable across all sites, but remained highest within the biodiversity sites (Fig. 5).

Across the complete study area, 70 plant species were identified (Table 3). *Pohlia nutans*, *Ceratodon purpureus*, *Polytrichum hyperboreum*, and *Polytrichum juniperinum* were the dominant taxa (>50% average frequency). The biodiversity sites had the most unique taxa, with 53 of the species being indicative of this zone. The overall richness was 2.5 greater than zone 5 (richest zone within the successional area), which is most attributed to the significant increase in bryophyte (3.3 times greater), and vascular plant richness (3.2 times greater; Fig. 5). With the inclusion of subfossil species, the diversity of zone 2 more than doubled. Four extant moss taxa were overserved (*Pohlia* nutans, *Pohlia drummondii*, *Polytrichum piliferum* and *Dicranum elongatum*), with 3 moss and 3 liverwort species determined from the subfossil material

(*Polytrichum juniperinum*, *Polytrichum hyperboreum*, *Ceratodon purpureus*, *Marsupella emarginata*, *Cephalozia bicuspidata* ssp. *ambigua*, and *Jungermannia sphaerocarpa*).

The subfossil assemblages had the lowest richness, containing nine species (Fig. 5) all of which were represented within the glacial foreland. Three bryophyte species were present in the subfossil communities (*Pogonatum urnigerum*, *Pohlia crudoides*, *Imbribryum alpinum*) and all successional stages except for stage 1 (zone 2). Based on frequency of determination within the subfossil samples, *Polytrichum juniperinum* (80% of samples), *Ceratodon purpureus* (78%), *Pohlia nutans* (68%), and *Polytrichum hyperboreum* (42%) were the dominant taxa, with *P. juniperinum* being indicative of the subfossil assemblage (Table 3). These species are commonly found in the alpine tundra colonizing disturbed or mesic habitats, with the exception of *Polytrichum juniperinum*, which can thrives under dryer to mesic conditions. Subfossil populations of *P. juniperinum* were a strong indicator of zone 1, and frequent within zone 2, indicating that at the time of ice entombment, environmental conditions were mesic to submesic.

Discussion

Successional Pattern

In the Granger ice patch foreland, primary succession forms three distinctive seral stages with increasing species diversity and richness (Table 4, Fig. 4). Populations that increase in richness with each successional stage are characteristic of directional non-replacement succession, which is commonly observed under harsh environmental conditions such as in high arctic polar semi-deserts (Svoboda and Henry 1987). Although the hydric-mesic conditions of the Mount Granger ice patch foreland would suggest directional replacement succession, where constraints from extrinsic factors are low, the high altitude environment limits competitive affects between plant functional groups (Bruun et al. 2006), allowing population stability.

There are three distinct successional stages at Mount Granger including: (1) 0-10m - Early Bryales (bryophyte) colonizers-> (2) 10-20m: Late Bryales colonizers-> (3) 20-40m: Polytrichales and Jungermanniales (bryophytes), and *Carex eleusinoides*. The ice patch foreland (40m from the IM) was overall dominated by mesic bryophyte taxa: a total of 17 moss and 12 liverwort taxa compared to 10 lichens, six vascular plants and one ascomycete fungi (Table 1). The extrinsic resistance of high altitudes generally limits vascular plant growth, whereas the adaptive nature of bryophytes allow them to flourish. Bryophytes are desiccation tolerant, allowing them to withstand diurnal freeze-thaw, as well as to survive extended periods of freezing with minimal intercellular damage (Proctor 2000, Lenne et al. 2010). They are also totipotent, possessing the capacity of cells to dedifferentiate and generate a completely new plant (gametophyte) from any viable cell, which has been attributed to their long term resilience (La Farge et al. 2013).

With glacial retreat, bryophyte dominance is often an early stage of succession, followed by vascular plant colonization (Chapin et al. 1994, Jones and Henry 2003, Breen and Levesque 2006, Garibotti et al. 2011). The bryophyte dominant successional pattern at Mount Granger indicates dynamic succession of specialized high alpine systems. A comparable succession pattern was observed following the retreat of a Signy Island glacier within the Maritime Antarctic, where pioneer bryophyte and lichen species form the major components of three successional stages, with overall diversity and total cover of the cryptogams increasing with terrain age (Favero-Longo et al. 2012). The succession with deglaciation of Sverdrup pass, Ellesmere Island, Canada was also cryptogam dominant, with early colonization of lichen and bryophyte species (Fahselt et al. 1988).

Within the first stage of succession (0-10m; zone 2), the presence of subfossil tissue indicate limited exposure following a recent ice margin retreat, with sparse colonization reflecting the short seasonal growth period (approximately two months, July 13 - September 9 2015). The relatively small size of the Granger ice patch makes it sensitive to climatic conditions, resulting in ice margin fluctuations as the ice mass accumulates or declines (Farnell et al. 2004). The ice patch variability creates constant disturbance, which has been shown to delay succession in deglaciated areas, particularly with vascular plants (Haughland and Beatty 2004). However, colonist bryophytes, such as observed in the glacial foreland, typically maintain the highest percent cover on the earliest exposed disturbed sites and remain constant in presence over time (Glime 2013). The increase in plant diversity and establishment within the second stage (10-20m; zone 3) suggests longer exposure and stability of this zone.

The dense bryophyte soil crusts formed in third successional stage (30-40m; zone 5) facilitate subsequent colonization through stabilization, water retention, and nutrient cycling (Bliss and Gold 1999, Belnap and Lange 2001, Hodkinson et al. 2003, Yoshitake et al. 2010, Prushkareva et al. 2016) supporting vascular plant development. Biological soil crusts also include of bacteria, algae, and cyanobacteria which were not surveyed within with study, but can be assumed present. Cyanobacteria-bryophyte associations have been shown to accelerate nitrogen fixation, augmenting successional processes (Arróniz-Crespo et al. 2014). Vascular plant and lichen establishment within this successional stage is congruent with prolonged exposure and soil crust establishment (Hodkinson et al. 2003, Nakatsubo et al. 2005). The lack of subfossil tissue (paleosols) indicates the complete evolution of the deglaciated foreland from subglacial assemblages to 100% cover of the extant flora.

Extrinsic contribution

Measured environmental factors (VMC, SM, pH) had minimal correlation with the successional pattern. The NMDS analysis on VWC (water content to soil ratio) showed some correlation with plant succession, based on strong variation of measurements within each zone. During the growing season the ice patch produced networks of melt water channels that were funneled to the central 30m of the ice patch (transects 7-10). Within each zone, measurements from the shoulders (transects 6 and 11, Fig. 1) experienced less melt water influx. VWC was overall lower across zone 5, which can be attributed to distance from the ice margin and percolation of glacial melt water into felsenmeer bedrock (Table 2). Soil moisture (SM) and pH had little variation throughout the entire foreland, suggesting the differences in VWC are also attributed to variation in soil volume across the terrain. Although moisture from ice patch melt did not influence the succession pattern, the ice patch vegetation is completely dependent on the melt water that forms an enriched alpine wetland (Bliss and Gold 1995, Bjork and Molau 2007). Glacial melt supplies water and often nutrients facilitating soil crust colonization (Elster et al. 1999, Colesie et al. 2014). Melt water from alpine snow accumulations (such as ice patches) introduce nitrogen, supporting plant growth and diversity (Bowman 1992), which is otherwise a limiting nutrients in tundra systems (Bowman et al., 1993; Jonasson et al., 1993, Chapin et al. 1994). The flora taxa ranged from mesic to hydric species which would conversely be subject to xeric conditions of the felsenmeer bedrock blocks that are dominated by lichens.

Limited nutrient availability has been attributed to restricted successional success following deglaciation (Svoboda and Henry 1897, Chapin at al. 1994, Elster et al. 2002, Goransson et al. 2011, Knelman et al. 2014, Darcy and Schmidt 2016, Kazemi et al. 2016). The millennia of accumulated dung that has been exhumed from the ice patch strata provide rich nutrients, promoting plant colonization. Dung decomposition will release nutrients to the soil within 2-3 years, facilitating rapid nutrient cycling (Dowding et al. 1981). In particular, bryophytes show accelerated growth with nutrient addition in polar environments (Robinson et al. 1998). In deglaciated areas with enriched nutrient from bird droppings, bryophytes formed dominant communities, whereas richness of vascular plants decreased (Hodkinson et al. 2003). The bryophyte dominant succession pattern at the Granger foreland is therefore highly reliant on the massive caribou dung deposits, in addition to the water and nutrient influx from ice patch melt.

Subfossil community

The similarity in dominant species composition of the succession zones and the emergent subglacial assemblages indicate that the ice patch bryophytes have been at this upland site up to 6470 years cal BP (Table 5), demonstrating long term temporal stability of the community structure. The ubiquitous nature of extant representatives of subfossil plants throughout the mesic terrain suggest that the conditions of zone 1 did not facilitate their establishment. The resiliency of bryophytes coupled with nutrient enriched dung substrate and constant water supply has contributed to their prolonged maintenance within this environment.

Marginal environments (ie. glacial forelands) constrain colonization to plants possessing the necessary physiological and genetic traits to thrive (Larsen 1964). Successful colonization following deglaciation is also highly dependent on protective microhabitats created by boulders and coarse soil, particularly for vascular plant seedling establishment (Jumpponen et al. 1999, Jones and del Moral 2005). The continued temporal persistence of this community structure can also be attributed to the dispersal ability of colonizing taxa (Erschbamer et al. 2008). The dominant foreland and subfossil species belong to the Polytrichales (*Polytrichum juniperinum*, *Polytrichum hyperboreum*, *Polytrichum piliferum*), which produce prolific spores (Hedderson and Longton 1995) capable of further colonization or contributing to the diaspore bank, remaining dormant within the soil and contributing to the persistence of future populations (During 2001, Longton 1997). At the time of the Mount Granger survey, the majority of the Polytrichales species were bearing sporophytes (spore producing structures), thus sustaining their dominance in a positive feedback system. Alternatively, dominant colonizing species *Pohlia drummondii*, and *Leptobryum pyriforme* maintain their presence through the production of gemmae, which are specialized asexual propagules. Asexual reproduction can occur in early stages of bryophyte development and requires less reproductive effort compared to sexual reproduction (spore production; During 1979). *Pohlia drummondii* produces axillary bulbil gemmae, whereas *Leptobryum pyriforme* produces axillary and rhizoidal gemmae, both contributing to long term colonization efforts of these species.

The strong difference between the biodiversity sites and the Granger foreland succession zones can be attributed to the differences in environmental factors. The biodiversity sites were situated along ‘rivulettes’ formed by the ice patch melt, analogous in moisture conditions to the glacial foreland and similarly selecting for growth of mesic taxa. The total richness and diversity of bryophytes was almost three times higher compared to the last succession stage (91 compared to 36 species; Table 4, Fig. 5) due to minimal perturbations and a broader range of microhabitats. Species with less adaptive plasticity colonize the stable sites, but cannot withstand the disturbances encountered within the ice patch foreland. Common subfossil and foreland species, *Polytrichum juniperinum* and *Polytrichum hyperboreum*, were frequent within the BD sites however many additional frequent taxa (ex. *Hylocomium splendens*, *Sanionia uncinata*, and *Dicranum muehlenbeckii*; found at 75% of BD sites) were not found in the subfossil or foreland communities. *Polytrichum sexangulare*, *Polytrichum commune*, and several liverwort species (Table 3) were observed within the foreland, but not within the biodiversity sites. Although they were not observed, their presence within the vicinity of Mount Granger cannot be ruled out considering surveys represent only subsets of the total diversity present.

Ecosystem significance

The Granger ice patch melt has formed a high altitude wetland oasis, providing an integral ecological niche to Yukon fauna (Hare et al. 2012). Caribou (*Rangifer tarandus*) utilize the ice patches as summer refuge from biting insects and for thermoregulation (Anderson and Nilssen 1998). The presence of caribou dung accumulations (spanning 8000 years BP, Farnell et al. 2004) emphasize the significance of the Granger ice patch for faunal support over millennia.

The rivulettes formed by ice patch melt also support diverse plant composition across the landscape (Bjork and Molau 2007). The preservation of these communities is dependent on continuous runoff during the growing season, as moisture inputs from snow and ice melt are essential to maintain polar oasis landscapes (Young 2008). The thick layers of accumulated dark caribou dung throughout the ice patch provide necessary nutrients to developing vegetation, that also decrease the ice surface albedo, contributing to accelerated ice patch retreat. Glacial darkening by mineral and biogenic surface deposition on the Vadret da Morteratsch glacier in Switzerland decreased albedo, directly enhancing melt rate (Oerlemans et al. 2009). With the loss of the Mount Granger ice patch, faunal migration may occur to areas with adequate summer refuge, and the mesic adapted plant communities would experience compositional shifts towards more xeric species.

Conclusions

The fluctuating retreat of the Granger ice patch supports a directional successional change without species replacement. The nutrient influx from caribou dung deposits and seasonal melt water provide unique alpine tundra growing conditions that support a diverse high altitude oasis comprised by a dynamic bryophyte dominant community over 6470 years (cal BP), that is highly specialized to moisture rich landscapes (Bjork and Molau 2007). The average annual summer temperature within Whitehorse, Yukon, has increase by 2°C over the past 50 years, and 4°C during the winter, (Streicker 2016). With this accelerated warming, the ice patch ecosystem, which is one of 87 in Southern Yukon, will be critically affected. Increased subglacial exposure with ice patch retreat will continue to enhance succession, unless climate change affects result in ultimate deterioration.

This study provides a framework for investigating succession at Yukon ice patches. The long term fauna reliance on the ice patches and the plant communities they support is profound; 1725 faunal specimens >6000 years BP, consisting mostly of Caribou (*Rangifer tarandus*) and Sheep (*Ovis dalli*) have been found collectively across ice patches (Hare et al. 2012). Future studies would determine if additional ice patches have pristine subfossil plant assemblages comparable to extant surrounding communities, supporting the current understanding of the ice patches in alpine systems, and further complementing on-going research on long term use of these sites by First Nations as ancestral hunting grounds dated back to 8360 years BP (Hare et al. 2004). The sensitivity the ice patch accentuates the need to understand the associated biological complexity it supports and the plant response with the inevitable ice retreat following climate warming.

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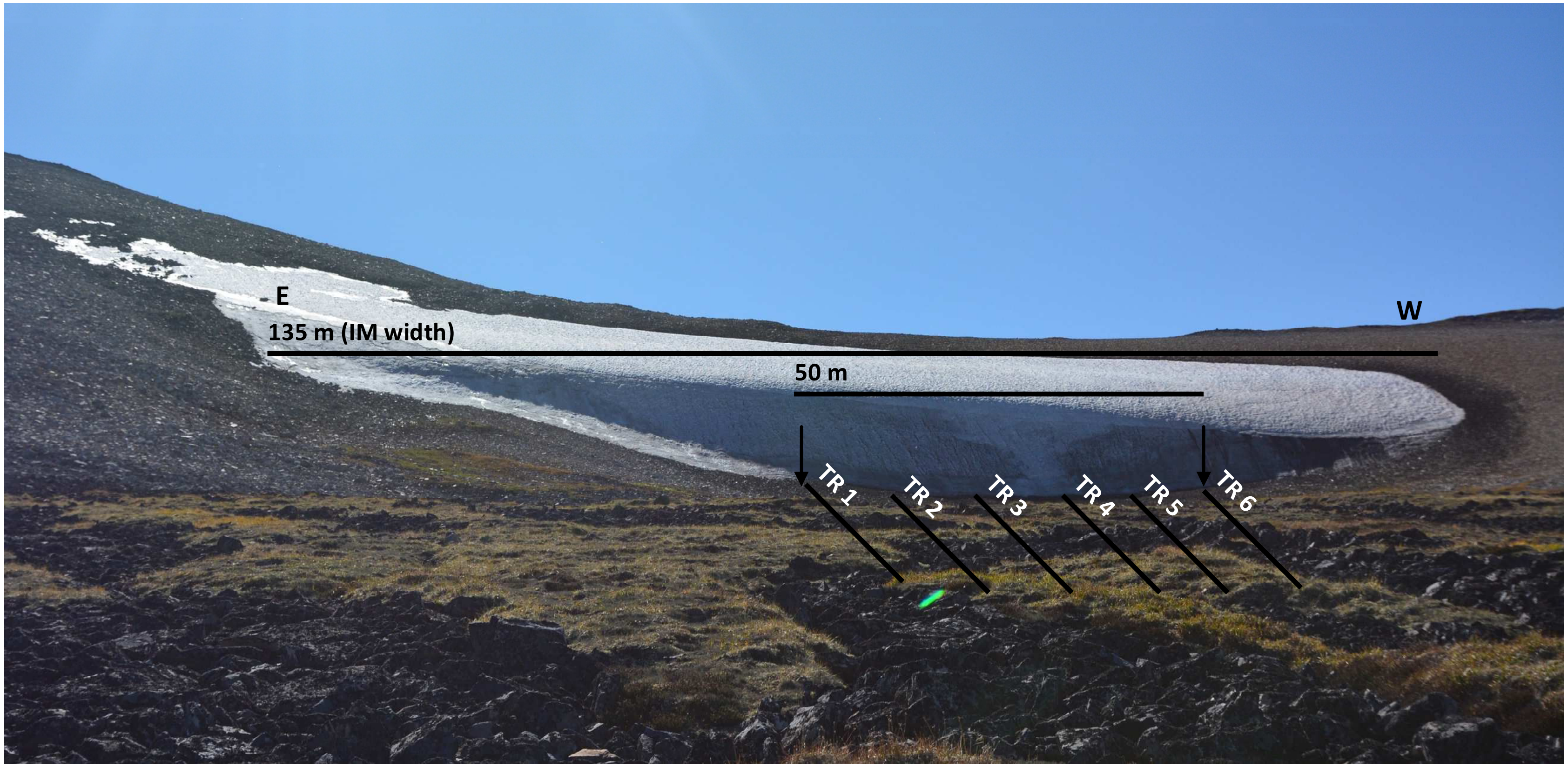


Figure 1. Mount Granger ice patch ice extent in 2015, indicating IM width (135m) and transects subtending the area of successional analysis (Transect (TR) 1-6, 50m span). E= east shoulder of ice patch, W= west shoulder of ice patch.

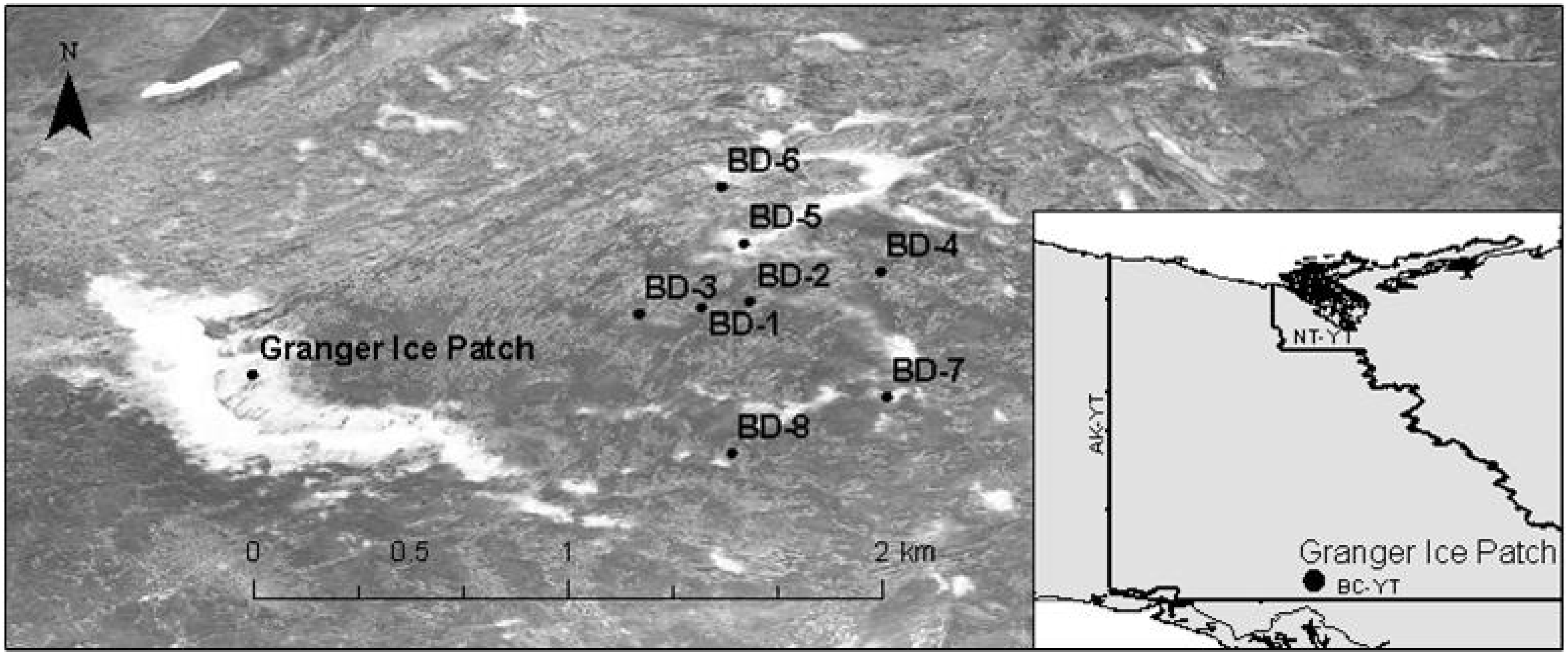


Figure 2. Locality of the Granger ice patch and sampled biodiversity sites. The ice extent depicted is during July 2010 (obtained from Google Earth^{TM}). Locations of biodiversity sites (1-8) surveys are indicated (>1km from ice patch). BD=Biodiveristy site; BC= British Columbia; YT=Yukon Territory; AK=Alaska; NT= Northwest Territores.

Taxon	**Frequency of Presence (%plots)**	**Indicator species analysis (ISA)**	
		Zone	**P-value**
Subfossil tissue	63	2	**0.0001**
Bryophytes			
Dicranum elongatum	2	2	1
Bryophytes			
Aulacomnium palustre	4	3	0.2376
Ceratodon purpureus	44	3	**0.0435**
Imbribryum alpinum	19	3	0.2846
Leptobryum pyriforme	2	3	1
Pohlia crudoides	17	3	0.5242
Pohlia drummondii	42	3	0.1842
Pohlia nutans	65	3	0.1346
Jungermannia sphaerocarpa	6	3	0.4187
Ascomycetes (sac fungi)			
Peziza sp.	13	3	0.6022
Vascular plants			
Dryas octopetala	2	3	1
Luzula confusa	4	3	1
Bryophytes			
Pogonatum urnigerum	17	4	0.2188
Polytrichastrum alpinum	8	4	0.8952
Polytrichum commune	4	4	1
Polytrichum piliferum	33	4	**0.041**
Cephalozia bicuspidata	19	4	0.6837
Jungermannia borealis	13	4	0.6053
Lophoiza incisa	8	4	0.1755
Marsupella brevissima	19	4	0.0502
Marsupella sparsifolia	4	4	1
Lichens			
Cetrariella delisei	6	4	0.5923
Flavocetraria cucullata	8	4	0.8973
Solorina crocea	8	4	0.8918
Vascular plants			
Silene acaulis	4	4	1
Bryophytes			
Niphotrichum canescens	2	5	1
Polytrichastrum sexangulare	10	5	0.3693
Polytrichum hyperboreum	52	5	**0.0141**
Polytrichum juniperinum	19	5	0.3707
Scorpidium cossonii	6	5	1

Taxon	**Frequency of Presence (%plots)**	**Indicator species analysis (ISA)**	
		Zone	**P-value**
Diplophyllum taxifolium	4	5	0.235
Lophozia attenuate	6	5	0.5974
Lophozia sudetica	17	5	0.1286
Lophozia ventricosa	23	5	0.1629
Marsupella emarginata	23	5	0.6977
Tritomaria quinquedentata	6	5	0.055
Lichens			
Cladonia chlorophaea	19	5	0.1294
Cladonia gracilis	25	5	0.2828
Cladonia macrocarpa	2	5	1
Cladonia pyxidata	19	5	0.0774
Dactylina arctica	2	5	1
Stereocaulon alpinum	29	5	0.1752
Thamnolia vermicularis	4	5	0.229
Vascular plants			
Carex eleusinoides	17	5	**0.0063**
Dryas integrifolia	2	5	1
Poa alpina	29	5	0.2627
Total # of species	**46**		

Table 1. Indicator species analysis (ISA) for Mount Granger succession zones 2-5. Distance from the ice margin is as follows: Z2: 1-10m; Z3: 10-20m; Z4: 20-30m; Z5: 30-40m, with 12 0.5m^2 plots surveyed in each zone. Significant species (P<0.05) are shown in bold. Percent frequency was calculated across all plots (n=48).

Zone	**Average**			**Diversity**		**# plots with subfossil material**
	pH	SM	VWC (%)	Shannon (H)	Jaccard (J)	
2 (10m)	7	0.98	30.67	0.15	0.11	12
3 (20m)	6.85	0.97	29.33	1.71	0.78	12
4 (30m)	6.72	2.46	35.67	2.03	0.8	5
5 (40m)	7.1	0.96	24.5	2.3	0.89	0

Table 2. Environmental variables and biodiversity measures for Mount Granger successional areas. Zone 2 representing 1-10m from the ice margin, zone 3 10-20m, zone 4 20-30m, and zone 5 20-40m with 12 0.5m^2 plots surveyed in each zone. Subfossil species were not included into richness and diversity indices, but were amalgamated into total subfossil tissue cover. pH= soil acidity measurement; SM= soil moisture; VMW= volumetric water content; Shannon (H) and Jaccard(J) = diversity indices where higher values represent more diversity.

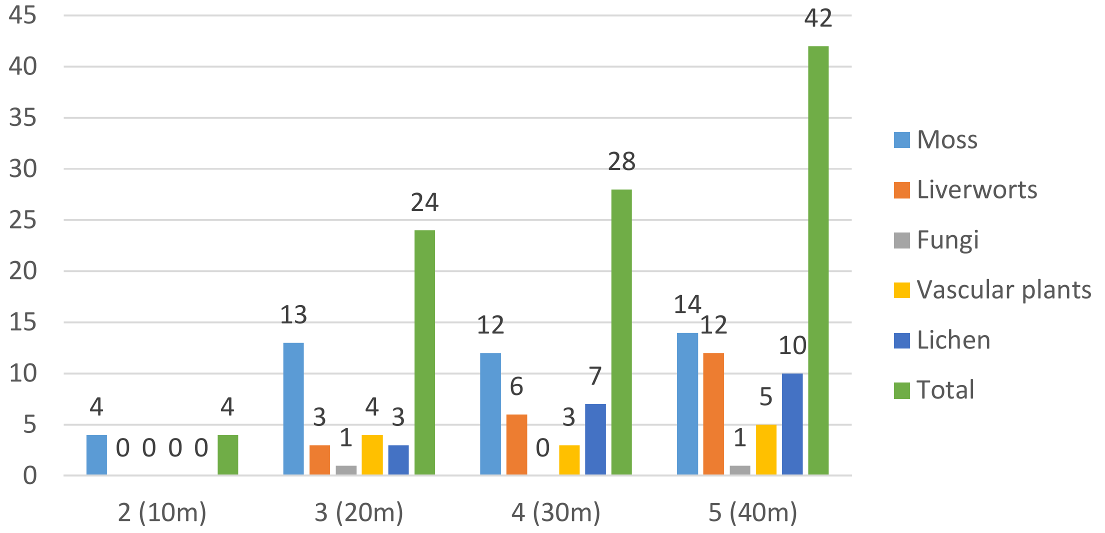


Figure 3. Species richness within in each plant functional group (moss, liverworts, fungi, vascular plants, and lichen) from zones surveyed for successional pattern determination (Z2-5, n=12 plots /zone).

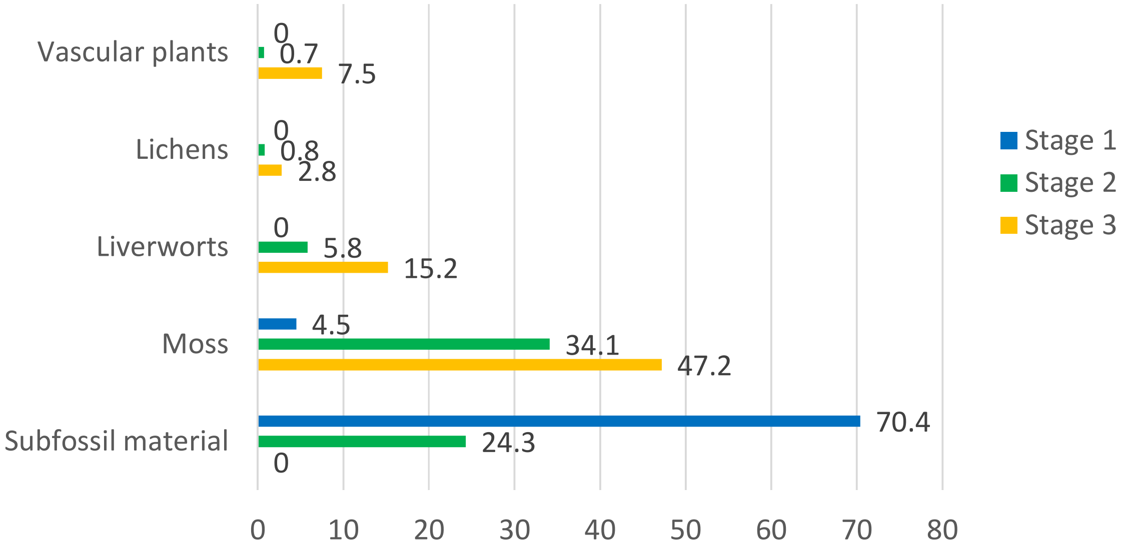


Figure 4. Average percent cover of plant functional groups for each statistically (MRPP) identified successional (seral) stage. Averages were calculated based on individual species percent cover estimates within 0.5m^2 plots, compiled into functional groups (n=12 plots/ each seral stage).

Taxon	Frequency of Presence (% plots)	Indicator species analysis (ISA)	
		Zone	P-value
*Polytrichum juniperinum**	53	1	0.1678
*Ceratodon purpureus**	61	2	**0.0269**
Aulacomnium palustre	5	3	0.2993
*Imbribryum alpinum**	18	3	0.1451
*Pohlia drummondii**	40	3	0.4705
*Pohlia nutans**	71	3	0.1796
Peziza sp.	3	3	1
*Polytrichastrum sexangulare***	4	4	0.2784
*Polytrichum commune***	3	4	1
*Polytrichum hyperboreum**	60	4	0.2172
*Polytrichum piliferum**	43	4	0.2681
Lophoiza incisa	9	4	0.2248
*Marsupella brevissima***	13	4	**0.0199**
*Marsupella sparsifolia***	3	4	1
Cephalozia bicuspidata ssp. ambigua	18	5	0.4948
Lophozia sudetica	13	5	**0.0299**
*Marsupella emarginata***	14	5	0.2067
Andreaea heinemannii	2	6	0.1241
Aulacomnium turgidium	4	6	**0.0149**
Bartramia ithyphylla	4	6	**0.0122**
Conostomum tetragona	7	6	**0.0002**
Cratoneuron filicinum	2	6	0.1204
Cynodontium alpestre	2	6	0.1204
Dicranoweisia crispula	2	6	0.1135
Dicranum acutifolium	11	6	**0.0001**
Dicranum elongatum	13	6	**0.0001**
Dicranum groenlandicum	2	6	0.1178
Dicranum muehlenbeckii	11	6	**0.0001**
Dicranum spadiceum	2	6	0.1178
Distichium capillaceum	2	6	0.1135
Hylocomnium splendens	11	6	**0.0001**
Hypnum hamulosum	2	6	0.1241
Leptobryum pyriforme	1	6	0.747
Niphotrichum canescens	3	6	0.3785
Niphotrichum canescens ssp. latifolium	2	6	0.1135
Philonotis fontana var. pumilla	2	6	0.1222
Plagiothecium denticulatum	4	6	**0.0131**
Plagiothecium piliferum	2	6	0.1135
Pogonatum dentatum	4	6	**0.0122**
*Pogonatum urnigerum**	22	6	0.7254

Pohlia cruda	2	6	0.1135
*Pohlia crudoides**	21	6	0.1229
Polytrichastrum alpinum	13	6	0.1237
Ptychostomum cryophilum	4	6	**0.0125**
Ptychostomum cyclophyllum	2	6	0.1222
Racomitrium lanuginosum	6	6	**0.0008**
Rhizomnium andrewsianum	2	6	0.1241
Rhytidium rugosum	2	6	0.1204
Sanionia uncinata	11	6	**0.0001**
Sarmentypnum pseudosarmentosum	2	6	0.1178
Sarmentypnum sarmentosum	2	6	0.1148
Scorpidium cossonii	10	6	**0.0381**
Sphagnum aongstroemii	2	6	0.1178
Sphagnum fuscum	2	6	0.1178
Sphagnum girgensohnii	2	6	0.1241
Sphagnum warnstorfii	2	6	0.1178
Tetraplodon palldius	2	6	0.1241
Barbalophozia hacterii	4	6	**0.0133**
Blepharostoma trichophyllum	2	6	0.1178
Cephalozia bicuspidata	6	6	**0.0014**
Diplophyllum taxifolium	3	6	0.1007
Jungermannia borealis	8	6	0.1803
Jungermannia sphaerocarpa	9	6	0.3341
Lophozia attenuate	10	6	**0.043**
Lophozia ventricosa	25	6	**0.0296**
Pleurocladula albescens	4	6	**0.0142**
Ptilidium ciliare	7	6	0.1241
Scapania hyperborea	2	6	0.1241
Tetralophozia setiformis	2	6	0.1135
Tritomaria quinquedentata	6	6	0.0549
Total # of species	**70**		

Table 3. Indicator species analysis (ISA) for Mount Granger succession zones 2-5, emergent subfossil communities (1) and biodviersty sites within the vicinity of Mount Granger (6; BD). Analysis was limited to bryophytes (moss and liverworts) at each site. Significant species (P<0.05) are shown in bold. Percent frequency was calculated across plots (n= 76). * indicates species that represent the subfossil assemblages. ** indicates species found within the Granger foreland, but not within the BD sites.

Zone	**Diversity**		**Pairwise comparison**					
			with site 1			**with site 6**		
	Shannon (H)	Jaccard (J)	A	T	P-value	A	T	P-value
1 (IM)	1.45	0.75	-	-	-	-	-	-
2 (10m)	1.4	0.73	0.006	0.396	0.602	0.195	-10.336	<0.0001
3 (20m)	1.83	0.81	0.042	-3.194	0.007	0.137	-9.124	<0.0001
4 (30m)	1.83	0.78	0.1	-7.281	<0.0001	0.122	-8.423	<0.0001
5 (40m)	1.7	0.74	0.122	-9.456	<0.0001	0.088	-7.568	<0.0001
BD (<1km)	2.54	0.88	-	-	-	-	-	-

Table 4. Biodiversity measures for Mount Granger successional areas (Zone 2-5), emergent subfossil assemblages (Z1; at the ice margin (IM)), and the biodiversity (BD) assemblages in the vicinity of Mount Granger. Analyses were from 19 subfossil assemblages, 12 0.5m^2 plots for each successional zone, and 8 BD sites. Measures included subfossil species were applicable. Multi-response permutation procedures (MRPP) comparisons between each zone with Z1 and BD were calculated with significant dissimilarity found with $p < 0.003$ (corrected for multiple comparisons).

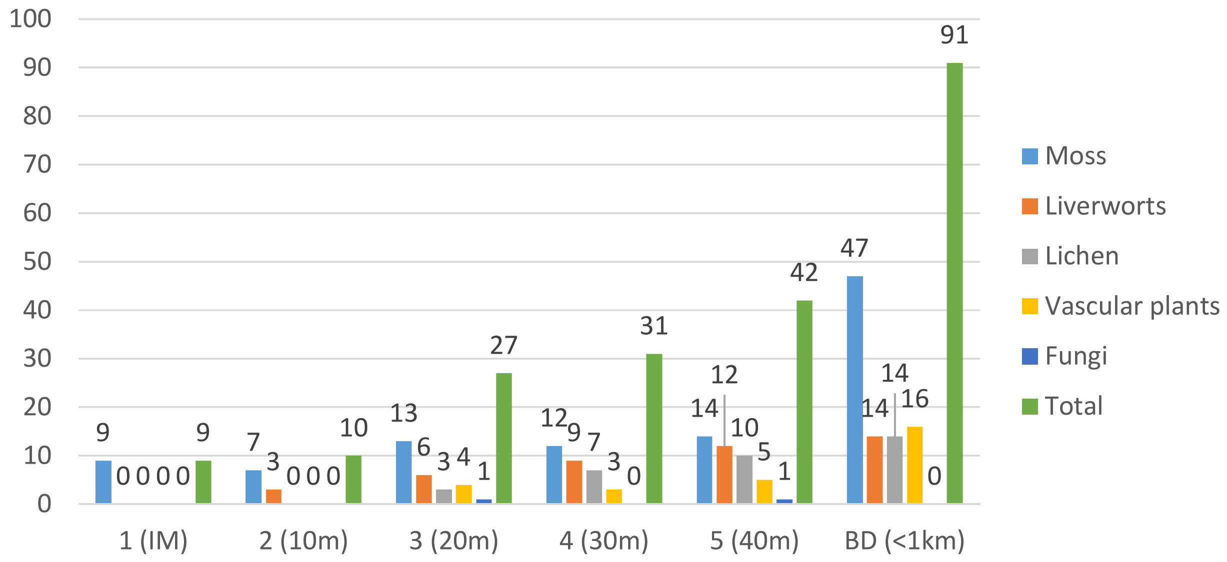
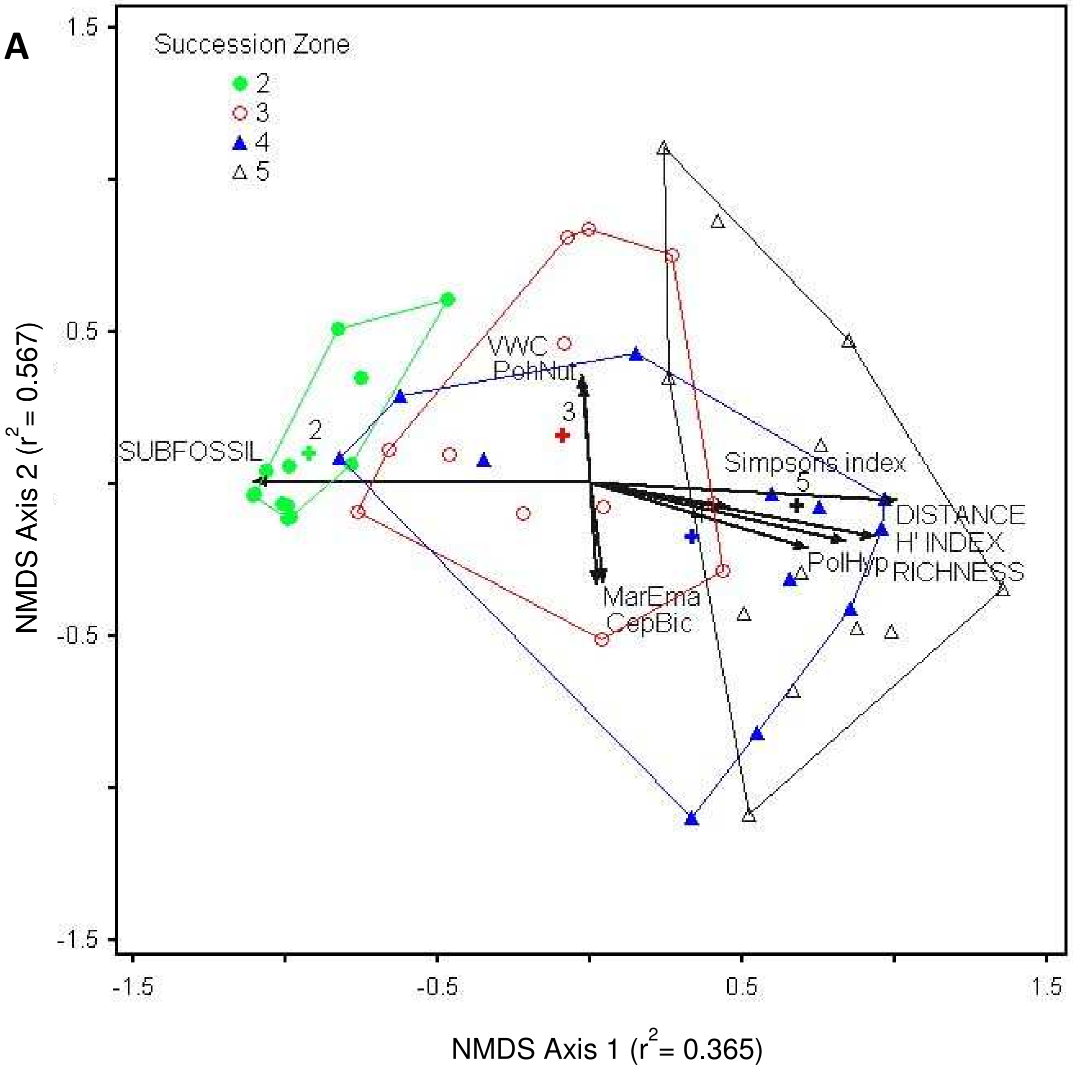


Figure 5. Cumulative richness of plant functional groups for emergent ice margin (IM) samples, foreland zones, and surrounding tundra sites (BD) of Mount Granger. Subfossil (IM=ice margin): previously ice-entombed species exhumed with Granger ice patch margin retreat (n=19); 2-5: successional zones with respective distances from the IM, included identified subfossil species within each zone (n=12/ zone); Biodiversity (BD): mesosites with mesic conditions comparable to the Mount Granger foreland.

UOC No.	Lab Sample ID	Collection Year	Distance from IM	Material	^{14}C yr BP ± error	F^{14}C ± error	Calibrated yr (2 sigma)
3725	2016-GRAN-3	2016	4cm from IM	*Polytrichum* sp. *Psilopilum* sp. *Ceratodon purpureus* *Ptychostomum* sp.	512 ± 38	0.9382 ± 0.0044	BP 560-501 (81.5%) BP 631-600 (13.9%)
3726	2016-GRAN-4	2016	IM	*Ceratodon purpureus* *Polytrichum* sp. *Pogonatum urnigerum* *Pohlia nutans* *Polytrichum juniperinum* *Ptychostomum* sp.	5608 ± 43	0.4975 ± 0.0026	BP 6470-6304 (95.4%)
3727	2015-GR-CD-15-2-73	2015	IM	*Polytrichum* sp.	Modern	1.0865 ± 0.0051	AD 1999-2003 (90.8%) AD 1956-1957 (4.6%)
UCIAMS No.							
187149	GR-CD-15-3	2015	IM	*Polytrichum* sp.	Modern	1.0515 ± 0.0018	AD 2007-2009 (87.0%) AD 1956-1957 (8.6%)
187150	GR-CD-15-1	2015	IM	*Polytrichum* sp.	Modern	1.0542 ± 0.0020	AD 2006-2009 (91.5%) AD 1956-1957 (5.6%)
187151	GR-CD-27-6	2015	20m from IM	*Polytrichum* sp.	Modern	1.0579 ± 0.0016	AD 2006-2009 (84.5%) AD 2005-2006 (9.7%)
187152	GR-CD-26-5	2015	10m from IM	*Polytrichum* sp.	Modern	1.0819 ± 0.0017	AD 2001-2004 (78.4%) AD 2001-2001 (18.4%)

Table 5. Radiocarbon dates (14C) of bryophytes from the Mount Granger ice patch, Yukon. Samples were submitted to A.E. Lalonde AMS (Accelerator Mass Spectrometry) Laboratory, University of Ottawa (UOC) or W. M. KECK Laboratory, University of California, Irvine (UCIAMS). Radiocarbon dates (yr BP) and calibrated ages (cal y BP) are given on stem apices of submitted samples. Calibrated age is give in range of sample age and chance (%) of material being older or younger than the date calculated. The two calibrated ages from UCIAMS samples with the highest chance (%) are listed.


A
Succession Zone
2
3
4
5
VWC
PohNut
3
2
SUBFOSSIL
Simpsons index
5
DISTANCE
H' INDEX
RICHNESS
PolHyp
MarEma
CepBic
1.5
0.5
-0.5
-1.5
-1.5
-0.5
0.5
1.5
NMDS Axis 2 (r^2= 0.567)
NMDS Axis 1 (r^2= 0.365)

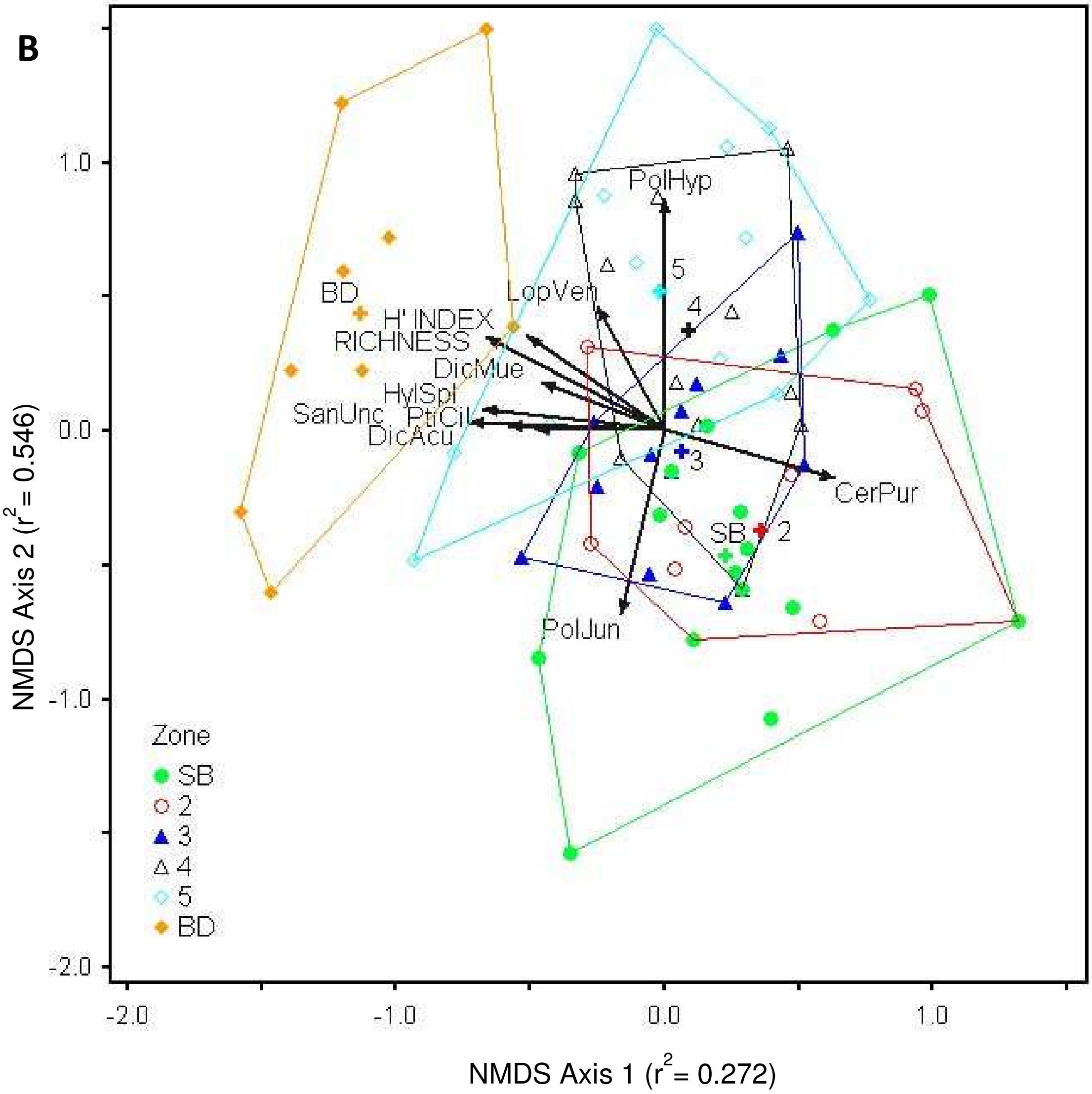


Figure 6. Ordination joint plots from nonmetric multidimensional scaling (NMDS) with overlays of environmental variables and biodiversity measures from Mount Granger ice patch foreland quantitative plot data. Vector length and direction indicate strength of correlation with each ordinal axis. All vectors r>0.2 are shown, with vectors r>0.5 capitalized.
A) Successional zones with percent cover of all plant taxa (moss, liverworts, lichens, fungi, and vascular plants; see Table 1) and exhumed subfossil assemblages. Successional zones (2-5) = Z2: 1-10m; Z3: 10-20; Z4: 20-30m; Z5: 30-40m. Final ordinal stress of 11.62965, 98 iterations, 0.00 instability. B) Presence or absence of bryophyte species from each successional site (2-5), SB (emergent subfossil tissue within 20cm of the ice margin; Z1), and BD (Biodiversity survey areas within the Mount Granger vicinity; selected for microhabitats analogous to the ice patch foreland). Final ordinal stress of 15.2470, 106 iterations, 0.00 instability. Abbreviations: VMC= volumetric water content, H' index= Shannon diversity index, PolHyp= *Polytrichum hyperboreum*, MarEma = *Marsupella emarginata*, DicMue= *Dicranum muehlenbeckii*, HypSpl= *Hylocomium splendens*, PtiCil= *Ptilidium cilliare*, SanUnc= *Sanionia uncinata*, DicAcu= *Dicranum acutifolium*, CetPur= *Certatodon purpureus*, PolJun= *Polytrichum juniperinum.*

Chapter III: Yukon Ice Patches: Bryophyte generation from ancient ice-entombed assemblages

Introduction

Within Arctic Canada, summer temperatures have been significantly higher over the past 100 years compared to historical records (Miller et al. 2013), contributing to the accelerated retreat and thinning of ice margins (Gardner et al. 2011). Recession of cold-based glaciers with basal ice frozen to the substrate, preserve the integrity of former ice-entombed terrain (Dyke 1993). In northern regions, emergent intact plant communities have been found in pristine condition (Falconer 1966; Bergsma et al. 1984, La Farge et al. 2013). Climate warming is predicted to have detrimental effects on high latitude and altitude bryophyte populations on a global scale by shifting the optimal temperature for photosynthesis, decreasing metabolic activity, and intensifying desiccation frequency beyond survival capacity (He et al. 2016). Bryophytes often form the dominant taxa of alpine and arctic communities of deglaciated forelands as pioneer species that facilitate vegetation re-establishment (Bliss and Gold 1999, Breen and Levesque 2006, Gornall et al. 2007) and as emergent subglacial substrate (La Farge et al. 2013). This study will address the role of alpine bryophytes beyond pioneer species that establish early in succession, or emergent organic substrate that enriches foreland succession, but as resilient, temporal continuity of successive generations of populations through millennia to alpine ice patch ecosystems.

Bryophytes have a suite of adaptive traits that maintain persistence in extreme climates (Longton 1997). Cold-adapted arctic and alpine bryophytes are often desiccation tolerant, facilitating cryptobiosis until rehydration (Proctor 2000). During environmental freezing minimal intracellular ice is formed that would otherwise damage the integrity of the cells (Lenne et al. 2010). As well, bryophytes express several molecular mechanisms that prevent cellular damage from diurnal freeze-thaw cycles. They continually produce dehydrins, late embryogenesis abundant (LEA) proteins that preserve membrane and enzyme integrity during freezing events (Bewley et al. 1993, Graether and Boddington 2014), and accumulate sucrose for vitrification, preserving cell viability (Buitink et al. 2002). Glutathione (GSH) antioxidants levels are also maintained to protect against reactive oxidative species (ROS) produced by photosynthesis inhibition during desiccation (Proctor et al. 2007). Bryophytes are also totipotent, referring to cells that can dedifferentiate (stem cells) to regenerate an entirely new organism from virtually any viable cell of the gametophyte (Ishikawa et al. 2011, Kofuji and Hasebe 2014). When faced with injury or isolation, the normal apical dominance is lost and regrowth will be stimulated. In addition to field observations of *in situ* regeneration at the glacial margin, research at the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut has shown that growth chamber assays of 400 years (cal BP) - Little Ice Age - entombed bryophytes confirmed successful *in vitro* regeneration (La Farge et al. 2013). The regeneration capacity of ice-entombed, ancient bryophyte populations has also been demonstrated for >1500 year (cal BP) moss gametophytes from of permafrost cores collected at Signy Island, Antarctic (Roads et al. 2014).

As a fundamental part of the bryophyte life cycle and often the dominant mode of reproduction in extreme environments, bryophytes contribute to diaspore banks, consisting of spores, specialized vegetative propagulae, and gametophytic fragments. Propagulae (i.e., gemmae, bulbils, and tubers) are desiccation tolerant and remain dormant in soil until ideal growth conditions arise (During 2001). These diaspores form genetic archives of successive generations of populations, encapsulating phenotypic variation produced under variable environmental conditions (Hock et al. 2008). This maintains genetic diversity and persistence in a habitat when faced with variable conditions through time (Thompson and Grime 1979, Frey and Kürschner 2011).

Within the Yukon, over 65 of ice patches have been systematically surveyed for exhumed biological remains and archeological artefacts, dating up to 8000 years old BP (Farnell et al. 2004, Hare et al. 2004, Hare et al. 2012), with three (Granger, Thandlät, and Friday Creek) surveyed in depth for glaciological and palynological history. The ice patches are formed as snow accumulations on north facing mountain slopes during ice free periods in the early Holocene, such as the Mount Granger ice patch (Farnell et al. 2004) or are glacial remnants of the Little Ice Age, as observed by flow patterns within the ice, such as the Gladstone ice patch (Dr. John England, personal communication) . Both the Granger and Gladstone had stratified layers of wind-blown sediment and dung accumulations from Caribou (*Rangifer tarandus*) populations that utilize the ice patches as summer refuge (Farnell et al. 2004). These ice patches are relatively small ice formations, 135m km wide at Granger and 1 km wide at Gladstone, making them highly susceptible to climate warming affects with evidence of rapid retreat (Farnell et al. 2004).

Ice patch forelands create a unique alpine wetland that are integral support to diverse flora and fauna (Farnell et al. 2004, Hare et al. 2004, Hare et al. 2012). Current understanding of the ice patch biology is limited to ^{14}C dating of subglacial vegetation in archeological surveys

(Hare et al. 2004), ice-entombed palynological analysis for paleo-environmental reconstruction (Bowyer et al. 2001). The composition of emergent ice patch vegetation and its relevance to understanding both past and present alpine ecosystems remains uninvestigated (see chapter 2). These ice patches also represent an opportunity to expand the current research on understanding the biological role of bryophytes in extreme environments. Our current study examines the role of bryophytes in alpine ice patch ecosystems. The objectives are to : 1) determine the radiocarbon age (^{14}C) composition, and regrowth potential of exhumed bryophyte and dung samples from the Granger, Gladstone and Little Gladstone ice patches (GRIP, GLIP, and little GLIP, respectively); 2) compare the composition of both subfossil and growth chamber assays of each ice patch ecosystem to determine regional variability through time. This study investigates the role of Yukon ice patches as biological reservoirs and their capacity to maintain a unique alpine wetland ecosystem that is an integral part of seasonal foraging by Yukon alpine fauna (i.e., Caribou -*Rangifer tarandus*, dall sheep - *Ovis dalli*). Understanding the biological maintenance of these critical alpine ecosystems is key in the face of climate change.

Methods

Study area

Mount Granger is within the southern-lakes ecoregion of the intermontane belt of the boreal cordillera ecozone, approximately 20 km SW of Whitehorse, Yukon (Fig. 1; Smith et al. 2004). This region is semi-arid, with a mean annual temperature of -1 to -2^{o}C, annual precipitation from 200-235 mm, and alkaline soils of glacial deposits and discontinuous areas of permafrost (Smith et al. 2004).

Approximately 170 km Northeast of Mount Granger is Gladstone, situated in the Ruby Ranges ecoregion of the boreal cordillera ecozone, East of Kluane Lake, Yukon. Annual temperature varies depending on elevation, ranging from -3 to -7^{o}C, and precipitation within this region is an average of 250-300 mm annually (Smith et al. 2004). Soils are predominately cryosols, also composed of glacial deposits and sporadic discontinuous permafrost. Little GLIP is approximately 2 km NW of Gladstone, within the same ecoregion and environmental regime (Fig. 1).

Experimental design

Emergent subfossil vegetation was collected from the GRIP (N 60.538975°, W 135.256047°) from August 3-12 2015 and on July 28 2016, GLIP (N 61.27098^{o}, W 137.97339^{o}) from July 17-24 2016, and the little GLIP (N 61.28699, W 37.99942^{o}; Fig. 1) on July 25 2016, following maximum seasonal ice retreat. Emergent bryophyte populations and caribou dung were collected within 1m of the ice margin (IM) as observed (Fig. 2). To preserve the integrity of exhumed tissue, samples were placed in polyethylene whirlPak bags™ (Nasco®) and stored in a cooler for transport to the University of Alberta where they were stored in a freezer at –20^{o}C. The bryophyte samples varied between 100-200g, depending on the size of the emergent population. Additional samples of fresh dung and extant vegetation up to 30m from the IM were collected to compare extant and subglacial samples for regrowth capacity.

To detect potential spore rain from the surrounding extant flora emergent IM subfossil samples that could contribute to false-positive subfossil growth in growth chamber assays, 14 spore traps were placed along the IM of the GRIP. Traps consisted of twice autoclaved soil samples (commercial brand Miracle-Gro® potting soil) in open petri dishes, to capture any wind-blown spores, propagules or fragments from surrounding areas and the IM foreland during the time of collection. Eight dishes were collected after the 2015 survey (10 days), and six were left *in situ* for collection in 2016. Collected plates were sealed with parafilm and transported back to the University of Alberta for growth chamber assays.

Subfossil Radiocarbon Dates

Five subfossil bryophyte samples from the Gladstone and Granger 2016 IM were submitted for radiocarbon dating (^{14}C) at A.E. Lalonde AMS (Accelerator Mass Spectrometry) Laboratory, University of Ottawa to determine the age range of emergent populations and regeneration. Apices from subfossil bryophyte stems of two Gladstone and three Granger populations (Table 1) were subsampled for age determination. Each sample was analyzed for species composition and washed in double-distilled H_20 to remove any plant debris (fungal hyphae, moss rhizoids, algae) prior to submission. Sampling of stems was limited to the youngest material (apices) to accurately represent the last growth period before ice entombment. Additional samples of exhumed dung from Gladstone were submitted to assess its potential contribution of diaspores to regeneration of the ice patch foreland.

Granger Ice Patch Retreat

The perimeter of the GRIP was measured and compared to previous measurements in Farnell et al. (2004) to determine shrinkage and exposure of successional areas. To estimate seasonal ice margin fluctuations and therefore vegetation emergence, thirteen metal stakes were placed along the margin on the first field day, August 4, 2015. Six stakes were collected after five days, and seven were left to be collected on July 28, 2016 (Table 2).

The duration of seasonal snow melt and IM exposure was estimated using eight Thermochron iButton data loggers, placed ~5 cm into the soil every 10m along the center of the Granger ice margin on August 12, 2015: (5) at each transect, (1) 10m E of transect 1, (2) 10 and 20m W of transect 5 (see chapter 2, Fig. 2). Data loggers were set to record temperatures every 240 minutes and to overwrite oldest data and continue to record temperatures ('rollover' was activated), capturing the 2016 growing season: September 4 2015-July 28 2016 when they were collected. Data loggers were analyzed using 1-Wire®/iButton® viewer (Maxim Integrated).

Growth Chamber Assays

Subfossil samples were assessed for regeneration capacity though *in vitro* growth chamber assays following field collection: 2015 Granger samples (September 2015), and 2016 Granger, Gladstone and Little Gladstone samples (August 2016). Approximately 20-30g portions of subsamples 'as is' were seeded into sterile, autoclaved 100ml Magneta^{TM} B-cap (Sigma) jars following 6 hours of thawing at room temperate (Fig. 2). A total of 90 bryophyte samples were selected for growth chamber assays: 1) 42 from the GRIP 2015 field season, including 31 emergent ice margin (IM) bryophyte populations, 1 emergent dung sample (Replicates were created for populations where ample material was collected, resulting in a total of 88 GRIP 2015 assays; Table 3; Appenix A), and 10 extant populations ≥1m from the IM to confirm species regrowth potential, 2) 4 emergent IM samples from GRIP (2016), 3) 39 GLIP samples without replication; 22 representing emergent IM populations, 10 populations > 1m from the IM, 4 emergent ice-entombed dung samples, and 2 of fresh dung collected >40m from the IM as a control of dung diaspore contribution, and 4) six samples from Little GLIP, including five populations < 1m from the IM and one population 2.5m from the IM (Table 3; Appendix A).

Assays were kept at consistent growth conditions with a mean irradiance of 74 ± 9.3 SD $\mu mol^{-2} \cdot s^{-1}$, simulating 16 h of daylight and 8 h of darkness with 215 W cool-white fluorescent bulbs, with temperature maintained at 15 °C (La Farge et al. 2013). The assay samples were hydrated using autoclaved distilled water every 7 days or as necessary. Observations were made monthly noting the chronological vegetative emergence. When gametophytes had matured enough to show the salient features necessary for identification, assays were harvested (2015 samples – 9 months and 2016 samples- 4 months).

The subfossil and newly generated taxa of each assay were determined by floating the populations in distilled water. Unequivocal regeneration was determined from new growth directly from subfossil tissue or juvenile growth of a species documented in the original subfossil sample. Species not documented on the original subfossil sample indicated evidence of diaspore germination. Regrowth was documented photographically, compiled in Zerene stacker^{TM} and edited in Adobe photoshop® CC 2015 version (Fig. 3-5).

Species determination and nomenclature followed Bryophyte Flora of North America Editorial Committee, eds. 1993+ (2007, 2014; bryophytes), Damsholt (2009; liverworts), Cody (1996; vascular plants), and Arora (1986; fungi). Some specimens were not determined to species, lacking diagnostic features. These included *Saxifraga, Pezzia, Sphagnum, Lophozia, Cephaloziella* and one juvenile fern species. Vouchers of all taxa are deposited in the Cryptogamic Herbarium (ALTA), Department of Biological Sciences, University of Alberta.

Secondary Regrowth Assays

To discern direct regeneration of gametophytes from subfossil material, nine assays containing taxa that were determined in the original subfossil sample were subjected to a secondary regrowth assays on plant growth media (Phytagel™ Sigma-Aldrich®). Eight to ten individual stems of the original subfossil material were extracted, rinsed with double distilled water, and inspected with a dissecting microscope to remove any debris or visible spore contaminants. Stems were then seeded onto Phytagel™ growth media and placed in the growth chamber for two months. Plates were hydrated with autoclaved distilled water and analyzed for plant development, weekly.

Spore Trap Controls

Petri dishes that functioned as spore traps were subjected to the same growing conditions and duration as the subfossil samples. Five controls were also placed in the growth chamber to test the autoclave efficacy of the soil substrate used, ensuring any growth observed in the exposed plates could be attributed to spore rain.

Statistical Analysis

Statistical analyses were used to compare the generated species composition between the ice patches (Granger 2015, 2016, Gladstone and Little Gladstone). Composition of growth chamber assays were assessed using with non-metric multidimensional scaling (NMDS; Legendre and Legendre 1998, McCune and Grace 2002) in PC-ORD 6.19 (McCune and Mefford 2011). The ordination was run with presence/absence species data of subfossil samples where material was discernable (54 samples and 17 species; Granger 2015 n=20, Granger 2016 n=4, Gladstone n=25, Little Gladstone n=5) The zero inflated data set with several single species accounts was navigated with a jaccard distance metric that minimizes the influence of outliers (Legendre and Legendre 1998). Joint plots overlays of the species variables with high correlations to ordinal axes (r>0.2) were included to indicate the species contributing most to the spatial organization (Fig. 6). Significant differences of subfossil composition at each ice patch was tested using multi-response permutation procedure (MRPP; McCune and Grace 2002) with a jaccard distance metric in PC-ORD 6.19 (McCune and Mefford 2011). Analysis of generated species composition between each ice patch to determine the similarity of regrowth potential between each ice patch was conducted with the same statistical procedure (66 samples and 43 species; Granger 2015 n=32, Granger 2016 n=4, Gladstone n=25, Little Gladstone n=5; Fig. 7). The similarity between subfossil and growth composition of each ice patch was also assessed with MRPP analysis.

The frequency of species regrowth at each ice patch was determined through Indicator Species Analysis (ISA; Dufrene and Legendre 1997) in PC-ORD 6.19 (McCune and Mefford 2011) with 9999 permutations for Monte Carlo analysis of indicator value significance (Table 4).

Results

Subfossil Radiocarbon Dates

Radiocarbon dates from subsamples of exhumed bryophyte assemblages from along the Granger ice margin in 2016 were up to 6407 years old (cal BP), but were subjected to more age mixing due to glacier melt, showing tissue as young as 501 years old (BP old; Table 1). Gladstone ice margin ranged in age from 4049-4815 calibrated years BP (Table 1). Subsamples of accumulated, emergent dung from the same site was similar in age, ranging from 4089-3873 calibrated years BP.

Granger Ice Margin Retreat

In 2015, the GRIP was estimated as ~1.71 ha, 4% of the LIA maximum size as determined by the lichen free zone (LFZ; Farnell et al. 2004). After five days of surveying in 2015, the margin had melted back a maximum of 1.17cm from stakes 10 stakes marking the IM (Table 2). In 2016 (July 28 2016) seven stakes were re-measured for distance from IM, revealing a maximum retreat rate of 4.73 m/yr (Table 2) at the center of the ice patch.

Data loggers recorded soil temperatures reaching above 0 ^{O}C between July 13 -24, indicating seasonal snow melt to the 2015 ice margin extent (point of data logger placement) within this twelve day period. Approximately 1900 temperatures reads were collected from seven data loggers, one failed to be recovered due to snow cover (data logger E of transect 1; see chapter 2 Fig. 2). From the date of the first reading above 0 ^{O}C to the collection of the data loggers on July 28 2016, recorded soil temperatures ranged from 0.5 ^{O}C - 6.2 ^{O}C, with an overall average of 3.7 ^{O}C. The data loggers were collected prior to the end of the 2016 summer season, however, records from 2015 show complete snow cover of the Mount Granger vicinity on September 9 (M. Svoboda, personal communication), approximating a two month seasonal exposure of the Granger ice margin.

Subfossil Composition

All exhumed bryophyte populations were preserved in pristine quality (leaf attachment, intact cellular structure), with 16 moss species from the three ice patches. The most frequent species from the ice patch subfossil samples, were *Certatodon purpureus* (35-100%), *Polytrichum juniperinum* (38-80%), and *Polytrichum piliferum* (12-75%; Table 4). The Gladstone subfossil assemblages had the highest richness (15 species, Table 4), which was roughly double the richness of Little Gladstone (8 species) and Granger 2015 (8 species). Granger 2016 only contained a third of the Gladstone richness (5 species), but was comparable to the Granger 2015 assemblage richness. The Granger 2015 and 2016 assemblages shared four taxa (*Ceratodon purpureus*, *Polytrichum juniperinum*, *Polytrichum piliferum*, and *Pogonatum urnigerum*, Table 4) but were differentiated by *Pohlia crudoides*, *Polytrichum hyperboreum*, and *Pohlia nutans*, which were restricted to the 2015 samples, and *Ptychostomum pallescens* which restricted to 2016. The Granger subfossil assemblages represented 10% of the total extant richness of Granger (glacial foreland and within the vicinity of Mount Granger; see chapter 2).

The NMDS analysis of subfossil composition shows overlap of all ice patches, (excluding Little Gladstone with Granger 2016 which did not overlap, Fig. 6) indicating similarity of assemblages. All sites were not significantly different ($p>0.008$) except for a comparison of Granger 2015 with Gladstone 2016 ($T=-5.81$, $A=0.04$, $p<0.000$). Ordinal axis 1 represented the

40% of the variation whereas Axis 2 represented 61% (Fig. 6). Sample size did not drastically influence the strength of the ordination; 8.914 stress from the 2-dimensional solution with Granger 2015 and Gladstone 2016 samples compared to a final stress of 10.91 for all ice patches, p<0.000). *Dicranum acutifolium* and *Dicranum elongatum* were negatively correlated with axis 2, due to their frequency in the Gladstone 2016 assemblages, whereas *Polytrichum juniperinum* was negatively correlated with axis 1, due to its high frequency within Little Gladstone and Granger 2015. *Pohlia nutans* was positively correlated with axis 2 due to its presence in all sites except for Granger 2016, where it was absent.

Phenology of Plant Emergence

After one month in the growth chamber, the Granger 2015 samples developed dense protonemal mats, covering the majority of substrate. Bryaceous (*Pohlia* spp*.* and *Ptychostomum* spp.) gametophores developed in abundance with a few stems of Polytrichaceae taxa, *Lophozia* spp. and fungal hyphae. At this stage most vegetative growth lacked salient features for classification beyond family or genus. At two months, gemmae were observed on *Pohlia* spp*.,* *Marchantia polymorpha* began to develop, and diagnostic characteristics for species level determination of *Polytrichum* (such as awns) began to develop. By three months, there were no additional species, but some *Pohlia* sp. *samples* developed sporophytes. At four months, the gametophores of established taxa such as *Pohlia* sp. and *Leptobryum pyriforme* proliferated, dominating assays and *Lophozia* spp. developed gemmae. The 2016 Granger, Gladstone and Little Gladstone assays followed a similar pattern, with the majority of assays showing prolific growth of several moss and liverwort taxa after 15 days. Vascular plant development did not occur until four months in the growth chamber.

Regrowth from Caribou Dung

Exhumed caribou dung from the IM of the GLIP contained *Ceratodon purpureus* and *Pogonatum urnigerum* stems, and produced *in vitro* generation of *Polytrichum juniperinum*, *Pohlia nutans*, and *Marchantia polymorpha* (Fig. 3). Three fresh dung samples were also assayed, two of which produced fungal hyphae, and one lacked detectable plant fragments, but developed *Tetraplodon mnioides* and *Splachnum vasculosum*, not present within the subfossil regrowth or subfossil assemblages (Appendix A).

Exhumed dung from the Granger 2015 IM contained subfossil fragments of *Certatodon purpureus* and *Polytrichum* sp. lacking critical diagnostic features for species determination, produced nine regrowth species *in vitro*: *Polytrichum hyperboreum*, *Polytrichum juniperinum*, *Pohlia nutans*, *Ceratodon purpureus*, *Pogonatum urnigerum*, *Imbribryum alpinum*, *Pohlia drummondii*, *Leptobryum pyriforme*, and *Cephalozia bicuspidata* ssp. *ambiguua* (Fig. 3).

Ice Patch Regrowth Capacity

GRIP 2015 subfossil assemblages were comprised of six species, all of which were present within the growth chamber assays (5-100% frequency, Table 4). Including subfossil representatives, 32 species grew *in vitro*: 20 mosses, 11 liverworts, and 1 ascomycete (Table 4). Of the 23 subfossil samples (including emergent dung; Table 3), 22 assays contained the generation of at least one species found in original subfossil material (95%; Table 4). All subfossil taxa were more frequently observed within the regrowth assays, with the exception of *Ceratodon purpureus,* which was more frequent in the subfossil record (1.3 times greater, Table 4). Based on number of observations, the most frequent taxa (≥59%) were *Ceratodon* *purpureus*, *Leptobryum pyriforme*, *Pohlia drummondii*, *Pohlia nutans*, and *Polytrichum juniperinum*. Several taxa were restricted to the Granger 2015 assays: *Gymnomitrion corallioides*, *Jungermannia borealis*, *Lophozia attenuata*, *Lophozia incisa*, *Lophozia sudetica*, *Marsupella emarginata* var. *pearsonii*, and *Niphotrichum ericoides*. Two assays showed initial protonemal development, but growth did not develop beyond this stage. Species that regrew were generated *in vitro* from the Mount Granger 2015 samples represented 65% of the extant foreland bryophyte diversity and 35% of the total bryophyte diversity of Mount Granger (see chapter 2, Table 4), five taxa were not observed in extant assemblages (*Cephalophoziella* sp., *Gymnomitrion corallioides*, *Niphotrichum ericoides*, *Ptychostomum pallescens*, *Trichostomum* cf. *arcticum*; Table 4).

The GRIP 2016 samples were collected along the ice margin, which was 1.5-4.73m from the previous 2015 August ice margin (Table 2). The subfossil assemblages contained five species, one of which was not observed in the 2015 assemblage (*Ptychostomum pallescens*; Table 4). Representatives of all subfossil taxa were found growing *in vitro*, including 11 species (10 mosses and 1 liverwort; Table 4), with all assays containing the generation subfossil taxa (Appendix A). *Polytrichum piliferum* and *Ceratodon purpureus* had the highest frequency within the subfossil assemblage (1.5 and 1.3 times greater frequency, respectively). The samples collected in 2016 were from areas not exposed in 2015, providing insights to temporal composition shifts in species presence.

The GLIP subfossil assemblage contained 15 species, 11 species were generated within the growth chamber assays (Table 4). Four subfossil taxa did not develop, including *Dicranum acutifolium*, *Dicranum groenlandicum*, *Imbribryum alpinum*, and *Niphotrichum canescens*.

Generated species richness was 21: 17 mosses, three liverworts, and two vascular plants (*Saxifraga* species and an immature fern unidentifiable to genus or species). From the 26 subfossil assays (including emergent dung; Table 3) 17 contained juvenile growth of species found the original subfossil assemblage (65%). The dominant taxa (≥56% frequency) were similar to Granger, including *Ceratodon purpureus*, *Leptobryum pyriforme*, *Pohlia nutans*, and *Polytrichum juniperinum*, however the generated species richness of Gladstone was only 65% that of the Granger 2015 richness. *Conostomum tetragonum*, *Hypnum revolutum*, *Pohlia filum*, *Ptychostomum cryophilum* and the Fern taxa were restricted to the Gladstone generated assay species/samples.

Little GLIP assays generated six species that were present within the subfossil assemblages. Two species, *Dicranum acutifolium* and *Pogonatum urnigerum*, were not determined in the subfossil samples (Table 4). Seventy-five percent of the assays showed species generated that were present in the original subfossil samples (Appendix A). The growth chamber assays contained 18 generated species (15 mosses and 3 liverworts), 86% of the generation richness at Gladstone, and 56% the generation richness of the 2015 Granger assemblages. The most frequent taxa were *Pohlia nutans* (100%) and *Ceratodon purpureus* (83%, Table 4). All 18 taxa (with the exception of *Ditrichum flexicaule*) were observed growing in the assays from other ice patches.

The growth chamber assays of emergent subfossil material (≤1m from the IM) indicated that 98% developed moss gametophores of at least one taxon (Table 3). All IM assays from Granger (2015, 2016) and Little Gladstone contained growth (100% success), whereas

Gladstone had a 95.7% success rate with one assay restricted to fungal hyphae development (Table 3). Growth chamber assays of the emergent ice margin samples (67 between Granger, Gladstone, and Little Gladstone), 49 had growth of at one species representing the subfossil assemblage (73%; Table 4), and 27 contained growth of all species within the original assayed subfossil assemblage (59%) showing high frequency of potential regeneration events. On average, 32.7% of growth within each assay represented the original assayed subfossil assemblage. Dissection of the assays did not indicate that the generated taxa was directly attached to the parental subfossil tissue. Over all, generated composition was more species rich compared to the original subfossil assemblages (40 versus 13 species, respectively), with six generated species shared by all ice patches (*Ceratodon purpureus*, *Leptobryum pyriforme*, *Pohlia nutans*, *Pohlia drummondii*, *Polytrichum juniperinum,* and *Polytrichum piliferum*; Table 4). Many of the *in vitro* taxa were not determined in the subfossil sample, suggesting that they developed from preserved diaspores (26 species, 57% of the total richness across sites).

All growth chamber of extant samples (>1m from the IM) contained species generation except for one Granger 2015 assay that lacked growth (98% success). Three extant populations (>1m from the IM) of *Polytrichum juniperinum* (Granger and Gladstone samples) *Aulacomnium turgidum* (Little Gladstone) showed direct regeneration from original gametophyte stems (Fig. 5). *Aulacomnium turgidum* regrew from lateral stem initials and *Polytrichum juniperinum* regrew from both lateral stem initials and from leaf lamellae. This demonstrates the regeneration capacity of these species where bryophyte material is viable. The *Aulacomnium turgdium* assay additionally contained *Polytrichum piliferum*, *Ceratodon purpureus*, and *Pohlia nutans* material but these species did not show any evidence of direct regeneration.

Regeneration is simulated following loss of apical meristematic dominance due to isolation or injury (Chopra and Kumar 1988) suggesting insufficient damage was sustained in the extant assayed material. The two samples showing direct regeneration of *Polytrichum juniperinum* contained only *Polytrichum juniperinum* in the assayed assemblages, but several additional species generated from diaspores (appendix I). Thirteen additional species were present in the extant assays but did not show direct regeneration (appendix I).

The NMDS analysis of Granger 2015 subfossil and the growth assay assemblages showed stronger similarity (T=-12.75, A=0.12, p<0.000) compared to Gladstone subfossil and regrowth assemblages which were more compositionally dissociated (T= -19.25, A=0.09, p<0.000). Granger 2016 assemblages were weakly dissociated (T=-2.86, A=0.19, p=0.013), and Little Gladstone was not considered significant (T=-1.83, A=0.048, p=0.051). The limited statistical strength of the Granger 2016 and Little Gladstone samples is likely due to the small sample sizes (n=4 and 6, respectively). An NMDS comparison of subfossil to generated assemblages for each ice patch was attempted with a jaccard distance metric. The ordination was unsuccessful due to a few heavily weighted taxa (more frequent) versus others and many species occur only once within the data set (3 present in > 50 samples). Alternative distance metrics obtained ordinal outputs, but due to the high frequency of zero data and significant influence of outliers, they did not accurately reflect relationships.

Secondary Regrowth Assays

Secondary assays including nice subfossil samples, showed that diaspores developed prolific gametophytes of species other than the seeded material**.** The most abundant taxa observed was *Pohlia nutans*, which was commonly found germinating from *Polytrichum* sp. leaves (Fig. 4). These results suggest that the species generated in the assays were attributed to ancient diaspores and that subfossil tissue provides the necessary substrate and microhabitat to facilitate germination of other moss taxa.

Spore Trap Controls

Granger (2015 & 2016) spore traps showed no observable growth after nine months in the growth chamber. Control samples (n=5) of unexposed autoclaved soil that were assayed for the same duration, under the same growth chamber conditions, did not yield growth. Seasonal retreat of the ice margin up to 4m (Table 2), samples collected within 1m were not exposed long enough to leave viable deposits of spores on their surface. Complete snow cover of the Mount Granger vicinity occurred on September 9 2015 (M. Svoboda, personal communication) ending the growing season. On August 18, 21 days prior to snowfall, many sporophytes of Polytrichales taxa maintained intact calpytrae on the capsules, indicating spores had not been disseminated. Ice margin samples represent paleodiaspore regrowth, not growth of modern spore rain.

Similarity of Generated Species between Ice Patches

The NMDS comparative analysis of the species generated composition from the three ice patches showed various degrees of similarity (Fig. 7). The projected relationship axis 2 represented 25% of the variation whereas axis 1 represented 47%. To ensure the differences in sample size did not dramatically affect the ordinal output, a NMDS was run with only Granger 2015 and Gladstone 2016. The resulting stress for the 2-dimensional solution was comparable to when all sites were included (17.62 and 17.77, respectively $p<0.000$). The species contributing most the pattern observed are shown as joint plot overlays. *Pohlia nutans*, *Cephalozia* sp., and *Pohlia drummondii* were negatively correlated with axis 1, having more strength in the Granger 2015 sample set. *Ceratodon purpureus* and *Ptychostomum pallescens* were positively correlated with axis 1, representing Gladstone 2016. *Pogonatum urnigerum*, *Polytrichum hyperboreum*, and *Leptobryum pyriforme* were positively correlated with axis 2, being most strongly represented in Granger 2015 and Gladstone 2016.

MRPP analysis showed that generated assemblages between each ice patch were overall dissimilar ($A=0.84$, $T=-16.14$, $p<0.000$). Granger 2015 and Gladstone were significantly distinct ($A=0.083$, $T=-24.30$, $p<0.000$), and differences between other sites were moderately strong (T between -5 to -1, $A < 0$, $p<0.008$). Granger 2016 was not distinct from Granger 2015 and Little Gladstone ($T=-1.2$, $p>0.008$) due to similar species composition.

Discussion

Exhumed bryophyte material was up to 6470 years old (cal BP) from 2016 mount Granger IM, and 4815 years old from the Gladstone IM (cal BP; Table 1). Material of multiple ages was collected at the Granger 2016 IM, ranging from 501 to 6470 years old (Table 1) indicating the IM has fluctuated to the 2016 extent multiple times over millennia. The wide range of dates coupled with the previous dating of emergent bryophyte populations to 8000 years BP (uncalibrated; Farnell et al. 2004) suggest plants have colonized the deglaciated terrain following ice patch fluctuations and undergone several periods of ice-entombment and re-exposure.

In 2015, the area of Granger was 4% of its Little Ice Age (LIA) maximum, as shown by the lichen free zone (LFZ; Farnell et al. 2004). The ice volume has fluctuated throughout the last 10 000 years, with the most recent maximum during the Little Ice Age (LIA) indicated by the LFZ around the ice patch estimated at 13.26 ha. It had reduced to 6% in 1995, and returned to 32% of its LFZ estimate size by 2001, correlated with Whitehorse summer temperature records (Farnell et al. 2004). The average temperature in July and August of 2015 was 14.5^{o}C and 12^{o}C, respectively. In 2016, average temperatures increased significantly with July recorded at 15^{o}C, and August at 14 ^{o}C (Streicker et al. 2016), which directly affected the ice patch, with an average retreat of 3.6m across the IM from 2015 to 2016 following seasonal melt, July 13th – Sept 9th 2016. Temperatures within the Yukon have been steadily increasing over the past 50 years, with an average increase of summer averages by 2^{o}C, and 4^{o}C increase in winters (Streicker 2016). Seasonal temperature increase will accelerate ice margin retreat and limit snow accumulation, resulting in a progressive net loss of ice of the ice patches. The exhumed IM subfossils from Gladstone ranged from 3656-4815 years BP; Table 1), suggesting the IM has been historically more stable than Granger. Understanding IM dynamics would be improved with more radiocarbon date control on emergent organic samples.

Subfossil Assemblages

Exhumed bryophytes from each ice patch represent paleo-community assemblages, providing insights to the long term temporal diversity found in each region. The emergent subfossil assemblages from Granger represent 13% of the foreland bryophyte composition with closer affinity than with the surrounding vegetation of the Mount Granger (>1km; see chapter 2, Fig. 7b). The 6470 years cal BP bryophyte material exhumed from Mount Granger (Table 1) shows that the community structure has persisted over thousands of years.

Comparison of Granger, Gladstone and Little Gladstone subfossil assemblages showed similarity between all three ice patches, with six species shared of the seventeen distinct species total. The GLIP had the most species rich subfossil assemblages (15 spp.), followed by Little Gladstone (8 spp.) and Granger (8 spp). Granger is located within the Southern Lakes ecoregion, characterized at semi-arid, whereas Gladstone falls within the Ruby Ranges ecoregion, which is generally classified with higher level of precipitation (up to 300 mm annually; Smith et al. 2004). Bryophyte diversity increases due to augmented moisture regimes, supporting plant diversity (Geffert et al. 2013). The environmental conditions of the Gladstone region supported a larger number of species prior to ice formation. The subfossil assemblages of Little Gladstone are considered and were composed of a subset of Gladstone species, corroborating their close proximity (Table 4, Fig 6). The species found at Gladstone, but not within Little Gladstone were likely present, but may have been missed due to constrained sampling time.

All subfossil taxa that were found at Gladstone were represented in Granger subfossil assemblages, with the exception of *Pohlia crudoides* and *Polytrichum hyperboreum*. However, the latter species was generated within Gladstone assays and can be assumed to have been present, but undetected in the subfossil assemblages. Exhumed subfossil assemblages from the GRIP contained three different species (*Pohlia crudoides*, *Pohlia nutans*, and *Ptychostomum pallescens*) between 2015 and 2016. Different species may have colonized the terrain at different times of exposure, following patterns of ice patch fluctuations. The subfossil sampling is considered a minimal subset of what existed at any given time. As the IM retreats, additional species may be exhumed that will contribute to the subfossil paleorecord.

Regeneration Capacity of Subfossil Material

Growth chamber assay results indicated that majority of samples (73%) produced juvenile populations of species determined in the original subfossil sample, representing potential regeneration events. Viable propagules dating up to 4089 years cal BP grew from emergent Caribou dung samples, showing long-term survival of paleo bryophyte material within the ice patches.

Bryophytes have been shown to survive long term cryopreservation due to their inherent adaptive traits, such as totipotency (Rowntree and Ramsey 2009, La Farge et al. 2013, Roads et al. 2014). Potential regeneration events occurred in 73% IM assays, with 32.7% on average representing growth analogous to subfossil assemblages. Direct observation of regeneration from subfossil gametophytes was lacking, but cannot be ruled out.

Potential loss of subfossil cell viability can be attributed to the ice margin fluctuations over time, exposing and refreezing the plant communities. Repeated annual freeze-thaw results in sucrose depletion (Melick and Seppelt 1992), affecting the ability of bryophytes to restore metabolic activity, or to withstand further freezing events. The longer plants remain frozen, the time required to regain metabolic recovery substantially increases (Proctor et al. 2007). Before subsequent ice-entombment events, exposed plants were not able to generate adequate new growth or replenish carbon storage resources for vitrification (Chopra and Kumar 1988), resulting in complete cell death.

The exhumed subfossil material provided an ideal substrate for paleodiaspore germination (Fig. 4). Ancient spores, gemmae, rhizoidal tubers, provide efficient means for a species to maintain itself through time at a particular habitat despite changing environmental conditions (Hock et al. 2008). The in rolled leaves of *Polytrichum juniperinum* provide protection and a warming greenhouse effect for superficial spores or gemmae of other taxa.

Regrowth of extant species from the foreland demonstrated successful regeneration (e.g., *Polytrichum juniperinum, Aulacomnium turgidum;* Fig. 5) is possible when cells are viable. In *Polytrichum commune*, a closely related taxa to *Polytrichum juniperinum*, regeneration is most prolific in photosynthetic (green) leaves and apices (Mickewik 1975). Regeneration of *Aulacomnium turgidum* has been shown from lateral stem initials, forming abundant regrowth *in vitro* (La Farge et al. 2013).

Growth Chamber Assay Assemblages

From the Granger, Gladstone, and Little Gladstone ice patches, exhumed IM samples have generated prolific *in vitro* germination of 40 distinct species, demonstrating preservation and resilience over millennia. Species richness of growth chamber assays was higher than subfossil richness at all sites (≥44%), with 27 species germinating *in vitro* that were not determined in the subfossil samples, emphasizing the contribution of resilient diaspores to biodiversity of the ice patch ecosystem. The generated species from Granger represented 35% of the total extant diversity, and 65% of the foreland diversity quantified, whereas the subfossil assemblage represented 10% of the extant diversity surveyed, and 13% of the foreland diversity. Similarity between generated and extant diversity suggest the exhumed diaspores contribute to establishment in the deglaciated foreland, and that the ice patch bryophyte flora has been maintained for thousands of years primarily through diaspore banks.

Generated species composition was overall variable between ice patches, but they shared a dominant composition of six bryophytes: *Polytrichum piliferum*, *Polytrichum juniperinum*, *Pohlia nutans*, Pohlia drummondii, *Leptobryum pyriforme*, and *Ceratodon purpureus*. These taxa are rapid colonizers of perturbed areas or stable perennial stayers (*Polytrichum* spp.) within alpine environments, optimizing their persistence and contribution to the diaspore bank through prolific spore or asexual propagule production (Miles and Longton 1999, During 2001). Polytrichales taxa sporophytes can release up to 85 000 millions spores per square meter of moss cover (Longton and Miles 1982).

The dominant species that generated *in vitro* were found within the subfossil assemblages of all ice patches (Table 4). Thousand year age gaps of exhumed material between ice patches shows that these species have formed the dominant floristic components of the high altitude Yukon environments over a long-term temporal scale. The strong correlation between subfossil and foreland plant composition (see chapter 2) further demonstrate that the abiotic conditions of the ice patches have supported a unique suite of taxa that are highly adapted to thrive under extreme high alpine environmental conditions since the mid Holocene (6407 years cal BP).

Three dominant extant foreland taxa (*Polytrichum juniperinum*, *Polytrichum piliferum*, and *Ceratodon purpureus*) rely on sexual reproduction through spore dispersal, producing prolific sporophytes (Fig. 8). These species were also dominant within the growth chamber assays, attributed to ice patch captured spore rain and regeneration from ancient populations of these species that colonized exposed subglacial terrain over long term IM fluctuations. On alpine summit snow drifts where diaspores were collected onto spore traps, gametophytic propagules showed successful germination (Miller and Ambrose 1976) with rare success of spores (Robinson and Miller 2013). In contrast to these studies of spore resilience and dispersal, cryopreservation of spores within or beneath the ice patches maintains their viability, expanding the persistence of moss species into future landscapes. In addition to maintain persistence through prolific spore production, Polytrichales taxa form rhizoidal gemmae from dense rhizoidal mats, capable of generating clonal gametophytes (Wigglesworth 1947, Longton and Schuster 1983).

The dominant taxa that were not producing sporophytes (*Pohlia nutans*, *Pohlia drummondii*, *Leptobryum pyriforme*), likely contributed to the diaspore bank through asexual vegetative propagules. Sexual (sporophyte) reproduction of bryophytes is generally less common in alpine and arctic environments, resulting in asexual reproduction in bryophytes being essential for habitat colonization and maintenance (Longton 1988, Frey and Kürschner 2011). *Pohlia drummondii* and *Leptobryum pyriforme* produce asexual propagules such as axillary bulbiform gemmae, and axillary or rhizoidal brood bodies, respectively (Flora of North America Editorial Committee, vol. 28 2014). In addition to sporophyte production, *Ceratodon purpureus* can produce multicellular stem filaments or rhizome nodules. *Pohlia nutans* does not produce specialized asexual structures, but is proliferated through clonal gametophyte development from dense rhizoidal mats, as seen in secondary regrowth assays (Fig. 4). The totipotency of bryophyte tissue also supports potential regrowth from gametophytic leaf or stem fragments (La Farge et al. 2013).

Species that germinated under growth chamber conditions without corresponding subfossil gametophytic presence (58% of species) represent diaspores that were not able to colonize the immediate exposed glacial terrain, but were deposited though anemochorous events into subglacial ice patch diaspore banks or onto the bryophyte assemblages prior to ice burial. The majority of these taxa do not frequently produce sporophytes, and more likely were dispersed from gametophytic propagules. Propagule density is generally largest in close proximity to the contributing gametophyte, favoring short distance dispersal for increased chance of survival, but propagules can be found at long range distances from the original source (Pohjamo et al. 2006, Lonnell et al. 2012, Sunberg 2013) particularity where anemochory is not limited by canopy cover (e.g., high alpine tundra). Pollen analysis on the stratified debris layers of the GRIP shows a dominance *Picea* sp. and *Pinus* sp. (Bowyer et al. 2001). These species are common within the lower altitude forests, supporting wind dispersion as a significant factor of spore contribution. The *in vitro* regrowth of a fern thallus, characteristic of insulated forested areas, further indicates long distance dispersion.

Due to the vast amount of caribou dung within the ice patches, it was important to determine its potential contribution to species enrichment. Growth chamber samples from extant dung samples suggests caribou dung does not function as a diaspore source initially. These dung assays were either overgrown with fungal hyphae, contained entomophilous and coprophilous taxa indicating insect dispersion events growth, or had development limited to protonemal mats (appendix I). Exhumed dung dating 4089-3873 years BP demonstrated that assays contained viable diaspores (Table 1), which generated similar taxa as in the subfossil assemblages, indicating spore rain deposition across all organic material present at the ice patch or are Caribou are dispersal vectors for ancient as well as extant alpine tundra floras.

Future environments

Simulated warming experiments in northern regions have shown generalized detrimental effects to cold-adapted bryophytes (Elmendorf et al. 2012, Alatalo et al. 2014). At elevated temperatures, arctic and alpine bryophytes decline in photosynthetic rate (Oechel and Sveinbjornsson 1978, Bejerke et al. 2011), resulting in limited growth or colony expansion. It has been predicted that with climate change in the north, bryophyte diversity will ultimately decrease (Hallingback and Tan 2010, He et al. 2016). Bryophytes contribute an estimated 25%

of the primary production within in arctic, as well as stabilize soil, fix nitrogen, and cycle carbon to support vascular plants (Street et al. 2013). The loss of bryophyte populations has implications for completely reshaping of the tundra vegetation.

The viable diaspores (propagules, gemmae, spores) stored within/beneath ice patches have demonstrated their capacity to regrow, and contribute to colonization of deglaciated terrain. Diaspore banks have been shown to accumulate genetic diversity, with stored spores representing haplotypes not present in extant populations (Hock et al. 2008). Genetic variability within successive plant populations produce diaspores adapted to a range of growing conditions. These provide the species with a collection of diaspores that can germinate under variable conditions, providing a mechanism to withstand the detrimental effects and adaptive pressure induced by climate warming (Jump et al. 2009). Diaspores preserved for millennia have a key role in contributing genetic diversity to the extant surrounding and establishing new populations, maintaining the vulnerable environment.

Conclusions

The regeneration capacity revealed by growth chamber assays demonstrate that the Yukon ice patches function as genetic reservoirs, containing subglacial bryophyte assemblages with viable cryopreserved diaspores. The data have shown that 95.7 -100% of the growth chamber assays generated new populations. Of these assayed samples, 73% generated taxa were present in the original subglacial samples. The life strategy of each of these species suggests the ice patch foreland ecosystem develops species with high reproductive effort and diaspore production. The majority of species generation was attributed to ancient diaspores, with 27 species not determined in the subfossil samples. Species generation from dated, exhumed dung samples (4089 years cal BP) demonstrates regeneration of diaspores, expanding the current understanding of the longevity and resilience of bryophyte material. Given that the retreat rate was 4.73m/yr, and the short period of IM exposure (July 13th- Aug 9th 2016) the samples collected and assayed within 1 m of the IM are presumed to be of ancient origin (≥ 500 years cal BP; Table 1).

The dominant foreland species represent the majority of the subfossil assemblages at Mount Granger, showing that the ice patch has preserved a unique bryophyte community over thousands of years. On deglaciated forelands, establishment requires initial nutrient input and soil stability (Hodkinson et al. 2003, Jones and del Moral 2009). The exhumed subfossil gametophytes provide an ideal substrate supporting establishment of the exhumed diaspores, which facilitate colonization of exposed terrain. The full biological impact of ice patches in alpine tundra ecosystems is poorly understood. This study provides insight to the role of bryophytes as temporally regenerative, components of alpine ice patch ecosystems. The ice patches serves as biological reservoirs that cryopreserve viable diaspores (spores, propagulae, fragments) through a changing high altitude landscape. The viable diaspore banks show that the ice patches are critical in the continued maintenance of Yukon alpine environments that are significantly affected by climate change.

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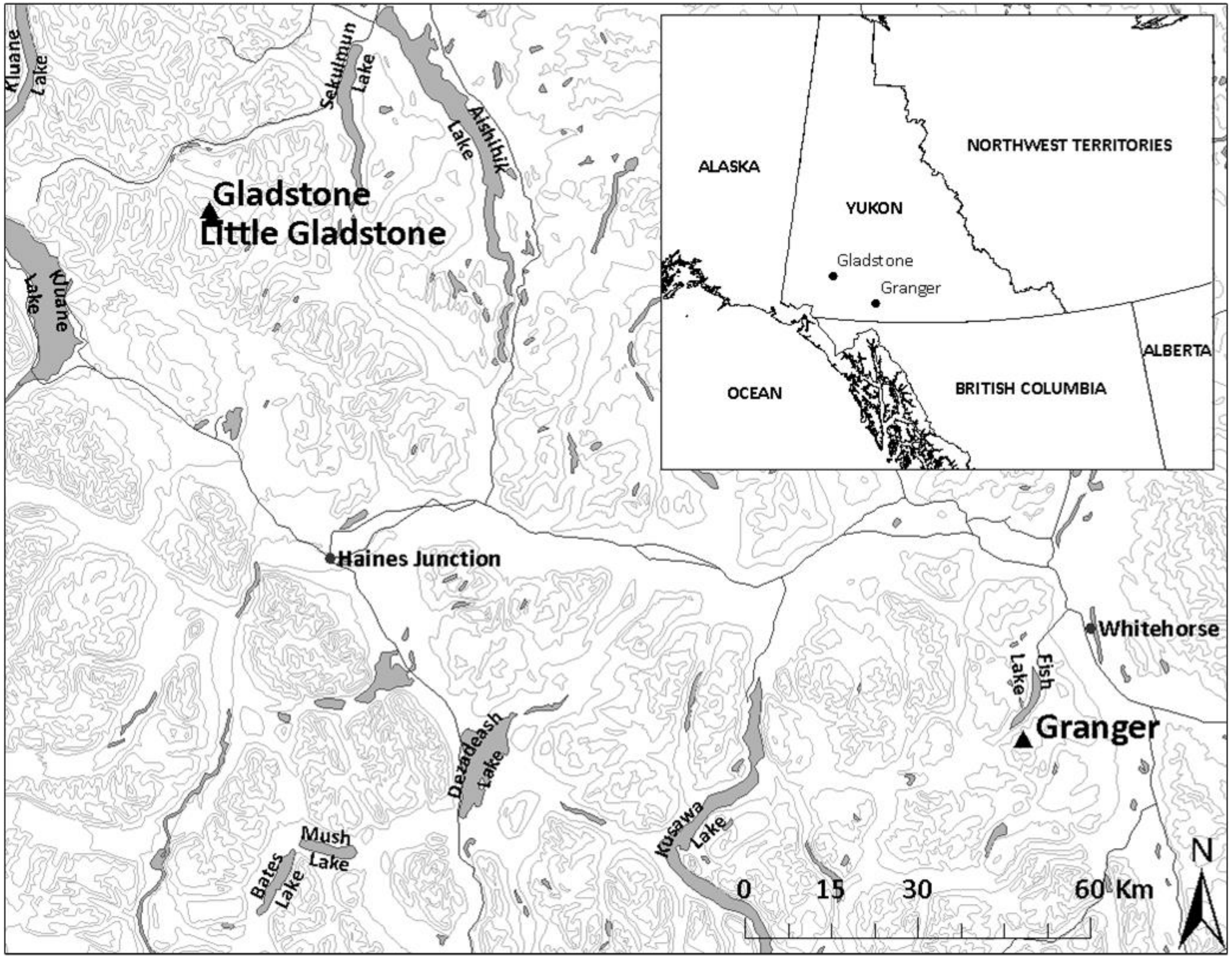

Figure 1. Locality of ice patches surveyed for exhumed subfossil material: Mount Granger (2015, 2016), Gladstone (2016), and Little Gladstone (2016).

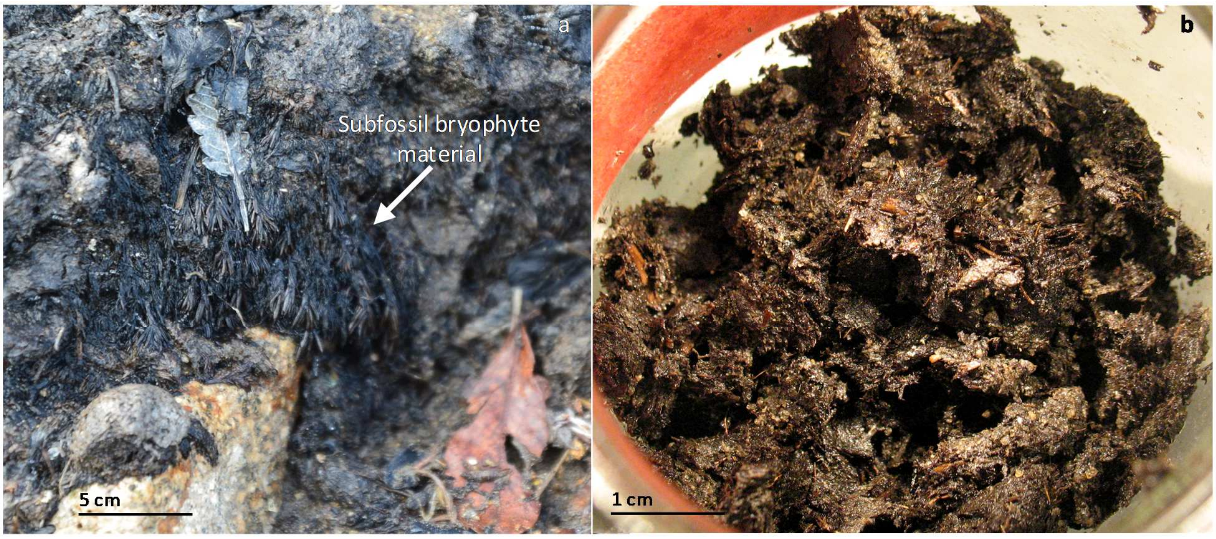

Figure 2. Exhumed subfossil material from the Granger ice patch margin (<1m) in 2015. (A) Pristine population of *Ceratodon purpureus*, (B) 'as is' subsample of exhumed material in a Magneta^{TM} B-cap (Sigma) jars for growth chamber assays.

UOC No.	Lab Sample ID	Ice Patch	Collection Yr	DIM (cm)	Taxa	^{14}C yr BP ± error	F^{14}C ± error	cal y BP at 2 sigma
3725	2016-GRAN-3	Granger	2016	4 cm from IM	*Polytrichum* sp. *Psilopilum* sp. *Ceratodon purpureus* *Ptychostomum* sp.	512 ± 38	0.9382± 0.004	631-600 (13.9%) 560-501 (81.5%)
3726	2016-GRAN-4	Granger	2016	IM	*Ceratodon purpureus* sp. *Polytrichum* sp. 1 *Pogonatum urnigerum* *Pohlia nutans* *Polytrichum juniperinum* *Ptychostomum* sp. 1	5608 ± 43	0.4975± 0.0026	6470-6304 (95.4%)
3727	2015-GR-CD-15-2-73	Granger	2015	IM	*Polytrichum* sp.	Modern	1.0856± 0.0051	AD 1956-1957 (4.6%) AD 1999-2003 (90.8%)
3722	2016-GLAD-3	Gladstone	2016	emergent dung/winter ice; 4 cm from IM	*Pogonatum urnigerum* *Polytrichum juniperinum* *Racomitrium lanuginosum* *Dicranum* sp. *Aulacomnium turgidum*	3656 ± 38	0.6344± 0.0030	4089-3873 (95.4%)
3723	2016-GLAD-6	Gladstone	2016	IM	*Polytrichum juniperinum* *Ceratodon purpureus* *Racomitrium lanuginosum* *Dicranum* sp. Woody vascular plant stems (cf *Salix* sp.)	3770 ± 38	0.6255± 0.0030	4248-4064 (83.1%) 4049-3987 (12.3%)

3724	2016-GLAD-19	Gladstone	2016	IM	*Hylocomium splendens* *Ditrichum flexicaule* *Encalypta* sp. *(calyptra only)* *Aulacomnium turgidum* *Aulacomnium palustre* *Dicranum* sp. *Polytrichastrum alpinum* *Racomitrium lanuginosum* *Pohlia nutans* *Ptychostomum* sp. 1 *Ptychostomum* sp. 2 *Polytrchum juniperinum* *Mnium* sp. *Fissidens* sp. *Dicranaceae* sp.	4092 ± 38	0.6009± 0.0029	4815-4753 (20.8%) 4712-4512 (73.2%) 4482-4443 (6%)

Table 1. Radiocarbon dates from exhumed material at the Granger and Gladstone ice margin in 2016. Samples were submitted to A.E. Lalonde AMS (Accelerator Mass Spectrometry) Laboratory, University of Ottawa (UOC) to determine the age range of subfossil material. DIM (cm) – distance from the ice margin in centimetres; IM – at the ice margin. ^{14}C yr BP – conventional radiocarbon date age; cal y BP- calibrated years before present. Collection Yr – year collected.

2015 IM stake Location		Distance from the ice margin (M)	
		2015	2016
Stake 1		1.17	-
Stake 2		1.39	-
Stake 3		0.75	-
Stake 4		0.81	-
Stake 5		0.72	-
Stake 6		1.01	-
Stake 7	Transect 2	0.52	4.73
Stake 8	Transect 3	1.08	3.56
Stake 9	Transect 4	1.14	3.76
Stake 10	Transect 5	1.13	3.65
Stake 11	Transect 6	-	4.02
Stake 12		-	4.07
Stake 13		-	1.5

Table 2. Granger ice margin retreat from August 5-August 10 2015 (5 days) August 5 2015-July 28 2016 (1 year). Stakes were placed 10m apart at seven flags along the center portion of the ice margin in 2015 (see chapter 2 methods), and measured against the ice margin in 2016.

	Subglacial samples (<1m from IM)		**Extant samples (>1m from the IM)**		**Emergent dung**	
Ice Patch	# of samples	Assay success (%)	# of samples	Assay success (%)	# of samples	Assay success (%)
Granger 2015	31 (+43 replicates)	100	10	100	1 (+3 replicates)	100
Granger 2016	4	100	-	-	-	-
Gladstone 2016	22	95.7	10 (+2 dung samples)	100	4	100
Little Gladstone 2016	5	100	1	100	-	-

Table 3. Growth chamber assays: summary of samples from each ice patch and percent success generated species. 100% success indicates all samples developed at least one bryophyte gametophyte. IM= ice margin.

	Granger 2015		Granger 2016		Little Gladstone 2016		Gladstone 2016	
Total no. of assays from IM samples	32		4		5		25	
	% Frequency							
Species	Regrowth	Subfossil	Regrowth	Subfossil	Regrowth	Subfossil	Regrowth	Subfossil
Aulacomnium palustre	2						19	
Aulacomnium turgidum	2				17	20	6	3
Bartramia ithyphylla	5						3	
*Cephalophoziella sp.**			25		33		3	
Cephalozia bicuspidata ssp. ambiguua	29							
Cephalozia sp.	18							
Ceratodon purpureus	59	80	75	100	83	80	94	35
Conostomum tetragonum							3	
Dicranum acutifolium						20		12
Dicranum elongatum	9				17		6	24
*Dicranum fuscescens**			25		17			
Dicranum groenlandicum	2							3
Ditrichum flexicaule					17			
Fern sp.							3	
*Gymnomitrion corallioides**	5							
Hypnum revolutum							3	3
Imbribryum alpinum	39							3
Jungermannia borealis	2							
Kiaeria glacialis					17			
Leptobryum pyriforme	60		50		50		56	
Lophozia attenuata	2							
Lophozia incisa	2							
Lophozia sp.	2				17			
Lophozia sudetica	13							
Lophozia ventricosa	20				17		3	
Marchantia polymorpha	11				50		67	

	Granger 2015		Granger 2016		Little Gladstone 2016		Gladstone 2016	
Total no. of assays from IM samples	32		4		5		25	
	% Frequency							
Species	Regrowth	Subfossil	Regrowth	Subfossil	Regrowth	Subfossil	Regrowth	Subfossil
Marsupella emarginata var. pearsonii	2							
*Niphotrichum ericoides**	2							
Niphotrichum canescens								3
Pezzia sp.	2							
Philonotis fontana	5							
Pogonatum urnigerum	57	20	50	25		20	8	15
Pohlia crudoides	11	5						
Pohlia drummondii	73	25	100		17		22	9
Pohlia filum							3	
Pohlia nutans	98	65	100		100	60	56	35
Polytrichastrum alpinum	2							
Polytrichum commune	4							
Polytrichum hyperboreum	43	30			17		3	
Polytrichum juniperinum	66	80	75	50	50	80	78	38
Polytrichum piliferum	13	20	50	75	17	60	11	12
Ptychostomum cryophilum							6	3
*Ptychostomum pallescens**			50	25	50	20	64	6
Sphagnum sp.	2				17			
*Trichostomum cf. arcticum**			25					
Richness	32	8	11	5	18	8	21	15

Table 4. Percent frequency of species generation and subfossil presence at each of the four surveyed ice patches. Frequency was determined by species counts (presence or absence) for each ice patch. Overall richness was calculated as species counts for each category. * indicates species that regrew from Mount Granger assays but were not present within the extant surveys of Mount Granger (see chapter 2). IM = ice margin; Regrowth= species regenerated *in vitro*; Subfossil= original material of assay.

Figure 3. Growth chamber assays prior to harvest, showing prolific establishment of bryophyte species.(A) Gladstone sample (GL-Z1-PT42; Table 1) showing growth of: *Ceratodon purpureus, Polytrichum juniperinum, Pohlia nutans, Marchantia polymorpha, Leptobryum pyriforme, Polytrichum piliferum, Aulacomnium palustre, Pogonatum urnigerum, Ptychostomum pallescens* (B) Little Gladstone (GL(2)-3): *Polytrichum hyperboreum, C. purpureus, P. juniperinum, P. nutans, M. polymorpha, L. pyriforme, P. pallescens,,* (C) Granger 15 (GR-SBG-11-1): *Pohlia drummondii, Cephalozia bicuspidata* ssp. *ambiguua*, *P. juniperinum, P. nutans, P. pallescens, P. urnigerum, L. pyriforme, M. polymorpha,* (D) Granger 16 (GR 2): *P. pallescens, P. piliferum, P. urnigerum, P. drummondii, P. juniperinum, P. nutans,* (E) Gladstone dung (SBG 6): *P. nutans, M. polymorpha, L. pyriforme, P. piliferum,* (F) Granger dung (GR-SBG-8-9) : *P. juniperinum, P. nutans, P. pallescens, C. purpureus, P. drummondii, L. pyriforme*.

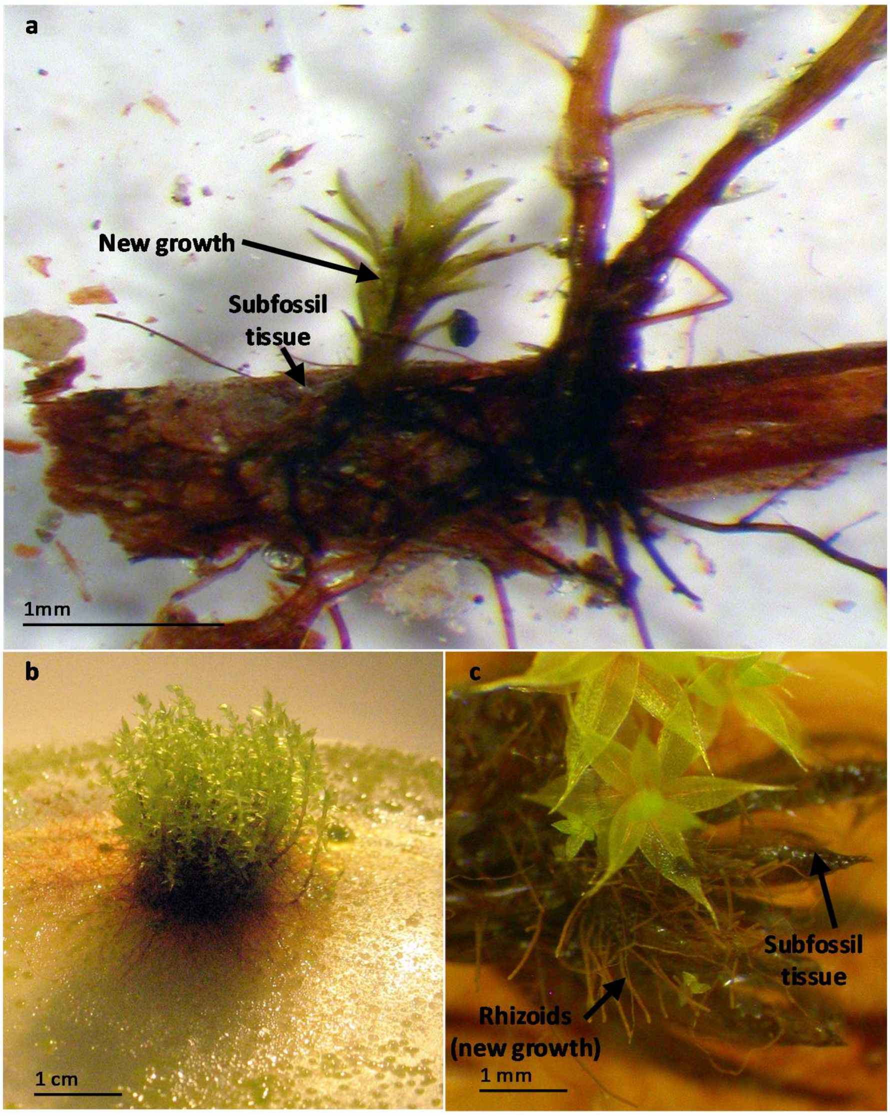

Figure 4. Diaspore generation on subfossil tissue. Species germinating from *Polytrichum* leaves within secondary greenhouse growth assays: (A) *Ceratodon purpureus* from the base of a detached *Polytrichum* sp. leaf, (B) dense population of clonal *Pohlia nutans* from rhizoidal mats on top of *Polytrichum* sp. leaves (not visible) within secondary regrowth assays, (C) *Ptychostomum pallescens* with prolific rhizoid development over *Polytrichum* sp. leaves.

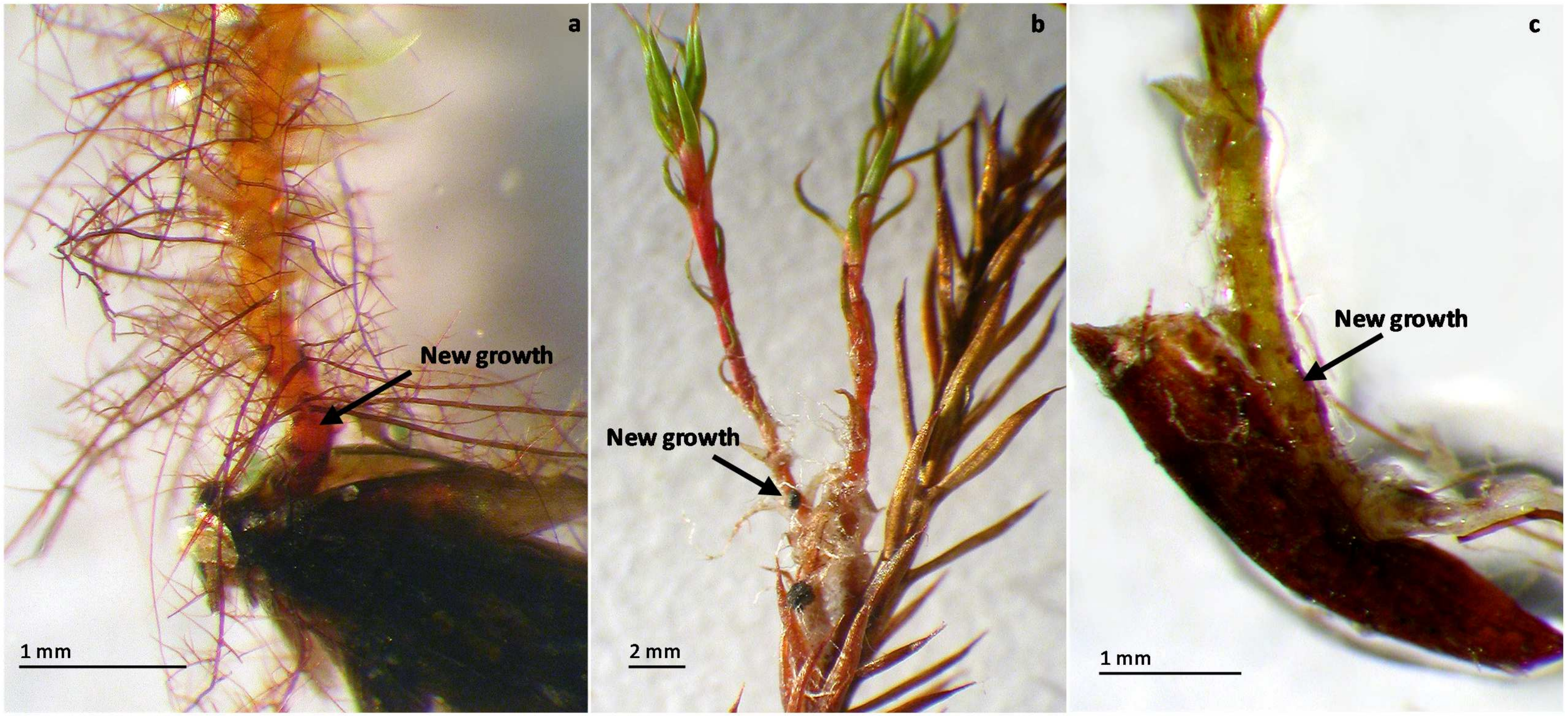

Figure 5. Extant bryophyte gametophytes demonstrating regrowth from fragmentation or from lateral stem initials. (A) *Aulacomnium turgidum* from the Little Gladstone, 2.5 m from IM (GL(2)-2; Table 1), (B) *Polytrichum juniperinum* regrowth 20m from the Granger 2015 IM (GR-SBG/EXT-23), and (C) *Polytrichum juniperinum* regrowth, 1.5 M from the Gladstone IM (SBG 19).

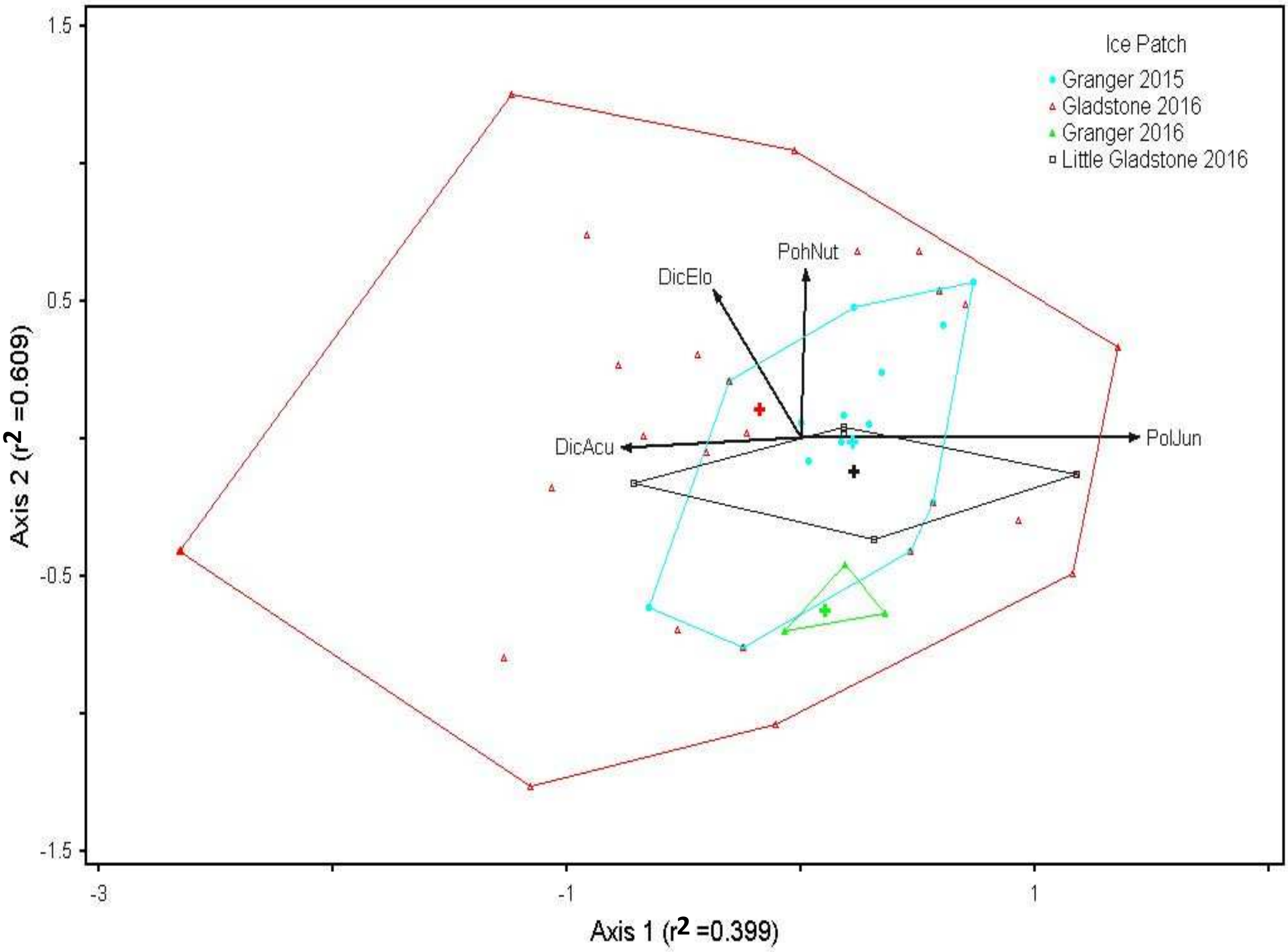

Figure 6. Comparison of subfossil compostion from Granger, Gladstone, and Little Gladstone ice patches using ordination joint plots from nonmetric multidimensional scaling (NMDS) with overlays of significant species vectors of subfossil composition. Analysis was based on presence/absence data. Species vectors with significant contribute to the ordinal output r>0.2 are shown. Vector length and direction indicate strength of correlation with each ordinal axis. Final stress for the 2-dimensional solution= 10.91001, number of iterations= 183, final instability= 0.000. PohNut= *Pohlia nutans*, PolJun= *Polytrichum juniperinum*, DicAcu= *Dicranum acutifolium*, DicElo= *Dicranum elongatum*.

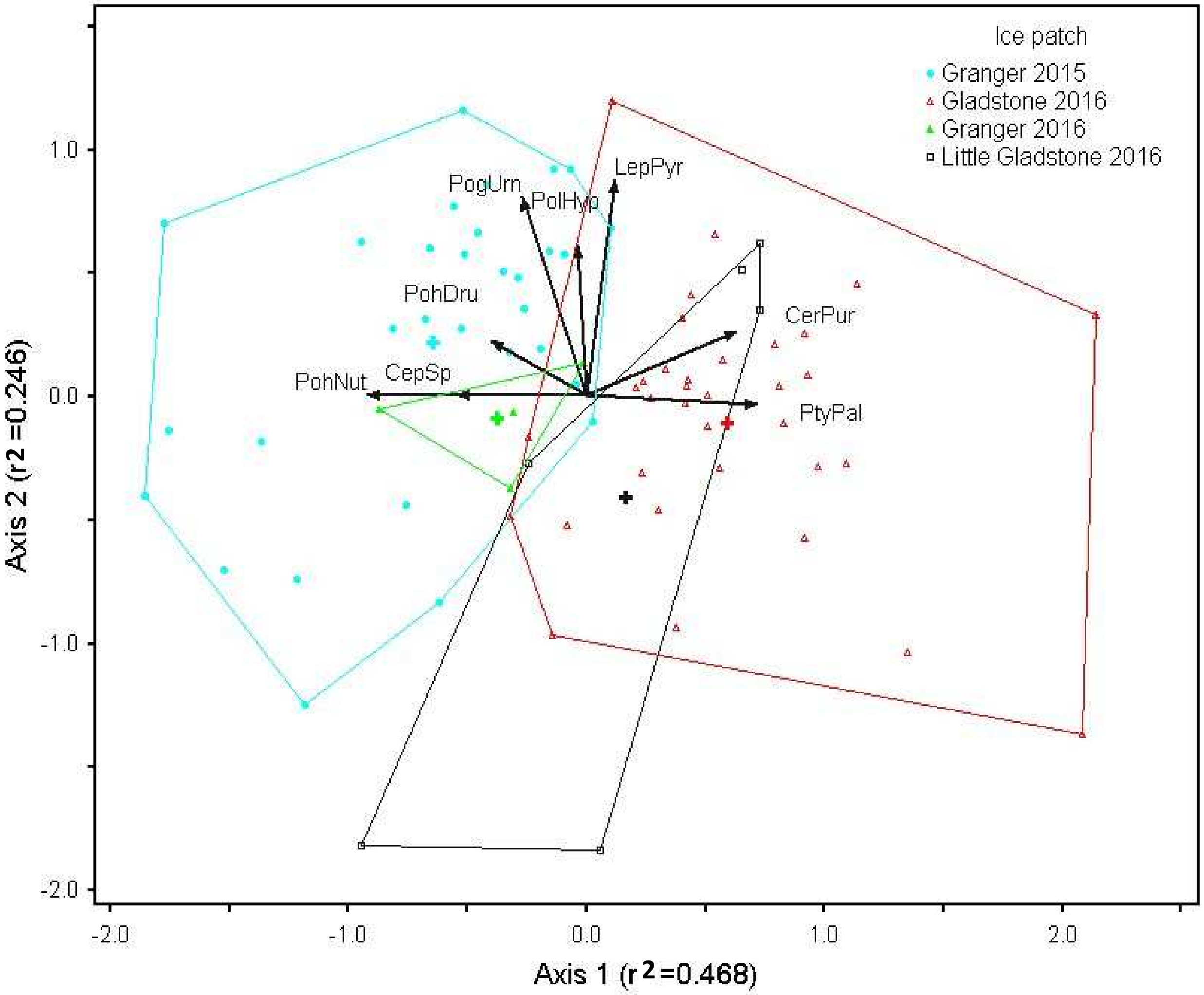

Figure 7. Comparison of *in vitro* growth assays from Granger, Gladstone, and Little Gladstone ice patcheses using ordination joint plots from nonmetric multidimensional scaling (NMDS) with overlays of significant species vectors, based on presence/absence data. Assemblages that have more similarity in species composition will show a higher degree of overlap. Species vectors with significant contribute to the ordinal output r>0.2 are shown. Vector length and direction indicate strength of correlation with each ordinal axis. Final stress for the 2-dimensional solution= 17.77608, number of iterations= 77, final instability= 0.000. PohNut= *Pohlia nutans*, CepSp= *Cephalozia* sp., PohDru= *Pohlia Drummondii*, PogUrn= *Pogonatum urnigerum*, PolHyp= *Polytrichum hyperboreum*, LepPyr= *Leptobryum pyriforme*, CerPur= *Ceratodon purpureus*, PtyPal= *Ptychostomum pallescens*.

Figure 8. Extant population of *Polytrichum hyperboreum* from the GRIP foreland (30 m from the IM) with abundant sporophyte production (August 5, 2015).

Appendix A.

Sample	***Ice patch***	***Field specimen***	***Collection year***	**Assay No.**	**Subfossil taxa**	**Generated taxa**	**Distance from IM**	**Growth duration**
Subfossil	*Granger*	*GR-SBG-2-2*	*2015*	*5*	-	*Polytrichum juniperinum* *Pohlia nutans* *Pohlia drummondii*	IM	Sept 14 - June 8 2015
(<1m from IM)		*GR-SBG-3-1*		6	-	*Polytrichum juniperinum* *Pohlia nutans* *Ceratodon purpureus* *Imbribryum alpinum* *Leptobryum pyriforme*	IM	Sept 14 - June 8 2015
		GR-SBG-4-1		7	***Polytrichum juniperinum*** ***Pohlia nutans***	***Polytrichum juniperinum*** ***Pohlia nutans*** *Pohlia drummondii*	IM	Sept 14 - June 9 2015
		GR-SBG-5-1		8	***Polytrichum sp.***	***Polytrichum juniperinum*** *Pohlia nutans* *Polytrichum hyperboreum* *Ceratodon purpureus* *Pogonatum urnigerum* *Imbribryum alpinum* *Pohlia drummondii*	IM	Sept 14 - June 9 2015
		GR-SBG-1-1		9	***Polytrichum sp.***	***Polytrichum juniperinum*** *Pohlia nutans* *Pogonatum urnigerum* *Pohlia crudoides* *Leptobryum pyriforme* *Marchantia polymorpha*	IM	Sept 14 - June 9 2015
		GR-SBG-6-2		10	-	*Polytrichum juniperinum* *Pohlia nutans* *Ceratodon purpureus* *Pogonatum urnigerum* *Pohlia drummondii* *Leptobryum pyriforme*	IM	Sept 14 - June 9 2015

Appendix A.

Sample	***Ice patch***	***Field specimen***	***Collection year***	**Assay No.**	**Subfossil taxa**	**Generated taxa**	**Distance from IM**	**Growth duration**
		GR-SBG-7-3		11 – 14	-	*Polytrichum juniperinum* *Pohlia nutans* *Polytrichum hyperboreum* *Polytrichum piliferm* *Ceratodon purpureus* *Pogonatum urnigerum* *Imbribryum alpinum* *Pohlia drummondii* *Leptobryum pyriforme*	IM	Sept 14 - June 10 2015
		GR-SBG-8-5		15 – 18	***Polytrichum juniperinum*** ***Ceratodon purpureus***	***Polytrichum juniperinum*** *Pohlia nutans* *Aulacomnium turgidum* *Polytrichum hyperboreum* *Polytrichum piliferum* ***Ceratodon purpureus*** *Polytrichum commune* *Pogonatum urnigerum* *Imbribryum alpinum* *Pohlia drummondii* *Leptobryum pyriforme* *Bartramia ithyphylla* *Cephalozia bicuspidata ssp. ambiguua* *Lophozia ventricosa* *Marchantia polymorpha*	IM	Sept 15 - June 11 2015
		GR-SBG-9-1		19 - 22, 43 – 44	***Ceratodon purpureus*** ***Polytrichum juniperinum***	***Polytrichum juniperinum*** *Pohlia nutans* *Polytrichum hyperboreum* ***Ceratodon purpureus*** *Dicranum elongatum* *Pogonatum urnigerum*	IM	Sept 15 - June 12/19 2015

Appendix A.

Sample	*Ice patch*	*Field specimen*	*Collection year*	Assay No.	Subfossil taxa	Generated taxa	Distance from IM	Growth duration
						Imbribryum alpinum *Pohlia crudoides* *Leptobryum pyriforme* *Cephalozia bicuspidata ssp. ambiguua* *Lophozia attenuata*		
		GR-SBG-10-2		23, 45	***Polytrichum hyperboreum*** ***Pogonatum urnigerum*** ***Ceratodon purpureus***	*Pohlia nutans* ***Polytrichum hyperboreum*** ***Ceratodon purpureus*** ***Pogonatum urnigerum*** *Imbribryum alpinum* *Pohlia drummondii* *Leptobryum pyriforme*	IM	Sept 15 - June 15/19 2015
		GR-SBG-11-1		24 – 27	***Polytrichum juniperinum*** ***Pogonatum urnigerum*** ***Ceratodon purpureus*** ***Polytrichum hyperboreum*** ***Pohlia nutans***	***Polytrichum juniperinum*** ***Pohlia nutans*** *Aulacomnium palustre* ***Polytrichum hyperboreum*** *Polytrichum piliferum* ***Ceratodon purpureus*** ***Pogonatum urnigerum*** *Imbribryum alpinum* *Pohlia drummondii* *Leptobryum pyriforme* *Philonotis fontana* *Cephalozia bicuspidata ssp. ambiguua* *Lophozia ventricosa* *Marchantia polymorpha* *Pezzia sp.*	IM	Sept 15 - June 15 2015

Appendix A.

Sample	*Ice patch*	*Field specimen*	*Collection year*	Assay No.	Subfossil taxa	Generated taxa	Distance from IM	Growth duration
		GR-SBG-12-1		31 -37	***Ceratodon purpureus*** ***Polytrichum juniperinum***	***Polytrichum juniperinum*** *Pohlia nutans* *Polytrichum hyperboreum* *Polytrichum piliferum* ***Ceratodon purpureus*** *Dicrnaum elongatum* *Polytrichastrum alpinum* *Dicranum groenlandicum* *Pogonatum urnigerum* *Imbribryum alpinum* *Pohlia drummondii* *Leptobryum pyriforme* *Philonotis fontana* *Lophozia incisa* *Cephalozia bicuspidata ssp. ambiguua* *Lophozia sudetica* *Lophozia ventricosa*	IM	Sept 15 - June 17 2015
		GR-SBG-(11-12)-1		28 - 30, 49, 50-57	***Polytrichum sp.***	*Pohlia nutans* ***Polytrichum hyperboreum*** *Ceratodon purpureus* *Pogonatum urnigerum* *Pohlia drummondii* *Leptobryum pyriforme* *Cephalozia bicuspidata ssp. ambiguua*	IM	Sept 15 - June 16/22-23 2016
		GR-SBG-13-1		38	-	*Pohlia nutans* *Ceratodon purpureus* *Pogonatum urnigerum* *Imbribryum alpinum* *Pohlia crudoides* *Leptobryum pyriforme*	IM	Sept 14 - June 18 2015

Appendix A.

Sample	***Ice patch***	***Field specimen***	***Collection year***	**Assay No.**	**Subfossil taxa**	**Generated taxa**	**Distance from IM**	**Growth duration**
		GR-SBG-14-1		39, 40, 58-60	***Polytrichum juniperinum***	***Polytrichum juniperinum*** *Pohlia nutans* *Polytrichum hyperboreum* *Polytrichum piliferum* *Ceratodon purpureus* *Pogonatum urnigerum* *Imbribryum alpinum* *Pohlia drummondii* *Leptobryum pyriforme* *Marchantia polymorpha*	IM	Sept 15 - June 18/24 2015
		GR-SBG-15-1		41, 42	***Polytrichum sp.***	***Polytrichum juniperinum*** *Pohlia nutans* ***Polytrichum hyperboreum*** *Ceratodon purpureus* *Polytrichum commune* *Imbribryum alpinum* *Pohlia drummondii* *Leptobryum pyriforme,*	IM	Sept 14 - June 18 2015
		GR-F2-SBG-1		61	*Polytrichum juniperinum* *Polytrichum piliferum* *Polytrichum hyperboreum* ***Pohlia nutans*** *Ceratodon purpureus*	***Pohlia nutans*** *Pohlia drummondii* *Cephalozia sp.* *Lophozia sp.*	IM	Sept 23 - June 24 2015
		GR15-SBG-10		62	*Ceratodon purpureus* *Polytrichum juniperinum* *Polytrichum piliferum* ***Pohlia nutans*** ***Pohlia crudoides***	***Pohlia nutans*** ***Pohlia crudoides*** *Pohlia drummondii* *Cephalozia sp.* *Lophozia sudetica*	IM	Sept 23 - June 24 2015

Appendix A.

Sample	***Ice patch***	***Field specimen***	***Collection year***	**Assay No.**	**Subfossil taxa**	**Generated taxa**	**Distance from IM**	**Growth duration**
		GR-SBG-17		64	***Polytrichum juniperinum*** ***Pogonatum urnigerum*** ***Pohlia nutans***	***Polytrichum juniperinum*** ***Pohlia nutans*** ***Pogonatum urnigerum*** *Pohlia crudoide* *Pohlia drummondii* *Leptobryum pyriforme*	IM	Sept 23 - June 24 2015
		GR-SBG-15		66	***Polytrichum juniperinum*** ***Pogonatum urnigerum*** ***Pohlia nutans*** *Polytrichum piliferum* ***Ceratodon purpureus***	***Polytrichum juniperinum*** ***Pohlia nutans*** ***Ceratodon purpureus*** ***Pogonatum urnigerum*** *Pohlia drummondii* *Leptobryum pyriforme* *Cephalozia sp.*	IM	Sept 23 - June 25 2015
		GR15-SBG-8		65, 68	*Ceratodon purpureus* ***Polytrichum juniperinum*** ***Pohlia nutans*** *Polytrichum hyperboreum* *Pohlia drummondii*	***Polytrichum juniperinum*** ***Pohlia nutans*** *Imbribryum alpinum* *Cephalozia sp.* *Lophozia sudetica*	IM	Sept 24 - June 25 2015
		GR-SBG-21		69	***Ceratodon purpureus*** ***Polytrichum juniperinum*** ***Pohlia nutans*** *Polytrichum hyperboreum* *Pohlia drummondii*	***Polytrichum juniperinum*** ***Pohlia nutans*** *Polytrichum piliferum* ***Ceratodon purpureus*** *Leptobryum pyriforme* *Bartramia ithyphylla* *Lophozia sudetica*	IM	Sept 24 - June 25 2015

Appendix A.

Sample	***Ice patch***	***Field specimen***	***Collection year***	**Assay No.**	**Subfossil taxa**	**Generated taxa**	**Distance from IM**	**Growth duration**
		GR-SBG-12		73	*Polytrichum juniperinum* ***Pohlia nutans*** *Polytrichum hyperboreum* *Pohlia drummondii*	***Pohlia nutans*** *Niphotrichum ericoides* *Dicranum elongatum* *Pogonatum urnigerum*	IM	Sept 24 - June 26 2015
		GR-SBG-18		74	*Ceratodon purpureus* ***Polytrichum juniperinum*** ***Pohlia nutans***	***Polytrichum juniperinum*** ***Pohlia nutans*** *Pogonatum urnigerum* *Leptobryum pyriforme* *Cephalozia sp.*	IM	Sept 24 - June 26 2015
		GR-SBG-11		46 - 48, 76	***Pohlia nutans*** *Polytrichum piliferum* *Polytrichum juniperinum* ***Pohlia drummondii***	***Pohlia nutans*** ***Pohlia drummondii***	under IM	Sept 15 - June 19/29 2015
		GR-SBG-13		77	***Polytrichum juniperinum*** ***Ceratodon purpureus*** *Pohlia drummonii*	***Polytrichum juniperinum*** *Pohlia nutans* *Polytrichum hyperboreum* ***Ceratodon purpureus*** *Pogonatum urnigerum* *Imbribryum alpinum* *Pohlia drummondii* *Leptobryum pyriforme* *Gymnomitrion corallioides* *Lophozia ventricosa* *Marchantia polymorpha*	IM	Sept 24 - June 29 2015

Appendix A.

Sample	***Ice patch***	***Field specimen***	***Collection year***	**Assay No.**	**Subfossil taxa**	**Generated taxa**	**Distance from IM**	**Growth duration**
		GR-SBG-13-2		78	-	*Polytrichum juniperinum* *Pohlia nutans* *Ceratodon purpureus* *Pogonatum urnigerum* *Pohlia drummondii* *Bartramia ithyphylla* *Philonotis fontana* *Marsupella emarginata var. pearsonii* *Cephalozia sp.* *Cephalozia bicuspidata ssp. ambiguua* *Lophozia ventricosa*	IM	Sept 24 - June 29 2015
		GR-SBG-16		85	-	*Polytrichum juniperinum* *Pohlia nutans* *Ceratodon purpureus* *Dicranum elongatum* *Pogonatum urnigerum* *Imbribryum alpinum* *Pohlia drummondii* *Leptobryum pyriforme* *Gymnomitrion corallioides* *Cephalozia sp.* *Lophozia sudetica* *Lophozia ventricosa*	IM	Sept 24 - July 1 2015
		GR-SBG-2		86	***Pohlia nutans*** *Ceratodon purpureus*	***Pohlia nutans***	IM	Sept 30 - July 2 2015

Appendix A.

Sample	***Ice patch***	***Field specimen***	***Collection year***	**Assay No.**	**Subfossil taxa**	**Generated taxa**	**Distance from IM**	**Growth duration**
		GR-SBG-6		87	*Ceratodon purpureus*	*Polytrichum juniperinum* *Pohlia nutans,*	IM	Oct 6 - July 2 2015
		GR-SBG-4		88	-	*Pohlia nutans* *Pogonatum urnigerum* *Cephalozia sp.*	IM	Oct 6 - July 2 2015
	Granger	*GR 1*	*2016*	1	***Polytrichum piliferum*** ***Ceratodon purpureus***	*Polytrichum juniperinum* *Pohlia nutans* ***Polytrichum piliferum*** ***Ceratodon purpureus*** *Pohlia drummondii* *Cephalophoziella sp.*	IM	Aug 1 - Dec 6 2016
		GR 2		2	***Pogonatum urnigerum*** *Ceratodon purpureus* ***Polytrichum juniperinum***	***Polytrichum juniperinum*** *Pohlia nutans* *Polytrichum piliferum* ***Pogonatum urnigerum*** *Pohlia drummondii* *Ptychostomum pallescens* *Dicranum fuscescens* *Trichostomum cf. arcticum*	IM	Aug 1 - Dec 6 2016
		GR 3		3	*Polytrichum piliferum* ***Ceratodon purpureus***	*Pohlia nutans* ***Ceratodon purpureus*** *Pohlia drummondii* *Leptobryum pyriforme*	IM	Aug 1 - Dec 6 2016

Appendix A.

Sample	*Ice patch*	*Field specimen*	*Collection year*	Assay No.	Subfossil taxa	Generated taxa	Distance from IM	Growth duration
	Little Gladstone	*GL(2)-1*	*2016*	5	*Polytrichum juniperinum* ***Polytrichum piliferum*** ***Ceratodon purpureus*** ***Pohlia nutans***	***Pohlia nutans*** ***Polytrichum piliferum*** ***Ceratodon purpureus*** *Dicranum elongatum* *Leptobryum pyriforme* *Marchantia polymorpha* *Polytrichum hyperboreum* *Ptychostomum pallescens*	25cm	Aug 1 - Dec 7 2016
		GL(2)-3		7	***Ceratodon purpureus*** ***Pytchostomum pallescens*** *Pogonatum urnigerum* ***Pohlia nutans*** *Dicranum acutifolium*	*Polytrichum juniperinum* ***Pohlia nutans*** *Polytrichum hyperboreum* ***Ceratodon purpureus*** *Leptobryum pyriforme* *Marchantia polymorpha* ***Ptychostomum pallescens***	20cm	Aug 1 - Dec 7 2016
		GL(2)-4		8	*Polytrichum juniperinum*	*Pohlia nutans* *Ceratodon purpureus* *Lophozia ventricosa* *Cephalophoziella sp.* *Ditrichum flexicaule* *Kiaeria glacialis*	70cm	Aug 1 - Dec 7 2016
		GL(2)-5		9	Fungal overgrowth could not dissect	*Polytrichum juniperinum* *Pohlia nutans* *Ceratodon purpureus* *Leptobryum pyriforme* *Marchantia polymorpha* *Ptychostomum pallescens*	IM	Aug 1 - Dec 7 2016

Appendix A.

Sample	*Ice patch*	*Field specimen*	*Collection year*	Assay No.	Subfossil taxa	Generated taxa	Distance from IM	Growth duration
		GL(2)-6		10	***Polytrichum juniperinum*** ***Ceratodon purpureus*** *Polytrichum piliferum*	***Polytrichum juniperinum*** *Pohlia nutans* ***Ceratodon purpureus*** *Pohlia crudoides*	10cm	Aug 1 - Dec 8 2016
	Gladstone	*GL-Z1-PT 37*	*2016*	13	*Niphotrichum canescens*	*Ptychostomum pallescens*	20cm	Aug 2 - Dec 12 2016
		GL-Z1-PT 42		15	***Pogonatum urnigerum*** ***Ceratodon purpureus*** *Pohlia nutans*	*Polytrichum juniperinum* *Polytrichum hyperboreum* ***Ceratodon purpureus*** *Dicranum elongatum* ***Pogonatum urnigerum*** *Pohlia drummondii* *Marchantia polymorpha* *Conostomum tetragonum* *Cephalophoziella sp.*	new ice, 1m	Aug 2 - Dec 12 2016
		GL-Z1-PT 38-2		16	***Pogonatum urnigerum***	*Polytrichum juniperinum* *Pohlia nutans* *Aulacomnium turgidum* *Aulacomnium palustre* *Polytrichum piliferum* *Ceratodon purpureus* ***Pogonatum urnigerum*** *Leptobryum pyriforme* *Marchantia polymorpha* *Ptychostomum pallescens*	new ice, 1m	Aug 2 - Dec 12 2016

Appendix A.

Sample	*Ice patch*	*Field specimen*	*Collection year*	Assay No.	Subfossil taxa	Generated taxa	Distance from IM	Growth duration
		GL-Z1-PT-22		17	Fungal overgrowth could not dissect	*Polytrichum juniperinum* *Aulacomnium palustre* *Ceratodon purpureus* *Leptobryum pyriforme* *Ptychostomum cryophilum*	IM	Aug 2 - Dec 13 2016
		T1-Z1-1		18	*Pogonatum urnigerum* *Dicranum elongatum* *Dicranum groenlandicum* ***Ceratodon purpureus*** *Niphotrichum canescens*	*Pohlia nutans* ***Ceratodon purpureus***	0.5m	Aug 2 - Dec 13 2016
		T3-Z1		19	***Polytrichum juniperinum***	***Polytrichum juniperinum*** *Ceratodon purpureus* *Pohlia drummondii* *Leptobryum pyriforme* *Marchantia polymorpha* *Ptychostomum pallescens*	IM	Aug 2 - Dec 13 2016
		T4-Z1-1		21	*Pohlia nutans* ***Aulacomnium turgidum*** ***Polytrichum juniperinum***	***Polytrichum juniperinum*** ***Aulacomnium turgidum*** *Polytrichum piliferum* *Ceratodon purpureus* *Leptobryum pyriforme* *Marchantia polymorpha* *Ptychostomum pallescens*	IM	Aug 2 - Dec 13 2016

Appendix A.

Sample	***Ice patch***	***Field specimen***	***Collection year***	**Assay No.**	**Subfossil taxa**	**Generated taxa**	**Distance from IM**	**Growth duration**
		T3-Z1		22	*Dicranum elongatum* ***Polytrichum juniperinum*** *Polytrichum piliferum*	***Polytrichum juniperinum*** *Pohlia nutans* *Ceratodon purpureus* *Ptychostomum pallescens*	IM	Aug 2 - Dec 13 2016
		T4-Z1-2		23	***Pohlia nutans***	*Polytrichum juniperinum* ***Pohlia nutans*** *Ceratodon purpureus* *Leptobryum pyriforme* *Marchantia polymorpha* *Ptychostomum pallescens*	IM	Aug 2 - Dec 14 2016
		T4-Z1-3		24	***Pohlia nutans***	*Polytrichum juniperinum* ***Pohlia nutans*** *Ceratodon purpureus* *Pohlia drummondii* *Leptobryum pyriforme* *Marchantia polymorpha* *Ptychostomum pallescens*	IM	Aug 2 - Dec 14 2016
		T1-Z1-2		26	***Polytrichum juniperinum*** ***Ceratodon purpureus***	***Polytrichum juniperinum*** *Aulacomnium palustre* ***Ceratodon purpureus*** *Leptobryum pyriforme* *Marchantia polymorpha* *Ptychostomum pallescens*	1m	Aug 2 - Dec 14 2016
		GL SBG 25		30	***Polytrichum piliferum*** ***Ceratodon purpureus*** ***Pohlia nutans***	*Polytrichum juniperinum* ***Pohlia nutans*** ***Polytrichum piliferum*** ***Ceratodon purpureus*** *Leptobryum pyriforme* *Marchantia polymorpha* *Ptychostomum pallescens*	<10cm	Aug 2 - Dec 15 2016

Appendix A.

Sample	*Ice patch*	*Field specimen*	*Collection year*	**Assay No.**	**Subfossil taxa**	**Generated taxa**	**Distance from IM**	**Growth duration**
		GL SBG 23		31	***Pohlia nutans*** ***Polytrichum juniperinum***	***Polytrichum juniperinum*** ***Pohlia nutans*** *Aulacomnium palustre* *Ceratodon purpureus* *Leptobryum pyriforme* *Marchantia polymorpha* *Ptychostomum pallescens*	IM	Aug 2 - Dec 16 2016
		SBG 24		32	***Pohlia nutans***	*Polytrichum juniperinum* ***Pohlia nutans*** *Ceratodon purpureus* *Ptychostomum pallescens*	IM	Aug 2 - Dec 16 2016
		SBG 24.1		33	***Pohlia nutans*** *Ceratodon purpureus*	*Polytrichum juniperinum* ***Pohlia nutans*** *Ceratodon purpureus* *Dicranum elongatum* *Leptobryum pyriforme* *Marchantia polymorpha* *Ptychostomum pallescens*	IM	Aug 2 - Dec 16 2016
		SBG 27		35	*Pohlia drummondii* ***Pohlia nutans*** ***Polytrichum juniperinum***	***Polytrichum juniperinum*** ***Pohlia nutans*** *Aulacomnium palustre* *Ceratodon purpureus* *Marchantia polymorpha* *Ptychostomum pallescens*	3-4cm	Aug 2 - Dec 17 2016
		SBG 18		37	*Dicranum elongatum*	*Polytrichum juniperinum* *Ceratodon purpureus* *Leptobryum pyriforme* *Ptychostomum pallescens*	on ice, sediment	Aug 2 - Dec 17 2016

Appendix A.

Sample	*Ice patch*	*Field specimen*	*Collection year*	Assay No.	Subfossil taxa	Generated taxa	Distance from IM	Growth duration
		SBG 26		38	*Pohlia nutans* ***Ceratodon purpureus*** *Dicranum elongatum*	*Polytrichum juniperinum* ***Ceratodon purpureus*** *Marchantia polymorpha*	IM	Aug 2 - Dec 17 2016
		SBG 8		43	***Ceratodon purpureus***	*Polytrichum juniperinum* *Pohlia nutans* ***Ceratodon purpureus*** *Leptobryum pyriforme* *Marchantia polymorpha*	10cm	Aug 2 - Dec 19 2016
		SBG 1		45	***Polytrichum juniperinum*** ***Ptychostomum pallescens***	***Polytrichum juniperinum*** *Ceratodon purpureus* *Bartramia ithyphylla* *Marchantia polymorpha* ***Ptychostomum pallescens***	snow, IM	Aug 2 - Dec 19 2016
		SBG 9		49	*Polytrichum juniperinum* *Polytrichum piliferum*	*Pohlia nutans* *Ceratodon purpureus* *Lophozia ventricosa* *Ptychostomum pallescens*	ice flow debris	Aug 3 - Dec 20 2016
		GL-Z1-PT 36		11	*Dicranum elongatum*	*Ceratodon purpureus* *Lophozia sp.* *Ptychostomum pallescens*	0.5m	Aug 2 - Dec 8 2016
Emergent Dung	*Granger*	*GR-SBG-8-9*	*2015*	1 – 4	***Ceratodon purpureus*** ***Polytrichum juniperinum***	***Polytrichum juniperinum*** *Pohlia nutans* ***Ceratodon purpureus*** *Polytrichum hyperboreum* *Pogonatum urnigerum*	IM	Sept 14 - June 16 2015

Appendix A.

Sample	*Ice patch*	*Field specimen*	*Collection year*	Assay No.	Subfossil taxa	Generated taxa	Distance from IM	Growth duration
						Imbribryum alpinum *Pohlia drummondii* *Leptobryum pyriforme* *Cephalophoziella sp.*		
	Gladstone	*GL-4*	*2016*	40	***Ceratodon purpureus*** ***Polytrichum juniperinum***	***Polytrichum juniperinum*** ***Ceratodon purpureus***	IM	Aug 3 - Dec 20 2016
		GL-3		41	*Dicranum elongatum* *Polytrichum piliferum*	*Fern sp.* *Ceratodon purpureus* *Aulacomnium palustre*	IM	Aug 3 - Dec 20 2016
		SBG 6		42	***Dicranum acutifolium***	***Dicranum acutifolium***	IM, on ice	Aug 3 - Dec 20 2016
		SBG 7		46	***Ceratodon purpureus*** ***Pogonatum urnigerum***	***Ceratodon purpureus*** ***Pogonatum urnigerum***	4cm	Aug 3 - Dec 20 2016
Modern samples	*Granger*	*GR-SBG/EXT-23*	*2015*	63, 67	***Polytrichum juniperinum***	***Polytrichum juniperinum*** *Pohlia nutans* *Aulacomnium palustre* *Lophozia ventricosa*	zone 3 (20m)	Sept 24 - June 24/25 2015

Appendix A.

Sample	*Ice patch*	*Field specimen*	*Collection year*	Assay No.	Subfossil taxa	Generated taxa	Distance from IM	Growth duration
(>1m from the IM)		*GR-SBG-19*		70	-	*Pohlia nutans* *Pogonatum urnigerum* *Pohlia drummondii* *Leptobryum pyriforme*	zone 2 (10m)	Sept 24 - June 26 2015
		GR-SBG-26		72	-	*Pohlia nutans* *Pogonatum urnigerum* *Cephalozia bicuspidata ssp. ambiguua* *Lophozia ventricosa*	zone 2 (10m)	Sept 24 - June 26 2015
		GR-SBG-22		75	*Polytrichum juniperinum* *Ceratodon purpureus* ***Pohlia nutans***	***Pohlia nutans*** *Pohlia drummondii* *Gymnomitrion corallioides* *Cephalozia bicuspidata ssp. ambiguua* *Lophozia ventricosa*	zone 2 (10m)	Sept 24 - June 29 2015
		GR-SBG-28		79	-	*Pohlia nutans* *Polytrichum hyperboreum* *Ceratodon purpureus* *Pohlia drummondii* *Cephalozia bicuspidata ssp. ambiguua* *Jungermannia borealis* *Lophozia ventricosa*	zone 3 (20m)	Sept 24 - June 30 2015
		GR-SBG-20		80	***Pohlia sp.*** ***Polytrichum juniperinum***	***Polytrichum juniperinum*** ***Pohlia nutans*** ***Pohlia crudoides*** ***Pohlia drummondii***	zone 2 (10m)	Sept 24 - June 30 2015

Appendix A.

Sample	*Ice patch*	*Field specimen*	*Collection year*	**Assay No.**	**Subfossil taxa**	**Generated taxa**	**Distance from IM**	**Growth duration**
						Cephalozia bicuspidata ssp. ambiguua		
		GR-SBG-14		81	***Pohlia nutans***	*Polytrichum juniperinum* ***Pohlia nutans*** *Ceratodon purpureus* *Pogonatum urnigerum* *Pohlia drummondii* *Leptobryum pyriforme* *Lophozia sudetica* *Lophozia ventricosa*	zone 2 (10m)	Sept 24 - June 30 2015
		GR-SBG-27-1		82	*Polytrichum juniperinum* *Polytrichum piliferum*	*Pohlia nutans* *Pohlia drummondii* *Cephalozia bicuspidata ssp. ambiguua*	zone 3 (20m)	Sept 24 - June 30 2015
		GR-SBG-27-2		83	***Pohlia nutans*** *Polytrichum piliferum* *Polytrichum juniperinum*	***Pohlia nutans*** *Pogonatum urnigerum* *Cephalozia sp.*	zone 3 (20m)	Sept 24 - July 1 2015
		GR-SBG/EXT-25		84	-	*Pohlia nutans* *Pohlia drummondii* *Cephalozia bicuspidata ssp. ambiguua* *Lophozia sudetica* *Lophozia ventricosa*	zone 3 (20m)	Sept 24 - July 1 2015

Appendix A.

Sample	*Ice patch*	*Field specimen*	*Collection year*	Assay No.	Subfossil taxa	Generated taxa	Distance from IM	Growth duration
	Gladstone	*GL-Z1-PT 38-1*	*2016*	14	***Pogonatum urnigerum*** *Hypnum revolutum* *Ptychostomum cryophilum*	*Polytrichum juniperinum* *Pohlia nutans* *Ceratodon purpureus* ***Pogonatum urnigerum***	2m	Aug 2 - Dec 12 2016
		T5-Z1		20	*Pohlia nutans* *Niphotrichum canescens* ***Ceratodon purpureus*** *Conostomum tetragona* *Polytrichum piliferum*	*Polytrichum juniperinum* ***Ceratodon purpureus*** *Leptobryum pyriforme* *Marchantia polymorpha* *Ptychostomum pallescens*	2m	Aug 2 - Dec 13 2016
		T4-Z1-4		25	vascular plant tissue	*Polytrichum juniperinum* *Ceratodon purpureus* *Ptychostomum pallescens*	3m	Aug 2 - Dec 14 2016
		Z1-1		27	***Polytrichum juniperinum***	***Polytrichum juniperinum*** *Pohlia nutans* *Ceratodon purpureus* *Pohlia drummondii* *Saxifraga sp.* (vascular plant) *Ptychostomum cryophilum*	2m	Aug 2 - Dec 15 2016
		Z1-2		28	***Ptychostomum pallescens*** *Ceratodon purpureus*	*Pohlia nutans* *Leptobryum pyriforme* *Marchantia polymorpha* ***Ptychostomum pallescens***	5m	Aug 2 - Dec 15 2016

Appendix A.

Sample	*Ice patch*	*Field specimen*	*Collection year*	**Assay No.**	**Subfossil taxa**	**Generated taxa**	**Distance from IM**	**Growth duration**
		Z1-3		29	*Polytrichum juniperinum* ***Pohlia drummondii*** *Ptychostomum pallescens*	*Pohlia nutans* *Ceratodon purpureus* ***Pohlia drummondii*** *Marchantia polymorpha*	1.5m	Aug 2 - Dec 15 2016
		SBG 20		34	***Polytrichum juniperinum*** *Dicranum elongatum* *Pohlia nutans*	***Polytrichum juniperinum*** *Aulacomnium palustre* *Ceratodon purpureus* *Leptobryum pyriforme* *Marchantia polymorpha* *Ptychostomum pallescens*	2.1m	Aug 2 - Dec 16 2016
	Little Gladstone	*GL(2)-2*	*2016*	6	*Polytrichum juniperinum* *Polytrichum pilififerum* ***Aulacomnium turgidium*** *Ceratodon purpureus* ***Pohlia nutans***	***Pohlia nutans*** *Lophozia sp.* ***Aulacomnium turgidum*** *Dicranum fuscescens* *Cephalophoziella sp.*	2.5m	Aug 1 - Dec 8 2016

Table 1. Generation results of subfossil and extant material from Granger, Gladstone, and Little Gladstone ice patches. Assays are highlighted where taxa present within the subfossil material demonstrated regrowth. Bolded taxa are present in both the subfossil and regrowth assemblage for specific assays they highlight.

Chapter IV: Conlcusions and Implications

Arctic and alpine glaciers have undergone substantial degradation as a result of climate warming (Gardner et al. 2011, IPCC 2013, WGMS 2016), with many relict ice formations predicted to disappear within the 21st century (Khan et al. 2014). The resilience of northern ecosystems is contingent on the response of plant communities to climate fluctuations. Bryophytes are a dominant component of northern vegetation (Longton 1988), and have been shown to account for 25% the net primary productivity in sub-arctic environments (Street et al. 2013). Together with cyanobacteria and algae (crust biota) they stabilize soils through retaining moisture, augmenting nitrogen content, and facilitating carbon nutrient cycling (Bliss and Gold 1999, Gornall et al. 2001, Pedersen et al. 2001, Breen and Levesque 2006, Pedersen et al. 2001, Tuba et al. 2011, Ciccazzo et al. 2016).

Ice patches throughout Southern Yukon, Canada, have been retreating with climate change (Farnell et al. 2004). They are an integral summer refuge for alpine fauna, with accumulations of prehistoric Caribou dung (*Rangifer tarandus*) forming stratified layers throughout ice patch surfaces (Farnell et al. 2004). Ice patch forelands create unique alpine wetlands supporting diverse flora and fauna (Farnell et al. 2004, Hare et al. 2004, Hare et al. 2012). Relative to extensive archeological (Hare et al. 2004, Hare et al. 2012) and palynological (Bowyer et al. 2001) analysis of the ice patches, the understanding of the ice patch biology in modern environments is limited to ^{14}C dating of subglacial vegetation used to determine ice patch formation (Hare et al. 2004).

The retreat of the Mount Granger ice patch, Yukon, Canada, has provided an opportunity to study succession in unique nutrient rich mesic alpine habitat, and how extant foreland bryophyte communities relate to the 6470 year old (cal BP) ice entombed plant assemblages. The exhumed diaspores from the Granger, Gladstone and Little Gladstone ice patches have expanded our understanding of the role of bryophytes in alpine tundra ecosystems. These bryophytes have been demonstrated to survive long-term cryopreservation for 4089 years of ice entombment.

Chapter II elucidated the pattern of plant colonization on the deglaciated foreland of the Granger ice patch. Three seral stages were statistically determined, representing directional succession without species replacement. Glacial forelands are usually nutrient limited (Chapin et al. 1994), however the ice patch melt water run-off has facilitated the establishment of a luxurious plant assemblage at Mount Granger. Within the first seral stage (surveyed zone 2; 0-10m from the IM) plants were able to colonize as early as eight years (2009 AD) following deglaciation expanding to complete cover by the third stage (30-40m from the IM).

Of the environmental variables measured volumetric water content (VWC) was the most influential edaphic property contributing to the foreland successional pattern. Soil moisture (SM) and acidity (pH) were relatively consistent across the foreland, indicating minimal significance. To determine the richness capacity of the foreland, eight surrounding mesosites (biodiversity sites; >1km from the ice patch) were surveyed for extant diversity comparable to the GRIP foreland. Sites were along ice patch melt water channels or ‘rivulettes’ and had dominant foreland taxa *Pohlia* spp. (*Pohlia nutans* or *Pohlia drummondii*) and *Polytrichum* spp. (*Polytrichum juniperinum* or *Polytrichum hyperboreum*). The dissimilarity between the surrounding biodiversity and the foreland community suggests the specific edaphic conditions at the foreland (pH and SM), influence the overall community structure. The autecology and life strategies of the dominant species also suggests that resilient species with prolific diaspore production thrive in Granger ice patch foreland.

Future studies on the biogeochemistry and edaphic composition of Yukon ice patch forelands would enhance our understanding of carbon and nitrogen cycles within the ice patch ecosystems by studying the ice margin and within each seral stage to confirm the nutrient cycling and the impact of the exhumed dung. Comparative analysis of edaphic composition and plant colonization of dung enriched to non-dung enriched ice patch forelands would also emphasize the signicance of the interplay between preserved dung and modern ecosystem dynamics. Succession data from Gladstone ice patch is in progress to provide a regional perspective of variation of ice patch communities.

Preserved subfossil bryophytes provided data on ecosystem stability and resilience of the foreland community structure. The subfossil assemblages contained the same dominant taxa as within the foreland, representing 13% of the total foreland bryophyte diversity. The shared dominant taxa of the subfossil and foreland assemblages suggest that this unique community composition has remained consistent over 6000 years.

Chapter III focused on the subfossil assemblages and their contribution to the establishment and maintenance of the ice patch tundra ecosystem. Granger ice patch is rapidly retreating in response global warming trends, having been reduced to 4% the LIA (Little Ice Age) maximum (Farnell et al. 2004) extent in 2015. This rapid retreat has exposed ice-entombed paleo bryophyte material up to 6470 years cal BP (Mount Granger) and viable propagules up to 4089 years old (cal BP; Gladstone). Growth chamber assays contained generation of the same species (juvenile populations) as the original subfossil material (parental assemblage) in 73% of the samples, indicating regeneration from subfossil bryophytes. Growth capacity of the subfossil samples was similar between all ice patches, all showing regeneration in over 98% of assays that shared the same dominant taxa: *Polytrichum piliferum, Polytrichum juniperinum, Pohlia nutans, Pohlia drummondii, Leptobryum pyriforme,* and *Ceratodon purpureus*. This similarity further supports that the abiotic conditions at the ice patches support a specific community of bryophytes. From the three ice patches (Granger, Gladstone, Little Gladstone) 40 species were generated in the assays, including, 26 species that were not present within the subfossil record, suggesting germination from diaspores.

From the Mount Granger ice patch, generated species from growth chamber assays represent 65% of the total emergent subfossil taxa, and 35% of the surrounding biodiversity (>1km from the IM), indicating that the Yukon ice patches function as significant alpine tundra reservoirs of biological diversity, and support a unique alpine plant community.

The life strategies of the foreland taxa are predominantly ruderal colonizers or perennial stayers. Colonizers such as *Pohlia drummondii, Ceratodon purpureus* and *Leptobryum pyriforme* thrive in unstable environments, and have short longevity of only a few years (Grime 1979, During 1992). To maintain their presence within an environment, these species produce prolific asexual gemmae (During 2001). Gemmae remain dormant within soil, expanding plant persistence into future generations where environmental conditions are ideal for establishment (During 2001). Reliance on asexual production is common in high stress and disturbance environments (Longton 1988). Perennial Polytrichales taxa form dense long-lived rhizoidal mats, capable of generating clonal gametophores from rhizoidal gemmae (Wigglesworth 1947, Longton and Schuster 1983), extending their life span on colonized terrain. *Polytrichum* species (*Polytrichum hyperboreum, Polytrichum juniperinum* and *Polytrichum piliferum*) in the foreland produced prolific sporophytes, indicating the mesic conditions were favorable for sexual reproduction. Each *Polytrichum* sp. sporophyte will produce millions of spores that will germinate in ideal conditions, or integrate into the diaspore bank (Miles and Longton 1990). The prevalence of diaspores within the subfossil material suggest that propagulae from ice patch foreland communities have been dispersed by anemochorous events and encapsulated within the ice patch foreland during times of exposure.

In addition to effective dispersal strategies, bryophytes possess a suite of adaptive traits, such as totipotency and desiccation tolerance, that has allowed them to flourish in harsh northern environments (Longton 1997). The results of this study support the findings of La Farge et al. (2013) and Roads et al. (2014), indicating that bryophyte adaptive traits have contributed to their viability after extended periods of ice entombment. This study has expanded the temporal limits of bryophyte survival from 400 years cal BP (La Farge et al. 2013), and 1500 years cal BP (Roads et al. 2014), to thousands of years (4089 years cal BP).

Additional research has been initiated on a genetic analysis of subfossil and extant populations of the dominant alpine bryophyte, *Polytrichum hyperboreum*, from the Granger and Gladstone ice patches. Preliminary result from successful DNA extraction of 36 populations, including Gladstone (15 extant) and Granger (15 extant, and six subfossil populations) have been sequenced using double digestion restriction site associated DNA next generation sequencing (ddRAD; Peterson et al. 2012) on a HiSeq$^{\mathrm{TM}}$ 500 Illumina platform. The ddRAD approach is a high through-put, effective sequencing technique for single nucleotide polymorphic (SNP) analysis that utilizes a reduced representation library (Davey et al. 2011). In this approach, genomic fragments from each individual are uniquely barcoded to allow for pooling of samples, decreasing time/cost ratios, and maximizing sequencing read outputs (Peterson et al. 2012). Next generation sequencing has only been done once prior with moss in Lewis et al. (2015) on *Tetraplodon mnioides*. Genetic diversity is correlated with the ability to adapt to changing environmental conditions (Jump et al. 2009). Molecular analyses of the exhumed plants compared to modern populations will provide insight to evolutionary relationships and potential genetic variation. High genetic diversity increases adaptive capacity, which is advantageous with increased rates of climate change. Sequencing data from cryopreserved bryophytes initiates the opportunity to assess genetic change spanning the Holocene (last 10,000 yrs).

Ice patches are an integral part of Yukon tundra ecosystems. In addition to supporting a unique community of plants within the immediate foreland, nutrient rich water from seasonal melt supports the surrounding floral diversity. Seventy bryophytes were found growing along melt water channels > 1km from the ice margin. Diverse alpine faunal also rely on the ice patches for sustenance (flora communities for foraging and melt water run off for hydration) and cooling effect of the ice as a summer refuge (Farnell et al. 2004). The gravitation of fauna towards this sites has made them ideal hunting grounds for first nations people (Hare et al 2004) for millennia as dated artefacts attest (8360 years BP , Hare et al. 2004, Hare et al 2012) from 43 distinct ice patches. In additional to the Yukon ice patches, ice patches have been recently the focus of intensified archeological research across North America, including the North West Territories (Andrews and McKay 2012, Meulendyk et al. 2012), Colorado Front Range, and the central Rocky Mountains of Wyoming and Montana (Lee 2012), providing insights into the past history of First Nations hunting ancestors (Brunswig 2014). This is the first study on the vegetation associated with these ice patches, expanding our understanding to the biological dynamics of ice patches past and present. These findings provide First Nation Peoples with a biological perspective on the regenerative capacity these ice patches for both the plants and fauna of the alpine tundra, documenting the role of ice patches within their ancestral heritage.

Simulated climate warming experiments across northern environments have projected vegetation shifts induced by climate change (Henry and Molau 1997, Elmendorf et al. 2012). Northern adapted bryophytes in particular are predicted to experience detrimental effects, with diversity overall decreasing (Hallingback and Tan 2010, He et al. 2016). This study has shown that with the retreat of Yukon ice patches, exhumed ancient viable diaspores have the potential to integrate plant diversity (Hock et al. 2008), stabilizing ice patch foreland vegetation. Alpine fauna have relied on the ice patches over an expansive temporal period, with faunal remains >6000 years 14^{C} BP found across ice patches (Hare et al. 2012), further emphasizing the necessity to monitor ice patch fluctuation and plant community response to climate warming.This study has also established a framework for investigating the biological relevance of Yukon ice patches (87 have been determined to date; Hare et al. 2012), contributed to current paleoenvironmental studies that are rapidly expanding in the Yukon (Zazula et al. 2006, Reyes et al. 2010), and provided a novel outlook subglacial systems and their role in the fate of the north.

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