

Future directions and priorities for Arctic bryophyte research¹

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Abstract: The development of evidence-based international strategies for the conservation and management of Arctic ecosystems in the face of climate change is hindered by critical knowledge gaps in Arctic floristic diversity and evolution. Particularly poorly studied are the bryophytes, which dominate the vegetation across vast areas of the Arctic and consequently play an important role in global biogeochemical cycles. Currently, much of what is known about Arctic floristic evolution is based on studies of vascular plants. Bryophytes, however, possess a number of features, such as poikilohydry, totipotency, several reproductive strategies, and the ability to disperse through microscopic diaspores, that may cause their responses to Arctic environments to differ from those of the vascular plants. Here we discuss several priority areas identified in the Arctic Council's "Arctic Biodiversity Assessment" that are necessary to illuminate patterns of Arctic bryophyte evolution and diversity, including dispersal, glacial refugia, local adaptation, and ecological interactions with bryophyte-associated microbiomes. A survey of digitally available herbarium data archived in the largest online aggregate, GBIF, across the Arctic to boreal zones indicates that sampling coverage of mosses is heterogeneous and relatively sparse in the Arctic *sensu stricto*. A coordinated international effort across the Arctic will be necessary to address knowledge gaps in Arctic bryophyte diversity and evolution in the context of ongoing climate change.

Key words: biodiversity, dispersal, local adaptation, microbiome, phylogeography.

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Résumé : Le développement de stratégies internationales, fondées sur des données probantes, visant la conservation et la gestion d'écosystèmes arctiques en présence du changement climatique se trouve entravé à cause de lacunes de connaissances critiques sur le plan de la diversité et de l'évolution floristique arctique. En particulier, les bryophytes, qui dominent la végétation à travers les vastes zones de l'Arctique, et par conséquent, jouent un rôle important dans des cycles biogéochimiques à l'échelle planétaire, sont mal étudiés. Actuellement, une grande partie de ce que l'on connaît de l'évolution floristique arctique est fondée sur des études de plantes vasculaires. Les bryophytes, cependant, possèdent un certain nombre de caractéristiques, comme le manque de capacité de maintenir ou de réguler la teneur en eau (« poikilohydry »), la totipotence, plusieurs stratégies reproductrices et la capacité de se disperser par diaspores microscopiques, ce qui peut causer leurs réponses aux environnements arctiques à être différentes de celles des plantes vasculaires. Ici nous discutons de plusieurs domaines prioritaires identifiés dans l'évaluation de la biodiversité arctique du Arctic Council, lesquels sont nécessaires afin de mettre en lumière les modèles d'évolution et de diversité des bryophytes arctiques, y compris la dispersion, les refuges glaciaires, l'adaptation locale et les interactions écologiques au sein des microbiomes liés aux bryophytes. Une étude des données disponibles en forme numérique archivées dans le plus important ensemble en ligne, le Système mondial d'informations sur la biodiversité, sur les herbiers à travers l'Arctique jusqu'aux zones boréales, indique que l'échantillonnage de la couverture de mousses est hétérogène et relativement clairsemé dans le *sensu stricto* d'Arctique. Un effort international coordonné à travers l'Arctique sera nécessaire afin de combler les lacunes de connaissances en matière de diversité et d'évolution des bryophytes en Arctique dans le contexte du changement climatique en cours.

Mots-clés : biodiversité, dispersion, adaptation locale, microbiome, phylogéographie.

Introduction

Arctic bryophytes are diverse, abundant, and ecologically significant

Bryophytes play a significant role in global carbon storage, both directly (Adams et al. 1990; Belyea and Malmer 2004) and through their ecological interactions with microorganisms (DeLuca et al. 2002; Lindo et al. 2013). Their contribution to primary productivity increases relative to vascular plants along a latitudinal gradient within the Arctic (Hassel et al. 2012). Despite their low nutritional value, bryophytes are foraged by herbivores (ruminants, rodents, and migratory birds) in the Arctic, probably due to their high biomass and availability within the tundra vegetation (Stech et al. 2011 and references therein). They also make a substantial contribution to circum-Arctic species richness, being the primary component of phytodiversity in some regional areas such as the High Arctic Svalbard archipelago, where they outnumber vascular plants 2:1 in species number (Daniëls et al. 2013). The Arctic Biodiversity Assessment (ABA), produced by the Arctic Council's Conservation of Arctic Flora and Fauna (<http://www.caff.is/>), reports approximately 900 species composing the Arctic bryoflora, with few regional endemics but many circum-boreal, circum-Arctic and, amphi-Beringian species (Daniëls et al. 2013). Similar to vascular plants, Arctic bryophyte species diversity is distributed across a small number of genera and families relative to lower latitudes (Yurtsev 1994). Bryophyte species diversity, however, may still be incompletely known, even for comparatively well-studied Arctic areas, as inferred from recent floristic studies (Hesse et al. 2012; Hassel et al. 2014).

Bryophytes dominate a number of vegetation types across often vast areas in the Arctic and sub-Arctic regions (Longton 1988; Daniëls et al. 2013). However, our current knowledge of floristic and genetic diversity, evolutionary history, and dispersal in the Arctic is sparse for these ecologically significant plants (but see Piñeiro et al. 2012; Kyrkjeeide et al. 2014, 2016a, 2016b). This is an increasingly conspicuous and important knowledge gap in the face of rapid climate change in the polar regions (Urban et al. 2016). Our limited understanding partly reflects that Arctic bryology is still a relatively young area of research. Early scientific expeditions to remote northern regions were rare in the 1800s. The earliest

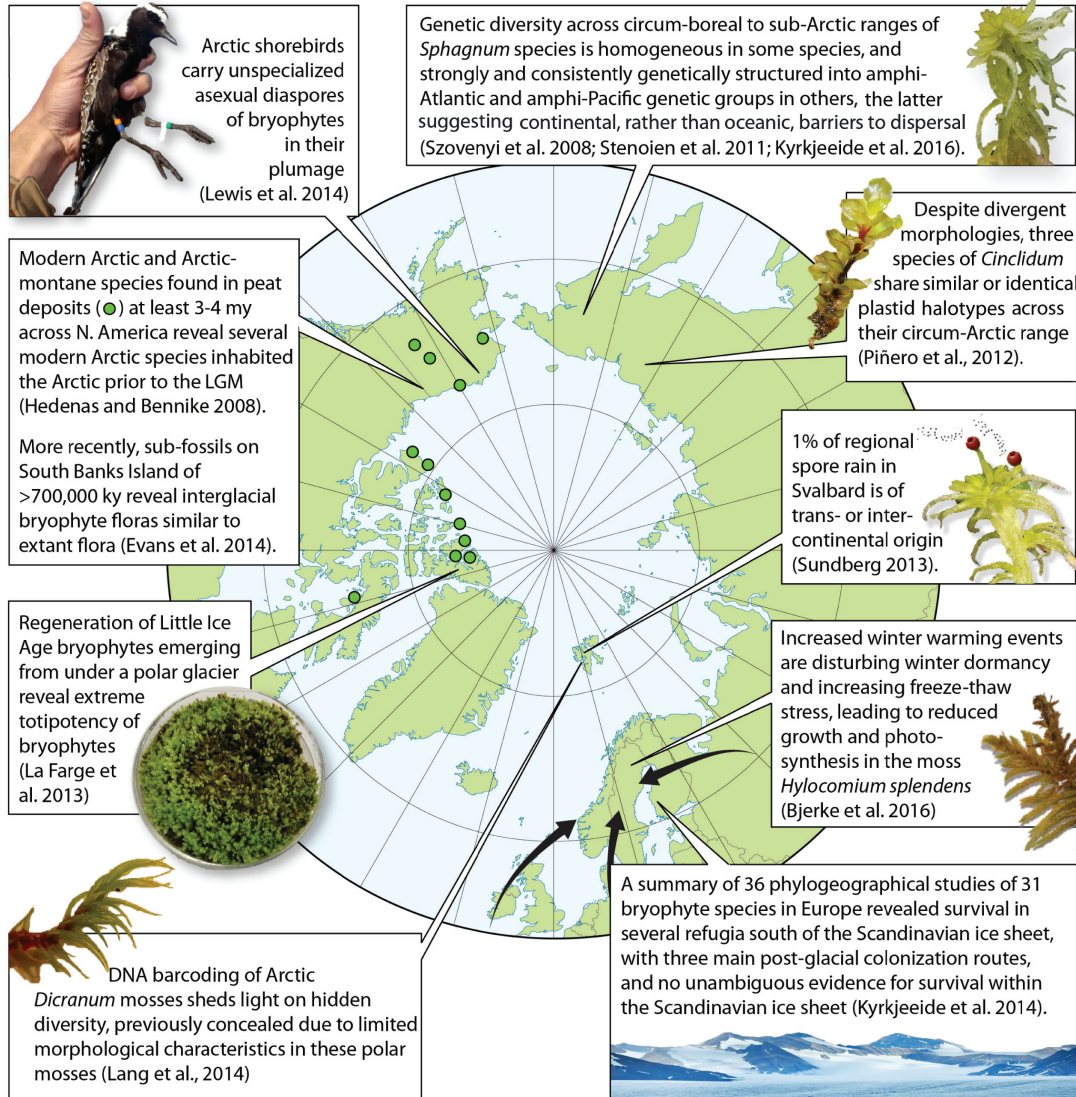
published scientific record of Arctic bryophytes in North America was from the HMS Discovery Expedition of Adolphus Greely who overwintered on northeastern Ellesmere Island between 1881 and 1884 (Lehnert and Greely 1886). In the Russian Arctic, bryological investigations began in the middle of the 19th century (Afonina and Czernyadjeva 1995). In the first half of the 20th century, advancing aviation technologies and infrastructure dramatically improved accessibility of the Arctic, promoting botanical and specifically bryological explorations (Steere 1971). Furthermore, infrastructure provided at newly accessible field sites as well as international programs to facilitate access to these stations (e.g., in the frame of the INTERACT network, <http://www.eu-interact.org/>) allowed for the collection of high-quality specimens from a broader geographic range across the Arctic.

This greater access to Arctic ecosystems and specimens provided evidence that (1) many Arctic bryophyte species were widely distributed across the Arctic, with presumed endemism of species resulting from sampling artifacts, and that (2) many species displayed an Arctic–montane disjunction, with populations in the Arctic and at high-altitude locations at lower latitudes (Steere 1954a; Brassard 1971; Schofield 1971). Starting in the late 1980s, molecular studies, initially based on isozymes and later DNA sequences, uncovered high levels of genetic diversity in many bryophytes (Shaw 2001; Shaw et al. 2002). In a number of cases, genetic diversity of broadly distributed morphologically defined bryophyte taxa were geographically highly structured and species were better considered assemblages of cryptic species (Heinrichs et al. 2009). The task of morphological species identification in bryophytes is especially difficult in speciose and taxonomically complex families such as the Bryaceae, Dicranaceae, Amblystegiaceae, Hypnaceae, and Brachytheciaceae, for example, which make up a considerable part of Arctic bryophyte diversity (Daniëls et al. 2013). Improvements have been made concerning taxonomy of some Arctic bryophyte species (Hesse et al. 2012); however, molecular studies are still needed for most Arctic bryophyte taxa to assess species circumscriptions. DNA barcoding tools (e.g., Hassel et al. 2013; Stech et al. 2013; Lang et al. 2014) would likely standardize identification across the Arctic and combined with other genetic tools promote the study of migration, mating system, and patterns of genetic diversity within consistent taxonomic entities (Zartman et al. 2006; McDaniel et al. 2013a, 2013b; Magdy et al. 2016).

Scope

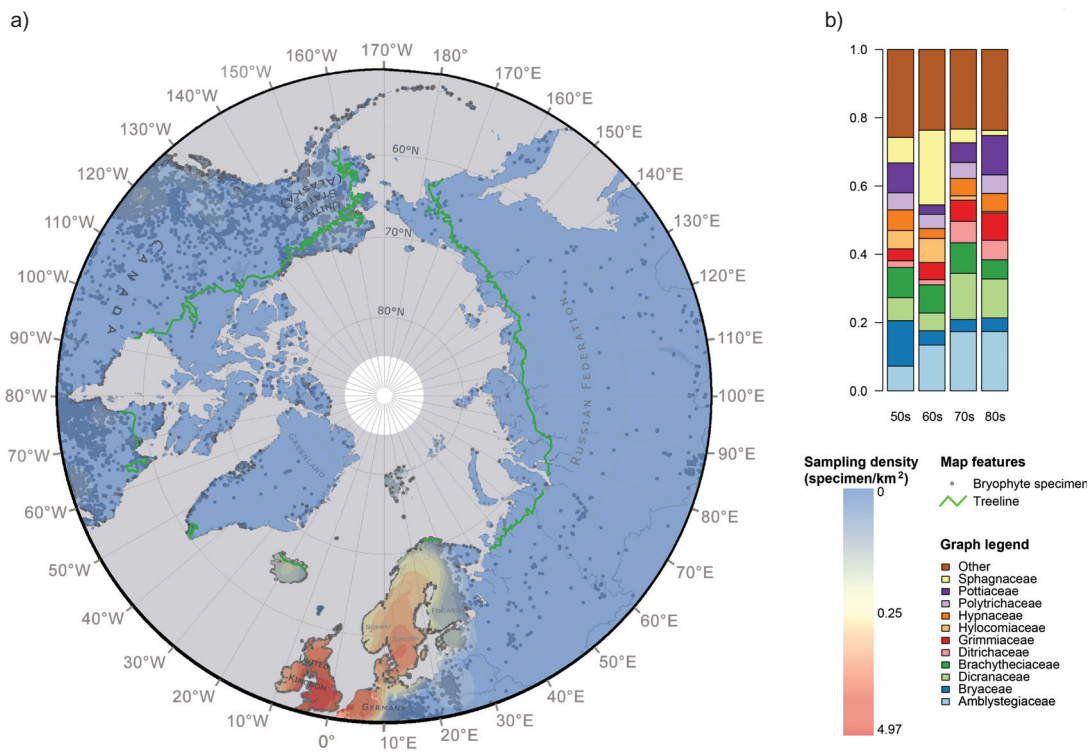
Here we examine recent progress in Arctic bryophyte phylogeography and diversity research (Fig. 1.) in the context of Arctic conservation priorities. Our discussion focuses on liverworts and mosses, with an emphasis on the latter, and excludes hornworts, which are absent from the Arctic flora. Given the limited literature on Arctic bryophytes at the circum-Arctic scale and employing molecular data, comparisons and inferences based on other land plant lineages are included to illuminate gaps and hypotheses that may guide studies on Arctic bryophyte phylogeography and diversity. We aim to complement a number of comprehensive reviews published over the past 5 years regarding the resilience and functional roles of Arctic and boreal bryophytes (Turetsky et al. 2012), the phylogeographic history of the European Quaternary bryoflora (Kyrkjeeide et al. 2014), the biogeography of polar photoautotrophs (Pointing et al. 2015), the *Sphagnum* microbiome (Kostka et al. 2016), and the physiological responses of bryophytes to increasing temperatures (He et al. 2016). We discuss the utility of museum collections, providing a brief discussion of digitally accessible specimen data, in conjunction with molecular data to understand how species richness, based on morphological species concepts, reflects genetic diversity. Genetic diversity and species richness are positively correlated for Arctic vascular plants (Stewart et al. 2016), but this hypothesis remains untested for Arctic bryophytes, as data for bryophyte genetic diversity are limited at both taxonomic and spatial scales (Daniëls et al. 2013).

Fig. 1. Some highlights among recent studies on the phylogeography, diversity, and dispersal of Arctic bryophytes. Green dots on the map indicate localities where modern Arctic and Arctic montane species have been recovered from peat deposits at least 3–4 My old (Hedenäs and Bennike 2008).



The Arctic is spatially and temporally dynamic, as is the process of defining the “Arctic.” Here we follow the ABA (Melfo et al. 2013), Walker et al. (2005), and Yurtsev (1994), defining the Arctic as the region north of the tree line (Fig. 2). We also consider regions south of the tree line to 50°N (Fig. 2.) because many Arctic bryophyte taxa have ranges extending to sub-Arctic and boreal zones (Brassard 1971; Schofield 1971; Steere 1971, 1978; Longton 1988) and migration between lower latitudes and the Arctic is at least historically significant (Kyrkjeeide et al. 2014). Additionally, bryophyte communities influence seedling environments (e.g., Soudzilovskaia et al. 2011), while trees alter the microclimate in which bryophytes grow (Longton 1988), making the tree line an ecologically relevant feature for delimitation.

Fig. 2. Distribution of Bryophyta (moss) collections above 50°N databased in GBIF as of July 2016. (a) Point occurrence data and density for specimen records are shown by color across all land masses and the lower limit of the Arctic, as delimited by tree line, marked by the green line. Blue regions have extremely sparse sampling and red regions have the greatest sampling density. Particularly large sampling gaps are in the Russian and eastern North American Arctic. This map was prepared by Toolik Field Station GIS and remote sensing group (<http://toolik.alaska.edu/gis/>). Note that ice cover is not shown, and the azimuthal equidistant projection increasingly distorts areas with increasing distance from the center point, making southern land masses appear larger. (b) Families with the greatest representation in specimen collections across four latitudinal increments. Listed families included are those that constitute 5% or more of samples in at least one of the latitudinal increments (i.e., 50s (≥ 50 to <60), 60s (≥ 60 to <70), 70s (≥ 70 to <80), and 80s (≥ 80 to <90)). Families with less than 5% representation in all latitudinal increment are grouped into the “Other” category, thus providing a summary of specimen-rich groups for Arctic research rather than providing a representation of Arctic diversity (see Daniëls et al. 2013 for a summary of Arctic bryophyte floristic studies). Given variable species concepts and the notably challenging families that dominate the northern high-latitude floras, future taxonomic revisions will likely result in changes to this summary of familial representation in digitally available collections data.



Arctic bryology in a conservation context

The ABA identifies fundamental knowledge gaps, including the need for a circum-polar checklist of bryophytes based on consistent taxonomic concepts and nomenclature and ideally informed by genetic data (Daniëls et al. 2013). Circum-Arctic checklists are currently available for the vascular flora (Elven et al. 2011), lichens, and lichenicolous fungi (Kristinsson et al. 2010). In addition to refining biodiversity estimates, intraspecific genetic data are essential for the identification of high-diversity localities (such as those potentially associated with refugia) and the reconstruction of dispersal patterns for Arctic taxa. Such data will be critical for comparative analyses between the Arctic and Antarctic, as called for in “The Arctic in 2045: a long-term vision” (Friedhuber 2016). In that spirit, we look also to the 2014 SCAR First Antarctic and Southern Ocean Horizon Scan, which

identified six scientific priorities, including “Learn how Antarctic life evolved and survived” (Kennicutt et al. 2014). This work is urgent, given the “greening of the Arctic” — the observed increase in trees and shrubs in tundra environments due to global climate warming — which may result in decreased abundance of bryophytes and changes in species composition and distributions (Callaghan et al. 2004). Consequences of a changing ecosystem structure may include reduced albedo, increased soil temperature, and higher ecosystem respiration and release of trace gases (summarized by Daniëls et al. 2013). Recently, “browning of the Arctic” associated with winter warming has also been reported in parts of the Arctic (Phoenix and Bjerke 2016) and has been shown to reduce photosynthesis and alter growth patterns in sub-Arctic populations of *Hylocomium splendens* (Bjerke et al. 2016). Currently, knowledge of patterns of floristic genetic diversity, evolutionary history, and dispersal in the Arctic is largely lacking for bryophytes, and this fragmentary baseline constitutes the main challenge for studying the effects of rapid climate change on polar biota (Urban et al. 2016).

Here we address the need for baseline biodiversity research across the Arctic bryoflora by focusing on three interrelated questions as follows.

(1) *What role does gene flow play in shaping the distribution of bryophyte genetic diversity across the Arctic?* In the context of ongoing environmental change, dispersal ability shapes an organism’s ability to shift ranges or track its niche. The ABA states that it is “essential to consider the vast spatial scales over which many organisms operate as well as the existing barriers to mobility that influence the current distribution...” (Meltofte et al. 2013). This is mirrored by an Antarctic Horizon Scan priority regarding the extent of gene flow in Antarctica, including sources and mechanisms of dispersal of propagules, and range shifts of indigenous species (Kennicutt et al. 2014).

(2) *What are the respective roles of historical demography (i.e., survival in refugia) and prevailing ecological conditions (i.e., selective pressure that may lead to local adaptation) in generating diversity hotspots?* Refugial areas are considered by the ABA to be “hotspots” of Arctic biodiversity that are of “paramount” importance (Meltofte et al. 2013). Prioritization of refugial areas for preservation of intraspecific genetic diversity may be critical to a species’ ability to adapt to change and for overall floristic resilience (Pauls et al. 2013). Alternatively, diversity may be maintained by ongoing selective processes. A clear understanding of local adaptation in high-latitude plants will also be critical for predicting responses to climate change (Souther et al. 2014). If populations are locally adapted, new conditions in a given site are likely to favor alleles that were previously advantageous elsewhere. Thus, in a rapidly changing climate, population structure may impose constraints on ecosystem dynamics (Eidesen et al. 2013; Vellend et al. 2014).

(3) *How will interactions between bryophytes and other community members change as the climate warms?* The importance of exploring and characterizing microbiome diversity and ecosystem contributions in polar regions was highlighted during the 2007–2008 International Polar Years as an important area of research and basis for formation of the Microbiological and Ecological Responses to Global Environmental Changes in Polar Regions working group (MERGE) (Naganuma and Wilmotte 2009; Pointing et al. 2015). The ABA similarly calls for improved “understanding of diversity (from species to populations) and interactions of vertebrates, invertebrates and microorganisms that collectively form the web of relationships within northern marine, freshwater and terrestrial systems” and points out that microbes are one of the most poorly studied groups of polar organisms (Meltofte et al. 2013). Given the challenges associated with Arctic bryology (Longton 1988; Daniëls et al. 2013), future work will require extensive bryophyte collecting efforts along with interdisciplinary training in bryophyte taxonomy, population and molecular genetics, experimental biology, ecosystem ecology, and modern statistical modeling.

What is the role of gene flow in shaping genetic structure across the Arctic bryoflora?

Much of what we can infer about the phylogeographic history and extant patterns of genetic diversity of the Arctic flora is based on studies of vascular plants (Daniëls et al. 2013; Meltofte et al. 2013). While micro- and macroclimatic conditions define the broad perimeter of the distribution for all plants, unique aspects of the life cycles, plant body architecture, symbionts, and physiology of bryophytes may dictate the processes that govern rates in range shifts and explain distinct responses to warming (He et al. 2016). Distinct trends in species–area relationships (Patiño et al. 2014), as well as variable latitudinal diversity patterns between vascular plants, mosses, and liverworts (Shaw et al. 2005; Mateo et al. 2016; Wang et al. 2017), as has also been demonstrated in South America (Rozzi et al. 2008), suggest distinct biogeographic consequences of features unique to bryophytes.

Long-distance dispersal

In the Arctic, many bryophyte species have broad distributions, potentially as a result of frequent and ongoing long-distance dispersal. The high dispersibility of bryophytes is supported by phylogenetic (Heinrichs et al. 2009; Piñeiro et al. 2012; Kyrkjeeide et al. 2016a, 2016b), experimental (van Zanten 1978), comparative floristic studies (Miller and McDaniel 2004; Muñoz et al. 2004), and field observations (Miller and Ambrose 1976; McDaniel and Miller 2000; Sundberg 2013). Dispersal potential of bryophytes is high due to the production of small spores as well as a suite of specialized (gemmae) and unspecialized asexual diaspores (gametophyte fragments), which may be wind- (Miller and Ambrose 1976; see Schofield 1971 for a detailed review) or animal-dispersed (Parsons et al. 2007; Pauliuk et al. 2011; Boch et al. 2013; Lewis et al. 2014). Recent work from the Eurasian Arctic has shown that sexually reproducing populations of *Sphagnum* are capable of intercontinental dispersal of spores (Sundberg 2013). Capture and culture of airborne bryophyte diaspores in eastern Canadian boreal forests have demonstrated that many species, independent of life strategy type, are dispersed regionally, and 19 taxa were recovered that were not present locally (Barbé et al. 2016). Despite the high dispersal potential of bryophytes associated with their small diaspores, Lenoir et al. (2012) found that bryophytes showed a very similar relationship between local and regional species composition to that found in seed plants, suggesting similar dispersal ranges. Limitations to effective dispersal (i.e., leading to establishment) for bryophytes are apparent in that “everything is not everywhere,” even when considering only seemingly suitable habitats for a given species (Medina et al. 2011).

Comparisons of spatial species turnover between local and regional scales in Eurasian Arctic bryophytes revealed that environmental variables had little effect on distance dissimilarity estimates, suggesting that relationships in species richness between local and regional scales are primarily controlled by dispersal factors rather than environmental limitations to establishment (Lenoir et al. 2012). Effective dispersal, that is dispersal concluded by establishment, is first dependent on spore viability and geographic connectivity. In the Southern Hemisphere, transoceanic disjunctions characterize species with spores resistant to extreme conditions associated with high-elevation winds (van Zanten 1978) and only if distant localities are connected by wind (Muñoz et al. 2004). In the Arctic, resistance to terrestrial connectivity is potentially high, such that vector-based dispersal limitations may not be as severe as in the sub-Antarctic, where land is scarce and transoceanic dispersal distances are large (e.g., McDaniel and Shaw 2003).

In addition to diaspore resistance to dispersal conditions, potentially limited spore or gemmae production by Arctic bryophytes may constrain dispersal potential. Schofield (1971)

discussed how low levels of free water along with the generally isolated patches of mostly dioicous (>60%) species (which may form single sex colonies) may limit sexual reproduction in the Arctic. Recent studies have shown, however, that sexual reproduction can occur in environments with only short-term availability of free water, as sperm cells and antheridia can withstand dehydration (Shortlidge et al. 2012; Stark et al. 2016). Monoicous acrocarpous taxa tend to reproduce sexually regularly (Schofield 1971; Longton 1988), but phenological data are lacking or incomplete for most taxa. Forty-two percent of the mosses of northern Ellesmere Island produce sporophytes but only 28% do so regularly (Brassard 1971). In North Greenland, 31% of moss species develop sporophytes (Holmen 1960) and nearly 48% of those in the Siberian sub-Arctic (Fedosov et al. 2011). For species with low rates of sexual reproduction, dispersal may be accomplished via asexual structures (gemmae) and gametophyte fragments (Schofield 1971).

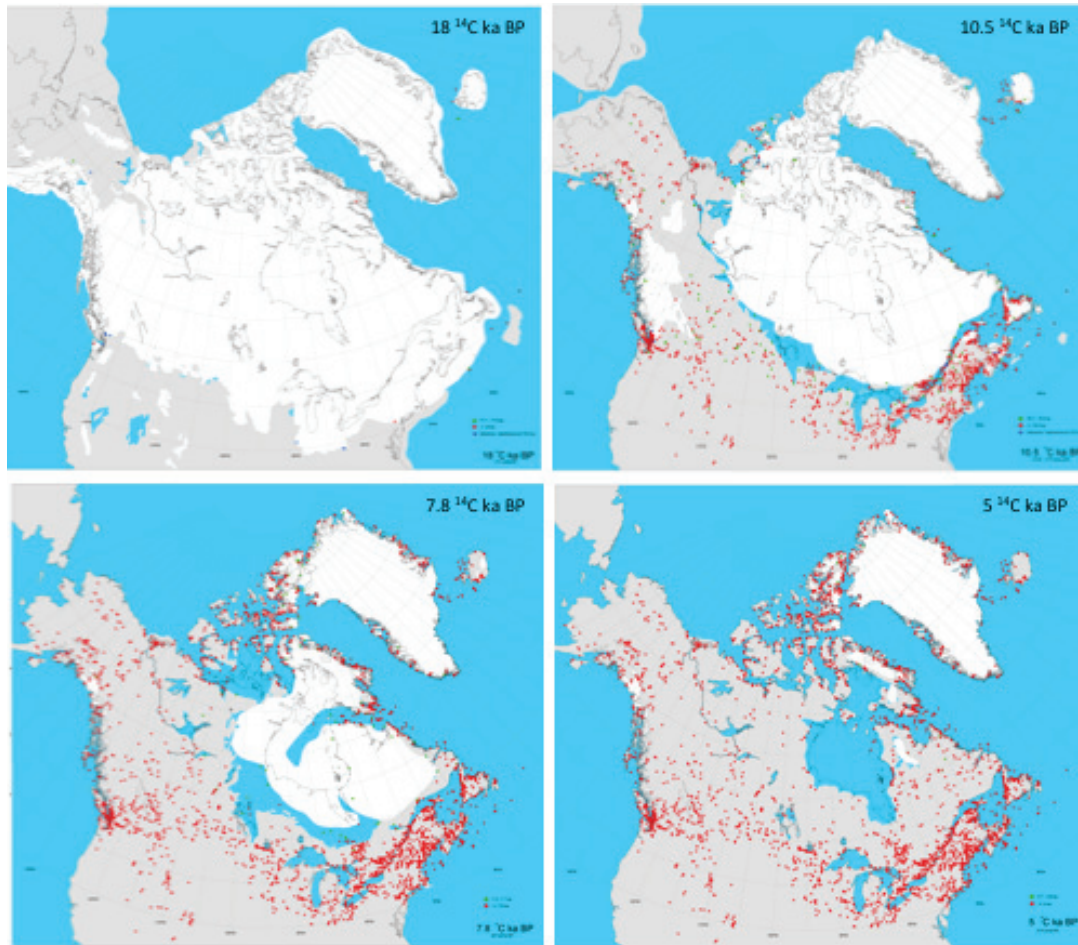
The potential correlation between sexual systems and mode of asexual reproduction has long attracted the attention of bryologists. In the United Kingdom, one of the best studied bryophyte floras (Fig. 2), dioicous species are considered less likely to produce sporophytes and hence spores (Longton 1992) but more likely to produce asexual propagules (Longton and Schuster 1983). Global comparative phylogenetic analyses suggest, however, a weak or no correlation between the presence of asexual propagules and dioicy in mosses and liverworts (Laenen et al. 2016). Gemmae production among Arctic bryophytes is relatively infrequent compared to bryophytes of boreal and tropical latitudes (Schofield 1971).

Lewinsky (1977) revised *Orthotrichum*, *Ulota*, and *Amphidium* from Greenland and only reported three dioicous taxa out of 11 species within those genera with asexual propagules. Likewise, in sub-Arctic Siberia (Anabar Peninsula), only 27 of the 520 species (19.3%) presented any signs of specialized vegetative reproduction (Fedosov et al. 2011). However, given that fragments of the vegetative body can typically regenerate entire plant bodies (Shaw 1986), establishment of Arctic bryophytes may result primarily from the dispersal of unspecialized vegetative fragments (Longton 1988), as is, for example, reported from alpine habitats (Robinson and Miller 2013). On High Arctic Bathurst Island, up to 4000 gametophyte fragments may be recovered per cubic metre of snow (Miller and Ambrose 1976), with similar results found in montane tundra (McDaniel and Miller 2000). Such vegetative fragments tend to more consistently produce protonema compared to spores and hence are more likely to lead to establishment (Maciel-Silva 2017).

DNA markers may be vital for accurately identifying Arctic bryophyte species (Lang et al. 2014), especially when only diaspores are sampled, and can provide an overall picture of the origin of diaspores and populations. A complete DNA barcode database for Arctic and sub-Arctic bryophytes is required in order to accurately identify bryophyte diaspores present in environmental samples taken from snow or air, for example. This would allow testing of the hypothesis that wind connectivity is a determining factor in shaping current patterns in biodiversity in the Arctic. Current concerted efforts to barcode Arctic mosses led by the Canadian Barcoding Initiative (<http://www.ccdb.ca>) and the Norwegian initiative for barcoding of polar bryophytes, with data hosted by BOLD (<http://www.boldsystems.org/>), are complemented by barcoding projects in temperate regions that include bryophytes (United Kingdom: Bell et al. 2013; Netherlands: Stech and Sparrius 2011; Germany: www.bolgermany.de) and are generating the essential tools required to assess the identity of bryophyte diaspores transported by wind currents.

The ability to effectively disperse is dependent not only on the potential and capacity to disperse but also on the opportunities for establishing. Greater availability of open niches following disturbance (such as that left by the retreating Laurentide Ice Sheet; Fig. 3) and changing climatic conditions create “windows of opportunity” for range expansions.

Fig. 3. Glacial Retreat in North America showing the demise of the Laurentide ice sheet between 18 and 5 ka BP (modified from Dyke 2004). Rapid retreat of ice cover over the past 13 000 years has radically changed the North American landscape. Retreat is based on radiocarbon dates from terrestrial organics (a high percentage are from peat) and marine shells indicated by the red dots.



The Miocene cooling and Pleistocene glaciations are recognized as creating the “window of opportunity” that has resulted in extant Arctic biodiversity (Abbott and Brochmann 2003; Shaw et al. 2010). Differences in species composition of viable airborne diaspores and locally occurring communities (Pettersen 1940; Barbé et al. 2016) highlight the role of environmental factors in limiting range expansions. However, little is known about the succession of bryophyte communities, in the Arctic or even temperate regions, or the biotic (including microbial) factors that may promote or impede establishment by particular species.

Migration across the Arctic may also be restricted by geographic barriers. The Arctic and Atlantic oceans, Greenland ice cap, Ural Mountains, and Lena and Kolyma rivers of Siberia have been identified as major barriers to dispersal and gene flow for Arctic angiosperms (Eidesen et al. 2013). These barriers may, however, be less effective in preventing the movement of microscopic bryophyte diaspores. Transoceanic floristic similarities and phylogeographic reconstruction reveal that gene flow is not completely interrupted by oceanic

barriers in bryophytes (Patiño et al. 2014) but may be more severely restricted by terrestrial barriers (Kyrkjeeide et al. 2016a). *Sphagnum* species tend to show a split between Beringian and Atlantic populations (Szövényi et al. 2008; Stenøien et al. 2011; Kyrkjeeide et al. 2016a), providing evidence that the North American and Eurasian continents act as barriers to dispersal. Other *Sphagnum* species and four species of *Cinclidium* are genetically homogeneous across their circum-Arctic to circum-boreal ranges (Piñeiro et al. 2012; Kyrkjeeide et al. 2016a), suggesting that barriers may act differently, on even closely related species.

The various limitations to dispersal in bryophytes likely act in a hierarchical way to shape distribution patterns in the Arctic. The role of dispersal limitations in bryophytes, however, has been explored to a very limited extent. The factors controlling bryophyte dispersal and range expansions remain elusive and mapping of genetic patterns across the landscape will be important in understanding the processes shaping genetic diversity in this vagile component of the Arctic flora. The significance of the barcode database and barcode availability would be to assess the migration potential, and hence migration “pressure,” which may be critical in understanding what shapes current patterns and in predicting how changes in climate may trigger changes in communities.

What are the respective roles of historical demographic and ongoing selective processes in shaping extant diversity?

Refugia

Global climate experienced fluctuations that led to several glacial–interglacial cycles during the Quaternary (last 2.4 My) (Hewitt 2000). Consequently, most species saw their geographical range expanded and contracted during the cyclical climatic changes of the Quaternary (Stewart et al. 2010). The age of extant bryophyte species is difficult to assess due to a limited number of fossils (see Tomescu 2016 for discussion on reasons behind the sparse fossil record, including insufficient paleobryological capacity). However, fossils with a minimum age of 4 My provide evidence for the historical presence of at least 16 mosses in Arctic North America prior to the last glacial maximum (LGM), including *Aulacomnium acuminatum*, *Bryobrittonia longipes*, and *Cinclidium latifolium* (Hedenäs and Bennike 2008). A similar minimum age was also inferred for fossils representing 12 Arctic-montane-distributed species. Thus, it is reasonable to assume that bryophytes have experienced the strong climatic oscillations throughout the Quaternary.

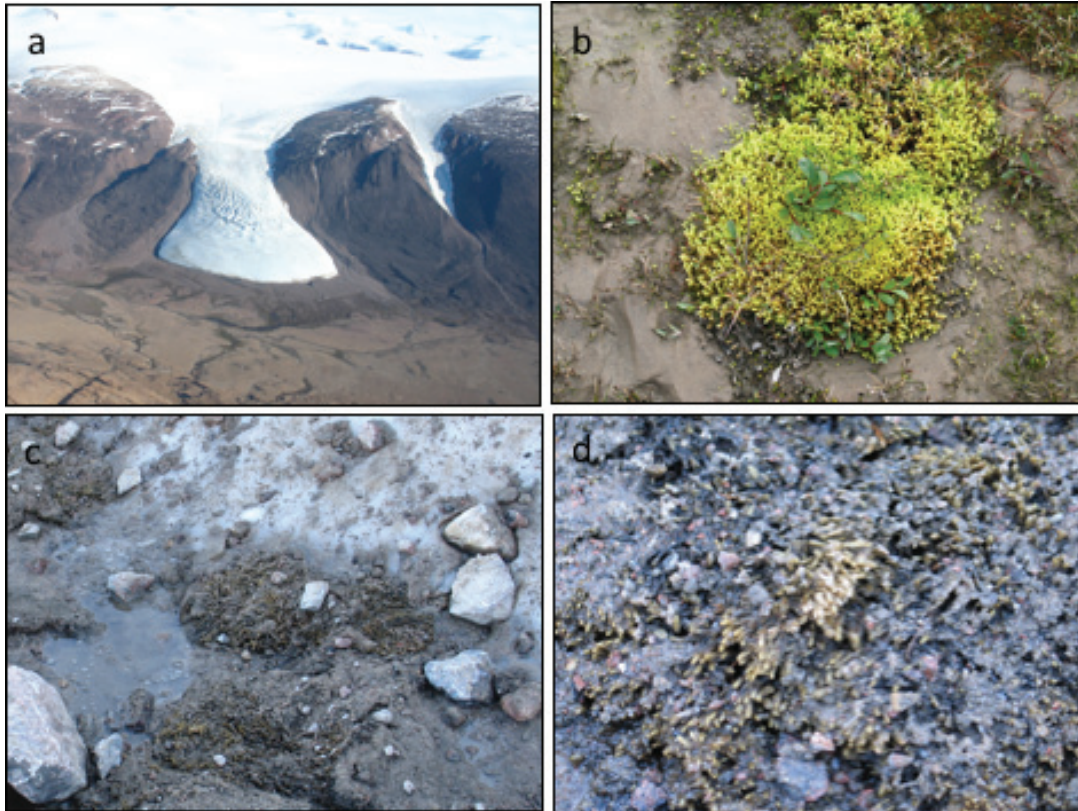
A refugium is a safe haven where one or more populations can escape the harsh conditions present beyond its perimeter. Here we use refugium to describe an area that was ice free and may have allowed for the survival of bryophytes during the LGM. Refugia are predicted to now harbor a higher diversity in terms of species richness and allelic diversity relative to surrounding areas (Hewitt 1996; Stewart et al. 2016). High relative diversity may also be attributed to contact zones for populations with high dispersal potential (Kyrkjeeide et al. 2014); however, refugial populations are expected to have more rare alleles (Comps et al. 2001; Petit et al. 2003). Refugial areas are thus likely to be characterized by high distinctiveness and high diversity, making them areas of conservation priority (Meltofte et al. 2013; Pauls et al. 2013). Contact zones are predicted to have high diversity but lower distinctiveness. Measures of distinctiveness may be used to estimate the relative importance of different refugia as sources for recolonization of postglacial landscapes (Eidesen et al. 2013). Surveys of species and genetic diversity are also likely to be critical for identifying regions that can serve as future refugia in a warming climate.

Since most Arctic bryophyte species predate the LGM, surveys of intraspecific genetic diversity will be critical for testing of the influence of putative refugia on current patterns of genetic variation and species diversity. Numerous authors have hypothesized that ice-free refugia existed throughout the Canadian Arctic Archipelago, along the coast of

Newfoundland, Peary Land and Jameson Land in Greenland, Andøya and Lofoten in western Scandinavia, in northern Siberia west of the Lena River to Taimyr peninsula (Hultén 1937; Dahl 1999; Abbott and Brochmann 2003; Walter et al. 2007; Stewart et al. 2010), the south island of the Russian archipelago Novaya Zemlya (Serebryanny et al. 1998; Velichko 2002), in parts of the Svalbard archipelago (e.g., Landvik et al. 2013), and high mountains and volcanoes, such as the Beerenberg on Jan Mayen (Imsland 1978). The most well-known refugium for Arctic species during the LGM was Beringia (Hultén 1937; Wen et al. 2016), stretching from the Lena River in Siberia east to the Mackenzie River in the Northwest Territories. Steere (1978) suggested that populations may have survived both in the Alaskan part of the Beringia refugium and in refugia north and south of the Laurentide ice sheet (see Fig. 3. for extent and retreat of the Laurentide ice sheet) (Dickson 1973 and references therein; Shafer et al. 2010; see Kyrkjeeide et al. 2014 for discussion on the Scandinavian ice sheet), with strictly circum-Arctic species possibly representing remnants of a widely distributed Tertiary or interglacial flora that only survived in northern refugia. This hypothesis was recently tested using molecular data in a phylogenetic context for the moss *Bryoxiphium norvegicum* and was rejected (Patiño et al. 2016). Other species, observed to be disjunct between temperate and Arctic zones (i.e., the “Umiat syndrome”), are also hypothesized as having survived in northern refugia (Steere 1965). Thirteen such species have been described for the Canadian Arctic archipelago (La Farge-England and Vitt 1985; La Farge-England 1989; Hedderson and Brassard 1992), including *Tayloria hornschurchii*, which is disjunct between northern Ellesmere Island and mainland Canada. This species has only been found from the site of its original discovery in the Arctic (C. La Farge, unpublished data), despite extensive sampling throughout the Canadian Archipelago for three decades (1974–2016) by La Farge and colleagues.

Correlation between landscape age and bryophyte species diversity at a fine scale suggests that there may be postglacial migration lag, and traces of the Pleistocene glaciations may still be apparent in the genetic diversity of the flora (Stewart et al. 2016). We can predict, then, that the bryophyte floras of formerly glaciated areas should be more species poor (and exhibit lower genetic diversity) compared to refugial areas. Large-scale comparisons between glaciated and nonglaciated areas to test this prediction are not yet possible given limited genetic data. Keeping in mind a possible bias by different sampling densities even between areas for which species checklists are available, we can, however, compare the moss flora of the formerly largely glaciated High Arctic Svalbard archipelago to that of the suggested refugial regions of Low to High Arctic Chukotka and Alaska. Currently, 288 mosses are reported from the 61 022 km² Svalbard (Frisvoll and Elvebakk 1996), whereas 415 and 467 moss species are reported from Alaska (Steere 1978) and Chukotka (Afonina 2004), respectively, with a combined area of 2 455 556 km². This quick comparison shows that Svalbard has 0.0047 moss species/km², while the combined area of Chukotka and Alaska (i.e., which constitute much of Beringia) has 0.0004 moss species/km². While this exercise does not account for differences in climate, physiography, or accessibility, it suggests that bryophyte diversity may deviate from predictions based solely on glaciation-driven demographic processes. Similar deviations from demographic hypotheses have been detected for the vascular flora. Nineteen of 30 circum-Arctic and northern temperate montane vascular plant species did not show patterns expected as a result of demographic history shaped by expansion from glacial refugia, namely decreasing genetic diversity correlated with distance from inferred refugia (Pellissier et al. 2016), suggesting that other factors, such as selection, may play a large role in shaping extant Arctic floristic diversity.

Fig. 4. Teardrop Glacier with extant and emergent Little Ice Age bryophytes (400 yr BP). (a) Teardrop Glacier at Sverdrup Pass (79°N), Ellesmere Island, Nunavut, Canada; (b) an extant population of *Aulacomnium turgidum* in the foreland of the Teardrop; (c and d) emergent Little Ice Age populations of *Aulacomnium turgidum*. Emergent populations were cultured in vitro by La Farge et al. (2013).



Could bryophytes have persisted in situ?

The small stature of bryophytes allows them to inhabit microhabitats and may have facilitated their survival in unglaciated microhabitats within otherwise glaciated areas (Anderson 1963; recently discussed by Patiño et al. 2016). Alternatively, bryophytes may be cryopreserved during glaciation with regeneration following glacial retreat, as recently observed, albeit over shorter periods of centuries to millennia, for Arctic and Antarctic mosses (Fig. 4) (La Farge et al. 2013; Roads et al. 2014). In a review of European Holocene bryophyte history, Kyrkjeide et al. (2014) found no cases of unambiguous evidence for *in situ* survival within the area of the Scandinavian ice sheet. This is in contrast to evidence of *in situ* survival of Antarctic populations of the moss *Bryum argenteum* (Pisa et al. 2014) as well as an increasingly wide range of Antarctic microorganisms and invertebrates (Convey et al. 2008, 2009; Pointing et al. 2015).

Local adaptation

Mapping of genetic diversity across the Arctic landscape will be an important first step in understanding the extent of gene flow among Arctic bryophytes as well as the interplay of historical demographic and ongoing selective processes in shaping extant diversity. Furthermore, it would likely provide necessary guidance on selection of species and populations in which to study local adaptation. Many Arctic bryophyte species exhibit distributions that extend south to the boreal regions and to lower latitude montane zones,

an ecologically heterogeneous expanse both today and throughout the Holocene at spatial and temporal scales. It is not surprising, then, that high levels of morphological variability characterize many Arctic bryophyte species (Longton 1988; Hesse et al. 2012; Daniëls et al. 2013). Such overall infraspecific variation may reflect phenotypic plasticity of specific genotypes along environmental gradients and differentiation due to demographic processes or local adaptation. The degree to which populations become adapted to particular environmental conditions depends on (1) the amount of genetic variation within and among populations, which is critically influenced by mating systems and demographic history, (2) the patterns and extent of migration among populations, and (3) the strength of divergent selection on populations. The extent of local adaptation and indeed knowledge of the relevant population parameters are virtually unknown for most bryophytes.

Historically, local adaptation has been detected using reciprocal transplant experiments requiring live material and recurrent visits to experimental study sites (Mooney and Billings 1961; Tieszen and Bonde 1967; McGraw and Antonovics 1983; Shaver et al. 1986; Souther et al. 2014). More recently, researchers have used trait-based approaches (Q_{ST} – F_{ST} comparisons: Keller et al. 2011; QTL analyses: Keller et al. 2012; Olson et al. 2013) to identify the genetic basis of adaptive differences among populations. Surveying polymorphic loci in many moss individuals from populations spanning an ecological gradient may facilitate the identification of loci that may be under selection. Candidate loci may exhibit elevated between-population allele frequency differences relative to the rest of the genome (often measured by the statistic F_{ST}) or allele frequencies that covary with an environmental variable or another trait of interest (Savolainen et al. 2013). Association (population-based) or QTL (pedigree-based) mapping could then be used to identify genes that are related to local adaptation, but this is contingent on identification of genetically differentiated populations. Restriction site associated DNA sequencing (RADseq) is an excellent tool for population genetic studies but may provide insufficient genomic coverage to detect regions under local selection (Lowry et al. 2017). In the absence of full genomic sequences, transcriptomic or exome capture techniques provide a relatively high coverage of genic regions (Lowry et al. 2017). While methods that provide a sampling of loci across the entire genome, such as RADseq, alone are insufficient tests of local adaptation, they are important in identifying patterns potentially associated with adaptation and provide a wealth of valuable information on population structure and allele frequencies.

Bryophytes in general offer several advantages that will enable researchers to more rapidly gain deeper insights into general biological processes in the Arctic. Larger mosses will be more suitable for obtaining high DNA yields for high throughput sequencing of individuals, as it is likely that sampling a patch of moss may result in mixing of individuals (McDaniel and Shaw 2005; Lewis et al. 2016). For smaller mosses, cultures may be necessary if sufficient DNA is required from an individual for high throughput sequencing, with new methods available to reduce contamination in cultures (Carey et al. 2015). Genotyping haploid gametophytes does not require distinguishing heterozygotes from homozygotes, and thus the genotype of an individual can be accurately inferred with less sequencing effort than is necessary for diploid or polyploid organisms. Second, because of the need to follow fewer genotypic classes when dealing with haploids (only two haploid genotypes rather than three as in diploid organisms — two homozygotes and one heterozygote), the statistical power for associating genotypes with traits (such as growth, carbon fixation, microbiome composition, or nitrogen fixation) is greater. Polyploidy will, however, complicate data generation and analysis and should be carefully considered for target species when designing studies (see Longton 1988 and Steere 1954b for discussions on polyploidy in Arctic bryophytes).

Large populations, as may be expected for many Arctic bryophyte species based on the vast areas that some species occupy, are more likely to exhibit local adaptation given the smaller effect of genetic drift (Kawecki and Ebert 2004; Savolainen et al. 2013). A meta-analysis of local adaptation studies on vascular plants found that population size had the greatest effect on selection for local adaptation (i.e., reciprocal transplant experiments had crossing reaction norms) but was observed only for plants with large population sizes, of which 52.3% had crossing reaction norms, while life history, habitat, and geographic distances between tested populations had no correlation with frequency of evidence for local adaptation (Leimu and Fischer 2008). However, if sexual reproduction is very low in Arctic populations, the population size may be effectively low and genetic drift is expected to have a larger effect, countering local adaptation. In discussing cryptic speciation in liverworts (i.e., strong genetic structuring within morphologically uniform species), Shaw (2001) proposed that restricted mating systems or ecological isolation (i.e., niche-based selection processes) rather than geographic isolation may be responsible for patterns of observed genetic diversity in liverworts. The frequency of sexual reproduction in many Arctic bryophytes, as discussed previously, is largely unknown, however, and more field observations (e.g., Lewis Smith and Convey 2002 showed that sexual reproduction is more common than previously assumed in Antarctic mosses) and molecular data are needed to provide insight into this aspect of bryophyte life history, as it has a profound impact on bryophyte evolution and diversity.

Perhaps the most important consideration for bryophytes is their anticipated high dispersal potential, which could offset a migration–selection balance that would allow for selection toward local adaptation. If migration is very high, it may overwhelm selective forces and genetic drift, just as it may erase genetic evidence of past demographic events, in which case, distribution of genetic diversity would reflect dispersal related processes and limitations (Piñeiro et al. 2012; Kyrkjeeide et al. 2016a). Elevational gradients are similar to those across latitudes but occur over shorter distances. In an assessment of AFLP signatures in the shuttle life strategist *Funaria hygrometrica*, genetic structuring along an elevational gradient in the Sierra Nevada Mountains of Spain are suggestive of local adaptation, even in this highly mobile and cosmopolitan species (Magdy et al. 2016). One theoretical expectation of local adaptation in species with high migration rates is evolution towards a small number of loci that have a strong effect on local fitness and thus are more likely to undergo strong local selection and remain polymorphic despite the homogenizing effect of migration (Savolainen et al. 2013). This requires the presence of alleles with strongly differential fitness between habitats; otherwise, the allele with highest overall fitness will dominate (i.e., adaptive phenotypic plasticity, as would be predicted by Rapoport's rule, recently discussed in terms of latitudinal diversity gradients by Mateo et al. 2016). As a general strategy for studying local adaptation, we suggest that initial insights from baseline genetic data regarding spatial partitioning of genetic diversity and correlations with environmental variables could be followed by identification of F_{ST} outliers to assist in identification of candidate genes that may be undergoing selection for local adaptation (Savolainen et al. 2013). Identifying genetically differentiated populations sets the stage for using common garden experiments in conjunction with association or QTL mapping to identify genes that are related to local adaptation.

Changing interspecies interactions in a warming climate: bryophyte microbiomes

Nutrient cycling in the Arctic growing season is heavily associated with microbial and fungal activity, either free-living or associated with plants (Longton 1988; and for boreal regions, see DeLuca et al. 2002; Davey et al. 2012; Zackrisson et al. 2009; Stewart et al. 2011; Vile et al. 2014; Skrzypek et al. 2015). Plants rely on bacteria and fungi to obtain

sufficient nitrogen in the form of nitrates and ammonium (DeLuca et al. 2002). Additionally, microbiomes may be directly involved in germination, growth, metabolism, and phenology of their bryophyte host (Bragina et al. 2014). Nitrogen fixation by Scandinavian boreal populations of the feather mosses *Pleurozium schreberi* and *Hylocomium splendens* microbiomes has been estimated at 1.4–2.0 kg N ha⁻¹ year⁻¹ (DeLuca et al. 2002; Zackrisson et al. 2009), with the highest fixation rates at 64°N latitude and higher (Zackrisson et al. 2009). Most knowledge on the compositional and functional aspects of the bryophyte microbiome comes from studies on *Sphagnum*-dominated peatlands (reviewed by Kostka et al. 2016) and the feather moss species mentioned above, as these species cover vast areas in boreal regions. Ground cover of the host–microbial community, however, does not necessarily mirror contributions to fixed nitrogen (Rousk et al. 2015). Furthermore, while the cyanobacterial components of bryophyte microbiomes have received the greatest attention, recent studies have shown that methanotrophs may play a greater role in N₂ fixation (Vile et al. 2014) and that distinct groups of nitrogen fixers contribute differently to habitat N₂ availability (Rousk et al. 2015).

The composition of epiphytic cyanobacterial communities varies across moss species (Zackrisson et al. 2009; Ininbergs et al. 2011). Additionally, communities vary with season (Zackrisson et al. 2009; Warshan et al. 2016), habitat (Zackrisson et al. 2009), and along disturbance gradients (Cutler et al. 2016) in terms of their composition and N₂ fixation in stands of *Pleurozium schreberi* and *Hylocomium splendens*. Host species specificity may be due to the production of host-species-specific chemo-attractants that encourage cyanobacterial colonization (Bay et al. 2013). Evidence from the model angiosperm *Arabidopsis thaliana* and potato cultivars suggests that the host genotype may have an effect on microbiome community composition (Inceoglu et al. 2010; Lundberg et al. 2012). Whether this applies to bryophytes, too, remains unknown.

Mapping of genetic diversity of Arctic bryophyte species will make it possible to detect patterns in microbiome community compositions. The same DNA extracts used for studies of mosses can also be used for sequencing a moss' microbiome by using primers to selectively amplify barcode markers such as the 16S or *nifH* (which targets nitrogen-fixing microbes) for parallel assessment of host genetics and microbiome composition. If using high-throughput methods for sequence generation, genome coverage of polymorphism should be sufficient to detect intraspecific host variation and correlate it with microbiome characteristics, similar to trait-based analyses suggested for the identification of putative locally adapted loci above.

It is possible that plants may be unable to migrate as fast as climate is changing, causing a decrease in fitness (i.e., an adaptive lag). Moreover, we do not know the extent to which plants and their microbiomes will respond in concert or the ecosystem consequences of asymmetries in their movement due to either plants and microbes experiencing different selective pressures or different capacities for migration. At the broad scale, the biogeography of polar cyanobacteria shows similar trends to polar bryophytes, with a number of lineages displaying widespread distributions across polar and montane regions (Jungblut et al. 2010; Christmas et al. 2015), suggesting similar processes. At a finer scale, however, distinct microbiome community compositions along fire and glacial disturbance gradients in boreal and sub-Antarctic ecosystems, respectively, suggest that selective pressures and colonization patterns will differ between host mosses and their microbiomes (Arróniz-Crespo et al. 2014; Cutler et al. 2016).

Digitally accessible Arctic bryophyte data

One of the greatest challenges for Arctic research is accessibility, and thus, existing collections may be important for achieving geographically comprehensive samplings for

genetic studies. Digitization of herbarium collections is improving accessibility of specimens and acquisition of specimen data. Major moves toward herbarium digitization in the United States, for instance, have been made through funding from the National Science Foundation (NSF) and the associated Integrated Digitized Biocollections (iDigBio) (<https://www.idigbio.org>). In particular, the USA-NSF-funded project *North American Lichens and Bryophytes: Sensitive Indicators of Environmental Quality and Change* now has made 4.2 million occurrence records of lichens and bryophytes (as of August 2016) available through two portals: the Consortium of North American Bryophyte Herbaria (CNABH) (<http://bryophyteportal.org/portal/>) and the Consortium of North American Lichen Herbaria (CNALH) (<http://lichenportal.org/portal/>). These data are also served to iDigBio and are available in the Global Biodiversity Information Facility (GBIF) (<http://www.gbif.org>; Edwards et al. 2000). Similarly, the Antarctic Plant Database (<https://data.bas.ac.uk/metadata.php?id=GB/NERC/BAS/AEDC/00023>) of the British Antarctic Survey Herbarium (BAS), with over 70 000 records of mostly lichens and mosses, is an important source of specimen occurrence data for the Southern Hemisphere and is also available through GBIF (Peat 1998; Cannone et al. 2013).

GBIF is the largest open-source aggregate of digitally accessible information (DAI) on species occurrences. Based on a data download from GBIF in January 2014 of ~1.2 million plant records, Meyer et al. (2016) compared taxonomic coverage of major plant groups versus total recorded global species diversity and estimated that only 28% of bryophyte species are represented on GBIF, highlighting that bryophyte floras are notably underrepresented. Here we provide a summary of DAI for Bryophyta (mosses) occurrence and major familial taxonomic representation across the Arctic and adjacent lower latitudes to 50°N (Fig. 2.) based on GBIF data download on 13 July 2016, excluding some records that were incorrectly georeferenced as occurring in oceans. Additional erroneous georeferencing is clear from the occurrence records distributed throughout the Greenland Ice Sheets and highlights issues with GBIF DAI. We provide the following points and Fig. 2 in order to highlight briefly the current state of GBIF DAI for Arctic bryology studies. Ultimately, there remains a clear need for greater bryological exploration in the Arctic along with greater digital mobilization of existing herbarium collections.

Bryophyte sampling north of the tree line (Fig. 2.) lacks a single area approaching one GBIF-databased specimen per square kilometre. Overall, the Arctic bryoflora is undercollected compared to adjacent southern regions, with 3 570 171 specimens sampled between 50°N and 60°N and only 1 179 294 above 60°N, a contrast likely reflecting the logistical and accessibility challenges in the Arctic. The greatest density of occurrence data is in northwestern European countries, accounting for 80.17% of all GBIF specimens 50°N and higher and reflected also by the well-developed literature on European holocene bryophyte phylogeography (Kyrkjeeide et al. 2014). Eleven families were identified to comprise 5% or more of occurrence records in at least one of four latitudinal increments (i.e., ≥ 50 to <60 , ≥ 60 to <70 , ≥ 70 to <80 , and ≥ 80 to <90) (Fig. 2b). Families represented by less than 5% of GBIF records were grouped as “Other,” highlighting groups with the greatest sampling. Families best represented by GBIF records closely match the most species-rich Arctic bryophytes families as discussed in the ABA (Daniëls et al. 2013). Much of the digitally accessible bryophyte samples above 50°N were collected more than 16 years ago, with 41% (1 948 634 out of 4 749 465) collected after the year 2000.

The actual records provide critical information on species, but for mining of genetic data, the specimens must also be adequately processed prior to storing, as drying temperature and speed determine the preservation of DNA more than age of the collection. For example, Hassel et al. (2013) found no relationship between specimen age and PCR and Sanger DNA sequencing success, and suitable DNA for sequencing of the ITS region has been isolated from a specimen of Polytrichaceae collected in 1888 (E. Biersma, unpublished data;

see also Epp et al. 2015 for sequencing of environmental DNA from a taxon of the Polytrichaceae found in lake sediments older than 5500 cal yr BP). The short DNA fragment lengths sequenced on Illumina platforms, however, may be suited for sequencing even degraded DNA. Library generation protocols such as RADseq can accommodate highly degraded DNA (Tin et al. 2014; Graham et al. 2015), and metabarcoding of Lepidoptera has been accomplished from century-old type specimens yielding 458–610 bp sequences (Prosser et al. 2016). Consequently, we suggest that given the low sampling density of Arctic bryophytes, older specimens should still be considered for molecular analysis, especially leveraging next-generation sequencing technologies.

There is a substantial amount of what Meyer et al. (2016) called “un-mobilized data,” and current DAI is an underestimate of existing Arctic bryological collections. For example, the largest collection of Arctic Russian mosses in the herbarium of the Russian Academy of Sciences in St. Petersburg (LE), with important collections from Taimyr and Chukotka, is not digitized. One example from the authors of the present paper are the specimens collected by M. Stech, J.D. Kruijer, and collaborators in Svalbard, East Greenland, and Jan Mayen during fieldwork in 2008–2016, but much older herbarium collections that still need to be made (digitally) accessible exist as well, e.g., the material collected by L.M. Jalink and M.M. Nauta on Svalbard during the 1980s (Jalink and Nauta 2004). Over 5000 specimens from the Canadian Arctic Archipelago have been collected between 1974 and 2016 by C. La Farge (ALTA), which will provide important North American samples from high latitudes. Funding for digitization, however, is limited and likely unavailable for many museums. Scientists are unlikely to “drop their science” and start digitizing herbaria, and without funding to support staff, the move toward digitally accessible bryophyte data for the Arctic is unlikely to progress rapidly. In some cases, GBIF data may be associated with sequence data. The Barcode of Life Data (BOLD) system (<http://www.boldsystems.org>) lists the global distribution of Bryophyta (mosses) collections with sequence data and also shows a low frequency of data from the Arctic. The Norwegian barcode initiative “Barcoding of Polar Bryophytes” currently consisting of 950 sequences of just under 400 species, all stored in BOLD, and the Canadian effort are actively filling this gap.

Conclusions

The Arctic is a floristically complex region with a critical role in the global carbon budget. Combining molecular and morphological observations can provide far more precise and generalizable insights than inferences based solely on morphological data, particularly in (Arctic) bryophytes where morphological characters are generally limited and the taxonomy is particularly challenging. Developments in molecular research have only just begun to illuminate patterns of diversity and phylogeographic history in this group of organisms. As next-generation sequencing approaches, which provide access to large numbers of loci, are becoming increasingly affordable, it will be possible to generate the higher resolution data required to address evolutionary as well as functional questions. Importantly, geographic sampling coverage of bryophytes in the Arctic is uneven, and concentrated in a few areas, with large sampling gaps particularly in Russia and eastern North America. Echoing Steere (1954a, 1971) and Schofield (1971), we emphasize that an essential step is training of a greater number of experienced bryologists to collect bryophytes in the Arctic and make these collections available to the global bryological community.

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