REVIEW

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Can bryophyte groups increase functional resolution in tundra ecosystems?[1]

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Abstract: The relative contribution of bryophytes to plant diversity, primary productivity, and ecosystem functioning increases towards colder climates. Bryophytes respond to environmental changes at the species level, but because bryophyte species are relatively difficult to identify, they are often lumped into one functional group. Consequently, bryophyte function remains poorly resolved. Here, we explore how higher resolution of bryophyte functional diversity can be encouraged and implemented in tundra ecological studies. We briefly review previous bryophyte functional classifications and the roles of bryophytes

in tundra ecosystems and their susceptibility to environmental change. Based on shoot morphology and colony organization, we then propose twelve easily distinguishable bryophyte functional groups. To illustrate how bryophyte functional groups can help elucidate variation in bryophyte effects and responses, we compiled existing data on water holding capacity, a key bryophyte trait. Although plant functional groups can mask potentially high interspecific and intraspecific variability, we found better separation of bryophyte functional group means compared with previous grouping systems regarding water holding capacity. This suggests that our bryophyte functional groups truly represent variation in the functional roles of bryophytes in tundra ecosystems. Lastly, we provide recommendations to improve the monitoring of bryophyte community changes in tundra study sites.

Key words: mosses, Arctic–Alpine, environmental change, functional traits, water holding capacity.

Résumé : La contribution relative des bryophytes à la diversité végétale, à la productivité primaire et au fonctionnement des écosystèmes s'accroît vers les climats plus froids. Les bryophytes répondent aux changements environnementaux au niveau de l'espèce, mais puisque les espèces de bryophytes sont relativement difficiles à identifier, elles sont souvent regroupées en un seul groupe fonctionnel. Par conséquent, la fonction des bryophytes reste mal résolue. Les auteurs explorent ici comment une meilleure résolution de la diversité fonctionnelle des bryophytes peut être encouragée et mise en œuvre dans les études écologiques de la toundra. Ils passent brièvement en revue les classifications fonctionnelles précédentes des bryophytes et les rôles des bryophytes dans les écosystèmes de la toundra et leur sensibilité aux changements environnementaux. Sur la base de la morphologie des pousses et de l'organisation des colonies, ils proposent ensuite douze groupes fonctionnels de bryophytes faciles à distinguer. Pour illustrer comment les groupes fonctionnels de bryophytes peuvent aider à élucider la variation des effets et des réponses des bryophytes, ils ont compilé les données existantes sur la capacité de rétention d'eau, une caractéristique clé des bryophytes. Bien que les groupes fonctionnels de végétaux puissent masquer une variabilité interspécifique et intraspécifique potentiellement élevée, ils ont constaté une meilleure séparation des moyennes des groupes fonctionnels de bryophytes par rapport aux systèmes de regroupement précédents concernant la capacité de rétention d'eau. Cela suggère que les groupes fonctionnels de bryophytes proposés par les auteurs représentent réellement la variation des rôles fonctionnels des bryophytes dans les écosystèmes de la toundra. Enfin, ils formulent des recommandations pour améliorer la surveillance des changements de la communauté bryophyte dans les sites d'étude de la toundra. [Traduit par la Rédaction]

E.J. Cooper. Department of Arctic and Marine Biology, Biosciences Fisheries and Economics, UiT-The Arctic University of Norway, N-9037 Tromsø, Norway.

J.H.C. Cornelissen. Department of Ecological Sciences, Vrije Universiteit, 1081 HV Amsterdam, The Netherlands.

E. Dorrepaal. Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, Sweden.

T.G. Elumeeva. Department of Ecology and Plant Geography, Biological Faculty, Lomonosov Moscow State University, Leninskie Gory, 1/12, 119234 Moscow, Russia.

A.K. Jägerbrand. Ecology and Environmental Science, RLAS, Halmstad University, Halmstad, Sweden.

F. Keuper. BioEcoAgro Joint Research Unit, INRAE, F-02000 Barenton-Bugny, France.

K. Klanderud* and K. Zuijlen. Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, 1432, Ås, Norway.

E. Lévesque. Département des Sciences de l'environnement et Centre d'études nordiques, Université du Québec à Trois-Rivières, Trois-Rivières, QC G8Z 4M3, Canada.

X. Liu. Chinese Academy of Sciences Key Laboratory of Mountain Ecological Restoration and Bioresource Utilization & Ecological Restoration and Biodiversity Conservation Key Laboratory of Sichuan Province, Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, China.

J. May.* Department of Biology, Florida International University, 11200 SW 8th Street, Miami, FL 33199-2156, USA.

M. Mörsdorf. Department of Geobotany, University of Freiburg, Schänzlestrasse 1, 79104 Freiburg, Germany.

C. Rixen.* WSL Institute for Snow and Avalanche Research SLF, Flüelastr. 11, 7260 Davos Dorf, Switzerland.

B.J.M. Robroek. Aquatic Ecology & Environmental Biology, Institute for Water and Wetland Research, Faculty of Science, Radboud University Nijmegen, AJ 6525 Nijmegen, The Netherlands.

N.A. Soudzilovskaia. Centre for environmental Sciences, Hasselt University, Martelarenlaan 42, 3500 Hasselt, Belgium.

A. Tolvanen. Natural Resources Institute Finland, B.O. Box 413, 90014 Oulu, Finland.

I. Volkov. Laboratory of Biodiversity and Ecology, Tomsk State University, Lenin pr., 36, 634050 Tomsk, Russia.

I. Volkova. Department of Botany and Laboratory of Ecosystem and Climate Change Studies, Tomsk State University, Lenin pr., 36, 634050 Tomsk, Russia.

Introduction

In the Arctic, bryophytes represent 30% of all plant species (Walker and Raynolds 2011). Unlike the general trend for vascular plants, regional bryophyte species richness does not decline when moving from the equator towards the poles (Geffert et al. 2013; Mateo et al. 2016). In many tundra ecosystem types, bryophytes contribute significantly (>50%) to primary production and standing biomass (Wielgolaski 1971; Huemmrich et al. 2010) and play important roles for soil moisture, biogeochemical cycling, surface energy balance, and species diversity (e.g., Lindo and Gonzalez 2010; Turetsky et al. 2012). Tundra ecosystems are facing dramatic shifts in structure and function due to environmental change, which affects the abundance of bryophytes (Elmendorf et al. 2012*a*, 2012*b*; Lang et al. 2012; Olofsson et al. 2014; Cooper et al. 2019). However, although both functionality of bryophytes and their responses to environmental change differ considerably among species (Cornelissen et al. 2007; Hudson and Henry 2010; Lang et al. 2012) very few field studies include bryophytes at the species or other subgroup level. Therefore, studies are largely inconclusive and speculative in predicting responses of tundra bryophyte communities to environmental changes (Elmendorf et al. 2012*a*, 2012*b*) and the potential consequences of these changes for ecosystem functioning.

The resolution of the bryophyte component in tundra vegetation and ecosystem studies could be increased considerably by applying relevant bryophyte functional groups. Traditionally, functional classification has been used in the opposite manner as an effort to reduce complexity in, for example, vascular plant ecology using "plant functional types". Such a priori functional grouping has been challenged because effect and response traits do not necessarily match. Therefore, a good starting point for establishing fine-resolution linkages between bryophyte abundance, environmental changes, and ecosystem functioning could be to assign bryophyte species to functional groups through post hoc trait-based aggregation. This is done increasingly for other primary producer groups (Thomas et al. 2019; Mauffrey et al. 2020), because it directly provides ecologically meaningful functional groups. Such groups translate and aggregate species responses to more general functional responses and allow cross-site comparisons of responses regardless of species (Lavorel et al. 1997). However, for bryophytes the challenge is not limited to translating species into function.

Bryophyte species identification, as such, is challenging, especially in the field. It is time-consuming and requires identification skills that few ecologists possess (Grace 1995). In practice, this causes most field ecologists to lump bryophytes into one group (e.g., bryophytes or even as "non-vascular plants", with lichens as "cryptogams"), or two or more bryophyte groups (e.g., "*Sphagnum*" and "other bryophyte species"). Consequently, important ecological information is lost, comparison between different studies is not straightforward and opportunities for addressing functional responses of bryophytes across sites and at larger scales are hampered. Therefore, for bryophytes, using a priori defined functional groups, based on coarse morphological characteristics that can be identified in the field, may be a more promising approach. Previous work on bryophyte classifications that has been based on life history traits (During 1979), position of sexual reproductive organs (La Farge-England 1996), and bryophyte colony structure (Mägdefrau 1982) offer useful insights about bryophyte ecology, but none of them focus primarily on functional diversity.

Here we propose a priori defined, field-identifiable "bryophyte functional groups" (BFGs) as a cost- and time-efficient, and meaningful way to increase bryophyte data resolution, allow measurement of change in bryophyte communities in response to environmental change, obtain comparable bryophyte data across tundra habitats and sites, and enhance understanding of bryophyte ecosystem effects and responses. To this end, we (1) provide an overview of the role of bryophytes in tundra ecosystems and their susceptibility to environmental change; (2) review previous efforts to group bryophytes; and (3) build on these efforts to propose twelve field identifiable BFGs. (4) We evaluate the relevance of these BFGs in relation to water holding capacity (WHC), a functionally important and commonly measured bryophyte trait, in a case study where we re-analyze existing data. As such, if BFGs separate into more than one cluster based on water holding capacity, the groups improve the functional resolution compared with the commonly used single "bryophytes" group for ecosystem function governed by this trait. Finally, we discuss how BFGs may differ in regard to other key bryophyte functions and provide recommendations on how to apply BFGs in tundra ecological studies.

Bryophytes in tundra ecosystems

Ecosystem functions and functional diversity of tundra bryophytes

An important feature of tundra bryophytes is that they often grow in dense carpets or colonies in many habitats. It is in the colony form that bryophytes most strongly affect the environment through their physical presence, as well as biogeochemically and biotically through interactions with other organisms in the ecosystem (Fig. 1). The physical properties of a dense and deep bryophyte layer may significantly control the soil environment by buffering substrate moisture and insulate soil from diurnal and annual air temperature variation with consequences for biogeochemical processes (Gornall et al. 2007; Soudzilovskaia et al. 2013; Jaroszynska 2019), active layer development and permafrost ice content (Jorgenson et al. 2010). Through their effects on water balance bryophytes affect energy partitioning and decrease ecosystem ground heat flux (Blok et al. 2011) and affect surface albedo (May et al. 2018). Biogeochemically, bryophytes are important as they contribute to the ecosystem carbon (C) balance through their great abundance, high C use efficiency and because they are active beyond the short vascular plant growing season (Douma et al. 2007; Woodin et al. 2009; Street et al. 2012, 2013). Bryophytes control the input of nitrogen (N) to the ecosystem through associations with N_2 fixing bacteria and by efficiently immobilizing N from deposition within the bryophyte layer (Jónsdóttir et al. 1995). Both C and N fixation rates are highly dependent on moisture conditions within the bryophyte tissue (Solheim and Zielke 2003; Turetsky 2003; Gavazov et al. 2010; Lett and Michelsen 2014; Rousk et al. 2015, 2017). Last, their recalcitrant litter and effects on pH are an important feature, which slows the release of C and N cycling in the ecosystem (Russell 1990; Lang et al. 2009; Soudzilovskaia et al. 2010).

Through a combination of these physical and biochemical effects, bryophytes interact with the biotic environment. As such, they affect vascular plant growth and establishment through competition and facilitation (Gornall et al. 2011; Soudzilovskaia et al. 2011; Keuper et al. 2011; Lett et al. 2017, 2018, 2020). For instance, bryophytes can grow in places where vascular plants cannot root, such as rocks and glacial forelands, where they over time form an organic substrate which can later be colonized by plants (Jones and Henry 2003; Gavini et al. 2019). Their colonies comprise a matrix for unique food webs of microfauna and microbes (Lindo and Gonzalez 2010; Glime 2012; Jonsson et al. 2015). Although their dietary value is low (Prop and Vulink 1992; Hübner 2007), bryophytes are also consumed by vertebrate herbivores such as rodents, geese, reindeer/caribou, and muskox, (Glime 2006; Ihl and Barboza 2007; Bjørkvoll et al. 2009; Soininen et al. 2013).

Fig. 1. Schematic overview of some of the structural and functional roles of the bryophyte layer (bryosphere) in tundra ecosystems. The bryosphere (green) does not substantially penetrate the soil but creates a zone between the active layer (brown) belowground and the atmosphere (light blue) aboveground. Teal-framed boxes are physical properties (solid) and conditions (dashed), yellow-framed boxes are biogeochemical pools (solid) and processes (dashed) and pink-framed boxes are the biota. Dashed arrow indicates an uncertain connection between boxes. The diagram does not include all environmental factors acting on bryophyte functioning.
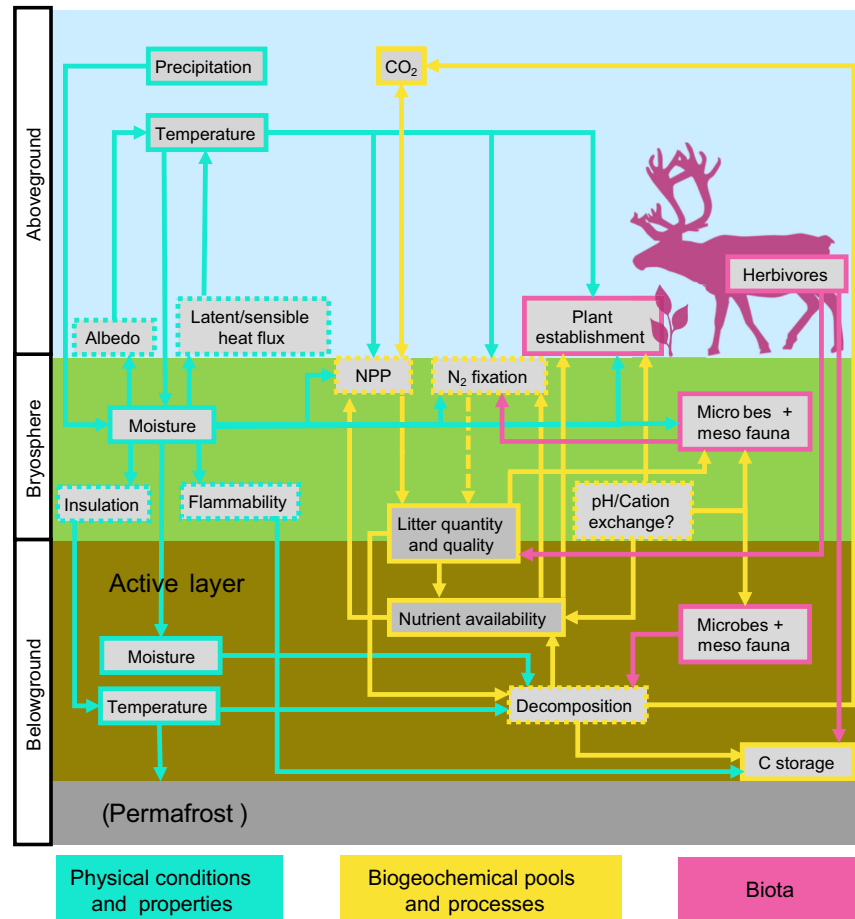
Bryophyte ecosystem functional trait data are still scarce in comparison to such data for vascular plants (St. Martin and Mallik 2017). Morphological shoot traits, and colony traits such as moss layer depth, colony density, and surface texture and color, are important for determining the physical effects of bryophytes on tundra ecosystems. For instance, decomposition rates can vary more than 10-fold between the extremely recalcitrant *Sphagnum* mosses and more nitrogen rich species such as *Ptilidium ciliare* (L.) Hampe and *Pleurozium schreberi* (Brid.) Mitt. (Lang et al. 2009; van Zuijlen et al. 2020) and water holding capacity may vary five-fold (Elumeeva et al. 2011). Such information is obtained by systematically screening species for important effect traits.

Responses in bryophyte cover to environmental change in tundra ecosystems

As for any tundra plant, climate warming is likely to promote bryophyte growth if water and nutrients are not limiting (Douma et al. 2007). Wetter and warmer climates, which are

now occurring and expected in much of the tundra biome (Bintanja and Andry 2017; Thomas et al. 2018), should, in principle, promote bryophyte growth and, thus, abundance. Data on bryophyte abundance responses to climate change are scarce compared with those on vascular plants, but available data from the North American and European Arctic show an overall decline in bryophyte abundance in response to climate warming across tundra ecosystems (Elmendorf et al. 2012a, 2012b). This decline seems more pronounced in moister sites and has been attributed to indirect effects of warming through competition from vascular plants (shading). However, bryophyte responses to warming vary substantially across species and sites, and habitats within sites. For example, no effect of experimental warming on bryophyte covers was observed in a subarctic *Racomitrium lanuginosum* (Hedw.) Brid. heath (Jónsdóttir et al. 2005), positive effects of warming were observed for common boreal bryophyte species in Arctic and subarctic alpine tundra plant communities (Lang et al. 2012) and for bryophytes in various habitats within a High Arctic tundra site (Hudson and Henry 2010; Edwards and Henry 2016).

Changes in water availability under warming, or susceptibility to other global change drivers may also contribute to the observed general negative trends. Unlike vascular plants, most bryophytes are poikilohydric and cannot actively control their water balance. They have no or only thin leaf cuticles and do not have leaf stomates. Most species do not have efficient vascular systems (but see Brodribb et al. 2020) nor true roots, and access water and nutrients passively through their leaves. Bryophytes can, to varying degrees, tolerate desiccation during dry periods after which they return to normal physiological activity (Proctor and Tuba 2002; Proctor et al. 2007). Increased herbivore pressure may disturb the bryophyte layer in the tundra, as, for example, through spring grubbing by the increasing goose populations in the Arctic (Kotanen and Jefferies 1997; Wal et al. 2007). Exclusion of lemmings and reindeer (Olofsson et al. 2014) and sheep (Jónsdóttir 1991) in subarctic alpine heath tundra increases bryophyte cover and colony depth through promotion of tall stature bryophytes. Furthermore, goose and sheep grazing can increase small scale bryophyte diversity at the species level (Jónsdóttir 1984; Jasmin et al. 2008). Increased snow depth may promote bryophyte biomass production and cover (Dorrepaal et al. 2004; Paradis et al. 2016; Cooper et al. 2019). Importantly, bryophytes show species-specific responses to multiple environmental factors operating at different spatial scales, with variable consequences for both community composition and total bryophyte cover across alpine and Arctic tundra regions.

Functional trait responses to the environment and intraspecific variation

By combining data for total bryophyte cover and species composition with data for bryophyte functional traits we can understand how environmental changes affect ecosystem functionality (Díaz and Cabido 2001). Some functional traits of bryophytes may, however, themselves be responsive to environmental change causing considerable intraspecific trait variation in addition to interspecific trait variation that is caused by species turnover. For example, bryophyte tissue phosphorus (P) content and shoot water holding capacity and growth showed high variation within species, whereas traits like pH, N content, and litter decomposability showed less intraspecific than interspecific variation in alpine ecosystems (Jägerbrand et al. 2014; Roos et al. 2019; Zuijlen et al. 2020). However, Roos et al. (2019) concluded that bryophyte species turnover rather than intraspecific variation drove changes in community abundance-weighted means of all six measured traits (N and P concentration and ratio, pH, specific leaf area, and water holding capacity) across an elevational gradient. This supports the possibility to assign bryophyte species to groups, which could represent certain ecosystem functions.

Grouping of bryophytes

Previous grouping of bryophytes

During (1979, 1992) identified life history types to classify bryophytes according to life strategies (e.g., life span and reproductive strategy, age and effort). Life history types may depend on the environment and life history traits are likely a key to understanding bryophyte population dynamics (Austrheim et al. 2005); however, they do not provide full insights into bryophyte functional roles in the ecosystem. Currently, the majority of trait data for bryophytes occurring in the TRY database are on life history traits (Kattge et al. 2020).

The growth form classification has often been used in combination with life form and (or) perichaetial position in the literature. La Farge-England (1996) distinguished growth form, life form, and perichaetial position and indicated which are environmentally modified versus genetically fixed. This provided a comprehensive and unambiguous way to assess the structure of moss (Bryophyta) individuals. They refer to growth form as the structure of individual shoots, including direction of growth and branch form. Here, growth form (modified by the environment) is differentiated from the perichaetial position (La Farge-England 1996). Perichaetial position, which classifies acrocarpy, cladocarpy, and pleurocarpy, is analyzed and reviewed with an evolutionary perspective within major Bryophyta lineages. Huttunen et al. (2018) mapped "carpy" phylogenetically across the lineages in an extensive review on bryophyte functional traits. They showed that perichaetial position alone does not determine the ecosystem function of bryophytes or how populations respond to environmental change. Growth form, by contrast, seems to influence how shoots are organized in colonies, which is thought to be important for ecosystem functioning (Bates 1998).

The life form classification of bryophytes was developed by Gimingham and Robertson (1950) and later refined and modified by Gimingham and Birse (1957); Mägdefrau (1982); Longton (1988); Grace (1995); Bates (1998); Hill et al. (2007) and Vanderpoorten and Goffinet (2009). The classification is based on the organization of the colony (group of shoots), although exact groups differ between authors. The life form classification integrates shoot morphology, such as branching pattern, growth direction, and colony structure. Grace (1995) showed that life forms are easily identifiable in the field across different levels of bryophyte identification skill. Importantly, it is convenient and meaningful to view bryophytes in terms of colonies rather than individuals to understand their effects on ecosystems (Bates 1998; Huttunen et al. 2018). Some physical colony properties, such as density and thickness, are directly related to ecosystem function, for example, insulation capacity and water holding capacity (Gornall et al. 2007; Elumeeva et al. 2011; Soudzilovskaia et al. 2013), whereas it is unknown whether chemical properties such as N content are linked to colony structure. Through their colony features bryophytes also affect the biotic environment, e.g., by hosting specific microfauna and mesofauna communities and through competition with or facilitation of other plants. Colonies in tundra ecosystems may be a mixture of several species (see below), which is a limitation to the life form classification. In conclusion, with their identifiability and ecological relevance, life forms integrate many of the desired features for a priori defined bryophyte functional groups.

Modified "life form" as BFGs

Our primary aim is to improve the representation of functionally different bryophytes in studies of tundra ecosystems by (1) focusing on the specific context of their responses to environmental changes and their effects on key ecosystem functions, and to encourage this by (2) proposing field-identifiable bryophyte functional groups as an alternative to determination at either the highest level, "species", and often not feasible level or the lowest level,

"bryophyte", of resolution, which is too coarse to be useful. Therefore, our BFGs are chosen to be as morphologically distinct as possible to aid field identification. The BFGs are organized as a key (Fig. 2). The first steps follow the British Field Flora for Mosses and Liverworts (Atherton et al. 2010) and rely on morphological differences in macro-characteristics of the shoots and thalli, including branching pattern, and later steps divide groups based on colony structure, i.e., life forms (Fig. 2). By combining the growth form and life form concepts, we optimize the possibility to have functionally and morphological distinct groups, which are also taxonomically distinct.

The first split divides bryophytes into those with thallus and those with leaves (Fig. 2*a*). The "Thalloid" group contains liverworts and hornworts (Marchantiophyta and Anthocerotophyta, Fig. A1). Leafy bryophytes are divided based on the characteristics and placement of the leaves (Fig. 2*b*). Leaves can be arranged either in 2–3 ranks, mostly rounded or 2-lobed, and always without nerves, "Leafy liverworts", or have leaves which are arranged in a spiral and often with a nerve and acute tip, mosses (Bryophyta). Mosses are further divided into those with a capitulum, i.e., "*Sphagnum*" and those without capitulum, i.e., non-*Sphagnum* (Fig. 2*c*). The group and genus *Sphagnum* is easily recognized in the field as no other bryophytes have a capitulum. Non-*Sphagnum* mosses are divided into those with branched shoots and those with shoots not or infrequently branching (Fig. 2*d*) roughly corresponding to pleurocarps and acrocarps; cladocarps fall into both groups.

Colonies with shoots not or infrequently branching are divided into those with thick, non-transparent leaves and those with thin, more transparent leaves (Fig. 2*e*). Non-transparent leaves are a feature of "Polytrichales" (Fig. A1) and are caused by lamellae on the surface of the leaves. These lamellae are usually visible with a hand lens but a common feature of this group is that stems and leaves tend to be sturdier than in individuals in the contrasting group. The contrasting group, mosses with thin, more transparent leaves, form a large group, which is divided into "Cushions" and "Unbranched turfs" (Fig. 2*f*). "Unbranched turfs" correspond to Bates' turfs (Bates 1998), except our group includes only acrocarps. All shoots grow vertically from the substrate and, depending on the length of the shoots, "Unbranched turfs" are divided into "Short unbranched turfs" (<5 cm) and "Tall unbranched turfs" (>5 cm, Fig. 2*g*). The "Cushions" have dome-shaped colonies (as in "cushion plants" such as *Silene acaulis* (L.) Jacq.). "Cushions" are divided into "Small cushions" and "Large cushions". Small cushions have shoots emerging from a shared, central origin so that shoots grow centrifugally and are less than 5 cm deep, Fig. 2*h*), e.g., genera *Grimmia* and *Andreaea*. "Large cushions" are more than 5 cm deep and may or may not have shoots growing from a central point. Species of this group also appear in other BFGs, e.g., *Racomitrium lanuginosum* in branched turf (see below) or *Leucobryum glaucum* (Hedw.) Ångstr., *Dicranum elongatum* Schleich. ex Schwägr., and *Anoectangium aestivum* (Hedw.) Mitt., in tall unbranched turfs.

Colonies with branched shoots are divided into "Dendroid", "Weft", "Mat" and "Branched turf" (Fig. 2*i*). The dendroid classification is technically a growth form. Dendroids have shoots that extend from horizontal stem and have branches placed towards the tip of the shoot making them resemble miniature trees. This is a small group and the most common species in tundra ecosystems is *Climacium dendroides* (Hedw.) F. Weber & D. Mohr, but also e.g., *Thamnobryum alopecurum* Nieuwl. and *Isothecium alopecuroides* (Lam. ex Dubois) Isov. are found in subarctic areas. Wefts also have strongly branched shoots, but branches are distributed throughout the entire stem giving rise to the colloquial name, feather moss. Colonies appear loose and chaotic with large heavily branched shoots growing both vertically and horizontally. The emblematic boreal species *Pleurozium schreberi* (Hedw.) Schimp. and *Hylocomium splendens* (Hedw.) Schimp. belong to this group. Shoots of the Mat group grow horizontal to the substrate. Tips of shoots can become erect, giving

Fig. 2. Bryophyte functional groups (BFGs) building on shoot morphology and life forms (Mägdefrau 1982). The left diagram functions as a key, which splits bryophytes into 12 BFGs listed in the right panel with their abbreviations (Abb.), short descriptions and examples of species. The key starts at the grey bubble and dichotomies leading from each step are indicated with a number and same color arrow. The 12 BFGs are placed at the periphery. Red crossed circles mark "not *Sphagnum*" or "not Polytrichales". Groups originating from orange bubbles can be collated to form broader functional groups. Note, in nature bryophytes often occur as a mixture of species, usually individuals occupy the same BFG, but if they do not, the most abundant BFG should be recorded.
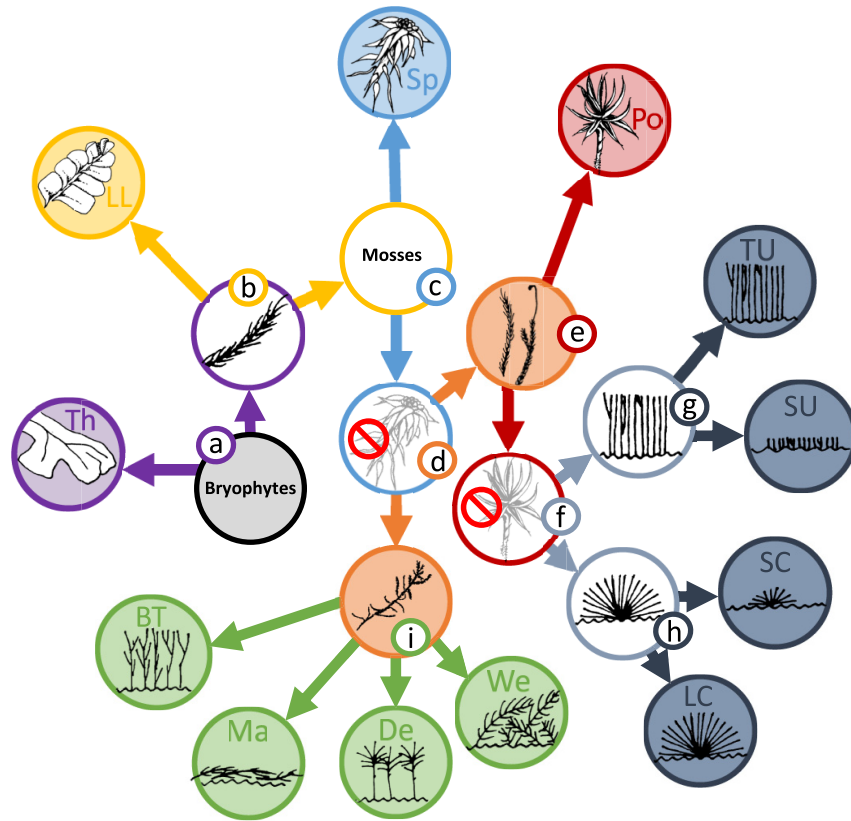

Abb	BFG	Short description	Examples of common/ typical species	
Th	Thallose liverwort and hornwort	Have undifferentiated vegetative tissue (no stems and shoots).	*Marchantia foliacea, Aneura pinguis*	
LL	Leafy liverwort	Shoots with leaves in 2-3 ranks, mostly rounded or 2-lobed and always without veins.	*Ptilidium ciliare, Lophozia floerkii*	
Sp	Sphagnum	Have capitulum. All Sphagnum species.	*Sphagnum fuscum, S. girgensohnii, S. warnstorfii*	
Po	Polytrichales	Unbranched shoots. Lanceolate leaves appear thick due to lamellae parallel to the vein (visible with hand lens). All Polytrichales	*Polytrichastrum alpinum, Polytrichum commune*	
SC	Small cushion	Dome-shaped colonies < 5 cm deep. Shoots grow from a central point with limited growth.	*Andreaea rupestris, Schistidium apocarpum, Grimmia spp.*	Shoots not or sparsely branched
LC	Large cushion	Dome-shaped colonies > 5 cm deep. Colonies may reach a radius of several decimeters.	*Racomitrium lanuginosum, Anoectangium aestivum, Dicranum elongatum*	
SU	Short unbranched turf	Colonies of unbranched (or sparsely branched) erect shoots. Shoots < 5 cm.	*Aulacomnium turgidum, Dicranum acutifolium, Cinclidium stygium*	
TU	Tall unbranched turf	Colonies of unbranched (or sparsely branched) erect shoots. Shoots > 5 cm.	*Dicranum majus, D. scoparium, Plagiomnium ellipticum, Paludella squarrosa*	
De	Dendroids	Main stem creeping and becomes erect. Branching stems from apex of main stem.	*Climacium dendroides, Thamnobryum alopecurum*	Shoots branched
We	Weft	Shoots grow erect and horizontally. Multiple branching stems distributed throughout the main stem. Sometimes appearance of a feather.	*Hylocomium splendens, Pleurozium schreberi*	
Ma	Mat	Branched shoots grow horizontal to substrate. Sometimes shoots possess erect lateral branches.	*Hypnum cupressiforme, Plagiothecium denticulatum*	
BT	Branched turf	Colonies of erect shoots with some branching.	*Tomentypnum nitens, Racomitrium spp., Drepanocladus revolvens*	

the mat a rougher surface as described by Bates (1998), but generally the branched shoots lie flat on the surface and, therefore, have a rather compact appearance. Mats are often found on solid substrates like logs or stones. Branched turf forms a new group containing pleuro-carp and cladocarp forming turfs. Like the unbranched turf, they have erect shoots but dif-fer in that their shoots are branched, although usually not as branched as the Wefts. The abundant tundra species *Tomentypnum nitens* (Hedw.) Loeske and species from the *Racomitrium* genus belong to this group.

The 12 BFGs (Fig. 2) do not encompass all tundra bryophyte species but focus on the perennial bryophytes, which constitute the vast majority of species (in the British bryo-phyte flora, 90% of species are perennial, Hill et al. 2007). Most species can be ascribed to only one BFG but some variable species will have a primary and a secondary life form, as recognized by Hill et al. (2007). For example, the cladocarpous *Racomitrium lanuginosum* is often quite branched and can form continuous and often deep layers, which would place it in the "branched turf" group. In more exposed sites with less vegetation cover, it can form dense cushions and would therefore be better placed within the "Large cushion" group. Furthermore, although species within each BFG do not necessarily share all charac-teristics (Dormann and Woodin 2002; Dorrepaal 2007) we argue that our bryophyte func-tional groups will increase resolution in tundra ecosystem studies compared with the frequent lumping of all bryophytes into one or very few functional groups.

Ecosystem functions of the BFGs

We assessed whether our choice of field-identifiable bryophyte functional groups can lead to a more meaningful representation of tundra bryophytes in the study of their ecosys-tem function by investigating how the groups separate for one key trait that is frequently measured, the WHC. As such, if BFGs separate into more than one cluster, we can conclude that the resolution for that trait is improved compared with the commonly used "bryophytes". Currently bryophyte trait data are poorly represented in global and regional trait databases such as the TRY (Kattge et al. 2020) and the tundra plant specific Tundra Trait Team database (Bjorkman et al. 2018), which limits the possibility to fully test the BFGs. However, a wide set of ecosystem functions are ultimately linked to bryophyte water balance. Water content, in turn, depends on habitat, seasonal climate and the species-specific ability of bryophytes to retain and hold water. The trait WHC is determined by a set of other traits, such as colony density, and leaf and shoot morphology (Elumeeva et al. 2011). Water content is important for key bryophyte traits such as insulation capacity, albedo, flammability, growth and association with N_2-fixing bacteria (Cornelissen et al. 2007; May et al. 2018).

To assess if our groups indeed perform better than those previously identified, we also compared our groups with three previous grouping systems. We chose the life form classification by Grace (1995), as this has been tested on non-expert people and found to be user-friendly, and it is most similar to our groups with *Sphagnum* defined as a separate group, "whorled branched turf". We included the primary life forms as defined by Bernhardt-Römermann et al. (2018), because these are the most recent of the life form clas-sifications. As a third grouping system, we included perichaetial position (La Farge-England 1996), with the only adaptation that we included liverworts as a separate group.

WHC data collection and analysis

We collated existing data on WHC, defined as maximum water held per gram of dry mass of bryophyte shoots or monospecific bryophyte colonies. The full data set included 1360 observations of 59 species from both published and unpublished studies. All data were from tundra ecosystems, except one Norwegian coastal heathland study (S.B. Rui,

V. Vandvik, and S. Haugum, unpublished data, 2018). Although the method across studies did not follow any standardized protocol the studies could be grouped into three methods of measuring WHC, as "internally" (Shoot$_{int}$) and "internal and externally" (Shoot$_{int+ext}$) held water in shoots and for whole bryophyte colonies (see Appendix Table A1 for the descriptions of methods for the individual studies). Although colonies represent the most realistic field situation, measurements at the shoot level are less destructive and, therefore, possible to conduct in long-term experimental plots and often data will, therefore, exist in this form. Internally held water is likely what directly links to physiological processes taking place inside bryophyte cells but is likely ultimately dependent on colony WHC. WHC Shoot$_{int}$ data included 36 species representing 7 BFGs (Elumeeva et al. 2011; Michel et al. 2012; Roos et al. 2019; van Zuijlen et al. 2021). WHC Shoot$_{int+ext}$, data included 28 species representing 8 BFGs (S.B. Rui, V. Vandvik, and S. Haugum, unpublished data, 2018; Elumeeva et al. 2011; A.M. Rzepczynska, A. Michelsen, and S. Lett, unpublished data, 2019) and WHC colony data included 33 species representing 7 BFGs (Elumeeva et al. 2011; I.S. Jónsdóttir, unpublished data, 2020; Lett et al. 2017; Liu and Rousk 2021; May et al. 2018; Michel et al. 2012; A.M. Rzepczynska, A. Michelsen, and S. Lett, unpublished data, 2019).

Correlation analyses with averaged species WHC values showed that WHC of whole colonies and WHC of Shoot$_{int+ext}$ were well correlated (Fig. A2a), whereas WHC Shoot$_{int}$ did not correlate with other ways of measuring WHC (Fig. A2b, c). Data for WHC Shoot$_{int}$ was, therefore, excluded from further analyses. The remaining data set included 963 observations of 37 bryophyte species, which we assigned to eight different BFGs (Fig. 3, Fig. A3) and to existing grouping schemes, namely "perichaetial position" (Liverworts grouped separately) (La Farge-England 1996), life form according to Grace (1995) and life form according to the BryForTrait database (Bernhardt-Römermann et al. 2018). Differences in WHC between groups within the different grouping schemes were analyzed with a mixed-effect model followed by Tukey's HSD test (see Appendix A). All data were handled and analyzed in R version 4.0.3 (R Core Team 2020).

Tundra bryophyte functional groups in relation to WHC

Three clusters with distinct WHC (Shoot$_{int+ext}$ and colony) materialized from our analysis (Fig. 3). "*Sphagnum*" had the highest WHC, with an average of 17 g water per g dry weight for colonies and Shoot$_{int+ext}$. The high WHC of *Sphagnum* species is primarily attributed to their specialized hyaline cells, which greatly increase their water holding capacity. With 2 g/g, "Polytrichales" had the lowest WHC and there was little variation between species within the group. Polytrichales are unique in several ways as they have relatively well-developed water conducting tissue and root-like structures, rhizoids and waxy leaves, a feature that reduces water evaporation rather than increasing water storage. The four groups, "Weft", "Mats", "Tall and Short unbranched turf", and "Branched turf" had intermediate WHC and did not differ from each other. Large variation between species within those groups (Fig. A3) shows that not all our groups distinguish themselves from each other in terms of WHC. Particularly the groups "Short unbranched turf" and "Tall unbranched turf" displayed almost as much variation between species within groups as the entire spectrum of the data set. A better separation between those groups might have been achieved by use of standardized protocols or a larger number of species representing each group. However, the groups possibly differ in other functional traits and thus represent functionally distinct species clusters, and this should be tested in future work.

Four of our groups were not represented in the analyses. Of these, "Thalloid" is, with its absence of leaves, the morphologically most distinct. From this group *Marchantia foliacea* Mitt. and *Monoclea forsteri* Hook. from New Zealand forests had WHC of 20 and 10 g/g, respectively (Green and Snelgar 1982), which is within the upper end the spectrum covered

Fig. 3.   Water holding capacity (WHC, g water per g dry mass bryophyte, g/g) analyzed across each of four grouping schemes. Black dots are species means and grey diamonds are group means. The data set includes 963 observations of 37 species. Each species was assigned a bryophyte functional group (BFG), perichaetial position (La Farge-England 1996), and life form according to Bernhardt-Römermann (2018), and life form following Grace (1995). BFGs are represented in the data set by Po, Polytrichales; BT, Branched turf; LL, Leafy liverworts; We, Weft; SU, Short unbranched turf; TU, Tall unbranched turf; Ma, Mat; Sp, *Sphagnum*). BryForTrait Life form following Bernhardt-Römermann et al (2018) are represented by Weft, Mat, Turf, cushion and species not assigned to groups (NA). Life form following Grace (1995) are represented by Large (L) cushion, Smooth mat, Tall (T) turf, Short (S) turf, Weft, Rough (R) mat, and Whorled branch (WB) turf. Groups with different lower-case letters are significantly different, N.S. indicate where groups that are not different (Tukey's HSD test, $p < 0.05$). Full variation within species for each BFG can be seen in the Appendix Fig. A3.
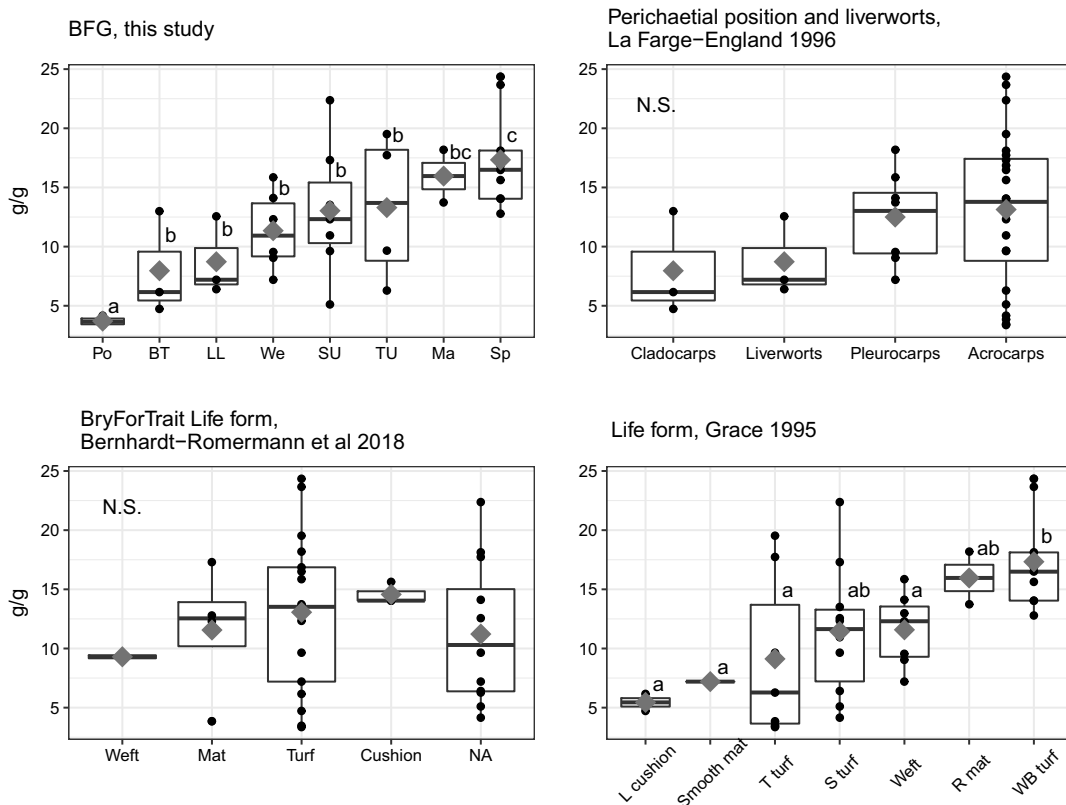
in our study. "Cushions", large and small, were also not represented by our data. Cushion growth is considered an adaptation to water conservation and low temperatures (Rice and Schneider 2004; Sand-Jensen and Hammer 2012). The WHC of "Dendroid" bryophytes has not been studied but the dendroid life form is associated with habitats of relatively high moisture or humidity (Atherton et al. 2010). Dendroids grow in loose patches, often intermingled with other species, and with limited branches at the lower stem, which could suggest that their WHC is not improved by colony structure.

Tundra bryophyte functional groups and other functional traits

Data at the species level for more than one functional trait are required to fully understand the functional roles of each BFG. Water holding capacity is only one of many important traits which relate bryophytes to key ecosystem functions (Cornelissen et al. 2007), and the BFGs are likely to cluster in unique ways for different functional traits. Here, we

Fig. 4. Selection of six bryophyte traits important for ecosystem functioning and their estimated relative value across the 12 bryophyte functional groups (BFGs). Three shades of green, light to dark indicate relative trait values (low, intermediate, high) assessed from the referenced sources (Furness and Grime 1982a; Lang et al. 2009; Elumeeva et al. 2011; Soudzilovskaia et al. 2013; Lett et al. 2017; Roos et al. 2019; A.M. Rzepczynska, A. Michelsen, and S. Lett, unpublished data, 2019). Diagonally split cells reflect that for a given BFG trait values range across the full spectrum. Striped cells are not covered by the given reference but are hypothesized based on authors' expert knowledge, no propositions are made for white cells; question marks indicate lack of data. Traits are water holding capacity (WHC), colony density, bryophyte colony layer depth/ shoot length, growth rate, tissue decomposability and nitrogen (N) content. References for a given trait do not necessarily use common protocols or units. No study covers all traits or all BFGs. Bryophyte functional groups are Sp, *Sphagnum*; De, Dendroid; We, Weft; Ma, Mat; BT, Branched turf; SC, Small cushion; LC, Large cushion; SU, Short unbranched turf; TU, Tall unbranched turf; Po, Polytrichales; LL, Leafy liverworts; Th, Thalloid.

discuss how additional functional traits, which are presumed to be of importance for ecosystem functioning, likely differ between the BFGs, i.e., colony density, bryophyte layer depth, relative growth rate, decomposability, and nutrient content, and identify the need for further research (Fig. 4).

Colony density together with bryophyte layer depth affect soil insulation efficiency, which in turn affects soil temperature, organic matter decomposition, nutrient cycling, active layer depth, and permafrost (Gornall et al. 2007; Soudzilovskaia et al. 2013). Colony density is relatively low in "*Sphagnum*", "Weft", and "Tall unbranched turf", whereas "Branched turf" and "Polytrichales" are BFGs that often have relatively higher density values (Fig. 4). Bryophyte layer depth or mat thickness is here defined as the distance from bryophyte layer surface to the point where bryophyte shoots or thalli begin to disintegrate. Mat thickness differs between some BFGs partly because size is an explicit character defining some groups ("Unbranched turf" and "Cushion"). Along with "*Sphagnum*", "Tall unbranched turf" and "Large cushion" create relatively deep bryophyte layers (Fig. 4). "Thalloid" bryophytes and "Mats" are never deep as they grow in close contact with the substrate.

The contribution of bryophytes to ecosystem C balance is manifested by the bryophyte layer depth as the balance between their net primary production and litter decomposability leads to variation in accumulation of bryophyte-derived organic matter. Both growth rate and decomposability show high variation between species and potentially between the BFGs. Studies comparing growth rates between multiple bryophyte species are relatively sparse and likely very sensitive to the method used. In growth chambers, length increment of "*Sphagnum*" was high compared with intermediate "Weft" and "Branched turf" and "Unbranched turf" and slow growing "Leafy liverworts" (Fig. 4, A.M. Rzepzynska, A. Michelsen, and S. Lett, unpublished data, 2019), whereas maximum biomass gain under

highly standardized conditions was the highest in "Short unbranched turf" and "Leafy liverworts" (Furness and Grime 1982*a*). Although both length and biomass gain may be relevant performance indicators, they are two different functional traits (Furness and Grime 1982*b*). This highlights the need for standardized bryophyte trait protocols. Bryophyte functional groups seem to have a relatively high variability in decomposability as "*Sphagnum*" had the lowest decomposition rates, followed by "Thalloid" bryophytes and "Branched turfs" (Fig. 4, Lang et al. 2009). "Unbranched turf", "Weft" and "Polytrichales" had intermediate decomposition rates, and "Leafy liverworts" had the highest decomposition rates. The rates of these two processes are likely influenced mostly by the contents of C-rich recalcitrant compounds, but also by tissue nutrient contents. Both bryophyte growth and decomposability are likely to be strongly affected by tissue nutrient content (Lang et al. 2009), and N content can be regarded as a separate functional trait.

Although there are indications from previous studies that BFGs are likely to differ in important functional traits (Fig. 4), there are big gaps in available data and the BFGs are not evenly represented. "Dendroids", "Mats", "Small and large cushion" and "Thalloids" are heavily understudied and focused efforts to include species representing these groups is crucial. In addition, there is a range of other important functional bryophyte traits which are less studied. For example, flammability has large impacts on ecosystem C and N balance and could become more important under future warmer and drier climate conditions. As water content greatly influences bryophyte flammability (Blauw et al. 2015), flammability could be linked to WHC and, thus, predicted by the BFGs. Bryophytes constitute an important substrate in many tundra ecosystems for N_2-fixing bacteria with substantial interspecies variation (Gavazov et al. 2010; Stuart et al. 2020). The mechanisms controlling N_2 fixation in bryophytes are poorly understood but traits like WHC and perhaps specific leaf area are potential important predictors of species differences (S. Lett, C.T. Christiansen, E. Dorrepaal, and A. Michelsen, unpublished data, 2018; Liu and Rousk 2021). In conclusion, the BFGs are likely to have unique combinations of trait values for a range of functional traits and the application of BFG could improve functional resolution in ecosystem studies.

Although BFGs may differ in one or many functional traits, many traits are plastic and may cause substantial intraspecific (or intra-BFG) variation. This variation needs to be further explored and it is possible that for some traits, the extent of the intraspecific variation may be predicted by the BFGs. For example, the trait "bryophyte albedo" is highly plastic for some species e.g., within the genera of *Sphagnum* and *Racomitrium*, which turn whiteish upon drought (May et al. 2018). In addition, trait plasticity could be important for understanding changes in bryophyte community composition in relation to environmental change as species or BFGs with higher trait plasticity may be less susceptible to environmental changes (Henn et al. 2018; Roos et al. 2019).

Using BFGs in vegetation surveys

The inclusion of bryophyte functional groups in vegetation assessments using standard methods such as the point-intercept method, a standard within the International Tundra Experiment (ITEX) network (Molau and Mølgaard 1996), and visual cover estimates could improve vegetation analyses in tundra ecosystems by providing greater resolution of the bryophyte component in plant communities. The BFGs are partly defined by the type of colony they appear in, but bryophytes do not always grow in monospecific patches. Often, they grow in complex assemblages of multiple species, which may or may not belong to the same functional group. If species growing in the same colony do not belong to the same BFG, how should a BFG then be determined based on colony type? For the point intercept method, this is partly solved in our classification system which combines shoot and colony

characteristics. The hierarchical organization (Fig. 2) of the BFGs allows group determination at a "lower" level in cases where colony type cannot be determined (Broad functional groups, Fig. 2). For visual cover estimates of bryophyte colonies, the BFG that the dominating species belongs to may be recorded. In relation to these issues, functional properties of mixed and single species bryophyte colonies can differ beyond the additive effect of the combination of species (Mulder et al. 2001; Rixen and Mulder 2005; Michel et al. 2012). In this way, the function of a given colony may not be the weighted mean of the species present in the colony. This is especially an issue when assessing bryophyte community function based on the species present in the ecosystem. Functional groups, like the ones suggested here, do not eliminate this issue. Despite these unresolved situations, we believe that the benefits of using BFGs will exceed the drawbacks.

In practice, we suggest using the proposed bryophyte functional group classification as a complement to the species approach. Thus, when a species cannot be determined due to issues such as time or skill limitation, hits are assigned to the group. It may also be advisable for field researchers to learn the two to three most common species in their plots and go to species level here. Importantly, the BFGs could also be used the "other way around" as a means to combine species allowing comparison of bryophyte-cover data across experiments and field sites. This type of aggregation is essential for enabling comparison when sites do not have the same species and has been done successfully for vascular plants within the ITEX network (Walker et al. 2006; Elmendorf et al. 2012a, 2012b). This would provide important insights into the responses of bryophyte communities to climate and environmental change and their ecosystem impacts and consequences.

Directions for future research

The BFGs suggested here are a first step to facilitate inclusion of bryophytes in vegetation surveys at a higher functional resolution than simply "bryophytes", while still accessible to non-experts and a means to lump bryophytes into meaningful groups that share important functional traits. However, the suggested BFGs need to be further evaluated for their usefulness by statistical testing for additional traits measured at the species level. With the WHC data, we provide an example of how this evaluation can be done and show that for WHC bryophyte functional resolution is increased from one to three by using the BFGs rather than the generic "bryophytes" and that the BFGs explain WHC better than previous grouping systems. The outcome might either support the grouping suggested here or require adjustments.

Further testing of the BFGs requires accessible functional trait data, which is currently limited. To allow robust analyses, these traits must be gathered using standardized protocols building on previous efforts (Jónsdóttir et al. 1999; Cornelissen et al. 2007; Hill et al. 2007). To improve or include bryophyte representation in current trait databases such as TRY and Tundra Trait Team (Kattge et al. 2020; Bjorkman et al. 2018), bryophyte functional trait data need to be geographically and taxonomically diverse for good representation of species. Unlike vascular plants, bryophyte functional traits are rarely recorded in field experiments, as this requires skills in species identification. For instance, in the database TRY, moss shoot length only has 716 entries and none of the observations are georeferenced, whereas vascular plant height has 249,551 observations (Kattge et al. 2020) and Arctic plant traits are generally highly under-represented (Bjorkman et al. 2018). Future challenges, therefore, lie in identifying and measuring bryophyte traits that underpin key ecological functions and to add these to existing trait databases. Importantly, species-level identification cannot be circumvented for these trait studies.

Bryophyte species identification will likely remain a struggle for many ecologists. This is further challenged by the lack of a comprehensive flora covering the Arctic region and poor

representation of bryophytes in plant-identification mobile phone applications such as SEEK-iNaturalist or PictureMe (the authors, personal observation). To date, there is not a comprehensive bryophyte flora that covers Greenland and North America. Fennoscandia and the Russian Arctic are covered by several regional floras (Table A2). As the Arctic biome consists of many countries, language can be another obstacle for identification. Comprehensive floras are needed to facilitate further focus on tundra ecosystem functioning where bryophytes are a major component both in terms of biomass, primary production and diversity. In the longer term, novel field-based genetic profiling technology (Parker et al. 2017) and plant identification applications may develop to become powerful tools for aiding field identification. Until then, our contribution seeks to minimize the loss of data in the long-term monitoring of the Arctic vegetation and elucidate the functional role and importance of bryophytes in tundra ecosystems. This may, in turn, stimulate further focus on species identification as well as facilitate openings for innovative research projects.

Final remarks

Today, bryophytes constitute a missing functional and evolutionary dimension in most tundra ecosystem studies, hindering our ability to understand ecosystem functionality and responses to environmental change. Using BFGs could be a means to include functional diversity of bryophytes in ecological studies while bypassing difficulties with species identification. Our example with bryophyte WHC shows some of the potentials and challenges of using BFGs and the groups can likely be improved through further studies at the species level. If proven robust, the groups could likely be expanded to include the boreal zone, another region where bryophytes play a major role (Turetsky et al. 2012). The hierarchical organization of the BFGs allows functional resolution to be adjusted to the scientific question in mind. Importantly, our suggestion to use the BFGs in ecological studies is not a suggestion to abandon studies of bryophyte functionality and responses at the species level. Rather it should be seen as an encouragement to include bryophytes at a higher functional resolution than simply "bryophyte" in more studies.

Contributors' statement

SL and ISJ conceived the original idea for the paper, which was developed with input from ABS, CTC, HD, FE, GHRH, SIL, AM, KR. ISJ, SB, SL, TGE, XL, JM, AMR, KvZ contributed data. SL analyzed the data and led the writing of the paper. All authors contributed to writing and editing of the manuscript.

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Appendix A

Methodology for water holding capacity

Water holding capacity (WHC) in all studies was measured as maximum held water per gram dry weight bryophyte. No recognized standardized protocol exists for measuring WHC and methodology therefore differed between studies (Table A2). However, across the WHC studies examined, three different general approaches were followed: WHC for $Shoot_{int+ex}$, WHC for $Shoot_{ext}$ and WHC for colonies. $Shoot_{int+ext}$ WHC was the weight difference of shoots at full water saturation and after complete drying. $Shoot_{int}$ WHC was measured in a similar manner except external water was removed before weighing by blotting shoots dry on a paper towel (Elumeeva et al. 2011). Bryophyte colony WHC was measured by weighing colonies at fully saturated conditions and after complete drying. For bryophyte colonies, volume varied between 20 and 3200 cm^3 between studies, though one study had volumes down to 2.5 cm^3 for some small statured bryophytes *Neoorthocaulis floerkii*, and *Dicranum elongatum* (A.M. Rzepczynska, A. Michelsen, and S. Lett, unpublished data, 2019).

To test if WHC measurements of the three approaches were correlated, we averaged species values and where species were represented for at least two approaches, these were fitted using linear models (Fig. A1). Colony WHC and $Shoot_{int+ext}$ WHC were significantly correlated ($p < 0.001$, $R^2 = 0.70$), whereas $Shoot_{int}$ WHC did not correlate with colony or $Shoot_{ext}$ WHC (Figure A1). This suggests that WHC can be measured on single shoots (WHC of $Shoot_{int+ext}$) in permanent plots where destructive measurement must be kept to a minimum and still represent colony WHC reasonably well. WHC of $Shoot_{int}$, by contrast, should perhaps be considered an entirely separate trait.

Because WHC of $Shoot_{int+ext}$ and colony were well-correlated (Fig. A2), differences between tundra bryophyte functional groups (BFGs) were analyzed for WHC of $Shoot_{int+ext}$ and colony together with a mixed effects model followed by Tukey's HSD test. To take into account potential structural biases across studies, study ID was included as a random factor. Species was nested inside study ID to take into account the expected smaller variation within compared with between bryophyte species.

Table A1. Methods of individual water holding capacity (WHC) studies. Full references for published studies can be found in the reference list for the main text. Water holding capacity was measured either for whole colonies, for shoots with internally and externally held water (WHC Shoot$_{int+ext}$) and for shoot only with internally held water (WHC Shoot$_{int}$). See above for overall description of methodology.

| Study	Description	Dimensions
WHC colony		
Elumeeva et al. 2011	Colonies kept in plastic containers. Shoots of non-target species removed to <1%. Colonies remoistened and surplus water drainage allowed. Samples weighed and full moisture and after oven-drying at 90 °C until a constant mass.	N: 5, area: 7.5×7.5 cm^2, depth: similar height as in field, green and basal parts included
Jónsdóttir, unpublished data, 2020	Colonies kept in plastic containers. Shoots of non-target species removed to <1% (usually not needed). Colonies sprayed with water until saturated and allowed to drain surplus water. Weighed at full saturation and after drying at 70 °C.	N: 10, area 19.6 cm^2 (circle, 5 cm in diameter), trimmed to 5 cm depth
Lett et al. 2017	Colonies kept in plastic containers. Shoots of non-target species removed to <1%. Colonies sprayed with water until field saturation and allowed to drain surplus water. Weighed at full water and after oven-drying at 85 °C until a constant mass.	N: 4, area: 11 x 11 cm^2, depth: 2.8–7.3 cm depending on species, green and basal parts included
Liu and Rousk 2021	Colonies kept in plastic containers. Shoots of non-target species removed to <1%. Placed in a tray of distilled water for 12 h to saturate and allowed to drain surplus water. Weighed at full water and after oven-drying at 65 °C until a constant mass.	N: 3, area: 10.75 cm^2 (circle, 3.7 cm Ø), depth: 2.1–7.8 cm depending on species, green and basal parts included
May et al. 2018	Vertical faces of colonies wrapped in cellophane and placed in trays. Colonies had vascular plants and soil removed and contained 95% target species moss. Placed in a tray of distilled water (3 cm depth) to hydrate. Soaked for 2 h until full saturation, then drained for 1 h. Colonies weighed after draining and at 0% water content after dried at 50 °C.	N: 4, area: 20×20 cm^2, depth: fixed depth, 8 cm
Michel et al. 2012	Colonies kept in plastic containers. Shoots of non-target species removed to <1%. Colonies sprayed with water until field saturation and allowed to drain surplus water. Weighed at full water and after oven-drying at 60 °C until a constant mass.	N: 6 for each colony, 16 colonies, area: 19.6 cm^2 (circle 5 cm in diameter), depth: fixed depth, 5 cm
Rzepczynska, Michelsen, and Lett, unpublished data, 2019	Colonies kept in plastic containers. Non-target species removed (~95%). Sprayed with distilled water until full saturation, allowing the excess water to drain. Samples were weighed and then dried at 85 °C for 48 h.	N: 20; dimensions varied among species (volume 3 to 248 cm^3)
WHC Shoot$_{int+ext}$		
Rui, Vandvik, and Haugum, unpublished data, 2018	Soil removed. Soaked in water for 30 min. Suspended in sealed container with water at the bottom for 24 h at 22 °C to allow excess of water drops and prevent evaporation. Then, weighed, oven-dried for 72 h at 70 °C and weighed again.	N: 30, Sample size: 1g dry weight
Elumeeva et al. 2011	Separate shoots remoistened in deionized water for min 12 h before weighing at full turgor. Less than 30 s before initial weighing every shoot was taken out of the water, shaken and lightly blotted to remove the extra external water not well connected with the shoot structures. Shoots dried at 90 °C until constant mass and weighed again.	N: 10, Sample size: 1 shoot
Rzepczynska, Michelsen, and Lett, unpublished data, 2019	Shoots collected from each sample placed in a glass vial and sprayed with distilled water until full turgor. Vials sealed with perforated parafilm for 24h, shoots then weighed before and after drying at 50 °C for 48h.	N: 20, number of shoots differed between species, always covering area of 1 cm^2

Table A1. (*concluded*).

| Study	Description	Dimensions
WHC Shoot_{int}		
Roos et al. 2019	Shoots submersed in demineralized water for 30 min. Placed on moistened filter paper in sealed Petri dishes for ~ 24 h. Shoots blotted dry and weighed, air-dried and weighed again. For each batch of samples, one replicate was oven-dried at 40 °C for 6 h and weighed to provide a conversion factor between air-dry and oven-dry mass.	*N*: 10, Sample size :1 shoot, (i.e., the top part of the shoot with green leaves)
van Zuijlen et al. 2021	Same as Roos et al. 2019, except one replicate per batch was oven-dried at 70 °C for 24 h (to provide a conversion factor between air-dry and oven-dry mass).	Same as Roos et al. 2019
Elumeeva et al. 2011	Shoots moistened in deionized water and shaken to remove water against gravity, then blotted to remove as much external water as possible and weighed. Shoots oven-dried at 90 °C.	*N*: 12, Sample size: 1 shoot.
Michel et al. 2012	Shoots moistened in deionized water and shaken to remove water, then blotted to remove as much external water as possible and weighed. Shoots oven-dried at 60 °C for 48 h.	*N*: 6 shoots for each species, 16 colonies, 8 species

Fig. A1. The twelve bryophyte functional groups (BFGs) and their abbreviations illustrated with photos of characteristic species, a–l. (a), *Sphagnum fuscum* (Schimp.) H. Klinggr.; (b), *Climacium dendroides* (Hedw.) F. Weber & D. Mohr; (c), *Hylocomium splendens* (Hedw.) Schimp.; (d), *Hypnum cupressiforme* Hedw.; (e), *Tomentypnum nitens* (Hedw.) Loeske; (f), *Grimmia pulvinata* (Hedw.) Sm.; (g), *Racomitrium lanuginosum* (Hedw.) Brid.; (h), *Aulacomnium turgidum* (Wahlenb.) Schwägr.; (i), *Dicranum fuscescens* (Brid.) Wilson; (j), *Polytrichum commune* Hedw.; (k), *Ptilidium ciliare*; and (l), *Marchantia foliacea*. White bars indicate approximate scale. Photos c, e, h by Signe Lett and a, b, d, f, g, i, j, k, l through Creative Commons (commons.wikimedia.org)((a) https://commons.wikimedia.org/wiki/File:Sphagnum_fuscum_(b,_150951-474701)_4200.JPG; (b) https://commons.wikimedia.org/wiki/File:Climacium_dendroides_-_Flickr_-_pellaea_(1).jpg; (d) https://commons.wikimedia.org/wiki/File:Hypnum.cupressiforme.jpg; (f) https://commons.wikimedia.org/wiki/File:Grimmia_pulvinata_91974896.jpg; (g) https://commons.wikimedia.org/wiki/File:Iceland_Crack_4328.JPG; (i) https://commons.wikimedia.org/wiki/File:Dicranum_flexicaule_(a,_141118-472329)_5339.JPG; (j) https://commons.wikimedia.org/wiki/File:Polytrichum_commune_(g,_144843-474723)_0636.JPG; (k) https://commons.wikimedia.org/wiki/File:Ptilidium_ciliare_(a,_132028-465914)_6839.JPG; (l) https://commons.wikimedia.org/wiki/File:Brunnenlebermoos_Marchantia_polymorpha_Regen_nahe_Viechtach-001.jpg).
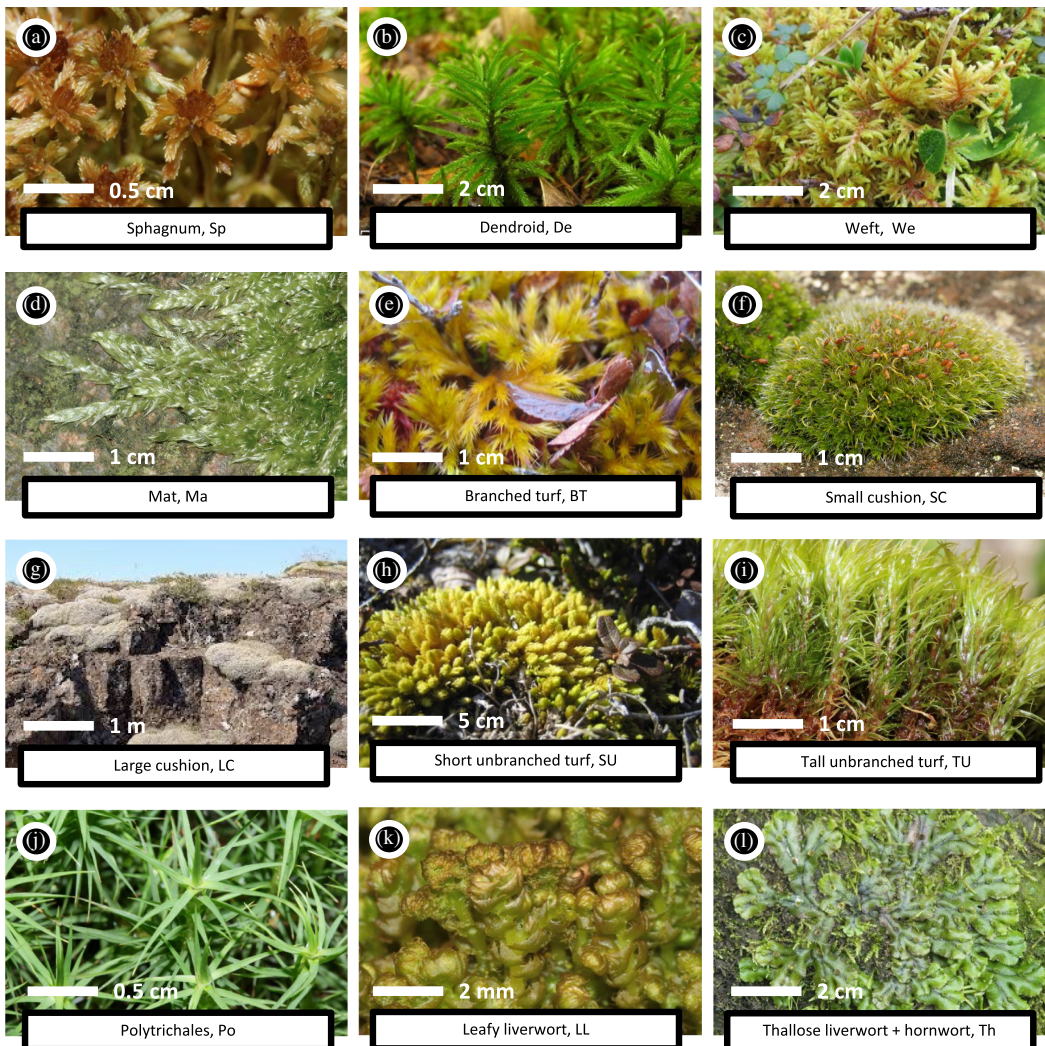
Fig. A2. Relationships between water holding capacity (WHC) in (a) bryophyte colonies, (b) shoots external and internal, and (c) in shoots only internal. Dots represent species means and are colored according to tundra bryophyte functional groups (TBFGs; We, Weft; Ma, Mat; BT, Branched turf; SU, Short unbranched turf; TU, Tall unbranched turf; Po, Polytrichales; Sp, *Sphagnum*, LL, Leafy liverworts). Colony WHC and Shoot$_{int+ext}$ WHC were significantly correlated, whereas Shoot$_{int}$ WHC did not correlate to colony or Shoot$_{ext}$ WHC (b,c).
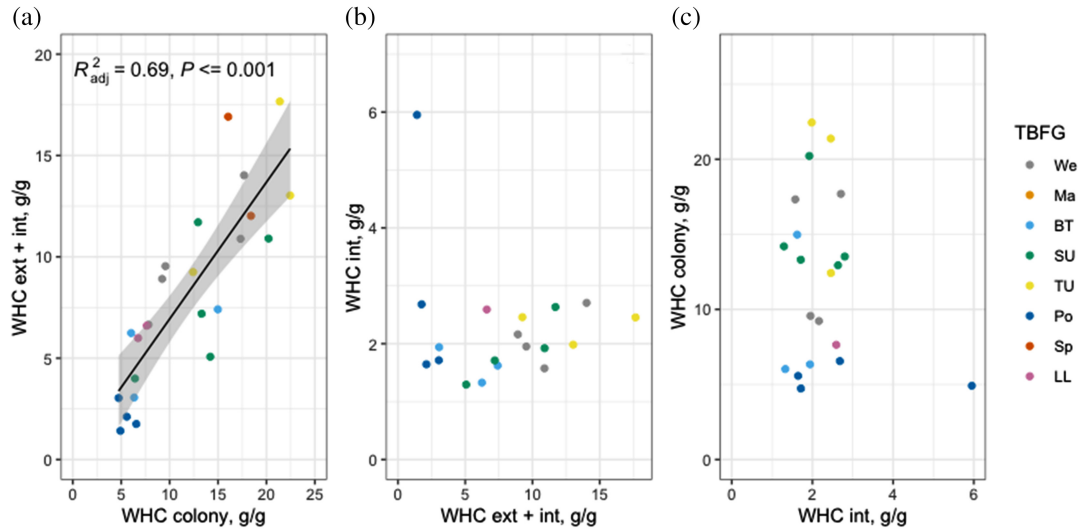
Fig. A3. Water holding capacity of bryophyte colonies (open circles) and shoot including external moisture (closed circles) measured in gram water per gram dry weight bryophyte. Bryophyte species are ordered according to tundra bryophyte functional groups (TBFGs; Po, Polytrichales; BT, Branched turf; LL, Leafy liverworts; We, Weft; SU, Short unbranched turf; TU, Tall unbranched turf; Ma, Mat; Sp, *Sphagnum*). Color of dots indicate study ID (Michel et al. 2012; Elumeeva et al. 2011; Lett et al. 2017; May et al. 2018; S.B. Rui, V. Vandvik, and S. Haugum, unpublished data, 2018; I.S. Jónsdóttir, unpublished data, 2020; Liu and Rousk 2021, A.M. Rzepczynska, A. Michelsen, and S. Lett, unpublished data, 2019). Boxes contain 1st and 3rd quartile and show median, dots outside whiskers indicate values more than 1.5 times the length of the box.
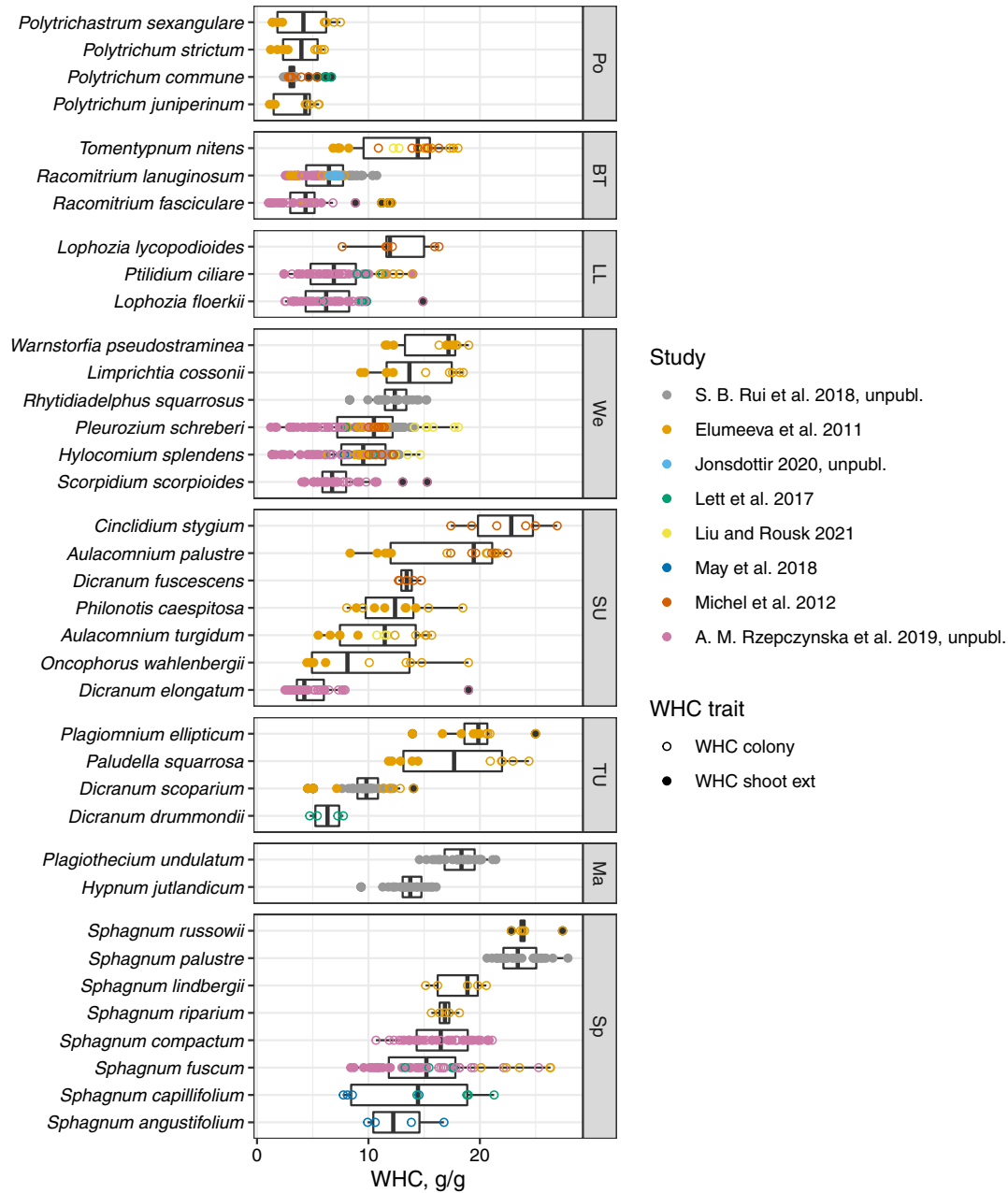
Table A2. List of recommended bryophyte floras and species lists (*) covering Arctic areas. The list is not comprehensive. Where available, number of species is given.

Arctic region	Flora/species list*	Language	Authors (ref)	Year	Comment
North America					
	Flora of North America, Vol. 27 and 28	English	Flora of North America Committee	2007, 2014	Mosses. Available as e-book, 621 + 698 species
USA	The mosses of Arctic Alaska*	English	W.C. Steere	1978	Mosses. 415 species Out of print
	A Bryophyte Species List for Denali National Park and Preserve, Alaska, with Comments on Several New and Noteworthy Records*	English	S.E. Stehn, J.K. Walton, C.A. Roland	2013	Bryophytes, Covers Denali National Park, 499 species
Canada	Flore des bryophytes du Québec et du Labrador, Vol. 1-3	French	J. Faubert	2012	Bryophytes, 892 species
	A key and annotated synopsis of the mosses of the northern lowlands of Devon Island, N.W.T., Canada	English	V.D. Vitt	1975	Mosses. Covers Devon Island. 131 species
	The Mosses of Northern Ellesmere Island, Arctic Canada. II. Annotated List of the Taxa*	English	G.R. Brassard	1971	Mosses. Covers North Ellesmere Island. 151 species
Greenland					
	Illustrated Moss Flora of Arctic North America and Greenland vol. 1-3	English	D. Long, H. Crum, B. Murray, G. Mogensen, *ed.*	1985	1. Polytrichaceae, 2. Sphagnaceae, 3. Andreaeobryaceae – Tetraphidaceae. Out of print
	Liverworts of Greenland	English	K. Damsholt	2013	Liverworts, 178 species
	Mosses (Bryophyta) and liverworts (Marchantiophyta) of the Zackenberg valley, northeast Greenland*	English	K. Hassel, H. Zechmeister, T. Prestø	2014	Mosses and liverworts, 212 species
Fennoscandia					
	Illustrated Moss Flora of Fennoscandia. II. Musci. Vol. 1-6	English	E. Nyholm	1954–1969	Bryophytes. Out of print
	Illustrated flora of Nordic Mosses, Vol. 1–4	English	E. Nyholm	1987–1998	Mosses; vol 4 out of print
	Illustrated moss flora of Nordic liverworts and hornworts	English	K. Damsholt	2009	Liverworts and hornworts. Out of print
Iceland	Íslenskir mosar	Icelandic	B. Jóhannsson	1989–2003	Bryophytes. Available as reports. 604 species, detailed descriptions and distribution maps for Iceland
	Mosar á Íslandi	Icelandic	Á. H. Bjarnsson	2018	Bryophytes. Key to all species in Iceland

Table A2. (*concluded*).

Arctic region	Flora/species list*	Language	Authors (ref)	Year	Comment
Norway	Norges torvmoser	Norwegian	K.I. Flatberg	2014	Sphagnaceae. 55 species
	Bryophytes of the Longyearbyen area*	English	T. Prestø, M. Lüth, K. Hassel	2014	Bryophytes
	Bryophytes, lichens and cyanoprocaryotes in surrounding of pyramiden (Svalbard): A consise handbook	English	M. Dodd, I. Tatarenko, N. Koroleva	2015	Bryophytes, subset of Svalbard species, 87 species
Sweden	National Nyckeln, 4 volumes	Swedish + English	T. Hallingbäck, N. Lönnel, H. Weibull, L. Hedenås	2005–2019	All mosses, 852 species
	Mossor	Swedish	T. Hallingbäck	2016	All bryophytes
	Bryophytes of the Tornetraesk area, northern Swedish Lapland*	English	O. Mårtensson	1956	Bryophytes
Russia					
	Moss Flora of Russia, Vol. 2, 4 and 5	Russian, English	M.S. Ignatov et al.	2017, 2018, 2020	Oedipodiales–Grimmiales; Bartramiales–Aulacomniales; Hypopterygiales - Hypnales (Plagiotheciaceae - Brachytheciaceae)
Other useful resources					
Britain and Ireland	Mosses and Liverworts of Britain and Ireland–a field guide	English	I. Atherton, S. Bosanquet, M. Lawley	2010	Mosses, Liverworts and Hornworts.

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