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Genetic variation and structure in peatmosses (*Sphagnum*)

Thesis for the degree of Philosophiae Doctor

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Norwegian University of Science and Technology
Faculty of Natural Sciences and Technology
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Acknowledgements

Working with peatmosses seems like the strangest occupations in the world considering peoples facial expression when I tell them. However, getting the opportunity to immerse myself in their historical traveling patterns makes for a fun workday in my world. Ending up loving bryophytes was somewhat random, and I would lie if I said it was love at first site. I remember thinking: “If plants, then why not the smallest and most difficult ones of them all?” What a great choice, less is really more.

I have had great support and help from a lot of people, making the difficult journey of finishing a PhD-thesis possible. I am grateful to my supervisors, Hans K. Stenøien and Kristian Hassel, for always keeping their doors open for me and my questions and always being fast and good at commenting on my manuscripts. Thank you for investing your time in my project, you have both taught me so much. Thanks to Hans for thinking big thoughts and paying attention to the details. Thanks to Kristian for giving me the opportunity to learn about bryophytes in a broad scale, reminding me that there is more out there (even birds) than *Sphagnum*. Thanks for the field experience you have provided me, it’s a pleasure doing field work with you.

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Magni Olsen Kyrkjeeide

Trondheim, May 2015

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List of papers

- I. Kyrkjeeide, M.O.; Stenøien, H.K.; Flatberg, K.I.; Hassel, K. Glacial refugia and post-glacial colonization patterns in European bryophytes. *Lindbergia* 2014 ;Volum 37. s. 47-59
- II. Kyrkjeeide, M.O., Hassel, K., Stenøien, H.K., Prestø, T., Boström, E., Shaw, A.J. & Flatberg, K.I. (2015) The dark morph of *Sphagnum fuscum* in Europe is conspecific with the North American *S. beothuk*. *Journal of Bryology* (accepted)
- III. Kyrkjeeide, M.O., Hassel, K., Flatberg, K.I., Shaw, A.J., Brochmann, C. & Stenøien, H.K. Long-distance dispersal and cryptic barriers shape the genetic structure of peatmosses (*Sphagnum*) across the Northern Hemisphere. (submitted to *Journal of Biogeography*)
- IV. Kyrkjeeide, M.O., Hassel, K., Flatberg, K.I., Shaw, Yousefi, N. & Stenøien, H.K. Is there more than one Lady in Red? Spatial genetic structure of the abundant and widespread peatmoss *Sphagnum magellanicum* Brid. (manuscript)

Declaration of contributions

I performed all work on which this thesis is based. Hans K. Stenøien and Kristian Hassel contributed significantly to the initiating and planning of all papers and were involved in the writing of all papers. HKS contributed on data analyses in all papers. KH and Kjell Ivar Flatberg collected herbarium material from Russia used in paper II, III, and IV. KIF were involved in the writing of all papers and initiated and contributed in morphological examination in paper II. A. Jonathan Shaw was involved in the final stages of writing papers II, III, and IV. Tommy Prestø and Erik Boström were involved in the final stages of writing paper II. TP collected the type material for paper II. EB contributed partly in the lab experiments perform in paper II and IV. Christian Brochmann was involved in the final stages of writing paper III. Narjes Yousefi was involved in the final stages of writing paper IV.

Introduction

Dispersal and vicariance events are the major determinants of species' distributions in space and time (Lomolino *et al.*, 2010). Even though vicariance and continental movement may explain the distribution of many taxa (Cowie & Holland, 2006), there is a growing consensus that dispersal generally plays a fundamental role for the distribution and structuring of diversity (Muñoz *et al.*, 2004; Nathan, 2006; Alsos *et al.*, 2007; Proches & Ramdhani, 2013). Organisms having high dispersal capacities can easily overcome barriers and colonize new areas long distances away from their origin (Gillespie *et al.*, 2012), and wide distribution ranges are indeed found in species such as birds, lichens and spore-producing plants (Schofield, 1988; Dahl, 1998; Proches & Ramdhani, 2013).

Historical events affect movement of species, and current species distributions are heavily influenced by the Pleistocene glaciations (Hewitt, 2000). The Northern Hemisphere ice-sheets fluctuated greatly during the last glaciation, with the last glacial maximum about 20,000 years ago (Svendsen *et al.*, 2004). In Europe, molecular studies of a wide range of organisms, including arctic-alpine plants, have provided support to post-glacial colonization of northern Europe from southern or eastern refugia after the ice retreated (e.g. Taberlet *et al.*, 1998; Hewitt, 1999; Ehrich *et al.*, 2008; Tollefsrud *et al.*, 2008; Alsos *et al.*, 2009). The extent of *in situ* glacial survival in plants has been debated (Brochmann *et al.*, 2003; Westergaard *et al.*, 2011), as extreme environmental conditions in glaciated areas make this seem unlikely. However, species able to survive in small populations may have existed in favourable microrefugia within the ice sheet (Holderegger & Thiel-Egenter, 2009; Rull, 2009) and *in situ* glacial survival likely explains the disjunct ampho-Atlantic distribution found in some plant species (Westergaard *et al.*, 2011). However, many arctic and boreal vascular plants have currently relatively broad distribution patterns in the Northern Hemisphere, and this is to a large degree the result of long-distance dispersal after the LGM (Abbott & Brochmann, 2003; Brochmann *et al.*, 2003; Alsos *et al.*, 2007; Brochmann & Brysting, 2008).

Microscopic organisms and organisms dispersing with microscopic propagules may differ from macroscopic organisms in distribution ranges and post-glacial history, because they theoretically can disperse across either hemisphere in short time (Wilkinson *et al.*, 2012). In fact, a study from the southern hemisphere show that floristic similarities of spore-producing plants and lichens are correlated to wind directions, rather than distances (Muñoz *et al.*, 2004). Thus, barriers observed for macro-organisms may not apply for species with dispersal

units around 20 μm . Lichens and spore-producing plants, for example ferns and mosses, reproduce by microscopic spores. Spore diameters are usually less than 40 μm in bryophytes (Frahm, 2008) and lichens (Pentecost, 1981), and 60 μm in ferns (Tryon, 1970). As numerous spores may be produced annually (Smith *et al.*, 2006; Flatberg, 2013), a high number of spores probably participate in long-distance dispersal by wind. Among spore-producing organisms, extraordinary large distribution ranges are often found (Schofield, 1988; Frahm & Vitt, 1993; Lücking, 2003; Printzen, 2008; Werth, 2011; Xiang *et al.*, 2015). Many species cover two or more continents, and sometimes they do occur in both hemispheres (Piñeiro *et al.*, 2012; Fernandez-Mendoza & Printzen, 2013). Genetic studies have shown that these wide ranges are likely a result of recent long-distance dispersal (Fernandez-Mendoza & Printzen, 2013; Lewis *et al.*, 2014a), rather than vicariance. This has also been suggested for the few vascular plants that have bipolar distribution (Popp *et al.*, 2011; Villaverde *et al.*, 2015). The dispersal vector between the hemispheres has been suggested to be migratory birds, dispersing plant fragments or seeds from the Northern Hemisphere to the Southern Hemisphere (Popp *et al.*, 2011; Lewis *et al.*, 2014a; Lewis *et al.*, 2014b).

Bryophytes comprises liverworts (Marchantiophyta), mosses (Bryophyta), and hornworts (Anthocerotophyta) and presents the earliest land plants (Qiu, 2008). In bryophytes, the photosynthetic, haploid gametophyte is free-living and usually perennial, while the diploid sporophyte is short-lived and completely dependent on the gametophyte. Bryophytes are found to occupy a wide range of habitats, growing from the tropics to the arctic, often in highly stressful environments (Goffinet & Shaw, 2009). The most important trait for the extreme tolerance is their poikilohydric nature, meaning that cell water content is directly determined by that of the environment. Hence, bryophytes lack the ability to prevent dehydration, but are still able to resume metabolism when rehydrated (Proctor *et al.*, 2007). Sexual system in bryophytes varies between monoicy (female and male gametangia are found at the same gametophyte) and dioicy (female and male gametangia are found on separated gametophytes).

Bryophytes have in general wide distribution ranges (Schofield & Crum, 1972; Schofield, 1988). For instance, 70% of moss species occurring in Europe, are also present in North America (Frahm & Vitt, 1993) as opposed to vascular plants, where only 6.5% of European species are shared with North America (Qian, 1999). There is generally a low degree of endemism in bryophytes even on archipelagos, with for example only 1.5% of bryophyte species found on the Canary Islands being endemic compared to 40% of angiosperms

(Vanderpoorten *et al.*, 2010). Traditionally, the wide distribution ranges have been explained by the old age of bryophytes, being characterized as “unmoving, unchanging sphinxes of the past” (Crum, 1972), meaning vicariance is the main factor leading to shared species across several continents. By contrast, most studies based on molecular analyses, show that wide distribution ranges are caused by recent intercontinental dispersal events (Szövényi *et al.*, 2008; Devos & Vanderpoorten, 2009; Kreier *et al.*, 2010; Shaw *et al.*, 2010; Vanderpoorten *et al.*, 2010; Stenøien *et al.*, 2011; Karlin *et al.*, 2012; Piñeiro *et al.*, 2012). Furthermore, populations found in widely separated regions can be genetically very similar (Szövényi *et al.*, 2008; Stenøien *et al.*, 2011; Shaw *et al.*, 2014a).

On the other hand, cryptic species are found in spore-producing organisms (Shaw, 2001; Crespo & Lumbsch, 2010), meaning that there are genetically distinct groups within species, but with no obvious morphological differences. Bryophytes and lichens are morphologically simple organisms with rather few characteristics suitable for species determination. Thus, widespread species might be more restricted than detected so far by morphological analyses. However, when phylogenetically separated lineages are found, re-examination of a taxon may lead to the detection of suitable characters that support the phylogenetic signal (Szweykowski *et al.*, 2005; Crespo & Pérez-Ortega, 2009). Still, this is not always the case, but genetically distinct lineages with no morphological distinction may be allopatric (Leavitt *et al.*, 2012), meaning they occur in different geographical areas.

Wide distribution ranges are also found among peatmosses *Sphagnum* L. (Bryophyta: Sphagnaceae), as species usually occur on two or more continents. For example, all but four European peat mosses are found in North America. The genus occur on all continents, except Antarctica, but are most abundant in the Northern Hemisphere. Peat mosses are the main plants in peatlands covering large areas in the northern boreal zone. As much as 1/3 of soil carbon is probably bound up in peatlands (Gorham, 1991), making *Sphagnum* one of the world’s most important carbon storing plant genera. The genus likely diversified when the climate cooled in the Miocene (Shaw *et al.*, 2010), meaning that long-distance dispersal have shaped the wide distribution ranges recognised today. *Sphagnum* spores are released by a shot-gun mechanism that increases the release height above ground (Sundberg, 2010; Whitaker & Edwards, 2010). They disperse by a fat-tailed kernel, found to lead to genetic homogeneity on a regional scale (Szövényi *et al.*, 2012). Sundberg (2012) estimated that as much as 1% of regional spore rain have intercontinental origin, indicating that genetic homogeneity might be found even on continental scales.

Genetic studies show that European and eastern North American populations are genetically similar and the Atlantic Ocean seems to be a weak barrier to gene flow (Hanssen *et al.*, 2000; Thinggaard, 2001; Szövényi *et al.*, 2008; Stenøien *et al.*, 2011). Also, across the northern Pacific Ocean extensive gene flow was observed in *S. miyabeaenum* Warnst. (Shaw *et al.*, 2014a), but in this species a barrier to dispersal was found to be situated in southern Alaska. On the other hand, no such barrier was recognised in the disjunctly distributed *S. subnitens* Russow & Warnst. (Karlín *et al.*, 2011), as all plants along the western North American coast were found to be genetically identical. Thus, how *Sphagnum* plants generally are structured genetically in the Pacific region is unknown.

Sampling the entire geographical distribution of a species, but also morphological and ecological variation, could strengthen phylogeographic studies (Pante *et al.*, 2015). Broad sampling, including close relatives with a somewhat uncertain taxonomic status, for example only based on morphology, would increase the chance of correctly delineating the focal species (Pante *et al.*, 2015). As most *Sphagnum* species are generally very widespread, it is important to sample specimens across the full distribution range to understand how spores may move across the entire Northern Hemisphere, especially between the Atlantic and Pacific region. However, few studies cover the entire distribution of circumboreal *Sphagnum* species or compare populations across the Northern Hemisphere continents. Whether genetic variation is homogenous across the Northern Hemisphere or whether there are barriers to dispersal on a global scale is currently unknown.

Aims of the thesis

The purpose of this thesis was to study the phylogeography of *Sphagnum* species mainly occurring across the Northern Hemisphere having disjunct or somewhat continuous distributions. The main aim was to better understand how dispersal patterns affect the contemporary distributions and genetic structure in widespread spore-producing plants.

Specifically, the aims of the thesis papers were:

- (1) Review the bryophyte history in Europe after the last ice-age and summarise insights concerning likely glacial refugia for bryophytes, identify major post-glacial colonisation routes, and discuss the probability of glacial survival within the ice-sheet (Paper I).
- (2) Test if life history traits (i.e., mating systems, spore production, and/or spore sizes), are associated with different geographical regions, range size, and genetic structure of European bryophytes based on meta-analyses of published results (Paper I).
- (3) Clarify the taxonomic status of two morphotypes within *S. fuscum* (dark and pale brown colour morphs) and compare them to the newly described North American species *S. beothuk* (Paper II).
- (4) Investigating the spatial genetic diversity and structure among several *Sphagnum* species to identify dispersal patterns and potential barriers in the Northern Hemisphere (Paper III and IV).
- (5) Examine if genetic diversity and structure are the same for disjunctly and continuously distributed species (Paper III).
- (6) Investigate the Northern Hemisphere-Southern Hemisphere disjunction of *S. magellanicum*, to evaluate where the South American plants have originated from (Paper IV).
- (7) Compare *S. magellanicum* and *S. alaskense* genetically to determine whether these morphologically similar species have the same ploidy level and evaluate their phylogenetic relationship (Paper IV).

Material and Methods

The material gathering of this thesis was twofold. First, 26 phylogeographical studies of 31 bryophytes published over 12 years were summarised to review the colonization history of bryophytes in Europe after the last glaciation (Paper I). In addition, meta-analyses was done on published data to test if life-history traits (sporophyte frequency and spore size) are associated with distribution ranges and genetic structuring in European bryophytes. Second, plant material from seven *Sphagnum* species were sampled for phylogeographic studies (Table 1), these were: *S. angustifolium* (Warnst.) C.E.O. Jensen, *S. austinii* Sull., *S. fuscum* (Schimp.) H. Klinggr., *S. magellanicum* Brid., *S. quinquefarium* (Lindb.) Warnst., *S. rubiginosum* Flatberg, and *S. wulfianum* Girg. The species are continuously or disjunctly distributed around the Northern Hemisphere. In addition, *S. alaskense* R.E. Andrus & Janssens and *S. beothuk* R.E. Andrus, which has amphi-Pacific and amphi-Atlantic distributions, respectively, were included. These two species are morphologically similar to other species included: *S. beothuk* to the dark colour morph of *S. fuscum* (see below) and *S. alaskense* to *S. magellanicum*. However, these species has not yet been analysed genetically and their taxonomic status are somewhat uncertain, at least for *S. beothuk*. *Sphagnum magellanicum* has a bipolar distribution as it occurs in South America. The disjunctly distributed species, *S. austinii*, *S. quinquefarium* and *S. rubiginosum*, show oceanic affinity and are found at the Northern Hemisphere coasts (Figure 1). The distribution ranges of three continuously distributed species, *S. angustifolium*, *S. fuscum*, and *S. wulfianum*, are shown in Figure 2. These six species are assumed to have rather similar dispersal capacity, but their micro-habitat requirements vary from narrow to broad (Flatberg, 2013).

I aimed at sampling specimens from as many localities as possible to cover the complete distribution ranges of the species (Figures 1 and 2). For this purpose, I used herbarium material from herbaria DUKE (Durham, USA), LN (St. Petersburg, Russia), MA (Madrid, Spain), MHA (Moscow, Russia), TRH (Trondheim, Norway), and UBC (Vancouver, Canada). By sampling from herbaria collections, most of the species habitat range and morphological variation were likely covered in addition to the full spatial distribution. One shoot was selected for DNA extraction from each chosen herbarium collection.

Table 1 Nine *Sphagnum* species from three different subgenera (Subgenus) were included in this thesis. Most species are dioecious (Sexuality), frequency of sporophyte production varies (Sporophytes), and all spore diameters (SD) lie within 20-30 µm. The species are either oceanic or continental (Section). Two species, *S. alaskense* and *S. beothuk* are not circumboreal, but are included as they are morphologically similar to *S. magellanicum* and the dark colour morph of *S. fuscum*, respectively. The other species occur throughout the Northern Hemisphere and *S. magellanicum* also occurs in South America (Continents and Distribution). The species varies from having general to specialised habitat requirements (Habitat and Type).

| Species | Subgenus | Sexuality | Sporophytes | SD (µm) | Section | Continents | Distribution | Habitat | Type |
|-------------------------|-------------------|-----------|-------------|---------|---------|--------------|--------------|----------|------------|
| <i>S. alaskense</i> | <i>Sphagnum</i> | D | - | - | Co | NA, A | Continuously | Mi, Fo | Generalist |
| <i>S. angustifolium</i> | <i>Cuspidata</i> | D | Occ.-fre. | 20-25 | Co | E, NA, A | Continuously | Fo,He,Mi | Generalist |
| <i>S. austinii</i> | <i>Sphagnum</i> | D | Occ.-fre. | 23-28 | O | E, NA | Disjunct | Mi | Specialist |
| <i>S. beothuk</i> | <i>Acutifolia</i> | D | Occ.-fre. | - | O | E, NA | Disjunct | Mi | Specialist |
| <i>S. fuscum</i> | <i>Acutifolia</i> | D | Occ.-fre. | 25-30 | Co | E, NA, A | Continuously | Mi | Generalist |
| <i>S. magellanicum</i> | <i>Sphagnum</i> | D | Occ.-com. | 25-30 | Co | E, NA, A, SA | Continuously | Fo,He,Mi | Generalist |
| <i>S. quinquefarium</i> | <i>Acutifolia</i> | M/P | Com.-abu. | 20-25 | O | E, NA, A | Disjunct | Fo,He | Generalist |
| <i>S. rubiginosum</i> | <i>Acutifolia</i> | M/P | Com.-abu. | 20-25 | O | E, NA, A | Disjunct | Fo,He | Specialist |
| <i>S. wulfianum</i> | <i>Acutifolia</i> | M/P | Occ.-com. | 20-25 | Co | E, NA, A | Continuously | Mi | Specialist |

Abbreviations: D-dioecious, M-monoecious, P-polyecious, Occ.-occasional, fre.-frequent, com.-common, abu.-abundant, C-continental, O-oceanic, E-Europe, NA-North America, A-Asia, SA-South America, Fo-forest, He-heath, Mi-mire. Literature: Flatberg (2013)

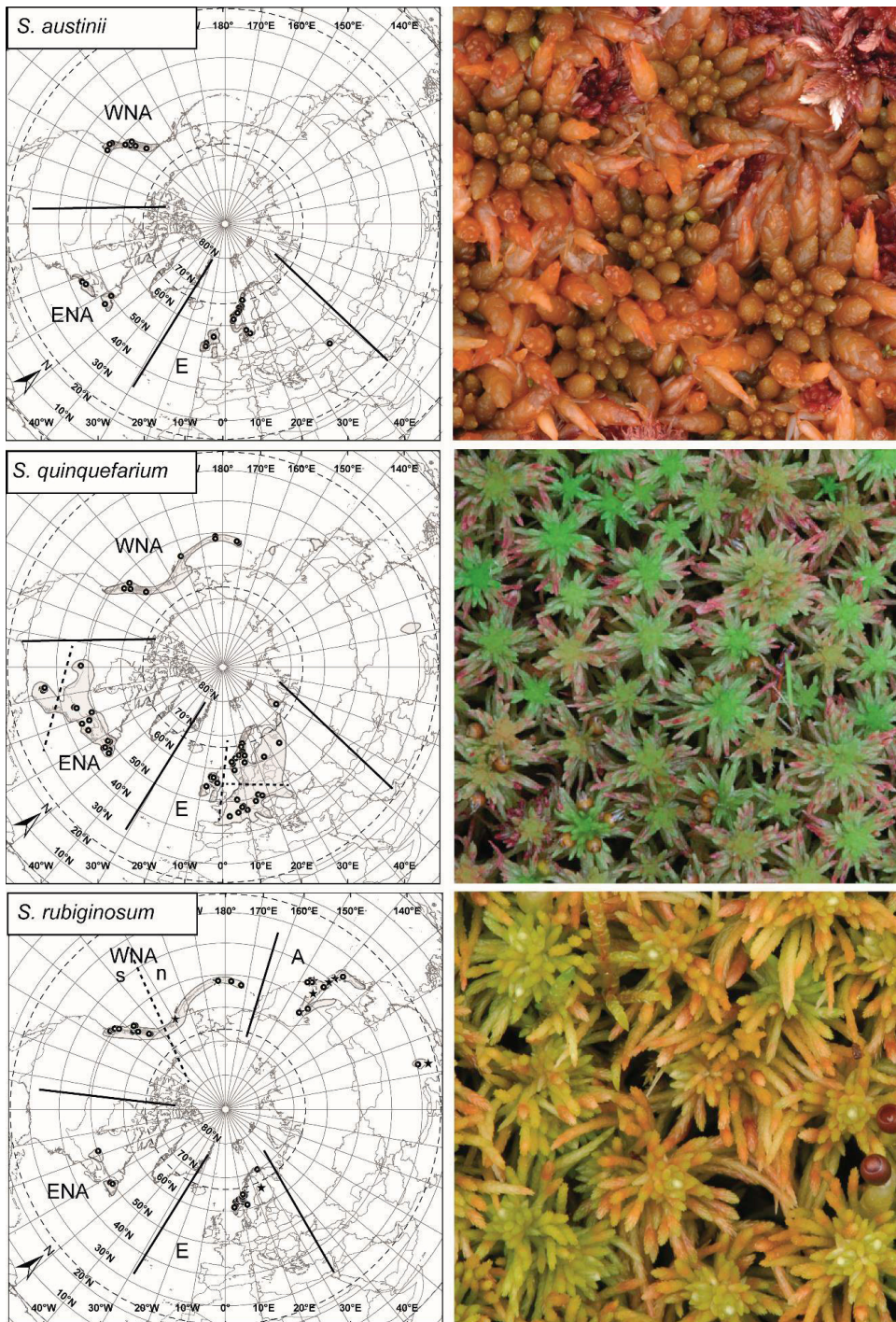


Figure 1: Distribution range (grey) and sampling location (black dots) of three disjunctly distributed *Sphagnum* species. Geographical regions are indicated by black lines.

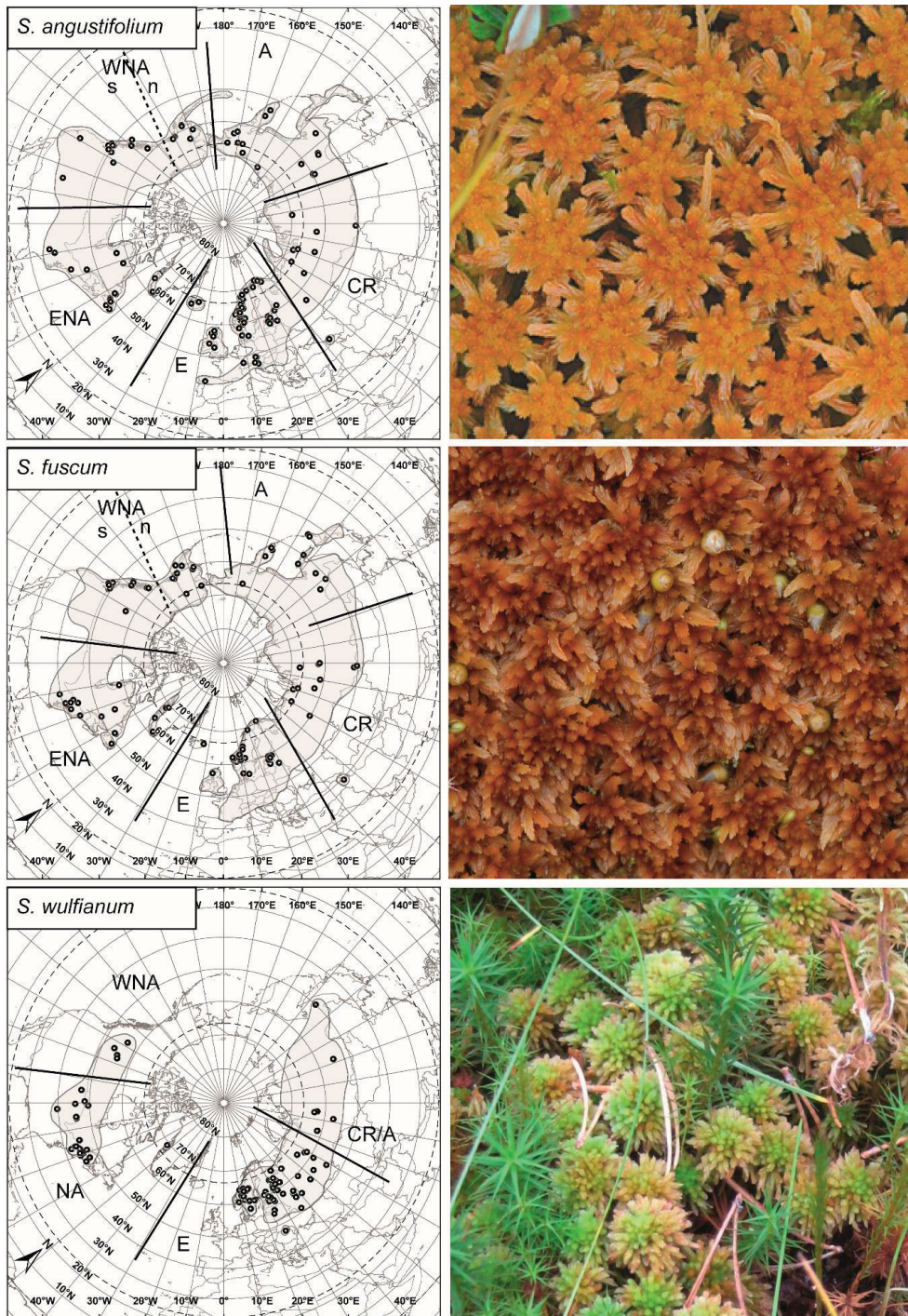


Figure 2: Distribution range (grey) and sampling location (black dots) of three continuously distributed *Sphagnum* species. Geographical regions are indicated by black lines.

Morphological analyses (Paper II)

Two colour morphs of *S. fuscum* and *S. beothuk* were examined for morphological diagnostic characters that separate them. Plants from both colour morphs were first screened for morphological characters suitable for species determination. Then, both quantitative and qualitative methods were applied to find differences. In the quantitative analysis, a mixed stand approach was applied, meaning that plants of the pale and dark colour morphs of *S. fuscum* growing next to each other were examined. Two mixed stand locations were used. From each location, five plants of both colour morphs of *S. fuscum* were picked and five stem leaves and five branch leaves measured. Thus, 50 leaves from each leaf type and morph were included in statistical analysis. Stem and branch leaves from both were measured in three ways: the full length of the leaves, the width at the middle of the leaves, and the width at the tip of the leaves (1/8 from the leaf tip). Altogether, five measurements were tested statistically: leaf length, leaf width (middle), leaf width (tip), ratio leaf length/leaf width (middle) and ratio leaf width (middle)/leaf width (tip). Leaf measurements were taken using the Leica DM6000 B transmission microscope, and photos were made applying the Leica Application Suite LASD V2.6 for stacking. Mixed models were used to analyse the characters, as the leaves from the same individual were not independent. All statistical analyses were done in the R Environment (R, Development Core Team. 2011).

For the qualitative part, the same mixed stand collections were used to find other diagnostic characters than analysed using the quantitative method. This part mainly focused on pore patterns of the branch leaf hyalocysts.

Herbarium plants were later examined to check if differences observed were universal. Additionally, characters observed in the field have been evaluated.

Molecular analyses (Paper II, III, IV)

DNA was extracted from a piece of the central part of the shoot apex of dried specimens. Extractions were performed using the CTAB protocol described in Shaw *et al.* (2003), DNeasy 96 Plant Kit (Qiagen, Oslo, Norway), or E.Z.N.A. SP Plant DNA Kit (Omega Biotek, Norway) following the manufacturer's protocol.

Altogether, 20 microsatellite markers developed for the genus *Sphagnum* were used (marker names are the same as in Shaw *et al.* (2008) and Stenøien *et al.* (2011)). Three to five markers were amplified in 8 µl of multiplex reactions using Qiagen Multiplex PCR Kit (Qiagen, Oslo, Norway). Multiplex reactions consisted of 2.5 µl multiplex mix, 1.7 µl doubled distilled H₂O, 0.8 µl primer mix, and 3 µl DNA diluted 1:10 in doubled distilled H₂O. Primer mixes were made based on expected microsatellite length and with three different fluorophores (HEX, FAM and NED) to avoid overlap between markers. The same thermocycling regime was implemented for all primer sets with an initial step at 95°C for 15 minutes, then 33 cycles at 94°C for 30 seconds, 53°C for 90 seconds, and 72°C for 60 seconds, and lastly a final step at 60°C for 30 minutes. 1 µL of PCR product, 8.85 µL of Hi-Di™ Formamide (Applied Biosystems, Norway) and 0.15 µL GSLizz500 were mixed for electrophoresis on an ABI 3730 sequencer. Alleles were sized and genotyped using GENEMAPPER® software (Applied Biosystems).

Phylogenetic relationships were investigated using DNA sequences. For this purpose, two loci from the plastid genome, *trnL* (UAA) 59 exon-*trnF* (GAA) and tRNA(Gly) (UCC), hereafter called *trnL* and *trnG*, respectively, were sequenced from a subset of samples of the total datasets. Three *trnG* sequences were obtained from each of *S. fuscum*, *S. beothuk*, *S. quinquefarium* and *S. rubiginosum*. Both genes were sequenced from 32 samples of *S. magellanicum* and *S. alaskense*. PCR amplifications were carried out using puReTaq Ready-To-Go PCR Beads (Amersham Biosciences) in solutions of 22.8 µL H₂O, 0.1 µL forward primer, 0.1 µL reverse primer, and 2.0 µL DNA extract. The PCR cycle profile was as follows: 95°C for 5 minutes, 51°C seconds for 45 seconds, 72°C for 45 seconds, with step 2 and 3 repeated 35 times, 72°C for 5 minutes. For *trnL*, step 2 and 3 were as follows: 54°C seconds for 45 seconds, 72°C for 190 seconds. DNA sequences was aligned using ClustalW with default parameters in Mega 6.0 (Tamura *et al.*, 2013).

Statistical analyses (Paper II, III, IV)

Samples occurring in the same geographical regions were pooled together in regional groups. Altogether six regional groups were defined; Europe, Eastern North America, Western North America, Asia, Central Russia, and South America. The number of regional groups used for each species varied according to distribution patterns in the species (see Figures 1 and 2). Genetic diversity estimates were obtained for regional groups in each species by calculating

number of polymorphic loci, expected heterozygosity (H_E ; Nei, 1987), and mean number of alleles. For *S. magellanicum*, genetic diversity measures were also estimated for specimens divided in genetic groups inferred by Structure (see below). To test for isolation-by-distance, Mantel tests were used to compare the relationship between genetic distance and geographical distance. Pairwise Φ_{PT} (used for haploid data as an analogue to F_{ST} , Peakall *et al.*, 1995) and Nei's genetic distance (Nei, 1973) was estimated to investigate population structure in each species. Genetic distance measurements were estimated between both regional groups and genetic groups inferred by Structure (see below) in *S. angustifolium*, *S. fuscum*, *S. magellanicum*, *S. quinquefarium*, and *S. rubiginosum*. All above analyses were performed in GenAlEx 6.501 (Peakall & Smouse, 2006, 2012).

Population structure in *Sphagnum* species was further investigated using principal coordinate analyses (PCoA) in GenAlEx 6.501 (Peakall & Smouse, 2006, 2012) and clustering analyses implemented in Structure 2.3.4 (Pritchard *et al.*, 2000; Falush *et al.*, 2003; Falush *et al.*, 2007; Hubisz *et al.*, 2009). The software Structure uses a Bayesian approach to identify genetically homogeneous clusters of individuals and the most likely number of such clusters in a datasets. The same analysis regime was used for all species, with 10 set as the maximum number of likely genetic clusters (K), using a burn-in period of 50,000 iterations followed by 200,000 iterations (longer runs returned the same results), and replicating this step 10 times for each K -value. The analyses included the admixture and independent allele frequencies models using all samples in the datasets. Structure Harvester (Earl & vonHoldt, 2012) was used for collating and visualising likelihood values obtained from Structure. The mean likelihood of the K -value, standard deviation for each K , and ΔK (Evanno *et al.*, 2005) were used to evaluate the likely number of genetic clusters in each species. Alignments of the different replicated analyses for the chosen K -values were made using the greedy option and 1000 random input orders in the software Clumpp 1.2.2. (Jakobsson & Rosenberg, 2007). The program Distruct 1.1 (Rosenberg, 2004) was used to graphically display the Structure results. In paper IV the online version of Clumpak (Kopelman *et al.*, 2015) was used for collating and visualising the results. In addition, the Best K option in Clumpak was used to estimate the most likely number of K .

Divergence time between main genetic groups inferred in *S. angustifolium*, *S. fuscum*, *S. magellanicum*, and *S. quinquefarium* by Structure was estimated using IMA (Hey & Nielsen, 2004). Preliminary test was performed following the recommendations in the user manual, while the full scale analyses were performed twice using 100,000 steps as burn-in followed by

at least 20 mill steps. A geometric heating scheme with parameters set to 0.8 and 0.9 and 30 Metropolis-coupled chains was applied. The upper boundary for population sizes was set to 1 and divergence time to maximum 5. Migration parameters were excluded to increase statistical power.

Phylogenetic relationships were investigated using the Maximum Likelihood option in Mega 6.0 (Tamura *et al.*, 2013), adding 1000 bootstrap replications and the general time reversible substitution model (GTR).

Results and Discussion

There is a growing consensus that long-distance dispersal shape the wide distribution ranges found in many bryophytes (Muñoz *et al.*, 2004; Szövényi *et al.*, 2008; Heinrichs *et al.*, 2009; Piñeiro *et al.*, 2012; Shaw *et al.*, 2014b). My results show that *Sphagnum* species are genetically homogeneous across large geographical ranges, supporting long-distance dispersal. However, five studied species are genetically structured across their distribution ranges, showing limitations to dispersal probably due to cryptic barriers. A general trend seems to be that main differentiated genetic groups occur in the Atlantic (Europe and eastern North America) and Beringian regions (Alaska and Asia). As found for other *Sphagnum* species (Szövényi *et al.*, 2008; Stenøien *et al.*, 2011; Shaw *et al.*, 2014a), the results further indicate that the Atlantic Ocean and northern Pacific Ocean are weak barriers to dispersal in *Sphagnum*. However, continents seem to be more difficult to overcome.

Bryophyte history in Europe after the last glacial maximum (paper I)

Several refugia and post-glacial colonisation routes were recognised for European bryophyte species based on literature. Colonisation routes and contact zones in bryophytes resemble those found for other organisms (Taberlet *et al.*, 1998; Hewitt, 1999). Some general trends are evident for bryophytes, and three main colonisation routes were recognised (Figure 1). Species colonising along the southern route (blue arrows in Figure 1) probably survived the LGM in southern Europe (Grundmann *et al.*, 2007, 2008). High levels of genetic variation and unique genetic lineages are found along the western coast of Europe for some species, supporting a western route (green arrows in Figure 2), colonising unglaciated areas from the

western coast of mainland Europe (Vanderpoorten *et al.*, 2008), southern parts of the British Isles (van der Velde & Bijlsma, 2003), but probably also from Macaronesia (Laenen *et al.*, 2011) and North America (Stenøien *et al.*, 2011). Species colonising along the third route (red arrow in Figure 3), likely survived in large non-glaciated areas east of the Scandinavian ice sheet (Hedenäs, 2012).

Even though some trends were found, more studies are needed to conclude if these colonisation routes are general among bryophytes, as most of the recognised refugia and colonisation routes inferred are based on relatively few studies. Specifically, more data are needed of potential *in situ* glacial survivors to evaluate to what extent bryophytes have survived within the limits of the last glacial ice-sheet. Moreover, the wide distribution ranges and potentially high dispersal ability of many bryophyte species emphasises the need for broad geographical sampling in phylogeographical studies of bryophytes to evaluate the importance of glacial survival outside of Europa, with post-glacial colonisation of Europe.

It seems like sporophyte and spore characteristics are associated with dispersal abilities in bryophytes (Sundberg, 2010). Thus, species having small spores and frequent sporophyte production should have wider distribution ranges than species with large spores and rare sporophyte production. The results of the meta-analyses performed here indicate that species with small spores indeed appear in more European regions than species with larger spores, but spore size was not significantly associated with F_{ST} -values between populations. On the other hand, F_{ST} -values were found to be significantly higher in species that rarely produce sporophytes compared to species with frequent spore production. The sample size for meta-analyses were low. Hence, the results should be interpreted with caution.

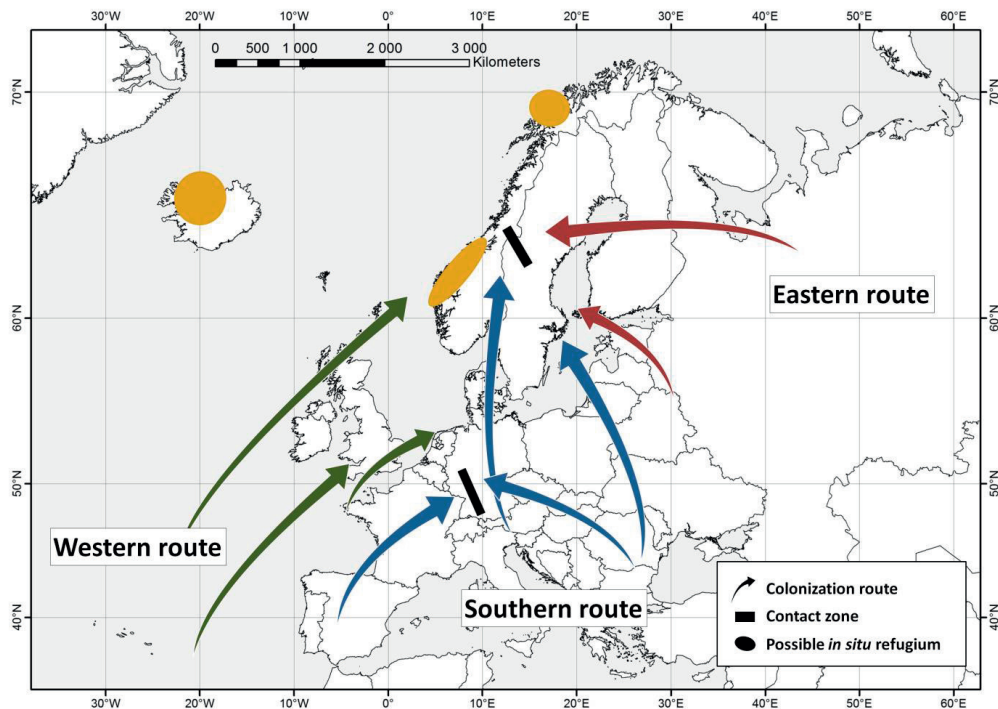


Figure 3: Hypothesised colonisation routes, contact zones, and possible *in situ* glacial refugia of bryophyte species in Europe during and after the last glacial maximum. Three main colonisation routes, western, southern, and eastern, are indicated by green, blue and red arrows, respectively. Solid yellow fields indicate potential *in situ* refugia during the LGM.

Delimitation of *Sphagnum fuscum* and *S. beothuk* (Paper II)

The results show that the pale and dark brown colour morphs observed in European *S. fuscum* are genetically and morphologically distinct taxa with different distribution patterns. Thus, they should be treated as separate taxa. Moreover, we show that the original material underlying the name *S. beothuk* is conspecific with the European and North American material collected as the dark brown colour morph of *S. fuscum*.

Morphological examinations, including quantitative analyses of specimens of both colour morphs collected from mixed stands and qualitative observations of herbarium material, reveal distinct differences in characters between the two colour morphs of *S. fuscum*. Characters associated with the dark colour morph are also found in *S. beothuk*. This support

that the dark colour morph is conspecific to *S. beothuk*. The stem leaf shape is usually a rather safe character for separating *S. fuscum* and *S. beothuk* when the average impression of several examined leaves from a plant is considered. However, the different pore pattern in the upper abaxial part of the branch leaf is the most diagnostic character separating the two species (Figure 4).

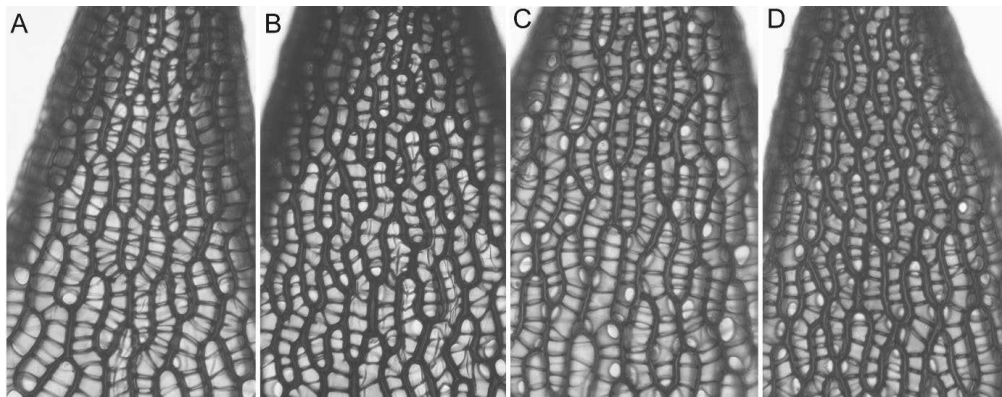


Figure 4: Pore patterns in the upper abaxial part of the branch leaves of the dark (A and B) and pale (C and D) colour morphs of *Sphagnum fuscum*. The dark colour morph is conspecific with *S. beothuk*.

Two genetic groups were inferred by the program Structure based on microsatellite data (Figure 5). Plants belonging to the pale colour morph of *S. fuscum* form one genetic group, while plants of the dark colour morph form another genetic group together with plants of *S. beothuk*. The phylogenetic relationship of the pale and dark colour morphs of *S. fuscum* within the subgenus *Acutifolia* were further analysed using sequences of the plastid gene *trnG*. The phylogenetic tree reveals that plants of the dark colour morph (*S. beothuk*) are separated from the pale colour morph of *S. fuscum* and other *Acutifolia* species by a long branch supported by a high bootstrap value (98%, results not shown).

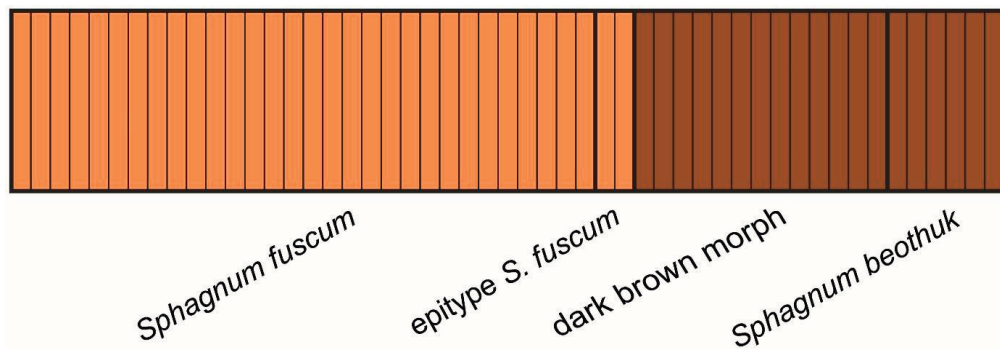


Figure 5: Genetic structure of *Sphagnum fuscum* and *S. beothuk* inferred by the software Structure based on microsatellite data. Different colours indicate different genetic clusters. The thick lines separate different species and colour morphs, while the thin lines separate individuals.

Sphagnum fuscum and *S. beothuk* differ in both distribution range and habitat preference. *Sphagnum fuscum* is found across the Northern Hemisphere mainly in the boreal zone. The current knowledge of the distribution range of *S. beothuk* includes the eastern coast of North America and the western coast of Europe, and it seems to be confined to the oceanic sections. In Britain and Ireland, *S. fuscum* and *S. beothuk* may occur at equal rates. Thus, it has a much more restricted distribution globally compared to several other oceanic *Sphagnum* species, that also occur in western North America and/or Asia (e.g. *S. quinquefarium*, *S. rubiginosum* (Flatberg, 1993), and *S. austinii* (McQueen & Andrus, 2007; Flatberg, 2013)). Only three other *Sphagnum* species are known to be amphi-Atlantic, making *S. beothuk* the fourth peat moss having this distribution.

Genetic structure and diversity of widely distributed *Sphagnum* species (Paper III and IV)

Genetic structure and diversity in seven *Sphagnum* species occurring continuously or disjunctly across the Northern Hemisphere were investigated. The results show that two species, *S. austinii* and *S. wulfianum* are genetically homogeneous throughout their distribution ranges. Between two and four genetic groups were recognised in *S. angustifolium*,

S. fuscum, *S. quinquefarium* and *S. rubiginosum* and these groups are geographically structured across the Northern Hemisphere (Figure 6). The main pattern seems to be that plants in the Atlantic region group together and are genetically different from plants from the Beringian region (Asia and Alaska). Plants from the Pacific Northwest (southern Alaska and southwards) group either with one of the two main groups (Atlantic in *S. fuscum* and *S. rubiginosum*, and Beringian in *S. quinquefarium*), or form a separate genetic group as in *S. angustifolium*.

In *S. magellanicum*, a similar pattern was found. However, the structuring in this species is at the ploidy level in this species. Almost all northeast Asian and Alaskan samples are diploid, while plants collected other places are haploid. Thus, the Atlantic region consists of haploid plants and the Beringian region of diploid plants (Figure 7). Haploid plants are also found outside the Atlantic region, reaching the Pacific coast in both North America (south of southern Alaska) and southern Asia and occurring throughout South America. Altogether, five differentiated genetic groups were inferred among the haploid plants, all having different geographical distribution ranges (Figure 7). The diploid group consist of plants collected as both *S. magellanicum* and *S. alaskense*. Even though three genetic groups were inferred among the diploids, they do not correspond to species nor geography. Thus, the diploid plants likely consist of one large homogeneous genetic pool. To evaluate the taxonomic status of the diploid plants, a thorough examination of morphology and other molecular markers are needed.

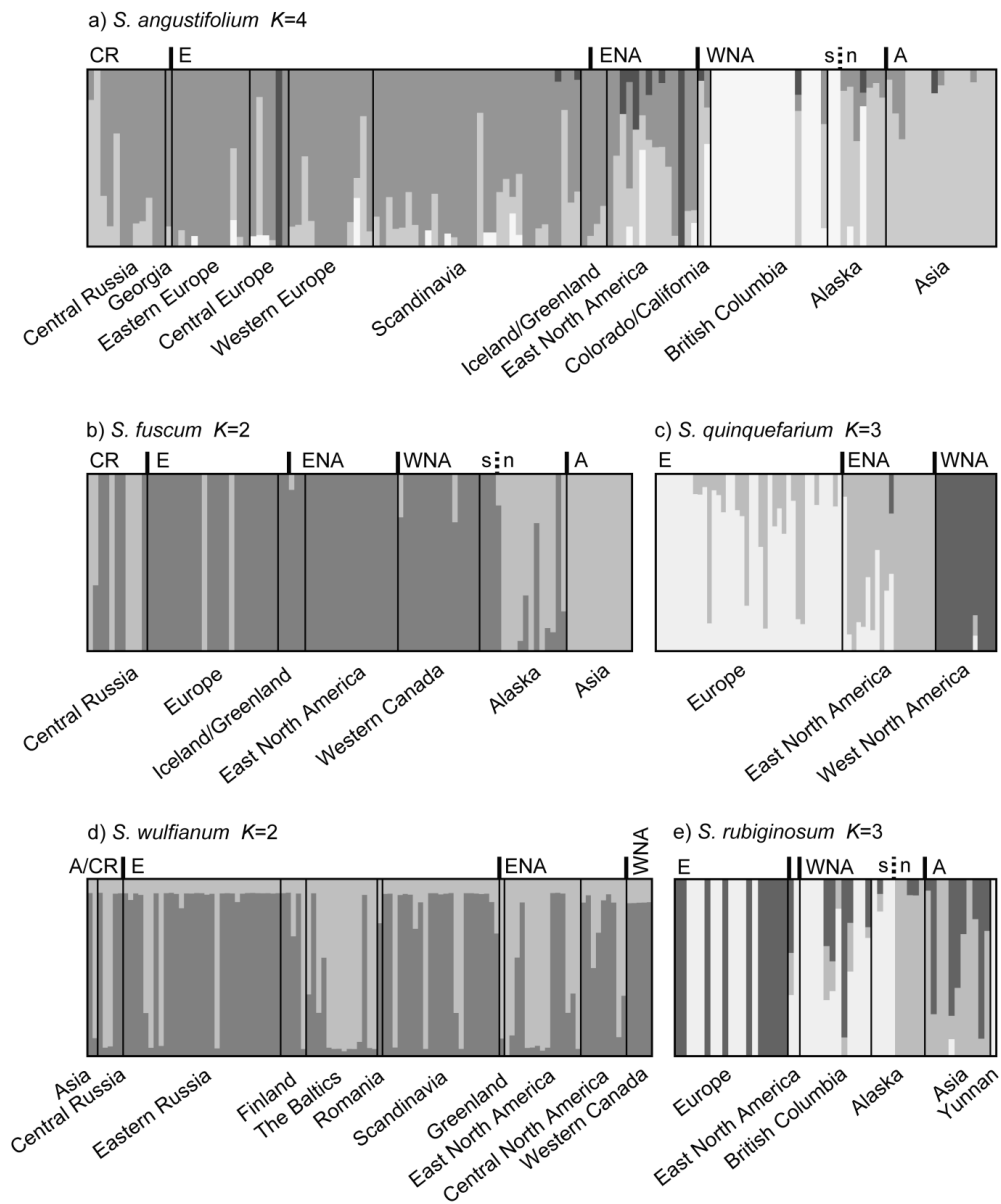


Figure 6: Genetic groups inferred by the software Structure in five species of *Sphagnum* (species names are denoted above the histograms together with the likely number of genetic groups). Regional groups are indicated above the histograms, separated by thick black lines (the division of southern and northern plants in western North America is indicated with dashed lines). Geographic belonging of the samples are indicated below the histograms and geographic areas are separated by black lines.

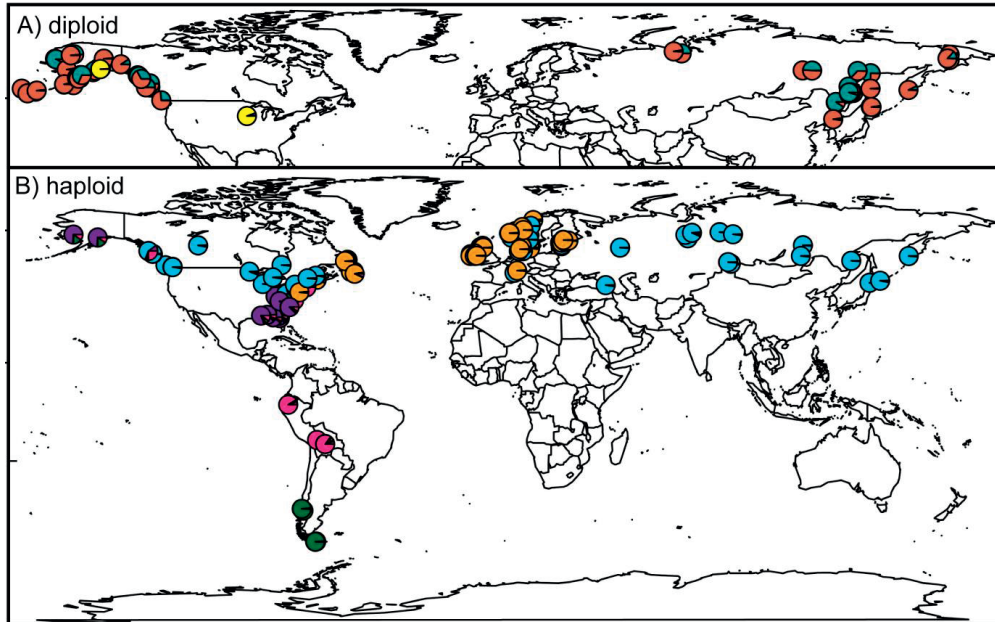


Figure 7: The maps show genetic clusters based on microsatellite data of diploid *S. magellanicum* and *S. alaskense* (A) and haploid *S. magellanicum* (B) inferred by the Structure software. There are likely three genetic groups among the diploid data and five among the haploid data. There is no geographical structuring in the diploid data, while the haploid genetic groups have different distributions.

The barriers found in *Sphagnum* species seems to be located on land, while oceans are seemingly weak barriers to gene flow. The patterns are somewhat opposite from those found in arctic vascular plants. In this group, oceans possess the strongest barriers together with the Ural Mountains in the Northern Hemisphere (Eidesen *et al.*, 2013). Both continents appear to be barriers to gene flow in some *Sphagnum* species, while the same genetic group are found across North America, except eastern and northern Alaska, and Eurasia in other species. Among the species that are structured across Eurasia, there are no abrupt genetic discontinuity around the Ural Mountains. Rather, this mountain range seems to be a somewhat weaker barrier in *Sphagnum* compared to vascular plants. Since bryophyte spores are wind dispersed, it is not unlikely that the barriers observed are caused by wind directions in the Northern Hemisphere (*sensu* Muñoz *et al.*, 2004), rather than physical barriers. There seems to be

frequent storms going from Asia towards Alaska, but avoiding the Pacific Northwest (Mendelsohn *et al.*, 2012). This could form the strong barrier observed in southern Alaska. Similarly, wind crossing the Atlantic Ocean may disperse spores from eastern North America to Europe or the other direction.

Plants of *S. magellanicum* in South America form two distinct genetic groups. However, all plants have identical plastid DNA as North American plants, indicating that establishment in South America happened relatively recently. The widespread moss *Cinclidium stygium* Sw. likely colonised Tierra del Fuego recently from the Northern Hemisphere (Piñeiro *et al.*, 2012). Recent dispersal from north to south has been hypothesised to have happen stepwise along the Andean mountain range or by migratory birds (Popp *et al.*, 2011; Villaverde *et al.*, 2015). Recently, a *Sphagnum* fragment was found in the plumage of a bird migrating between the Northern and Southern Hemispheres (Lewis *et al.*, 2014b), indicating that this could be a dispersal vector for bryophytes across the equator (Lewis *et al.*, 2014a), including *S. magellanicum*.

Genetic variation differs among species and regions. The least variable species is *S. austinii*, with one haplotype dominating Europe and being the only one present in North America. Similarly, all plants of *S. subnitens* along the coast of western North America share the same haplotype (Karlin *et al.*, 2011), but this haplotype was not found elsewhere and the level of genetic variation found in Europa was comparable to other *Sphagnum* species. Thus, *S. austinii* is the most genetically uniform *Sphagnum* studied so far. Also, *S. wulfianum* are genetically depauperate. Both species have narrow habitat niches and available habitats during the last glacial maximum could have been scarce. Hence, they may have been going through severe bottlenecks recently. Current wide distribution ranges are likely due to recent long-distance dispersal events. On the other hand, *S. rubiginosum* also has narrow habitat range, but is more genetically variable. The species is currently found in the Beringian area, and could have survived there, in addition to somewhere else, maintaining higher levels of genetic variation during the last glacial maximum.

Both *S. angustifolium* and *S. magellanicum* (the haploid plants) are continuously and widely distributed, and both species have broad habitat requirements. This could possibly explain the high genetic variation found in these species. However, differences in genetic variation found in vascular plants are sometimes connected to post-glacial history (e.g., Eidesen *et al.*, 2007). Thus, glacial and/or post-glacial history is probably also shaping the genetic patterns

observed. Several genetic groups are observed in most of the *Sphagnum* species, and this may reflect historical events, such as survival in multiple refugia during the last glacial maximum (Beatty & Provan, 2010; Marr *et al.*, 2012). The current distributions of genetic groups are likely shaped by long-distance dispersal, with wind being the main dispersal vector.

Species within the genus *Sphagnum* are relatively young and they probably diversified in the Northern Hemisphere during the cooling of the climate in the Miocene (Shaw *et al.*, 2010). Genetic differences found within the *Sphagnum* species may seem small, but they can nonetheless indicate ongoing or recent speciation in these widespread species. There seems to be little gene flow between Beringian and Atlantic genetic groups, and similarities may be due to incomplete lineage sorting. Thus, the widespread distribution ranges traditionally assumed for many *Sphagnum* species across the Northern Hemisphere may be more restricted than they appear. Instead of circum-boreal distribution, there may rather be two other wide ranges: one mainly covering Asia and Alaska (northern of southern Alaska) and one mainly covering the Atlantic regions, but with extensions into western North America (southern Alaska and southwards) and through Russia into southern Asia.

Conclusion

Although phylogeography of *Sphagnum* species is relatively well studied, genetic structuring was found within widespread species in this thesis. By sampling the full-scale range of widespread species, the results show that there are limitations to dispersal across the Northern Hemisphere in peatmosses. Specifically, there is little gene flow between plants in the Beringian (northern Pacific) and the Atlantic regions. My findings indicate that plants from genetically differentiated groups within species should be examined morphologically to determine whether the taxonomic status of such groups should be changed. The genetic differences detected may be an indication of recent or ongoing speciation. Thus, circum-boreal distribution ranges in many *Sphagnum* species, may be more limited than assumed based on morphological uniformity. Rather, there seem to be two other broad ranges: one Beringian distribution which includes Asia and Alaska (except the southernmost part) and one broad Atlantic, spanning from western North America (from southern Alaska and southward), across the Atlantic region, through Russia into southern Asia.

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Glacial refugia and post-glacial colonization patterns in European bryophytes

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Most species are assumed to have survived south or east of the ice sheet covering northern Europe during the last glacial maximum. Molecular and macrofossil evidence suggests, however, that some species may have survived in ice-free areas in Scandinavia. In plants, inbreeding and vegetative growth are associated with low genetic load and enhanced survival in small, isolated populations. These characteristics are often found in bryophytes, possibly allowing them to survive extreme conditions in isolated refugia and also within ice sheets. Here, we review the Holocene bryophyte history in Europe highlighting main glacial refugia and post-glacial colonization routes. Also, meta-analyses are performed to investigate if distribution ranges and genetic structure are associated with life-history traits. Bryophytes survived the last glaciation in several refugia, but there is no unequivocal evidence of survival within the Scandinavian ice sheet. Northern Europe was colonized from southern, eastern and western Europe, as well as North America. Species with small spores have broader distribution ranges than species with large spores, and high frequency of sporophyte production is associated with limited genetic differentiation between populations.

Bryophytes have a long history in Europe, with fossils dating to the Miocene, about 23 million years ago (Frahm 2004, Hedenäs and Bennike 2008, Lewis et al. 2008), resembling extant species. This suggests that some European species were exposed to multiple glacial cycles during the Quaternary. The extent of the northern European ice sheet fluctuated greatly during the Pleistocene, and the last glacial maximum (LGM, ~20 000 year BP) was particularly severe with the Weichselian ice sheet covering most of Fennoscandia and extending into mainland Europe and the British Isles (Svendsen et al. 2004). The Mediterranean region (Taberlet et al. 1998) together with Asia Minor (Ansell et al. 2011) and central Europe (Provan and Bennett 2008) are recognized as refugia for a range of species during this period, acting as large-scale sources for recolonization of glaciated areas after the LGM.

An unknown fraction of extant species in northern areas may have survived glaciated periods within or at the periphery of the Weichselian ice sheet (in situ survival, Dahl 1998). Even though extreme environmental conditions in glaciated areas make this seem unlikely, species able to survive in small populations may have existed in favour-

able microrefugia within the ice sheet (Holderegger and Thiel-Egenter 2009, Rull 2009). Recent studies support glacial survival of both arctic angiosperms (Westergaard et al. 2011) and conifers (Parducci et al. 2012) in Scandinavia during the LGM. Moreover, based on radiocarbon dating, Kullman (2008) concluded that *Betula* trees grew on Andøya in northern Norway approximately 17 000 year BP. These findings support the in situ survival theory, long considered to be of minor relevance for explaining contemporary diversity in Scandinavia (but see Birks et al. 2012). The in situ glacial survival hypothesis has been disfavoured because of little fossil evidence from areas within the ice sheet (Birks 1994, Paus et al. 2011), and molecular studies have found patterns compatible with post-glacial colonization for many species (Taberlet et al. 1998, Alsos et al. 2007). Molecular studies often depend on probabilities of glacial survival based on observed patterns of genetic structure, with low levels of differentiation between separated populations (measured by F_{ST}) indicating post-glacial colonization. Low divergence between populations within and outside the ice sheet areas does not necessarily imply recent divergence, though, since this could also be

caused by large ancestral sizes or recent gene flow (Nielsen and Beaumont 2009). Alternatively, high F_{ST} could instead of long-time survival result from little genetic variation within versus among populations (Stenøien et al. 2011a, Kyrkjeeide et al. 2012).

Populations of limited sizes often contain reduced adaptive variability and accumulated detrimental alleles, and organisms will have different capacities of surviving such conditions (Bhagwat and Willis 2008). Specifically, species with low genetic load and vegetative growth may have a high capacity to survive in small, stable microrefugia over time (Mosblech et al. 2011). Species able to survive in scattered microrefugia might also have been able to expand rapidly into glaciated areas when the ice retreated. Indeed, species surviving the LGM in central Europe are typically asexuals and generalists with small, wind-dispersed seeds, while species restricted to climatically more favourable southern refugia usually reproduce sexually, are often specialists, and produce large seeds (Bhagwat and Willis 2008).

If vascular plants survived in northern areas during the LGM (Westergaard et al. 2011, Parducci et al. 2012, Vorren et al. 2013), other plants should also have been able to survive the extreme environments in the north (cf. Stenøien et al. 2011a, b, Kyrkjeeide et al. 2012, Vorren et al. 2013). Bryophytes exhibit traits that might make them better suited than vascular plants for survival in small, northern refugia, including their poikilohydric nature, enabling survival through unfavourable periods (Proctor et al. 2007; see also Segreto et al. 2010). Furthermore, asexual reproduction is widespread in bryophytes (Frey and Kürschner 2011) and haploidy might enable efficient purging of genetic load, even though inbreeding depression is also expressed during the diploid sporophyte stage (Taylor et al. 2007). Bryophytes have combined or separated sexes (monoicy and dioicy, respectively), and fertilization is limited by dispersal as spermatozooids must move through water. This may lead to low rates of sexual reproduction in dioicous species and possibly high levels of inbreeding in monoicous species (McDaniel and Perroud 2012). Inbreeding depression is expected to be low in plants where selfing is the dominant mating system (Lande and Schemske 1985), as demonstrated in a study using a moss model system (Taylor et al. 2007). Also, there are examples of bryophyte populations primarily established and maintained through vegetative diaspores (Pfeiffer et al. 2006), implying that bryophyte populations may be stable and expanding despite low levels of sexual reproduction.

The spatial distribution of wind-dispersed organisms depends mainly on the size of propagules, and it has been suggested that microbes being $\sim 20 \mu\text{m}$ or less should efficiently spread worldwide in a short time (Wilkinson et al. 2012). Bryophyte spore sizes typically range from 7 to 100 μm (Frahm 2008) and they may easily be dispersed by wind (van Zanten and Pocs 1982, Muñoz et al. 2004).

Sundberg (2012) trapped peat moss spores across a large spatial scale and concluded that a major fraction of spores are dispersed regionally in boreal areas, but as much as 1% of the spore rain may have intercontinental origin. Wide distribution ranges in bryophytes suggest that they in general are exceptional dispersers (Szövényi et al. 2008, Stenøien et al. 2011a). For instance, about 70% of moss species occurring in Europe are also present in North America (Frahm and Vitt 1993), while less than 7% of European vascular plant species are shared with North America (Qian 1999). There are few bryophyte endemics on various geographical levels, even on relatively small archipelagos, exemplified by only 1.5% of bryophyte species on the Canary Islands being endemic compared to 40% of angiosperms (Vanderpoorten et al. 2010).

Here we review phylogeographical studies of bryophytes based on molecular marker information, and our aim is twofold. First, we want to review the bryophyte history in Europe after the last ice age and summarize insights concerning likely glacial refugia for bryophytes, identify major post-glacial colonization routes, and discuss the probability of glacial survival within the ice sheet. Second, we will, based on meta-analyses of published results, test if life history traits (i.e. mating systems, spore production and/or spore sizes), are associated with different geographical regions, range size and genetic structure of European bryophytes.

Material and meta-analyses

Altogether, 26 phylogeographical studies of 31 bryophytes published over the last 13 years were summarized to review the colonization history of bryophytes in Europe after the last glaciation. All papers and species mentioned in the text and included in meta-analyses are listed in Table 1.

We tested if life-history traits (frequency of sporophyte production and spore size) are associated with presence in different regions of Europe, range size (i.e. number of European regions a species is found in) and genetic structuring. The number of bryophyte biogeographical regions of Europe varies between authors, but we follow Mateo et al. (2013), and recognise their Alpine, Atlantic and Boreal elements, while merging the Mediterranean–Macaronesian and Continental elements. Altogether we distinguish four regions; the arctic, western, boreal and southern regions, and these regions were used to describe the range sizes of the reviewed species (Table 1). Spore size was estimated as mean spore diameter taken from the minimum and maximum spore diameter (references in Table 1). Two categories of frequency of sporophyte production were included in the analysis: rare (rare to occasional) and frequent (frequent to abundant, Table 1). For species whose reproduction varies from rare to frequent between geographical areas, sporophyte production was set to be frequent. Mating system was not included in the analysis since the majority

Table 1. List of species included in this review. The table shows sexuality (Sex), frequency of sporophyte production (SP), minimum and maximum spore diameter in μm (SD), floristic region(s) (Region), global distribution, genetic differentiation between studied populations measured by F_{ST} or related measures, genetic markers used in various studies (Marker), and sampling scale in the different studies (Sampling).

| Species | Sex ²⁶ | SP | SD ^{26,42} | Region | Global distribution ⁴⁵ | F_{ST}/C_{ST} | Marker | Sampling |
|---|-------------------|---|---------------------|--------|-----------------------------------|-----------------|-----------------|----------|
| Liverwort | | | | | | | | |
| <i>Radula lindenbergiana</i> ¹ | D | F ²⁷ R ²⁸ | 25–38 ²⁸ | SWB | Circ,Af,Mac | 0.2 | pDNA | Regional |
| Moss | | | | | | | | |
| <i>Anitrichia curtispindula</i> ² | D | R ²⁷ R ²⁹ | 32–40 | SWBA | Eu, Af, As, ENAm | - | ITS, pDNA | Global |
| <i>Cinclidium arcticum</i> ³ | D | R ³⁰ | 25–70 ³⁰ | A | Circ | - | pDNA | Global |
| <i>Cinclidium latifolium</i> ³ | D | R ^{30,31} | 20–45 ³⁰ | A | Circ | - | pDNA | Global |
| <i>Cinclidium stygium</i> ³ | M | R ²⁷ F ³⁰ | 25–70 ³⁰ | BA | Circ,SAm | - | pDNA | Global |
| <i>Cinclidium subrotundum</i> ³ | M | F ^{30,31} | 25–70 ³⁰ | BA | Circ | - | pDNA | Global |
| <i>Drepanocladus aduncus</i> ⁴ | D | R ^{27,32,33} | 11–18 | SWBA | Circ,Af,C-SAm,O | - | ITS, pDNA | Global |
| <i>Grimmia montana</i> ⁵ | D | R ^{27,34,35} | 8–15 | SWBA | Circ,Mac,CAm,Saf | 0.32 | pDNA | Global |
| <i>Hamatocaulis vernicosus</i> ⁶ | D | R ^{27,32} | 10–22 | BA | Circ,CAm | - | ITS, pDNA | Regional |
| <i>Homalothecium sericeum</i> ^{7,8} | D | O ²⁷ R ¹⁶ | 11–23 | SWBA | Eu,WAs,NAf,Mac,EAm | 0.181 | ITS, pDNA | Regional |
| <i>Kindbergia praelonga</i> ⁹ | D | F ²⁷ N ¹⁶ | 11–14 | SWB | Eu,Mac,NAm,Saf,O | - | ITS, pDNA | Global |
| <i>Leucodon sciuroides</i> ¹⁰ | D | R ^{27,37,29} | 18–55 | SWB | Eu,As,NAf,Mac | 0.437 | iso | Regional |
| <i>Platyhypnidium riparioides</i> ¹¹ | M | F ²⁷ R ¹⁶ | 14–22 | SWB | Circ | 0.177 | msat | Regional |
| <i>Pleurochaete squarrosa</i> ^{12,13} | D | N ¹⁰ R ¹⁵ | 10–14 | S | Cosm | 0.443, 0.892 | ITS, pDNA, allo | Regional |
| <i>Polytrichastrum formosum</i> ¹⁴ | D | F ^{27,35} N ¹⁸ | 12–16 | SWB | Cosm,Ex,SAm,O | 0.395, 0.047 | allo, msat | Regional |
| <i>Polytrichum commune</i> ¹⁴ | D | F ^{27,35,38} | 8–12 | SWBA | Holarct,SEAs | 0.070, 0.047 | allo, msat | Regional |
| <i>Polytrichum juniperinum</i> ¹⁴ | D | A ²⁷ F ^{35,38} | 8–12 | SWBA | Cosm | 0.341, 0.167 | allo, msat | Regional |
| <i>Polytrichum piliferum</i> ¹⁴ | D | A ²⁷ O ³⁵ F ³⁸ | 9–14 | SWBA | Cosm | 0.087 | allo | Regional |
| <i>Polytrichum uliginosum</i> ¹⁴ | D | - | 8–12 | SWB | - | 0.091 | allo | Regional |
| <i>Sanonia uncinata</i> ^{15,16} | M | F ^{27,33,39} | 10–18 | SWBA | Cosm | - | ITS, pDNA | Global |
| <i>Sarmentypnum exannulatum</i> ¹⁷ | D | F ³⁰ R ^{27,33} | 12–24 | SWBA | Cosm | - | ITS, pDNA | Global |
| <i>Scopidium cossonii</i> ¹⁸ | D | F ³⁰ R ²⁷ N ¹³ | 12–21 | SWBA | Circ,SAm,O | - | ITS, pDNA | Global |
| <i>Scopidium scorpioides</i> ¹⁸ | D | F ³⁰ R ^{27,33} | 12–22 | SWBA | Circ,C-SAm | - | ITS, pDNA | Global |
| <i>Sphagnum affine</i> ¹⁹ | D | R ^{27,35} | 24–28 ⁴⁴ | WB | Eu,ENAm | 0.512 | iso | Regional |
| <i>Sphagnum angermanicum</i> ²⁰ | D | R ⁴⁰ | 26–34 ⁴⁰ | W | Eu,WNAm | 0.15 | msat | Global |
| <i>Sphagnum capillifolium</i> ²¹ | D/M | F ²⁷ R ¹⁵ N ⁴¹ | 24–28 ⁴⁴ | WBA | Circ,Af,SAm | 0.252 | iso | Local |

Table 1. Continued.

| Species | Sex ²⁶ | SP | SD ^{26,42} | Region | Global distribution ⁴⁵ | F_{ST}/G_{ST} | Marker | Sampling |
|--|-------------------|---|---------------------|--------|-----------------------------------|-----------------|------------|----------|
| <i>Sphagnum fimbriatum</i> ^{22,23} | M | A ²⁷ R ³⁵ E ⁴¹ | 24–28 ⁴⁴ | WBA | Circ,SAI,SAm,NZ,An | - | ITS, nDNA | Regional |
| <i>Sphagnum squarrosum</i> ^{22,23} | M | A ²⁷ O ^{35,41} | 22–30 ⁴⁴ | WBA | Circ,Mac,CAm,O | - | ITS, nDNA | Regional |
| <i>Sphagnum troendelagicum</i> ²⁴ | - | N | - | W | Eu | 0.12, 0.16 | msat, pDNA | Global |
| <i>Sphagnum wulfianum</i> ²⁵ | D/M | R ²⁶ O ⁴² | 22–24 ⁴⁴ | B | Circ | 0.72 | msat | Regional |
| <i>Tortula muralis</i> ²⁶ | M | A ^{27,34,35} | 7–12 | SWB | Cosm | 0.185 | pDNA | Global |

Abbreviations: Sex: D-dioicous; M-monoicous; SP: A-abundant; F-frequent; N-not observed; O-occasional; R-rare; Region: A-arctic; B-boreal; S-Mediterranean-Macaronesian/southern/central; W-atlantic/western; Global distribution: AI-Africa; Am-America; An-Antarctica; As-Asia; E-east; Eu-Europe; Ex-excluding; C-central; Circ-northern circumpolar or circumboreal; Cosm-cosmopolitan; Disj-disjunct; Holarct-holarctic; Mac-Macaronesia; N-north; O-Oceania; S-south; W-west; Marker: allo-allozymes; iso-isozymes; ITS-internal transcribed spacer; msat-microsatellites; pDNA-plastid markers
Literature: ¹Laenen et al. 2011; ²Hedenäs 2008a; ³Piñero et al. 2012; ⁴Hedenäs 2008a; ⁵Vanderpoorten et al. 2008; ⁶Hedenäs and Eldenäs 2007; ⁷Hedderson and Nowell 2006; ⁸Desamóré et al. 2012; ⁹Hedenäs 2010a; ¹⁰Cronberg 2000; ¹¹Hutsemekers et al. 2011; ^{12,13}Grundmann et al. 2007, 2008; ¹⁴van der Velde and Bijlsma 2003; ^{15,16}Hedenäs 2010b, 2012; ^{17,18}Hedenäs 2009a, 2009b; ¹⁹Thinggaard 2001; ²⁰Stenøien et al. 2011a; ²¹Natcheva and Cronberg 2003; ^{22,23}Szövényi et al. 2006, 2007; ²⁴Stenøien et al. 2011b; ²⁵Kyrkjeteide et al. 2012; ²⁶Werner and Guerra 2003; ²⁷Hill et al. 2007; ²⁸Damsholt 2002; ²⁹Johannsson 1990a; ³⁰Hallingbäck et al. 2008; ³¹Johannsson 1995; ³²Nyholm 1974a; ³³Johannsson 1998; ³⁴Hallingbäck et al. 2006; ³⁵Pedrotti 2001; ³⁶Johannsson 1990b; ³⁷Nyholm 1974b; ³⁸Johannsson 1990b; ³⁹Hedenäs pers. comm.; ⁴⁰McQueen and Andrus 2007; ⁴¹Johannsson 1989; ⁴²Field experience and herbarium collections from Europe; ⁴³Nyholm 1958; ⁴⁴Sundberg et al. 2006; ⁴⁵Dierssen 2001

of species in this dataset are dioicous. Genetic divergence among populations measured by the fixation indexes F_{ST} (Weir and Cockerham 1984) and G_{ST} (Nei 1973), hereafter collectively called F_{ST} , was used to describe genetic structure. Whenever F_{ST} was measured twice (e.g. for different geographical scales or molecular markers), the mean value was used. In all analyses, the F_{ST} values were log transformed to obtain normal distribution of the data. χ^2 -tests and one-way ANOVA were performed to test if there were any associations between range sizes and life-history traits, and F_{ST} respectively (Supplementary material Appendix 1). Furthermore, an analysis of covariance (ANCOVA) was used to test the relationship between range size and spore sizes and frequency of sporophyte production. Finally, we tested whether F_{ST} is associated with spore size and frequency of sporophyte production using linear regression and Welch t-test, respectively. Analyses were also performed at the genus level due to similar life-history traits within genera (see Supplementary material Appendix 1 for results of analyses of phylogenetic constraints). Analyses were performed in the R environment.

Results

Refugia and postglacial colonization routes in Europe

Here we present a short overview of the southern, western, boreal and arctic floristic elements of Europe, give examples of species likely surviving the LGM in different regions, and also present likely post-glacial colonization routes (Fig. 1). Life-history traits and range sizes for all species considered are listed in Table 1. Table 2 gives an overview of different historical scenarios and how genetic patterns may indicate different scenarios.

The southern element

The Mediterranean area is characterized by warm, dry summers and mild, wet winters, leading to a high fraction of the bryophyte flora being winter ephemerals (Frahm 2010), and the majority of species being acrocarpous (Størmø 1983). In the mountain areas, the species composition largely overlaps with that found in more central parts of Europe (Frahm 2010). The Mediterranean is not a worldwide hot-spot of species diversity for bryophytes as it is for vascular plants and vertebrates, probably due to the arid climate (Goffinet and Shaw 2009).

Southern populations of *Pleurochaete squarrosa* (Brid.) Lindb. are more variable than northern populations (Grundmann et al. 2007, 2008), a pattern resembling that of several southern European vascular plants (Taberlet et al. 1998). *Pleurochaete squarrosa* seems to have survived in the Mediterranean Basin and later colonized northwards

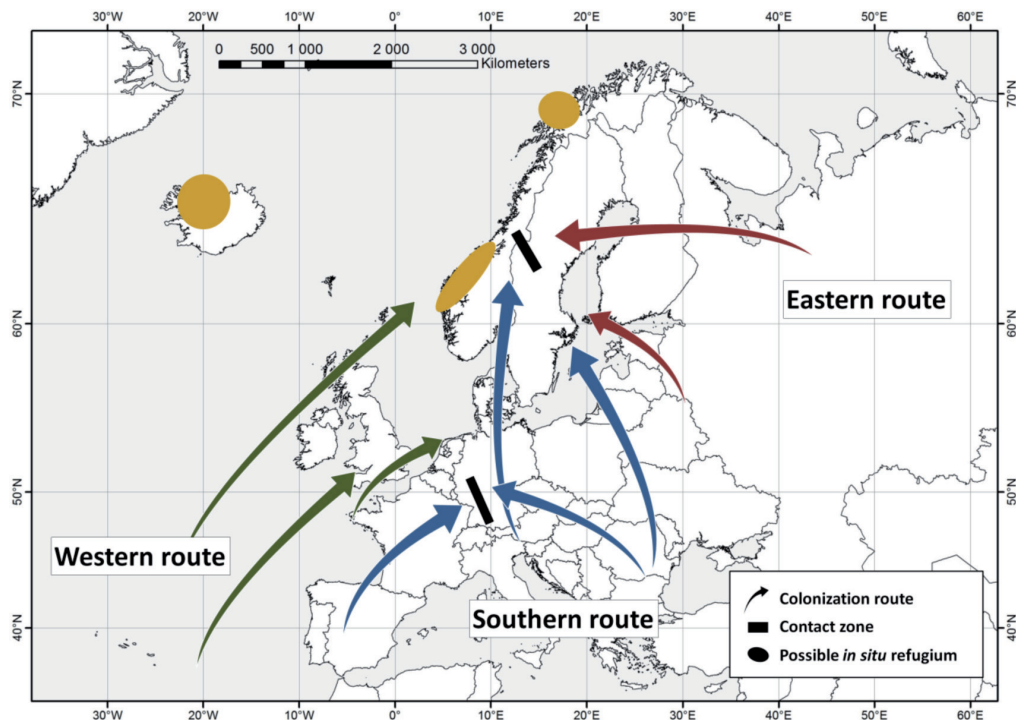


Figure 1. Hypothesized colonization routes, contact zones, and possible in situ glacial refugia of bryophyte species in Europe during and after the last glacial maximum. Three main colonization routes, western, southern, and eastern, are indicated by green, blue and red arrows, respectively. Solid yellow fields indicate potential in situ refugia during the LGM.

from both the Iberian Peninsula and the Balkans, hence a contact zone is recognized in central Europe (Grundmann et al. 2007, 2008). Also, *Leucodon sciuroides* (Hedw.) Schwaegr. (Cronberg 2000, Stech et al. 2011) has higher genetic diversity in southern versus northern populations.

Homalothecium sericeum (Hedw.) Schimp. also shows high genetic variation in the Mediterranean region, but high levels of unique haplotypes on the British Isles and adjacent mainland, indicate that this species may also have had a western refugium during the LGM (Hedderson and Nowell 2006). The authors estimate divergence between British Isles and mainland populations to have occurred 0.45 Myr ago (i.e. long before the LGM). Désamoré et al. (2012) found northern refugia the most likely origin of the northern European colonization. Haplotype groups restricted to southwestern genetic clusters are also found in *Kindbergia praelonga* (Hedw.) Ochyra, suggesting southern survival, whereas the most widespread haplotype group probably survived in other, larger refugia and colonized all of Europe after the LGM (Hedenäs 2010a). *Antitrichia curtipendula* (Hedw.) Brid. has one widespread haplotype group throughout the distribution range, making refugia hard to localize, while another haplotype group is more restricted to western Europe, indicating that it

colonized fewer available areas after the LGM (Hedenäs 2008a).

Hutsemékers et al. (2011) compared genetic variation of island and mainland populations of the southern temperate moss *Platyhypnidium riparioides* (Hedw.) Dixon using Macaronesian, southwestern European, and north African populations to test if islands can act as source rather than sink to mainland. The authors found no indication of bottlenecks in the island population and argued that these archipelagos might have been important in post-glacial colonization of Europe. Also, no monophyletic haplotype groups were observed within Macaronesia in the temperate *Grimmia montana* Bruch & Schimp., most likely due to transatlantic gene flow (Vanderpoorten et al. 2008). The authors found that the root of their inferred haplotype network was close to haplotypes residing in south-western Europe and the Canary Islands, and, hypothesised that the species could have survived the LGM there.

The western element

The western element is found along the Atlantic coast, containing so-called atlantic vascular plants and oceanic bryophytes. The distribution of atlantic vascular plants

Table 2. Overview of possible historical scenarios, genetic signatures that may be caused under these scenarios and alternative explanations for the patterns observed. Each pattern is exemplified by a bryophyte species included in the present review.

| Historical scenario | Genetic signature | Alternative explanation |
|-------------------------|---|--|
| Refugial area | Relatively high genetic variation in an area compared to other studied areas (Hewitt 2004) e.g. <i>Pleurochaete squarrosa</i> (Grundmann et al. 2007) | Rapid population growth maintaining polymorphisms in an area despite recent colonization (Waxman 2012) and/or the area being a post-glacial contact zone (Provan and Bennett 2008) |
| | High level of unique alleles and haplotypes (Ehrich et al. 2008) e.g. <i>Homalothecium sericeum</i> (Hedderson and Nowell 2006) | Admixture in contact zone leading to unique haplotypes (Hassel et al. 2005) |
| | Root of gene trees or haplotype network close to haplotypes found in an area e.g. <i>Grimmia montana</i> (Vanderpoorten et al. 2008) | |
| Several refugial areas | Long time since divergence between genetic lineages found in two or more areas e.g. <i>Homalothecium sericeum</i> (Hedderson and Nowell 2006) | Estimated mutation rate used to date divergence times may be too high, thereby giving the false impression of ancient divergence (discussed in Stenøien et al. 2011a) |
| Colonized area | Relatively low genetic variation in a given area compared to one or more other studied areas (Hewitt 2004) e.g. <i>Leucodon sciurioides</i> (Cronberg 2000, Stech et al. 2011) | Genetic swamping, i.e. colonizing individuals have removed signals of refugial survivors, either due to selective advantages of immigrants or by genetic drift |
| Contact zone | Relatively high genetic variation due to genetically differentiated lineages (Provan and Bennett 2008) e.g. <i>Pleurochaete squarrosa</i> (Grundmann et al. 2008) | Refugial area, species originating in this area |
| Dispersal | | |
| Effective gene flow | No genetic structure e.g. <i>Polytrichum commune</i> (van der Velde and Bijlsma 2003) | Low mutation rate and/or large effective population size causing incomplete lineage sorting (Stenøien and Sæstad 1999) |
| Long distance dispersal | Widespread haplotypes e.g. <i>Radula lindenbergiana</i> (Laenen et al. 2011) | Low mutation rate and/or large effective population size causing incomplete lineage sorting (Stenøien and Sæstad 1999) |

correlates mostly with winter temperatures, while oceanic bryophytes are mainly constrained by amount and frequency of rainfall (Dahl 1998). Consequently, the highest bryophyte species richness of the western element occur in areas with frequent precipitation, i.e. the British Isles and southwestern Scandinavia (Dahl 1998), areas mostly covered by ice during the LGM. There are many species confined to the northwestern Atlantic coast of Europe and there are even a few endemic species in this area, such as the liverwort *Lepidozia pearsonii* Spruce and the mosses *Anoetangium warburgii* Crundw. & M.O. Hill and *Weisia perssonii* Kindb. (Dahl 1998). Some of the oceanic species found in Europe have disjunct occurrences along the

western coast of North America and the Himalayas, but lack specialized vegetative diaspores and do not reproduce sexually (Damsholt 2002), making recent long distance dispersal less likely. The oceanic species may have escaped harsh climate during the last glaciation by surviving in ice-free areas between the British Isles and the mainland now situated below current sea level (Frahm 2012). This scenario has also been suggested as an explanation of the presence of unique AFLP markers in the British populations of the temperate herb *Meconopsis cambrica* Vig (Valtueña et al. 2012).

The endemic allopolyploid *Sphagnum troendelagicum* Flatberg known from coastal central Norway, has a

probable origin before the LGM (Stenøien et al. 2011b). This could indicate glacial survival in Scandinavia, but it could also mean that the species originated outside the ice sheet and colonized Norway after the ice retreated (Stenøien et al. 2011b). A similar scenario has been suggested for another amphi-Atlantic peat moss, *Sphagnum angermanicum* Melin, with European populations only found in Norway, Sweden and Iceland. Two genetic clusters have been recognized in this species in European and North American populations, both occurring on the two continents (Stenøien et al. 2011a). One lineage may have colonized Europe from North America before the LGM (~40 000 year BP) and the other after the LGM, and *S. angermanicum* may have survived the LGM in a southern cryptic refugium where it later went extinct after colonizing Scandinavia (Stenøien et al. 2011a). North American origin could also be suggested for *S. affine* Renaud & Cardot, as higher genetic variation is found along the eastern coast of North America than in Scandinavia (Thingsgaard 2001).

The boreal element

The boreal region is dominated by coniferous forest and bryophytes composition broadly overlaps with that found in central Europe, though the latter is more diverse due to warmer climate (Størmer 1983). There are few endemic boreal bryophytes in Europe (e.g. the mosses *Cynodontium suecicum* (Arnell & C.E.O. Jensen) I. Hagen and *Schistidium bryhni* I. Hagen (Dahl 1998)), and many species are circumboreal (Frahm 2012). Most of Russia, except the westernmost parts and north-western coast, remained ice-free during the LGM (Svendsen et al. 2004). Molecular studies support the hypothesis of glacial refugia east of the ice for several vascular plants (Ehrich et al. 2008, Tollefsrud et al. 2008), implying that the area also was suitable for a range of bryophytes during the LGM.

As an example, the boreal peat moss *Sphagnum wulfianum* Girg. is hypothesised to have colonized Scandinavia from the southeast and perhaps also from eastern refugia, even though some uncertainty exists due to low genetic variation and hence low confidence as to where glacial refugia could have been situated (Kyrkjæide et al. 2012). Small populations of *Sphagnum capillifolium* (Ehrh.) Hedw. seem to have survived the last glaciation in the Balkan mountains, but the distinct haplotypes found here suggest that this area was not the source for postglacial colonization of northern Europe (Natcheva and Cronberg 2003). Also, one of the European cryptic species of *Hamatocaulis vernicosus* (Mitt.) Hedenäs (Hedenäs and Eldenäs 2007) may have survived in southern refugia during the LGM. Another cryptic species has a more northern distribution and one main haplotype, spread throughout the distribution range.

Several refugia have been hypothesized for *Sphagnum squarrosum* Crome, and three genetic clusters are found

in this species (Szövényi et al. 2006, 2007). However, the clusters are only weakly structured in Europe, possibly due to extensive gene flow. *Sphagnum fimbriatum* Wilson on the other hand, is found to be highly structured in one 'Atlantic' and one 'non-Atlantic' clade (Szövényi et al. 2006, 2007). The Atlantic clade likely survived the LGM along the western coast and is currently found from southern England to northern Spain, while the non-Atlantic clade is widespread in Europe and probably recolonized the continent rather rapidly after the LGM. This discrepancy between lineage distributions could be explained by the widespread clade being able to fill niches becoming available after the ice retreated, while the Atlantic clade possibly was unable to do the same, and hence became restricted to the southwestern coast of Europe (Szövényi et al. 2007).

Southwestern refugia have been suggested for bryophytes with wide distribution ranges, i.e. not restricted to the western element. van der Velde and Bijlsma (2003) studied five *Polytrichum* species in Europe and found low levels of genetic structure in four of them, suggesting that gene flow is high enough to prevent genetic differentiation between European populations. In contrast, *P. juniperinum* Hedw. may have had a unique evolutionary history, with recolonization of Europe occurring from two refugia, one being western, possibly in southern parts of the British Isles. Western genetic lineages in both *P. juniperinum* and *S. fimbriatum* are geographically restricted, indicating that recolonization of the European mainland from western refugia was limited. On the other hand, colonization from western refugia does not seem to be limited in the liverwort *Radula lindenbergiana* Gottsche ex Hartm., which is found to be more variable in western versus eastern Europe, with most diversity found in Macaronesia (Laenen et al. 2011).

Some boreal bryophytes maintain their highest diversity in northern areas. Hedenäs (2009a) found higher haplotype variation in Scandinavia versus southern and central Europe in *Sarmentypnum exannulatum* (Shimp.) Hedenäs. The lineages found in southern and central Europe may have survived the LGM there and later colonized northern Europe. However, other lineages found in Scandinavia were hypothesized to have survived in northern and/or immigrated from northeastern refugia (Hedenäs 2009a), a scenario also suggested for *Scorpidium cossonii* (Schimp.) Hedenäs and *S. scorpioides* (Hedw.) Limpr. (Hedenäs 2009b). The cosmopolitan *Sanionia uncinata* (Hedw.) Loeske also has higher genetic variation in northern versus southern European populations, indicating colonization of northern Europe from several refugia, including northeastern ones (Hedenäs 2010b). Alternatively, the species may have survived in ice-free areas in Scandinavia. Furthermore, a global study of *S. uncinata* showed that haplotype diversity was highest in eastern Eurasia, indicating more severe bottlenecks in western compared to eastern European populations during glacial periods (Hedenäs 2012). One haplotype group, found in

Africa, western Europe, and southeast Greenland, probably colonized northern Europe from southern or western rather than northeastern glacial refugia.

The arctic element

The European arctic bryophyte flora belongs to a wider circumarctic floristic element spanning the polar part of the northern hemisphere and consists of species restricted to the arctic (e.g. *Sphagnum arcticum* Flatberg & Frisvoll), but also occurring in some alpine areas further south (Steere 1978, e.g. *Rhizomnium andreusianum* (Steere) T.J. Kop.). One such European endemic is *Orthothecium lapponicum* (Schimp.) C. Hartm. (Dahl 1998), and this species may be an ancient relict that survived in large ice-free areas, potentially Beringia, since the Tertiary (Steere 1978). Northeast Russia and northwest America remained ice-free during the Pleistocene, and fossil and molecular data show that this area served as a large refugium for arctic vascular plant species (Abbott and Brochmann 2003). For northern species, long distance dispersal may be common, and colonization of the arctic may primarily be limited by establishment opportunities (Alsos et al. 2007). Few phylogeographic studies of arctic areas have included bryophytes, but the four species in the arctic and boreal moss genus *Cinclidium* Sw. are found to have identical haplotypes throughout large areas, suggesting recent dispersal as the main mechanism shaping the circumpolar distribution in this genus (Piñeiro et al. 2012). It is presently unknown where glacial refugia for these species may have been located. Good dispersal ability is also suggested for *Scorpidium cossonii* occurring in the arctic (Hedenäs 2009b).

In situ glacial survival

Nunataks existing in glaciated areas of Alaska and Greenland today hold several species, including lichens, bryophytes, vascular plants, and insects (Heusser 1954, Gjærevoll and Ryvarden 1977). Nunataks or other ice-free refugia probably also existed along the coast of Norway and the island Andøya, which were partly ice-free during the LGM (Mangerud et al. 2011, Vorren et al. 2013).

Although studies of bryophytes have found unique genetic lineages in Scandinavia for some species (e.g. *Radula lindenbergiana*, *Sanionia uncinata*, *Sphagnum angermanicum* and *S. wulfianum*) no studies have unequivocally concluded that in situ glacial survival has taken place (Laenen et al. 2011, Hedenäs 2012, Kyrkjæide et al. 2012), even though it seems likely (Stenøien et al. 2011a, b). In the study of *Sanionia uncinata*, global sampling was applied and one of the haplotype groups recognized occur only in Scandinavia and Svalbard (Hedenäs 2012). The haplotype group was suggested to have survived in a cryptic northern glacial refugium south of the ice sheet, but these results

do not preclude that *S. uncinata* could have survived on a nunatak somewhere within the ice sheet.

Meta-analyses

There is no significant association between different European regions and life-history traits or F_{ST} , respectively (see Supplementary material Appendix 1 for results). The interaction between spore size and sporophyte production is non-significant, hence, likelihood ratio tests were used to find the best model explaining range size (for details regarding model test, see results in Supplementary material Appendix 1). The most parsimonious model only includes spore size as an explanatory variable, and linear regression was used to test the relationship between range size and spore size. There is a significant effect of spore size on range size (DF = 27, MS = 0.99, $F = 9.05$, $p = 0.006$, Fig. 2): species with small spores appear in more regions than species with larger spores. On the other hand, spore size is not significantly associated with F_{ST} between populations (DF = 13, MS = 0.46, $F = 1.72$, $p = 0.21$). F_{ST} is found to be significantly higher in species that rarely produce sporophytes (mean = 0.36) compared to species with frequent spore production (mean = 0.16, $t = -2.36$, DF = 7.43, $p = 0.048$, Fig. 3, the means are given using untransformed F_{ST}). The results were not significant at the genus level (results in Supplementary Material Appendix 1), but this may be due to very low sample sizes.

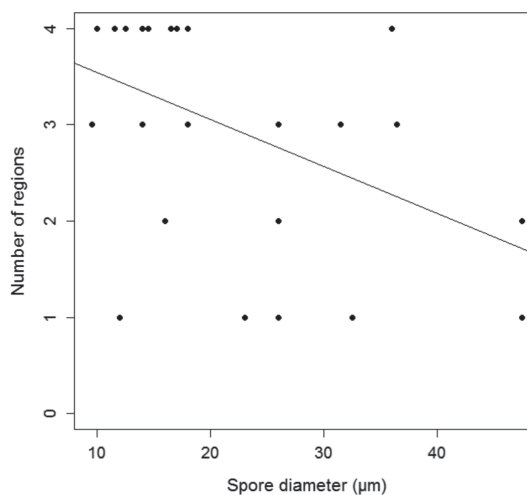


Figure 2. Relationship between the spore size of a bryophyte species and the number of European regions in which it occurs. Species with small spores occur in more regions than species with large spores ($R^2 = 0.25$, $F_{1,27} = 9.05$, $p = 0.006$).

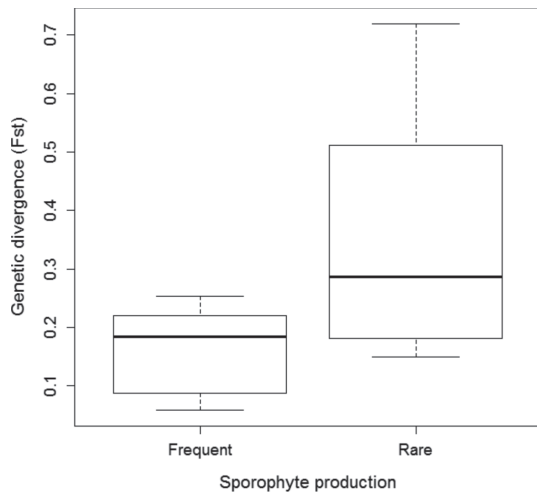


Figure 3. Relationship between F_{ST} -values between populations of bryophytes and the frequency of sporophyte production (rare and frequent) in 14 bryophyte species. Bryophytes reproducing frequently (mean = 0.16) seem to be less genetically differentiated than bryophytes reproducing rarely (mean = 0.38, $t = -2.49$, $DF = 7.73$, $p = 0.04$).

Discussion

There seems to be different responses among different bryophyte species to climate change after the LGM, with several refugia and several post-glacial colonization routes. For many bryophyte species, more than one glacial refugial area is suggested, indicating that a species could have survived virtually anywhere. For example, *Drepanocladus aduncus* (Hedw.) Warnst. had potential refugia along the Atlantic coast, in the Alps, southeastern Europe, east of the ice sheet, and Scandinavia (Hedenäs 2008b). Nevertheless, some general trends are evident, and three main colonization routes are recognized (Fig. 1). First, a southern route (blue arrows in Fig. 1) representing bryophyte species like *Pleurochaete squarrosa* (Grundmann et al. 2007, 2008) and *Leucodon sciuroides* (Cronberg 2000), that likely survived the LGM in southern Europe (Iberian peninsula, Italy and the Balkans). Second, high levels of genetic variation and unique genetic lineages are found along the western coast of Europe for some species, supporting a western route (green arrows in Fig. 1) with refugia in Macaronesia (e.g. *Radula lindenberghiana* (Laenen et al. 2011) and *Platyhypnidium riparioides* (Hutsemekers et al. 2011)), southwestern European mainland (e.g. *Grimmia montana* (Vanderpoorten et al. 2008)), south in the British Isles (e.g. *Polytrichum juniperinum* (van der Velde and Bijlsma 2003)), and also North America (e.g. *Sphagnum angermanicum* (Stenøien et al. 2011a)). Third, the large non-glaciated area east of the Scandinavian ice sheet seems to have served as a refugium resulting in an eastern

route (red arrow in Fig. 1). *Sanionia uncinata* (Hedenäs 2012), *Sarmentypnum exannulatum* (Hedenäs 2009a), and *Sphagnum wulfianum* (Kyrkjeeide et al. 2012) likely recolonized northern Europe along such an eastern route. The two former species also recolonized along the southern route, making Scandinavia a contact zone for some species.

In addition to the three routes recognized, there may possibly be a 'northern route' from refugia located within the ice sheet (yellow dots in Fig. 1). The few signs of in situ glacial bryophyte survivors could imply that this has occurred only rarely, that our tools for inferring glacial survival are too imprecise, or, as an extension, it could also be that ancient genetic variants are regularly swamped by post-glacial colonizers. Genetic swamping implies removal of genetic signals of glacial survival (e.g. the presence of old alleles and genetic differentiation from other populations), and this phenomenon could be particularly pronounced in organisms with high dispersal capacity. Due to the small spore sizes and potentially high dispersal abilities of many bryophytes, one may expect genetic swamping to be a potential problem in studies aimed at detecting glacial refugia. It is also worth keeping in mind that mutation models profoundly affect historical time estimates, and estimated divergence time between *Sphagnum angermanicum* populations would be more recent, perhaps more recent than the LGM, if actual mutation rates are higher than the approximations used in the calculation of divergence time (Stenøien et al. 2011a). The most likely glacial refugia of *S. angermanicum* would in that case be in North America, not southern Europe or in situ. Mutation rate would also affect estimated species age (e.g. *Sphagnum troendelagicum*, Stenøien et al. 2011b), and speciation after the LGM could explain endemics in previously glaciated areas. To our knowledge, marker mutation rates are quite low in many bryophytes (cf. Stenøien 2008), but it is pivotal for future phylogeographic studies to obtain more precise measures of mutation rates of the markers employed. More studies are needed to assess the importance of northern refugial populations, including studies of arctic species occurring in harsh environments and species known as macrofossils from ice-free areas in Scandinavia (Vorren et al. 2013).

Care must be taken when inferring refugia, plausible range expansions and other factors from genetic data (Table 2). Range expansion typically leads to a decline in heterozygosity with increasing distance from the ancestral populations, as well as increased frequency of specific alleles through genetic surfing (Slatkin and Excoffier 2012). High levels of genetic variability will often provide information for hypothesizing where refugial areas have been located (Hewitt 2004), but this association between age and levels of variability will not always hold. For instance, rapid population growth may cause increased probability of maintaining genetic polymorphisms (Waxman 2012), and differences in population size fluctuations could ex-

plain at least part of the observed differences in genetic variability levels among populations. Also, if an area has acted as a contact zone, with high genetic variation caused by immigration of multiple lineages during colonization, then levels of variation may be misleading for pinpointing populations of origin (Hassel et al. 2005, Provan and Bennett 2008). On the other hand, refugial populations may have a higher level of unique haplotypes than recolonized regions (Ehrich et al. 2008), and the latter may often contain only a few very different haplotypes (Provan and Bennett 2008, Ansell et al. 2011). Similarly, ancient haplotypes that are closely related to one another can sometimes be found in refugial areas, as demonstrated in vascular plants (Ansell et al. 2011).

It has been hypothesized that sporophyte and spore characteristics should be associated with dispersal abilities in bryophytes (Sundberg 2010). Thus, bryophytes reproducing frequently with small spores should have wider distribution ranges than species that reproduce rarely and/or have large spores. Indeed, the results of the meta-analyses performed here indicate that species with small spores have wider distribution ranges in Europe than species with large spores. This indicates that spore size may be important for long distance dispersal events to occur and that spore sizes may explain the wide distribution ranges of bryophytes on a global scale. On the other hand, frequency of sporophyte production seems to be more important than spore size in preventing genetic differentiation, as species that produce spores frequently have lower F_{ST} between populations than species that produce spores rarely. No such pattern is found between F_{ST} and spore size. Moreover, no association is found between European regions and life-history traits and F_{ST} , respectively. This could be due to species being geographically limited by other factors than the ones we studied, such as temperature or precipitation. This could also be an effect of low sample size, since most species included in the meta-analyses occur in two or more elements.

In general, we cannot rule out the possibility that the observed pattern in bryophytes to some extent could be influenced by sampling bias, since sampling was conducted on different geographical scales in the various studies included and different molecular markers have been used. There are also problems with relatively few species being included in the test, many of them belonging to the same genera. Recently, Szövényi et al. (2012) showed that dispersal of *Sphagnum* spores are likely highly efficient and can be approximated by a random colonization model preventing genetic structuring on regional scales. Several bryophyte species reviewed here have one or more haplotypes that are widespread throughout Europe (Werner and Guerra 2004, Vanderpoorten et al. 2008, Hedenäs 2012, Kyrkjeeide et al. 2012), indicating that little genetic structure may also be found on a broader geographical scale. Also, Sundberg (2012) found that spore size did not have a large influence on dispersal abilities in *Sphagnum*. These

findings fit well with our results as we found no significant relationship between spore size and F_{ST} . Dispersal ability does not seem to explain why one or a few haplotypes are widespread while others are limited geographically. It might be that some haplotypes were faster at occupying available habitats when the climate changed or that spore production has been more successful in these haplotypes.

Conclusion

Eastern, southern and western refugial areas similar to those found in vascular plants seem to have harboured bryophytes during the LGM, and colonization routes and contact zones in bryophytes resemble those found for other organisms. More studies are needed to conclude if these are general trends among bryophytes, as most of the recognized refugia and colonization routes are inferred based on relatively few studies and hence, a limited number of species. Specifically, more data are needed regarding potential survivors of ice-free refugia in arctic areas and potential nunatak areas in Iceland, Scotland, Faeroe Islands and Norway, to elucidate to what extent in situ glacial survival occurred during the LGM. Applying statistical phylogeographical methods (Knowles 2009) for estimating historical demographic parameters seems to be a promising way to infer more accurately the evolutionary history of bryophytes. The wide distribution ranges and potentially high dispersal ability of many bryophyte species emphasises the need for broad sampling in phylogeographical studies of bryophytes to study the importance of glacial refugia also outside of Europe for post-glacial colonization of this continent.

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Supplementary material (available online as Appendix L1046 at <www.lindbergia.org/readers/volume-37>). Appendix 1.

Supplementary material

χ^2 -tests and ANOVA

χ^2 -tests were performed to test if different bryophyte regions in Europe (southern, western, boreal, and arctic) are associated with specific life-history characteristics, i.e. frequency of sporophyte production (Tables S1 and S2) and spore size (Tables S3 and S4). One test was performed for frequency of sporophyte production and spore size, respectively, including all species recorded for each geographic region they occur. For all χ^2 -tests (see below), spore sizes were divided in two categories, small and large, with the limit between small and large spores being set to 20 μm (During, 1979). There are too few species occurring in only one element to do a separate test including only these species (Tables S2 and S4). In addition, one-way ANOVA was performed to test if the four floristic elements are characterized by different levels of genetic structuring as measured by overall F_{ST} values (log transformed), including all species' F_{ST} recorded for each of the elements the species occur in.

There is no significant association between floristic elements in Europe and frequency of sporophyte reproduction ($\chi^2=0.32$, d.f.=3, p -value=0.96), spore size ($\chi^2=5.02$, d.f.=3, p -value=0.17), or F_{ST} (d.f.=42, $R^2=0.02$, $p=0.87$, Table S5).

Table S1 Number of species producing sporophytes frequently and rarely of four floristic elements in Europe.

| Region | Reproduction frequent | Reproduction rare |
|----------|--------------------------|----------------------|
| southern | 10 | 7 |
| western | 11 | 11 |
| boreal | 13 | 12 |
| arctic | 10 | 9 |

Table S2 Frequency of sporophyte reproduction in species occurring in only one floristic element.

| Region | Reproduction frequent | Reproduction rare |
|----------|--------------------------|----------------------|
| southern | 0 | 1 |
| western | 0 | 1 |
| boreal | 0 | 1 |
| arctic | 0 | 2 |

Table S3 Number of species having small or large spores in four floristic elements of Europe.

| Region | Small spores | Large spores |
|----------|--------------|--------------|
| southern | 16 | 2 |
| western | 15 | 8 |
| boreal | 16 | 10 |
| arctic | 11 | 8 |

Table S4 Spore size of species occurring in only one floristic element.

| Region | Small spores | Large spores |
|----------|--------------|--------------|
| southern | 1 | 0 |
| western | 0 | 1 |
| boreal | 0 | 1 |
| arctic | 0 | 2 |

Table S5 Degrees of freedom (d.f.), sum of squares (SS), mean of squares (MS), F-value, and p -value for the ANOVA analysis of floristic elements and F_{ST} values.

| | d.f. | SS | MS | F-value | p -value |
|-----------|------|-------|------|---------|------------|
| Elements | 3 | 0.32 | 0.11 | 0.24 | 0.87 |
| Residuals | 42 | 18.60 | 0.44 | | |

Model testing

To find which variables best explain distribution ranges in bryophytes, different models were compared using likelihood ratio tests. The models include distribution range (calculated as number of regions in which a species is found) as the response variable and spore size (mean spore diameter) and frequency of sporophyte production (rare or frequent) as explanatory variables. The different models are listed below.

Model 1: Regions~Spore size*Sporophyte production

Model 2: Regions~Spore size+Sporophyte production

Model 3: Regions~Spore size

Model 4: Regions~Sporophyte production

There is no significant difference between Models 1, 2 and 3, but Model 4 is significantly worse than Model 2 (Table S6). The simplest model (Model 2) of the two best ones was thus chosen for further analysis of distribution range.

Table S6 likelihood ratio test between different models explaining distribution ranges in bryophytes. For model explanation see text. Only Model 3 and 4 is significantly worse than the others.

| Source | d.f. | <i>F</i> | <i>p</i> |
|--------------------|------|----------|----------|
| Model 1 vs Model 2 | 26 | 0.38 | 0.545 |
| Model 2 vs Model 3 | 27 | 4.13 | 0.052 |
| Model 2 vs Model 4 | 27 | 6.79 | 0.015 |

Analyses of phylogenetic relationship

Fig. S1 shows the spore size of species included in the meta-analyses performed in this review (see main text for details on statistical methods employed). Species that belong to the same genus tend to cluster regarding spore sizes, indicating that the data points are not independent from one another. However, there are several non-related species having the same spore size as the two largest genera included here. There is no clear clustering of related species in frequency of sporophyte production (Fig. S2) and F_{ST} (Fig. S3). We did the meta-analyses again using estimates at the genus level, i.e. the mean of all species in one genus, to compare the results with results found in the main text. The relationship between range size and spore size is not significant when considering data at the genus level (d.f.=16, MS=0.92, F=1.43, $R^2=0.08$, $p=0.25$), but the non-significant result could be due to low sample size. Also, F_{ST} is not significantly higher in species rarely producing sporophytes (mean=0.34) compared to species with frequent spore production (mean=0.18, $t=-2.25$, d.f.=7.42, $p=0.057$, Fig. 3) using the genus level. The relationship between spore size and F_{ST} was not tested again, as this relationship was non-significant at the species level.

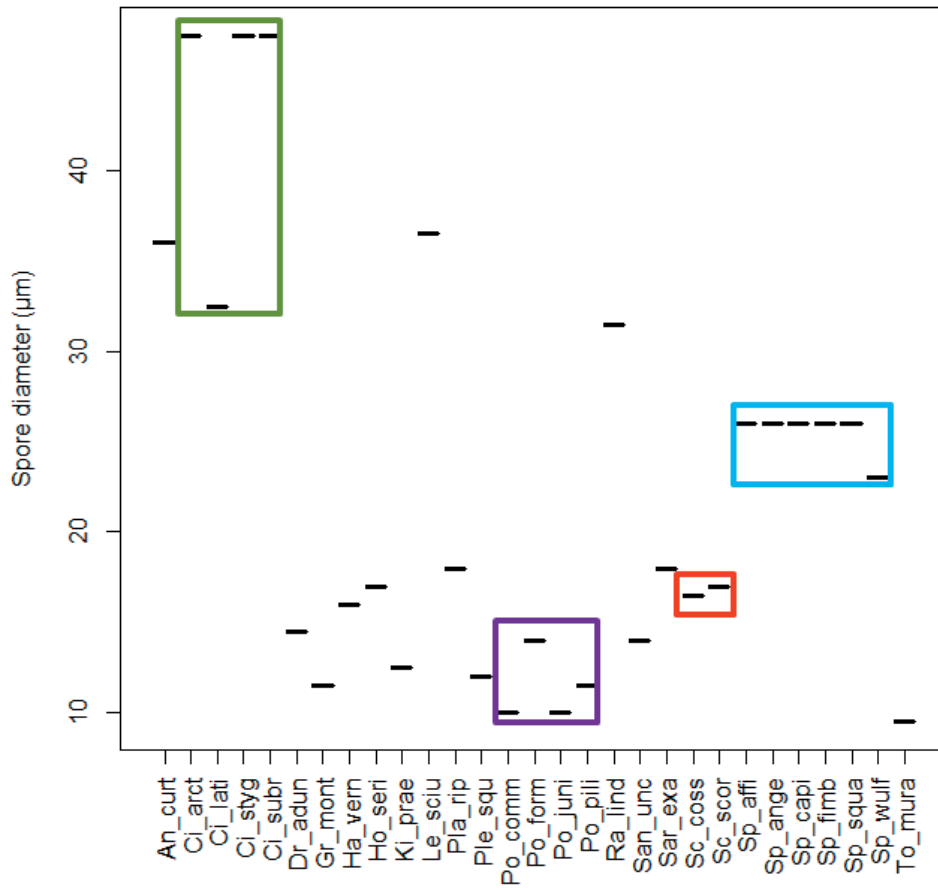


Figure S1 The graph shows the spore size (mean spore size) of all bryophyte species mentioned in the main text. Genera with two or more species are encircled with colour (*Cinclidium* – green, *Polytrichum* – purple, *Scorpidium* – red, and *Sphagnum* – blue). Species in the same genus cluster together around the same spore size.

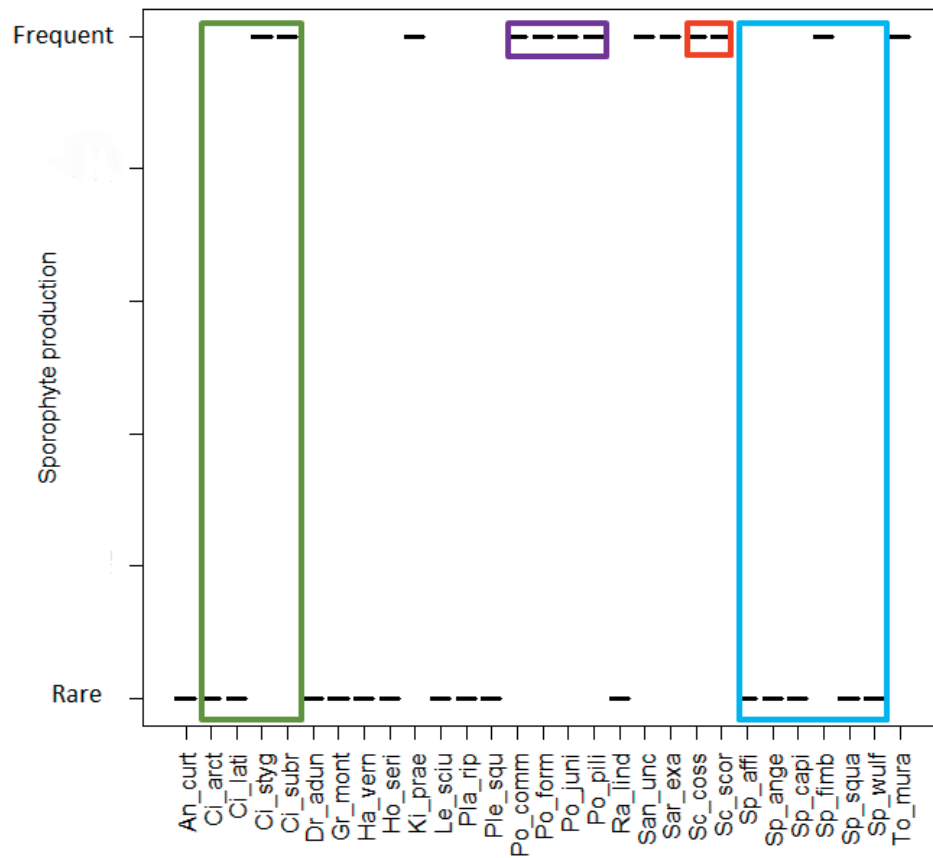


Figure S2 The graph show frequency of sporophyte production, rare or frequent, for all bryophyte species mentioned in the main text. Sporophyte production differs within genera (colours as in Fig. S1).

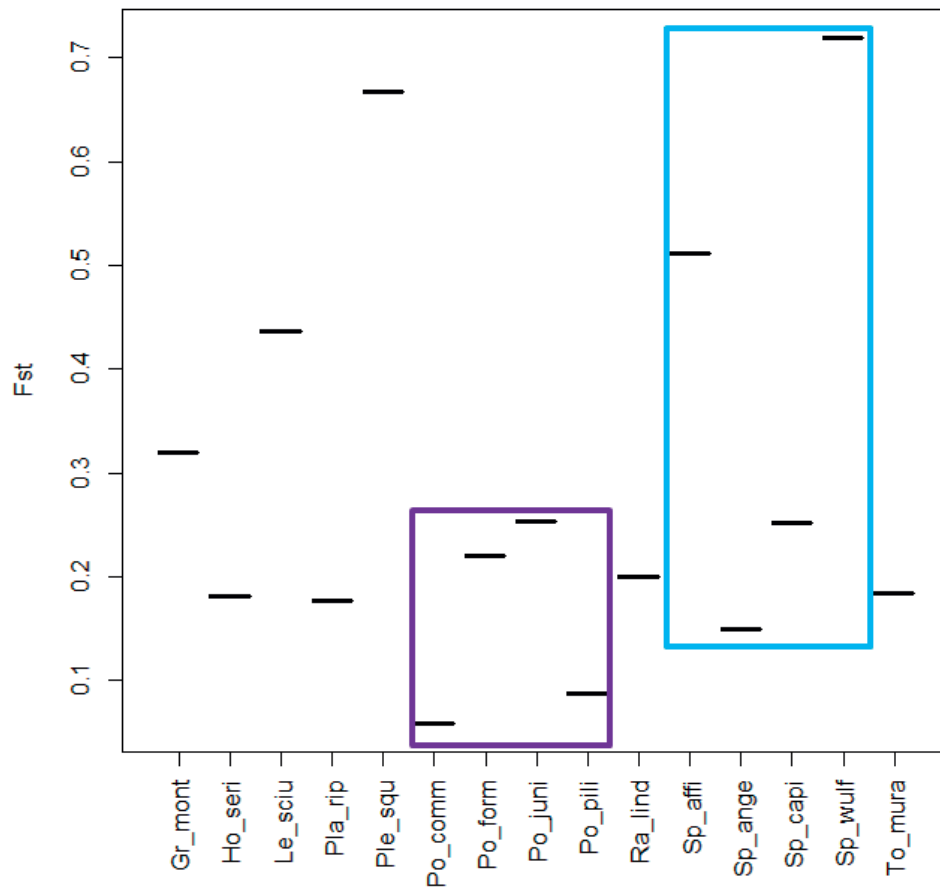


Figure S3 The scatterplot shows F_{ST} values for all bryophyte species included in the meta analyses in the main text. There are only two genera (*Polytrichum* – purple and *Sphagnum* – blue) represented by more than one species and F_{ST} varies greatly within both genera, i.e. phylogeny has no influence on F_{ST} .

The dark morph of *Sphagnum fuscum* in Europe is conspecific with the North American *S. beothuk*

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Running title: Taxonomy of *S. fuscum*

Abstract

Peat mosses (*Sphagnum*) are known to be difficult to identify, especially in the field, because of extensive morphological variation that can blur distinctions among closely related species. The extent to which phenotypic variation reflects genetic differentiation versus environmentally induced plasticity is, however, poorly understood. The common and widespread *Sphagnum fuscum* is relatively easy to recognize, but two different colour morphs, dark and pale brown, have been observed along the western coast of Europe for some time. In this study we aimed to test whether the two colour morphs are genetically differentiated, and assess their phylogenetic relationship to the recently described *S. beothuk* from eastern North America. We used a combination of morphological characters and genetic markers (microsatellites and cpDNA sequences). Our results indicate that the dark colour morph of *S. fuscum* in Europe is conspecific with *S. beothuk* from eastern North America. On the other hand, the pale morph of *S. fuscum* and *S. beothuk* differ in morphology, are separated genetically, and have different habitat preferences and distribution ranges. The known occurrences of *S. beothuk* are restricted to the oceanic regions along the North Atlantic coast. It is one of few peat mosses restricted to the amphi-Atlantic region. We show that by combining morphology, genetic data, distributional information, and habitat knowledge it is possible to evaluate taxonomic uncertainties in *Sphagnum*. We also epitypify the name *S. fuscum*.

Keywords: amphi-Atlantic, bryophyte, distribution, microsatellite, morphology, peat moss, species delimitation, *Sphagnum*

Introduction

Sphagnum L. (peat mosses) is a species rich and ecologically important moss genus in the northern hemisphere. Even though the genus is easy to recognize, many closely related species are difficult to separate morphologically. Many species show pronounced infraspecific morphological variation in “field” traits such as growth form, plant size, colour, and leaf characteristics (Flatberg, 2013).

Interpretations about what should constitute species in *Sphagnum* vary substantially among taxonomists and as a result, the numbers of taxa and their defining features differ among bryophyte handbooks even within North America (e.g. Crum, 1984; McQueen & Andrus, 2007) and Europe (e.g. Daniels & Eddy, 1990; Flatberg, 2013). For example, the taxonomic status of *S. capillifolium* (Ehrh.) Hedw. and *S. rubellum* Wilson has long been and is still controversial, with recent classification as different species in Flatberg (2013), but as subspecies of *S. capillifolium* in Atherton *et al.* (2010). They seem to be both morphologically and genetically distinct (Cronberg, 1989, 1998; Shaw *et al.*, 2005).

The basis for morphological variation (e.g. environmental conditions or genetic variability) in *Sphagnum* may not always be known, or difficult to trace. However, there are some studies showing that observed morphological differentiation found in variable species and species complexes is most likely due to phenotypic plasticity, e.g. *Sphagnum recurvum* complex (Stenøien *et al.*, 1997; Såstad, 1999; Szurdoki *et al.*, 2014), *S. comosum* Müll.Hal. (Karlin *et al.*, 2008), and *S. palustre* L. (Stenøien *et al.*, 2014). On the other hand, an extremely divergent growth form of *S. cribrosum* seems to be genetically based, as reversal to normal form was not observed in a reciprocal transplant experiment (Johnson *et al.*, 2012). Another mechanism confusing morphological appearance may be hybridisation between closely related species (Cronberg, 1998; Natcheva & Cronberg, 2007) or between allopolyploids and their parental species (Flatberg *et al.*, 2006; Ricca *et al.*, 2011).

Description of new species and taxonomic revisions have usually been based on morphological characters. Complex species groups have been separated into several species after closer morphological examination, as in the *S. imbricatum* complex (Flatberg, 1984; Andrus, 1987). Here, five species (*S. austinii* Sull., *S. affine* Renauld & Cardot., *S. steerei* R.E. Andrus, *S. portoricense* Hampe, and *S. imbricatum* Hornsch. ex Russow) are now commonly recognised (Hill *et al.*, 2006; Ignatov *et al.*, 2006; McQueen & Andrus, 2007). Recently, molecular methods make it possible to investigate genetic correlates of morphologically differentiated species, and genetic analyses of taxa suggested in the *S. imbricatum* complex are separated genetically (Thingsgaard, 2002).

Furthermore, there are several examples of recently described new species based on morphology that are found to be genetically differentiated as well, e.g. *S. inexpectatum* Flatberg (Flatberg, 2005; Shaw *et al.*, 2014a), *S. mirum* Flatberg & Thingsg. (Flatberg & Thingsgaard, 2003), and *S. concinnum* (Berggr.) Flatberg (Flatberg, 2007; Shaw *et al.*, 2012). On the other hand, no significant genetic differences were found within the widely distributed species *S. fimbriatum* Wilson with seemingly clearly differentiated morphotypes (Shaw *et al.*, 2012). Similarly, no genetic differences were found comparing two newly described species from North America, *S. atlanticum* R.E. Andrus and *S. bergianum* R.E. Andrus, with *S. torreyanum* Sull. and *S. subfulvum* Sjors, respectively, using microsatellite markers (Shaw *et al.*, 2009). This indicates that the description of two new species was superfluous, and that the morphological differences found may rather be due to e.g. phenotypic plasticity.

Even though species delimitation may be challenging, using a combination of morphological characterization and molecular data seems to be a good way of evaluating species distinctness in *Sphagnum*. Furthermore, if morphologically separated taxa differ in geographical distribution and ecological preferences, this strongly support that they have different evolutionary histories and may be treated as separate species (Shaw, 2008a). For morphological studies, the mixed stand approach has been used to compare similar taxa (e.g. Isoviita, 1966; Frisvoll, 1988; S  stad & Flatberg, 1994; Stech *et al.*, 2013), as plants growing close together are likely to be influenced by the same micro-

ecological environment. Morphological differentiation found can therefore give valuable information of taxonomic relationships (but see Stenøien *et al.*, 2014).

Sphagnum fuscum (Schimp.) Klinggr. (subgenus *Acutifolia*) is one of the most common peat mosses in boreal peatlands. It is traditionally considered to be one of the easier *Sphagnum* species to recognize in the field as there are few other similar species. However, the existence of two morphological variants of *S. fuscum* was recognised by Flatberg during field work in 1971, when mires in western Norway were investigated to outline a national plan for establishment of mire reserves (Flatberg, 1971). One of these variants was characterised by a dark brown colour and rather convex capitula, the other being more pale brown with rather flat capitula, corresponding to the traditional morphological form of *S. fuscum*. But, as no obvious morphological differences were found in microscopic details between the two variants at that time, herbarium collections of *S. fuscum* with dark brown colour made during subsequent years were marked as the “dark brown morph”, leaving further examination to come.

Two distinct haplotype groups were found when studying genetic structure in *S. fuscum* on a local scale at one particular ombrotrophic mire (bog) in Central Norway (Gunnarsson *et al.*, 2007). These two groups also differed in microhabitat preferences: one being found in acidic, dry hummocks higher above the water table and the other in slightly less acidic, wetter hummocks. The authors speculated that the two genetic groups represented different ecotypes, and concluded that they had different histories, having colonised the mire independently (Gunnarsson *et al.*, 2007). If the differences found are due to sampling of the two colour morphs or not is unknown, but both colour morphs are present at the sampling locality (Flatberg, pers. obs.).

In 2006, Andrus (Andrus) described a new brown-coloured *Acutifolia* species based on material collected in Newfoundland, Canada. Even though *S. beothuk* R.E. Andrus was described as close to *S. fuscum*, the morphological characterisation and differentiation described were rather ambiguous (see also McQueen & Andrus, 2007). Its taxonomic status has therefore remained unclear.

The purpose of our study is to (1) clarify the taxonomic status of the dark and pale brown colour morphs of *S. fuscum* by using both genetic and morphological methods, supplied with knowledge of their distributions and habitat preferences, (2) investigate the genetic and morphological relationship of the two morphs compared to the newly described species *S. beothuk*, and (3) clarify the relationship between *S. fuscum* and *S. beothuk* within the subgenus *Acutifolia*.

Material and Methods

Specimen collection

All material used for genetic and morphological analysis and examinations are from publicly available herbarium collections. Two mixed stand collections of the pale and dark brown colour morphs of *S. fuscum* from two geographically separated areas in Norway were used for detailed morphological analyses. These were collected near the coast of central (TRH 158326) and northern (TRH 157468) Norway from poor fen hummock habitats.

Specimen sampling for genetic analyses was performed by picking one shoot from herbarium collections for DNA extraction (Table S1 in Supplementary Material provides a list of voucher specimens with locality information). Altogether, 13 samples of the dark brown colour morph of *S. fuscum* and seven samples of *S. beothuk* were collected from herbarium TRH (Trondheim, Norway) and herbarium DUKE (Durham, NC, USA), respectively. A subsample of 30 specimens from a larger dataset of *S. fuscum* (Kyrkjeeide *et al.* unpublished) was used to represent the pale brown colour morph of *S. fuscum*. As this dataset contains samples from the global distribution of *S. fuscum*, both geographically and genetically separated specimens were chosen in the subsample to represent the complete variability found. Additionally, two shoots of the selected epitype collection (see below) of *S. fuscum* were included.

Morphological analyses and examinations

The mixed stand approach was applied to look at leaf and cell characteristics of the two colour morphs of *S. fuscum* growing intimately mixed in the same micro-habitat. From each of two mixed stand collections, five shoots of the pale and dark brown colour morph, respectively, were arbitrarily picked for morphometric measurements and qualitative observation. A number of stem leaves were removed from the upper 1–2 cm of the stem, and branch leaves from the middle part of two spreading branches from the same part of the stem, and semi-permanently mounted in glycerol on microscopic slides.

In the morphometric part of the mixed stand study, five stem leaves (ST) and five branch leaves (BR) from each shoot were measured. Both leaf types were scored for length (STL, BRL), width at mid-leaf (STM, BRM), and width at 1/8 length from distal leaf end (STT, BRT). Altogether, five characters for each leaf type were included in statistical analyses: leaf length, leaf mid-width, leaf tip-width (1/8 from distal end), the leaf mid-width/leaf tip-width ratio, and leaf length/mid-width ratio. In total, 100 data points were included in statistical analyses for each character (2 species, 2 location, 5 individuals, 5 leaves). Differences in morphological characters between species were analysed using mixed models to account for repeated measurements (leaves from same individual). Locations were chosen randomly and were treated as a part of the random error with individuals nested within location. All analyses were done in the R environment (R Development Core Team, 2011).

The qualitative part of the mixed stand study was concentrated on observations made on pore pattern of the branch leaf hyalocysts, as preliminary herbarium studies had indicated this to be a possibly good distinguishing character between the two putative species. The observations made in this part of the study were not quantified.

The mixed stand study was followed by extensive examination of herbarium plants from various parts of the known distributions of the two colour morphs in order to check if differences observed could be used universally to separate the morphs. In addition, characters such as the shape of the capitula and colour were considered, as these can be used to distinguish *Sphagnum* species in the field.

Leaf measurements were taken using the Leica DM6000 B transmission microscope, and photos were made applying the Leica Application Suite LASD V2.6 for stacking.

Molecular analyses

DNA extractions were done using DNeasy 96 Plant Kit (Qiagen, Oslo, Norway) or E.Z.N.A. SP Plant DNA Kit (Omega Biotek, Norway). Both microsatellite markers and cpDNA were used in the present study. Nineteen microsatellite markers were amplified following Shaw *et al.* (2008b). The markers used were 1, 4, 7, 9, 10, 12, 14, 17, 18, 19, 20, 22, 28, 30, 56, 65, 68, 78, and 93 (Shaw *et al.*, 2008b; Stenøien *et al.*, 2011). GENEMAPPER® software (Applied Biosystems) was used to size and genotype the alleles. In addition, three samples of each colour morph of *S. fuscum*, were amplified for the loci tRNA(Gly) (UCC) (referred to here as *trnG*) representing the chloroplast genome. The samples chosen for sequencing were geographically separated and genetically different based on microsatellite results. For amplification and sequencing of *Sphagnum* specimens, see Shaw *et al.* (2010).

The genetic relationships between the two colour morphs of *Sphagnum fuscum*, and *S. beothuk* were examined by analysing variation in microsatellite markers. The software Structure 2.3.4. (Pritchard *et al.*, 2000; Falush *et al.*, 2003; Falush *et al.*, 2007; Hubisz *et al.*, 2009) estimates the optimal number of genetic clusters in a dataset using a Bayesian approach. Based on genetic similarities, individuals are clustered together and the likely number of clusters (K) estimated. The analyses

were performed using 150,000 iterations after a burn-in period of 50,000 iterations, with eight as the maximum number of K and 10 replicates for each K. The admixture and independent allele frequency models were used. Alignments of the different replicated analyses for the chosen K-values were made using the greedy option and 1000 random input orders in the software Clumpp 1.2.2. (Jakobsson & Rosenberg, 2007). The program Distruct 1.1 (Rosenberg, 2004) was used to graphically display the Structure results. Genetic structuring was further analysed using principal coordinate analyses (PCoA) implemented in GenAlEx 6.501 (Peakall & Smouse, 2006, 2012). The percentage of polymorphic loci, expected heterozygosity (Nei, 1987), and mean number of alleles were estimated for the two species using GenAlEx. Additionally, pairwise Φ_{PT} (used for haploid data as an analogue to F_{ST} , Peakall *et al.*, 1995) and Nei's genetic distance (Nei, 1973) between the two species were calculated using GenAlEx.

Furthermore, the genetic relationship between *S. fuscum* and *S. beothuk* and their phylogenetic relationship within the subgenus *Acutifolia* section *Acutifolia* was explored using *trnG*. In addition to three samples of *S. fuscum* and *S. beothuk*, respectively, *trnG* sequences of seven *Acutifolia* species were downloaded from GenBank (Table S2 in Supplementary Material for GenBank accession numbers). Also, three *trnG* sequences each of *S. quinquefarium* (Braithw.) Warnst. and *S. rubiginosum* Flatberg, and one sequence of *S. warnstorffii* Russow were included in the analyses, as these species were poorly represented in GenBank. *Sphagnum wulfianum* Girg. section *Polyclada* and *S. squarrosum* Crome section *Squarrosa* in subgenus *Acutifolia* were used as out-group. All sequences were aligned using ClustalW with default parameters in Mega 6.0 (Tamura *et al.*, 2013). The phylogenetic relationship between the species was investigated using the Maximum Likelihood option in Mega 6.0, adding 1000 bootstrap replications and the general time reversible substitution model (GTR).

Distribution ranges and habitat

The Norwegian and global distribution ranges of *S. fuscum* and *S. beothuk* were delineated by examining specimens from herbaria, also including literature records of *S. fuscum* (see below). All herbarium collections of *S. fuscum* from the four main Norwegian herbaria (BG, O, TRH, and TROM) have been revised (based on new knowledge of morphological differences) to map the distribution ranges of the two colour morphs in Norway. The global distribution of *S. beothuk sensu* R. E. Andrus was based on records deposited in DUKE. In addition, all specimens of *S. fuscum* from LE and MHA were screened in 2011 and no samples corresponding to the dark brown colour morph of *S. fuscum* were found.

Habitat preferences for *S. fuscum* and *S. beothuk* were investigated based on literature (see below) and field experience.

Results

Our results (see below) show that the pale and dark brown colour morph of *S. fuscum* are genetically and morphologically distinct taxa with different distribution patterns and deserve to be treated as separate species. Moreover, we show that the original material underlying the name *S. beothuk* is conspecific with the European and North American material collected as the dark brown colour morph of *S. fuscum*, and therefore makes the description of a new species superfluous. However, an epitypification of the name *S. fuscum* is necessary (see below). The material sampled and/or identified as the dark colour morph of *S. fuscum* will hereafter be referred to as *S. beothuk*.

Morphology

Mixed stand analyses and examinations

Both species vary considerably in the shape and size of both branch and stem leaves (Figure 1), and it proved difficult to find leaf size differences that clearly separate them throughout their whole micro-habitat and distribution ranges. However, the statistical analyses showed that all stem leaf characters were significantly different in *S. beothuk* and *S. fuscum*, except the ratio between stem leaf length and mid-width (Table 1). In branch leaves, only branch leaf mid-width and the ratio between branch leaf length and mid-width were significantly different (Table 1).

The most diagnostic character separating *S. beothuk* and *S. fuscum* is the pore pattern in the hyalocysts in the upper 1/3-1/2 abaxial (convex) part of the branch leaves of spreading branches (Figure 3). The latter have scattered elliptic to circular, more or less ringed, perfect pores along the commissures/cell ends in all or nearly all cells in the upper 1/3-1/2 part of the leaf. These pores vary in number from (1-)2-3(-5) in each cell, and gradually diminish in size towards leaf the apex. Near the leaf apical end, the pores are often rather tiny, elliptic to circular and ringed, and occur both along the commissures and are often free-lying (Figure 3). The branch leaf hyalocysts of *S. beothuk* are either aporse on the upper 1/3-1/2 abaxial part, or a few cells have 1-2 ± circular to broadly elliptic, perfect pores, confined mostly to the proximal cell ends (Figure 3). Some diffuse imperfect pores with membrane thinnings may occur. In addition, the hyalocysts close to the apical end of the leaves usually possess a few, tiny, ringed, mostly circular pores, but these tiny pores can be absent. They do not differ in size and shape from the tiny pores in *S. fuscum*. Rarely, as in the type specimen of *S. beothuk*, they can be rather numerous.

Examination of herbarium plants and field observations

The characters further focused on were colour and shape of capitulum, stem leaf shape, the arrangement and shape of branch leaves on spreading branches, and branch leaf hyalocyst pores (for summary, see Table 2).

Although both species vary considerably in leaf shape in examined herbarium material, and sometimes identification is difficult based on this characteristic alone, the relative differences observed in the mixed stand study, have been confirmed. In general, *S. fuscum* has stem leaves that are larger and broader close to the leaf apex with more obtuse apices, than *S. beothuk* (Figure 2). Also, the branch leaves are usually shorter and broader in *S. fuscum*, than in *S. beothuk*. The observed difference in pore patterns of branch leaves in the mixed stand study, were consistent in examined herbarium material. The absence of perfect pores in many or most hyalocysts in the upper 1/3–1/2 part of the leaves in *S. beothuk* appears to be the best distinguishing character in comparison to *S. fuscum* (see Figure 3), in both European and North American plants examined. Noticeably, *S. beothuk* lacks the gradual diminishing pore size from about the middle of the leaf towards the apical end which is typical in *S. fuscum*. Other leaf cell patterns of the two species have not been studied in detail, but screening of other possible leaf characters has not given additional information of obvious diagnostic value in their separation.

Sphagnum beothuk forms cushions or mats with somewhat elevated (convex) capitula of a deep brown colour (Figure 4A, B, E), often furnished with a purplish sheen during autumn. The spreading branches often have the leaves in visible rows (5-ranked), but not always. *Sphagnum fuscum* has rather flat to only slightly elevated (convex) capitula with a usually pale brown colour, and a purplish sheen is not obvious during autumn (Figure 4C, D, E). The different capitulum shape makes the surface of the *S. fuscum* hummocks more even and less facet-looking than in *S. beothuk*. The capitulum colour varies in *S. fuscum*, and particularly in fen mire habitats the capitula can be as dark as in *S. beothuk* (Figure 4D), but the surface structure differs. When found growing in the same

habitat, the colour difference between the two species is obvious (Figure 4E, see also Flatberg (2013, Pl. 61)). The branch leaves of *S. fuscum* are non-ranked in hummock habitat, but plants from fen lawn communities can have distinctly 5-ranked leaves as *S. beothuk*.

Both *S. beothuk* and *S. fuscum* are dioicous. In Norway both species occur rather frequently with sporophytes (Figure 4B, C, E), but with considerable variation between years, and seemingly also between species from year to year (Flatberg, pers. obs.). Morphology of perichaetial leaves and spores of the two species have not been included in our work.

The morphology of the holotype of *S. beothuk* (herbarium DUKE) deviates from the typical appearance of this species. However, re-examination of the type material based on the new knowledge of the total morphological ranges of *S. fuscum* s. lat., suggests that *S. beothuk* and the dark brown colour morph belong to the same species.

Molecular analyses

There were no missing data among *S. fuscum*. In *S. beothuk*, the accepted value of missing data was set arbitrarily to 40%. One specimen had more than 40% missing data and was excluded. The total amount of missing data among *S. beothuk* was 7.5%. There are fixed differences between *S. beothuk* and *S. fuscum* at eight out of 19 microsatellite loci. Four loci are homozygous in *S. fuscum* compared to 13 loci in *S. beothuk*. The percentage of polymorphic loci was 79% and 32% in *S. fuscum* and *S. beothuk*, respectively, and the mean number of alleles per locus was more than two times higher in *S. fuscum* (4.0) than in *S. beothuk* (1.7). Only one allele was present at each locus, strongly supporting the interpretation that both species are gametophytically haploid.

Genetic clustering analyses show that there are two main genetic clusters in the dataset (Figures 5 and 6). One cluster includes the pale brown morph of *S. fuscum* and the epitype of *S. fuscum*, while the other cluster contains *S. beothuk* and the dark brown morph of *S. fuscum*. Nei's genetic distance

between the two species is 1.02 and $\Phi_{PT}=0.58$ ($p<0.01$). Genetic variation was higher in *S. fuscum* ($H_E=0.42$) than in *S. beothuk* ($H_E=0.13$).

The aligned length of the pDNA sequences was 678 bp. No genetic variation was found within either *S. fuscum* or *S. beothuk*. The two taxa differed at six sites. The maximum likelihood tree in Figure 7 shows that *S. beothuk* is separated from all other compared *Acutifolia* species, by a long branch length supported by a high bootstrap value (98%).

Distribution ranges

Following the terminology and distribution of vegetation sections and zones in Moen (1999), the Norwegian records of *S. beothuk* lie within the highly and markedly oceanic sections (O3 and O2, respectively) in the boreo-nemoral and southern to middle boreal vegetation zones (Figure 8A). The northernmost locality known is in Troms County (TROM B-1119), close to the sea level (O2) in the middle boreal zone. The southernmost Norwegian record lies within O3 in the boreo-nemoral zone in Vest-Agder County (O 38489). The known altitudinal limit is in the middle boreal zone located in O2 in Central Norway at an altitude of about 400 m asl.

Seven specimens of *S. beothuk* are deposited at herbarium DUKE (Table 3). The records were sampled at three localities, one in Maine, USA, and two in Newfoundland, Canada. The type material is collected at Lark Harbour, Newfoundland (DUKE 10687). Additionally, 11 records outside Norway are revised as *S. beothuk* after genetic and morphological examination of *S. fuscum* material in TRH. Of these are nine from Newfoundland and Labrador, Canada, and two from the western coast of Scotland (Table 3). These records are currently the basis for the known distribution range of *S. beothuk* outside Norway (Figure 9).

Sphagnum fuscum is widely distributed in most of mainland Norway (Figure 8B). The distribution covers all vegetation zones from boreo-nemoral areas in the south via boreal to southern arctic areas

in the northernmost mainland, and it ascends above the tree limit into the low-alpine zone.

Moreover, the distribution embraces all sections from O3 along the western coast, to slightly continental areas (C1) in the east and northeast. Hence, it occurs in all areas where *S. beothuk* is found.

Sphagnum fuscum is widespread in the northern hemisphere (Figure 9, literature used to draw distribution boundaries confirm *S. fuscum* when diagnostic illustrations are present, for references see below). The species occurs in many countries in Europe (TRH), but the main distribution lies in northern Europe (Daniels & Eddy, 1990; Söderström *et al.*, 1998). Furthermore, herbarium material from LE and MHA confirms that the species occurs throughout northern Russia. In North America, *S. fuscum* is common in most of Canada and is only unrecorded from some states in the Midwest and southern USA (McQueen & Andrus, 2007). The main distribution of *S. fuscum* lies in the boreal vegetation zone, but with extensions southward into the nemoral (e.g. Andrus, 1980; Bouman, 2002) and sub-meridional zones (e.g. Guerra & Cros, 2004; Anderson *et al.*, 2009; Matsuda, 2012), and northwards into the arctic zones on all continents (Ignatov & Afonina, 1992; McQueen & Andrus, 2007). The occurrences of *S. fuscum* in the nemoral and especially in the sub-meridional zones seem to be located at rather high-elevation sites (Europe: Alps (e.g. Miserere *et al.*, 1997), Pyrenees (e.g. Guerra & Cros, 2004), Carpathians (A. Ganeva, pers. com., identity not confirmed), Dinaric Alps (M. Sabovljevi, pers. com., identity not confirmed); North America: Blue Ridge Mountains (Anderson *et al.*, 2009; identity of *S. fuscum* confirmed; DUKE specimens 0017158, 0023720, 0023720); Japan: Hokkaido (Takita, 1999; identity of *S. fuscum* confirmed; DUKE specimens 0017169, 0017170, 0158778, 0158779, 0158781, 0158782, 0158783, 0158784), Honshu (Matsuda, 2012; identity of *S. fuscum* confirmed; DUKE specimens 0017168, 0017171, 0023209)). *Sphagnum fuscum* reaches the coast on all continents, including the western coast of Greenland (TRH). Thus, it is found in all vegetation sections, from O3 to highly continental (C3).

Habitat

The typical habitat of *Sphagnum beothuk* in Norway is elevated hummocks in ombrotrophic mires (bogs) of various kinds. In the ericaceous coastal heath region along the western coast it occurs scattered in open, treeless Atlantic bogs. Inland, it occurs in open expanse mire communities and close to the margin in bogs with open treeless expanses and *Pinus sylvestris*-wooded margins, and the main niche is hummocks in transitional sites where small pines often occur. It is not found in pine-wooded, ericaceous and hummock-dominated margins (bog forests). Its habitat preference is similar to that of *S. austinii*, and often they grow together on elevated hummocks in oceanic sections in the boreo-nemoral and southern boreal zones. According to the local “poor–rich” mire ecogradient, nearly all records of *S. beothuk* in Norway are from ombrotrophic (bog mire) sites. It is also recorded from poor fen sites, though never from rich fens. The habitat of *S. beothuk* in North America is reported to be medium rich fen hummocks (Andrus, 2006; McQueen & Andrus, 2007), and records from ombrotrophic (bog) habitats are unmentioned. This is not in accordance with our observations and collections in Newfoundland (Flatberg, field work 1996) and Labrador (Flatberg, field work 2007). The common habitat of *S. beothuk* also seems here to be ombrotrophic hummocks, although the type collection is from medium rich fen (Andrus, 2006). *Sphagnum beothuk* is mostly confined to the hummock level along the “hummock–lawn–carpet” vegetation gradient (the “dry–wet” ecogradient), but occasionally also occurs in lawns. In Isle of Skye, western Scotland, *S. beothuk* was found growing in Atlantic bog hummocks (Flatberg, field work 1987), corresponding well with its habitat in the O3 section of western Norway.

Sphagnum fuscum often occupies similar hummock habitats as *S. beothuk* in southern and middle boreal, O2 section areas, such as in Central Norway, but *S. fuscum* has a wider habitat range. Along the “hummock-lawn-carpet” gradient, *S. fuscum*, like *S. beothuk*, is primarily a hummock species, but it is more common in lawn communities than the latter, and occasionally occurs in carpets. In lowland, southern boreal ombrotrophic mires (bogs) *S. fuscum* occurs from open expanses to pine-

wooded margins along the “mire expanse-margin” gradient, and thus, contrary to *S. beothuk*, it is common in forested bogs. In Norway, it occupies a wider range along the “poor–rich” gradient than *S. beothuk*. The most common habitat is hummocks in ombrotrophic mires (bogs), but it is also common in elevated hummocks in poor fen mires, and even in rich fens, particularly in northern boreal mires, where it sometimes co-occurs with *S. warnstorffii*. In middle and northern boreal areas in more continental areas of Norway, it often is the dominant hummock peat moss in mixed ombrotrophic and poor fen mires. The habitat of *S. fuscum* in the low-alpine zone in Norway is hummocks in intermediate to rich fens on shallow peat.

Outside Norway, the habitat of *S. fuscum* in boreal areas in Eurasia and North America seems to be rather similar. In nemoral zone areas of Europe, its main habitat seems to be hummocks in bog and poor fen mires as well (e.g. Hölzer, 2010). The high-elevation occurrences of *S. fuscum* in Italy are reported to be from bog communities (Miserere *et al.*, 1997). In tundra (southern arctic zone), *S. fuscum* form small hummocks in flat, mostly poor fen mires on shallow treeless peat (Flatberg field observations: Yukon-Kuskokwim Area, Alaska 2001, Nunavik, northern Hudson Bay 2007, western Greenland 2006; Hassel & Prestø field observations: western Greenland 2010 (cf. TRH-specimens)).

Discussion

We combined morphology, genetic data, distribution and habitat knowledge to evaluate the taxonomic uncertainty concerning different colour morphs in *S. fuscum*, and also the relationship to *S. beothuk*. The results clearly show that the dark brown colour morph of *S. fuscum* belongs to the same taxon as the newly described *S. beothuk*. Furthermore, our genetic and morphological studies give unambiguous support to treating *S. beothuk* and *S. fuscum* as two different species, strengthened by their morphological distinctness in mixed stands. Their different distributional patterns together with different habitat preferences further support this view.

The mixed stand approach has been debated (see e.g. Frisvoll, 1988). However, in our study we found the method very useful in tracing possible leaf and cell characters separating the two colour morphs of *S. fuscum*. The differences observed using this method were easy to follow up and check diagnostically during morphological screening of herbarium material representing *S. fuscum*.

The morphology of *S. beothuk* and *S. fuscum* seems to overlap in some degree concerning colour and leaf shapes. The stem leaf shape is usually a rather safe character for species identification when the average impression of several leaves examined from a plant is considered. But, the most diagnostic character separating the two species is the different pore pattern in the upper abaxial part of the branch leaf. The pore characterization (see Figures 21-26 in Andrus, 2006) of *S. beothuk* given by Andrus (2006) and McQueen & Andrus (2007) is imprecise and misleading. A plant fragment from the type specimen examined had branch leaves with rather many tiny pores in the apical part hyalocysts. This may be caused by the habitat of the type collection being medium rich fen (Andrus, 2006). In Scandinavia the typical habitat of the species is bogs and to a less degree, poor fens. Thus, plants from rather rich fen habitats of *S. beothuk* may possess more tiny pores than in poorer mire habitats. When both species show a typical habit appearance in field, they are fairly easy to separate.

The tiny pores of *S. beothuk* – when present – are rather similar to those found in *S. fuscum* and *S. warnstorffii*, and do not alone distinguish the species from *S. fuscum*. In fact, *S. beothuk* was suggested to be an allopolyploid hybrid between *S. fuscum* and *S. warnstorffii* (Andrus, 2006). Allodiploids usually have two alleles in several microsatellite loci (e.g. Ricca & Shaw, 2010), and we found only one allele in all loci of *S. beothuk*. Thus, if this species has a hybrid origin it must be a homoploid at haploid ploidy level. However, the chloroplast DNA haplotype (*trnG*) of *S. beothuk* is not similar to the haplotypes of *S. fuscum* or *S. warnstorffii*. As chloroplast DNA is maternally inherited in *Sphagnum* (Natcheva & Cronberg, 2007), this indicates that neither species could be the

maternal species of *S. beothuk*. Thus, *S. beothuk* is probably not a hybrid between *S. fuscum* and *S. warnstorffii*.

Microsatellite markers are highly variable, and usually species-specific. However, in *Sphagnum* these markers can generally amplify across all species. Thus, they have been used for species determination of closely related species (Shaw *et al.*, 2009) and studies of allodiploid origins (Ricca & Shaw, 2010; Stenøien *et al.*, 2011b) and allotriploid origins (Karlin *et al.*, 2009; Karlin *et al.*, 2014). In our study, several microsatellite loci were fixed for different alleles in *S. fuscum* and *S. beothuk*, and the two species are clearly separated in these markers.

The maximum likelihood tree is poorly resolved and the different clades have low bootstrap support. However, the purpose of this study was not to resolve the phylogeny of subgenus *Acutifolia*, but to investigate if differences in the nuclear genome (microsatellites) found between *S. fuscum* and *S. beothuk* correspond to differences found between other valid species in the subgenus. The tree is only based on a single chloroplast gene (*trnG*), but shows the same distinct pattern as the microsatellite data. The *trnG* tree corresponds rather well to the trees in both Shaw *et al.* (2005) and Johnson *et al.* (2014), with *S. girgensohnii* Russow, *S. fimbriatum* Wilson, and *S. rubiginosum* in one clade and *S. fuscum*, *S. capillifolium*, and *S. russowii* Warnst. in another clade. Complex phylogenetic patterns among members of the *S. fimbriatum* complex (Shaw *et al.*, 2012) is evident in the tree. The *trnG* marker seems to be conservative within species, but shows moderate variation between species. The branch length and bootstrap values of *S. fuscum* and *S. beothuk* are comparable to that found in *S. rubiginosum* and *S. quinquefarium*, supporting that *S. beothuk* is a distinct phylogenetic entity.

Genetic variation appears to be higher in *S. fuscum* than in *S. beothuk*. This could be due to different evolutionary histories. *Sphagnum beothuk* has a much more restricted distribution than *S. fuscum*, and it probably went through a more severe bottleneck during the last glacial maximum (LGM), decreasing its genetic variability. The current European population sites were mainly covered by ice

during the LGM. As *Sphagnum* spores have high dispersal capacity (Muñoz *et al.*, 2004; Szövényi *et al.*, 2008; Sundberg, 2012; Wilkinson *et al.*, 2012; Shaw *et al.*, 2014b), survival along the eastern coast of North America with post-glacial colonization of the western coast of Europe is a plausible historical scenario. This is, for instance, the likely explanation for the current distribution of one of two genetic clusters recognized in *S. angermanicum* Melin (Stenøien *et al.*, 2011).

Genetic differentiation found between *S. fuscum* haplotypes at one site located in Trondheim, Norway, by Gunnarsson *et al.* (2007), is likely due to sampling of both *S. fuscum* and *S. beothuk*. The authors argue that the two groups found had different immigration histories at the locality. They found that one haplotype group was similar to a specimen from a locality in New Brunswick, while they found similar sequences for the other haplotype group in North America, but also in Japan. Thus, the former could be *S. beothuk*, and the latter *S. fuscum*. However, the habitat preferences described for the two groups are opposite of our observations. Nevertheless, this could simply be due to the sampling scheme. The specimens in that study were sampled along transects and thus, untypical habitats may occur by chance.

In Europe, *S. beothuk* seems to occur in highly oceanic areas. As indicated by the Norwegian distribution, it is likely to be confined to the western, coastal areas near the Atlantic Ocean. In fact, the total Norwegian distribution of this species is restricted to markedly and highly oceanic areas (Fig 5a). This distribution is rather similar to the distribution of *S. austinii* (Flatberg, 2013). However, *S. austinii* has a marginally less oceanic affinity and also occurs in the slightly oceanic section (O1, sensu Moen, 1999). Both *S. fuscum* and *S. beothuk* are often found growing together at the same mire sites in sections O2 and O3, also in mixed stands, but both species are rather rare in the treeless westernmost, Atlantic heath and mire region facing the North Sea. This is an area that has been heavily influenced by humans for a long time, with regular burning of ericaceous heaths and bogs, scything, sheep grazing and trampling, drainage, and extensive peat cuttings for fuel. These activities may be the main reason for the rarity of bog species like *S. austinii* in such areas

(Flatberg, 1984). As in Norway, increased land use intensity has reduced the abundance of *S. austinii* in Wales (Hughes *et al.*, 2007). As *S. beothuk* and *S. austinii* seem to have overlapping distributions, the former species may also be declining in parts of Europe.

Sphagnum beothuk is so far only known from the coast of Norway and northwest Scotland in Europe. With the Scottish records, the species extends its distribution from the boreal zone into the nemoral zone. No records of *S. beothuk* are currently known from Ireland. However, here and in western parts of Britain, *S. beothuk* may be as common as *S. fuscum* since oceanicity resembles that along the Norwegian coast. In fact, the picture illustrating *S. fuscum* in the flora “Mosses and Liverworts of Britain and Ireland” (Atherton *et al.*, 2010) seems to be of *S. beothuk* as the capitula are rather convex and the colour is dark brown. *Sphagnum beothuk* may occur in lowland, oceanic areas in mainland Europe. Revision of more herbarium material and field work are needed to confirm this.

The current knowledge of the distribution range of *S. beothuk* includes the eastern coast of North America and the western coast of Europe. Thus, it has a much more restricted distribution globally compared to several other oceanic *Sphagnum* species, occurring in western North America and/or Asia (e.g. *S. quinquefarium*, *S. rubiginosum* (Flatberg, 1993), and *S. austinii* (McQueen & Andrus, 2007; Flatberg, 2013)). This makes *S. beothuk* one of few amphi-Atlantic peat mosses, as only three other species are known to have this pattern of distribution: *S. angermanicum* (Gunnarsson *et al.*, 2005; Stenøien *et al.*, 2011), *S. venustum* Flatberg (Flatberg, 2008, 2013), and *S. affine* Renaud & Cardot (Thinggaard, 2001). In a phylogeographic study of *Sphagnum* (Kyrkjeeide *et al.*, unpublished), material of *S. fuscum* (from DUKE, TRH, LE, and MHA) were sampled covering the species' entire distribution range. No samples were genetically similar to *S. beothuk*. If *S. beothuk* occurs along the Pacific coast, one or a few samples of *S. beothuk* would likely by chance have been sampled for that study, but we cannot eliminate the possibility that it occurs there. As no material of *S. fuscum* was included from Japan in this study, 10 collections from Japan deposited at DUKE

were examined morphologically. All samples belong to *S. fuscum*. Additionally, only *S. fuscum*, i.e. the “pale brown colour morph”, has been observed or sampled during field work in western North America (British Columbia and Alaska, Flatberg field work, 1996, 2001, 2008).

Typification

Our taxonomic revision implies the necessity for typification of the name *Sphagnum fuscum* (Schimp.) H.Klinggr. 1872 p. 4 (Klinggräff, 1872). The basionym underlying this specific name is *S. acutifolium* var. *ε. fuscum* Schimper 1857, p. 64, tab. XIII, *ε*.

Schimper’s description (1857) lacks significant morphological information defining the differentiation towards other brown-coloured species in subgenus *Acutifolia*, including *S. beothuk*. The protologue does not cite any original specimens, nor any geographical locations where he had collected or seen material, except for the rather anonymous sentence: “In turfosis profundis ubi sæpe tractus oblegit” [“In deep cushions where often in large extent covering in the regions/tracts”]. We have not been able to trace any original specimens of his *S. acutifolium* var. *ε. fuscum* in the herbaria cited by Vitt *et al.* (1985) to contain Schimper’s bryophytes specimens, thus making it impossible with present knowledge to select a suitable specimen as a lectotype. The ICN (Melbourne Code, McNeill *et al.*, 2012) opens the possibility to designate his single shoot illustration of *ε. fuscum* as the lectotype (Figure 10). However, this illustration does not give clear evidence of the taxonomic relationship to *S. beothuk*, and we therefore find it necessary to epitypify the name. We know from a type specimen of *Bryum microstegium* Bruch & Schimp. (= *B. intermedium* (Brid.) Blandow) preserved in herb. TRH and collected by Schimper, that he visited the Kongsvoll area, Dovrefjell mountains in Central Norway in 1844. We have been unsuccessful in finding more information of his stay there, or whether he collected sphagna or not. *Sphagnum fuscum* is common in the Kongsvoll area, and lies far outside the known lowland, coastal

occurrences of *S. beothuk* in Norway (Figure 8). We therefore designate an epitype of the name *S. fuscum* from the Kongsvoll area based on new material selected for this particular purpose, and which gives unambiguous genetic, morphological and taxonomic distinction of *S. fuscum* from *S. beothuk*.

Sphagnum fuscum (Schimper) H. Klinggräff. 1872 p. 4.

Basionym: *Sphagnum acutifolium* var. *ε. fuscum* Schimper 1857, p. 64, tab. XIII, *ε*.

Lectotype (designated here): [icon in] Schimper 1857, tab. XIII, *ε*. (see Figure 10).

Epitype (designated here): Norway. Sør-Trøndelag county, Oppdal municipality, Dovrefjell, Kongsvoll, just S of Blæsterbekken. Ombrotrophic hummock in bog. 19 August 2014, leg. & det. Tommy Prestø (TRH B-676595; isoepitypes DUKE, H, LE, UBC).

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Tables

Table 1 Mixed models were used to test if five different morphological characters in stem and branch leaves, respectively, differ between *S. beothuk* and *S. fuscum*. The measurements are given in micrometers (μm).

| Measurement | <i>S. beothuk</i> mean | <i>S. fuscum</i> mean | Standard error | t-value | DF | p-value |
|----------------------|---------------------------|--------------------------|-------------------|---------|----|---------|
| <i>Stem leaves</i> | | | | | | |
| STL | 1083.1 | 1180.3 | 29.8 | 3.26 | 17 | 0.005 |
| STM | 575.2 | 636.2 | 12.2 | 4.98 | 17 | <0.001 |
| STT | 342.8 | 457.5 | 9.8 | 11.74 | 17 | <0.001 |
| STM/STT | 1.67 | 1.40 | 0.05 | -6.06 | 17 | <0.001 |
| STL/STM | 1.89 | 1.86 | 0.04 | -0.63 | 17 | 0.540 |
| <i>Branch leaves</i> | | | | | | |
| BRL | 1144.5 | 1081.1 | 32.13 | -2.0 | 17 | 0.065 |
| BRM | 331.7 | 386.8 | 14.56 | 3.8 | 17 | 0.002 |
| BRT | 191.1 | 210.7 | 10.23 | 1.9 | 17 | 0.073 |
| BRM/BRT | 1.75 | 1.85 | 0.05 | 2.1 | 17 | 0.053 |
| BRL/BRM | 3.48 | 2.81 | 0.08 | -7.8 | 17 | <0.001 |

Abbreviations: STL-Stem leaf length; STM-Stem leaf middle width; STT-Stem leaf tip width;

BRL-Branch leaf length; BRM-Branch leaf middle width; BRT-Branch leaf tip width.

Table 2 Morphological characters separating *Sphagnum fuscum* and *S. beothuk*. See text for more detailed characteristics.

| Character | <i>S. fuscum</i> | <i>S. beothuk</i> |
|--|--|----------------------------------|
| Capitulum colour | usually pale brown | dark brown |
| Capitulum shape seen from sides | rather flat to slightly convex | often markedly convex |
| Capitulum arrangement/surface appearance | rather even surface | often faceted surface |
| <i>Branch leaves of spreading branches</i> | | |
| Arrangement | usually non-ranked | varying, but often 5-ranked |
| Shape above | not narrowed | often narrowed |
| Hyalocyst pores on abaxial surface in upper 1/3-1/2 part of leaf | all or nearly all cells with perfect pores, gradually diminishing in size towards apex | many cells lacking perfect pores |
| Presence of minute, ringed pores towards distal end of leaf | usually present | often present but can lack |
| Stem leaf apex | obtuse to broadly obtuse-rounded | acute-obtuse to narrowly obtuse |

Table 3 Records of *Sphagnum beothuk* collected outside Norway.

| Country | County | Collector | Year | Herbarium | Genetic data |
|----------|--------------|--|------|-----------|--------------|
| Canada | Labrador | Flatberg, K.I., Flatberg, B. | 2007 | TRH | Yes |
| Canada | Labrador | Flatberg, K.I., Flatberg, B. | 2007 | TRH | Yes |
| Canada | Labrador | Flatberg, K.I., Flatberg, B. | 2007 | TRH | Yes |
| Canada | Newfoundland | Andrus, R. E., Flatberg, K.I., McQueen, C. | 1996 | TRH | No |
| Canada | Newfoundland | Andrus, R. E., Flatberg, K.I., McQueen, C. | 1996 | TRH | No |
| Canada | Newfoundland | Andrus, R. E., Flatberg, K.I., McQueen, C. | 1996 | TRH | No |
| Canada | Newfoundland | Andrus, R. E., Flatberg, K.I., McQueen, C. | 1996 | TRH | No |
| Canada | Newfoundland | Andrus, R. E., Flatberg, K.I., McQueen, C. | 1996 | TRH | No |
| Canada | Newfoundland | Andrus, R. E., Flatberg, K.I., McQueen, C. | 1996 | TRH | Yes |
| Canada | Newfoundland | Andrus, R. E., Flatberg, K.I., McQueen, C. | 1996 | TRH | No |
| Canada | Newfoundland | Andrus, R. E., Flatberg, K.I., McQueen, C. | 1996 | TRH | No |
| Canada | Newfoundland | Andrus, R. E. | 2005 | DUKE | Yes |
| Canada | Newfoundland | Andrus, R. E. | 2005 | DUKE | Yes |
| Canada | Newfoundland | Andrus, R. E. | 2005 | DUKE | Yes |
| Canada | Newfoundland | Andrus, R. E. | 2005 | DUKE | Yes |
| USA | Maine | Andrus, R. E. | 2007 | DUKE | Yes |
| USA | Maine | Andrus, R. E. | 2007 | DUKE | Yes |
| USA | Maine | Andrus, R. E. | 2007 | DUKE | Yes |
| Scotland | Highland | Flatberg, K.I. | 1987 | TRH | Yes |
| Scotland | Highland | Kyrkjeide, M.O, Kyrkjeide, K.O | 2011 | TRH | Yes |

Figures

Figure 1 The box-plots show stem (left) and branch (right) leaf morphometric measurements of five different characters (top to bottom: leaf length, leaf mid-width, leaf tip-width, leaf mid-width/leaf tip width ratio, and leaf length/leaf mid-width ratio) in *Sphagnum beothuk* and *S. fuscum*.

Figure 2 Stem leaves (above) and branch leaves (below) of *Sphagnum beothuk* (A, B, E, F) and *S. fuscum* (C, D, G, H).

Figure 3 Pore patterns of *Sphagnum beothuk* (A, B) and *S. fuscum* (C, D) in the upper abaxial part of the branch leaves. The pictures are oriented with the leaf apex pointing upwards. See text for details about pore patterns.

Figure 4 Field habit of *Sphagnum beothuk* (A, B, E) and *S. fuscum* (C, D, E). Sporophytes of *S. beothuk* can be seen in picture B and of *S. fuscum* in picture C and E. © Kjell Ivar Flatberg

Figure 5 Genetic structure of *Sphagnum fuscum* and *S. beothuk* inferred in the software Structure based on microsatellite data. Different colours indicate different genetic clusters. The thick lines separate different species and colour morphs, while the thin lines separate individuals.

Figure 6 PCoA based on microsatellite markers of *Sphagnum fuscum* (filled circles), including the epitype (open circles), *S. beothuk* (filled squares), and samples of *S. fuscum* collected as the dark brown colour morph (open squares).

Figure 7 Maximum likelihood tree of *Acutifolia* species based on the chloroplast marker *trnG*. *Sphagnum squarrosum* section *Squarrosa* was chosen as outgroup. The numbers below the branches are bootstrap support.

Figure 8 Distribution maps of *Sphagnum beothuk* (A) and *S. fuscum* (B) in Norway, based on revised material of *S. fuscum* deposited in herbaria BG, O, TRH, and TROM.

Figure 9 Coarse distribution of *Sphagnum fuscum* (grey area) and samples of *S. beothuk* (dots) presently included in molecular studies. The open circles are samples collected as *S. beothuk*, while the black dots are samples identified as the “dark brown colour morph” of *S. fuscum*.

Figure 10 Illustration of *Sphagnum acutifolium* var. *ε. fuscum* from Schimper 1857.

Figure 1

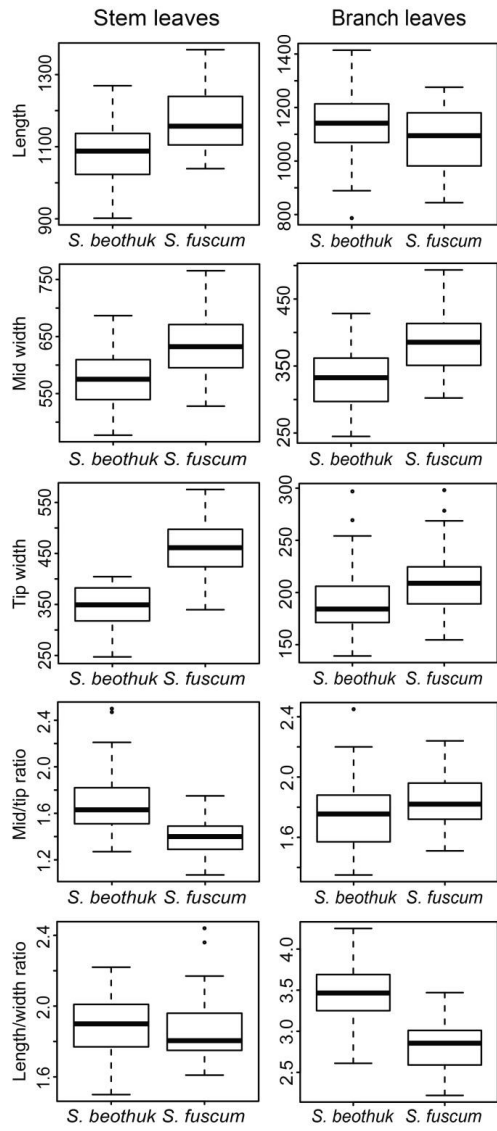


Figure 2

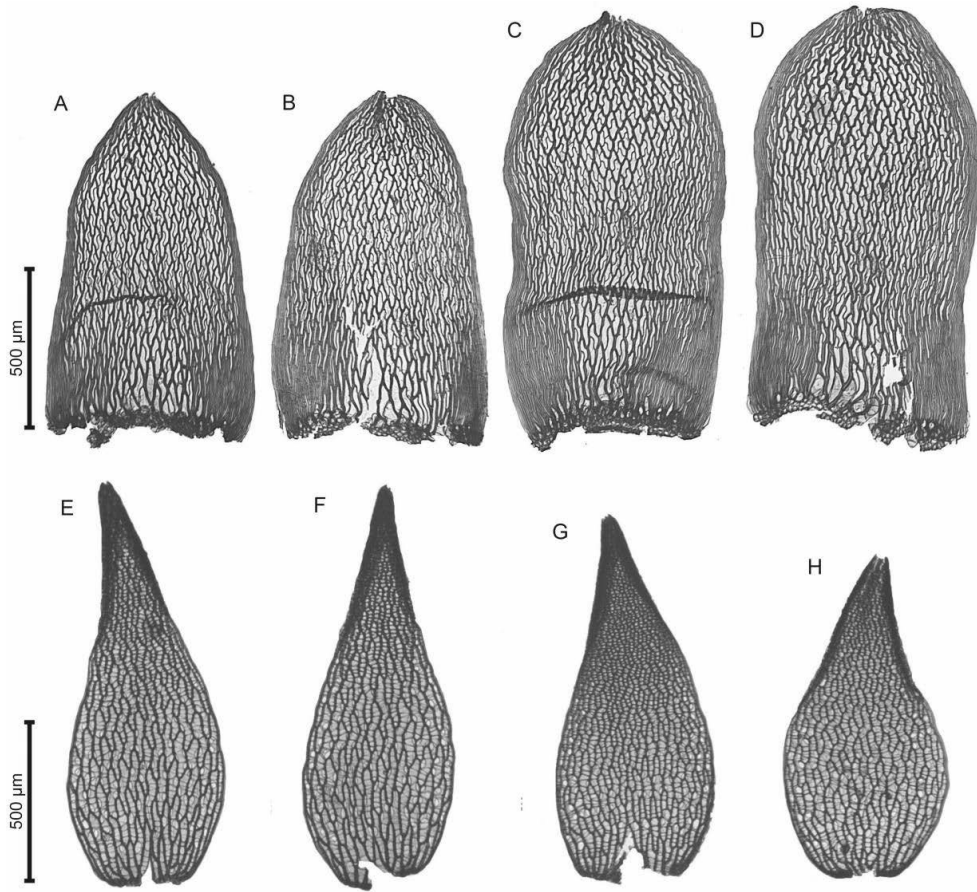


Figure 3

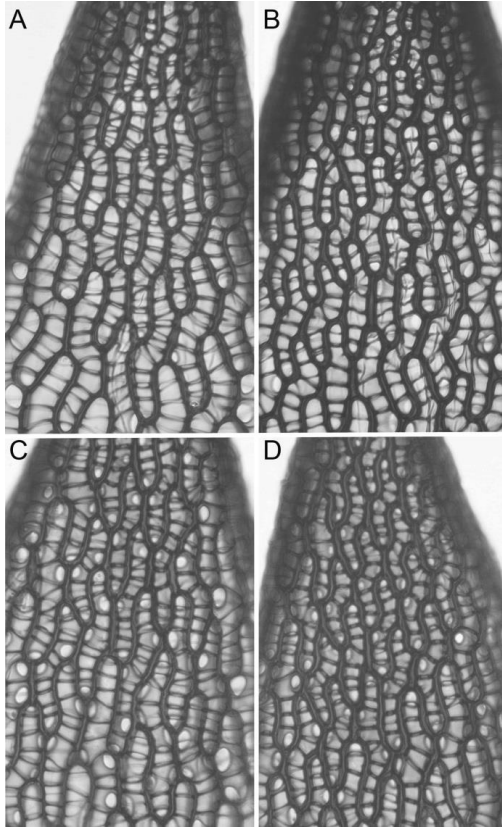


Figure 4

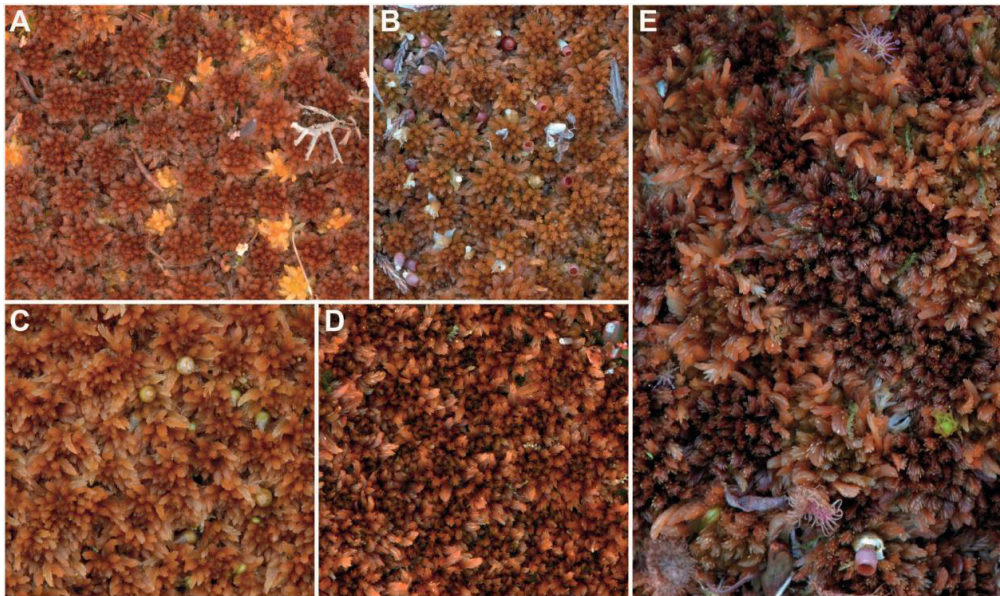


Figure 5

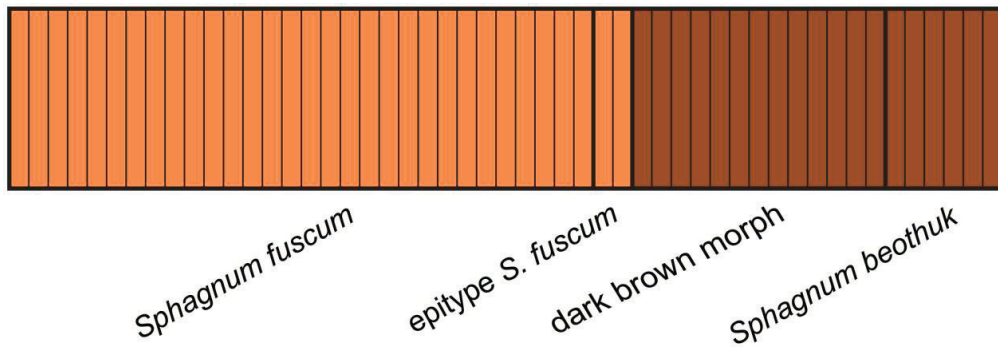


Figure 6

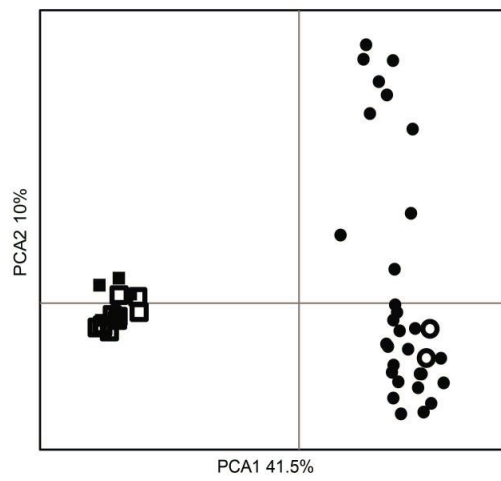


Figure 7

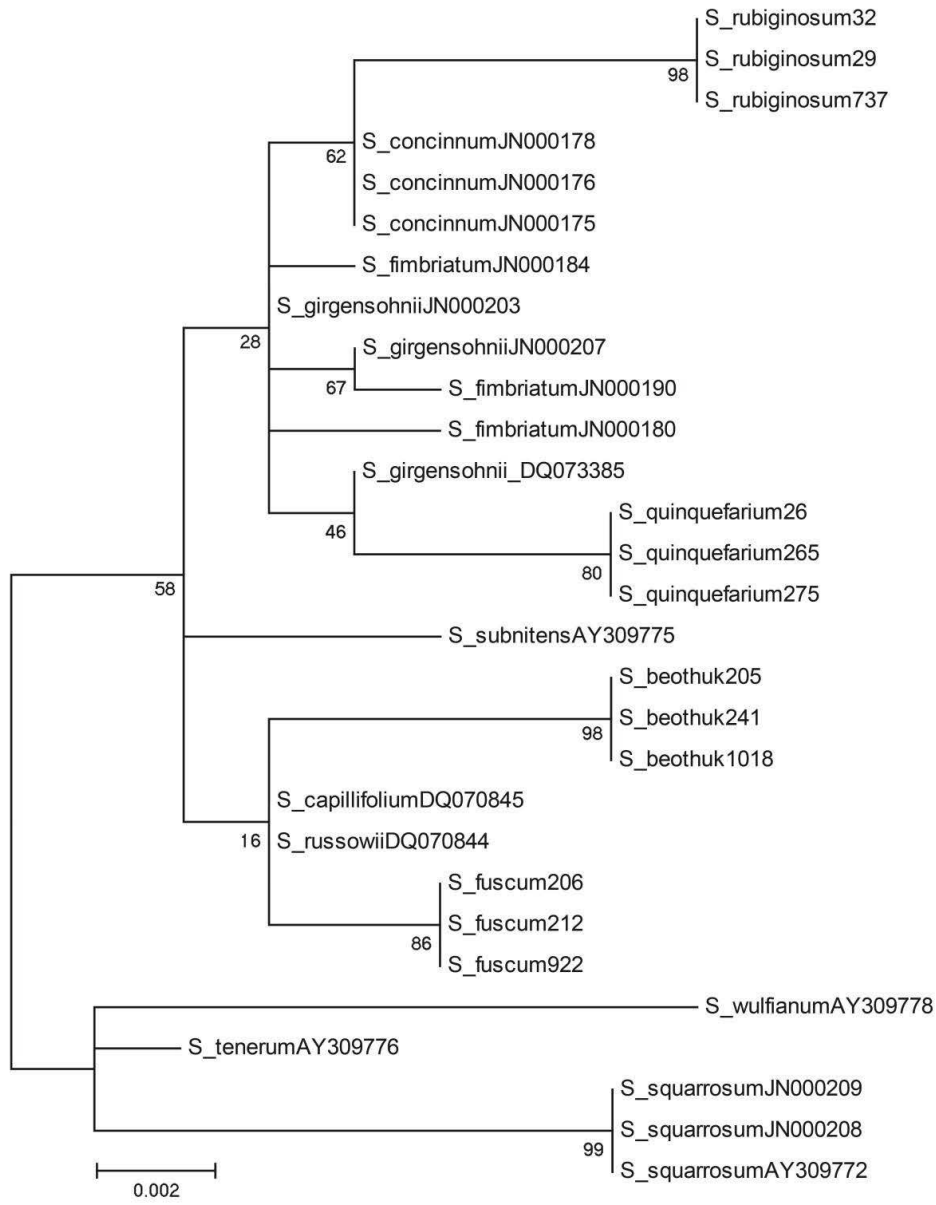


Figure 8

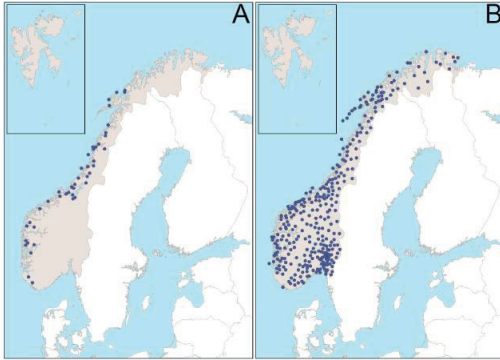


Figure 9

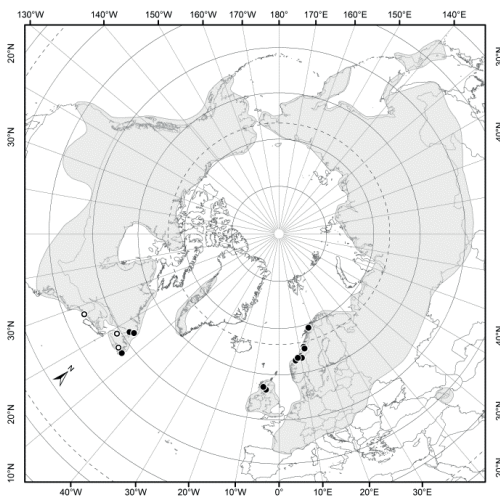


Figure 10



Supplementary Material: Voucher information (Table S1) for samples included in the microsatellite analyses and list of GenBank accession numbers used to build the ML tree.

Table S1 Herbarium, country, county and collectors of all *Sphagnum* specimens used in the study.

| Species | Herb. | Herb. No. | Country | County | Collector |
|------------------------|--------------|------------------|----------------|---------------------------|---|
| <i>Sphagnum fuscum</i> | TRH | 724527 | USA | Alaska | K. I. Flatberg |
| <i>Sphagnum fuscum</i> | TRH | 740592 | Norway | Hedmark | K. I. Flatberg |
| <i>Sphagnum fuscum</i> | TRH | 10127 | Danmark | Nordjylland | K. Thingsgaard |
| <i>Sphagnum fuscum</i> | TRH | 740397 | Norway | Nord-Trøndelag | K. I. Flatberg |
| <i>Sphagnum fuscum</i> | TRH | 724522 | Canada | Newfoundland and Labrador | K. I. Flatberg, B. Flatberg |
| <i>Sphagnum fuscum</i> | TRH | 724535 | USA | Alaska | K. I. Flatberg, K. Thingsgaard |
| <i>Sphagnum fuscum</i> | TRH | 724537 | USA | Alaska | K. I. Flatberg, K. Thingsgaard |
| <i>Sphagnum fuscum</i> | TRH | 724526 | USA | Alaska | K. I. Flatberg |
| <i>Sphagnum fuscum</i> | TRH | 155823 | Norway | Finnmark | K. I. Flatberg |
| <i>Sphagnum fuscum</i> | TRH | 158646 | Norway | Hordaland | K. I. Flatberg |
| <i>Sphagnum fuscum</i> | TRH | 120063 | Norway | Oppland | M. O. Kyrkjeide |
| <i>Sphagnum fuscum</i> | TRH | 690553 | Norway | Nord-Trøndelag | K. Hassel |
| <i>Sphagnum fuscum</i> | LE | - | Russia | Yamal | I. V. Czernyadjeva |
| <i>Sphagnum fuscum</i> | LE | - | Russia | Yamal | I. V. Czernyadjeva, E. Yu. Kuzmina |
| <i>Sphagnum fuscum</i> | LE | - | Russia | Kamtchatka | I. V. Czernyadjeva |
| <i>Sphagnum fuscum</i> | MHA | - | Russia | Krasnoyarsk | S. Popov |
| <i>Sphagnum fuscum</i> | MHA | - | Russia | Sakhalin | V. A. Bakalin |
| <i>Sphagnum fuscum</i> | MHA | - | Russia | Sakhalin | M. Ignatov |
| <i>Sphagnum fuscum</i> | TRH | 741322 | Greenland | Aasiaat | K. I. Flatberg |
| <i>Sphagnum fuscum</i> | TRH | 741342 | Greenland | Ilulissat | K. I. Flatberg |

| | | | | | |
|-------------------------|-----|--------|-----------|---------------------------|--|
| <i>Sphagnum fuscum</i> | TRH | 693759 | Greenland | Sermersooq | K. Hassel, T. Prestø |
| <i>Sphagnum fuscum</i> | TRH | 742351 | Canada | Newfoundland and Labrador | R. E. Andrus, K. I. Flatberg, C. McQueen |
| <i>Sphagnum fuscum</i> | TRH | 724572 | USA | Pennsylvania | R. E. Andrus |
| <i>Sphagnum fuscum</i> | TRH | 724571 | USA | New York | R. E. Andrus, M. Corey |
| <i>Sphagnum fuscum</i> | TRH | 724568 | USA | Maryland | R. E. Andrus, D. D. Boone |
| <i>Sphagnum fuscum</i> | TRH | 724566 | USA | Maryland | R. E. Andrus |
| <i>Sphagnum fuscum</i> | TRH | 724532 | USA | Alaska | K. I. Flatberg, K. Thingsgaard |
| <i>Sphagnum fuscum</i> | TRH | 724553 | USA | Alaska | S. Talbot |
| <i>Sphagnum fuscum</i> | TRH | 724479 | Canada | British Columbia | G. K. Golinski, P. Williston |
| <i>Sphagnum fuscum</i> | MHA | | Russia | Sakhalin | O.Yu. Pisarenko |
| <i>Sphagnum fuscum</i> | TRH | 676595 | Norway | Sør-Trøndelag | T. Prestø |
| <i>Sphagnum fuscum</i> | TRH | 676595 | Norway | Sør-Trøndelag | T. Prestø |
| <i>Sphagnum beothuk</i> | TRH | 724504 | Canada | Newfoundland and Labrador | R. E. Andrus, K. I. Flatberg, C. McQueen |
| <i>Sphagnum beothuk</i> | TRH | 724518 | Canada | Newfoundland and Labrador | K. I. Flatberg, B. Flatberg |
| <i>Sphagnum beothuk</i> | TRH | 724521 | Canada | Newfoundland and Labrador | K. I. Flatberg, B. Flatberg |
| <i>Sphagnum beothuk</i> | TRH | 724524 | Canada | Newfoundland and Labrador | K. I. Flatberg, B. Flatberg |
| <i>Sphagnum beothuk</i> | TRH | 158611 | Norway | Møre og Romsdal | K. I. Flatberg |
| <i>Sphagnum beothuk</i> | TRH | 740050 | Norway | Møre og Romsdal | K. I. Flatberg |
| <i>Sphagnum beothuk</i> | TRH | 10065 | Norway | Nordland | K. Thingsgaard |
| <i>Sphagnum beothuk</i> | TRH | 10089 | Norway | Nordland | K. Thingsgaard |
| <i>Sphagnum beothuk</i> | TRH | 740608 | Norway | Sør-Trøndelag | K. I. Flatberg |
| <i>Sphagnum beothuk</i> | TRH | 740580 | Norway | Sør-Trøndelag | K. I. Flatberg |
| <i>Sphagnum</i> | TRH | 158998 | Norway | Troms | K. I. Flatberg |

| | | | | | |
|---------------------|------|--------|----------|------------------------------|---|
| <i>beothuk</i> | | | | | |
| <i>Sphagnum</i> | | | | | |
| <i>beothuk</i> | TRH | 727119 | Scotland | Highland | K. I. Flatberg |
| <i>Sphagnum</i> | | | | | |
| <i>beothuk</i> | TRH | 120145 | Scotland | Highland | M. O. Kyrkjeide, K. O. Kyrkjeide |
| <i>Sphagnum</i> | | | | | |
| <i>beothuk</i> | DUKE | 130635 | Canada | Newfoundland and Labrador | R. E. Andrus |
| <i>Sphagnum</i> | | | | | |
| <i>beothuk</i> | DUKE | 130640 | Canada | Newfoundland and Labrador | R. E. Andrus |
| <i>Sphagnum</i> | | | | | |
| <i>beothuk</i> | DUKE | 130634 | Canada | Newfoundland and Labrador | R. E. Andrus |
| <i>Sphagnum</i> | | | | | |
| <i>beothuk</i> | DUKE | 130636 | Canada | Newfoundland and Labrador | R. E. Andrus |
| <i>Sphagnum</i> | | | | | |
| <i>beothuk</i> | DUKE | 146898 | USA | Maine | R. E. Andrus |
| <i>Sphagnum</i> | | | | | |
| <i>beothuk</i> | DUKE | 146899 | USA | Maine | R. E. Andrus |
| <i>Sphagnum</i> | | | | | |
| <i>beothuk</i> | DUKE | 146900 | USA | Maine | R. E. Andrus |
| <i>Sphagnum</i> | | | | | |
| <i>warnstorffii</i> | DUKE | 9818 | Europe | Finland | J. A. Shaw |

Table S2 List of species and corresponding GenBank accession numbers included in the maximum likelihood tree of *Acutifolia* species. Voucher identification numbers from herbarium TRH are given for newly generated sequences.

| <i>Species</i> | DNA ID/ GenBank | Voucher |
|-------------------------------|--------------------|------------|
| <i>Sphagnum beothuk</i> | MOK241 | TRH 158998 |
| <i>Sphagnum beothuk</i> | MOK205 | TRH 724521 |
| <i>Sphagnum beothuk</i> | MOK1018 | TRH 727119 |
| <i>Sphagnum capillifolium</i> | DQ070845.2 | |
| <i>Sphagnum concinnum</i> | JN000178.1 | |
| <i>Sphagnum concinnum</i> | JN000175.1 | |
| <i>Sphagnum concinnum</i> | JN000176.1 | |
| <i>Sphagnum fimbriatum</i> | JN000190.1 | |
| <i>Sphagnum fimbriatum</i> | JN000184.1 | |
| <i>Sphagnum fimbriatum</i> | JN000180.1 | |
| <i>Sphagnum fuscum</i> | MOK206 | TRH 724522 |
| <i>Sphagnum fuscum</i> | MOK212 | TRH 724537 |
| <i>Sphagnum fuscum</i> | MOK922 | TRH 120318 |
| <i>Sphagnum girgensohnii</i> | DQ073385.2 | |
| <i>Sphagnum girgensohnii</i> | JN000203.1 | |
| <i>Sphagnum girgensohnii</i> | JN000207.1 | |
| <i>Sphagnum quinquefarium</i> | MOK26 | TRH 690268 |
| <i>Sphagnum quinquefarium</i> | MOK265 | TRH 725187 |
| <i>Sphagnum quinquefarium</i> | MOK275 | TRH 7621 |
| <i>Sphagnum rubiginosum</i> | MOK29 | TRH 740712 |
| <i>Sphagnum rubiginosum</i> | MOK32 | TRH 158850 |
| <i>Sphagnum rubiginosum</i> | MOK737 | TRH 155020 |
| <i>Sphagnum russowii</i> | DQ070844.2 | |
| <i>Sphagnum squarrosum</i> | JN000209.1 | |
| <i>Sphagnum squarrosum</i> | JN000208.1 | |
| <i>Sphagnum squarrosum</i> | AY309772.1 | |
| <i>Sphagnum subnitens</i> | AY309775.1 | |
| <i>Sphagnum tenerum</i> | AY309776.1 | |
| <i>Sphagnum warnstorffii</i> | SB580 | DUKE 9818 |
| <i>Sphagnum wulfianum</i> | AY309778.1 | |

Original article

Long-distance dispersal and cryptic barriers shape genetic structure of peatmosses (*Sphagnum*) across the Northern Hemisphere

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Word count: 6 966

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1 Is there more than one Lady in Red? Spatial genetic structure of the abundant
2 and widespread peatmoss *Sphagnum magellanicum* Brid.

3

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15 Running title: Spatial structure in a widespread peatmoss

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Department of Biology

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| 1978 | Tore Slagsvold | Dr. philos Zoology | Breeding events of birds in relation to spring temperature and environmental phenology |
| 1978 | Egil Sakshaug | Dr. philos Botany | "The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton" |
| 1980 | Arnfinn Langeland | Dr. philos Zoology | Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake |
| 1980 | Helge Reinertsen | Dr. philos Botany | The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton |
| 1982 | Gunn Mari Olsen | Dr. scient Botany | Gravitropism in roots of <i>Pisum sativum</i> and <i>Arabidopsis thaliana</i> |
| 1982 | Dag Dolmen | Dr. philos Zoology | Life aspects of two sympatric species of newts (<i>Triturus, Amphibia</i>) in Norway, with special emphasis on their ecological niche segregation |
| 1984 | Eivin Røskaft | Dr. philos Zoology | Sociobiological studies of the rook <i>Corvus frugilegus</i> |
| 1984 | Anne Margrethe Cameron | Dr. scient Botany | Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinizing hormone in male mature rats |
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| 1985 | Jarle Mork | Dr. philos Zoology | Biochemical genetic studies in fish |
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| 1986 | Bernt-Erik Sæther | Dr. philos Zoology | Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach |
| 1986 | Torleif Holthe | Dr. philos Zoology | Evolution, systematics, nomenclature, and zoogeography in the polychaete orders <i>Owenimorpha</i> and <i>Terebellomorpha</i> , with special reference to the Arctic and Scandinavian fauna |
| 1987 | Helene Lampe | Dr. scient Zoology | The function of bird song in mate attraction and territorial defence, and the importance of song repertoires |
| 1987 | Olav Hogstad | Dr. philos Zoology | Winter survival strategies of the Willow tit <i>Parus montanus</i> |
| 1987 | Jarle Inge Holten | Dr. philos Botany | Autecological investigations along a coast-inland transect at Nord-Møre, Central Norway |
| 1987 | Rita Kumar | Dr. scient Botany | Somaclonal variation in plants regenerated from cell cultures of <i>Nicotiana sanderae</i> and <i>Chrysanthemum morifolium</i> |

| | | | |
|------|-------------------------|-----------------------|---|
| 1987 | Bjørn Åge Tømmerås | Dr. scient Zoology | Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction |
| 1988 | Hans Christian Pedersen | Dr. philos Zoology | Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care |
| 1988 | Tor G. Heggberget | Dr. philos Zoology | Reproduction in Atlantic Salmon (<i>Salmo salar</i>): Aspects of spawning, incubation, early life history and population structure |
| 1988 | Marianne V. Nielsen | Dr. scient Zoology | The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (<i>Mytilus edulis</i>) |
| 1988 | Ole Kristian Berg | Dr. scient Zoology | The formation of landlocked Atlantic salmon (<i>Salmo salar</i> L.) |
| 1989 | John W. Jensen | Dr. philos Zoology | Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth |
| 1989 | Helga J. Vivås | Dr. scient Zoology | Theoretical models of activity pattern and optimal foraging: Predictions for the Moose <i>Alces alces</i> |
| 1989 | Reidar Andersen | Dr. scient Zoology | Interactions between a generalist herbivore, the moose <i>Alces alces</i> , and its winter food resources: a study of behavioural variation |
| 1989 | Kurt Ingar Draget | Dr. scient Botany | Alginate gel media for plant tissue culture |
| 1990 | Bengt Finstad | Dr. scient Zoology | Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season |
| 1990 | Hege Johannesen | Dr. scient Zoology | Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung |
| 1990 | Åse Krøkje | Dr. scient Botany | The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test |
| 1990 | Arne Johan Jensen | Dr. philos Zoology | Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (<i>Salmo salar</i>) and brown trout (<i>Salmo trutta</i>): A summary of studies in Norwegian streams |
| 1990 | Tor Jørgen Almaas | Dr. scient Zoology | Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues |
| 1990 | Magne Husby | Dr. scient Zoology | Breeding strategies in birds: Experiments with the Magpie <i>Pica pica</i> |
| 1991 | Tor Kvam | Dr. scient Zoology | Population biology of the European lynx (<i>Lynx lynx</i>) in Norway |
| 1991 | Jan Henning L'Abée Lund | Dr. philos Zoology | Reproductive biology in freshwater fish, brown trout <i>Salmo trutta</i> and roach <i>Rutilus rutilus</i> in particular |
| 1991 | Asbjørn Moen | Dr. philos Botany | The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Solendet nature reserve; haymaking fens and birch woodlands |
| 1991 | Else Marie Løbersli | Dr. scient Botany | Soil acidification and metal uptake in plants |
| 1991 | Trond Nordtug | Dr. scient Zoology | Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods |
| 1991 | Thyra Solem | Dr. scient Botany | Age, origin and development of blanket mires in Central Norway |
| 1991 | Odd Terje Sandlund | Dr. philos Zoology | The dynamics of habitat use in the salmonid genera <i>Coregonus</i> and <i>Salvelinus</i> : Ontogenic niche shifts and polymorphism |

| | | | |
|------|--------------------------|-----------------------|--|
| 1991 | Nina Jonsson | Dr. philos Zoology | Aspects of migration and spawning in salmonids |
| 1991 | Atle Bones | Dr. scient Botany | Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase) |
| 1992 | Torggrim Breiehagen | Dr. scient Zoology | Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher |
| 1992 | Anne Kjersti Bakken | Dr. scient Botany | The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (<i>Phleum pratense</i> L.) |
| 1992 | Tycho Anker-Nilssen | Dr. scient Zoology | Food supply as a determinant of reproduction and population development in Norwegian Puffins <i>Fratercula arctica</i> |
| 1992 | Bjørn Munro Jenssen | Dr. philos Zoology | Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks |
| 1992 | Arne Vollan Aarset | Dr. philos Zoology | The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans. |
| 1993 | Geir Slupphaug | Dr. scient Botany | Regulation and expression of uracil-DNA glycosylase and O ⁶ -methylguanine-DNA methyltransferase in mammalian cells |
| 1993 | Tor Fredrik Næsje | Dr. scient Zoology | Habitat shifts in coregonids. |
| 1993 | Yngvar Asbjørn Olsen | Dr. scient Zoology | Cortisol dynamics in Atlantic salmon, <i>Salmo salar</i> L.: Basal and stressor-induced variations in plasma levels and some secondary effects. |
| 1993 | Bård Pedersen | Dr. scient Botany | Theoretical studies of life history evolution in modular and clonal organisms |
| 1993 | Ole Petter Thangstad | Dr. scient Botany | Molecular studies of myrosinase in Brassicaceae |
| 1993 | Thrine L. M. Heggberget | Dr. scient Zoology | Reproductive strategy and feeding ecology of the Eurasian otter <i>Lutra lutra</i> . |
| 1993 | Kjetil Bevanger | Dr. scient Zoology | Avian interactions with utility structures, a biological approach. |
| 1993 | Kåre Haugan | Dr. scient Botany | Mutations in the replication control gene trfA of the broad host-range plasmid RK2 |
| 1994 | Peder Fiske | Dr. scient Zoology | Sexual selection in the lekking great snipe (<i>Gallinago media</i>): Male mating success and female behaviour at the lek |
| 1994 | Kjell Inge Reitan | Dr. scient Botany | Nutritional effects of algae in first-feeding of marine fish larvae |
| 1994 | Nils Røv | Dr. scient Zoology | Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant <i>Phalacrocorax carbo carbo</i> |
| 1994 | Annette-Susanne Hoepfner | Dr. scient Botany | Tissue culture techniques in propagation and breeding of Red Raspberry (<i>Rubus idaeus</i> L.) |
| 1994 | Inga Elise Bruteig | Dr. scient Botany | Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers |
| 1994 | Geir Johnsen | Dr. scient Botany | Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses |
| 1994 | Morten Bakken | Dr. scient Zoology | Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, <i>Vulpes vulpes</i> |
| 1994 | Arne Moksnes | Dr. philos Zoology | Host adaptations towards brood parasitism by the Cuckoo |
| 1994 | Solveig Bakken | Dr. scient Botany | Growth and nitrogen status in the moss <i>Dicranum majus</i> Sm. as influenced by nitrogen supply |

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|------|-------------------------|-----------------------|--|
| 1994 | Torbjørn Forseth | Dr. scient Zoology | Bioenergetics in ecological and life history studies of fishes. |
| 1995 | Olav Vadstein | Dr. philos Botany | The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions |
| 1995 | Hanne Christensen | Dr. scient Zoology | Determinants of Otter <i>Lutra lutra</i> distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink <i>Mustela vison</i> |
| 1995 | Svein Håkon Lorentsen | Dr. scient Zoology | Reproductive effort in the Antarctic Petrel <i>Thalassoica antarctica</i> ; the effect of parental body size and condition |
| 1995 | Chris Jørgen Jensen | Dr. scient Zoology | The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity |
| 1995 | Martha Kold Bakkevig | Dr. scient Zoology | The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport |
| 1995 | Vidar Moen | Dr. scient Zoology | Distribution patterns and adaptations to light in newly introduced populations of <i>Mysis relicta</i> and constraints on Cladoceran and Char populations |
| 1995 | Hans Haavardsholm Blom | Dr. philos Botany | A revision of the <i>Schistidium apocarpum</i> complex in Norway and Sweden |
| 1996 | Jorun Skjærmo | Dr. scient Botany | Microbial ecology of early stages of cultivated marine fish; impact fish-bacterial interactions on growth and survival of larvae |
| 1996 | Ola Ugedal | Dr. scient Zoology | Radiocesium turnover in freshwater fishes |
| 1996 | Ingibjörg Einarsdóttir | Dr. scient Zoology | Production of Atlantic salmon (<i>Salmo salar</i>) and Arctic charr (<i>Salvelinus alpinus</i>): A study of some physiological and immunological responses to rearing routines |
| 1996 | Christina M. S. Pereira | Dr. scient Zoology | Glucose metabolism in salmonids: Dietary effects and hormonal regulation |
| 1996 | Jan Fredrik Børseth | Dr. scient Zoology | The sodium energy gradients in muscle cells of <i>Mytilus edulis</i> and the effects of organic xenobiotics |
| 1996 | Gunnar Henriksen | Dr. scient Zoology | Status of Grey seal <i>Halichoerus grypus</i> and Harbour seal <i>Phoca vitulina</i> in the Barents sea region |
| 1997 | Gunvor Øie | Dr. scient Botany | Eevaluation of rotifer <i>Brachionus plicatilis</i> quality in early first feeding of turbot <i>Scophthalmus maximus</i> L. larvae |
| 1997 | Håkon Holien | Dr. scient Botany | Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters |
| 1997 | Ole Reitan | Dr. scient Zoology | Responses of birds to habitat disturbance due to damming |
| 1997 | Jon Arne Grøttum | Dr. scient Zoology | Physiological effects of reduced water quality on fish in aquaculture |
| 1997 | Per Gustav Thingstad | Dr. scient Zoology | Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher |
| 1997 | Torgeir Nygård | Dr. scient Zoology | Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as |
| 1997 | Signe Nybø | Dr. scient Zoology | Impacts of long-range transported air pollution on birds with particular reference to the dipper <i>Cinclus cinclus</i> in southern Norway |
| 1997 | Atle Wibe | Dr. scient Zoology | Identification of conifer volatiles detected by receptor neurons in the pine weevil (<i>Hylobius abietis</i>), analysed by gas chromatography linked to electrophysiology and to mass spectrometry |

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| 1997 | Rolv Lundheim | Dr. scient Zoology | Adaptive and incidental biological ice nucleators |
| 1997 | Arild Magne Landa | Dr. scient Zoology | Wolverines in Scandinavia: ecology, sheep depredation and conservation |
| 1997 | Kåre Magne Nielsen | Dr. scient Botany | An evolution of possible horizontal gene transfer from plants to soil bacteria by studies of natural transformation in <i>Acinetobacter calcoaceticus</i> |
| 1997 | Jarle Tufto | Dr. scient Zoology | Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models |
| 1997 | Trygve Hesthagen | Dr. philos Zoology | Population responses of Arctic charr (<i>Salvelinus alpinus</i> (L.)) and brown trout (<i>Salmo trutta</i> L.) to acidification in Norwegian inland waters |
| 1997 | Trygve Sigholt | Dr. philos Zoology | Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (<i>Salmo salar</i>) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet |
| 1997 | Jan Østnes | Dr. scient Zoology | Cold sensation in adult and neonate birds |
| 1998 | Seethaledsumy Visvalingam | Dr. scient Botany | Influence of environmental factors on myrosinases and myrosinase-binding proteins |
| 1998 | Thor Harald Ringsby | Dr. scient Zoology | Variation in space and time: The biology of a House sparrow metapopulation |
| 1998 | Erling Johan Solberg | Dr. scient Zoology | Variation in population dynamics and life history in a Norwegian moose (<i>Alces alces</i>) population: consequences of harvesting in a variable environment |
| 1998 | Sigurd Mjøen Saastad | Dr. scient Botany | Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity |
| 1998 | Bjarte Mortensen | Dr. scient Botany | Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro |
| 1998 | Gunnar Austrheim | Dr. scient Botany | Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach |
| 1998 | Bente Gunnveig Berg | Dr. scient Zoology | Encoding of pheromone information in two related moth species |
| 1999 | Kristian Overskaug | Dr. scient Zoology | Behavioural and morphological characteristics in Northern Tawny Owls <i>Strix aluco</i> : An intra- and interspecific comparative approach |
| 1999 | Hans Kristen Stenøien | Dr. scient Botany | Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts) |
| 1999 | Trond Arnesen | Dr. scient Botany | Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway |
| 1999 | Ingvar Stenberg | Dr. scient Zoology | Habitat selection, reproduction and survival in the White-backed Woodpecker <i>Dendrocopos leucotos</i> |
| 1999 | Stein Olle Johansen | Dr. scient Botany | A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis |
| 1999 | Trina Falck Galloway | Dr. scient Zoology | Muscle development and growth in early life stages of the Atlantic cod (<i>Gadus morhua</i> L.) and Halibut (<i>Hippoglossus hippoglossus</i> L.) |
| 1999 | Marianne Giæver | Dr. scient Zoology | Population genetic studies in three gadoid species: blue whiting (<i>Micromisistius poutassou</i>), haddock (<i>Melanogrammus aeglefinus</i>) and cod (<i>Gadus morhua</i>) in the North-East Atlantic |

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|------|--------------------------|-----------------------|--|
| 1999 | Hans Martin Hanslin | Dr. scient Botany | The impact of environmental conditions of density dependent performance in the boreal forest bryophytes <i>Dicranum majus</i> , <i>Hylocomium splendens</i> , <i>Plagiochila asplenigides</i> , <i>Ptilium crista-castrensis</i> and <i>Rhytidiadelphus lokeus</i> |
| 1999 | Ingrid Bysveen Mjølnerød | Dr. scient Zoology | Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (<i>Salmo salar</i>) revealed by molecular genetic techniques |
| 1999 | Else Berit Skagen | Dr. scient Botany | The early regeneration process in protoplasts from <i>Brassica napus</i> hypocotyls cultivated under various g-forces |
| 1999 | Stein-Are Sæther | Dr. philos Zoology | Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe |
| 1999 | Katrine Wangen Rustad | Dr. scient Zoology | Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease |
| 1999 | Per Terje Smiseth | Dr. scient Zoology | Social evolution in monogamous families: Young Atlantic salmon (<i>Salmo salar</i> L.) and Brown trout (<i>Salmo trutta</i> L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions |
| 1999 | Gunnbjørn Bremset | Dr. scient Zoology | Host specificity as parameter in estimates of arthropod species richness |
| 1999 | Frode Ødegaard | Dr. scient Zoology | Expressional and functional analyses of human, secretory phospholipase A2 |
| 1999 | Sonja Andersen | Dr. scient Zoology | Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture |
| 2000 | Ingrid Salvesen | Dr. scient Botany | The Cuckoo (<i>Cuculus canorus</i>) and its host: adaptations and counteradaptations in a coevolutionary arms race |
| 2000 | Ingar Jostein Øien | Dr. scient Zoology | Methods for the microbial control of live food used for the rearing of marine fish larvae |
| 2000 | Pavlos Makridis | Dr. scient Botany | Sexual segregation in the African elephant (<i>Loxodonta africana</i>) |
| 2000 | Sigbjørn Stokke | Dr. scient Zoology | Seawater tolerance, migratory behaviour and growth of Charr, (<i>Salvelinus alpinus</i>), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard |
| 2000 | Odd A. Gulseth | Dr. philos Zoology | Biochemical impacts of Cd, Cu and Zn on brown trout (<i>Salmo trutta</i>) in two mining-contaminated rivers in Central Norway |
| 2000 | Pål A. Olsvik | Dr. scient Zoology | Maternal effects in fish: Implications for the evolution of breeding time and egg size |
| 2000 | Sigurd Einum | Dr. scient Zoology | Production and nutritional adaptation of the brine shrimp <i>Artemia</i> sp. as live food organism for larvae of marine cold water fish species |
| 2001 | Jan Ove Evjemo | Dr. scient Zoology | Lichen response to environmental changes in the managed boreal forest systems |
| 2001 | Olga Hilmo | Dr. scient Botany | Male dimorphism and reproductive biology in corkwing wrasse (<i>Symphodus melops</i> L.) |
| 2001 | Ingebrigt Uglem | Dr. scient Zoology | Coevolutionary adaptations in avian brood parasites and their hosts |
| 2001 | Bård Gunnar Stokke | Dr. scient Zoology | Spatio-temporal dynamics in Svalbard reindeer (<i>Rangifer tarandus platyrhynchus</i>) |
| 2002 | Ronny Aanes | Dr. scient Zoology | Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses |
| 2002 | Mariann Sandsund | Dr. scient Zoology | |

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|------|---------------------------|-----------------------|--|
| 2002 | Dag-Inge Øien | Dr. scient Botany | Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway |
| 2002 | Frank Rosell | Dr. scient Zoology | The function of scent marking in beaver (<i>Castor fiber</i>) |
| 2002 | Janne Østvang | Dr. scient Botany | The Role and Regulation of Phospholipase A ₂ in Monocytes During Atherosclerosis Development |
| 2002 | Terje Thun | Dr. philos Biology | Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material |
| 2002 | Birgit Hafjeld Borgen | Dr. scient Biology | Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth |
| 2002 | Bård Øyvind Solberg | Dr. scient Biology | Effects of climatic change on the growth of dominating tree species along major environmental gradients |
| 2002 | Per Winge | Dr. scient Biology | The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in <i>Arabidopsis thaliana</i> and the Ral GTPase from <i>Drosophila melanogaster</i> |
| 2002 | Henrik Jensen | Dr. scient Biology | Causes and consequences of individual variation in fitness-related traits in house sparrows |
| 2003 | Jens Rohloff | Dr. philos Biology | Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control |
| 2003 | Åsa Maria O. Espmark Wibe | Dr. scient Biology | Behavioural effects of environmental pollution in threespine stickleback <i>Gasterosteus aculeatur</i> L. |
| 2003 | Dagmar Hagen | Dr. scient Biology | Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach |
| 2003 | Bjørn Dahle | Dr. scient Biology | Reproductive strategies in Scandinavian brown bears |
| 2003 | Cyril Lebogang Taolo | Dr. scient Biology | Population ecology, seasonal movement and habitat use of the African buffalo (<i>Syncerus caffer</i>) in Chobe National Park, Botswana |
| 2003 | Marit Stranden | Dr. scient Biology | Olfactory receptor neurones specified for the same odorants in three related Heliothine species (<i>Helicoverpa armigera</i> , <i>Helicoverpa assulta</i> and <i>Heliothis virescens</i>) |
| 2003 | Kristian Hassel | Dr. scient Biology | Life history characteristics and genetic variation in an expanding species, <i>Pogonatum dentatum</i> |
| 2003 | David Alexander Rae | Dr. scient Biology | Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Arctic environments |
| 2003 | Åsa A Borg | Dr. scient Biology | Sex roles and reproductive behaviour in gobies and guppies: a female perspective |
| 2003 | Eldar Åsgard Bendiksen | Dr. scient Biology | Environmental effects on lipid nutrition of farmed Atlantic salmon (<i>Salmo Salar</i> L.) parr and smolt |
| 2004 | Torkild Bakken | Dr. scient Biology | A revision of Nereidinae (Polychaeta, Nereididae) |
| 2004 | Ingar Pareliussen | Dr. scient Biology | Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar |
| 2004 | Tore Brembu | Dr. scient Biology | Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in <i>Arabidopsis thaliana</i> |
| 2004 | Liv S. Nilsen | Dr. scient Biology | Coastal heath vegetation on central Norway; recent past, present state and future possibilities |
| 2004 | Hanne T. Skiri | Dr. scient Biology | Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (<i>Heliothis virescens</i> , <i>Helicoverpa armigera</i> and <i>Helicoverpa assulta</i>) |

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| 2004 | Lene Østby | Dr. scient Biology | Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment |
| 2004 | Emmanuel J. Gerreta | Dr. philos Biology | The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania |
| 2004 | Linda Dalen | Dr. scient Biology | Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming |
| 2004 | Lisbeth Mehli | Dr. scient Biology | Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (<i>Fragaria x ananassa</i>): characterisation and induction of the gene following fruit infection by <i>Botrytis cinerea</i> |
| 2004 | Børge Moe | Dr. scient Biology | Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage |
| 2005 | Matilde Skogen Chauton | Dr. scient Biology | Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples |
| 2005 | Sten Karlsson | Dr. scient Biology | Dynamics of Genetic Polymorphisms |
| 2005 | Terje Bongard | Dr. scient Biology | Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period |
| 2005 | Tonette Røstelien | ph.d Biology | Functional characterisation of olfactory receptor neurone types in heliothine moths |
| 2005 | Erlend Kristiansen | Dr. scient Biology | Studies on antifreeze proteins |
| 2005 | Eugen G. Sørmo | Dr. scient Biology | Organochlorine pollutants in grey seal (<i>Halichoerus grypus</i>) pups and their impact on plasma thyrid hormone and vitamin A concentrations |
| 2005 | Christian Westad | Dr. scient Biology | Motor control of the upper trapezius |
| 2005 | Lasse Mork Olsen | ph.d Biology | Interactions between marine osmo- and phagotrophs in different physicochemical environments |
| 2005 | Åslaug Viken | ph.d Biology | Implications of mate choice for the management of small populations |
| 2005 | Ariaya Hymete Sahle Dingle | ph.d Biology | Investigation of the biological activities and chemical constituents of selected <i>Echinops</i> spp. growing in Ethiopia |
| 2005 | Anders Gravbrøt Finstad Shimane | ph.d Biology | Salmonid fishes in a changing climate: The winter challenge |
| 2005 | Washington Makabu | ph.d Biology | Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana |
| 2005 | Kjartan Østbye | Dr. scient Biology | The European whitefish <i>Coregonus lavaretus</i> (L.) species complex: historical contingency and adaptive radiation |
| 2006 | Kari Mette Murvoll | ph.d Biology | Levels and effects of persistent organic pollutants (POPs) in seabirds, Retinoids and α -tocopherol – potential biomarkers of POPs in birds? |
| 2006 | Ivar Herfindal | Dr. scient Biology | Life history consequences of environmental variation along ecological gradients in northern ungulates |
| 2006 | Nils Egil Tokle | ph.d Biology | Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on <i>Calanus finmarchicus</i> |
| 2006 | Jan Ove Gjershaug | Dr. philos Biology | Taxonomy and conservation status of some booted eagles in south-east Asia |
| 2006 | Jon Kristian Skei | Dr. scient Biology | Conservation biology and acidification problems in the breeding habitat of amphibians in Norway |
| 2006 | Johanna Järnegren | ph.d Biology | Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity |

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|------|---------------------------|--------------|--|
| 2006 | Bjørn Henrik Hansen | ph.d Biology | Metal-mediated oxidative stress responses in brown trout (<i>Salmo trutta</i>) from mining contaminated rivers in Central Norway |
| 2006 | Vidar Grøtan | ph.d Biology | Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates |
| 2006 | Jafari R Kideghesho | ph.d Biology | Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania |
| 2006 | Anna Maria Billing | ph.d Biology | Reproductive decisions in the sex role reversed pipefish <i>Syngnathus typhle</i> : when and how to invest in reproduction |
| 2006 | Henrik Pärn | ph.d Biology | Female ornaments and reproductive biology in the bluethroat |
| 2006 | Anders J. Fjellheim | ph.d Biology | Selection and administration of probiotic bacteria to marine fish larvae |
| 2006 | P. Andreas Svensson | ph.d Biology | Female coloration, egg carotenoids and reproductive success: gobies as a model system |
| 2007 | Sindre A. Pedersen | ph.d Biology | Metal binding proteins and antifreeze proteins in the beetle <i>Tenebrio molitor</i> - a study on possible competition for the semi-essential amino acid cysteine |
| 2007 | Kasper Hancke | ph.d Biology | Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae |
| 2007 | Tomas Holmern | ph.d Biology | Bushmeat hunting in the western Serengeti: Implications for community-based conservation |
| 2007 | Kari Jørgensen | ph.d Biology | Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth <i>Heliothis virescens</i> |
| 2007 | Stig Ulland | ph.d Biology | Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (<i>Mamestra brassicae</i> L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry |
| 2007 | Snorre Henriksen | ph.d Biology | Spatial and temporal variation in herbivore resources at northern latitudes |
| 2007 | Roelof Frans May | ph.d Biology | Spatial Ecology of Wolverines in Scandinavia |
| 2007 | Vedasto Gabriel Ndibalema | ph.d Biology | Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania |
| 2007 | Julius William Nyahongo | ph.d Biology | Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania |
| 2007 | Shombe Ntaraluka Hassan | ph.d Biology | Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania |
| 2007 | Per-Arvid Wold | ph.d Biology | Functional development and response to dietary treatment in larval Atlantic cod (<i>Gadus morhua</i> L.) Focus on formulated diets and early weaning |
| 2007 | Anne Skjetne Mortensen | ph.d Biology | Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios |
| 2008 | Brage Bremset Hansen | ph.d Biology | The Svalbard reindeer (<i>Rangifer tarandus platyrhynchus</i>) and its food base: plant-herbivore interactions in a high-arctic ecosystem |
| 2008 | Jiska van Dijk | ph.d Biology | Wolverine foraging strategies in a multiple-use landscape |
| 2008 | Flora John Magige | ph.d Biology | The ecology and behaviour of the Masai Ostrich (<i>Struthio camelus massaicus</i>) in the Serengeti Ecosystem, Tanzania |

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|------|-----------------------------|--------------------|--|
| 2008 | Bernt Rønning | ph.d Biology | Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (<i>Taeniopygia guttata</i>) |
| 2008 | Sølvi Wehn | ph.d Biology | Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen |
| 2008 | Trond Moxness Kortner | ph.d Biology | "The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (<i>Gadus morhua</i>): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations" |
| 2008 | Katarina Mariann Jørgensen | Dr. scient Biology | The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation |
| 2008 | Tommy Jørstad | ph.d Biology | Statistical Modelling of Gene Expression Data |
| 2008 | Anna Kusnierczyk | ph.d Biology | <i>Arabidopsis thaliana</i> Responses to Aphid Infestation |
| 2008 | Jussi Evertsen | ph.d Biology | Herbivore sacoglossans with photosynthetic chloroplasts |
| 2008 | John Eilif Hermansen | ph.d Biology | Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania |
| 2008 | Ragnhild Lyngved | ph.d Biology | Somatic embryogenesis in <i>Cyclamen persicum</i> . Biological investigations and educational aspects of cloning |
| 2008 | Line Elisabeth Sundt-Hansen | ph.d Biology | Cost of rapid growth in salmonid fishes |
| 2008 | Line Johansen | ph.d Biology | Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution |
| 2009 | Astrid Jullumstrø Feuerherm | ph.d Biology | Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease |
| 2009 | Pål Kvello | ph.d Biology | Neurons forming the network involved in gustatory coding and learning in the moth <i>Heliothis virescens</i> : Physiological and morphological characterisation, and integration into a standard brain atlas |
| 2009 | Trygve Devold Kjellsen | ph.d Biology | Extreme Frost Tolerance in Boreal Conifers |
| 2009 | Johan Reinert Vikan | ph.d Biology | Coevolutionary interactions between common cuckoos <i>Cuculus canorus</i> and <i>Fringilla</i> finches |
| 2009 | Zsolt Volent | ph.d Biology | Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter |
| 2009 | Lester Rocha | ph.d Biology | Functional responses of perennial grasses to simulated grazing and resource availability |
| 2009 | Dennis Ikanda | ph.d Biology | Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (<i>Panthera leo</i>) in Tanzania |
| 2010 | Huy Quang Nguyen | ph.d Biology | Egg characteristics and development of larval digestive function of cobia (<i>Rachycentron canadum</i>) in response to dietary treatments - Focus on formulated diets |
| 2010 | Eli Kvingedal | ph.d Biology | Intraspecific competition in stream salmonids: the impact of environment and phenotype |
| 2010 | Sverre Lundemo | ph.d Biology | Molecular studies of genetic structuring and demography in <i>Arabidopsis</i> from Northern Europe |
| 2010 | Iddi Mihijai Mfunda | ph.d Biology | Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania |

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|------|------------------------------------|----------------------------|---|
| 2010 | Anton Tinchov Antonov | ph.d Biology | Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis |
| 2010 | Anders Lyngstad | ph.d Biology | Population Ecology of <i>Eriophorum latifolium</i> , a Clonal Species in Rich Fen Vegetation |
| 2010 | Hilde Færevik | ph.d Biology | Impact of protective clothing on thermal and cognitive responses |
| 2010 | Ingerid Brønne Arbo | ph.d Medical technology | Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans |
| 2010 | Yngvild Vindenes | ph.d Biology | Stochastic modeling of finite populations with individual heterogeneity in vital parameters |
| 2010 | Hans-Richard Brattbakk | ph.d Medical technology | The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits |
| 2011 | Geir Hysing Bolstad | ph.d Biology | Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy |
| 2011 | Karen de Jong | ph.d Biology | Operational sex ratio and reproductive behaviour in the two-spotted goby (<i>Gobiusculus flavescens</i>) |
| 2011 | Ann-Iren Kittang | ph.d Biology | <i>Arabidopsis thaliana</i> L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity |
| 2011 | Aline Magdalena Lee | ph.d Biology | Stochastic modeling of mating systems and their effect on population dynamics and genetics |
| 2011 | Christopher Gravningen Sørmo | ph.d Biology | Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in <i>Arabidopsis thaliana</i> |
| 2011 | Grethe Robertsen | ph.d Biology | Relative performance of salmonid phenotypes across environments and competitive intensities |
| 2011 | Line-Kristin Larsen | ph.d Biology | Life-history trait dynamics in experimental populations of guppy (<i>Poecilia reticulata</i>): the role of breeding regime and captive environment |
| 2011 | Maxim A. K. Teichert | ph.d Biology | Regulation in Atlantic salmon (<i>Salmo salar</i>): The interaction between habitat and density |
| 2011 | Torunn Beate Hancke | ph.d Biology | Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology |
| 2011 | Sajeda Begum | ph.d Biology | Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh |
| 2011 | Kari J. K. Attramadal | ph.d Biology | Water treatment as an approach to increase microbial control in the culture of cold water marine larvae |
| 2011 | Camilla Kalvatn Egset | ph.d Biology | The Evolvability of Static Allometry: A Case Study |
| 2011 | AHM Raihan Sarker | ph.d Biology | Conflict over the conservation of the Asian elephant (<i>Elephas maximus</i>) in Bangladesh |
| 2011 | Gro Dehli Villanger | ph.d Biology | Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals |
| 2011 | Kari Bjørneraas | ph.d Biology | Spatiotemporal variation in resource utilisation by a large herbivore, the moose |
| 2011 | John Odden | ph.d Biology | The ecology of a conflict: Eurasian lynx depredation on domestic sheep |
| 2011 | Simen Pedersen | ph.d Biology | Effects of native and introduced cervids on small mammals and birds |
| 2011 | Mohsen Falahati- Anbaran | ph.d Biology | Evolutionary consequences of seed banks and seed dispersal in <i>Arabidopsis</i> |

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| 2012 | Jakob Hønborg Hansen | ph.d Biology | Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance |
| 2012 | Elin Noreen | ph.d Biology | Consequences of diet quality and age on life-history traits in a small passerine bird |
| 2012 | Irja Ida Ratikainen | ph.d Biology | Theoretical and empirical approaches to studying foraging decisions: the past and future of behavioural ecology |
| 2012 | Aleksander Handå | ph.d Biology | Cultivation of mussels (<i>Mytilus edulis</i>): Feed requirements, storage and integration with salmon (<i>Salmo salar</i>) farming |
| 2012 | Morten Kraabøl | ph.d Biology | Reproductive and migratory challenges inflicted on migrant brown trout (<i>Salmo trutta</i> L) in a heavily modified river |
| 2012 | Jisca Huisman | ph.d Biology | Gene flow and natural selection in Atlantic salmon |
| | Maria Bergvik | ph.d Biology | Lipid and astaxanthin contents and biochemical post-harvest stability in <i>Calanus finmarchicus</i> |
| 2012 | Bjarte Bye Løfaldli | ph.d Biology | Functional and morphological characterization of central olfactory neurons in the model insect <i>Heliothis virescens</i> . |
| 2012 | Karen Marie Hammer | ph.d Biology | Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia |
| 2012 | Øystein Nordrum Wiggen | ph.d Biology | Optimal performance in the cold |
| 2012 | Robert Dominikus Fyumagwa | Dr. Philos Biology | Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania |
| 2012 | Jenny Bytingsvik | ph.d Biology | Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs |
| 2012 | Christer Moe Rolandsen | ph.d Biology | The ecological significance of space use and movement patterns of moose in a variable environment |
| 2012 | Erlend Kjeldsberg Hovland | ph.d Biology | Bio-optics and Ecology in <i>Emiliana huxleyi</i> Blooms: Field and Remote Sensing Studies in Norwegian Waters |
| 2012 | Lise Cats Myhre | ph.d Biology | Effects of the social and physical environment on mating behaviour in a marine fish |
| 2012 | Tonje Aronsen | ph.d Biology | Demographic, environmental and evolutionary aspects of sexual selection |
| | Bin Liu | ph.d Biology | Molecular genetic investigation of cell separation and cell death regulation in <i>Arabidopsis thaliana</i> |
| 2013 | Jørgen Rosvold | ph.d Biology | Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective |
| 2013 | Pankaj Barah | ph.d Biology | Integrated Systems Approaches to Study Plant Stress Responses |
| 2013 | Marit Linnerud | ph.d Biology | Patterns in spatial and temporal variation in population abundances of vertebrates |
| 2013 | Xinxin Wang | ph.d Biology | Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (<i>Salmo salar</i>) farming |
| 2013 | Ingrid Ertshus Mathisen | ph.d Biology | Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia |
| 2013 | Anders Foldvik | ph.d Biology | Spatial distributions and productivity in salmonid populations |
| 2013 | Anna Marie Holand | ph.d Biology | Statistical methods for estimating intra- and inter-population variation in genetic diversity |
| 2013 | Anna Solvang Båtnes | ph.d Biology | Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night |

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| 2013 | Ane Kjersti Vie | ph.d Biology | Molecular and functional characterisation of the IDA family of signalling peptides in <i>Arabidopsis thaliana</i> |
| 2013 | Marianne Nymark | ph.d Biology | Light responses in the marine diatom <i>Phaeodactylum tricorutum</i> |
| 2014 | Jannik Schultner | ph.d Biology | Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird |
| 2014 | Craig Ryan Jackson | ph.d Biology | Factors influencing African wild dog (<i>Lycaon pictus</i>) habitat selection and ranging behaviour: conservation and management implications |
| 2014 | Aravind Venkatesan | ph.d Biology | Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences |
| 2014 | Kristin Collier Valle | ph.d Biology | Photoacclimation mechanisms and light responses in marine micro- and macroalgae |
| 2014 | Michael Puffer | ph.d Biology | Factors influencing African wild dog (<i>Lycaon pictus</i>) habitat selection and ranging behaviour: conservation and management implications |
| 2014 | Gundula S. Bartzke | ph.d Biology | Effects of power lines on moose (<i>Alces alces</i>) habitat selection, movements and feeding activity |
| 2014 | Eirin Marie Bjørkvoll | ph.d Biology | Life-history variation and stochastic population dynamics in vertebrates |
| 2014 | Håkon Holand | ph.d Biology | The parasite <i>Syngamus trachea</i> in a metapopulation of house sparrows |
| 2014 | Randi Magnus Sommerfelt | ph.d Biology | Molecular mechanisms of inflammation – a central role for cytosolic phospholipase A2 |
| 2014 | Espen Lie Dahl | ph.d Biology | Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway |
| 2014 | Anders Øverby | ph.d Biology | Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity |
| 2014 | Kamal Prasad Acharya | ph.d Biology | Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient. |
| 2014 | Ida Beathe Øverjordet | ph.d Biology | Element accumulation and oxidative stress variables in Arctic pelagic food chains: Calanus, little auks (alle alle) and black-legged kittiwakes (<i>Rissa tridactyla</i>) |
| 2014 | Kristin Møller Gabrielsen | ph.d Biology | Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants |
| 2015 | Gine Roll Skjærvø | dr.philos Biology | Testing behavioural ecology models with historical individual-based human demographic data from Norway |
| 2015 | Nils Erik Gustaf Forsberg | ph.d Biology | Spatial and Temporal Genetic Structure in Landrace Cereals |