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Source: Lindbergia, 37(2) : 47-59

Published By: Dutch Bryological and Lichenological Society and Nordic Bryological Society

URL: https://doi.org/10.25227/linbg.01046

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Lindbergia 37: 47–59, 2014
ISSN 0105-0761
Accepted 2 September 2014

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 favourable 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

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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 spermatozoids 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 ~20 µm 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 (Szövenyi 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

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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}/G_{ST}	Marker	Sampling
Liverwort								
Radula lindenbergiana[1]	D	F[27]R[28]	25–38[28]	SWB	Circ,Af,Mac	0.2	pDNA	Regional
Moss								
Antitrichia curtipendula[2]	D	R[27]R[29]	32–40	SWBA	Eu, Af, As, ENAm	-	ITS, pDNA	Global
Cinclidium arcticum[3]	D	R[30]	25–70[30]	A	Circ	-	pDNA	Global
Cinclidium latifolium[3]	D	R[30,31]	20–45[30]	A	Circ	-	pDNA	Global
Cinclidium stygium[3]	M	R[27]F[30]	25–70[30]	BA	Circ,SAm	-	pDNA	Global
Cinclidium subrotundrum[3]	M	F[30,31]	25–70[30]	BA	Circ	-	pDNA	Global
Drepanocladus aduncus[4]	D	R[27,32,33]	11–18	SWBA	Circ,Af,C-SAm,O	-	ITS, pDNA	Global
Grimmia montana[5]	D	R[27,34,35]	8–15	SWBA	Circ,Mac,CAm,SAf	0.32	pDNA	Global
Hamatocaulis vernicosus[6]	D	R[27,32]	10–22	BA	Circ,CAm	-	ITS, pDNA	Regional
Homalothecium sericeum[7,8]	D	O[27]R[36]	11–23	SWBA	Eu,WAs,NAf,Mac,EAm	0.181	ITS, pDNA	Regional
Kindbergia praelonga[9]	D	F[27]N[36]	11–14	SWB	Eu,Mac,NAm,SAf, O	-	ITS, pDNA	Global
Leucodon sciuroides[10]	D	R[27,37,29]	18–55	SWB	Eu,As,NAf,Mac	0.437	iso	Regional
Platyhypnidium riparioides[11]	M	F[27]R[36]	14–22	SWB	Circ	0.177	msat	Regional
Pleurochaete squarrosa[12,13]	D	N[30]R[35]	10–14	S	Cosm	0.443, 0.892	ITS, pDNA, allo	Regional
Polytrichastrum formosum[14]	D	F[27,35]N[38]	12–16	SWB	Cosm,Ex:SAm,O	0.395, 0.047	allo, msat	Regional
Polytrichum commune[14]	D	F[27,35,38]	8–12	SWBA	Holarct,SEAs	0.070, 0.047	allo, msat	Regional
Polytrichum juniperinum[14]	D	A[27]F[35,38]	8–12	SWBA	Cosm	0.341, 0.167	allo, msat	Regional
Polytrichum piliferum[14]	D	A[27]O[35]F[38]	9–14	SWBA	Cosm	0.087	allo	Regional
Polytrichum uliginosum[14]	D	-	8–12	SWB	-	0.091	allo	Regional
Sanionia uncinata[15,16]	M	F[27,33,39]	10–18	SWBA	Cosm	-	ITS, pDNA	Global
Sarmentypnum exannulatum[17]	D	F[39]R[27,33]	12–24	SWBA	Cosm	-	ITS, pDNA	Global
Scorpidium cossonii[18]	D	F[39]R[27]N[33]	12–21	SWBA	Circ,SAm,O	-	ITS, pDNA	Global
Scorpidium scorpioides[18]	D	F[39]R[27,33]	12–22	SWBA	Circ,C-SAm	-	ITS, pDNA	Global
Sphagnum affine[19]	D	R[27,35]	24–28[44]	WB	Eu,ENAm	0.512	iso	Regional
Sphagnum angermanicum[20]	D	R[40]	26–34[40]	W	Eu,WNAm	0.15	msat	Global
Sphagnum capillifolium[21]	D/M	F[27]R[35]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
Sphagnum fimbriatum[22,23]	M	$A^{27}R^{35}F^{41}$	24–28[44]	WBA	Circ,SAf,SAm,NZ,An	-	ITS, nDNA	Regional
Sphagnum squarrosum[22,23]	M	$A^{27}O^{35,41}$	22–30[44]	WBA	Circ,Mac,CAm,O	-	ITS, nDNA	Regional
Sphagnum troendelagicum[24]	-	N	-	W	Eu	0.12, 0.16	msat, pDNA	Global
Sphagnum wulfianum[25]	D/M	$R^{28}O^{42}$	22–24[44]	B	Circ	0.72	msat	Regional
Tortula muralis[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: Af-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: [1]Laenen et al. 2011; [2]Hedenäs 2008a, [3]Piñero et al. 2012, [4]Hedenäs 2008a; [5]Vanderpoorten et al. 2008; [6]Hedenäs and Eldenäs 2007; [7]Hedderson and Nowell 2006; [8]Désamoré et al. 2012; [9]Hedenäs 2010a; [10]Cronberg 2000; [11]Hutsemékers et al. 2011; [12,13]Grundmann et al. 2007, 2008; [14]van der Velde and Bijlsma 2003; [15,16]Hedenäs 2010b, 2012; [17,18]Hedenäs 2009a, 2009b; [19]Thingsgaard 2001; [20]Stenøien et al. 2011a; [21]Natcheva and Cronberg 2003; [22,23]Szövényi et al. 2006, 2007; [24]Stenøien et al. 2011b; [25]Kyrkjeeide et al. 2012; [26]Werner and Guerra 2003; [27]Hill et al. 2007; [28]Damsholt 2002; [29]Jóhannsson 1990a; [30]Hallingbäck et al. 2008; [31]Jóhannsson 1995; [32]Nyholm 1974a; [33]Jóhannsson 1998; [34]Hallingbäck et al. 2006; [35]Pedrotti 2001; [36]Jóhannsson1997; [37]Nyholm 1974b; [38]Jóhannsson 1990b; [39]Hedenäs pers. comm.; [40]McQueen and Andrus 2007; [41]Jóhannsson 1989; [42]Field experience and herbarium collections from Europe; [43]Nyhom 1958; [44]Sundberg et al. 2006; [45]Dierssen 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 (Størmer 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

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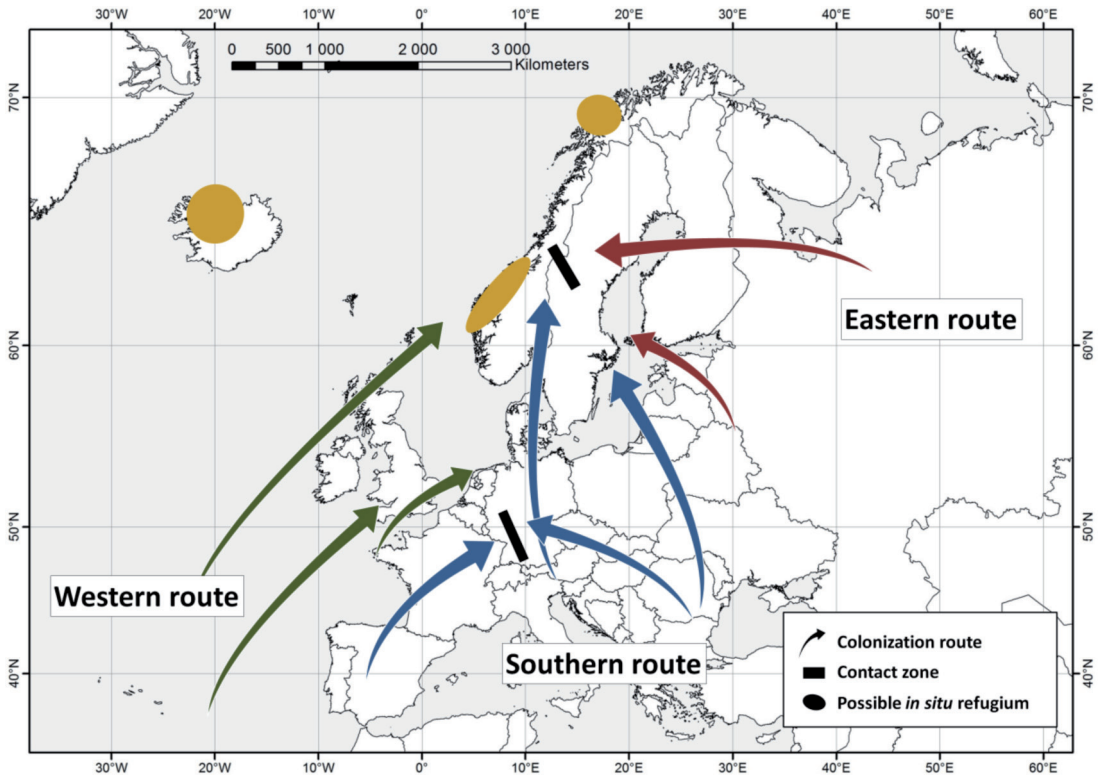


Figure 1. Hypothesized colonization routes, contact zones, and possible in situ glacial refugia of bryophyte species in Europe during and after the last glacial maximum. Three main colonization routes, western, southern, and eastern, are indicated by green, blue and red arrows, respectively. Solid yellow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

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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. *Pleurochaete squarrosa* (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. *Homalothecium sericeum* (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. *Grimmia montana* (Vanderpoorten et al. 2008)	
Several refugial areas	Long time since divergence between genetic lineages found in two or more areas e.g. *Homalothecium sericeum* (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. *Leucodon sciuroides* (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. *Pleurochaete squarrosa* (Grundmann et al. 2008)	Refugial area, species originating in this area
Dispersal		
Effective gene flow	No genetic structure e.g. *Polytrichum commune* (van der Velde and Bijlsma 2003)	Low mutation rate and/or large effective population size causing incomplete lineage sorting (Stenøien and Såstad 1999)
Long distance dispersal	Widespread haplotypes e.g. *Radula lindenbergiana* (Laenen et al. 2011)	Low mutation rate and/or large effective population size causing incomplete lineage sorting (Stenøien and Såstad 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 *Anoectangium warburgii* Crundw. & M.O. Hill and *Weissia 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

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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 linage 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* Renauld & 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 bryhnii* 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 (Kyrkjeeide 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 (Szövenyi 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 (Szövenyi 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 (Szövenyi 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 hypothesised 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

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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 andrewsianum* (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, Kyrkjeeide 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 1for 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.

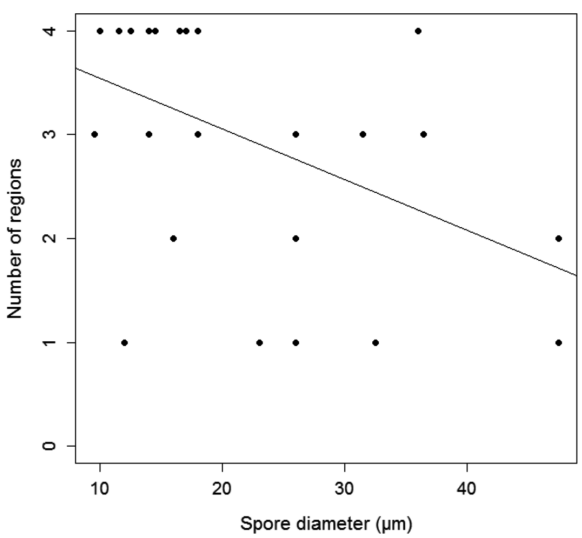


Figure 2. Relationship between the spore size of a bryophyte species and the number of European regions in which it occurs. Species with small spores occur in more regions than species with large spores (R^2 = 0.25, $F_{1,27}$ = 9.05, p = 0.006).

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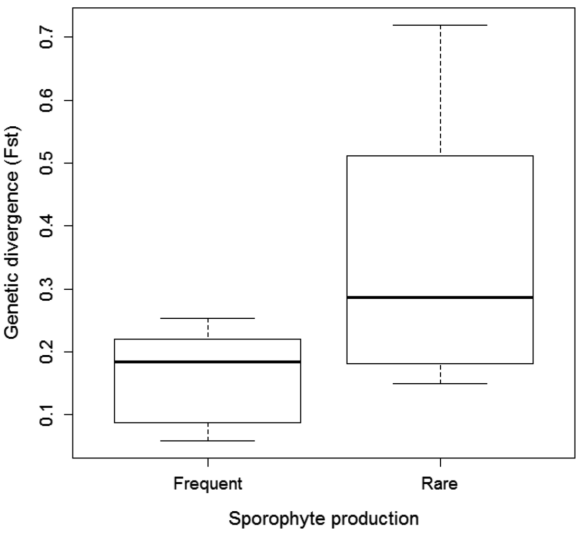


Figure 3. Relationship between F_{ST}-values between populations of bryophytes and the frequency of sporophyte production (rare and frequent) in 14 bryophyte species. Bryophytes reproducing frequently (mean = 0.16) seem to be less genetically differentiated than bryophytes reproducing rarely (mean = 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 lindenbergiana* (Laenen et al. 2011) and *Platyhypnidium riparioides* (Hutsemékers 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-

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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.

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