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Is interspecific gene flow and speciation in peatmosses (*Sphagnum*) constrained by phylogenetic relationship and life-history traits?

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Peatmosses are interesting for studies of speciation processes not only because of their frequent hybridization and recent diversification, but also their phenotypic diversity, ecological importance and ancient history. Diverse and widespread hybridization has been widely documented in the genus, but little is known about what factors underlie this phenomenon. We hypothesize that these factors include phylogenetic distance and variation in life-history traits of parental species. We summarize current knowledge about the occurrence of hybridization in peatmosses and explore how it is associated with phylogenetic distance and life-history trait variation of parental species. Possibly as much as one out of five (or more) peatmoss species hybridize, mostly producing allopolyploid hybrids. Parents of admixed haploids are more closely related to each other than parents of allopolyploids. Hybridization seems to be most frequent in 1) monoicous and polyoicous species exhibiting 2) relatively high sporulation frequency, 3) producing relatively small spores, as well as 4) growing in poor habitats. Surprisingly, neither phylogenetic proximity nor life-history trait variation explain patterns of hybridization in peatmosses, and other likely explanations for patterns observed are discussed.

Hybrid speciation has been acknowledged to be important for speciation and biological diversity in many organism groups (Levin and Kerster 1974), but has traditionally been considered to be of limited importance in explaining overall large-scale biodiversity (Mayr 1942, Ehrlich and Raven 1969, Levin 1981). More recently, accumulating evidence have revealed patterns of parapatric and sympatric speciation with past or ongoing gene flow in many taxa (Morjan and Rieseberg 2004, Arnold 2006, Feder et al. 2012). Ellstrand (2014) showed that in a diverse set of plants, interspecific gene flow is much more prevalent than what previously thought (Levin 1984), and polyploid hybridization is now acknowledged as one of the most common mechanisms of plant speciation (Soltis et al. 2009, 2014). For a glossary of genetic expressions see Box 1.

Numerous studies have demonstrated that hybridization is common across old, species-rich lineages of bryophytes and might have been one of the key factors underlying speciation in these plants (Wyatt et al. 1988, Natcheva and Cronberg 2004, Stenøien et al. 2011b, Shaw et al. 2015). One of the largest bryophyte genera, *Sphagnum* (peatmoss), has been extensively studied, and introgression, hybridization, polypoidization, reticulate evolution and cryptic speciation is common in the genus (Såstad et al. 2001, McDaniel and Shaw 2003, Natcheva and Cronberg 2007, Shaw 2008, Ricca et al. 2011).

One of the oldest known fossil remains of land plants is morphologically similar to extant peatmosses (Cardona-Correa et al. 2016), dated 455–454 Ma. Today *Sphagnum* includes almost 300 species (Michaelis 2011), often growing in peatlands which occupy in total ca 3% of terrestrial land, storing more carbon than any other plant genus (at least 25% of all terrestrial carbon, Yu et al. 2010, Glime 2017a). Peatmosses thus play a key role in global carbon balance and climate (Weston et al. 2015). Many peatmoss species are ecologically variable and exhibit high phenotypic plasticity (Stenøien et al. 2014). Genetic structure of modern peatmoss populations is shaped by past and on-going gene flow and intercontinental distributions of many species are thought to reflect high potential of dispersal in the genus (Sundberg 2000, Szövényi et al. 2008, Stenøien et al. 2011b, Karlin et al. 2013, Shaw et al. 2014, Kyrkjeeide et al. 2016b). There is a considerable species diversity in certain areas of the world (Goffinet and Shaw 2008), even though the last peak of diversification in peatmosses was surprisingly recent, only 7–20 Ma (Shaw et al. 2010). The combination of ancient history, recent diversification, high gene flow potential and

Box 1. Genetic glossary

Gene flow: the movement of alleles between populations.
Genetic admixture: the integration of a genomic region from one population/species into the genome of another population/species, hereafter referred to as admixture.
Homoploid hybrid species: a species having resulted from homoploid hybrid speciation.
Homoploid hybrid speciation: speciation by interspecific hybridization without change in chromosome number.
Hybrid: an individual having resulted from hybridization.
Hybridization: the interbreeding of individuals from two distinct populations/species.
Introgression: gene flow between populations of different species.
Polyploidization: hybridization leading to formation of hybrid progeny with multiple sets of chromosomes.
Admixed individual: here referred to an individual showing evidence of admixture with another species of the same ploidy level, but not in itself considered as a taxonomically separate species.
Allopolyploid: a hybrid individual with ploidy level of two (or more), and having resulted from interspecific crosses.
Autopolyploid: a hybrid individual with ploidy level of two (or more), and having resulted from intraspecific crosses.

ecological variability makes peatmoss an interesting model for studying patterns and processes of speciation.

There is evidence of past and extant polyploid hybridization in peatmosses (examples discussed in details below), and possible mechanisms of polyploids formation are reviewed in detail elsewhere (Natcheva and Cronberg 2004, Såstad 2005). For instance, Devos et al. (2016) has revealed multiple whole genome duplication events in evolutionary history of Sphagnopsida, two of which could have contributed to the rapid diversification of peatmosses. Furthermore, numerous studies have described extant polyploid peatmoss species and many have emphasized the importance and relative commonness of hybridization and polyploidization within the genus (Karlin et al. 2009, Ricca et al. 2011, Shaw et al. 2012a, 2013, Karlin 2014). In contrast to angiosperms, interploidal hybridization is rather commonly observed in *Sphagnum* (Flatberg et al. 2006, Karlin et al. 2009, 2014). Nevertheless, we still do not know exactly the extent to which peatmosses experience interspecific gene flow, and even less about what factors promote the ability to hybridize in these plants.

Difference in mating system might have profound evolutionary implications in peatmosses (Stenøien and Såstad 1999, Szövényi et al. 2014, Johnson and Shaw 2015). The gametophyte, which is the dominant phase in the life cycle, carries sexual reproductive organs producing gametes mitotically. Most species are dioicous, i.e. unisexual (Wyatt and Anderson 1984), and the sexes must therefore grow in close proximity to be capable of sexual reproduction (Longton and Schuster 1983). Many species are monoicous (i.e. bisexual) and exhibit both outcrossing and intragametophytic selfing. Gametophytic sex expression seems to be a fixed trait in most peatmosses (Szövényi et al. 2009, Ricca et al. 2011), but many monoicous species may occur with separate male plants (i.e. they are andropolyoicous sensu Kyrkjeeide et al. 2018, hereafter referred to as polyoicous). Mating system might not in itself affect allelic diversity (Stenøien and Såstad 2001), but in haploid-dominant plants 'selfers' diversify faster and seem more effective in purging genetic load compared to 'outcrossers' (McDaniel et al. 2013, Szövényi et al. 2014). In addition, mating system strongly influences sporulation frequency in mosses (Longton 1992), that could in turn affect gene flow rates, since frequently sporulating monoicous and polyoicous species might have a higher gene flow potential than less frequently sporulating dioicous species (Stenøien and Såstad 1999, 2001).

As a result of sexual reproduction, a diploid sporophyte develops on a mother gametophyte, where spore mother cells undergo meiosis and produces spores. Mature spores are explosively discharged via so-called air-gun mechanism (Nawaschin 1897, Goffinet and Shaw 2008, Sundberg 2010b). Spores are easily dispersed by wind and can eventually establish by germination and production of a protonema, which gives rise to one or more genetically identical gametophytes. Peatmoss species exhibit considerable variation in spore size and colour (Sundberg and Rydin 1998). Compared to larger spores, small spores remain viable longer (Sundberg and Rydin 2000), and provide a dispersal advantage over short distances (Sundberg 2010a). Spore colour is associated with viability of spores after the dispersal event, because it might influence resistance to mutagenic effect of UV light (Sundberg and Rydin 2000). Consequently, spore size and colour might affect levels of gene flow.

It has been shown, that pre- and postzygotic isolation between lineages tends to increase with time (Coyne and Orr 1997). Interspecific hybridization should then be more likely in closely related species, which have not developed reproductive barriers. Establishment of postzygotic barriers is shown to often take very long time in plants (probably, millions of years), especially for plants with long generation times (Levin 2012). Peatmoss species are long-lived and we can therefore expect hybridization to occur even between non-sister species. High genetic divergence between parents may actually facilitate allopolyploidization by prevention of normal chromosome pairing during meiosis in hybrids (reviewed by Karlin et al. 2014).

It is currently unclear how phylogenetic distance and life-history traits influence the occurrence of interspecific hybridization in peatmosses. In this paper we aim to 1) summarize evidence of hybridization in peatmosses, 2) explore how phylogenetic distance and life-history traits are associated with hybridization and interspecific gene flow, and 3) discuss in what way interspecific gene flow can influence speciation in peatmosses. To address these questions, we use results from published literature to first identify hybrid species and their parents, and then do comparative analyses to identify how different factors contribute to the occurrence and commonness of hybridization.

Material and methods

Data collection and summarizing

We first gathered reports already known to us with evidence for interspecific gene flow and polyploidy between peatmoss species. References from those papers were checked

to identify other possible papers. Then, we conducted a literature search using the Web of Science Core Collection online database (ver. 5.26.2, Web of Science, Clarivate Analytics 2017) and in Google Scholar for articles published between 1960 and 2017. We searched for different combinations of such terms as 'Sphagnum', 'peatmoss', 'introgression', 'hybridization', 'hybrid', 'polyploid' and 'admixture'. We performed the search in November 2017 but did not find new papers in addition to those we had collected earlier. To differentiate between reported cases of hybridization, we assigned the cases to the following groups: allopolyploid hybrids, admixed haploid individuals (hereafter – admixed individuals) and homoploid hybrids (see Glossary in Box 1).

Based on the collected information, we calculated a minimum coefficient of hybridization for each subgenus as the ratio of the number of identified hybridizing species to the total number of species within the subgenus. We also collected information about certain life-history traits of the identified parental species: mating system type, observed frequency of sporulation, spore colour, position of a species along the mire water table ('hummock–hollow') and the nutrient ('poor–rich') gradients (Eddy 1985, McQueen and Andrus 2007, Flatberg 2013, Johnson 2013, Kyrkjeeide et al. 2018), and maximum and minimum spore size (Suzuki 1958, McQueen and Andrus 2007, Kyrkjeeide et al. 2018). Mire is here used in a wide sense, also including moist heaths and forests.

Estimation of phylogenetic distance between the parents

We found no published phylogenetic tree including all species of interest that matched our objectives. In order to summarize the phylogeny of parental species, we constructed a composite cladogram using all available published phylogenetic trees containing species of interest. The cladogram was visualized with Dendroscope (ver. 3.5.8, Huson and Scornavacca 2012). In several cases, one or both parents could not be unambiguously identified. For example, there are 22 observed cases of species from subgenus *Subsecunda* being involved in hybridization, but parental species were only determined to subgenus in 11 cases, and to a species complex in two cases. As no information about the specific position in the phylogeny is available in these cases, we combined them for each subgenus into one 'unknown species' and placed it within the subgenus on the composite cladogram in order to visualize all reported evidence of hybridization simultaneously. Assuming, that all these unknown species represent different species, we added these cases to the number of unequivocally identified parental species in a subgenus. We then calculated a maximum hybridization coefficient by dividing this number by the total number of species in a subgenus. In this way, we can get an overview of the possible upper extent of hybridization for each subgenus.

The composite cladogram unites a broad spectrum of species from different subgenera, but it does not include many species within subgenera. Parental species might thus seem to be more related within subgenera than they actually are. Due to this, we counted the number of nodes separating parental species in each possible tree, and calculated the average number for each parental species pair as a measure of phylogenetic distance between the parents (Vellend et al. 2010). Because not all parents were identified, we estimated phylogenetic distances for 22 parental species pairs. The portion of the inter-subgeneric hybrids among these species pairs was the same as in the general sample.

Comparative analysis

We were interested in testing for associations between occurrence of hybridization on one hand, and life-history traits of the parental species on the other. Hence, we combined a dataset with seven life-history traits of parental species listed above with two additional factors: subgenus and intensity of hybridization, which corresponds to the number of hybrid species produced by each individual parental species. *Sphagnum australe*, *S. irritans*, *S.* 'sp-3' (Shaw et al. 2015) and *S.* 'sp-4' (Shaw et al. 2015) were excluded from the analysis because most of their life-history traits are unknown. As our data set contained both categorical and continuous variables, we explored it with factorial analysis of mixed data (FAMD) using the FactoMineR package in R (Lê et al. 2008), and used the missMDA package in R (Josse and Husson 2016) to account for missing trait values within some species. All analyses were conducted and visualized in the R statistical environment (ver. 3.4.1, <www.r-project.org>).

Results

Occurrence of interspecific hybridization

There are 36 documented allopolyploid hybrids, seven cases of genetic admixture and one case of homoploid hybridization in our data set, respectively (Table 1, Fig. 1). Peatmoss autopolypoids have not been registered, although Shaw et al. (2012b) discuss potential autopolyploidy of diploid *Sphagnum tescorum* based on registered genetic admixture between parental *S. fimbriatum* and *S. girgensohnii*, which in turn might be the second evidence of homoploid hybridization for the genus. So far, we treat the latter as an example of admixture. The parentage is completely unknown for five allopolyploid hybrids and partially unknown for 18 allopolyploid and admixed hybrids. In total, there are 37 parental species, each producing from one to four hybrids (Fig. 2A, Table 2). Some species are involved in both admixture and polyploid hybridization (Table 2). Hybridization events often occur within subgenera, but as many as 13 out of 39 hybrids are the results of inter-subgeneric crosses (Table 1, Fig. 1).

Hybridization is common in all subgenera, and the fraction of species hybridizing varies from 9 to 20% (Fig. 2B). The maximum coefficient of hybridization is of the same magnitude and reaches 27% in *Cuspidata*, while the lowest coefficient is observed in subgenus *Sphagnum*, but here parentage is unknown for half of the registered hybrid species. In general, up to one out of five (21%) of peatmoss species potentially hybridize.

Table 1. Polyploid hybrids and admixed haploid individuals registered in *Sphagnum*. Phylogenetic distance calculated as a number of nodes separating species in published phylogenetic trees (see 6, References). We refer to all studies which include information about 1) taxonomic status, 2) parentage, 3) ploidy level and/or 4) phylogenetic trees with the species of interest, which were used to obtain phylogenetic distance estimates. * – homoploid hybrid, NA – data is not available.

1. Subgenus	2. Hybrid species	3. Ploidy level	4. Parental species	5. Phylo-genetic distance	6. References
	S. × *alaskense*	2	unknown	NA	Kyrkjeeide et al. 2016a
	S. × *centrale*	2	unknown	NA	Temsch et al. 1998, Karlin et al. 2010a
	S. × *cristatum*	2	unknown	NA	Karlin et al. 2008
Sphagnum	*S.* × *palustre (*including *S. henryense)*	2	unknown	NA	Bryan 1955, Temsch et al. 1998, Shaw et al. 2008, Karlin et al. 2010a
	S. × *papillosum*	2	unknown	NA	Temsch et al. 1998, Karlin et al. 2010b
	S. austinii × *S. affine*	1	*S. austinii* × *S. affine*	2	Shaw and Goffinet 2000, Thingsgaard 2002, Johnson 2013, Johnson et al. 2015
	S. medium × *S. divinum*	1	*S. medium* × *S. divinum*	1.3	Kyrkjeeide et al. 2016a, Yousefi et al. 2017, Hassel et al. 2018
Sphagnum × *Rigida*	*S.* × *australe*	2	*S.* cf. *strictum* (subgenus *Rigida*) × subgenus *Sphagnum* (unknown species)	NA	Karlin et al. 2009, Karlin 2014, Shaw et al. 2016
Sphagnum × *Acutifolia*	*S.* × *australe*	3	*S. australe* (2n) × *S. fimbriatum*	5.9	Karlin et al. 2009, Karlin 2014
Sphagnum × *Subsecunda*	*S.* × *cuculliforme*	?	unknown *Sphagnum* (Neotropical, maternal) × uknown *Subsecunda*	NA	Crum 1987, Shaw and Goffinet 2000, Karlin et al. 2010b
	S. × *jensenii*	2	*S. balticum* × *S. annulatum*	6.5	Såstad et al. 1999, Johnson 2013, Johnson et al. 2015
	S. × *majus*	2	*S. cf. cuspidatum* × unknown *Cuspidata*	NA	Såstad et al. 2000
	S. × *torreyanum*	2	*S. cuspidatum* × unknown *Cuspidata (S. recurvum?)*	NA	Shaw et al. 2009, Karlin et al. 2014
Cuspidata	*S.* × *troendelagicum*	2	*S. balticum* × *S. tenellum*	4	Såstad et al. 2001, Stenøien et al. 2011a
	S. angustifolium × *S. flexuosum*	1	*S. angustifolium* × *S. flexuosum*	3.4	Såstad et al. 1999, 2001, Johnson 2013, Szurdoki et al. 2014, Karlin et al. 2014, Johnson et al. 2015
	S. × *irritans*	2	unknown *Cuspidata* × unknown *Subsecunda* (maternal)	NA	Karlin et al. 2009, 2013, Karlin and Robinson 2017
	S. × *falcatulum*	3	*S. irritans* × *S. cuspidatum*	5.2	Karlin et al. 2009, Karlin 2014
	S. × *mendocinum*	2	unknown *Cuspidata* × unknown *Subsecunda*	NA	Shaw and Goffinet 2000, Karlin et al. 2010b
Cuspidata × *Subsecunda*	*S.* × *slooveri*	2	*S. cf. recurvum* × *Subsecunda (S. africanum* complex)	7	Shaw 2000, Karlin et al. 2014, Karlin 2014
	S. × *planifolium 1*	3	*S. slooveri* × *Subsecunda (S. capense* complex*)*	4	Karlin et al. 2014
	S. × *planifolium 2*	3	*S. slooveri* × *S. cuspidatum*	5	Karlin et al. 2014
	S. × *lenense*	2	*S. lindbergii* × unknown *Subsecunda*	NA	Shaw et al. 2016
	S. × *contortum**	1	unknown *Cuspidata* × unknown *Subsecunda*	NA	Shaw et al. 2016
	S. contortum × S. *subsecundum*	1	*S. contortum* × *S. subsecundum*	NA	Ricca and Shaw 2010, Shaw et al. 2012a
	S. × *carolinianum*	2	*S. lescurii* × unknown *Subsecunda*	NA	Ricca et al. 2008, Shaw et al. 2012a
	S. × *guwassanense*	2	*S. inexspectatum/orientale* (female) × unknown *Subsecunda*	NA	Shaw et al. 2013

(Continued)

Table 1. Continued

1. Subgenus	2. Hybrid species	3. Ploidy level	4. Parental species	5. Phylo-genetic distance	6. References
	S. × *inundatum*	2	*S. auriculatum* × *S. subsecundum*	1	Ricca et al. 2008, Shaw et al. 2012a, b, Karlin et al. 2013
	S. × *missouricum*	2	*S. lescurii* × *S. subsecundum*	5	Ricca and Shaw 2010, Shaw et al. 2012a
	S. × *triseriporum*	2	*S. inexspectatum/orientale* (maternal) × unknown *Subsecunda*	NA	Shaw et al. 2013
Subsecunda	*S.* × *perfoliatum*	2	*S. orientale/inexspectatum* × unknown *Subsecunda*	NA	Shaw et al. 2015
	S. ×*"microporum"*	2	*S. kushiroense/microporum* × *S. miyabeanum*	4.7	Shaw et al. 2015
	S. ×"sp-5"	2	*S.* 'p-3' × *S.* 'sp-4'	1.3	Shaw et al. 2015
	S. × *platyphyllum* 2n	2	S. *platyphyllum* × unknown *Sphagnum*	NA	Ricca and Shaw 2010, Shaw et al. 2012a
	S. × *missouricum* × *S. lescurii*	3, 4	*S.* × *missouricum* × *S. lescurii*	1	Ricca and Shaw 2010, Ricca et al. 2011
Acutifolia × *Subsecunda*	*S.* sp. nov.	3	*S. incundum* × unknown *Subsecunda*	NA	Kyrkjeeide et al. 2018
	S. × *arcticum*	2	*S. incundum* × unknown *Acutifolia*	NA	Greilhuber et al. 2003, Shaw et al. 2005, Kyrkjeeide et al. 2018
	S. × *olafii*	2	*S. incundum* × unknown *Acutifolia*	NA	Greilhuber et al. 2003, Shaw et al. 2005, Kyrkjeeide et al. 2018
	S. russowii	2	*S. girgensohnii* × *S. rubellum*	7.8	Cronberg 1996a, Temsch et al. 1998, Shaw 2000, Shaw et al. 2005, 2016, Kyrkjeeide et al. 2018
	S. × *girgensohnii* × *S. russowii*	3	*S. girgensohnii* × *S. russowii*	6.6	Shaw et al. 2005, Flatberg et al. 2006, Karlin 2014, Kyrkjeeide et al. 2018
Acutifolia	*S.* × *skyense*	2	*S. quinquefarium* × *S. subnitens*	4.4	Shaw 2000, Shaw et al. 2005, Karlin 2014, Kyrkjeeide et al. 2018
	S. × *tescorum*	2	*S. girgensohnii* × *S. fimbriatum*	2	Shaw 2000, Shaw et al. 2005, 2012b, Karlin 2014, Kyrkjeeide et al. 2018
	S. capillifolium × *S. rubellum*	1	*S. capillifolium* × *S. rubellum*	3.4	Cronberg 1997, 1998, Shaw and Goffinet 2000, Natcheva and Cronberg 2003, Shaw et al. 2005, 2016, Johnson 2013, Johnson et al. 2015, Kyrkjeeide et al. 2018
	S. capillifolium × *S. warnstorfii*	1	*S. capillifolium* × *S. warnstorfii*	4	Cronberg 1997, Shaw and Goffinet 2000, Natcheva and Cronberg 2003, Shaw et al. 2005, Johnson 2013, Johnson et al. 2015, Kyrkjeeide et al. 2018
	S. capillifolium × *S. quinquefarium*	1	*S. capillifolium* × *S. quinquefarium*	3.2	Shaw 2000, Natcheva and Cronberg 2007, Karlin 2014, Kyrkjeeide et al. 2018

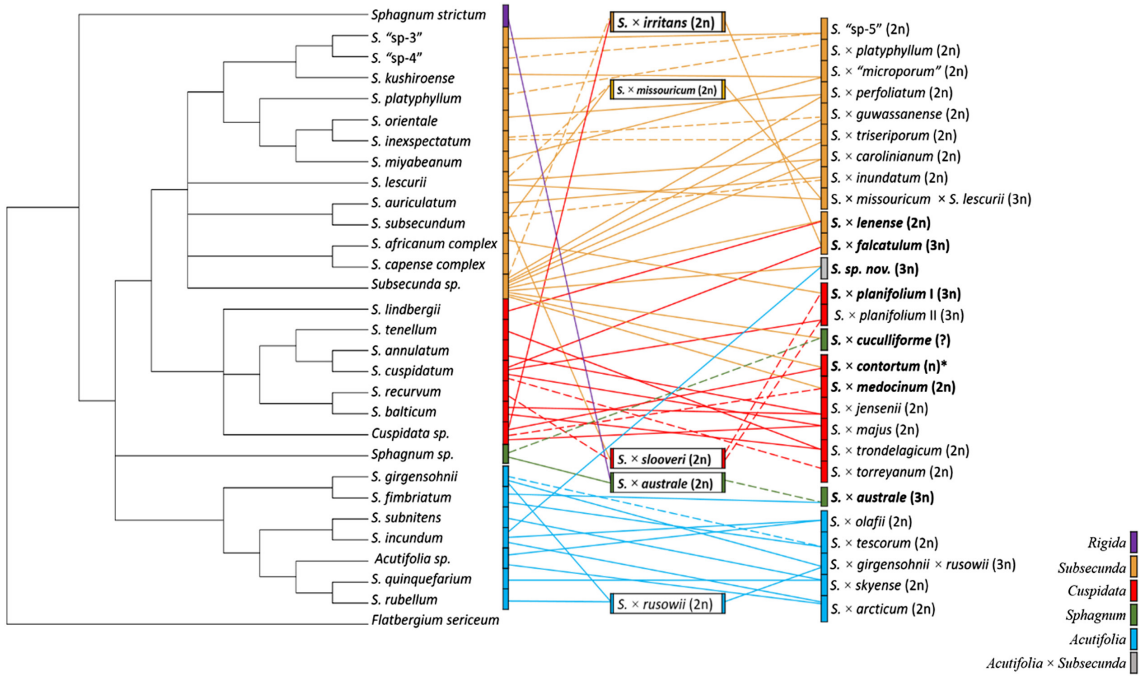

Figure 1. Hybridization in *Sphagnum*. All cases of allopolyploid and homoploid hybridization (species to the right) when at least one parent was identified (species to the left). Other cases, including admixture, are listed in Table 1. Coloured bars indicate subgenera as showed in the lower right corner. Dashed lines correspond to maternal parents, solid lines – to paternal or unidentified parents. Ploidy level is stated in brackets and otherwise is 1n, * – homoploid hybrid. Intersubgeneric hybrids are in bold, some of these hybrids are assigned to that subgenus, which their maternal plant belongs to. For references see Table 1.

Phylogenetic distance of parental species and life-history trait analysis

The majority of allopolyploid hybrids are produced by non-sister species, with a mean phylogenetic distance of 4.68 (SE = 0.56) nodes between parental species (Fig. 3). Distributions of phylogenetic distances between parents do not deviate from normal distribution (Shapiro test, $p = 0.43$ and $p = 0.36$ for parents of the allopolyploid hybrids and the admixed individuals, respectively). The average phylogenetic distance between parents of admixed individuals seems lower than between parents of allopolyploids, albeit insignificantly so (2.88 (SE = 0.41) versus 4.68 (SE = 0.56) nodes, respectively, Student's t-test, $p = 0.06$).

The FAMD based on the collected life-history trait information (Table 2) shows that subgenus and spore colour contribute the most to the variation in characters between parental species, followed by maximum spore size, mating system and sporulation frequency (Table 3). The contribution of spore colour to axis 1 is 23.1%, and contribution of the maximum spore size variable to axis 2 is 23.6% (Table 3). Contribution of subgenus variable to axis 1 and axis 2 is 23.4% and 16.7%, respectively (Table 3). The intensity of hybridization explains 2.6% of variance between species. Although we distinguish several groups, species producing different number of hybrids are scattered evenly across all of them (Fig. 4A). The FAMD individual factor plot shows that intensity of hybridization tends to be associated with polyoicous and monoicous reproductive systems, high sporulation frequency, poor habitats (low pH and few minerals), small spore sizes and high position along the water table (Fig. 4B). Data on spore sizes and sporulation frequency is unavailable for many parental species, because they are rarely or never observed with sporophytes.

Discussion

Occurrence and a potential role of interspecific gene flow in speciation of peatmosses

The majority of hybrids in peatmosses result from allopolyploid hybridization (82%). Polyploidy represents a very important mechanism of speciation in these plants, and this seems primarily related to immediate postzygotic reproductive isolation between hybrid progeny and parents (Ricca and Shaw 2010, Abbott et al. 2013). Despite this, complete reproductive isolation is sometimes not established, and polyploids are able to backcross with their parents, preventing the establishment of new 'distinct evolutionary lineages' and also increasing the genetic diversities of both polyploid and parental species. In peatmosses, several allopolyploids are reported to undergo interploidal backcrossing with haploid parents (e.g. *Sphagnum russowii, S. troendelagicum, S. missouricum*, Flatberg et al. 2006, Ricca et al. 2011, Stenøien et al. 2011a).

It has been suggested that high levels of fixed heterozygosity can increase ecological amplitudes in hybrid plant taxa, even beyond the habitat and niche limitations of the parents (Levin 2002). Well-established allopolyploid species are relatively often found in habitats which parental species do not occupy. From this perspective, it seems that environmental heterogeneity can promote and contribute to the establishment of new hybrid species (Brochmann et al.

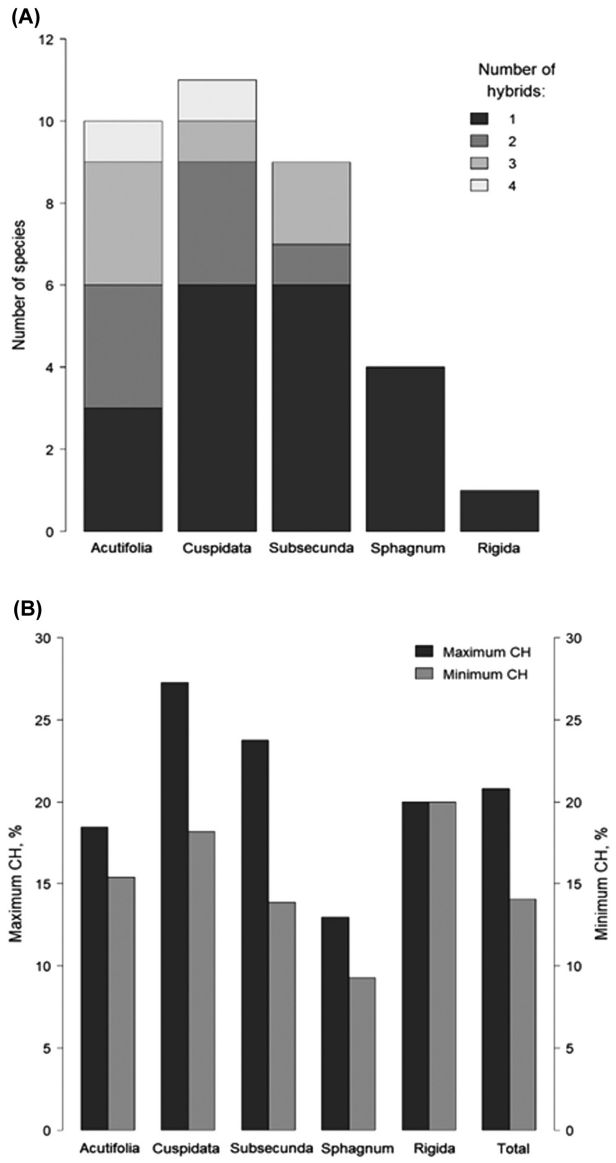

Figure 2. Characteristics of hybridization across *Sphagnum* subgenera. (A) Intensity of hybridization across *Sphagnum* subgenera. Intensity of hybridization corresponds to the number of hybrids produced by an individual parental species. Bars on the X-axis represent subgenera, coloured according to the number of hybrid species produced by individual parental species as shown on the right. Y-axis represent number of parental species of each category within subgenera. Inter-subgeneric hybrid parents are assigned to that subgenus, which their maternal plants belongs to. (B) Occurrence of hybridization across *Sphagnum* subgenera. Maximum CH – the maximum coefficient of hybridization counted as the ratio of the maximum possible number of parental species to the total number of species in a subgenus. Minimum CH – the minimum coefficient of hybridization counted as the ratio of the number of the identified parental species to the total number of species in a subgenus.

2004, Abbott et al. 2013). This might be the case for several peatmoss allopolyploids, for example *S. missouricum* and *S. australe* (Shaw et al. 2012a, Karlin et al. 2014). It could also be the other way around, when ecological divergence originates after the establishment of new species (Abbott et al. 2010). Polyploid plants are often characterized by greater vigour compared to their diploid progenitors, possibly facilitating their dispersal to and establishment in new habitats (Grant 1981). Brochmann et al. (2004) suggested that polyploid arctic plants might have been more successful in colonizing areas after the last glaciation than diploids, because fixed highly heterozygous duplicated genomes of polyploids contain much of the ancestral diversity. In peatmosses, an increase of genetic diversity through polyploidization has been hypothesized to facilitate successful colonization of new habitats in allotriploid *S. falcatulum* (Karlin et al. 2014). Genetic diversity and frequency of polyploids in populations can also be increased via recurrent polyploidization, which thus may play an important role in the successful establishment of polyploid lineages (Ricca and Shaw 2010). This is probably the case for several peatmoss polyploids which have originated more than once, e.g. *S. russowii* (Shaw et al. 2005), *S. jensenii* (Såstad et al. 1999), *S. carolinianum* (Ricca et al. 2008), *S. falcatulum* and *S. australe* (Karlin 2014).

Registered admixture between peatmoss species might result from hybrid speciation sensu stricto, but introgression in itself is not evidence of successful speciation. In order for speciation to take place, more complete reproductive isolation between newly formed admixed lineages and parental species must subsequently develop (Abbott et al. 2013). Nonetheless, extensive genomic admixture clearly indicates an early phase in speciation. In peatmosses, one case of admixture (*S. girgensohnii* and *S. fimbriatum*) presumably resulted in polyploidization and subsequent establishment of a separate species, *S. tescorum* (Shaw et al. 2012b). In other cases, however, observed admixture is an ongoing process in zones of contact, which does not affect distinctiveness of parental gene pools, as for *S. capillifolium* × *S. warnstorfii* (Cronberg 1997), *S. capillifolium* × *S. quinquefarium* (Cronberg and Natcheva 2002), *S. capillifolium* × *S. rubellum* (Cronberg 1996b), *S. angustifolium* × *S. flexuosum* (Szurdoki et al. 2014), or is a consequence of secondary contact, as for *S. magellanicum* expanse × *S. magellanicum* margin (cf. Yousefi et al. 2017, *S. divinum* and *S. medium*, respectively, in Hassel et al. 2018). There are also examples of past hybridization events, e.g. *S. rubellum* × *S. capillifolium* (Natcheva and Cronberg 2003) and *S. austinii* × *S. affine* (Thingsgaard 2001). The latter has been suggested to represent an example of past adaptive introgression (Thingsgaard 2001). Comparing to allopolyploid hybridization, admixture and homoploid hybridization in peatmosses might be underestimated since hybrid individuals remain undetected because of their morphological resemblance to one of the parents.

The age of admixed taxa can be important for distinguishing hybrid speciation from more or less "neutral" admixture (Abbott et al. 2013). Yet, there is modest information available about the age of hybrid taxa in peatmosses, particularly for admixed hybrids. Several allopolyploid species seem to have originated before the last glaciation maximum, e.g. *S. troendelagicum* (Stenøien et al. 2011a); *S. guwassanense*, *S. triseriporum* (Shaw et al. 2013); *S. alaskense* (Kyrkjeeide et al. 2016a), while others probably are of more recent origin, e.g. *S. jensenii* (Såstad et al. 1999), *S. falcatulum* (Karlin et al. 2013) and both the diploid and

Table 2. Reproductive and microhabitat characteristics of identified parental species. Key to the columns abbreviations: 5 – Number of hybrid species produced by the parental one (Table 1); 6 – Reproductive system: m – monoicous, d – dioicous, p – polyoicous (including andro-polyoicous species sensu Kyrkjeeide et al. 2018, i.e. which are reported with separate male plants, but with certainty not with pure female plants); 7 – Sporulation frequency: F – frequent, R – rare; 8 – Position along the water table ('hummock–hollow') mire gradient: H – hummock, L – lawns/carpets, I – intermediate (both in hummocks and lawns/carpets); 9 – Position along the nutrient ('poor–rich') mire gradient: R – rich fen habitat, P – poor fen and bog habitat, I – intermediate fen; 10 – Spore colour, sources: Eddy 1985, McQueen and Andrus 2007, Flatberg 2013, Johnson 2013, Hassel et al. 2018, Kyrkjeeide et al. 2018; 11 – Maximum spore size, µm; 12 – Minimum spore size, µm, sources: Suzuki 1958, McQueen and Andrus 2007, Kyrkjeeide et al. 2018; * – homoploid hybrid; ♂ – male parent of the hybrid, ♀ – female parent of the hybrid; NA – data is not available. Mire is here used in a wide sense, also including moist heaths and forests.

1. No	2. Parental Species	3. Subgenus	4. Produced hybrid species	5	6	7	8	9	10	11	12
1	*Sphagnum strictum*	*Rigida*	*S.* × *australe* (2n)	1	m	F	I	P	yellow-brown	31	43
2	*S. medium*	*Sphagnum*	*S. medium* × *S. divinum* (n)	1	d	R	I	P	yellow-brown	NA	NA
3	*S. divinum*	*Sphagnum*	*S. medium* × *S. divinum* (n)	1	d	R	H	P	yellow-brown	21	31
4	*S. austinii*	*Sphagnum*	*S. austinii* × *S. affine* (n)	1	d	R	H	P	light-brown	23	28
5	*S. affine*	*Sphagnum*	*S. austinii* × *S. affine* (n)	1	d	F	I	I	yellow-brown	27	31
6	*S. annulatum*	*Cuspidata*	*S.* × *jensenii* (2n)	1	d	R	L	I	light-brown	25	32
7	*S. balticum*	*Cuspidata*	*S.* × *jensenii* (2n) *S.* × *troendelagicum* (2n) ♂	2	d	F	I	P	yellow	25	33
8	*S. tenellum*	*Cuspidata*	*S.* × *troendelagicum* (2n) ♀	1	p	F	L	P	yellow	27	44
9	*S. cuspidatum*	*Cuspidata*	*S.* × *falcatulum* (3n) *S.* × *planifolium* (3n) ♂ *S.* × *majus* (2n) *S.* × *torreyanum* (2n)	4	d	R	L	P	light-brown	29	38
10	*S. recurvum*	*Cuspidata*	*S.* × *slooveri* (2n)	1	d	R	I	P	light-brown	22	28
11	*S.* × *slooveri*	*Cuspidata*	*S.* × *planifolium1* (3n) ♀ *S.* × *planifolium2* (3n) ♀	2	d	NA	NA	NA	NA	NA	NA
12	*S. lindbergii*	*Cuspidata*	*S.* × *lenense* (2n)	1	p	F	L	P	yellow-orange	22	40
13	*S. angustifolium*	*Cuspidata*	*S. angustifolium* × *S. flexuosum* (n)	1	d	F	I	I	light-brown	21	25
14	*S. flexuosum*	*Cuspidata*	*S. angustifolium* × *S. flexuosum* (n)	1	d	R	I	I	light-brown	23	25
15	*S. lescurii*	*Subsecunda*	*S.* × *carolinianum* (2n) *S.* × *missouricum* (2n) ♀ *S.* × *missouricum* × *S. lescurii* (3n, 4n)	3	d	R	L	I	NA	27	34
16	*S. inexspectatum*	*Subsecunda*	*S.* × *guwassanense* (2n) ♀ *S.* × *triseriporum* (2n) ♀	2	d	NA	I	I	NA	36	39
17	*S. auriculatum*	*Subsecunda*	*S.* × *inundatum* (2n) ♂	1	d	R	I	I	light-brown	NA	NA
18	*S. subsecundum*	*Subsecunda*	*S.* × *inundatum* (2n) ♀ *S.* × *missouricum* (2n) ♂ *S.* × *contortum* ♀ × *S. subsecundum* (n)	3	d	R	I	R	light-brown	30	35
19	*S. orientale*	*Subsecunda*	*S.* × *perfoliatum* (2n)	1	d	R	I	R	light-brown	NA	NA
20	*S. kushiroense*	*Subsecunda*	*S.* × *'microporum'* (2n)	1	d	R	L	NA	NA	NA	NA
21	*S. miyabeanum*	*Subsecunda*	*S.* × *'microporum'* (2n)	1	d	R	L	NA	NA	NA	NA
22	*S.* × *missouricum*	*Subsecunda*	*S.* × *missouricum* × *S. lescurii* (3n, 4n)	1	d	R	I	I	NA	NA	NA
23	*S. platyphyllum*	*Subsecunda*	*S.* × *platyphyllum* (2n) ♀	1	d	R	L	R	brownish	23	35
24	*S.* × *contortum**	*Subsecunda*	*S.* × *contortum* × *S. subsecundum* (n)	1	d	R	I	R	light-brown	22	28
25	*S. fimbriatum*	*Acutifolia*	*S.* × *australe* (3n) ♂ *S.* × *tescorum* (2n) *S. fimbriatum* × *S. girgensohnii* (n)	3	p	F	I	R	yellow-brown	20	27
26	*S. rubellum*	*Acutifolia*	*S.* × *rusowii* (2n) *S. capillifolium* × *S. rubellum* (n)	2	d	R	I	P	yellow-brown	18	33
27	*S. girgensohnii*	*Acutifolia*	*S.* × *rusowii* (2n) *S.* × *girgensohnii* × *S. rusowii* (3n) *S.* × *tescorum* (2n) ♀ *S. fimbriatum* × *S. girgensohnii* (n)	4	d	R	H	P	yellow-brown	21	27
28	*S. russowii* 2n	*Acutifolia*	*S.* × *girgensohnii* × *S. rusowii* (3n)	1	d	R	I	P	yellow-brown	18	33
29	*S. quinquefarium*	*Acutifolia*	*S.* × *skyense* (2n) *S.* × *capillifolium* × *S. quinquefarium* (n) ♀	2	p	F	H	P	yellow-brown	19	27
30	*S. subnitens*	*Acutifolia*	*S.* × *skyense* (2n)	1	m	F	I	I	yellow-brown	22	32
31	*S. incundum*	*Acutifolia*	*S.* × *artcticum* (2n) *S.* × *olafii* (2n) S. sp. nov. (3n)	3	p	R	I	R	yellow-brown	24	29
32	*S. capillifolium*	*Acutifolia*	*S.* × *capillifolium* × *S. quinquefarium* (n) ♂ *S. capillifolium* × *S. warnstorfii* (n) *S. capillifolium* × *S. rubellum* (n)	3	p	F	H	P	yellow-brown	20	28
33	*S. warnstorfii*	*Acutifolia*	*S. capillifolium* × *S. warnstorfii* (n)	1	d	R	I	R	light-brown	17	26

triploid *S. australe* cf. Karlin et al. (2009). For admixed hybrids the age is only estimated for those formed between *S. divinum* and *S. medium*, which seem to be around 20 000 years old (Yousefi et al. 2017).

Abbott et al. (2013) point out that admixed individuals resulted from secondary contact can evolve into a separate species by occupying a niche not yet occupied by its parents. Early homoploid hybrid plant lineages are characterized

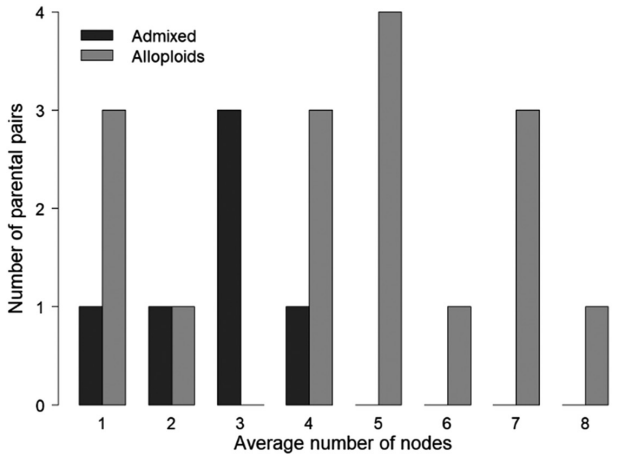

Figure 3. Phylogenetic distance between parental species in *Sphagnum*. X-axis represents averaged rounded number of nodes separating identified parental species pair in published phylogenetic trees, Y-axis represents counts of parental species pairs with the corresponding number of nodes. Dark grey bars represent counts for parents of admixed haploid individuals, light-grey bars – parents of allopolyploid hybrids as showed on the right. n = 22 species pairs.

by rapid and sometimes large-scale changes in gene expression patterns, which might increase phenotypic novelty and facilitate differentiation into new species (Abbott et al. 2010). Even if reproductive barriers are not complete at the initial stage of speciation, environmental based (exogenous) selection can maintain the distinctness of hybrid species. It is, however, not clear whether admixed peatmoss hybrids occupy different ecological spaces and are reproductively isolated from parents at any level. In addition, their morphological distinctiveness has not been examined in the majority of cases. Further research is thus needed to assess evolutionary significance of admixture observed in peatmosses and to define their taxonomical status.

Does phylogenetic distance explain occurrence of interspecific hybridization within the genus?

It has been suggested that certain degrees of genetic divergence between parents is required in order for allopolyploidization to occur as a result of impaired meiotic chromosome pairing in peatmosses (Natcheva and Cronberg 2007, Karlin et al. 2014). Although the only recorded homoploid hybrid species in peatmosses (*S. contortum*) is not included in our analysis because of unknown parentage, we do observe that parents of allopolyploids are less related compared to parents of haploid admixed individuals. At the same time, several allopolyploid hybrids are formed by closely related species, while several distantly related species are involved in admixture, which is not expected assuming that divergence ultimately leads to problems in meiosis during spore production. Patterns observed in allopolyploids and admixed species indicates that phylogenetic distance in itself does not define the success of interspecific crosses. It is worth noting that the homoploid *S. contortum* is thought to be an inter-subgeneric species, whose parents are rather distantly related. *Sphagnum contortum* also hybridizes inter-subgenerically with *S. subsecundum*, producing admixed individuals. But it cannot be ruled out that instead of being a homoploid hybrid, this species could have originated through polyploidization followed by chromosome number reduction, or also through introgression of genes between the subgenera and subsequent divergent speciation (Shaw et al. 2016).

Levin (2013) argues that low divergence between parents leads to formation of homoploids, whereas strong and modest divergence result in strict and segmental polyploids (i.e. allopolyploids whose chromosomes are partially homologous), respectively. These patterns are observed in vascular plants (Chapman and Burke 2007), and might also explain formation of allopolyploid hybrids by closely related parents in peatmosses. It is unclear whether these hybrids are strict or segmental polyploids since strict disomic inheritance usually serves as a null-hypothesis in revealing allopolyploids (Karlin and Smouse 2017). So far, evidence of recombination between parental genomes has only been registered in two allopolyploids: *S. tescorum* (Shaw et al. 2012b) and *S. palustre*, the latter a hybrid species with unknown parentage (Stenøien et al. 2014). Otherwise, recombination between parental genomes has only been reported for admixed haploid individuals (Natcheva and Cronberg 2007).

Do life-history traits explain intensity of interspecific hybridization?

We show that intensity of hybridization tends to be associated with polyoicous and monoicous reproductive systems, high sporulation frequency, poor habitats (low pH and low concentration of minerals), small spore size and light spore

Table 3. Contribution of the variables to the axes in the FAMD. * – Number of species produced by individual parental species.

		Contribution of a variable to the axes				
Variable	Type	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Subgenus	categorical	23.66	16.76	26.30	46.78	32.11
Spore colour	categorical	23.18	12.34	12.97	4.17	9.51
Minimum spore size	continuous	13.23	6.42	1.16	0.13	7.02
Water gradient	categorical	12.68	5.08	14.11	6.58	22.65
Reproductive system	categorical	8.83	15.59	31.81	6.49	1.01
Nutrient gradient	categorical	8.25	4.87	3.33	27.07	6.15
Spore frequency	categorical	5.28	13.63	0.00	0.00	7.25
Maximum spore size	continuous	3.32	24.52	0.04	0.01	4.71
No_sp_prod*	continuous	1.59	0.80	10.28	8.78	9.59

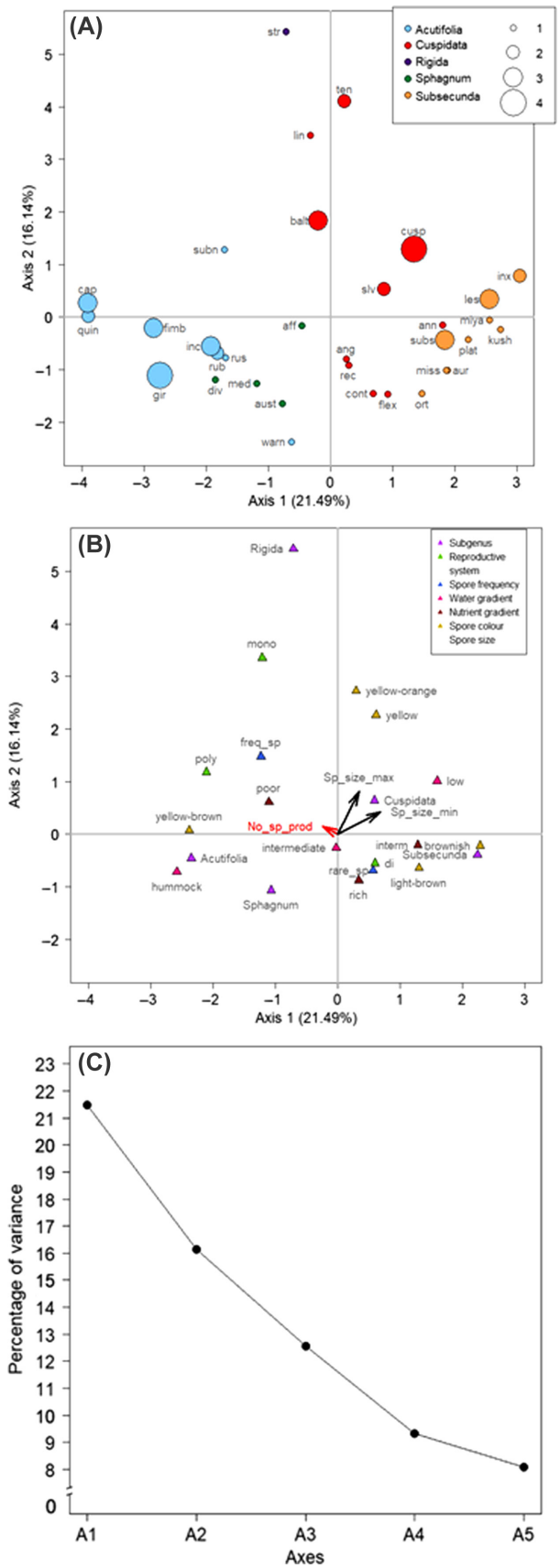

Figure 4. Two-dimensional FAMD plots for 33 parental species. Based on seven life-history variables (Table 2, column 6–12), as well as subgenus and intensity of hybridization as factors (Table 2, column 3 and 5, respectively). Percentage of the variance explained by the axis is given along each axis. (A) Individual species plot. Size and colour of point markers corresponds to the number of hybrids produced by the species and to the subgenus, respectively, as showed on the upper right corner. Key to the species abbreviations: aff - *S. affine*, ang - *S. angustifolium*, ann - *S. annulatum*, aur - *S. auriculatum*, aust - *S. austinii*, balt - *S. balticum*, cap - *S. capillifolium*, cont - *S. contortum*, cusp - *S. cuspidatum*, div - *S. divinum*, fimb - *S. fimbriatum*, gir - *S. girghensonii*, inc - *S. incundum*, inx - *S. inexspectatum*, kush - *S. kushiroense*, les - *S. lescurii*, lin - *S. lindbergii*, med - *S. medium*, miss - *S. missouricum*, miya - *S. miyabeanum*, ort - *S. orientale*, pla - *S. platyphyllum*, quin - *S. quinquefarium*, rec - *S. recurvum*, rub - *S. rubellum*, rus - *S. russowii*, slv - *S. slooveri*, str - *S. strictum*, sub - *S. subnitens*, subs - *S. subsecundum*, warn - *S. warnstorfii*, ten - *S. tenellum*. (B) Individual factor plot for quantitative and qualitative variables. Shape and colour of point markers correspond to different variables used in analysis as showed on the upper right corner. Key to the factor abbreviations: Reproductive system: *di* – dioicous, *mono* – monoicous, *poly* – polyoicous (including andro-polyoicous species sensu Kyrkjeeide et al. 2018, i.e. which are reported with separate male plants, but with certainty not with pure female plants); Spore frequency: *freq_sp* – frequent sporulation, *rare_sp* – rare sporulation; Water gradient (i.e. position along the water table ('hummock–hollow') mire gradient): *hummock* – hummock, *low* – lawns/carpets, *intermediate* – intermediate (both in hummocks and lawns/carpets); Nutrient gradient (i.e. position along the nutrient ('poor–rich') mire gradient): *rich* – rich fen habitat, *poor* – poor fen and bog habitat, *interm* – intermediate fen. Mire is here used in a wide sense, also including moist heaths and forests. Black arrows correspond to maximum and minimum spore sizes, and the red arrow – to the number of species produced by individual parental species, according to the labels. (C) A scree plot from the FAMD: X-axis represents Axis 1–5 according to the labels, Y-axis represents the percentage of variance explained by the axis.

colour. The latter is in line with theoretical expectations, as small spores and high sporulation frequency can give an advantage of dispersal to longer distances. More frequent hybridization found in monoicous and polyoicous species might result from their higher reproductive and dispersal success, and hence colonization ability, compared to dioicous species. Consequently, we can expect the portion of dioicous species to be smaller among hybridizing species than among non-parental species. This is indeed what we observe, even though we find that the difference is insignificant. Yet, one of the two species that have produced the highest observed number of hybrids is *S. cuspidatum*, a dioicous species which have the largest spores within the genus and rarely sporulate (Glime 2017b). According to the conducted FAMD, intensity of hybridization only explains about 2.6% of the total variance in life-history traits between species. Thus, other factors might certainly be more important in explaining the observed contradictions.

Johnson et al. (2015) showed a considerable phylogenetic signal for interspecific variation along the hummock–hollow gradient in peatlands. Based on this finding, we treat the position along the water table as a phylogenetically constrained trait and do not interpret how it is associated with intensity of hybridization. The same apparently applies to spore colour (Flatberg 2013). Phylogenetic constraints imply that traits of related species cannot be considered as

independent and identically distributed, by that violating assumptions of most of the statistical tests (Sober and Orzack 2001). Because of the amount and incompleteness of the available data, we were not able to account for relatedness in the FAMD. In light of this, it should be kept in mind that the relatedness between species might contribute to the patterns we observe.

Nevertheless, the association between more intensive hybridization and monoicous and polyoicous reproductive system, high sporulation frequency and smaller spores in peatmosses makes biological sense and provides a rationale for further testing. Unfortunately, there is lacking knowledge about mating system and other life-history traits in many parental and non-parental species. Available floras (Chien et al. 1999, McQueen and Andrus 2007, Flatberg 2013) list 104 *Sphagnum* species out of 289 species known worldwide (McQueen and Andrus 2007, Michaelis 2011), mostly describing the peatmoss diversity in the Northern Hemisphere. In particular, mating system is only known for 89 of the listed species, and the fraction of polyoicous species might be generally underestimated (Kyrkjeeide et al. 2018). To that end, it is likely that with more knowledge about the reproductive biology of peatmosses, we will be able to show the importance of these life-history traits for the occurrence of hybridization.

What other factors can potentially affect interspecific gene flow in *Sphagnum*?

There are other factors that might explain occurrence and intensity of interspecific hybridization in peatmosses, including levels of intraspecific gene flow. Generally, interspecific gene flow has been viewed insignificant compared to intraspecific rates of gene exchange (Mayr 1942, Ehrlich and Raven 1969). However, recent meta-analyses of a range of different organism groups show that distribution of interspecific and intraspecific rates of gene flow sometimes overlaps (Hey and Pinho 2012). Substantial intraspecific gene flow and frequent mating could in itself lead to frequent introgression between highly dispersing species in plants (Levin and Kerster 1974, Levin 1979), leading to a positive correlation between intra- and interspecific gene flow rates. Despite the high number of studies linking patterns of inter- and intraspecific gene flow and speciation in plants (Currat et al. 2008, Zhou et al. 2010), this has not been studied in bryophytes. Because of high ability of long-distance dispersal, peatmosses have high levels of intraspecific gene flow between populations, located even on different continents (Kyrkjeeide et al. 2016b, Désamoré et al. 2016). Therefore, intraspecific gene flow can potentially be important in explaining levels of interspecific introgression between species.

It was shown, that interaction of genetic and demographical factors, such as population size, time of season and relatedness, is important for explaining gene flow rates in plants (Goodell et al. 1997). Thus, studying speciation by gene flow in peatmosses primarily requires clarification of the relationships between inter- and intraspecific gene flow using genomic data and accounting for possible interaction between different factors.

Conclusion

Interspecific introgression is very common in peatmosses. Allopolyploidization seems to be a prominent process for speciation in the genus, while evaluation of the evolutionary significance of admixture requires further research. Up to 21% of all peatmosses are involved in intra- and intersubgeneric hybridization, producing mainly allopolyploid species, but also homoploid species and haploid admixed hybrids. This number might be substantially underestimated, since many parents of described allopolyploid hybrids are still unknown.

Parents of allopolyploids are on average less related than parents of admixed hybrids. Key life-history traits tend to be associated with intensity of hybridization as monoicous and polyocious species with high sporulation frequency and smaller spores preferring poor habitats produce more hybrids than other species. Overall occurrence of hybridization, however, is not constrained by phylogenetic distance and life-history traits of the parents. We suggest that differences in levels of intraspecific gene flow and/or interaction of population genetics and demographical history factors have a high potential in explaining occurrence and level of interspecific introgression. Finally, more studies are needed to determine the actual occurrence of hybridization in nature, as well as more detailed comparative data regarding reproductive biology and ecology of parental and hybrid species.

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