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Evidence for interspecific hybridization in bryophytes during pre-molecular and molecular eras

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Abstract

Interspecific hybridization had been long recognized as a widespread evolutionary process in vascular plants. In the present review, we summarize knowledge concerning studies of interspecific hybridization in bryophytes before and after the advent of molecular methods. The available data indicate that hybridization is an important evolutionary phenomenon among bryophytes. Evidence for hybridization events before the molecular era is mainly based on studies of intermediacy of parental morphology. The recent molecular marker technology has revolutionized studies of hybridization, generating new insights into the genetic and evolutionary consequences of homoploid and allopolyploid speciation. The current molecular approaches support the prevalence of allopolyploidy in bryophytes. However, we anticipate that homoploid hybridization is under-reported. Finally, we suggest some directions for future studies of hybrid speciation among bryophytes.

Key words: Allopolyploid, bryophytes, homoploid, interspecific hybridization, introgression, molecular marker

Introduction

For many years, natural interspecific hybridization has been considered an important process in plant, animal and fungal evolution (Gross & Rieseberg 2005; Mallet 2007; Soltis & Soltis 2009, Schmickl *et al.* 2017), and it is estimated that more than 50% of vascular plant species (Stebbins 1950) and about of 50–70 % of flowering plant species have some form of hybrid origin (Stace 1987). Based on recent genetic evidence, hybrid speciation is more common than earlier expected not only in plants but also in animals (Mallet 2007). In nature, some hybrid progeny is soon lost by natural selection, but others may survive beyond the initial generation by intercrossing between other hybrids forming “hybrid zones” and sometimes backcrossing with parental genomes forming “hybrid swarms” (Rhymer & Simberloff 1996). Repeated backcrossing of a hybrid with one of its parent species (introgression) may transfer genes between different evolutionary units. Hybridization and introgression (sometimes collectively called ‘introgressive hybridization) contribute to an increase of intraspecific genetic diversity (Anderson 1948), genetic adaptation (Stebbins 1950), increase of genetic, ecotype and species diversity (Dobzhansky 1937; Mayr 1942; Grant 1981; Whitham *et al.* 1994; Coyne & Orr 2004; Natcheva & Cronberg 2004; Wissemann 2007) or hybrid breakdown or reinforcement of reproductive barriers between closely related taxa (Ellstrand & Elam 1993; Rieseberg & Gerber 1995; Levin *et al.* 1996; Petit *et al.* 1999). Hybridization could also lead to extinction through genetic swamping, the loss of a rarer species, when subject to hybridization and back-crossing to a more common species, or demographic swamping, when excess production of maladapted hybrid progeny causes population decline (Todesco *et al.* 2016).

By definition, hybridization is a union between differentiated genetic materials in new individuals derived from parents which belong to different species, subspecies (Rieseberg 1997; Wagenitz 2003) or distinct populations (Arnold *et al.* 1991). Empirical data implies that hybridization has an important role in speciation (Mallet 2007, reviewed in Wissemann 2007). Two principal types of hybrid speciation are generally recognized, allopolyploidy and homoploid (recombinational) hybrid speciation (Mallet 2007; Hegarty & Hiscock 2005). Allopolyploidy involves hybridization between two taxa, in which hybrid offspring acquires a genome composed of more or less the full chromosome sets

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of both the parental individuals. The processes involved in allopolyploidy are well documented and a large body of knowledge has accumulated over the past history. Homoploid hybrid speciation involves a union between two taxa without change in chromosome number and is associated with recombination of the parental genomes.

Bryophytes constitutes the second most diverse group of higher plants, followed only by flowering plants, with some 20,000 species globally. They consist of three remotely related major groups, mosses (Bryophyta), liverworts (Marchantiophyta) and hornworts (Anthocerotophyta) (Nickrent *et al.* 2000; Kugita *et al.* 2003), which represent evolutionary lineages related to the first algal colonizers of terrestrial habitats. The relevance to bring them together in the context of hybridization is that they share a similar life cycle in terms of a dominant haploid gametophytic phase and a short-lived diploid sporophytic phase which is physically attached to the female parent. Bryophytes can reproduce both sexually and vegetatively. The sexual reproduction of bryophytes depends on water, by which mobile male gametes can swim to fertilize sessile female gametes. Successful fertilization of bryophytes is determined by both water availability and distance between male and female plants. This means that species that are involved in hybridization must grow in close vicinity, which is sometimes the case in intermediate or mosaic habitats (reviewed in Natcheva & Cronberg 2004).

Interspecific hybridization in bryophytes occurs after fertilization and the resulting diploid hybrid sporophyte is physically connected to the haploid female gametophyte (Nicholson 1931; Anderson 1980). The two paternal genomes are recombined during numerous meiotic events taking place in the sporophyte prior to the formation of spores. Thus, the true hybrid is the sporophyte (comparable to the F1 generation in of angiosperms with hybrid origin) and the spores are referred to as "recombinants" or "hybrid segregates" (comparable to the F2 generation of angiosperms), containing a combination of genes from both parents. If viable, recombinant spores may germinate and develop into the haploid gametophytes, which are directly exposed to natural selection since no variants are hidden as recessive alleles.

Long-term impacts of hybridization depend on circumstances, for example, it may slow or reverse genetic differentiation by allowing gene flow and recombination between species. Hybridization may also accelerate speciation by adaptive introgression or give rise to near-instantaneous speciation by allopolyploid formation (Abbott *et al.* 2013). Although speciation by homoploid hybridization is considered rare, sporadic hybridization is well documented to mediate horizontal transfer of adaptive genetic variation in both plants and animals (Burke & Arnold 2001).

Interspecific hybridization was long ignored by bryologists as an evolutionary process although hybrids were identified based on morphological characters already in the mid 1800s (Natcheva & Cronberg 2004). In most of the first observed cases, which included fairly distantly related species, hybrid breakdown took place during sporophyte initiation or spore formation, leading to a general conception that bryophyte hybrids were evolutionary insignificant failures. Hybridization in bryophytes was claimed more common following the discovery of allopolyploid species (Persson 1954; Wyatt 1994). Homoploid hybridization is historically rarely reported in bryophytes, even though its presence has been well-established in several groups of vascular plants (Anderson & Stebbins 1954; Grant 1981; Buerkle *et al.* 2000; reviewed in Natcheva & Cronberg 2004; Mallet 2007). In the present review, we aim to summarize different kinds of evidence among various groups of bryophytes in both nature and *in vitro*, both before and after molecular era. We survey the two major types of hybrid speciation processes in bryophytes (allopolyploid vs. homoploid). We account for the prevalence of different methods for detection of bryophyte hybridization in a historic perspective. The objective is also to provide prospects for future bryological studies on hybridization.

Materials and methods

To retrieve articles that report natural and experimental interspecific hybridization among bryophytes, we performed online-searches for full articles or abstracts from the databases Web of Science® and Google Scholar (available at http://scholar.google.com/). We also collected references that were cited by various authors that did not appear in the above-mentioned searches. Keywords, i.e. "Bryophyte + Hybrid" "Bryophyte + Hybrid + Hybridization" "Bryophyte + Interspecific Hybridization" "Bryophyte + Allopolyploid" "Bryophyte + Homoploid", were chosen for searches in the databases. The time span for searches was set from early 1900's until September 2020.

Results and discussion

Based on our literature search we found 207 records dealing with bryophyte hybrididzation in 132 articles, including for example, observations in nature, hybrid specimens from museum vouchers, experimental cross fertilization, spontaneous fertilization and hybridization detection by various molecular tools (**Appendix 1**). Records of hybridization are not evenly distributed among taxonomic groups—a large proportion of (putative) hybrids and their (putative) parental species belong to the acrocarpous moss groups (108 records) and peat mosses (54 records) and thallose liverworts (25 records). Notably, we found no record of hybridization in hornworts (**Fig. 1**). The three moss families most frequently reported to hybridize are Sphagnaceae, Funariaceae and Pottiaceae (**Fig. 2**). The three most studied bryophyte families prior to the molecular era are Funariaceae, Pottiaceae, and Bryaceae, whereas the three most studied bryophyte families during the molecular era are Sphagnaceae, Pottiaceae and Mniaceae (**Fig. 3**).

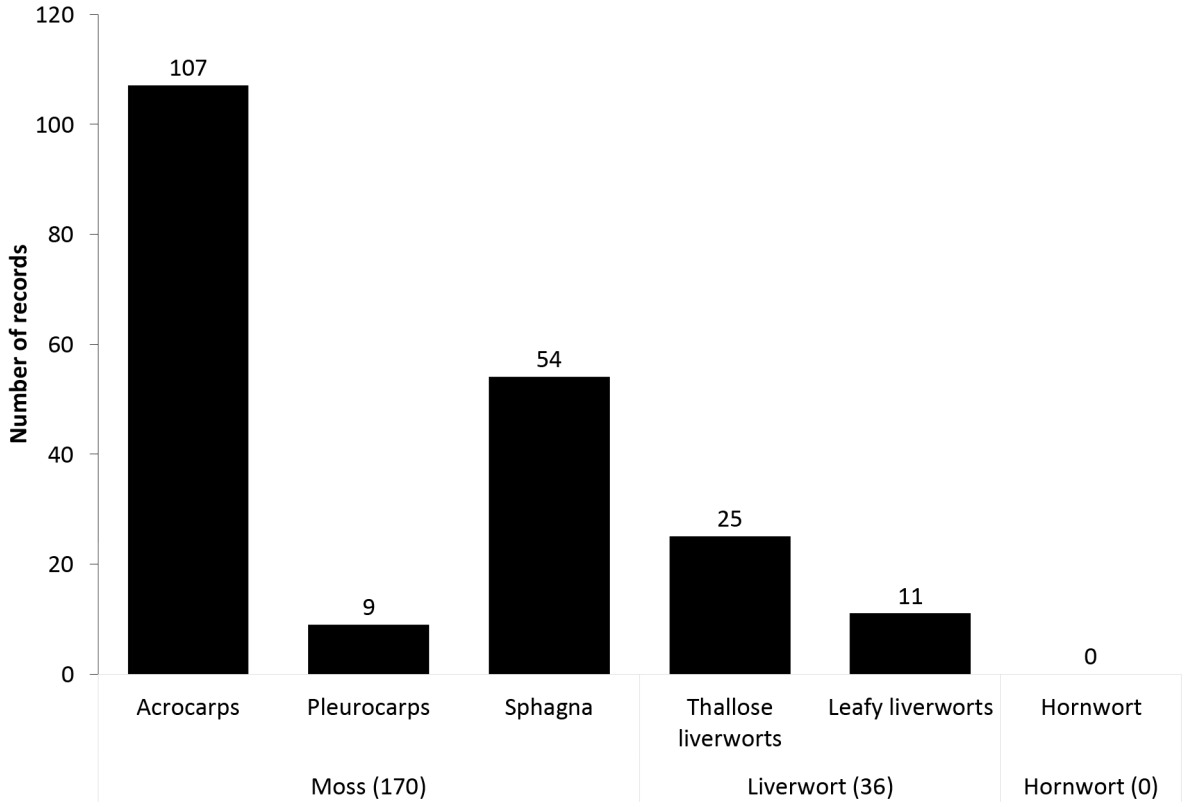

FIGURE 1. Number of literature records of interspecific hybridization in bryophytes categorized by growth form.

Initially, hybrid identification was based solely on morphological studies or a combination of morphology and spore germination/spore characters, subsequently by cytological ploidy level determination and analyses of secondary chemical substances and more recently by DNA markers at the turn of the 20th century (**Fig. 4**). Therefore, we divide the records into two major periods—the first period during 1900–1988 (Pre-molecular era) and the second period during 1989–present (Molecular era) (**Fig. 4**).

Recognizing hybrid offspring in bryophytes in the pre-molecular and molecular periods

First period (1900–1988): *Hybrid characterization based on morphological intermediacy of sporophytes, gametophytes, spore characters, spore germination test and/or chromosome counts.*

During this period hybrid identification was mainly restricted to morphological studies or a combination of morphological studies and other methods (**Appendix 1**). Morphological observations were used as preliminary indicators of hybridization, which was subsequently confirmed by complementary and more reliable methods. In quantitative terms we see that the markers that were used for identifying hybrid offspring in bryophytes are based on five key characters e.g. 1) sporophyte morphology 2) gametophyte morphology 3) F1 spore viability 4) F1 spore

morphology and 5) ploidy level, respectively (**Appendix 1**). Observations of hybrid morphology in bryophytes during this period were made by looking for a combination of traits characteristic of the putative parental species:

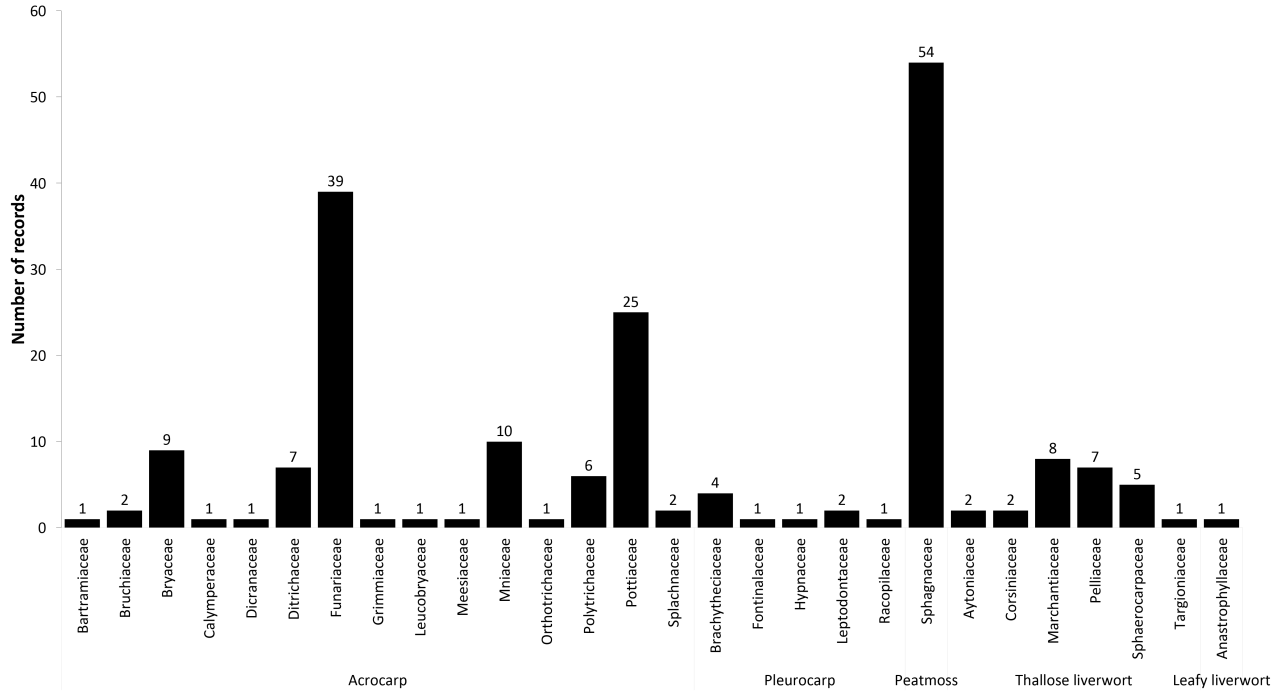

FIGURE 2. Number of literature records of interspecific hybridization in bryophytes categorized by family.

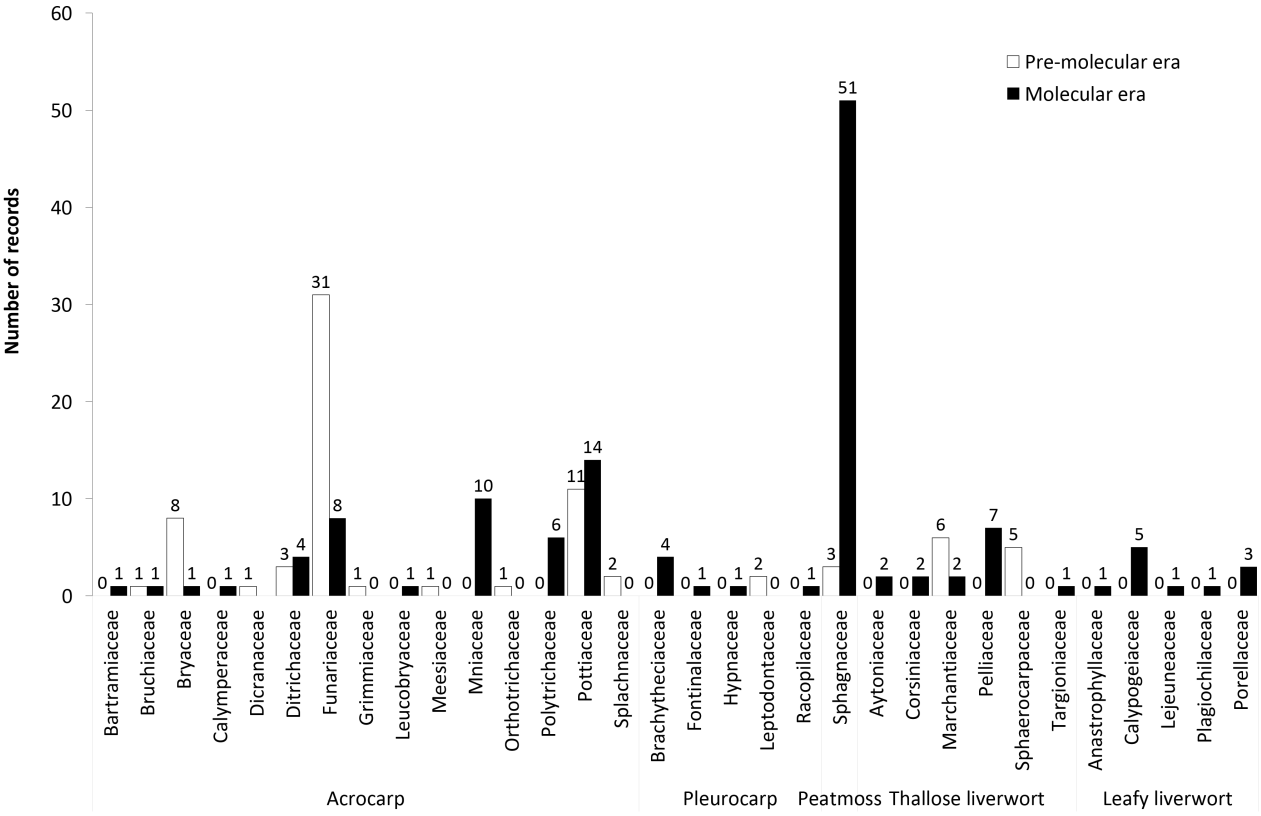

FIGURE 3. Comparison of the number of literature records of interspecific hybridization in bryophytes during the pre-molecular and molecular eras categorized by family.

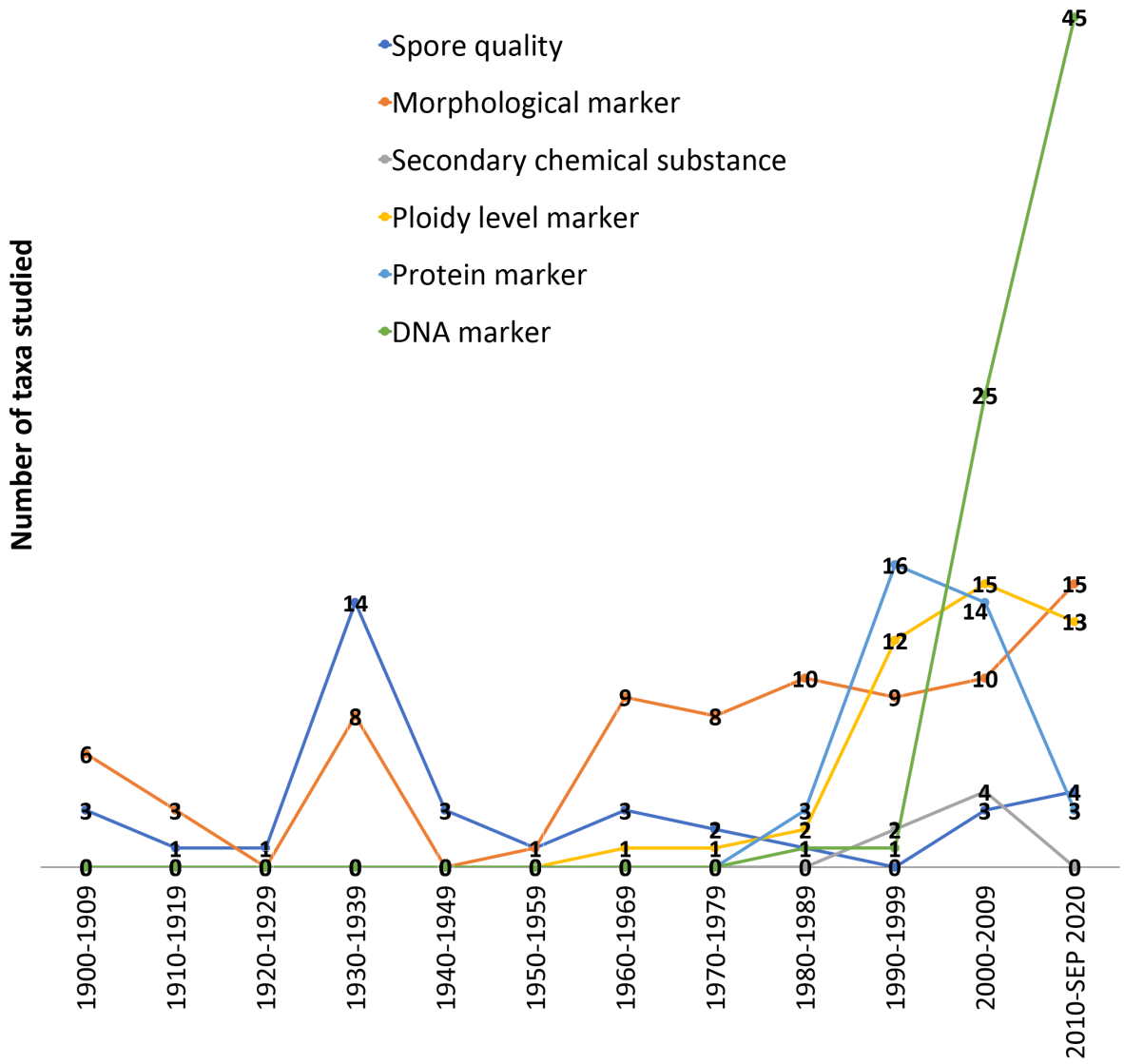

FIGURE 4. Number of literature records of hybrid progeny in bryophytes recognized by each type of character (marker).

i. Hybrid sporophytes

In most reported cases (**Appendix 1**), hybrid sporophytes were intermediate in terms of external and internal morphology (Allen 1935), capsule colour (Allen 1935), seta colour and presence/absence of calyptra (Pettet 1964), capsule shape (Khanna 1960; Anderson & Lemmon 1972; Hedderson 1986), form, colour and anatomical structure of seta in cross section (Frisvoll 1978), numbers and positions of stomata on capsule walls (Hedderson 1986) or exothecial cell characters (Andrews & Hermann 1959; Frisvoll 1978; Hedderson 1986). Generally, the hybrid sporophytes showed intermediate characters of both parents (Allen 1935), but there are some exceptions where hybrid sporophytes closely resembled the female parent (Allen 1935; Doyle 1960). If sought for, intermediate sporophytes were rarely encountered in nature (Crundwell & Nyholm 1964; Pettet 1964). The rare observation of intermediate sporophytes means that it is difficult to assess the evolutionary significance of these reports. In addition, hybrid sporophytes with intermediate characters will remain undetected if closely related parental species have similar sporophytes, which is the case in many acrocarps, most pleurocarps, peat mosses, and almost all liverworts (Natcheva & Cronberg 2004).

ii. Hybrid gametophytes

In bryophytes it is often difficult to assess whether morphological intermediacy has arisen as a consequence of

plasticity, ecotypic differentiation or hybridization. Hybrid gametophytes (also known as recombinant gametophytes) with intermediacy of parental character combination are therefore rarely reported according to Natcheva & Cronberg (2004). Gametophyte characters used to identify hybrid gametophytes include shape of leaves (Khanna 1960), gemma colour (Crundwell & Nyholm 1964), leaf arrangement (Holmen & Scotter 1971), and numbers of rhizoidal tubers (Risse 1985). Gametophytic morphology generally shows high phenotypic plasticity in bryophytes (Campbell 1971; Vanderpoorten & Goffinet 2009. In more than half of the articles (**Appendix 1**), gametophytes of putative hybrid origin showed an intermediate mix of parental characters, but several articles instead reported hybrid gametophytes to more closely resemble the female parent (Nicholson 1910; Wettstein 1928; Allen 1935; Pettet 1964; Holmen & Scotter 1971; Anderson & Lemmon 1972). Two exceptions included 1) *Physcomitrium* (haploid) × *Funaria* (haploid); the haploid gametophytes from hybrid spores showed similar characters to the female parent but diploid gametophytes from hybrid spores showed similar characters to the male parent (Allen 1935), and 2) *Bryum rubens* × *Bryum microerythrocarpum* (maternal/paternal unknown); the hybrid gametophytes produced gemmae that were similar to those of *B. rubens* (Crundwell & Nyholm 1964).

iii. F1 hybrid spores

Many cases of F1 hybrid spores were detected in bryophytes during the first period (**Appendix 1**). Inference of hybridization from spores was generally based on two types of observations; a) spore quality assessment via germination experiments, and b) studies of spore morphology (size and shape). Hybrid spores are frequently imperfect and wrinkled (Andrews & Hermann 1959; Reese & Lemmon 1965; Hedderson 1986), show a high degree of sterility (Nicholson 1905, 1906; Allen 1935, 1945; Nyholm 1954; Crundwell & Nyholm 1964; Williams 1966; Anderson & Lemmon 1972), and a variable degree of developmental disorder after germination (Andrews 1918; Burgeff 1943), suggesting that there is an internal sterility barrier to hybridization (Smith 1978). Typically, spore germination was investigated only on putative hybrid species but not systematically compared with that of the putative parental species (**Appendix 1**). Hybridization often result in sterile or inviable progeny owing to divergent evolution and genomic incompatibility (Mallet 2007), but spores could be inviable for other reasons than hybridization and some species are known to show large within-species variation in spore fertility (for example *Ceratodon purpureus*; Norrell *et al.* 2014) Furthermore, Allen (1935) reported that (putative) hybrid spores sometimes displayed a high germination rate (≥ 50%). As for the size, hybrid spores did not always show intermediate size of the parents, but rather spore size classes associated to each of the parents in the same hybrid capsules (Allen 1935), variable sizes of spores in the same hybrid capsules (Nyholm 1954; Andrews & Hermann 1959) or spore size similar to the female parent (Doyle 1960).

Unlike hybrid sporophytes and gametophytes, morphological intermediacy of hybrid spores between two putative parental taxa is rarely reported. Spore morphology is rarely useful below the genus level in mosses, and more important as diagnostic character in acrocarpous than pleurocarpous species (Clarke 1979; Ireland 1987). Some hepatics, especially thallous liverworts have species-specific spore morphology. Studies performed by Allen (1930) on external morphology of spores from the dioicous liverwort genus *Sphaerocarpos* demonstrated maternal inheritance of this trait (actually, said to be the first example of maternal inheritance in plants). Consequently, spore wall markings resembled spores belonging to the female parent rather than the male parent in cross experiments between *Sphaerocarpos* species (Doyle 1960).

iv. Hybrid bryophytes with different ploidy levels

Chromosome numbers in bryophytes are either studied in mitotic gametophyte cells or meiotic spore mother cells (Smith 1978). Observations on bryophyte chromosomes are time consuming and sometimes lead to inaccurate results (Smith 1978). From our literature search, Khanna (1960) was the first to provide evidence of allopolyploidy in bryophytes by chromosome counts from spore mother cells. Detection of hybrid species by ploidy level estimates based on chromosome counts alone might be problematic unless the karyotypes are distinctly different; 1) chromosome counts usually fail to differentiate between autopolyploids (containing more than two complete sets of homologous chromosomes and multisomic inheritance) and allopolyploids (contain separate sets of non-homologous chromosomes resulting from hybridization between different species and displaying disomic inheritance) (reviewed in Såstad 2005); 2) estimates of DNA content from chromosome counts is inclined to uncertainty due to a lack of overall relationship between chromosome number and genome size for mosses and a lack of cytological evidence for polyploidy in bryophytes containing high chromosome numbers (Vogelmayer 1998). Accordingly, Vogelmayer (1998) suggested that chromosomal rearrangements, such as translocations and deletions are the most common reason for differences in chromosome numbers, and that polyploidization may be important only in certain families and genera of bryophytes (e.g. Sphagnaceae). Såstad (2005) added that estimation of ploidy level by chromosome counting may be flawed by

chromosome fission and fusion events. In the case of liverworts, which have a more stable basic chromosome number of 8, 9 or 10, it is easier to assess if genomes are haploid or polyploid (Schuster 1966; Smith 1978; Newton 1983).

Second period (1988–present): *Hybrid characterization based on combined methods of cellular ploidy determination, biochemical properties and genetic markers (biological and molecular markers)*.

From 1988 to the present days, hybrid progeny identification based on combined morphology of parental species characters in sporophytes, gametophytes and F1 spores are still practiced for screening of hybrids, but lose in popularity (**Appendix 1**). Ploidy level analysis based on various microscopic methods (see below) is more widely used to confirm species hybridization through allopolyploidy in this period than the first period. At the same time, more precise methods for identification of hybrids in bryophytes are introduced: protein markers (e.g. isozymes), DNA markers (e.g. microsatellite DNA, nuclear DNA, cpDNA, mtDNA, SNPs) and cell chemical markers (e.g. flavonoids, oil bodies) (**Appendix 1**). Protein markers were gradually replaced by DNA markers, whereas secondary chemical substance markers were only used for a short period (**Fig. 2**). The various markers to identify bryophyte hybridization events in the second period are summarized below.

i. Hybrid sporophytes

Recognition of hybrid sporophytes based on intermediacy of parental species characters is rare during this period. In case of non-intermediacy, hybrid sporophytes showed similarity to one parent (McIntosh 1989), variable characters (van der Velde & Bijlsma 2004), or more robustness than both parents (Flatberg *et al.* 2006; Ricca *et al.* 2011). Thus, observations of intermediate characters of sporophytes are used rather as a preliminary screening method for hybrid species preceding other more accurate investigations (**Appendix 1**).

ii. Hybrid gametophytes

Hybrid gametophytes or recombinant gametophytes with parental character combination are rather frequently reported in various taxa in our survey (**Appendix 1**). Gametophyte characters chosen to identify hybrid gametophytes include the pattern of sex organ arrangement (Lobachevs'ka & Ulychna 1994), thallus cell size (Boisselier-Dubayle *et al.* 1998a; Orzechowska *et al.* 2006), leaf size (Såstad *et al.* 2001), anatomy of stem cross section (Werner *et al.* 2014). In general, gametophytic characters mentioned in the surveyed literature show high phenotypic plasticity. In cases of non-intermediacy, hybrid gametophytes showed different degrees of parental character inheritance e.g. highly variable (Shaw & Bartow 1992; Cronberg 1996; Boisselier-Dubayle *et al.* 1998b), similar to female parent or one parent (Delgadillo 1989; Ros *et al.* 1994; Ricca & Shaw 2010; Shaw *et al.* 2012b; Shaw *et al.* 2013; Werner *et al.* 2014), indistinct to non-hybrid populations (Boisselier-Dubayle & Bischler 1998; Boisselier-Dubayle & Bischler 1999), or more robust size than both parents (Boisselier-Dubayle *et al.* 1998a; Såstad *et al.* 2001; Orzechowska *et al.* 2006). Like hybrid sporophytes, morphological identification of hybrid gametophytes is used as a complementary method, together with other more reliable studies.

iii. F1 hybrid spores

Hybrid spores were reported in some cases of bryophyte species in the second period but did not increase over time (**Appendix 1**). Hybrid spores with non-intermediate sizes showed more highly variable sizes than those of their parents (Delgadillo 1989; Košnar *et al.* 2012) or similar sizes to those of one parent (often female) (Guerra *et al.* 1994; Ros *et al.* 1994) or larger spore size than those of the parents (Flatberg *et al.* 2006) or the same size and shape as their parents (Natcheva & Cronberg 2007a, b) or irregular size and shape compared to the parents (Frahm & Ho 2010).

iv. Hybrid bryophytes with different ploidy level

Earlier cytological techniques are gradually replaced by improved methods to compare chromosome morphology, ploidy level and estimate DNA content e.g. the squash technique (Boisselier-Dubayle & Bischler 1998; Boisselier-Dubayle *et al.* 1998a; Boisselier-Dubayle *et al.* 1998b; Orzechowska *et al.* 2010), the fluorochrome 4, 6-diamidino-2-phenylindole (DAPI) technique (Abderrahman 1998; Abderrahman 2004; Buczkowska *et al.* 2004), flow cytometry (Såstad *et al.* 2001; Ricca *et al.* 2008; Karlin *et al.* 2009; Košnar & Kolář 2009; Orzechowska *et al.* 2010; Ricca *et al.* 2011; Buczkowska *et al.* 2012; Nieto-Lugilde *et al.* 2018), Fluorescent differential staining, C-banding and fluorescent *in situ* hybridization (FISH) with 26S and 5S ribosomal DNA probes (Orzechowska *et al.* 2010), Feulgen DNA image densitometry (Ricca *et al.* 2008; Karlin *et al.* 2009; Kyrkjeeide *et al.* 2019) and ploidy estimation by microsatellite pattern (Karlin *et al.* 2013, 2014). The use of fluorescent *in situ* hybridization (FISH) of specific DNA probes to specific chromosomes or chromosome segments has recently proved straightforward and useful in studies of

chromosomal rearrangements and homologue associations, which can generate chromosome maps for the subsequent study of chromosome evolution during hybridization event (Lysak *et al.* 2001; Hegarty & Hiscock 2005) (**Appendix 1**).

v. Hybrid bryophytes with different concentration of secondary chemical substances

Wyatt and his colleagues in 1991 were the first to use flavonoids to study hybridization among seven taxa of *Plagiomnium* section *Rosulata* and found that hybrids express a combination of the flavonoids characteristic of their parental species. Buczkowska *et al.* (2004) demonstrated that the distribution pattern of oil bodies (presence/absence) in leaf and underleaf cells were highly correlated with isozyme variants of four enzymes of six *Calypogeia* liverwort species from Poland. The fixed heterozygosity pattern of two enzymes (TPI and GOT) found in all studied samples of the polyploid *C. azurea*, *C. muelleriana* and *C. sphagnicola* may suggest the three species having allopolyploid origins.

vi. Hybrid bryophytes via molecular marker studies

Gradually improved molecular techniques have over the years become employed for studies of variation and hybridization at the genomic level in flowering plants (Hegarty & Hiscock 2005) and bryophytes (Pardo *et al.* 2014). Starting around 1988, a range of molecular techniques based on various kinds of markers have been used to identify hybrid progeny in bryophytes. Marker-based techniques to identify hybrids assume that the given markers are species-specific to either parent, in order to be detected in combination in putative hybrids. Molecular markers can be divided into two major classes 1) protein markers (e.g. isozymes or allozymes) and 2) DNA markers such as RFLPs, RAPDs, Microsatellites, ISSR, PCR-RFLP, QTL-associated markers, specific DNA sequences, and SNP markers.

Isozymes or allozymes. The isozymes were important sources of information about infraspecific population structure and genetic relationships among species because they are cost-effective, easy to detect, highly reproducible (Shaw 2009; Gibson 2015), and co-dominant so that diploid/polyploid individuals can be identified as homozygotes or heterozygotes at a given locus (Parker *et al.* 1998). Wyatt *et al.* (1988) introduced isozymes as molecular markers to identify interspecific hybridization and chromosome doubling in the moss, *Plagiomnium medium*. Due to co-dominant expression, allopolyploids were readily identified by fixed heterozygosity at multiple loci. Isozyme analyses have been replaced by DNA markers in recent years, although useful in studies of hybrid speciation in conjunction with other techniques such as RFLP analysis of chloroplast DNA, RAPD and microsatellite assays. (**Appendix 1**).

Restriction Fragment Length Polymorphisms (RFLPs). RFLPs were the first widespread markers that quantified variation in DNA sequences by using restriction enzymes to cut DNA into small pieces and then run in agarose gel and to see DNA profiles. Wyatt *et al.* (1988) used chloroplast DNA (cpDNA) extracted from three *Plagiomnium* species to identify *P. insigne* as the female parent of the alloploid *P. medium* on the assumption that cpDNA was maternally inherited. Studies of chloroplast DNA using RFLP are useful for identifying the maternity of the hybrid progeny.

Random Amplified Polymorphic DNA (RAPDs). RAPDs markers are the simplest PCR-based method by amplifying arbitrarily derived DNA segments for genotyping individuals at multiple loci (Welsh and McClelland 1990, Gibson 2015). Due to some drawbacks of this technique such as a lack of knowledge on amplification products, co-migration of non-homologous fragments of similar size, a lack of reproducibility of bands and dominant nature (Shaw 2009; Pardo *et al.* 2014), it was soon abandoned for more accurate methods (**Appendix 1**). Only two studies have used RAPD technique for identifying hybrid bryophytes. Stenøien & Flatberg (2000) and Såstad *et al.* (2001) indicated two progenitor species of allopolyploid species, *Sphagnum troendelagicum* and hypothesized that it had multiple origins from recurrent hybridization events based on a moderately high haplotypic variation in the RAPD profiles.

Microsatellites. Microsatellites (also known as simple sequence repeats, SSRs or short tandem repeats, STRs) are nucleotide tandem repeats of 1–6 bp in DNA sequences located in nuclear, chloroplast and mitochondrial genomes (Freeland *et al.* 2011). Van der Velde & Bijlsma (2001) applied microsatellite markers to detect the second parental taxon of the allopolyploid hybrid acrocarpous moss *Polytrichum longisetum*, which was not resolved by allozyme data. The numbers of bryophyte species from which microsatellite loci have been characterized have accumulated over time, so that they have been accessible for studies of hybridization events (**Appendix 1**). The co-dominant property of microsatellites provides a major benefit over other markers such as RAPDs, AFLPs and ISSRs, in studies of hybridization and mating systems in bryophytes (Shaw *et al.* 2008c).

Inter-simple sequence repeat or ISSR. The ISSR method is similar to RAPD method but ISSR primers are designed from microsatellite regions and are longer than RAPD primers (Pardo *et al.* 2014), producing more reliable and reproducible bands than RAPD (Vanderpoorten *et al.* 2003). Natcheva & Cronberg (2007a, b) introduced this technique to demonstrate recombination and introgression of nuclear and chloroplast genomes between the two peat

mosses, *Sphagnum capillifolium* and *S. quinquefarium*. Recombinant progeny from hybrid sporophytes, only a few of which were viable, showed asymmetrical nuclear inheritance—possessing a majority of nuclear markers typical for *S. capillifolium* (as a paternal progenitor), whereas cpDNA markers were maternally inherited.

PCR-Restriction Fragment Length Polymorphism (PCR-RFLP). This method involved two processes, a digestion by a restriction endonuclease of a specific amplified DNA segments and the presence/absence of a given restriction site in the DNA sequence to determine polymorphism (Pardo *et al.* 2014). Natcheva & Cronberg (2007a, b) used this method in their study to assess two chloroplast haplotypes in the two sympatric species of peat mosses, *Sphagnum capillifolium* and *S. quinquefarium* and identified gametophyte hybrids possessing a single chloroplast haplotype interited only from *S. quinquefarium* (as a maternal progenitor).

QTL-associated markers. QTL is quantitative trait loci, which refers to specific DNA regions that are responsible for controlling the expression of a quantitative phenotype (Freeland *et al.* 2011). McDaniel *et al.* (2008) demonstrated an intrinsically reproductive isolation mechanism, contributing to hybrid breakdown in interpopulation progeny of the moss *Ceratodon purpureus* by using markers linked to a gene that influences the expression of the quantitative trait, protonemal development size. The observations by McDaniel and his colleagues suggested that multiple complex genetic factors contribute to divergence among populations of *C. purpureus*.

DNA sequence markers. DNA sequence markers are more reliable than markers based on banding pattern if homologous loci are compared and paralogous genes are absent (Pardo *et al.* 2014). Stech & Quandt (2010) showed that the number of markers applied in bryophytes phylogenetic studies has increased considerably since 2001, with an increase of about 250% in the plastid, 470% in the nuclear, and 550% in the mitochondrial DNA. The most difficult problem of DNA sequence marker analysis lies in the selection of the region of the genome that not only reveals allelic variation but can also be sequenced efficiently. DNA sequence markers from the three types of genomes nrDNA (nuclear), cpDNA (from chloroplasts) and mtDNA (mitochondrial) are used to study hybridization in bryophytes as shown below.

1) nrDNA markers: ITS (rRNA gene) regions are extensively used as markers because these sequences are transcribed but not translated, thus they tend to evolve rapidly and have relatively high rates of mutation that are useful for determining the phylogenies of closely related taxa (Bhatia *et al.* 1996). In contrast to organellar genomes (cpDNA and mtDNA), nuclear markers are biparentally inherited (Stech & Quandt 2010).

2) cpDNA markers: Loci which are widely targeted in cpDNA sequences includes genes, spacers and introns of the following regions: trnG, trnL, rbcL, trnL-trnF, rpL16, atpB-rbcL, rps4-trnS, trnL-F, trnH-psbA, and rpoC1 (Shaw & Goffinet 2000; Jankowiak & Szweykowska-Kulinska 2004; Shaw *et al.* 2005; Jankowiak *et al.* 2005; Jankowiak-Siuda *et al.* 2008; Shaw *et al.* 2008a,b; Bell & Hyvönen 2010; Ricca & Shaw 2010; McDaniel *et al.* 2010; Heinrichs *et al.* 2011; Buczkowska *et al.* 2012; Shaw *et al.* 2012a; Vilnet *et al.* 2012; Shaw *et al.* 2013; Karlin *et al.* 2014; Werner *et al.* 2014; Shaw *et al.* 2015). The cpDNA markers are useful in studying hybridization because they are maternally inherited (McDaniel et al 2007, Natcheva & Cronberg 2007a).

3) mtDNA markers: The mtDNA offers few loci for bryophyte studies primarily due to lower variability as compared to the cpDNA (Stech & Quandt 2010; Liu *et al.* 2012). The mtDNA genes have been used for phylogenetic studies involving genera, families, and order (Cox *et al.* 2004). However, some genes recently proved useful as markers for studies of species-level hybridization in bryophytes such as the trnS and the coxIII genes, the nad5 gene, and the nad4 (Jankowiak & Szweykowska-Kulinska 2004; Jankowiak *et al.* 2005; Jankowiak-Siuda *et al.* 2008; Bell & Hyvönen 2010). Like the cpDNA markers, the mtDNA markers are maternally inherited in bryophytes (Stech & Quandt 2010).

Single Nucleotide Polymorphisms or SNPs. SNPs are single base pair positions in the genome that vary between individuals. Due to a high abundance in the genome, SNPs serve as useful biological markers (Jin *et al.* 2016). Species-specific SNP markers can be selected, which allow direct identification of hybrid genotypes by heterozygous allele combinations (Clarke *et al.* 2014; Rusek *et al.* 2015). Despite these obvious advantages, there are only a limited number of examples of application of SNP markers in bryophyte hybridization by 2020. SNP markers were used by Sawangproh *et al.* (2020a, b) to detect hybrids and to estimate the degree of genetic mixing in the pleurocarpous mosses *Homalothecium lutescens* and *H. sericeum*, through three generations; haploid gametophytes, diploid sporophytes and recombinant sporelings.

Records on mode of hybridization in bryophytes in the pre-molecular and molecular periods

First period (1870–1988): *Modes of hybridization (homoploid/allopolyploid) are mostly undetermined.*

Studies of hybridization events based mainly on a combination of intermediate morphological characters allowed bryologists to detect parental progenitors, but usually not to reconstruct the hybridization process. Out of 76 cases of putative hybridization among bryophytes, only 14 aimed at revealing the evolutionary processes underlying the hybridization events (**Appendix 1**). Studies which propose a more or less well-documented mode of hybridization sum up to: allopolyploidy (11 records), autopolyploidy (5 records), homoploid origin (3 records), and allopolyploid-autopolyploid combination (1 record) (**Fig. 5)**. Smith (1978) claimed that interspecific polyploids in both mosses and liverworts seem to be autopolyploids based on cytological analyses. However, some authors disagreed with the view of prevalent autopolyploidy and argued that allopolyploidy is underestimated in bryophytes (reviewed in Wyatt *et al.* 1992). The modes of hybrid speciation found from our literature survey were from interpretation of cross-fertilization experiments (e.g. Doyle 1960) except one study by Khanna (1960), in which hybridization by allopolyploidy was inferred by cytological analysis through chromosome counting. The relatedness of hybridizing entities as judged by taxonomic ranking was: intraspecific (1 record), interspecific (42 records), and intersectional (36 records) (**Fig. 6**).

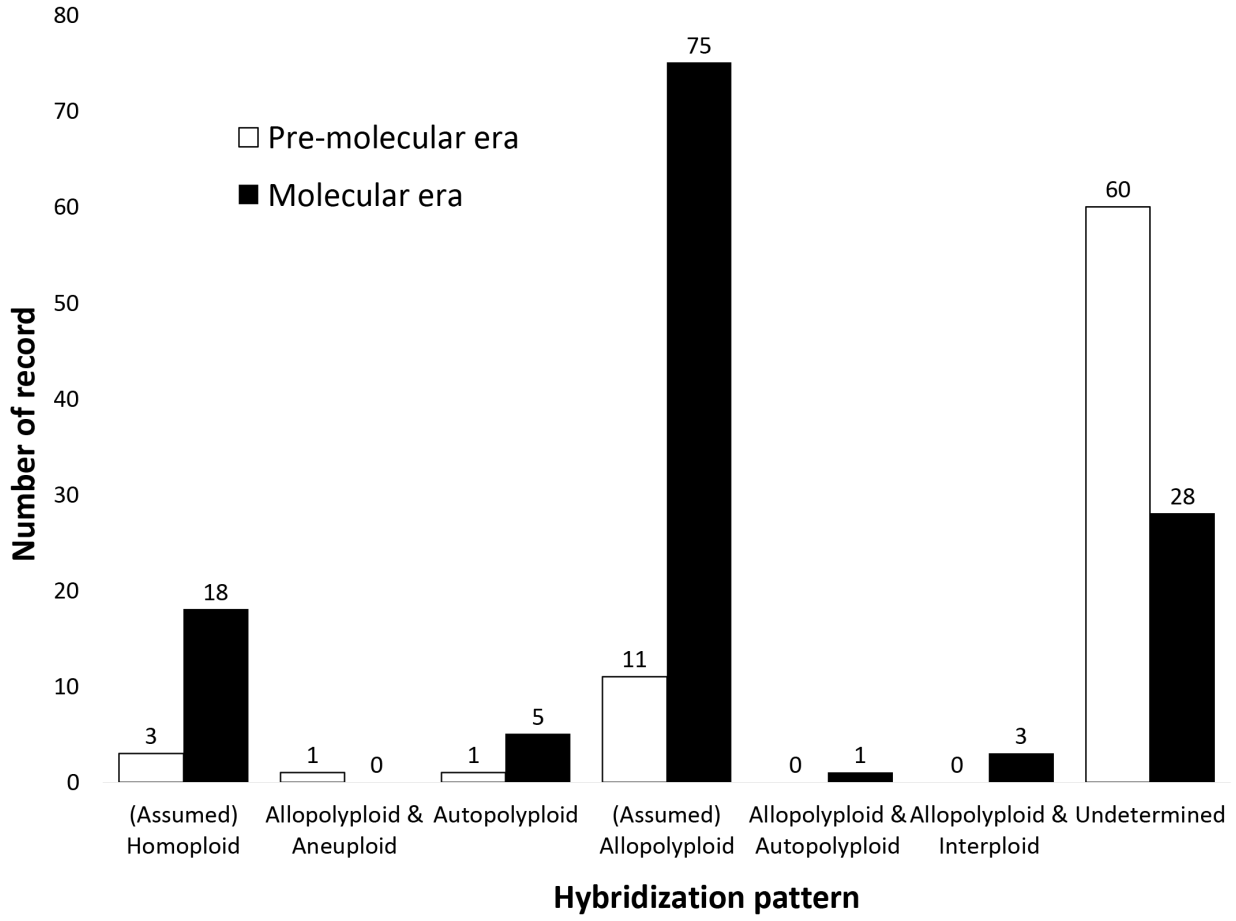

FIGURE 5. Comparison of literature records with respect to modes of hybridization in bryophytes during the pre-molecular and molecular eras.

Second period (1988–present): *Modes of hybridization in bryophytes are mainly studied by more accurate methods and most of the studied cases involve allopolyploidy.*

During this period, the modes of hybridization are investigated by more reliable and sophisticated cytological and molecular studies—revealing more information about the hybrid events. The cytological and molecular techniques made it possible to characterize the mode of hybridization in 101 out of 132 records (**Appendix 1**). The most common mode was allopolyploidy (76 records), followed by (assumed) homoploid (16 records), autopolyploid (5 records), allopolyploid-interploid combination (3 records), and allopolyploid-autopolyploid combination (1 record) respectively

(**Fig. 5**). Classified by divergence level, we found hybrid records involving i) parental pair at the same ploidy level, i.e., interspecific hybridization (87 records) and intraspecific hybridization (14 records) and ii) the parental pair at different ploidy levels i.e., interploidal hybridization (2 records). Other cases were intersectional hybridization (18 records), intergeneric hybridization (10 records), and interfamiliar hybridization (1 record) (**Fig. 6**).

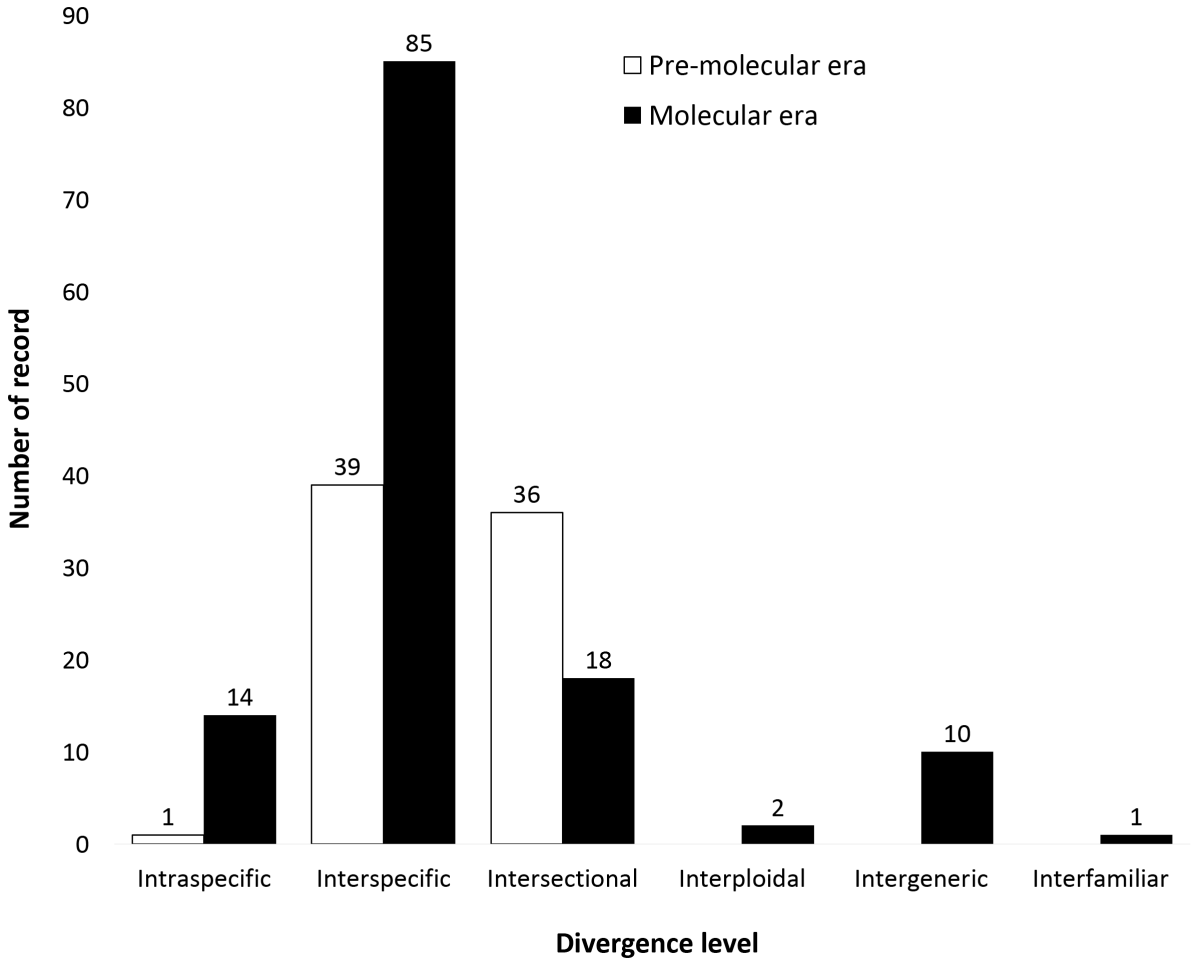

FIGURE 6. Comparison of literature records in the pre-molecular and molecular eras regarding the divergence of putative parental species to hybrids in terms of separation at different taxonomical levels.

More and more cases of hybridization by allopolyploidy are being discovered among bryophytes as cytological and molecular studies progress, following the first pioneering findings of fixed heterozygosity based on isozyme markers in *Plagiomnium medium* by Wyatt *et al.* (1988) (**Appendix 1**). Såstad noted in a review 2005 that all polyploid bryophytes studied so far (at the time mostly by isozymes) had turned out to be allopolyploids. He estimated that about 5–10% of liverwort species and 6–19% of moss species have polyploid origins and suggested that most are allopolyploids. Evidence for autopolyploidy is still missing among peat mosses (*Sphagnum*) (Meleshko *et al.* 2018), the most well-studied group in this respect, with a possible exception for diploid *S. tescorum* (Shaw *et al.* 2012a). The low number of confirmed autopolyploid bryophytes is puzzling, since ploidy level series exist for many taxa (Fritsch 1982), in particular among mosses. Due to the haploid-dominant life cycle in bryophytes, allopolyploidy potentially provide adaptive flexibility to hybrids by allowing heterozygosity to be expressed in the free-living gametophyte generation, unlike the haploid parents, in which the genome is directly exposed to natural selection (Wyatt *et al.* 1992). In theory, an allopolyploid hybridization event therefore leads to the formation of a genotype with superior fitness and a higher chance to establish and proliferate vegetatively and sexually (Natcheva & Cronberg 2004). Shaw *et al.* (2008b) corroborate that allopolyploid species appear to be common among the mosses. However, speciation by homoploid hybridization is also increasingly reported among bryophytes as a result of the progress of molecular technologies. Homoploid speciation has been proposed for *Physcomitrium eurystomum* (McDaniel *et al.* 2010), *Sphagnum contortum*

(Shaw *et al.* 2012b), *Ceratodon* × *conicus* (Nieto-Lugilde *et al.* 2018), but on the other hand, Linde *et al.* (2020) refuted on basis of genomic data the old hypothesis that *Marchantia polymorpha* subspecies *ruderalis* is a homoploid hybrid between subspecies *polymorpha* and *montivagans*. Our literature survey suggests that homoploid hybridization without speciation (admixture) may occur between differentiated geographic populations (McDaniel *et al.* 2008) or between more or less closely related species in the same genus (Cronberg & Natcheva 2002; Flatberg 2005; Natcheva & Cronberg 2007a,b; Ricca & Shaw 2010; Shaw *et al.* 2012a,b; Meleshko *et al.* 2018), but rarely among more distantly related species. Ignatov *et al.* (2019) review the question how remote hybridization can be in bryophytes.

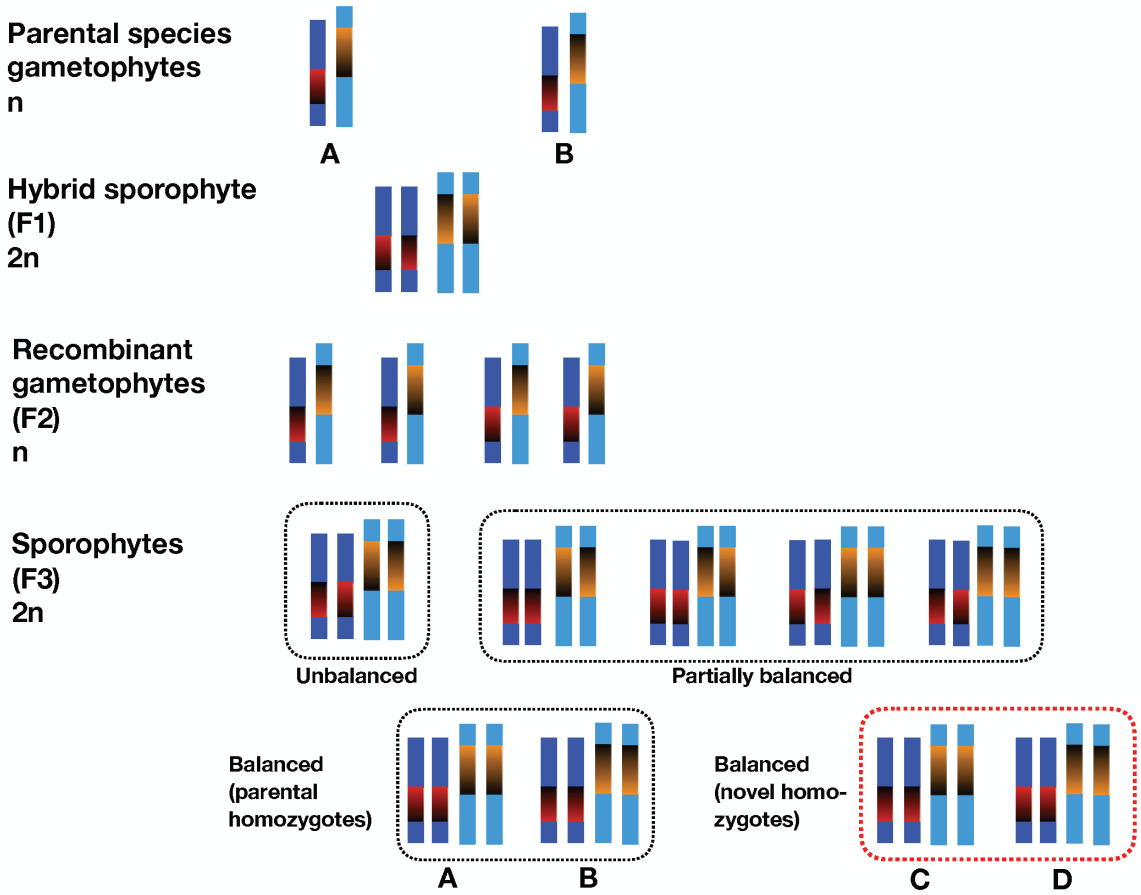

FIGURE 7. Schematic representation of the Grant (1975, 1981) model of "recombinational speciation" adopted for bryophytes. Note that gametophyte generations are haploid (n) and sporophyte generations diploid (sn). The parental species (A and B) differ by having two chromosomal inversions (red and orange chromosomal blocks; inversions indicated by inverted shading). Hybridization result in F1 sporophytes that are heterozygous for both the inversions and thus expected to have low fertility. Mating among the F2 recombinant spores can give rise to partially balanced genotypes (homozygous for one inversion; four examples illustrated) in the F3 sporophyte generation, re-establishment of the F1 genotype or the parental genotypes (A and B; homozygous for both inversions) as well as two novel balanced genotypes (C and D; homozygous for both inversions). Such a novel balanced genotype is expected to produce viable progeny that shows higher interfertility with other hybrid progeny with the same novel homozygotes as compared to if it would have been back-crossed to the parental species.

New perspectives on hybrid formation in bryophytes after the advent of molecular tools

Isolation mechanisms can be subdivided into prezygotic and postzygotic mechanisms (before and after fertilization). Spatial isolation is probably the major prezygotic barrier acting against hybridization in bryophytes. This phenomenon is pronounced compared to most vascular plant by short fertilization distances in bryophytes (Natcheva & Cronberg 2004). Spatial and/or ecological separation may therefore prevent hybridization throughout most of overlapping distributions areas, unless intermediate habitats exist. This is illustrated by *Homalothecium lutescens* and *H. sericeum* which are normally ecologically separated, growing on soil and on tree trunks or stone walls, respectively, but found

to be extensively hybridizing when growing in mixed populations in regionally occurring intermediate habitats on the island of Öland, Sweden (Sawangproh *et al.* 2020a,b). Adding to this, the two species of *Homalothecium* are nannandric, meaning that male spores germinating on female shoots develop into minute but sexually active dwarf males which can readily fertilize the female. Rosengren and Cronberg (2015) demonstrated experimentally that females of *H. lutescens* could prevent spore germination of an unrelated species (*Isothecium alepecuroides*) but spores of *H. sericeum* germinated equally well as the *H. lutescens* spores and developed into dwarf males. This discrimination failure between related species expose an obvious mechanism for hybridization in nannandric species, as it reduces the spatial isolation barrier in mixed or adjacent populations. Nannandry is a widespread phenomen among both acrocarpous and pleurocarpous mosses so the question raises to what extent females can discriminate between native and alien spores in other groups.

Partial or full postzygotic reproductive isolation among allopatric taxa in bryophytes have been demonstrated in crossing experiments (Allen 1937; Burgeff 1943, Proskauer 1969; Proctor 1972; McDaniel *et al.* 2008). It is not known to what extent reproductive isolation in bryophytes depends on chromosomal or other structural rearrangements at genomic level, incompatibility between the nuclear genome and a foreign chloroplast (or mitochondrium) or some kind of "speciation genes" (related to a reinforcement process). Burgeff (1943) made reciprocal crossings involving the three taxa in the *Marchantia polymorpha* complex, with varying degrees of reproductive isolation, in particular he observed strikingly different hybrid fertility in reciprocal crosses between subspecies *polymorpha* and *montivagans*, suggesting an influence of sex chromosomes or maternally inherited chloroplast or mitochondrial genomes.

The question how polyploids arise in bryophytes have been discussed for a long time. Polyploid hybrids evolve in bryophytes by 1) syndiploidy-doubling of the gametic chromosome number by fusion of daughter cell nuclei in the capsules or diplospory—the production of unreduced spores (Flatberg *et al.* 2006), by 2) apospory—the regeneration of diploid gametophytes from immature sporophyte tissues (e.g., Anderson, 1980; Shaw 2009) and possibly by 3) endopolyploidy—DNA replication in hybrid spores without nuclear or cell division. The latter is widespread in mosses but rare in liverworts (Bainard & Newmaster 2010) and a rather recent finding, observed through flow cytometry. Since bryophyte tissue is totipotent (Lal, 1984), any cell can form a new individual, endoploid cells (if disrupted from the normal haploid cells) could possibly form autopolyploid gametophytes. In the case of endopolyploidy, both parental species must have undergone endopolyploid duplication and subsequently hybridized to acquire a progeny that could be interpreted as allopolyploid. In contrast, allopolyploidy is aquired directly if the sporophyte undergoing syndiploidy or apospory is of hybrid origin.

Allopolyploid individuals are believed to rarely introgress with their parental taxa because of differences in ploidy levels (Petit *et al.* 1999), but several exceptions have been found in *Sphagnum*. Modern molecular and cytological methods have made it possible to trace secondary hybridization and polyploidization of allopolyploids giving rise to allotriploids, auto-allotriploids and double allopolyploids and to disentangle the various involved parental genomes. Most of these reports have emanated from molecular analyses of herbarium specimens, but the first observation came from a wild population with hybrid sporophytes carried on *Sphagnum girgensohnii* (maternal parent), apparently fertilized by allopolyploid *S. russowii* (paternal parent), which in turn is a hybrid between *S. girgensohnii* and *S. rubellum* (Flatberg *et al.* 2006). The genome in the sporophyte was thus 1 × *rubellum* and 2 × *girgensohnii* and the triploid was transmitted through syndiploidy or diplospory to the spores, of which 5 % were viable. The resulting gametophytes matched spontaneous gametophytes in the population. This observation was soon followed by several reports of allotriploid and double allopolyploid species (having three and four separate genomes, respectively) by Karlin *et al.* (2009, 2013, 2014), Karlin (2014) and Kyrkjeeide *et al.* (2019). These separate genomes originated from close relatives but sometimes also from parental species representing different subgenera of peatmosses.

Grant (1975, 1981) proposed the two models for speciation by homoploid hybridization: 1) "The recombinational speciation model", that the two parental species with the same chromosome number differ by two or more chromosomal rearrangements. Due to the chromosomal rearrangements, some F2 progeny with novel homozygotes shows higher interfertility with other hybrid progeny with the same novel homozygotes than when back-crossed to the parental species (Rieseberg 1997). This model might apply also to bryophytes although the sporophytes are comparable to the F1 generation and the recombinant spores to the F2 generation, meaning that the novel homozygotes should turn up in the second generation of sporophytes (Fig. 7).

2) "The transgressive segregation model", that new combinations of parental alleles may generate hybrids that can survive in new ecological niches unavailable to either parent (Vicente & Tanksley 1993). Currently, only few cases of speciation by homoploid hybridization have been pointed out for bryophytes, so it is an open question to what extent and under what circumstances these models are realized.

In molecular studies, recombinant bryophyte gametophytes have been proved to display not only asymmetrical

phenotypic expression but also asymmetrical genomic contribution from the two parental species (Cronberg 1989; Shaw 1998; Cronberg & Natcheva 2002, Sawangproh *et al.* 2020a,b). Asymmetrical parental genome could reflect differential levels of fitness of recombinant offspring or secondary back-crossing of hybrid offspring to one of the parental species (Shaw 2009). From what we know from sowing experiments (Flatberg 2006, Natcheva & Cronberg 2007b), recombinant spores from hybrid sporophytes showed low viability but not complete sterility, and the few viable spores displayed a quite skew inheritance of parental genomes (Natcheva & Cronberg 2007b; Sawangproh *et al.* 2020a). The interpretation of skew inheritance was that among the many thousand meiosis events taking place in a sporophyte some may by pure stochasticity have inherited a major part of the genome from one parent, a situation where hybridization results in immediate introgression in the next gametophyte generation rather than hybrids with intermediate expression of traits. The recombinant sporelings had maternally inherited chloroplasts in combination with almost complete paternal dominance of the nuclear genome (Natcheva & Cronberg 1997a)—the process appears to mimic what is known as chloroplast capture in vascular plants. From what we know today, homoploid hybridization in bryophytes may involve transfer of only few genes between the genomic backgrounds, rather than complete mixing. Sawangproh *et al.* (2020a,b) found a few sporophytes and gametophytes with strongly admixed genomes in a hybrid zone of *Homalothecium lutescens* and *H. sericeum*, but a majority of sporophytes and recombinant gametophytes were only mildly admixed, possibly as a consequence of extensive back-crossing. Similarly, when comparing whole autosomal genomes from 12 individuals belonging to the three taxa of the *Marchantia polymorpha*-complex, Linde *et al.* (2020) observed two individuals from separate sites in which small parts on a single chromosome was transferred from one taxon to the other, suggesting limited introgression. At both sites the involved taxa occurred together in sympatry.

Could hybridization explain poor consensus in phylogenetic studies of bryophytes?

Incongruence between morphology and genomic markers may suggest horizontal gene transfer through interspecific hybridization. For example, some individuals of peat mosses in mixed populations of *Sphagnum capillifolium* with *S. rubellum* (Cronberg 1989) and *S. capillifolium* with *S. quinquefarium* (Cronberg & Natcheva 2002) were identified as one species by isozyme markers but were identified as the other species by the morphological expression of the gametophytes. Apparently, hybrid progeny expresses a high degree of variability in morphological expression not only in the characters of gametophytes but also in other life stages such as sporophytes and spores (Natcheva & Cronberg 2004; Sawangproh *et al.* 2020a,b). Hegarty & Hiscock (2005) addressed that hybrid speciation may occur repeatedly at different times and at different geographical locations, and, furthermore, backcrossing to either parent or to a related taxon may occur regionally. Consequently, regional morphological differences among hybrids may sometimes lead them to be recognized under different names by different authors.

Observations of cytoplastic introgression and incongruences between rDNA and cpDNA sequences in phylogenetic analyses of vascular plants have been put forward as evidence for past hybridization and historic introgression (Sytsma 1990; Rieseberg 1991; Rieseberg *et al.* 1996). Phylogenetic incongruence of nuclear and chloroplast DNA sequences supported the hypothesis of hybridization among widely divergent (intersectional) taxa of peat mosses (Shaw & Goffinet 2000), which partially explains the historic problems to reach a consensus on the taxonomy of the genus *Sphagnum* (Shaw & Goffinet 2000). Hernández-Maqueda *et al.* (2008) found sectional placement of most species in family Grimmiaceae to be congruent based on plastid DNA. However, some species seemingly combine nuclear sequences of one section with chloroplast sequences of another. Similarly, Heinrichs *et al.* (2011) observed phylogenetic incongruence between chloroplast and nuclear sequences for the leafy liverwort species *Porella platyphylloidea*, which possibly originated by ancient hybridization between *P. cordaeana* and *P. platyphylla*. Werner *et al.* (2014), Hedenäs (2015), Köckinger & Hedenäs (2017) found incongruences between nuclear and two chloroplast genes in *Tortella*, indicating that hybridization is widespread in this acrocarpous moss genus. For example, haplotype networks displayed significant reticulation in a study of the classic hybrid taxon *Tortella rigens* and its related species, suggesting local backcrossing to the putative parental species *T. inclinata* and *T. fragilis* as well as to *T. tortuosa*. Furthermore, sporophytes were observed on *T. rigens*, with morphological affinities to *T. inclinata* and T. *tortuosa*, which are likely fathers because males are lacking in *T. rigens*.

When studying closely related taxa it is often difficult or even impossible to differentiate between gene transfer by hybridization and retention of ancient polymorphisms (incomplete lineage sorting). Comparison across whole genomes is now possible and less arbitrary than studies based on occasional genes, but this wealth of data does not automatically

make it easier to detect hybridization. In a whole genome comparison between the three taxa in the *Marchantia polymorpha*-complex (including subspecies *polymorpha*, *montivagans* and *ruderalis*) with *M. paleacea* as outgroup all three possible phylogenetic topologies were richly represented among sequences across the genomes (Linde *et al.* 2020) although concensus analyses singled out *montivagans* as the earliest diverging branch. Statistical tests did not reveal any signature of hybridization, but it turned out that chromosome 2 of *montivagans* was more diverged than any other part of the genomes. This could only happen if it was captured by hybridization from a more divergent unknown taxon or if the rest of the chromosomes had converged by hybridization. The second hypothesis was favoured because chromosome 2 of *montivagans* displayed a higher degree of structural rearrangements, apparently protecting it from intermittent or ongoing hybridization. It is well known from other organisms that genomic regions show differential porosity to gene transfer during hybridization (Harrison & Larson 2014). The failure of the statistical tests to detect hybridization in this case may be explained if many hybridization events have taken place, each involving only a small part of the genome.

Conclusions and perspectives for future study

Historically, studies of hybridization in bryophytes were based on observations of gross morphology or chromosomal characteristics of hybrid progeny. More or less intermediate morphological markers and mismatched types of capsules in case of polysetous gametophytes were used for preliminary identification of putative cases of hybridization. A major limitation of morphological or chromosomal traits is the fact that closely related taxa often do not show distinct morphological differences, or the differences are obscured by phenological plasticity (Natcheva & Cronberg 2004; Maki & Murata 2001). Therefore, it is evident that recently developed more powerful molecular tools and cytological methods are useful to trace past hybridization and reveal its importance for speciation and differentiation.

This review summarizes a growing body of evidence for interspecific hybridization in bryophytes, both synthesized *in vitro* and observed in wild populations. The available data indicates that hybridization is important for adaptation and speciation. There is still a large unexploited potential to further study details of hybridization processes and the hitherto gathered data is strongly focused on few groups of bryophytes. In *Sphagnum* mosses, enough data has accumulated to make it possible to search for patterns underlying evolutionary processes. Accordingly, a review compiled from more than 50 *Sphagnum* hybridization records by Meleshko *et al.* (2018) showed that homoploid hybridization takes place among closely related species, whereas allopolyploidy potentially involve more distantly related parental species. Their meta-analysis also suggests some traits that are associated with hybridization in *Sphagnum*, such as monoicy/polyoicy, high sporulation frequency, small spores, and propensity to grow in poor habitats.

In comparison to organisms with a dominant diploid generation, bryophytes have been expected to accumulate comparatively little adaptive genetic variation, because mutations, effecting a change in what is apparently the only one copy of a particular allele of genes, must be beneficial or at least not lethal. Thus, Newton (1988) predicted the accumulation of such variation in haploid gametophytes to be slow. Combination of genomes in allopolyploids and transfer of adaptive genes between lineages through homoploid polyploidization could compensate for low mutation rate by transfer of adaptive genes to new genomic backgrounds. Until now there are few studies that have assessed the adaptive value of such gene transfer and for most cases of homoploid hybridization we do not even know if the recombinants are able to transmit such genes to the next generation, to what extent back-crossing takes place or if populations behave as true hybrid zones. Similarly, we know little about infraspecific variability in allopolyploids (or autopolyploids) and if allopolyploidy expands or changes the fundamental and/or realized niches relative to the paternal species.

DNA fingerprint methods such as RFLPs, ISSRs and microsatellites are valuable markers for recently diverged bryophytes (Vanderpoorten & Shaw 2010), but Schmickl *et al.* (2017) suggested that future work should focus on population genomic studies that can provide detailed insights into the genetic basis of adaptive divergence. With an increasing genome-wide view of the divergence landscape, population genomic studies can overcome key limitations of previous approaches. For example, they can detect polygenic adaptation provided markers are dense and they can leverage sufficient resolution and statistical power to detect non-random patterns of introgression (Schmickl *et al.* 2017). The advent of high-throughput sequencing and phylogenomic tests/softwares such as Phylo-Net (network and tree methods), D statistics or ABBA-BABA statistics (detection SNP window-based or genome-wide evidence of shared alleles in a four-taxon case), and HybridCheck (detection of introgressed genomic blocks and visualization of the heterogeneous, mosaic-like genome structure and dating of introgressed blocks) reveals hybridization and introgression

events at genomic and demographic levels (reviewed in Schmickl *et al.* 2017; Linde *et al.* 2020). Although it is now possible to search for signs of hybridization across whole genomes it is still challenging to differentiate between gene transfer by hybridization and incomplete lineage sorting, especially if multiple hybridization events have taken place, each involving transfer of only a small part of the genome and/or if extensive back-crossing against one parent has taken place. For this reason, genomic studies should be complemented by populations level studies of putatively hybridizing parental species, comparing allopatric and sympatric populations.

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Appendix A. References which have inferred hybridization during the period from January 1900 to September 2020. For each record information about phylum, family, major growth form, putative parental species (maternal and paternal species pointed out, if known), gametophytic hybrid species name (if any), type of hybridization (allopolyploid vs. homoploid; intra-vs. interspecific, intergeneric, intersectional etc.), quality of hybrid spores in F1 generation sporophytes (if known). The characters used for identifcation of hybrids in the gametophyte phase are also indicated as sporophyte, spore or gametophyte morphology, chemical markers (secondary metabolites), ploidy level identifiers, protein markers (isozymes or allozymes) and DNA markers. (Uploaded separately as Supplementary file)