

REVIEW PAPER

Diversity, phylogeny, and adaptation of bryophytes: insights from genomic and transcriptomic data

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Received 28 November 2021; Editorial decision 11 March 2022; Accepted 24 March 2022

Editor: Francesca Degola, University of Parma, Italy

Abstract

Bryophytes including mosses, liverworts, and hornworts are among the earliest land plants, and occupy a crucial phylogenetic position to aid in the understanding of plant terrestrialization. Despite their small size and simple structure, bryophytes are the second largest group of extant land plants. They live ubiquitously in various habitats and are highly diversified, with adaptive strategies to modern ecosystems on Earth. More and more genomes and transcriptomes have been assembled to address fundamental questions in plant biology. Here, we review recent advances in bryophytes associated with diversity, phylogeny, and ecological adaptation. Phylogenomic studies have provided increasing supports for the monophyly of bryophytes, with hornworts sister to the Setophyta clade including liverworts and mosses. Further comparative genomic analyses revealed that multiple whole-genome duplications might have contributed to the species richness and morphological diversity in mosses. We highlight that the biological changes through gene gain or neofunctionalization that primarily evolved in bryophytes have facilitated the adaptation to early land environments; among the strategies to adapt to modern ecosystems in bryophytes, desiccation tolerance is the most remarkable. More genomic information for bryophytes would shed light on key mechanisms for the ecological success of these ‘dwarfs’ in the plant kingdom.

Keywords: Adaptation, genome, hornworts, liverworts, mosses, plant terrestrialization, transcriptome.

Introduction

Bryophytes (including mosses, liverworts, and hornworts) are an extraordinary group among land plants (embryophytes) and have high species diversity, second only to flowering plants (angiosperms) (Christenhusz and Byng, 2016). They are small in size and lack a true root and vascular system. In the life cycle of bryophytes, the gametophyte is dominant and free living,

while the sporophyte is partially or wholly dependent on the gametophyte for water and nutrient supply. The gametophyte of bryophytes shows a thalloid organization, or differentiates into root-like, stem-like, and leaf-like structures named rhizoids, cauloids, and phylloids, respectively. This structural organization is intermediate between that of green algae and vascular plants,

and thus bryophytes are considered to have arisen soon after the origin of land plants (Bowman *et al.*, 2007). Therefore, the phylogenetic placement of mosses, liverworts, and hornworts among land plants has attracted a lot of attention over time (reviewed in Donoghue *et al.*, 2021). Importantly, bryophytes play an important role in the ecosystem in many aspects: maintenance of forest biodiversity; water retention; soil improvement; as ecological indicators; and in nutrient cycling (Gao *et al.*, 2017; Rousk *et al.*, 2017; Moore *et al.*, 2019; Glime, 2020; Xiao and Bowker, 2020; Zuijlen *et al.*, 2020).

During the early evolution of land plants, bryophytes were among the pioneers in adapting to the terrestrial environment—a dry and nutrient-poor habitat with elevated UV radiation. Land plants have evolved an array of morphological changes in order to live on land, such as stomata, cuticles, water-conducting structures, and the rooting system (Pires and Dolan, 2012; Harrison, 2017; Ishizaki, 2017; Szövényi *et al.*, 2019). In the three bryophyte lineages, these traits have been reflected to different degrees morphologically and genetically.

Since evolving ~500 million years ago (Mya; Magallón *et al.*, 2013; Morris *et al.*, 2018), bryophytes have achieved great ecological success in various habitats, from desert to aquatic and from tropical to arctic. Their species composition and distribution are associated with microhabitats (e.g. forest floors, tree trunks, and rocks) and microclimates (e.g. humidity, temperature, and light intensity). Accordingly, bryophytes exhibit a wide variety of adaptations in their morphology, physiology, and reproductive strategies, such as desiccation tolerance and dormancy, to respond quickly to environmental changes (Kürschner, 2004; Glime, 2020).

Nowadays, the rapid development of high-throughput sequencing technologies has resulted in a dramatic increase in plant genomic and transcriptomic data (Kersey, 2019; Leebens-Mack *et al.*, 2019; Wong *et al.*, 2020; Marks *et al.*, 2021a; Sun *et al.*, 2022). These omics data contain critical molecular information for phylogenetic, morphological, and physiological analyses, and further comparative genomics and transcriptomics will be a foundation for evolutionary developmental biology (evo-devo) (Fig. 1). Here we aim to provide insight into the diversity, phylogeny, and adaptation of bryophytes from the omics data, and explore the putative molecular basis for: (i) the formation of species richness and morphological diversity among bryophyte lineages; (ii) the adaptation to early land environments by bryophytes; and (iii) the adaptation to modern ecosystems by bryophytes.

Genomes and transcriptomes

Plant genomes hold the key to revealing the evolutionary history of plants and understanding how plant diversity occurs (Soltis and Soltis, 2021). Although the species richness of bryophytes is the second largest among land plants after angiosperms, only 14 genome assemblies of bryophytes (five

chromosome-level assemblies) have been reported to date, comprising eight mosses (two genome species from *Sphagnum* released by JGI, but without detailed publication), three liverworts, and three hornworts (Fig. 1; see Table S1 at Zenodo repository <https://doi.org/10.5281/zenodo.6176732>; Wang *et al.*, 2022) in sharp contrast to 763 genomes available for angiosperms (Marks *et al.*, 2021a). The genomes have been sequenced and assembled for *Physcomitrium* (*Physcomitrella*) *patens* (Rensing *et al.*, 2008; Lang *et al.*, 2018), *Sphagnum fallax* and *S. magellanicum* (Weston *et al.*, 2018; <http://phytozome.jgi.doe.gov/>), *Pleurozium schreberi* (Pederson *et al.*, 2019), *Calohypnum plumiforme* (Mao *et al.*, 2020), *Fontinalis antipyretica* (Yu *et al.*, 2020), *Ceratodon purpureus* (Carey *et al.*, 2021), and *Syntrichia caninervis* (Silva *et al.*, 2021) in mosses (Table S1 at Zenodo). The sequenced mosses are mainly from the classes Bryopsida and Sphagnopsida (Fig. 2B; (Table S1 at Zenodo). In comparison, all currently published liverwort genomes are limited to one genus, *Marchantia*, including *M. polymorpha* (Bowman *et al.*, 2017; Diop *et al.*, 2020; Montgomery *et al.*, 2020), *M. inflexa* (Marks *et al.*, 2019), and *M. paleacea* (Radhakrishnan *et al.*, 2020). Likewise, the published hornwort genomes are also all from one genus, *Anthoceros*, including *A. angustus* (J. Zhang *et al.*, 2020), *A. agrestis* (Li *et al.*, 2020), and *A. punctatus* (Li *et al.*, 2020). The sizes of the published genomes are different among these three lineages, with a median size of 373.7 Mb in mosses, 224.4 Mb in liverworts, and 122.9 Mb in hornworts. Thanks to the release of transcriptomic data for >1000 species of green plants by the 1000 Plants (1KP) initiative (Matasci *et al.*, 2014; Leebens-Mack *et al.*, 2019; Carpenter *et al.*, 2019; <https://db.cngb.org/onekp/>) and a series of individual studies on bryophyte RNA sequencing, the transcriptome sequences are available for at least 151 bryophyte species, comprising 77 mosses, 64 liverworts, and 10 hornworts (Fig. 1; Table S1 at Zenodo). These data covered most of the bryophyte diversity at the ordinal level (Table S1 at Zenodo); however, it is still far from encompassing the bryophyte diversity at the genus or species level (Fig. 1).

Diversity and phylogeny

Bryophytes are among the early land plants. Whether bryophytes are a paraphyletic or monophyletic group, the phylogenetic relationships among hornworts, liverworts, and mosses, and their relationships to other land plant groups have been disputed for a long time (reviewed in Donoghue *et al.*, 2021). The initial phylogenetic framework has been already established in mosses, liverworts, and hornworts, and the monophyly of each lineage has been well supported (Fig. 2B; Shaw and Renzaglia, 2004; Shaw *et al.*, 2011; Villarreal and Renner, 2012; Villarreal and Renzaglia, 2015). However, the incongruences among different reconstructions are present not only at higher level classification but also in the in-depth relationship of rapidly diversified clades based on the limited DNA sequence

information from plastid, mitochondrial, and nuclear loci (reviewed in [Dong *et al.*, 2019](#); [Su *et al.*, 2021](#)).

Using an initial 1KP dataset of 852 nuclear genes from 103 plant species, [Wickett *et al.* \(2014\)](#) revealed that bryophytes are paraphyletic with a clade of liverworts and mosses as sister to vascular plants, and hornworts as sister to all other land plants in the maximum likelihood analysis, while in the coalescent

analysis bryophytes were demonstrated to be monophyletic and sister to vascular plants, with hornworts as the earliest diverged among the three lineages. Subsequently, a series of phylogenomic/phylotranscriptomic studies regarding the evolution of land/green plants sprang up ([Fig. 1](#)). Some utilized more sophisticated strategies of data processing such as reducing the effects of compositional heterogeneity, conducting

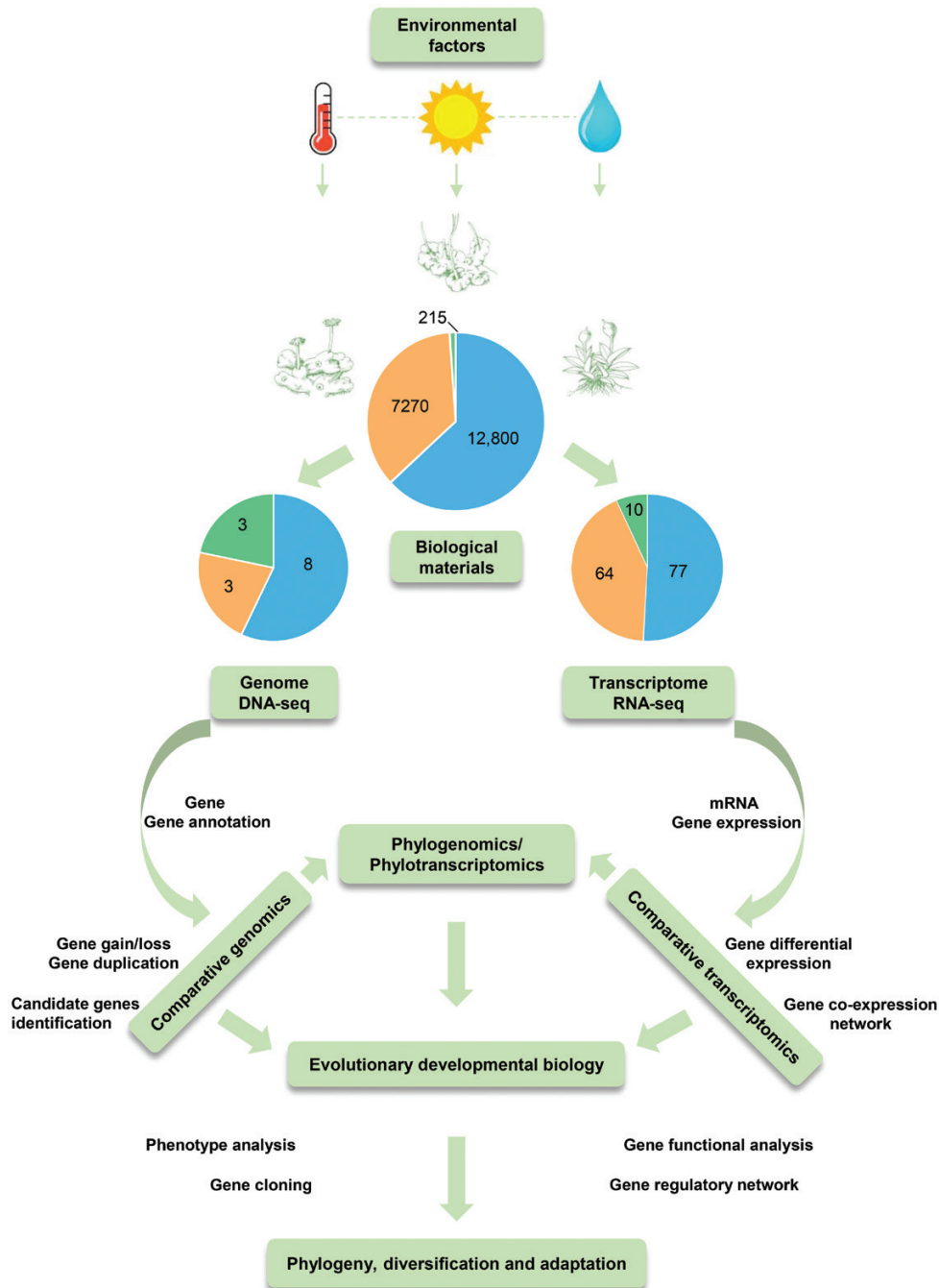


Fig. 1. Genomic and transcriptomic studies in bryophytes. The number of total world bryophyte species in their natural distribution and the number of bryophyte species with genomic/transcriptomic data are shown in pie charts. Blue indicates mosses, orange shows liverworts, and green represents hornworts. The workflow includes the important approaches to explore the phylogeny, diversity, and adaptation of bryophytes during the era of omics such as comparative genomics/transcriptomics, phylogenomics, and evolutionary developmental biology. Drawings courtesy of Ying-Bao Sun.

topology tests, or using Bayesian supertree inference (Puttick *et al.*, 2018; de Sousa *et al.*, 2019); some further extended the sampling number to represent more taxonomic diversity (Leebens-Mack *et al.*, 2019; Harris *et al.*, 2020; Su *et al.*, 2021). These large-scale phylogenetic studies together reached a congruence that bryophytes are monophyletic, with hornworts sister to the Setaphyta clade consisting of liverworts and mosses, and the concept of monophyly for bryophytes has already been widely accepted as the working hypothesis to illustrate the evolution of genotype and phenotype in the early land plants (Fig. 2A; Donoghue *et al.*, 2021). Within bryophytes, there are 30 orders

in mosses, 15 orders in liverworts, and five orders in hornworts (Goffinet and Shaw, 2009; Söderström *et al.*, 2016). The phylogenetic backbone relationships for each bryophyte lineage have been almost fully resolved by combining recent phylogenomic data (Fig. 2B; Villarreal *et al.*, 2010; Villarreal and Renzaglia, 2015; Liu *et al.*, 2019; Bell *et al.*, 2020; Dong *et al.*, 2021).

Compared with the more recently derived angiosperms, bryophytes exhibit substantially lower species richness, which probably resulted from massive extinctions and low diversification rates (Laenen *et al.*, 2014). The extant bryophytes comprise ~20 000 species, and these species are not evenly

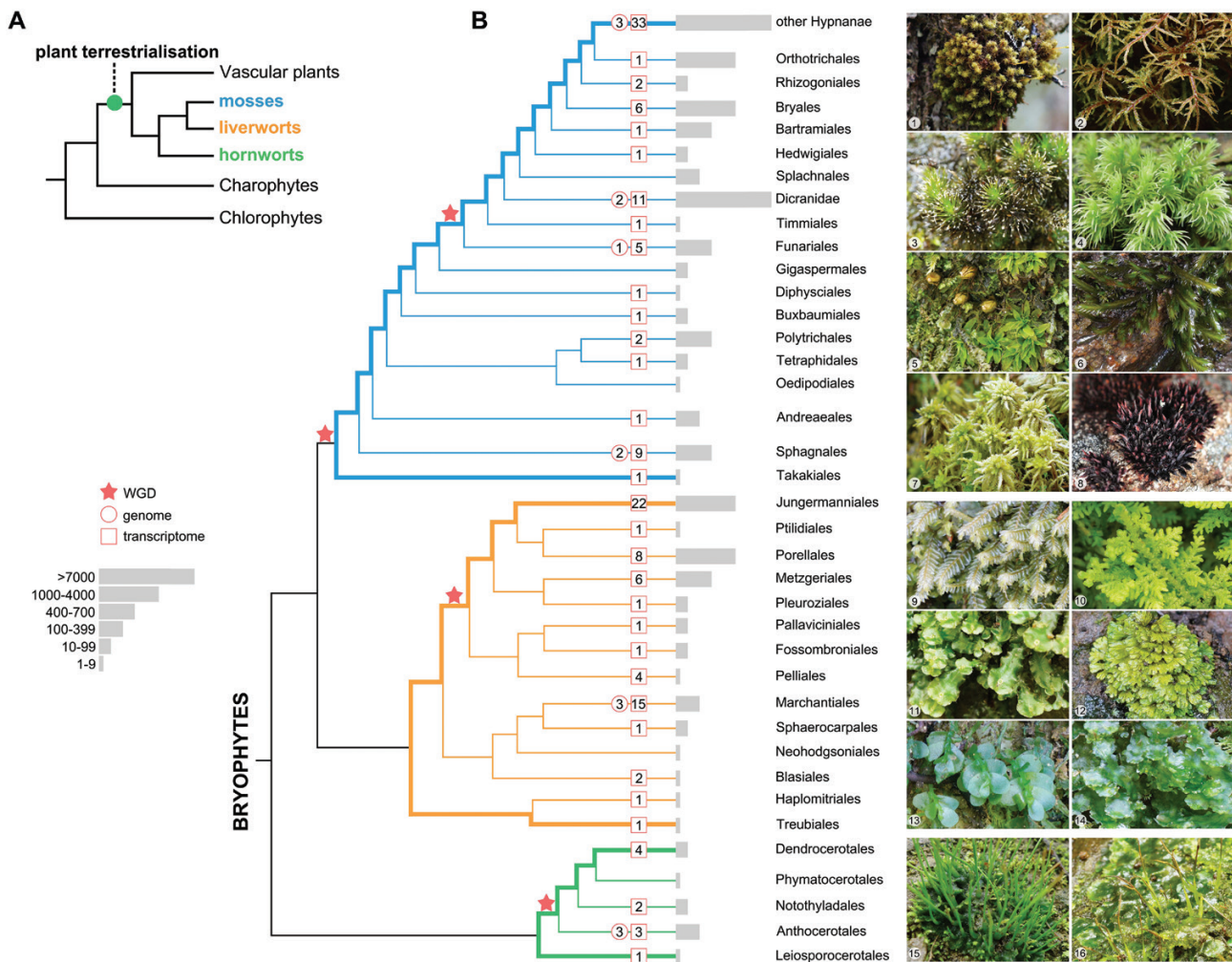


Fig. 2. The diversity and phylogeny of bryophytes. (A) A simplified framework shows the earliest divergence of bryophytes among green plants. (B) The three lineages of bryophytes and their ordinal phylogeny (Villarreal and Renzaglia, 2015; Long *et al.*, 2016; Liu *et al.*, 2019; Flores *et al.*, 2020; Dong *et al.*, 2021). The clade ‘other Hypnanae’ comprises seven orders (Aulacomniales, Hypnales, Hookeriales, Hypnodendrales, Hypopterygiales, Orthodontiales, and Ptychomniales) and the Dicranidae comprises three orders (Dicranales, Grimmiales, and Pottiales). The gray bars show the approximate species number in each branch with species number inside represent genome and transcriptome data, respectively, already available for each branch. The red stars indicate four ancient whole-genome duplications in bryophytes. The photos on the right are numbered: 1, *Ulota crispa* (Hedw.) Brid.; 2, *Pleurozium schreberi* (Willd. ex Brid.) Mitt.; 3, *Dicranum* sp.; 4, *Leucobryum* sp.; 5, *Diphyscium fulvifolium* Mtt.; 6, *Fissidens* sp.; 7, *Sphagnum* sp.; 8, *Andreaea wangiana* P.C. Chen; 9, *Plagiochila* sp.; 10, *Trichocolea tomentella* (Ehrh.) Dumort.; 11, *Dumortiera hirsuta* (Sw.) Nees; 12, *Cyathodium aureonitens* (Griff.) Schiffn.; 13, *Haplomitrium* sp.; 14, *Blasia pusilla* L.; 15, *Phaeoceros* sp.; and 16, *Megaceros flagellaris* (Mitt.) Steph. Photos 2 and 8 courtesy of Wen-Zhang Ma.

distributed among the three lineages, with ~60% (~12 800 species) in mosses, nearly 36% in liverworts (~7270 species), and only 4% (~215 species) in hornworts (Fig. 1; Crosby *et al.*, 1999; Magill, 2010; Villarreal *et al.*, 2010; von Konrat *et al.*, 2010; Cox *et al.*, 2010; Söderström *et al.*, 2016). In plants, species evolution and diversity are driven by multiple factors, such as genomic changes, ecological opportunity, co-diversification with pollinators, and phenotypic associations (Vamosi *et al.*, 2018; Soltis *et al.*, 2019).

Whole-genome duplication (WGD) often leads to profound genomic changes and provides raw genetic material for evolutionary innovation and adaptation, and diversification (Schranz *et al.*, 2012; Soltis and Soltis, 2016; Alix *et al.*, 2017; Van de Peer *et al.*, 2017; Clark and Donoghue, 2018). In plants, WGDs are widespread and frequently coincide with global climatic change events, especially the Cretaceous–Tertiary (KT) extinction event ~65 Mya (Fawcett *et al.*, 2009; Vanneste *et al.*, 2014; Wu *et al.*, 2020). In addition to angiosperms or ferns as a whole (Jiao *et al.*, 2011; Ren *et al.*, 2018; Huang *et al.*, 2020), ancient WGDs has also been suggested to contribute to species diversification in a series of individual lineages, such as Asteraceae (Zhang *et al.*, 2021), Cucurbitaceae (Guo *et al.*, 2020), and Malpighiales (Cai *et al.*, 2019). Likewise, several WGDs were found in published moss genomes, including two rounds in *P. patens* (Lang *et al.*, 2018), and one in each species of *Pleurozium schreberi* (Fig. 2B; Pederson *et al.*, 2019), *Calohyphnum plumiforme* (Mao *et al.*, 2020), *Syntrichia caninervis* (Silva *et al.*, 2021), and *Ceratodon purpureus* (Szövényi *et al.*, 2015; Carey *et al.*, 2021). A comprehensive survey of WGDs across lineages of green plants using the 1KP data indicated that multiple rounds of WGDs occurred in mosses, but only a small number of WGDs took place deep in liverworts and hornworts (Fig. 2B; Leebens-Mack *et al.*, 2019). Among these WGD events in mosses, a large-scale ancestral event was shared by all mosses, an ancient event was shared by species in the BDTF clade (Bryidae, Dicranidae, Timmiidae, and Funariidae), and two recent events were reported at least in the common ancestor of the Funariales and in the common ancestor of the Sphagnales (Devos *et al.*, 2016; Leebens-Mack *et al.*, 2019; Gao *et al.*, 2022). The BDTF duplication and the Funariales-wide duplication correspond to the WGD1 (57–70 Mya) and WGD2 (38–50 Mya) events within the Late Cretaceous and the Early Cenozoic intervals, respectively, in *P. patens* (Lang *et al.*, 2018). The transcriptome data of both *Funaria hygrometrica* and *P. pyriforme* also supported that the common ancestor of the Funariales may have undergone an ancient WGD (Rahmatpour *et al.*, 2021). The WGDs in *Syntrichia caninervis* and *Ceratodon purpureus* all belong to the BDTF duplication (Szövényi *et al.*, 2015; Carey *et al.*, 2021; Silva *et al.*, 2021). The ancient large-scale gene duplication events are also detected in the common ancestor of the Jungermanniopsida (liverworts) and Anthocerotopsida (hornworts) (Leebens-Mack *et al.*, 2019), although no recent WGD has been found to date in the published liverwort (Bowman *et al.*, 2017) and hornwort genomes (Li *et al.*, 2020; J. Zhang

et al., 2020). In addition, the previous cytological analyses also showed that genome duplication is rare in liverworts (~8% of species) and nearly absent in hornworts (using $n>10$ as a threshold for polyploidy), while at least 20% of moss species are polyploid (reviewed in Husband *et al.*, 2013). Based on available data, WGDs seem to be more frequent in mosses than in liverworts and hornworts, which coincides with the higher species diversity and wider environmental range of mosses.

WGDs could provide redundant genetic resources that confer robustness against deleterious mutations, and the retained duplicates might be rewired to execute novel functions albeit followed by massive gene loss (Smet and Van de Peer, 2012; Wu *et al.*, 2020; Van de Peer *et al.*, 2021). Polyploidy might confer a selective advantage under stresses, and the preferential retention of stress-related duplicated genes after WGDs promotes plant responses to both abiotic and biotic stresses (Ren *et al.*, 2018; Song *et al.*, 2020; Wu *et al.*, 2020; L.S. Zhang *et al.*, 2020; X. Zhang *et al.*, 2020; Van de Peer *et al.*, 2021). The significant retention of stress-related gene duplicates in mosses implies in return the potential contribution of WGDs to ecological adaptation of mosses (Gao *et al.*, 2022).

Adaptation to early land environments

Pioneer plants need to cope with a series of environmental challenges, such as desiccation, UV light radiation, and greater temperature variation (Beraldi-Campesi, 2013; Weber *et al.*, 2016), and are restricted to the soil and rock surfaces occupied by bacteria, fungi, lichens, and protists (Heckman *et al.*, 2001; Graham *et al.*, 2004). Although bryophytes have simple structures morphologically, they already possess the key innovations of land plants for the early adaptations to terrestrial habitats, namely a multicellular embryo, cuticle, stomata, water-conducting cells (WCCs), and a rooting system (Fig. 3A; Pires and Dolan, 2012; Harrison, 2017; Szövényi *et al.*, 2019). Furthermore, the degree of morphological diversity during early adaptation differs among mosses, liverworts, and hornworts (Fig. 3A). In mosses and most liverworts, the stem-like and leaf-like structures are present in their gametophytes, while the hornwort gametophytes are fairly simple thalli. In bryophyte gametophytes, the rhizoid-based rooting system mainly functions in anchoring the plant to the substrate, although some indications also show its functions in the uptake of water and nutrients (reviewed in Jones and Dolan, 2012). Rhizoids are multicellular in mosses, but unicellular in liverworts and hornworts. The WCCs are present in mosses (commonly referred to as hydroids) and liverworts, but absent in hornworts (Ligrone *et al.*, 2000, 2002). Most mosses and hornworts have stomata on the sporophytes, but liverworts do not possess stomata. The primary role of stomata in mosses and hornworts appears to be to promote sporophyte desiccation and spore dispersal, in comparison with the functions of helping photosynthetic gas exchange and preventing water loss in vascular plants

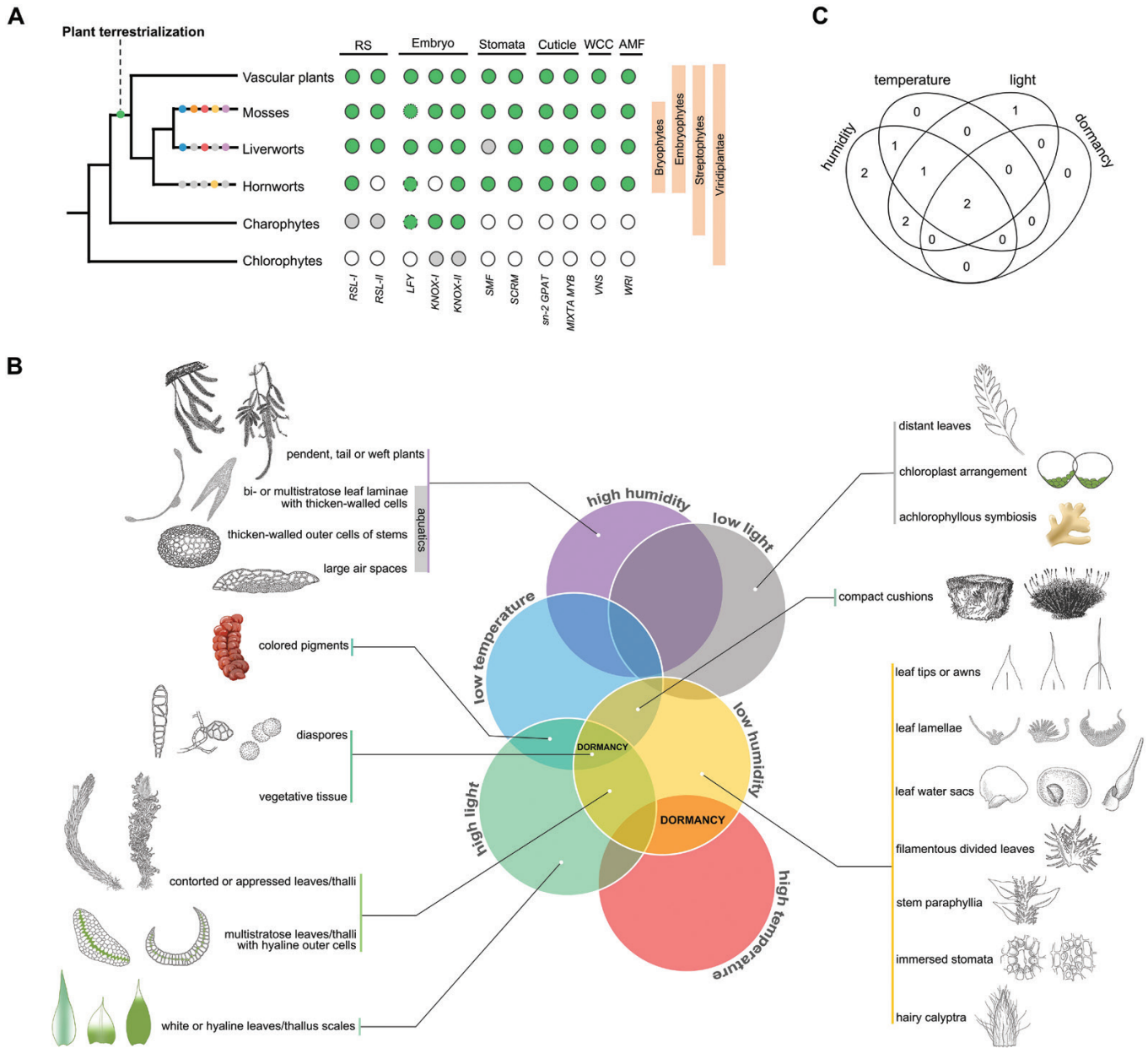


Fig. 3. The terrestrial adaptation of bryophytes. (A) Genetic novelties and morphological innovations for plant terrestrialization. A cladogram shows the phylogenetic backbone of green plants. The morphological innovations of land plants are shown on the top, and the corresponding genetic novelties are displayed on the bottom. RS, rooting system, here regarding rhizoids and root hairs; WCC, water-conducting cell; AMF, associations with arbuscular mycorrhizal fungi. The green circles represent the presence of the classical and functional genes. The gray circles display that the sequences are divergent from the classical genes. The white circles show the absence of the corresponding genes. The different green circles for LFY genes in different lineages indicate that they have different DNA binding specificity. The blue dot along the branch indicates the position of plant terrestrialization, and the orange dot shows the monophyly of bryophytes with the features and adaptive strategies highlighted. The major morphological differences among the three bryophyte lineages (row of dots): the blue dot shows the differentiation into stems and leaves; the gray dot shows no corresponding differentiation; the orange dot, multicellular rhizoids versus gray dot, unicellular rhizoids; red dot, presence of WCCs versus gray dot, absence of WCCs; yellowish brown dot, presence of stomata versus gray dot, absence of stomata; purple dot, presence of seta versus gray dot, absence of seta. (B) Main adaptive strategies of bryophytes to different humidity, temperature, and light intensity in modern ecosystems. The overlapping area between different stresses roughly reflects the frequency of their association in the field. We here classified both aquatic and wet environments as high humidity, although they are not completely the same. The dormant strategy is shown directly in the corresponding stress to indicate its importance for bryophytes. (C) The species number of bryophytes with molecular studies on adaptations under different environmental factors. The morphological drawings courtesy of Mu-Sen Guo and Ai-Li Li.

(Chater *et al.*, 2016; Renzaglia *et al.*, 2017; Duckett and Pressel, 2018; Sussmilch *et al.*, 2019; McAdam *et al.*, 2021). Both mosses and liverworts possess setae supporting the spore-bearing capsule of the sporophytes. However, the hornwort sporophyte grows continuously from a basal meristem but lacks a seta.

Discovering the genomic changes during plant evolution is critical to reveal the molecular basis for morphological and physiological innovations. With the increasing accumulation of genome and transcriptome data, comparative genomic analysis revealed two consecutive bursts of genetic novelties before the colonization of the land by plants: the first is in the origin of streptophytes and the second is in the common ancestor of land plants (Bowles *et al.*, 2020). In both bursts, a large proportion of the genetic novelties were identified as transcription factors (TFs) (Catarino *et al.*, 2016; Bowman *et al.*, 2017; L.S. Zhang *et al.*, 2020). The increase in the number of TFs is in line with the evolution of plant complexity and plasticity in environmental responses (Lang *et al.*, 2010; Catarino *et al.*, 2016; Lehti-Shiu *et al.*, 2017; Wilhelmsson *et al.*, 2017). Therefore, the stepwise increase of genetic novelties that pre-dates the origin of land plants might have driven biological innovations that helped plants to adapt to terrestrial habitats. In addition, genes encoding TFs tend to be highly retained following polyploidy, and the WGD events could explain expansion of these genes to a certain extent (Lang *et al.*, 2010; Bowles *et al.*, 2020). Most of the important TF families in land plants have already evolved in bryophytes (J. Zhang *et al.*, 2020). However, the TF number in the sequenced bryophyte species is not balanced. The moss *P. patens* genome with recent WGDs retains a large number of TF genes with a high proportion of multiple-copy TFs (Rensing *et al.*, 2008; J. Zhang *et al.*, 2020). In comparison, the genomes of the liverwort *M. polymorpha* and hornwort *A. angustus* without a recent WGD contain a small number of TF genes with a high proportion of single-copy TFs (Bowman *et al.*, 2017; Li *et al.*, 2020; J. Zhang *et al.*, 2020). This pattern might affect the degree of morphological diversity among mosses, liverworts, and hornworts (J. Zhang *et al.*, 2020).

With genomic and genetic approaches (Fig. 1), significant insights have been obtained into the origin and evolution of the genes associated with the early adaptive innovations for plant terrestrialization (Fig. 3A). Rhizoids, as a rooting system in bryophytes which are similar in structure and function to the root hairs in angiosperms, are important for the early adaptation of plants to land (Jones and Dolan, 2012). The *ROOT HAIR DEFECTIVE SIX-LIKE* (RSL) class I genes, a group of basic helix-loop-helix (bHLH) TF genes, control rhizoid development in bryophytes as well as root hair formation in angiosperms (Menand *et al.*, 2007; Pires *et al.*, 2013; Proust *et al.*, 2016). The RSL class II genes are involved in protonema differentiation in *P. patens* or initiation and elongation of root hairs in *Arabidopsis thaliana* (Pires *et al.*, 2013). Rhizoids also develop in some lineages of the streptophyte algae, such as *Chara* (Charophytales) (Jones and Dolan, 2012). The *Chara braunii* bHLH gene (*CbbHLH*), sister to the land plant RSL clade, is

not expressed in rhizoids, and is unable to replace the RSL gene in *M. polymorpha* or *A. thaliana*, involved in rhizoid development that was functionally different from land plant RSL genes. This suggests that the function of the *CbbHLH* gene is different from that of land plant RSL genes, and involvement of RSL genes in rhizoid differentiation in land plants evolved by neofunctionalization in the common ancestors shared by land plants (Bonnot *et al.*, 2019). In addition, the hornwort *A. angustus* genome lacks the class II RSL genes (Fig. 3A), corresponding to the morphological simplification of this organism with respect to its tip-growing filamentous structures (Goffinet and Buck, 2013).

The formation of a multicellular embryo is crucial for plants to survive in dry environments, separating the land plants from their close algal charophyte relatives (Radoeva *et al.*, 2019). LEAFY (LFY) and KNOTTED-LIKE HOMEODOMAIN (KNOX) are two well-known TFs that play key roles in embryogenesis. In *P. patens*, the LFY homolog is required for the progression of the first cell division of the zygote; however, in angiosperms, the LFY homologs function in floral identity determination (Tanahashi *et al.*, 2005), which is due to specific variations in their DNA-binding domain to promote expression of different gene sets (Maizel *et al.*, 2005). The LFY genes originated in the streptophytes and the changes of DNA binding specificity for LFY proteins resulted in several motif-binding types: type I for angiosperms, gymnosperms, ferns, lycophytes, liverworts, and a small number of mosses, type II for most of the mosses, type III for charophytes, and a promiscuous one for hornworts (Fig. 3A; Sayou *et al.*, 2014; Gao *et al.*, 2019). Corresponding to the DNA binding specificity, the expression of the LFY homolog in *A. agrestis* is mainly in the gametophyte stages as distinct from the predominantly sporophytic expression in *P. patens*, which implies the functional divergence within LFY genes of land plants (Li *et al.*, 2020). A similar divergence is also found in KNOX genes which have been identified in all green plant lineages (Fig. 3A; Frangedakis *et al.*, 2017; J. Zhang *et al.*, 2020). They have differentiated into class I and class II subclasses in the common ancestor of land plants and charophytes (Fig. 3A; Frangedakis *et al.*, 2017; J. Zhang *et al.*, 2020). The ancient KNOX gene *Gamete-specific minus1* (*GSM1*) in the chlorophyte *Chlamydomonas reinhardtii* has a function in formation of the diploid zygote (Lee *et al.*, 2008). In *P. patens*, the class I KNOX genes are required for cell division and differentiation in sporophytes, and their activity is necessary for seta differentiation (Sakakibara *et al.*, 2008; Renzaglia *et al.*, 2018; Coudert *et al.*, 2019). In *M. polymorpha*, the *KNOX1* gene is required to initiate zygotic development, similar to that in *C. reinhardtii* (Dierschke *et al.*, 2021; Hisanaga *et al.*, 2021). In comparison, the hornwort genomes of both *A. angustus* and *A. agrestis* lack the class I KNOX genes (Fig. 3A), corresponding to the absence of seta in hornworts (Goffinet and Buck, 2013; Renzaglia *et al.*, 2018). In angiosperms, the class I KNOX genes play a major role in the regulation of leaf shape (reviewed in Maksimova *et al.*, 2021). The class II KNOX

genes function in haploid to diploid morphological transition in all land plants (Sakakibara *et al.*, 2013).

Stomata have been gained in land plants, but following multiple independent losses in various lineages, including liverworts, some mosses and hornworts, and some aquatic vascular plants such as *Isoetes tegetiformans* and *Zostera marina* (Harris *et al.*, 2020). Among bryophytes, stomata are restricted to the sporophytes, and seem to have undergone reductive evolution (Harris *et al.*, 2020). Stomata development is regulated by a set of genes (reviewed in Frangedakis *et al.*, 2021), and the bHLH TFs SPCH/MUTE/FAMA/SMF and ICE/SCREAM (SCRM) are key regulators (Chater *et al.*, 2016, 2017; Harris *et al.*, 2020). SMF and SCRM have evolved in the common ancestor of land plants (Fig. 3A; Chater *et al.*, 2017; Harris *et al.*, 2020; J. Zhang *et al.*, 2020). Lack of true stomata in the liverwort *M. polymorpha* and moss *Sphagnum fallax* could be due to the significant divergence of their SMF proteins in bHLH motifs (Fig. 3A; Chater *et al.*, 2017). The full function of stomata in water conservation and gas exchange is achieved by cooperation of intercellular gas spaces, cuticles, and wax (Chen *et al.*, 2017). The formation of the cuticle is considered as one of the fundamental innovations that facilitated the transition of plants from aquatic to terrestrial environments, by protecting plants from environmental stresses, such as water loss and UV irradiation (Dominguez *et al.*, 2017). In *P. patens*, *sn-2 Glycerol-3-phosphate acyltransferase* (*GPAT*) genes play roles in cuticle biosynthesis (Lee *et al.*, 2020), and, in *M. polymorpha*, the TF gene *MIXTA MYB* is a key regulator of cuticle biosynthesis (Xu *et al.*, 2021). These two types of genes are land plant specific (Fig. 3A; Brockington *et al.*, 2013; Kong *et al.*, 2020; Lee *et al.*, 2020; J. Zhang *et al.*, 2020; Xu *et al.*, 2021). In addition, land plants developed WCCs for efficient conduction of water, such as hydroids in mosses and xylem cells in vascular plants, which enabled the transition of plants from water to land (Ohtani *et al.*, 2017). The VNS (VND, NST/SND, SMB-related) TFs function in vascular tissues and secondary cell wall thickening in *A. thaliana*, and they regulate hydroid cell differentiation by inducing programmed cell death in *P. patens* (Xu *et al.*, 2014). The VNS homologs are specific to land plants (Fig. 3A; Xu *et al.*, 2014; J. Zhang *et al.*, 2020). All these suggest that the VNS-based genetic network evolved during gametophytic generation of the common ancestor of land plants, and subsequently was co-opted in the sporophyte generation contributing to vascular plant evolution (Xu *et al.*, 2014).

Besides the phenotypic novelties of land plants, the mutualistic associations with arbuscular mycorrhizal fungi (AMF) also contribute to the colonization of land by plants (Heckman *et al.*, 2001; Bonfante and Genre, 2008; Field *et al.*, 2015). Most land plants benefit from symbiosis with mutualistic AMF by facilitating the uptake of nutrients and water (Begum *et al.*, 2019). A comprehensive phylogenetic analyses with available transcriptomes and genomes of green plants revealed the deep conservation of the genetic basis for colonization regulation and arbuscule formation in the common ancestor of land

plants (Delaux *et al.*, 2015; Radhakrishnan *et al.*, 2020). The land plant-specific TF WRINKLED (WRI) (Fig. 3A) in *M. paleacea* regulates the formation of mutualism with AMF by the biosynthesis of fatty acids and then their transfer to the symbiont (Rich *et al.*, 2021).

In addition, some species in bryophytes can establish symbiotic relationships not only with AMF but also with cyanobacteria (Adams and Duggan, 2008; Ligrone *et al.*, 2012; Radhakrishnan *et al.*, 2020). The cyanobacterial symbionts (cyanobionts) generally supply these bryophytes with fixed nitrogen, which is an important source of plant-available nitrogen (Adams and Duggan, 2008). In the hornworts *A. punctatus* and *A. agrestis*, there were 40 genes found to be highly induced when the cyanobionts are present (Li *et al.*, 2020), including the homolog of the SWEET sugar transporter in *Medicago truncatula* which is responsible for arbuscule maintenance during arbuscular mycorrhizal symbiosis (An *et al.*, 2019). With more opportunities to interact with fungi and bacteria, genomes of bryophytes also show a high frequency of horizontal gene transfers (HGTs), which are reported in the representative species from all three bryophyte lineages, namely the moss *P. patens* (Yue *et al.*, 2012), the liverwort *M. polymorpha* (Bowman *et al.*, 2017), and the hornwort *A. angustus* (J. Zhang *et al.*, 2020). These foreign genes are mainly related to DNA repair, pathogen resistance, and stress response, serving as a genetic pool for environmental adaptation (Yue *et al.*, 2013; J. Zhang *et al.*, 2020; Chen *et al.*, 2021).

Adaptation to modern ecosystems

After the prosperity of vascular plants, particularly angiosperms, the ecosystem on Earth becomes more and more complex (Fiz-Palacios *et al.*, 2011), which has provided numerous new ecological habitats for bryophytes (Fig. 4). These new microclimates vary greatly in humidity, temperature, and light intensity, while bryophytes exhibit their strong adaptability to the modern terrestrial environment through complex phenotypic and physiological modifications (Fig. 3B). The molecular basis for the ecological adaptation has been illustrated in some bryophytes with the help of genomic/transcriptomic data and further evo-devo analyses (Fig. 3C).

Humidity

Bryophytes are considered the ‘amphibians’ of the plant kingdom and they are more sensitive to environmental humidity than vascular plants. They are abundant in moist habitats. In the wet tropical forest, most bryophytes are epiphytic, on tree trunks, branches, or even leaves. They usually grow in pendent, tail, or weft forms that can take the greatest advantage of air moisture (Fig. 3B; Pardow *et al.*, 2012). Many bryophytes have leaves with grooves to support draining of surplus water in the wet season. For the mosses living in streams, they need to adapt to other stresses coupled with the aquatic environments,

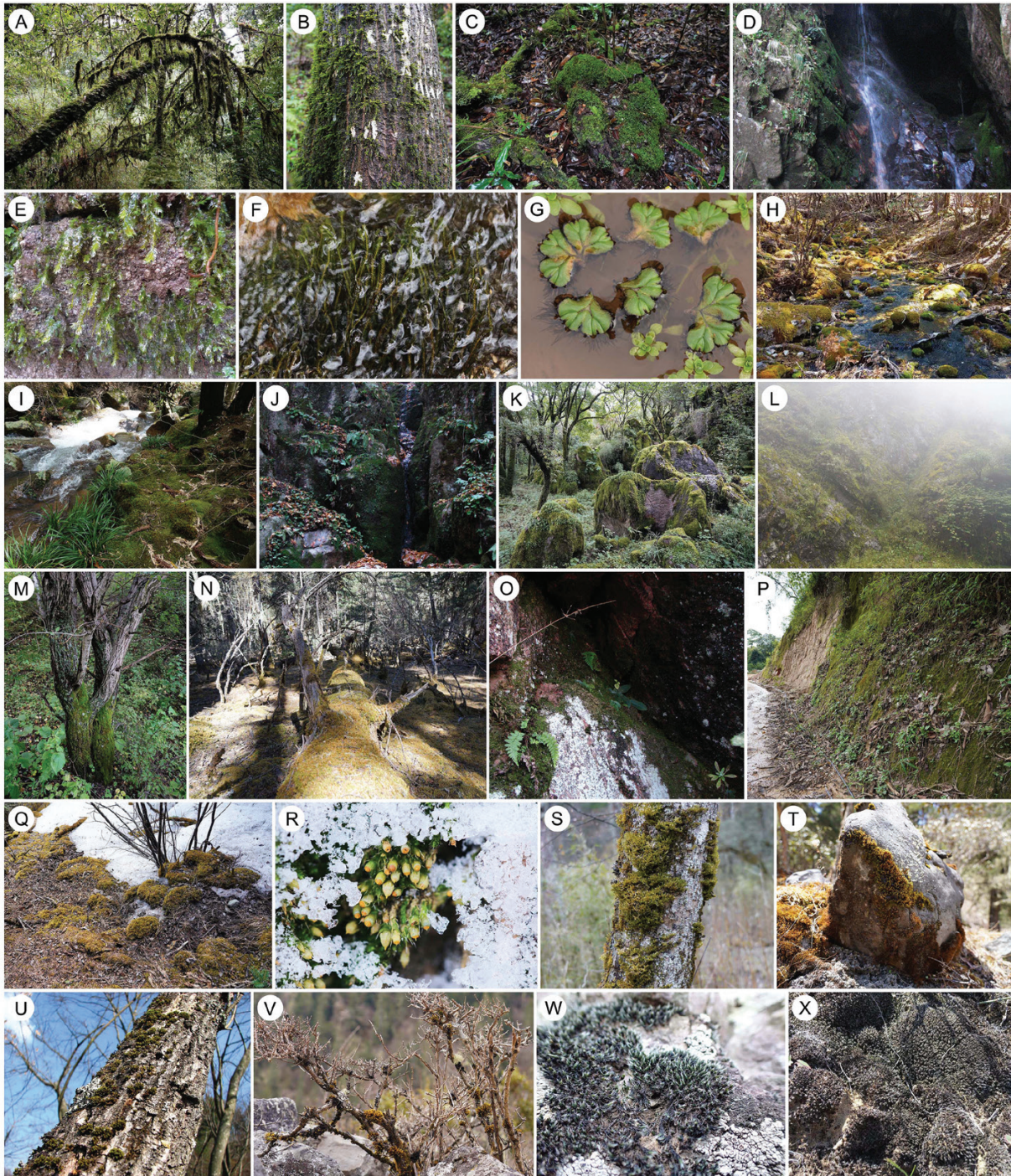


Fig. 4. The microenvironment diversity of bryophytes showing habitats from high to low humidity. (A–G) Extremely wet and aquatic: A, wet tropical forest (Ailao Mts., Yunnan); B, wet trunks (Puer, Yunnan); C, wet fallen wood in shaded area (Puer, Yunnan); D, waterfall in front of a cave (Yichang, Hubei); E, rocks with dripping water (Malipo, Yunnan); F, aquatic habitat with submerged mosses (Jiulong, Sichuan); G, aquatic habitat with floating mosses (Lanshan, Hunan). (H–L) Moderately wet: H, wet rocks and soil near stream with sunfleck (Jiulong, Sichuan); I, wet and shaded rocks and soil near river (Meihuashan, Fujian); J, wet rocks near a vertical brook in shaded area (Yichang, Hubei); K, wet rocks in forest (Jiaozi Snow Mt., Yunnan); L, wet rocks with heavy fog (Jiaozi Snow Mt., Yunnan). (M–P) Wet: M, moist trunks in temperate region (Xiaowutai, Hebei); N, fallen wood in forest with sunfleck (Jiulong, Sichuan); O, a small cave under rocks (Yichang, Hubei); P, a moist roadside slope (Mengla, Yunnan). (Q–T) Dry: Q, a slope partially covered with snow (Jiulong, Sichuan); R, epiphytic mosses covered by snow and ice (Institute of Botany, CAS, Beijing); S, dry trunks (Yaan, Sichuan); T, dry rocks in open area (Jiulong, Sichuan). (U and V) Moderately dry: U, dry trunks with high light (Yichang, Hubei); V, dry shrubs in high altitude region (Kangding, Sichuan). (W and X) Extremely dry: W, dry rocks in temperate region (Xiaowutai, Hebei); X, crust in desert (Gurbantüנגgüt Desert, Xinjiang). All locations are in China. Photos F, H, and R courtesy of Lian Luo; photo G courtesy of De-Chang Meng, and photo X courtesy of Dao-Yuan Zhang.

especially the abrasion and drag force of flowing water, for which mosses have bi- or multistratose leaf laminae, or at least leaf borders, with thickened cell walls (Fig. 3B), as seen in *Fissidens grandifrons* and *Vittia pachyloma*. Their stems likewise tend to be rigid due to strong thick-walled outer cells and flexible due to thin-walled inner cells (Fig. 3B). In liverworts, the aquatic *Riccia fluitans* has large air spaces for gas exchange and flotation (Fig. 3B; Glime, 2020).

In their long evolutionary history, bryophytes have formed a series of ways to adapt to water-limited environments. They utilize two major strategies, desiccation tolerance and avoidance, although controversies still exist between them (Proctor, 2000; Glime, 2020). Xerophytic mosses often grow in large cushions or compact mats to obtain and retain water (Fig. 3B; Sand-Jensen and Hammer, 2012), as seen in *Syntrichia caninervis*. However, more drought-related adaptation in morphology is seen in their leaves or thalli. For example, mosses contain crisped or appressed leaves when dry as in *Ceratodon purpureus* and *Ulota hutchinsiae*; leaf awns or hair tips may help to trap and absorb water from fog and dew as in many species of *Grimmia*; numerous hyaline cells (hyalocysts) serve as a water reservoir, partially or completely surrounding the photosynthetic cells, such as in *Leucobryum*; and some vertical filaments (lamellae) on the adaxial surface of leaves that provide capillary spaces to absorb and retain water as seen in *Aloina* and *Polytrichum*. In liverworts such adaptation includes the lobules that develop into small water sacs, as found in tropical epiphytics of *Frullania*, *Lejeunea*, and the most sophisticated one in *Colura*; and the filamentous divided leaves that using the same capillary principle to increase water absorption and retention as in *Trichocolea* and *Trichocoleopsis* (Fig. 3B; Vitt et al., 2014; Glime, 2020). As well as the leaf, paraphyllia around stems such as those in *Thuidium* mosses also use the same capillary principle (Fig. 3B). In addition to gametophytes, sporophytes in some mosses also exhibit adaptations to drought. Stomata located at the capsules are rarely immersed, covering the pores partially or completely by protruding cells, to reduce water loss, like those seen in the moss *Orthotrichum* (Fig. 3B; Q.H. Wang et al., 2021). Calyptra hairs in moss taxa such as *Polytrichum* and *Orthotrichum* could also function to prevent desiccation (Fig. 3B; Glime, 2020).

Another way to survive dry periods is to avoid them, by going into dormancy as diaspores or remaining in a vegetative state. Diaspores of bryophytes include spores and any other vegetative structures for dispersal (Fig. 3B). For example, the ephemeral moss *Ephemerum* has a shortened life cycle to rapidly produce spores before the dry season, while *Haplodontium notarisii* and *Phaeoceros pearsonii* develop tubers (Fig. 3B), and *Funaria hygrometrica* has subterranean bulbils to span the drought period. Certainly, the most striking strategy is vegetative dormancy (Vitt et al., 2014). In the desert mosses *Bryum argenteum*, *Syntrichia caninervis*, and *Crossidium crassinervium*, their high dehydration can result in metabolic shutdown when

they are drought stressed, but after rehydration they will begin to photosynthesize quickly (Zhang et al., 2007).

The desiccation-tolerant (DT) bryophytes clearly have remarkable phenotypes, but the molecular and physiological mechanisms are still uncertain. Desiccation-induced proteins that act as protectants [e.g. late embryogenesis abundant (LEA) proteins and early light-induced proteins (ELIPs)] or as enzymes to catalyze the synthesis of protective molecules (e.g. antioxidants) during desiccation and rehydration have been identified in some DT bryophyte genomes/transcriptomes, such as the mosses *P. patens*, *Syntrichia caninervis*, *S. ruralis*, *Bryum argenteum*, *Pohlia nutans*, *Sphagnum fallax*, and *S. denticulatum*, and the liverworts *M. polymorpha* and *M. inflexa* (Oliver et al., 2004; Cui et al., 2012; Gao et al., 2017; Winnicka and Melosik, 2019; VanBuren et al., 2019; Zhang et al., 2019; Liu et al., 2020; Ekwealor and Mishler, 2021; Marks et al., 2021b; Silva et al., 2021). In particular, ELIPs have significantly further expanded in DT bryophytes (VanBuren et al., 2019; Silva et al., 2021; Gechev et al., 2021). Moreover, a series of other desiccation-induced genes have been found in bryophyte species (e.g. *Syntrichia caninervis*, *Pohlia nutans*, *Bryum argenteum*, and *M. polymorpha*) through transcriptome sequencing and/or analysis of differentially expressed genes upon dehydration-rehydration (Oliver et al., 2004; Gao et al., 2014, 2015, 2017; Zhang et al., 2019; Wang et al., 2020; Ghosh et al., 2021; Marks et al., 2021b; Silva et al., 2021). However, further analysis and functional verification of these DT-related genes are still rare in bryophytes.

Studies of the dormancy mechanism in bryophytes are also rare. The *DELAY OF GERMINATION1* (*DOG1*) family genes (*DFG* genes) that are involved in seed dormancy have been suggested to have diverged from the TGACG motif-binding TF genes before the divergence of the bryophyte lineage (Nishiyama et al., 2021). In *M. polymorpha*, the dormancy of gemmae is not only regulated by auxin that is synthesized by the indole-3-pyruvic acid (IpyA) pathway (Eklund et al., 2015), but is also controlled by abscisic acid (ABA) signaling components (Eklund et al., 2018).

Temperature and light intensity

The temperature of the microclimate often determines the growth rate and distribution of bryophytes (Gabriel, 2000; Acebey et al., 2003; Belland, 2005; Pharo et al., 2005). However, the water content is of great importance in the thermal tolerance of bryophytes. Dry bryophytes are typically much more resistant to heat than wet ones due to dehydration into dormancy (Dulai et al., 2002; Zhang et al., 2011). Even tropical bryophytes do not seem to be as resistant to heat as we would expect, because their net photosynthesis decreases drastically at temperatures above 26 °C (Wagner et al., 2013, 2014). Actually, most extant bryophytes can be regarded as cool- or cold-adapted plants due to the temperature range for their

photosynthetic gain being from -10°C to 26°C (Wagner *et al.*, 2013, 2014). In the Antarctic region, bryophytes are frequently red which can help to increase their leaf temperature by absorbing more energy from sunlight that is further turned into heat (Fig. 3B). Their growth in large cushions or compact mats likewise facilitates retaining heat (Fig. 3B; Glime, 2020). Similarly, desiccated bryophytes are more likely to survive in freezing conditions than those which are hydrated (Lenne *et al.*, 2010; Segreto *et al.*, 2010). At the molecular level, there has been very limited research on the response to temperature changes in bryophytes. The core components of the heat-responsive signaling pathway are likely to be conserved in bryophytes and angiosperms, based on the signaling pathways that were found in the *M. polymorpha* genome (Marchetti *et al.*, 2021). Liu *et al.* (2013) found that 3796 unigenes were significantly up-regulated after cold treatment, while 1405 were significantly down-regulated in the *Pohlia nutans* transcriptome. Elzanati *et al.* (2020) revealed that some genes with rapid and transient heat activation in *P. patens* could be direct targets of a heat shock TF called HsfA1E. Zhuo *et al.* (2020) showed that the expression of nine genes (*HSF3*, *HSP70*, *ERF*, *LEA*, *ELIP*, *LHCA*, *LHCB*, *Tf288*, and *DHN*) could be induced under heat shock stress in *Bryum argenteum*.

Bryophytes are generally adapted to low light intensities compared with other land plants. In a dark environment, in order to optimize light capture, they often arrange leaves distantly, or even always orient chloroplasts towards the most intensely lit spot on one side of cell, such as occurs in the mosses *Schistostega pennata* and *Mittenia plumula*, and the liverwort *Cyathodium* (Fig. 3B; Zhang *et al.*, 2004; Glime, 2020; Ren *et al.*, 2021). However, the most remarkable species is the European thalloid liverwort, *Aneura mirabilis*, which completely lacks chlorophyll and depends on a type of fungus to obtain its energy. This liverwort is the only land plant with a dominant non-photosynthetic haploid generation (Fig. 3B; Brundrett, 2002; Bidartondo, 2005; Wickett and Goffinet, 2008). Nevertheless, some photophilic bryophytes can resist high light by structural modifications, most commonly reflecting sunlight through white or hyaline surfaces (Lovelock and Robinson, 2002). The reflective surfaces in mosses are on leaves, from the whole leaves (*Leucobryum*), the upper half leaves (*Bryum argenteum*), to only the leaf tips (*Syntrichia caninervis*) (Fig. 3B; Tao and Zhang, 2012), while in liverworts they are on scales (*Mannia fragrans* and *Riccia trichocarpa*) or thalli (some species of *Exormochea* and *Riccia*) (Kürschner, 2004). Perhaps because high light intensities are often coupled with drought, some adaptation of bryophytes to the latter is also applicable to the former, for example the contorted or erect dry leaves which can reduce exposure to sun and the photosynthetic cells of leaves or thalli protected by many hyaline cells which can filter the sunlight before it reaches the chlorophyll (Fig. 3B). Colored pigment is another major route often seen in bryophytes, which can absorb the UV light before it damages the chlorophyll, although this process must be coupled with low temperatures (Bukhov *et al.*, 2001).

Molecular research efforts on the response to light intensity in bryophytes are limited. In *Pohlia nutans*, through transcriptional profiling and physiological analysis, antioxidant enzyme, flavonoid biosynthesis-related, and photolyase genes were found to be the main defense components involved in the adaptation to UV-B radiation (Li *et al.*, 2019). A type I flavone synthase-type enzyme (PnFNSI) in *P. nutans* was suggested to participate in flavone metabolism against drought stress and UV-B radiation (Wang *et al.*, 2020). A CPD photolyase gene (*PnPHR1*) in *P. nutans* was revealed to participate in the adaptation to UV-B radiation and salinity stress (H.J. Wang *et al.*, 2021). In the transcriptomes of *Syntrichia caninervis* and *S. ruralis*, transcripts involved in oxidative stress and in desiccation tolerance (such as LEA and ELIP genes) were suggested to be in response to UV radiation, implying the possible crosstalk between UV tolerance and desiccation tolerance (Ekwealor and Mishler, 2021). In the Antarctic moss *Leptobryum pyriforme*, integrative analysis using transcriptome and metabolome data showed that UVR8-mediated signaling, jasmonate signaling, the flavonoid biosynthesis pathway, and the DNA repair system might contribute to its acclimating to UV-B radiation (Liu *et al.*, 2021). A genome-wide analysis showed that ~ 400 genes in *P. patens* exhibited the differential expression in response to UV-B radiation, and *P. patens* is more capable of surviving UV-B stress than is *A. thaliana* (Wolf *et al.*, 2010). The mechanism by which UVR8 mediates photomorphogenic responses to UV-B is strongly conserved in *P. patens* and *M. polymorpha* (Clayton *et al.*, 2018; Soriano *et al.*, 2018; Kondou *et al.*, 2019).

Conclusion

Here, we drew a general picture of the diversity, phylogeny, and adaptation of bryophytes, and reviewed the phenotypic traits and molecular basis for the adaptations of the three bryophyte lineages to both early land environments and modern ecosystems. The monophyly of bryophytes has been accepted as the most suitable hypothesis, with hornworts sister to the clade including liverworts and mosses. Both molecular and ecological factors contribute to the unbalanced diversifications among the three bryophyte lineages. The frequent WGD events provide the genetic basis for phenotypic innovations, and might promote the flourishing of mosses among bryophytes. Many molecular and morphological novelties associated with plant terrestrialization have primarily evolved in bryophytes through gain of new genes or via duplication or neofunctionalization. During the adaptation to early land environments, mosses evolved with relatively high genetic redundancy via WGDs, while liverworts and hornworts retained low redundancy along with gene loss and genome reduction. Horizontal gene transfer also contributes to the emergence of novel genes in bryophyte species for ecological adaptations. Through morphological and physiological innovations, the stress resistance to humidity, temperature, and light intensity of mosses, liverworts, and hornworts seems to decrease in turn

according to previous studies. For the adaptation to modern ecosystems, desiccation tolerance is the most important strategy for bryophytes, especially mosses. Once dehydration becomes unavoidable, they will use an effective escape strategy, namely dormancy, in particular vegetative dormancy, which is the 'last resort' for escaping from an extreme drought environment. Desiccation-induced proteins, especially LEA proteins and ELIPs, play important roles during the response to desiccation, and the crosstalk of genetic pathways in response to different environmental stresses is also vital in bryophytes.

To date, genomic and transcriptomic data for bryophytes have only uncovered the tip of the iceberg, and future work needs to sequence more bryophyte genomes and transcriptomes to cover the species diversity and represent the ecological adaptive diversity, such as sequencing species in the basal groups of the three lineages (i.e. Takakiales in mosses, Haplomitriales and Treubiales in liverworts, and Leiosporocerotales in hornworts) and species that live in various environments (e.g. caves, desert, aquatic habitats, and polar regions). In addition to genomics/transcriptomics, studies on other omics such as proteomics, metabolomics, and epigenomics are still rare in bryophytes to date. In addition, the molecular mechanisms of specific morphological and physiological strategies of bryophytes to cope with various modern environments are still unclear, and most of those that are known are related to drought, with little known about temperature and light intensity. Comparative multi-omics and evo-devo studies are urgently needed to elucidate the molecular basis for the formation of adaptive traits in bryophytes and insight into the ecological success of these 'dwarfs' in the plant kingdom.

Acknowledgements

We thank Lian Luo, De-Chang Meng, Wen-Zhang Ma, and Dao-Yuan Zhang for providing field photos, and Mu-Sen Guo, Ai-Li Li, and Ying-Bao Sun for drawing morphological features.

Author contributions

ZDC: conceptualization; QHW and JZ: collecting opinions from all authors and writing the original draft with editorial input from ZDC; QHW and JZ: designing the figures with editorial input from ZDC. All authors reviewed and approved the final manuscript.

Conflict of interest

The authors declare no competing financial interests.

Funding

This work was supported by the National Natural Science Foundation of China (grant nos NNSF 32070233 and 31970214) and the Open

Research Foundation of State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences (grant no. LSEB2021-2).

Data availability

Supporting information is openly available at the Zenodo repository <https://doi.org/10.5281/zenodo.6176732> (Wang *et al.*, 2022).

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