

## eXtra Botany

Special Issue Editorial

# Bryophytes: how to conquer an alien planet and live happily (ever after)

**There are many push and pull factors that commonly drive individuals to leave their homeland. For example, escaping competition and occupying a novel habitat undoubtedly offer the advantage of new opportunities to pilgrims, but the absence of unfavorable biotic interactions can be counterbalanced by other antagonistic abiotic forces. After all, conquering an alien planet is not now nor ever was an easy task. We cannot know how many attempts and failures have punctuated the journey that led ancestral, photosynthetic organisms to leave the aquatic world and successfully establish on dry land. However, some traits developed by the ancestors of modern bryophytes that allowed them to adapt their life cycle to such a different habitat and persist there, have been undoubtedly identified.**

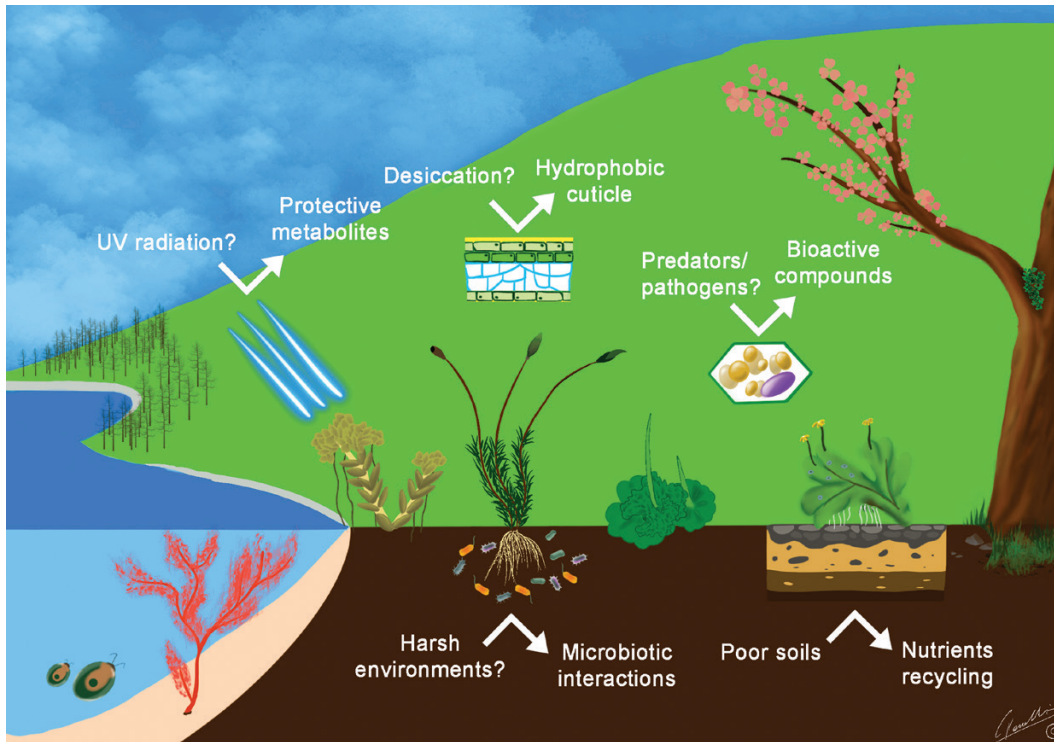
In past decades, research emphasizing taxonomy, biogeography and morphology studies has led to substantial advances in understanding bryophyte species description, distribution and phenology. This has contrasted with the genetic or morphogenetic insights obtained from flowering and other vascular plants. However, the gaps in understanding bryophyte genetics and morphogenesis are now being filled ever faster by researchers engaged in exploring some of these fundamental aspects of plant biology, from evolutionary ecology to a molecular scale (Bippus *et al.*, 2022; Fernandez-Pozo *et al.*, 2022; Wang *et al.*, 2022; Sakuraba *et al.*, 2022). In fact, since bryophytes are the closest modern relatives of the ancestors of the earliest terrestrial plants, the fascination of potentially finding in them traces of the transition and origin of higher plants from their algal lineages has driven considerable scientific interest in this group. Nonetheless their phylogeny is still under debate. The accepted hypothesis of their origin as paraphyletic—with liverworts, mosses and hornworts being successive sister lineages to tracheophytes (Qiu *et al.*, 2006)—has recently been challenged, as there is mounting evidence that bryophytes could be monophyletic (Morris *et al.* 2018; Su *et al.*, 2021).

Even if their vascular cousins undeniably dominate current plant landscapes in the majority of biomes, bryophytes,

despite their supposed ‘simplicity’, successfully manage to inhabit almost all environments, shape some of them and modulate ecosystem functions such as carbon and nitrogen cycling. In turn, the adaptive strategies that made bryophytes pioneers of colonization and resilience are crucial for water management, nutrition optimization, biotic interactions and stress responses (Fig. 1). Hence, when it comes to understanding how these tiny plants managed to conquer an alien planet and become such a fundamental part of it, we should look at five tasks they have achieved.

### Task one: adapt

The move from aquatic to terrestrial habitats brought multiple challenges, including the absence of a hydrostatic pressure assuring mechanical support, exposure to very much stronger ultraviolet radiation, and overall the urgent need to re-think both substrate adhesion and water management. All these evolutionary forces that helped to shape their development and physiology made terrestrial plant ancestors talented colonizers, as they have resourcefully succeeded in adapting to the most wide-ranging environmental variables. From desert to wetlands, from tropical to arctic, modern ecosystems are populated by bryophytes that currently show those morphological as well as strategic innovations—desiccation tolerance, cuticle and water-saving configuration to cite some—optimized for a life on land. Despite differing degrees of structural complexity among mosses, liverworts, and hornworts, the molecular bases for adaptive innovations that bryophytes inherited from the common ancestor of land plants have been identified in a burst of genetic novelty predominantly involving transcription factors (TFs), whose increased appearance is consistent with plant plasticity in environmental responses (Bowles *et al.*, 2020; Zhang *et al.*, 2020b). Retention of genes encoding TFs that follow polyploidy could partially explain this plasticity in bryophytes, as whole genome duplication events, which contributed heavily to gene expansion during terrestrial evolution, have been suggested to correlate with the higher morphological complexity of mosses than that of liverworts and hornworts



**Fig. 1.** Successful strategies adopted by bryophytes to cope with life on land, and efficiently populate the most diverse dry land ecosystems. Image by Gianluigi Giannelli (University of Parma).

(Zhang *et al.*, 2020a). However, this hypothesis does not seem to apply to some TFs such as RWP-RK, plant specific proteins that have a key role in nitrogen sensing and have recently been suggested as a pivotal element for the development of sophisticated nitrogen- and gametogenesis-related regulatory processes (Chardin *et al.* 2014).

Amid all the pre-requisites for successfully exploiting the many opportunities of terrestrial life, one first line of defense must be included. Bryophytes certainly express in their cell wall composition and organization the traits of success, but whether these traits are the artifacts of major changes in this structural element or if there was no substantial innovation in cell wall arrangement following terrestrial colonization, is still to be fully addressed (Sørensen *et al.*, 2010). Nonetheless, some interesting differences in polysaccharide components have been useful for clarifying different phylogenetic positions of hornworts and liverworts, as well as for unraveling the relationships between mosses and other lineages. An additional surface improvement decisively supported bryophytes during terrestrialization—the cuticle—ensured protection against water loss and multiple environmental stressors. To cope with highly dehydrating habitats – where surroundings are characterized by gaseous air that constantly drive water to evaporate – the availability of a biosynthetic machinery able to synthesize a hydrophobic skin to coat the exposed surfaces and protect tissues against desiccation, ultraviolet radiation, extreme temperature and pathogen penetration is essential. Profiling techniques

and comparative analyses have revealed how cuticle quantity and composition vary between bryophytes (Lee *et al.*, 2020; Machado Matos *et al.*, 2021). In fact, while liverworts and hornworts generally show a minimal cuticle with prevalence of phenolic compounds in the cutin fraction and very long-chained waxy components, the cuticles of mosses share more similarities with those of lycophytes, suggesting that selective pressures to evolve specific types of cuticle may have acted differently across phylogenetic clades (Kong *et al.*, 2020).

While phenolics are highly correlated with the need to shield UV radiation, so challenging for life outside water in general, as well as for surviving in specific ecosystems, the enrichment in fatty acids has also been recognized for rehydration and water content equilibration processes that define the poikilohydric behavior of bryophytes. Intriguingly, although bryophytes typically colonize moist habitats, the cellular mechanisms they have developed for enhancing survival in dehydrating conditions are sophisticated and effective (Morales-Sanchez *et al.*, 2022). This has produced crucial ecophysiological features that allow bryophytes to colonize extreme environments with limited and fluctuating precipitation – an ability that vascular plants acquired through the development of water-conducting structures and a more complex organization, at the expense of desiccation tolerance at the organism level. After all, saving water was not a linear process. For instance, investigations on the origin of stomata have recently revealed that bryophytes diverged

from an ancestral stomatophyte, and underwent a reductive evolution that led to a secondary loss of these structures. As a result, liverworts and some early-diverged mosses completely lost stomata and only later evolved specific air pores (Harris *et al.*, 2020).

### Task two: engage with natives

For the ancestors of terrestrial plants and for their modern descendants, the association with microorganisms has been central for a more profitable exploitation of nutrients and response to stressors (Fürst-Jansen *et al.*, 2020). Interactions with microbes have been observed in liverworts as well as mosses, in which mutualistic relationships with a diverse set of microorganisms substantially contribute to plant carbon and nitrogen management. In addition, the growth of plants with their microbiomes has been found to be deeply intertwined (Knack *et al.*, 2015). For example, all hornworts are known to harbor endosymbiotic colonies of *Nostoc*, which form recognizable clusters throughout the thallus.

Nonetheless, bryophytes from all lineages have proven to be capable of symbiotic interactions with mycorrhizal fungi, associated with their rhizoids (Pressel *et al.*, 2014; Rimington *et al.*, 2018). Phylogenetic analyses conducted on mycorrhization-related genes recently revealed that the genetic machinery governing pivotal aspects of plant–fungal partnerships is largely conserved and co-regulated across distantly related land plants. The understanding that a mycorrhizal symbiosis-associated function seems to have been acquired before the last common ancestor of land plants (and inherited since then by modern descendants), changes forever our interpretation of how non-vascular clades interact with the substrate, as well as sheds new light on the establishment of bryophytes on land environments (Wang *et al.*, 2010; Hoysted *et al.*, 2018; Sgroi and Paszkowski, 2020, Preprint).

Although intercourse between bryophilous mycorrhizal fungi and bryophytes have been periodically investigated, interactions with the rest of endophytic populations still remain largely unstudied, even when it has highlighted how several species contain more fungi than the morphologically obvious mutualists. Many researchers tend to explain the high degree of biochemical complexity offered by bryophytes as a consequence not only of their ecological and genetic diversification, but also of their multifaceted relationship with a wide range of endophytes that provide their hosts with advantageous adaptive features, like tolerance to extreme pH levels and resilience to extreme environments. This has been particularly evidenced in Antarctica, where some bryophyte populations represent the richest endophyte microhabitats of the Antarctic environment (Yu *et al.*, 2014). Either way, the establishment of a ‘non-belligerent’ attitude to some microbial natives clearly represents one of the key points for bryophytes to efficiently occupy otherwise impossible ecosystems.

### Task three: defend

Biochemical adaptation for colonization and diversification on such diverse niches certainly requires taking advantage of more than a few chemical weapons, mostly functioning to limit the detrimental effects of biotic stressors. New worlds may lack predators and competitors, but hidden threats of some phyto-pathogenic microorganisms would not be unnoticed for long. Presumably from the very beginning, bryophytes were able to synthesize secondary metabolites tailored for a wide-range of defense against pathogens; in turn, they developed a bioactive ‘treasure chest’ as diverse as the inhabited environment requires (Commisso *et al.*, 2021). Their ability to produce constitutive or inducible compounds with antimicrobial properties leave them largely unaffected by microbial diseases, despite their tendency to grow in humid habitats. For example, various classes of phenolic derivatives that are released from wet thalli have prevented the germination of fungal spores landing on plant surfaces. Secondary metabolites like polyphenols, terpenoids, flavonoids and anthocyanins (and more recently cannabinoids), the well characterized arsenal of biochemical defenses for mitigating pathogen infection in angiosperms, are also found in bryophytes, and probably represented an advantage in the terrestrialization process (Novaković *et al.*, 2021; Asakawa *et al.*, 2020). However, even if the phytochemistry of bryophytes attracts the interest of researchers for its stunning diversity of biologically active compounds, their ‘secretory secrets’ offer perhaps more fascination. The structures developed to accumulate a high concentration of specialized compounds while avoiding autotoxicity perfectly exemplify one of these enigmas. The structures that have evolved this function in liverworts are oil bodies, which are suggested to provide defense against herbivores in some species (Romani *et al.*, 2020). How the differentiation of secretory structures proceeded in land plants lineages with different evolutionary histories and the implication that similar metabolites may have repurposed their molecular mechanisms to solve similar physiological challenges (such as jasmonic acid and other oxylipins, whose phylogenetic distribution was speculated to be a consequence of interactions and/or adaptations of common ancestors to the surroundings) have not yet been fully elucidated.

### Task four: spread

Amongst extant land plants, bryophytes are the only plants in which the gametophyte (the haploid generation) represents the dominant generation in the life cycle with respect to the sporophyte (the diploid generation). However, although both generations are usually conspicuous, the reduction of one or the other is not uncommon, as observed in some mosses and liverworts that possess extremely reduced gametophytic phases. To invest in a multicellular diploid generation whose reproductive cells divide via meiosis must have facilitated the dissemination

of bryophytes and their capacity to persist, despite the cost of resources spent on the retention of zygote and embryo development. At present, since the sporophytes of mosses, liverworts, and hornworts are very different, it is widely accepted that they evolved largely in parallel from ancestors with simpler structures, proceeding in the direction of progressively more elaborate sporophytes. In contrast, the relative absence of complexity found in the sporophytes of various bryophyte lineages has often been regarded as an adaptation to dry habitats. From an architectural point of view, one innovation above all that has been critical for terrestrialization was to grow in 3D, as shooting systems with organs positioned radially around an up-right stem were a primer for greatly increased biomass production and diversity (Whitewoods *et al.*, 2018). Modern mosses still show this transition during development, when the filamentous protonema (2D) gives rise to 3D gametophores. To a lesser extent than flowering plants, bryophytes have managed to fruitfully exploit the opportunity to occupy space by developing a variety of shapes.

How does sex impact on spatial colonization by pioneer plants? The role of sexual reproduction in allowing bryophytes to successfully disseminate on colonized lands is still controversial. If asexual reproduction warrants that offspring will already be adapted to a stable (when not predictable) niche, sexual reproduction furnishes a population with the genetic variation essential for adapting to new or changing environments. These plants apply both strategies, but some features like mating that occur locally within the area defined by the range of sperm movement, and a typical outcompetition of male individuals by females (probably due to fewer resources expended by females for gamete production), still contribute to maintain uncertainty about the significance of sexuality in driving bryophytes to acquire and retain their space (Haig, 2016).

### Task five: shape the niche

Bryophytes are found almost everywhere from the tropics to Arctic regions, in aquatic and terrestrial habitats, from sea level to mountain summits, and are undoubtedly among the major contributors to diversity and functioning of numerous ecosystems that characterize several biomes such as tropical forests, boreal coniferous forests and tundra. The large number of adaptive strategies they gained was crucial for their ability to establish, develop and cope with different environmental conditions, but also for their ability to build new niches for a large diversity of microflora and mesofauna. The latter shows how these organisms, despite their supposed lack of complex adaptations, developed their architecture and functionality to explore a large number of possible solutions to allow them to overcome all kinds of environmental constraints, including an increasing number of biotic interactions. Even though their impact on nutrient production and decomposition has been

acknowledged, as bryophytes proved to be important players in both carbon and nitrogen cycles (Turetsky, 2003), little is known about the dynamics of nutrient regeneration that substantially contributes to aboveground vegetative leaf area and biomass. For example, the potential of stream bryophytes to influence organic matter composition of lotic ecosystems has been attributed to their relatively large C, N and P content, but very few studies have investigated nutrient assimilation, retention and cycling, which is surprising given their strong representation in the total autotrophic biomass.

It is clear that during evolution these organisms became highly desirable elements of biotic soil-crusted, providing ecological services important for soil stabilization, nutrient uptake and reallocation, and seed germination control that made possible the colonization of areas uninhabitable for the majority of other plants (Oliveira and Maciel-Silva, 2022). Species abundance, an important ecological role in several ecosystems and an extremely generous foundation of niches for other species, emphasizes the positioning of bryophytes as functional components for habitat quality, but much more deserves to be studied and brought to light about their real contribution to environmental ecology (Ladrón de Guevara and Maestre, 2022).

### Concluding remarks

This special issue summarizes the latest insights into questions such as ‘what have we learnt about the story behind the incredible colonization of the land by bryophytes?’ and ‘can we still use them to trace those adaptive processes that shaped, in plants, the key features for both an evolutionary success and the capability of persisting in highly dynamic—often harsh—environments?’. Exploring the biology of bryophytes might not only provide a privileged window from which we can observe and comprehend exactly how modern plants overcame the challenges of terrestrialization, but also shed light on those evolutionary strategies that still allow them to tenaciously preserve their flourishing existence on Earth: from the biosynthesis of specialized metabolites (Kulshrestha *et al.*, 2022) to light radiation response (Martínez-Abáigar *et al.*, 2022), from the development of dedicated structures (Romani *et al.*, 2022) to the sophistication of inherited structures (Ye and Zhong, 2022; Pfeifer *et al.*, 2022), from the interaction with the microbial population (Alvarenga *et al.*, 2022; Bonhomme and Guillory, 2022; Chen and Nelson, 2022) to the response of external and internal cues (Mohanasundaram and Pandey 2022; Nibau *et al.*, 2022; Pietrykowska *et al.*, 2022; Reboledo *et al.*, 2022), even to the tuning of a positive carbon balance interlaced with their capacity to deal with extreme conditions (Perera-Castro *et al.*, 2022a; Perera-Castro *et al.*, 2022b). Who knows, could bryophytes be exploited in the (future) colonization of other new worlds?

**Keywords:** Adaptation strategies, bryophytes, evolutionary pioneers, hornworts, liverworts, mosses, terrestrialization.

**Francesca Degola<sup>1\*</sup>, Luigi Sanità di Toppi<sup>2</sup> and Alessandro Petraglia<sup>1</sup>**

<sup>1</sup> Department of Chemistry, Life Science and Environmental Sustainability, University of Parma, 43124 Parma, Italy

<sup>2</sup> Department of Biology, University of Pisa, 56126 Pisa, Italy

\* Correspondence: [francesca.degola@unipr.it](mailto:francesca.degola@unipr.it)

## References

- Alvarenga DO, Rousk K.** 2022. Unraveling host-microbe interactions and ecosystem functions in moss-bacteria symbioses. *Journal of Experimental Botany* **73**, 4473–4486.
- Asakawa Y, Nagashima F, Ludwiczuk A.** 2020. Distribution of bibenzyls, prenyl bibenzyls, bis-bibenzyls, and terpenoids in the liverwort genus *Radula*. *Journal of Natural Products* **83**, 756–769.
- Bippus AC, Flores J, Hyvnen J, Tomescu AMF.** 2022. The role of paleontological data in bryophyte systematics. *Journal of Experimental Botany* **73**, 4273–4290.
- Bonhomme S, Guillory A.** 2022. Synthesis and signaling of strigolactone and KA12-Ligand signals in Bryophytes. *Journal of Experimental Botany* **73**, 4487–4495.
- Bowles AMC, Bechtold U, Paps J.** 2020. The origin of land plants is rooted in two bursts of genomic novelty. *Current Biology* **30**, 530–536.
- Chardin C, Girin T, Roudier F, Meyer C, Krapp A.** 2014. The plant RWP-RK transcription factors: key regulators of nitrogen responses and of gametophyte development. *Journal of Experimental Botany* **65**, 5577–87.
- Chen K-H, Nelson J.** 2022. A scoping review of bryophyte microbiota: diverse microbial communities in small plant packages. *Journal of Experimental Botany* **73**, 4496–4513.
- Commisso M, Guarino F, Marchi L, Muto A, Piro A, Degola F.** 2021. Bryo-activities: A review on how bryophytes are contributing to the arsenal of natural bioactive compounds against fungi. *Plants* **10**, 203.
- Fernandez-Pozo N, Haas FB, Gould SB, Rensing SA.** 2022. An overview of bioinformatics, genomics and transcriptomics resources for bryophytes. *Journal of Experimental Botany* **73**, 4291–4305.
- Fürst-Jansen JMR, de Vries S, de Vries Jan.** 2020. Evo-physio: on stress responses and the earliest land plants. *Journal of Experimental Botany* **71**, 3254–3269.
- Haig D.** 2016. Living together and living apart: the sexual lives of bryophytes. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**, 20150535.
- Harris BJ, Harrison CJ, Hetherington AM, Williams TA.** 2020. Phylogenomic evidence for the monophyly of bryophytes and the reductive evolution of stomata. *Current Biology* **30**, 2001–2012.e2.
- Hoysted GA, Kowal J, Jacob A, Rimington WR, Duckett JG, Pressel S, Orchard S, Ryan MH, Field KJ, Bidartondo MI.** 2018. A mycorrhizal revolution. *Current Opinion in Plant Biology* **44**, 1–6.
- Knack JJ, Wilcox LW, Delaux PM, Ané JM, Piotrowski MJ, Cook ME, Graham JM, Graham LE.** 2015. Microbiomes of streptophyte algae and bryophytes suggest that a functional suite of microbiota fostered plant colonization of land. *International Journal of Plant Sciences* **176**, 405–420.
- Kong L, Liu Y, Zhi P, Wang X, Xu B, Gong Z, Chang C.** 2020. Origins and evolution of cuticle biosynthetic machinery in land plants. *Plant Physiology* **184**, 1998–2010.
- Kulshrestha S, Jibrán R, van Klink JW, Zhou Y, Brummell DA, Albert NW, Schwinn KE, Chagné D, Landi M, Bowman JL, Davies KM.** 2022. Stress, senescence, and specialized metabolites in bryophytes. *Journal of Experimental Botany* **73**, 4396–4411.
- Ladrón de Guevara M, Maestre FT.** 2022. Ecology and responses to climate change of biocrust-forming mosses in drylands. *Journal of Experimental Botany* **73**, 4380–4395.
- Lee SB, Yang SU, Pandey G, Kim MS, Hyoung S, Choi D, Shin JS, Suh MC.** 2020. Occurrence of land-plant-specific glycerol-3-phosphate acyltransferases is essential for cuticle formation and gametophore development in *Physcomitrella patens*. *New Phytologist* **225**, 2468–2483.
- Machado Matos T, Fernandes Peralta D, Paradizo Roma L, Alves Cursino dos Santos DY.** 2021. The morphology and chemical composition of cuticular waxes in some Brazilian liverworts and mosses. *Journal of Bryology* **43**, 129–137.
- Martínez-Abaigar J, Núñez-Olivera E.** 2022. Bryophyte ultraviolet-omics: from genes to the environment. *Journal of Experimental Botany* **73**, 4412–4426.
- Mohanasundaram B, Pandey S.** 2022. Effect of environmental signals on growth and development in mosses. *Journal of Experimental Botany* **73**, 4514–4527.
- Morales-Sanchez JA, Mark K, Souza JPS, Niinemets U.** 2022. Desiccation-rehydration measurements in bryophytes: current status and future insights. *Journal of Experimental Botany* **73**, 4338–4361.
- Morris JL, Puttick MN, Clark JW, Edwards D, Kenrick P, Pressel S, Wellman CH, Yang Z, Schneider H, Donoghue PCJ.** 2018. The time-scale of early land plant evolution. *Proceedings of the National Academy of Science USA* **115**, E2274–E2283.
- Nibau C, van de Koot W, Spiliotis D, Williams K, Kramaric T, Beckmann M, Mur LAJ, Hiwatashi Y, Doonan JH.** 2022. Molecular and physiological responses to desiccation indicate the ABA pathway is conserved in the peat moss, *Sphagnum*. *Journal of Experimental Botany* **73**, 4576–4591.
- Novaković M, Ludwiczuk A, Bukvicki D, Asakawa Y.** 2021. Phytochemicals from bryophytes: Structures and biological activity: Review. *Journal of the Serbian Chemical Society* **86**, 1139–1175.
- Oliveira MF, Maciel-Silva A.** 2022. Biological soil crusts and how they might colonize other worlds: insights from these Brazilian ecosystem engineers. *Journal of Experimental Botany* **73**, 4362–4379.
- Perera-Castro AV, González-Rodríguez ÁM, Fernández-Marín B.** 2022a. When time is not of the essence: constraints to the carbon balance of bryophytes. *Journal of Experimental Botany* **73**, 4562–4575.
- Perera-Castro AV, Waterman MJ, Robinson SA, Jaime F.** 2022b. Limitations to photosynthesis in bryophytes: certainties and uncertainties regarding methodology. *Journal of Experimental Botany* **73**, 4592–4604.
- Pfeifer L, Mueller K-K, Classen B.** 2022. The cell wall of hornworts and liverworts: innovations in early land plant evolution? *Journal of Experimental Botany* **73**, 4454–4472.
- Pietrykowska H, Sierocka I, Zielezinski A, Alisha A, Carrasco-Sanchez JC, Jarmolowski A, Karlowski WM, Szweykowska-Kulinska Z.** 2022. Biogenesis, conservation, and function of miRNA in liverworts. *Journal of Experimental Botany* **73**, 4528–4545.
- Pressel S, Bidartondo MI, Ligrone R, Duckett, J.G.** 2014. Fungal symbioses in bryophytes: New insights in the twenty first century. *Phytotaxa* **9**, 238–253.
- Qiu YL, Li L, Wang B, et al.** 2006. The deepest divergences in land plants inferred from phylogenomic evidence. *Proceedings of the National Academy of Sciences USA* **103**, 15511–15516.
- Reboledo G, Agorio A, Ponce De Leon I.** 2022. Moss transcription factors regulating development and defense responses to stress. *Journal of Experimental Botany* **73**, 4546–4561.
- Rimington WR, Pressel S, Duckett JG, Field KJ, Read, DJ, Bidartondo MI.** 2018. Ancient plants with ancient fungi: Liverworts associate with early-diverging arbuscular mycorrhizal fungi. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20181600.

- Romani F, Banic E, Florent SN, et al.** 2020. Oil body formation in *Marchantia polymorpha* is controlled by MpC1HDZ and serves as a defense against arthropod herbivores. *Current Biology* **30**, 2815–2828.
- Romani F, Flores JR, Tolopka JI, Suarez G, He X, Moreno JE.** 2022. Liverwort oil bodies: diversity, biochemistry, and molecular cell biology of the earliest secretory structure of land plants. *Journal of Experimental Botany* **73**, 4427–4439.
- Sakuraba Y, Zhuo M, Yanagisawa S.** 2022. RWP-RK domain-containing transcription factors in the Viridiplantae: biology and phylogenetic relationships. *Journal of Experimental Botany* **73**, 4323–4337.
- Sgroi M, Paszkowski U.** 2020. Transcriptional responses to arbuscular mycorrhizal symbiosis development are conserved in the early divergent *Marchantia paleacea*. *BioRxiv* doi: [10.1101/2020.12.14.422721](https://doi.org/10.1101/2020.12.14.422721).
- Sørensen I, Domozych DS, Willats WGT.** 2010. How have plant cell walls evolved? *Plant Physiology* **153**, 366–372.
- Su D, Yang L, Shi X, Ma X, Zhou X, Hedges SB, Zhong B.** 2021. Large-scale phylogenomic analyses reveal the monophyly of bryophytes and neoproterozoic origin of land plants. *Molecular Biology and Evolution* **38**, 3332–3344.
- Turetsky MR.** 2003. The role of bryophytes in carbon and nitrogen cycling. *Bryologist* **106**, 395–409.
- Wang B, Yeun LH, Xue J-Y, Liu Y, Ané J-M, Qiu Y-L.** 2010. Presence of three mycorrhizal genes in the common ancestor of land plants suggests a key role of mycorrhizas in the colonization of land by plants. *New Phytologist* **186**, 514–525.
- Wang Q-H, Zhang J, Liu Y, Jia Y, Jiao Y-N, Xu B, Chen, Z-D.** 2022. Diversity, phylogeny and adaptation of bryophytes: insights from genomic and transcriptomic data. *Journal of Experimental Botany* **73**, 4306–4322.
- Whitewoods CD, Cammarata J, VENZA ZN, et al.** 2018. CLAVATA was a genetic novelty for the morphological innovation of 3D growth in land plants. *Current Biology* **28**, 2365–2376.e5.
- Yu NH, Kim JA, Jeong MH, Jeong M-H, Cheong YH, Hong SG, Jung JS, Koh YJ, Hur J-S.** 2014. Diversity of endophytic fungi associated with bryophyte in the maritime Antarctic (King George Island). *Polar Biology* **37**, 27–36.
- Zhang J, Fu XX, Li RQ, et al.** 2020a. The hornwort genome and early land plant evolution. *Nature Plants* **6**, 107–118.
- Zhang LS, Wu SD, Chang XJ, Wang XY, Zhao YP, Xia YP, Trigiano RN, Jiao YN, Chen F.** 2020b. The ancient wave of polyploidization events in flowering plants and their facilitated adaptation to environmental stress. *Plant, Cell & Environment* **43**, 2847–2856.
- Ye ZH, Zhong R.** 2022. Cell wall biology of the moss *Physcomitrium patens*. *Journal of Experimental Botany* **73**, 4440–4453.