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## Unveiling the nature of a miniature world: a horizon scan of fundamental questions in bryology

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### ABSTRACT

**Introduction.** Half a century since the creation of the International Association of Bryologists, we carried out a review to identify outstanding challenges and future perspectives in bryology. Specifically, we have identified 50 fundamental questions that are critical in advancing the discipline.

**Methods.** We have adapted a deep-rooted methodology of horizon scanning to identify key research foci. An initial pool of 258 questions was prepared by a multidisciplinary and international working group of 32 bryologists. A series of online surveys completed by a broader community of researchers in bryology, followed by quality-control steps implemented by the working group, were used to create a list of top-priority questions. This final list was restricted to 50 questions with a broad conceptual scope and answerable through realistic research approaches.

**Key results.** The top list of 50 fundamental questions was organised into four general topics: Bryophyte Biodiversity and Biogeography; Bryophyte Ecology, Physiology and Reproductive Biology; Bryophyte Conservation and Management; and Bryophyte Evolution and Systematics. These topics included 9, 19, 14 and 8 questions, respectively.

**Conclusions.** Although many of the research challenges identified are not newly conceived, our horizon-scanning exercise has established a significant foundation for future bryological research. We suggest analytical and conceptual strategies and novel developments for potential use in advancing the research agenda for bryology.

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## Introduction

The horizon-scanning method consists of systematically searching for and identifying emerging research trends, limitations and opportunities that might determine future pathways in a given research field. Horizon

scanning is a valuable and increasingly popular approach because it allows input and synthesis from a large and diverse scientific community (Sutherland et al. 2011). Several previous initiatives have successfully sought to identify and prioritise research

questions within scientific fields, including ecology (Sutherland et al. 2013), global change biology (Sutherland et al. 2020), invasion biology (Ricciardi et al. 2017), island biology (Patiño et al. 2017), palaeoecology (Seddon et al. 2014) and subterranean biology (Mammola et al. 2020).

To date, most horizon-scanning exercises have dealt with the state of the art in broad research areas rather than focusing on specific taxonomic groups. However, there is significance in conducting horizon scans that are narrow in their focus, to spotlight taxon-specific priorities (e.g. Trevathan-Tackett et al. 2019). In this paper, we present the results of the first horizon scan for bryology to identify future research avenues and priorities with the aim of significantly advancing our understanding of the biology of bryophytes.

### Why bryophytes?

Bryophytes comprise three major lineages: hornworts, liverworts and mosses (Vanderpoorten and Goffinet 2009). All three lineages possess a dominant gametophyte onto which the unbranched and monosporangiate sporophyte is permanently attached. Bryophytes are characterised by a unique combination of structural and physiological traits, such as their generally small size, poikilohydric condition, vegetative desiccation tolerance, physiological resistance to low-temperature regimes, and production of spores as their main dispersal unit (Patiño and Vanderpoorten 2018). This combination of traits has allowed bryophytes to thrive under a wide range of climatic and environmental conditions from polar to tropical regions, and from continents to remote oceanic islands, playing key ecological roles including their influence on the global climate since the Ordovician (Lenton et al. 2012). Bryophytes are indeed dominant organisms in several ecosystems, such as many forest and wetland systems (Vitt et al. 1995; Fenton et al. 2015). Several other life-history features of bryophytes are unique among embryophytes, such as evolutionarily labile mating systems and high levels of dioecy. It is unsurprising, therefore, that compelling answers to major questions in physiology (e.g. Proctor et al. 2007), evolution (e.g. Shaw et al. 2011), global change biology (e.g. He et al. 2016), and ecology and biogeography (e.g. Patiño and Vanderpoorten 2018) are increasingly being provided by studies of bryophytes.

Half a century since the International Association of Bryologists (IAB; <https://bryology.org/>) was established, bryological research is now embracing a golden era, propelled by new technologies for data management, molecular biology, genomics and ecological modelling. Such advances have been reflected by recent special issues addressing the state of the art of different fields of bryological research (Budke et al. 2018; Stech et al. 2021). However, key questions

have only started to be largely resolved, most notably those concerning phylogenetic relationships among the three main bryophyte lineages and with respect to the vascular plants (Puttick et al. 2018; de Sousa et al. 2019; Harris et al. 2020; Su et al. 2021). The monophyly of bryophytes and their sister relationship with tracheophytes challenge the long-held perception of bryophytes as the earliest extant land plants, and hence interpretations regarding how adaptations to land were acquired in the group and in tracheophytes (Donoghue et al. 2021; McDaniel 2021). The integration of bryophytes in land plant phylogenomics, that is, the study of the evolution of genes and their function, is thus essential for estimating how the function of genes changed during the early diversification of land plants. Additionally, this crucial task is contributing to uncovering which gene or gene families originated or expanded during terrestrialisation (Bowles et al. 2020; Naramoto et al. 2022).

It is thus time to consider both outstanding and new challenges facing the botanical discipline of bryology, with the ultimate goal of identifying promising research avenues and horizon issues. Such an exercise may help to answer general questions, facilitate hypothesis-driven research, and ensure the long-term conservation of this ecologically and evolutionarily important group of land plants.

To celebrate the fiftieth anniversary of the IAB, 32 bryologists engaged in different fields of bryological research initiated and developed a horizon-scanning exercise. This international team sought to bring forward 50 ranked fundamental questions for bryological research. The outcomes of this survey-based approach were presented during the 50th IAB conference in 2019 (IAB 2019), held at the Royal Botanical Garden in Madrid (9–12 July 2019). More recently, a selection of these fundamental research foci were presented by members of the core team of this initiative during a dedicated symposium at the online Bryophytes and Lichens BL2021 Conference (6–9 July 2021), co-organised by the IAB.

## Materials and methods

### The horizon-scanning approach

The horizon-scanning method used in the present study is based on the approach developed during a former initiative carried out to identify key research foci in island biology (Patiño et al. 2017). Before IAB 2019, the five initial survey coordinators (B. Goffinet, L. Hedenäs, J. Patiño, S. Pressel and A. Vanderpoorten) invited several other bryologists to form the '50 fundamental questions in bryology' working group. Each member provided expertise in at least one of eight main research fields: (i) Ecology; (ii) Systematics and Taxonomy; (iii) Floristics, Biodiversity and Biogeography;

(iv) Evolution; (v) Genomics, Evolutionary Developmental (Evo-Devo) and Developmental Biology; (vi) Reproductive Biology and (Eco-)Physiology; (vii) Conservation and Management; and (viii) Palaeobryology. Two to four working group members were asked to contribute to a specific research field, with the option to recruit one more member to their panel if deemed critical in providing complementary expertise. The final international working group comprised 32 bryologists (see author list), who had the main task of identifying 10–15 fundamental questions within their assigned research field (Figure 1). Members of each panel were encouraged to consult broadly with colleagues outside the working group.

This first phase (Phase 1 in Figure 1) produced 258 questions, which were then screened by the survey coordinators for duplication or ambiguity. The survey coordinators also took care to homogenise wording to ensure that the proposed questions were presented in a straightforward style with a consistent level of readability (Mammola et al. 2020). This first phase resulted in a curated list of 224 questions (hereafter termed List #1). To facilitate practical implementation of the first round of voting (Survey 1), questions from List #1 were redistributed into four general topics (GTs; adapted from Patiño et al. 2017), as follows.

- GT1 – Bryophyte Biodiversity and Biogeography: 39 questions from the subject areas of Macroecology; Floristics, Biodiversity and Biogeography; and Palaeobryology
- GT2 – Bryophyte Ecology, Physiology and Reproductive Biology: 59 questions from Ecology, Community Ecology, Reproductive Biology and (Eco-)Physiology
- GT3 – Bryophyte Conservation and Management: 39 questions pertaining to Conservation Biology and Global Change
- GT4 – Bryophyte Evolution and Systematics: 87 questions on Evolution, Genomics, Evo-Devo and Developmental Biology, and Systematics and Taxonomy.

The subscribers ( $n = 1536$ ) of the listserv e-mail discussion group Bryonet (bryonet-L@mtu.edu), supported by IAB, were invited to participate in Survey #1. This first step was structured into four online surveys (Phase 2 in Figure 1), one for each of the four GTs. Across the four online surveys, Bryonet subscribers had the opportunity to score each question as 'fundamental' or 'not fundamental', or to leave the answer blank. The order in which the questions were presented was randomised for each new online login, so that a specific order would not bias the outcome of the surveys (see Patiño et al. 2017); this strategy was retained for the two subsequent online surveys (see below). For each of the four GTs, survey

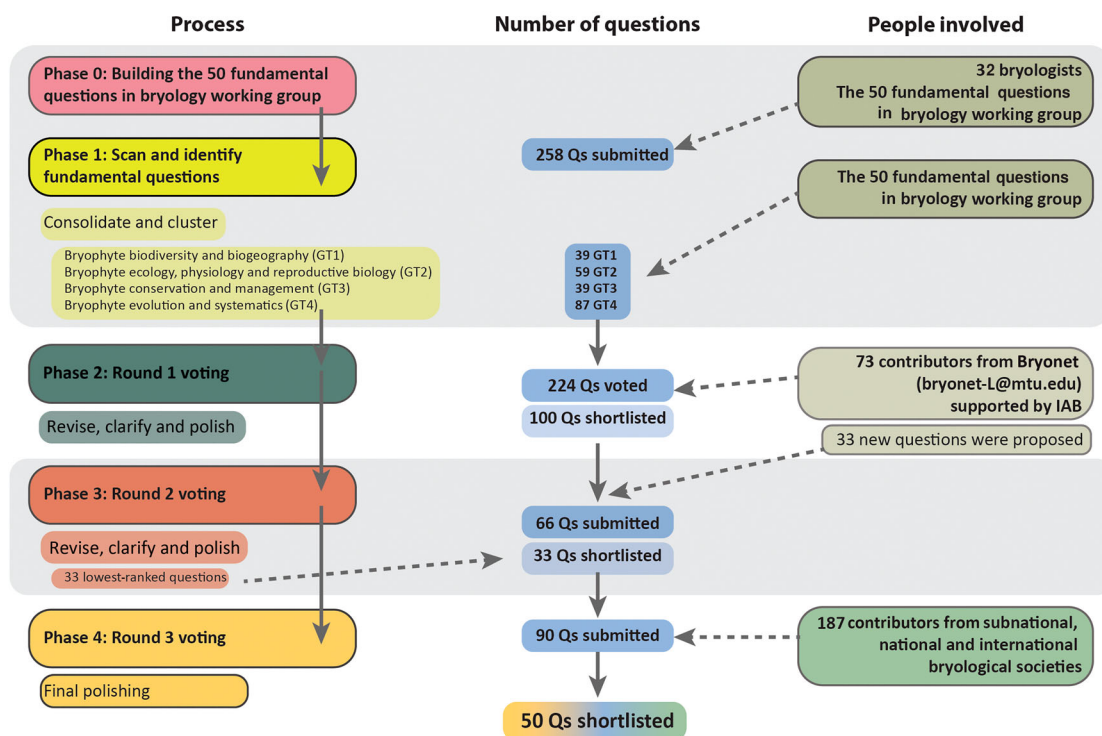
participants were also given the opportunity to propose one or two additional questions, to fill a perceived important gap in List #1. At the end of Survey #1, the original set of questions were ranked according to the total number of participants who scored a given question as 'fundamental', and the top 100 questions were selected (List #2).

A total of 33 new questions were proposed by participants in Survey #1 (List #3); these questions were merged with an equivalent number of questions from List #2, specifically the 33 lowest ranked questions (Phase 3 in Figure 1). This resulting new set of 66 questions (List #4) was used in a second online survey (Survey #2) in which only the 32 members of the '50 fundamental questions in bryology' working group participated. The questions from List #4 were voted and ranked during Survey #2 as 'fundamental' or 'not fundamental'. The top 33 questions of List #4 were then refined to eliminate redundant questions or ambiguities through discussions among the survey coordinators, and then merged with the top 67 questions retained from List #2. A final round of rewording to improve readability and to eliminate ambiguities and overlap (*sensu* Mammola et al. 2020) reduced the number of questions from 100 to 90 (see Figure 1).

The list of 90 questions (List #6) was then subjected to a third and final online survey (Survey #3) involving the broader participation of several international and national bryological societies, including the IAB; the Latinoamerican, Central European, Dutch, Nordic, Spanish–Portuguese, British, Australian and Chinese bryological societies; and the members of Bryonet and the International Molecular Moss Science Society (Phase 4 in Figure 1). During this online survey, we collected professional information such as the main research field(s) and the geographical area(s) of study to enable characterisation of the scientific profiles and interests of the participants. Survey #3 was completed by a total of 187 respondents. The final ranking of the questions was based on the proportion of 'fundamental' votes relative to the total numbers of votes received for each question (Patiño et al. 2017), and eventually resulted in selection of the 50 highest ranked questions.

### Procedural shortcomings

When applying horizon-scanning approaches, it is crucial to discuss transparently the potential caveats and uncertainties that can emerge from the participants, particularly from their background knowledge and areas of expertise (Sutherland et al. 2011; Patiño et al. 2017; Mammola et al. 2020). Individual subjective components are always consequential, because they will influence the selection of initial topics, the formulation of questions, and the final voting procedure. For



**Figure 1.** The procedure used to identify the 50 fundamental questions in bryology. The actions performed by the 32 bryologists of the ‘50 fundamental questions in bryology’ working group are highlighted in grey.

instance, a significant imbalance can be observed in the final questions selected for each GT (see *Results*), which may have resulted from bryologists interested in a given topic being underrepresented in the bryological community.

Despite such caveats, we sought to minimise the consequences of individual preferences and other sources of subjectivity by (i) including a broad spectrum of expertise in our core working group, and (ii) performing several rounds of voting involving a diverse group of both societies and research-interest groups from a wide range of institutions, geographical regions and study fields (see *Results*). Furthermore, by allowing participants in Survey #1 to suggest additional questions, we aimed to broaden the range of fundamental questions while minimising the biases inherent to horizon-scanning initiatives (Sutherland et al. 2011, 2013; Patiño et al. 2017).

## Results

During Survey #1, the number of voters (from a total of 93) and the maximum and minimum percentage of ‘fundamental’ votes (i.e. for the questions considered the most and least fundamental, respectively) varied across the four online surveys, as follows.

GT1 – Bryophyte Biodiversity and Biogeography (73 voters): 86% and 16%

GT2 – Bryophyte Ecology, Physiology and Reproductive Biology (58 voters): 84% and 15%

GT3 – Bryophyte Conservation and Management (55 voters): 85% and 16%

GT4 – Bryophyte Evolution and Systematics (48 voters): 79% and 10%.

All 32 members of the ‘50 fundamental questions in bryology’ working group participated in Survey #2, providing support for a given question for which the percentage of ‘fundamental’ votes ranged between 89% and 11%.

A total of 187 people contributed to the third and final round of online voting (Survey #3), of whom 88% identified a bryological field as their primary field of research. Although voters’ geographical areas of study were clearly skewed towards Europe and the Americas, with 78 and 60 participants, respectively, all the other continents were represented: Asia (32), Australasia including New Zealand (15), Africa (14), Antarctica (9), and worldwide, as involving at least four different floristic regions (9); thus, most regions of the world were to some degree represented in this survey. The 90 questions in Survey #3 received a mean ( $\pm$  SD) of 169.5 ( $\pm$  2.5) votes, with the majority (70/90) scored as ‘fundamental’ by most survey participants.

In the following sections and the Appendix, we present the 50 questions most highly ranked and hence perceived as fundamental in bryology through our horizon-scanning initiative. For ease of presentation, questions are organised in the same four general bryological topics used during Survey #3:

GT1 – Bryophyte Biodiversity and Biogeography (9 questions); GT2 – Bryophyte Ecology, Physiology and Reproductive Biology (19 questions); GT3 – Bryophyte Conservation and Management (14 questions); and GT4 – Bryophyte Evolution and Systematics (8 questions). We also provide information on each question's final rank (#) and the percentage of 'fundamental' votes received in Survey #3 (%).

## GT1 – Bryophyte Biodiversity and Biogeography

### Biodiversity patterns

- Q1. What are the main drivers of taxonomic, phylogenetic and functional diversity in bryophytes? [Rank #3, votes 81.9%.]
- Q2. Which are the main ecological factors shaping bryophyte species diversity along latitudinal and climatic gradients? [Rank #14, votes 75.0%.]
- Q3. How is phylogenetic diversity in bryophytes geographically structured? [Rank #33, votes 65.7%.]
- Q4. How does environmental heterogeneity affect species and intraspecific diversity patterns of bryophytes at different spatial and time scales? [Rank #45, votes 62.3%.]

Mounting evidence from ecological analyses of bryophyte functional traits (Ah-Peng et al. 2014; Spitale 2016; Henriques et al. 2017a; Berdugo and Dovciak 2019), although still limited by the availability of relevant databases (Henriques et al. 2017b), suggests that taxonomic and functional diversity represent complementary diversity metrics. Although the two metrics are sometimes strongly correlated (Ah-Peng et al. 2014), species assemblages may change functionally without significant changes in species richness (Lelli et al. 2019). The four highest-ranked questions in this section [Q1–Q4] emphasise the importance of improving our understanding of the factors shaping taxonomic, phylogenetic and functional diversity metrics across spatial and time scales.

The factors controlling diversity patterns typically vary depending on spatial scale, and two questions [Q3, Q4] are focused on how this variation is structured. For example, cover, species richness and functional diversity of bryophyte biocrust communities increase with shrub cover at the site scale, but the reverse applies at the microsite level (Soliveres and Eldridge 2020). These interactions within the bryophyte community and between bryophytes and vascular plants also vary along gradients of nutrient availability (Gunnarsson et al. 2004). A recent study on the long-term effects of nutrient enrichment has shown that the addition of phosphorus (P), unlike that of nitrogen (N), had a considerable impact on

plant communities of boreal rich fens (Øien et al. 2018). The increase in bryophyte diversity was explained by the fact that bryophytes receive N through their association with cyanobacteria, presumably affording them a greater ability to utilise the added P than that of vascular plants, which were affected by N shortage.

At larger spatial scales, recent surveys focused on altitudinal gradients (Patiño and González-Mancebo 2011; Hernández-Hernández et al. 2017; Boch et al. 2019; Iskandar et al. 2020), which offer substantial climatic variation across short distances. In turn, variation of diversity metrics along latitudinal gradients remains poorly studied. This knowledge gap can be explained by the lack of distribution data in a spatially standardised framework. In mosses, the absence of a standard checklist at the world scale, similar to that available for liverworts (Söderström et al. 2016), is a further impediment to macroecological and broad-scale biogeographical studies; this limitation is reflected in Q1.

For now, an entire field of research on phylogenetic diversity, which is the focus of Q3, has been addressed in a surprisingly low number of bryological studies (Shaw et al. 2005; Collart et al. 2021b; Sanbonmatsu and Spalink Forthcoming 2022; Wu et al. 2021), considering its growing importance in ecology, evolution and conservation. Phylogenetic diversity measures the genetic divergence among species within a community (alpha diversity) or the extent to which species within a community tend to be more phylogenetically related than species among communities (beta diversity) (see Graham and Fine 2008). These metrics can be usefully applied to address a broad range of questions, from the evolutionary origin of floras to the question of niche conservatism, according to which species are evolutionarily restricted within their niche. Niche conservatism has become one of the major foci in ecology, because it appears to be a primary driver of present-day distribution patterns of plant biodiversity (Crisp et al. 2009) and also has major consequences for the ability of species to adapt as a response to ongoing global change.

The development of efficient protocols for rapidly generating large numbers of sequences of unicopy nuclear genes in mosses (Liu et al. 2019; Medina et al. 2019) will undoubtedly open new avenues for research in community phylogenetics and its application to such major questions as the factors driving species distributions and diversity patterns at large spatial and temporal scales. Such efforts should also be extended to liverworts and hornworts. Despite this increasing interest in exploring patterns in taxonomic, functional and phylogenetic diversity, the predominant drivers, and the relationships among these three biodiversity components, remain unclear in bryophytes.

## The central role of historical collections for biodiversity research

- Q5. How can we realise the full potential of bryophyte herbaria for biodiversity research? [Rank #25, votes 69.0%.]

Renewed interest in herbaria, brought about by their use in integrative taxonomy and a growing awareness of their value as ‘windows into the past’ in global change research (Lang et al. 2019), underpins the relevance of Q5. Bryophyte herbarium collections have been used to reconstruct the historical composition of floras (Lavoie 2013), shed light on the timing of colonisation events (Calleja et al. 2020), analyse altitudinal range shifts (Bergamini et al. 2009), study phenology or functional trait variation (Hedenäs et al. 2010; Bisang et al. 2014; Stark et al. 2017), measure pollutant concentrations to retrace changes in pollution loads over time (Martinez-Swatson et al. 2020; Wu et al. 2020), reconstruct past levels of stratospheric ozone and ultraviolet (UV) radiation (Otero et al. 2009), and assess increases and decreases in bryophyte abundance to help trace predicted changes in nature (Hedenäs et al. 2002; Hofmann et al. 2007). Most recently, the application of high-throughput sequencing methods to the analysis of museum collections has revolutionised the study of biodiversity, offering a unique opportunity to obtain temporal snapshots of past population genetic diversity and quantify the extent and dynamics of the current biodiversity crisis (Gauthier et al. 2020).

In bryophytes, as in other organisms stored in natural science collections, such techniques open new avenues of research. For example, these approaches have allowed quantification of the impact of air and water pollution on patterns of genetic structure and diversity over time in ecological groups such as epiphytic and aquatic bryophytes, and the impact of ongoing human-mediated habitat fragmentation in biodiversity hotspots such as Amazonia or oceanic archipelagoes. It is therefore crucial that collecting efforts and collection infrastructures are not only maintained but also renewed to ensure the future of herbaria as fundamental research resources (Bebber et al. 2010; Soltis 2017; Lang et al. 2019).

### Distribution patterns

- Q6. At what spatial and temporal scales are dispersal limitations and environmental conditions shaping bryophyte distributions and diversity? [Rank #23, votes 69.9%.]
- Q7. What geographical regions exhibit the highest levels of bryophyte endemism, both taxonomic and phylogenetic, and what geographical

attributes do these regions present in common, if any? [Rank #30, votes 67.1%.]

- Q8. Are there bryophyte species that are truly cosmopolitan in distribution, and if so, what mechanism(s) explain such a capacity? [Rank #41, votes 63.9%.]
- Q9. How do stochastic (e.g. natural disturbance, population dynamics) and deterministic (e.g. habitat filters) processes influence bryophyte diversity and community composition, and how do these processes vary along environmental gradients? [Rank #42, votes 63.4%.]

Bryophytes have traditionally been perceived as organisms characterised by high dispersal capacities, based on their large distribution ranges and low levels of endemism (Patiño and Vanderpoorten 2018). Experimentally derived dispersal kernels (Lönnell et al. 2012) and community analyses demonstrating substantial differences between the species composition of spore clouds and ground vegetation (Barbé et al. 2016b) support the notion that bryophytes generally exhibit extremely good dispersal capacities that might erase any signal of isolation by distance. However, the widely held view that bryophyte species exhibit large, disjunct distribution ranges has increasingly been challenged by emerging phylogeographical evidence supporting a predominant role of within-continent speciation versus intercontinental dispersal (for review, see Vigalondo et al. 2019). This debate is reflected in three top-ranked questions concerning the role of dispersal capabilities in shaping distribution ranges [Q6, Q8], and the factors underpinning levels of endemism in bryophytes from both taxonomic and phylogenetic perspectives [Q7].

Although substantial phylogeographical evidence supports the idea that bryophytes exhibit high long-distance dispersal capacities, significant spatial genetic structures have been found in virtually all species at all spatial scales (Vanderpoorten et al. 2019). This suggests that successful colonisation events are determined by environmental filtering, geographical distance or barriers, and wind connectivity, rather than stochasticity [Q9]. Dispersal capacity may further be modulated by species intrinsic traits (van Zanten 1978; Estébanez et al. 2018). In particular, mating systems have long been identified as a major factor controlling variation in dispersal capacities among species. Recent analyses of epiphyll metacommunities have shown that early arrivals have greater rates of male and female sexual expression and reproductive output than late colonisers, suggesting that dispersal ability is reflected in establishment order (Sierra et al. 2019). The roles of dispersal- and establishment-related species traits (e.g. mating systems, spore ultrastructure and ornamentation, specialised

vegetative propagules) in shaping diversity patterns of apparently efficient dispersers such as bryophytes needs to be explored in greater detail (see GT2).

## GT2 – Bryophyte Ecology, Physiology and Reproductive Biology

### Life-history strategies and reproduction

- Q10. What are the functions of bryophyte morphological structures (e.g. hair points, papillae, paraphyllia, paraphyses) in terms of the ecophysiology (e.g. photosynthesis dynamics) and fitness (e.g. reproductive performance)? [Rank #21, votes 70.4%.]
- Q11. How does vegetative reproduction versus sexual reproduction influence population establishment and dynamics? [Rank #24, votes 69.6%.]
- Q12. What are the main intrinsic factors (e.g. life-history traits, habitat specificity, genetic diversity) governing rarity and vulnerability in bryophytes? [Rank #26, votes 68.9%.]
- Q13. What are the life-history traits of bryophytes that allow them, as a plant group, to persist and compete in the broad range of environments they occupy, and how do those traits vary across lineages? [Rank #29, votes 67.7%.]
- Q14. What biotic and abiotic factors determine the development of bryophyte gametophytes from propagule banks? [Rank #47, votes 60.9%.]
- Q15. Which (extrinsic versus intrinsic) cues determine the reproductive strategies of a bryophyte species (e.g. sexual, asexual or both)? [Rank #49, votes 60.0%.]

The characteristics of the bryophyte life cycle have a major bearing on nearly every aspect of bryophyte biology. The differences in reproductive modes (sexual, asexual; see Q11), which in turn are coupled to mating systems and other life-history attributes outlined above, affect establishment and demography of populations, plant community composition, and eventually species distribution and richness patterns (During 2007; Löbel and Rydin 2009; Laenen et al. 2016b).

Both spores and asexual diaspores of bryophytes can survive years, or even centuries, of unsuitable conditions while buried in different substrates (During 2007; Bisang et al. 2009; Caners et al. 2009; Bu et al. 2017). Also, the regeneration capacity of bryophyte fragments after several centuries of ice entombment in polar environments has been recently demonstrated (La Farge et al. 2013; Cannone et al. 2017). A persistent diaspore bank is critical for population regeneration and maintenance of genetic diversity, and it can serve as a reservoir for dispersal over time (During 2007; Hock et al. 2008; Maciel-Silva et al. 2012). However, diaspore longevity in, movement to and

emergence from the diaspore bank, and factors controlling these, have been investigated for only a handful of species and habitats [Q14]. What are the effects of species-inherent traits, environmental factors and biotic vectors, and how do they interact? These questions also pertain to species and habitat management in a conservation context [GT3].

We currently lack sufficient data to enable assessment of which factors drive selection for different reproductive modes and other life-history traits [Q15], which are the intrinsic phylogenetic and developmental constraints that limit phenotypic expression of these traits [Q15], and how these traits shape population dynamics [Q11]. This relates to another top-ranked question [Q10] concerning the function of morphological traits for reproductive performance and ecophysiology. For example: Do paraphyses affect gamete dispersal? What role does the maternal cuticular structure play in offspring development? What are the effects of gametophore size on mate availability (Budke et al. 2013)? How do leaf shape or leaf hair points affect a species' water economy (Tao and Zhang 2012; Pan et al. 2016; Hájek 2020)?

Other characteristics of bryophytes determine to a high degree where they can thrive and how large they can grow, including their limited structural (e.g. conducting tissues; but see Brodribb et al. 2020) or functional mechanisms to regulate tissue water content. The cellular water content of bryophyte gametophytes largely depends on environmental humidity ('poikilohydry'). However, most species tolerate some level of dehydration of their vegetative tissues over long periods. The processes that determine bryophyte recovery from dehydration have received considerable attention lately (Oliver et al. 2005; Stark 2017). Nevertheless, the function of bryophyte-specific morphological structures in these and other physiological processes remains poorly explored [Q10]. Thus, many crucial issues related to bryophyte life histories, functions and strategies, and how these relate to, for example, distribution or population dynamics, and the environment, remain unsolved, whereas they have received detailed attention in seed plants. Addressing these key questions [Q11–Q15; see also Q47 in section GT4] will not only advance bryology but add significantly to the understanding of plant biology and life-history evolution (Stearns 2000).

The questions outlined above need to be addressed in a phylogenetic framework to take into account phylogenetic relatedness (Crawford et al. 2009; Bisang et al. 2014), and with input from molecular biology to address the underlying mechanisms of trait expressions (e.g. Smith and Donoghue 2008). A comprehensive compilation of species traits for species from all the major bryophyte orders, at the scale of continents or regions, as has been accomplished for



Europe (Dierssen 2001), the Azores (Henriques et al. 2017b) and the UK (Hill et al. 2007), for example, will be a prerequisite for: (i) testing for trade-offs between different reproductive modes and other life-history characters (e.g. Bisang and Ehrlén 2002; Pohjamo and Laaka-Lindberg 2003; Löbel and Rydin 2009); and (ii) comparing traits and trait combinations between lineages and environments [Q13]. Ultimately, identifying genes contributing to focal phenotypes will provide a means to assess homology among distantly related taxa, or identify the extent to which distantly related species use the same mechanisms for solving biological challenges.

Research into life-history traits should be supplemented by studies of other species-inherent characteristics, for example habitat specificity, niche breadth, gametophytic ploidy level and intraspecific genetic variation, and their relationships with environmental factors and vulnerability [Q12] should be evaluated (Kotiaho et al. 2005; Löbel et al. 2018; Zettlemoyer et al. 2019). The recent Red List assessments of >1800 European bryophytes (Hodgetts et al. 2019) has enabled such an analysis for Europe. This step will provide crucial insights into extinction risks to bryophytes and the possibility of modelling them [Q12] for other regions and environments.

### Dispersal ecology

- Q16. To what extent do bryophyte species differ in their capacity for long-distance dispersal, and how does this variation in dispersal ability correlate with ecological, physiological or reproductive traits? [Rank #12, votes 75.4%.]
- Q17. What are the main environmental factors affecting dispersal of bryophytes, and how do they vary across habitats and geographical areas? [Rank #18, votes 71.7%.]
- Q18. What is the role of biotic and abiotic vectors for bryophyte dispersal at various spatial scales? [Rank #34, votes 65.7%.]
- Q19. What are the effective dispersal distances of bryophytes, and how do these vary with their life-history traits, in particular the type of diaspore? [Rank #38, votes 64.9%.]

The generally wide geographical distributions of bryophyte species suggest that they have great dispersal abilities (Medina et al. 2011; Patiño and Vanderpoorten 2018), as already discussed in the earlier subsection *Distribution patterns*. Spores or vegetative diaspores < 20 µm can be transported by wind across very large distances of several thousands of kilometres (Muñoz et al. 2004; Wilkinson et al. 2012). However, spore size as an estimate of dispersal potential is certainly too simplistic. Bryophyte diaspores can be dispersed by different mechanisms. Besides wind, water in the

form of rain or running water is an important vector, and rain ends dispersal events by washing out wind-blown diaspores from the air (Kimmerer 1991; Korpe-lainen et al. 2013). Animals serve as dispersal agents over short (Boch et al. 2013, 2015), moderate (Marino et al. 2009; Barbé et al. 2016a), and even long distances (Lewis et al. 2014; Chmielewski and Eppley 2019). Additionally, spatial and temporal factors constrain diaspore production. For instance, long-distance spore dispersal may occur from localised or regional source populations, or only during years with suitable weather conditions (Lönnell et al. 2014; Hedenäs 2015; Barbé et al. 2017; Hedenäs and Bisang 2019).

Thus, besides diaspore size, numerous other biotic or abiotic factors must be considered to enable realistic estimates of the dispersal potential of bryophytes. Their relative importance at different spatial scales remains, however, poorly understood [Q18]. Indeed, only some of these factors have been studied thoroughly and often only in a few model species, as reflected in the questions included in this subsection [Q16–Q19]. Therefore, to improve our understanding of bryophyte dispersal processes and their influence on relevant ecological aspects (e.g. community assembly), it is crucial to shed new light on (i) the influence of environmental (e.g. weather) conditions [Q17]; and (ii) adaptations in life-history traits (e.g. diaspore shape and ornamentation, density or mass of individual diaspores) and physiology (e.g. survival ability during dispersal) [Q16]. This will facilitate comprehension of when and how the production and release of diaspores increase dispersal efficiency (van Zanten 1978; Hedenäs 2001; Sundberg 2013; Lönnell et al. 2015; Zanatta et al. 2016, 2018).

Although many studies have analysed diverse aspects of bryophyte dispersal, we remain far from the general understanding required for quantitative estimates of how dispersal affects bryophytes and their distributions or survival in many natural and anthropogenic contexts. To date, bryophyte dispersal distances and mechanisms [Q19] have been studied for relatively few species (e.g. Lönnell et al. 2012; Sundberg 2013; Zanatta et al. 2018). Reaching the general understanding needed requires data from a much wider selection of species and over different spatial and temporal scales. These species need to represent diverse dispersal modes, habitats, distribution types, life histories, diaspore types and physiological adaptations. Future investigations should also consider whether similar dispersal adaptations in different lineages are a result of a single evolutionary event or the outcome of convergence through independent evolutionary episodes resulting from, for instance, common responses to adaptive forces.

Finally, large-scale analyses incorporating numerous species must be based on data assembled and scored in a consistent way or in ways that make

comparisons possible. For example, can we compare dispersal distances estimated (i) from species' distribution and abundance patterns at different scales (Pharo and Zartman 2007; Patiño and Vanderpoorten 2018), (ii) from tracing the origin or studying the fate of spores or vegetative diaspores by means of spore traps (e.g. Pohjamo et al. 2006; Lönnell et al. 2012; Sundberg 2013; Ingimundardóttir et al. 2014), and (iii) from molecular or phylogeographical approaches (e.g. Shaw et al. 2003; Pfeiffer et al. 2006; Hedenäs 2008)? Despite the formidable challenges, given the small size of both diaspores and plants compounded by often complicated micrometeorological and other microecological conditions (Moncrieff et al. 1997; Buzorius et al. 2001), broad approaches will provide a much deeper understanding of bryophyte dispersal.

### Biotic interactions and productivity

- Q20. How do bryophytes contribute to water retention, carbon and nitrogen budgets in ecosystems where their productivity and biomass are most significant? [Rank #2, votes 83.0%.]
- Q21. How common are the symbiotic associations with fungi and/or cyanobacteria, and through what mechanisms do they increase the ecological performance of bryophytes? [Rank #15, votes 73.9%.]
- Q22. How large is the contribution of bryophytes as primary producers across ecosystem types? [Rank #16, votes 73.9%.]
- Q23. What are the interrelationships between bryophytes and the microbiome, and how do they influence bryophyte community composition and ecosystem function? [Rank #20, votes 71.0%.]
- Q24. How do symbioses with fungi affect bryophyte development? [Rank #27, votes 68.8%.]
- Q25. What is the contribution of cyanobacteria associated with bryophytes to global fixation of atmospheric nitrogen, and in which ecosystem is this more prominent? [Rank #48, votes 60.9%.]

Bryophytes are key components of several biomes worldwide, where they contribute fundamentally to biomass and productivity and exert a major influence on ecosystem processes, including water, carbon (C) and N cycles (Turetsky 2003; Cornelissen et al. 2007; Turetsky et al. 2012; Michel et al. 2013; Song et al. 2016; Ah-Peng et al. 2017; Horwath et al. 2019). Although appreciation for the roles of bryophytes in ecosystem functioning has increased in the past few decades, especially for peat mosses (Bengtsson et al. 2016), major questions remain unanswered as to the mechanisms involved and how differences among species in key traits such as water retention capacity, productivity, litter quality and decomposition, N

interception, retention and fixation, and in the community composition of their microbiomes, shape the functional significance of bryophytes across ecosystem types [Q20–Q25].

In pristine, N-limited northern ecosystems, biological N<sub>2</sub> fixation by cyanobacteria and other diazotrophic microbes associated epiphytically with dominant feathermosses and *Sphagnum* contributes up to 50% of the total N input in these systems (DeLuca et al. 2002, 2007, 2008; Turetsky et al. 2012; Rousk et al. 2015; Holland-Moritz et al. 2018), characterising productivity and with putative crucial roles in overall N and C budgets (Rousk et al. 2013a, 2013b). In many other ecosystems, including tropical environments (Cusack et al. 2009), cyanobacteria probably contribute significantly to N<sub>2</sub> fixation, because they are frequently observed on bryophytes collected in many habitats and regions (L. Hedenäs, unpublished data). Transfer of cyanobacteria-fixed N<sub>2</sub> to moss hosts increases their biomass growth (Berg et al. 2013), directly influencing C fixation, while the N stored in moss tissue provides a major soil N input before and after decomposition (Coxson et al. 1992; Lindo and Gonzalez 2010), further affecting ecosystem C sequestration. However, current gaps in understanding of the physiological and genetic mechanisms governing bryophyte–cyanobacteria symbiosis (Warshan et al. 2016), and of the processes, routes and timescales by which the N from cyanobacterial-N-enriched moss tissue becomes available for N cycling in the soil (Lindo et al. 2013; Rousk et al. 2013a, 2013b), severely limit our appreciation of the role of this association in ecosystem functioning [Q20, Q21, Q25].

A better understanding of how different groups of nitrogen fixers may contribute to habitat N<sub>2</sub> fixation (Rousk et al. 2015), and how the composition of symbiotic cyanobacteria communities is influenced by host (Bay et al. 2013), habitat and season (Zackrisson et al. 2009; Ininbergs et al. 2011; Warshan et al. 2016), is also required, together with improved appreciation of the impact of habitat traits, including nutrient status (N deposition and P availability), temperature, water relations and atmospheric CO<sub>2</sub> concentrations on bryophyte productivity, N<sub>2</sub> fixation and ecosystem C and N cycling (Turetsky 2003; Rousk et al. 2013a, 2013b; van den Elzen et al. 2020). The latest research indicates that host identity may be a more important factor than the environment in structuring moss-associated bacterial communities, although local site conditions, such as light and temperature, also appear to have an effect, albeit subtler (Holland-Moritz et al. 2021 and literature within).

Cyanobacterial associations have been well characterised in hornworts (Frangedakis et al. 2021) and in the liverwort order Blasiales (Adams and Duggan 2008; Rikkinen and Virtanen 2008), with a recent focus on those of feathermosses and *Sphagnum*

species. However, as reflected by Q20 and Q24, a comprehensive understanding of the taxonomic extent of these partnerships across bryophytes, and their significance across ecosystem types, remains patchy (Turtsky 2003; Deane-Coe 2015). Also required is a deeper understanding of the types and roles of other microbes that associate with bryophytes [Q23], and how microbiomes may impact not only host nutrient acquisition but also germination, growth, metabolism and phenology (Bragina et al. 2014) across ecosystem types [Q22]. Mosses associate with a diverse community of potential N<sub>2</sub>-fixing microbes, including non-photosynthetic bacteria (Holland-Moritz et al. 2021 and references therein). Methanotrophic bacteria are important N<sub>2</sub>-fixing members of the *Sphagnum* microbiome (Larmola et al. 2014), contributing up to 20% of the CO<sub>2</sub> necessary for host photosynthesis (Raghoebarsing et al. 2005; Vile et al. 2014), and play a significant role in reducing methane fluxes from arctic freshwater systems through their mutually beneficial associations with submerged brown mosses (Amblystegiaceae) (Liebner et al. 2011).

Mutualistic, mycorrhizal-like associations involving diverse members of the Mucoromycota (Mucoromycotina and Glomeromycotina or Glomeromycota) (Spatafora et al. 2016) and Ascomycota (Rimington et al. 2020) have been demonstrated in a number of liverworts (e.g. Field et al. 2015, 2016; Kowal et al. 2018) and shown to enhance host P and N uptake and increase host fitness (Humphreys et al. 2010); however, the spread, functional significance and biogeochemical impact of these symbioses across bryophytes and ecosystems remain to be determined [Q24]. Besides these mutualistic groups, bryophyte microbiomes include a wide range of prokaryotes and fungi (Nelson et al. 2018), which may act as pathogens, parasites, saprobes or commensals (Davey and Currah 2006), and make possible a wide range of outcomes for host development (Nelson et al. 2018). However, our understanding of the variation in microbiome community composition among species and habitat type, the metabolic roles of these associations, the impacts of ecological factors on microbiome structure and function, their influence on bryophyte community composition, and ultimately the roles of bryophyte microbiomes in ecosystem functioning (Kostka et al. 2016; Carrell et al. 2020; Holland-Moritz et al. 2021; Stuart et al. 2021), is in its infancy [Q23, Q24]. An improved understanding of bryophyte-microbiome interactions is needed to predict the potential impact of climate and anthropogenic change on bryophyte-mediated biogeochemical cycles. Given the major influence of bryophytes on ecological processes in several biomes worldwide (Lindo et al. 2013; Weston et al. 2015), environmentally induced changes in bryophyte communities and their microbiomes are likely

to provide major feedback in carbon, nitrogen and water cycles at the global scale [Q25].

## Community ecology

- Q26. Which environmental factors determine establishment success in bryophytes, ultimately shaping bryophyte community composition? [Rank #9, votes 77.8%.]
- Q27. How does the interaction between macroclimate and microhabitat structure bryophyte community composition? [Rank #28, votes 68.2%.]
- Q28. How common and intense are competitive interactions in bryophytes, and to what extent do they influence their coexistence along environmental gradients? [Rank #39, votes 64.2%.]

Community ecology encompasses “the study of patterns in the diversity, abundance and composition of species in communities, and the processes underlying those patterns” (Vellend 2010, page 183). Modern community ecology seeks to integrate the description of patterns within a mechanistic framework, with the ultimate goal of understanding how communities assemble over time and space (Weiher et al. 2011; Thompson et al. 2020). Both deterministic and stochastic processes can operate during community assembly (Bannar-Martin et al. 2018). Interspecific competition and other biotic interactions are frequently assumed to work at a local scale while environmental changes and dispersal operate at larger scales (Ovaskainen et al. 2017).

Bryophytes are ideal organisms in which to investigate influences of deterministic and stochastic factors across scales. Because they are small, they are influenced by a broad array of large-scale environmental factors combined with small-scale microhabitat variables; this enables analysis of the across-scales effects of environmental drivers. Furthermore, bryophytes compete mainly for above-ground resources, with scarce experimental evidence suggesting that competitive exclusion is probably rare at best (Mälson and Rydin 2009). In fact, bryophytes have been used to challenge the view that stochastic versus deterministic factors operate uniquely at different scales (Medina et al. 2014, 2018a), and to disentangle the importance of dispersal versus niche assembly processes (Mota de Oliveira et al. 2009; Mota de Oliveira and ter Steege 2015).

Although major progress has been made towards a unified community assembly theory (e.g. Vellend 2016), in organisms such as bryophytes much more theoretical and empirical evidence needs to be obtained through both natural and manipulative experiments (Zamfir and Goldberg 2000; Snäll et al. 2003; but see Löbel et al. 2006). In particular, community dynamics should be studied at different spatial

and temporal scales and include an array of approaches such as experiments, modelling, population genetics and metapopulation theory (e.g. Pharo and Zartman 2007; Rydgren et al. 2010; Rosengren et al. 2015). This need is highlighted in the questions of this subsection [Q26–Q28].

Owing to the high dispersal capabilities of many bryophytes (see subsections *Distribution patterns* and *Dispersal ecology*), geographical isolation typically plays a negligible role, compared with that of environmental filtering, in the assembly of bryophyte communities (Sundberg et al. 2006; Mota de Oliveira and ter Steege 2015; Tiseliu et al. 2019; Liu et al. 2020; but see Löbel et al. 2006). In this context, Barbé et al. (2016a) have shown that environmental tolerance during establishment and species' ability to produce substantial amounts of diaspores are more important selective forces in bryophyte community dynamics than dispersal distance per se (see also Crum 1972). A similar pattern has been observed among island bryophyte communities and those expected under a null model in which species can disperse randomly among islands (Liu et al. 2020). By contrast, indirect estimates of dispersal derived from analyses of spatial genetic structures have mostly revealed significant isolation-by-distance patterns, indicating dispersal limitations (Vanderpoorten et al. 2019; Ledent et al. 2020). Such a discrepancy between the results of studies based on the spatial structure of communities and those of genetic analyses of the dispersal capacities of bryophytes is striking and opens an avenue for research on the role of environmental filters in colonisation and the spatial scale at which these filters operate [Q26, Q27], as well as the potential role of biotic interactions [Q28].

When looking into the factors that shape bryophyte communities, in addition to dispersal and environmental filters, we need to consider a third filter: interactions with other species (Weiher et al. 2011; HilleRisLambers et al. 2012) [Q28]. Few studies have assessed biotic filters in bryophytes, and therefore the degree of interspecific competitive exclusion and facilitation remains largely unknown. Former studies have accordingly suggested that competitive exclusion may (Udd et al. 2016; Ma et al. 2020) or may not (Mälson and Rydin 2009) play a role during bryophyte community assembly; however, facilitation can be important in specific ecological bryophyte groupings and environmental conditions (Bu et al. 2013).

A number of theoretical, experimental and empirical approaches have been proposed to assess the role of biotic interactions in shaping assemblages of species (HilleRisLambers et al. 2012), including species distribution modelling (Wisiz et al. 2013), which might emerge as a complementary method to be applied in studies of bryophytes (but see König et al. 2021). However, several assumptions underlying

these approaches, which utilise presence–absence data, undermine our ability to disentangle the role of biotic interactions from that of environmental filters and dispersal limitations (Blanchet et al. 2020; König et al. 2021). This shortcoming calls for the implementation of alternative approaches involving abundance data associated with mechanistic models and experimental methodologies, in order to advance the study of bryophyte community ecology.

## GT3 – Bryophyte Conservation and Management

### Global change

- Q29. What is and will be the impact of global climate change on bryophyte species' distribution, abundance, and composition in ecosystems? [Rank #1, votes 87.0%.]
- Q30. How will global climate change affect extinction risk (i.e. genetic diversity) of bryophyte species and, consequently, their ability to adapt to changing environmental conditions? [Rank #4, votes 81.3%.]
- Q31. What are the key drivers of decline in bryophyte species and intraspecific diversity, at both the global and regional level? [Rank #5, votes 79.4%.]
- Q32. What are the highest priority areas (i.e. regions, habitats) for the conservation of bryophytes in the face of land-use change, habitat destruction and climate change? [Rank #7, votes 79.2%.]
- Q33. How are biotic interactions between bryophytes and other organisms affected by climate change? [Rank #35, votes 65.7%.]

The earth is increasingly affected by anthropogenic change, and one of the forecasted consequences, foreshadowed by the ongoing dramatic reduction of biodiversity, is a most likely sixth mass extinction (Barnosky et al. 2011; Steffen et al. 2011; Sage 2020): the so-called Anthropocene extinction. Severe and consistent shifts have been observed in species distribution ranges, community composition and biodiversity levels, including losses of taxonomic, genetic and functional diversity across several terrestrial taxonomic groups (Ceballos et al. 2017; Gray 2019). In turn, most bryological studies have focused on understanding how Pleistocene or earlier climate change events have shaped species distribution and genetic diversity patterns (e.g. Shaw et al. 2011; Patiño et al. 2015; Ledent et al. 2019). Thus, it is essential to address the question of how bryophyte species and assemblages might respond to ongoing global change [Q29–Q33; see also Q34, Q37, Q38 in the next subsection] (Tuba et al. 2011; He et al. 2016; Bengtsson et al. 2021).

Species distribution modelling has become a common approach by which to forecast the potential

responses of bryophyte distributions to climate change scenarios. The models often depend, however, on large-scale climatic predictors and rarely include small-scale variables accounting for microenvironmental differences such as the microclimatic ones (Zellweger et al. 2019). Indeed, because bryophytes are small organisms, the environment they experience may be strongly decoupled from macroclimatic conditions. Not accounting for small-scale ecological conditions that may lead to an overestimation of climate-warming effects, as has been shown for alpine (Scherrer and Körner 2011) and boreal plants (Greiser et al. 2020).

Furthermore, the extent to which bryophyte species can compensate for climate warming-induced loss of suitable habitats by shifting their distribution ranges remains an area of debate. Projected rates of range loss derived from dispersal simulations under changing climate conditions in Europe significantly exceeded projected rates of range expansion, suggesting that even highly dispersive organisms such as bryophytes might not be fully equipped to cope with projected trends of climate change in the coming decades (Zanatta et al. 2020).

The need for this crucial information on the effects of global change is captured by the first two questions of this subsection, which focus on how bryophyte floras will respond to changing climatic conditions [Q29, Q30]. Spatial analyses across continental (e.g. Désamoré et al. 2012; Ruete et al. 2012) and insular systems (e.g. Ferreira et al. 2016; Patiño et al. 2016), predicting future changes in the geographical ranges of bryophyte species, allow us to assess the efficacy of existing protected reserves and the need for new ones [Q32, but also see Q34 in the next subsection] in order to meet present and future conservation needs.

Mounting evidence for local adaptation among infra-specific lineages raises the question of the taxonomic level at which species distribution modelling should be performed [Q31; see also Q40] (Smith et al. 2019, and references therein). This question is especially relevant in taxa with reduced morphologies, such as bryophytes, in which cryptic species have been increasingly reported. Such cases necessitate testing of the hypothesis of niche conservatism versus divergence among the investigated lineages or taxa, in order to inform subsequent modelling analyses (Collart et al. 2021a). A related and similarly neglected aspect is the genetic dimension at the intraspecific level of diversity (Cronberg 2002; Habel and Schmitt 2018). Biodiversity loss due to reduction in intraspecific genetic diversity at different spatial scales [Q30] has not been considered sufficiently for bryophytes (Hedenäs 2019).

Efforts devoted to understanding how species respond to diverse agents of global change are growing, following concerns about the capacity of species to cope with rapid anthropogenic global

change. However, current predictions of global and regional change responses and subsequent conservation strategies are largely incomplete, particularly for inconspicuous species-rich plant groups such as bryophytes [Q29, Q30, Q32, Q33]. Despite major efforts to assess the extinction risk at national or even continental levels through Red List assessments over time (Sim-Sim et al. 2014; Ingerpuu et al. 2018; Hodgetts et al. 2019) and through long-term monitoring of habitats and species (Pharo and Zartman 2007; Ingerpuu and Vellak 2017), many regions lack a quantitative assessment of how much of their bryophyte biodiversity is threatened [Q32]. Such a limitation is strongly correlated with the lack of knowledge about species' geographical ranges, population size and habitat conservation (Bergamini et al. 2019). This further points to the necessity for floristic explorations [see Q34, Q41, Q42] and an urgent need to assess geographical range loss, ecological processes and biological traits that render species vulnerable to extinction under anthropogenic disturbance regimes [Q31, Q32; see also Q12 and Q43 in panels GT2 and GT4, respectively]. This will enable assessment of the underlying causes of extinction risks at broad evolutionary and spatial scales (Pharo and Zartman 2007; Bergamini et al. 2009; Hylander and Weibull 2012; Hodgetts et al. 2019).

In this pressing context, we have limited knowledge about the effects of global warming on biotic interactions (Bragina et al. 2012), and how taxon-specific life-history traits interact to modify community composition (Pardow and Lakatos 2013). Inclusion of bryophyte-plant interactions in species-richness models has been shown to significantly increase their predictive power while decreasing bias (Mod et al. 2015). Thus, answering questions regarding the impact of global change on plant-plant interactions in bryophytes [Q33] might have crucial implications for improving existing approaches to preserving and restoring bryophyte assemblages across heavily human-disturbed landscapes.

## Disturbance, management and policies

- Q34. Which geographical areas and ecosystems are in urgent need of bryological exploration before being destroyed by human impact? [Rank #8, votes 78.5%.]
- Q35. How do bryophyte diaspore banks contribute to the long-term persistence of species, the preservation of genetic variation, and the restoration of habitats? [Rank #11, votes 76.0%.]
- Q36. How should bryological information be communicated to government, policy makers and managers to influence most effectively policies and decision-making? [Rank #13, votes 75.4%.]

- Q37. How effective are existing nature conservation reserves and networks for the conservation of bryophytes? [Rank #17, votes 72.1%.]
- Q38. Which ecosystems, ecosystem functions and services are most sensitive to changes in bryophyte composition? [Rank #22, votes 70.4%.]
- Q39. How could bryophyte conservation be better integrated into modern forestry to improve significantly the bryophyte diversity levels in managed forests? [Rank #36, votes 65.3%.]
- Q40. What are the best protocols for cultivation, reinforcement and reintroduction (ex situ conservation) of threatened bryophyte species into their original habitats? [Rank #50, votes 60.0%.]

Documenting biodiversity patterns, ecosystem functioning, and extinction rates is one of the most fundamental steps taken to effectively preserve natural resources (Cornwell et al. 2019; Le Roux et al. 2019), particularly in regions with high rates of human-induced habitat destruction. This crucial conservation task [reflected in Q34, Q38] is nowhere more critical than in tropical hotspots across Africa, Asia, the Americas and Oceania, which are severely threatened by rapid land-use transformation (Di Marco et al. 2019) but where so little is known about bryophyte diversity and its distribution (Figure 2) (Patiño and Vanderpoorten 2018; Cornwell et al. 2019; Van Rooy et al. 2019). The questions in this subsection [Q34–Q40] therefore highlight the growing need to design management and conservation strategies for bryophytes (Hallingback and Tan 2014). Forests were particularly highlighted [Q39], because they offer important habitats and are under enormous pressure on a global scale (e.g. Leberger et al. 2020; Karger et al. 2021). More specifically, the integration of potential historical in situ (e.g. diaspore banks) and contemporaneous ex situ (e.g. culture collections) diaspore pool reservoirs (Barbé et al. 2016b; Ingerpuu et al. 2019; Bisang et al. 2021) may prove valuable approaches by which to preserve and possibly even restore diversity and composition of bryophyte assemblages in anthropogenically influenced environments [Q35, Q40]. Additionally, there is an urgent need to document bryophytes in urban environments as key markers of the effects of changes in climate and air quality (Duckett and Pressel 2019).

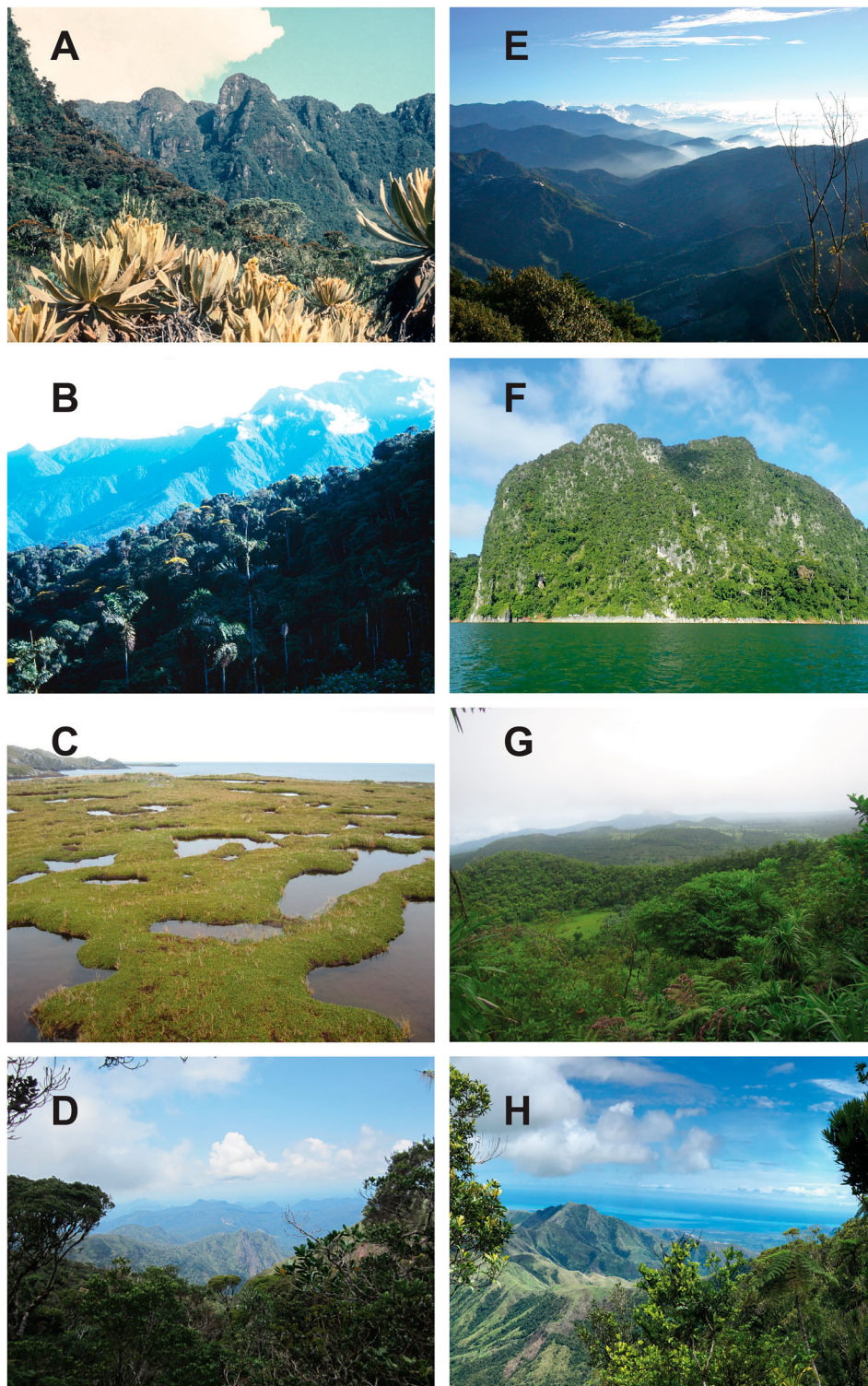
Moreover, conservation actions are implemented from national to subnational scales, and consensus has emerged on the need to reach stakeholders, managers and politicians to transmit the scientific outcomes (Carwardine et al. 2019) and to convey the significance of bryophyte species to biodiversity and ecosystem functions (Vanderpoorten and Hallingbäck 2009). Connecting scientists and decision makers has

important consequences, from boosting the application of novel conservation strategies to fostering in local policymakers and managers a long-term interest in plant conservation. The Cape Horn Biosphere Reserve represents a particularly successful case of integration of bryophytes into education and conservation programmes (Rozzi et al. 2004, 2006). To tackle the complex but necessary integration of bryophyte diversity loss into political agendas globally, it is fundamental to investigate and improve approaches that promote the incorporation of scientific bryological research into nature conservation policies [Q36, Q39]. This goal greatly relies on future levels of investment in the bryological training of early-career botanists and biodiversity managers (e.g. Lewis et al. 2017), as well as in the development of standardised methodologies for long-term biodiversity monitoring (e.g. Borges et al. 2018).

### Rarity, threat and Red Lists

- Q41. Where are the global hotspots of rare or threatened bryophyte species, and how do these relate to hotspots of species and intraspecific diversity? [Rank #6, votes 79.4%.]
- Q42. Which regions and habitats are most in need of increasing assessment efforts in red listing of bryophytes? [Rank #19, votes 71.1%.]

Over recent decades, assessments of rarity and threat have become the cornerstones of conservation efforts, and the study of extinction-prone species identified as a priority when seeking to implement efficient conservation strategies and policies (Myers et al. 2000; Orme et al. 2005; Grenyer et al. 2006). A mounting number of studies have highlighted limited cross-taxon congruence in distribution patterns of rare and threatened species, with the researchers calling for high-resolution data from multiple taxa in order to inform biodiversity conservation decisions (Grenyer et al. 2006). Taxa traditionally considered in this type of study include angiosperms, mammals, amphibians and birds (Orme et al. 2005; Grenyer et al. 2006; Kier et al. 2009); bryophytes have been completely, or to a large extent, neglected. Indeed, there are regions across tropical America, Africa, Asia and Polynesia (see Figure 2), among others, whose bryophyte floras remain poorly known and where the need for Red Lists has been emphasised (González-Mancebo et al. 2012; Geffert et al. 2013; Hallingback and Tan 2014; Van Rooy et al. 2019). Therefore, there is an urgent need not only to carry out a global examination of distributions of all rare and threatened bryophyte species in order to assess potential patterns of endangerment, but also to evaluate the degree of



**Figure 2.** Eight geographical regions considered hotspots of biodiversity and unexplored bryologically. (A) Tatama Massif in the Western Cordillera, Colombia. (B) Chocó in the Western Cordillera, Colombia. (C) Freshwater ponds in the Cape Horn, Chile. (D) Marojejy National Park, Madagascar. (E) Central Taiwan Mountains around Taroko National Park, Taiwan. (F) Gua Bewah in Tasik Kenyir, Terengganu, Peninsular Malaysia. (G) Siga, Upolu Island, Samoa. (H) Nadarivatu, Viti Levu, Fiji. Photographs: Guido van Reenen (A), Jan-Peter Frahm (B), Bernard Goffinet (C, D), Alfons Schäfer-Verwimp (E), Gaik Ee Lee (F), Mereia Tabua (G, H).

congruence regarding interspecific but also intraspecific biodiversity hotspots in bryophytes [Q41, Q42; see also Q31, Q32, Q34]. Because the spatial scale probably influences the degree of congruence

among cross-taxon biodiversity hotspots, the distribution of threatened bryophyte species across fine spatial (habitat) gradients should be critically examined [Q42; see also Q27].

## GT4 – Bryophyte Evolution and Systematics

### Speciation, diversification and extinction

- Q43. What is the current extinction rate in bryophytes, and what are the most appropriate data to estimate this? [Rank #10, votes 77.4%.]
- Q44. How does variation in bryophyte diversity throughout time correlate with past global climate changes, with emphasis on the most recent epochs (i.e. Pleistocene and Holocene)? [Rank #31, votes 66.5%.]
- Q45. What is the relative importance of geographical (e.g. geographical isolation) and ecological speciation (e.g. adaptive radiation) in bryophytes? [Rank #37, votes 65.3%.]
- Q46. What is the early branching pattern that explains the evolution of the relationships among the three main bryophyte lineages? [Rank #40, votes 64.0%.]
- Q47. What life-history traits can be associated with high diversification rates in bryophytes? [Rank #43, votes 63.3%.]
- Q48. Which factors enable bryophytes to survive as predominantly haploid, and if there are different mechanisms of DNA repair, what is the template? [Rank #44, votes 62.8%.]

Bryophytes comprise approximately 17,900 extant species (Magill 2010; Söderström et al. 2016). Although the relationships among the major bryophyte lineages remain somewhat contentious, their origin early in the conquest of land at least half a billion years ago is uncontested (Morris et al. 2018, Su et al. 2021). Their long evolutionary history is marked by periods of rapid diversification in several lineages of liverworts (Porellales), mosses (Funariaceae, Hypnales) and hornworts (Anthocerotales) (Laenen et al. 2014; Medina et al. 2018b), from which much of the extant diversity of bryophytes originated. These diversification patterns may have been triggered by a broad variety of mechanisms, such as geographical speciation (Patiño and Vanderpoorten 2018), whole-genome duplications (Devos et al. 2016), global climatic shifts (Shaw et al. 2010; Medina et al. 2018b), and key innovations such as shifts in mating systems (Wall 2005; Laenen et al. 2016a).

Five questions in this subsection illustrate the need to study factors and processes that shaped bryophyte diversity in the past and continue to shape it in the present: extinction [Q43], past climate change [Q44], speciation mode [Q45], specific life-history traits [Q47], and the bryophyte-specific dominant haploid phase of the life cycle [Q48]. Question 46 highlights the ongoing discussion about the phylogenetic relationships of the main bryophyte lineages in the context of land plant evolution.

Given the current biodiversity crisis, it may not be surprising that the question related to estimation of historical extinction rates [Q43] was rated as the top-priority question, and it is one that connects to several questions in GT3 related to identification of knowledge gaps and data sources in order to assess extinction risk. Additionally, comparative studies of bryophytes across both taxonomic groups (including fossils) and spatial scales are necessary to estimate extinction rates, their trait dependence, and variation among lineages. Past levels of bryophyte diversity [Q44] are probably underestimated, because the bryophyte fossil record, despite ongoing discoveries (Feldberg et al. 2021; Ignatov and Maslova 2021; Edwards et al. 2022a, 2022b), remains scarce due to either the limited resistance of the plant body to decay or taphonomic biases and related issues (Tomescu et al. 2018). Furthermore, phylogenetic reconstructions highlight high levels of homoplasy in morphological evolution, challenging the assignment of extinct taxa to extant lineages (Edwards et al. 2022c). Although several fossils, especially from amber, were considered suitable for calibrating molecular trees (Feldberg et al. 2021; Ignatov and Maslova 2021), the identity of many older fossils remains ambiguous. The ambiguity of assigning fossils to the most terminal phylogenetic lineage further lowers their calibration potential and hence their contribution to estimation of the timing of evolutionary events. Therefore, advances in bryophyte taphonomy (the branch of palaeontology that deals with the processes of fossilisation) and focused searches for fossils will be crucial in future efforts to unravel bryophyte evolution and extinction rates (Tomescu et al. 2018).

In this context, the ability to link diversification events to time periods of significant global environmental changes (e.g. Shaw et al. 2010; Bechteler et al. 2017) strongly depends on the underlying calibration assumptions (Feldberg et al. 2013; Laenen et al. 2014). Information on the relative timing of speciation events across the Plant Tree of Life, such as major radiations in bryophytes and angiosperms, could be obtained from uncalibrated trees. However, this analytical strategy would rely on the assumption of homogeneous rates of molecular evolution across lineages, a hypothesis unlikely to hold true (Villarreal et al. 2016). Despite these limitations, such an approach has recently provided evidence for consistent bursts of diversification in several bryophyte groups during important global events of climatic and ecological change (Shaw et al. 2010; Feldberg et al. 2014; Laenen et al. 2014). Because the number of such case studies based on high-resolution geographical and species samplings is still low, Q44 remains largely unanswered.

The relative importance of specific evolutionary mechanisms in driving bryophyte diversification



remains difficult to assess [Q45]. Allopatric speciation remains the default assumption, at least for species whose spores or asexual propagules can withstand the stresses of aerial dispersal (van Zanten 1978; Estébanez et al. 2018), but what constitutes a geographical barrier to gene flow in bryophytes is uncertain. For example, unlike vascular plants, bryophytes exhibit low levels of speciation and insular endemism on oceanic islands (Patiño et al. 2014), suggesting either that (i) bryophytes tend to prefer long-term environmentally stable habitats, which do not seem to fuel plant speciation on islands (Patiño et al. 2014); or (ii) long-distance gene flow precludes isolation (Vanderpoorten et al. 2008; Patiño and Vanderpoorten 2021).

The latter hypothesis suggests that in organisms with high dispersal capacities, such as bryophytes, gene flow among diverging species may not be completely disrupted; therefore, factors other than geographical distance or barriers must promote reproductive isolation. It was initially thought that bryophytes largely fail to diversify along environmental gradients (Shaw 1985), which would offer a straightforward explanation for their failure to ecologically radiate on islands (Patiño et al. 2014). Mounting evidence points, however, to the genetic structuring of genetic variation along ecological gradients (e.g. Sim-Sim et al. 2015; Magdy et al. 2016; Ledent et al. 2020), which suggests ecotypic differentiation, a hypothesis congruent with the unexpectedly wide gene space of bryophytes (e.g. Bowman et al. 2017; Lang et al. 2018; Li et al. 2020; Zhang et al. 2020; Carey et al. 2021; Rahmatpour et al. 2021). Studies that employ reciprocal transplant or crossing experiments (Schwarzer and Joshi 2017), combined with broad comparative studies of diversification and population genetic structure, will be critical for identifying traits linked to local adaptation, reproductive isolation, or altered extinction probabilities.

Post-zygotic isolation due to differences in ploidy levels between closely related species (i.e. polyploid speciation) is also clearly important (Beike et al. 2014; Perley and Jesson 2015; Nieto-Lugilde et al. 2018a; 2018b), but many closely related species pairs lack ploidy differences. Populations may further differ in the timing of gametogenesis, such that changes in phenology may generate temporal isolation. Intriguingly, limited evidence has pointed to the idea that mosses may use odours to attract sperm-dispersing microarthropods (Cronberg et al. 2006; Cronberg 2012; Rosenstiel et al. 2012; Shortlidge et al. 2021), offering the possibility of isolation mechanisms analogous to pollination syndromes in flowering plants. Identifying the key factors driving speciation in bryophytes [Q44, Q45, Q47] will require a combination of comparative, experimental and genetic analyses. Because bryophytes have nearly equal numbers of

bisexual and unisexual species, they are particularly well suited for answering questions concerning the role of sexual conflict in speciation, a key research focus in other eukaryotic groups (Crespi and Nosil 2013).

As far as phylogenetic relationships of the three major bryophyte lineages are concerned [Q46], inferences from variation in DNA sequences offer support for the full array of sister relationship hypotheses (Puttick et al. 2018). Recent phylogenomic analyses converge to a Plant Tree of Life wherein mosses and liverworts ('setaphytes') are sister groups and all three bryophyte lineages together compose the sister group to extant vascular plants (Wickett et al. 2014; Puttick et al. 2018; de Sousa et al. 2019; Sousa et al. 2020a, 2000b; Su et al. 2021), a hypothesis previously supported by inferences from spermatogenesis (Garbary et al. 1993). The challenges of reconstructing the early radiation of land plants are rooted in the difficulty of reassembling events that happened half a billion years ago, and which may have occurred in rapid succession following the colonisation of land by plants and given rise to some lineages that have long since become extinct.

Despite considerable knowledge of the life forms, life strategies and reproduction of bryophytes (see GT2), links between life-history traits and phylogenetic history and diversification rates in bryophytes are poorly understood [Q47] (but see Crawford et al. 2009). Detailed information on individual species traits, which is organised in databases (e.g. Dierssen 2001; Hill et al. 2007; Henriques et al. 2017b; Bernhard-Römermann et al. 2018; Stanton and Coe 2021), will be highly beneficial for assessing such associations. Combined with phylogenetic analyses, this will allow large-scale analyses of character evolution. For example, Coudert et al. (2017) demonstrated that the diversification of branching forms during moss evolution was especially prominent in the diverse lineages that radiated after the origin of pleurocarpy. Bisang et al. (2014) suggested that phylogenetic history is more important than the current environment in explaining reproductive traits in dioicous pleurocarpous wetland mosses. These case studies illustrate how the integration of functional differences among species, phylogenetic relatedness and geographical data can contribute towards a more universal theory of plant functional ecology (Stanton and Coe 2021).

Question 48 covers different aspects related to the dominance of the haploid generation in the bryophyte life cycle. In haploid organisms, natural selection is more efficient because recessive deleterious or adaptive mutations are not masked; they therefore have a direct effect on the phenotype (Martin-Roy et al. 2021). This should be analogous to the situation in bryophytes (Szövényi et al. 2014). In bryophytes,

however, selection in the haploid and diploid phases is difficult to compare, given that the sporophyte is dependent on the gametophyte and many species do not regularly produce sporophytes. How natural selection acting on the haploid gametophyte phase influences the evolution of bryophyte genomes and populations remains a major question.

Furthermore, different types of mutations (single-nucleotide mutations versus larger structural changes) may affect haploid versus diploid cells differently, as observed in the yeast *Saccharomyces cerevisiae* (Sharp et al. 2018). Thus, the gametophyte and sporophyte of bryophytes may experience different dynamics of DNA replication and repair. Whether this is true, and how it would relate to the finding that differentiation in gene expression between both generations is weaker in *Funaria hygrometrica* than in *Ara-bidopsis thaliana* (Szövényi et al. 2013), despite the fact that the bryophyte gametophyte is more exposed to mutagens in the environment, needs to be investigated.

It should be also noted that cell cycle arrest is variable among different tissues in *Physcomitrium patens* (also referred to as *Aphoanorrhagma patens*) (Schween et al. 2003; Ishikawa and Hasebe 2015). For the gametophytes of different liverwort and moss species, DNA damage from artificially enhanced UV-B radiation has been demonstrated, whereas exposure to natural ambient UV-B levels mostly does not result in DNA damage (summarised in Fabón et al. 2011). Consequently, efficient protection and repair mechanisms in bryophytes acclimated to their specific environmental conditions seem to be in place (Fabón et al. 2011), and in some species at least vegetative desiccation may provide protection against DNA damage (Turnbull et al. 2009). Furthermore, DNA damage induces reprogramming of gametophore leaf cells to chloronema apical stem cells, rather than cell death, as in other organisms (Gu et al. 2020). The molecular mechanisms of DNA repair in bryophytes have, to date, been addressed only in the model species *Physcomitrium patens* (also referred to as *Aphoanorrhagma patens*) (Kamisugi et al. 2016; Wiedemann et al. 2018; Kobayashi et al. 2020).

### Species concepts and taxonomy

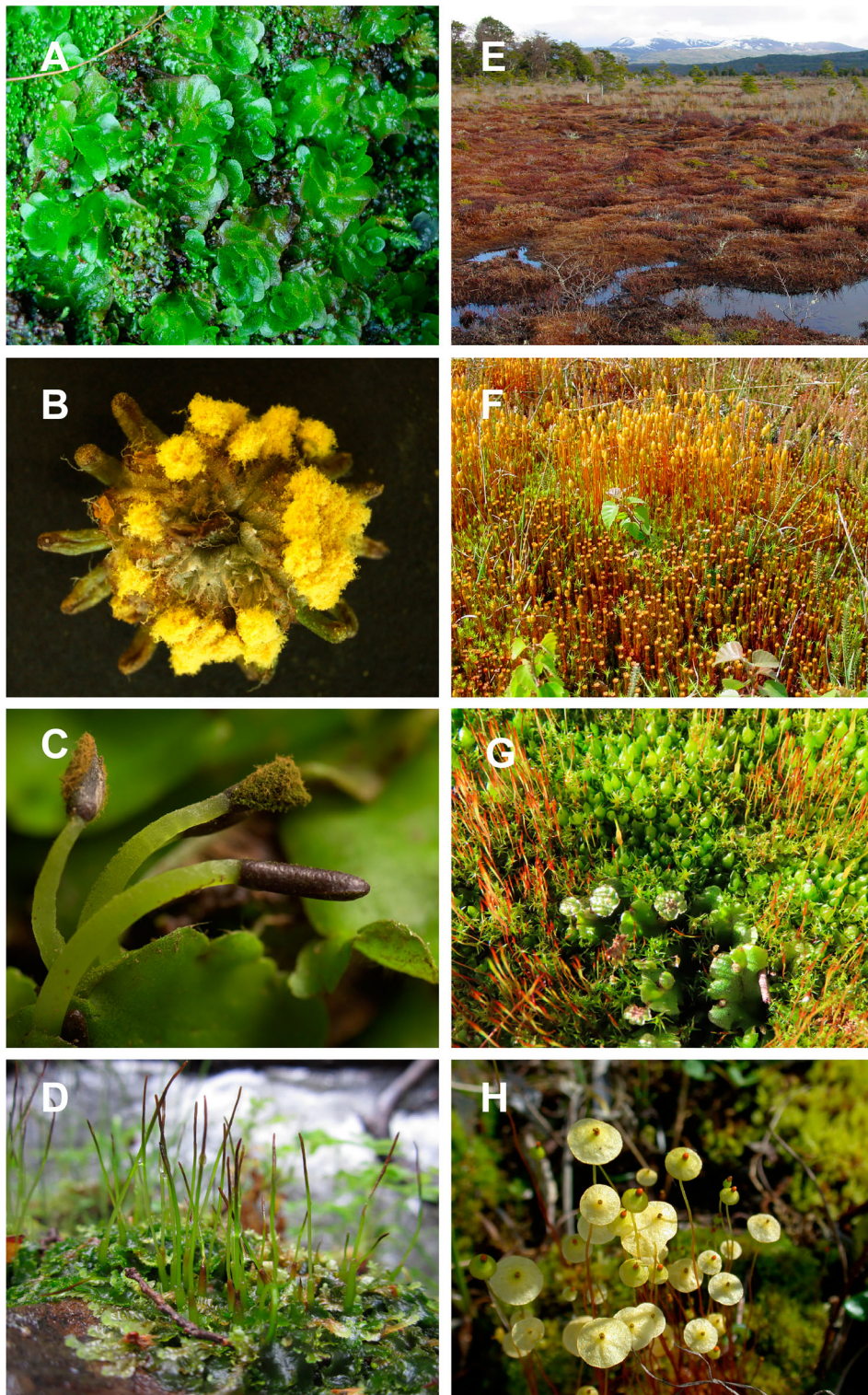
- Q49. How should we rationalise the dilemma between classic morphometric taxonomy and molecular based rearrangements of taxonomic order in the case of bryophytes? [Rank #32, votes 65.9%.]  
 Q50. Which species concepts are most adequate for assessing bryophyte diversity? [Rank #46, votes 61.8%.]

As in other organisms, analyses of DNA sequence data complement studies of traditional morphological

characters for assessing the species diversity of bryophytes and for classifying species into higher taxa. Taxonomic revisions based on classic approaches led to striking reductions in the actual number of species. During the period of active bryological exploration of extra-European regions during the nineteenth century in particular, hundreds of new ‘species’ were described based in large part on the assumption that populations from distant regions must represent distinct taxa (Shaw 2001). Frahm (1999), for example, reduced the initial number of ca 1000 species in the moss genus *Campylopus* to 150, indicating that morphological diversity could have been overrated, at least for specific groups. Conversely, an increasing number of morphologically defined species (e.g. Heinrichs et al. 2010; Renner et al. 2013; Lang et al. 2015), genera and families (e.g. *Bryum*, *Hypnum*, *Orthotrichum*, families in the Dicranidae and Hypnales) have been split based on molecular data. This trend is ongoing, as further genera (e.g. *Aongstroemia* and *Dicranella* in Bonfim Santos et al. 2021) and families (e.g. Ditrichaceae in Fedosov et al. 2016) are resolved as polyphyletic; these findings will have to be addressed taxonomically.

That the taxonomic diversity of bryophytes may be “vastly” underestimated is further suggested by the frequency of polyploidy (Patel et al. 2021 and references therein), in which either genome doubling (autopolyploidy; Fritsch 1991) or genome merger (hybridisation; Natcheva and Cronberg 2004; Shaw 2009; Olena et al. 2018; Sawangproh et al. 2020; Sawangproh and Cronberg 2021) may result in immediate reproductive isolation and hence act as a speciation mechanism. Within this context, studies that employ reciprocal transplant or crossing experiments, combined with broad comparative phylogenetic approaches and new sequencing technologies (Ravinet et al. 2017; Harvey et al. 2019), will be critical for providing a mechanistic understanding of the processes that generate diversity.

An increasing number of studies based on denser population-level and marker sampling have revealed an until-now unappreciated molecular diversity that may not be covered by the morphological species concept traditionally applied to bryophytes [Q50]. Complex interspecific and intraspecific evolutionary patterns may result from molecular variation without corresponding morphological variation, as well as genealogical conflict suggesting hybridisation (e.g. Sukkharak et al. 2011; Buchbender et al. 2014; Myszczyszki et al. 2017; Nieto-Lugilde et al. 2018a; Patel et al. 2021; Sawangproh and Cronberg 2021) or horizontal gene transfer (Hedenäs et al. 2021). Molecular lineages within morphological species may represent “cryptic species” (Struck et al. 2018), which are potentially widespread among bryophytes (e.g. Hedenäs



**Figure 3.** Bryophyte species illustrating the broad diversity of bryophytes and their potential use for education and outreach through citizen science. (A) The base of the liverwort tree: *Treubia lacunosa* (Colenso) Prosk. (B) Dehiscent sporophytes in the model liverwort *Marchantia polymorpha* subsp. *ruderalis* Bischl. & Boisel.-Dub. (C) Mature sporophytes of the largest thalloid liverwort in the world, *Monoclea forsteri* Hook. (D) *Nothoceros endiviaefolius* (Mont.) J.Haseg. ex J.C.Villarreal, Hässel de Menéndez & N.Salazar, from Navarino island, Chile, an endemic hornwort from the subantarctic Magellanic ecoregion. (E) About 6% of global carbon is locked up in *Sphagnum* living and dead; pristine *Sphagnum magellanicum* Brid. from Tierra del Fuego. (F) Representative of the most robust mosses, the Polytrichaceae; male and female colonies of *Polytrichum juniperinum* Hedw. (G) Primary colonists after a heathland fire: *Ceratodon purpureus* (Hedw.) Brid., *Funaria hygrometrica* Hedw. and male *Marchantia polymorpha*. (H) *Splachnum luteum* Hedw. from Alaska is an example of insect-mediated spore dispersal. Photographs: Jeffrey Duckett (A–C, E–G) and Bernard Goffinet (D and H).

and Eldenäs 2007; Fuselier et al. 2009; Bączkiewicz et al. 2017; Hedenäs 2020), although the use of that term needs to be evaluated critically (Renner 2020) [see Q49]. In particular, developing morphometrical tools offer increasing opportunities to identify more informative characters, especially in taxa mostly characterised by plastic, continuous traits, such as thalloid liverworts (Reeb et al. 2018). To tackle Q50, and to some extent Q49, integrating comprehensive information from morphological and molecular sources, together with other geographical or ecological data, should become the preferred approach by which to (re-)circumscribe bryophyte taxa (e.g. Medina et al. 2012; Nieto-Lugilde et al. 2018b; Vigalondo et al. 2019; Hanusch et al. 2020).

### Concluding remarks

Through a comprehensive and diverse horizon scanning exercise, we have identified 50 top-priority questions in bryology to commemorate the fiftieth anniversary of the IAB. Four interconnected GTs emerged (GT1–GT4), which encompass challenging questions and emerging research foci in a broad variety of bryological disciplines, including biodiversity, ecology, physiology, conservation, evolution and systematics. The fundamental questions presented in this paper signal: (i) an increasing need for phylogenetic and functional data to be incorporated into investigations of mechanisms underlying the shaping of global patterns of bryophyte diversity; (ii) greater recognition of the importance of life-history theory and biotic interactions in explaining bryophyte biology, population dynamics, community assembly and ecosystem functioning; (iii) expansion of multidisciplinary roles for bryophyte conservation biology in climate change research, ecosystem management, and assessment of extinction risk; (iv) growing applications for cutting-edge sequencing technologies and statistical-mechanistic models in biogeography and systematics; and (v) the use of experimental approaches to assess the importance of adaptation, reproductive barriers, and the genetic basis of trait variation in bryophyte evolution. When possible, we have suggested potential avenues for the research needed to answer the proposed questions.

Our horizon scan, the results of which reflect major challenges in bryology over the coming decades, was based on identification of the most highly ranked questions. This approach may, however, lead to undervaluation of the importance of some potentially overlooked questions. In particular, outreach was not represented in the final list of selected questions. This might reflect the often-invoked challenge that botanists, although eager to participate in and

deliver outreach activities, face critical limitations in the implementation of effective outreach efforts. There is an increasing demand for botanical information from people outside the scientific community. Therefore, it is plausible that a key question will be how we can best stimulate the imagination of a significant proportion of society to appreciate and focus attention on bryology (Figure 3). The involvement of undergraduate students and postdoctoral scholars to tenured professors and researchers in outreach activities and citizen science is a key step forward. An important challenge will be to design more innovative and inclusive outreach programmes and activities that engage with more diverse student and citizen communities (von Konrat et al. 2018; Raven 2019).

Although we recognise that our list of fundamental questions is not without its limitations, particularly regarding the truly emerging nature of a given topic, the possible bias introduced by the participants' interests, and the fact that some of the approaches proposed are rather nascent, it seems that our scanning initiative is sufficiently broad and diverse to delineate some of the most crucial research priorities for years to come. Indeed, along with other important recent initiatives (e.g. Renzaglia et al. 2007; Budke et al. 2018; Câmara et al. 2021; Stech et al. 2021), we have sought to contribute and advance the bryophyte research agenda. Despite our large and ambitious list of research foci, much of hypothesis-driven and well-executed research discussed here has the full potential to inspire theoretical and empirical research in the near future. We envision that our final list of 50 key questions in bryology will become a fruitful arena for early-career bryologists and contribute to fostering international and interdisciplinary collaborations, both important long-term goals of the IAB.

### Dedication

This paper is dedicated to the memory of our colleague Jochen Heinrichs, who sadly passed away in 2018.

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## Appendix

### The 50 fundamental questions in bryology

#### GT1 – Bryophyte Biodiversity and Biogeography

##### Biodiversity patterns

- Q1. What are the main drivers of taxonomic, phylogenetic and functional diversity in bryophytes?
- Q2. Which are the main ecological factors shaping bryophyte species diversity along latitudinal and climatic gradients?
- Q3. How is phylogenetic diversity in bryophytes geographically structured?
- Q4. How does environmental heterogeneity affect species and intraspecific diversity patterns of bryophytes at different spatial and time scales?

##### The central role of historical collections for biodiversity research

- Q5. How can we realise the full potential of bryophyte herbaria for biodiversity research?

##### Distribution patterns

- Q6. At what spatial and temporal scales are dispersal limitations and environmental conditions shaping bryophyte distributions and diversity?
- Q7. What geographical regions exhibit the highest levels of bryophyte endemism, both taxonomic and phylogenetic, and what geographical attributes do these regions present in common, if any?
- Q8. Are there bryophyte species that are truly cosmopolitan in distribution, and if so, what mechanism(s) explain such a capacity?
- Q9. How do stochastic (e.g. natural disturbance, population dynamics) and deterministic (e.g. habitat filters) processes influence bryophyte diversity and community composition, and how do these processes vary along environmental gradients?

## Appendix (continued)

### GT2 – Bryophyte Ecology, Physiology and Reproductive Biology

#### Life-history strategies and reproduction

- Q10. What are the functions of bryophyte morphological structures (e.g. hair points, papillae, paraphyllia, paraphyses) in terms of the ecophysiology (e.g. photosynthesis dynamics) and fitness (e.g. reproductive performance)?
- Q11. How does vegetative reproduction versus sexual reproduction influence population establishment and dynamics?
- Q12. What are the main intrinsic factors (e.g. life-history traits, habitat specificity, genetic diversity) governing rarity and vulnerability in bryophytes?
- Q13. What are the life-history traits of bryophytes that allow them, as a plant group, to persist and compete in the broad range of environments they occupy, and how do those traits vary across lineages?
- Q14. What biotic and abiotic factors determine the development of bryophyte gametophytes from propagule banks?
- Q15. Which (extrinsic versus intrinsic) cues determine the reproductive strategies of a bryophyte species (e.g. sexual, asexual or both)?

#### Dispersal ecology

- Q16. To what extent do bryophyte species differ in their capacity for long-distance dispersal, and how does this variation in dispersal ability correlate with ecological, physiological or reproductive traits?
- Q17. What are the main environmental factors affecting dispersal of bryophytes, and how do they vary across habitats and geographical areas?
- Q18. What is the role of biotic and abiotic vectors for bryophyte dispersal at various spatial scales?
- Q19. What are the effective dispersal distances of bryophytes, and how do these vary with their life-history traits, in particular the type of diaspore?

#### Biotic interactions and productivity

- Q20. How do bryophytes contribute to water retention, carbon and nitrogen budgets in ecosystems where their productivity and biomass are most significant?
- Q21. How common are the symbiotic associations with fungi and/or cyanobacteria, and through what mechanisms do they increase the ecological performance of bryophytes?
- Q22. How large is the contribution of bryophytes as primary producers across ecosystem types?
- Q23. What are the interrelationships between bryophytes and the microbiome, and how do they influence bryophyte community composition and ecosystem function?
- Q24. How do symbioses with fungi affect bryophyte development?
- Q25. What is the contribution of cyanobacteria associated with bryophytes to global fixation of atmospheric nitrogen, and in which ecosystem is this more prominent?

#### Community ecology

- Q26. Which environmental factors determine establishment success in bryophytes, ultimately shaping bryophyte community composition?
- Q27. How does the interaction between macroclimate and microhabitat structure bryophyte community composition?
- Q28. How common and intense are competitive interactions in bryophytes, and to what extent do they influence their coexistence along environmental gradients?

### GT3 – Bryophyte Conservation and Management

#### Global change

- Q29. What is and will be the impact of global climate change on bryophyte species' distribution, abundance, and composition in ecosystems?
- Q30. How will global climate change affect extinction risk (i.e. genetic diversity) of bryophyte species and, consequently, their ability to adapt to changing environmental conditions?
- Q31. What are the key drivers of decline in bryophyte species and intraspecific diversity, at both the global and regional level?
- Q32. What are the highest priority areas (i.e. regions, habitats) for the conservation of bryophytes in the face of land-use change, habitat destruction and climate change?
- Q33. How are biotic interactions between bryophytes and other organisms affected by climate change?

#### Disturbance, management and policies

- Q34. Which geographical areas and ecosystems are in urgent need of bryological exploration before being destroyed by human impact?
- Q35. How do bryophyte diaspore banks contribute to the long-term persistence of species, the preservation of genetic variation, and the restoration of habitats?
- Q36. How should bryological information be communicated to government, policy makers and managers to influence most effectively policies and decision-making?
- Q37. How effective are existing nature conservation reserves and networks for the conservation of bryophytes?
- Q38. Which ecosystems, ecosystem functions and services are most sensitive to changes in bryophyte composition?

## Appendix (continued)

- Q39. How could bryophyte conservation be better integrated into modern forestry to improve significantly the bryophyte diversity levels in managed forests?
- Q40. What are the best protocols for cultivation, reinforcement and reintroduction (ex situ conservation) of threatened bryophyte species into their original habitats?

### Rarity, threat and red Lists

- Q41. Where are the global hotspots of rare or threatened bryophyte species, and how do these relate to hotspots of species and intraspecific diversity?
- Q42. Which regions and habitats are most in need of increasing assessment efforts in red listing of bryophytes?

## GT4 – Bryophyte Evolution and Systematics

### Speciation, diversification and extinction

- Q43. What is the current extinction rate in bryophytes, and what are the most appropriate data to estimate this?
- Q44. How does variation in bryophyte diversity throughout time correlate with past global climate changes, with emphasis on the most recent epochs (i.e. Pleistocene and Holocene)?
- Q45. What is the relative importance of geographical (e.g. geographical isolation) and ecological speciation (e.g. adaptive radiation) in bryophytes?
- Q46. What is the early branching pattern that explains the evolution of the relationships among the three main bryophyte lineages?
- Q47. What life-history traits can be associated with high diversification rates in bryophytes?
- Q48. Which factors enable bryophytes to survive as predominantly haploid, and if there are different mechanisms of DNA repair, what is the template?

### Species concepts and taxonomy

- Q49. How should we rationalise the dilemma between classic morphometric taxonomy and molecular based rearrangements of taxonomic order in the case of bryophytes?
- Q50. Which species concepts are most adequate for assessing bryophyte diversity?