Naturalis Repository

Unveiling the nature of a miniature world: a horizon scan of fundamentalquestions in bryology

Jairo Patiño, Irene Bisang, Bernard Goffinet, Lars Hedenäs, Stuart McDaniel, Silvia Pressel, Michael Stech [et al.]

DOI:
https://doi-org.naturalis.idm.oclc.org/10.1080/03736687.2022.2054615

Downloaded from
Naturalis Repository

Article 25fa Dutch Copyright Act (DCA) - End User Rights

This publication is distributed under the terms of Article 25fa of the Dutch Copyright Act (Auteurswet) with consent from the author. Dutch law entitles the maker of a short scientific work funded either wholly or partially by Dutch public funds to make that work publicly available following a reasonable period after the work was first published, provided that reference is made to the source of the first publication of the work.

This publication is distributed under the Naturalis Biodiversity Center 'Taverne implementation' programme. In this programme, research output of Naturalis researchers and collection managers that complies with the legal requirements of Article 25fa of the Dutch Copyright Act is distributed online and free of barriers in the Naturalis institutional repository. Research output is distributed six months after its first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and copyrights owner(s) of this work. Any use of the publication other than authorized under this license or copyright law is prohibited.

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the department of Collection Information know, stating your reasons. In case of a legitimate complaint, Collection Information will make the material inaccessible. Please contact us through email: collectie.informatie@naturalis.nl. We will contact you as soon as possible.

JOURNAL OF BRYOLOGY
2022, VOL. 44, NO. 1, 1–34
https://doi.org/10.1080/03736687.2022.2054615

Taylor & Francis
Taylor & Francis Group

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

Jairo Patiño [a,b], Irene Bisang [c], Bernard Goffinet [d], Lars Hedenäs [c], Stuart McDaniel [e], Silvia Pressel [f], Michael Stech [g,h], Claudine Ah-Peng[i], Ariel Bergamini [j], Richard T. Caners [k], D. Christine Cargill [l], Nils Cronberg [m], Jeffrey Duckett [f], Sarah Eppley [n], Nicole J. Fenton [o], Kirsten Fisher [p], Juana González-Mancebo[b], Mitsuyasu Hasebe [q], Jochen Heinrichs†, Kristoffer Hylander [r], Michael S. Ignatov [s,t], Javier Martínez-Abaigar [u], Nagore G. Medina [v,w], Rafael Medina [x], Dietmar Quandt[y], Stefan A. Rensing [z], Karen Renzaglia[aa], Matthew Renner[ab], Rosa M. Ros [ac], Alfons Schäfer-Verwimp [ad], Juan Carlos Villarreal [ae] and Alain Vanderpoorten [af]

[a]Island Ecology and Evolution Research Group, Instituto de Productos Naturales y Agrobiología–Consejo Superior de Investigaciones Científicas (IPNA-CSIC), Tenerife, Canary Islands, Spain; [b]Department of Botany, Ecology and Plant Physiology, University of La Laguna, Tenerife, Canary Islands, Spain; [c]Department of Botany, Swedish Museum of Natural History, Stockholm, Sweden; [d]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, USA; [e]Department of Biology, University of Florida, Gainesville, Florida, USA; [f]Life Sciences Department, The Natural History Museum, London, UK; [g]Naturalis Biodiversity Center, RA Leiden, The Netherlands; [h]Leiden University, Leiden, The Netherlands; [i]UMR PVBMT, Université de La Réunion, Saint-Pierre, France; [j]WSL Swiss Federal Research Institute, Birmensdorf, Switzerland; [k]Royal Alberta Museum, Edmonton, Alberta, Canada; [l]Australian National Herbarium, Centre for Australian National Biodiversity Research, Canberra, Australia; [m]Department of Biology, Lund University, Ecology Building, Naturvetarvägen, Lund, Sweden; [n]Center for Life in Extreme Environments, Portland State University, Portland, Oregon, USA; [o]Forest Research Institute, Université du Québec en Abitibi-Témiscamingue, Québec, Canada; [p]Biological Sciences, California State University, Los Angeles, California, USA; [q]National Institute for Basic Biology, Okazaki, Japan; [r]Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, Sweden; [s]Tsitsin Main Botanical Garden of Russian Academy of Sciences, Moscow, Russia; [t]Faculty of Biology, Lomonosov Moscow State University, Moscow, Russia; [u]Faculty of Science and Technology, University of La Rioja, Logroño, La Rioja, Spain; [v]Departamento de Biología (Botánica), Facultad de Ciencias, Universidad Autónoma de Madrid, Madrid, Spain; [w]Centro de Investigación en Biodiversidad y Cambio Global, Madrid, Spain; [x]Department of Biodiversity, Ecology, and Evolution, Complutense University of Madrid, Madrid, Spain; [y]Nees-Institut für Biodiversität der Pflanzen, Rheinische, Friedrich-Wilhelms-Universität, Bonn, Germany; [z]University of Freiburg, Freiburg, Germany; [aa]Department of Plant Biology, Southern Illinois University Carbondale, Illinois, USA; [ab]Royal Botanic Garden and Domain Trust, Mrs Macquaries Road, Sydney, Australia; [ac]Department of Plant Biology (Botany), University of Murcia, Murcia, Spain; [ad]Mittlere Letten 11, Herdwangen-Schoenach, Germany; [ae]Département de Biologie, Pavillon C.-E. Marchand Université Laval, Québec (Québec), Canada; [af]Institute of Botany, University of Liege, Liège, Belgium

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.

ARTICLE HISTORY
First Published Online 28 April 2022

KEYWORDS
Biogeography; bryophytes; conservation; dispersal; diversity; ecology; evolution; physiology; reproduction; systematics; taxonomy

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

---

CONTACT Jairo Patiño ✉ jpatino@ipna.csic.es

† Deceased.

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

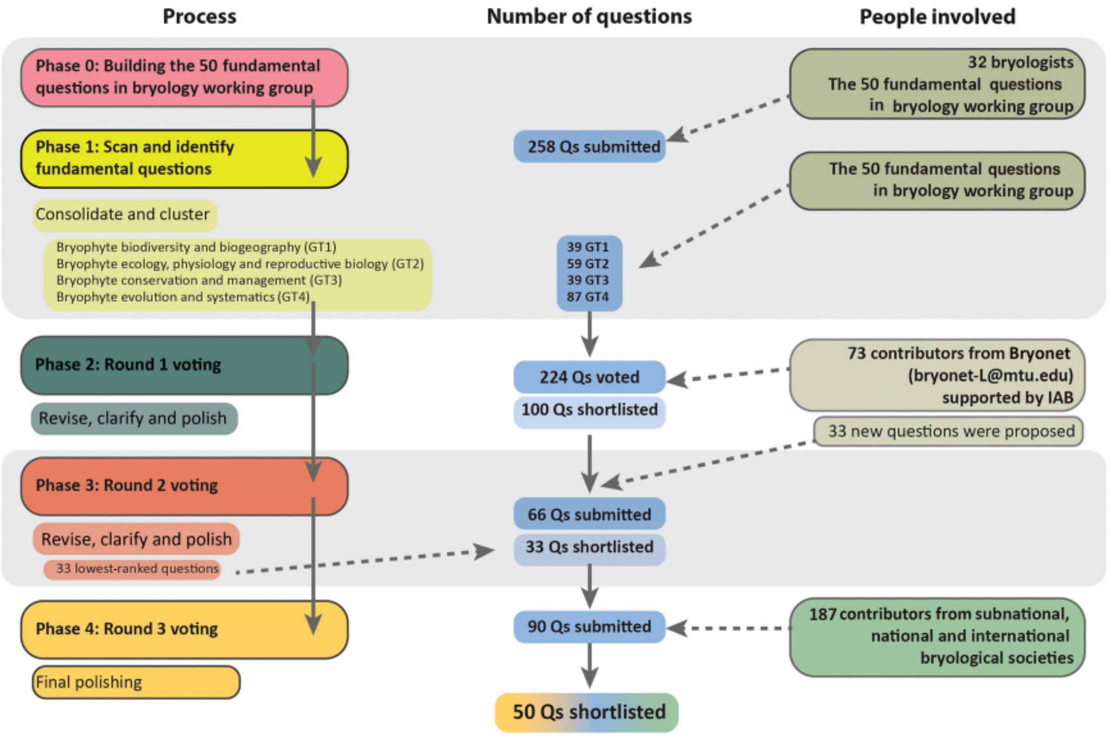

Figure 1. The procedure used to identify the 50 fundamental questions in bryology. The actions performed by the 32 bryologists of the '50 fundamental questions in bryology' working group are highlighted in grey.

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 (± SD) of 169.5 (± 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; Korpelainen 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_2 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_2 fixation, because they are frequently observed on bryophytes collected in many habitats and regions (L. Hedenäs, unpublished data). Transfer of cyanobacteria-fixed N_2 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_2 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_2 concentrations on bryophyte productivity, N_2 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 (Turetsky 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_2-fixing microbes, including non-photosynthetic bacteria (Holland-Moritz et al. 2021 and references therein). Methanotrophic bacteria are important N_2-fixing members of the *Sphagnum* microbiome (Larmola et al. 2014), contributing up to 20% of the CO_2 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; Tiselius 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 (Wisz 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 infraspecific 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

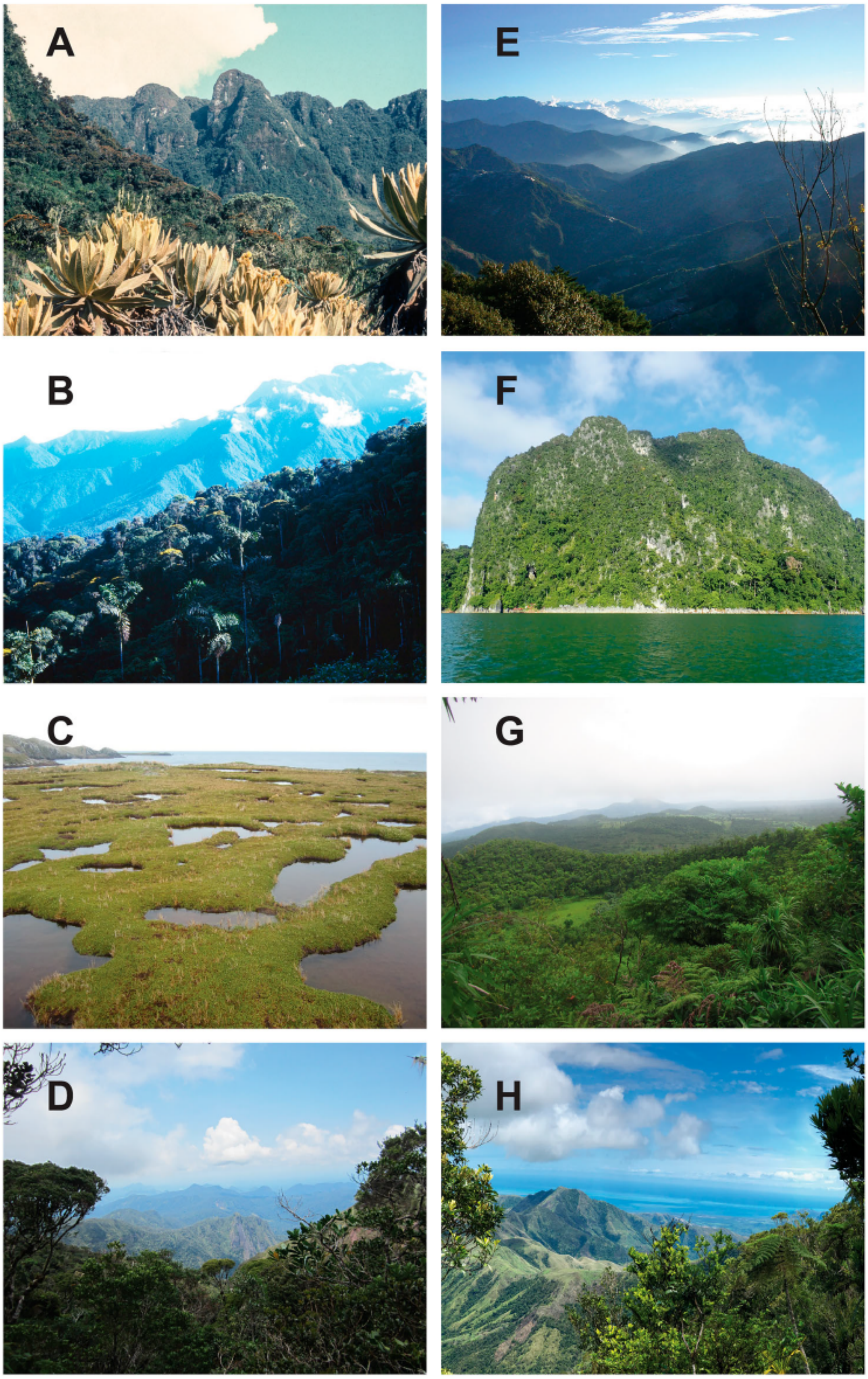

Figure 2. Eight geographical regions considered hotspots of biodiversity and unexplored bryologically. (A) Tatama Massif in the Western Cordillera, Colombia. (B) Chocó in the Western Cordillera, Colombia. (C) Freshwater ponds in the Cape Horn, Chile. (D) Marojejy National Park, Madagascar. (E) Central 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; Bernhardt-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 *Arabidopsis 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 *Aphoanorrhegma 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 *Aphoanorrhegma 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; Myszczyński 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

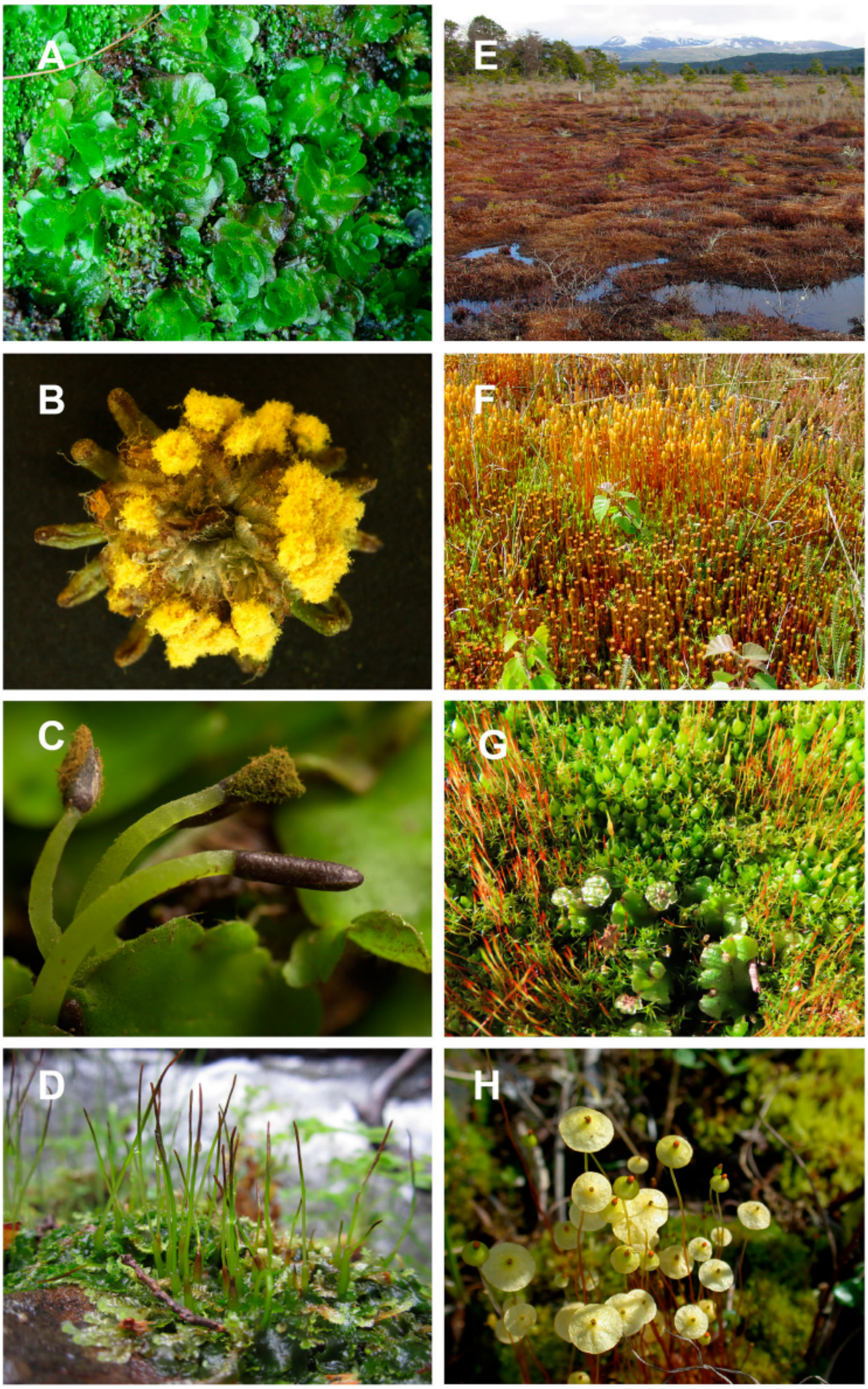

Figure 3. Bryophyte species illustrating the broad diversity of bryophytes and their potential use for education and outreach through citizen science. (A) The base of the liverwort tree: *Treubia lacunosa* (Colenso) Prosk. (B) Dehisced sporophytes in the model liverwort *Marchantia polymorpha* subsp. *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 and Silvia Pressel (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.

Acknowledgements

The '50 fundamental questions in bryology' working group is grateful to all persons who contributed their time to participate in the different rounds of voting and the proposal of questions that ultimately made this paper possible. We also thank S. Robbert Gradstein, Guido van Reenen, Jan-Peter Frahm, Gaik Ee Lee and Mereia Tabua for allowing us to reproduce his photographs. We finally thank Neil Bell and two anonymous reviewers for their constructive comments on an earlier version of the manuscript.

Disclosure statement

No potential conflicts of interest were reported by the authors.

Funding

J. Patiño was funded by the Spanish Ministerio de Ciencia e Innovación (MICINN) through the Ramón y Cajal Program (RYC-2016-20506) and supported by the Fundación BBVA project (PR19_ECO_0046) and the MICINN project (PID2019-110538GA-I00). S. McDaniel was supported by grants from the NSF (DEB 1542609, 1541005, 1541506). J. Martínez-Abaigar was supported by the grant PGC2018-093824-B-C42, funded by MCIN/AEI/10.13039/501100011033 and by the European Regional Development Fund. B. Goffinet was supported by NSF grant DEB-1753811.

ORCID

Jairo Patiño http://orcid.org/0000-0001-5532-166X
Irene Bisang http://orcid.org/0000-0002-0403-6196
Bernard Goffinet http://orcid.org/0000-0002-2754-3895
Lars Hedenäs http://orcid.org/0000-0003-1763-1696
Stuart McDaniel http://orcid.org/0000-0002-5435-7377
Silvia Pressel http://orcid.org/0000-0001-9652-6338
Michael Stech http://orcid.org/0000-0001-9804-0120
Ariel Bergamini https://orcid.org/0000-0001-8816-1420
Richard T. Caners http://orcid.org/0000-0002-7504-2462
D. Christine Cargill http://orcid.org/0000-0001-8390-3245
Nils Cronberg http://orcid.org/0000-0002-3369-8420
Jeffrey Duckett http://orcid.org/0000-0001-7101-6673
Sarah Eppley http://orcid.org/0000-0002-2094-9454
Nicole J. Fenton http://orcid.org/0000-0002-3782-2361
Kirsten Fisher http://orcid.org/0000-0001-6505-1309
Mitsuyasu Hasebe http://orcid.org/0000-0001-7425-8758
Kristoffer Hylander http://orcid.org/0000-0002-1215-2648
Michael S. Ignatov http://orcid.org/0000-0001-6096-6315
Javier Martínez-Abaigar http://orcid.org/0000-0002-9762-9862
Nagore G. Medina http://orcid.org/0000-0003-4702-1610
Rafael Medina http://orcid.org/0000-0001-5629-1503
Stefan A. Rensing http://orcid.org/0000-0002-0225-873X
Rosa M. Ros http://orcid.org/0000-0003-2115-2911
Alfons Schäfer-Verwimp http://orcid.org/0000-0002-2720-6055
Juan Carlos Villarreal http://orcid.org/0000-0002-0770-1446
Alain Vanderpoorten http://orcid.org/0000-0002-5918-7709

References

Adams DG, Duggan PS. 2008. Cyanobacteria–bryophyte symbioses. Journal of Experimental Botany. 59(5):1047–1058. https://doi.org/10.1093/jxb/ern005.

Ah-Peng C, Cardoso AW, Flores O, West A, Wilding N, Strasberg D, Hedderson TAJ. 2017. The role of epiphytic bryophytes in interception, storage, and the regulated release of atmospheric moisture in a tropical montane cloud forest. Journal of Hydrology. 548:665–673. https://doi.org/10.1016/j.jhydrol.2017.03.043.

Ah-Peng C, Flores O, Wilding N, Bardat J, Marline L, Hedderson TAJ, Strasberg D. 2014. Functional diversity of subalpine bryophyte communities in an oceanic island (La Réunion). Arctic, Antarctic, and Alpine Research. 46(4):841–851. https://doi.org/10.1657/1938-4246-46.4.841.

Bączkiewicz A, Szczecińska M, Sawicki J, Stebel A, Buczkowska K. 2017. DNA barcoding, ecology and geography of the cryptic species of *Aneura pinguis* and their relationships with *Aneura maxima* and *Aneura mirabilis* (Metzgeriales, Marchantiophyta). PLoS One. 12(12): e0188837. https://doi.org/10.1371/journal.pone.0188837.

Bannar-Martin KH, Kremer CT, Ernest SKM, Leibold MA, Auge H, Chase J, Declerck SAJ, Eisenhauer N, Harpole S, Hillebrand H, et al. 2018. Integrating community assembly and biodiversity to better understand ecosystem function: the Community Assembly and the Functioning of Ecosystems (I) approach. Ecology Letters. 21(2):167–180. https://doi.org/10.1111/ele.12895.

Barbé M, Chavel ÉE, Fenton NJ, Imbeau L, Mazerolle MJ, Drapeau P, Bergeron Y. 2016a. Dispersal of bryophytes and ferns is facilitated by small mammals in the boreal forest. Ecoscience. 23(3–4):67–76. https://doi.org/10.1080/11956860.2016.1235917.

Barbé M, Fenton NJ, Bergeron Y. 2016b. So close and yet so far away: long-distance dispersal events govern bryophyte metacommunity reassembly. Journal of Ecology. 104 (6):1707–1719. https://doi.org/10.1111/1365-2745.12637.

Barbé M, Fenton NJ, Caners R, Bergeron Y. 2017. Interannual variation in bryophyte dispersal: linking bryophyte phenophases and weather conditions. Botany. 95(12):1151–1169. https://doi.org/10.1139/cjb-2017-0054.

Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, Marshall C, McGuire JL, Lindsey EL, Maguire KC, et al. 2011. Has the Earth's sixth mass extinction already arrived? Nature. 471:51–57. https://doi.org/10.1038/nature09678.

Bay G, Nahar N, Oubre M, Whitehouse MJ, Wardle DA, Zackrisson O, Nilsson M-C, Rasmussen U. 2013. Boreal feather mosses secrete chemical signals to gain nitrogen. New Phytologist. 200(1):54–60. https://doi.org/10.1111/nph.12403.

Bebber DP, Carine MA, Wood JRI, Wortley AH, Harris DJ, Prance GT, Davidse G, Paige J, Pennington TD, Robson NKB, et al. 2010. Herbaria are a major frontier for species discovery. Proceedings of the National Academy of Sciences of the United States of America. 107(51):22169. https://doi.org/10.1073/pnas.1011841108.

Bechteler J, Schäfer-Verwimp A, Lee GE, Feldberg K, Pérez-Escobar OA, Pócs T, Peralta DF, Renner MAM, Heinrichs J. 2017. Geographical structure, narrow species ranges, and Cenozoic diversification in a pantropical clade of epiphyllous leafy liverworts. Ecology and Evolution. 7(2):638–653. https://doi.org/10.1002/ece3.2656.

Beike AK, von Stackelberg M, Schallenberg-Rüdinger M, Hanke ST, Follo M, Quandt D, McDaniel SF, Reski R, Tan BC, Rensing SA. 2014. Molecular evidence for convergent evolution and allopolyploid speciation within the *Physcomitrium–Physcomitrella* species complex. BMC Evolutionary Biology. 14(1):158. https://doi.org/10.1186/1471-2148-14-158.

Bengtsson F, Granath G, Rydin H. 2016. Photosynthesis, growth, and decay traits in *Sphagnum* – a multispecies comparison. Ecology and Evolution. 6(10):3325–3341. https://doi.org/10.1002/ece3.2119.

Bengtsson F, Rydin H, Baltzer JL, Bragazza L, Bu Z-J, Caporn SJM, Dorrepaal E, Flatberg KI, Galanina O, Gałka M, et al. 2021. Environmental drivers of *Sphagnum* growth in peatlands across the Holarctic region. Journal of Ecology. 109(1):417–431. https://doi.org/10.1111/1365-2745.13499.

Berdugo MB, Dovciak M. 2019. Bryophytes in fir waves: forest canopy indicator species and functional diversity decline in canopy gaps. Journal of Vegetation Science. 30 (2):235–246. https://doi.org/10.1111/jvs.12718.

Berg A, Danielsson Å, Svensson BH. 2013. Transfer of fixed-N from N_2-fixing cyanobacteria associated with the moss *Sphagnum riparium* results in enhanced growth of the moss. Plant and Soil. 362(1):271–278. https://doi.org/10.1007/s11104-012-1278-4.

Bergamini A, Bisang I, Hodgetts N, Lockhart N, van Rooy J, Hallingbäck T. 2019. Recommendations for the use of critical terms when applying IUCN red-listing criteria to bryophytes. Lindbergia. 2019(1):1–6. https://doi.org/10.25227/linbg.01117.

Bergamini A, Ungricht S, Hofmann H. 2009. An elevational shift of cryophilous bryophytes in the last century – an effect of climate warming? Diversity and Distributions. 15(5):871–879. https://doi.org/10.1111/j.1472-4642.2009.00595.x.

Bernhardt-Römermann M, Poschlod P, Hentschel J. 2018. BryForTrait – a life-history trait database of forest bryophytes. Journal of Vegetation Science. 29(4):798–800. https://doi.org/10.1111/jvs.12646.

Bisang I, Bergamini A, Lienhard L. 2009. Environmental-friendly farming in Switzerland is not hornwort-friendly. Biological Conservation. 142(10):2104–2113. https://doi.org/10.1016/j.biocon.2009.04.006.

Bisang I, Ehrlén J. 2002. Reproductive effort and cost of sexual reproduction in female *Dicranum polysetum*. The Bryologist. 105:384–397.

Bisang I, Ehrlén J, Persson C, Hedenäs L. 2014. Family affiliation, sex ratio and sporophyte frequency in unisexual mosses. Botanical Journal of the Linnean Society. 174(2):163–172. https://doi.org/10.1111/boj.12135.

Bisang I, Lienhard L, Bergamini A. 2021. Three decades of field surveys reveal a decline of arable bryophytes in the Swiss lowlands despite agri-environment schemes. Agriculture, Ecosystems and Environment. 313:107325. https://doi.org/10.1016/j.agee.2021.107325.

Blanchet FG, Cazelles K, Gravel D. 2020. Co-occurrence is not evidence of ecological interactions. Ecology Letters. 23(7):1050–1063. https://doi.org/10.1111/ele.13525.

Boch S, Berlinger M, Fischer M, Knop E, Nentwig W, Türke M, Prati D. 2013. Fern and bryophyte endozoochory by slugs. Oecologia. 172(3):817–822. https://doi.org/10.1007/s00442-012-2536-0.

Boch S, Fischer M, Knop E, Allan E. 2015. Endozoochory by slugs can increase bryophyte establishment and species richness. Oikos. 124(3):331–336. https://doi.org/10.1111/oik.01536.

Boch S, Martins A, Ruas S, Fontinha S, Carvalho P, Reis F, Bergamini A, Sim-Sim M. 2019. Bryophyte and macrolichen diversity show contrasting elevation relationships and are negatively affected by disturbances in laurel forests of Madeira Island. Journal of Vegetation Science. 30(6):1122–1133. https://doi.org/10.1111/jvs.12802.

Bonfim Santos M, Fedosov V, Hartman T, Fedorova A, Siebel H, Stech M. 2021. Phylogenetic inferences reveal deep polyphyly of Aongstroemiaceae and Dicranellaceae within the haplolepideous mosses (Dicranidae, Bryophyta). Taxon. 70(2):246–262. https://doi.org/10.1002/tax.12439.

Borges PAV, Cardoso P, Kreft H, Whittaker RJ, Fattorini S, Emerson BC, Gil A, Gillespie RG, Matthews TJ, Santos AMC, et al. 2018. Global Island Monitoring Scheme (GIMS): a proposal for the long-term coordinated survey and monitoring of native island forest biota. Biodiversity and Conservation. 27:2567–2586. https://doi.org/10.1007/s10531-018-1553-7.

Bowles AMC, Bechtold U, Paps J. 2020. The origin of land plants is rooted in two bursts of genomic novelty. Current Biology. 30(3):530–536. https://doi.org/10.1016/j.cub.2019.11.090.

Bowman JL, Kohchi T, Yamato KT, Jenkins J, Shu S, Ishizaki K, Yamaoka S, Nishihama R, Nakamura Y, Berger F, et al. 2017. Insights into land plant evolution garnered from the *Marchantia polymorpha* genome. Cell. 171(2):287–304. https://doi.org/10.1016/j.cell.2017.09.030.

Bragina A, Berg C, Cardinale M, Shcherbakov A, Chebotar V, Berg G. 2012. *Sphagnum* mosses harbour highly specific bacterial diversity during their whole lifecycle. The International Society for Microbial Ecology Journal. 6(4):802–813. https://doi.org/10.1038/ismej.2011.151.

Bragina A, Oberauner-Wappis L, Zachow C, Halwachs B, Thallinger GG, Müller H, Berg G. 2014. The *Sphagnum* microbiome supports bog ecosystem functioning under extreme conditions. Molecular Ecology. 23(18):4498–4510. https://doi.org/10.1111/mec.12885.

Brodribb TJ, Carriquí M, Delzon S, McAdam SAM, Holbrook NM. 2020. Advanced vascular function discovered in a widespread moss. Nature Plants. 6(3):273–279. https://doi.org/10.1038/s41477-020-0602-x.

Bu Z-J, Sundberg S, Feng L, Li H-K, Zhao H-Y, Li H-C. 2017. The Methuselah of plant diaspores: *Sphagnum* spores can survive in nature for centuries. New Phytologist. 214(4):1398–1402. https://doi.org/10.1111/nph.14575.

Bu Z-J, Zheng X-X, Rydin H, Moore T, Ma J. 2013. Facilitation vs. competition: does interspecific interaction affect drought responses in *Sphagnum*? Basic and Applied Ecology. 14(7):574–584. https://doi.org/10.1016/j.baae.2013.08.002.

Buchbender V, Hespanhol H, Krug M, Sérgio C, Séneca A, Maul K, Hedenäs L, Quandt D. 2014. Phylogenetic reconstructions of the Hedwigiaceae reveal cryptic speciation and hybridisation in *Hedwigia*. Bryophyte Diversity and Evolution. 36(1):1–21.

Budke JM, Bernard EC, Gray DJ, Huttunen S, Piechulla B, Trigiano RN. 2018. Introduction to the special issue on bryophytes. Critical Reviews in Plant Sciences. 37(2–3):102–112. https://doi.org/10.1080/07352689.2018.1482396.

Budke JM, Goffinet B, Jones CS. 2013. Dehydration protection provided by a maternal cuticle improves offspring fitness in the moss *Funaria hygrometrica*. Annals of Botany. 111(5):781–789. https://doi.org/10.1093/aob/mct033.

Buzorius G, Rannik Ü, Nilsson D, Kulmala M. 2001. Vertical fluxes and micrometeorology during aerosol particle formation events. Tellus B: Chemical and Physical Meteorology. 53(4):394–405. https://doi.org/10.3402/tellusb.v53i4.16612.

Calleja JA, Vigalondo B, Mazimpaka V, Draper I, Garilleti R, Lara F. 2020. Earliest herbarium evidence for the occurrence of *Lewinskya acuminata* (Orthotrichaceae) in East Africa. Journal of Bryology. 42(2):186–188. https://doi.org/10.1080/03736687.2019.1655871.

Câmara PEAS, Carvalho-Silva M, Stech M. 2021. Antarctic bryophyte research – current state and future directions. Bryophyte Diversity and Evolution. 43:221–233.

Caners RT, Ellen Macdonald S, Belland RJ. 2009. Recolonization potential of bryophyte diaspore banks in harvested boreal mixed-wood forest. Plant Ecology. 204(1):55–68. https://doi.org/10.1007/s11258-008-9565-0.

Cannone N, Corinti T, Malfasi F, Gerola P, Vianelli A, Vanetti I, Zaccara S, Convey P, Guglielmin M. 2017. Moss survival through in situ cryptobiosis after six centuries of glacier burial. Scientific Reports. 7(1):4438. https://doi.org/10.1038/s41598-017-04848-6.

Carey SB, Jenkins J, Lovell JT, Maumus F, Sreedasyam A, Payton AC, Shu S, Tiley GP, Fernandez-Pozo N, Healey A, et al. 2021. Gene-rich UV sex chromosomes harbor conserved regulators of sexual development. Science Advances. 7(27):eabh2488. https://doi.org/10.1126/sciadv.abh2488.

Carrell AA, Lawrence TJ, Cabugao KGM, Carper DL, Pelletier DA, Jawdy S, Grimwood J, Schmutz J, Hanson PJ, Shaw AJ, et al. 2020. *Sphagnum* peat moss thermotolerance is modulated by the microbiome. bioRxiv 2020.2008.2021.259184. https://doi.org/10.1101/2020.08.21.259184.

Carwardine J, Martin TG, Firn J, Reyes RP, Nicol S, Reeson A, Grantham HS, Stratford D, Kehoe L, Chadès I. 2019. Priority threat management for biodiversity conservation: a handbook. Journal of Applied Ecology. 56(2):481–490. https://doi.org/10.1111/1365-2664.13268.

Ceballos G, Ehrlich PR, Dirzo R. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences of the United States of America. 114(30):E6089. https://doi.org/10.1073/pnas.1704949114.

Chmielewski MW, Eppley SM. 2019. Forest passerines as a novel dispersal vector of viable bryophyte propagules. Proceedings of the Royal Society B: Biological Sciences. 286(1897):20182253. https://doi.org/10.1098/rspb.2018.2253.

Collart F, Hedenäs L, Broennimann O, Guisan A, Vanderpoorten A. 2021a. Intraspecific differentiation: implications for niche and distribution modelling. Journal of Biogeography. 48(2):415–426. https://doi.org/10.1111/jbi.14009.

Collart F, Wang J, Patiño J, Hagborg A, Söderström L, Goffinet B, Magain N, Hardy OJ, Vanderpoorten A. 2021b. Macroclimatic structuring of spatial phylogenetic turnover in liverworts. Ecography. 44(10):1474–1485. https://doi.org/10.1111/ecog.05659.

Cornelissen JHC, Lang SI, Soudzilovskaia NA, During HJ. 2007. Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. Annals of Botany. 99(5):987–1001. https://doi.org/10.1093/aob/mcm030.

Cornwell WK, Pearse WD, Dalrymple RL, Zanne AE. 2019. What we don't know about global plant diversity. Ecography. 42(11):1819–1831. https://doi.org/10.1111/ecog.04481.

Coudert Y, Bell NE, Edelin C, Harrison CJ. 2017. Multiple innovations underpinned branching form diversification in mosses. New Phytologist. 215(2):840–850. https://doi.org/10.1111/nph.14553.

Coxson DS, McIntyre DD, Vogel HJ. 1992. Pulse release of sugars and polyols from canopy bryophytes in tropical montane rain forest (Guadeloupe, French West Indies). Biotropica. 24(2):121–133. https://doi.org/10.2307/2388665.

Crawford M, Jesson LK, Garnock-Jones PJ. 2009. Correlated evolution of sexual system and life-history traits in mosses. Evolution. 63(5):1129–1142. https://doi.org/10.1111/j.1558-5646.2009.00615.x.

Crespi B, Nosil P. 2013. Conflictual speciation: species formation via genomic conflict. Trends in Ecology and Evolution. 28(1):48–57. https://doi.org/10.1016/j.tree.2012.08.015.

Crisp MD, Arroyo MTK, Cook LG, Gandolfo MA, Jordan GJ, McGlone MS, Weston PH, Westoby M, Wilf P, Linder HP. 2009. Phylogenetic biome conservatism on a global scale? Nature. 458:754–756.

Cronberg N. 2002. Colonization dynamics of the clonal moss *Hylocomium splendens* on islands in a Baltic land uplift area: reproduction, genet distribution and genetic variation. Journal of Ecology. 90:925–935. https://doi.org/10.1046/j.1365-2745.2002.00723.x.

Cronberg N. 2012. Animal-mediated fertilization in bryophytes – parallel or precursor to insect pollination in angiosperms? Lindbergia. 35:76–85.

Cronberg N, Natcheva R, Hedlund K. 2006. Microarthropods mediate sperm transfer in mosses. Science. 313 (5791):1255–1255. https://doi.org/10.1126/science.1128707.

Crum H. 1972. The geographic origins of the mosses of North America's eastern deciduous forest. Journal of the Hattori Botanical Laboratory. 35:269–298.

Cusack DF, Silver W, McDowell WH. 2009. Biological nitrogen fixation in two tropical forests: ecosystem-level patterns and effects of nitrogen fertilization. Ecosystems. 12(8):1299–1315. https://doi.org/10.1007/s10021-009-9290-0.

Davey ML, Currah RS. 2006. Interactions between mosses (Bryophyta) and fungi. Canadian Journal of Botany. 84 (10):1509–1519. https://doi.org/10.1139/b06-120.

Deane-Coe KK. 2015. Cyanobacteria associations in temperate forest bryophytes revealed by $\delta^{15}N$ analysis. The Journal of the Torrey Botanical Society. 143(1):50–57. https://doi.org/10.3159/TORREY-D-15-00013.

de Sousa F, Foster PG, Donoghue PCJ, Schneider H, Cox CJ. 2019. Nuclear protein phylogenies support the monophyly of the three bryophyte groups (Bryophyta Schimp.). New Phytologist. 222(1):565–575. https://doi.org/10.1111/nph.15587.

DeLuca TH, Zackrisson O, Gentili F, Sellstedt A, Nilsson M-C. 2007. Ecosystem controls on nitrogen fixation in boreal feather moss communities. Oecologia. 152(1):121–130. https://doi.org/10.1007/s00442-006-0626-6.

DeLuca TH, Zackrisson O, Gundale MJ, Nilsson M-C. 2008. Ecosystem feedbacks and nitrogen fixation in boreal forests. Science. 320(5880):1181. https://doi.org/10.1126/science.1154836.

DeLuca TH, Zackrisson O, Nilsson M-C, Sellstedt A. 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. Nature. 419(6910):917–920. https://doi.org/10.1038/nature01051.

Désamoré A, Laenen B, Stech M, Papp B, Hedenäs L, Mateo RG, Vanderpoorten A. 2012. How do temperate bryophytes face the challenge of a changing environment? Lessons from the past and predictions for the future. Global Change Biology. 18(9):2915–2924. https://doi.org/10.1111/j.1365-2486.2012.02752.x.

Devos N, Szövényi P, Weston DJ, Rothfels CJ, Johnson MG, Shaw AJ. 2016. Analyses of transcriptome sequences reveal multiple ancient large-scale duplication events in the ancestor of Sphagnopsida (Bryophyta). New Phytologist. 211(1):300–318. https://doi.org/10.1111/nph.13887.

Di Marco M, Ferrier S, Harwood TD, Hoskins AJ, Watson JEM. 2019. Wilderness areas halve the extinction risk of terrestrial biodiversity. Nature. 573(7775):582–585. https://doi.org/10.1038/s41586-019-1567-7.

Dierssen K. 2001. Distribution, ecological amplitude and phytosociological characterization of European bryophytes. Bryophytorum Bibliotheca. 56:1–289. https://doi.org/10.1639/0007-2745(2002)105[0503:]2.0.CO;2.

Donoghue PCJ, Harrison CJ, Paps J, Schneider H. 2021. The evolutionary emergence of land plants. Current Biology. 31(19):R1281–R1298.

Duckett JG, Pressel S. 2019. The epiphyte flora of roadside trees in the London conurbation with a North American perspective on its possible future. Field Bryology. 122:35–51.

During HJ. 2007. Relations between clonal growth, reproduction and breeding system in the bryophytes of Belgium and The Netherlands. Nova Hedwigia. 131:133–145.

Edwards D, Morris JL, Axe L, Duckett JG, Pressel S, Kenrick P. 2022a. Piecing together the eophytes – a new group of ancient plants containing cryptospores. New Phytologist. 233(3):1440–1455. https://doi.org/10.1111/nph.17703.

Edwards D, Morris JL, Axe L, Duckett JG. 2022c. Picking up the pieces: new charcoalified plant mesofossils (eophytes) from a Lower Devonian Lagerstätte in the Welsh Borderland, UK. Review of Palaeobotany and Palynology. 297:104567. https://doi.org/10.1016/j.revpalbo.2021.104567.

Edwards D, Morris JL, Axe L, Taylor WA, Duckett JG, Kenrick P, Pressel S. 2022b. Earliest record of transfer cells in Lower Devonian plants. New Phytologist. 233(3):1456–1465. https://doi.org/10.1111/nph.17704.

Estébanez B, Medina NG, Caparrós R, Monforte L, Del-Castillo-Alonso M-Á, Martínez-Abaigar J, Núñez-Olivera E. 2018. Spores potentially dispersed to longer distances are more tolerant to ultraviolet radiation: a case study in the moss genus *Orthotrichum*. American Journal of Botany. 105(6):996–1008. https://doi.org/10.1002/ajb2.1118.

Fabón G, Monforte L, Tomás R, Núñez-Olivera E, Martínez-Abaigar J. 2011. Ultraviolet radiation-induced DNA damage in bryophytes: what is already known and new results on rapid repair in a liverwort in an artificial diel cycle. Boletín de la Sociedad Española de Briología. 37:39–52.

Fedosov VE, Fedorova AV, Fedosov AE, Ignatov MS. 2016. Phylogenetic inference and peristome evolution in haplolepideous mosses, focusing on Pseudoditrichaceae and Ditrichaceae s. l. Botanical Journal of the Linnean Society. 181(2):139–155. https://doi.org/10.1111/boj.12408.

Feldberg K, Gradstein SR, Gröhn C, Heinrichs J, von Konrat M, Mamontov Y, Renner MAM, Roth M, Schäfer-Verwimp A, Sukkharak P, Schmidt AR. 2021. Checklist of fossil liverworts suitable for calibrating phylogenetic reconstructions. Bryophyte Diversity and Evolution. 36:14–71.

Feldberg K, Heinrichs J, Schmidt AR, Váňa J, Schneider H. 2013. Exploring the impact of fossil constraints on the divergence time estimates of derived liverworts. Plant Systematics and Evolution. 299(3):585–601. https://doi.org/10.1007/s00606-012-0745-y.

Feldberg K, Schneider H, Stadler T, Schäfer-Verwimp A, Schmidt AR, Heinrichs J. 2014. Epiphytic leafy liverworts diversified in angiosperm-dominated forests. Scientific Reports. 4:5974. https://doi.org/10.1038/srep05974.

Fenton N, Hylander K, Pharo E. 2015. Bryophytes in forest ecosystems. In: Peh KS-H, Corlett RT, Bergeron Y, editors. Handbook in forest ecology. London: Routledge; p. 239–249.

Ferreira MT, Cardoso P, Borges PAV, Gabriel R, de Azevedo EB, Reis F, Araújo MB, Elias RB. 2016. Effects of climate change on the distribution of indigenous species in oceanic islands (Azores). Climatic Change. 138(3):603–615. https://doi.org/10.1007/s10584-016-1754-6.

Field KJ, Rimington WR, Bidartondo MI, Allinson KE, Beerling DJ, Cameron DD, Duckett JG, Leake JR, Pressel S. 2015. First evidence of mutualism between ancient plant lineages (Haplomitriopsida liverworts) and Mucoromycotina fungi and its response to simulated Palaeozoic changes in atmospheric CO_2. New Phytologist. 205(2):743–756. https://doi.org/10.1111/nph.13024.

Field KJ, Rimington WR, Bidartondo MI, Allinson KE, Beerling DJ, Cameron DD, Duckett JG, Leake JR, Pressel S. 2016. Functional analysis of liverworts in dual symbiosis with Glomeromycota and Mucoromycotina fungi under a simulated Palaeozoic CO_2 decline. The International Society for Microbial Ecology Journal. 10(6):1514–1526. https://doi.org/10.1038/ismej.2015.204.

Frahm J-P. 1999. A type catalogue of Campylopodioideae and Paraleucobryoideae (Musci, Dicranaceae), Part II, *Campylopus*. Tropical Bryology. 16(1):17–102. https://doi.org/10.11646/bde.16.1.6.

Frangedakis E, Shimamura M, Villarreal JC, Li F-W, Tomaselli M, Waller M, Sakakibara K, Renzaglia KS, Szövényi P. 2021. The hornworts: morphology, evolution and development. New Phytologist. 229(2):735–754. https://doi.org/10.1111/nph.16874.

Fritsch R. 1991. Index to bryophyte chromosome counts. Bryophytorum Bibliotheca. 40:1–352.

Fuselier L, Davison PG, Clements M, Shaw B, Devos N, Heinrichs J, Hentschel J, Sabovljevic M, Szövényi P, Schuette S, et al. 2009. Phylogeographic analyses reveal distinct lineages of the liverworts *Metzgeria furcata* (L.) Dumort. and *Metzgeria conjugata* Lindb. (Metzgeriaceae) in Europe and North America. Biological Journal of the Linnean Society. 98(4):745–756. https://doi.org/10.1111/j.1095-8312.2009.01319.x.

Garbary DJ, Renzaglia KS, Duckett JG. 1993. The phylogeny of land plants: a cladistic analysis based on male gametogenesis. Plant Systematics and Evolution. 188(3):237–269. https://doi.org/10.1007/BF00937730.

Gauthier J, Pajkovic M, Neuenschwander S, Kaila L, Schmid S, Orlando L, Alvarez N. 2020. Museomics identifies genetic erosion in two butterfly species across the 20th century in Finland. Molecular Ecology Resources. 20(5):1191–1205. https://doi.org/10.1111/1755-0998.13167.

Geffert JL, Frahm J-P, Barthlott W, Mutke J. 2013. Global moss diversity: spatial and taxonomic patterns of species richness. Journal of Bryology. 35(1):1–11. https://doi.org/10.1179/1743282012Y.0000000038.

González-Mancebo JM, Dirkse GM, Patiño J, Romaguera F, Werner O, Ros RM, Martín JL. 2012. Applying the IUCN Red List criteria to small-sized plants on oceanic islands: conservation implications for threatened bryophytes in the Canary Islands. Biodiversity and Conservation. 21(14):3613–3636.

Graham CH, Fine PVA. 2008. Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. Ecology Letters. 11(12):1265–1277. https://doi.org/10.1111/j.1461-0248.2008.01256.x.

Gray A. 2019. The ecology of plant extinction: rates, traits and island comparisons. Oryx. 53(3):424–428. https://doi.org/10.1017/S0030605318000315.

Greiser C, Ehrlén J, Meineri E, Hylander K. 2020. Hiding from the climate: characterizing microrefugia for boreal forest understory species. Global Change Biology. 26:471–483. https://doi.org/10.1111/gcb.14874.

Grenyer R, Orme CDL, Jackson SF, Thomas GH, Davies RG, Davies TJ, Jones KE, Olson VA, Ridgely RS, Rasmussen PC, et al. 2006. Global distribution and conservation of rare and threatened vertebrates. Nature. 444(7115):93–96. https://doi.org/10.1038/nature05237.

Gu N, Tamada Y, Imai A, Palfalvi G, Kabeya Y, Shigenobu S, Ishikawa M, Angelis KJ, Chen C, Hasebe M. 2020. DNA damage triggers reprogramming of differentiated cells into stem cells in *Physcomitrella*. Nature Plants. 6(9):1098–1105. https://doi.org/10.1038/s41477-020-0745-9.

Gunnarsson U, Granberg G, Nilsson M. 2004. Growth, production and interspecific competition in *Sphagnum*: effects of temperature, nitrogen and sulphur treatments on a boreal mire. New Phytologist. 163(2):349–359. https://doi.org/10.1111/j.1469-8137.2004.01108.x.

Habel JC, Schmitt T. 2018. Vanishing of the common species: empty habitats and the role of genetic diversity. Biological Conservation. 218:211–216. https://doi.org/10.1016/j.biocon.2017.12.018.

Hájek T. 2020. Interlinking moss functional traits. A commentary on: 'Mechanisms behind species-specific water economy responses to water level drawdown in peat mosses'. Annals of Botany. 126(2):iv–v. https://doi.org/10.1093/aob/mcaa108.

Hallingback T, Tan BC. 2014. Past and present activities and future strategy of bryophyte conservation. Phytotaxa. 9 (1):266–274.

Hanusch M, Ortiz EM, Patiño J, Schaefer H. 2020. Biogeography and integrative taxonomy of *Epipterygium* (Mniaceae, Bryophyta). Taxon. 69(6):1150–1171.

Harris BJ, Harrison CJ, Hetherington AM, Williams TA. 2020. Phylogenomic evidence for the monophyly of bryophytes and the reductive evolution of stomata. Current Biology. 30(11):2001–2012.

Harvey MG, Singhal S, Rabosky DL. 2019. Beyond reproductive isolation: demographic controls on the speciation process. Annual Review of Ecology, Evolution, and Systematics. 50(1):75–95. https://doi.org/10.1146/annurev-ecolsys-110218-024701.

He X, He KS, Hyvönen J. 2016. Will bryophytes survive in a warming world? Perspectives in Plant Ecology, Evolution and Systematics. 19:49–60. https://doi.org/10.1016/j.ppees.2016.02.005.

Hedenäs L. 2001. Environmental factors potentially affecting character states in pleurocarpous mosses. The Bryologist. 104:72–91.

Hedenäs L. 2008. Molecular variation and speciation in *Antitrichia curtipendula* s.l. (Leucodontaceae, Bryophyta). Botanical Journal of the Linnean Society. 156(3):341–354. https://doi.org/10.1111/j.1095-8339.2007.00775.x.

Hedenäs L. 2015. *Rhytidium rugosum* (Bryophyta) colonized Scandinavia from at least two glacial refugial source populations. Botanical Journal of the Linnean Society. 179 (4):635–657. https://doi.org/10.1111/boj.12341.

Hedenäs L. 2019. On the frequency of northern and mountain genetic variants of widespread species: essential biodiversity information in a warmer world. Botanical Journal of the Linnean Society. 191(4):440–474. https://doi.org/10.1093/botlinnean/boz061.

Hedenäs L. 2020. Cryptic speciation revealed in Scandinavian *Racomitrium lanuginosum* (Hedw.) Brid. (Grimmiaceae). Journal of Bryology. 42(2):117–127. https://doi.org/10.1080/03736687.2020.1722923.

Hedenäs L, Bisang I. 2019. Episodic but ample sporophyte production in the moss *Drepanocladus turgescens* (Bryophyta: Amblystegiaceae) in SE Sweden. Acta Musei Silesiae, Scientiae Naturales. 68(1–2):83–93. https://doi.org/10.2478/cszma-2019-0009.

Hedenäs L, Bisang I, Korpelainen H, Cronholm B. 2010. The true sex ratio in European *Pseudocalliergon trifarium* (Bryophyta: Amblystegiaceae) revealed by a novel molecular approach. Biological Journal of the Linnean Society. 100(1):132–140. https://doi.org/10.1111/j.1095-8312.2010.01408.x.

Hedenäs L, Bisang I, Tehler A, Hamnede M, Jaederfelt K, Odelvik G. 2002. A herbarium-based method for estimates of temporal frequency changes: mosses in Sweden. Biological Conservation. 105(3):321–331. https://doi.org/10.1016/S0006-3207(01)00212-9.

Hedenäs L, Eldenäs P. 2007. Cryptic speciation, habitat differentiation, and geography in *Hamatocaulis vernicosus* (Calliergonaceae, Bryophyta). Plant Systematics and Evolution. 268:131. https://doi.org/10.1007/s00606-007-0529-y.

Hedenäs L, Larsson P, Cronholm B, Bisang I. 2021. Evidence of horizontal gene transfer between land plant plastids has surprising conservation implications. Annals of Botany. 127(7):903–908. https://doi.org/10.1093/aob/mcab021.

Heinrichs J, Hentschel J, Bombosch A, Fiebig A, Reise J, Edelmann M, Kreier H-P, Schäfer-Verwimp A, Caspari S, Schmidt AR, et al. 2010. One species or at least eight? Delimitation and distribution of *Frullania tamarisci* (L.) Dumort. s. l. (Jungermanniopsida, Porellales) inferred from nuclear and chloroplast DNA markers. Molecular Phylogenetics and Evolution. 56(3):1105–1114. https://doi.org/10.1016/j.ympev.2010.05.004.

Henriques DSG, Rigal F, Borges PAV, Ah-Peng C, Gabriel R. 2017a. Functional diversity and composition of bryophyte water-related traits in Azorean native vegetation. Plant Ecology and Diversity. 10(2–3):127–137. https://doi.org/10.1080/17550874.2017.1315839.

Henriques DSG, Ah-Peng C, Gabriel R. 2017b. Structure and applications of BRYOTRAIT-AZO, a trait database for Azorean bryophytes. Cryptogamie, Bryologie. 38(2):137–152. https://doi.org/10.7872/cryb/v38.iss2.2017.137.

Hernández-Hernández R, Borges PAV, Gabriel R, Rigal F, Ah-Peng C, González-Mancebo JM. 2017. Scaling α- and β-diversity: bryophytes along an elevational gradient on a subtropical oceanic island (La Palma, Canary Islands). Journal of Vegetation Science. 28(6):1209–1219. https://doi.org/10.1111/jvs.12573.

Hill MO, Preston CD, Bosanquet SDS, Roy DB. 2007. BRYOATT: attributes of British and Irish mosses, liverworts and hornworts. Huntingdon, UK: Centre for Ecology and Hydrology.

HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM. 2012. Rethinking community assembly through the lens of coexistence theory. Annual Review of Ecology, Evolution, and Systematics. 43(1):227–248. https://doi.org/10.1146/annurev-ecolsys-110411-160411.

Hock Z, Szövényi P, Schneller JJ, Urmi E, Tóth Z. 2008. Are sexual or asexual events determining the genetic structure of populations in the liverwort *Mannia fragrans*? Journal of Bryology. 30(1):66–73. https://doi.org/10.1179/174328208X282120.

Hodgetts N, Cálix M, Englefield E, Fettes N, García Criado M, Patin L, Nieto A, Bergamini A, Bisang I, Baisheva E, et al. 2019. A miniature world in decline: European Red List of mosses, liverworts and hornworts. Brussels: International Union for Conservation of Nature.

Hofmann H, Urmi E, Bisang I, Müller N, Küchler M, Schnyder N, Schubiger C. 2007. Retrospective assessment of frequency changes in Swiss bryophytes over the last two centuries. Lindbergia. 32(1):18–32.

Holland-Moritz H, Stuart J, Lewis LR, Miller S, Mack MC, McDaniel SF, Fierer N. 2018. Novel bacterial lineages associated with boreal moss species. Environmental Microbiology. 20(7):2625–2638. https://doi.org/10.1111/1462-2920.14288.

Holland-Moritz H, Stuart JEM, Lewis LR, Miller SN, Mack MC, Ponciano JM, McDaniel SF, Fierer N. 2021. The bacterial communities of Alaskan mosses and their contributions to N_2-fixation. Microbiome. 9(1):53. https://doi.org/10.1186/s40168-021-01001-4.

Horwath AB, Royles J, Tito R, Gudiño JA, Salazar Allen N, Farfan-Rios W, Rapp JM, Silman MR, Malhi Y, Swamy V, et al. 2019. Bryophyte stable isotope composition, diversity and biomass define tropical montane cloud forest extent. Proceedings of the Royal Society B: Biological Sciences. 286(1895):20182284. https://doi.org/10.1098/rspb.2018.2284.

Humphreys CP, Franks PJ, Rees M, Bidartondo MI, Leake JR, Beerling DJ. 2010. Mutualistic mycorrhiza-like symbiosis in the most ancient group of land plants. Nature Communications. 1(1):103. https://doi.org/10.1038/ncomms1105.

Hylander K, Weibull, H. 2012. Do time-lagged extinctions and colonizations change the interpretation of buffer strip effectiveness? – a study of riparian bryophytes in the first decade after logging. Journal of Applied Ecology. 49 (6):1316–1324. https://doi.org/10.1111/j.1365-2664.2012.02218.x.

Ignatov MS, Maslova EV. 2021. Fossil mosses: what do they tell us about moss evolution? Bryophyte Diversity and Evolution. 36:72–97.

Ingerpuu N, Kupper T, Vellak K, Kupper P, Sõber J, Tullus A, Zobel M, Liira J. 2019. Response of bryophytes to afforestation, increase of air humidity, and enrichment of soil diaspore bank. Forest Ecology and Management. 432:64–72. https://doi.org/10.1016/j.foreco.2018.09.004.

Ingerpuu N, Vellak K. 2017. Methods for monitoring threatened bryophytes. Biodiversity and Conservation. 26(14):3275–3287. https://doi.org/10.1007/s10531-017-1405-x.

Ingerpuu N, Vellak K, Ehrlich L. 2018. Revised Red Data List of Estonian bryophytes. Folia Cryptogamica Estonica. 55 (0):97–104. https://doi.org/10.12697/fce.2018.55.10.

Ingimundardóttir GV, Weibull H, Cronberg N. 2014. Bryophyte colonization history of the virgin volcanic island Surtsey, Iceland. Biogeosciences. 11(16):4415–4427. https://doi.org/10.5194/bg-11-4415-2014.

Ininbergs K, Bay G, Rasmussen U, Wardle DA, Nilsson M-C. 2011. Composition and diversity of *nifH* genes of nitrogen-fixing cyanobacteria associated with boreal forest feather mosses. New Phytologist. 192(2):507–517. https://doi.org/10.1111/j.1469-8137.2011.03809.x.

Ishikawa M, Hasebe M. 2015. Cell cycle reentry from the late S phase: implications from stem cell formation in the moss *Physcomitrella patens*. Journal of Plant Research. 128(3):399–405. https://doi.org/10.1007/s10265-015-0713-z.

Iskandar EAP, Stech M, Mota de Oliveira S. 2020. The two faces of Mt Gede, Java – species richness, composition and zonation of epiphytic bryophytes. Cryptogamie, Bryologie. 41(6):69–81. https://doi.org/10.5252/cryptogamiebryologie2020v41a6.

Kamisugi Y, Whitaker JW, Cuming AC. 2016. The transcriptional response to DNA-double-strand breaks in *Physcomitrella patens*. PLoS One. 11(8):e0161204. https://doi.org/10.1371/journal.pone.0161204.

Renzaglia KS, Schuette S, Duff RJ, Ligrone R, Shaw AJ, Mishler BD, Duckett JG. 2007. Bryophyte phylogeny: advancing the molecular and morphological frontiers. The Bryologist. 110(2):179–213. https://doi.org/10.1639/0007-2745(2007)110[179:BPATMA]2.0.CO;2

Karger DN, Kessler M, Lehnert M, Jetz W. 2021. Limited protection and ongoing loss of tropical cloud forest biodiversity and ecosystems worldwide. Nature Ecology and Evolution. 5(6):854–862. https://doi.org/10.1038/s41559-021-01450-y.

Kier G, Kreft H, Lee TM, Jetz W, Ibisch PL, Nowicki C, Mutke J, Barthlott W. 2009. A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences of the United States of America. 106(23):9322–9327. https://doi.org/10.1073/pnas.0810306106.

Kimmerer RW. 1991. Reproductive ecology of *Tetraphis pellucida*. I. Population density and reproductive mode. The Bryologist. 94(3):255–260. https://doi.org/10.2307/3243962.

Kobayashi Y, Odahara M, Sekine Y, Hamaji T, Fujiwara S, Nishimura Y, Miyagishima S-y. 2020. Holliday junction resolvase MOC1 maintains plastid and mitochondrial genome integrity in algae and bryophytes. Plant Physiology. 184(4):1870. https://doi.org/10.1104/pp.20.00763.

König C, Wüest RO, Graham CH, Karger DN, Sattler T, Zimmermann NE, Zurell D. 2021. Scale dependency of joint species distribution models challenges interpretation of biotic interactions. Journal of Biogeography. 48 (7):1541–1551. https://doi.org/10.1111/jbi.14106.

Korpelainen H, von Cräutlein M, Kostamo K, Virtanen V. 2013. Spatial genetic structure of aquatic bryophytes in a connected lake system. Plant Biology. 15(3):514–521. https://doi.org/10.1111/j.1438-8677.2012.00660.x.

Kostka JE, Weston DJ, Glass JB, Lilleskov EA, Shaw AJ, Turetsky MR. 2016. The *Sphagnum* microbiome: new insights from an ancient plant lineage. New Phytologist. 211(1):57–64. https://doi.org/10.1111/nph.13993.

Kotiaho JS, Kaitala V, Komonen A, Päivinen J. 2005. Predicting the risk of extinction from shared ecological characteristics. Proceedings of the National Academy of Sciences of the United States of America. 102(6):1963. https://doi.org/10.1073/pnas.0406718102.

Kowal J, Pressel S, Duckett JG, Bidartondo MI, Field KJ. 2018. From rhizoids to roots? Experimental evidence of mutualism between liverworts and ascomycete fungi. Annals of Botany. 121(2):221–227. https://doi.org/10.1093/aob/mcx126.

La Farge C, Williams KH, England JH. 2013. Regeneration of Little Ice Age bryophytes emerging from a polar glacier with implications of totipotency in extreme environments. Proceedings of the National Academy of Sciences of the United States of America. 110(24):9839–9844. https://doi.org/10.1073/pnas.1304199110.

Laenen B, Machac A, Gradstein SR, Shaw B, Patiño J, Désamoré A, Goffinet B, Cox CJ, Shaw AJ, Vanderpoorten A. 2016a. Increased diversification rates follow shifts to bisexuality in liverworts. New Phytologist. 210(3):1121–1129. https://doi.org/10.1111/nph.13835.

Laenen B, Machac A, Gradstein SR, Shaw B, Patiño J, Désamoré A, Goffinet B, Cox CJ, Shaw AJ, Vanderpoorten A. 2016b. Geographic range in liverworts: does sex really matter? Journal of Biogeography. 43(3):627–635.

Laenen B, Shaw B, Schneider H, Goffinet B, Paradis E, Désamoré A, Heinrichs J, Villarreal JC, Gradstein SR, McDaniel SF, et al. 2014. Extant diversity of bryophytes emerged from successive post-Mesozoic diversification bursts. Nature Communications. 5:5134. https://doi.org/10.1038/ncomms6134.

Lang AS, Bocksberger G, Stech M. 2015. Phylogeny and species delimitations in European *Dicranum* (Dicranaceae, Bryophyta) inferred from nuclear and plastid DNA. Molecular Phylogenetics and Evolution. 92:217–225. https://doi.org/10.1016/j.ympev.2015.06.019.

Lang D, Ullrich KK, Murat F, Fuchs J, Jenkins J, Haas FB, Piednoel M, Gundlach H, Van Bel M, Meyberg R, et al. 2018. The *Physcomitrella patens* chromosome-scale assembly reveals moss genome structure and evolution. The Plant Journal. 93(3):515–533. https://doi.org/10.1111/tpj.13801.

Lang PLM, Willems FM, Scheepens JF, Burbano HA, Bossdorf O. 2019. Using herbaria to study global environmental change. New Phytologist. 221(1):110–122. https://doi.org/10.1111/nph.15401.

Larmola T, Leppänen SM, Tuittila E-S, Aarva M, Merilä P, Fritze H, Tiirola M. 2014. Methanotrophy induces nitrogen fixation during peatland development. Proceedings of the National Academy of Sciences of the United States of America. 111(2):734. https://doi.org/10.1073/pnas.1314284111.

Lavoie C. 2013. Biological collections in an ever changing world: herbaria as tools for biogeographical and environmental studies. Perspectives in Plant Ecology, Evolution and Systematics. 15(1):68–76. https://doi.org/10.1016/j.ppees.2012.10.002.

Le Roux JJ, Hui C, Castillo ML, Iriondo JM, Keet J-H, Khapugin AA, Médail F, Rejmánek M, Theron G, Yannelli FA, et al. 2019. Recent anthropogenic plant extinctions differ in biodiversity hotspots and coldspots. Current Biology. 29(17):2912–2918.e2912. https://doi.org/10.1016/j.cub.2019.07.063.

Leberger R, Rosa IMD, Guerra CA, Wolf F, Pereira HM. 2020. Global patterns of forest loss across IUCN categories of protected areas. Biological Conservation. 241:108299. https://doi.org/10.1016/j.biocon.2019.108299.

Ledent A, Désamoré A, Laenen B, Mardulyn P, McDaniel SF, Zanatta F, Patiño J, Vanderpoorten A. 2019. No borders during the post-glacial assembly of European bryophytes. Ecology Letters. 22(6):973–986. https://doi.org/10.1111/ele.13254.

Ledent A, Gauthier J, Pereira M, Overson R, Laenen B, Mardulyn P, Gradstein SR, de Haan M, Ballings P, Van der Beeten I, et al. 2020. What do tropical cryptogams reveal? Strong genetic structure in Amazonian bryophytes. New Phytologist. 228(2):640–650. https://doi.org/10.1111/nph.16720.

Lelli C, Bruun HH, Chiarucci A, Donati D, Frascaroli F, Fritz Ö, Goldberg I, Nascimbene J, Tøttrup AP, Rahbek C, et al. 2019. Biodiversity response to forest structure and management: comparing species richness, conservation relevant species and functional diversity as metrics in forest conservation. Forest Ecology and Management. 432:707–717. https://doi.org/10.1016/j.foreco.2018.09.057.

Lenton TM, Crouch M, Johnson M, Pires N, Dolan L. 2012. First plants cooled the Ordovician. Nature Geoscience. 5(2):86–89. https://doi.org/10.1038/ngeo1390.

Lewis LR, Behling E, Gousse H, Qian E, Elphick CS, Lamarre J-F, Bêty J, Liebezeit J, Rozzi R, Goffinet B. 2014. First evidence of bryophyte diaspores in the plumage of transequatorial migrant birds. PeerJ. 2:e424. https://doi.org/10.7717/peerj.424.

Lewis LR, Ickert-Bond SM, Biersma EM, Convey P, Goffinet B, Hassel K, Kruijer H, Farge CL, Metzgar J, Stech M, et al. 2017. Future directions and priorities for Arctic bryophyte research. Arctic Science. 3(3):475–497. https://doi.org/10.1139/as-2016-0043.

Li F-W, Nishiyama T, Waller M, Frangedakis E, Keller J, Li Z, Fernandez-Pozo N, Barker MS, Bennett T, Blázquez MA, et al. 2020. *Anthoceros* genomes illuminate the origin of land plants and the unique biology of hornworts. Nature Plants. 6(3):259–272. https://doi.org/10.1038/s41477-020-0618-2.

Liebner S, Zeyer J, Wagner D, Schubert C, Pfeiffer E-M, Knoblauch C. 2011. Methane oxidation associated with submerged brown mosses reduces methane emissions from Siberian polygonal tundra. Journal of Ecology. 99(4):914–922. https://doi.org/10.1111/j.1365-2745.2011.01823.x.

Lindo Z, Gonzalez A. 2010. The bryosphere: an integral and influential component of the Earth's biosphere. Ecosystems. 13(4):612–627. https://doi.org/10.1007/s10021-010-9336-3.

Lindo Z, Nilsson M-C, Gundale MJ. 2013. Bryophyte–cyanobacteria associations as regulators of the northern latitude carbon balance in response to global change. Global Change Biology. 19(7):2022–2035. https://doi.org/10.1111/gcb.12175.

Liu Y, Johnson MG, Cox CJ, Medina R, Devos N, Vanderpoorten A, Hedenäs L, Bell NE, Shevock JR, Aguero B, et al. 2019. Resolution of the ordinal phylogeny of mosses using targeted exons from organellar and nuclear genomes. Nature Communications. 10(1):1485. https://doi.org/10.1038/s41467-019-09454-w.

Liu J, Zheng S, Tiwari RM, Liu L, Han W, Liu J. 2020. Similar mechanisms underlie beta diversity of bryophytes in two archipelagos with different isolation time. Ecosphere. 11(11):e03296. https://doi.org/10.1002/ecs2.3296.

Löbel S, Mair L, Lönnell N, Schröder B, Snäll T. 2018. Biological traits explain bryophyte species distributions and responses to forest fragmentation and climatic variation. Journal of Ecology. 106(4):1700–1713. https://doi.org/10.1111/1365-2745.12930.

Löbel S, Rydin H. 2009. Dispersal and life history strategies in epiphyte metacommunities: alternative solutions to survival in patchy, dynamic landscapes. Oecologia. 161(3):569–579.

Löbel S, Snäll T, Rydin H. 2006. Species richness patterns and metapopulation processes – evidence from epiphyte communities in boreo-nemoral forests. Ecography. 29(2):169–182. https://doi.org/10.1111/j.2006.0906-7590.04348.x.

Lönnell N, Hylander K, Jonsson BG, Sundberg S. 2012. The fate of the missing spores – patterns of realized dispersal beyond the closest vicinity of a sporulating moss. PLoS One. 7(7):e41987. https://doi.org/10.1371/journal.pone.0041987.

Lönnell N, Jonsson BG, Hylander K. 2014. Production of diaspores at the landscape level regulates local colonization: an experiment with a spore-dispersed moss. Ecography. 37(6):591–598. https://doi.org/10.1111/j.1600-0587.2013.00530.x.

Lönnell N, Norros V, Sundberg S, Rannik Ü, Johansson V, Ovaskainen O, Hylander K. 2015. Testing a mechanistic dispersal model against a dispersal experiment with a wind-dispersed moss. Oikos. 124(9):1232–1240. https://doi.org/10.1111/oik.01886.

Ma J-Z, Chen X, Mallik A, Bu Z-J, Zhang M-M, Wang S-Z, Sundberg S. 2020. Environmental together with interspecific interactions determine bryophyte distribution in a protected mire of Northeast China. Frontiers in Earth Science. 8:32. https://doi.org/10.3389/feart.2020.00032.

Maciel-Silva AS, Válio IFM, Rydin H. 2012. Diaspore bank of bryophytes in tropical rain forests: the importance of breeding system, phylum and microhabitat. Oecologia. 168(2):321–333. https://doi.org/10.1007/s00442-011-2100-3.

Magdy M, Werner O, McDaniel SF, Goffinet B, Ros RM. 2016. Genomic scanning using AFLP to detect loci under selection in the moss *Funaria hygrometrica* along a climate gradient in the Sierra Nevada Mountains, Spain. Plant Biology. 18(2):280–288. https://doi.org/10.1111/plb.12381.

Magill RE. 2010. Moss diversity: new look at old numbers. Phytotaxa. 9(1):167–174. https://doi.org/10.11646/phytotaxa.9.1.9.

Mälson K, Rydin H. 2009. Competitive hierarchy, but no competitive exclusions in experiments with rich fen bryophytes. Journal of Bryology. 31(1):41–45. https://doi.org/10.1179/174328209X404916.

Mammola S, Amorim IR, Bichuette ME, Borges PAV, Cheeptham N, Cooper SJB, Culver DC, Deharveng L, Eme D, Ferreira RL, et al. 2020. Fundamental research questions in subterranean biology. Biological Reviews. 95(6):1855–1872. https://doi.org/10.1111/brv.12642.

Marino P, Raguso R, Goffinet B. 2009. The ecology and evolution of fly dispersed dung mosses (family Splachnaceae): Manipulating insect behaviour through odour and visual cues. Symbiosis. 47(2):61–76. https://doi.org/10.1007/BF03182289.

Martin-Roy R, Nygård E, Nouhaud P, Kulmuni J. 2021. Differences in thermal tolerance between parental species could fuel thermal adaptation in hybrid wood ants. The American Naturalist. 198(2):278–294. https://doi.org/10.1086/715012.

Martinez-Swatson K, Mihály E, Lange C, Ernst M, Dela Cruz M, Price MJ, Mikkelsen TN, Christensen JH, Lundholm N, Rønsted N. 2020. Biomonitoring of polycyclic aromatic hydrocarbon deposition in greenland using historical moss herbarium specimens shows a decrease in pollution during the 20th century. Frontiers in Plant Science. 11:1085.

McDaniel SF. 2021. Bryophytes are not early diverging land plants. New Phytologist. 230(4):1300–1304. https://doi.org/10.1111/nph.17241.

Medina NG, Albertos B, Lara F, Mazimpaka V, Garilleti R, Draper D, Hortal J. 2014. Species richness of epiphytic bryophytes: drivers across scales on the edge of the Mediterranean. Ecography. 37(1):80–93. https://doi.org/10.1111/j.1600-0587.2013.00095.x.

Medina NG, Bowker MA, Hortal J, Mazimpaka V, Lara F. 2018a. Shifts in the importance of the species pool and environmental controls of epiphytic bryophyte richness across multiple scales. Oecologia. 186(3):805–816. https://doi.org/10.1007/s00442-018-4066-x.

Medina NG, Draper I, Lara F. 2011. Biogeography of mosses and allies: does size matter? In: Fontaneto D, editor. Biogeography of micro-organisms. Is everything small everywhere? Cambridge: Cambridge University Press; p. 209–233.

Medina R, Johnson MG, Liu Y, Wickett NJ, Shaw AJ, Goffinet B. 2019. Phylogenomic delineation of *Physcomitrium* (Bryophyta: Funariaceae) based on targeted sequencing of nuclear exons and their flanking regions rejects the retention of *Physcomitrella*, *Physcomitridium* and *Aphanorrhegma*. Journal of Systematics and Evolution. 57(4):404–417. https://doi.org/10.1111/jse.12516.

Medina R, Johnson M, Liu Y, Wilding N, Hedderson TA, Wickett N, Goffinet B. 2018b. Evolutionary dynamism in bryophytes: phylogenomic inferences confirm rapid radiation in the moss family Funariaceae. Molecular Phylogenetics and Evolution. 120:240–247. https://doi.org/10.1016/j.ympev.2017.12.002.

Medina R, Lara F, Goffinet B, Garilleti R, Mazimpaka V. 2012. Integrative taxonomy successfully resolves the pseudo-cryptic complex of the disjunct epiphytic moss *Orthotrichum consimile* s.l. (Orthotrichaceae). Taxon. 61(6):1180–1198. https://doi.org/10.1002/tax.616002.

Michel P, Payton IJ, Lee WG, During HJ. 2013. Impact of disturbance on above-ground water storage capacity of bryophytes in New Zealand indigenous tussock grassland ecosystems. New Zealand Journal of Ecology. 37(1):114–126.

Mod HK, le Roux PC, Guisan A, Luoto M. 2015. Biotic interactions boost spatial models of species richness. Ecography. 38(9):913–921. https://doi.org/10.1111/ecog.01129.

Moncrieff J, Valentini R, Greco S, Guenther S, Ciccioli P. 1997. Trace gas exchange over terrestrial ecosystems: methods and perspectives in micrometeorology. Journal of Experimental Botany. 48(5):1133–1142. https://doi.org/10.1093/jxb/48.5.1133.

Morris JL, Puttick MN, Clark JW, Edwards D, Kenrick P, Pressel S, Wellman CH, Yang Z, Schneider H, Donoghue PCJ. 2018. The timescale of early land plant evolution. Proceedings of the National Academy of Sciences of the United States of America. 115(10):E2274. https://doi.org/10.1073/pnas.1719588115.

Mota de Oliveira S, ter Steege H. 2015. Bryophyte communities in the Amazon forest are regulated by height on the host tree and site elevation. Journal of Ecology. 103(2):441–450. https://doi.org/10.1111/1365-2745.12359.

Mota de Oliveira S, Ter Steege H, Cornelissen JHC, Robbert Gradstein S. 2009. Niche assembly of epiphytic bryophyte communities in the Guianas: a regional approach. Journal of Biogeography. 36(11):2076–2084. https://doi.org/10.1111/j.1365-2699.2009.02144.x.

Muñoz J, Felicísimo ÁM, Cabezas F, Burgaz AR, Martínez I. 2004. Wind as a long-distance dispersal vehicle in the Southern Hemisphere. Science. 304(5674):1144–1147. https://doi.org/10.1126/science.1095210.

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature. 403(6772):853–858. https://doi.org/10.1038/35002501.

Myszczyński K, Bączkiewicz A, Buczkowska K, Ślipiko M, Szczecińska M, Sawicki J. 2017. The extraordinary variation of the organellar genomes of the *Aneura pinguis* revealed advanced cryptic speciation of the early land plants. Scientific Reports. 7(1):9804. https://doi.org/10.1038/s41598-017-10434-7.

Naramoto S, Hata Y, Fujita T, Kyozuka J. 2022. The bryophytes *Physcomitrium patens* and *Marchantia polymorpha* as model systems for studying evolutionary cell and developmental biology in plants. The Plant Cell. 34(1):228–246. https://doi.org/10.1093/plcell/koab218.

Natcheva R, Cronberg N. 2004. What do we know about hybridization among bryophytes in nature? Canadian Journal of Botany. 82:1687–1704.

Nelson JM, Hauser DA, Hinson R, Shaw AJ. 2018. A novel experimental system using the liverwort *Marchantia polymorpha* and its fungal endophytes reveals diverse and context-dependent effects. New Phytologist. 218(3):1217–1232. https://doi.org/10.1111/nph.15012.

Nieto-Lugilde M, Werner O, McDaniel SF, Koutecký P, Kučera J, Rizk SM, Ros RM. 2018a. Peripatric speciation associated with genome expansion and female-biased sex ratios in the moss genus *Ceratodon*. American Journal of Botany. 105(6):1009–1020. https://doi.org/10.1002/ajb2.1107.

Nieto-Lugilde M, Werner O, McDaniel SF, Ros RM. 2018b. Environmental variation obscures species diversity in southern European populations of the moss genus

Ceratodon. Taxon. 67(4):673–692. https://doi.org/10.12705/674.1.

Øien D-I, Pedersen B, Kozub Ł, Goldstein K, Wilk M. 2018. Long-term effects of nutrient enrichment controlling plant species and functional composition in a boreal rich fen. Journal of Vegetation Science. 29(5):907–920. https://doi.org/10.1111/jvs.12674.

Olena M, Hans KS, James DMS, Kjell IF, Magni OK, Kristian H. 2018. Is interspecific gene flow and speciation in peat-mosses (*Sphagnum*) constrained by phylogenetic relationship and life-history traits? Lindbergia. 41(1):1–14. https://doi.org/10.25227/linbg.01107.

Oliver MJ, Velten J, Mishler BD. 2005. Desiccation tolerance in bryophytes: a reflection of the primitive strategy for plant survival in dehydrating habitats? Integrative and Comparative Biology. 45(5):788–799. https://doi.org/10.1093/icb/45.5.788.

Orme CDL, Davies RG, Burgess M, Eigenbrod F, Pickup N, Olson VA, Webster AJ, Ding T-S, Rasmussen PC, Ridgely RS, et al. 2005. Global hotspots of species richness are not congruent with endemism or threat. Nature. 436(7053):1016–1019. https://doi.org/10.1038/nature03850.

Otero S, Núñez-Olivera E, Martínez-Abaigar J, Tomás R, Huttunen S. 2009. Retrospective bioindication of stratospheric ozone and ultraviolet radiation using hydroxycinnamic acid derivatives of herbarium samples of an aquatic liverwort. Environmental Pollution. 157(8–9):2335–2344. https://doi.org/10.1016/j.envpol.2009.03.025.

Ovaskainen O, Tikhonov G, Norberg A, Guillaume Blanchet F, Duan L, Dunson D, Roslin T, Abrego N. 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. Ecology Letters. 20(5):561–576. https://doi.org/10.1111/ele.12757.

Pan Z, Pitt WG, Zhang Y, Wu N, Tao Y, Truscott TT. 2016. The upside-down water collection system of *Syntrichia caninervis*. Nature Plants. 2(7):16076. https://doi.org/10.1038/nplants.2016.76.

Pardow A, Lakatos M. 2013. Desiccation tolerance and global change: implications for tropical bryophytes in lowland forests. Biotropica. 45(1):27–36. https://doi.org/10.1111/j.1744-7429.2012.00884.x.

Patel N, Medina R, Johnson M, Goffinet B. 2021. Karyotypic diversity and cryptic speciation: have we vastly underestimated moss species diversity? Bryophyte Diversity and Evolution. 36:150–163.

Patiño J, Carine MA, Fernández-Palacios JM, Otto R, Schaefer H, Vanderpoorten A. 2014. The anagenetic world of the spore-producing plants. New Phytologist. 201:305–311. https://doi.org/10.1111/nph.12480.

Patiño J, Carine MA, Mardulyn P, Devos N, Mateo RG, González-Mancebo JM, Shaw AJ, Vanderpoorten A. 2015. Approximate Bayesian computation reveals the crucial role of oceanic islands for the assembly of continental biodiversity. Systematic Biology. 64(4):579–589. https://doi.org/10.1093/sysbio/syv013.

Patiño J, González-Mancebo JM. 2011. Exploring the effect of host tree identity on epiphyte bryophyte communities in different Canarian subtropical cloud forests. Plant Ecology. 212(3):433–449.

Patiño J, Mateo RG, Zanatta F, Marquet A, Aranda SC, Borges PAV, Dirkse G, Gabriel R, Gonzalez-Mancebo JM, Guisan A, et al. 2016. Climate threat on the Macaronesian endemic bryophyte flora. Scientific Reports. 6:29156. https://doi.org/10.1038/srep29156.

Patiño J, Vanderpoorten A. 2018. Bryophyte biogeography. Critical Reviews in Plant Sciences. 37(2–3):175–209. https://doi.org/10.1080/07352689.2018.1482444.

Patiño J, Vanderpoorten A. 2021. Island biogeography: an avenue for research in bryology. Bryophyte Diversity and Evolution. 43:206–220.

Patiño J, Whittaker RJ, Borges PAV, Fernández-Palacios JM, Ah-Peng C, Araújo MB, Ávila SP, Cardoso P, Cornuault J, de Boer EJ, et al. 2017. A roadmap for island biology: 50 fundamental questions after 50 years of *The Theory of Island Biogeography*. Journal of Biogeography. 44(5):963–983. https://doi.org/10.1111/jbi.12986.

Perley DS, Jesson LK. 2015. Hybridization is associated with changes in sexual system in the bryophyte genus *Atrichum*. American Journal of Botany. 102(4):555–565. https://doi.org/10.3732/ajb.1400494.

Pfeiffer T, Fritz S, Stech M, Frey W. 2006. Vegetative reproduction and clonal diversity in *Rhytidium rugosum* (Rhytidiaceae, Bryopsida) inferred by morpho-anatomical and molecular analyses. Journal of Plant Research. 119(2):125–135. https://doi.org/10.1007/s10265-005-0255-x.

Pharo EJ, Zartman CE. 2007. Bryophytes in a changing landscape: the hierarchical effects of habitat fragmentation on ecological and evolutionary processes. Biological Conservation. 135(3):315–325. https://doi.org/10.1016/j.biocon.2006.10.016.

Pohjamo M, Laaka-Lindberg S. 2003. Reproductive modes in the epixylic hepatic *Anastrophyllum hellerianum*. Perspectives in Plant Ecology, Evolution and Systematics. 6(3):159–168. https://doi.org/10.1078/1433-8319-00074.

Pohjamo M, Laaka-Lindberg S, Ovaskainen O, Korpelainen H. 2006. Dispersal potential of spores and asexual propagules in the epixylic hepatic *Anastrophyllum hellerianum*. Evolutionary Ecology. 20(5):415–430.

Proctor MCF, Oliver MJ, Wood AJ, Alpert P, Stark LR, Cleavitt NL, Mishler BD. 2007. Desiccation-tolerance in bryophytes: a review. The Bryologist. 110(4):595–621.

Puttick MN, Morris JL, Williams TA, Cox CJ, Edwards D, Kenrick P, Pressel S, Wellman CH, Schneider H, Pisani D, et al. 2018. The interrelationships of land plants and the nature of the ancestral embryophyte. Current Biology. 28(5):733–745.e732. https://doi.org/10.1016/j.cub.2018.01.063.

Raghoebarsing AA, Smolders AJP, Schmid MC, Rijpstra WIC, Wolters-Arts M, Derksen J, Jetten MSM, Schouten S, Sinninghe Damsté JS, Lamers LPM, et al. 2005. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. Nature. 436(7054):1153–1156. https://doi.org/10.1038/nature03802.

Rahmatpour N, Perera NV, Singh V, Wegrzyn JL, Goffinet B. 2021. High gene space divergence contrasts with frozen vegetative architecture in the moss family Funariaceae. Molecular Phylogenetics and Evolution. 154:106965. https://doi.org/10.1016/j.ympev.2020.106965.

Raven PH. 2019. Saving plants, saving ourselves. Plants, People, Planet. 1:8–13. https://doi.org/10.1002/ppp3.3.

Ravinet M, Faria R, Butlin RK, Galindo J, Bierne N, Rafajlović M, Noor MAF, Mehlig B, Westram AM. 2017. Interpreting the genomic landscape of speciation: a road map for finding barriers to gene flow. Journal of Evolutionary Biology. 30(8):1450–1477. https://doi.org/10.1111/jeb.13047.

Reeb C, Kaandorp J, Jansson F, Puillandre N, Dubuisson J-Y, Cornette R, Jabbour F, Coudert Y, Patiño J, Flot J-F, et al. 2018. Quantification of complex modular architecture in plants. New Phytologist. 218(2):859–872. https://doi.org/10.1111/nph.15045.

Renner MAM. 2020. Opportunities and challenges presented by cryptic bryophyte species. Telopea. 23:41–60.

Renner MAM, Devos N, Patiño J, Brown E, Orme A, Elgy M, Wilson T, Gray L, von Konrat M. 2013. Integrative taxonomy resolves the cryptic and pseudo-cryptic *Radula buccinifera* complex (Porellales, Jungermanniopsida), including two reinstated and five new species. PhytoKeys. 27(0):1–113. https://doi.org/10.3897/phytokeys.27.5523.

Ricciardi A, Blackburn TM, Carlton JT, Dick JTA, Hulme PE, Iacarella JC, Jeschke JM, Liebhold AM, Lockwood JL, MacIsaac HJ, et al. 2017. Invasion science: a horizon scan of emerging challenges and opportunities. Trends in Ecology and Evolution. 32(6):464–474. https://doi.org/10.1016/j.tree.2017.03.007.

Rikkinen J, Virtanen V. 2008. Genetic diversity in cyanobacterial symbionts of thalloid bryophytes. Journal of Experimental Botany. 59(5):1013–1021. https://doi.org/10.1093/jxb/ern003.

Rimington WR, Duckett JG, Field KJ, Bidartondo MI, Pressel S. 2020. The distribution and evolution of fungal symbioses in ancient lineages of land plants. Mycorrhiza. 30(1):23–49. https://doi.org/10.1007/s00572-020-00938-y.

Rosengren F, Hansson B, Cronberg N. 2015. Population structure and genetic diversity in the nannandrous moss *Homalothecium lutescens*: does the dwarf male system facilitate gene flow? BMC Evolutionary Biology. 15(1):270. https://doi.org/10.1186/s12862-015-0545-4.

Rosenstiel TN, Shortlidge EE, Melnychenko AN, Pankow JF, Eppley SM. 2012. Sex-specific volatile compounds influence microarthropod-mediated fertilization of moss. Nature. 489(7416):431–433.

Rousk K, DeLuca TH, Rousk J. 2013a. The cyanobacterial role in the resistance of feather mosses to decomposition – toward a new hypothesis. PLoS One. 8(4):e62058. https://doi.org/10.1371/journal.pone.0062058.

Rousk K, Jones D, DeLuca T. 2013b. Moss–cyanobacteria associations as biogenic sources of nitrogen in boreal forest ecosystems. Frontiers in Microbiology. 4:150. https://doi.org/10.3389/fmicb.2013.00150.

Rousk K, Sorensen PL, Lett S, Michelsen A. 2015. Across-habitat comparison of diazotroph activity in the subarctic. Microbial Ecology. 69(4):778–787. https://doi.org/10.1007/s00248-014-0534-y.

Rozzi R, Massardo F, Anderson CB. 2004. The Cape Horn Biosphere Reserve: a proposal for conservation and tourism to achieve sustainable development at the southern end of the Americas. Punta Arenas, Chile: Ediciones Universidad de Magallanes.

Rozzi R, Massardo F, Berghöfer A, Anderson CB, Mansilla A, Mansilla M, Plana J, Berghöfer U, Araya P, Barros E. 2006. Cape Horn biosphere reserve: nomination document for the incorporation of the cape horn archipelago territory into the world biosphere reserve network. Punta Arenas, Chile: MaB Program–UNESCO Ediciones de la Universidad de Magallanes.

Ruete A, Yang W, Bärring L, Stenseth NC, Snäll T. 2012. Disentangling effects of uncertainties on population projections: climate change impact on an epixylic bryophyte. Proceedings of the Royal Society B: Biological Sciences. 279(1740):3098–3105. https://doi.org/10.1098/rspb.2012.0428.

Rydgren K, Halvorsen R, Cronberg N. 2010. Infrequent sporophyte production maintains a female-biased sex ratio in the unisexual clonal moss *Hylocomium splendens*. Journal of Ecology. 98(5):1224–1231. https://doi.org/10.1111/j.1365-2745.2010.01639.x.

Sage RF. 2020. Global change biology: a primer. Global Change Biology. 26(1):3–30. https://doi.org/10.1111/gcb.14893.

Sanbonmatsu K, Spalink D. Forthcoming 2022. Spatial phylogenetics of mosses (Bryopsida) at a global scale: current status and future directions. Journal of Biogeography.

Sawangproh W, Cronberg N. 2021. Evidence for interspecific hybridization in bryophytes during pre-molecular and molecular eras. Bryophyte Diversity and Evolution. (36):180–205.

Sawangproh W, Hedenäs L, Lang AS, Hansson B, Cronberg N. 2020. Gene transfer across species boundaries in bryophytes: evidence from major life cycle stages in *Homalothecium lutescens* and *H. sericeum*. Annals of Botany. 125(4):565–579. https://doi.org/10.1093/aob/mcz209.

Scherrer D, Körner C. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. Journal of Biogeography. 38(2):406–416. https://doi.org/10.1111/j.1365-2699.2010.02407.x.

Schwarzer C, Joshi J. 2017. Parallel adaptive responses to abiotic but not biotic conditions after cryptic speciation in European peat moss *Sphagnum magellanicum* Brid. Perspectives in Plant Ecology, Evolution and Systematics. 26:14–27. https://doi.org/10.1016/j.ppees.2017.03.001.

Schween G, Gorr G, Hohe A, Reski R. 2003. Unique tissue-specific cell cycle in *Physcomitrella*. Plant Biology. 5(1):50–58. https://doi.org/10.1055/s-2003-37984.

Seddon AWR, Mackay AW, Baker AG, Birks HJB, Breman E, Buck CE, Ellis EC, Froyd CA, Gill JL, Gillson L, et al. 2014. Looking forward through the past: identification of 50 priority research questions in palaeoecology. Journal of Ecology. 102(1):256–267. https://doi.org/10.1111/1365-2745.12195.

Sharp NP, Sandell L, James CG, Otto SP. 2018. The genome-wide rate and spectrum of spontaneous mutations differ between haploid and diploid yeast. Proceedings of the National Academy of Sciences of the United States of America. 115(22):E5046. https://doi.org/10.1073/pnas.1801040115.

Shaw AJ. 1985. The relevance of ecology to species concepts in bryophytes. The Bryologist. 88:199–206.

Shaw AJ. 2001. Biogeographic patterns and cryptic speciation in bryophytes. Journal of Biogeography. 28:253–261.

Shaw AJ. 2009. Bryophyte species and speciation. In: Goffinet B, Shaw AJ, editors. Bryophyte biology, 2nd ed. Cambridge: Cambridge University Press; p. 445–486.

Shaw AJ, Cymon JC, Goffinet B. 2005. Global patterns of moss diversity: taxonomic and molecular inferences. Taxon. 54(2):337–352. https://doi.org/10.2307/25065362.

Shaw AJ, Devos N, Cox CJ, Boles SB, Shaw B, Buchanan AM, Cave L, Seppelt R. 2010. Peatmoss (*Sphagnum*) diversification associated with Miocene Northern Hemisphere climatic cooling? Molecular Phylogenetics and Evolution. 55:1139–1145. https://doi.org/10.1016/j.ympev.2010.01.020.

Shaw AJ, Szövényi P, Shaw B. 2011. Bryophyte diversity and evolution: windows into the early evolution of land plants. American Journal of Botany. 98(3):352–369. https://doi.org/10.3732/ajb.1000316.

Shaw AJ, Werner O, Ros RM. 2003. Intercontinental Mediterranean disjunct mosses: morphological and molecular patterns. American Journal of Botany. 90(4):540–550. https://doi.org/10.3732/ajb.90.4.540.

Shortlidge EE, Carey SB, Payton AC, McDaniel SF, Rosenstiel TN, Eppley SM. 2021. Microarthropod contributions to fitness variation in the common moss *Ceratodon purpureus*. Proceedings of the Royal Society B: Biological Sciences. 288(1947):20210119. https://doi.org/10.1098/rspb.2021.0119.

Sierra AM, Toledo JJ, Salazar Allen N, Zartman CE. 2019. Reproductive traits as predictors of assembly chronosequence patterns in epiphyllous bryophyte metacommunities. Journal of Ecology. 107(2):875–886. https://doi.org/10.1111/1365-2745.13058.

Sim-Sim M, Lopes T, Ruas S, Stech M. 2015. Does altitude shape molecular diversity and richness of bryophytes in Madeira's natural forest? A case study with four bryophyte species at two altitudinal levels. Plant Ecology and Evolution. 148(2):171–180. https://doi.org/10.5091/plecevo.2015.1041.

Sim-Sim M, Ruas S, Fontinha S, Hedenäs L, Sergio C, Lobo C. 2014. Bryophyte conservation on a North Atlantic hotspot: threatened bryophytes in Madeira and Selvagens Archipelagos (Portugal). Systematics and Biodiversity. 12 (3):310–330.

Smith SA, Donoghue MJ. 2008. Rates of molecular evolution are linked to life history in flowering plants. Science. 322 (5898):86–89.

Smith AB, Godsoe W, Rodríguez-Sánchez F, Wang H-H, Warren D. 2019. Niche estimation above and below the species level. Trends in Ecology and Evolution. 34(3):260–273. https://doi.org/10.1016/j.tree.2018.10.012.

Snäll T, Ribeiro Jr PJ, Rydin H. 2003. Spatial occurrence and colonisations in patch-tracking metapopulations: local conditions versus dispersal. Oikos. 103(3):566–578. https://doi.org/10.1034/j.1600-0706.2003.12551.x.

Söderström L, Hagborg A, von Konrat M, Bartholomew-Began S, Bell D, Briscoe L, Brown E, Cargill DC, da Costa DP, Crandall-Stotler BJ, et al. 2016. World checklist of hornworts and liverworts. PhytoKeys. 59:1–828. https://doi.org/10.3897/phytokeys.59.6261.

Soliveres S, Eldridge DJ. 2020. Dual community assembly processes in dryland biocrust communities. Functional Ecology. 34(4):877–887. https://doi.org/10.1111/1365-2435.13521.

Soltis PS. 2017. Digitization of herbaria enables novel research. American Journal of Botany. 104(9):1281–1284. https://doi.org/10.3732/ajb.1700281.

Song L, Lu H-Z, Xu X-L, Li S, Shi X-M, Chen X, Wu Y, Huang J-B, Chen Q, Liu S, et al. 2016. Organic nitrogen uptake is a significant contributor to nitrogen economy of subtropical epiphytic bryophytes. Scientific Reports. 6(1):30408. https://doi.org/10.1038/srep30408.

Sousa F, Civáň P, Brazão J, Foster PG, Cox CJ. 2020a. The mitochondrial phylogeny of land plants shows support for Setaphyta under composition-heterogeneous substitution models. PeerJ. 8:e8995. https://doi.org/10.7717/peerj.8995.

Sousa F, Civáň P, Foster PG, Cox CJ. 2020b. The chloroplast land plant phylogeny: analyses employing better-fitting tree- and site-heterogeneous composition models. Frontiers in Plant Science. 11:1062. https://doi.org/10.3389/fpls.2020.01062.

Su D, Yang L, Shi X, Ma X, Zhou X, Hedges SB, Zhong B. 2021. Large-scale phylogenomic analyses reveal the monophyly of bryophytes and neoproterozoic origin of land plants. Molecular Biology and Evolution. 38(8):3332–3344. https://doi.org/10.1093/molbev/msab106.

Spatafora JW, Chang Y, Benny GL, Lazarus K, Smith ME, Berbee ML, Bonito G, Corradi N, Grigoriev I, Gryganskyi A, et al. 2016. A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. Mycologia. 108(5):1028–1046. https://doi.org/10.3852/16-042.

Spitale D. 2016. The interaction between elevational gradient and substratum reveals how bryophytes respond to the climate. Journal of Vegetation Science. 27(4):844–853. https://doi.org/10.1111/jvs.12403.

Stanton DE, Coe KK. 2021. 500 million years of charted territory: functional ecological traits in bryophytes. Bryophyte Diversity and Evolution. 36:234–252.

Stark LR. 2017. Ecology of desiccation tolerance in bryophytes: a conceptual framework and methodology. The Bryologist. 120(2):130–165. https://doi.org/10.1639/0007-2745-120.2.130.

Stark LR, Greenwood JL, Brinda JC. 2017. Desiccated *Syntrichia ruralis* shoots regenerate after 20 years in the herbarium. Journal of Bryology. 39(1):85–93. https://doi.org/10.1080/03736687.2016.1176307.

Stearns SC. 2000. Life history evolution: successes, limitations, and prospects. Naturwissenschaften. 87(11):476–486.

Stech M, Câmara PEAS, Medina R, Muñoz J. 2021. Advances and challenges in bryophyte biology after 50 years of International Association of Bryologists. Bryophyte Diversity and Evolution. 43:6–9.

Steffen W, Persson Å, Deutsch L, Zalasiewicz J, Williams M, Richardson K, Crumley C, Crutzen P, Folke C, Gordon L, et al. 2011. The Anthropocene: from global change to planetary stewardship. AMBIO. 40(7):739. https://doi.org/10.1007/s13280-011-0185-x.

Struck TH, Feder JL, Bendiksby M, Birkeland S, Cerca J, Gusarov VI, Kistenich S, Larsson K-H, Liow LH, Nowak MD, et al. 2018. Finding evolutionary processes hidden in cryptic species. Trends in Ecology and Evolution. 33 (3):153–163. https://doi.org/10.1016/j.tree.2017.11.007.

Stuart JEM, Holland-Moritz H, Lewis LR, Jean M, Miller SN, McDaniel SF, Fierer N, Ponciano JM, Mack MC. 2021. Host identity as a driver of moss-associated N_2 fixation rates in Alaska. Ecosystems. 24(3):530–547. https://doi.org/10.1007/s10021-020-00534-3.

Sukkharak P, Gradstein SR, Stech M. 2011. Phylogeny, taxon circumscriptions, and character evolution in the core Ptychanthoideae (Lejeuneaceae, Marchantiophyta). Taxon. 60(6):1607–1622. https://doi.org/10.1002/tax.606006.

Sundberg S. 2013. Spore rain in relation to regional sources and beyond. Ecography. 36(3):364–373. https://doi.org/10.1111/j.1600-0587.2012.07664.x.

Sundberg S, Hansson J, Rydin H. 2006. Colonization of *Sphagnum* on land uplift islands in the Baltic Sea: time, area, distance and life history. Journal of Biogeography. 33:1479–1491. https://doi.org/10.1111/j.1365-2699.2006.01520.x.

Sutherland WJ, Dias MP, Dicks LV, Doran H, Entwistle AC, Fleishman E, Gibbons DW, Hails R, Hughes AC, Hughes J, et al. 2020. A horizon scan of emerging global biological conservation issues for 2020. Trends in Ecology and Evolution. 35(1):81–90. https://doi.org/10.1016/j.tree.2019.10.010.

Sutherland WJ, Fleishman E, Mascia MB, Pretty J, Rudd MA. 2011. Methods for collaboratively identifying research priorities and emerging issues in science and policy. Methods in Ecology and Evolution. 2(3):238–247. https://doi.org/10.1111/j.2041-210X.2010.00083.x.

Sutherland WJ, Freckleton RP, Godfray HCJ, Beissinger SR, Benton T, Cameron DD, Carmel Y, Coomes DA, Coulson T, Emmerson MC, et al. 2013. Identification of 100 fundamental ecological questions. Journal of Ecology. 101(1):58–67. https://doi.org/10.1111/1365-2745.12025.

Szövényi P, Devos N, Weston DJ, Yang X, Hock Z, Shaw JA, Shimizu KK, McDaniel SF, Wagner A. 2014. Efficient purging of deleterious mutations in plants with haploid selfing. Genome Biology and Evolution. 6(5):1238–1252. https://doi.org/10.1093/gbe/evu099.

Szövényi P, Ricca M, Hock Z, Shaw JA, Shimizu KK, Wagner A. 2013. Selection is no more efficient in haploid than in diploid life stages of an angiosperm and a moss. Molecular Biology and Evolution. 30(8):1929–1939. https://doi.org/10.1093/molbev/mst095.

Tao Y, Zhang YM. 2012. Effects of leaf hair points of a desert moss on water retention and dew formation: implications for desiccation tolerance. Journal of Plant Research. 125(3):351–360. https://doi.org/10.1007/s10265-011-0449-3.

Thompson PL, Guzman LM, De Meester L, Horváth Z, Ptacnik R, Vanschoenwinkel B, Viana DS, Chase JM. 2020. A process-based metacommunity framework linking local and regional scale community ecology. Ecology Letters. 23(9):1314–1329. https://doi.org/10.1111/ele.13568.

Tiselius AK, Lundbäck S, Lönnell N, Jansson R, Dynesius M. 2019. Bryophyte community assembly on young land uplift islands – dispersal and habitat filtering assessed using species traits. Journal of Biogeography. 46(10):2188–2202. https://doi.org/10.1111/jbi.13652.

Tomescu AMF, Bomfleur B, Bippus AC, Savoretti A. 2018. Why are bryophytes so rare in the fossil record? A spotlight on taphonomy and fossil preservation. In: Krings M, Harper CJ, Cúneo NR, Rothwell GW, editors. Transformative paleobotany. London: Academic Press; p. 375–416.

Trevathan-Tackett SM, Sherman CDH, Huggett MJ, Campbell AH, Laverock B, Hurtado-McCormick V, Seymour JR, Firl A, Messer LF, Ainsworth TD, et al. 2019. A horizon scan of priorities for coastal marine microbiome research. Nature Ecology and Evolution. 3(11):1509–1520. https://doi.org/10.1038/s41559-019-0999-7.

Tuba Z, Slack NG, Stark LR. 2011. Bryophyte ecology and climate change. Cambridge, UK: Cambridge University Press.

Turetsky MR. 2003. The role of bryophytes in carbon and nitrogen cycling. The Bryologist. 106(3):395–409. https://doi.org/10.1639/05.

Turetsky MR, Bond-Lamberty B, Euskirchen E, Talbot J, Frolking S, McGuire AD, Tuittila ES. 2012. The resilience and functional role of moss in boreal and arctic ecosystems. New Phytologist. 196(1):49–67. https://doi.org/10.1111/j.1469-8137.2012.04254.x.

Turnbull JD, Leslie SJ, Robinson SA. 2009. Desiccation protects two Antarctic mosses from ultraviolet-B induced DNA damage. Functional Plant Biology. 36(3):214–221. https://doi.org/10.1071/FP08286.

Udd D, Sundberg S, Rydin H. 2016. Multi-species competition experiments with peatland bryophytes. Journal of Vegetation Science. 27(1):165–175. https://doi.org/10.1111/jvs.12322.

van den Elzen E, Bengtsson F, Fritz C, Rydin H, Lamers LPM. 2020. Variation in symbiotic N_2 fixation rates among *Sphagnum* mosses. PLoS One. 15(2):e0228383. https://doi.org/10.1371/journal.pone.0228383.

Van Rooy J, Bergamini A, Bisang I. 2019. Fifty shades of red: lost or threatened bryophytes in Africa. Bothalia. 49(1):a2341. https://doi.org/10.4102/abc.v49i1.2341.

van Zanten BO. 1978. Experimental studies on trans-oceanic long-range dispersal of moss spores in the southern hemisphere. Journal of the Hattori Botanical Laboratory. 44:455–482.

Vanderpoorten A, Devos N, Goffinet B, Hardy OJ, Shaw AJ. 2008. The barriers to oceanic island radiation in bryophytes: insights from the phylogeography of the moss *Grimmia montana*. Journal of Biogeography. 35(4):654–663. https://doi.org/10.1111/j.1365-2699.2007.01802.x.

Vanderpoorten A, Goffinet B. 2009. Introduction to bryophytes. Cambridge, UK: Cambridge University Press.

Vanderpoorten A, Hallingbäck T. 2009. Conservation biology. In: Goffinet B, Shaw AJ, editors. Bryophyte biology. 2nd ed. Cambridge, UK: Cambridge University Press; p. 487–533.

Vanderpoorten A, Patiño J, Désamoré A, Laenen B, Górski P, Papp B, Holá E, Korpelainen H, Hardy O. 2019. To what extent are bryophytes efficient dispersers? Journal of Ecology. 107(5):2149–2154. https://doi.org/10.1111/1365-2745.13161.

Vellend M. 2010. Conceptual synthesis in community ecology. The Quarterly Review of Biology. 85(2):183–206.

Vellend M. 2016. The theory of ecological communities. Princeton (NJ): Princeton University Press. (Monographs in Population Biology; 57).

Vigalondo B, Garilleti R, Vanderpoorten A, Patiño J, Draper I, Calleja JA, Mazimpaka V, Lara F. 2019. Do mosses really exhibit so large distribution ranges? Insights from the integrative taxonomic study of the *Lewinskya affinis* complex (Orthotrichaceae, Bryopsida). Molecular Phylogenetics and Evolution. 140:106598. https://doi.org/10.1016/j.ympev.2019.106598.

Vile MA, Kelman Wieder R, Živković T, Scott KD, Vitt DH, Hartsock JA, Iosue CL, Quinn JC, Petix M, Fillingim HM, et al. 2014. N_2-fixation by methanotrophs sustains carbon and nitrogen accumulation in pristine peatlands. Biogeochemistry. 121(2):317–328. https://doi.org/10.1007/s10533-014-0019-6.

Villarreal JC, Crandall-Stotler BJ, Hart ML, Long DG, Forrest LL. 2016. Divergence times and the evolution of morphological complexity in an early land plant lineage (Marchantiopsida) with a slow molecular rate. New Phytologist. 209(4):1734–1746. https://doi.org/10.1111/nph.13716.

Vitt DH, Li Y, Belland RJ. 1995. Patterns of bryophyte diversity in peatlands of continental Western Canada. The Bryologist. 98(2):218–227.

von Konrat M, Campbell T, Carter B, Greif M, Bryson M, Larraín J, Trouille L, Cohen S, Gaus E, Qazi A, et al. 2018. Using citizen science to bridge taxonomic discovery with education and outreach. Applications in Plant Sciences. 6(2):e1023. https://doi.org/10.1002/aps3.1023.

Wall DP. 2005. Origin and rapid diversification of a tropical moss. Evolution. 59(7):1413–1424. https://doi.org/10.1111/j.0014-3820.2005.tb01792.x.

Warshan D, Bay G, Nahar N, Wardle DA, Nilsson M-C, Rasmussen U. 2016. Seasonal variation in nifH abundance and expression of cyanobacterial communities associated with boreal feather mosses. The International Society for Microbial Ecology Journal. 10(9):2198–2208. https://doi.org/10.1038/ismej.2016.17.

Weiher E, Freund D, Bunton T, Stefanski A, Lee T, Bentivenga S. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. Philosophical Transactions of the Royal Society B: Biological Sciences. 366(1576):2403–2413. https://doi.org/10.1098/rstb.2011.0056.

Weston DJ, Timm CM, Walker AP, Gu L, Muchero W, Schmutz J, Shaw AJ, Tuskan GA, Warren JM, Wullschleger SD. 2015. *Sphagnum* physiology in the context of changing climate: emergent influences of genomics, modelling and host–microbiome interactions on understanding ecosystem function. Plant, Cell and Environment. 38(9):1737–1751. https://doi.org/10.1111/pce.12458.

Wickett NJ, Mirarab S, Nguyen N, Warnow T, Carpenter E, Matasci N, Ayyampalayam S, Barker MS, Burleigh JG, Gitzendanner MA, et al. 2014. Phylotranscriptomic analysis of the origin and early diversification of land plants. Proceedings of the National Academy of Sciences of the United States of America. 11(45):4859–4868. https://doi.org/10.1073/pnas.1323926111.

Wiedemann G, van Gessel N, Köchl F, Hunn L, Schulze K, Maloukh L, Nogué F, Decker EL, Hartung F, Reski R. 2018. RecQ helicases function in development, DNA repair, and gene targeting in *Physcomitrella patens*. The Plant Cell. 30(3):717–736. https://doi.org/10.1105/tpc.17.00632.

Wilkinson DM, Koumoutsaris S, Mitchell EAD, Bey I. 2012. Modelling the effect of size on the aerial dispersal of microorganisms. Journal of Biogeography. 39(1):89–97. https://doi.org/10.1111/j.1365-2699.2011.02569.x.

Wisz MS, Pottier J, Kissling WD, Pellissier L, Lenoir J, Damgaard CF, Dormann CF, Forchhammer MC, Grytnes J-A, Guisan A, et al. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biological Reviews. 88(1):15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x.

Wu L, Fu S, Wang X, Chang X. 2020. Mapping of atmospheric heavy metal deposition in Guangzhou city, southern China using archived bryophytes. Environmental Pollution. 265:114998. https://doi.org/10.1016/j.envpol.2020.114998.

Wu ETY, Liu Y, Jennings L, Dong S, Davies TJ. 2021. Detecting the phylogenetic signal of glacial refugia in a bryodiversity hotspot outside the tropics. Diversity and Distributions. https://doi.org/10.1111/ddi.13449.

Zackrisson O, DeLuca TH, Gentili F, Sellstedt A, Jäderlund A. 2009. Nitrogen fixation in mixed *Hylocomium splendens* moss communities. Oecologia. 160(2):309. https://doi.org/10.1007/s00442-009-1299-8.

Zamfir M, Goldberg DE. 2000. The effect of initial density on interactions between bryophytes at individual and community levels. Journal of Ecology. 88:243–255. https://doi.org/10.1046/j.1365-2745.2000.00442.x.

Zanatta F, Engler R, Collart F, Broennimann O, Mateo RG, Papp B, Muñoz J, Baurain D, Guisan A, Vanderpoorten A. 2020. Bryophytes are predicted to lag behind future climate change despite their high dispersal capacities. Nature Communications. 11(1):5601. https://doi.org/10.1038/s41467-020-19410-8.

Zanatta F, Patiño J, Lebeau F, Massinon M, Hylander K, de Haan M, Ballings P, Degreef J, Vanderpoorten A. 2016. Measuring spore settling velocity for an improved assessment of dispersal rates in mosses. Annals of Botany. 118(2):197–206. https://doi.org/10.1093/aob/mcw092.

Zanatta F, Vanderpoorten A, Hedenäs L, Johansson V, Patiño J, Lönnell N, Hylander K. 2018. Under which humidity conditions are moss spores released? A comparison between species with perfect and specialized peristomes. Ecology and Evolution. 8(23):11484–11491. https://doi.org/10.1002/ece3.4579.

Zellweger F, De Frenne P, Lenoir J, Rocchini D, Coomes D. 2019. Advances in microclimate ecology arising from remote sensing. Trends in Ecology and Evolution. 34(4):327–341. https://doi.org/10.1016/j.tree.2018.12.012.

Zettlemoyer MA, McKenna DD, Lau JA. 2019. Species characteristics affect local extinctions. American Journal of Botany. 106(4):547–559. https://doi.org/10.1002/ajb2.1266.

Zhang J, Fu X-X, Li R-Q, Zhao X, Liu Y, Li M-H, Zwaenepoel A, Ma H, Goffinet B, Guan Y-L, et al. 2020. The hornwort genome and early land plant evolution. Nature Plants. 6(2):107–118. https://doi.org/10.1038/s41477-019-0588-4.

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?