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Antarctic bryophyte research—current state and future directions

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Abstract

Botany is one of the oldest sciences done south of parallel 60 °S, although few professional botanists have dedicated themselves to investigating the Antarctic bryoflora. After the publications of liverwort and moss floras in 2000 and 2008, respectively, new species were described. Currently, the Antarctic bryoflora comprises 28 liverwort and 116 moss species. Furthermore, Antarctic bryology has entered a new phase characterized by the use of molecular tools, in particular DNA sequencing. Although the molecular studies of Antarctic bryophytes have focused exclusively on mosses, molecular data (fingerprinting data and/or DNA sequences) have already been published for 36 % of the Antarctic moss species. In this paper we review the current state of Antarctic bryological research, focusing on molecular studies and conservation, and discuss future questions of Antarctic bryology in the light of global challenges.

Keywords: Antarctic flora, conservation, future challenges, molecular phylogenetics, phylogeography

Introduction

The Antarctic is the most pristine, but also most extreme region on Earth in terms of environmental conditions. It is geopolitically defined as comprising all lands and waters south of 60 °S, and can be biogeographically divided into the Maritime Antarctic zone and the Continental Antarctic zone (Ochyra *et al.* 2008).

Antarctica is currently administered by the Antarctic Treaty and related agreements (Antarctic Treaty System). In 1959, twelve countries originally signed the Treaty, banning the commercial and military use of Antarctica as well as nuclear tests and garbage disposal. The importance of protecting the Antarctic environment was reinforced by the Protocol on Environmental Protection to the Antarctic Treaty (Madrid Protocol) in 1998. The Antarctic Treaty also clearly states that a country has to demonstrate its interest in the region by means of performing significant scientific research in order to achieve a consultative status, i.e. having voting rights over the region.

Antarctic scientific research is organized in different ways by the consultative members, e.g. by Antarctic Institutes (e.g. Argentina, Chile), Antarctic programs (e.g. Australia, Brazil, UK), or as part of polar programs (e.g. Netherlands). To date, 29 of the 54 countries that are party to the Treaty have a consultative status and, together with three further countries, run research facilities in Antarctica (operated during summer only or year-round). To manage the complex and expensive logistics in Antarctica, some countries rely on military support (e.g. Brazil, Chile), invest in civilian research vessels (e.g. UK, Germany) or a mix of both (e.g. Spain). Predominant research fields, such as geology, glaciology, oceanography, marine and terrestrial biology, differ between countries, but very few have focused on Antarctic vegetation, in particular bryophytes.

Only 0,18% of the Antarctic terrestrial area is ice-free in summer (Burton-Johnson *et al.* 2016), and the extreme climatic conditions and low diversity of substrates (mostly rock, soil, bones) severely limit the formation of (vascular plant) vegetation. In the Maritime Antarctic, which south of 60 °S comprises the archipelagoes of the South Shetland Is. and South Orkney Is. as well as parts of the west coast of the Antarctic Peninsula, conditions are less severe, and the vegetation is more diverse and abundant than in the much harsher Continental Antarctic with only 24 species (Ochyra *et al.* 2008). In the latter, bryophytes can be found, e.g. in melt pools and streams, in rock fissures, and on geothermal

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ground, which is one of the main habitats for Antarctic liverworts (Bednarek-Ochyra *et al.* 2000). However, some ice-free areas of Continental Antarctica are near the cold-arid limit for life, where bryophytes only survive as part of hypolithic communities associated with the underside of translucent quartz rocks (Khan *et al.* 2011).

While overall plant diversity decreases with increasing latitude, the relative diversity of bryophytes compared to vascular plants increases in the polar regions, most drastically so in the Antarctic. In contrast to only two native flowering plants, *Deschampsia antarctica* E.Desvaux (1854: 338) (Antarctic hairgrass, Poaceae) and *Colobanthus quitensis* (Kunth 1823: 19) Bartling (1831: 13) (Caryophyllaceae) as well as one invasive grass (*Poa annua* L. 1753: 68), 116 species of mosses (Ochyra *et al.* 2008; Ellis *et al.* 2013a, 2013b; Sollman 2015; Câmara *et al.* 2019a) and 28 species of liverworts (Bednarek-Ochyra *et al.* 2000, Suárez *et al.* 2019) are recorded from Antarctica, which form a major component of the Antarctic terrestrial vegetation.

The history of Antarctic bryology as well as problems and advances of bryological research in Antarctica have previously been discussed by Greene (1964, 1967), Ando (1979) and Seppelt *et al.* (1998). Thereafter, Ochyra *et al.* (2008) updated and extended the knowledge on the Antarctic moss flora in terms of botanical history, taxonomy and biogeography, including early molecular data based on DNA fingerprinting. Since then, phylogenetic reconstructions from DNA sequences have had a considerable impact on our understanding of polar bryophyte diversity. Most recently, Câmara & Carvalho-Silva (2020) published an overview on botanical research in Antarctica, focusing on the role of Brazil.

The polar regions face the accelerating threats of global climate change. As Lewis *et al.* (2017a) discussed for the Arctic, the development of strategies for ecosystem conservation and management in the face of climate change is hindered by knowledge gaps in Arctic bryology. Since this may be true for the Antarctic as well, here we present an update on the current state of Antarctic bryological research, focusing on molecular studies and conservation, and discuss future research questions of Antarctic bryology in the light of global challenges.

Antarctic bryophyte diversity—Recent history and current state of knowledge

The 'classical' knowledge on the taxonomy and species diversity of Antarctic bryophytes is largely based on the collections and scientific work of relatively few professional botanists, taxonomists and ecologists, starting from Joseph Dalton Hooker, more than 180 years ago, and later especially Stanley Greene (1928–1989), Royce Longton, Ronald I. Lewis Smith, Rod Seppelt, Ryszard Ochyra, Halina Bednarek-Ochyra, and Peter Convey. Many years of collecting and taxonomic work resulted in the comprehensive *Illustrated Moss Flora of Antarctica* (Ochyra *et al.* 2008), which serves as main reference for the Antarctic moss flora. Less attention has been given to the Antarctic liverwort flora, despite the likewise important publication *The Liverwort Flora of Antarctica* (Bednarek-Ochyra *et al.* 2000). Liverworts are not only less diverse in Antarctica, they can also be more easily missed during field collecting than many moss species, due to their small size and stems growing intermingled with mosses.

The knowledge comprised in Bednarek-Ochyra *et al.* (2000) and Ochyra *et al.* (2008) may suggest that little remains to be studied about the Antarctic bryophyte flora. On the contrary, the knowledge from these two atlases form a foundation for addressing remaining taxonomic problems and interpret new results from floristic and taxonomic studies (e.g. Li *et al.* 2009; Kurbatova & Ochyra 2012; Ellis *et al.* 2013a, 2013b; Sollman 2015; Suárez *et al.* 2019), and especially molecular studies, considering that both books were published before the more intensive use of DNA sequence data from Antarctic bryophytes.

The use of molecular tools to study Antarctic bryophyte diversity started in the 1990's, initially applying isozymes (Melick *et al.*1994) or isozymes together with Random Amplified Polymorphic DNA (RAPD) fingerprinting (Adam *et al.* 1997). The latter technique was extensively used in a number of papers by Australian researchers P. M. Selkirk, M. L. Skotnicki and collaborators (Dale *et al.* 1999; Selkirk *et al.* 1997, 1998; Skotnicki *et al.* 1997, 1998a, 1998b, 1998c, 1999a, 1999b, 2000, 2001, 2002, 2004a, 2004b). Skotnicki *et al.* (2000) summarized the inferences made from RAPD analysis until then. They concluded that the method was suitable to infer population-level genetic diversity, analyse dispersal patterns, such as long-distance dispersal events by air and localized dispersal by meltwater streams in several moss species, and identify unknown plant material such as moss protonema. Subsequent studies (partly combining RAPD and ITS sequence data) indicated, for example, single colonization events of moss populations on isolated geothermal grounds in Continental Antarctica (Skotnicki *et al.* 2001, 2002). The high levels of genetic diversity within moss colonies, as observed in the RAPD studies, were initially ascribed mainly to mutagenesis (Skotnicki *et al.* 2000, 2004b). However, it was revealed that RAPD studies had incorrectly reported high levels of genetic diversity, likely due to contaminants (Stevens *et al.* 2007), and the RAPD method has not been used for Antarctic mosses ever since. In fact, microsatellite data revealed that *Ceratodon purpureus* (Hedwig 1801: 36) Bridel (1826: 480) populations from Continental Antarctica display less intra-population genetic diversity than populations from temperate and sub-Antarctic sites, as opposed to RAPD data (Clarke *et al.* 2008, 2009). Populations of *Sanionia uncinata* (Hedwig (1801: 289) Loeske (1907: 309) showed similar or lower mean values for intra-population genetic diversity as other, non-Antarctic moss species based on Amplified Fragment Length Polymorphism (AFLP) fingerprinting (Hebel *et al.* 2018).

The nuclear ribosomal internal transcribed spacer (nrITS) region became the first DNA sequence marker to be used in Antarctic bryophytes, either together with RAPD (Skotnicki *et al.* 2002, 2004a, 2004b; Stevens *et al.* 2007), as a single marker (Skotnicki *et al.* 2005, 2012; Pisa *et al.* 2014; Biersma *et al.* 2018a), together with other nuclear markers (phy2: Hills *et al.* 2010; 18S: Khan *et al.* 2011; Liu *et al.* 2014), or, most frequently, in combination with one or more chloroplast markers (Hedenäs 2012; Kato *et al.* 2013; Biersma *et al.* 2017, 2018b, 2020; Rankin *et al.* 2017; Saługa *et al.* 2018; Câmara *et al.* 2019a, 2019b; Zaccara *et al.* 2020). Most frequently sequenced chloroplast markers were *trn*L-*trn*F and *trn*S-*rps*4, followed by *rpl*16, *atp*B-*rbc*L, *trn*G, and *atp*H-*atp*I (see Stech & Quandt 2010 for detailed descriptions of these markers, except *atp*H-*atp*I which has only rarely been used for bryophytes, starting with Piñeiro *et al.* 2012).

The 'DNA sequence era' is characterized by a diversification in terms of research groups and institutions (including the authors of this review), participation of a new generation of scientists contributing to study Antarctic bryophyte diversity, and broader research aims and geographic focus in many studies. Studies on global phylogeographic patterns focused on cosmopolitan species (*Bryum argenteum* Hedwig (1801: 181), Pisa *et al.* 2014; Zaccara *et al.* 2020; *Ceratodon purpureus*, Biersma *et al.* 2020) and especially on bipolar species. Bipolarity, i.e., species with occurrence in both polar (Arctic and Antarctic) and cool-temperate regions, with or without intermediate occurrences in tropical mountain areas, is quite a common phenomenon in Antarctica, with about 45% of its flora being bipolar, including some of the most common species (Ochyra *et al.* 2008). Recent molecular phylogenetic analyses supported the monophyly of a number of bipolar moss species (*Polytrichastrum alpinum* (Hedwig 1801: 92) G.L. Smith (1971: 37) and three species of *Polytrichum* Hedwig (1801: 88), Biersma *et al.* 2017; *Schistidium rivulare* (Bridel 1801: 276) Podp., Biersma *et al.* 2018a) and suggested a Holarctic origin for all of them except *Polytrichum juniperinum* Hedwig (1801: 89), (Biersma *et al.* 2017). In *Sanionia* Loeske (1907: 309) (Hedenäs 2012), the (molecular) species delimitations were less clear, but Northern Hemisphere origins of Southern Hemisphere populations of the bipolar *S. uncinata* were inferred as well. A corresponding pattern of Northern Hemisphere origins of sub-Antarctic populations was observed in the bipolar *Cinclidium stygium* Swartz (1803: 27) (Piñeiro *et al.* 2012) and *Tetraplodon fuegianus* Bescherelle (1885: 64) (Lewis *et al.* 2017b). Another important phylogeographic inference based on molecular data of the cosmopolitan or bipolar species was that the contemporary Antarctic moss flora is a mix of both relictual survivors of the last glacial maximum and recent colonists from multiple long-range dispersal events (Pisa *et al.* 2014; Biersma *et al.* 2017, 2018a, 2018b, 2020). In *Ceratodon purpureus*, both an ancient Antarctic clade as well as several genotypes more recently introduced in Antarctica were observed (Biersma *et al.* 2020). Different inferences were made concerning connectivity within Antarctica. For example, Biersma *et al.* (2018a) suggested that the mountainous spine on the Antarctic Peninsula forms a strong barrier to gene flow in *Schistidium antarctici* (Cardot 1906: 15) L.I.Savicz & Smirnova (1965: 252), whereas Zaccara *et al.* (2020) inferred strong connectivity and the existence of intra-Antarctic dispersal routes for *Bryum argenteum*.

As mentioned before, bryophyte plants in the Antarctic grow under extreme environmental conditions, and consequently are very difficult to identify by a traditional morphological approach. DNA sequencing has proven a powerful tool for species identification as well as to understand species delimitations and relationships. Molecular species identification (DNA barcoding) has been applied to mosses in aquatic (Antarctic lakes, Kato *et al.* 2013; Rankin *et al.* 2014), terrestrial (Liu *et al.* 2014) and saxicolous (Khan *et al.* 2011) habitats.

Phylogenetic analyses and the use of a molecular species delimitation method (Automatic Barcode Gap Discovery, ABGD; Puillandre *et al.*, 2012) provided additional insights into Antarctic *Schistidium* Bruch & Schimper (1845: 1) (Biersma *et al.* 2018a) and *Bartramia* Hedwig (1801: 164) (Câmara *et al.* 2019a), including a potential new species of *Schistidium* in South Georgia and southern Chile (Biersma *et al.* 2018a) and *Bartramia subsymmetrica* Cardot (1906: 8) new to Antarctica (Livingston Island; Câmara *et al.* 2019a). However, ABGD may also tend to overlump species compared to phylogenetic analysis, as observed in *Bartramia* (Câmara *et al.* 2019a), and further comparative analyses of automated species delimitation methods may be needed. Furthermore, analyses of molecular variation have allowed for a better understanding of the effects of such extreme environmental conditions on morphological plasticity (Câmara *et al.* 2018b).

At higher taxonomic levels, the application of DNA tools resulted in separating the bipolar species *Hypnum revolutum* (Mitten 1859: 97) Lindberg (1866: 542) in a new moss genus (*Roaldia* P.E.A.S. Câmara & Carvalho-Silva 2018: 257) and its transfer from Hypnaceae Schimper (1856: 113) to Pylaisiaceae Schimper (1860: 518) (Câmara *et al.* 2018). Taxonomic changes from phylogenetic studies not addressing Antarctic species directly impact on the family composition of the Antarctic moss flora as well. Compared to Ochyra *et al.* (2008), these include transfers between families of *Amphidium* Schimper (1856: 39) (Dicranaceae Schimper (1856: 11) to Amphidiaceae Stech (2008: 14), *Campylopus* Bridel (1819: 71) (Dicranaceae to Leucobryaceae Schimper (1856: 19), *Kiaeria* I.Hagen (1915: 109) (Dicranaceae to Rhabdoweisiaceae Limpricht (1886: 271), *Distichium* Bruch & Schimper (1846: 153) (Ditrichaceae Limpricht (1887: 482) to Distichiaceae Schimper (1860: 135)), *Holodontium strictum* (Hooker f. & Wilson 1844: 540) Ochyra (1993: 84) and *Hymenoloma* Dusén (1905: 19) (Seligeriaceae Schimper (1856: 22) to Hymenolomataceae Ignatov & Fedosov (2016: 128)), *Leptobryum* (Bruch & Schimper) Wilson (1855: 219) (Bryaceae Schwägr. (1830: 47) to Meesiaceae Schimper (1856: 82)), *Pohlia* Hedwig (1801: 171) and *Schizymenium* Harvey (1838: 384) (Bryaceae to Mniaceae Schwägrichen (1830: 25)), *Sanionia* (Amblystegiaceae G.Roth (1899: 6) to Scorpidiaceae Ignatov & Ignatova (2004: 942)), *Warnstorfia* Loeske (1907: 310) (Amblystegiaceae to Calliergonaceae Vanderpoorten, Hedenäs, C.J.Cox & A.J.Shaw (2002: 120)) as well as *Isopterygiopsis* Z.Iwatsuki (1970: 379) and *Platydictya* Berkeley (1863: 145) (Hypnaceae to Plagiotheciaceae M.Fleischer (1912: 748)) (Frey & Stech 2009 and references therein, Fedosov *et al.* 2016a, 2016b, 2020). Nine of these families represent new families for Antarctica. Except for Mniaceae, they all belong to the two largest moss lineages, the Dicranidae (Amphidiaceae, Distichiaceae, Hymenolomataceae, Leucobryaceae, Rhabdoweisiaceae) or the Hypnales (Calliergonaceae, Pylaisiaceae, Scorpidiaceae), respectively, and were resurrected or newly described based on molecular phylogenetic inferences. The polyphyly of *Ditrichum* and the Ditrichaceae (Fedosov *et al.* 2016a) may lead to further taxonomic changes involving the Antarctic species, however, the taxonomic diversity of Antarctic mosses at family level is already much more accurate due to the insights from molecular data.

So far, molecular studies of Antarctic bryophyte species have focused exclusively on mosses. Molecular data (fingerprinting data and/or DNA sequences) have been published for 31 (36 %) of the 116 Antarctic moss species (Fig. 1). The cosmopolitan species *Bryum argenteum* and *Ceratodon purpureus* were studied most frequently, followed by the bipolar species *Bryum pseudotriquetrum* (Hedwig 1801: 190) G.Gaertner, B.Meyer & Scherbius (1802: 102). The majority of species have, however, only been included in a single study (Fig. 1).

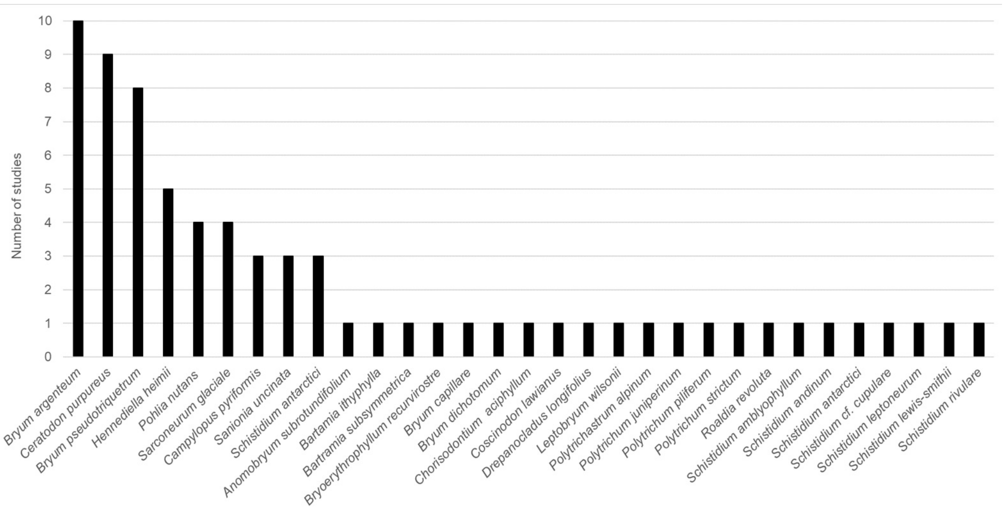

FIGURE 1. Antarctic moss species for which molecular data (fingerprinting and/or DNA sequence data) are available, and numbers of studies addressing these species.

With the advances in sequencing technology, the first studies using Next Generation Sequencing (NGS) for Whole Genome Sequencing (WGS) of organellar genomes of Antarctic bryophyte species (Freitas *et al.* 2018; Park *et al.* 2018; Byun *et al.* 2019; Kim *et al.* 2019) were published. Currently, the use of NGS for eDNA metabarcoding of environmental samples (soil, air) is starting up as well. Recent studies on algae (Câmara *et al.* 2021) and fungi (Rosa *et al.* 2020) detected yet unknown diversity in the soil at a protected and a human-impacted site on Deception Island, South Shetland Islands, and demonstrated that important differences exist between both sites in terms of diversity, richness, and abundance of algal and fungal taxa. The detection of DNA of non-native taxa highlighted concerns about human impacts, primarily through tourism and research operations, on future biological colonization processes in Antarctica. Ongoing studies of air and soil samples are expected to provide a better understanding of dispersal and colonization processes of bryophytes in Antarctica as well (own unpublished data), which may be facilitated by an increase in ice-free areas due to climate change.

Conservation of Antarctic bryophyte diversity

There are currently 71 Antarctic Specially Protected Areas (ASPAs), of which the terrestrial ones vary in size between 0.03 and 91.76 km^2, and seven mostly (much) larger Antarctic Specially Managed Areas (ASMAs) with ca 30,246 km^2. Of these, 18 mention mosses or liverworts in the summary description in the Antarctic Protected Areas Database (https://www.ats.aq/devph/en/apa-database). Furthermore, areas destined to protect other values may also end up protecting the bryophyte flora, and the ASPA management plans provided in the database may give more details on bryophytes worth of protection. For example, ASPA 140, in Deception Island (South Shetland Islands), is divided into 11 subsites, most of them created to protect some unique aspect of the local island flora. Although bryophytes are not mentioned in the summary, subsite E (Stonethrow ridge), for example, is designated to protect "several very rare mosses, liverworts and lichens" according to its management plan. Currently, 15 Antarctic Conservation Biogeographic Regions (ACBRs), originally proposed in 2012 and representing biologically distinct ice-free areas (a 16th ACBR was proposed by Terauds & Lee 2016), are used as an important tool in Antarctic science, conservation, management and policy, e.g. in proposing new ASPAs (Terauds & Lee 2016).

However, Coetzee *et al.* (2017) pointed out that the network of terrestrial protected areas of Antarctica should be expanded since the ASPAs are generally small, unrepresentative of the continent's biodiversity, and subject to a range of pressures, including local human (research) activities (Hughes *et al.* 2013). Yet little is known about how effective the ASPAs or ASMAs actually are in protecting the local bryophyte flora, since generally few studies have focused on monitoring of bryophyte populations and comparison of species composition through time in Antarctica (e.g. Wasley *et al.* 2012; King 2017; Robinson *et al.* 2018; Câmara *et al.* 2020). These studies demonstrated that changes in the composition of local moss floras occur and could be linked with environmental changes, in particular climatic changes. Observations such as an increase in populations size of cosmopolitan species (*Bryum pseudotriquetrum* and *Ceratodon purpureus*) at the expense of the Antarctic endemic *Schistidium* (King 2017; Robinson *et al.* 2018) and disappearance of species from local communities (Câmara *et al.* 2020) not only indicate the importance of monitoring populations over long periods of time, but may also indicate the need of threat assessment of Antarctic bryophyte species. So far there is no Red List of threatened plant species in Antarctica, and the flora has been generally considered to be at low threat. This, however, may not be true for all species, especially not for the rare or very rare species, which together comprise 40 % of the Antarctic moss flora (Ochyra *et al.* 2008) and 67% of the Antarctic liverwort flora (Bednarek-Ochyra *et al.* 2000).

Knowledge on the distribution and population sizes of species is obviously important to make accurate threat assessments, which will mainly rely on the existing floras (Bednarek-Ochyra *et al.* 2000; Ochyra *et al.* 2008), complemented by new data. For example, recent fieldwork and morphological identification allowed the expansion of geographical ranges of several Antarctic bryophyte species (Henriques *et al.* 2018; Câmara *et al.* 2017; Suarez *et al.* 2019). Furthermore, intraspecific molecular analyses allow scientists to incorporate genetic diversity in conservation planning and threat assessment. While DNA sequence variation was found to be low in some Antarctic moss species, e.g. the bank-forming *Chorisodontium aciphyllum* (Hooker f. & Wilson 1844: 541) Brotherus (1924: 205) (Biersma *et al.* 2018b), other species like *Bryum argenteum*, *Ceratodon purpureus, Polytrichum juniperinum* and *Schistidium antarctici* show a considerable genetic diversity in Antarctica, including Antarctic exclusive haplotypes (Pisa *et al.* 2014; Zaccara *et al.* 2020; Biersma *et al.*, 2017, 2018a, 2020). The use of both traditional and molecular approaches is therefore useful to assess biodiversity and provide data for decision making processes on conservation.

Future challenges

Antarctic ecosystems face increasing threats due to global environmental change, despite their remoteness and formal protection status (Bergstrom *et al.* 2021). Invasive species are a matter of concern as they pose big threats to the native local flora, as are pollution, tourism as well as current (fishery) and possible future economic exploitation (e.g. Chown *et al.* 2012). The latter should not be underestimated, since the region holds about 70 % of the world's freshwater resources as well as yet untouched fossil energy (oil, gas, coal) and mineral (e.g., chromium, copper, gold, iron ore) resources, and the ban on mineral exploitation by the Antarctic Treaty may be revised in 2048.

To better understand the importance of bryophytes for the Antarctic terrestrial ecosystem, assess the impact of the diverse threats on the Antarctic bryophyte diversity and vegetation, and further develop conservation measures, several research strategies and knowledge gaps should be addressed.

Like in the Arctic (Lewis *et al.* 2017a), access to collections is still a challenge for Antarctic research. There are few institutions that house significant plant collections from Antarctica, including herbaria BM, BR, PC, NY and US for historical collections and AAS, HO, KRAM and UB for more recent ones, not all are (fully) digitalized and available online. For example, of 6206 occurrences of Antarctic mosses on GBIF (www.gbif.org; search parameters: administrative areas: Antarctica, scientific name: Bryophyta, occurrence status: present, basis of record: preserved specimen; accessed 15-10-2020), 5291 (85%) were retrieved from herbaria AAS (British Antarctic Survey Antarctic Plant Database), HO and UB.

There may also be (sometimes rare) collections from more remote and inaccessible areas, usually obtained for ecological or chemical studies, that are not properly deposited in a regular collection, making it difficult to access them for systematic research. It is of paramount importance that Antarctic collections are properly deposited and curated in herbaria, and made available to everyone online. As already pointed out by Lewis *et al.* (2017a), existing collections remain an important considering the high logistics costs associated with polar expeditions to collect new material. Online specimen information for GIS-based research and physical specimens for taxonomic and molecular research, (in particular, NGS approaches that enable the generation of short sequences from old plant material), would foster Antarctic bryology (and polar bryology in general) considerably.

The high costs and complexity of Antarctic logistics, and also the need to comply with the Madrid Protocol for Environmental Protection, and to keep up the Antarctic Treaty spirit of collaboration among parties, make the international collaboration of countries and the bryological community very important, both in sharing logistics and in science. Some countries like Brazil require that a proposal demonstrates the interactions with other research groups within the Treaty parties in order to secure funds. Unfortunately, nowadays there are very few bryologists actively working on Antarctic bryophytes, especially in systematics and taxonomy. There are, however, a considerable number of scientists using Antarctic mosses in studies of ecology, biochemistry, plant physiology, and other scientific areas, which are not the focus of this review.

In terms of species delimitation, relationships and genetic diversity, one obvious knowledge gap is that only about one third of the Antarctic moss species and none of the liverwort species have so far been studied based on molecular data. Furthermore, the studied moss species are unevenly distributed taxonomically. Data on relatively species-rich and taxonomically complex families like Brachytheciaceae, Ditrichaceae, and especially Pottiaceae are still rare, but also Bryaceae are still represented by only few species in the molecular studies. Pottiaceae and Bryaceae in particular contain species of which Antarctic material is difficult to identify based on (gametophytic) morphological characters (Ochyra *et al.* 2008). Given the results of the recent genus-level studies discussed above (Biersma *et al.* 2018a, Câmara *et al.* 2019a), molecular analyses of extended taxon samplings of other genera will likely result in further taxonomic changes and a more accurate assessment of the bryophyte species diversity in Antarctica. One limiting factor, however, may be the availability of collections from rare or very small species that are suitable for DNA sequencing, such as the bipolar *Platydictya jungermannioides* (Bridel 1812: 255) H.A.Crum (1964: 60), the smallest moss species in Antarctica (Ochyra *et al.* 2008), and several liverwort species (Bednarek-Ochyra *et al.* 2000).

To better understand the geographic and evolutionary origins, and patterns of diversification, of the Antarctic bryophyte flora, further taxa from all main phytogeographic elements (Antarctic endemic, sub-Antarctic, south-temperate, bipolar, and cosmopolitan; Ochyra *et al.* 2008) should be studied by phylogenetic and phylogeographic analyses with appropriate global sampling. At the same time, further analyses of intraspecific genetic variation are needed to understand (i) the role of gene flow (by dispersal to and within Antarctica) in shaping genetic structure, and the roles of historical demography (i.e., survival in refugia) versus local adaptation (as a result of ongoing selective pressure by ecological conditions) in shaping extant diversity (Kennicutt *et al.* 2014, Lewis *et al.* 2017a, Zaccara *et al.* 2020). These questions are particularly important in the light of the contemporary global climate change. Antarctic species may benefit from modest warming and newly available, ice-free terrestrial areas, however, potentially at the expense of loss of genetic diversity and competition by non-native species (Siegert *et al.* 2019). Specimen-based analyses are necessary to infer the present genetic diversity of Antarctic bryophyte species, as a baseline to monitor future changes. Such data should be complemented by eDNA metabarcoding to infer which diaspores arrive in

Antarctica by air currents and are deposited in the soil diaspore bank, and may colonize Antarctic terrestrial ecosystems under climate change.

Final remarks

By force of the Treaty, the whole Antarctic region became dedicated to science 60 years ago, and more professional botanists became involved in Antarctic research than ever before. The first peak of bryological research, characterized by taxonomic studies of newly available collections, culminated in the publication of Antarctic moss and liverwort floras. The local bryophyte flora is now well documented as a basis for ongoing and future research. Improved research facilities in Antarctica, national research programs, international collaborations, and the use of molecular tools like Sanger sequencing and eDNA metabarcoding, offer opportunities for systematic, evolutionary, ecological and biochemical studies. These will bring new insights, perspectives and, surely enough, raise new questions concerning Antarctic bryophyte diversity. Bryology in Antarctica is still far from being well understood, and progress may be challenged due to few scientists currently being dedicated to Antarctic bryophytes. However, considering the accelerating environmental changes and the geopolitical importance of science in Antarctica, together with the opportunities described above, Antarctic bryological research may reach another peak in the near future.

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