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Bryophyte Ecosystem Services:
How Bryophytes Impact Ecosystem Processes and Their Use in Urban Systems

by

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1. Introduction

As climate change and urbanization effect biodiversity and change ecosystems, understanding the relationships among species and how these relationships will change is important in developing effective conservation efforts. One powerful tool to estimate the effects of climate change on biodiversity has been the use of empirical niche models to identify exposure to climate change (Schwartz 2012). However, because climate change and its effects on biodiversity is a complex issue, examining vulnerability, exposure, sensitivity, and adaptive capacity of a species or population is necessary to accurately predict losses and plan conservation methods (Dawson et al. 2011). Therefore, it is critical to research species' sensitivities, vulnerability, and ability to adapt in order to potentially mitigate the effects of climate change over the next century particularly for understudied groups.

Bryophytes, which include mosses, liverworts, and hornworts, are one understudied group of plants and expected to be negatively impacted by climate change and land use changes. Bryophytes are non-vascular plants (without roots or xylem to move water through their stems); they are poikilohydric (they have the inability to regulate water content independently of their environment); and they reproduce by spores rather than by seeds. However, research regarding the effects of climate change on plants and land use changes is heavily skewed towards vascular plants (e.g., flowering plants and conifers). Due to differences between bryophytes and vascular plants, such as size differences and the life strategy of bryophytes, studies on vascular plants cannot be used to predict the response of bryophytes to climate change (He et al. 2016, Turetsky 2003, Zanatta et al. 2020). Although many bryophytes are desiccation tolerant (the ability to withstand long periods of dryness), He et al. (2016) suggests that temperate species of bryophytes may only tolerate a 2-3°C increase in temperature before photosynthetic rates will be negatively impacted. Climate change is not the only threat to bryophytes though. Research

suggests that bryophyte diversity will decrease in areas where development and habitat degradation occur (Gignac 2001, Pykälä 2019). Despite the gap in research compared to vascular plants, bryophytes represent the second largest group of green land plants after flowering plants with approximately 20,000 species (Patiño & Vanderpoorten 2018) and a nearly global distribution (Gignac 2001, Pharo & Zartman 2007).

Although bryophytes may be small and inconspicuous compared to many vascular species, that does not imply that they are less important than vascular plants in their communities. Many bryophyte species, such as *Sphagnum* species (Jassey et al. 2013), are ecosystem engineers (organisms that modify their environment to create habitat) which can help to maintain community biodiversity (Gavini et al. 2019). In addition, bryophytes provide important ecosystem services such as altering nutrient availability and cycling carbon and water (Turetsky 2003). Bryophytes can benefit humans directly as well. Bryophytes have been used as a garden substrate in countries like Japan and have been used by Indigenous peoples as medicine (Glime 2017, Martin 2015). Although more research is needed, bryophytes may be useful as green roof vegetation (Anderson et al. 2010, Glime 2017), as bioindicators (Govindaparyi 2010, Koroleva 2020, Oishi & Hiura 2017, Shi et al. 2017), in horticulture (Glime 2017, Martin 2015), and in modern medicine (Decker & Reski 2020). Given that their future in the face of climate change remains unclear, conservation efforts will be needed to assure that bryophyte ecosystem services are not significantly reduced. Generating interest in bryophytes through their benefits to humans may be an effective conservation strategy.

2. Bryophyte Ecosystem Services in Natural Systems

Bryophytes are considered ecosystem engineers that strongly influence ecosystem processes. In natural systems, these services include but are not limited to global nutrient and carbon cycling (Cornelissen et al. 2007, Crowley and Bedford 2011, Porada et al. 2013, Turetsky 2003), regulation of soil temperature (Gornall et al. 2007, Sun et al. 2017), water retention (Gignac 2001, Michel et al. 2013, Turetsky et al. 2012), and maintenance of community level biodiversity (Buchholz 2016, Cornelissen et al. 2007, Crowley and Bedford 2011, Gavini et al. 2019, Glime 2017). It is important to understand the extent to which bryophytes influence these processes and how losses to diversity and biomass of bryophytes could have cascading effects for communities. The following will explore the role of bryophytes in carbon cycling, water cycling, nutrient cycling, and community level biodiversity.

2.1 Carbon Cycling

Carbon cycling occurs as carbon from the atmosphere moves to reservoirs such as the ocean, organisms, soil, and rocks. Like vascular plants, bryophytes influence this cycle through their growth and metabolic processes such as photosynthesis and respiration (Turetsky 2003). Net primary production (the rate at which biomass is stored; NPP) represents the difference between the carbon gained through photosynthesis and carbon lost through respiration; this difference can be used to determine the amount of carbon stored by plants (Bowman et al. 2017). A global estimate of NPP is an important parameter to determine because it quantifies the carbon cycle and storage of plants and informs predictions of the effects of climate change (Ito 2011). A study on three moss species' NPP in a subarctic system found that twenty-five percent of the system's carbon was stored by non-vascular plants (Campioli et al. 2008). While the NPP of vascular plants has been studied intensely (Gower et al. 2001, Potter et al. 2012, Xing et al. 2010),

research on the NPP of bryophytes and how climate change will impact their role in carbon cycling remains understudied particularly for tropical species.

Peatland, terrestrial wetland ecosystems that are often dominated by mosses, serve as important carbon sinks that hold at least 20 percent of stored carbon in terrestrial systems despite representing approximately 2.84 percent of total terrestrial land (4.23 million km²) (Bragazza et al. 2006, Heijmans et al. 2008, Xu et al. 2018). Many dominant mosses in cool peatlands are in the genus *Sphagnum* (also known as peat mosses), but understanding whether climate change will increase or decrease carbon storage in *Sphagnum* peatlands depends on a broad understanding of these complex systems. A model based on vegetation changes of peatlands in Denmark and the UK by Heijmans et al. (2008) found that colonization by vascular plants as peat decomposition occurs may prevent these ecosystems from ultimately becoming carbon sources in the future. However, a meta-analysis by Hugelius et al. (2020) of over 7,000 field analyses of northern peatlands found that warmer climate and permafrost thawing may cause peatlands to have a net warming effect especially at their southern regions. Similarly, a review of 52 field experiments on the effects of warming, nitrogen addition, and vegetations composition change on greenhouse gas emissions from peatlands found highly variable results and suggests that multiple studies across a wide range of locations is needed to understand the response of peatlands to climate change (Gong et al. 2020).

Although the carbon storage of peatlands has been studied fairly intensely, the NPP of many tropical species of bryophytes remains largely unknown (Turetsky 2003). As stated above, photosynthetic rates of temperate species of bryophytes are hypothesized to suffer as global temperatures increase (He et al. 2016). Additionally, changes in precipitation patterns are expected to impact the carbon balance of tropical bryophytes as proper hydration is needed for

growth and for preventing high respiration rates (Wagner et al. 2014). Much like peatlands in cold and temperate systems, tropical peatlands are important carbon sinks that are threatened by climate change and human activities such as land degradation (Hirano et al. 2012, Posa et al. 2011). Since the NPP for tropical bryophytes is not well researched, it is not possible to estimate the increase in CO₂ emission from these species as the climate warms. Understanding how these species will react to climate change and how this will impact the global atmospheric carbon levels is key to mitigating the harmful effects of climate change.

2.2 Water Cycling

Due to their poikilohydric nature, bryophytes act as a temporary water storage space and alter water cycling within their community (Gignac 2001, Michel et al. 2013, Turetsky et al. 2012). For example, in semiarid climates, bryophytes significantly increase soil moisture content at shallow depths (5cm) (Xiao et al. 2016). Bryophyte also regulate soil moisture through evaporation; Chen et al. (2019) found that soil water evaporation increased underneath mosses with increasing temperatures. These results suggest that mosses regulate soil temperature through evaporation similarly to how vascular plant regulate temperatures through transpiration. However, bryophytes' greatest impact on water cycling is through rainfall interception. Porada et al. (2018) found that including lichens and bryophytes in a model of global rainfall interception increase total evaporation by 61 percent compared to a model that only included vascular plants.

Rainfall interception by bryophytes has been studied intensively in tropical montane cloud forests (high altitude tropical forests which experience regular cloud immersion). Epiphytic biomass of these forests, of which bryophytes can make up to seventy-five percent, play a key role in the uptake of water from cloud cover (Gotsch et al. 2016, Lakatos 2011). Ah-Peng et al. (2017) found that two liverwort species, *Bazzania decrescens* and *Mastigophora*

dielados, stored the equivalent of 3.46 mm of rainwater through atmospheric water interception in a tropical montane cloud forest on the Mascarene Islands. Tropical montane cloud forests are expected to be negatively impacted by climate change as cloud cover moves upward and their range contracts. If cloud cover moves to locations where these communities cannot disperse to or to areas without suitable habitat, it is likely that losses to biodiversity will occur (Foster 2001). Due to their importance in capturing and storing atmospheric water, losses to bryophytes diversity and biomass could alter community level water cycling and have cascading effects on community structure in these forests. Research into how bryophytes alter the water cycling in montane cloud forests and other communities is critical to understanding their current importance in these systems as well as how their potential loss due to climate change may affect cycling in these systems.

2.3 Nutrient Cycling

In order for an ecosystem to function properly, nutrients need to be available for plants and other organisms to use. For example, nitrogen and phosphorus must be made available through fixation (de Bruijn 2015, Herridge et al. 2008) or mineralization (Bünemann 2015, Spohn & Kuzyakov 2013). However, bryophytes also have a critical role in the nutrient cycling of communities. Bryophytes are ecosystem engineers that modify abiotic and biotic factors such as soil pH, rocky substrate, and microbe biomass which can alter nutrient availability (Palozzi & Lindo 2017, Turetsky et al. 2012) A study by Crowley and Bedford (2011) found that mosses in rich fens increased phosphorus availability for other plants through redox reaction which oxidize soils and resulted in greater arbuscular mycorrhizal fungi activity. The increase in phosphorus led to more growth of vascular species suggesting that the presences of mosses increase biodiversity in rich fens through nutrient cycling. Bryophytes can also cycle phosphorus without utilizing symbionts.

Unlike most other land plants, bryophytes lack true roots and can grow on rocky surfaces. It is hypothesized that bryophytes living on rocks and in soils release weathering agents that make phosphorus available for their communities (Porada et al. 2014, Porada et al. 2016, Seppelt et al. 2016). Porada et al. (2014) estimates that bryophytes and lichens process 0.46 to 4.6 Tg of phosphorous and weather 0.06 to 1.1 km³ of rock per year.

Bryophytes are also important for global nitrogen fixation and fix nitrogen through multiple pathways. Two significant forms of fixation by bryophytes occur through atmospheric deposition and biological fixation (symbiosis with cyanobacteria) (Lindo & Whiteley 2011, Markham & Fernández Otárola 2021, Turetsky 2003). In arctic systems, mosses influence microorganisms that fix nitrogen by regulating soil temperature and moisture (Gornall et al. 2007). Similarly, Sun et al. (2017) found that the removal of bryophytes from the understory of shrubland and coniferous habitats decreased the biomass of the microbial community. Decreases in nitrogen fixing microbes could lead to lower plant growth and higher stress if the decrease is significant enough. Although a global estimation for the amount of nitrogen made available by bryophytes is not known, the nitrogen requirements (requirement and fixation estimates are usually similar) of lichens and bryophytes is estimated to be 3.5 to 34 Tg per year (Porada et al. 2014). Similarly, a study by Elbert et al. (2012) estimated the global nitrogen fixation of cryptogams (plants that reproduce by spores) and their symbiotic cyanobacteria to be 49 Tg per year. These studies suggest that bryophytes are important for global nitrogen fixation, and suggest that fixation rates are increased in ecosystems where demand for nitrogen is higher, such as deserts.

2.4. Community Biodiversity

In order to have a healthy ecosystem, a diverse range of organisms are needed to provide critical ecosystem services (Ranius et al. 2018, Thom & Seidl 2016). Biodiversity, is a measurement of the diversity of biological organisms in a system; it can measure genetic diversity within and among species across a range of scales including communities, ecosystems, or even globally (Bowman et al. 2017). In recent years, global losses to biodiversity cannot be understated; current extinction rates range from 1000 to 10,000 times higher than historic rates derived from fossil records (Barnosky et al. 2011, Singh 2002). Although extinction is a normal process, the rate at which is currently occurring is hypothesized to have negative cascading effects such as the collapse of seed dispersal (Butt et al. 2015, Pérez-Méndez et al. 2016), breakdown of plant-pollinator relationships (Pires et al. 2020, and trophic collapse (Dobson et al. 2006). With losses to biodiversity at an all-time high, research should focus not just on how to conserve individual populations and species but on how to conserve the habitats in which threatened species occur.

Bryophytes serve as a habitat for a variety of organisms. Micro and macroinvertebrates such as nematodes, rotifers, and Chironomidae are commonly found in bryophytes ranging from species that are exclusively found on bryophytes to those that associate with but do not required bryophytes to survive (Glime 2017). Additionally, symbionts such as cyanobacteria (Adams & Duggan 2008, Lindo et al. 2013) and arbuscular mycorrhizal fungi (Rimington et al. 2018, Zhang & Guo 2007) associate with bryophytes and increase nutrient availability. Birds also interact significantly with bryophytes (Chmielewski & Eppley 2019); birds rely on bryophytes as a preferred or emergency food source, a place for foraging on invertebrates, and as a nesting material (Glime 2017).

Bryophytes can also alter the communities in which they grow. A study by Rehm et al. (2019) on reforestation in Hawaii concluded that bryophytes were the most important substrate for seedling recruitment of 'ōhi'a (*Metrosideros polymorpha*) and koa (*Acacia koa*) trees. This study found that the mean seedling abundance was ten times higher for bryophytes than the second best substrate, woody leaf litter, and that in koa corridors only bryophytes supported seedlings. Soil temperature regulation by bryophytes may also keep communities with healthy levels of plant, microbe (Gornall et al. 2007), and macroinvertebrate biodiversity (Neven 2000). Warming soil temperatures have been found to decrease plant and invertebrate diversity (Robinson et al. 2018) and negatively impact the efficiency of soil microbe communities (Frey et al. 2013, Sun et al. 2017). As soil microorganisms can increase nutrient and water availability for plants (Jeffries, et al. 2013), losses to bryophyte diversity and subsequent changes to soil microorganism communities may have a larger impact to communities than currently hypothesized.

Additionally, bryophytes also alter communities through allelopathy. Allelopathy is a defense mechanism found in some plant species where secondary metabolites produced by the plant negatively impact the growth of nearby organisms (Meiners et al. 2012). Allelopathy has been observed in *Sphagnum* species (Liu et al. 2020), and allelopathic compounds have been identified in the moss species, *Rhynchostegium pallidifolium* (Kato-Noguchi et al. 2010). In forest ecosystems of New Zealand, allelopathic activity of bryophytes negatively impact tree seedlings and their growth (Michel et al. 2011). Although allelopathic activity may seem to only have negative impacts, it also has a crucial role in maintaining biodiversity by influencing plant succession, dominance, and invasion (Chou 1999, Koocheki 2013). Additionally, secondary metabolites of bryophytes that have allelopathic activity may be an alternative source of

pesticides and herbicides (Jabran et al. 2015, Latif et al. 2017, Zaynab et al. 2018). Although there is some research on the interactions with vascular plants, little research has looked at allelopathic interactions between bryophytes and non-vascular plants (Whitehead et al. 2018). In order to better understand the role of bryophytes in community biodiversity, it is important to research how their secondary metabolites are affecting the species growing around them.

Because bryophytes have such strong effects on biodiversity and community structure, future losses of bryophyte due to climate change will have large effects at the community level and these effects are already being seen in some moss communities. A good example would be the decomposition of peatlands. The range of peatland has been reduced significantly in the past century due to human activities, such as extraction, and are currently faced with the threat of climate change (Buchholz 2016, Gallé et al. 2019, Roucoux et al. 2017, Saarimaa et al. 2019). Peatlands provide habitat for many types of organisms, particularly in the order Odonata (dragonflies and damselflies) (Glimes 2017), and they contain a number of rare and specialist species, especially spiders. A study of spider assemblages in northern Germany found that different successional stages of bogs contained different assembles of spider species and that habitat specialists were negatively correlated with succession (Buchholz 2016). Sperle & Bruelheide (2021) surveyed bog species in the Black Forest of Germany from 1972 to 1980 and from 2017 to 2020. Of a total of 88 species, 37 decline during the study period and 2 went extinct; the authors concluded that higher temperatures and lower precipitation caused the decline since abundance declined the most at low elevations. These studies suggest, it is worth the effort to conserve some peatlands for specialist and rare species. Much of the research on peatland specialists has been on European bogs; however, research on tropical peatlands show that they contain unique plant assemblages and provide crucial habitat for at risk species (Posa et

al. 2011, Yule 2010). Research should aim to identify specialists in tropical or other understudied bryophyte communities as they could be at extreme risk.

3. Bryophyte Ecosystem Service in Urban Systems and Human Uses

Urban areas have drastic impacts on ecosystems in the form of habitat fragmentation and degradation (Seto et al. 2011), increased pollution (Yuan et al. 2021), increased insecticide and herbicide use (Wittmer et al. 2011), and losses to biodiversity (Shochat et al. 2010). However, there has been a growing interest in sustainability and how lessen the effects of humans and our lifestyles on the environment (Kim & Kwon 2018, Trencher et al. 2014). Bryophytes can play a role in efforts to make urban spaces and human needs more sustainable. On the one hand, bryophytes can be obstacles to a perfect lawn and roof, and unwanted bryophytes can be removed with herbicides and other means. However, these methods can have unwanted effects. For example, the cosmetic use of pesticides and herbicides is one of the main factors in the decline in insect abundance worldwide (Kawahara et al. 2021). Instead of removing bryophytes with environmentally damaging methods, there are beneficial ways to utilize them in urban spaces such as in green roofs, as bioindicators, and for humans benefits such as medicine and for horticulture.

3.1 Green Roofs

The use of green roofs is one topic related to sustainability that has generated interest in urban areas. Green roofs can help mitigate the negative effects of urbanization in cities. Benefits of green roofs include stormwater retention with improved water quality (Razzaghmanesh et al. 2014; Rowe 2011), reduced urban heat island effect (Razzaghmanesh et al. 2016; Susca et al. 2011), and improved urban biodiversity for insects, birds, and other organisms (Colla et al. 2009;

MacIvor & Lundholm 2001). Bryophytes may serve as a useful substrate for green roofs alone or in combination with other plants as they can spontaneously colonize roofs, are primary colonizers, and are desiccation tolerant (Anderson et al. 2010). Another benefit of using bryophytes is that they do not require fertilizer and may need less maintenance than other types of green roof vegetation (Glime 2017, Martin 2015). A study by Heim et al. (2014) on green roofs in Nova Scotia, Canada found that planting moss alongside *Festuca rubra*, a grass species, resulted in the grass species having a higher growth rate. This suggests that mosses may help a greater diversity of plants grow on green roofs. Because bryophytes are desiccation tolerant, they may be a good substrate choice in regions that experience arid weather where traditional green roof vegetation may struggle to survive drought. However, not all bryophyte species are equally suited for use as green roof substrate. Most bryophytes grow as colonies and can be classified into seven categories of life-forms (turfs, cushions, dendroids, mats, wefts, fans, and pendants) which can correlate to properties such as desiccation tolerance, light requirement, and moisture content (Bates 1998, Mägdefrau 1982, Oishi 2009). Cruz de Carvalho et al. (2019) identified 43 potential moss species for green roof in the Mediterranean basin and concluded that different moss life forms, such as turf and cushion forms, were more suitable for dry climates than other forms. Since climate change will lead to desertification in many areas, bryophytes may be a good choice as green roof substrates for their ability to dry out and remain alive. Most likely, individuals installing a green roof will not be experts in identifying bryophyte species and life-form may be an easier, more accessible way to determine if a bryophyte is well suited for their needs. Unfortunately, bryophyte life-form categories are not systematically assigned and their associated properties may not solely be a result of a species' life-form (Bates 1998). A more systematic categorization paired with quantitative data on the properties of different life-forms is

needed before suggesting what bryophyte species should be used on green roofs. Additionally, more research is needed to determine what specific species or life-forms would be best across a wide range of locations.

3.2 Bioindicators

Pollution is a serious issue for human health especially in urban areas. Pollutants can cause multiple health issues ranging from respiratory problems to cancer. Although pollution can harm anyone, research suggests that a person's socioeconomic status and race may correlate to the amount of pollutants that they are exposed to throughout their life (Gray et al. 2013, Vrijheid et al. 2012). As many of the instruments used to measure air quality and pollutants are costly, data often have low geographic resolution, and bioindicators are a cheaper alternative which can provide much needed geographic resolution to pinpoint pollution hotspots. Bryophytes, particularly epiphytic species, have been used as bioindicators to monitor heavy metals, atmospheric nitrogen deposition, and other pollutants (Govindaparyi 2010, Koroleva 2020, Oishi & Hiura 2017, Shi et al. 2017, Turetsky 2003). For example, a study by Donovan et al. (2016) used an epiphytic moss species to identify the source of cadmium pollution. Compared to traditional methods of measuring air quality, bryophytes may potentially be a cost-effective way to monitor pollutants. However, the age of the epiphytic bryophytes is often unknown which may cause issues for long term monitoring. Bryophytes on green roofs may be beneficial as bioindicators. Since the age of a green roof is known, bryophytes on green roofs could serve as bioindicators where time is a known and measurable variable. Further research is needed to determine whether this method would give comparable results to traditional instrumentation. If bryophytes on green roofs are reliable bioindicators, they would provide communities not only

with air quality monitoring but also with the benefits of green roofs such as a reduction of the urban heat island effect.

3.3 Horticulture

Although bryophytes have historically been used in horticulture as a substrate, often in the form of peat, moss gardens are slowly becoming more popular. In 2015, Annie Martin, also known as Mossin' Annie, published her book *The Magical World of Moss Gardening* which details the history of moss gardens, the basics of bryophyte biology, descriptions of species useful for gardeners, and how to take care of and maintain a moss garden. Moss gardens are particularly popular in Japan where they have a long history, however moss gardens can also be found in the UK, the US, Canada and elsewhere (Glime 2017, Martin 2015). Compared to traditional lawns, moss gardens offer unique benefits. For example, moss gardens do not require fertilizer (addition may be detrimental); they provide habitat for beneficial insect, salamanders, and other organism that traditional lawns do not support; the need for herbicides and pesticides is lower due to naturally occurring secondary metabolites; water usage is decrease compared to lawns; and machine powered garden tools are not needed (Martin 2015, Glime 2017). However, care needs to be taken as moss gardens gain popularity. Overharvesting is a serious conservation issue and usually occurs when there is a growing demand for a product. For example, many rare succulents and other popular houseplants are threatened by overharvesting (Liu et al. 2018, Victor & Makwarela 2011). Overharvesting of bryophytes is not just a potential issue with horticulture; mosses for green roofs and other uses also need to be harvested in a sustainable way.

3.4 Uses by Indigenous Peoples

In 2003, Robin Wall Kimmerer, a professor at the State University of New York College of Environmental Science and Forestry and a member of the Potawatomi Nation, published

Gathering Moss: A Natural and Cultural History of Mosses. Her book explores mosses through personal essays with topics ranging from ecological succession to urban areas. In her chapter entitled “The Web of Reciprocity: Indigenous Uses of Moss,” Kimmerer details how mosses have been used by indigenous peoples of North America in a variety of ways including diapers, sanitary napkins, insulation, and food preparation (Kimmerer 2003). Janice Glime also reviews the potential medicinal uses of bryophytes in her book *Bryophyte Ecology*. Bryophytes have been used in herbal medicines in China, India, North America, and elsewhere to treat various health issues such as liver disease, fungal infections, cardiovascular disease, inflammation, and lung disease (Glime 2017). For example, *Polytrichum* species were traditionally used by indigenous women of North America to assist with childbirth (Martin 2015, Glime 2017). In Chinese herbal medicine, *Polytrichum commune* has been used to treat symptoms of menopause and isolated secondary compounds from this species have shown anti-neuroinflammatory activity in vitro (Glime 2017, Guo et al. 2020). Compounds isolated from bryophytes may have a huge potential for modern medicine and their use in traditional medicine may be a great place to start investigating.

3.5 In Modern Medicine

As some of the first land plants, bryophytes have evolved to produce a vast number of secondary compounds. For example, liverwort species have been found to contain over 1600 terpenoids (a class of organic chemicals some of which exhibit bioactivity) (Chen et al. 2018). Similar to the research on *Polytrichum commune* by Guo et al. (2020), bryophytes have recently generated interest in pharmaceutical and biotechnology industries. In 2017, an enzyme replacement therapy drug for treating Morbus Fabry, a genetic disease, was made from *Physcomitrella patens*, a moss species, and has completed the first stage of its clinical trial (Decker & Reski 2020). Although

much of the research in phytochemistry (the study of plant produced chemicals), is focused on vascular plants, bryophytes contain many biologically active compounds, some unique to bryophytes, including lipids, proteins, terpenoids, and aromatic compounds (Commisso et al. 2021, Ludwiczuk & Asakawa 2020).

Although the activity of many of these compounds is unknown, recent studies have demonstrated that they may be useful for human health and medicine. For example, bryophytes have also shown antiproliferative (cell growth suppressing) activity; a study by Vollár et al. (2018) of 168 extracts isolated from bryophytes found that extracts from the families Brachytheciaceae and Amblystegiaceae had the most antiproliferative activity for gynecological cancer cells. A review of liverwort and moss species' secondary metabolites by Ludwiczuk & Asakawa (2019) found that activities of isolated compounds included phytotoxicity (toxic to plant grow), insect antifeedant, molluscicidal (poisonous to mollusks) activity, piscicidal (poisonous to fish) activity, antifungal activity, antimicrobial, cytotoxicity (toxic to cells), anti-inflammatory, and more. Although not enough research has been done about the activities of these compounds, they may have great potential for medicine in the future.

4. Bryophyte Conservation

Bryophytes play a critical role in ecosystem services and have a wide range of use for humans indicating that conservation may be crucial for some species if they are threatened and endangered. Bryophyte diversity, range, biomass, and photosynthetic rates are expected to be negatively impacted by global warming (Gignac 2001, He et al. 2016, Turetsky 2003), and therefore research and development is needed into effective conservation strategies. As Dawson et al. (2011) suggests, it is not enough to only identify exposure to climate change as there is also a need to research species' sensitivities, vulnerability, and ability to adapt. In addition,

investigations are critical into how humans are impacting bryophytes through means other than climate change such as habitat fragmentation and degradation, overharvesting, and the introduction of invasive species and diseases. Unlike vascular plants, bryophytes reproduce by spores rather than seeds which allows for greater dispersal ability (Gignac 2001, Patiño & Vanderpoorten 2018). This ability may help bryophytes negate the harm of climate change as they will be able to move to suitable habitat with more ease compared to seed plants.

However, there is debate on whether bryophyte dispersal ability will be able to keep up with suitable habitat loss. Zanatta et al. (2020) argues that although the dispersal ability of bryophytes is quite good, simulations of climate and wind conditions over approximately the next 30 years suggest that even highly dispersive species will struggle to match the rate of range contractions due to climate change. Urban development may also negatively impact the range of suitable habitats available for species as their current habitats are degraded. Range contractions are not the only threat to bryophytes. Increased temperatures are hypothesized to negatively affect photosynthetic rates of bryophytes specifically for species adapted to specific habitats such as tropical montane cloud forests, alpine areas, and temperate regions (He et al. 2016).

Predicting how threatened, if at all, many bryophyte species are by climate change is difficult as data are lacking for many species. The International Union for Conservation of Nature (IUNC) lists 23 species as near threatened, 37 as vulnerable, 39 as endangered, 25 as critically endangered, 4 as extinct, and 18 as data deficient of 182 total species. Considering that current estimate of bryophytes species globally is around 20,000 species (Patiño & Vanderpoorten 2018), data are certainly on many species. With extinction rates at an all-time high, research efforts may not be able to keep up and species may go extinct before they are even classified as at risk or even named (Howard & Bickford 2014, Lees & Pimm 2015). In addition

to the large number of species without data, the current IUCN red list criteria are not easily applied to colonial and asexually reproducing organisms such as bryophytes, and Bergamini et al. (2019) suggests that definitions of generation length, mature individual, and fragmentation may need to be modified for bryophyte conservation. However, this does not suggest the IUCN red list for bryophytes is not useful. Similar to suggestions made by Bergamini et al. (2019), a study on the status of bryophyte species in the Canary Islands used modified IUCN criteria and found that 105 out of 501 species were either critically endangered (7), endangered (20), or vulnerable (78) (González-Mancebo et al. 2012). Identifying all bryophyte species and evaluating their risk will not be possible in one go. Given the number of species with insufficient data and the nearly global range of bryophyte, efforts to document local species or species in particularly damaged habitats may be more effective. Once data on a status of a species is sufficient, assessing its sensitivities, vulnerability, and ability to adapt to climate change will be easier.

However, research on how bryophytes will respond to upcoming challenges will not be enough for effective conservation. An interdisciplinary approach that combines scientific, local, and indigenous knowledge is necessary for effective conservation as policies that are not livable are more likely to be ignored (Bartel 2014, Heller & Zavaleta 2009, Reyes-García & Benyei 2019). While traditional conservation approaches such as nature reserves and protected lands have been successful, they are not enough to combat the impacts of climate change (Corrigan et al. 2018, Reside et al. 2018) and can have negative social impacts, such as the removal of indigenous peoples from their home (Moola & Roth 2018). Although not traditionally included, indigenous voices are important for conservation as they help avoid knowledge gaps such as culturally important species, unique ecosystems services, and data deficient species (Fernández-

Llamazares et al. 2021, Reyes-García & Benyei 2019). For example, bryophytes have been historically used in indigenous medicines but are just now being used in modern medicine (Glime 2017, Kimmerer 2003, Martin 2015). A study by Schuster et al. (2019) on indigenous-managed lands found equal or greater vertebrate biodiversity compared to nature reserves in Australia, Brazil and Canada. Similarly, Inuit management practices have positively impacted local biodiversity, created unique plant assemblages, and increased soil nutrients (Oberndorfer et al. 2020). Climate change and urbanization will undeniably make conservation efforts more difficult than they already are. An interdisciplinary effort including local and indigenous voices will be crucial to conservation efforts in the coming years.

5. Conclusion

Bryophytes have a broad range of uses for humans and provide important ecosystem services that keep communities healthy. As interest in a more sustainable future grows, bryophytes may help humans have a more sustainable life style particularly in urban areas. When used a substrate for green roofs, bryophyte will help reduce problem such as the urban heat island effect while simultaneously being a better substrate choice in areas that experience times of arid weather due to their desiccation tolerance. In urban areas experiencing high levels of pollution, bryophyte can be used a bioindicators. Not only will this be a cheaper alternative to traditional air quality monitoring methods, combining bryophytes with green roofs may be more effective at monitoring pollution long term compared to just using epiphytic bryophytes. For individuals in the right climate, mosses may be a good alternative to a traditional lawn as they provide habitat for local fauna while decreasing the need for harmful upkeep like the use of pesticides. Although they have long been used by indigenous peoples as traditional medicines, interest in the use bryophytes' secondary compounds in modern medicine is just beginning. Isolated compounds

from bryophytes have been found to have activities including antifungal, antimicrobial, cytotoxicity, and anti-inflammatory properties. Although there are many possible research paths, researching focusing on green roofs and medicine would most likely benefit the greatest amount of people. Green roofs benefit communities by alleviating some negative aspects of urbanization while also creating much needed habitat for urban insects and other organisms. For moss green roofs to be successful, research needs to be done to determine what climates support mosses and what species are best suited as green roof substrate. Similarly, research is needed to not only identify the broad range of secondary compounds of bryophytes but also to determine what biological activity they express. Given the large number of bryophyte species, it may necessary to continue to examine how bryophytes were used in traditional medicines in order to identify potentially helpful species.

However, for all of the positive possibilities of bryophytes for human use, there remains the possibility that climate change and habitat degradation will cause significant losses to bryophyte biodiversity. Considering the important ecosystem services bryophytes provide such a carbon, water, and nutrient cycling as well as maintaining community biodiversity, a reduction in bryophyte biodiversity may have cascading effects. The most noticeable effect of climate change on bryophytes may be increase in greenhouse gas emissions from peatlands. As these systems hold at least 20 percent of terrestrial carbon, the decomposition of peatlands could significantly increase the amount of carbon dioxide in the atmosphere. However, there are numerous species of bryophytes whose risk levels have yet to be evaluated. Although it may be the case that the high dispersal ability of many bryophyte species will be able to keep up with range contractions due to climate change, it remains understudied. Before assuming bryophytes will be able to withstand climate change, researchers need to define and implement criteria on how to classify

the risk status of bryophyte species. In addition to whether a species is at risk currently, research is needed to assess how bryophytes will respond as the effects of climate change worsen particularly for data deficient species. As more research is focused on bryophytes and people are induced to bryophytes' benefits, interest may increase in their conservation and their use in sustainable urban environments.

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