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Impact of changing climate on bryophyte contributions to terrestrial water, carbon, and nitrogen cycles

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Tansley review

Impact of changing climate on bryophyte contributions to terrestrial water, carbon, and nitrogen cycles

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Contents

Summary	2	VI. Bryophyte restoration and conservation	13
I. Introduction	2	VII. Conclusion	13
II. Bryophyte contributions to terrestrial water cycles	3	Acknowledgements	14
III. Bryophyte contributions to the C cycle	7	References	14
IV. Bryophyte contributions to the N cycle	10		
V. Other effects of bryophytes and their associated biota on ecosystem function	12		

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Summary

Bryophytes, including the lineages of mosses, liverworts, and hornworts, are the second-largest photoautotroph group on Earth. Recent work across terrestrial ecosystems has highlighted how bryophytes retain and control water, fix substantial amounts of carbon (C), and contribute to nitrogen (N) cycles in forests (boreal, temperate, and tropical), tundra, peatlands, grasslands, and deserts. Understanding how changing climate affects bryophyte contributions to global cycles in different ecosystems is of primary importance. However, because of their small physical size, bryophytes have been largely ignored in research on water, C, and N cycles at global scales. Here, we review the literature on how bryophytes influence global biogeochemical cycles, and we highlight that while some aspects of global change represent critical tipping points for survival, bryophytes may also buffer many ecosystems from change due to their capacity for water, C, and N uptake and storage. However, as the thresholds of resistance of bryophytes to temperature and precipitation regime changes are mostly unknown, it is challenging to predict how long this buffering capacity will remain functional. Furthermore, as ecosystems shift their global distribution in response to changing climate, the size of different bryophyte-influenced biomes will change, resulting in shifts in the magnitude of bryophyte impacts on global ecosystem functions.

1. Introduction

Bryophytes are widely distributed across terrestrial ecosystems where they often contribute a substantial portion of the photosynthetic biomass (peatlands: 250–300 g C m⁻² yr⁻¹, Gunnarsson, 2005; boreal: 162 g C m⁻² yr⁻¹, Turetsky *et al.*, 2010). However, even in systems where bryophytes are the dominant vegetation, they are frequently overlooked in assessments of biodiversity and ecosystem function even though they contribute significantly, and perhaps disproportionately, to ecosystem

processes like water, carbon (C), and nitrogen (N) cycling (Turetsky, 2003; Eldridge *et al.*, 2023). Furthermore, the combined effects of bryophytes on these biogeochemical cycles may be nonlinear and may present as feedbacks within and between cycles (Fig. 1). For example, bryophytes are dependent on and can alter hydrological cycles, but changes in water availability can also impact C and nutrient dynamics for bryophyte communities. Inversely, increased bryophyte abundance (C stock) increases water retention and storage capacity. Unfortunately, changing climate has been shown to negatively influence bryophyte function and

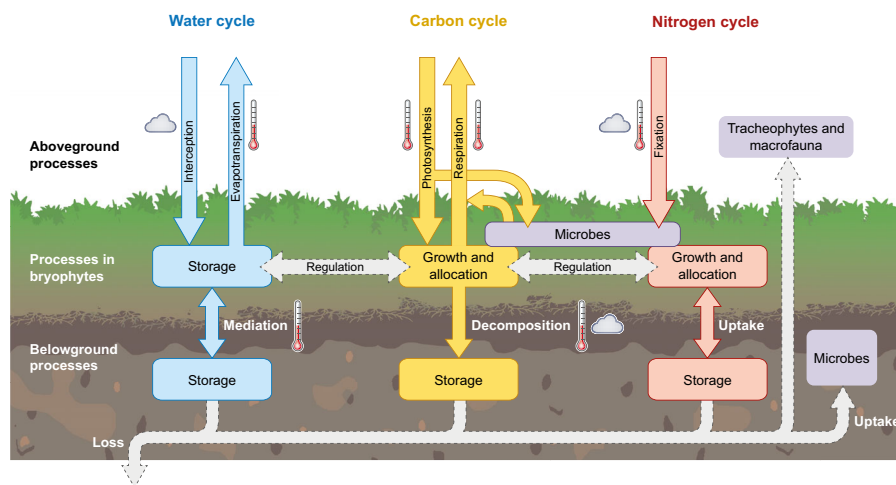


Fig. 1 Bryophytes mediate multiple processes occurring within terrestrial water, carbon (C), and nitrogen (N) cycles. These processes include uptake and release of water, C, and nutrients, storage and allocation within bryophytes, and interactions with microbes, macrofauna, and vascular plants. Many of these processes occur within the bryosphere (the area in and around bryophytes influenced by bryophyte traits), yet bryophyte-mediated ecosystem processes extend beyond the bryosphere and overlap in space and time, hence impacts on one process can have cascading effects across cycles. Regulation between cycles occurs due to processes such as trade-offs in water and C acquisition and nutrient dependence on growth and allocation. Because bryophyte mediation of ecosystem processes is affected by global changes in temperature and water availability, we indicate bryophyte processes shown to be particularly sensitive to these aspects of global change with either a thermometer icon (denoting temperature sensitivity) and/or a cloud icon (denoting sensitivity to water availability). Note that while this and subsequent figures illustrate biogeochemical effects of soil-dwelling bryophytes, bryophytes that grow on trees and rocks will foster similar ecosystem dynamics. Find expanded views of the role of bryophytes in each of the water, C, and N cycles in Figs 3–5.

survival (Tuba *et al.*, 2011; Alatalo *et al.*, 2020; Fig. 2). Given that ongoing changes in climate (temperature and moisture availability) will affect how all plants interact with hydrological and biogeochemical cycles, a comprehensive review of how climate change will alter bryophyte-mediated impacts on water, C, and N cycling is warranted.

As a group, bryophytes possess unique sets of ecophysiological traits that set them apart from vascular plants and relate to their impacts on biogeochemical cycling (Cornelissen *et al.*, 2007). Many bryophytes have low-temperature optima for photosynthesis (He *et al.*, 2016), but bryophyte temperature tolerance is linked to water relations, and many bryophytes can only withstand higher temperatures when desiccated and dormant compared to when rehydrated and physiologically active (Gignac, 2001). Bryophytes are unique in their interactions with water because they lack roots and often other vascular structures, and their cellular-level hydration is equilibrated with that of the atmosphere (i.e. their vegetative tissues are poikilohydric). This lack of complex internal conducting structures and laminar stomata to mediate water foraging, transport, loss, or storage, results in both morphological adaptations to retain, transport, and store external water (Fig. 3), and a widely spread ability to tolerate desiccation. Despite these adaptations, cellular desiccation is an intense process that fractures the cell membrane (Hoekstra *et al.*, 2001) which leads to the loss of intracellular C, N, and other molecules (Wilson & Coxson, 1999; Slate *et al.*, 2019b) before membrane repair. If bryophyte rehydration is too brief and/or repeated dry-wet cycles are too frequent, bryophytes will develop a C deficit or negative C balance and this will eventually lead to mortality (e.g. Coe *et al.*, 2012b). The physical environment formed by live and senescent bryophytes due to their anatomical and chemical structure, along with the microfauna that reside within, on, and inside the above to below bryophyte areas of influence, has been termed the 'bryosphere' (Lindo & Gonzalez, 2010). Alterations in bryosphere presence, conditions, and constituents have consequences for C and N cycling, both at the level of the individual bryophyte and at the ecosystem.

Future climate will be warmer, and the direct metabolic effects of higher temperatures on bryophytes and associated C and N cycles have been studied and reviewed elsewhere (Lindo *et al.*, 2013; He *et al.*, 2016; Ruklani *et al.*, 2021; Zhang *et al.*, 2023). Future precipitation levels will also vary in total amount, frequency, and intensity, and this will further impact bryophyte influences on the amount of water, C, and N being fixed, stored, or lost from ecosystems (Wang *et al.*, 2019; Liu *et al.*, 2020). However, our understanding of bryophyte-mediated interconnected ecosystem processes of water, C, and N cycling is limited across ecosystems globally. Brown & Bates (1990) and Turetsky *et al.* (2012) provide reviews of bryophyte-mediated C and N cycling across multiple ecosystems, Elbert *et al.* (2012) examine the impact of cryptogamic covers more broadly on ecosystem C and N fluxes, and multiple authors have studied bryophyte impacts on water, C, or N cycling from the perspective of a specific ecosystem (i.e. boreal and Arctic ecosystems: Turetsky *et al.*, 2012; tropical cloud forest: Metcalfe & Ahlstrand, 2019) or processes (i.e. C cycling: Grau-Andrés *et al.*, 2021; water cycling: Porada *et al.*, 2018). Yet changes to the abundance and distribution of bryophytes and their unique

physiological and metabolic response under climate change have not been extensively examined with respect to the consequences for ecosystem processes, specifically the interconnected cycles of water, C, and N.

II. Bryophyte contributions to terrestrial water cycles

Bryophytes mediate water interception and storage across all biomes (Fig. 4) in proportion to bryophyte dominance and abundance. These effects are particularly pronounced in areas with dense and continuous bryophyte carpets, such as in peatlands, as well as in areas where bryophyte carpets coexist with dominant vascular vegetation, like in boreal forests. In forests where dense leaf litter covers soils, bryophytes occupy other substrates and grow more or less abundantly as epiphytes intercepting and retaining water. Whether in the form of large and dense multispecies carpets or of sporadic colonies, bryophyte structural traits, from subcellular to colony level, facilitate rapid water absorption, increase storage, reduce water loss, or reduce evaporative pressure (Fig. 3; e.g. Schofield, 1981; Glime, 2017).

1. Water interception

Across biomes, bryophyte interception of water varies greatly with ecosystem-level vegetation structure. Epiphytic bryophytes in forest canopies increase rain throughfall, whereas epiphytic bryophytes on tree trunks reduce stemflow (García-Santos & Bruijnzeel, 2011). In turn, the ground bryophyte layer and biocrust bryophytes mediate water movement from the atmosphere to the soil (Xiao *et al.*, 2015; Gall *et al.*, 2022). Studies indicate that forest type and age can greatly impact potential epiphyte bryophyte interception (and short-term storage), which can vary from < 1 mm of incoming precipitation in continental temperate (Hembre *et al.*, 2021) and tropical secondary forest to nearly 5 mm in an old-growth tropical cloud forest (Köhler *et al.*, 2007). Consequently, it is not surprising that in a global modeling effort, Porada *et al.* (2018) estimated that epiphytic bryophytes in forests may increase rainfall interception by more than 60%, but with great spatial heterogeneity. Looking at ground bryophyte layers, they alone can intercept *c.* 25% of throughfall in a boreal forest, with much of this water (*c.* 80%), making its way through the bryophyte layer over subsequent days rather than later evaporating (Price *et al.*, 1997). In a temperate tussock grassland, bryophytes intercepted three times more water per dry mass than vascular plants (Michel *et al.*, 2013).

Beyond rainfall, bryophytes can also intercept fog (wind-entrained water droplets), collect dew (condensation of water vapor), and retain snow. Fog and dew can increase inputs of water into ecosystems, either by solely hydrating bryophytes or by adding significant water volumes to soils through dripping. Although this occurs over a wide range of climates, bryophyte fog interception is best studied in tropical montane forests (Cavelier & Goldstein, 1989), páramos (Villegas *et al.*, 2008), and subtropical forests (Chang *et al.*, 2002; Ah-Peng *et al.*, 2014). Bryophyte fog interception can reach high rates (0.17 mm h⁻¹; Chang *et al.*, 2002) and once bryophytes are saturated with fog water,



Fig. 2 Summary of the main impacts changing climate is having on bryophyte-mediated biogeochemical processes and bryophyte communities in seven types of globally abundant ecosystems. Ecosystems that cannot shift latitudinally (b, tundra), or where the frequency of disturbances like wildfire are having such catastrophic impacts that a different type of ecosystem is expected to regenerate (a, peatlands; d, temperate forests) are noted in parentheses as having high vulnerability to changing climate (Gonzalez *et al.*, 2010). By contrast, ecosystems able to shift latitudinally (c, boreal), expanding in area (deserts), or being more functionally robust to changing climate (e, tropical evergreen broadleaf forests) are identified as having lower vulnerability to changing climate (Gonzalez *et al.*, 2010). Across ecosystems, the effects of changing climate are generally decreasing the abundance of bryophytes which will decrease the magnitude of bryophyte impacts on biogeochemical processes. In many cases, bryophyte communities may also change in composition. More research is needed to understand how changes in bryophyte community composition will impact the biogeochemical functioning of bryophytes within and across ecosystems. Photographs: Des Callaghan (a), Nicole Fenton (c), Daniel Stanton (b, d), Daniel Tucker (e), Stephanie Freund (f).

throughfall of rain may also increase (García-Santos & Bruijnzeel, 2011). In deserts, dew can be an important source of moisture (Kidron & Starinsky, 2019), especially when captured with morphological adaptations such as leaf awns (Fig. 3n; Tao & Zhang, 2012; Pan *et al.*, 2016). Direct uptake of humid air can also be a water source for bryophytes (Lange, 1969), but remains understudied. Snow retained by bryophytes can be an important component of snow cover at higher latitudes and altitudes, however, the impacts of bryophytes on snow retention are less clear than the impacts of changing snow cover on bryophytes (Cooper *et al.*, 2019).

2. Water storage

Across diverse ecosystems, bryophytes exhibit an impressive capacity to absorb and store two to several hundred times their dry weight in water (DeLucia *et al.*, 2003). This results in increased water content in substrates beneath both bryophyte layers and biocrust bryophytes. In Arctic tundra, the water storage capacity of bryophytes surpasses that of lichens or short-stature vascular vegetation (Migala *et al.*, 2014). Epiphytic bryophytes in temperate forests can hold 10 times their dry mass in water (Pypker *et al.*, 2017). Although bryophytes only contributed *c.* 4% of the biomass in New Zealand tussock grasslands (Michel *et al.*, 2013), they are the second-largest contributor to plant water storage.

The remarkable ability of bryophytes to store water relates to the structural traits discussed previously. In particular, bryophyte colony density, cover, biomass, and life form, rather than the morphology or structure of individual shoots or cells, dictate water storage capacity, and colony water saturation level governs desiccation rates (Fig. 3m–r; Elumeeva *et al.*, 2011; Grau-Andrés *et al.*, 2021). Variation in water storage capacity is also species-specific (Davey, 1997; Michel *et al.*, 2013) and can be related to bryophyte functional groups (Lett *et al.*, 2021), providing evidence that not all bryophytes should be categorized as one functional group and that community composition drives bryophyte impacts on the water cycle (Hembre *et al.*, 2021). An example of this is that deeper bryophyte layers (a functional trait) have a greater capacity for water storage, which results in colder soils and better temperature insulation compared to thinner bryophyte layers that hold less water. This observation is consistent in biomes as divergent as Arctic tundra (Gornall *et al.*, 2007), shrublands and grasslands of Argentina (Kröpfl *et al.*, 2022), and dry shrubland of New Zealand (Dollery *et al.*, 2022).

3. Impacts on soil hydrology

Water movement through the bryophyte layer to underlying soil or organic layers (hereafter substrate) is also influenced by the water-holding capacity of bryophytes, whether ground-dwelling or epiphytic. Dry or partially hydrated bryophytes may prevent precipitation from reaching the underlying substrate; however, this effect decreases as bryophytes hydrate (García-Santos & Bruijnzeel, 2011). Thus, substrates under bryophytes may receive more water in ecosystems where bryophytes tend to remain hydrated (e.g. peatlands, tropical montane regions). By contrast, substrates under

bryophytes in systems with less frequent and/or less abundant precipitation (e.g. drylands, some temperate forests, and grasslands) may only receive water after bryophytes are rehydrated. Importantly, even within the same ecosystem, different bryophyte species will vary in their impact on soil moisture (e.g. Wang *et al.*, 2019).

Bryophytes not only impact how much water enters soils but also influence soil water retention (Fig. 4). Water movement from soil through the bryophyte layer and to the atmosphere is driven by a vapor pressure gradient (lower in atmosphere and higher in soil). The evaporation of water from soils through bryophytes varies in time (diurnally and seasonally) and space. Differences in temperature between the upper and lower bryophyte layers can result in the distillation of soil moisture to the surface bryophyte layer (Carleton & Dunham, 2003), slowing the loss of soil moisture during morning hours. During the day, as bryophytes desiccate, they lose moisture through evaporation, which increases the vapor pressure gradient between air and soil, increasing the loss of soil water through evaporation (Carleton & Dunham, 2003). Thus, evapotranspiration in systems with bryophytes can be a multi-step process including transfers between soil and bryophytes as well as evaporation from both soil and bryophytes. This complexity can lead to contrasting effects on soil water across ecosystems. For example, in the Arctic tundra, higher evapotranspirative losses from bryophyte-covered soils compared with bare soil are attributed to both the retention of large amounts of water that later evaporates, and bryophyte uptake of deeper soil water via capillary action (e.g. Raz-Yaseef *et al.*, 2017; Clark *et al.*, 2023). Conversely, soil moisture content under bryophytes can be much higher than under other vegetation such as in grasslands (two to four times; Van Tooren *et al.*, 1985) and boreal forests (Grau-Andrés *et al.*, 2021), especially in the top 10 cm (Michel *et al.*, 2013). In alpine shrub tundra, bryophyte removal leads to increases in evapotranspiration rates from previously buffered soil or organic layers (e.g. Liu *et al.*, 2022). Bryophyte-covered sites can also have lower evapotranspiration rates than vascular-covered sites because bryophyte evaporative losses cease once bryophytes are desiccated while deeper-rooted plants continue to transpire (Liu *et al.*, 2022).

In addition to these direct effects on soil water movement, bryophytes also influence soil moisture indirectly through impacts on soil temperature, soil structure, porosity, and organic matter content. Cooler soils have lower evaporative losses than warmer soils meaning that the buffering effects of bryophytes on soil temperature fluctuations (Huntley, 1971; Gold *et al.*, 2001) can indirectly influence soil water retention. It is also likely that the coloration of dryland bryophytes within soil biocrust communities alters surface temperatures (Xiao & Bowker, 2020) such that evaporation rates of existing surface water is greater. In peatland and dryland systems, bryophyte-driven micropore channels not only influence water infiltration but also stabilize soils and reduce erosion (e.g. Eldridge, 2003; Grover & Baldock, 2013). Dryland bryophytes and their associated biocrust communities also harbor large soil invertebrate communities whose burrowing creates additional soil micro and macropores (Belnap, 2003).

In sum, bryophyte contributions to water cycles involve key processes that regulate the speed at which water flows through their

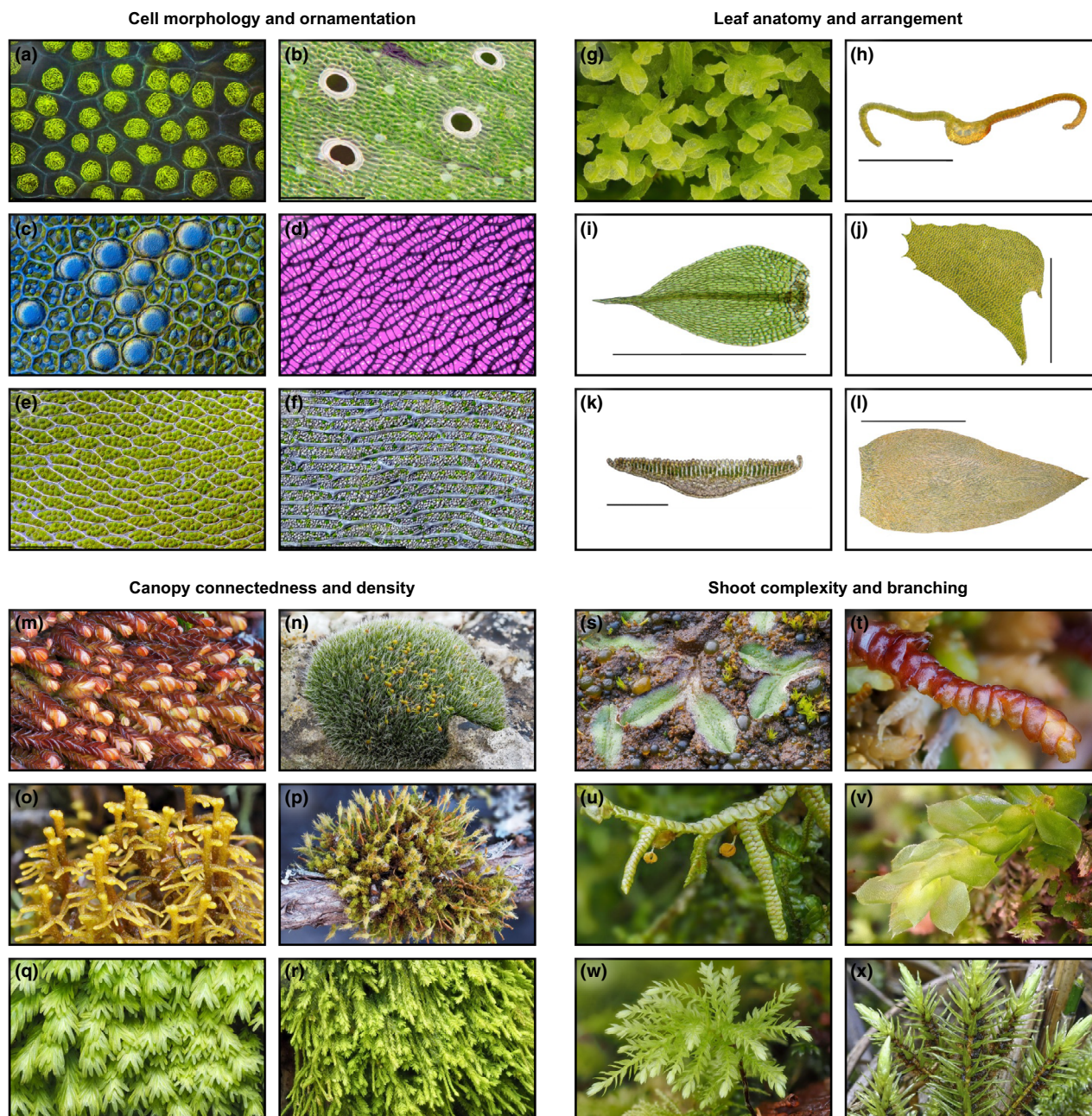


Fig. 3 Bryophyte structures and forms across scales enhance functions such as water capture and retention; carbon (C) assimilation, retention, and storage; and nitrogen (N) retention and fixation, by providing a suitable habitat for microorganisms. At the cell scale (a–f), hyaline cells in *Sphagnum* spp. (d), formed by programmed cell death, create water-holding spaces within reinforced walls which can prolong hydration and facilitate water uptake during rehydration. Elongated hyaline leaf tips (awns; n) in certain species reduce water loss by creating a boundary layer above the bryophyte surface (e.g. *Grimmia* spp.; Schofield, 1981), and can facilitate water uptake via interception from the atmosphere (Pan *et al.*, 2016). Leaf components (g–l) such as scales and/or hairs and fringes on thalloid liverworts (g) and hornworts create capillary spaces for ventral water movement and a lipid-containing dorsal cuticle reduces evaporation (Glime, 2017). At the shoot scale (s–x), a thick cover of hairs on stems (tomentum; x), overlapping leaf arrangement of mosses and leafy liverworts (t–v), and modified leaves (for instance lobes in Lejeuneaceae or vaginant laminae in *Fissidens*; q) increase surface area and capillarity (Schofield, 1981; Glime, 2017). Beyond leaf arrangement and branching, colony-level complexity (m–r) emerging from the interaction between the growth form and the environment (known as life form; Bates, 1998) moderates external water movement and bryophyte water storage capacity. These effects of life form on the boundary-layer diffusion resistance to water loss (Proctor, 2000) vary with contexts (Kürschner *et al.*, 1999; Spitale *et al.*, 2020). For instance, subalpine mosses that form large cushions and compact mats (e.g. n) have lower evaporation rates by dry weight than mosses forming smooth mats, wefts, and tall turfs (o, r; Nakatsubo, 1994). Finally, cellular, leaf, shoot, and canopy scales are a spatial continuum, structures at different scales contribute simultaneously to multiple bryophyte functions. Because the water, C, and N cycles are also interconnected within the bryosphere, some structures enhance several bryophyte functions simultaneously; for example, lamellae (k) increase C assimilation per unit leaf area while also increasing capillary spaces occupied by both N-fixing microorganisms and water. Photographs: Des Callaghan; see Supporting Information Notes S1 for additional photo descriptions, scale, and taxonomy (Brinda & Atwood, 2023).

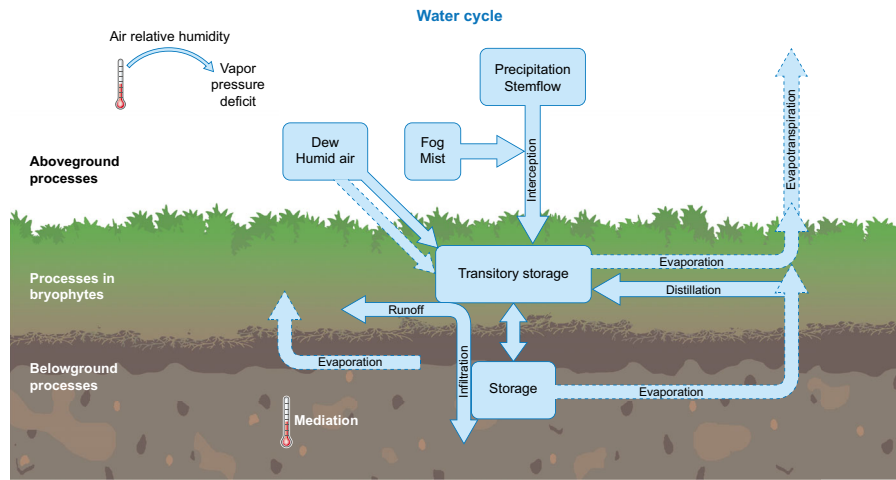


Fig. 4 Bryophytes play a key role in water interception, storage, and soil hydrology by physically occupying the space between their substrate and the air. Bryophytes intercept water in the form of precipitation, fog/mist, and humid air, and can also take up water from the substrate. Water stored internally and externally in bryophytes can be lost to the surrounding environment through evaporation to the atmosphere and infiltration into the soil. Arrows represent fluxes of water through pools of the water cycle. Dashed borders on arrows represent vapor phase processes. The curved arrow connecting temperature (indicated by the thermometer icon) and vapor pressure deficit (VPD) by touching relative humidity (top right) indicates that atmospheric water vapor conditions, which drive evaporation rates, vary with temperature and are modulated by relative humidity (Anderson, 1936). VPD, calculated from temperature and relative humidity, allows fair comparisons of atmospheric water vapor conditions in different ecosystems.

host terrestrial ecosystems. The absolute magnitude of these contributions, expressed as water volumes and/or as rates (i.e. water volumes per time unit) per area of the host ecosystem, vary in proportion to bryophyte abundance (cover or biomass, depending on the ecosystem) and, in some cases, in proportion to bryophyte functional diversity. For instance, interception of horizontal precipitation is higher in ecosystems where bryophytes occupy vertical epiphytic habitats in addition to edaphic and other horizontal habitats. Our review highlights important biases and identifies several research priorities. For example, bryophyte contributions to water cycles are mainly characterized in deserts and Arctic locations. Bryophyte contributions are also reported in different units depending on the process under assessment, the units describing absolute magnitudes facilitate impartial comparisons but hamper our ability to develop ecologically significant comparisons of the role of bryophytes in supporting water-related processes across ecosystems. Finally, drying dynamics have been evaluated in a number of contexts (but still need more study), while rehydration dynamics, particularly in natural settings, are essentially unknown.

4. Impacts of changing climate

Expected changes in precipitation regimes (rain frequency and intensity as well as duration of rainfall events) with climate change are likely to have large effects on the capacity of bryophytes to intercept and store water, as both are closely related to bryophyte hydration status. Thus, variation in the amount, frequency, and intensity of precipitation could result in lower amounts of water moving through systems where bryophytes are under-hydrated to excessive amounts of water moving across the landscape when the ability of bryophytes to absorb water is overwhelmed. Temperature

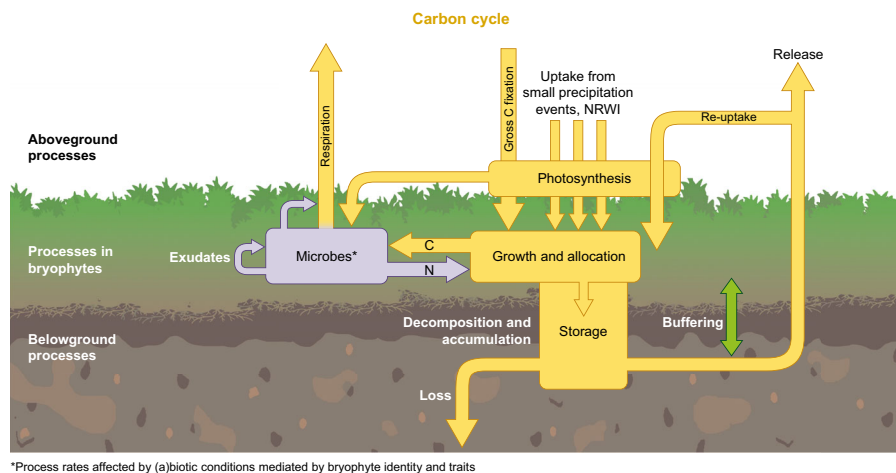
increases may further affect bryophyte hydrology by increasing evaporative demand and shortening periods of hydration. If hydration periods shorten excessively, bryophytes will no longer be able to maintain a positive C balance and their water retention capacity will be lost. Additional indirect effects of climate change on surrounding vascular plants are also likely to impact bryophyte hydrology. For example, disturbances can induce changes in bryophyte community composition, replacing species that intercept and retain more water with species with lower water interception and storage capacity abilities, or eliminate bryophyte layers entirely.

III. Bryophyte contributions to the C cycle

At a global scale, bryophytes exert direct and indirect control on the C cycle (e.g. Yu *et al.*, 2010; Piatkowski *et al.*, 2021). As photoautotrophs with physiological ranges of tolerance that can exceed those of vascular plants, bryophytes contribute to C uptake and can account for a substantial fraction of net primary productivity (NPP) in systems such as forests and peatlands and during times of the year when other plants are inactive (e.g. Woodin *et al.*, 2009; Street *et al.*, 2013). Because of slow decomposition (organic matter breakdown) rates in many bryophyte-dominated systems, this uptake also contributes to belowground C storage (i.e. short- or long-term sequestration; e.g. Gorham, 1991). Often existing at or near the soil-atmosphere interface, bryophytes also mediate soil-atmosphere C fluxes (Fig. 5).

1. C uptake

As prominent groundcovers across peatland, boreal, and alpine systems (including páramos), and as components of biocrusts in



*Process rates affected by (a)biotic conditions mediated by bryophyte identity and traits

Fig. 5 Carbon uptake, storage, and loss as mediated by bryophytes. Through photosynthesis, bryophytes take up C from the atmosphere as gross fixation and when hydrated by nonrainfall water inputs (NRWI) and re-uptake C released from belowground processes that release CO₂ (e.g. soil respiration). Within the bryophyte layer, C is also allocated to growth and structural/reproductive tissues as well as support of symbiotic microbes. Bryophyte-associated microbes also take up C via photosynthesis (if autotrophic), contribute to respiratory C release from the bryophyte layer to the atmosphere, and stimulate their own activity and growth via release of various exudates. Decomposition and accumulation (e.g. peat) contribute to belowground C pools, and properties of the bryophyte layer (i.e. temperature and moisture regulation) affect soil C fluxes and storage. Arrows represent C fluxes between pools in the aboveground, bryophyte, and belowground components of the C cycle.

globally vast drylands, bryophytes contribute significantly to global C uptake. In some ecosystems, gross C uptake by bryophytes can vastly exceed that of other plants due to bryophyte presence in diverse and widespread soil surface communities. The C use efficiency (the ratio of net C gain to gross C assimilation; CUE) of mosses has been examined by Street *et al.* (2013) and Woodin *et al.* (2009) with both studies finding similar CUE values of *c.* 70%, a value slightly higher than the 40–60% estimated for most vascular plants. In addition to their gross C uptake on an annual basis, bryophytes can also dominate C uptake during times of year when vascular plants are not active (e.g. before and after the typical vascular plant growing season; the ‘shoulder season’) because they can be physiologically activated (thus capable of C fixation) by very small water inputs or while soils remain frozen and temperatures near or below zero. Because of this unique responsiveness to hydration, bryophytes can also contribute to C uptake during small rainfall or snowfall events that may go unrecorded by traditional instruments or ignored in terrestrial C cycling models.

Across systems, C uptake in bryophytes is controlled primarily by water availability, and secondarily by a suite of other factors such as light intensity, temperature, nutrient availability, atmospheric CO₂ concentration, and diversity of the bryophyte community. Scaling from the individual colonies (i.e. C uptake) to an area basis suitable for ecosystem-scale analyses (i.e. NPP), hydration status has been shown to be a dominant factor controlling C uptake and NPP in peatlands, tundra systems, boreal forests, and drylands. In peatlands, water stress in *Sphagnum* can result in a shift from net C assimilation to net C loss (Jassey & Signarbieux, 2019), and reductions in water table depth can result in *Sphagnum* transitioning from a net C sink from the atmosphere to a source (Kwon *et al.*, 2022). Likewise, soil warming that causes permafrost thaw and increased soil water in tundra systems has been shown to increase NPP in *Sphagnum*

(Deane-Coe *et al.*, 2015). The growth, and consequently C assimilation, of common forest-floor bryophytes in boreal forests is strongly controlled by moisture availability and precipitation (Busby *et al.*, 1978; Vitt, 1990). In water-limited drylands, inter- and intra-annual moisture availability drives C fixation in bryophytes. Specifically, the C balance following hydration from precipitation events is related to the size, timing, and season of events (Coe *et al.*, 2012b), and repeated exposure to small hydration events can cause declines in net C uptake in dryland bryophytes (Reed *et al.*, 2012) due to the metabolic cost of rehydration. Finally, thallus water content is also expected to drive C dynamics in tropical bryophytes (Nikolic *et al.*, 2023).

Temperature can also control C uptake in bryophytes (as long as they are not also water-limited), where in most cases increases in temperatures beyond photosynthetic optima reduce C fixation. This has been shown in field and laboratory studies that exposed mosses to short-term simulated warming conditions (Harley *et al.*, 1989; Xu *et al.*, 2009; Coe *et al.*, 2012a), as well as in boreal and tundra systems exposed to long-term experimental air warming, with the latter showing a reduction in bryophyte photosynthesis by 40% (Bjerke *et al.*, 2017) and reductions in bryophyte NPP by up to 90% (Deane-Coe *et al.*, 2015; Norby *et al.*, 2019). Water tends to exert primary control on C fixation (and NPP) as it determines the timing of photosynthetic activity and temperature changes interact with hydration (i.e. increased temperatures causing desiccation and cessation of metabolism). Finally, as with other C₃ plants, exposure to elevated atmospheric CO₂ can stimulate C uptake (Csintalan *et al.*, 2005; Coe *et al.*, 2012a), and in temperate forests, bryophytes often rely on CO₂ from soil respiration (which is likely elevated within the boundary layer of the forest floor) as a source of C (DeLucia *et al.*, 2003).

Estimates of bryophyte NPP vary across ecosystems and among species. The highest estimates for bryophyte NPP come from peatlands, where values up to $1450 \text{ g C m}^{-2} \text{ yr}^{-1}$ have been reported (Gunnarsson, 2005). Other estimates from these systems range from $8 \text{ g C m}^{-2} \text{ yr}^{-1}$ on the lower end (Gunnarsson, 2005) to values in the $200 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Norby *et al.*, 2019; Bengtsson *et al.*, 2020) to $600 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Vitt *et al.*, 2003) range. Bryophyte NPP rates from other northern latitude systems can be nearly as high but display more variability depending on the species and habitat. In boreal regions, bryophyte NPP estimates range from $3.1 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Bona *et al.*, 2016) up to $162 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Turetsky *et al.*, 2010), with feather mosses and *Sphagnum* spp. contributing the most to total NPP. In tundra systems, estimates range from 2 to $80 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Deane-Coe *et al.*, 2015; Riis *et al.*, 2016), depending on the species. In drylands, bryophyte NPP rates are much lower overall, and while estimates are scarce, one study from Western North America provided a mean NPP estimate of $3.8 \text{ mg C m}^{-2} \text{ yr}^{-1}$ (Coe & Sparks, 2014). This NPP estimate is notably between three and five orders of magnitude lower than C uptake values from other ecosystems on an area basis, likely due to the diminutive size of most dryland bryophytes and frequent water limitation on photosynthesis. However, when considered alongside the global extent of drylands and the abundance of bryophytes in dryland biocrusts that, as soil surface communities, can occupy over 80% of vascular plant interspace regions (Eldridge *et al.*, 2020; Miralles *et al.*, 2020), dryland bryophyte NPP is likely globally significant to C cycling and storage.

Evaluating bryophyte-C uptake as a fraction of total NPP (from all photoautotrophs) across ecosystems can be helpful in conceptualizing the importance of bryophytes to C cycling. In peatlands and black spruce forests with *Sphagnum* understories, bryophytes can account for the majority of aboveground NPP, with reported values ranging from 50% to over 75% of NPP (Bond-Lamberty *et al.*, 2004; Vitt, 2007). Bryophyte NPP is estimated to range from 11% of total NPP in temperate forests (DeLucia *et al.*, 2003) up to 20% in boreal systems (Turetsky *et al.*, 2012). In Arctic systems, bryophyte NPP contribution ranges from 10% to 35%, depending on the dominant community type (Campioli *et al.*, 2009; Turetsky *et al.*, 2012). While percent of total NPP contributed by bryophytes has not explicitly been examined in drylands, evidence suggests that biocrust bryophytes can dominate C uptake, especially during small precipitation events when other plants are not active (Tucker *et al.*, 2019), thus bryophytes may account for 100% of NPP during certain times of the year. In the future, researchers should also consider the potentially more scalable comparison between bryophytes and other plants of photosynthetic biomass.

2. C storage and loss

Bryophyte-driven C storage is a significant part of the global C budget. This is partially due to the slow decomposition rates of bryophytes which leads to soil C accumulation at globally significant levels, especially in northern peatlands (see Gorham, 1991). Despite the prevalence of bryophytes across ecosystems, information on bryophyte-C storage rates in

nonpeatland ecosystems is rare. However, the low decomposition rate of bryophytes compared to vascular plants and lichens (Lang *et al.*, 2009), coupled with their relatively high C uptake rates, suggests that bryophyte contributions to soil C are likely several orders of magnitude higher than vascular plants or lichens even in ecosystems where they may not be the dominant plant functional group (e.g. alpine regions).

The chemical composition of bryophyte living tissues exerts controls on soil C stability and persistence in these ecosystems. For example, non-*Sphagnum* mosses decompose on average slower than vascular plants and lichens, partially due to structural lignin-like compounds (Lang *et al.*, 2009). *Sphagnum* litters decompose more slowly compared to vascular plants due to cell-wall polysaccharides explaining their low rate of C mineralization (Hájek *et al.*, 2011). Within peatlands, *Sphagnum* species demonstrate niche differentiation based primarily on water availability (Andrus *et al.*, 1983). These microhabitat preferences of *Sphagnum* are reflected in species-specific strategies in C storage and cycling. Turetsky *et al.* (2008) found that the ratio of metabolic to structural carbohydrates predicted 84% of the variability in the decomposition in *Sphagnum*. Species characterized by resource-acquisition life-history strategies, such as *S. angustifolium* (Warnst.), decompose faster than species that use resource-conservation strategies, like *S. fuscum* (Schimp) (Turetsky *et al.*, 2008; Bengtsson *et al.*, 2018). Vertical peat deposits also promote nutrient immobilization (oligotrophication; Loisel & Yu, 2013), curtailing colonization of peatlands by vascular species with high nutrient requirements and more mineralizable litter (Oke & Hager, 2020). Finally, *Sphagnum* vegetation often promotes wet, anoxic and acidic conditions that constrain microbial and plant activities, thereby limiting decomposition (Van Breemen, 1995).

Whether bryophyte-dominated systems remain net C sinks into the future depends on both NPP rates and CO_2 losses through autotrophic as well as heterotrophic respiration in the overall ecosystem response to global change factors. Climate- or disturbance-related changes in bryophyte species composition will heavily drive the magnitude of these responses and shifts in vascular plant diversity, biomass, and community composition will also be influential (Jonsson *et al.*, 2015). Ground-covering bryophytes help reduce belowground heterotrophic respiration through several mechanisms, including reduction of decomposition rates by maintaining low soil temperatures (Startsev *et al.*, 2007) and production of litter that requires more time to decompose (Lang *et al.*, 2009; Palozzi & Lindo, 2017) due to low nutrient to C ratios and complex C compounds.

3. Impacts of changing climate

Global change-induced increases in temperature and changes in precipitation are likely to alter bryophyte community structure across the globe and associated bryophyte-driven C cycling processes. In northern and temperate peatlands, warming-mediated lowering of the peatland water table can lead to increases in the abundance of vascular plants, resulting in decreases in *Sphagnum* abundance and increases in N availability, thereby relaxing controls on C accumulation, which could shift

these systems from a C sink to a C source (e.g. Dieleman *et al.*, 2015; Oke & Hager, 2020). In drylands, bryophyte-C balance (the net gain or loss of C resulting from physiological responses to hydration) is negatively impacted by both smaller precipitation events and increased temperatures, leading to reduced survival and compromised ecosystem functions of the biocrusts in which they carry a keystone role. Most of our current knowledge of bryophyte-C cycling processes related to global change factors comes from peatlands, northern forests, and select arctic and dryland systems. Contrastingly, it is hypothesized that in tropical lowland forests, bryophyte-C gains are likely restricted by frequent wetting events that may saturate the bryophyte thallus and either limit C assimilation or increase respiration (Wagner *et al.*, 2014). Therefore, if wetting events are less frequent in tropical lowland forests under warmer future climate, bryophytes may reach their physiological limits due to high temperatures (He *et al.*, 2016) but also, less frequent water saturation may expand the time window in which bryophytes can photosynthesize. Aside from these biomes, our understanding of how C cycling processes contributed by bryophytes will be impacted by global change is limited. Despite these knowledge gaps, the existence of ecophysiological traits shared across bryophytes can allow for global change-related predictions across regions. In all biomes (even those regions for which we possess scant data on bryophyte-C cycling processes such as other tropical forests), the dependence of all bryophytes on hydration for C uptake and survival suggests that global changes resulting in drier conditions and more irregular rainfall will substantially modify bryophyte-C cycling processes in the future. We know that the intensity of these impacts will vary among bryophyte species but have a limited amount of data on very few species of bryophytes and a poorly developed understanding of bryophyte-driven C-cycling processes outside of peatland systems.

IV. Bryophyte contributions to the N cycle

Bryophytes carry out key functions related to N cycling in various ecosystems, including interception and storage of different N forms and habitat provision for N fixers (Fig. 6). This is particularly true where bryophytes are abundant and/or where N availability is low, such as in the tundra or boreal forest. Elsewhere, bryophytes can have local but pronounced impacts on N cycling, for example when found in the tree canopy of temperate or tropical forests or in dryland biocrusts. Bryophytes intercept and take up N from dry and wet deposition and store this N in their slow-decomposing tissues, thus serving as a N sink. Bryophytes can also serve as a N source when N is lost via disturbances, decomposition, or leakage during dehydration-rehydration cycles. Biological N₂-fixation (BNF) carried out by the diverse microbiota hosted by bryophytes is an important source of available N across ecosystems (Gundale *et al.*, 2011). The relative importance of BNF varies according to ecosystem type (Table 1) and bryophyte species.

1. N uptake

Bryophytes are a major source of N uptake across the vast boreal, Arctic, and dryland ecosystems (Rosswall & Granhall, 1980; Van

Cleve & Alexander, 1981; Marion *et al.*, 1982). The ecological role that N uptake by bryophytes plays in regulating N cycling varies across terrestrial systems and ranges from competing with vascular plants (Nordin *et al.*, 1998; Bobbink *et al.*, 2010; Gundale *et al.*, 2011), serving as slow-release sinks that may benefit vascular plants (Hobbie, 1996; Malmer *et al.*, 2003; Turetsky *et al.*, 2010, 2012), to buffering against excessive N flux to sub-rhizosphere soils (Koranda & Michelsen, 2021). Bryophytes obtain N from a variety of sources, including both wet and dry atmospheric deposition, canopy throughfall, leaf litter leachates, soil, and by hosting N-fixing cyanobacteria (Turetsky, 2003; Ayres *et al.*, 2006; Koranda & Michelsen, 2021). While bryophytes most readily take up N as NH₄⁺ and NO₃⁻, with NH₄⁺ being the form most readily assimilated (Schuurkes *et al.*, 1986; Brown, 1992; Turetsky, 2003), bryophytes also assimilate organic N forms such as amino acids and dipeptides (reviewed in Turetsky, 2003). The rate of N uptake is fairly consistent across ecological systems, despite varying levels of bryophyte prevalence. In tundra and boreal systems, bryophyte N uptake can account for up to 60% of the total aboveground plant N uptake (Marion *et al.*, 1982). *Sphagnum* spp. uptake of N in high-latitude peatlands varies widely from 0.36 to 1.9 ± 2.7 g N m⁻² yr⁻¹ compared with 0.67 N m⁻² yr⁻¹ by vascular plants. The high end of this amount of N uptake exceeds the estimated input of 0.33–0.5 ± 0.4 g N m⁻² yr⁻¹ by atmospheric deposition in subantarctic and northern peatlands (Rosswall & Granhall, 1980; Yin *et al.*, 2022), suggesting a significant contribution from other potential N sources. Similar rates of bryophyte N uptake from throughfall have been demonstrated in boreal forests (0.336 g N m⁻² yr⁻¹; Oechel & Van Cleve, 1986). Dense aggregations of bryophytes cover the forest floor of Pacific northwest temperate forests, USA, and can uptake 0.40 g N m⁻² yr⁻¹, a rate comparable to boreal and tundra systems (Binkley & Graham, 1981), constituting 11% of all aboveground plant N uptake (Perakis & Sinkhorn, 2011). N uptake by moss-dominated biocrusts in arid drylands can reach 0.4 g N m⁻² yr⁻¹ (Zhao *et al.*, 2010). Temperature and water availability influence the rates of N uptake by bryophytes within these ecosystems (Van Cleve & Alexander, 1981) through their direct impacts on bryophyte physiology. For example, experimental additions of N demonstrated that bryophytes below a threshold of oversaturation can rapidly uptake N, incorporating up to 89% of the applied N within the bryophyte layer (Koranda & Michelsen, 2021).

2. Biological N₂-fixation

Bryophytes host a diverse endophytic and epiphytic microbiome that includes various N₂-fixing diazotrophs such as cyanobacteria (Ininbergs *et al.*, 2011; Holland-Moritz *et al.*, 2018). BNF by bryophyte-associated microbes is one of the largest inputs of new N in high-latitude and high-altitude ecosystems and can sometimes equal or exceed N deposition rates (DeLuca *et al.*, 2002; Zackrisson *et al.*, 2004; Gundale *et al.*, 2011). Multiple bryophyte species host diazotrophic microbes, including *Sphagnum* spp., numerous forest-floor species (e.g. *Pleurozium schreberi*), and epiphyllic and epiphytic species (e.g. *Isoetecium myosuroides*; Opelt *et al.*, 2007; Ininbergs *et al.*, 2011; Lindo & Whiteley, 2011; Stuart *et al.*, 2021).

Fig. 6 Nitrogen uptake, storage, transformation, and loss through the bryosphere is illustrated by the red arrows. Arrows do not represent the size of fluxes, as these tend to vary greatly between ecosystems or even bryophyte species. The bryosphere is the area influenced by bryophyte traits, including bryophyte and substrate moisture, temperature, and microbial community assemblage and process rates.

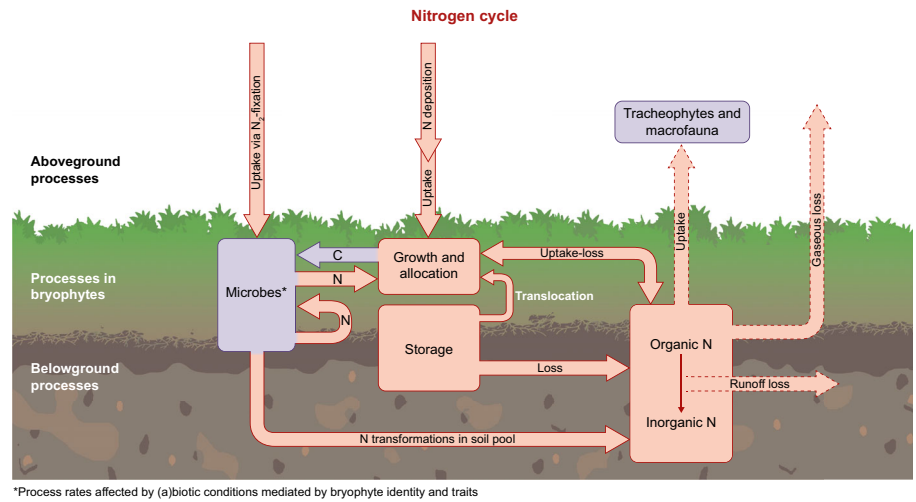


Table 1 Overview of bryophyte-associated biological nitrogen fixation (BNF) rates from the literature.

Ecosystem type	Minimum	Maximum	Average	Reference
Polar and alpine tundra regions				
Arctic	< 0.1	24.04	–	Deslippe <i>et al.</i> (2005) (Canada) Chapin <i>et al.</i> (1991) (Alaska, USA)
Antarctic	1	4.9	–	Vincent (2007)
Alpine	–	–	4.9	Bowman <i>et al.</i> (1996)
Boreal regions				
Subarctic	0.9	24.6	–	Sonesson (1967)
Boreal forests	< 0.1	15	3–4	Sorensen & Michelsen (2011) Lagerström <i>et al.</i> (2007) DeLuca <i>et al.</i> (2008) Jean <i>et al.</i> (2018) Van Cleve & Alexander (1981) Reviewed in Yin <i>et al.</i> (2022)
Northern peatlands (bogs and fens)	< 0.1	11.5	1.9 ± 2.7	
Temperate regions ¹				
Grasslands ²	0.008	0.124	–	Calabria <i>et al.</i> (2020)
Temperate forests	0.26 (forest floor)	0.76 (epiphytes)	0.26	Lindo & Whiteley (2011)
Tropical regions				
Tropical forests	–	–	0.2	Zheng <i>et al.</i> (2019) ³
Cloud forests	–	–	4.8	Markham & Fernández (2021)

All values are in kg N ha⁻¹ yr⁻¹. Note that the table only comprises the minimum and maximum values found in the literature, or an indication of the mean rate if only one could be found. Table extended from Lindo *et al.* (2013) through a nonsystematic review.

¹Knorr *et al.* (2015) published BNF rates associated with *Sphagnum* in Patagonian bogs, but incubation temperatures used were above the growing season average, possibly leading to inflated estimates.

²Vlassak *et al.* (1973) measured BNF associated with the moss *Ceratodon purpureus* in grasslands, but their rates could not be scaled up.

³Assuming 215 d growing season.

Aside from the well-known Cyanobacteria clade, other groups of N-fixing microbial taxa have been reported, such as methanotrophs in peatlands (Larmola *et al.*, 2010; Warren *et al.*, 2017; Holland-Moritz *et al.*, 2018; Saiz *et al.*, 2019). Molecular analyses of bryophytes have repeatedly found evidence for specificity in microbial communities related to bryophyte identity (Holland-Moritz *et al.*, 2021; Wicaksono *et al.*, 2021). The specificity of these communities may be driven in part by exchanges of material between bryophytes and microbes (Warshan *et al.*, 2017). The microenvironment created by bryophyte anatomy and community traits influences moisture, temperature, and organic matter composition (Fig. 3; Elumeeva *et al.*, 2011),

which in turn influences microbial community composition and process rates (Klarenberg *et al.*, 2023). Biotic and abiotic controls over bryophyte-associated BNF have been reviewed extensively by Rousk (2022).

Estimates of bryophyte-associated BNF rates vary widely across ecosystems (Table 1). The highest BNF rates are usually found in northern regions, although this could also reflect a sampling bias with most of the research on that topic conducted in boreal, subarctic, and Arctic regions of North America and Europe. Arctic tundra, subarctic and boreal forests, and northern peatlands have high fixation rates (up to 11.5–24.6 kg N ha⁻¹ yr⁻¹) but also show a wide range of variation (Table 1). By contrast, lower BNF

rates have been measured in alpine tundra and temperate regions (averages of 4.9 and 0.26 kg N ha⁻¹ yr⁻¹, respectively). Unfortunately, there currently are few reports of BNF rates in tropical biomes but higher BNF rates have been associated with dense epiphyllic bryophyte cover and biomass (Bentley, 1987). In particular, Yin *et al.* (2022) identify tropical peatlands as an important knowledge gap, since their high N accumulation rates suggest that their associated BNF could be even higher than in their northern counterparts. In terms of relative contribution to N requirements for primary productivity in various ecosystems, bryophyte-associated BNF typically contributes 2–10% of annual requirements in Alaskan coniferous forests (Jean *et al.*, 2018), but only *c.* 0.1–2.5% in temperate grasslands (Calabria *et al.*, 2020). Globally, BNF in peatlands was estimated at 8.0 Tg N yr⁻¹, a value that could have accounted for *c.* 14% of preindustrial BNF in terrestrial ecosystems (Vitousek *et al.*, 2013; Yin *et al.*, 2022). The fate of the fixed N (uptake, transfer, and loss) remains an object of active research, with some evidence suggesting a direct uptake by bryophytes (Jones & Wilson, 1978; Bentley & Carpenter, 1984; Berg *et al.*, 2013; Arróniz-Crespo *et al.*, 2022), while other works have suggested partial (Kardol *et al.*, 2016; Arróniz-Crespo *et al.*, 2022) or no transfer (Hyodo *et al.*, 2013).

3. N storage and loss

Bryophytes are efficient at retaining absorbed or adsorbed nutrients for extended periods of time within their tissues and have the capacity to recycle nutrients by translocating them from older to newer tissue (Turetsky, 2003; Glime, 2007; Fenton *et al.*, 2015). Studies in the tundra, shrublands, and temperate forests found higher N concentrations (NH₄⁺, NO₃⁻, or dissolved organic N) in bare soils than under bryophytes, suggesting that N intercepted and stored by bryophytes is held tightly (Koranda & Michelsen, 2021; Chen *et al.*, 2022; Dollery *et al.*, 2022). In some ecosystems, N sinks in bryophytes can be larger than in vascular plants, and the size of those sinks is influenced by temperature and precipitation (Liu *et al.*, 2020).

N losses from bryophyte tissues are primarily attributed to leaching and decomposition (Carleton & Read, 1991; Koranda & Michelsen, 2021). Various disturbances, particularly those related to desiccation-rehydration and freeze-thaw cycles, have been found to enhance N loss in several bryophyte species (Carleton & Read, 1991; Lindo *et al.*, 2013; Slate *et al.*, 2019b). In boreal ecosystems, it can take anywhere from 3 to 7 yr to detect a measurable level of N loss from bryophytes (Liu *et al.*, 2020; DeLuca *et al.*, 2022), with incremental loss gradually returning N to other plants (Oechel & Van Cleve, 1986). Under substantial N deposition, bryophytes may transition into a N source with net N release from their tissues (Gundale *et al.*, 2011). The fate of N outside the bryophyte but still within the bryosphere is affected in part by transformations between different forms of N. For example, rates of gaseous N loss depend on soil conditions (temperature, moisture, and pH) to produce N compounds via ammonification and nitrification and the volatilization of NH₄⁺ or denitrification (Maag & Vinther, 1996). Some evidence suggests that the amount of leached C from bryophytes and ratio of leached C to N may also influence rates of gaseous N loss from the bryosphere (Slate *et al.*, 2019b).

4. Impacts of changing climate

Climate change impacts on temperature and precipitation as well as increases in N deposition are having profound impacts on bryophyte contributions to the N cycle. Decreases in bryophyte cover related to the physiological stress of higher temperatures, altered precipitation patterns, or N deposition (Koranda *et al.*, 2007; Gundale *et al.*, 2011; He *et al.*, 2016) are being exacerbated by negative global change impacts on the plants that bryophytes co-occur with. N deposition, particularly inorganic N, decreases the ability of bryophytes for N uptake, causing a deterioration in their physiological condition in a few evaluated ecosystems (Koranda *et al.*, 2007; Gundale *et al.*, 2011; Zhang *et al.*, 2016). Increased temperatures could accelerate bryophyte decomposition rates, leading to increased ecosystem N loss. The implications of this on plant communities and biogeochemical processes remain undetermined. Warming field experiments have been shown to have both direct and indirect negative impacts on bryophytes and BNF in Arctic tundra most likely related to decreases in bryophyte cover, increases in vascular plant cover, and reductions in BNF activity (Permin *et al.*, 2022). Given the ecological importance of BNF as a source of N, reductions in this N input will have consequences for plant productivity and soil C storage that are currently poorly understood.

V. Other effects of bryophytes and their associated biota on ecosystem function

Water, C, and N cycles are not the only broad impacts that bryophytes have on ecosystems. Due to their physical structures and position at the substrate-atmosphere interface, bryophytes also impact matter and energy fluxes as well as food webs and terrestrial community dynamics. Bryophytes intercept and store air-borne soil and most other nutrient elements carried in throughfall, decomposing plant litter, and dust (Oechel & Van Cleve, 1986; Hájek & Adamec, 2009). Externally stored nutrients and stored soil serve as a substrate and provide resources for co-occurring epiphytic and nonepiphytic plants (Pócs, 1982; Leary *et al.*, 2004). Significant physical effects and biotic interactions have also been reported for numerous environments and merit further attention, even if they are not the primary focus of this review, not least due to their interactions with water and nutrient cycles.

Thick bryophyte mats can have large impacts on the exchange of energy between atmosphere and earth surfaces. These effects include changing surface albedo (Stoy *et al.*, 2012; Xiao & Bowker, 2020), radiative heat transfer from soil (effectively insulating soil temperature from air temperature; Soudzilovskaia *et al.*, 2013; Porada *et al.*, 2016) and changing boundary-layer thickness (Rice *et al.*, 2018). Bryophyte insulative effects are probably best studied in regions with permafrost where bryophytes contribute to permafrost persistence (Matthews *et al.*, 1997). While these effects have received attention in ecosystem models of high-latitude systems (Stoy *et al.*, 2012; Porada *et al.*, 2018), they are likely to be important in other ecosystems with high bryophyte cover or biomass such as montane tropical forests. Thermal properties of bryophytes also change with hydration status (Rice

et al., 2018) and can reduce the severity or frequency of extreme events such as freeze–thaw cycles. Many of the biotic effects of bryophytes, described below, can be related to these effects on the thermal environment, as well as water, C, and N impacts.

Bryophytes regularly interact with vascular plants, bacteria, micro and macro invertebrates, and vertebrates. For vascular plants, bryophytes sometimes provide a moist microsite that facilitates the recruitment of native plants (e.g. Van Tooren *et al.*, 1985; Berdugo *et al.*, 2022), and in some systems (e.g. deserts, boreal, and grasslands) inhibit invasive species establishment (Slate *et al.*, 2019a; Vandvik *et al.*, 2020). In desert, grassland, alpine, and Arctic ecosystems, the impact of bryophytes tends to be mostly positive on later stages of vascular plant growth and survival due to their influence on water, C, and N cycling outlined above. However in peatlands, *Sphagnum* spp. inhibit the productivity of older plants as the waterlogged environmental conditions they create lead to low nutrient availability (Pacé *et al.*, 2018). We suggest this as an important topic for a future review as the literature is vast, diverse, and unresolved.

The ubiquitous bacteria, cyanobacteria, fungi, algae, micro and meso invertebrates, and other microflora and microfauna within the bryosphere (Lindo & Gonzalez, 2010), are important drivers of biogeochemical cycling and also influence bryophyte growth. For example, methanotrophic biota within the *Sphagnum* microbiome not only play a key role in BNF but also supply CO₂ that supports *Sphagnum* photosynthesis (Raghoebarsing *et al.*, 2005). Bryophytes also support diverse suites of free-living and vascular plant-associated fungi, many of which are generalists, while others seem to associate with specific bryophyte species (Döbbeler, 1997; Davey *et al.*, 2013) where they may even be relegated to certain bryophyte tissue (Redhead & Spicer, 1981). Fungi can account for up to 4% of bryophyte biomass and the magnitude of bryophyte-associated fungal communities is comparable to that of vascular plant rhizosphere fungal communities (Davey *et al.*, 2009, 2012). Microeukaryotes and microarthropods (i.e. collembola and oribatid mites), are particularly diverse and abundant in bryophyte mats (Darby *et al.*, 2011), and contribute to C fixation and nutrient cycling directly as decomposers, but mostly indirectly through multi-trophic dynamics (Kardol *et al.*, 2016; Barreto *et al.*, 2023). Allelochemicals produced by these microbiota can also inhibit vascular plant establishment (Chiapusio *et al.*, 2013, 2022) and maintain the composition and function of bryophyte communities (Norby *et al.*, 2019). Herbivory of bryophytes is not as common as in vascular plants due to their high production of secondary metabolites, high phenolic and cellulose content, which makes bryophytes difficult to digest (Glime, 2006). These overall low levels of bryophyte herbivory further support ecosystem C accumulation, water retention, and water storage (see Section II).

VI. Bryophyte restoration and conservation

The effects of changing climate on bryophyte abundance and ecosystem function should not be overlooked. Changing climate is reducing the cover and/or altering the composition of bryophyte communities globally (Fig. 2) and efforts to restore and conserve

bryophytes should continue to be improved and expanded on. Research on bryophyte restoration has been primarily focused on drylands and peatlands, locations where large amounts of bryophyte research have occurred, and should be expanded across additional ecosystem types. Bryophyte restoration is a slow and challenging process involving site preparation, bryophyte/propagule collection, and bryophyte re-introduction with the amount and type of attention needed after re-introduction still being refined. While this workflow doesn't vary from vascular plant restoration efforts, the scale of time needed for bryophyte restoration and general lack of familiarity with bryophytes results in a slower rate of methodological improvement. Progress made in recent years and certain systems (Chimner *et al.*, 2017), however, suggests that successful bryophyte restoration may become a viable strategy. The main hindrances to bryophyte restoration that remain include (1) the general oversight of bryophyte restoration in favor of vascular plant restoration, (2) restoration of the wrong bryophyte species, and (3) the fact that harvesting bryophytes for re-introduction creates a new disturbance. Efforts have been made to better coordinate bryophyte salvaging for reinoculation from areas where disturbances are planned (Rocheffort *et al.*, 2003; Bowker, 2007; Tucker *et al.*, 2020). Likewise, cultivation efforts are also being developed in the glasshouse, field, and fog chamber (Doherty *et al.*, 2015, 2020; Antoninka *et al.*, 2016) and should be considered more broadly.

In terms of conservation, environmental features are key determinants of the abundance of any bryophyte species. The diminutive size of bryophytes combined with their unique physiology makes microenvironmental features specific to growth substrates, associated plant communities, and water levels more important than macroenvironmental features in determining the ability of individual species to establish and expand (Vitt *et al.*, 2023). Indeed, rare bryophytes are thought to be rare because their specific microhabitat is lacking (Heinlen & Vitt, 2003). This tight microenvironmental connection combined with widespread disturbance has contributed to 23% of European bryophyte species being recently identified by the IUCN as threatened (Hodgetts *et al.*, 2019). Compared with vascular plants, conversations on bryophyte conservation are in their infancy but as awareness increases, attention to developing tools and strategies for conserving bryophytes should be a high priority.

VII. Conclusion

While broad commonalities exist for some ecosystems, there may be key differences not only between but also within ecosystem types, both in functional impact of bryophytes and in vulnerability. Major climatic stressors and vulnerabilities may also differ greatly between seasons: high temperatures are damaging to hydrated bryophytes during the wet season, but may have minimal impact on dormant bryophytes in the dry season. Divergent responses to the same environmental stress such as this need to be evaluated in greater depth across terrestrial ecosystems. From our review, we identified a set of eight unanswered questions of key importance to better estimate and compare the current contributions of bryophytes to water, C, and N cycles and to assess the direct effects

of climate change on bryophyte abundance and subsequent indirect effects on ecosystem and global water, C, and N dynamics:

- (1) How do bryophyte rehydration rates (varying with alternative water sources) modulate bryophyte effects on water, C, N, and other nutrient cycles within and across ecosystems?
- (2) How much does nonrainfall water (dew, fog, distillation, etc.) and snow contribute to bryophyte water storage and C fixation?
- (3) What are the ecosystem effects of bryophytes in ecosystems where they have been historically overlooked (e.g. tropical lowland rainforest, tropical dry forest, drier temperate forest, etc.)?
- (4) What is the relationship between bryophyte diversity and ecosystem functions?
- (5) What is the diversity, extent, and global fraction of bryophyte-associated N fixation?
- (6) What is the global contribution of bryophytes to 'shoulder season' C and N fixation?
- (7) How do the functional effects of bryophytes vary across lineages and growth forms?
- (8) What are the biophysical impacts of bryophytes outside of high-latitude environments?

While evidence suggests that global change factors that directly or indirectly reduced water availability will be detrimental to bryophyte ecophysiology across terrestrial biomes, with cascading effects on ecosystem functions, it is equally important to note that bryophytes are incredibly resilient plants. Bryophytes are among the first colonizers, regrowing after being dry or entombed in glaciers for months to years (e.g. La Farge *et al.*, 2013; Roads *et al.*, 2014; Stark *et al.*, 2017). Recent research notes that in the absence of experimental warming, dryland moss recovery was more dynamic than expected (Phillips *et al.*, 2022), suggesting that the variability of changing climate may provide unanticipated opportunities for natural recovery and adaptation. Bryophyte microbiomes may even increase the thermotolerance of their hosts by inducing a physiological stress response to increasing temperatures (Carrell *et al.*, 2022) but the complexity of this and associated responses to changing climate (Davey *et al.*, 2017) needs greater attention across species, circumstances, and ecosystems. Bryophytes also have strong positive impacts on the resilience of the ecosystems in which they occur (Rodríguez-Rodríguez *et al.*, 2023). For example, ruderal dryland bryophytes that colonize after severe wildfires increase soil bacterial diversity and promote succession of microbial communities on fire-affected soils (García-Carmona *et al.*, 2022), leaving us reason to hope that by conserving and restoring bryophytes we may continue to reap the benefits these plants provide for the foreseeable future.

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Competing interests

None declared.

Author contributions

MLS and KKC conceived the study, recruited the coauthors, and coordinated the manuscript writing. AA, LB, MBB, DAC, MC, MWC, NJF, HH-M, SH, MJ, BEK, ZL, AM, TO, DS, JS, and DT contributed to the writing and editing.

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Supporting Information

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Notes S1 Additional descriptions of what each image in Fig. 2 shows.

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