The ecology and function of soil mosses and their associated microbiome under global change

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Abstract

Mosses represent one of the most ubiquitous groups of non-vascular plants on Earth, occurring across diverse climates and habitats. Emblematic mosses, such as *Sphagnum*, have key physiological adaptations, including high cation-exchange capacity and the production of recalcitrant phenolic compounds that can facilitate long-term C preservation and peat accumulation. They also provide habitat for highly functional microbiomes, which are key in regulating major nutrient cycles, e.g., via biological nitrogen fixation (BNF) or helping in C sequestration. Unfortunately, climate change is impacting the moss-associated microbiome, leading to critical implications for moss microbiome-mediated biogeochemical cycles. This review seeks to summarize the current state of knowledge about the ecology and function of the microbiome of mosses and their vulnerability to climate change.

Impact Statement

Mosses are ecologically significant non-vascular plants that contribute to multiple ecosystems functioning across diverse terrestrial habitats. Their associated microbiomes also facilitate these processes by taking an active part in various functions linked with nutrient cycles (e.g., BNF). However, climate change may alter these moss-microbe interactions, with potential consequences for microbiome-mediated biogeochemical processes. This manuscript provides a comprehensive overview of moss ecology and associated microbiomes, highlighting their role in regulating soil nutrient cycles in regions where vascular plant abundance is scarce. In this review, we discuss the fundamental ecological and biogeochemical functions of moss-associated microbiomes and evaluate the vulnerability of these vital microbial associations to ongoing climate change.

Keywords: Moss microbiome, Biological nitrogen fixation (BNF), Carbon sequestration, Moss biocrust, Climate change

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1. Introduction

Mosses, as part of the bryophytes, are among the most ubiquitous life forms found in nearly any terrestrial and freshwater habitat, across all climatic regimes, from deserts to boreal forests, and across contrasting land uses, from natural to urban environments. Mosses are the earliest-diverging lineages of modern land plants, with an evolutionary history spanning over 450 million years (Donoghue *et al.* 2021; Laenen *et al.* 2014). The present-day major clades of land plants, bryophytes and tracheophytes, have both evolved from a common ancestor (Ligrone *et al.* 2012). The evolution of all land plants' fundamental characters takes place in the bryophyte grade. Bryophytes carry the history of the earliest plants to have colonized land (Clarke *et al.* 2011). As such, these organisms are largely regarded as a model system for studying land plant evolution, stress-induced cellular responses and plant-microbe coevolution (Yadav *et al.* 2023).

Mosses are an entirely different group of plants, often referred to as non-vascular plants, lacking a proper root system for the absorption of nutrients and water directly from the soil surface; instead, they have less-developed rhizoids. They usually appear as thick mats in moist habitats of terrestrial ecosystems and are associated with soil particles to form thin moss biocrusts in dryland ecosystems. Moreover, we have a relatively good understanding on the structure and function of mosses. A recent study mapping the global distribution of soil mosses suggested that soil moss cover is negatively influenced by vascular plant cover and climate seasonality (Eldridge et al. 2023). The moss cover tended to be greater in environments with relatively stable temperature conditions and limited vascular-plant competition. This might reflect their specialized adaptations for moisture retention and tolerance to prolonged desiccation. Mosses are further fundamental for supporting soil microbial diversity and ecosystem functions (Delgado-Baquerizo *et al.* 2016, 2018). They are the primary producers of the boreal ecosystem, and their associated diazotrophic communities substantially contribute to terrestrial nitrogen (N) fixation (Elbert et al. 2012; Renaudin et al. 2022a). Mosses also have a crucial role in C sequestering and are responsible for more than one-fifth of global soil organic C storage in peatland ecosystems (Holden 2005; Macdonald *et al.* 1998). Moreover, moss biocrusts serve as an important hotspot for microbial genetic resources that link with different ecological processes (Xiao and Veste, 2017). Moss biocrusts have a significant contribution to soil nutrients such as N by shaping the below-ground microbial community that promotes N mineralization while reducing the microbial assimilation of available N (Tang et al., 2023; Xiao et al., 2023). Moss biocrusts also have the potential to expedite the restoration of severely degraded ecosystems by maintaining soil fertility (Cheng et al., 2021).

Even so, most studies have focused on a few moss species. For instance, *Sphagnum* and its close relatives receive the main focus while representing only 2.5% of moss species globally, which also highlights the ecological significance of peatlands. This bias is concerning since *Sphagnum* is an evolutionarily distinct lineage, making it distant from the rest of the mosses (Newton *et al.* 2000; Shaw *et al.* 2010). Moreover, the ecological characteristics of this particular genus, which predominantly thrives in cold, acidic, water-saturated, nutrient-poor and oxygen-deprived conditions, may not adequately represent the ecology and functional diversity of other moss lineages. Therefore, expanding our knowledge beyond *Sphagnum* to encompass the ecology and distribution of a wider range of moss species is critical for better understanding their contributions to ecosystem functioning.

Mosses are major microbial habitats hosting diverse groups of organisms from archaea and bacteria to eukaryotes like chromista, fungi, metazoa and protists (Câmara *et al.* 2021). We know that moss host species identity and their phylogenetic relationships play a role in shaping moss microbiome composition (Tveit *et al.* 2020). Moreover, light availability, climate

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(temperature and precipitation), pH, soil nutrients and surrounding tree abundances and canopy structure are also key drivers of the moss microbiome (Delgado-Baquerizo *et al.* 2018; Korn *et al.* 2024; Renaudin *et al.* 2022b; Rodríguez-Rodríguez *et al.* 2022; Stuart *et al.* 2021). Microbial symbiosis plays a significant role in moss survivability in adverse environments and assists in the establishment of land plants (Delaux and Schornack 2021; Knack *et al.* 2015). Also, mosses are known to provide habitat for microbes in drylands, mitigating the impacts of aridity on the soil microbiome when compared with soils uncovered by mosses (Delgado-Baquerizo *et al.* 2018). Millions of years of plant-microbe symbioses have led to the selection of functionally adapted microbial groups within the moss microbiome, including key N fixers (Wicaksono *et al.* 2021).

Unfortunately, mosses are highly vulnerable to global environmental change (Eldridge *et al.* 2023). Alterations in global climatic patterns can have a profound effect on moss microbial communities, which have a fundamental role in global nutrient fixation. Experimental evidence suggests that changes in present climate conditions lead to a shift in the community composition of the moss-associated microbiome that further disrupts their ability to fix C and N (Klarenberg *et al.* 2022). Such changes could have implications for nutrient cycling in ecosystems where moss-microbe associations contribute substantially to biogeochemical processes, highlighting the need for investigating the moss microbiome across diverse habitats and environmental conditions. This review emphasizes on the ecological perspectives of moss-associated microbiome, their associated role in global nutrient fixation and the consequences of climate change on their ecological functionality. Here, our discussions are primarily confined to the microbiomes of soil-associated mosses, considering diverse growing habitats, from drylands to waterlogged peatland ecosystems, cold regimes to artificial warming environments and high altitudes mountain to low-altitude landforms. We have excluded the microbiome of parasitic mosses or those that are attached to different substrata, as there are lacking in information or research. The main purpose of this synthesis is to deliver a deeper understanding of moss-microbe interactions, which have been essential in shaping the function of terrestrial ecosystems worldwide.

2. Mosses as a model-system for understanding climate change and the evolution of plant-microbe interactions

Given their global scale distribution and their small size which allow easy manipulations in lab and field micro and mesocosm experiments, mosses provide useful model systems for addressing significant questions concerning the impacts of global environmental change (Maestre *et al.* 2016). Yet, despite recent advancements, our understanding of how moss-microbial relationships were first formed remains relatively limited. Moreover, we posit that mosses can help deepen our understanding of plant-microbe interactions. Diverse mosses can provide contrasting information given their evolutionary histories, constituting different model-systems. The early-diverging moss, such as *Takakia* is Earth's most archaic modern land plant. It can be viewed as a model for studying symbiosis-related aspects of the evolutionary transition of plant-associated microbiomes. It may partially mirror the microbial symbiosis adaptation to challenging environmental conditions, like scarcity of nutrients. The homology of *Takakia* root-analogs with the lateral roots of angiosperms, also having the capability of mucilage production, helps them to maintain N-fixation symbiosis. Some members of mycorrhizal fungi, like *Rhizophagus irregularis,* have been identified in the microbiome of *Takakia* but were later lost from mosses during the course of evolution (Radhakrishnan *et al.* 2020; Read *et al.* 2000; Satjarak *et al.* 2022). Likewise, studies at the genomic level have revealed that mosses like *Sphagnum* exhibit no gene colinearity with other available reference genomes, representing it as a novel lineage of land plant evolution (Healey

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et al. 2023). Thus, bog ecosystems serve as another model systems to study the evolution of plant-microbe interactions, owing to their long-term ecological stability, abiotic factors and ombrotrophic lifestyle that is not easily influenced by soil and presents a bridge between terrestrial and aquatic habitats (Chaudhary *et al.* 2018; Pedrotti *et al.* 2014). Most of the existing studies have predominantly focused on N-fixing bacterial communities associated with the mosses of these environments (e.g. *Sphagnum*), creating a bias in our knowledge regarding bacterial footprints of other moss species. Such an imbalance may hinder a comprehensive understanding of the potentiality of moss-associated microbiome, particularly in the context of global moss-microbial diversity and their role in the establishment of plant-microbe symbiotic associations throughout land plant history.

Other living labs where mosses can constitute significant model systems are dryland ecosystems (Bowker *et al.* 2018; Li *et al.* 2022; Young *et al.* 2024). In the arid and semiarid regions of the globe, which are often characterized by relatively sparse vascular plant cover, moss biocrusts occupy the plant interspaces (Pombubpa *et al.* 2020; Tian *et al.* 2023b). Moss biocrust covers a major portion of the terrestrial soil surface and provides multiple ecosystem services in dryland ecosystems (Tian *et al.* 2023b). Biocrust-forming mosses showed a positive influence on belowground microbial activities as well as their abundances, especially in the regions of high aridity (Delgado-Baquerizo et al. 2016). In arid ecosystems, biocrust-associated microorganisms are highly involved in biogeochemical cycles related to C and N metabolism. However, the functional potential of microbial communities varies with different stages of succession (Liu et al. 2018; Zhao et al. 2020). For example, the genes related to C degradation and denitrification were found to be at the highest abundance at the later stages of succession in desert ecosystems (Liu et al. 2018). In addition, the identity of dominant biocrust-forming species can substantially influence the composition and functional potential of their associated soil microbiome (Concostrina-Zubiri *et al.* 2021; Liu *et al.* 2017; Pombubpa *et al.* 2020). Together, these findings highlight mosses as potential model systems for investigating how species-specific effects and successional dynamics shape soil microbial communities and influence biogeochemical functioning.

3. Unveiling the moss microbiome: community architecture and diversity drivers

3.1 Bacterial taxonomic architecture across the moss

Mosses and microbes support complex and long-term co-evolved relationships which we are just starting to understand. Mosses have been shown to support a unique and globally distributed core microbiome across contrasting habitats at a global scale. This microbiome is dominated by *Pseudomonadota*, *Chloroflexota*, *Myxococcota* and *Cyanobacteriota*, and is known to conform complex soil ecological networks which can be found worldwide (Ochoa-Hueso *et al.* 2024). The diversity and richness of these moss-associated microbial groups can be even higher than those of vascular plants living in close vicinities (Ramakrishnan et al., 2025). Furthermore, the colonization patterns of moss-associated bacteria are uneven along moss shoot, with bacteria occupying distinct ecological niches that partially overlap (Renaudin *et al.* 2022b). For example, the basal region of the moss gametophytes is associated with bacterial phyla having potential for N fixation, C fixation and methane metabolism, while anoxygenic photoautotrophs dominate bacterial phyla of the apical part (Ishak *et al.* 2024). Furthermore, the environmental perturbations, along with the moss host trait, regulate the overall microbial community composition of the moss microbiome (Ramakrishnan et al., 2025).

Moreover, the dominant moss species present in the biocrust can shape the overall microbial community of the moss-dominated biocrust (Song *et al.* 2022). The moss biocrust microbiome

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largely depends upon carbohydrate substrates as its primary C source (Tian *et al.* 2023b). These microbiomes usually have higher bacterial species richness than their fungal counterparts (Pombubpa *et al.* 2020; Song *et al.* 2022). It was also observed that these bacterial populations maintain a distinct depth-dependent organization along with the vertical axis of moss biocrust. They had lower species richness within biocrust samples than in their soil underneath (Mueller *et al.* 2015; Pombubpa *et al.* 2020). Moss biocrusts are usually rich in bacterial phyla such as *Actinobacteria*, *Bacteroidetes*, *Proteobacteria*, *Acidobacteria* and *Cyanobacteria* (Pombubpa *et al.* 2020; Tian *et al.* 2023b). The presence of *cyanobacteria* in different biocrust types symbolizes their reliance on sunlight for photoautotrophic metabolism (Garcia-Pichel *et al.* 2003; Steven *et al.* 2013). However, in the case of a moss-dominated biocrust, *cyanobacteria* abundance is low, as most of the photoautotrophic activity is attributed to mosses (Fisher *et al.* 2020). In addition, some key microbial taxa such as *Microcoleus*, *Microvirga*, *Pseudonocardia*, *Belnapia* and *Methylobacterium* act as microbial hubs in moss-dominated biocrusts (Pombubpa *et al.* 2020). These microorganisms possess specific traits, including the production of extracellular polysaccharides and antifungal compounds, which can influence microbial interactions by promoting microbial adhesion and biofilm formation while suppressing the growth of fungal parasites (Belnap and Gardner 1993; Cafaro *et al.* 2011; Carr *et al.* 2012). Thus, these bacterial taxa have an essential role in maintaining overall microbial community dynamics and functioning. However, future studies are needed to provide deeper insights into specific functional guilds and community-level regulation of these species.

3.2 Major drivers of microbial community assembly

3.2.1 Host-mediated deterministic factors

The evolutionary divergence between bryophytes and vascular plant is characterized by a profound structural trajectory; while the tracheophyte lineage evolved intricate internal compartmentalization and specialized vascular tissues, moss gametophytes maintained a relatively simpler, highly conserved anatomical organization (Huttunen *et al.* 2018). Such a uniform, non-complex architecture may provide a standardized, ubiquitous interface for plant-microbe interactions. To the best of our knowledge, few studies have examined relationships between host morphological traits and their associated microbiome assembly patterns. A prominent example is found in *Sphagnum*, whose specialized dead, hollow, water-filled hyaline cells create suitable microsites for moss-microbe interactions (Bragina *et al.* 2012). The relatively elevated pH of hyaline cells provides a favourable microhabitat for microbes in the harsh, acidic peatland environment. However, metabolites released by *Sphagnum* exerted a greater influence on their associated microbial community structure and function than its anatomical and morphological features (Sytiuk *et al.* 2022). The micro-topographical variations of moss surfaces, like the presence of papillae, paraphyllia and lamellae, give them an additional advantage in engineering microhabitats for better microbial colonization. For example, the presence of paraphyllia (filaments or leaf-like photosynthetic structures present between the moss leaf and stem) showed substantial cyanobacterial colonization compared to the rest of the moss shoots (Liu and Rousk 2022). However, their occurrence was restricted to only a few moss families, such as Brachytheciaceae, Hylocomiaceae and Thuidiaceae. In addition, the macro-structural geometries of moss leaves help them to retain moisture that shields microbial communities from rapid drying. For example, some species like *Sphagnum* can curve their leaves for better water retention (Bengtsson et al. 2020). Furthermore, moss hosts provide specific microenvironments that select characteristic microbial communities in their associated microbiomes (Holland-Moritz *et al.* 2018; Ininbergs *et al.* 2011; Jean *et al.* 2020; Opelt *et al.* 2007a; Wang *et al.* 2024). The microbiome similarity index is found to be highest in the case of moss species with the closest phylogeny compared to distant ones (Ishak *et al.* 2024). In addition, mosses maintain a distinct bacterial community structure throughout

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their life by vertical transmission of microbes over gametophytes to the sporophytes (Bragina *et al.* 2012; Escolástico-Ortiz *et al.* 2023; Holland-Moritz *et al.* 2021; Klarenberg *et al.* 2023). Unlike some hornworts and liverworts, mosses generally lack specialized structures dedicated to housing microbial symbionts such as *cyanobacteria* (Rikkinen 2017). Consequently, the associated microbiome may be shaped more strongly by host and local environmental conditions, potentially resulting in greater variation in colonization potential and community composition across moss taxa and habitats. Furthermore, the extent of variation in colonization potential of microbes across moss taxa further creates some bias in their ecological functional roles (Holland-Moritz *et al.* 2018; Liu and Rousk 2022; Salemaa *et al.* 2019; Stuart *et al.* 2020). Moreover, this influence of moss-host genetic makeup on microbial community composition cannot be separated from their prevailing environmental conditions. Thus, it is challenging to disentangle the species-specific effects on microbiome composition from their native micro-environmental influences. Future studies on variation of microbial diversity relative to different clades within the similar moss host and environmental conditions will provide a deeper understanding of the eco-evolutionary process of moss-microbe interactions.

3.2.2 Environmental filters

The microbiome of soil mosses has recently been demonstrated to be highly correlated with changes in water availability, with mosses in more arid ecosystems usually associated with higher relative abundance of microbial taxa as compared to mesic environments (Ochoa-Hueso *et al.* 2024). Temperature is another significant driver of moss microbial associations (Ishak *et al.* 2024; Renaudin *et al.* 2022a). However, the impact of temperature on moss microbiome can vary depending on host species, physiological condition, ecological context, and the thermal history of the associated microbial community. For example, bacterial communities associated with the feather moss, *Racomitrium lanuginosum* exhibit greater thermal resistance compared to those of *Sphagnum* (Carrell *et al.* 2019; Klarenberg *et al.* 2022). Interestingly, the *Sphagnum* microbiome exposed to warm field conditions has the potential to acclimate and respond to warming by thermal reprogramming of host defense mechanisms, including upregulation of heat shock proteins (HSP70) and genes involved in jasmonic acid biosynthesis (Carrell *et al.* 2022a). Together, these findings suggest that temperature-mediated responses of moss-associated microbiomes are context-dependent and may reflect complex interactions among host physiology, microbial adaptation, and environmental conditions. Moreover, moss-associated bacterial community composition can shift under warming environments. However, the responses of diazotrophic communities to warming are taxon-specific. For example, the relative abundance of heterocystous cyanobacterial diazotrophs, including *Fischerella* and *Stigonema*, as well as alphaproteobacterial diazotrophs, decreases under warming, whereas certain bacterial taxa involved in nitrification increase in relative abundance (Carrell *et al.* 2019; Klarenberg *et al.* 2022). Normally, long-term warming increases the relative abundance of taxa that are engaged in the initial step of the N cycle, such as diazotrophic genera *Rhizobium*, *Rhizobacter*, *Pararhizobium*, *Neorhizobium*, *Allorhizobium*, *Sphingomonas* and nitrifying bacteria *Nitrobacter* (Klarenberg *et al.* 2022). However, the changes in microbial composition may not be the direct consequence of warming, but instead an indirect effect of some other temperature-mediated variables like soil moisture level (Allison and Treseder 2008), moss layer thickness (Björnsdóttir *et al.* 2022), etc. The temperature also influences the moss's photosynthetic activities. A higher temperature reduces the moss photosynthate production, thereby secreting little exudates for their associated microbiome (Haraguchi and Yamada 2011). The change in the C-rich exudate, polyphenols, and other secondary metabolites released from *Sphagnum* is itself responsible for the shift in microbial community structure under warming (Jassey *et al.* 2012) (Figure-2).

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Most of the moss-associated microbial community structures are influenced by the physical and chemical characteristics of their underlying soil (Ramakrishnan *et al.* 2025). Soil pH has been shown to be another major driver of the microbiome of soil mosses across global environments (Ochoa-Hueso *et al.* 2024), with more alkaline soils supporting a higher relative abundance of these specialized microbial assemblages. Moreover, soil pH has a deterministic role in the maintenance of the abundance of bacterial taxa, like *cyanobacteria*. The growth rate of nostocalean cyanobacterial communities is significantly inhibited with rising soil pH (Alvarenga and Rousk 2021; Garby *et al.* 2017; Kannaujiya *et al.* 2020). Furthermore, the acidification of moss microhabitat reduces the cyanobacterial abundance and ultimately impacts the N cycle (Alvarenga and Rousk 2021). An elevated concentration of soil N may also trigger negative feedback on the differentiation of vegetative cells to heterocyst cells in *cyanobacteria* (Flores *et al.* 2019). The higher availability of soil N in low light conditions supplants the niche with non-diazotrophic *cyanobacteria* in moss that is previously occupied by active cyanobacterial diazotrophic communities (Alvarenga and Rousk 2021). However, the effects of soil N enrichment depend on its chemical form, abundance and time of exposure in dryland moss biocrust. Notably, the addition of N in the form of ammonium results in microhabitat acidification, leading to the collapse of cyanobacterial biomass in moss biocrust. Soil nitrate amendments enhance moss-cyanobacterial associations at lower doses and inhibit moss functional potential at higher doses. Surprisingly, soil urea abundance has shown a positive influence on moss microbial biomass by maintaining neutral pH (Qian *et al.* 2025). Nonetheless, a low-level addition of soil N can increase the diversity and richness of moss belowground microorganisms, which indirectly promotes the soil respiration rate, resulting in loss of soil organic C content in dryland ecosystems (Dou *et al.* 2024). Soil litter also has different influences on moss-microbial associations depending on the various biochemical nature of litter from different plant species. For instance, birch litter, rich in phosphorus, stimulates moss-*cyanobacteria* association, while willow litter, high in N, inhibits these associations (Rousk and Michelsen 2017; Sorensen and Michelsen 2011).

4. Functional traits and microbiome-mediated ecosystem services

Functional traits are measurable plant characteristics that influence responses to environmental conditions and interactions with associated organisms, while trade-offs among these traits reflect different ecological strategies. Mosses are associated with a highly diverse group of symbiotic microorganisms that mediate vital ecological processes, extending beyond host health. These interactions are inherently dynamic and span a highly plastic continuum ranging from beneficial to neutral or even detrimental interactions (Leung & Poulin, 2008). The stability, functioning and health of moss-dominated ecosystems are largely dependent on their associated microbiome services. These microbiome services are mainly related to nutrient input, biosynthesis of essential molecules, support in host-plant growth and metabolism, etc. (Lan *et al.* 2020; Opelt *et al.* 2007b; Renaudin *et al.* 2022b; Shcherbakov *et al.* 2013; Wicaksono *et al.* 2021). Although intensive frameworks for vascular plant functional traits have been developed, bryophytes still lag, despite an increasing number of studies on their ecological attributes across multiple ecosystems over the last few decades. In the case of mosses, particularly considering functional traits, approximately two-thirds of records involve nutrient cycling, emphasizing their potential roles in various biogeochemical cycles (Eldridge *et al.* 2023). A recent synthesis of 282 studies has characterized more than 10,000 moss-associated functional traits. Among them, the traits based on morphological characters and those related to nutrient storage and cycling dominate the existing literature (Coe *et al.* 2024). Recent studies have increasingly explored moss functional traits being linked to microbiome composition and ecosystem services. For example, moss leaf architecture and hydration rate can modulate moss-cyanobacterial associations, hence regulating cyanobacterial N-fixing

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activity. In a comparative study of four mosses, the species with a greater hydration rate showed better cyanobacterial colonization and had a higher N-fixation rate (Liu and Rousk 2022). The moss species with higher hydration rates could promote maximum cyanobacterial colonization by facilitating their movement along the moss shoot (Brahamsha B and Bhaya D 2014). Moreover, mosses characterized by a high frequency of small leaves possess greater surface area, potentially enhancing water retention and providing more colonization sites for cyanobacterial colonization than species with fewer and larger leaves (Liu and Rousk 2022). Evidence from successional studies using *Racomitrium* species growing along a glacier-forefield chronosequence further demonstrates that moss traits such as moss C/N ratio and moisture content are directly associated with variation in their associated bacterial community (Klarenberg *et al.* 2023). Thus, the relationship between moss traits and ecosystem functioning is not necessarily direct but may be mediated through restructuring the composition and functional potential of the associated microbiome.

Despite considerable evidence for these relationships, most studies remain concentrated on N fixation and C-related processes, while the links between a broader range of moss traits and their associated microbiome function and ecosystem service remain poorly resolved. Moreover, much of the available evidence originates from boreal and temperate regions of Europe, North America and East Asia, and that represents only a small fraction of global moss diversity. Thus, a comprehensive understanding of plant-environment interactions requires greater insights into the functional diversity linking moss traits to community or ecological processes, particularly under current environmental change scenarios. Future studies should aim to better understand the contribution of moss traits to explaining the moss microbiome. This information could contribute, for example, to selecting the best moss species for ecosystem restoration, aiming to bring back microbial diversity and function (Lan et al. 2020; Opelt et al. 2007b; Renaudin et al. 2022b; Shcherbakov et al. 2013; Wicaksono et al. 2021).

4.1 Moss-diazotroph associations: Mechanisms and budgets of nitrogen fixation

Moss-cyanobacterial association is one of the fundamental drivers of N cycling and serves as a root of 'new N' in many ecosystems (DeLuca *et al.* 2022; Renaudin *et al.* 2022a). Although putative diazotrophic proteobacterial taxa can also occur in relatively high abundance within moss-associated microbial communities, their relative contribution to overall BNF remains uncertain and may be lower than that of cyanobacterial diazotrophs (Arróniz-Crespo *et al.* 2022; DeLuca *et al.* 2008; Turetsky *et al.* 2012). In the association between mosses and *cyanobacteria*, nutrient transfer has been viewed through the lens of reciprocal exchange, where fixed N is provided to the host while *cyanobacteria* benefit from physical shelter, moisture, and potentially host-derived nutrients such as sulfur (S) (Carrell *et al.* 2022b; Stuart *et al.* 2020). However, direct C transfer from the moss host to photoautotrophic *cyanobacteria* remains putative and lacks definitive empirical verification, as depicted by the dashed path in Figure 1. Trehalose serves as the primary C source for cyanobionts partners in moss-cyanobacterial association. In return, the inorganic ammonium released by c*yanobacteria* acts as a N currency for the mosses except in epiphytic *cyanobacteria,* where a diverse array of amino acids contributes as an N currency for their associated moss host (Carrell *et al.* 2022a; Warshan *et al.* 2017). The moss-c*yanobacteria* endophytic association leads to a decrease in *cyanobacteria* photoautotrophic C fixation activity and RubisCO protein abundance, and the resulting lower rate of photosynthesis is compensated by moss-released carbohydrate sources (Khamar *et al.* 2010; Meeks and Elhai 2002). In contrast, epiphytic c*yanobacteria* are actively photosynthetic and exhibit higher levels of photosynthetic gene expression (Warshan *et al.* 2017). Despite their ability to fix C, they can also utilize fixed C from their moss hosts (Stuart *et al.* 2020). Unlike in more tightly coupled symbioses with plants, it appears that relying on

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the host for C may not be a viable strategy for c*yanobacteria* in epiphytic associations (Alvarenga *et al.* 2024). However, there does not exist any exchange exclusivity in moss-*cyanobacteria* association as most of the exudates are available to some opportunistic or cheating partners (Arróniz-Crespo *et al.* 2022; Stuart *et al.* 2020). Conversely, the flow of nutrients between mosses and *cyanobacteria* may not be an active, regulated process, but rather mostly driven by constitutive release of host-derived nutrients irrespective of symbiont or environmental stimuli (Alvarenga *et al.* 2024). Moreover, moss could secrete certain signalling molecules, such as heterocyte-differentiating factors (HDFs) that trigger morphophysiological changes in associated epiphytic cyanobionts. This can stimulate the N-fixation potential of cyanobionts irrespective of their symbiotic compatibility with host plants (Alvarenga *et al.* 2023). Nonetheless, moss-associated BNF rates are mainly regulated by the abundance and structure of their bacterial communities, especially diazotrophs. It is also noted that not all members possessing *nifH* are actively participating in BNF activity, rather indicating the possible contribution of diazotrophs to the overall host N budget (Klarenberg *et al.* 2023; Kolton *et al.* 2022). Furthermore, moss-associated *Nostoc* often employ a 'cheating strategy'; despite its higher biomass, it exhibits a lower expression of the *nifH* gene (Warshan *et al.* 2016). This may be explained by the expression selectivity of the *nifH* gene to only heterocyst cells. Additionally, there are also some biases in methodological approaches for measuring BNF rates (Saiz *et al.* 2019). Apart from c*yanobacteria*, other non-cyanobacterial members also took an active role in moss-associated BNF activity. They mainly contribute to BNF activity in colder regions, where cyanobacterial nitrogenase activities are hindered by suboptimal temperatures (Gentili *et al.* 2005). Bacterial phyla such as *Proteobacteria* (genera such as *Azorhizobium, Rhodomicrobium, Methylocapsa, and Methyloferula*), *Actinobacteria*, *Verrucomicrobia*, and *Planctomycetes* are actively associated with moss-related BNF activities (Escolástico-Ortiz *et al.* 2023; Holland-Moritz *et al.* 2021; Jean *et al.* 2020; Leppänen *et al.* 2013; Renaudin *et al.* 2022b).

The fate of fixed N to transfer into the soil depends upon two possible pathways: 'Slow turnover pathway' and 'Rapid pathway' (Figure-1). In 'slow turnover pathway', the fixed N is initially integrated into the moss tissue in a highly conserved manner, then gradually becomes available to moss litter as moss tissues decay and decompose over years (DeLuca *et al.* 2022; Guo *et al.* 2024; Lang *et al.* 2009; Lindo *et al.* 2013; Rousk *et al.* 2013). In 'rapid pathway', fixed N is readily passed on to next trophical cascades within microbial and mesofaunal food web, potentially supporting microbial and faunal activity and thereby reinforcing an influence on organic matter decomposition and nutrient cycling, with indirect consequences for ecosystem C dynamics (Arróniz-Crespo *et al.* 2022; Bragina *et al.* 2014; Jonsson *et al.* 2015; Kardol *et al.* 2016; Rousk *et al.* 2017b). Although BNF associated with mosses represents an important pathway of nitrogen input in nutrient-poor ecosystems, the fate of fixed nitrogen and the mechanisms linking moss-associated N fixation to ecosystem productivity and carbon cycling remain poorly understood.

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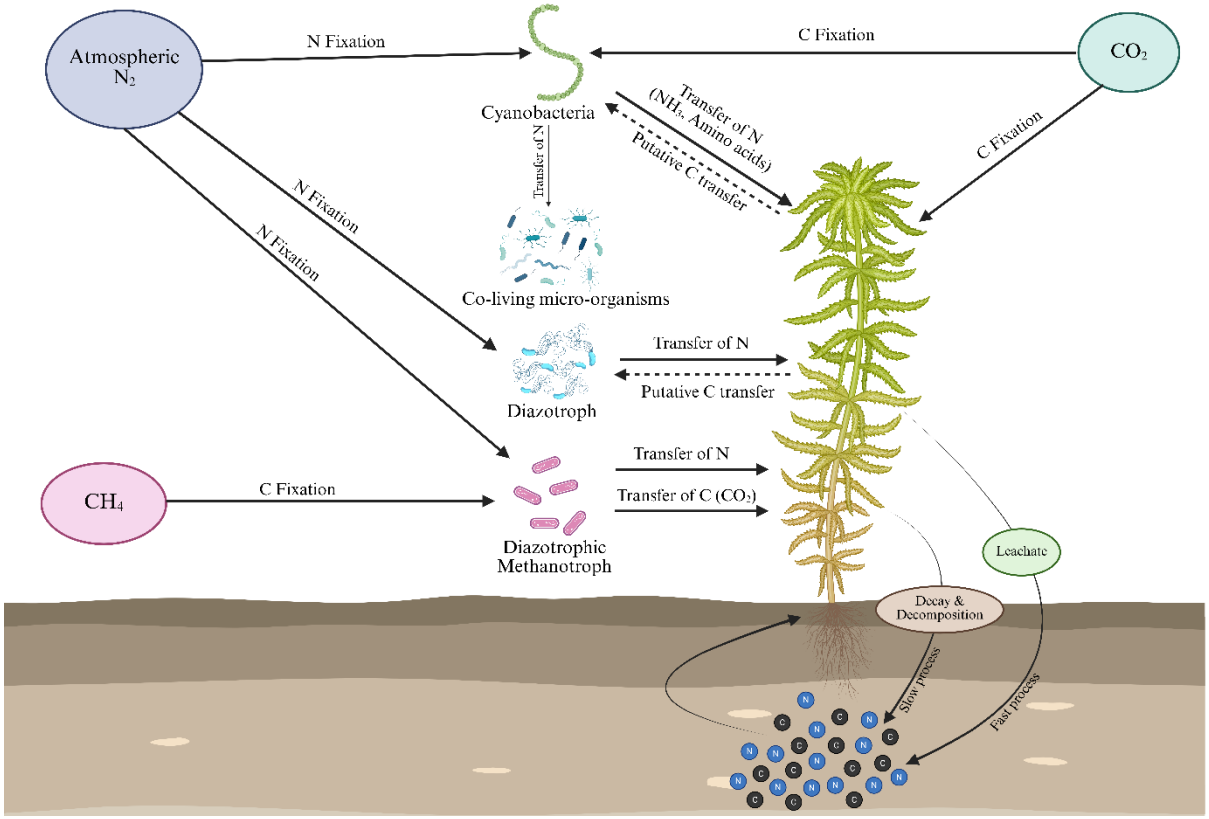


Figure-1: Schematic representation of the contributions of the moss microbiome to global biogeochemical cycling, highlighting carbon and nitrogen exchanges between mosses and their associated microorganisms. Solid arrows indicate established processes, whereas dashed arrows denote proposed or insufficiently demonstrated interactions. Created in https://BioRender.com.

4.2 Moss-bacteriome interactions in carbon dynamics and biogeochemical cycling

Soil mosses have a positive influence on the sequestration of soil C, from local to global scales (Eldridge et al. 2023), particularly in systems with persistent moss cover and in sandy soils. Mosses are also critical in peatlands, constituting an enormous sink of C that stores approximately one-third of the Earth's terrestrial C (Treat *et al.* 2019). The accumulated peat C has surpassed its decomposition as a result of a cold, acidic, waterlogged, nutrient-poor, and anoxic environment over millennia. Hence, the C reservoirs of peatlands are not easily accessible, making peatlands significant C sinks. *Sphagnum* is mainly responsible for creating these environments and can be capable of storing more C than any other plant genus (Kostka *et al.* 2016). The cell walls of *Sphagnum* are rich in polyuronic acid polymers, which impart a high cation-exchange capacity by binding basic cations and releasing protons, thereby maintaining the characteristic low pH of peatlands (Voragen *et al.* 2009). Such low pH and cold conditions support the accumulation of C, inhibiting the decomposition of soil organic matter. Again, *Sphagnum* cell walls can disintegrate under certain conditions and release some antimicrobial substance known as sphagnan. Sphagnan can inhibit microbial metabolism by inactivating extracellular enzymes, thereby helping in preventing microbial degradation of peat and supporting C storage in peatlands (Kostka *et al.* 2016). Additionally, the high resistance to degradation of *Sphagnum* litters makes them ideal for C accumulation in peat (Fujii and Hayakawa 2022; Kasimir *et al.* 2021). Moreover, *Sphagnum* shows a higher magnitude of average recombination rate, and the presence of short putative sex chromosomes gives them an additional advantage in C sequestration within acidic peat environments (Healey *et al.* 2023). However, a small amount of methane can still be released into the atmosphere from the anaerobic degradation of peat (Gorham 1991; Kip *et al.* 2010). Furthermore, *Sphagnum*

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engages in chemical 'biowarfare' to outcompete other vascular plants, helping to maintain the health and longevity of the peatland ecosystem (Stalheim *et al.* 2009). Hence, they are often referred to as an "ecological engineer" of the peatland ecosystem.

Mosses also influence soil methane emissions. The association of methanotrophs and *Sphagnum* is loose and facultative. Different environmental perturbations like water table level, temperature and light can significantly influence their association (Putkinen *et al.* 2014). The methane flux rate of peatlands is largely regulated by water table levels, via influencing the methanotroph community composition (Tian *et al.* 2023c). Normally, the moss that grows below the water table level has a higher methane oxidation rate in comparison to those that grow above the water (Kip *et al.* 2010). Temperature has a pronounced effect on methanotrophic activity; elevated temperatures may suppress methane oxidation by methanotrophs, resulting in increased peatland methane emissions (Winden et al., 2012). Light also regulates the methane oxidation rate of the *Sphagnum*-associated microbiome, likely due to the dependency of this process directly or indirectly on photosynthates (Kox *et al.* 2020). Moreover, the metabolites released from *Sphagnum* also have a greater influence on peatland microbial dynamics than other traits (Sytiuk *et al.* 2022). Beyond influences on their native microbiomes, *Sphagnum* mosses contribute to the microbial community composition of underlying peat layers. As a primary source of organic input in peat soils comes from the decomposition of *Sphagnum*. Thereby, they can modulate the chemical and nutrient environment of peat, fostering unique microbial networks in the peat (James *et al.* 2021a, 2021b). While there is a distinct microbial community separation between living, green *Sphagnum* and decomposing tissue (Tian *et al.* 2019), a limited number of studies focus on exploring the link between above and below ground microbial communities in peatlands will be a prime area for future research.

4.3 Biocrust functionality and surface stabilization

In dryland ecosystems, moss biocrust supports multiple ecosystem services, including primary production, prevention of soil erosion, and regulation of local hydrological dynamics that help in the improvement of soil stability as well as soil fertility (Kidron and Benenson 2014; Li *et al.* 2021; Sun *et al.* 2021; Zhang *et al.* 2008). Thus, they facilitate suitable microhabitats for the regeneration of vegetation and vascular plant establishment (Seppelt *et al.* 2016). Microbial communities associated with moss biocrust can positively regulate soil extracellular enzymatic activities (Xu *et al.* 2022), thereby exerting an indirect influence on soil nutrient cycles (Cheng *et al.* 2022; Tian *et al.* 2023b). These influences are predicted to be higher at their early stages of succession compared to the later stages (Ferrenberg *et al.* 2022). Previous reports suggested that the effects of moss microbial community are mostly limited to soil organic C and N, with the least influence observed on the abundance of soil available P (Delgado-Baquerizo *et al.* 2016). In general, the diazotrophs associated with different biological crusts provide the key N input in most of the arid ecosystems (Delgado-Baquerizo *et al.* 2013; Strauss *et al.* 2012). However, low diversity and abundances of genes related to N-fixation pathways in moss-dominated biocrust may indicate that it does not solely depend upon diazotrophic activity for its N metabolism (Li *et al.* 2020; Tian *et al.* 2023b). The N metabolism pathway of moss biocrust was mostly represented by nitrogen reduction, followed by denitrification, with nitrogen fixation having the least (Tian *et al.* 2023b). Subsequently, most of the soil nitrogen is available as ammonium and helps in the fulfilment of N currency for further vegetation propagation (Yang *et al.* 2014). Moss crusts also have better C fixation rates compared to bare soil (Pietrasiak *et al.* 2013). Previous reports on moss biocrust found a higher abundance of carbon monoxide (CO) dehydrogenase genes over ribulose 1,5-bisphosphate carboxylase/oxygenase (RuBisCo), suggesting a clear dominance of respiration pathways over

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C fixation in moss biocrust (Tian *et al.* 2023b). This CO dehydrogenase gene might participate in C fixation through the Calvin cycle or chemosynthetic C fixation in some dryland ecosystems like the Antarctic desert and Tengger desert (Ji *et al.* 2017; King and Weber 2007; Li *et al.* 2020). In future, in-depth and more systematic studies will reveal the comprehensive knowledge of nutrient cycles associated with moss biocrust.

Moss biocrust also serves as a sustainable approach for many dryland restoration programmes. Researchers have been interested in identifying several exogenous microorganisms, such as *Chlorella vulgaris*, *Bacillus mucilaginosus*, *Streptomyces pactum*, *Actinomyces bovis*, *etc.*, that can further improve the applicability of moss biocrust. These microorganisms act as a microbial hub that strengthens moss microbial interconnections as well as stability and accelerates the recovery of degraded dry soil conditions via nutrient enrichment (Tian *et al.* 2022, 2023a). Moss biocrust can be used as a rehabilitation technique to mitigate the detrimental consequences of fire-affected soil. Studies showed that moss-dominated biocrust increases the resilience of the microbial community in fire disturbance areas and helps in revegetation establishment (García-Carmona *et al.* 2022). Recently, moss biocrust has also gained interest for its integration with intercropping methods. The application of moss biocrust significantly alleviates soil erosion and nutrient losses from agricultural fields (Wang *et al.* 2023). Further research on moss biocrust will provide its usefulness too in some other forest management practices.

5. Moss bacteriome responses to multiple global change stressors

Mosses are subjected to an increasing number of global change factors, including climate change and land use intensification. Both climate change and land use intensification are known to impact soil mosses and their microbiomes negatively. Soil compaction, erosion, tilling and grazing are known to negatively impact the structure and function of biocrusts (Chung *et al.* 2019; Cofre *et al.* 2025; Gao *et al.* 2020; Li *et al.* 2025; Mallen-Cooper *et al.* 2018). Moreover, climate change, including droughts and warming, can also impact mosses and their microbiome (Keane *et al.* 2025; Maestre *et al.* 2013; Reed *et al.* 2012). In most of the field-warming experiments, rising temperatures have sharply declined the moss growth, productivity, as well as ground coverages, leading to a disturbance in various ecological processes mainly involved in N cycle (Hao and Chu 2021; Norby *et al.* 2023; Permin *et al.* 2022). In dryland ecosystems, warming causes a decrease in moss cover and biomass, resulting in the disturbances of biogeochemical function (C and N fixation), soil enzyme activities, as well as water balance of global drylands (Li *et al.* 2023). Climate warming is expected to be more pronounced in the northern hemisphere as compared to the southern latitudes (IPCC, 2023). Most of the landmasses of these northern latitudes are filled with peatlands serving as global C sinks over millennia. However, the fate of climate warming in these regions is unclear, with conflicting model outcomes showing both potential increase and decrease in net C accumulation (Gallego-Sala *et al.* 2018). Some reports on warming effects have shown a significant loss of C from peatland as a result of increased peat decomposition rates (Bell *et al.* 2018; Gao *et al.* 2022) and accelerated microbial CO_2 (Dorrepaal *et al.* 2009; Gavazov *et al.* 2018) and CH_4 emissions (Hopple *et al.* 2020). Although the impact of the warming might vary across seasons, except in the winter season, increasing temperature reduced the net primary productivity of mosses (Osaki and Nakatsubo 2021). However, the resistivity of individual moss species depends on their own physiological and biochemical characteristics. For example, feather moss *Pleurozium schreberi* is more resistant toward warming in comparison to other feather mosses like *Hylocomium splendens* (Permin *et al.* 2022). Furthermore, the impact of warming on moss BNF activities was not consistent across different studied ecosystems, showing positive, negative or neutral results (Rousk and Michelsen 2017; Sorensen and

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Michelsen 2011). Interestingly, two common mosses, namely *P. schreberi* and *Tomentypnum nitens* (Hedw.) Loeske, collected from subarctic and arctic environments, respectively, showed a positive result of BNF activity when incubated alone at 30 °C in a moist environment under the laboratory set-up (Rousk *et al.* 2017a). These contrasting results at different levels of investigation, like individual moss species as well as ecosystems, might suggest the influences of some other factors in moss-mediated BNF activities besides temperature and moisture. Fortunately for microbes, mosses can also buffer some of these impacts for their microbiomes, supporting stable environments across, for example, aridity gradients (Delgado-Baquerizo *et al.* 2018). Mosses are mainly responsible for maintaining the fluctuations of soil average temperature as well as reducing the frequency of freeze-thaw cycles in subarctic and boreal forests. Understanding how microbial and moss species abundance and interactions will adapt to multiple global change stressors is a major priority in this field of knowledge (Figure-2).

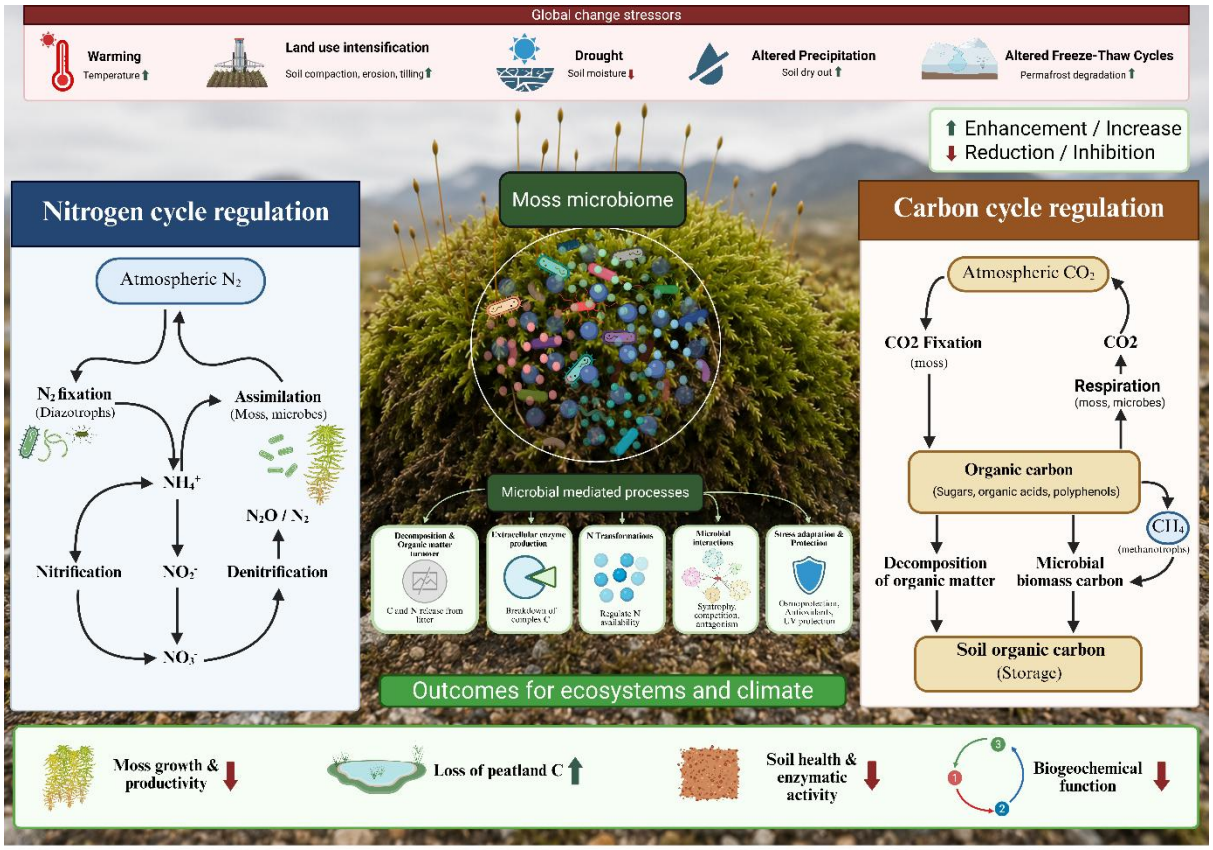


Figure-2: Conceptual illustration of the role of moss microbiome in regulating biogeochemical cycles under global change stressors. The diagram shows the global stressors like warming, drought and altered precipitation impact microbial-mediated ecological processes. Consequently, these changes lead to broader ecosystem outcomes, including reduced moss growth, loss of peatland carbon, and negative influences on biogeochemical functions. Created in https://BioRender.com.

6. Conclusion

The studies of the moss microbiome are biased toward the Northern hemisphere, limiting their knowledge to only a few ecosystems (Delgado-Baquerizo *et al.* 2018; Holland-Moritz *et al.* 2018; Holland-Moritz *et al.* 2021). For a comprehensive understanding of the overall moss microbial communities and their influences on various ecological functions, future studies must incorporate the less-studied moss habitats from tropical, subtropical and Southern Hemisphere. Moreover, there are also notable gaps in microbiome studies from epiphytic mosses, as most researchers have been interested only in mosses attached to the soil, leaving little information

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about the epiphytic moss microbiome. Furthermore, while moss-associated microbial communities are highly vulnerable to climate-driven environmental shifts, mechanistic assessments of these vulnerabilities remain largely confined to temperate and boreal systems (Carrell *et al.* 2019; Klarenberg *et al.* 2022). The climate change sensitivity of moss-rich mountain areas in tropical and sub-tropical regions has been scarcely studied. The impact of climate change on the structure, function and biomass of moss microbiomes is an active area of research. Mosses are versatile plants that can grow on a variety of substrates. However, the impacts of these substrates on their associated microbiomes have not been well explored. Most research on moss microbiomes has emphasized only beneficial symbiosis, often overlooking other associated microorganisms such as non-diazotrophic bacteria or non-mycorrhizal fungi, which may play a role in establishing complex microbial interactions (Alvarenga and Rousk 2022). Molecular approaches have revealed considerable knowledge about moss microbial communities, while the metabolic and functional potential of this microbiota is still not well understood. Recently, moss biocrusts have gained interest for their effectiveness in dryland soil restoration strategies by enhancing the accumulation of soil C and N (Hu *et al.* 2019; Xiao *et al.* 2023). Future in-depth comprehensive studies will further pave the way for more effective application of mosses in the recovery of degraded ecosystems. In situ studies of moss-microbiome are challenging due to fluctuations in the natural environmental conditions that enduringly influence moss microbial community structures. Hence, developing novel mesocosm setups that mimic actual environmental conditions under controlled laboratory settings is crucial for appropriately depicting moss-microbial interactions. With the advancement of different methodological approaches and the evolution of gnotobiotic systems for moss microbiome research, more comprehensive details of moss microbial communities and their functional attribution will be anticipated in the foreseeable future.

Moss microbiome has a long co-evolutionary history, making them a unique and ideal system for studying plant-microbiome interactions compared to other tracheophyte-microbial systems. These dynamic and vital microbial communities of soil mosses regulate the terrestrial ecosystem stability through modulating multiple biogeochemical cycles. As rapid global changes continue to shift environmental baselines, these microbial communities potentially influence and contribute to destabilizing climate feedback loops. Consequently, integrating moss-microbial dynamics into global climate and biogeochemical models is no longer optional, but an absolute necessity to accurately predict, mitigate and navigate the future state of our biosphere.

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Author contributions
RB wrote the first draft of this manuscript. MDB and NA intellectually contributed to the development of this review, and significantly contributed to the subsequent draft. All authors read and approved the final version of the manuscript.

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Conflict of Interest
None declared.

Data Availability
Not applicable.

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