CHAPTER

6

Moss-inhabiting microalgae and cyanobacteria

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Bryophytes are nonvascular plants that occupy ecological niches across a wide range of habitats, from temperate forests and wetlands to extreme environments such as deserts and polar regions (Hájek, 2013; Lewis et al., 2017; Müller et al., 2019). Mosses are characterized by their lack of true roots, stems, and leaves, possessing instead rhizoids for anchorage and water absorption (Huttunen et al., 2018; Shaw & Goffinet, 2000). Despite their relatively simple structure, mosses play a significant role in ecological system functioning (Turetsky et al., 2012), particularly in soil stabilization (Seitz et al., 2017), water retention (Michel et al., 2013), and microclimate regulation (Jaroszynska et al., 2023).

The symbiotic relationships between mosses and microorganisms, such as algae and cyanobacteria, are fundamental to the functioning of moss-dominated ecological systems (Dangar et al., 2024; Zhao et al., 2019). Cyanobacteria, particularly nitrogen-fixing species, provide a crucial source of bioavailable nitrogen to mosses, enhancing their growth in nutritionally limited habitats (Rousk, 2022). This process is particularly significant in ecological systems where nitrogen availability constrains primary production (Berg et al., 2013). Cyanobacteria and algae can also contribute to the overall photosynthetic capacity of the moss system, thus increasing carbon fixation (Colesie et al., 2012; Lindo & Gonzalez, 2010). The association between algae and mosses in polar and alpine regions can improve the resilience of mosses to ecological stress (Elster & Benson, 2004).

The objective of this review is to provide a comprehensive synthesis of current knowledge regarding the symbiotic relationships between mosses, algae, and cyanobacteria. Specifically, the review will examine the diversity of algal and cyanobacterial species associated with mosses, the ecological functions of these interactions, and the underlying mechanisms facilitating these symbioses. In addition, the review will discuss the implications of these relationships for ecological system processes, such as nitrogen cycling, and their potential applications in ecological system restoration and climate change mitigation. Special attention will be given to the role of *Sphagnum*-dominated peatlands, due to their significance in global carbon storage and nitrogen cycling. Finally, this review aims

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to conclude by identifying 12 key research areas that require further investigation, advancing our understanding of the ecological and evolutionary significance of moss-algae-cyanobacteria associations.

6.1 Methodologies to study moss-algae-cyanobacteria interactions

6.1.1 Microscopy

Microscopy remains a fundamental tool in the study of moss-algae-cyanobacteria interactions, enabling the visualization of the physical associations between these organisms at various levels of resolution. Scanning electron microscopy (SEM) and transmission electron microscopy (TEM) are two techniques widely employed to study the structural relationships and morphological characteristics of moss-associated microorganisms (Adams & Duggan, 2008; Knapp & Lowe, 2009). SEM provides high-resolution, three-dimensional images of the surfaces of mosses and their symbiotic partners, allowing researchers to observe the spatial distribution and physical attachment of algae and cyanobacteria on moss tissues (Nguyen & Harbison, 2017; Solheim et al., 2004). SEM is particularly useful for studying the surface topography of moss gametophytes, including leaves and rhizoids, where biofilms of algae and cyanobacteria often form. It allows for the detailed analysis of biofilm formation, cellular adhesion mechanisms, and the structural organization of microbial communities in relation to the moss surface (Scheirer & Dolan, 1983). Microscopic techniques also provide insight into the extent of colonization, the microhabitats created within the moss tissues (Alvarenga & Rousk, 2022), and the quantification of cyanobacteria (Renaudin et al., 2021).

6.1.2 Molecular techniques

Molecular techniques have revolutionized the study of microbial diversity in all ecological systems. These methods, including Polymerase Chain Reaction (PCR), sequencing, metagenomics, and omics approaches, have significantly increased richness estimates and provided insights into community composition and ecological system processes (Kumari & Rai, 2020; Singer et al., 2021). Direct PCR approaches enable analysis of low-biomass samples from cryptogam-associated communities, such as the free-living cyanobacteria (Jung et al., 2024). Metabarcoding approaches uncover a more diverse and complex cyanobacterial and algal communities compared to traditional morphological identification methods (Kamberović et al., 2024; Li et al., 2019). Notably, novel bacterial lineages, including potential nitrogen fixers and anoxygenic phototrophs, have been discovered in moss microbiomes (Holland-Moritz et al., 2018). Metagenomics studies reveal complex interactions between mosses and their associated microbiomes (Baev et al., 2024; Ishak et al., 2024). Metagenomics methods highlight that *Sphagnum*-dominated bogs host a diverse microbiome with unique genetic traits that support ecological system functions, including stress resistance, nutritional cycling, and biofilm formation (Bragina et al., 2014). Functional gene analysis, such as nitrogenase genes (nifH), provides valuable insights into symbiotic nitrogen fixation by cyanobacteria associated with mosses (Ininbergs et al., 2011; Kubota et al., 2023). These associations show host specificity and seasonal variations in nifH gene abundance and expression (Warshan et al., 2016). Overall, molecular approaches are indispensable for uncovering the diversity, functional capabilities, and ecological roles of algae and cyanobacteria in moss-dominated ecological systems. These methods offer unparalleled resolution in studying both the taxonomic composition and the functional dynamics of symbiotic interactions.

6.1.3 Stable isotope analysis

Stable isotope analysis, particularly of carbon and nitrogen, has emerged as a powerful tool for investigating nutritional exchange and metabolic processes in moss-algae-cyanobacteria interactions (Stuart et al., 2020). Stable isotope analysis relies on the natural abundance or enrichment of stable isotopes, such as nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$), to track the flow of nutrients between ecological system components (Ataeian et al., 2022; Wannicke et al., 2024). These methods have demonstrated that cyanobacteria–moss associations significantly contribute to biogeochemical cycle and can be used as proxies to monitor climate changes (Stuart et al., 2021). By integrating isotopic data from mosses, algae, and cyanobacteria, researchers can gain a comprehensive understanding of the biogeochemical processes that sustain moss-dominated habitats, including the role of symbiotic interactions in modulating nutritional availability and ecological system productivity.

6.2 Diversity of algae and cyanobacteria associated with mosses

Mosses serve as substrates for diverse communities of microorganisms in various ecological systems (Szczepocka et al., 2024). The major clades of soil and moss-associated algae include Cyanobacteria, Bacillariophyta, and Chlorophyta.

Common cyanobacterial genera associated with mosses include *Nostoc*, *Calothrix*, and *Stigonema* (Gentili et al., 2005). New genus and species of cyanobacteria have been isolated and described from mosses, such as *Neosynechococcus sphagnicola* from *Sphagnum* mosses (Dvořák et al., 2014) or *Microcoleus vaginatus* associated with the moss *Mnium cuspidatum* (Zhang et al., 2014). Other novel bacterial lineages, including potential nitrogen fixers, have been identified in moss microbiomes (Holland-Moritz et al., 2018; Ishak et al., 2024).

Bacillariophyta (stramenopiles), commonly referred to as diatoms associated with mosses, exhibit significant diversity. A study of moss-associated diatoms from Malay Peninsula montane cloud forests revealed that one-third of the observed diatom species could not be identified or affiliated with any known species (Rybak et al., 2023). Molecular analyses have further shown that certain taxa, such as the terrestrial diatom *Pinnularia borealis*, represent species complexes, comprising multiple cryptic species, some of which may be endemic (Souffreau et al., 2013). Nevertheless, the use of metabarcoding for soil diatom biomonitoring is still in its infancy (Maidana et al., 2024).

Trebouxiophyceae (Chlorophyta) is also a common class of green algae frequently associated with mosses. Genera such as *Pseudochlorella* and *Pseudostichococcus* are often identified in bryophyte samples (Szczepocka et al., 2024). New species and genera within Trebouxiophyceae, such as the genus *Coleochlamys*, have been described based on both morphological and genetic analyses (Redkina et al., 2022). Another study on *Sphagnum* mosses demonstrated that operational taxonomic units (OTUs) affiliated with Cryptophyceae can be detected through metabarcoding approaches utilizing universal genetic markers (Singer et al., 2019). Notably, OTUs related to the genus *Desmodesmus* serve as bioindicators of tropical and subtropical ecological systems, while those associated with *Plagioselmis* indicate temperate regions (Singer et al., 2019). Other algal groups, such as Dinophyceae (Alveolata), Mamiellophyceae (Chlorophyta), Klebsormidiophyceae (Streptophyta), and Eustigmatophyceae (Stramenopiles), have also been detected in ecological samples using metabarcoding approaches (Reczuga et al., 2020; Singer et al., 2019). The current knowledge of the taxonomic diversity of algae remains poor in comparison with other organisms associated with mosses, such as bacteria (Bragina et al., 2012; Renaudin et al., 2022) or fungi (Davey & Currah, 2006; Kauserud et al., 2008). Knowledge of the diversity of algae and cyanobacteria associated with mosses is incomplete, often constrained by the limited phylogenetic information provided by short sequence lengths, which hinders accurate taxonomic classification (Salmaso et al., 2024). Therefore, taxonomic work is essential to improve the reliability and completeness of reference databases.

6.3 Ecological roles and functions

The main habitat where the bryophytes are found will affect cyanobacterial and algal community composition. At a large scale, Rodríguez-Rodríguez et al. (2022) have demonstrated a significant difference in community composition between coniferous and broadleaf forests. At a smaller scale, the composition and diversity of cyanobacterial communities are influenced by moss species identity, with host-specific clusters observed (Ininbergs et al., 2011). Ecological features, such as hypolithic niches, further shape communities (Fisher et al., 2020). Host species and evolutionary history are strong predictors of microbiome composition, demonstrating phylogenetic coherence (Holland-Moritz et al., 2021). Moss traits, particularly hydration rate and morphology, play a crucial role in cyanobacterial colonization and nitrogen fixation (Liu & Rousk, 2021). Finally, cyanobacterial abundance and nitrogen fixation rates vary seasonally and between moss species (Warshan et al., 2016). These findings highlight the complex interactions between mosses and their associated microbiomes in various ecological systems.

The micro-environment formed by bryophyte cushions is distinct and strongly shaped by the physiological and structural characteristics of the bryophytes themselves. This unique zone of influence has been termed the “bryosphere” (Lindo & Gonzalez, 2010). A specific compartment of the bryosphere will be the *Sphagnum* mosses-dominated ecological system. Due to the specific physical and physiological properties of these mosses, the associated microbial communities within *Sphagnum* mats are even more strongly constrained (Clymo & Hayward, 1982; van Breemen, 1995), leading to the proposal of the term “sphagnosphere” to describe this specialized habitat (Jassey et al., 2011; Singer, 2017). Because of the specificity of this particular habitat, the bryosphere and the sphagnosphere serve as an excellent model systems for investigating the ecology and the function of cyanobacteria and microalgae.

Mosses form symbiotic relationships with diverse microorganisms, creating unique microenvironments that maintain high humidity levels (Cao et al., 2020). They form symbiotic associations with cyanobacteria, which play an essential role in nitrogen fixation in various ecological systems, such as boreal and temperate forests (Alvarenga & Rousk, 2022; Deane-Coe & Sparks, 2016; Rousk et al., 2013). In pristine environments, such as *Sphagnum*-dominated peatlands, these cyanobacterial associations can supply up to 50% of the nitrogen required by the ecological system, often exceeding atmospheric nitrogen deposition (Alvarenga & Rousk, 2022; Kolton et al., 2022). Finally, associations between cyanobacteria and mosses play crucial roles in primary succession and soil development in newly exposed terrains (Arróniz-Crespo et al., 2014).

Environmental factors such as substrate humidity and temperature will be the main factors influencing both the diversity and the distribution of moss-associated organisms (Gentili et al., 2005; Szczepocka et al., 2024). For cyanobacterial colonization, nitrogen fixation is closely regulated by moisture, temperature, and nutritional access (Meeks, 2018). Another factor can be the feather mosses, which can secrete chemical signals to attract cyanobacteria under nitrogen-limited conditions (Bay et al., 2013). Recent studies indicate that cyanobacterial biomass and nitrogen (N_2) fixation in mosses are controlled by distinct factors: cyanobacterial biomass is primarily influenced by temperature, precipitation, and phosphorus, while N_2 fixation depends on temperature and molybdenum, with a negative impact from vanadium (Renaudin et al., 2022). This negative relationship with vanadium, a cofactor for the alternative V-nitrogenase enzyme, suggests that moss-associated cyanobacteria may rely on V-nitrogenase in molybdenum-limited environments, where it provides an adaptive advantage despite its lower efficiency compared to Mo-nitrogenase (Renaudin et al., 2022). Prolonged drought conditions have been shown to reduce the N_2 fixation capacity of cyanobacteria–moss associations, while sustained moisture availability enhances this capacity (Gundale et al., 2009). This relationship likely accounts for the commonly observed declines in N_2 fixation rates during mid-summer, when conditions are typically at their driest (DeLuca et al., 2002; Zackrisson et al., 2004). Nitrogen fixation is extremely sensitive to external nitrogen deposition. Studies have shown that inorganic nitrogen inputs generally inhibit N_2 fixation in moss-cyanobacteria associations (Gundale et al., 2013; Rousk et al., 2016; Wang et al., 2021), while low levels of organic nitrogen can stimulate it (Wang et al., 2021). The sensitivity to nitrogen inputs, anthropogenic pollution, and moisture variability may differ between moss species and forest ages (Gundale et al., 2013; Sjøgren et al., 2023).

Photosynthetic microorganisms, including cyanobacteria and microalgae, play a significant role in carbon uptake within moss-dominated ecological systems across boreal and tropical regions (Hamard et al., 2021; Jassey et al., 2022). These microbes contribute approximately 2%–4% of bryophyte carbon uptake in tropical and boreal systems, respectively (Jassey et al., 2022), and up to 10% of peatland carbon uptake (Hamard et al., 2021). The contribution of algae to carbon cycling within moss systems is not limited to their photosynthetic activity. Microalgae also play a role in the production of extracellular polysaccharides (EPSs), which contribute to various ecological functions (Rossi & De Philippis, 2016). These EPSs, along with proteins, nucleic acids, and lipids, form a hydrated biofilm matrix that facilitates cell adhesion and interaction (Xiao & Zheng, 2016). In moss-dominated ecological systems, biofilms can regulate carbon flux by influencing the balance between autotrophic and heterotrophic processes (Rober et al., 2023). Finally, *Sphagnum*-dominated ecological systems host diverse microbial communities, including cyanobacteria and algae, which form biofilms that enhance water retention (Bragina et al., 2014). The *Sphagnum* microbiome supports ecological system functioning under extreme conditions by providing nutrition, fixing nitrogen, and helping the moss cope with ecological stresses (Bragina et al., 2014; Carrell et al., 2022). Understanding bryophyte-microbe interactions and their responses to climate change is crucial for accurately assessing global carbon dynamics (Alvarenga & Rousk, 2022; Slate et al., 2024).

6.4 Interaction between cyanobacteria, moss, and algae

In the early 2000s, the nature of the relationship between hosts and cyanobacteria was a subject of debate, with some evidence suggesting it might be more commensal or even parasitic rather than mutualistic (Hyvärinen et al., 2002). Contemporary perspectives have evolved to recognize that cyanobacterial symbioses exist along a continuum from parasitism to mutualism, with their nature varying depending on the specific partners involved and ecological conditions (Rousk, 2022; Tamarit & Andersson, 2020). Cyanobacteria are primarily epiphytic, frequently located between the stem and leaf of their moss hosts (Gentili et al., 2005; Solheim & Zielke, 2002; Solheim et al., 2004). A specific case occurs in *Sphagnum* species, where cyanobacteria inhabit water-filled, dead (hyaline) cells, likely providing protection from the acidic conditions of bog environments (Solheim & Zielke, no date; Dvořák et al., 2014). Direct contact with sunlight can also have a significant impact on the interaction between the moss and the cyanobacteria. A study has demonstrated that ozone depletion and increased UV-B exposure in the Arctic significantly reduce nitrogen fixation in moss-associated cyanobacteria, especially where cyanobacteria are located on moss surfaces and directly exposed (Solheim et al., 2006). In contrast, subarctic moss-associated cyanobacteria, possibly less exposed or shielded by moss structures, remain unaffected by UV-B but show increased nitrogen fixation with higher precipitation (Solheim et al., 2006). The fixed nitrogen is transferred to moss tissues either directly or via diffusion through the biofilm matrix (Arróniz-Crespo et al., 2014). This transfer occurs rapidly, with nitrogen made available as ammonium (Sprent & Meeks, 2013). Recent studies have revealed a bidirectional nutritional exchange between mosses and cyanobacteria, where mosses supply carbon, nitrogen, and potentially signaling molecules through sulfur compounds to cyanobacteria (Stuart et al., 2020). However, the relationship may be more complex, as gene expression analysis suggests cyanobacteria may receive limited nutrition from the host during early stages of symbiosis (Alvarenga et al., 2024).

The organic carbon produced by algae may be transferred to the moss in several ways. Algae may release dissolved organic carbon (DOC) into the surrounding water film, which can support the growth of bacterial biomass (Hulatt & Thomas, 2010) or be absorbed by the moss. Additionally, the decomposition of algal cells within the moss mat contributes to the pool of organic carbon available for moss and microbial growth. This carbon exchange is particularly significant in ecological systems with low nutritional availability, such as *Sphagnum*-dominated peatlands (Hamard et al., 2021).

In summary, the physical association between mosses and their symbiotic partners, coupled with the efficient exchange of nutrients, creates a highly integrated and resilient system. These interactions enhance the ability of moss-dominated ecological systems to persist in nutrient-poor and ecologically challenging conditions, contributing to the stability and productivity of a wide range of terrestrial habitats.

6.5 Environmental and evolutionary significance

The symbiotic relationships between mosses, algae, and cyanobacteria have a long evolutionary history dating back to the origin of land plants ~500 million years ago (Alvarenga & Rousk, 2022). These associations have likely facilitated plant colonization of land and continue to shape plant diversity (Reboledo & de León, 2021). In terrestrial systems, the resilience of moss-algae-cyanobacteria systems to ecological stresses has been observed, suggesting their potential significance in early terrestrial ecological systems (Graham et al., 2017). These symbiotic interactions between mosses, algae, and cyanobacteria are critical for the survival and ecological success of these organisms in extreme environments, such as arctic tundra, deserts, and high-altitude ecological systems (Solheim & Zielke, 2002). Mosses, algae, and cyanobacteria exhibit remarkable adaptations to extreme environments through their capacity for cryptobiosis, enabling them to survive desiccation and temperature fluctuations (Lakatos, 2011; Seckbach et al., 2007). These poikilohydric organisms can rapidly reactivate their metabolism upon rehydration, allowing them to exploit transient periods of favorable ecological conditions (Adessi et al., 2021).

6.6 Human and ecological applications

Moss-cyanobacteria communities function as sensitive bioindicators of ecological change due to anthropogenic sources, like eutrophication (Salemaa et al., 2020). Their responsiveness to ecological shifts underscores their utility in monitoring ecological system health (Alvarenga & Rousk, 2022). Given the ongoing impact of climate change on northern ecological systems, research on moss-cyanobacteria-algae associations is crucial for forecasting and managing ecological system dynamics (Lindo et al., 2013). Elevated nitrogen deposition due to human activities in peatlands exerts complex and variable impacts on cyanobacterial-moss associations. Some studies have demonstrated significant suppression of biological nitrogen fixation, with reductions of up to 74% under conditions of chronic nitrogen loading (Gundale et al., 2013; Saiz et al., 2021). However, other research has reported no significant effect on nitrogen fixation, even under high levels of nitrogen deposition, as observed in specific species, such as *Sphagnum capillifolium* (van den Elzen et al., 2018).

Cyanobacteria and mosses have been identified as promising biotechnological resources for land restoration in degraded ecological systems (Adessi et al., 2021). Restoration of biological soil crusts, including moss-cyanobacteria associations, can rapidly recover ecological system functions in disturbed areas (Chiquoine et al., 2016). Greenhouse cultivation methods have been developed to produce moss-based biocrusts for restoration purposes (Antoninka et al., 2016). Cyanobacteria-rich biocrusts have shown promise in rehabilitating postmining and degraded landscapes. These organisms can rapidly colonize disturbed soils, improving soil structure, stability, and fertility (Doudle et al., 2011; Williams et al., 2019). Cyanobacteria aid in nutritional cycling, desalination, and contaminant degradation, making them valuable for restoring various types of human-impacted soils (Hooda et al., 2023). Recent research has also explored the relationship between ecological system degradation and cyanobacterial community composition, identifying potential key species for efficient inoculum production (Roncero-Ramos et al., 2020) and using them toward large-scale biocrust restoration (Roncero-Ramos et al., 2022). While challenges remain, the use of cyanobacterial crusts shows promise in rehabilitation, particularly in arid environments (Zhao et al., 2016).

6.7 Key research areas

6.7.1 Diversity (taxonomic and functional)

1. **Microbial community composition:** Use advanced sequencing and metagenomic approaches to characterize the diversity of microalgae, cyanobacteria, and other microorganisms associated with mosses. This research could identify novel species and functional traits, contributing to a more accurate reference database and comprehensive understanding of the ecological roles of these microbial communities.
2. **Functional diversity in contrasting environments:** Conduct comparative studies of moss-microbe interactions in diverse ecological systems, such as polar tundra, temperate forests, and arid deserts. This research could highlight how ecological factors influence the diversity, stability, and ecological significance of these symbioses, providing insights into their adaptive strategies.

6.7.2 Molecular mechanisms

1. **Molecular mechanisms of symbiosis:** Study the genetic and biochemical pathways involved in establishing and maintaining symbiotic relationships between mosses and their microbial partners. This research could focus on the identification of symbiosis-related genes, signaling molecules, and regulatory networks that enable nutritional exchange and stress tolerance.
2. **Metagenomics and functional profiling:** Utilize high-throughput omics technologies, including metagenomics and metatranscriptomics, to study the functional potential and gene expression profiles of moss-associated microbial communities. This research could provide a detailed understanding of how microbial activity responds to ecological changes and drives ecological system processes.

6.7.3 Interactions

1. **Host-specific interactions:** Investigate the degree to which specific moss species form preferential or exclusive partnerships with microalgae or cyanobacteria. This research could elucidate how evolutionary history, habitat specificity, and physiological traits influence host-microbe interactions, shedding light on the ecological significance of these associations in different environments.
2. **Nutrient exchange pathways:** Delve into the processes that facilitate the transfer of essential nutrients, such as carbon and nitrogen, between mosses and

their symbionts. Understanding these pathways can provide insights into the role of moss-microbe interactions in nutritional cycling and ecological system productivity, with a particular focus on the mutual benefits of these associations.

3. **Influence of microbial metabolites on moss physiology:** Investigate how metabolites produced by associated microalgae and cyanobacteria, such as growth hormones, antioxidants, or antimicrobial compounds, affect moss physiology and stress tolerance. This research could provide insights into the biochemical interactions that enhance the resilience and growth of mosses in challenging environments.
4. **Biofilm dynamics and community structure:** Investigate the formation and ecological roles of biofilms that develop on moss surfaces. This research could explore how biofilm architecture influences microbial community composition, nutritional retention, and interactions with external ecological factors, such as light and pollutants.

6.7.4 Climate change

1. **Impact of climate change:** Assess how global warming, shifts in precipitation patterns, and extreme weather events influence moss-microbe symbioses. Research could explore how changes in temperature and water availability affect microbial metabolism, nitrogen fixation, and the overall resilience of moss-dominated ecological systems.
2. **Long-term studies on ecological system impact:** Implement long-term research to track the contributions of moss, algae, and cyanobacteria interactions to ecological system dynamics over time. These studies could focus on how these interactions influence soil development, plant succession, and ecological system resilience, particularly in response to ecological disturbances and global change.

6.7.5 New technologies

1. **Remote sensing for ecological system monitoring:** Develop and use advanced remote sensing technologies, such as satellite imagery, drone surveys, and hyperspectral sensors, to monitor the distribution, health, and productivity of moss-microbe communities at a landscape scale. This research could provide valuable data for assessing the impacts of climate change and land-use changes on moss-dominated ecological systems, informing conservation and management efforts.
2. **Synthetic biology applications:** Explore the potential of engineering moss-cyanobacteria-algae consortia for biotechnological applications, such as ecological system restoration, soil stabilization, and carbon sequestration. Research could focus on designing microbial communities with enhanced nitrogen-fixing or photosynthetic capabilities, tailored to specific ecological challenges.

6.8 Conclusion

Moss-associated microalgae and cyanobacteria play crucial roles in ecological system functions, particularly in nutritional cycling, primary production, and ecological system resilience. Despite advancements in understanding these interactions, knowledge gaps persist in areas such as host specificity, the molecular basis of symbiosis, and the ecological factors governing nutritional exchange pathways. Addressing these knowledge gaps is critical, especially as climate change and anthropogenic disturbances pose significant threats to moss-microbe symbioses. Future research should focus on elucidating the molecular and ecological mechanisms of these associations, assessing their responses to ecological change, and leveraging innovative technologies like high-throughput sequencing, metagenomics, and remote sensing for ecological system monitoring. Additionally, the potential for synthetic biology applications and engineered moss-microbe consortia offers exciting prospects for biotechnological and conservation efforts. These insights will be fundamental for predicting the resilience of moss-dominated ecological systems and their contribution to global carbon and nitrogen cycles.

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