Sub-tropical mosses harbour a consistent bacterial community irrespective of their host identity

Ramen Barman
Gauhati University
Niraj Agarwala
niraj_botany@gauhati.ac.in

Gauhati University

Research Article

Keywords: Moss Phyllosphere, Sub-tropical moss, Metagenomics, Bacterial diversity

Posted Date: June 12th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-9893137/v1

Additional Declarations: No competing interests reported.

Abstract

Moss phyllosphere represents a unique and ecologically significant microhabitat, harbouring a distinct microbial consortium thriving under harsh environmental conditions. The role of host identity in shaping the moss microbial assemblies in sub-tropical ecosystems remains largely unknown. This study characterized the bacterial communities associated with three taxonomically distinct moss species, namely *Garckea phascoides*, *Philonotis nitida* and *Pogonatum aloides* from sub-tropical regions. The taxonomic profiling showed a dominance of Pseudomonadota, Bacillota, Cyanobacteria, Acidobacteriota and Actinomycetota in the moss phyllosphere. Overall, our findings demonstrated that the moss phyllosphere hosts a consistent bacterial assembly in an identical ecological condition, irrespective of host species. While a host-specific microbial variation was still found across moss hosts. The functional prediction analysis showed that the moss microbiome maintains a baseline level of functional redundancy involved in essential biogeochemical cycles that support host survivability over challenging environments. This study highlights the significance of the local environment as well as host traits for protecting microbial biodiversity and implementing them in global strategies for biodiversity restoration.

1. Introduction

Mosses represent one of the earliest divergent lineages of modern land plants. It is characterized by a lack of true roots and traditional vascular systems. Despite their smaller size and structural simplicity, they exhibited a higher range of ecological adaptability across diverse habitats, from arid desert biomes to moisture-saturated subtropical mountain forests [1]. The ecological success and stress resilience of mosses are largely driven by their complex symbiotic relationships with highly diverse microbial groups, particularly bacteria, which colonize their phyllosphere and rhizoids [2]. They play a significant role in various ecosystem functions, including biogeochemical cycles, stabilization and moisture retention, etc. In the regions of high humidity and a biodiversity-rich environment like sub-tropical forests, mosses provide a stable as well as moist microhabitat that serves as an extraordinary reservoir for microbial diversity, yet the major driver of these microbial assemblies remains poorly understood. The phyllosphere, defined as the exposed aerial parts of plants, represents one of the least studied dynamic microhabitats on Earth. Most of the research targeting the phyllosphere is limited to vascular and crop plants, often underestimating the unique and ecologically significant plants from the lower plant group, like Mosses [3, 4]. In the case of vascular plants, the phyllosphere is often viewed as a highly selective environment where plant host-traits, including leaf morphology, secondary metabolite production and nutrient exudation pattern, determine distinct microbial assemblies on leaf surface [5, 6]. However, the unique physiology of moss presents a different ecological scenario. Being poikilohydric in nature, mosses cannot regulate their internal hydration status as they do not possess a complex cuticle and stomatal regulation is often observed in higher plants. So, the hydration status of mosses mostly equilibrates with their surroundings [7]. However, recent studies found that moss may control a level of water loss through a non-stomatal mechanism as identified in angiosperms [8]. This constant exchange with the atmosphere and the surrounding environment suggests that moss phyllosphere may be more susceptible to external ecological drivers, such as habitat filtering and regional species pool, rather than

strict host-driven selection [9, 10]. Because of their pronounced environmental susceptibility, mosses are recognized as ideal model systems for studying the effects of environmental extremity on their associated microbial assemblies. For instance, sub-tropical regions like India, mosses are subjected to intense environmental pressures, including high UV radiation, seasonal desiccation and nutrient scarcity. To capture complex microbial dynamics in such environments, recent advancements in sequencing technology (e.g. ONT) have enabled higher taxonomic resolution, allowing researchers to move beyond phylum-level to identify specific microbial players and their ecological associations. Previous studies on moss-associated microbiomes in sub-tropical forests suggested that the phyllosphere core microbiota consists of both host-specific and environment-derived components. The host-specific core members make a stable communitywhereas environmentally derived core members enhance resilience to environmental extremes [11]. Whether this pattern applies to other moss species outside the genus *Sphagnum* is still under debate. To address this study gap, we have characterized and compared the bacterial communities associated with three distinct moss species, namely *Garckea phascoides*, *Philonotis nitida*, and *Pogonatum aloides*. The central question of the present study is the extent to which moss host identity shapes the structure of the associated microbiome. We also studied the predicted functional profiles of each moss-associated microbiome under similar environmental conditions. We hypothesize that the unique physiological traits of each moss host species exert strong selective pressure, resulting in divergent and host-specific microbial assemblies and interaction networks. Secondly, the function of the associated microbiomes is largely determined by the specific physiological needs of the individual moss hosts. Understanding the microbial dynamics in the moss phyllosphere provides crucial insights into the plant-microbe interaction in the lower group of plants. Our findings contribute to a deeper understanding on the bacterial assembly determinants of the moss phyllosphere and highlight the microbial networks in one of the world's most vital forest ecosystems.

2. Methods

2.1 Site description

Moss sample collections were conducted in August and September of 2025 from forest cover areas of Garbhanga Wildlife Sanctuary (26°02′29″ N, 91°61′71″ E). It is situated on the southwestern outskirts of Guwahati, Assam (India), alongside the border of Meghalaya. The forest is a moist deciduous type, and its dense canopy cover is supported by sal forest, semi-evergreen patches, bamboo groves and lush undergrowth. The forest's terrain mostly consists of rolling hills, deep river valleys and dense tropical canopies. The altitude of the forest ranges from approximately 50 meters to 600 meters above mean sea level. This sanctuary often experiences a subtropical monsoon climate, with cold and foggy weather in winter and hot and humid weather in summer. The weather gets a little warmer in March and April, marking a distinct transition from cold, dry winter to the humid spring season. The temperature begins to rise gradually at the beginning of March and reaches its maximum during July-August. The mean maximum temperature fluctuates within the range of 20 to 33°C. Precipitation mostly occurs during the monsoon (May-September) and slowly reduces by the arrival of winter (November-January). The highest

average rainfall was observed in June (485.7 mm), whereas the lowest value of rainfall (0.5 mm) was recorded in December.

2.2 Moss sample collection

To investigate the host-specific assembly of the moss-associated microbiome, three distinct acrocarpous moss species, namely *Garckea phascoides*, *Philonotis nitida* and *Pogonatum aloides*, were collected from their natural field habitat. Pictures are provided in supplementary information (Figure A, B and C). To ensure the representative natural microbial diversity and biological variability, moss samples were collected from three independent moss cushions separated by at least 5 meters. The top phyllospheric region (approx. 2 cm) of healthy and green gametophyte shoots from each moss species was carefully removed to minimize the possible contamination from rhizoid-associated microbes and soil particles. To prevent cross-contamination during the collection process, sampling was performed using sterile forceps and spatulas while wearing nitrile gloves. The moss samples were gently shaken to remove loosely attached soil particles and plant debris before being placed into properly labelled sterile 50 ml falcon tubes. After collection, the samples were immediately transferred to the laboratory on ice inside insulated coolers. Upon arrival at the laboratory, the samples were stored at -20°C until total genomic DNA extraction was performed.

2.3 Bacterial isolation and total DNA extraction

The moss phyllosphere bacteria were extracted as per the previously described protocol with slight modifications [12]. Briefly, around 3 g of sample from each moss species were placed directly into 50 ml falcon tubes containing 30 ml of sterile phosphate-buffered saline (1x) with tween-20 (pH = 7.4). Then, the samples were kept in agitation at 200 rpm for 1 hour at room temperature and followed by vortexing six times for 30 sec at 10 min intervals. From the obtained solution, moss phyllosphere parts were carefully removed and the resulting solutions were finally filtered with 0.22 µm cellulose nitrate membrane. The membranes were taken and then were cut into pieces (2 x 2 mm) with sterilized scissors to proceed for metagenomic DNA extraction using the DNeasy PowerSoil Pro Kit (Cat. No. 47014, QIAGEN, Germany) according to the manufacturer's guidelines. The quality of the extracted DNA was visualized by electrophoresis in 1% agarose gel and quantified with a UV-Vis spectrophotometer (Eppendorf AG, Hamburg, Germany). Finally, the extracted DNA from each sample were stored at − 20°C prior to sequencing.

2.4 Library preparation and sequencing

The PCR amplification was performed targeting the full-length bacterial 16S rRNA gene (~ 1500 bp) using the universal primer pair 27F (5'-AGRGTTYGATYMTGGCTCAG-3') and 1492R (5'-CGGTTACCTTGTTACGACTT-3'). The metagenomic DNA samples from each moss were used as templates for the PCR reactions. The PCR was carried out in a total reaction volume of 50 µL, containing ~ 1 ng template DNA, 2X NEB Q5® high-fidelity master mix and 5 pmol of each barcoded primer. A negative control was maintained by using molecular-grade water in place of DNA. The PCR conditions were as follows: initial denaturation at 98°C for 30 seconds; 30 cycles of denaturation at 98°C for 10

seconds, annealing at 58°C for 20 seconds, and elongation at 72°C for 3 min; followed by a final extension at 72°C for 2 min. All the 3 replicates for each moss, a total of 9 samples, were amplified with a unique barcode. The PCR amplicons were loaded onto a 0.8% agarose gel, and the presence of a band approximately 1.5 kb in size was verified. All PCR products were purified using the Zymo DNA Clean & Concentrator-25 (D4034) kit and quantified using Qubit® dsDNA BR Assay Kits (Cat. No. Q32853) in Qubit 3 Fluorometer (Thermo Fisher Scientific, Oregon, USA). Amplicon libraries were generated using a native barcoding kit 96 V14 (SQK-NBD114.96) kit (Oxford Nanopore Technologies Nanopore, Oxford, UK) following the Oxford Nanopore 1D library protocol. Equimolar concentrations of all barcoded products were pooled together for sequencing performed by using MinION OXFORD NANOPORE device (Flow cell version: 10.4.1) at the NGS facility of Institute of Life Sciences, India. Base-calling and demultiplexing of the raw signal data were performed using Dorado basecaller, with read quality above 10 and read length between 1200 and 1700 bp. The resulted FASTQ files were deposited at the NCBI under accession number PRJNA1469936.

2.5 Bioinformatic analysis

The passed high-quality reads were taxonomically classified using EPI2ME Labs platform with NextFlow wf-16 pipeline (v1.6.1) (https://github.com/epi2me-labs/wf-16s). The reads were filtered based on quality (Q-score > 10) and read length (1400–1600 bp), followed by alignment-based classification using the Minimap2 tool (v2.28) (Li, 2018) against a curated full-length NCBI 16S rRNA reference database (ncbi_16s_18s). Default parameters (minimum percentage identity = 95 and minimum reference coverage = 90) were used to assign bacterial taxa with maximum coverage. The generated abundance table was used for further statistical analyses and visualized using R, incorporating the microeco package [14]. The low feature counts were removed from the abundance table by setting standard parameters (relative abundance ≥ 0.01% and occurrence frequency ≥ 2). To minimize biases arising from uneven sequencing depth, rarefaction was performed to normalize all samples to the same number of reads. Alpha diversity was measured using the Shannon, Simpson and Chao1 indices, and statistical significance among groups was evaluated using the Kruskal-Wallis rank-sum test with multiple-testing corrections. Beta-diversity was calculated by computing Bray-Curtis dissimilarities from normalized ASV abundance data. For the differential abundance analysis, Linear Discriminant Analysis Effect Size (LEfSe) was applied with an LDA score > 2 and a significant p-value < 0.05 [15]. Additionally, a machine learning Random Forest model [16] was performed using the Mean Decrease Gini value. The microbial co-occurrence patterns were evaluated using the relative abundance data at genus level. Pairwise Spearman rank correlation coefficients (r) and network topology were computed using the igraph package in R. The final network was visualized through Gephi software (v0.11.2). The ecological and biogeochemical functions of the annotated bacterial communities were predicted using the FAPROTAX (Functional Annotation of Prokaryotic Taxa) database (v1.2.12) [17, 18].

3. Results

3.1 Bacterial community composition of moss phyllosphere

In total, we obtained 25,795, 31,360 and 32,331 bacterial ASVs from the phyllosphere of mosses, *G. phascoides P. nitida and P. aloides*, respectively. Out of an average of 11,293 (43.78%), 25,384 (80.94%) and 21,609 (66.84%) reads from moss samples, accordingly, *G. phascoides, P. nitida* and *P. aloides* were mapped to known bacterial taxonomic groups, leaving 14,502 (56.22%), 5,976 (19.06%) and 10,722 (33.16%) reads per sample of moss as unclassified. Overall, across all studied moss phyllospheres, the bacterial community is dominated by Pseudomonadota (59.88%), Bacillota (15.88%), Cyanobacteriota (8.63%), Acidobacteriota (6.06%) and Actinomycetota (4.95%). At the genus level, the overall microbial community was characterized by a high abundance of *Priestia* (8.80%) and *Paraburkholderia* (8.56%), followed closely by *Methylobacterium* (7.08%), *Bacillus* (5.97%), and *Methylocella* (4.40%). Moreover, the variation of the relative abundance of bacterial taxa across the samples, highlighting a potential influence of host-specific microbiome partitioning in the moss phyllosphere. In *G. phascoides*, Pseudomonadota (60.47%) constituted a major portion of the bacterial community, followed by a notably high proportion of Cyanobacteriota (18.67%) and Actinomycetota (9.14%) Figure-1(A). At the genus level, the community was primarily composed of *Methylobacterium* (11.12%) and the cyanobacterial genus *Porphyrosiphon* (10.37%), as well as *Methylocella* (7.27%). While the bacterial community associated with *P. nitida* showed a co-dominance of Pseudomonadota (44.43%) and Bacillota (42.14%), marking a significant divergence from the other host species. Consequently, at the genus level, this moss species was largely colonized by Bacillota representatives, primarily *Priestia* (26.28%) and *Bacillus* (13.38%), alongside *Rhizobium* (4.23%) Figure-2. In contrast, *P. aloides* displayed the highest relative abundance of Pseudomonadota among all samples, comprising 74.73% of its microbiome, followed by Acidobacteriota (10.80%) and Bacillota (4.15%). The prominent genera thriving in this community were *Paraburkholderia* (19.07%), *Alloacidobacterium* (6.95%), and *Lichenibacterium* (6.76%) Figure-1(B).

The Venn diagram analysis revealed the structural overlap and host-specific distribution pattern of the bacterial community across studied moss samples. Out of the total detected taxa, a substantial proportion of the moss bacterial community remained as a highly conserved core microbiome, comprising more than half of all detected taxa (332 ASVs; 51.6%) Figure-1(C). Taxonomically, these ubiquitous taxa were mainly from bacterial phyla Pseudomonadota (227 ASVs) and Bacillota (32 ASVs), specifically generalist genera related to nitrogen fixation and robust environmental adaptability, such as *Bradyrhizobium*, *Methylobacterium*, *Bacillus* and *Rhizobium*. In contrast, the portion of bacterial taxa restricted to a single moss host was relatively low (103 ASVs; 16%). *P. nitida* harboured the highest number of unique taxa (67 ASVs; 10.4%), uniquely enriching members of the phyla Cyanobacteriota and Bacteroidota (e.g. *Chryseobacterium* and *Flavobacterium*). Conversely, *P. aloides* and *G. phascoides* possessed highly reduced exclusive communities of only 24 (3.7%) and 12 (1.9%) unique ASVs, respectively, with *P. aloides* uniquely recruiting specific Acidobacteriota and genera like *Legionella*. Furthermore, pairwise comparisons showed consistent degrees of structural similarity among the hosts,

with the highest overlap observed between *G. phascoides* and *P. aloides* (79 ASVs; 12.27%), followed by *P. nitida* sharing exactly 65 exclusive ASVs (10.09%) with both *G. phascoides* and *P. aloides* Figure-1(D). This indicated that while distinct host-specific microbial signatures exist, the overall bacterial community of these mosses is overwhelmingly driven by the recruitment of a large, shared functional core.

3.2 Moss microbial diversity and community structure

To evaluate the species richness and evenness of the moss-associated bacterial communities, alpha diversity was assessed using Chao1, Shannon and Simpson indices. The highest community richness was observed in *P. nitida* (Chao1 = 468.48 ± 51.62), followed by *P. aloides* (Chao1 = 446.06 ± 24.90) and *G. phascoides* (Chao1 = 434.47 ± 32.37) Figure-3(A). However, *G. phascoides* exhibited the highest microbial diversity (Shannon = 4.61 ± 0.08, Simpson = 0.975), closely mirrored by *P. aloides* (Shannon = 4.56 ± 0.06, Simpson = 0.974). In contrast, *P. nitida* displayed the lowest and most variable bacterial community structure (Shannon = 4.07 ± 0.78, Simpson = 0.931) Figure-3(B,C). This lower value of bacterial diversity indices in *P. nitida* was explained by the disproportionate hyper-dominance of Bacillota (genera such as *Priestia* and *Bacillus*). To measure the bacterial community dissimilarity among the moss samples, beta diversity was calculated using Bray-Curtis dissimilarity matrices. The analysis revealed strong host-specific clustering, with the variation between different moss species significantly outweighing the variation within the same moss species. The pairwise comparisons of the microbial communities showed the most drastic structural separations of *P. nitida* from both two mosses, *P. aloides* (Bray-Curtis distance = 0.838) and *G. phascoides* (Bray-Curtis distance = 0.822) Figure-3(D). Conversely, the microbiomes of *G. phascoides* and *P. aloides* were relatively more similar to each other, exhibiting the lowest inter-species dissimilarity (Bray-Curtis distance = 0.624). Further, we had investigated whether specific bacterial taxa were differentially abundant across the studied moss samples. We performed both LEfSe (LDA score > 2, $p < 0.05$) and a Random Forest model to identify specific bacterial clades associated with each moss. But we did not find any significantly enriched bacterial taxa across the moss species, indicating an absence of distinct taxonomic biomarkers distinguishing each of the moss samples. Thus, these results showed that the overall bacterial community structure of the moss phyllosphere tended to be homogeneous.

3.3 Co-occurrence Network Analysis

To elucidate the complex microbial interactions and potential symbiotic relationships within the moss-associated phyllosphere microbiome, a co-occurrence network analysis was performed. The resulting global microbial network was comprised of a total 280 nodes with 770 edges. The overall network topology revealed a graph density of 0.0197 and an average node degree of 5.5, suggesting that each bacterial taxon in the network directly interacts with an average of between five to six other taxa. In this network, most of the microbial interactions were dominated by positive co-occurrences (network edge = 754; 97.9%), while only 16 edges (2.1%) represented negative interactions or mutual exclusions. This highly skewed distribution indicates synergistic and shared environmental niche preferences among the microbial communities, rather than competitive exclusion. Taxonomically, the structural framework of

the network was heavily anchored by the phylum Pseudomonadota, which constituted the vast majority of the interconnected nodes (161). Other prominent phyla deeply integrated into the microbial network included Actinomycetota (27 nodes), Cyanobacteriota (25 nodes), Bacteroidota (25 nodes) and Bacillota (19 nodes) Figure-3(E). The high prevalence of Pseudomonadota within the network indicates that species belonging to this phylum likely act as keystone taxa, playing critical roles in maintaining the stability and connectivity of the broader moss-associated community. Furthermore, the network exhibited a highly modular structure, clustering into several distinct sub-communities or “modules” of strongly interconnected taxa. These modules typically represent functional guilds or consortia of microbes that respond similarly to environmental gradients. The most prominent modules identified within the network were M1 and M2 (each clustering 26 interacting taxa), followed closely by M3 (24 taxa), M4 (22 taxa), and M5 (18 taxa). The presence of these densely connected sub-networks highlights that the moss microbiome is organized into highly structured, cooperative microbial hubs rather than being randomly assembled. Furthermore, subnetwork analysis revealed distinct variations in network size, connectivity and taxonomic structure of bacterial communities associated with each individual moss species. Out of three mosses, *P. nitida* exhibited the highest level of complexity and interconnectivity, containing 205 nodes and a massive 606 edges. The synergistic relationships of this moss sample were heavily dominated by positive interactions (597 positive edges) compared to only 9 negative edges. In contrast, *P. aloides* had an intermediate level of network complexity, comprising 194 nodes and 243 edges. Its microbial community was more sparse, with a density of 0.013 and an average degree of 2.51. The bacterial community associated with *G. phascoides* assembled into the most fragmented and least connected network (173 nodes; 187 edges) yielding the lowest network density (0.0126) and an average node degree of just 2.16. Despite the lower connectivity, the interactions among the taxa remained highly cooperative (171 positive vs. 16 negative edges).

3.4 Functional prediction of moss associated microbiome

To infer the ecological roles and metabolic functions of the moss-associated bacterial communities, functional prediction analysis was performed based on the 16S rRNA gene amplicons. It was observed that despite significant variations in taxonomic profiles across the different moss host species, the overall microbiome maintains a baseline of functional redundancy. A core set of metabolic pathways was maintained across all samples, heavily dominated by broad-spectrum functions such as aerobic chemoheterotrophy, general carbon cycling and fundamental nitrogen metabolism Figure-4. This suggests that although the change in occurrence of taxa noted depending on the host, the essential biogeochemical roles required to sustain the moss phyllosphere microenvironment remain highly conserved.

However, the differential abundance analysis revealed significant host-specific enrichment of distinct metabolic pathways. *G. phascoides* microbiome had significantly enriched in traits related to methanotrophy, methylotrophy and methanol oxidation, suggesting a specialised C1-compound-driven carbon cycling niche. In contrast, *P. nitida* showed a marked elevation in the pathways linked with the degradation of complex organic matter (e.g., chitinolysis). The microbiome associated with *P. aloides*

demonstrated a strong diversification in functions tied to complex nitrogen cycling, including nitrate denitrification and nitrite denitrification Figure-5. Overall, the results from functional prediction analysis showed that the moss-associated microbes are highly adaptive and conserved among host species. The differential enrichment of metabolic pathways across moss host species ensures micro-ecosystem stability of moss microbiomes tailored to their specific physiological and environmental needs.

4. Discussion

Our results showed a significant and high proportion of taxonomically unclassified sequences (34.86%) from the phyllosphere of all three moss species. The prevalence of a large number of unassigned reads suggests that a significant portion of the moss-associated microbiome remains undocumented in global databases. The presence of unique evolutionary lineages of bacteria in the moss microbiome that were hard to culture or sequence underscores the moss phyllosphere as a substantial reservoir of microbial dark matter and taxonomic entities, comparable to other well-studied plant microenvironments.

4.1 Mosses maintain a consistent bacterial assembly over different host species

We initially hypothesized that the distinct physiological characteristics of each moss species would impose strong selective pressures, leading to divergent microbial assemblies and host-specific patterns of interaction. However, our findings demonstrated that the phyllosphere of the subtropical mosses such as *Garckea phascoides*, *Philonotis nitida* and *Pogonatum aloides* maintained similar bacterial communities inhabiting identical environmental and ecological conditions. The negative results in our LEfSe and Random Forest models, coupled with highly overlapping beta-diversity profiles, suggest that the influence of the host identity on moss microbial assembly becomes secondary compared to the selective pressures of the local environmental and ecological characteristics. Consequently, these lead to the rejection of our initial hypothesis. The phyllosphere of sub-tropical mosses appears to be colonized by a shared and ubiquitous pool of microbial consortia that are predominantly regulated by ecological conditions rather than host plant identity. This partially aligns with previous findings by Rodríguez-Rodríguez et al. (2022), in which microbial assembly of feather mosses, such as *Pleurozium schreberi* and *Ptilium crista-castrensis* was largely predicted by site-specific ecological conditions rather host phylogeny. Interestingly, while accounting for only about half of the overall bacterial diversity, this shared bacterial core community comprised more than 82% of the total sequencing reads across the studied samples. This suggests that the vast majority of bacterial taxa inhabiting the moss phyllosphere were broadly shared bacterial consortia, while the observed minor variation between samples arises from rare taxa responding to the transient environment of host surfaces [19]. In contrast to our data, while host taxonomy is often recognized as a primary driver of phyllosphere microbiome composition in vascular plants [20]. This divergence can be largely attributed to the unique anatomical and physiological traits of mosses. As mosses lack a proper vascular system, they are primarily dependent on their immediate surroundings for water and nutrition [7]. Most of the water absorbed by mosses comes from

either atmospheric deposition or flow-over water through their surfaces. As a result, the chemistry of the thin water layer on the moss surface is largely governed by external environmental conditions instead of host-mediated control, thereby diminishing the host-filtering effect commonly observed in higher plants [21, 22]. The evolution of structural and physiological adaptations in vascular plants, including stomatal architecture, leaf chemistry and specific host-microbe signalling, enables them to recruit distinct epiphytic microbial guilds buffering environmental control [23, 24]. This may suggest that the moss species with different genetic backgrounds that grow under similar microhabitats may possess functionally identical surface micro-environments from the perspective of a colonizing bacterium [25]. However, the moss host identity plays a greater role in shaping the composition of endophytic microbial communities compared to epiphytic assemblages, as proposed by previous researchers [26–28]. Our findings support the ecological bottleneck filtering hypothesis, suggesting that under the extreme or highly fluctuating microhabitats, environmental factors create an ecological bottleneck that only a specific subset of environmentally adapted taxa can pass through, regardless of the host species on which they reside [29–31]. Consequently, the physicochemical properties of the moss phyllosphere, such as moisture retention, pH and surface nutrient profile, are essentially extensions of the ambient environment. These colonizing bacteria are subject to intense environmental filtering, overriding the more nuanced selective pressures that might be exerted by host-specific traits.

Overall, the microbial communities across the studied moss phyllosphere were dominated by the bacterial phyla Pseudomonadota (formerly known as Proteobacteria), Acidobacteriota (Acidobacteria), Actinomycetota (Actinobacteria), Planctomycetota (Planctomycetes) and Cyanobacteriota (Cyanobacteria). This similar pattern of bacterial diversity was also found in global surveys of the moss microbiome, including boreal, temperate and high-latitude mountain ecosystems (Ochoa-Hueso et al. 2024). The higher abundance of Pseudomonadota within the moss phyllosphere was consistent with the current study, highlighting this phylum as a ubiquitous colonizer of bryophytes [34]. The ecological and metabolic versatility of this bacterial phylum, from photoautotrophy to generalist heterotrophy, enables them to persist in the nutrient-scarce and fluctuating microenvironments of the moss canopy [33]. Conversely, high prevalence of Bacillota (40%) in the phyllosphere of *P. nitida*, driven primarily by the genus *Priestia* (including *P. aryabhattai* and *P. megaterium*), suggests a specialized ecological role of this phylum in transient phyllosphere environments. These taxa were formerly classified under *Bacillus* and are well-documented from higher plants in both epiphytic and endophytic habitats [35, 36]. Furthermore, the high relative abundance of Cyanobacteriota (20%) in *G. phascoides* suggests the critical role of diazotrophic activity in moss ecosystems, facilitating the gap between the host nutrient requirement and limited environmental availability [37, 38]. The persistent presence of bacterial genera like *Methylobacterium* and *Paraburkholderia* across the studied samples indicates that the moss phyllosphere is a curated assembly of bacterial taxa rather than a random collection of environmental transients. Our co-occurrence network analysis revealed that the dominance of positive interactions (over 97%) across all the subnetworks, providing a profound insight into microbial assembly rules and ecological strategies governing the moss phyllosphere. The extreme scarcity of negative edges indicates a synergistic, cross-feeding relationship of the moss microbiome that has mostly shared environmental

niches rather than competitive exclusion [39]. This observation strongly aligns with Stress Gradient Hypothesis, which suggests the prevalence of facilitative interactions among microbial taxa under environmental extremes and unstable conditions (He et al. 2013). Furthermore, high positive interaction may indicate strong habitat filtering in the moss phyllosphere that clusters together a compatible group of microbes adaptable to a unique phyllosphere microhabitat. Our results identified Pseudomonadota as a keystone bacterial group within the moss phyllosphere. However, the microbial network architecture was not uniform across the studied samples. *P. nitida* had a massive and highly interconnected web of taxa in comparison to the other two moss samples, *G. phascoides* and *P. aloides*. This suggested that the stability of the bacterial community in *P. nitida* was achieved by functional redundancy and tight bacterial crosstalk, whereas the stability of microbial assembly of the other two mosses was maintained via fewer but more highly specialized core interactions. Ultimately, our results suggest that the moss phyllosphere acts as a passive physical scaffold for microbial colonization rather active biological filter. Hence, the composition of the phyllosphere bacterial assembly is mostly determined by the ecological readout of the surrounding microclimate.

4.2 Moss phyllosphere microbiomes maintain a baseline level of functional redundancy ensuring their survivability over challenging conditions

Our results suggest that the phyllosphere of the subtropical mosses harbours a consistent bacterial community found in similar environmental conditions, irrespective of host identity. They play a profound role in forest ecosystem functioning by providing essential services such as nitrogen input, carbon sequestration, and methane mitigation. In the absence of strong host-driven selection, the moss phyllosphere becomes dominated by highly resilient environmental generalists [9]. The survivability and colonization potential of phyllosphere bacteria are fundamentally limited by the water retention capacity of host tissue and exposure to ultraviolet (UV) radiation [41]. Our taxonomic profiling revealed that the moss phyllosphere is consistently co-dominated by bacterial genera including *Paraburkholderia*, *Methylobacterium*, *Bacillus*, and *Methylocella.* These taxa were frequently isolated from extreme or highly variable environmental conditions and possess essential adaptations critical for survival in the epiphytic habitat (Lindow and Brandl, 2003). For instance, the members of *Paraburkholderia* were mostly reported for their impact on plant growth promotion and disease control by either the inhibition of phytopathogens or the induction of plant systemic resistance [42]. Similarly, *Methylobacterium* was another dominant phyllospheric symbiont capable of utilizing single-carbon compounds [43]. This genus can resist intense UV radiation and desiccation common to an epiphytic lifestyle, and support plant growth by the production of plant hormones (e.g. cytokinin and IAA) and help in nutrient acquisition [44, 45]. The flexible metabolic capabilities of *Methylocella* and *Methylocapsa* species enable them to thrive under the dynamic and nutrient-fluctuating environments of the moss phyllosphere. The presence of a soluble methane monooxygenase (sMMO) gene cluster in these organisms provides a broader range of substrate versatility than the commonly found methanotrophs with a particulate membrane-bound enzyme (pMMO) gene cluster [46, 47]. These bacteria can utilize multi-carbon substrates under low-methane conditions. The colonization of the moss surface by these methanotrophs substantially reduces methane emissions to the atmosphere by functioning as a biological methane filter.

Concurrently, they can supply an additional source of carbon dioxide derived from methane oxidation for the host moss. *Bacillus*, a spore-forming bacterial genus, is a well-studied bacterial group for its biofilm-producing nature. Besides their active role in plant growth promotion, this genus may act as a biocontrol agent and support other phyllospheric life forms, as well as host plants from both biotic and abiotic stresses [48]. We have found a high prevalence of the bacterial genus *Lichenibacterium* from family Lichenibacteriaceae under Hyphomicrobiales (formerly Rhizobiales) across the studied samples. Previously, it was reported as a carotenoid-producing bacterial lineage predominantly associated with lichen thalli [49]. A recent global phylogenomic meta-analyses study by Leducq et al. (2026) had redefined their existence as a core member of the broader plant foliar interface. The presence of this bacterial genus in our datasets extends its ecological niche from lichen symbioses to the microlayer of non-vascular plant canopies. *Lichenibacterium* likely occupies a complementary niche to classic foliar dominants like *Methylobacterium*. It can thrive in complex polysaccharides and organic acids exuded by the moss cellular surface, ensuring its stability even when the host undergoes desiccation. The presence of bacterial genus *Porphyrosiphon*, which belongs to the non-heterocystous order Oscillatoriales on the moss epiphytic surfaces, likely complements the heterocystous diazotrophs like *Nostoc* or *Scytonema* and the associative alphaproteobacterial. This genus is recognized as a key pioneer of terrestrial biocrusts and lithophytic surfaces [51, 52], rarely highlighted as a core component of moss phyllosphere microbiome. They are actively associated with the secretion of sticky mucilaginous matrix that aids in the structural retention of moisture and organic debris, which indirectly helps in nourishing the entire epiphytic bacterial communities. They can also perform diurnal partitioning of oxygenic photosynthesis and nitrogenase activity under the micro-aerobic pockets created within the thick EPS matrix. The recruitment of all these bacterial taxa to form a functional team in the moss phyllosphere is a common strategy by the host plant for adaptation in harsh environments, where the symbiotic partnership provides benefits that neither organism could achieve alone. The ubiquitous presence of these specific functional groups aligns with the physiological demands of survival on a moss leaf, further supporting the idea that the surrounding environment largely dictates bacterial community assembly rather than the moss host plant.

A significant characteristic of moss microbiome is its contribution to biogeochemical cycling, particularly through nitrogen fixation and methane oxidation. The functional repertoire of the taxa identified in subtropical mosses reveals a high degree of redundancy, ensuring the maintenance of their vital ecosystem services regardless of the specific moss host species. Our Venn analysis showed a massive core of shared taxa across all three studied moss samples. This ubiquitous core was overwhelmingly dominated by Pseudomonadota, specifically genera such as *Bradyrhizobium*, *Methylobacterium*, and *Rhizobium*, involved in nitrogen fixation, methylotrophy and robust environmental adaptability. Mosses typically grow in nutrient-limited environments and the persistent occurrence of these diazotrophic and methylotrophic taxa suggests that moss phyllosphere actively recruits a foundational consortium of generalists to fulfil essential baseline biogeochemical activities, particularly nitrogen and carbon acquisitions. While a striking divergence was observed in *P. nitida*, due to the massive hyper-dominance of Bacillota, specifically, *Priestia* and *Bacillus*. This taxonomic shift directly

correlated with our predicted functional profile, which showed a significant enrichment in endospore formation and chemoheterotrophic stress responses. The members of Bacillota exhibited a high tolerance to desiccation and UV radiation for their sporulation capabilities. The specific enrichment of these taxa in association with a highly complex and tightly knit co-occurrence network suggests that this moss harbours a highly collaborative, stress-resilient microbial consortium, potentially as an adaptive mechanism to survive in highly fluctuating or harsh environments. In contrast, *G. phascoides* and *P. aloides* shared a much closer ecological and evolutionary relationship. However, *G. phascoides* established a highly specialized niche enriched in Cyanobacteriota such as *Porphyrosiphon*. This suggests a symbiotic reliance of this moss on cyanobacteria for supplementary carbon fixation and additional nitrogen input. Furthermore, the presence of more than half of the taxonomically unclassified reads from this moss phyllosphere highlights it as a significant reservoir of novel, undescribed branching of bacterial lineages that warrant further research. Meanwhile, *P. aloides* fostered a highly balanced and diverse community enriched in Acidobacteriota, reflecting their microbiome for a distinct soil-like microenvironment. This host-independent nature of the moss microbiome has significant implications for ecosystem functioning. It is likely because the stability of their vital biogeochemical processes is directly tied to environmental conservation rather than the preservation of specific moss species. Future shifts in climatic conditions, like altered precipitation patterns or canopy cover reduction, could rapidly disrupt these microbe-mediated cycles by altering the environmental filters that sustain this core bacterial community.

5. Conclusion

The overall findings of our study demonstrate that the moss phyllosphere harbours a consistent bacterial assembly in similar environmental conditions irrespective of their host species. An individual moss host may recruit specific microbial cohorts suited to its functional requirements. But these taxonomic variations did not show any statistically significant differences in genus-level abundance. The harsh and challenging environment of the leaf surfaces mostly selects the bacterial assemblies with mutualistic synergies over competitive relationships. These phyllosphere microbiomes maintain a base-level functional redundancy of some essential biochemical functions related to the nitrogen cycle (nitrogen fixation, nitrate reduction, ureolysis), carbon cycle (Methylotrophy, methanotrophy, hydrocarbon degradation) and methanol oxidation that ensures their survivability over challenging situations. These findings significantly advance our understanding of moss-microbe interaction in sparsely studied sub-tropical regions.

Declarations

Competing Interests

None declared.

Funding

Anusandhan National Research Foundation, Govt of India funded Core Research Grant project (CRG/2023/002423).

Author Contribution

RB and NA designed the research. RB drafted the manuscript. NA critically reviewed and edited the manuscript. All authors read and approved the final version of the manuscript.

Acknowledgement

The authors would like to express their sincere gratitude to Professor Prem Lal Uniyal, Department of Botany, University of Delhi, India, for his invaluable expertise and help in the taxonomic identification of the moss species. We extend our sincere gratitude to the scientists and technical staff at the Institute of Life Sciences (ILS) for their technical expertise and assistance with the ONT metagenomic sequencing. Additionally, RB extends heartfelt thanks to Arnav Patowary, Bhaskar Jyoti Parasar, Nilutpal Baruah, Dhan Pratim Chetry, and Abhijit Sanyashi for their dedicated support and assistance during the field sampling and sample collection process. We are also thankful to DST, Govt. of India, for providing DST-FIST Support to the Department of Botany, Gauhati University, and DST-PURSE [file no: SR/ PURSE/2022/116 (C)] support to Gauhati University.

Data Availability

All the raw files obtained in FASTQ format were deposited at the NCBI under accession number PRJNA1469936 (http://www.ncbi.nlm.nih.gov/bioproject/1469936).

References

1. Alessa O, Ogura Y, Fujitani Y, et al (2021) Comprehensive Comparative Genomics and Phenotyping of *Methylobacterium* Species. Front Microbiol 12:. https://doi.org/10.3389/fmicb.2021.740610
2. Alvarenga DO, Rousk K (2022) Unraveling host–microbe interactions and ecosystem functions in moss–bacteria symbioses. J Exp Bot 73:4473–4486. https://doi.org/10.1093/jxb/erac091
3. Bashir I, War AF, Rafiq I, et al (2022) Phyllosphere microbiome: Diversity and functions. Microbiol Res 254:126888. https://doi.org/10.1016/j.micres.2021.126888
4. Bragina A, Maier S, Berg C, et al (2012) Similar diversity of Alphaproteobacteria and nitrogenase gene amplicons on two related *Sphagnum* mosses. Front Microbiol 2:18723. https://doi.org/10.3389/FMICB.2011.00275/BIBTEX

5. Breiman L (2001) Random Forests. Mach Learn 45:5–32. https://doi.org/10.1023/A:1010933404324
6. Crombie AT, Murrell JC (2014) Trace-gas metabolic versatility of the facultative methanotroph *Methylocella silvestris*. Nature 510:148–151. https://doi.org/10.1038/nature13192
7. Delaux P-M, Schornack S (2021) Plant evolution driven by interactions with symbiotic and pathogenic microbes. Science (1979) 371:. https://doi.org/10.1126/science.aba6605
8. Faust K, Raes J (2012) Microbial interactions: from networks to models. Nat Rev Microbiol 10:538–550. https://doi.org/10.1038/nrmicro2832
9. Fessia A, Barra P, Barros G, Nesci A (2022) Could Bacillus biofilms enhance the effectivity of biocontrol strategies in the phyllosphere? J Appl Microbiol 133:2148–2166. https://doi.org/10.1111/jam.15596
10. Hardie DC, Hutchings JA (2010) Evolutionary ecology at the extremes of species' ranges. Environmental Reviews 18:1–20. https://doi.org/10.1139/A09-014
11. He Q, Bertness MD, Altieri AH (2013) Global shifts towards positive species interactions with increasing environmental stress. Ecol Lett 16:695–706. https://doi.org/10.1111/ele.12080
12. Holland-Moritz H, Stuart J, Lewis LR, et al (2018) Novel bacterial lineages associated with boreal moss species. Environ Microbiol 20:2625–2638. https://doi.org/10.1111/1462-2920.14288
13. Holland-Moritz H, Stuart JEM, Lewis LR, et al (2021) The bacterial communities of Alaskan mosses and their contributions to N2-fixation. Microbiome 9:53. https://doi.org/10.1186/s40168-021-01001-4
14. Huttunen S, Bell N, Hedenäs L (2018) The Evolutionary Diversity of Mosses – Taxonomic Heterogeneity and its Ecological Drivers. CRC Crit Rev Plant Sci 37:128–174. https://doi.org/10.1080/07352689.2018.1482434
15. Ishak S, Rondeau-Leclaire J, Faticov M, et al (2024) Boreal moss-microbe interactions are revealed through metagenome assembly of novel bacterial species. Sci Rep 14:22168. https://doi.org/10.1038/s41598-024-73045-z
16. Kim D-H, LEE N-J, YOON S-R, et al (2022) *Porphyrosiphon annulatus* sp. nov. (Oscillatoriales, Cyanobacteria) isolated on moist soil in Suwon, Republic of Korea. Phytotaxa 532:288–300. https://doi.org/10.11646/phytotaxa.532.3.6
17. Kubin E, Lippo H, Poikolainen J (2000) Heavy metal loading. pp 60–71
18. Lajoie G, Dariel L (2025) How Useful Are Plant Traits in Explaining Variation in Phyllosphere Microbial Abundance and Composition Across Hosts? Environ Microbiol 27:. https://doi.org/10.1111/1462-2920.70123
19. Leducq J-B, St-Amand L-P, Ross D, Kembel SW (2026) A phylogenomic and metagenomic meta-analysis of bacterial diversity in the phyllosphere lifts a veil on hyphomicrobiales dark matter. Syst Appl Microbiol 49:126697. https://doi.org/10.1016/j.syapm.2026.126697

20. Li H (2018) Minimap2: pairwise alignment for nucleotide sequences. Bioinformatics 34:3094–3100. https://doi.org/10.1093/bioinformatics/bty191
21. Li J, Jin M-K, Neilson R, et al (2023) Plant identity shapes phyllosphere microbiome structure and abundance of genes involved in nutrient cycling. Science of The Total Environment 865:161245. https://doi.org/10.1016/j.scitotenv.2022.161245
22. Lindow SE, Brandl MT (2003) Microbiology of the Phyllosphere. Appl Environ Microbiol 69:1875–1883. https://doi.org/10.1128/AEM.69.4.1875-1883.2003
23. Liu C, Mansoldo FRP, Li H, et al (2026) A workflow for statistical analysis and visualization of microbiome omics data using the R microeco package. Nat Protoc 21:1300–1324. https://doi.org/10.1038/s41596-025-01239-4
24. Louca S, Jacques SMS, Pires APF, et al (2016a) High taxonomic variability despite stable functional structure across microbial communities. Nat Ecol Evol 1:0015. https://doi.org/10.1038/s41559-016-0015
25. Louca S, Parfrey LW, Doebeli M (2016b) Decoupling function and taxonomy in the global ocean microbiome. Science (1979) 353:1272–1277. https://doi.org/10.1126/science.aaf4507
26. Machado-de-Lima NM, Fernandes VMC, Roush D, et al (2019) The compositionally distinct cyanobacterial biocrusts from brazilian savanna and their environmental drivers of community diversity. Front Microbiol 10:. https://doi.org/10.3389/fmicb.2019.02798
27. Maqsood A, Aslam MN, Khaliq H, et al (2024) Endophytic *bacillus* spp. mediated plant growth promotion of tomato seedlings and suppression of *Meloidogyne incognita* and *Fusarium oxysporum* Disease Complex. J Plant Growth Regul 43:2454–2469. https://doi.org/10.1007/s00344-024-11279-x
28. Noble AS, Abbaszadeh J, Lee CK (2025) Host selection is not a universal driver of phyllosphere community assembly among ecologically similar native New Zealand plant species. Microbiome 13:35. https://doi.org/10.1186/s40168-024-02000-x
29. Ochoa-Hueso R, Eldridge DJ, Berdugo M, et al (2024) Unearthing the soil-borne microbiome of land plants. Glob Chang Biol 30:. https://doi.org/10.1111/gcb.17295
30. Ottesen AR, Gorham S, Reed E, et al (2016) Using a control to better understand phyllosphere microbiota. PLoS One 11:e0163482. https://doi.org/10.1371/journal.pone.0163482
31. Palberg D, Kisiała A, Jorge GL, Emery RJN (2022) A survey of *Methylobacterium* species and strains reveals widespread production and varying profiles of cytokinin phytohormones. BMC Microbiol 22:49. https://doi.org/10.1186/s12866-022-02454-9
32. Pankratov TA, Grouzdev DS, Patutina EO, et al (2020) *Lichenibacterium ramalinae* gen. nov, sp. nov., *Lichenibacterium* minor sp. nov., the first endophytic, beta-carotene producing bacterial representatives from lichen thalli and the proposal of the new family Lichenibacteriaceae within the order Rhizobiales. Antonie Van Leeuwenhoek 113:477–489. https://doi.org/10.1007/s10482-019-01357-6

33. Perera-Castro A V., Márquez DA, Busch FA, Hanson DT (2026) Evidence for regulation of transpiration in nonstomatal plants: insights from bryophyte gametophytes. New Phytologist. https://doi.org/10.1111/nph.71206
34. Pishchik VN, Filippova PS, Mirskaya G V., et al (2021) Epiphytic PGPB *Bacillus megaterium* AFI1 and *Paenibacillus nicotianae* AFI2 Improve Wheat Growth and Antioxidant Status under Ni Stress. Plants 10:2334. https://doi.org/10.3390/plants10112334
35. Renaudin M, Laforest-Lapointe I, Bellenger J-P (2022) Unraveling global and diazotrophic bacteriomes of boreal forest floor feather mosses and their environmental drivers at the ecosystem and at the plant scale in North America. Science of The Total Environment 837:155761. https://doi.org/10.1016/j.scitotenv.2022.155761
36. Rodríguez-Rodríguez JC, Bergeron Y, Kembel SW, Fenton NJ (2022) Dominance of coniferous and broadleaved trees drives bacterial associations with boreal feather mosses. Environ Microbiol 24:3517–3528. https://doi.org/10.1111/1462-2920.16013
37. Rojas-Rojas FU, Gómez-Vázquez IM, Estrada-de los Santos P, et al (2025) The potential of *Paraburkholderia* species to enhance crop growth. World J Microbiol Biotechnol 41:62. https://doi.org/10.1007/s11274-025-04256-3
38. Rousk K, Jones DL, DeLuca TH (2013) Moss-cyanobacteria associations as biogenic sources of nitrogen in boreal forest ecosystems. Front Microbiol 4:. https://doi.org/10.3389/fmicb.2013.00150
39. Samanta D, Rauniyar S, Saxena P, Sani RK (2024) From genome to evolution: investigating type II methylotrophs using a pangenomic analysis. mSystems 9:. https://doi.org/10.1128/msystems.00248-24
40. Segata N, Izard J, Waldron L, et al (2011) Metagenomic biomarker discovery and explanation. Genome Biol 12:R60. https://doi.org/10.1186/gb-2011-12-6-r60
41. Singh PK, Martins CSC, Jayaramaiah RH, et al (2026) Leaf microbiome assembly is linked to plant phylogeny. Plant Soil 520:1177–1192. https://doi.org/10.1007/s11104-026-08318-9
42. Sohrabi R, Paasch BC, Liber JA, He SY (2023) Phyllosphere microbiome. Annu Rev Plant Biol 74:539–568. https://doi.org/10.1146/annurev-arplant-102820-032704
43. Stegen JC, Lin X, Konopka AE, Fredrickson JK (2012) Stochastic and deterministic assembly processes in subsurface microbial communities. ISME J 6:1653–1664. https://doi.org/10.1038/ismej.2012.22
44. Tang JY, Ma J, Li XD, Li YH (2016) Illumina sequencing-based community analysis of bacteria associated with different bryophytes collected from Tibet, China. BMC Microbiol 16:276. https://doi.org/10.1186/s12866-016-0892-3
45. Thapa S, Prasanna R (2018) Prospecting the characteristics and significance of the phyllosphere microbiome. Ann Microbiol 68:229–245. https://doi.org/10.1007/s13213-018-1331-5
46. Thomas G, Kay WT, Fones HN (2024) Life on a leaf: the epiphyte to pathogen continuum and interplay in the phyllosphere. BMC Biol 22:168. https://doi.org/10.1186/s12915-024-01967-1

47. Turetsky MR (2003) The role of bryophytes in carbon and nitrogen cycling. Bryologist 106:395–409. https://doi.org/10.1639/05
48. Wang Q-H, Zhang J, Liu Y, et al (2022) Diversity, phylogeny, and adaptation of bryophytes: insights from genomic and transcriptomic data. J Exp Bot 73:4306–4322. https://doi.org/10.1093/jxb/erac127
49. Whitlow TH, Bassuk NL (1988) Ecophysiology of urban trees and their management—the North American experience. HortScience 23:542–546. https://doi.org/10.21273/HORTSCI.23.3.542
50. Yin X, Ang LP, Zhu R-L, et al (2025) Host-specific and environmental core bacteria differentially shape the stability and function of the *Sphagnum* phyllosphere. ISME Communications 5:. https://doi.org/10.1093/ismeco/ycaf221
51. Yin X, Martineau C, Samad A, Fenton NJ (2023) Out of site, out of mind: Changes in feather moss phyllosphere microbiota in mine offsite boreal landscapes. Front Microbiol 14:. https://doi.org/10.3389/fmicb.2023.1148157
52. Zhang C, Zhou D-F, Wang M-Y, et al (2024) Phosphoribosylpyrophosphate synthetase as a metabolic valve advances *Methylobacterium*/*Methylorubrum* phyllosphere colonization and plant growth. Nat Commun 15:5969. https://doi.org/10.1038/s41467-024-50342-9

Figures

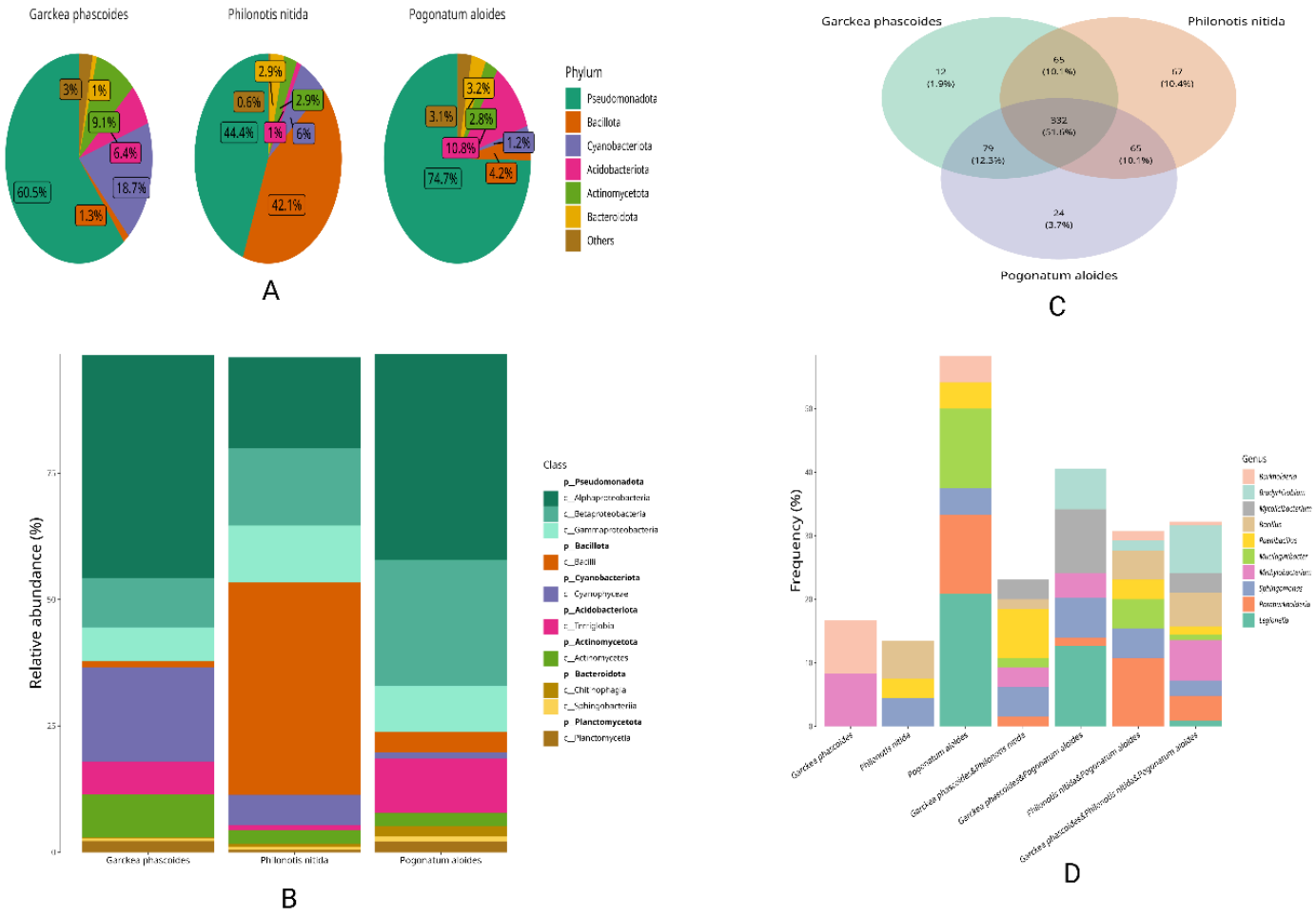

Figure 1

The bacterial communities associated with moss species, *Garckea phascoides*, *Philonotis nitida* and *Pogonatum aloides*. (A) Pie charts showing the relative abundance of dominant bacterial taxa at the Phylum level, (B) Stacked bar charts showing the relative abundance of the bacterial phyla, broken down to the class level. (C) Venn diagram showing the number and percentage of unique and shared ASV. (D) Stacked bar plots showing the frequency of the top bacterial genera found uniquely within specific moss hosts and shared across different hosts.

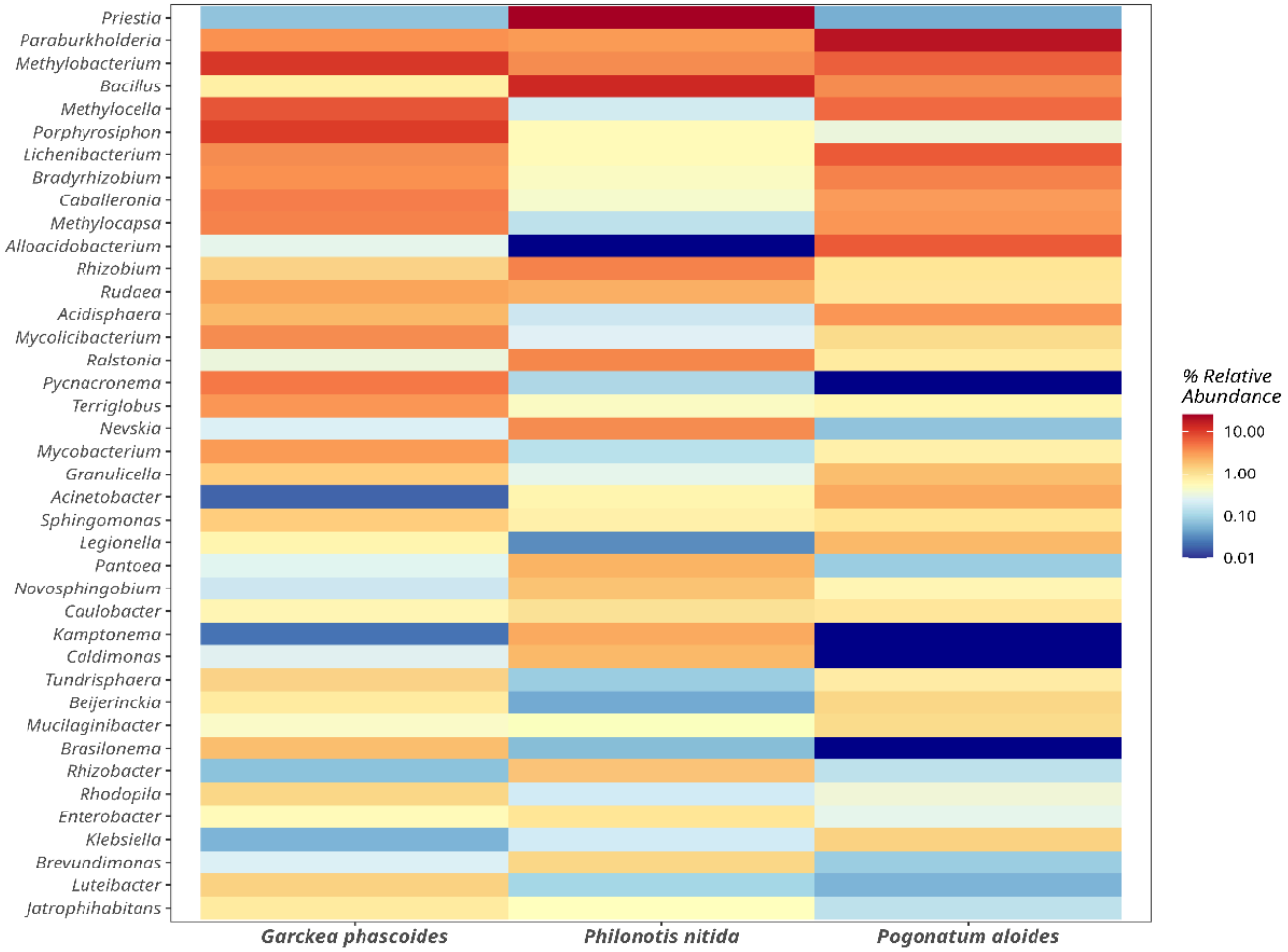

Figure 2

Heatmap illustrating the distribution and relative abundance of dominant bacterial genera across three moss species.

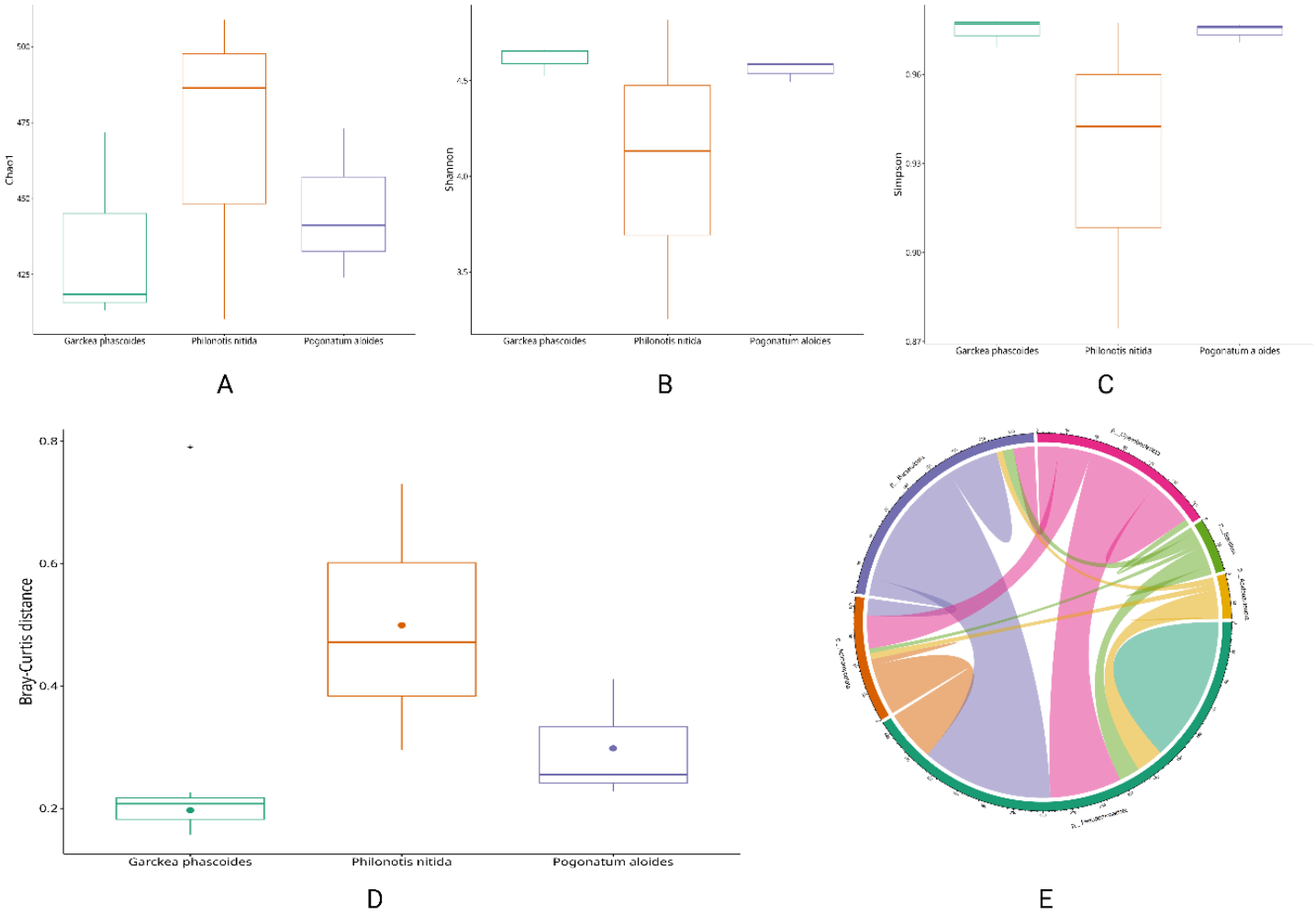

Figure 3

The diversity and interaction network of moss-associated microbiome. A-C – alpha diversity analysis of moss microbial community. The boxplots illustrate Chao1 (A), Shannon (B) and Simpson (C) indices. D – Beta diversity analysis of moss microbiome using Bray-Curtis distance. E – A chord diagram showing the interaction network of moss microbial taxa.

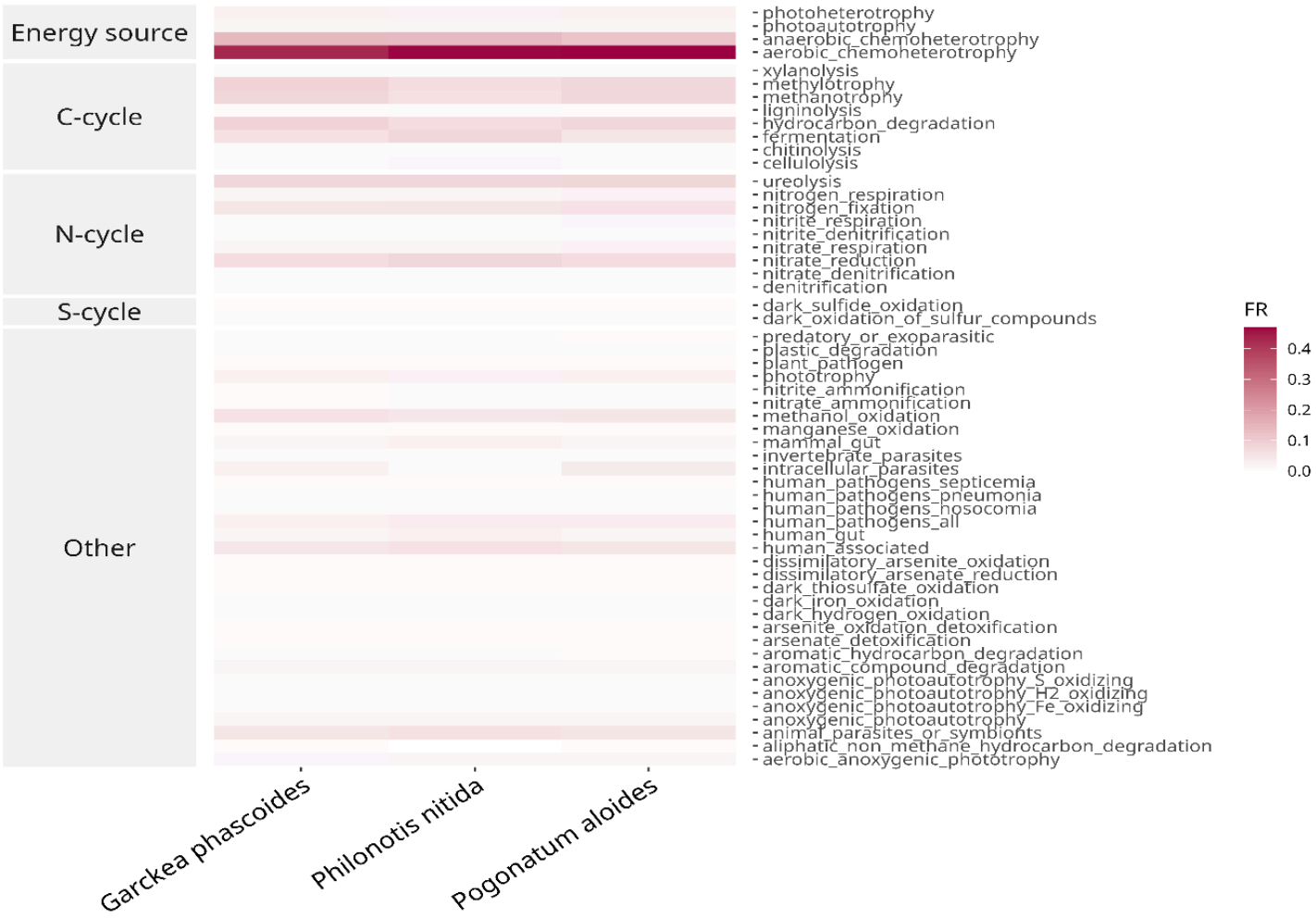

Figure 4

Heatmap showing the predicted functional profiles of moss microbial communities. Here, the color gradient represents the functional redundancy (FR) of these pathways.

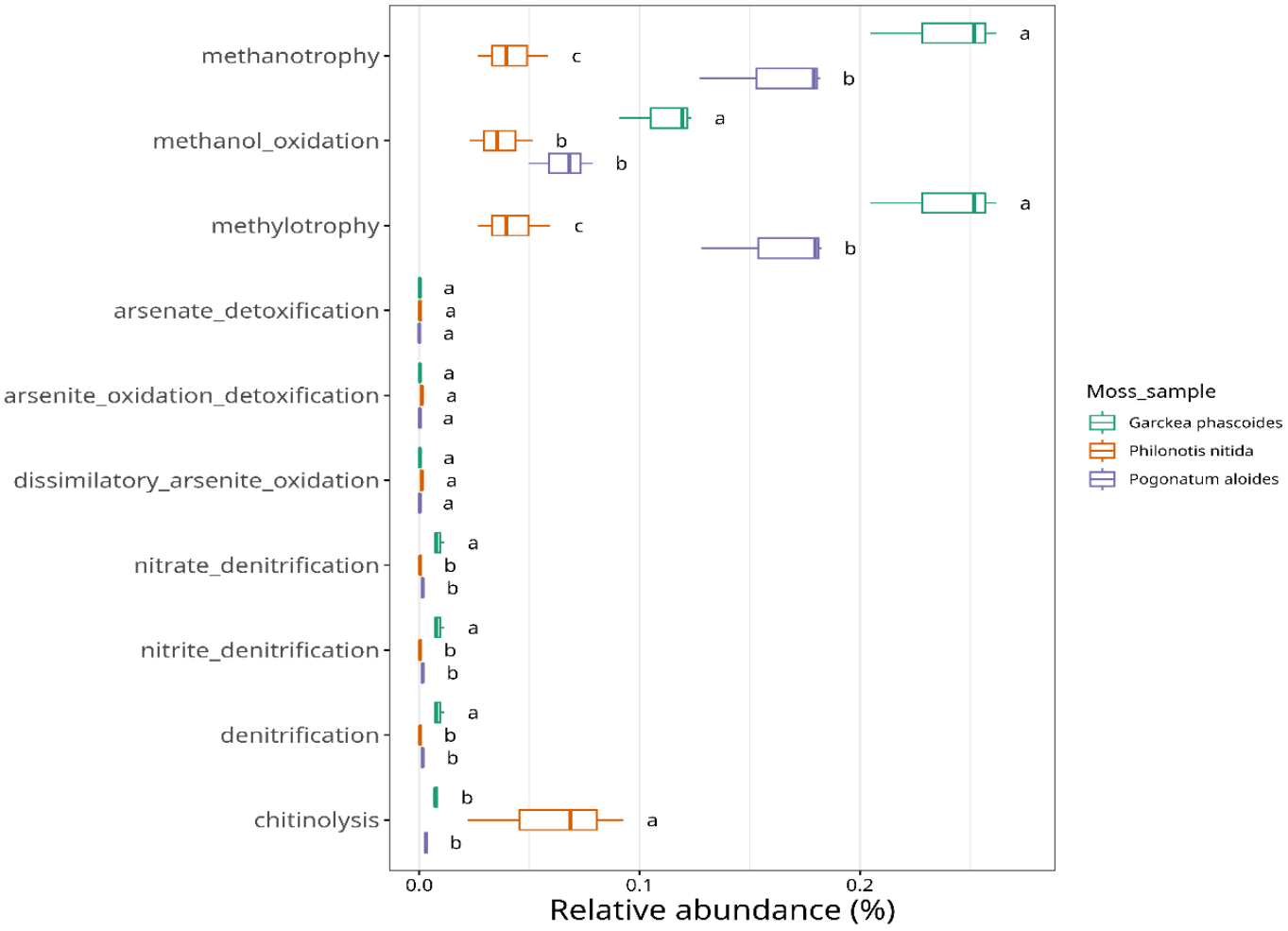

Figure 5

Boxplots showing the differential abundance of predicted functional traits of moss microbiomes.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryInformation.docx