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Original Research

Shading Reduces Root Aluminum Content and Restructures Epiphytic Microbial Communities on the Subtropical Plateau of Southwest China

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Abstract

The aim of this work is to determine the influence of one-year shading on soil physical and chemical attributes, moss leaf and root traits, and bacterial and fungal communities of the moss phyllosphere and rhizoplane on the subtropical plateau in Southwest (SW) China, as well as to explore the biological drivers of moss traits. Results show that shading significantly reduces the moss root aluminum content ($p = 0.032$). Five bacterial and nine fungal lineages are significantly enriched on moss phyllosphere under shading treatment, nine bacterial and two fungal lineages on moss phyllosphere under non-shading treatment, sixteen bacterial and eight fungal lineages on moss rhizoplane under shading treatment, and seventeen bacterial and fourteen fungal lineages on moss rhizoplane under non-shading treatment [linear discriminant analysis scores (LDA) ≥ 4, $p < 0.05$]. The relative abundance of the moss phyllosphere *Granulicella* genus ($r = -0.74$, $p = 0.014$) is inversely related to the moss root aluminum content, while that of the moss phyllosphere *Saitozyma* genus ($r = 0.72$, $p = 0.018$) is positively related. This study emphasizes the importance of the epiphytic microbiome in shaping moss traits in subtropical moss production in China.

Keywords: phyllosphere, rhizoplane, microbiome, aluminum, moss

Introduction

Moss is among the oldest nonvascular vegetation [1] and the most widely distributed plants across the planet [2]. Because of the high adaptability of moss to highly acidic and nutrient-deprived habitats [1], and its positive role in restoring and conserving degraded lands [3, 4], moss has seen increasing attention.

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Most of the previous works concentrated on the distribution of mosses and their relationship with the environment [5]. Few works analyzed the impact of shading on moss, hindering our understanding and response to the impacts of future global changes. Shade is a passive means of relieving stresses by lowering heat and increasing available resources by increasing soil water. For most mosses, lowered light is not a stress since they tolerate or desire low light contexts [6, 7]. On the one hand, increasing global shade causes shifts from mosses to vascular vegetation [8]. On the other hand, moss growers introduce extensive shading treatment to reduce water loss and the impacts of increasing drought. Although many efforts provided assistance in understanding the ecological impact of moss from the perspectives of soil physicochemical attributes, plant productivity, and microorganisms, the influence of shading on soil attributes, moss traits, and moss-related microbiomes is poorly understood.

Studies have reported the effects of mosses on soil physicochemical attributes. The presence of moss significantly alters many attributes of the soil, especially electrical conductivity, and pH [9]. Moss releases hydrogen ions to acidify the soils or releases phenolics [1], thus changing soil pH. Their morphological and architectural properties and cell traits exhibit a high capacity for water storage and retention, can conserve soils [2], and reduce runoff [10] and water loss [11]. Moss thus increases soil moisture [12]. Some studies found that moss changes the soil organic matter density [12] and has positive effects on all soil nutrients [13, 14]. For example, moss increases soil organic carbon, total nitrogen, and available nitrogen concentrations [3], and converts unavailable potassium to available potassium [14]. Moreover, moss activates aluminum and iron oxides in the soil, thereby promoting the increase in mineral-bound organic carbon [1]. Besides, the capillary action of mosses in absorbing water can minimize the losses of soil organic matter, nitrogen, and phosphorus [14, 15]. However, others confirmed that moss maintains the contents of most fundamental nutrients at constant levels, whereas it shows minimal effects on soil macronutrients, such as the contents of soil phosphorus and potassium [16]. This discrepancy suggests the necessity of additional study.

Inconsistent conclusions remain exist regarding the effect of shading on moss traits. Some studies found that species often exhibit a maximum number of branches in fairly high-light contexts; however, higher radiation can expedite moss dehydration, consequently reducing growth [17]. Others showed the positive effect of shade on the yields of mosses [7, 18, 19]. Some degree of shading increases the cover, density, and productivity of mosses [7]. This discrepancy suggests the necessity of additional study. Furthermore, carbon, nitrogen, phosphorus, potassium, iron, and aluminum are the basis of plant physiology, growth, reproduction, structure, and functioning [20, 21]. Despite the significant roles the moss traits (i.e., the carbon, nitrogen, phosphorus, potassium, aluminum, and iron contents of moss) play in moss growth, photosynthesis, and environmental adaptability [20], the effect of shading on the moss traits is still not fully understood.

Like vascular plants [22], mosses host diverse microbiomes that have a significant and essential effect on host phenotype, environment adaptability, nutrient acquisition, productivity, and reproduction [1, 23-26]. Since the microbial community of mosses is hypersensitive to their physical environments, even when planted in almost homogenous environments [27], we speculate that the shading would restructure moss-related microbiomes. Furthermore, many previous studies have shown the diversity and composition of soil- or moss-related microbiomes [25, 28-30], their roles in the development of moss, and the biotechnological capability of microbiomes [31]; however, despite the important role moss epiphytic microbiomes play in moss adaptability [25, 28], how the shading reshapes moss epiphytic microbiome, and how moss epiphytic microbiomes link to moss traits remain unclear, especially for the bacterial and fungal communities on mosses' phyllosphere and rhizoplane. Moreover, it remains unknown whether the shading changes the phyllosphere and rhizoplane microbial community composition, function, and network.

Therefore, in this study, we manipulated one-year-shading and non-shading treatments on artificially cultivated moss in the fields to determine the impacts of one-year-shading on the soil physical and chemical attributes, moss leaf and root traits, and bacterial and fungal communities on mosses' phyllosphere and rhizoplane on the subtropical plateau of SW China, and to identify the biological drivers of moss trait. The following hypotheses (H) were tested: (a) one year-shading would change the phyllosphere and rhizoplane microbial community composition, function, and network (H1); (b) rhizoplane microbial community shows a more tightly relationship with the moss trait than phyllosphere microbial community does (H2).

Material and Methods

Study Area, Design, and Sample Collection

The study area (25°50′N – 26°10′N, 107°30′E – 107°50′E, 1412 m above sea level) was in a 100 mu common garden in Dushan county of Guizhou, SW China. This area is a subtropical monsoon humid region with an annual temperature of 13.9 °C and an annual precipitation of 1570 mm. Gleyed paddy soils cover this area.

Between late May and early June 2024, five sites under the treatments of shading and non-shading (i.e., five 1 m × 2 m plots) were established in short-term (one year) shading and non-shading areas, respectively. The shade was achieved by setting up shading nets, which can block 85% of the sunlight. First, in the 1m× 1 m subplot, 500 g fresh moss green part (leaves) and the yellow part (pseudo roots) were collected separately in sterile bags, stored under ice bags, and sent to Yangling Xinhua Ecological Technology Co., Ltd (Yangling, China) for testing the bacterial and fungal communities attached to the moss surface (i.e., phyllosphere and rhizoplane). To avoid cross-contamination, separate ring knives and sterile gloves were employed [32]. In the adjacent 1m × 1m subplot, the green part (leaves) and yellow part (pseudo roots) of all mosses were collected in sterile bags, killed at 105 ℃ and dried at 65 ℃ to constant weight, crushed by a grinder, sieved through a 2mm sieve, and used to determine plant traits. Three soil cores were collected using ring knives at each site. One was used to determine soil bulk density and soil porosity [32], while the other two were used to determine soil water holding capacity. Ca. 1kg 0-5 cm soil was collected for the assay of soil physicochemical attributes.

Assay of Soil Physicochemical Attributes and Moss Traits

This part was performed by Yangling Xinhua Ecological Technology Co., Ltd (China). Briefly, pH was tested using a pH meter [33]. Soil bulk density, total porosity, capillary porosity, and non-capillary porosity were tested [34] using an oven at 105 °C and an electronic balance (Shanghai Baiyinghengqi Corporation, China). Soil organic carbon content was tested using an elemental analyzer, available nitrogen content was analyzed by the alkali diffusion approach [35], available phosphorus content was tested using the sodium bicarbonate extraction-molybdenum antimony anti-colorimetric method [36], available potassium content was tested by the flare photometer method [32], available aluminum content was determined by the Hac-NaAc extraction and UV spectrophotometer and available iron content was determined by an atomic absorption spectrophotometer. Moss carbon content was tested using the potassium dichromate concentrated sulfuric acid external heating method [37], moss nitrogen content was determined using the H_2SO_4-H_2O_2 digestion and indigo phenol blue colorimetric method, moss phosphorus content was determined using the HNO_3-$HClO_4$ digestion method, moss potassium content was tested using the H_2SO_4-H_2O_2 digestion and flame photometry method, moss aluminum content was determined using the Nitric acid-perchloric acid digestion method, and moss iron content was determined using HNO_3-$HClO_4$ digestion method.

DNA (Deoxyribonucleic acid) Extraction, Amplicon Sequencing and Bioinformatics Analysis

This part was carried out by Novogene Biotech. Co., Ltd (CN). The method is available in supplementary documents. DNA isolation kits were applied to extract DNA. 16S rRNA and ITS genes of distinct regions (16SV3- V4 and ITS1-5F) were amplified. DADA2 (Divisive Amplicon Denoising Algorithm 2) was used to denoise [Version (Quantitative Insights Into Microbial Ecology) QIIME2-202202] for obtaining Amplicon Sequence Variants (ASVs). The bacteria and fungi were taxonomically named through QIIME2 with Silva and Unite Databases, respectively. The Chao1, Pielou evenness, Simpson, and Good coverage were calculated using QIIME2. To compare the differences between treatments, principal coordinate analysis was performed using "ade4" package and "ggplot2" package in R (v4.0.3). LEfSe (linear discriminant analysis effect size) was used to identify the indicators with linear discriminant analysis (LDA) scores ≥4 and statistically significant differences ($p < 0.05$) among treatments [35]. PICRUSt2 (Phylogenetic Investigation of Communities by Reconstruction of Unobserved States, V2.3.0) and FunGuild were applied to annotate the bacterial and fungal community's functions. A bar chart and heat map with clusters were used to display the relative abundance through the "ggplot2" package and the "pheatmap" function. The network was established using the "igraph" package with removing the connections with Spearman correlation coefficient < 0.6 and connections with node abundance less than 0.005%. The raw data on bacterial (Accession number: SAMN43039897—SAMN43039878) and fungal (Accession number: SAMN43039877—SAMN43039858) microbiomes were uploaded to the National Center for Biotechnology Information (NCBI) in the name of PRJNA1144507.

Statistical Analysis

Wilcoxon test or Kruskal-Wallis test was applied to test the significance of difference [32] in the soil physicochemical attributes, moss traits, and microbial community diversity. To explore the relationships between moss traits and microbial properties, Pearson correlation analysis was applied using the "psych" and "igraph" packages in R v3.6.1. $p < 0.05$ suggests significant.

Results and Discussion

Shading Marginally Altered Soil Physicochemical Properties but Significantly Reduced Moss Root Aluminum

Shading treatment slightly changed the soil's physical and chemical properties (Wilcoxon test, p = 0.15-1, Fig. 1). The shading reduced soil and water loss [38], this might increase the soil organic carbon [3] (Fig. 1g). The shading increased nitrogen mineralization and nitrification rate and increased inorganic nitrogen [39]; this might increase soil available nitrogen [3] (Fig. 1h). Moss can release H+ to acidify soils (Wang et al. 2024), convert unavailable potassium to available potassium

[14], and activate soil aluminum and iron oxides [1]. The shading might enhance this effect, thus increasing soil-available potassium (Fig. 1j), soil-available aluminum (Fig. 1k), and soil-available iron (Fig. 1m). Our evidence supported that the slightly positive effect of shading on soil chemical properties, although this needs further study. Nevertheless, further research is still needed on the mechanism by which shading decreases soil total porosity, soil non-pore porosity, soil pore porosity, and soil water holding capacity, and increases soil bulk density. Consistent with previous findings, shading increased the carbon and nitrogen content of dry mass [40] (Fig. 2a-d).

Compared with the non-shading, the shading did not significantly change the moss leaf carbon, moss root carbon, moss leaf nitrogen, moss root nitrogen, moss leaf phosphorus, moss root phosphorus, moss leaf potassium, moss root potassium, moss leaf aluminum, moss leaf iron, and moss root iron (Wilcoxon test, *p* = 0.056-1), however, shading significantly reduced the moss root aluminum content (Wilcoxon test, *p* = 0.032). Many studies have confirmed that aluminum in acidic soils has toxic effects on plants [41] and is a predominant cause restricting plant productivity in acidic soil [42]. The increase in soil available aluminum (Fig. 1k) might threaten the growth of moss; however, the shading marginally reduced the moss leaf aluminum content (Fig. 2i) and significantly reduced root aluminum content (Fig. 2j), implying that moss had strong adaptability to soil aluminum.

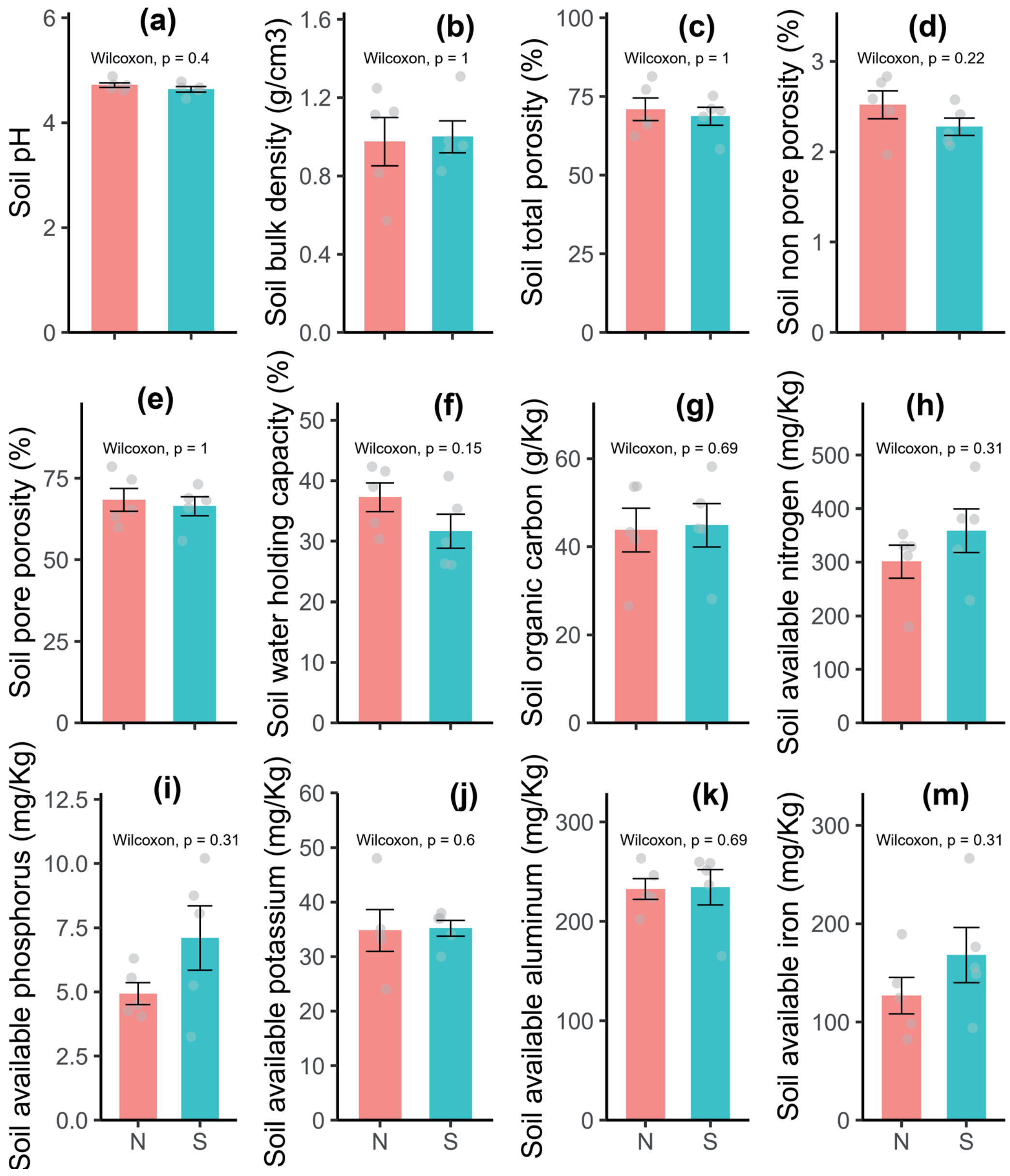

Fig. 1. The bar plots with points showing the effect of shading on soil physicochemical attributes (mean ± standard error). Wilcoxon, Wilcoxon test; N, non-shading; S, shading.

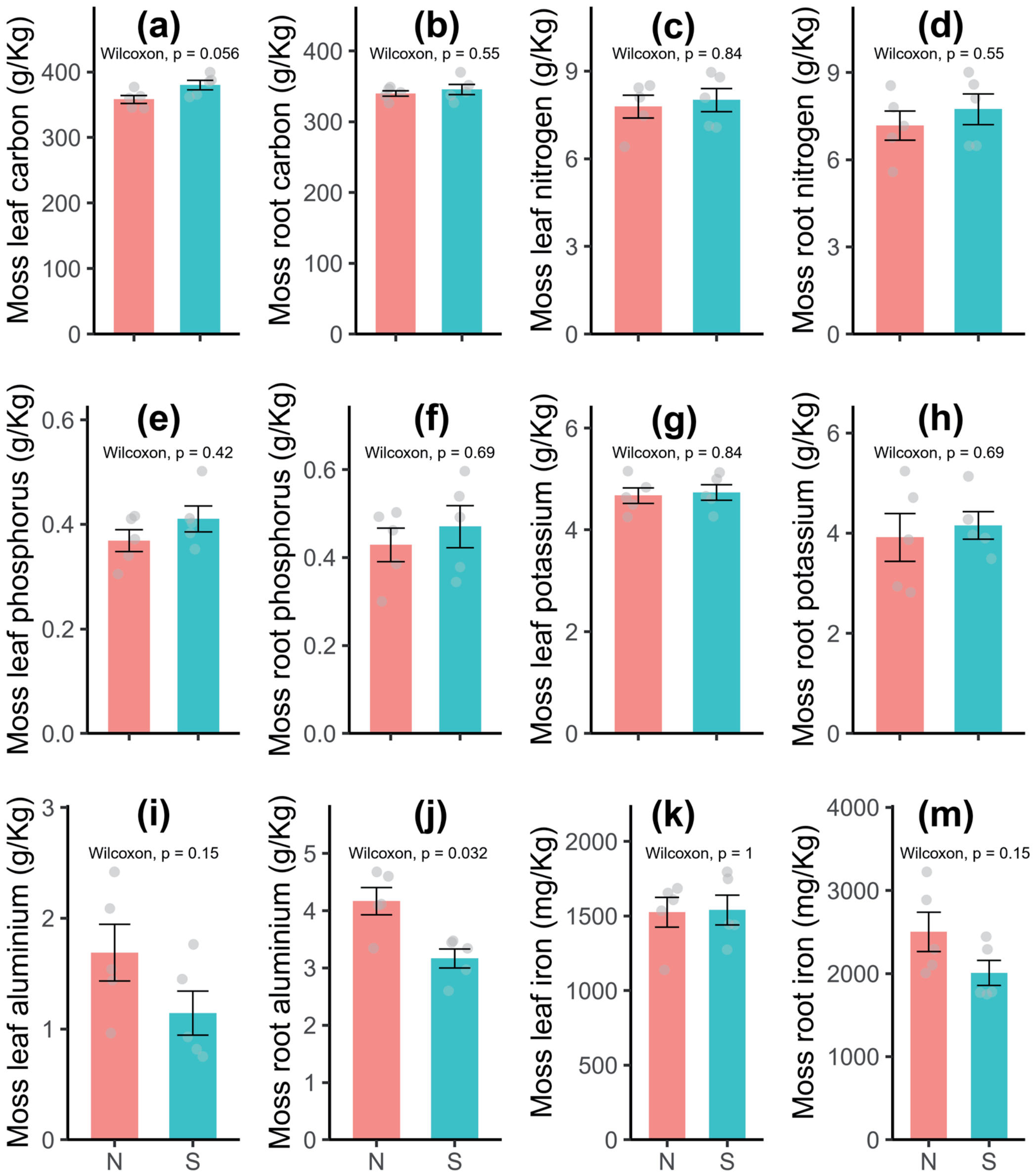

Fig. 2. The bar plots with points showing the effect of shading on the moss traits (mean ± standard error). Wilcoxon, Wilcoxon test; N, non-shading; S, shading.

Shading Restructures Epiphytic Microbial Community

All good coverage was > 99.7% (Fig. S1), indicating an overall good sampling and sequencing depth [35, 43]. The chao1 (p = 0 – 0.0003), pielou evenness (p = 0 – 0.0003), Simpson (p = 0 – 0.0003) of rhizoplane bacterial community and the chao1 (p = 0.0003 – 0.0125) of rhizoplane fungal community were significantly higher than those of phyllosphere community (Fig. 3, Table S1). Although the shading increased the Chao1, Pielou evenness, Simpson of phyllosphere bacterial and fungal community and decreased the rhizoplane fungal community, compared with the non-shading, these changes were found to be insignificant (p = 0.2640 – 0.9208). In a word, the shading did not significantly change the phyllosphere and rhizoplane microbial community diversity. This result is similar to the effect of shading on the diversity of grass rhizosphere bacteria [44].

Overall, principal co-ordinates analysis (Fig. 4) suggested that there was a clear separation between the phyllosphere and rhizoplane microbial community composition, but there was no separation between microbial community composition under shading treatment and non-shading treatment, regardless of the phyllosphere or rhizoplane microbial community composition. At the phylum level, the bar chart showed that the shading increased the relative abundance of phyllosphere *Proteobacteria*, *Acidobacteriota*, *Verrucomicrobiota*, *Bacteroidota*, the relative abundance of rhizoplane *Firmicutes*, *Verrucomicrobiota*, *Chloroflexi*, the relative abundance of rhizoplane

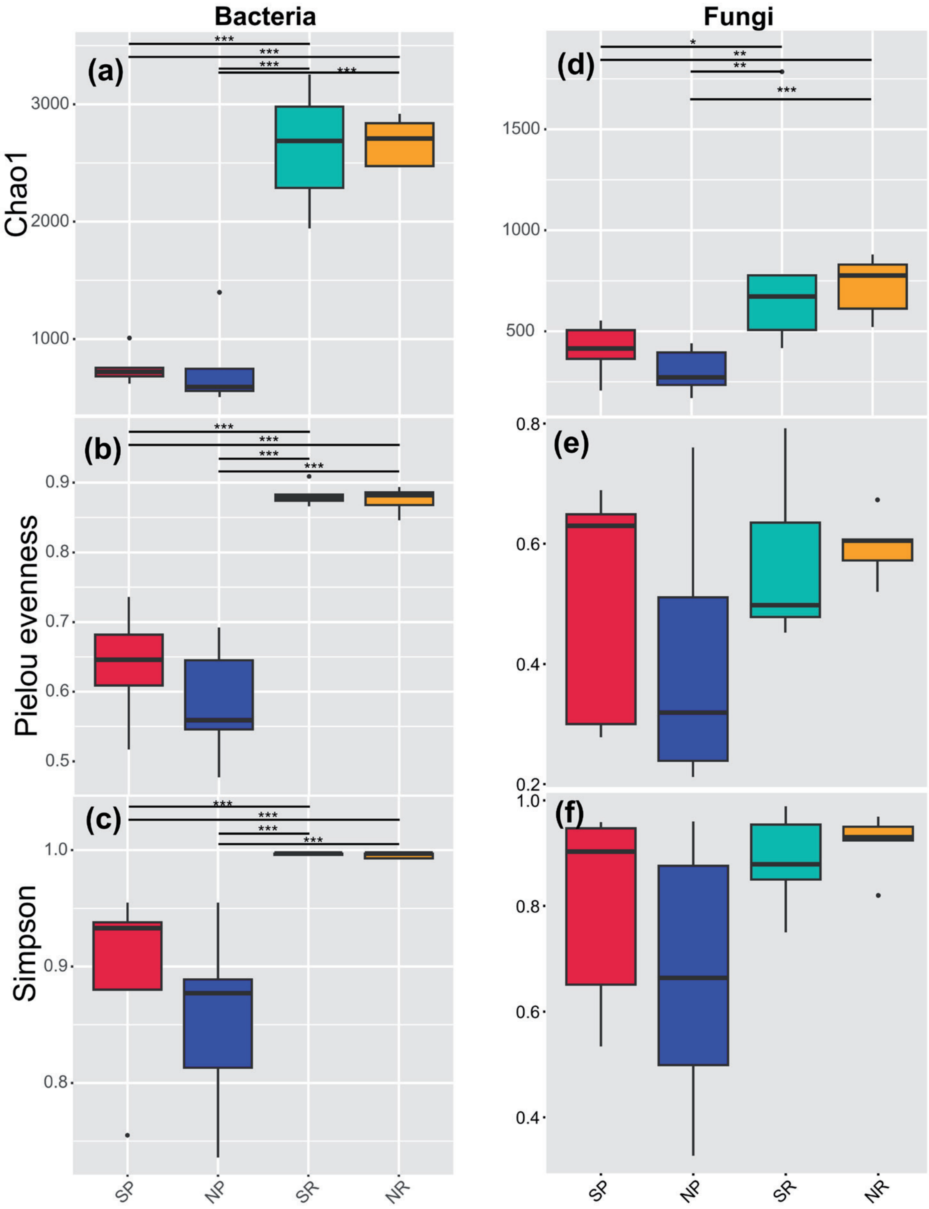

Fig. 3. The boxplot showing the effect of shading on the phyllosphere and rhizoplane bacterial (a-c) and fungal (d-f) community diversity. SP, moss phyllosphere under shading treatment; NP, moss phyllosphere under non-shading treatment; SR, moss rhizoplane under shading treatment; NR, moss rhizoplane under non-shading treatment; *, Kruskal-Wallis test $p < 0.05$; **, Kruskal-Wallis test $p < 0.01$; ***, Kruskal-Wallis test $p < 0.001$; non-significant (Kruskal-Wallis test $p > 0.05$) differences were not shown.

Ascomycota, and the relative abundance of phyllosphere *Basidiomycota*; however, the shading decreased the relative abundance of phyllosphere *Firmicutes*, *Actinobacteriota*, the relative abundance of rhizoplane *Cyanobacteria*, *Proteobacteria*, the relative abundance of phyllosphere *Ascomycota*, and the relative abundance of rhizoplane *Glomeromycota*. Previous studies showed that moss-related bacterial communities are dominated by the phyla *Proteobacteria* and *Actinobacteria* [25, 26, 28, 45, 46]. In this study, this situation was only found in the rhizoplane communities of moss, the phyla *Proteobacteria* and *Cyanobacteria*, rather than the phyla *Proteobacteria* and *Actinobacteria* dominated the phyllosphere bacterial communities of moss. *Cyanobacteria,* as epiphytes of mosses, are the dominant nitrogen-fixing organisms [47]; however, additional works are needed to test the effect of these differences on moss. Moreover, consistent with the previous findings [48, 49], the phyla *Ascomycota* and *Glomeromycota* dominated the phyllosphere and rhizoplane fungal communities of moss (Fig. 5c). Previous studies suggested that host phylogeny has a strong effect on the related microbiome and that niches also play key roles if the hosts are phylogenetically more similar [25, 46]. The present work showed a more important role of the moss compartment niche in structuring the moss epiphytic microbial community. Besides, this study provided more information than before, showing that the shading changed the relative abundance of the bacterial and fungal-dominated phyla (Fig. 5a, c).

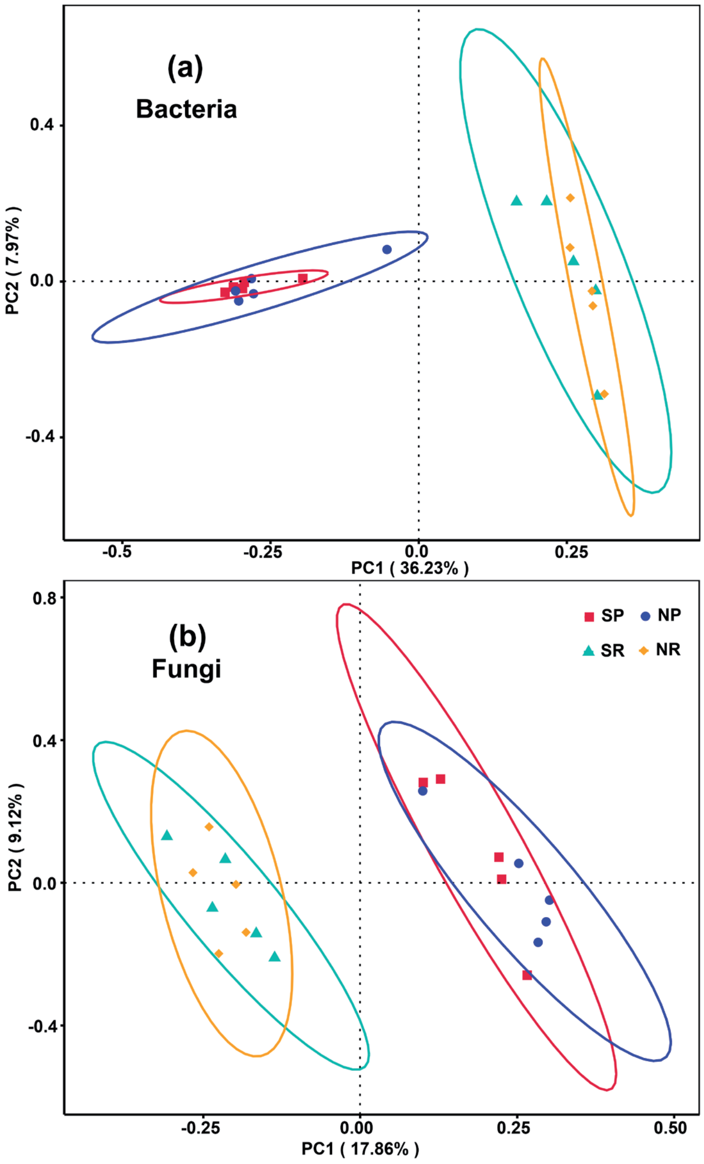

Fig. 4. Principal coordinates analysis (PCoA) showing the effect of shading on the phyllosphere and rhizoplane microbial community composition. SP, moss phyllosphere under shading treatment; NP, moss phyllosphere under non-shading treatment; SR, moss rhizoplane under shading treatment; NR, moss rhizoplane under non-shading treatment.

Restructuring the epiphytic microbial community by the shading not only occurred at the phyla level but also at the genus level (Fig. 5b, d). The heatmap diagram (Fig. 5) showed that the shading changed the relative abundance of the phyllosphere and rhizoplane bacterial and fungal genus. At the lineage level, LEfSe analysis of the bacterial community (Fig. 6a) found that five lineages were significantly enriched on moss phyllosphere under shading treatment, nine lineages on moss phyllosphere under non-shading treatment, sixteen lineages on moss rhizoplane under shading treatment, seventeen lineages on moss rhizoplane under non-shading treatment (LDA score ≥ 4, $p< 0.05$). LEfSe analysis of the fungal community (Fig. 6b) found that nine lineages were significantly enriched on moss phyllosphere under shading treatment, two lineages on moss phyllosphere under non-shading treatment, eight lineages on moss rhizoplane under shading treatment, fourteen lineages on moss rhizoplane under non-shading treatment (LDA score ≥ 4, $p< 0.05$). Collectively, partly in line with our first hypothesis (H1), the shading changed the phyllosphere and rhizoplane microbial community composition. The heatmap diagram (Fig. 7) showed that the shading changed the relative abundance of the phyllosphere and rhizoplane bacterial and fungal community functions. For bacterial communities, there was a clear distribution pattern of the abundance of genes encoding enzymes in the phyllosphere and rhizoplane (Fig. 7a); for fungal communities, the fungal mode distribution pattern differed among phyllosphere and rhizoplane, and shading and non-shading treatments (Fig. 7b). Besides, divergent network patterns were found (Fig. S2a-h), suggesting that shading changed the microbial network [50]. Collectively, the shading

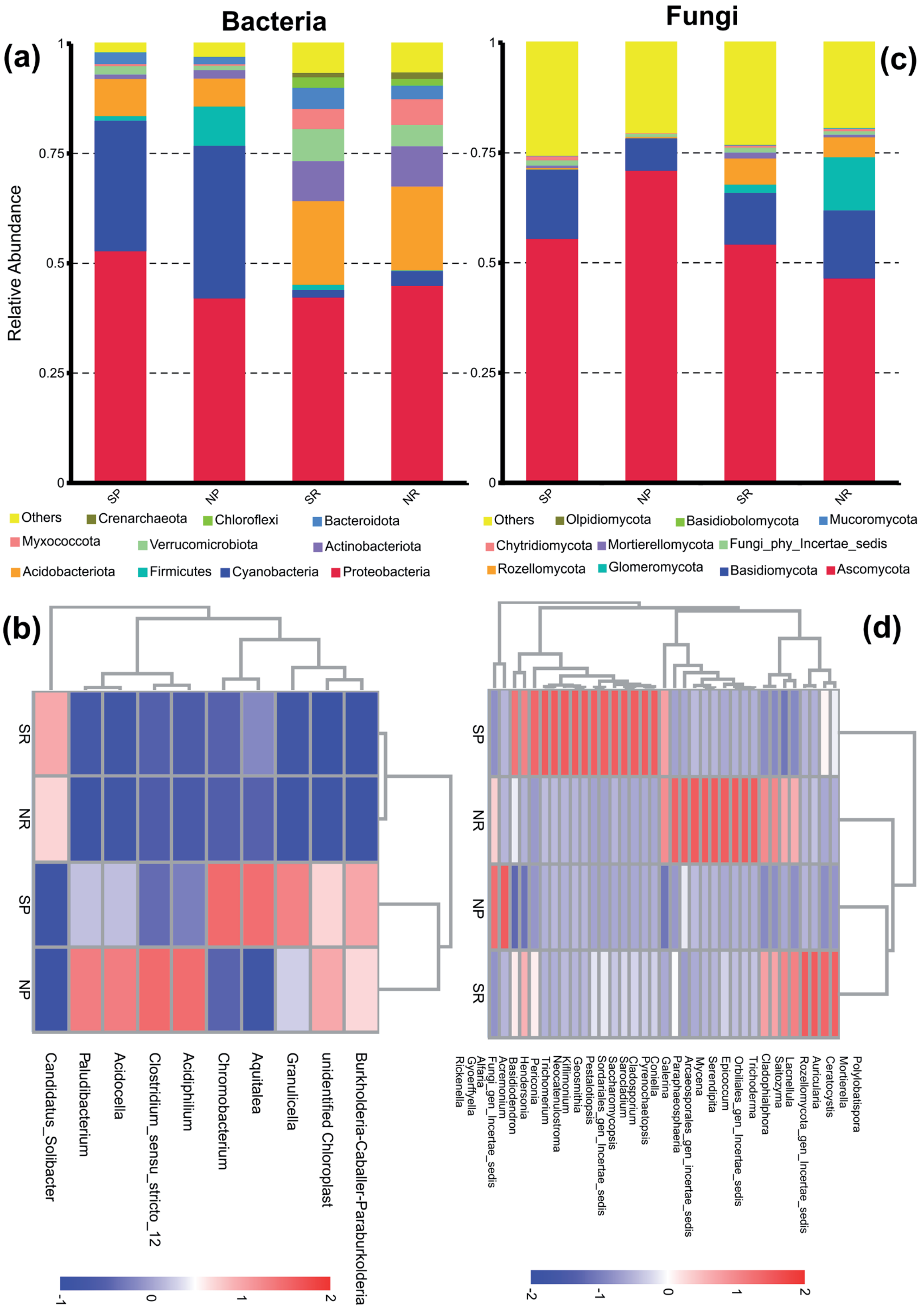

Fig. 5. Bar chart (a, c) and heatmap (b, d) showing the effect of shading on the phyllosphere and rhizoplane bacterial (a, b) and fungal (c, d) community composition at the phylum (a, c) and genus (b, d) levels, respectively. SP, moss phyllosphere under shading treatment; NP, moss phyllosphere under non-shading treatment; SR, moss rhizoplane under shading treatment; NR, moss rhizoplane under non-shading treatment.

changed the phyllosphere and rhizoplane microbial community composition, function, and network, supporting our first hypothesis (H1). These alterations may have functional implications. Revealing their functional abilities is decisive for understanding their ecological significance [26]. Earlier research has shown the functions of moss-associated microbes. For instance, moss-associated microbes fix nitrogen, oxidize methane, and contribute to the decomposition of organic matter [51]. Moss-associated diazotrophs are assessed to supply more than 40% of nitrogen input to peatlands with a high accumulation of fixed nitrogen in vegetation biomass

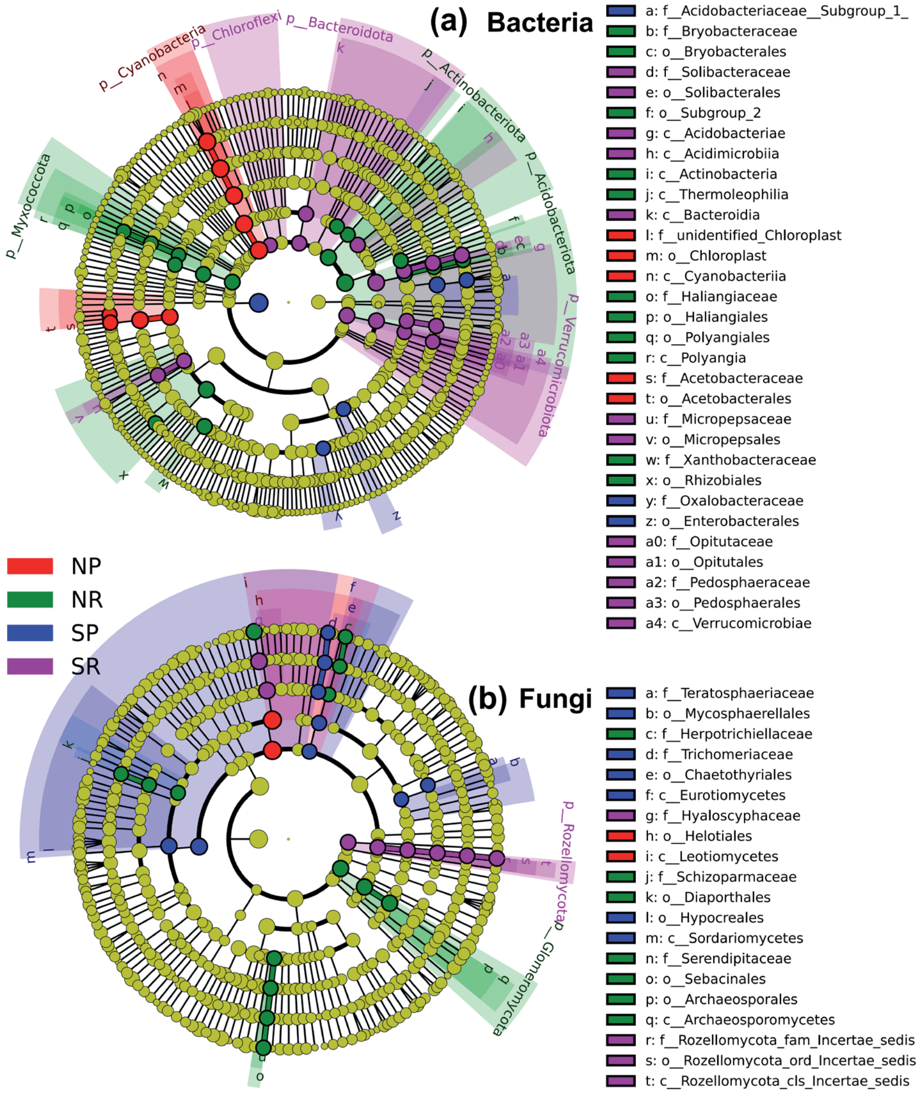

Fig. 6. Cladogram showing the phylogenetic distribution of the phyllosphere and rhizoplane bacterial (a) and fungal (b) lineages and indicator with linear discriminant analysis scores (LDA) of ≥ 4 and $p < 0.05$ under shading and non-shading treatments. SP, moss phyllosphere under shading treatment; NP, moss phyllosphere under non-shading treatment; SR, moss rhizoplane under shading treatment; NR, moss rhizoplane under non-shading treatment.

[52]. Moss-associated methanotrophic bacteria can convert methane to CO_2 [52]. In this study, the genera *Burkholderia* [46, 53], *Trichoderma* [47] (Fig. 5d), and *Granulicella* [46] (Fig. 5b) were typical inhabitants of moss. Most fungi in peatlands are saprophytes that participate in the decay of organic matter [48]. Over three hundred species of *Ascomycota* are found to parasitize mosses [30]. *Mortierella* and *Cladosporium* are opportunistic plant pathogens [30]. *Saitozyma* has a lignin-degrading capacity [54]. The alterations in the relative abundance of the bacterial and fungal genus would have significance for the elemental cycling, moss traits, and health.

Linking Phyllosphere and Rhizoplane Microbial Community to Moss Root Aluminum

In the past, the growth and development of moss were influenced by soil water content, light and temperature, and nutrient availability [7]. Relationships between moss and fungus were long supposed to be uncommon [55]. However, in recent years, researchers have studied the feasibility of rapid artificial cultivation and restoration of moss and have gained some important findings [7]. For instance, moss manganese, iron, and molybdenum contents were positively related to moss-related soil biological nitrogen fixation and diazotrophic community [56]. In the present study, the bacterial and fungal community diversity (r = -0.3356 – 0.1557, p = 0.3431 – 0.9532, Table S2) and functions (r = -0.5505 – 0.5017, p = 0.09919 – 0.9918, Table S3) of the phyllosphere and rhizoplane were not significantly related to the moss

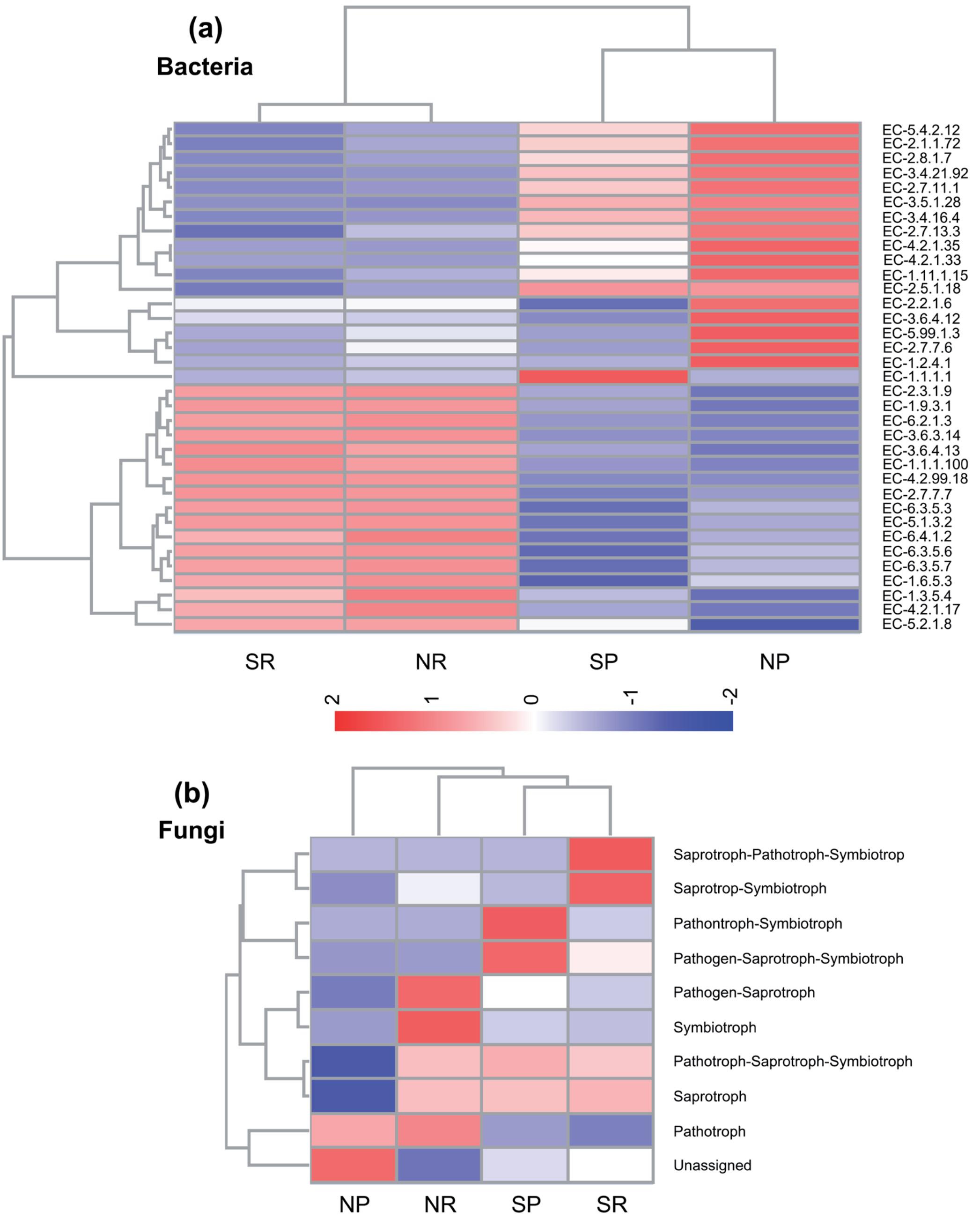

Fig. 7. Heatmap diagram showing the effect of shading on the phyllosphere and rhizoplane microbial community function. SP, moss phyllosphere under shading treatment; NP, moss phyllosphere under non-shading treatment; SR, moss rhizoplane under shading treatment; NR, moss rhizoplane under non-shading treatment.

root aluminum content. However, the higher relative abundance of the phyllosphere *Granulicella* genus (bacteria, Fig. 5b) and the lower relative abundance of the phyllosphere *Saitozyma* genus (fungi, Fig. 5d) under shading significantly facilitated the significant decline in the moss root aluminum content (Fig. 8, Table S4). A previous study showed that increasing temperature decreased the relative abundance of *Granulicella* [57]. The shading reduced temperature, which resulted in the higher relative abundance of the phyllosphere *Granulicella* genus under the shading. *Granulicella* is capable of utilizing various organic compounds [58] and degrading plant polymers [59] and toxins produced by the plant pathogenic fungus [60]. It is a potentially beneficial plant and a biocontrol microorganism [61]. Thus, the shading-induced higher relative abundance of the phyllosphere *Granulicella* genus was beneficial for moss. Furthermore, *Saitozyma*, a typical soil-borne yeast, was reported to suppress acetic acid fermentation [62, 63], and its occurrence was strongly associated with a high Al^{3+} [64]. The shading-induced lower relative abundance of the phyllosphere *Saitozyma* genus (fungi, Fig. 5d) was beneficial for moss. Ultimately, both decreased the moss root aluminum content growing in the acid soils. This finding has not been reported previously but rejects our second hypothesis (H2). The

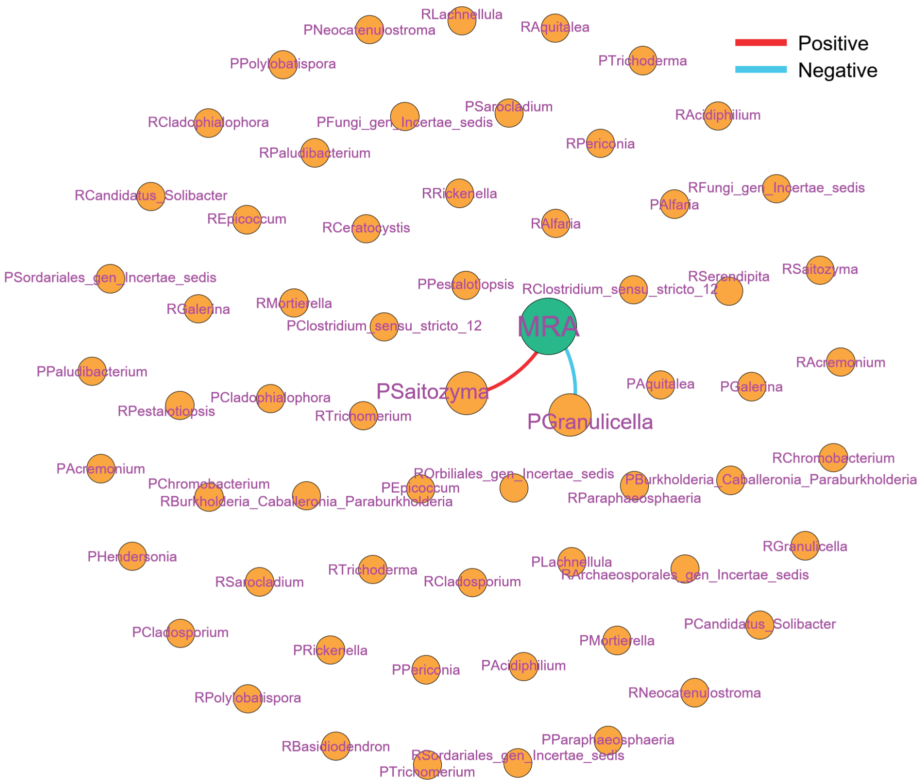

Fig. 8. Pearson correlation analysis showing the significant ($p < 0.05$) relationship between the moss root aluminum (MRA) and the relative abundance of phyllosphere (P) and rhizoplane (R) bacterial and fungal genus. The insignificant ($p > 0.05$) relationship was not displayed.

phyllosphere genus showed a tighter relationship with the moss trait than the rhizoplane genus did. This study emphasized the importance of the genus *Granulicella* and Saitozyma in shaping moss traits and updated the current knowledge regarding the positive interactions between moss and microbiome. However, the cause-and-effect mechanisms behind it remain understudied.

Conclusion

One year-shading sightly changed the soil physicochemical properties and most of the moss traits, whereas it significantly reduced the moss root aluminum content. The shading restructured the phyllosphere and rhizoplane microbial community composition, function, and network. The relative abundance of the *Granulicella* genus and *Saitozyma* genus of the moss phyllosphere were positively and negatively related to the moss root aluminum content. These findings will be useful for future improvements in moss production in southwest China.

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Conflict of Interest

All authors confirm no conflict of interest.

References

1. WANG Y., XUE D., CHEN X., QIU Q., CHEN H. Structure and functions of endophytic bacterial communities associated with Sphagnum mosses and their drivers in two different nutrient types of peatlands. Microbial Ecology, **87** (1), **2024**.

2. MENG W., DAI Q., REN Q., TU N., LENG T. Ecological stoichiometric characteristics of soil-moss C, N, and P in restoration stages of karst rocky desertification. PloS one, **16** (6), e0252838, **2021**.
3. BAO T., ZHAO Y., GAO L., YANG Q., YANG K. Moss-dominated biocrusts improve the structural diversity of underlying soil microbial communities by increasing soil stability and fertility in the Loess Plateau region of China. European Journal of Soil Biology, **95**, 103120, **2019**.
4. BU C., ZHANG K., ZHANG C., WU S. Key factors influencing rapid development of potentially dune-stabilizing moss-dominated crusts. PLoS one, **10** (7), e0134447, **2015**.
5. LI Z.-K., WU Q.-M., WANG Z.-H., ZZHANG H.-H. Diversity and ecological characteristics of bryophytes from peak cluster under the background of Karst Urban. Bulletin of Botanical Research, **38** (3), 433, **2018**.
6. ALPERT P., OECHEL W.C. Comparative patterns of net photosynthesis in an assemblage of mosses with contrasting microdistributions. American Journal of Botany, **74** (12), 1787, **1987**.
7. BU C., LI R., WANG C., BOWKER M.A. Successful field cultivation of moss biocrusts on disturbed soil surfaces in the short term. Plant Soil, **429**, 227, **2018**.
8. BONNETT S.A.F., OSTLE N., FREEMAN C. Short-term effect of deep shade and enhanced nitrogen supply on Sphagnum capillifolium morphophysiology. Plant Ecology, **207** (2), 347, **2009**.
9. BALL B.A., VIRGINIA R.A. The ecological role of moss in a polar desert: implications for aboveground–belowground and terrestrial–aquatic linkages. Polar Biology, **37**, 651, **2014**.
10. BU C., WU S., HAN F., YANG Y., MENG J. The combined effects of moss-dominated biocrusts and vegetation on erosion and soil moisture and implications for disturbance on the Loess Plateau, China. Plos one, **10** (5), **2015**.
11. SAND-JENSEN K., HAMMER K.J., MADSEN-ØSTERBYE M., DENCKER T., KRAGH T. Positive interactions between moss cushions and vascular plant cover improve water economy on Öland's alvar, Sweden. Botany, **93** (3), 141, **2015**.
12. TURETSKY M.R. The role of bryophytes in carbon and nitrogen cycling. The Bryologist, **106** (3), 395, **2003**.
13. CHENG C., LI Y., LONG M., GAO M., ZHANG Y., LIN J., LI X. Moss biocrusts buffer the negative effects of karst rocky desertification on soil properties and soil microbial richness. Plant Soil, **475** (1-2), 153, **2020**.
14. SHEN J.C., ZHANG Z.H., LIU R., WANG Z.H. Ecological restoration of eroded karst utilizing pioneer moss and vascular plant species with selection based on vegetation diversity and underlying soil chemistry. International Journal of Phytoremediation, **20** (14), 1369, **2018**.
15. WU Y.H., CHENG G.D., GAO Q. Bryophyte's ecology functions and its significances in revegetation. Journal of Desert Research, **23** (3), 215, **2003**.
16. SIWACH A., KAUSHAL S., BAISHYA R. Effect of Mosses on physical and chemical properties of soil in temperate forests of Garhwal Himalayas. Journal of Tropical Ecology, **37** (3), 126, **2021**.
17. ARIEL B., MARKUS P. Effects of light and nitrogen on morphological plasticity of the moss Calliergonella cuspidata. Oikos, **96**, 355, **2002**.
18. SCANDRETT E., GIMINGHAM C.H. Experimental investigation of bryophyte interactions on a dry heathland. The Journal of Ecology, **77** (3), 838, **1989**.
19. MA J.Z., BU Z.J., ZHENG X.X., LI S.L., ZENG J., ZHAO G.L. Effects of shading on two sphagnum species growth and their interactions. The Journal of Applied Ecology, **23** (2), 357, **2012**.
20. LI Y.G., ZHOU X.B., LU Y., ZHANG Y.M. Moss C, N, P and K stoichiometry and their relationships are related to soil nutrients and environment in a temperate desert of central Asia. Journal of Plant Ecology, **16** (3), rtac070, **2023**.
21. OFOE R., THOMAS R.H., ASIEDU S.K., WANG-PRUSKI G., FOFANA B., ABBEY L. Aluminum in plant: Benefits, toxicity and tolerance mechanisms. Frontiers in Plant Science, **13**, **2023**.
22. HOLLAND-MORITZ H., STUART J., LEWIS L.R., MILLER S., MACK M.C., MCDANIEL S.F., FIERER N. Novel bacterial lineages associated with boreal moss species. Environmental Microbiology, **20** (7), 2625, **2018**.
23. MARAIST C.A. Effect of microbes on the growth and physiology of the Dioecious Moss, Ceratodon purpureus Portland State University, **2018**.
24. WANG P., DING L., ZOU C., ZHANG Y., WANG M. Rhizosphere element circling, multifunctionality, aboveground productivity and trade-offs are better predicted by rhizosphere rare taxa. Frontiers in Plant Science, **13**, **2022**.
25. WANG S., TANG J.Y., MA J., LI X.D., LI Y.H. Moss habitats distinctly affect their associated bacterial community structures as revealed by the high-throughput sequencing method. World Journal of Microbiology and Biotechnology, **34**, 1, **2018**.
26. BAEV V., GECHEVA G., APOSTOLOVA E., GOZMANOVA M., YAHUBYAN G. Exploring the metatranscriptome of bacterial communities of two moss species thriving in different environments—terrestrial and aquatic. Plants, **13** (9), 1210, **2024**.
27. JEAN M., HOLLAND-MORITZ H., MELVIN A.M., JOHNSTONE J.F., MACK M.C. Experimental assessment of tree canopy and leaf litter controls on the microbiome and nitrogen fixation rates of two boreal mosses. New Phytologist, **227** (5), 1335, **2020**.
28. MA J., TANG J.Y., WANG S., CHEN Z.L., LI X.D., LI Y.H. Illumina sequencing of bacterial 16S rDNA and 16S rRNA reveals seasonal and species-specific variation in bacterial communities in four moss species. Applied Microbiology and Biotechnology, **101**, 6739, **2017**.
29. HUANG T., LIU W., LONG X.E., JIA Y., WANG X., CHEN Y. Different responses of soil bacterial communities to nitrogen addition in moss crust. Frontiers in Microbiology, **12**, 665975, **2021**.
30. ROSA L.H., DE SOUSA J.R.P., DE MENEZES G.C.A., DA COSTA COELHO L., CARVALHO-SILVA M., CONVEY P., CÂMARA P.E.A.S. Opportunistic fungi found in fairy rings are present on different moss species in the Antarctic Peninsula. Polar Biology, **43** (5), 587, **2020**.
31. OPELT K., BERG G. Diversity and antagonistic potential of bacteria associated with bryophytes from nutrient-poor habitats of the Baltic Sea Coast. Applied and Environmental Microbiology, **70** (11), 6569, **2004**.
32. DING L., CHEN H., WANG M., WANG P. Shrub expansion raises both aboveground and underground multifunctionality on a subtropical plateau grassland: coupling multitrophic community assembly to multifunctionality and functional trade-off. Frontiers in Microbiology, **14**, 1339125, **2024**.

33. DING L., CHEN H., WEI X., QIN T., LEI X., LI J., ZHANG Y., ZHAO L., WANG P. Soil cations explain the variation of soil extracellular activities and microbial elemental limitations on subtropical grassland, China. Polish Journal of Environmental Studies, **33** (4), 4061, **2024**.
34. LI W., TIAN Y., LIU C., YANG R., JIN Y., LI T. Biochar application: A viable and pyrolysis temperature dependent option for enhancing leaf secondary metabolites of Cyclocarya paliurus. Forests, **14** (7), **2023**.
35. DING L., SHANG Y., ZHANG W., ZHANG Y., LI S., WEI X., ZHANG Y., SONG X., CHEN X., LIU J., YANG F., YANG X., ZOU C., WANG P. Disentangling the effects of driving forces on soil bacterial and fungal communities under shrub encroachment on the Guizhou Plateau of China. Science of the Total Environment, **709**, **2020**.
36. LV Y., XU L., GUO X., LIU J., ZOU B., GUO Y., ZHANG Y., LI H., ZHENG G., GUO Y., ZHAO M. Effect of biochar on soil physiochemical properties and bacterial diversity in dry direct-deeded rice paddy fields. Agronomy, **13** (1), **2022**.
37. LI W., YU W., BAI L., LIU H., YANG D. Effects of nitrogen addition on the mixed litter decomposition in Stipa baicalensis Steppe in Inner Mongolia. American Journal of Plant Sciences, **07** (03), 547, **2016**.
38. DE CARVALHO A.F., FERNANDES-FILHO E.I., DAHER M., GOMES L.D.C., CARDOSO I.M., FERNANDES R.B.A., SCHAEFER C.E.G.R. Microclimate and soil and water loss in shaded and unshaded agroforestry coffee systems. Agroforestry Systems, **95** (1), 119, **2020**.
39. CHENG X., LUO Y., SU B., WAN S., HUI D., ZHANG Q. Plant carbon substrate supply regulated soil nitrogen dynamics in a tallgrass prairie in the Great Plains, USA: results of a clipping and shading experiment. Journal of Plant Ecology, **4** (4), 228, **2011**.
40. MA J.Z., BU Z.J., ZHENG X.X., GE J.L., WANG S.Z. Effects of shading on relative competitive advantage of three species of Sphagnum. Mires Peat, **16** (04), 1, **2015**.
41. KONG F.-X., SANG W.-L., JIANG X., WANG L.-S. Aluminum toxicity and tolerance in plants. Acta Ecologica Sinica, **20** (5), 854, **2000**.
42. EMMANUEL D., PETER R.R. Aluminum toxicity and tolerance in plants. Plant Physiology, **107**, 315, **1995**.
43. DING L., WANG P. Afforestation suppresses soil nitrogen availability and soil multifunctionality on a subtropical grassland. Science of the Total Environment. **761**, **2021**.
44. FU J., LUO Y., SUN P., GAO J., ZHAO D., YANG P., HU T. Effects of shade stress on turfgrasses morphophysiology and rhizosphere soil bacterial communities. BMC Plant Biology, **20** (1), **2020**.
45. WICAKSONO W.A., CERNAVA T., BERG C., BERG G. Bog ecosystems as a playground for plant–microbe coevolution: bryophytes and vascular plants harbour functionally adapted bacteria. Microbiome, **9**, 1, **2021**.
46. TANG J.Y., MA J., LI X.D., LI Y.H. Illumina sequencing-based community analysis of bacteria associated with different bryophytes collected from Tibet, China. BMC Microbiology, **16** (1), **2016**.
47. SPIESS L.D., LIPPINCOTT B.B., LIPPINCOTT J.A. Facilitation of moss growth and development by bacteria. The Journal of the Hattori Botanical Laboratory, **55**, 67, **1984**.
48. THORMANN M.N., RICE A.V. Fungi from peatlands. Fungal Diversity, **24** (2415), 299, **2007**.
49. XIAO B., VESTE M. Moss-dominated biocrusts increase soil microbial abundance and community diversity and improve soil fertility in semi-arid climates on the Loess Plateau of China. Applied Soil Ecology, **117**, 165, **2017**.
50. LI C., LIU J., BAO J., WU T., CHAI B. Effect of Light Heterogeneity Caused by Photovoltaic Panels on the Plant–Soil–Microbial System in Solar Park. Land, **12** (2), **2023**.
51. HOLLAND-MORITZ H., STUART J.E.M., LEWIS L.R., MILLER S.N., MACK M.C., PONCIANO J.M., MCDANIEL S.F., FIERER N. The bacterial communities of Alaskan mosses and their contributions to N 2-fixation. Microbiome, **9**, 1, **2021**.
52. CARRELL A.A., KOLTON M., GLASS J.B., PELLETIER D.A., WARREN M.J., KOSTKA J.E., IVERSEN C.M., HANSON P.J., WESTON D.J. Experimental warming alters the community composition, diversity, and N2 fixation activity of peat moss (Sphagnum fallax) microbiomes. Global Change Biology, **25** (9), 2993, **2019**.
53. OPELT K., CHOBOT V., HADACEK F., SCHöNMANN S., EBERL L., BERG G. Investigations of the structure and function of bacterial communities associated with Sphagnum mosses. Environmental Microbiology, **9** (11), 2795, **2007**.
54. ALIYU H., GORTE O., ZHOU X., NEUMANN A., OCHSENREITHER K. In silico proteomic analysis provides insights into phylogenomics and plant biomass deconstruction potentials of the Tremelalles. Frontiers in Bioengineering and Biotechnology, **8**, **2020**.
55. DAVEY M.L., CURRAH R.S. Interactions between mosses (Bryophyta) and fungi. Botany, **84** (10), **2006**.
56. GROß C., HOSSEN S., DITTRICH S., KNORR K.H., BORKEN W., NOLL M. Biological nitrogen fixation, diversity and community structure of diazotrophs in two mosses in 25 temperate forests. Environmental Microbiology, **26** (1), e16555, **2024**.
57. WU X., LI J., ZHU J., JIANG Y., HUANG Z., WU P., MA X. Effects of simulated warming on bacterial community structure in litters of Chinese Fir based on displacement test. Forests, **15** (6), **2024**.
58. MESSYASZ A., MÄNNISTÖ M.K., KERKHOF L.J., HÄGGBLOM M.M. Genome analysis and description of Tunturibacter gen. nov. expands the diversity of Terriglobia in tundra soils. Environmental Microbiology, **26** (5), **2024**.
59. PANKRATOV T.A., DEDYSH S.N. Granulicella paludicola gen. nov., sp. nov., Granulicella pectinivorans sp. nov., Granulicella aggregans sp. nov. and Granulicella rosea sp. nov., acidophilic, polymer-degrading acidobacteria from Sphagnum peat bogs. International Journal Of Systematic And Evolutionary Microbiology, **60** (12), 2951, **2010**.
60. SHAO S., LI Y., LI Z., MA X., ZHU Y., LUO Y., CAI P., JIA X., RENSING C., LI Q. Impact of tea tree cultivation on soil microbiota, soil organic matter, and nitrogen cycling in mountainous plantations. Agronomy, **14** (3), **2024**.
61. LI B., YANG P., FENG Y., DU C., QI G., ZHAO X. Rhizospheric microbiota of suppressive soil protect plants against Fusarium solani infection. Pest Management Science, **2024**.
62. SUN Q., SUN B., XU S., ZHANG H., GUO J., QIAN Z., ZHUANG X. Fermentation characteristics and microbiota during the ensiling of myriophyllum aquaticum Inoculated with lactic acid bacteria. Applied Sciences, **12** (10), **2022**.

63. YURKOV A.M. Yeasts of the soil – obscure but precious. Yeast, **35** (5), 369, **2018**.
64. MOREIRA G.A.M., VALE H.M.M.D. Occurrence of yeast species in soils under native and modified vegetation in an iron mining area. Revista Brasileira De Ciência Do Sol, **42**, e0170375, **2018**.

Supplementary Data

Supplementary documents and data are available at https://github.com/dlltargeting/epiphytic_microbiome.