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RESEARCH ARTICLE

Different vegetation communities did not amplify spatial heterogeneity of soil microbial diversity and community in a subtropical *Sphagnum*-dominated peatland

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Abstract

Background and Aims Critical peatland functions are intricately linked to biogeochemical processes mediated by soil microbes. The belowground microbial activities are associated and interacted with aboveground vegetation types. Vegetation shifts from *Sphagnum* mosses to vascular plants in peatlands may alter soil microbial community, leading to changes in ecological functions. However, our knowledge in this area is still limited.

Methods We selected four sites (two core areas and two marginal areas) in the *Sphagnum*-dominated wetland in Zhejiang *Hynobius amjiensis* National Nature Reserve. At each site, peat soils under three common peatland vegetation communities (OW: only *Sphagnum*; HW: herbaceous plants with *Sphagnum* carpet; SW: shrubs with *Sphagnum* carpet) were collected at two depths. A high-throughput sequencing method was adopted to investigate the alteration in soil bacterial and fungal communities.

Results Vascular plant did not significantly alter soil properties and microbial α-diversity, given that mosses are still the dominant plants and have higher resistance levels to multiple environmental-changes than vascular plants. The features of bacterial co-occurrence network in HW revealed higher stability than that in OW and SW, indicating that herbaceous plants may contribute to the stable coexistence with *Sphagnum*. The microbial diversity, community structure and putative functions differed between core and marginal areas of the peatland.

Conclusion The results demonstrated that the spatial heterogeneity of environmental factors may play a more important role in microbial activities than vegetation types at the early successional stages. These insights provide a novel perspective for development of management practices to preserve subtropical peatlands.

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Keywords Peatland · *Sphagnum* mosses · Vascular plant · Microbial community and function · Spatial heterogeneity

Abbreviations

OW	Only *Sphagnum*
HW	Herbaceous plants with *Sphagnum* carpet
SW	Shrubs with *Sphagnum* carpet
ASV	Amplicon sequence variant
ANOVA	One-way analysis of variance
NMDS	Non-metric multidimensional scaling
PERMANOVA	Permutational multivariate analysis of variance
PCA	Principal component analysis

Introduction

Peatlands are estimated to cover just 3% of the earth's land surface, but contain one-third of soil carbon (C), serving as the largest terrestrial soil C pool (Dargie et al. 2017). Peatlands are sensitive ecosystems that provide globally critical ecological functions such as soil C sequestration, water and climate regulation and biodiversity conservation (van der Velde et al. 2021). Peat soils are sedentarily accumulated substances consisting of partially decomposed organic matter due to the low temperature, wet and anaerobic soil conditions (Minasny et al. 2019). Most of the accumulated peat is derived from *Sphagnum* mosses, which are the dominant vegetation in peatlands (Laine et al. 2021). With the recalcitrant and antimicrobial nature, *Sphagnum* mosses can create acidic, oligotrophic, waterlogged, and oxygen-limited conditions to inhibit the growth of specific microbial groups and further decrease decomposition rates (Dieleman et al. 2015; Ma et al. 2022). Moreover, they have the ability to produce phenolic compounds as potent inhibitors of hydrolytic enzymes responsible for organic matter decomposition (Freeman et al. 2001). The peat accumulation and high water-holding capacity form a positive-feedback loop, which powerfully reinforces the dominance of *Sphagnum* mosses (van der Velde et al. 2021). Thus, peatlands have accumulated a substantial amount of organic C over a long period, some over 20, 000 years (Minasny et al. 2019).

However, anthropogenic-driven climate changes (global warming and drought) and land use changes have reduced the dominance of *Sphagnum* mosses in favor of vascular plants, resulting in the succession of peatlands (Ritson et al. 2021; Ma et al. 2022). The changes in vegetation phenology and composition, particularly the declining ratio of *Sphagnum* mosses to vascular plants, have weakened the stability of peat soils, compromising the carbon sink function of peatlands and turning peatlands into net sources of C emissions (Laine et al. 2021). Soil microorganisms are vital components of ecosystems, playing a significant role in terrestrial biogeochemical processes by being involved in organic matter turnover (Sokol et al. 2022). The aboveground and belowground systems are linked and interacted mainly through plants (De Deyn and Van der Putten 2005). Alterations in soil properties, such as pH, water-holding capacity and nutrient availability, driven by vegetation shifts together with the biological traits of plants, can influence the soil microbial diversity and community structure, thereby changing the crucial ecological functions (Ho and Chambers 2019; Zeh et al. 2020). Li et al. (2022) concluded that the succession pattern of aboveground plants significantly influenced the composition of soil bacteria. Sui et al. (2021) revealed that the structure and composition of microbial communities varied significantly along a wetland-forest successional series. The variation was primarily attributed to differences in soil physicochemical properties induced by vegetation shifts, rather than variations in vegetation composition. Also, microorganisms can reciprocally influence soil conditions, creating spatial heterogeneity and ecological niches that are suitable for specific vegetation types (Sokol et al. 2022). However, it still remains unclear specifically how aboveground vegetation types and underground microbes interact with each other in peatlands, and to what extent microbial communities can reflect the successional stages and functions of the ecosystems.

The Zhejiang *Hynobius amjiensis* National Nature Reserve in Anji County, Huzhou City (Zhejiang Province, China) has become a unique geographic unit owing to the rare peatland in subtropics and endangered *Hynobius amjiensis* (Gu et al. 1999). *H. amjiensis* is a salamander species firstly found in Longwangshan Nature Reserve, which is the

predecessor of Zhejiang *Hynobius amjiensis* National Nature Reserve (Gu 1992). This species is classified to be endangered according to the IUCN Red List of Threatened Species (IUCN SSC Amphibian Specialist Group 2021) and is being promoted to the highest protection level (Class I Wildlife species) in China according to the List of National Key Protected Wild Species (National Forestry and Grassland Administration 2021). The Anji subpopulation is believed to comprise only 150–300 breeding females (IUCN SSC Amphibian Specialist Group 2021). The very limited range and number of breeding sites makes *H. amjiensis* particularly susceptible to habitat alteration. The peatland within the core area of the National Nature Reserve, which is the main habitat for *H. amjiensis*, has rapidly degraded in recent decades (Chen et al. 2016). The peatland is mainly dominated by *Sphagnum palustre* L., but is at continuous risk of succession due to the global warming and human-disturbance, posing a significant threat to the survival of *H. amjiensis*. Thus, a rigorous study of soil properties and microbial community in response to the growth of vascular plants in *Sphagnum*-dominated peatland is essential to disentangle ecological and functional changes occurring across the successional series of subtropical peatland in Zhejiang *Hynobius amjiensis* National Nature Reserve.

Herein, we selected four sites in a subtropical peatland (*Sphagnum* wetland), including two core areas and two marginal areas of the peatland, to explore the spatial heterogeneity of soil properties and soil microbial communities in peatlands. Moreover, three different vegetation types (only *Sphagnum;* herbaceous plants with *Sphagnum* carpet; shrubs with *Sphagnum* carpet) were selected in each site, to elucidate the effects of vascular plants on microbial traits and putative microbial functions in peatlands dominated by *Sphagnum*. Specific objectives were to (1) investigate the role of herbaceous plants and shrubs on bacterial and fungal communities in *Sphagnum* wetlands; (2) assess the spatial heterogeneity of soil properties and microbial traits between the core and marginal areas of the wetlands; and (3) examine whether the growth of vascular plants amplify spatial variations. We hypothesized that if vegetation in peatlands shifted from *Sphagnum* mosses to vascular plants, the soil properties would differ and the soil microbial communities would become more complex and stable along the successional gradient, enlarging the spatial heterogeneity.

Materials and methods

Sites and soil sampling

The *Sphagnum* wetland (30°23'N, 119°26'E) is the core region of the Zhejiang *Hynobius amjiensis* National Nature Reserve, which is located in Anji County (Zhejiang Province, China) with a subtropical monsoon climate. The altitude of the study area is 1338 m and the average annual precipitation is 1870 mm. The minimum and maximum temperatures are 2.6 °C and 28 °C, respectively, while the average temperatures range from 8.9 °C to 15.8 °C. The solar radiation changes from 3770 to 4460 MJ m^{-2} y^{-1} (Ding et al. 2006). The predominant soil type in *Sphagnum* wetlands is peat bog soil (Zhang et al. 2015).

Soil sampling was performed at four sites (S1, S2, S3 and S4) in *Sphagnum* wetland to furnish a diversity of soil properties relevant to microbial community. The S1 and S2 were at the edge of the main *Sphagnum* wetland (marginal areas), while the S3 and S4 were the core areas of the isolated and the main *Sphagnum* wetland, respectively (Fig. 1). Three different vegetation types were selected within each of the four sites: only *Sphagnum* (OW), herbaceous plants with *Sphagnum* carpet (HW), shrubs with *Sphagnum* carpet (SW). OW, HW, and SW all exhibited nearly complete coverage of *Sphagnum*. In addition, HW and SW had approximately 70% coverage of herbaceous plants (such as *Osmundastrum cinnamomeum*, *Hemerocallis fulva*, *Arundinella hirta*) and shrubs (such as *Hydrangea paniculata*, *Rhododendron mole*, *Rhododendron simsii*), respectively. Sampling was performed in three replicate plots at two depths (top, 0–20 cm; bottom, 20–40 cm) in each vegetation type. There are a total of 72 soil samples (4 sites × 3 vegetation types × 2 soil layers × 3 replicates).

The covered vegetation was removed before soil sampling in April, 2021. Three soil cores were randomly collected in each plot and combined into one composite sample. The samples were transported to the laboratory at 4 °C and homogenized within 24 h of sampling. A subsample of each soil sample was stored at -80 °C for DNA extraction, whereas the rest

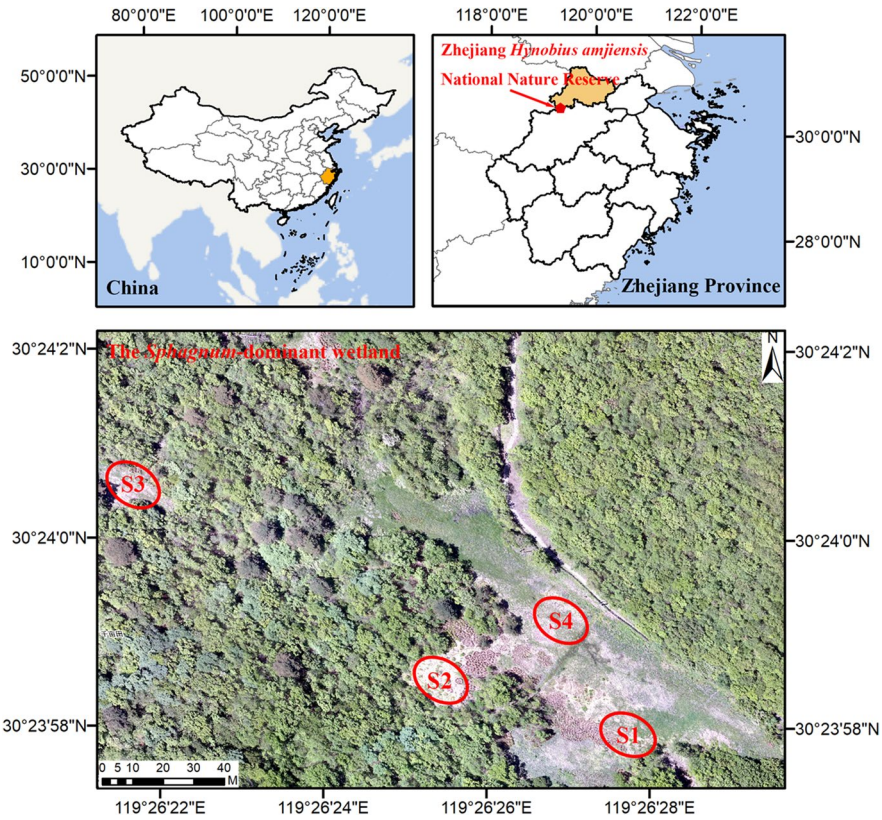

Fig. 1 Sampling sites including two marginal areas (S1 and S2) and two core areas (S3 and S4) in the peatland in Zhejiang *Hynobius amjiensis* National Nature Reserve, China

was air-dried, ground and passed through a 2-mm or 0.15-mm sieve for the analysis of physicochemical properties. The methods to determine soil properties (pH, total C, total N, dissolved organic C, NH_4^+-N and NO_3^--N) were presented in SI.

Illumina high-throughput sequencing

Soil DNA was extracted with Mag-Bind® Soil DNA Kit M5635 (Omega Bio-Tek, USA). The quantity and quality of extracted DNA were determined by a Nanodrop NC2000 spectrophotometer (Thermo Fisher Scientific, USA) and agarose gel electrophoresis, respectively. The V4-V5 region of the bacterial 16S rRNA gene was amplified with 515F (5'-GTGCCAGCMGCCGCGGTAA-3') and 907R (5'-CCGTCAATTCCTTTGAGTTT-3') primers. The fungal ITS gene was amplified with ITS5-1737F (5'-GGAAGTAAAAGTCGTAACAAGG-3') and ITS2-2043R (5'-GCTGCGTTCTTCATCGATGC-3') primers. Barcodes were linked with the 5' end of both primers for multiplex sequencing. Each sample was amplified in a 25-μL system containing 5 μL of buffer (5×), 0.25 μL of Fast pfu DNA Polymerase (5U/μL), 2 μL of dNTPs (2.5 mM), 1 μL of each primer (10 μM), 1 μL of DNA sample, and 14.75 μL of ddH_2O. The thermal cycling consisted of 98 °C for 5 min, then 25 cycles of 98 °C for 30 s, 53 °C for 30 s, 72 °C for 45 s, and a final extension of 72 °C for 5 min. Amplified samples were purified with VAHTS® DNA Clean Beads (Vazyme, China) and quantified using the Quant-iT™ PicoGreen™ dsDNA Assay Kit (Invitrogen, USA). After the amplicons were pooled in equal amounts, pair-end 2×250 bp sequencing was performed using the Illlumina NovaSeq platform with NovaSeq™ 6000 S Prime Reagent Kit (Illlumina USA). The amplification, library preparation and high-throughput sequencing processes were completed by Shanghai Personal Biotechnology Co., Ltd, China. Sequences were submitted to the Genome Sequence Archive (GSA) database under accession number CRA005854 and CRA005855.

The paired-end raw sequence data were demultiplexed using the "demux" plugin and the primers were cut using the "cutadapt" plugin with QIIME2

platform (Bolyen et al. 2019). Then, the sequences were quality-filtered, denoised, merged and chimeras were removed using the "DADA2" plugin (Callahan et al. 2016). Non-singleton amplicon sequence variants (ASVs) were aligned with "mafft" (Katoh et al. 2002). Naive Bayes classifiers (Bokulich et al. 2018) was used to annotate taxonomy for each sequence of 16S rRNA and ITS genes based on SILVA-132 database (Quast et al. 2013) and UNITE 8.0 (Koljalg et al. 2013), respectively. All sequencing data were rarefied to a minimum sequencing depth of 14,474 (16S rRNA) or 9802 (ITS) reads.

Co-occurrence network construction

The soil microbial co-occurrence networks were constructed independently within individual vegetation types (n = 24 each network) or sampling sites (n = 18 each network). Only the ASVs with the relative abundances of total samples higher than 0.5% were selected to reduce rare ASVs in the dataset. ASVs with a relative abundance of zero in more than eight (vegetation type) or three (sampling site) replicates were also removed. The co-occurrence networks were constructed using the "Hmisc" (Harrell and Harrell 2019) and "igraph" packages (Csardi and Nepusz 2006) in R (v. 4.2.1) based on the Spearman's rank correlations with *p*-value adjusted using the Benjamini–Hochberg false discovery rate (FDR) controlling procedure (Benjamini and Hochberg 1995). The values of adjusted-$p < 0.01$ were taken as statistically significant. A valid network based on the threshold of correlation coefficients was above 0.7 (vegetation type) or 0.8 (sampling site). The Gephi software (v. 0.9.7) was used to visualized the network and calculate topological properties (Bastian et al. 2009).

Connectivity of each node was determined by connectivity within module (*Zi*) and connectivity among module (*Pi*) (Olesen et al. 2007). Nodes can be classified into four categories based on *Zi* and *Pi* values: network hubs ($Zi \geq 2.5$ and $Pi \geq 0.6$), module hubs ($Zi \geq 2.5$ and $Pi < 0.62$), connectors ($Zi < 2.5$ and $Pi \geq 0.6$) and peripherals ($Zi < 2.5$ and $Pi < 0.6$). Network hubs, module hubs and connectors have been proposed as potential keystone taxa due to their critical roles in network topology. The clusters of the unique and shared keystone taxa were performed by R package "UpSetR" (Conway et al. 2017).

Statistical analysis

One-way analysis of variance (ANOVA) followed by Turkey's honestly significant difference (HSD) test was adopted to assess differences among sampling sites. Two-way ANOVA with Turkey's HSD was performed to test the effects of vegetation types and soil layers on soil properties. Analysis were deemed significant if $p < 0.05$. Alpha-diversity indexes, including Chao1 and Shannon-Weiner, were calculated for both bacterial and fungal communities. Bray–Curtis similarity coefficients were assessed among samples and visualized using non-metric multidimensional scaling (NMDS). Permutational multivariate analysis of variance (PERMANOVA) was performed to evaluate the effect of sampling site, vegetation type and soil layer on microbial community structures based on Bray–Curtis distance. A Mantel test assessed correlations between soil properties (based on Euclidean distance) and microbial communities (based on Bray–Curtis distance). Principal component analysis (PCA), alpha-diversity, PERMANOVA, Mantel test and NMDS were all performed using the R package "vegan" (Oksanen et al. 2007). The bipartite association networks of the unique and shared microbial species were visualized using Cytoscape software (v. 3.9.1) (Shannon et al. 2003).

To further predict the ecologically relevant functions, a functional annotation was performed using FAPROTAX database (v. 1.2.4), which has been extensively used to screen functional groups in a variety of environments (Louca et al. 2016). The FUNGuild database (v. 1.1) was adopted to predict functional guild of fungal community (Nguyen et al. 2016). In order to avoid over-interpreting, only ASVs with either "probable" or "highly probable" confidence was included in further analysis. The violin plots and bar plots were created using Origin 2021, while additional plots were created with "ggplot2" (Wickham 2016) in R.

Results

Soil properties

Principal component analysis (PCA) was applied to analyze the overall structural variations of soil

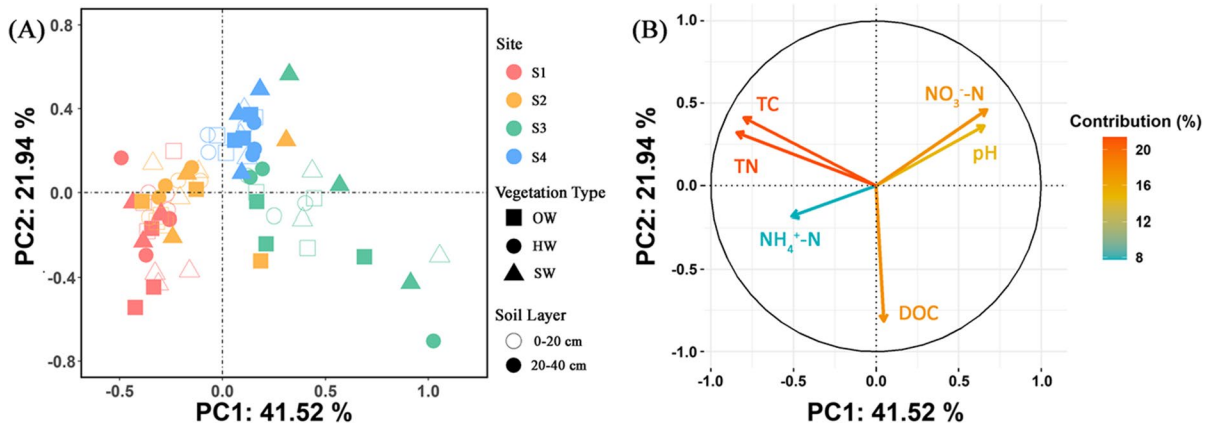

Fig. 2 The principle component analysis of soil properties (**A**) and their contributions to the variance (**B**) in various zones ($n = 72$). OW: only *Sphagnum*; HW: herbaceous plants with *Sphagnum* carpet; SW: shrubs with *Sphagnum* carpet

properties with different vegetation types in four sites (two layers, n = 72). The first two PCs accounted for 63.5% of the cumulative variance. The distribution of edaphic factors presented significant variations among different sampling sites (Fig. 2A). Clear separation of core areas (S3 and S4) from marginal areas (S1 and S2) along PC1 was observed, highlighting the categories of edaphic factors with close association, such as pH and the concentrations of total N (Fig. 2B). The soil pH in S3 and S4 were much higher than those in S1 and S2, contrary to the total N concentrations (Fig. S1). Meanwhile, the concentrations of dissolved organic C, total C and NO_3^- contributed the differences between S1 and S2, S3 and S4. Soils in S3 contained lower total C concentrations than other sites (Fig. S1B). However, PCA ordinations showed no clear variation among vegetation types or soil layers, though the significant differences between soil layers were still observed in terms of total C. There was a substantial increase of total C concentrations in soils at 0–20 cm depth compared to those at 20–40 cm depth, especially in marginal areas (Fig. S2B).

Alteration of soil microbial diversity and community structure

The bacterial α-diversity differed among sampling site and soil layers, while the vegetation type did not have significant impact on bacterial diversity (Figs. 3 and S3). The bacterial Chao1 and Shannon-Weiner indices in core areas (S3 and S4) were significantly higher than that in marginal areas (S1 and S2). Losses of bacterial diversity were observed with increasing soil depth. Both Chao1 and Shannon-Weiner indices were higher at 20–40 cm depth compared to 0–20 cm depth. Weak or non-significant differentiation of fungal α-diversity among different sampling sites were recorded. The changes in fungal α-diversity did not show a consistent trend with respect to vegetation type and soil layer.

Compared to the effect of vegetation type, the bacterial community was more influenced by site and soil depth. NMDS ordination showed a clear separation of the bacterial communities among sampling sites across the first principal, especially between core areas and marginal areas, while soil layers also significantly separated the samples across the second principal coordinate (Fig. 3C). However, soil layers and vegetation types did not contribute to the variation of fungal community distinctly according to NMDS analysis, while different sampling sites still had an effect on fungal community (Fig. 3F). Accordingly, PERMANOVA analysis revealed a strong effect on both bacterial and fungal communities with respect to sampling site, soil layer and vegetation type (Table 1). Sampling site explained the largest portion of the variation ($p < 0.0001$). Meanwhile, the interactive effects of sampling site and soil layer, sampling site and vegetation type on microbial communities were also significant. Furthermore, a Mantel test revealed that edaphic parameters significantly affected bacterial community structure, including pH ($p < 0.0001$),

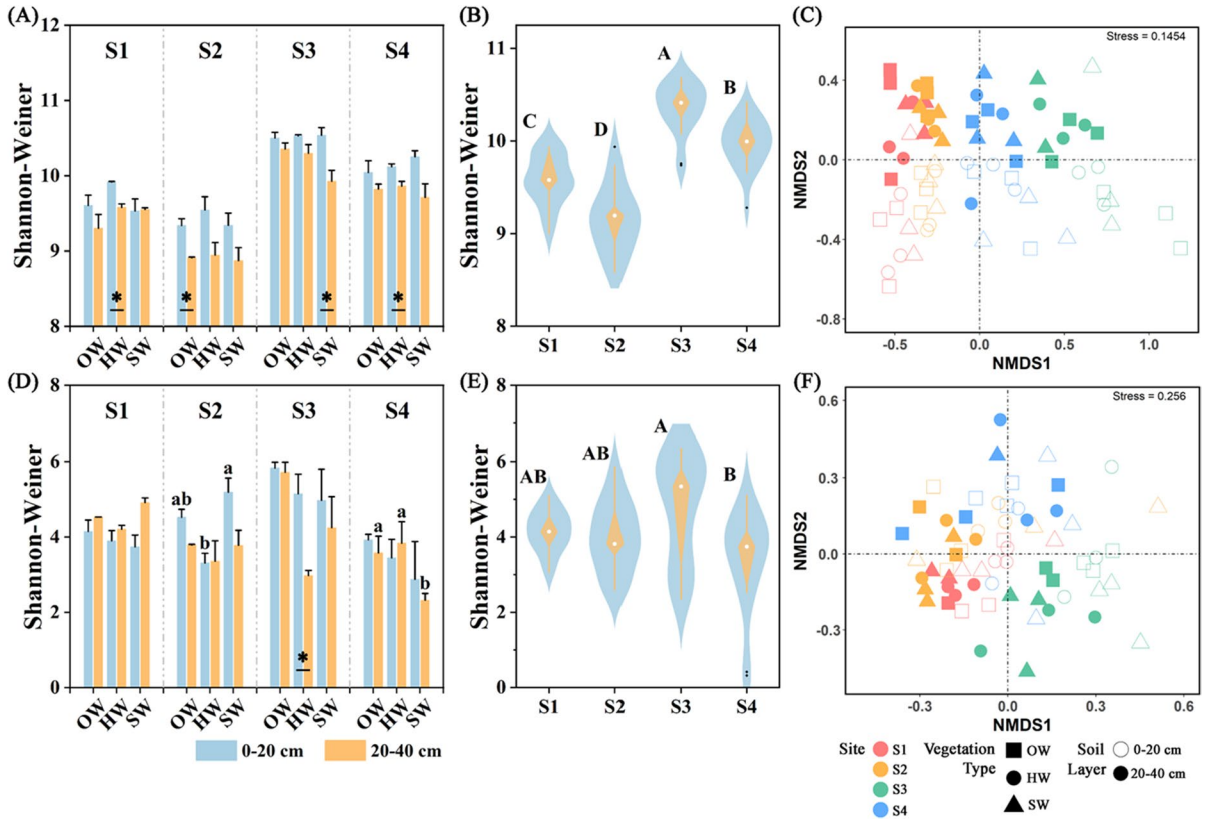

Fig. 3 Bacterial (**A** and **B**) and fungal (**D** and **E**) α-diversity as revealed by Shannon–Wiener index in various zones (**A** and **D**) and in each site (**B** and **E**). Non-metric multidimensional scaling ordination plot (NMDS) based on the Bray–Curtis matrix of the soil bacterial (**C**) and fungal (**F**) community composition ($n = 72$). Asterisks, different lower- and upper-case letters indicate significant differences between soil layers, vegetation types or sites ($p < 0.05$). Error bars indicate the standard error of three replicates. The boxplots embedded within violin plots represent median, interquartile range and 95% confidence interval. Black dots represent outlying data. OW: only *Sphagnum*; HW: herbaceous plants with *Sphagnum* carpet; SW: shrubs with *Sphagnum* carpet

Table 1 Permutation Multivariate Equation Analysis (PERMANOVA) of the effects of sites, soil layers and vegetation types on soil microbial communities

	Bacteria			Fungi		
	R^2	F	*p*	R^2	F	*p*
Site	0.28	10.82	< 0.0001	0.16	3.92	< 0.0001
Soil layer	0.07	8.03	< 0.0001	0.04	1.54	0.0026
Vegetation type	0.02	1.42	0.0457	0.04	2.72	0.0009
Site × Layer	0.06	2.45	0.0001	0.11	1.35	0.0012
Site × Type	0.08	1.52	0.0011	0.05	1.22	0.0493
Layer × Type	0.01	0.73	n.s.	0.02	0.79	n.s.
Site × Layer × Type	0.04	0.83	n.s.	0.06	0.76	n.s.
Residuals	0.4			0.53		

Table 2 Mantel correlation between microbial communities and soil properties

Soil properties	Bacteria		Fungi	
	R	*p*-value [a]	R	*p*-value [a]
All properties	0.234	< 0.0001	−0.117	n.s.
pH	0.267	< 0.0001	0.009	n.s.
Dissolved organic C	0.133	0.004	−0.018	n.s.
NH_4^+	0.053	n.s.	0.093	0.048
NO_3^-	0.142	0.003	−0.092	n.s.
Total C	0.076	n.s.	−0.074	n.s.
Total N	0.058	n.s.	−0.086	n.s.

[a] *p*-value was tested on 9999 permutations

dissolved organic C ($p < 0.005$) and NO_3^--N ($p < 0.005$), whereas only NH_4^+-N concentrations ($p < 0.05$) were significantly correlated with fungal community structure (Table 2).

Microbial community composition

Bacterial communities in soils were primarily comprised of six major phyla: Proteobacteria, Acidobacteria, Planctomycetes, Bacteroidetes, Chloroflexi and Nitrospirae, accounting for 83% of the relative abundance (Fig. S4A). Soil samples from same site shared similar compositions of predominant bacterial phyla regardless of the vegetation types. Nevertheless, soil layers affected their relative abundances and the impacts varied among the taxa. For instance, the relative abundances of Proteobacteria phylum were higher at 0–20 cm depth compared to those at 20–40 cm depth in marginal areas (S1 and S2), whereas the Nitrospirae phylum was more abundant at 20–40 cm depth. The fungal community was predominated by Ascomycota and Basidiomycota regardless of the sampling sites, soil layers or vegetation types (Fig. S4B).

Of the 2191 bacterial species detected across all samples, the major numbers of species ($n = 1529$) were shared by OW, HW and SW, which were primarily belonging to Proteobacteria, Acidobacteria, and Planctomycetes phyla. Only 54, 48, and 35 bacterial species were unique to OW, HW, and SW, respectively (Fig. 4A). OW and HW shared 215 bacterial species, which was the highest compared to OW and SW, HW and SW. The 243 core fungal species were commonly found in wetland with each vegetation type (Fig. 4B). Surprisingly, no unique fungal species was found in HW and SW, while 90 species were enriched in OW. Moreover, OW shared 85 and 94 common fungal species with HW and SW, respectively, whereas HW and SW did not share any species.

Bacterial co-occurrence networks

To identify the co-occurrence patterns of bacterial communities in soils with different vegetation types and sites, bacterial networks were modulated for three vegetation types (Fig. 5) and four sites (Fig. S5), separately. The fungal networks contained few nodes and edges due to the strict restriction (Data not shown). Multiple network topological metrics consistently showed that bacterial co-occurrence patterns differed in three kinds of vegetation types (Fig. 5 and Table 3). HW formed greater networks with more nodes (166) than SW (147) and OW (129). Meanwhile, the HW networks contained more connections (edges: 767) which increased the density of connections, but less

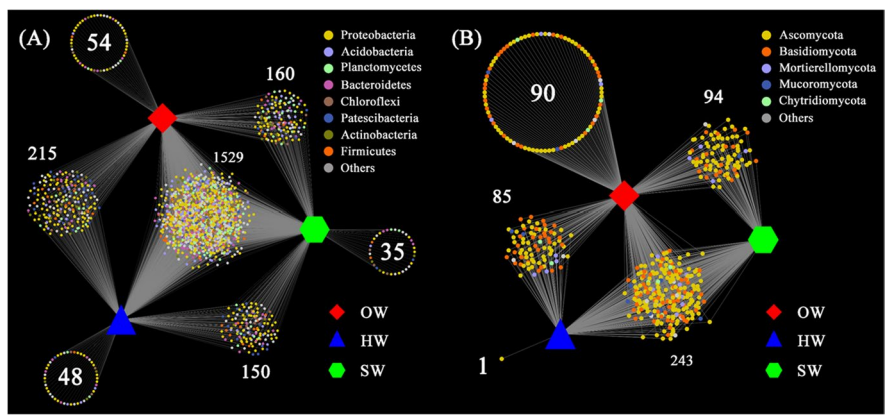

Fig. 4 Bipartite association networks of the unique and shared microbial species (**A**: bacteria; **B**: fungi) in response to different vegetation types; The number of species is provided for each cluster (singleton is exclusive). OW: only *Sphagnum*; HW: herbaceous plants with *Sphagnum* carpet; SW: shrubs with *Sphagnum* carpet

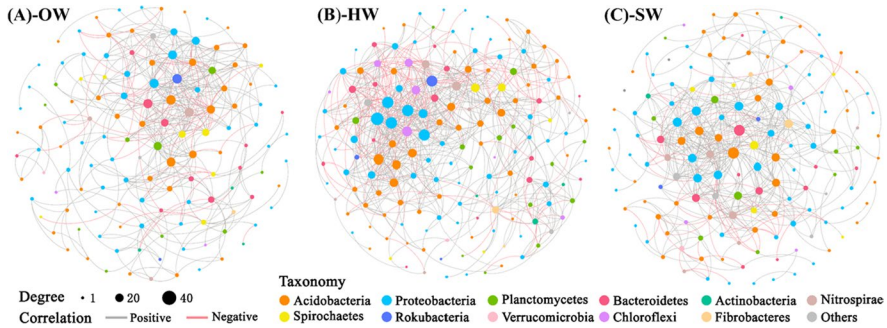

Fig. 5 The bacterial co-occurrence networks of soils under *Sphagnum* only (**A**, OW), herbaceous plants with *Sphagnum* carpet (**B**, HW) and shrubs with *Sphagnum* carpet (C, SW). The size of each node is proportional to the number of degrees, as is shown in the legend. The thickness of each edge is proportional to the value of Spearman's correlation coefficients. A connection stands for a strong (Spearman's $\rho > 0.7$) and significant ($p < 0.01$) correlation. Detailed network properties were listed in Table 3

Table 3 The topological metrics of networks in soils under *Sphagnum* only (OW), herbaceous plants with *Sphagnum* carpet (HW), shrubs with *Sphagnum* carpet (SW)

Topological metrics	OW	HW	SW
Number of nodes	129	166	147
Number of links	412	767	522
Positive links (%)	83.01	75.62	88.70
Negative links (%)	16.99	24.38	11.30
Average degree	6.388	9.241	7.102
Average betweenness centrality	151.2	203.2	183.8
Modularity	0.503	0.477	0.504
Average clustering coefficient	0.453	0.461	0.463
Average path length	3.775	3.523	3.938

positive connections (edges: 75.6%) between nodes than SW and OW. The average degree and betweenness centrality in HW were also considerably higher than OW and SW. Most of the highly connected nodes belonged to Acidobacteriia, Alphaproteobacteria and Deltaproteobacteria. The *Zi-Pi* plot showed that most of the putative keystone taxa were classified as connectors, only 1 and 2 ASVs were classified as module hubs for networks of HW and OW, respectively, while the network of SW did not have any module hub (Fig. 6A). However, the SW network had the highest number of unique connectors, followed by HW and OW (Fig. 6B). In addition, the bacterial networks of marginal areas (S1 and S2) contained more nodes and

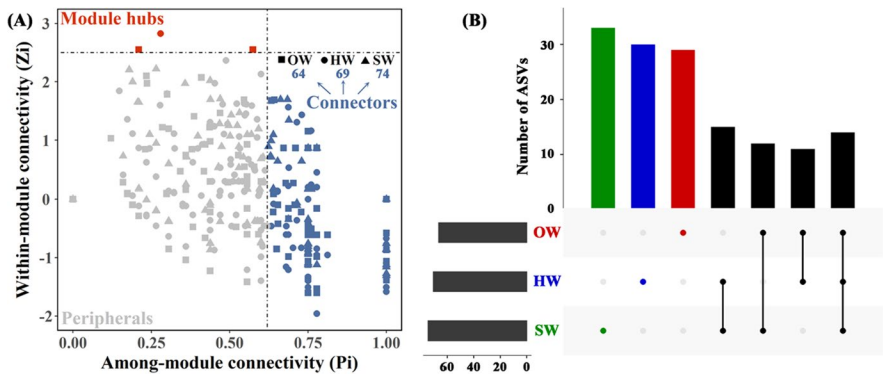

Fig. 6 **A** The *Zi-Pi* plot showing the distribution of bacterial ASVs based on their topological roles. The threshold values of *Zi* and *Pi* for categorizing ASVs are 2.5 and 0.6, respectively. The number of connectors is provided for each vegetation type. **B** The UpSetR cluster showing the number of unique and shared keystone taxa (module hubs and connectors) in response to different vegetation types. OW (square): only *Sphagnum*; HW (circle): herbaceous plants with *Sphagnum* carpet; SW (triangle): shrubs with *Sphagnum* carpet

connections than those of the core areas (S3 and S4). The average degree, average betweenness centrality, average clustering coefficient and average path length for networks in S1 and S2 were also higher than those in S3 and S4, indicating greater network robustness in marginal areas (Fig. S5 and Table S1).

Functional profiles of bacterial and fungal communities

The FAPROTAX database was adopted to predict the potential functions of the bacterial community across the sampling sites (Fig. 7). The assigned bacterial ASVs covered versatile metabolic functions and were highly enriched in nitrification, fermentation and N fixation. In N-cycling, bacterial nitrification, including aerobic ammonia oxidation and nitrite oxidation, was lowest in S4 than in other soils. Denitrification and N respiration were more enriched in the marginal areas (S1 and S2), particularly in S2. In C-cycling, the bacterial fermentation and methanogenesis were significantly higher in core areas than in the marginal areas, contrary to the bacterial methanotrophy. The celluloysis

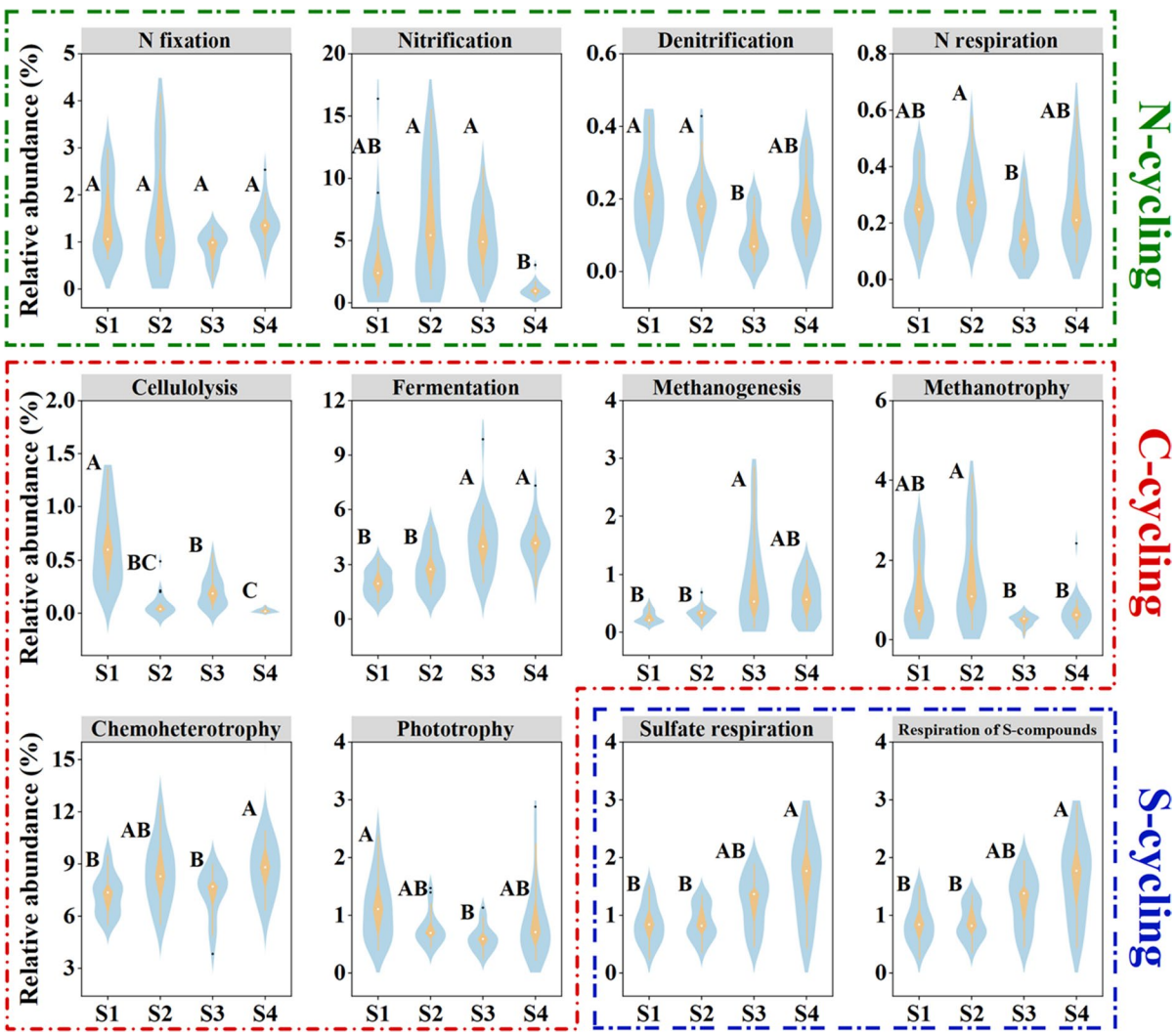

Fig. 7 Violin plots showing the relative abundances of ASVs predicted to be involved in N, C and S cycling processes in each site. The boxplots embedded within violin plots represent median, interquartile range and 95% confidence interval. The black dots represent outlying data. Different upper-case letters indicate significant differences among sites ($p < 0.05$)

and phototrophy were more abundant in S1. The S-respiration in S-cycling was significantly higher in S4 (core area) than in the marginal areas. FUNGuild database was used to annotate fungi, and three types of trophic modes were provided: symbiotroph, saprotroph, and pathoproth (Fig S7). The relative abundances of saprotroph and pathoproth groups increased significantly in core areas (S3 and S4) compared to marginal areas (S1 and S2), while the symbiotroph group was not significantly affected by sampling sites.

Discussion

Variation in microbial composition among vegetation types

It was anticipated that the relative share of *Sphagnum* mosses and vascular plants in the vegetation covers would have an effect on microbial groups during the development of *Sphagnum* wetland (Laine et al. 2021). However, contrary to our expectations, the α-diversity of bacterial and fungal communities, as well as soil properties, were not significantly affected by vegetation types (Figs. 2 and 3). Furthermore, only 6.3% and 17.7% of the bacterial and fungal ASVs were exclusive to a single vegetation type according to the bipartite association networks (Fig. 4). Previous studies have demonstrated that the significance of identifying the plant attributes in predicting the soil microbial communities, considering the fact that plant communities are greatly influenced by climate, nutrients and human activities (van der Velde et al. 2021). The shifts in vegetation covers might alter the soil microbial compositions and activities due to that: (1) various vegetation types form diverse microhabitats and promote niche differentiation, which lay foundation for distinct microbes gathering (De Deyn and Van der Putten 2005); (2) the substances exchange between plants and soil might change the soil chemical properties (e.g., pH, and nutrient availability), which is a selective factor for microbial species (Bennett and Klironomos 2019); (3) the litter types from distinct mosses and vascular plants provide various resources with differential rates of decomposition (Zeh et al. 2020). However, no remarkable differences in soil properties and microbial diversities were observed among vegetation types in current study, for a couple of reasons. First, mosses were considered to have higher resistance level to multiple environmental-changes compared to vascular plants (Laine et al. 2021). Despite the growth of herbaceous plants and shrubs in *Sphagnum* wetland, the *Sphagnum* was still the dominant plant species in moss layer, especially in the core areas (S3 and S4). Besides, the flooding conditions accelerated the diffusion and exchange of root exudation and nutrients (Neori and Agami 2016). Thus, the heterogeneity of soil properties and microbial compositions among vegetation types in same sampling site was not obvious. Moreover, anoxic conditions induced by high water levels limited decomposition of litters, leading to the accumulation of peat (Marschner 2021). The total C stock can be rather sufficient owing to the deep peat layer, contributing to the resistance and resilience of the *Sphagnum* wetland (Ritson et al. 2021).

The co-occurrence networks were constructed to explore the overall co-occurrence patterns of soil bacterial communities, providing a holistic view of interactions in bacterial communities under different vegetation covers (Fig. 5). Distinctive consequences were observed among three different vegetation types, particularly for HW (Table 3). Proteobacteria and Acidobacteria phyla substantially dominated in all three co-occurrence networks. The higher links and nodes exhibited stronger and more significant correlations in HW than other two networks (Zhang et al. 2023). Strong positive links indicated that most soil bacteria might adapt to vascular plant growth via symbiotic relationships, including commensalism and mutualism, while negative associations could be the result of competition, predation or amensalism (Chen et al. 2020; Guan et al. 2021). Several studies have reported that networks with a lower ratio of positive and negative links between nodes were more likely to endure environmental changes, given that negative links could stabilize co-oscillation in microbial communities (Coyte et al. 2015; de Vries et al. 2018). Higher centrality and lower modularity confirmed that bacterial community in HW were more stable during degradation, while networks in OW and SW exhibited properties indicating lower stability (de Vries et al. 2018). In other words, herbaceous plants may

contribute to the stable coexistence with *Sphagnum*, because they required similar living conditions and were more-or-less equally fit. On the contrary, the unstable microbial communities in wetland with shrub growth may be the result of a poorer fitness in the presence of seedlings of woody species than herbaceous plants.

Spatial heterogeneity in microbial communities and function

Ecosystems, including wetlands, can supply diverse habitats and services due to their fine-scale heterogeneity. Soil microbial compositions and structures may reflect and support the spatial heterogeneity under rapid environmental change (Gravuer et al. 2020). The spatial variabilities in the *Sphagnum* wetland were evident both between two soil depths and among sampling sites, especially between the core and marginal areas of the wetland. The soil microbial diversities and structures of core areas (S3 and S4) significantly differed with those of marginal areas (S1 and S2) (Fig. 3). The bacterial networks in marginal areas were more complicated than those in core areas (Fig. S5 and Table S1). The differences in soil microbial communities could be attributed to the differences in soil properties (Fig. 2). The results from PCA analysis indicated a clear separation of soil properties including pH, C and N contents among different sampling sites. Therefore, the spatial variabilities prevailed over vegetation types as a factor shaping the microbial communities. Different vegetation types did not amplify spatial heterogeneity of microbial diversity and community. Many studies have reported that bacterial and fungal community structure varied obviously along vegetation succession or degradation gradients (Ho and Chambers 2019; Sui et al. 2021). Notably, our results showed that the vegetation types did not play a critical role at the initial stages of the successional series. Both moss, herbaceous plants and shrubs could coexist because vascular plants did not sharply alter soil properties. However, the shift (wetland degradation) would occur when critical limits were exceeded, which explained the differences in microbial diversity and communities and soil properties between marginal and core areas (Verhoeven et al. 2006; Salimi et al. 2021).

The FAPROTAX analysis indicated that soils in core areas (S3 and S4) had lower metabolic potential in N cycling, such as nitrification, denitrification and N respiration (Fig. 7). Mechanisms proposed to explain the low nutrient process efficiency in peatlands include the effects on microbial activities of phenolic compounds accumulation, and limited oxygen and nutrient supply (Freeman et al. 2001). Due to a higher water-table, the oxygen conditions in the core areas of *Sphagnum* wetland were more limited compared to marginal areas, which contributed the accumulation of phenolic compounds (Freeman et al. 2001). The relative abundances of ASVs involved in methanogenesis (CH_4 production by methanogens under anaerobic conditions) and methanotrophy (CH_4 oxidation by methanotrophs under aerobic conditions) were different among sampling sites, which decided the net CH_4 emissions (Serrano-Silva et al. 2014). The methanotrophs were more abundant in marginal areas indicated that the core areas of wetland may have higher metabolic potential in CH_4 production. This phenomenon also resulted from the differential oxygen conditions between core areas and marginal areas. Zhang et al. (2021) reported that the CH_4 emissions and methanogenic gene abundances declined along the hydrological gradient from submerged to emerged soil conditions in an alpine wetland, which is consistent with our results. Abundant sulfur species play a critical part in the C- and S-cyclings. Previous studies indicated that sulfate-reducing bacteria could limit CH_4 emissions by inhibiting methanogenesis (Muyzer and Stams 2008). Our study also demonstrated that the microorganisms involved in methanogenesis and sulfate respiration were both more abundant in core areas of *Sphagnum* wetland. Dalcin Martins et al. (2017) reported that the sulfate reduction bacteria probably accounted for rapid C mineralization in wetland, while the processing of C pools generated substrates for anaerobic respiration, such as methanogenesis, especially in the presence of a great fraction of labile C. Fungi also contribute significantly to soil C-cycling and nutrient mobilization (Maaroufi et al. 2019). Saprotrophic fungi have received increasing attention lately due to their important effects in soil C budget, such as decomposition of cellulose and lignin (Wu et al. 2023; Ye et al. 2023). The higher relative abundance of saprotrophs in core areas (S3 and S4) compared to marginal areas (S1 and S2) indicated higher microbial metabolic potential in

C decomposition, especially at 0–20 depth (Fig. S7). Saprotrophs tend to colonize relatively fresh litter and degrade complex polymeric organic substances for capturing nutrients and energy (Cao et al. 2022). The accumulation of partially decomposed *Sphagnum* tissues in core areas provided a mass of organic matter for saprotrophs. Meanwhile, the higher abundances of symbiotrophic fungi helped *Sphagnum* access to nutrients and water, further contributed to the growth of saprotrophs (Maaroufi et al. 2019).

Conclusions

Peatlands are sensitive to environmental alterations and threatened by global warming and drought, which favor vascular plants over *Sphagnum*, initiating shifts in vegetation succession. Our study demonstrated that herbs or shrubs did not significantly alter the soil properties and microbial community structures when the *Sphagnum* were still the dominant plants in the *Sphagnum* wetland, indicating that the vascular plants did not prevail over moss at the initial stages of the successional series. Only when the critical limits are exceeded, the vegetation succession would be accelerated. Therefore, removal of vascular plants in the Nature Reserve is important to powerfully reinforce the dominance of *Sphagnum* mosses. However, the effects of vascular plants removal on greenhouse gas emissions, C conservation and biological diversity should be taken into consideration to better protect wetlands. Furthermore, controlling the water-table is an effective way to preserve pristine peatlands since the oxygen conditions plays an irreplaceable role in microbial composition and ecological function. It is a huge challenge to protect peatlands in the face of climate change and anthropologic disturbance. Meeting these challenges requires a more integrative understanding of water, soil, microorganisms, plants and animals in peatlands. Future studies need to focus on above- and below-ground biodiversity linkages at spatial and temporal scales.

Authors contributions Mengjie Yu: Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft. Yuexin Rui: Data curation, Formal analysis, Investigation, Methodology. Ting Wang: Methodology, Writing – review & editing. Qunli Shen: Writing – review & editing. Xianting Wang: Resources, Supervision. Yuhuan Wu: Conceptualization, Supervision, Funding acquisition, Validation, Writing – review & editing.

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Data availability All data generated or analyzed during this study are included in this published article. Sequences were submitted to the Genome Sequence Archive (GSA) database under accession number CRA005854 and CRA005855.

Declarations

Competing interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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