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Metagenomics reveals the functional profiles of soil microorganisms and nutrient cycling under long-term grass vegetation cropping

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ABSTRACT

Soil microbes are crucial for biogeochemical cycles and their functional potential is greatly affected by ecosystem management. Yet, how does grass vegetation affect the composition of soil microbial communities and the abundance of key nutrient-cycling functional genes? In this study, based on an experimental plot built for 7 years, the long – term influence of two grass vegetation types (*Carex breviculmis* and *Festuca arundinacea* Schreb) on soil microbial community structure and C, N, P, and S cycles were explored by metagenomics. The results showed that both plants significantly increased the diversity and richness of soil bacteria and fungi, and the abundance of Pseudomonadota and Ascomycota in *Carex breviculmis* increased significantly, while those of Actinomycetota and Mucoromycota decreased. Microbial network analysis shows that *Carex breviculmis* forms a highly modular, low - complexity microbial interaction network, indicating specialized and stable microbial community functions. Conversely, *Festuca arundinacea* Schreb has a more complex and less modular network, suggesting enhanced microbial interactions. *Carex breviculmis* significantly increased the abundance of genes related to carbon fixation (*fumA/B, pps, ppc*) and phosphorus mineralization (*phoR/P/B, phnF/P*), and also enhanced soil denitrification potential. In contrast, *Festuca arundinacea* Schreb showed a enrichment of soil nitrogen fixation genes (*nifh*). Additionally, growing *Carex breviculmis* and *Festuca arundinacea* Schreb induced the growth of sulfur - oxidizing bacteria (e.g., Thiobacillus), enriching the abundance of sulfur - metabolism - related genes (*apr, sox*). Genes related to microbial C, N, P, and S cycles are positively correlated with soil pH, available P, and alkali-hydrolyzed nitrogen. Overall, this study reveals how different grass vegetation types regulate microbial community structure and functional gene abundance to drive nutrient cycling differentiation in grassland ecosystems, thereby providing a theoretical basis for optimizing grass vegetation configuration in managed and restored grasslands to enhance soil ecological functions.

1. Introduction

Soil microbial communities are crucial for organic matter formation and decomposition, driving the global cycles of C, N, P, and S, and play a significant ecological role in the biogeochemical balance (Kaye et al., 2005; Oberson et al., 2005; Wieder et al., 2013; Zhou et al., 2025). They decompose plant, animal and their own remains, sequester organic matter, fix atmospheric N_2 into usable ammonia (Sun et al., 2021), and transform sulfur into soluble forms, thus promoting nutrient cycling and reuse (Zhou et al., 2025). During these processes, microbial genes related to nutrient cycling encode enzymes that catalyze specific protein synthesis, which are vital for soil carbon respiration, N mineralization and fixation, redox transformations of sulfur, and P solubilization and uptake (Oberson et al., 2005; Wilhelm Scherer et al., 2009; Li et al., 2017). Therefore, how do specific soil microbial functional genes regulate the rates and efficiencies of key nutrient cycling processes in different grassland ecosystems?

In recent years, the degradation of ecosystem caused by human

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pressure and environmental change has become more and more serious (Song et al., 2016; Yu et al., 2024). As the most widely distributed vegetation, planting grass vegetation has become one of the scientific management strategies to alleviate the degradation and improve the ecological environment (Ge et al., 2022). Planting grass vegetation improves ground cover and dust capture, and results in changes in soil biological and abiotic parameters such as soil fertility, pH, extracellular enzyme activity, microbial biomass, and nutrient input associated with root exudates (Han et al., 2021; Tian et al., 2021; Li et al., 2023). In an experiment planting *Hairy Vetch* and *Ryegrass*, these plants significantly boosted soil enzyme activities, including catalase and urease (Hansen et al., 2022). Also, the composition, structure, and functional gene abundance and potential of microbial communities respond uniquely to grass vegetation planting. Zhou et al. found that grass species (*Paspalum notatum*) alter soil organic carbon and rhizosphere microbes due to high organic carbon input. However, legume species (*Stylosanthes guianensis*) more significantly impact rhizosphere microbial community structure and function. Both grass types significantly change soil microbial nitrogen and phosphorus cycling (Zhou et al., 2018). In another pot experiment, planting *Medicago sativa* increased the abundance of genes involved in nitrification and denitrification (Zhang et al., 2017). Thus, grass vegetation, as a dominant component of terrestrial ecosystems, plays an important role in shaping soil microbial diversity and nutrient cycling.

Carex breviculmis, a perennial herb in the Sedge family, features a long green period, strong stress tolerance, and vigorous reproduction (Jiang et al., 2023; Wang et al., 2023). *Festuca arundinacea* Schreb a perennial cool-season grass, has extensive roots and forms turf rapidly, making it excellent for forage, turf, and ecological restoration (Zhang et al., 2006; Ferreira et al., 2023). Both plants boost soil microbial activity while enhancing soil nutrition and the environment. A study on planting *Carex praeclara* in Zoige desertified alpine grassland found it significantly boosted soil fertility (available potassium, phosphorus, total nitrogen, organic carbon), and increased Actinobacteria and Proteobacteria abundance, while decreasing Acidobacteria, Chloroflexi, and Gemmatimonadetes. Additionally, genes related to microbial N cycling, including those involved in denitrification, transport, and the synthesis of cyanase and urease, were significantly enriched after planting *Carex praeclara*, while genes related to nitrification and nitrogen fixation were significantly reduced. At the same time, genes related to organic phosphorus mineralization, the dissolution of insoluble inorganic phosphorus, and transport proteins, which are associated with phosphorus cycling, were significantly increased (Jian et al., 2022). In a study comparing cultivation of different crops, Ghosh et al. (2024) found that the monoculture of *Festuca arundinaceae* could significantly increase the abundance of genes encoding nitrite oxidoreductase (NXR) and dissimilatory nitrate reductase (NAR). The results indicated that *Festuca arundinaceae* could enhance nitrification and denitrification from NO_2^- to NO_3^- during soil nitrogen cycle, which might be related to the increase of the abundance of *Nitrospirota* community (Ghosh et al., 2024). Different grass vegetation types can change soil properties and lead to the formation of unique microbial communities. Therefore, it is crucial to investigate the changes in soil microbial communities and key functional genes in nutrient cycling, as well as their relationship with soil nutrients, under the cultivation of different grass vegetation types (*Carex breviculmis* and *Festuca arundinacea* Schreb).

Consequently, this study proposes the following hypotheses: (1) Grass vegetation ecological strategies drive divergent shifts in soil microbial community diversity and the functional potential for nutrient cycling; (2) Changes in soil physicochemical properties induced by plant community composition are key mediators linking grass vegetation types to microbial-mediated nutrient cycling processes. To test these hypotheses, this study will: (1) Quantify soil physicochemical properties (including nutrients) under contrasting grass vegetation types (*Carex breviculmis* and *Festuca arundinacea* Schreb representing); (2) Characterize soil microbial community composition and diversity using high-throughput sequencing; (3) Assess the abundance and diversity of key functional genes involved in nutrient cycling (e.g., N, P, C cycling) via metagenomic analysis; (4) Employ statistical modeling to elucidate the relationships between vegetation type, soil properties, microbial communities, and functional gene profiles. The specific objectives are: (1) to investigate the influence of planting *Carex breviculmis* and *Festuca arundinacea* Schreb on functional genes in soil microbial nutrient cycling; (2) to determine their influence on soil properties and the relationship between soil nutrients and microbial nutrient cycling.

2. Materials and methods

2.1. Experimental design and sample collection

The experiment was conducted in May 2017 at the National Precision Agriculture Research and Demonstration Base in Xiaotangshan Town, Changping District, Beijing, China (116°27′E, 40°10′N). The area is located in the plain region south of the Yan Mountains, with a warm temperate continental monsoon climate, distinct seasons. The study area has a mean annual temperature of approximately 15 °C and an average annual precipitation of around 600 mm. Detailed monthly climatic data during the study period are provided in Supplementary Table S2 to better characterize interannual and seasonal variability in environmental conditions. The soil used in this experiment is classified primarily as Calcic Kastanozem (chestnut soil). A randomized block design was used, with two treatments: planting *Festuca arundinacea* Schreb (F) and *Carex breviculmis* (C), and a plot size of 10 m × 10 m. Seeds were broadcast at a rate of 2 kg/m^2. The control (CK) consisted of naturally fallow abandoned farmland with spontaneous vegetation, rather than bare soil, ensuring that microbial baselines reflect natural field conditions. No fertilization was applied after planting in order to avoid external nutrient inputs that could obscure the intrinsic effects of vegetation type on soil nutrient cycling. Annual cutting management was conducted each September. The initial soil properties (the soil conditions measured before planting) were: pH 8.15, total nitrogen 1.54 $g{\cdot}kg^{-1}$, available potassium 120.09 $mg{\cdot}kg^{-1}$, available phosphorus 0.6 $mg{\cdot}kg^{-1}$, alkali-hydrolyzed nitrogen 58.832 $mg{\cdot}kg^{-1}$, and organic matter 12.16 $g{\cdot}kg^{-1}$. The vegetation is dominated by *Digitaria sanguinalis* (L.) Scop. (10% coverage), *Euphorbia hirta* L. (6%), *Cirsium arvense* var. *integrifolium* Wimm. & Grab. (5%), *Setaria viridis* (L.) P. Beauv. (3%), and *Acalypha australis* L. (2%).

In August 2024, during the peak vegetative growth stage of the plants, four 1 m × 1 m quadrats were established for each treatment (*Festuca arundinacea, Carex breviculmis*, and the unplanted control). From each quadrat, three soil cores (0–20 cm depth, 5 cm diameter) were collected and homogenized into one composite sample. These four composite samples per treatment served as biological replicates. In total, 12 soil samples (three treatments × four replicates) were analyzed for chemical properties and metagenomic analysis. All samples collected under each grass type were analyzed separately. Prior to analysis, we removed all visible living plant residues from the screened soil (<2 mm in diameter). Sieved soil samples for metagenomic and soil chemical analysis are stored at −80 °C and 4 °C, respectively.

2.2. Analysis of soil physicochemical properties

Soil organic matter (SOM) was determined by potassium dichromate oxidation method. After shaking soil-water suspensions (1:2.5 water/soil) for 30 min, soil pH was determined with a potentiometer. Olsen's extract method was used to measure soil available phosphorus (AP). Acetic acid and ammonium leaching extracted soil AK (available potassium), quantified by inductively coupled plasma-atomic emission spectrometry. The chloroform fumigation-K_2SO_4 extraction method assessed microbial biomass carbon (MBC) and nitrogen (MBN). Alkali-hydrolyzed nitrogen (AN), nitrate nitrogen (NO_3—N) and ammonium nitrogen (NH_4—N) were determined by Kjeldahl method (Table S3).

2.3. Soil DNA extraction, metagenomic sequencing, and bioinformatics analyses

Total soil microbial DNA was extracted from 0.5 g of mixed fresh soil following the manufacturer's instructions for the E.Z.N.A.® Soil DNA Kit (Omega Bio-TEK). Prior to metagenomic sequencing, DNA quality and concentration were assessed using a NanoDrop 2000 spectrophotometer (Thermo Scientific, USA). Approximately 1 μg of DNA was taken from each sample and sent to Majorbio Bio-pharm Technology Co., Ltd. (Shanghai, China) for analysis by an Illumina HiSeq 4000 platform (Illumina Inc., San Diego, CA, USA). The original sequencing data were quality - controlled using fastp to obtain high - quality clean data for subsequent analysis. Megahit software was used to assemble the obtained clean data into the contig with the best splicing effect. The shortest contig retained after splicing and assembly was 300 bp. Next, MetaGene software was used to predict ORFs of Contigs in the splicing results, screen out ORFs with a length ≥100 bp and translate them into amino acid sequences. The nucleic acid and amino acid sequences of ORFs were obtained for subsequent analysis. Utilizing CD-HIT version 4.6.1 (accessible at http://www.bioinformatics.org/cd-hit/), a non-redundant gene catalog was constructed with a threshold of 90% identity and 90% coverage (Bahram et al., 2018). SOAPaligner was used to align high-quality reads from each sample to the non-redundant gene catalog, generating raw read counts for each gene. To reduce sparsity and ensure comparability across samples, extremely low-abundance genes were removed (present in fewer than two samples or with total read counts <10). Gene abundances were then normalized using the RPKM (Reads Per Kilobase Million) method, which corrects for both gene length and sequencing depth. RPKM values were calculated using the following formula: $\text{Genei} = \left((\mathrm{R_i}/\mathrm{L_i}) \times 10^6\right)/\sum_1^n(\mathrm{R_j})$, where R_i is the number of reads mapped to gene i; L_i is the nucleotide length of gene i and $\sum_1^n(R_j)$ is the total number of reads mapped to all genes within the sample. DIAMOND software was used to compare the non-redundant gene set with NR, eggNOG, KEGG, CAZy and other databases (parameters: blastp; E-value ≤ 1e-5) to obtain information such as species annotation and functional annotation. The raw sequence data generated in this study have been deposited in the National Center of Biotechnology Information (NCBI) with Accession No PRJNA1430137.

2.4. Statistical analysis

R software was used for data analysis. The "vegan" package assessed microbial diversity and performed NMDS analysis. We constructed microbial co-occurrence networks using Spearman correlations with data-driven, optimized thresholds. The final cutoff ($|r| \geq 0.22$ and $p < 0.05$) was selected based on threshold optimization and sensitivity analysis implemented in the microeco package, and the resulting networks were visualized in Gephi. The average degree was calculated as (k) = 2E/N, where E is the total number of edges and N is the number of nodes. Modularity (Q) was calculated using the fast greedy optimization algorithm implemented in the igraph package, following the Newman–Girvan modularity definition. The "reshape2" package tested differences in gene abundance related to C, N, P, and S cycling.

To evaluate the influence of soil physicochemical properties on microbial C, N, P, and S cycling genes, independent partial least squares (PLS) models were constructed within each treatment group (CK, C, and F). For each sample, the total abundances of genes belonging to C, N, P, and S cycle categories were summed as response variables (Y), while soil variables including NO_3^-–N, NH_4^+–N, AN, MBC, MBN, pH, SOM, AK, and AP were used as predictors (X). All X and Y variables were standardized prior to modelling. PLS was used to extract the first two latent components that maximize covariance between soil properties and functional gene categories. Model performance was assessed using R^2X (variance in X explained), R^2Y (variance in Y explained). Variable importance in projection (VIP) scores were computed to identify the dominant soil factors associated with variations in C/N/P/S cycles. Pearson correlation analysis linked soil properties to nutrient - cycling genes, with significance at 0.05, 0.01, and 0.001 levels.

3. Results

3.1. Soil microbial community composition and network structure under long-term grass vegetation cultivation

A total of 12 soil metagenomic data were obtained from two grass vegetation types (C: *Carex breviculmis* and F: *Festuca arundinacea* Schre) and CK. After sequence splicing and quality control assessment, the average clean reads and contigs were 86,530,077 and 998,015, respectively (Table S1). After planting C and F, the diversity and richness of bacteria and fungi in soil increased significantly (Fig.S1). From the phylum level of bacteria, the relative abundance of Pseudomonadota, the dominant community, increased in both C and F, while that of Actinomycetota decreased significantly. At the phylum level of fungi, the relative abundance of the dominant communities in C and F increased in Ascomycota, but decreased significantly in Mucoromycota. In addition, the changes of these dominant microorganisms were more significant in C than in F (Fig. 1).

Additionally, to investigate potential shifts in microbial interactions and community stability, we constructed co-occurrence networks for soils under long-term planting of these contrasting grass vegetation types. (Fig. 2). Compared to CK and F, C had a less complex network, with fewer edges (bacteria: 1188; fungi: 171) and lower average degrees (bacteria: 16.163; fungi: 4.071), but a higher degree of modularity, with modularity indices (bacteria: 0.827; fungi: 0.918) much higher than those of CK (bacteria: 0.525; fungi: 0.641). The F bacterial network was the most complex, with more edges (1715) and a higher average degree (25.589) than CK, but its modularity (0.425) was lower than the other two groups.

3.2. Abundance of soil microbial functional genes under long-term grass vegetation cultivation

In this study, we first analyzed gene families encoding carbon - fixing enzymes, identifying 14 functional genes related to carbon fixation. Compared to the CK group, the relative abundance of genes related to carbon fixation (*fumA/B, IDH1/2, pps, ppc*) was significantly higher in group C (Fig. 3).

In the nitrogen cycling genes, the relative abundance of *nifH* did not differ significantly among treatments, although numerically higher values were observed in the F group, while the relative abundance of genes related to nitrification (*amoA/B/C, hao*) showed a trend of decreasing under the two types of plant cultivation. The relative abundance of (*norB/C*, etc.) was higher in group C (Fig. 4).

Of the 14 identified soil phosphorus - cycling genes, including P - starvation response regulators (*phoP/B*), inorganic P solubilization and organic P mineralization genes (*ppx, phnP*), and P uptake and transport genes (*phnC/D/E*), their relative abundance was significantly higher in group C (Fig. 5).

In the sulfur cycle pathway, we identified related genes responsible for dissimilated sulfate reduction and sulfide oxidation. Among these, the relative abundances of genes encoding key enzymes involved in dissimilatory sulfate reduction (e.g., *apr*), which mediate the stepwise reduction of adenosine-5′-phosphosulfate (APS) to sulfite and subsequently to sulfide, were higher in the C and F plots compared with the reference treatment. In addition, the relative abundance of *sox* gene families involved in sulfur oxidation pathways was significantly higher in the C and F plots (Fig. 6).

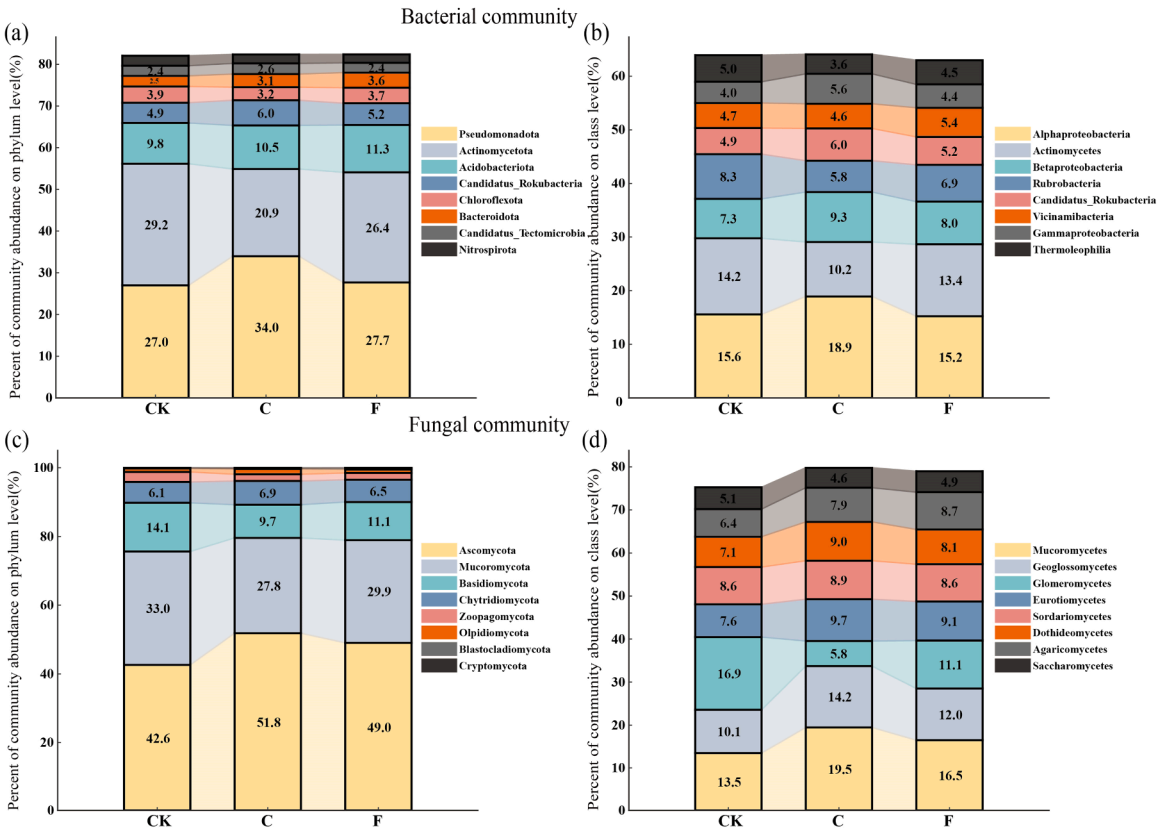

Fig. 1. Relative abundance of dominant bacterial phylum (a)/class (b) and fungal phylum (c)/class (d) in the soil under long-term cultivation of different grass vegetations. CK, control; C, *Carex breviculmis*; F, *Festuca arundinacea* Schreb.

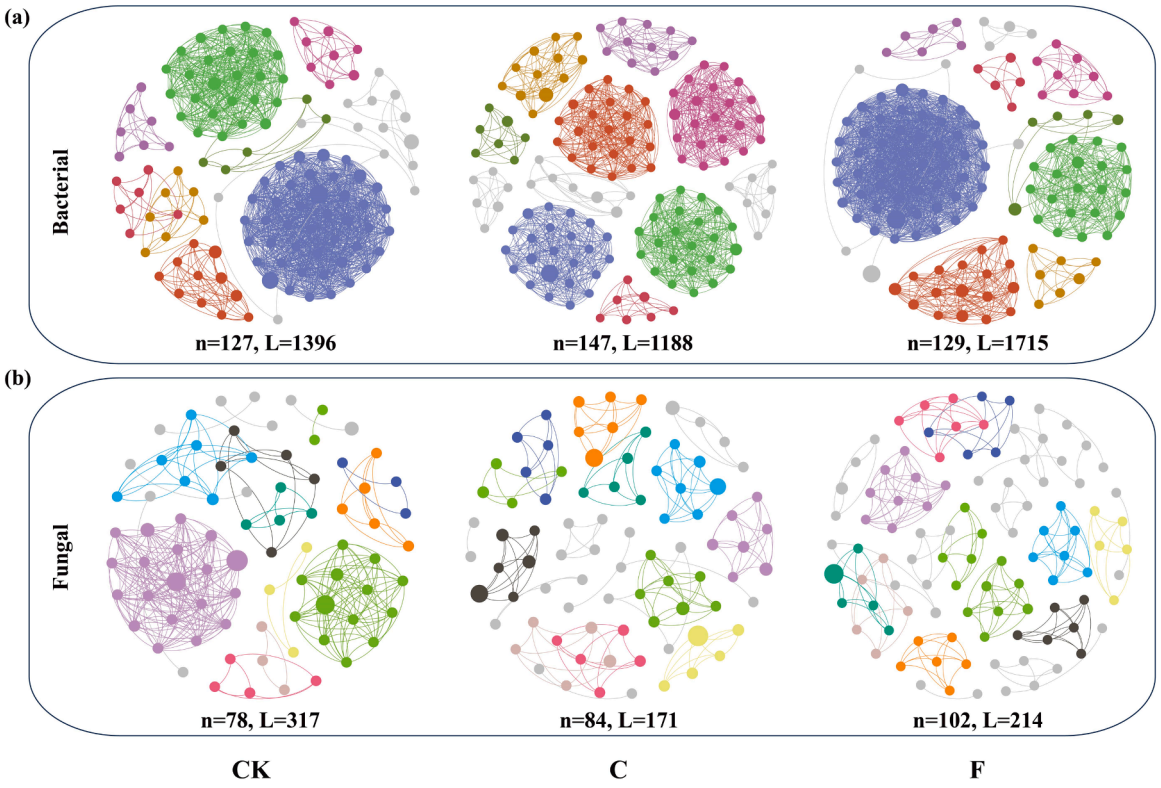

Fig. 2. Microbial network structures of soil bacterial phylum (a) and fungal phylum (b) under long - term cultivation of different grass vegetations. n, the number of nodes; L, the number of edges. CK, control; C, *Carex breviculmis*; F, *Festuca arundinacea* Schreb. Different colors represent network modules detected using the fast greedy community detection algorithm.

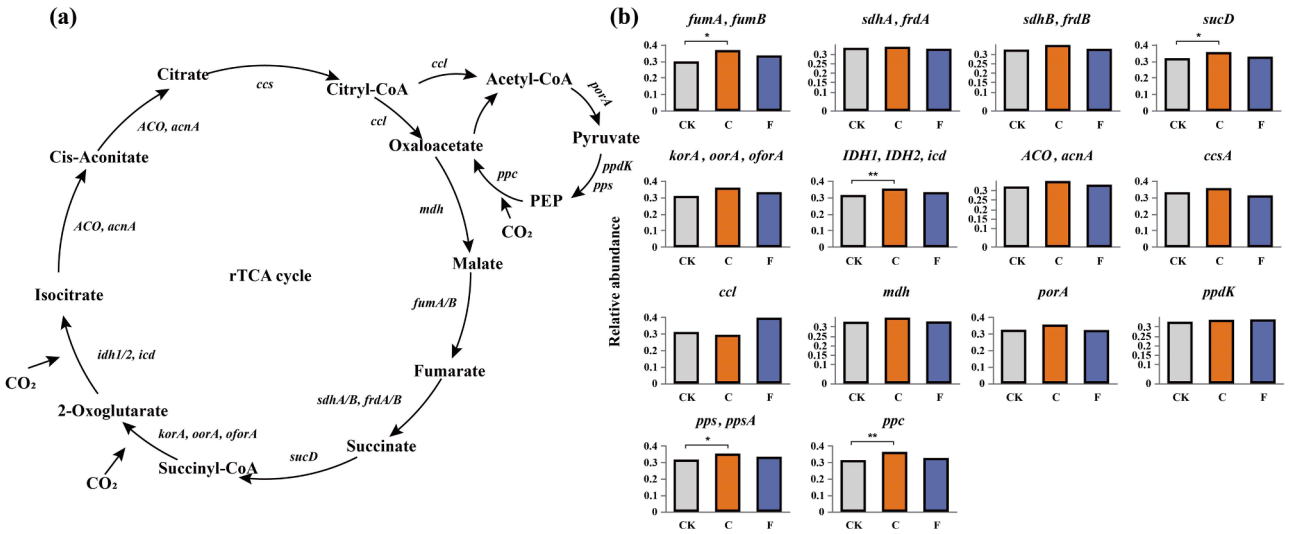

Fig. 3. The relative abundance of carbon - cycling functional genes in soil microbes under long - term cultivation of different grass vegetations. (a) Schematic representation of the carbon cycle. (b) Relative abundances of major carbon-cycle-related genes. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. CK, control; C, *Carex breviculmis*; F, *Festuca arundinacea* Schreb.

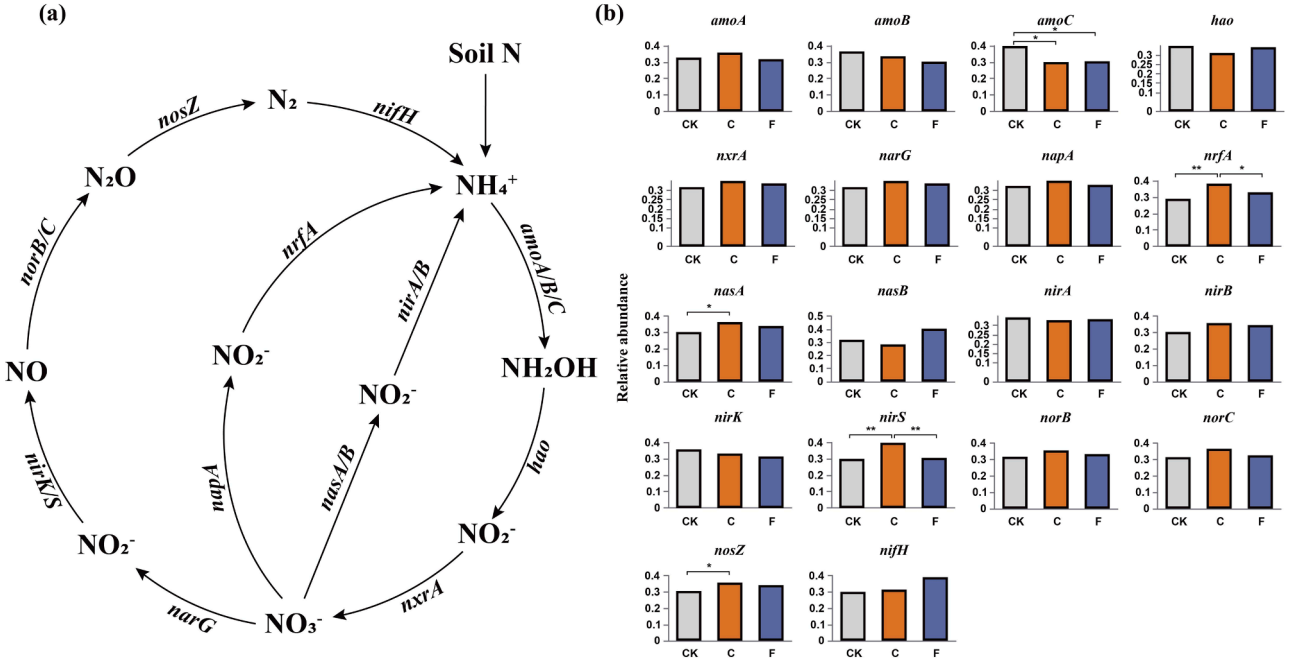

Fig. 4. The relative abundance of nitrogen - cycling functional genes in soil microbes under long - term cultivation of different grass vegetations. (a) Schematic representation of the nitrogen cycle. (b) Relative abundances of major nitrogen-cycle-related genes. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. CK, control; C, *Carex breviculmis*; F, *Festuca arundinacea* Schreb.

3.3. Factors driving the variation in the abundance of soil microbial functional genes

To evaluate how soil physicochemical properties are associated with microbial C/N/P/S functional gene categories under different treatment conditions, independent PLS models were constructed separately for CK, C, and F groups (Fig. 7). In the CK group, the first two latent components explained 57% of the variation in soil properties ($R^2X = 0.57$) and 97.8% of the variation in functional gene cycles ($R^2Y = 0.98$), indicating a strong association between soil conditions and microbial functions under control conditions. AK, pH, and AP showed the highest loadings and more coherent loading directions, indicating their relative importance within the CK group (Fig. 7; Table S4). In group C (*Carex breviculmis*), in addition to AP and pH, AN displayed relatively high loadings, indicating its close association with functional gene variation in this treatment (Fig. 7; Table S4). In group F (*Festuca arundinacea*), pH and AN showed relatively strong contributions to the first two components, suggesting their importance within this group (Fig. 7; Table S4).

Furthermore, through correlation heatmaps, the Pearson correlation relationships between soil physical and chemical properties and the functional genes involved in carbon (C), nitrogen (N), phosphorus (P), and sulfur (S) cycles were illustrated separately for CK, C, and F. The correlation heatmaps revealed that gene–environment association patterns varied among the three treatment groups (Fig. 7).

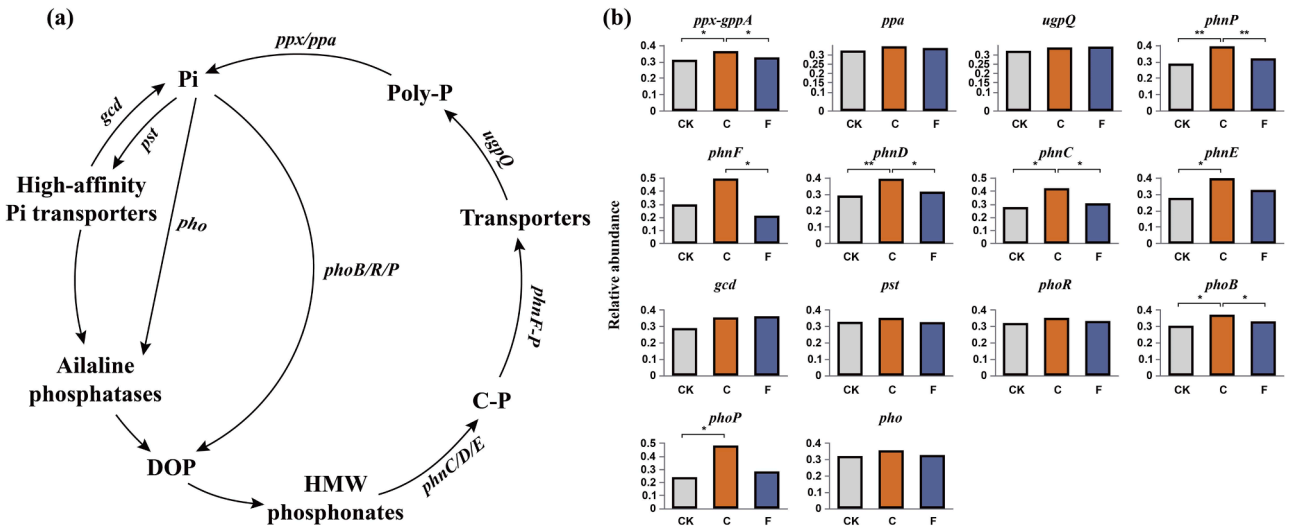

Fig. 5. The relative abundance of phosphorus - cycling functional genes in soil microbes under long - term cultivation of different grass vegetations. (a) Schematic representation of the phosphorus cycle. (b) Relative abundances of major phosphorus-cycle-related genes. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. CK, control; C, *Carex breviculmis*; F, *Festuca arundinacea* Schreb.

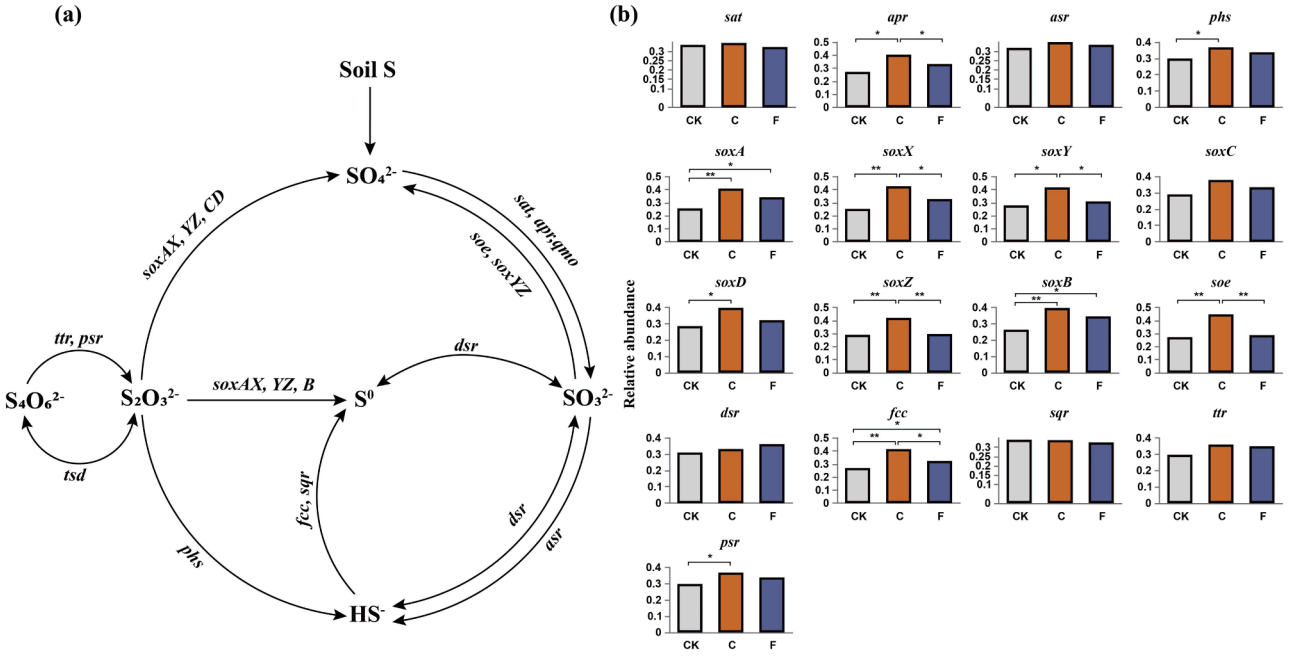

Fig. 6. The relative abundance of sulfur - cycling functional genes in soil microbes under long - term cultivation of different grass vegetations. (a) Schematic representation of the sulfur cycle. (b) Relative abundances of major sulfur-cycle-related genes. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. CK, control; C, *Carex breviculmis*; F, *Festuca arundinacea* Schreb.

4. Discussion

4.1. Changes in soil microbial ecological strategies induced by long-term grass vegetation cultivation

Long-term cultivation of distinct grass vegetation types fundamentally reshapes soil microbial communities by altering resource inputs and physicochemical conditions, thereby selecting for microbes with divergent ecological strategies. The diversity patterns shown in Supplementary Figure 1 further supports these shifts. Although bacterial Shannon diversity did not differ significantly among treatments, bacterial richness (Ace) increased under *Carex breviculmis*, while fungal diversity and richness showed increasing trends from CK to *Carex breviculmis* and *Festuca arundinacea* Schreb. These results indicate that vegetation establishment enhances both bacterial and fungal diversity relative to the pre-planting soils, and that different grass species exert distinct filtering pressures on microbial communities.

According to resource-modulation theory, plant-induced shifts in carbon availability, nutrient stoichiometry, and rhizodeposition fundamentally filter microbial taxa by favoring either copiotrophic or oligotrophic strategies rather than simply increasing or decreasing abundance (Zelenev et al., 2005). Xiang et al. (2023) found that orchards with grass cover had 61.2% higher bacterial abundance, 78.7% higher fungal abundance, and 47.3% higher Actinobacteria abundance than those without cover, driven largely by elevated carbon inputs and enzyme activities (Xiang et al., 2023). In this study, we found that the

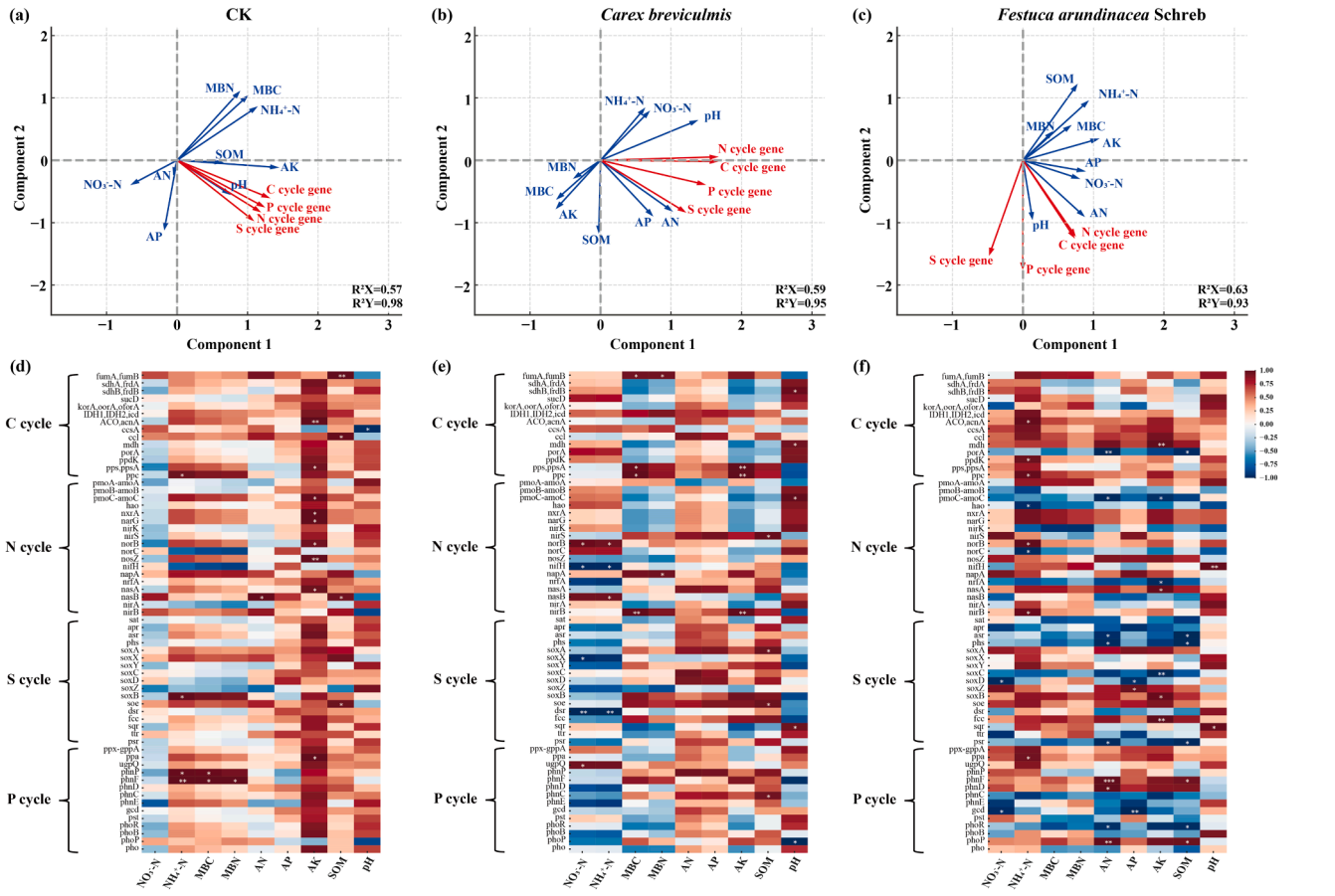

Fig. 7. (a–c) PLS biplots showing relationships between soil physicochemical properties and C/N/P/S functional gene categories in CK, C, and F treatments. Red arrows indicate gene-cycle categories (C, N, P, S), and blue arrows represent soil variables. R^2X and R^2Y denote the variance explained for soil properties and gene categories. (d–f) Correlation heatmaps showing Pearson correlations between functional gene abundances and soil physicochemical properties. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. SOM: Soil organic matter; MBC: microbial biomass carbon; MBN: microbial biomass nitrogen; AP, available phosphorus; AK: available potassium; AN, alkali-hydrolyzable nitrogen; NO_3^--N: nitrate nitrogen; NH_4^+-N: ammonium nitrogen; CK, control; C, *Carex breviculmis*; F, *Festuca arundinacea* Schreb.

rise in Pseudomonadota abundance may stem from its metabolic flexibility (H. Xu et al., 2024). Pseudomonadota can swiftly respond to carbon - source changes and adjust growth strategies according to environmental conditions (Mangin et al., 2025). Conversely, the drop in Actinomycetota abundance after planting *Carex breviculmis* and *Festuca arundinacea* Schreb may result from the disruption of its long-term stable environment (Dos Santos, et al., 2024). Actinomycetota are often r-strategists adapted to richer and more labile carbon pool (Yang et al., 2023), however a culture-independent study revealed that Actinobacteria are sensitive to physical disturbances in the soil, which break the actinomycetal hyphae that are difficult to repair (Wolińska et al., 2019). The increase in the relative abundance of Ascomycota in fungi reflects the improvement of soil nutrient resources after planting *Carex breviculmis* and *Festuca arundinacea* Schreb, which is more conducive to the propagation of these eutrophic microorganisms (L.M. Manici et al., 2024a). Ascomycetes are thought to be fast – growing copiotrophic soil microorganism that produce enzymes to break down fresh organic matter and feed on unstable organic carbon (Bi et al., 2021; Llewellyn et al., 2023; L.M. Manici et al., 2024b). In a grassland restoration study, the abundance of Ascomycota increased significantly during the later stages of grassland restoration. These microbes quickly respond to nutrient - rich environments, efficiently use complex organics like proteins and lipids, and degrade polymers like cellulose. In the late restoration stage, abundant soil nutrients promote organic matter decomposition and mineralization, creating favorable microbial growth conditions and aiding in the formation of competitive and stable populations such as Ascomycota. These fast - growing microbes stimulate plant root nutrient uptake, increasing litter and root exudates, and balancing nutrient cycling and decomposition (Yang et al., 2023). In our study, the decrease in Mucoromycota suggests that planting *C. breviculmis* and *F. arundinacea* may reshape decomposition pathways (Kowal, et al., 2022; Zhang et al., 2022). This pattern likely reflects functional replacement rather than simple loss, where fast-growing Ascomycota outcompete Mucoromycota under altered carbon quality regimes (Louca et al., 2018). Moreover, compared with *Festuca arundinacea* Schreb, the changes in these dominant microbes in *Carex breviculmis* were more significant, possibly due to different root exudates (Zhao et al., 2021; Agarwal et al., 2024). This supports the growing evidence that plant identity regulates microbial assembly via exudate chemistry, which modulates energy channels and constrains microbial network topology (Farkas et al., 2025).

Network complexity and modularity reflect microbial ecological strategy differences after planting *Carex breviculmis* and *Festuca arundinacea* Schreb. In ecological network theory, high modularity typically indicates functional compartmentalization, which can buffer ecosystems against disturbances by preventing cascading failures (Chagnon et al., 2012). Compared to CK and F, group C had a higher modularity index (bacteria: 0.827; fungi: 0.918), indicating that the *C. breviculmis*–derived organic inputs may induce niche differentiation among microbial groups, promoting specialized carbon-processing guilds and reducing cross-module dependencies (Matchado et al., 2024; Guseva et al., 2022). For example, in grassland soils, there are specialized modules of microorganisms responsible for breaking down cellulose, which are able to rapidly break down the cellulose component of plant residues and

convert it into simple sugars that provide nutrients for other microorganisms or plants (Li, et al., 2025). This efficient functional division makes grassland ecosystem more efficient in the process of organic decomposition and nutrient release (Zheng et al., 2021). At the same time, the low number of connected edges indicates a relatively simple community structure. Such simplified but well-defined modules typically emerge when resource types are partitioned among microbial guilds, reflecting environmental filtering rather than random assembly. By adding specific microbial agents or changing the environmental conditions of the soil (such as pH value), the microbial modules responsible for specific nutrients can be targeted to achieve accurate management of the grassland ecosystem and promote their sustainable development (Cornell et al., 2023; Thakur et al., 2024). The high complexity (1715 edges, average degree 25.589) and low modularity (0.425) of the bacterial network in group F indicate enhanced microbial interactions (Matchado et al., 2021; Guseva et al., 2022), which typically perform multiple ecological functions such as more nutrient cycling, organic matter decomposition and pollutant degradation (Xue et al., 2022). This enables the ecosystem to better cope with external changes and stress (Hernandez et al., 2021). Studies have found that cultivating forage ryegrass and white clover increases the node number, edge number, and modularity index of the AMF (arbuscular mycorrhizal fungi) network in soil, thereby expanding the scale and complexity of the AMF network (Xiao et al., 2022). Overall, the contrasting network patterns between *C. breviculmis* and *F. arundinacea* reflect two distinct microbial assembly pathways: one dominated by functional specialization (high modularity), and the other characterized by interaction-rich, redundant networks (high complexity). These pathways correspond to different ecosystem strategies for processing carbon inputs and maintaining stability.

4.2. *Effects of planting different grass vegetation on functional genes of microbial communities in soil nutrient cycling*

Previous research has confirmed that different types of plants can drive carbon fixation and storage pathways by altering the abundance and diversity of soil microbial genes related to carbon degradation and fixation. In a study assessing the effect of different tree species on soil microbial diversity, it was found that tree species can mediate the abundance of multiple key functional genes in soil microbes that encode the degradation of aromatic and lignin compounds (Kelly et al., 2021). In our study, after planting *Carex breviculmis*, the enrichment of genes such as *fumA/B* and *sucD* in soil microbes enhanced the rTCA cycle, a crucial central biosynthetic pathway that can acquire carbon from existing organic compounds (heterotrophic) or fix carbon dioxide from the atmosphere (autotrophic), depending on the availability of carbon sources and energy in the surrounding environment (Ragsdale, 2018; Song et al., 2025). Combined with the lignin-degrading ability of Ascomycota, *Carex breviculmis* may influence soil carbon turnover dynamics through shifts in dominant fungal functional groups (Yang et al., 2024; Wu et al., 2024). The abundance of carbon fixation genes in soil microorganisms planted with *Festuca arundinacea* Schreb is generally lower than that of *Carex breviculmis*, indicating weaker function in carbon fixation and long-term sequestration, which may favor its rapid growth and reproduction (Zhou et al., 2012; Du et al., 2023). These patterns collectively indicate that vegetation identity may shape the microbial functional potential related to carbon transformation, although future work incorporating direct measurements of soil carbon pools or mineral-associated carbon fractions is necessary to verify its consequences for long-term carbon storage.

Typically, after planting grass vegetation, soil nitrogen input increases, but more nitrogen may be absorbed by plants (Chen, et al., 2021). Consequently, the functional gene differentiation of soil microbial communities can lead to diverse ecological impacts. Our prior study indicated that *Medicago sativa* significantly increased the abundance of genes related to nitrogen nitrification and denitrification in soil microorganisms, suggesting that planting *Medicago sativa* can accelerate nitrogen turnover in soil. Conversely, *Smooth brome* significantly increased denitrification and DNRA, but reduced the abundance of the *amoA/pmoA* gene associated with nitrification (H. Xu et al., 2024). In this study, after planting *Festuca arundinacea* Schreb, the rise in the abundance of the *nifh* gene may offset the decline in nitrification gene (*amoA/B/C*), mitigating nitrogen loss via biological nitrogen fixation (Zhang et al., 2024). In contrast, *Carex breviculmis* raises the abundance of denitrification genes (*nirS, norB/C*), promoting soil nitrogen cycling but potentially increasing N_2O emissions. Future research should combine field monitoring to evaluate the net environmental effect (Jetten, 2008; Ouyang et al., 2018). Additionally, nitrate (NO_3^--N), as a plant-available nitrogen form, showed contrasting relationships with the *nirA* gene among vegetation types: it was negatively correlated with *nirA* abundance in the CK and F groups, whereas a weak positive correlation was observed in the C group. This pattern suggests that the regulation of microbial nitrogen acquisition by nitrate availability differs across vegetation contexts (Li et al., 2020). Soil pH may indirectly regulate nitrification by affecting ammonia - oxidizing bacteria activity (Li and Cupples, 2021; Zhu, et al., 2022).

Plants have specific activation mechanisms for phosphorus and sulfur cycling, including absorption, transport, metabolism, storage, and reuse of phosphorus and sulfur (Padhy et al., 2022; H. Zhang et al., 2025). The importance of phosphorus is due to the high phosphorus availability, and we found that after planting *Carex breviculmis*, the significantly increased of the abundance of *phnF/P* and *pst* genes in soil microbes, along with the positive correlation with AP and AN. And the abundance of Pseudomonadota, which binds to the phosphorus-soluble microbes, was significantly increased in group C, indicates that *Carex breviculmis* enhances organic phosphorus mineralization and transport by recruiting such bacterial communities, showing its phosphorus-activation advantage (Khomutovska et al., 2024; Zheng et al., 2024). Sulfur cycling is closely related to the biogeochemical cycles of carbon, nitrogen, and phosphorus, as well as plant growth (Granat et al., 1976). As a component of nitrogenase, sulfur involved in biological nitrogen fixation and is crucial for enhancing soil nitrogen and phosphorus availability and promote the absorption and utilization of nitrogen and phosphorus by crops (Chaudhary et al., 2023; Zenda, et al., 2021). In this study, the abundance of genes such as *apr* and *sox* in soil microorganisms increased simultaneously with the planting *Carex breviculmis* and *Festuca arundinacea* Schreb, indicating enhanced sulfur cycling integrity, likely due to root exudates promoting the growth of sulfur-oxidizing bacteria like *Thiobacillus* (Amin et al., 2021; Liu et al., 2023). And PLS -DA results consistently show that soil pH, AP and AN are the strongest predictors shaping microbial functional gene composition and nutrient-cycling pathways across treatments. These functional insights suggest potential implications for species selection in grassland restoration, although the ecological outcomes should be interpreted with caution. *Carex breviculmis* may contribute to improved carbon turnover and phosphorus availability, while *Festuca arundinacea* appears associated with microbial traits linked to nitrogen cycling. Implementing vegetation-based restoration strategies may benefit from considering plant–microbe interactions, but additional field experiments and long-term measurements are needed to verify their broader ecological effects and practical applicability in soil rehabilitation.

5. Conclusions

This study found that different grass vegetation types drive distinct ecological strategies by influencing soil microbial community structure and functional genes. *Carex breviculmis* enhanced microbial modularity (bacterial: 0.827 vs. CK 0.525; fungal: 0.918 vs. CK 0.641), significantly increasing the abundance of carbon fixation-related genes (e.g., *fumA/B*, *sucD*), phosphorus starvation response genes and organic phosphate mineralization genes (e.g., *phoR*, *ppx*), indicating *Carex breviculmis* tended to form a modular, high carbon/phosphorus cycle function of the

steady-state system. *Festuca arundinacea* Schreb promoted microbial interactions (edges: 1715; average. degree: 25.589 vs. *Carex breviculmis* 1188 and 16.163) and nitrogen - fixation gene (*nifh*) enrichment, its tendency to form a competitive strategy dominated by high complexity and nitrogen-fixing. Soil pH, AP, and AN are key factors regulating nutrient cycling under both plants. Overall, this study deepens our understanding of how different grass vegetation types mediate soil nutrient cycling in grassland ecosystems. Future research will focus on assessing the recovery potential and specialized functions of different plant species within these systems, with the aim of informing more targeted soil and vegetation improvement strategies.

Data availability statement

The raw data generated in this study are not yet publicly available because additional analyses are still in progress, and the dataset must remain confidential at this stage. All finalized data will be deposited in a recognized public repository upon completion of the subsequent experiments and analyses.

Declaration of 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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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.crmicr.2026.100583.

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Further reading

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