



Evaluating the optimal land use pattern for saline-sodic soils from the perspective of nitrogen metabolism

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ABSTRACT

Enhancing soil nitrogen storage is a global concern, particularly in soils affected by salinization. Land use changes significantly affect soil nitrogen cycle and its metabolic processes; however, their impacts on nitrogen availability and microbial nitrogen transformation in saline-sodic soils remain unclear. To address this knowledge gap, soils of six land use types – paddy field (PF), dryland (DL), converted paddy field to dryland (SGH), forestland (FL), grassland (GL), and wasteland (WL) – were collected to investigate the underlying mechanism of nitrogen transformations. Compared to WL, agricultural land use systems (PF, DL, SGH) significantly decreased ($p < 0.05$) soil pH (10.65–8.38 units), electrical conductivity (EC) (1.51–0.19 dS m^{-1}), exchangeable sodium percentage (ESP) (86–8 %), sodium adsorption ratio (SAR) (203 to 13), and water-soluble salt ions. Moreover, agricultural land use systems significantly increased soil organic matter (SOM), available phosphorus (AP), available potassium (AK), and nitrogen fraction contents relative to WL and enriched nitrogen-metabolizing microorganisms. Furthermore, agricultural land use systems were more advantageous than non-agricultural land use systems in improving soil nitrogen availability, through affecting N fixation, nitrification, and dissimilatory nitrate reduction to ammonium (DNRA). In addition, network analysis revealed that soil physicochemical properties shaped soil nitrogen-metabolizing microbial communities. Crucially, ammonium nitrogen ($\text{NH}_4^+\text{-N}$) and nitrite nitrogen ($\text{NO}_2\text{-N}$) were critical determinants of soil nitrogen metabolism dynamics. Therefore, agricultural land use systems, especially PF and DL, were conducive to the improvement of soil salinization and the promotion of soil nitrogen metabolism and storage in saline-sodic soils.

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1. Introduction

Nitrogen is a fundamental nutrient for life, underpinning growth and development across ecosystems. Soil nitrogen cycle, a pivotal component of global biogeochemical cycling, governs the transformation of inert atmospheric nitrogen into bioavailable forms, primarily mediated by diverse microbial communities (Kuypers et al., 2018). This intricate cycle encompasses key processes such as nitrogen fixation, organic N mineralization (ammonification), nitrification, denitrification, and dissimilatory/assimilatory nitrate reduction (DNRA/ANRA) (Xiao et al., 2019), each orchestrated by specialized functional microbial groups (e.g., ammonia-oxidizing archaea/bacteria, nitrite reducers). Critically, the structure and function of these microbial communities form a kinetic core that regulates the rates of decomposition, mineralization, and overall nitrogen flux within soils (Wang et al., 2020). Consequently, deciphering the mechanisms controlling soil nitrogen transformations is paramount for enhancing nitrogen retention and utilization efficiency in terrestrial systems.

In recent decades, serious land degradation problems, especially soil salinization, have been increasingly prominent across the globe due to climate change and human activities (Ivushkin et al., 2019). Saline-alkaline soils are widely distributed around the world in regions such as Central Asia, the Middle East, South America, North Africa, and the Pacific. It is estimated that 950 million hectares of soil in more than 100 countries around the world are affected by salinization (Chang et al., 2014), which poses a threat to global food security, restricts agricultural production, and endangers soil health (Han et al., 2021). Among them, China is one of the regions severely affected by soil salinization, with a total area of 99.13 million hectares, which is still growing at a rate of 1 % per year (Liu et al., 2019; Li and Wang, 2018).

Soil salinization led to increased soil pH, soil nutrient imbalance, reduced water availability, and altered microbial diversity, which further affected plant health through osmotic stress, ionic toxicity, and low nutrient bio-availability (Zhang et al., 2019a). Meanwhile, soil salinization showed a non-negligible impact on soil nitrogen content and transformation. Excess soluble salts increase soil osmotic pressure, and generate toxic ions in highly concentrated cells, thereby disrupting soil structure, increasing soil nitrogen loss, and inhibiting plant water and nitrogen uptake (Xu et al., 2016; Zhang et al., 2017). Soil salinization also alters nitrogen transformation processes such as soil N mineralization (Noe et al., 2013), nitrification (Osborne et al., 2015), denitrification (Giblin et al., 2010), and reduction of DNRA (Yang et al., 2015). Microbial nitrogen cycling processes drive and regulates nitrogen compounds (e.g., N_2O , $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$); therefore, soil salinization could directly affect soil nitrogen transformations and nitrogen losses by altering soil microbial communities and their biochemical activities (Teixeira et al., 2013). Hence, there is an urgent need for searching rational means to reduce nitrogen loss, enhance nitrogen utilization efficiency, and land productivity in saline-alkaline soils, which will help to improve soil quality and plant growth, increase agricultural yields, and improve the ecological environment.

Land use represents a primary manifestation of human interaction with natural resources, significantly shaping regional ecology, soil conservation, and biogeochemical cycles (Shi et al., 2014; Wang et al., 2014). Critically, land use change (such as conversions between forest, grassland, cropland, and wetlands) induces profound shifts in vegetation cover, soil physicochemical properties, and microbial community structure and function (Fuchs et al., 2015; Bargali et al., 2019). These changes inevitably cascade to impact core ecosystem processes, including the soil nitrogen cycle. Rational land management practices can enhance soil nitrogen fixation, reduce losses, improve soil quality, and contribute to climate change mitigation (Blaud et al., 2018). For instance, rice cultivation has been shown to promote soil nitrogen fixation compared to natural forests or banana plantations (He et al., 2024), while optimized management can significantly increase global cropland nitrogen recovery efficiency (You et al., 2023). Land use-induced differences in the transformation characteristics of soil N cycling may be due to (a) oxygen availability (regulating nitrification/denitrification balance) (Wang et al., 2025); (b) soil carbon to nitrogen ratio (driving microbial N immobilization and mineralization) (Gao et al., 2024); and (c) synergistic microbial community effects (Zhang et al., 2023). While wise land management can improve nitrogen retention and utilization efficiency in non-saline soils, the efficacy and mechanistic pathways are severely understudied in saline environments, where stressors such as high pH, ionic toxicity and osmotic stress inherently disrupt microbial function and nutrient cycling. This constitutes a critical knowledge gap: How do land use types reconfigure soil biotic-abiotic interactions to regulate nitrogen transformation pathways under saline-alkaline stress? Therefore, understanding these differences is essential for tailoring land management to optimize nitrogen cycling in degraded soils.

The western part of the Songnen Plain in northeastern China is one of the world's three largest concentrations of saline-sodic soils, covering an area of up to 3.73 million ha (Zhao et al., 2022). The western Songnen Plain provides a compelling model system to address the above knowledge gap. This region is experiencing rapid and significant land use change, driven by agricultural intensification and development, manifesting as conversions of grassland (GL), wetland (WL), and unused land to cropland (e.g., PF, DL, SGH) and forestland (FL) (Xia et al., 2014; Lu et al., 2024). This convergence of intense land use conversion and persistent saline-sodic stress establishes an urgent experimental context to resolve how land use trajectories rewire nitrogen cycling mechanisms. Therefore, we studied six saline-sodic land use type soils (PF, DL, SGH, FL, GL and WL) in the Songnen Plain, including changes in soil salinity and nutrients and biotic and abiotic mechanisms of soil nitrogen transformations in different land use types. Our specific objectives are to: (a) quantify land use effects on soil salinity, nutrients, and nitrogen partitioning; (b) determine how different land use practices affect microbial communities that are key functions of the nitrogen cycle, as well as nitrogen metabolism processes; (c) elucidate the dominant mechanisms driving variations in soil nitrogen transformation processes by disentangling the relative contributions of microbial community attributes versus soil physicochemical properties. We hypothesize that agronomic practices under specific land uses alleviate saline-sodic stress, restructuring microbial communities to favor nitrogen-conserving microorganism, thereby enhancing nitrogen retention in saline-sodic soils.

2. Materials and methods

2.1. Description of the study area

The study was conducted in the Qiangolos Mongolian Autonomous County (44°17'-45°28'N, 123°35'-125°18'E), Songyuan City, Jilin Province, China, located in the northwestern part of Jilin Province and the southern part of the Songnen Plain. The county has a temperate continental monsoon climate with four distinct seasons, an average annual temperature of 4.5 °C, an average annual precipitation of 400–500 mm, an annual evaporation of more than 1200 mm and a frost-free period of 130–140 days. The soil type of the site is mostly black calcium soil, meadow soil, saline soil, and wind sandy soil. The local topography is alluvial plain along the river, the terrain is low and flat, and the altitude is about 150 m.

2.2. Experimental design and soil collection

Six land management practices were established, including paddy field (PF), dryland (DL), wasteland (WL), grassland (GL), forestland (FL), and converted paddy field to dryland (SGH). The six land management measure plots were each 1–2 km apart. We define PF, DL, and SGH as agricultural land use systems and FL, GL and WL as non-agricultural land use systems. The surface of WL investigated in this study is degraded grassland with low cover, the surface of GL is vegetated with alkali ponies or goat grass, the surface of FL is vegetated with poplar, the crop grown in DL is maize, and the crop grown in PF is rice. FL, GL and WL systems shared little anthropogenic external material inputs and agricultural management measures (including fertilizer application, ploughing, irrigation). It has been five years since the WL was reclaimed as FL and GL. Both DL and PF both follow an annual cropping pattern, and have been continuously monocultured for five years. SGH involves a shift from rice to maize after three years of rice cultivation and has been growing maize for five years. Wasteland is reclaimed as agricultural soils, then tilled, irrigated, and sown beginning in early May. It is managed for water level, weed control, and fertilization between May and October (Zhou et al., 2024). Nitrogen fertilizers used in PF, DL and SGH were based on compound fertilizers and ammonium sulphate at a dosage of 60–80 kg hm⁻² per year (N-P₂O₅-K₂O=12:8:7). Crops were harvested in October each year, after which some or all of the crop residues were crushed and returned to the field. The residues were then ploughed into the soil tillage layer (0–30 cm) with spring ploughing the following year. All fields were managed with 100 % straw return and fertilizer application.

Samples (0–20 cm and 20–40 cm) were collected on April 28, 2023, prior to spring cultivation (for croplands) and during early vegetation growth (all land use systems), to capture baseline nitrogen transformation conditions with minimal recent disturbance. There were three plots for each land use pattern. Soil samples were collected at five random locations in each plot using a 5 cm diameter auger and combined into a composite sample, which was then transported to the laboratory below 0 °C. Soil samples were naturally air-dried to remove residues such as debris and plant roots for soil physicochemical property analysis. The majority of the microbial communities are present in the 0–20 cm soil layer; therefore, samples were collected from this layer for microbial molecular testing and stored at -80 °C.

2.3. Soil physicochemical properties

Soil pH and electrical conductivity (EC) were measured in a ratio of 1:5 (soil weight/ water volume) (Luo et al., 2018b). Soil cation exchange capacity (CEC) was determined using the sodium acetate method and measured with a flame photometer (AP1200, Aopu Company, Shanghai, China). Soil exchangeable sodium percentage (ESP) was measured using the flame atomic absorption spectrometry method (Feng et al., 2019). Soil sodium adsorption ratio (SAR) was calculated using the formulae method (Murtaza et al., 2006). Soil water-soluble K⁺, Na⁺, Ca²⁺ and Mg²⁺ ions were first extracted with deionised water and then determined by the ICP-AES method (Yayintas et al., 2007). Soil water-soluble CO₃²⁻ and HCO₃⁻ were determined by leaching with deionised water followed by dual indicator-neutralisation titration. Soil organic matter (SOM) was determined using the potassium dichromate external heating method (Zhu et al., 2020). Soil total carbon (TC) and total nitrogen (TN) were determined using a Vario Max CNS analyser (Elementar Instrument, Mt. Laurel, NJ, USA). Soil available phosphorus (AP) was determined using the molybdenum-antimony colorimetric method (Rowell, 1994). Soil available potassium (AK) was determined by flame photometric method (Rowell, 1994). Soil ammonium nitrogen (NH₄⁺-N) and nitrate nitrogen (NO₃⁻-N) were extracted with KCl and measured with a flow injection analyser (SAN+++; Skalar Analytical B.V., Breda, The Netherlands). Soil nitrite nitrogen (NO₂⁻-N) was extracted with KCl solution and then determined by N-(1-naphthyl)-ethylenediamine hydrochloride colorimetric method (Chengdu Baihui Biotechnology Co., Ltd., China). Soil dissolved organic nitrogen (DON) was determined by differential subtraction method (Wang et al., 2022). Soil microbial nitrogen (MBN) was determined using chloroform fumigation extraction-TOC method (Vance et al., 1987).

2.4. Metagenome sequencing and bioinformatics analysis

Metagenome sequencing and analysis were conducted by OE biotech Co., Ltd. (Shanghai, China). Genomic DNA was extracted from soil samples using Mag Pure Soil DNA LQ Kit (Magen Biotechnology Co., Ltd, Guangzhou, China), after which the DNA concentration was detected using agarose gel electrophoresis and NanoDrop2000. Library amplification was carried out as follows: 95 °C, 3 min; 7–8cycle (98 °C 20 s, 60 °C 15 s, 72 °C 30 s); 72 °C, 5 min; 4 °C hold. Reads were trimmed and filtered using fastp (v0.20.1) (Chen et al., 2018b). Assembly was performed using MEGAHIT (v1.2.9) (Li et al., 2015). ORF prediction of assembled contigs (longer than 500 nt) was carried out using prodigal (v2.6.3) (Hyatt et al., 2010). Non-redundant gene sets were built for all predicted genes using MMSeqs2

(v13.45111) (Steinegger et al., 2017). Clustering parameters were 95 % identity and 90 % coverage. The longest gene was selected as representative sequence of each gene set. Clean reads of each sample were aligned against the non-redundant gene set (95 % identity) using salmon (v1.8.0) and the abundant information of the gene in the corresponding sample was counted. The gene set representative sequence (amino acid sequence) was annotated using the NR, KEGG and GO databases with an e-value of $1e^{-5}$ through DIAMOND (v0.9.10.111) (Buchfink et al., 2015). The taxonomy of the species was obtained as a result of the corresponding taxonomy database of the NR Library.

2.5. Statistical analysis

All values are presented as mean \pm standard error (SE). Lower case letters on the bar graphs indicate significant differences between treatments. Significant differences in the soil variables were tested using oneway analysis of variance (ANOVA), followed by the least significant difference (LSD) at $p < 0.05$. ANOVA and Pearson correlation analyses were performed using SPSS 20.0 (IBM Corp., Armonk, NY, USA). DNA was extracted from five replicate samples per land use type, with triplicate PCR amplifications per extract. Fig. 3 data reflect means of biological replicates ($n = 5$). Mothur 1.30.2 (Michigan, Ann Arbor, MI, USA) was used for α diversity analysis, Qiime 1.9.1 (Nau, Flagstaff, AZ, USA) was used for β diversity distance calculation. The “psych” and “reshape2” packages were used for symbiotic network analysis, the “vegan” package for Mantel test correlation analysis, and the “plspm” package for partial least squares path modeling (PLS-PM), all implemented in RStudio 4.2.2 (RStudio Inc., Boston, MA, USA).

3. Results

3.1. Soil physicochemical properties

Compared to non-agricultural land use systems (FL, GL, WL), soil pH, EC, ESP, and SAR values were significantly lower ($p < 0.05$) in the agricultural land use systems (PF, DL, SGH) (Fig. 1 a, b, d, e). Specifically, agricultural land use systems reduced soil pH from 10.65

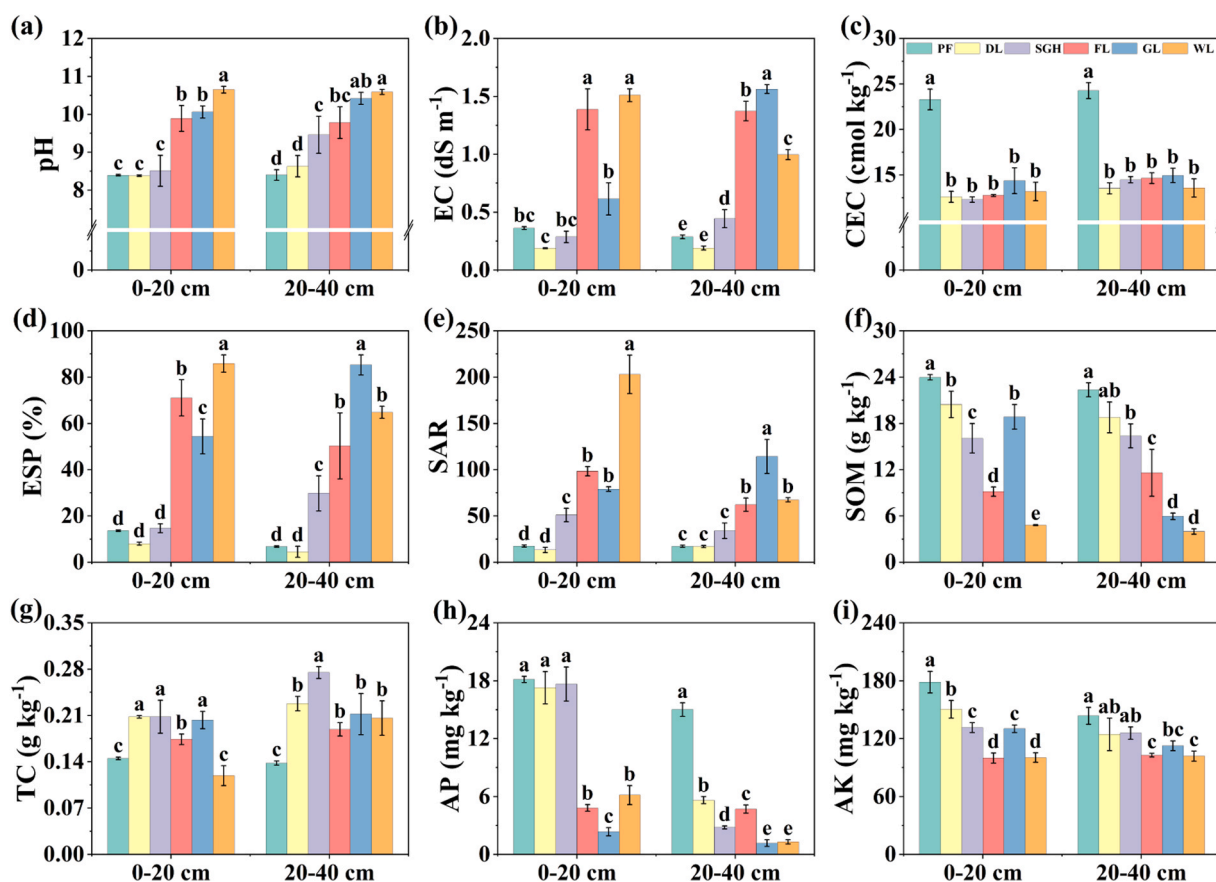


Fig. 1. Soil salinity, alkalinity and nutrient contents under different land uses. Different letters on each column indicate statistically significant differences ($p < 0.05$). pH (a), EC-electric conductivity (b), CEC-cation exchange capacity (c), ESP-exchangeable sodium percentage (d), SAR-sodium adsorption ratio (e), SOM-soil organic matter (f), TC-total carbon (g), AP-available phosphorus (h), AK-available potassium (i). PF-paddy field, DL-dryland, SGH-converted paddy field to dryland, FL-forestland, GL-grassland, WL-wasteland, same below.

units (WL) to 8.38 units, EC from 1.51 dS m⁻¹ to 0.19 dS m⁻¹, ESP from 86 % to 8 %, and SAR from 203–13 ($p < 0.05$). The CEC values of PF were significantly higher ($p < 0.05$) than the other five land use systems (Fig. 1c). Agricultural land use systems also significantly reduced ($p < 0.05$) the soil water-soluble Ca²⁺, Na⁺, K⁺, Mg²⁺, CO₃²⁻ and HCO₃⁻ ion contents (Fig. S1).

Our results showed that SOM content ranged from 4.0 to 24.0 g kg⁻¹, which were significantly higher ($p < 0.05$) in the agricultural land use systems (PF and DL) compared to the other systems (Fig. 1f). Soil TC content ranged from 0.12 to 0.27 g kg⁻¹ with the lowest value for WL and the highest values for DL and SGH in the 0–20 cm soil layer ($p < 0.05$) (Fig. 1g). Soil AP content ranged from 1.2 to 18.1 mg kg⁻¹, with the lowest values for GL and the highest values for PF in both soil horizons ($p < 0.05$) (Fig. 1h). Soil AK content ranged from 99.8 to 178.5 mg kg⁻¹ and was significantly greater in the 0–20 cm soil layer for PF and DL than for the other land types ($p < 0.05$) (Fig. 1i). Thus, SOM, AP and AK were higher in the agricultural land use systems and generally lower in the WL.

Land use practices significantly affected nitrogen fractions in saline-sodic soils (Fig. 2). Soil TN content ranged from 0.25 to 1.51 g kg⁻¹ and was significantly greater in PF and DL than in the other land use systems, with WL having the lowest ($p < 0.05$) TN

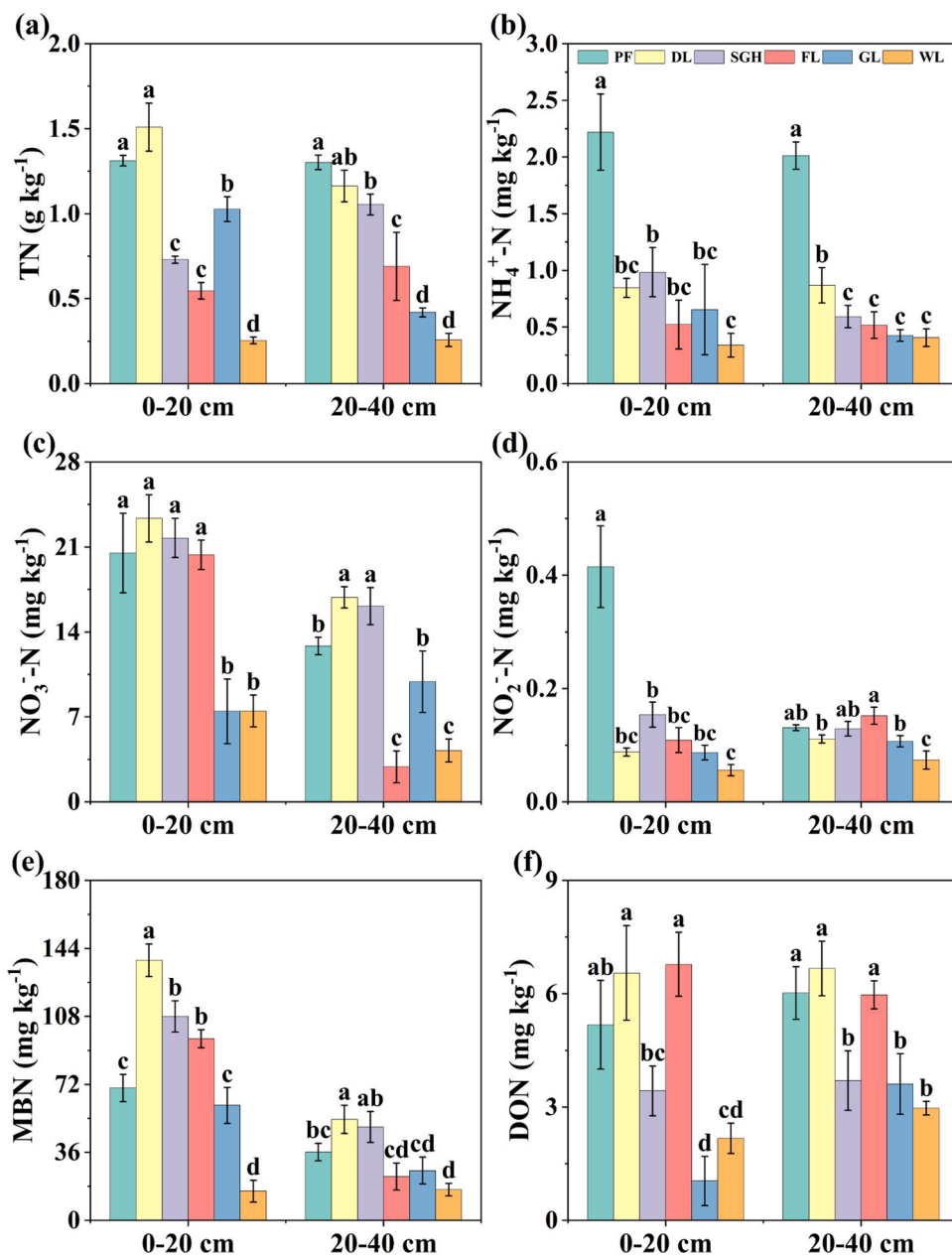


Fig. 2. Soil TN, NH₄⁺-N, NO₃⁻-N, NO₂⁻-N, MBN and DON contents under different land uses. Different letters on each column indicate statistically significant differences ($p < 0.05$). TN-total nitrogen (a), NH₄⁺-N-ammonium nitrogen (b), NO₃⁻-N-nitrate nitrogen (c), NO₂⁻-N-nitrite nitrogen (d), MBN-microbial biomass nitrogen (e), DON-dissolved organic nitrogen (f).

content (Fig. 2a). Soil $\text{NH}_4^+\text{-N}$ content ranged from 0.34 to 2.22 mg kg^{-1} and was significantly higher in PF, while WL had the lowest $\text{NH}_4^+\text{-N}$ content ($p < 0.05$) (Fig. 2b). Soil $\text{NO}_3^+\text{-N}$ content ranged from 2.9 to 23.4 mg kg^{-1} , with DL having highest $\text{NO}_3^+\text{-N}$ content, with values of 23.4 mg kg^{-1} and 16.8 mg kg^{-1} in two soil horizons, respectively ($p < 0.05$) (Fig. 2c). Soil $\text{NO}_2^+\text{-N}$ content of PF was highest with a value of 0.41 mg kg^{-1} and WL had the lowest $\text{NO}_2^+\text{-N}$ content with a value of 0.06 mg kg^{-1} ($p < 0.05$) (Fig. 2d). Soil MBN content ranged from 15.5 to 137.8 mg kg^{-1} and the MBN content of DL was significantly higher ($p < 0.05$) than that of the other land use systems in the 0–20 cm soil layer (Fig. 2e). Soil DON content ranged from 1.0 to 6.7 mg kg^{-1} , and PF, DL and FL store more DON ($p < 0.05$) (Fig. 2f). As a result, agricultural land use systems had higher TN content. In particular, paddy field stored more $\text{NH}_4^+\text{-N}$ and $\text{NO}_2^+\text{-N}$, while dryland stored more $\text{NO}_3^+\text{-N}$, MBN and DON.

3.2. Soil nitrogen cycling microorganisms

3.2.1. Diversity analysis

The diversity of microbial communities involved in the soil nitrogen cycle is shown in Fig. 3. At the phylum level, the microbial communities involved in the soil nitrogen cycle were dominated by the *Proteobacteria*, *Actinobacteria*, *Acidobacteria*, *Gemmatimonadetes* and *Chloroflexi* (Fig. 3a). The relative abundance of *Proteobacteria* was significantly higher ($p < 0.05$) in the PF, DL and SGH than in the FL, GL and WL. Whereas the relative abundance of *Actinobacteria* was significantly lower ($p < 0.05$) in the PF and SGH than in the other land type systems and the relative abundance of *Acidobacteria* was significantly lower in PF than in the other land use systems (Fig. 3a). At the genus level, the dominant genera of PF were *Polaromonas* and *Thiobacillus*, the dominant genus of SGH was *Bradyrhizobium*, the dominant genera of DL were *Pseudomonas* and *Flavobacterium*, the dominant genus of WL was *Streptomyces*, the dominant genera of FL were *Streptomyces*, *Nitriiliruptor* and *Sphingosinicella*, and the dominant genus of GL was *Pontibacter* (Fig. 3b). Taken together, the relative abundance of dominant genera was significantly higher in the PF, DL and SGH than in the FL, GL and WL. The number of species observed and community richness were lowest in DL, with higher values found in the non-agricultural land use system compared to the agricultural land use system (Fig. 3c and d). The Shannon index was highest in PF, which exhibited the greatest community diversity (Fig. 3e).

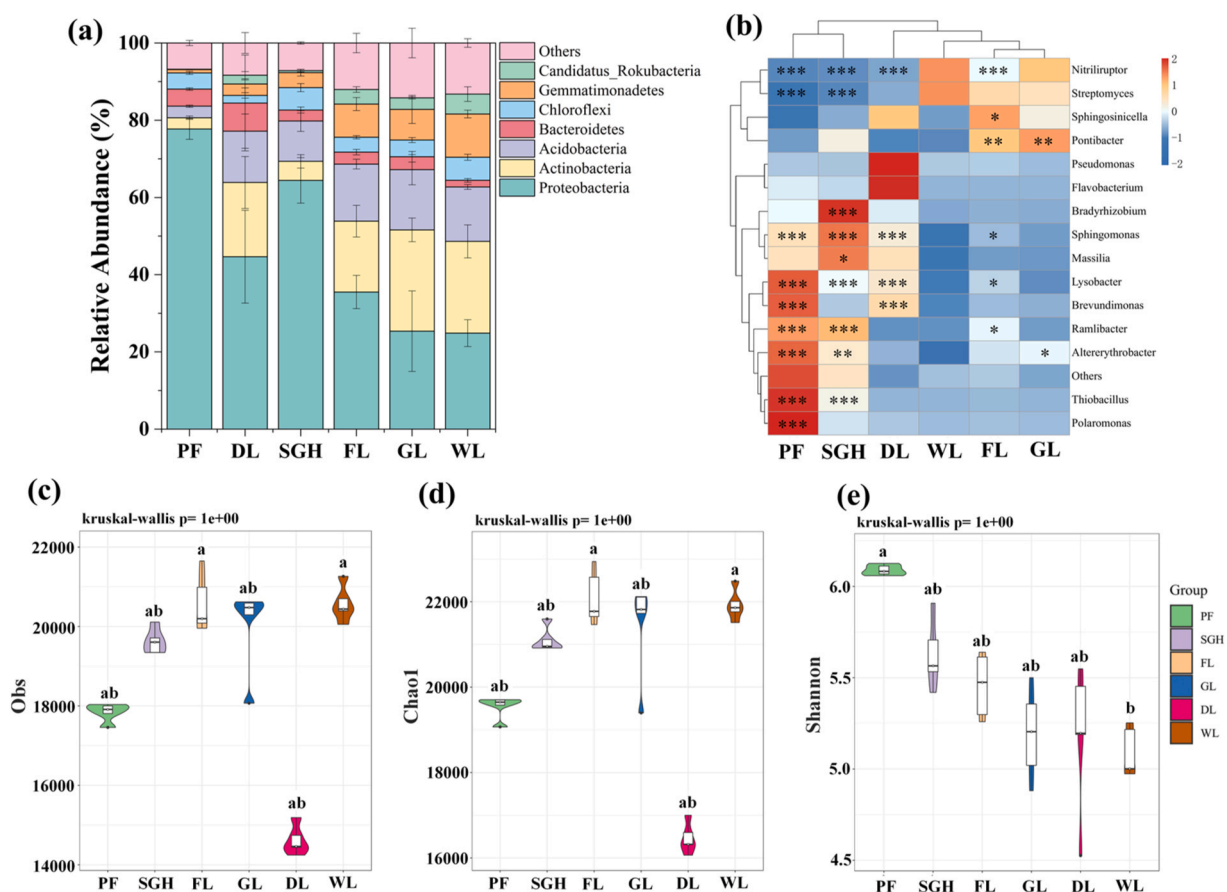


Fig. 3. Species composition and diversity analysis of soil nitrogen cycle under different land uses. Species composition at the phylum level (a), species composition at the genus level (b), Alpha diversity (c-e). Different letters on each column indicate statistically significant differences ($p < 0.05$). *, $0.01 < p < 0.05$, **, $p < 0.01$, ***, $p < 0.001$.

3.2.2. LEfSe analysis

LEfSe analysis used to identify soil nitrogen-metabolizing microbial community taxa as biomarkers under different land use practices. The LDA filtering threshold for the LEfSe analysis was set to 4. In the cladogram, the circles radiating from inside to outside represented the taxonomic level from phylum to genus (Fig. 4a). Statistically distinct biomarkers were also distributed from phylum to genus in Fig. 4b. The highest number of species with significant differences was found in DL with 29 microbial taxa, the lowest in FL with only 4 microbial taxa, and the agricultural land use system had a higher number of significantly different species (Fig. 4b). *Gammaproteobacteria* and *Actinobacteria* in DL, *Betaproteobacteria* in PF, *Proteobacteria* and *Alphaproteobacteria* in SGH, *Actinobacteria* in GL, *Gemmatimonadetes* in WL and *Pseudonocardia* in FL could be used as biomarkers in different treatment groups (Fig. 4b).

3.2.3. KEGG analysis of soil nitrogen metabolism

Soil nitrogen metabolism usually proceeds through six modular pathways, which are nitrogen fixation (M00175), nitrification (M00528), denitrification (M00529), dissimilatory Nitrate Reduction to ammonium (DNRA) (M00530), assimilatory nitrate reduction to ammonium (ANRA) (M00531), and complete ammonia oxidation (M00804) (Fig. 5a-f). The abundance of functional genes corresponding to these six soil nitrogen metabolism modules was shown in Fig. 5g-l. The relative abundance of soil nitrogen fixation modules of PF and SGH was significantly higher ($p < 0.05$) than in the other four land types (Fig. 5a). Additionally, the relative abundance of nitrogen fixation functional genes was highest ($p < 0.001$) in PF (Fig. 5g). The relative abundance of the soil nitrification module was highest ($p < 0.05$) in DL (Fig. 5b), with the nitrification functional genes *pmoA-amoA*, *pmoB-amoB* and *pmoC-amoC* showing the highest ($p < 0.001$) relative abundance (Fig. 5h). Additionally, the highest ($p < 0.05$) relative abundance of soil denitrification, DNRA, and complete ammonia oxidation modules were found in PF (Fig. 5c, d, f). The relative abundance of soil denitrification functional genes (*narG*, *narH*, *norC* and *norB*, etc.), DNRA functional genes (*nrfA*), and complete ammonia oxidation functional genes (*hao*) were significantly higher ($p < 0.001$) in PF than in the other land types (Fig. 5i, j, l). There was no significant

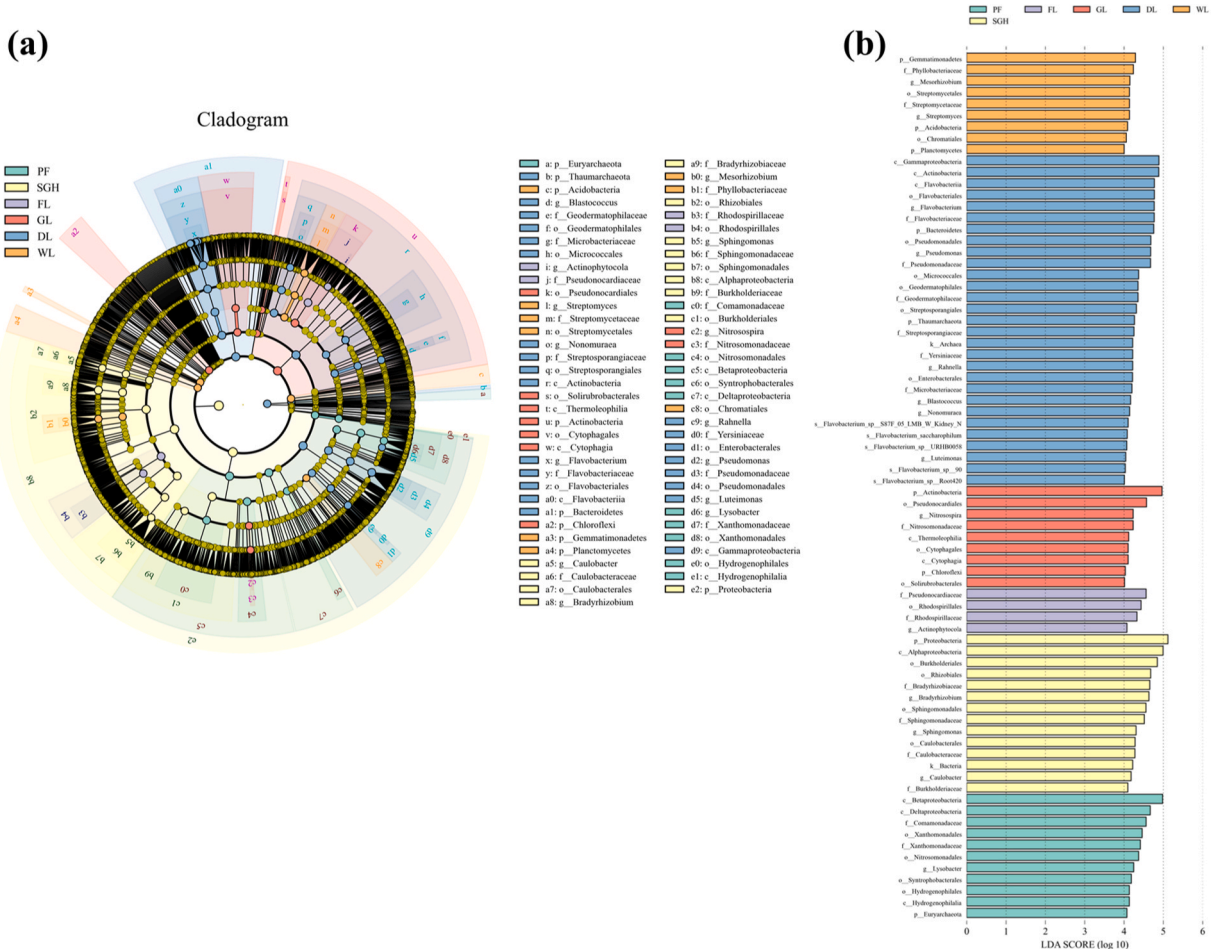


Fig. 4. Linear discriminant analysis (LDA) Effect Size (LEfSe) of soil nitrogen cycle under different land uses. LDP evolutionary cladogram (a) and histogram of LDA value distribution (b). In the cladogram, the taxa associated with small circles and the shading in the colour of a specific soil played an important part in the structure of the microbial community in that soil (significantly different from other soils). The diameter of the small circle represents the relative abundance of the taxa. The taxa without a significant difference are coloured yellow.

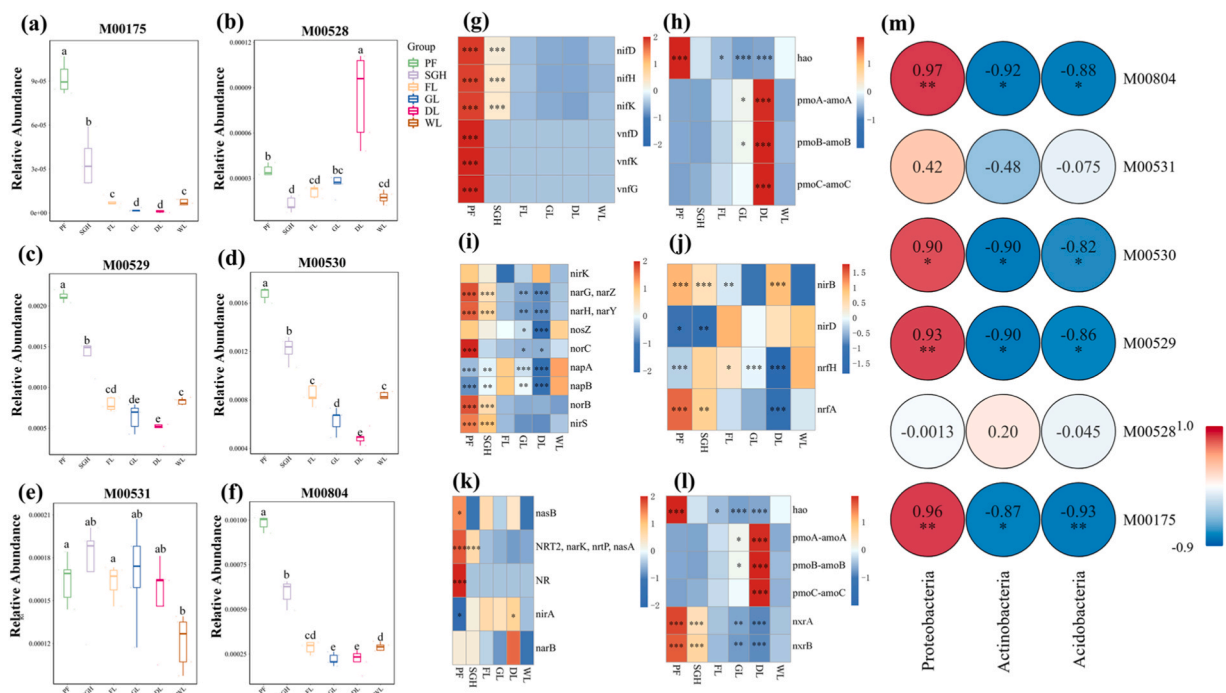


Fig. 5. KEGG analysis of soil nitrogen cycle under different land uses. Module abundance (a-f) and functional gene abundance (g-l) for soil nitrogen fixation (a, g), nitrification (b, h), denitrification (c, i), DNRA (d, j), ANRA (e, k) and complete ammonia oxidation (f, l). Pearson correlation analysis of abundance of three microbial communities and abundance of nitrogen metabolism modules at the phylum level (m). *, ** and *** Significant effects at 0.05, 0.01 and 0.001 probability level, respectively.

difference in the relative abundance of ANRA modules among the land types (Fig. 5e). The highest ($p < 0.05$) relative abundance of soil ANRA functional genes *NR*, *nasA* and *nasB* was found in PF (Fig. 5k).

3.3. Correlation analysis of soil physicochemical properties, microbial communities and functional genes abundance

3.3.1. Symbiotic network analysis

The symbiotic network of microbial communities and soil environmental factors at the level of soil nitrogen metabolizing genera is shown in Fig. 6. In PF soils, MBN, $\text{NO}_2\text{-N}$, SOM, Mg^{2+} , and DON showed correlation with soil nitrogen metabolizing microbial genera (Fig. 6a). *Pseudoxanthomonas* showed positive correlation with SOM, MBN, and Mg^{2+} , and negative correlation with $\text{NO}_2\text{-N}$ and DON (Fig. 6a). *Thiobacillus* was negatively correlated with MBN, Mg^{2+} and SOM (Fig. 6a). In DL soils, ESP, CO_3^{2-} , and $\text{NO}_3\text{-N}$ correlated with soil nitrogen-metabolizing microbial genera (Fig. 6b). *Rubrobacter* showed a negative correlation with ESP, while *Agrobacterium* and *Pseudomonas* showed a positive correlation (Fig. 6b). *Novosphingobium* and *Blastococcus* were negatively correlated with CO_3^{2-} , whereas *Sphingosinella*, *Luteimonas*, *Nonomuraea*, and *Steroidobacter* were positively correlated with $\text{NO}_3\text{-N}$ (Fig. 6b). In FL soils, *Kutzneria* and *Actinophytocola* were negatively correlated with ESP, EC and Mg^{2+} (Fig. 6d). In GL soils, *Nitrosospora* was positively correlated with CO_3^{2-} (Fig. 6e). In WL soils, *Gemmatirosa* showed positive correlation with $\text{NO}_3\text{-N}$, TN and negative correlation with DON. *Janthinobacterium* was positively correlated with SOM and AK, and negatively correlated with pH, CEC, and K^+ (Fig. 6f). Comparison of the topological characteristics of the networks revealed that the co-occurring networks of DL, PF, and WL exhibited higher nodes, edges, average degree, network diameter, and average path length, suggesting that the networks were more connected and that nitrogen-metabolizing microbial communities were more intricately and tightly linked to each other (Table S1). The modularity indices of the co-occurring networks of FL, DL, GL, and PF were greater than 0.44, suggesting that the nitrogen-metabolizing microbial communities and environmental factors have formed a certain modularity (Table S1).

3.3.2. Mantel test and PLS-PM analysis

Mantel test analysis of soil physicochemical properties and abundance of functional genes classified into six nitrogen metabolism modules was shown in Fig. 7. Soil salinity and alkalinity indicators (pH, EC, ESP, SAR, water-soluble salt ions) were significantly positively correlated ($p < 0.05$) with each other, whereas SOM, AP, AK, TN, and soil salinity and alkalinity were significantly negatively correlated ($p < 0.05$) (Fig. 7). Soil $\text{NH}_4^+\text{-N}$ was significantly positively correlated ($p < 0.05$) with CEC and AK (Fig. 7). Soil $\text{NO}_3\text{-N}$ and pH were significantly negatively correlated ($p < 0.05$) (Fig. 7). Soil $\text{NO}_2\text{-N}$ was significantly positively correlated ($p < 0.01$) with CEC and $\text{NH}_4^+\text{-N}$ (Fig. 7). Soil MBN was significantly negatively correlated ($p < 0.05$) with CO_3^{2-} and positively correlated ($p < 0.05$) with $\text{NO}_3\text{-N}$ (Fig. 7). Soil DON and $\text{NO}_3\text{-N}$ were significantly positively correlated ($p < 0.05$) (Fig. 7). Notably, there were significant

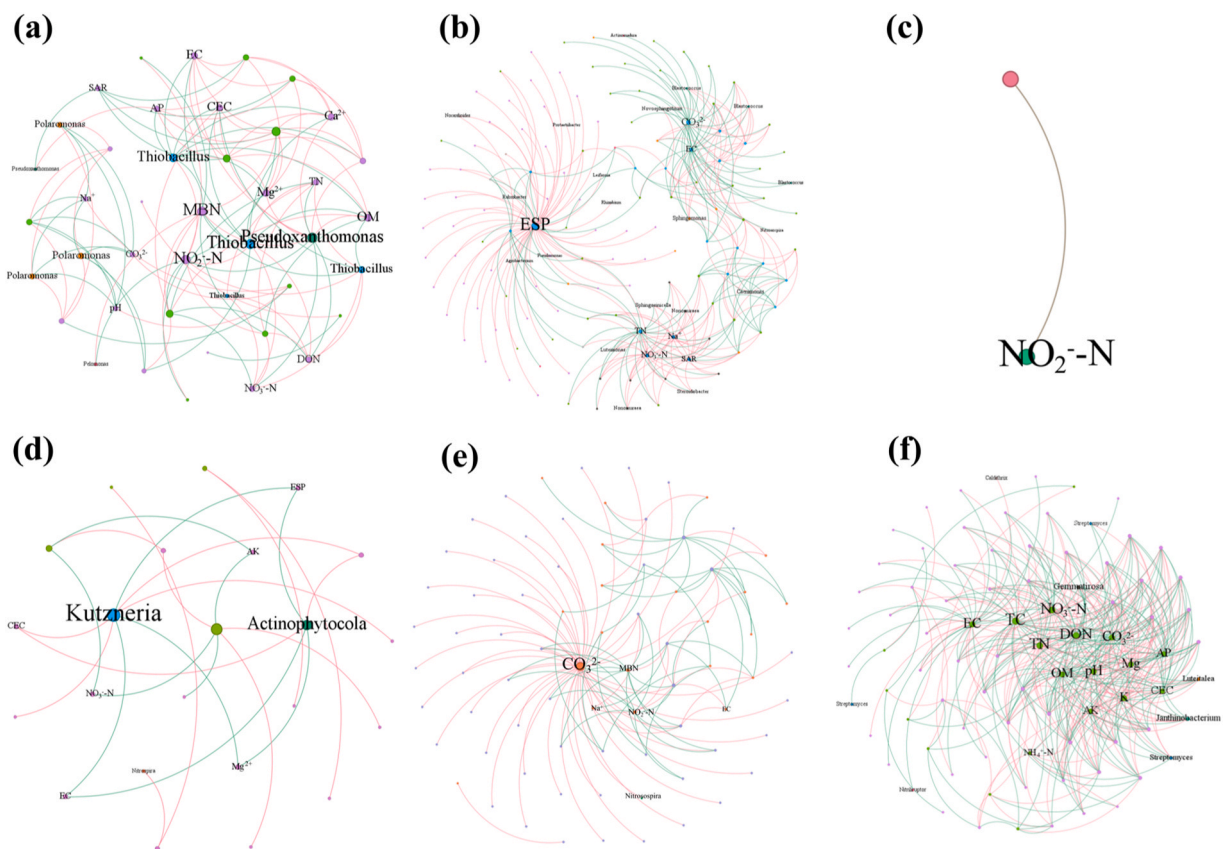


Fig. 6. Symbiotic network analysis of soil physicochemical properties and nitrogen metabolizing microbial genera in different land uses. Paddy field (a), dryland (b), converted paddy field to dryland (c), forestland (d), grassland (e) and wasteland (f). (Red line indicates positive correlation, green line indicates negative correlation.).

correlations between soil nitrogen fixation, nitrification, denitrification, ANRA, and complete ammonia oxidation metabolism gene abundance with soil $\text{NH}_4^+\text{-N}$ and $\text{NO}_2\text{-N}$, as well as significant correlation between soil DNRA metabolism gene abundance and soil pH (Fig. 7). Therefore, we conducted PLS-PM analysis to further investigate the direct and indirect effects of soil physicochemical properties on soil $\text{NH}_4^+\text{-N}$, $\text{NO}_2\text{-N}$, pH and soil nitrogen metabolism processes under different land uses (Fig. 8). Soil nutrients had significant positive indirect effects on soil nitrogen fixation, denitrification, ANRA, and complete ammonia oxidation processes by influencing $\text{NH}_4^+\text{-N}$ and $\text{NO}_2\text{-N}$ (Fig. 8a, c, d, f). Soil nutrients directly influenced soil nitrification and DNRA processes (Fig. 8b, e). Soil salinity and alkalinity had a direct significant negative effect on soil nitrogen fixation, denitrification, ANRA and complete ammonia oxidation processes (Fig. 8a, c, d, f). Soil $\text{NO}_2\text{-N}$ had the largest standardized positive total effect on soil nitrogen fixation, denitrification, ANRA and complete ammonia oxidation processes, whereas salinity metrics had the largest standardized negative total effect on these five processes (Fig. 8g, i, j, l). Soil nutrients had the largest standardized positive total effect on soil nitrification and DNRA processes (Fig. 8h, k).

4. Discussion

4.1. Soil salinization mitigation and nutrient enrichment through agricultural land use systems

Traditionally, land use transformation involved mutual transformation of forestland, grassland, and cropland, among others. (Fuchs et al., 2015). Reasonable land use practices not only mitigate soil salinization, improve soil carbon and nitrogen fixation capacity, and reduce nutrient loss, but also improve soil quality and mitigate climate change (Blaud et al., 2018). In this study, compared to non-agricultural land use systems, agricultural land use systems significantly reduced soil pH, EC, ESP, and SAR while significantly increased SOM, AP and AK contents (Fig. 1). This could be attributed to the fact that salt leaching effect during the cultivation of crops, such as rice and maize, along with the substances secreted by the roots of the crops, could lower the soil pH and salinity (Xu et al., 2020). In addition, straw return measures could replenish organic acids in saline-sodic soils and lower soil pH (Shao et al., 2022). Elevated SOM and AP/AK under agriculture are attributed to organic amendments (e.g., manure) and phosphate/potash fertilization (Cui et al., 2018; Qi et al., 2021). These inputs offset salt-induced nutrient immobilization, promoting microbial mineralization. The

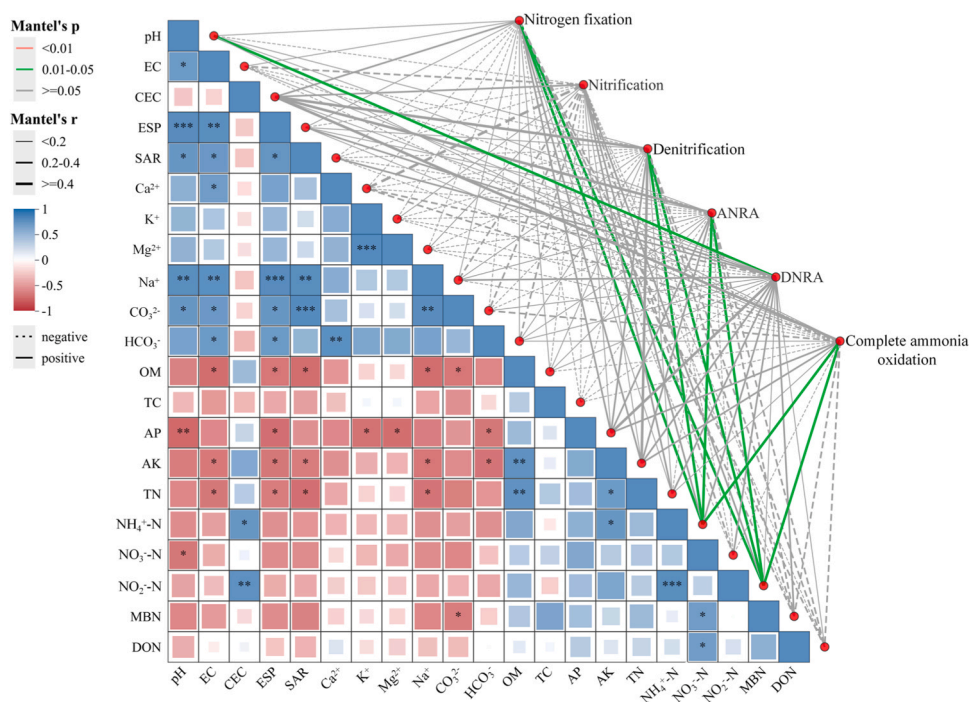


Fig. 7. Mantel test analysis of soil nitrogen cycle under different land uses. Pairwise correlations of soil properties are shown, with red and blue indicating Pearson's correlation. Vector length and angle are related to each soil property by the Mantel test. Edge width corresponds to Mantel's r value, edge color denotes statistical significance. Shaded areas show 95 % confidence intervals of the fit in the line regression analysis.

SOM content in the 0–20 cm soil layer of FL soils was significantly lower than that of GL soils, while in the 20–40 cm layer, it was significantly higher in FL soils than in GL soils (Fig. 1f). This might be because grass roots were short and die easily, storing organic matter at the surface, while forestland plants had long roots and tended to store more organic matter at deeper depths (Anderson et al., 2019). Therefore, artificial agricultural management measures could reduce soil saline-alkali stress and increase soil nutrient through crop-root secreted substances and straw returning measures.

It has been reported that soil nitrogen inputs vary widely depending on the type of vegetation cover under different land use practices. In this study, the highest soil TN was observed in PF and DL soils, with highest $\text{NH}_4^+\text{-N}$ found in PF soils, and highest $\text{NO}_3^+\text{-N}$ and MBN in DL soils (Fig. 2). These results are similar to those of Gao et al. (2014), who proposed that orchard and farmland soils exhibited higher N density and storage than forest soils. As is widely known, soil nitrogen in paddy fields mainly exists in the form of NH_4^+ , while in dryland soils, it primarily exists as $\text{NO}_3^+\text{-N}$ (Chen et al., 2018a; Liu et al., 2015). $\text{NO}_3^+\text{-N}$ is easily lost due to runoff and water leaching when planting rice. Meanwhile, the anaerobic environments of paddy field tends to promote soil denitrification and $\text{NH}_4^+\text{-N}$ accumulation (Wang et al., 2022). As a result, the $\text{NO}_3^+\text{-N}$ content in paddy fields is usually lower than that in dryland soils, while the $\text{NH}_4^+\text{-N}$ content follows the opposite trend. Dryland is mostly an aerobic environment, which provides a suitable habitat for soil microorganisms and improves the decomposition efficiency of apoplastic materials (Gong et al., 2022). These could be the reasons why dryland soils shared great MBN content. In addition, compared to wasteland, grassland and agricultural soils exhibit higher DON content due to fertilizer inputs, and forestland has higher DON content due to the input and decomposition of apoplastic matter from plants (Liu et al., 2016). Thus, we propose that agricultural land use practices contribute to enhancing soil nitrogen storage in saline soils.

4.2. Microbial community enhancement driving nitrogen transformation in agricultural land use systems

Changes in land use practices can directly affect soil physicochemical properties and reshape the community composition. In this study, land use practices significantly altered the microbial community composition (Fig. 3a). Specifically, the relative abundance of *Proteobacteria* was significantly higher in the three agricultural soils (PF, DL and SGH) than in non-agricultural soils, a pattern also observed by Bai et al. (2022) in their study of grassland-to-cropland conversion in North China. Conversely, the abundance of *Actinobacteria* and *Acidobacteria* was significantly lower in PF and SGH than in other land types (Fig. 3a). Dominance of *Proteobacteria* aligns with studies of saline-alkali soils (Gu et al., 2022), where their halotolerance and role in N-cycling under stress are established. The disruption of soil aggregates and accelerated mineralization of organic matter induced by anthropogenic tillage alters physicochemical properties (e.g., aeration, moisture distribution, nutrient availability) and creates localized microenvironments, thereby favoring the proliferation of copiotrophic bacterial phyla such as the *Proteobacteria* (Goldfarb et al., 2011). It has been reported that *Actinobacteria* can easily survive in neutral and alkaline conditions, while *Acidobacteria* thrive in low nutrient environments (Peng

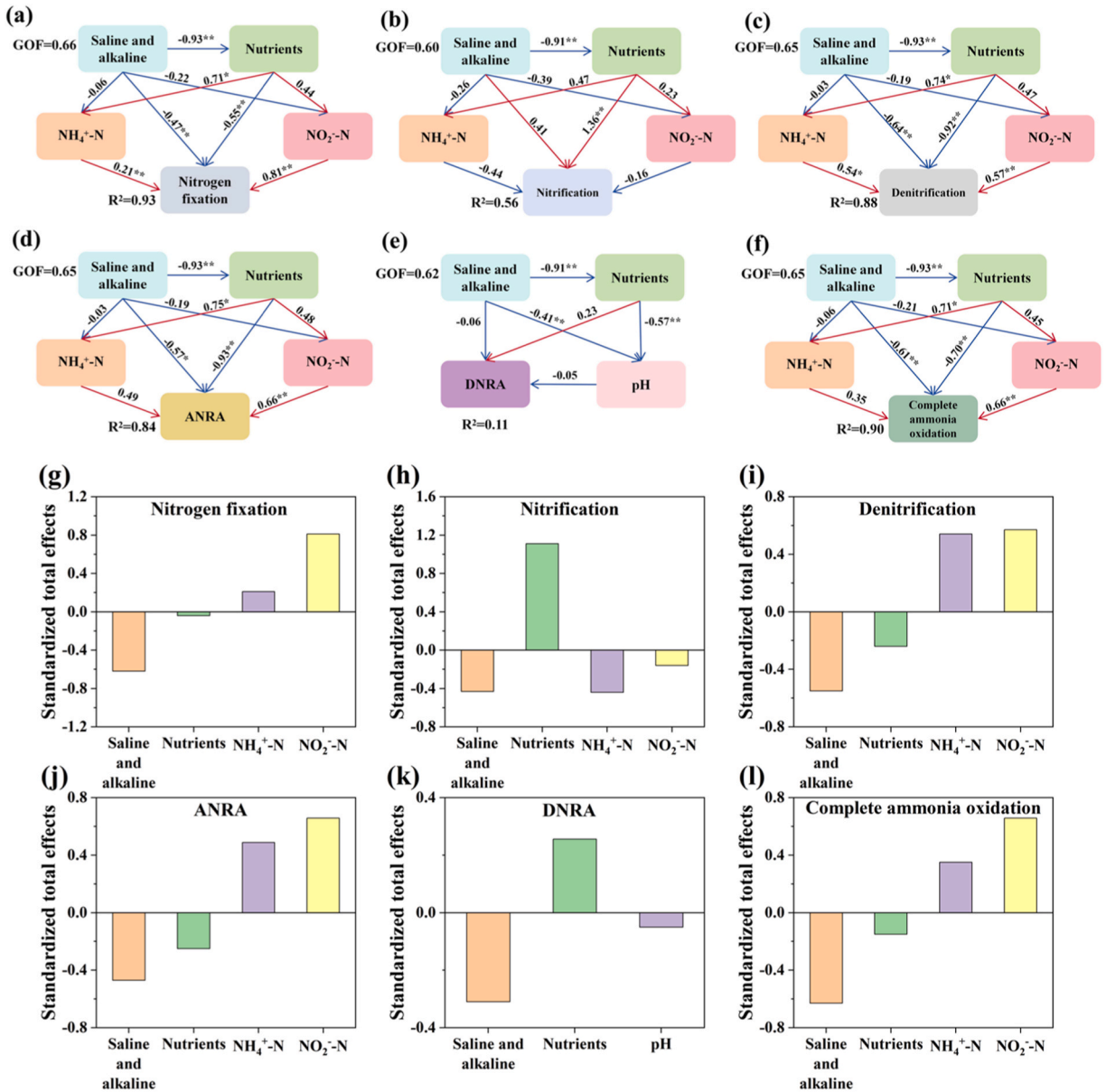


Fig. 8. Partial least squares path model (PLS-PM) analysis showing effect of soil environmental factors on soil nitrogen cycle under different land uses (a-f) and standardized total effects of variables (g-l). Note: The numbers adjacent to arrows are standardized path coefficients. Goodness-of-fit statistics for model is shown below the model. *, 0.01 < p < 0.05, **, p < 0.01, ***, p < 0.001.

et al., 2017); thus, these two phyla are well adapted to salinized and non-agricultural soils. Additionally, our study found that species diversity and community richness were greater in non-agricultural systems (Fig. 3c, d). This is likely because agricultural system is ploughed for monoculture cropping, which reduces species richness (Beckmann et al., 2019). The increased diversity in PF and SGH (Fig. 3e) was likely due to improved soil structure and pore space resulting from plowing method of tillage, which enhanced microbial community distribution and diversity (Connell, 1978). LEfSe analysis revealed that the number of biomarkers was significantly higher in agricultural soils than in non-agricultural systems, with the highest number observed in DL (Fig. 4). This findings aligns with earlier studies by Zheng et al. (2022), who suggested that dryland could enrich microbial species due to factors such as tillage, fertilization and aerobic environment, compared to abandoned land. Therefore, the microbial communities in agricultural land systems exhibited greater responsiveness to soil conditions than those in non-agricultural land use systems. Thus significant enrichment of microbial communities may be associated with their role in resisting salinity stress and promoting nitrogen conversion functions.

A nitrogen metabolism (ko00910) functional gene set was constructed to annotate nitrogen metabolism-related functions. KEGG analysis showed that nitrogen metabolism genes were most abundant in paddy field for fixation, denitrification, DNRA, and ammonia

oxidation, whereas in dryland, they were most abundant for nitrification (Fig. 5). Consequently, we assumed that agricultural land use systems exhibited a superior capacity to facilitate the metabolic transformation of soil nitrogen compared to non-agricultural land use systems. Paddy field are affected by nutrient and fertilizer inputs during ploughing, which significantly enhance their nitrogen fixation capacity (Li et al., 2022). Whereas the anaerobic environment promote denitrification and DNRA processes in paddy soil nitrogen (Tang et al., 2024; Wei et al., 2022). Moreover, DNRA process has the potential to reduce nitrogen loss by competing with denitrification and anaerobic ammonia oxidation processes in paddy soils (Putz et al., 2018). The high abundance of *hao* and *narG/H* genes in paddy field and their high capacity for complete ammonia oxidation also echoed the high $\text{NO}_2\text{-N}$ content in paddy field (Fig. 5). Besides, Luo et al. (2023) found that land use conversion from dryland to paddy field increase soil nitrogen fixation and decrease soil nitrification and N_2O production, which was similar with our study. Dryland soils had the highest gene abundance of *pmoA/B/C-amoA/B/C* (Fig. 5h), as they were well aerated and had a high nitrification potential; however, future studies should further investigate nitrate accumulation in these soils. Notably, *Proteobacteria* played a major role in soil N metabolism processes in agricultural land use soils (Hou et al., 2023; Zhang and Lv, 2021), which aligns with our results on soil nitrogen fixation, denitrification, DNRA, and complete ammonia oxidation processes (Fig. 5m). These processes were particularly significant in paddy fields (Figs. 3a and 5). Our results further suggest that agricultural practices, especially fertilizer use and crop management, can facilitate key processes in soil nitrogen cycling by enhancing microbial communities.

4.3. Determinants of N-metabolizing microbial communities and nitrogen transformation: Soil pH, $\text{NH}_4^+\text{-N}$ and $\text{NO}_2\text{-N}$

Changes in land use practices affect the physicochemical properties of soils, thereby shifting the soil microbial communities (Sui et al., 2019; Turley et al., 2020). Our study showed a strong relationship between the abundance of soil nitrogen-metabolizing microbial community and soil properties under different land use types (Fig. 6). For instance, *Pseudoxanthomonas* and *Thiobacillus* in paddy fields were associated with soil SOM, MBN and Mg^{2+} (Fig. 6a). Higher SOM content elevated the abundance of *Pseudoxanthomonas* (Fig. 6a), thereby promoting nitrogen fixation (Gao et al., 2024). Additionally, *Thiobacillus* increase was accompanied by a decrease in mg^{2+} (Fig. 6a). This is similar to a previous study in which *Thiobacillus* could lower soil saline by increasing soil sulfate content (Xiao et al., 2023). Furthermore, changes in soil salinity and nutrients are important factors affecting microbial diversity, especially in agricultural ecosystems. Increased nutrient inputs from fertilizers, manure, and crop residues can enhance bacterial and fungal interactions with soil nitrogen metabolizing nutrients (Kang et al., 2024). In summary, soil salinity and nutrients were key factors affecting soil nitrogen metabolism microbial communities, which differ with land use practices.

Both Mantel test and PLS-PM analysis showed that soil salinity, alkalinity, and nutrients influence nitrogen processes (Figs. 7–8). Soil properties (SOM and pH) emerged as important drivers influencing the abundance of functional genes (*nifH*, *amoA*, *norB*, and *nosZ*) during the nitrogen cycle (Li et al., 2024). This is similar to our findings that soil salinity and nutrients drive nitrogen metabolic processes and functional genes for nitrogen metabolism (Fig. 8). Additionally, Soil pH and $\text{NO}_2\text{-N}/\text{NH}_4^+\text{-N}$ were significantly correlated with the abundance of microbial functional genes during the nitrogen transformation processes, which is consistent with our findings that $\text{NO}_2\text{-N}$ and $\text{NH}_4^+\text{-N}$ are key determinants of soil N metabolism processes (Fig. 8) (Chen et al., 2021). NH_4^+ is the main substrate of nitrification and its availability directly constrains the rate of nitrification, whereas the concentration of NO_2^- as a central intermediate in nitrification and denitrification-regulates denitrification efficiency and N loss pathways (e.g., N_2O emissions) (Chen et al., 2015; Zhang et al., 2019b). In contrast, $\text{NO}_3\text{-N}$ is more stable but less biochemically constrained, thus $\text{NH}_4^+\text{-N}$ and $\text{NO}_2\text{-N}$ are closer to regulators of microbial activity and N fluxes (Zhang et al., 2018). However, since changes in soil properties affected the denitrification, future research should focus on nitrogen loss from this process. Additionally, our results showed that agricultural land use systems, especially paddy fields and drylands, played an important role in increasing soil nitrogen content and promoting nitrogen metabolism transformation processes. This is because management practices (e.g. tillage and fertilization) can directly and indirectly affect soil nutrient transformation. Therefore, the research and development of new, efficient fertilizers is urgent for enhancing nitrogen use efficiency and ensuring the sustainable management of salinity-affected farmland.

5. Conclusion

In conclusion, agricultural land use systems (PF, DL and SGH) significantly decreased soil pH, EC, ESP, SAR, and water-soluble salt ion contents, while significantly increasing SOM, AP and AK contents, compared to non-agricultural land use systems (FL, GL and WL). Moreover, agronomic management practices, especially in PF and DL, significantly enhanced microbial community diversity and enriched nitrogen metabolism-related microorganisms, thereby contributing to soil nitrogen gene abundance and transformation (N fixation, nitrification and DNRA). Soil ESP, CO_3^{2-} , $\text{NO}_2\text{-N}$, $\text{NO}_3\text{-N}$, and MBN were important factors for soil nitrogen-metabolizing microbial communities. More importantly, $\text{NH}_4^+\text{-N}$, and $\text{NO}_2\text{-N}$ were critical determinants of the dynamics of soil nitrogen metabolism. In summary, in the saline-sodic soils of the Songnen Plain, compared to abandoned land, the selection of salt-tolerant crops, combined with optimized fertilizer management (particularly organic amendments or balanced NPK to boost nutrients) and improved water management (controlled irrigation or drainage to leach salts), were effective measures to improve soil salinization, promote N cycling, and increase N efficacy. Practices in paddy field and dryland systems were most impactful for enhancing microbial-mediated N processes. Further research should focus on the sustainable practices for managing saline-sodic soils and the development of new, efficient fertilizers, to reduce soil salinization, increase soil nitrogen storage, and improve soil nitrogen utilization.

CRedit authorship contribution statement

Xueqin Ren: Supervision, Formal analysis. **Qilin Lv:** Resources, Investigation. **Tairan Zhou:** Methodology, Investigation, Data curation. **Marcela Hernández:** Writing – review & editing, Methodology. **Hong Pan:** Writing – review & editing, Resources, Formal analysis. **Haojie Feng:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Shuwen Hu:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Xu Yang:** Methodology, Investigation. **Xuepeng Zhou:** Methodology, Investigation. **Tianhao Wang:** Software, Methodology, Formal analysis. **Yunshan Meng:** Writing – review & editing, Writing – original draft, Methodology, Investigation.

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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.eti.2025.104363](https://doi.org/10.1016/j.eti.2025.104363).

Data Availability

The raw reads were deposited into the NCBI Sequence Read Archive (SRA) database (Accession Number: PRJNA1226390).

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