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Rhizosphere microbial community construction during the latitudinal spread of the invader *Chromolaena odorata*

Ming-zhu Zhang[1], Wei-tao Li[1*], Wen-jun Liu[1] and Yu-long Zheng[1*]

Abstract

The colonization of alien plants in new habitats is typically facilitated by microorganisms present in the soil environment. However, the diversity and structure of the archaeal, bacterial, and fungal communities in the latitudinal spread of alien plants remain unclear. In this study, the rhizosphere and bulk soil of *Chromolaena odorata* were collected from five latitudes in Pu' er city, Yunnan Province, followed by amplicon sequencing of the soil archaeal, bacterial, and fungal communities. Alpha and beta diversity results revealed that the richness indices and the structures of the archaeal, bacterial, and fungal communities significantly differed along the latitudinal gradient. Additionally, significant differences were observed in the bacterial Shannon index, as well as in the structures of the bacterial and fungal communities between the rhizosphere and bulk soils. Due to the small spatial scale, trends of latitudinal variation in the archaeal, bacterial, and fungal communities were not pronounced. Total potassium, total phosphorus, available nitrogen, available potassium and total nitrogen were the important driving factors affecting the soil microbial community structure. Compared with those in bulk soil, co-occurrence networks in rhizosphere microbial networks presented lower complexity but greater modularity and positive connections. Among the main functional fungi, arbuscular mycorrhizae and soil saprotrophs were more abundant in the bulk soil. The significant differences in the soil microbes between rhizosphere and bulk soils further underscore the impact of *C. odorata* invasion on soil environments. The significant differences in the soil microbiota along latitudinal gradients, along with specific driving factors, demonstrate distinct nutrient preferences among archaea, bacteria, and fungi and indicate complex microbial responses to soil nutrient elements following the invasion of *C. odorata*.

Keywords *Chromolaena odorata*, Rhizosphere, Soil microorganisms, Amplicon sequencing

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Introduction

Plant invasion can change soil biochemical properties, nutrient cycling and microbial diversity, leading to ecological imbalances [1]. As crucial components of the soil ecosystem, soil microorganisms play important roles in decomposing organic matter and promoting soil nutrient cycling [2–4]. Invasive plants can modify the structure of soil microbial communities, creating a favourable soil environment for their own growth [5]. Soil microbial communities can mitigate the effects of invasive plants on local plant communities through allelochemical degradation, symbiotic interactions with arbuscular mycorrhizae fungi, or inhibition through pathogen accumulation [6]. The interaction between invasive plants and soil microorganisms has gained increasing attention, and understanding their interrelationship is highly important.

Soil microbial communities encompass a wide array of organisms, including bacteria, archaea, fungi, protists, nematodes, and viruses [7]. Among them, archaea, bacteria, and fungi constitute vital components of the soil microbiota and are often regarded as the cornerstone of soil food webs, playing indispensable roles in the global cycling of elements such as carbon, nitrogen, and sulfur, as well as in soil structure formation [8]. It is generally believed that the global richness of most soil taxonomic groups follows a similar trend to that of aboveground taxa, with richness increasing towards warm and humid tropical regions [9]. However, studies suggest that soil microbes may exhibit different latitudinal trends at the global scale. Some research has indicated a decrease in soil bacterial diversity with increasing latitude [10], whereas fungal diversity shows a unimodal distribution along latitudinal gradients [11]. Alternatively, bacterial diversity may exhibit a hump-shaped pattern with latitude, and fungal diversity may decrease with latitude [12], or even show weak or nonexistent latitudinal patterns in soil microbial community composition [13]. There is no consensus on the latitudinal trends of soil microbial richness and diversity. Similarly, archaea, bacteria, and fungi respond differently to environmental factors across various ecological scales. In temperate forests, average temperature, soil pH, and total nitrogen content are key environmental factors influencing bacterial diversity and composition across latitudes [10]. In continental forest systems, pH and the N: P ratio are the best predictors of the latitudinal distribution of bacterial diversity [12]. These studies have focused mainly on larger-scale latitudinal gradients, and little is known about the effects of environmental factors on microbial community assembly in consistent ecosystems along smaller-scale latitudinal gradients. It remains unknown whether soil microbial communities (archaea, bacteria, fungi) associated with *C. odorata* are subject to changes with latitude and what the primary influencing factors are.

The "rhizosphere" refers to the interface between plant roots and soil, which often exhibits "rhizosphere effects" [14]. Owing to these effects, specific microbial communities are typically enriched in the rhizosphere [15]. In this context, root exudates play a significant role and have been proven to be important driving factors in shaping the composition of rhizosphere microbial communities [16]. Plant roots release compounds that alter available substrates and signalling molecules, thereby attracting and determining the rhizosphere microbiota [17]. Bulk soil serves as a reservoir for microbial diversity, from which rhizosphere-associated microbial communities can absorb and select [18]. Although the rhizosphere and bulk soils are interrelated, differences in the construction, structure, and function of microbial communities occur [19]. For instance, the rhizosphere of the invasive plants *Mikania micrantha* has a distinct bacterial community structure that is clearly separated from the bulk soil [20]. A widespread invasive tree, *Acacia dealbata* whose rhizospheric microbial communities differ significantly in structure and composition from those of the bulk soil, with two bacterial (Alpha-proteobacteria and Gamma-proteobacteria) and two fungal (Pezizomycetes and Agaricomycetes) classes were enriched in the rhizosphere compared with those in bulk soils [21]. The rhizosphere soil microbial diversity of *Bidens pilosa* is greater than that of bulk soil, with pH being the primary environmental factor causing differences in microbial community composition between rhizosphere and bulk soils [22]. Understanding the diversity and composition of soil microbial communities following invasion by *C. odorata*, as well as differences between rhizosphere and bulk soil microbial communities, is crucial for exploring the mechanisms of plant invasion.

In this study, we investigated the soil microbial community diversity in rhizosphere and bulk soils at five latitudes naturally invaded by *C. odorata* in Pu' er city. *Chromolaena odorata* (Linnaeus) R. M. King & H. Robinson is a common invasive species in tropical and subtropical areas [23] and is known for its strong competitive ability [24]. By altering the soil nutrient cycle and enhancing nutrient utilization, *C. odorata* creates a favourable soil environment for its own growth and propagation [25]. It is considered one of the most noxious plant species worldwide and poses a severe threat to invaded ecosystems [26]. Previous research on *C. odorata* has focused largely on its invasive competitive ability, with a limited understanding of its influence on the latitudinal patterns of soil microbial communities. In this study, we examined the differences in archaeal, bacterial and fungal communities between the rhizosphere and bulk soils of *C. odorata* among different latitudinal regions, as well as their main influencing factors. We hypothesized that (1) the diversity and structure of archaeal, bacterial, and

fungal communities in the rhizosphere and bulk soils may be significantly different along the latitudinal gradient; (2) the composition of archaeal, bacterial, and fungal communities is influenced by different soil factors. Therefore, the main objectives of our study were to (1) investigate the variations along latitudinal gradients in the rhizosphere and bulk soils microbial communities of the *C. odorata*; (2) explore whether changes in latitudinal gradients have different impacts on archaeal, bacterial and fungal communities; and (3) determine the primary driving factor in archaeal, bacterial and fungal community composition.

Materials and methods

Site description and soil Sampling

The sampling sites are located in Pu' er, Yunnan Province, Southwest China (99°09′~102°19′E, 22°46′~24°26′N) (Fig. 1), with an altitude of 376~3,306 m. The climate here is warm and humid, with an average annual temperature of 15 ℃~20.3 ℃ and an annual rainfall of 1,100~2,800 mm. The abundant landforms and favourable climate, coupled with the border location, are typical invasion areas of *C. odorata*.

Soil samples were collected by selecting typical invasion sites of *C. odorata* along the latitudinal path in Pu' er, and rhizosphere and bulk soil samples were collected at each site. Rhizosphere soil was obtained from the surface layer of 1–2 mm thickness surrounding the roots of *C. odorata*, whereas bulk soil was obtained from the general soil. A total of 40 samples (5 invasion sites × 4 repetitions × 2 locations) were obtained. Some of the soil samples were filtered through a 2 mm sieve, refrigerated at −40 °C and sent to Shanghai Maiyobio Biopharm Technology Co., Ltd. (Shanghai, China) for subsequent DNA extraction and sequencing. The remaining soil samples were air-dried, ground, and sieved by a 2 mm sieve to determine the soil nutrients.

PCR amplification of DNA and sequence data processing

Total genomic DNA was extracted from 0.5 g of fresh soil via the Fast DNA™SPIN Kit (MP Biomedicals, Santa Ana, CA, USA) in accordance with the manufacturer's protocol. The microbial diversity was analysed via Illumina HiSeq sequencing. The hypervariable regions of the archaea were amplified with the primers 524F10extF (5′-TGYCAGCCGCCGCGGTAA-3′) and Arch958RmodR (5′-YCCGGCGTTGAVTCCAATT-3′) [27]. The hypervariable regions of the bacteria were amplified via the primers 515F (5' -GTGYCAGCMGCCGCGGTAA-3') and 907R (5′-CCGTCAATTCMTTTRAGTTT-3′) [28]. The hypervariable regions of the fungi were amplified via the primers SSU0817F (5'-TTAGCATGGAATAATRRAATAGGA-3') and 1196R (5'-TCTGGACCTGGTGAGTTTCC-3') [29]. Amplicons were paired and sequenced on the Illumina HiSeq platform, generating 250 bp paired-end reads. The HiSeq sequence was deposited in the GenBank database of the National Center for Biotechnology Information (NCBI) with accession numbers PRJNA973797, PRJNA973801, and PRJNA973803.

The paired end reads of the raw DNA fragments were merged via FLASH [30]. Amplicon and metagenomic analysis pipelines [31] were used to obtain feature tables for the archaea, bacteria and fungi, respectively. During this process, low-quality sequences were removed by USEARCH [32], the representative sequences were obtained through -unoise3 pipeline denoising [33]. The low abundance sequences were filtered out via vsearch (https://sourceforge.net/projects/vsearch/), and then the zero-radius operational taxonomic units (zOTUs) feature tables were generated. The archaeal and bacterial sequences were classified via the rdp_16s_v18 database, and the fungal sequences were classified via the silva_18s_v123 database (http://www.drive5.com/usearch/manual/sintax_downloads.html), and mitochondria, chloroplast and unassigned sequences were removed. Finally, the feature tables were normalized via the vegan package, 550, 4915, and 850 zOTUs were obtained for Archaea, Bacteria, and Fungi, respectively. The functional traits of the fungal taxa were obtained via FUNGuild [34]. The fungal functional traits of 217 (25.53%) of the 850 zOTUs were identified.

Soil physicochemical properties

The soil physicochemical properties were determined via routine methods described by Lu (1999) [35]. The soil organic matter content was determined via potassium dichromate oxidation and the external heating method, total nitrogen (N) and available nitrogen (N) contents were measured via the Kjeldahl-N and alkalolysis diffusion methods, respectively, total phosphorus (P) and available phosphorus (P) contents were measured via HF–$HClO_4$ digestion and the molybdenum blue method, respectively, and total potassium (K) and available potassium (K) contents were measured via HF–$HClO_4$ digestion and atomic absorption spectroscopy, respectively.

Statistical analyses

On the basis of the zOTUs table, the alpha diversity and beta diversity of archaea, bacteria and fungi were calculated via USEARCH. A linear mixing model was used to analyse latitudinal patterns of the alpha diversity of the archaeal, bacterial, and fungal communities. One-way analysis of variance (ANOVA) based on least significant difference (LSD) was used to test for significant differences in the alpha diversity among different latitudes (SPSS Statistics 26.0). Two-way ANOVAs were employed to assess the effects of latitude, location (rhizosphere or

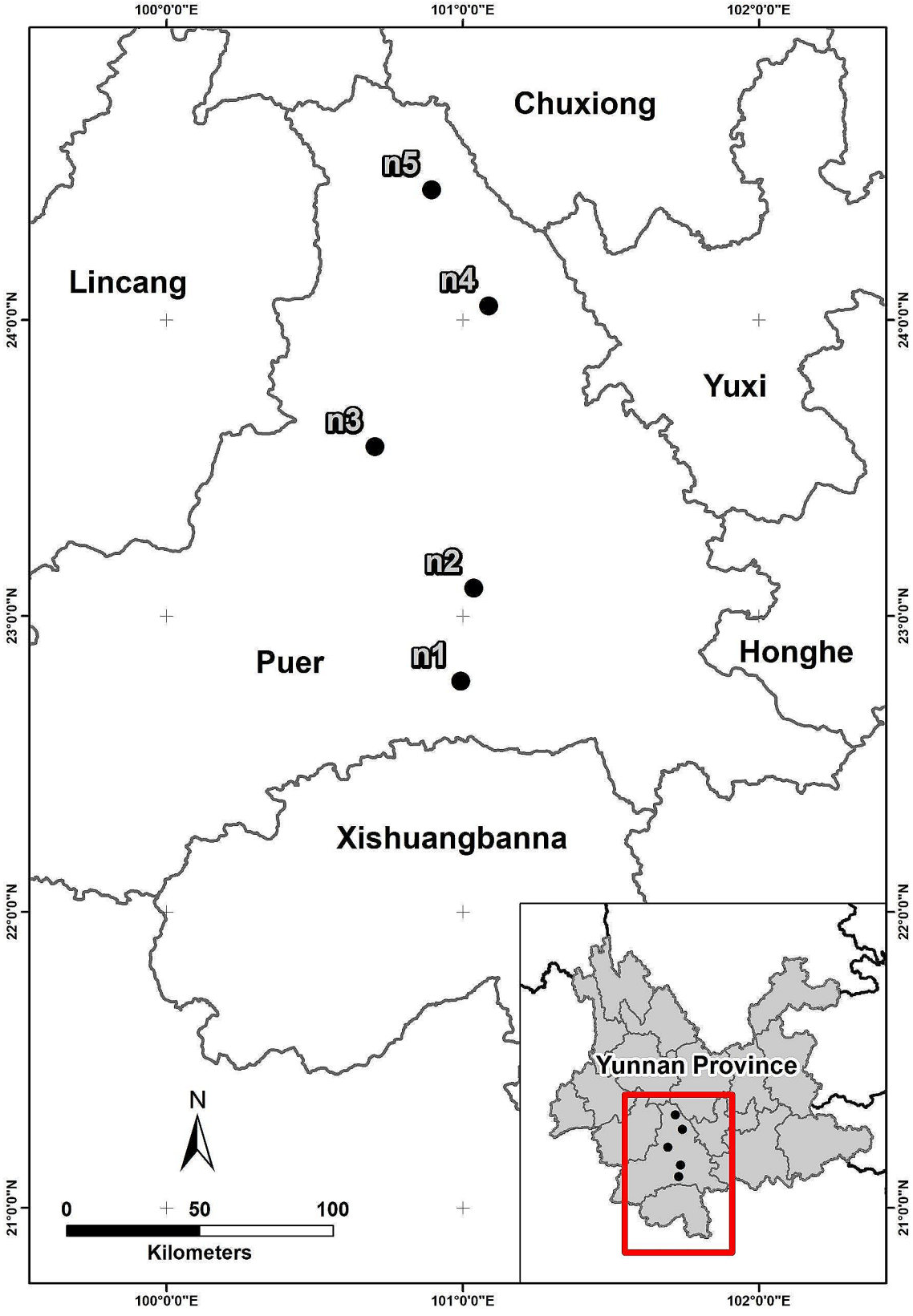

Fig. 1 Soil collection locations along latitude in Pu'er city. Points n1–n5 on the map represent sampling sites at latitudes ranging from 22°46′ to 24°26′N. The map comes from the standard map service system of the Ministry of Natural Resources, PRC. The map is authorized for free. http://bzdt.ch.mnr.gov.cn/, and the base map has not been modified

bulk), and their interaction on microbial diversity/functional fungi/network properties (SPSS Statistics 26.0). The structure of the bacterial, archaeal, and fungal communities was analyzed via principal coordinates analysis (PCoA) on the basis of Bray-Curtis dissimilarity matrices, employing the "vegan" R package (https://cran.r-project.org/web/packages/vegan/index.html). Additionally, a two-way permutational multivariate analysis of variance was conducted to examine the effects of latitude, location, and their interaction on microbial Bray–Curtis dissimilarity. The relative abundances of the microbial communities were analysed at the phylum level, and the relationships between the soil nutrients and dominant phyla were evaluated via Pearson correlation analysis. Monte Carlo permutation tests (499 permutations) and redundancy analysis (RDA) in CANOCO 5.0 software [36] were employed to test the relationships between the soil nutrients and the soil microbial community compositions. Cooccurrence networks were constructed via the "WGCNA" R package (https://cran.r-project.org/web/packages/igraph/index.html), and network properties were calculated via the "igraph" R package (https://cran.r-project.org/web/packages/igraph/index.html) before visualization in Gephi (https://gephi.org/).

Results

Latitudinal variation of microbial community diversity under-ground of *Chromolaena odorata*

The richness index and Shannon index were used to estimate the alpha diversity of the archaea, bacteria and fungi in the rhizosphere and bulk soils (Fig. 2, Table S1). Bacteria presented the highest richness index (1762.25 ~ 2289.75) and Shannon index (6.07 ~ 7.13); followed by fungi, with a richness index of 262.00 ~ 366.75 and a Shannon index of 3.39 ~ 4.43, whereas archaea presented the lowest richness index (77.25 ~ 235.75) and Shannon index (2.80 ~ 4.01). The alpha diversity of bacterial communities was greater than that of archaeal and fungal communities at each latitude, and the alpha diversity of bacterial communities in the rhizosphere was generally lower than that in the bulk soils. The alpha diversity of the archaeal and fungal communities did not significantly differ between the rhizosphere and bulk soils. Significant differences were observed in the richness indices of the archaeal, bacterial, and fungal communities along latitudinal gradients, but there was no discernible latitudinal distribution pattern (Table S2).

The overall dissimilarity percentages for the archaeal, bacterial, and fungal communities along the latitudinal gradient were 48.1%, 46.65%, and 33.51%, respectively (Fig. 3). The archaeal communities significantly differed among latitudes (F = 8.3103, P = 0.001), whereas

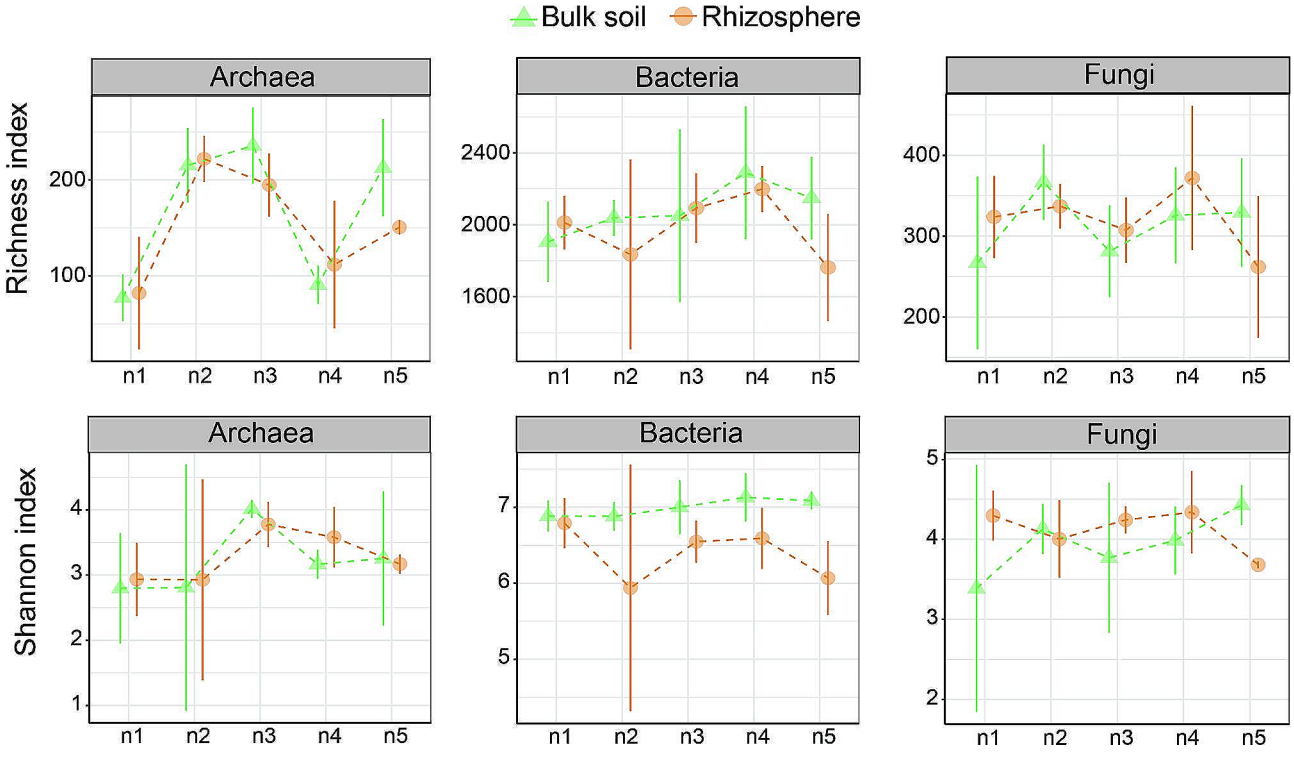

Fig. 2 Richness and Shannon indices of archaea, bacteria and fungi in the rhizosphere and bulk soils. n1–n5 represent sampling sites at latitudes of 22°46′ to 24°26′N

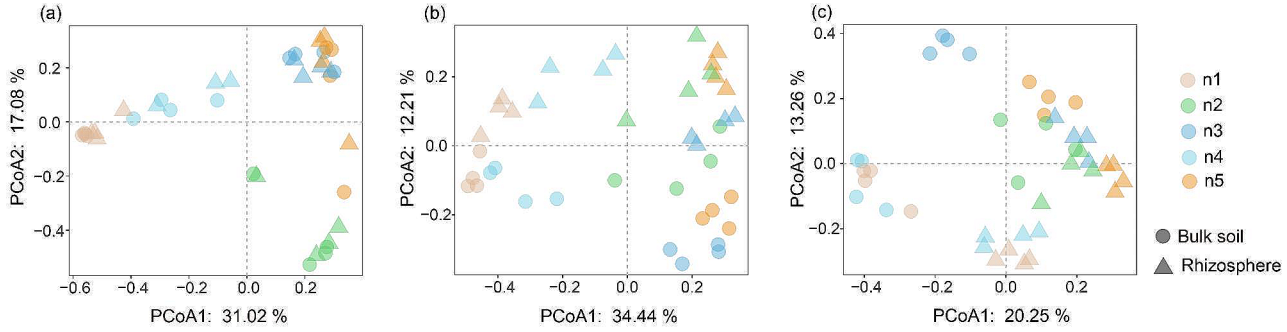

Fig. 3 Principal coordinate analysis of latitudinal variation patterns of the archaeal (**a**), bacterial (**b**) and fungal (**c**) communities of *C. odorata* in rhizosphere and bulk soils. n1–n5 represent sampling sites at latitudes of 22°46′ to 24°26′N

Table 1 Latitudinal variations in soil nutrients around the roots of *Chromolaena odorata*

Latitude	SOM(g/kg)	TN(g/kg)	AN(mg/kg)	TP (%)	AP(mg/kg)	TK(%)	AK(mg/kg)
n1	27.86 ± 3.18^{ab}	1.58 ± 0.12^{a}	154 ± 29.29^{a}	0.51 ± 0.03^{b}	7.78 ± 3.12^{a}	1.83 ± 0.2^{a}	181.2 ± 54.84^{a}
n2	29.81 ± 8.33^{a}	1.38 ± 0.3^{ab}	143 ± 18.46^{ab}	1.37 ± 0.52^{a}	8.14 ± 1.14^{a}	0.5 ± 0.41^{c}	261.8 ± 78.57^{a}
n3	24.67 ± 2.84^{ab}	1.3 ± 0.27^{ab}	136 ± 10.58^{ab}	0.49 ± 0.08^{b}	2.67 ± 0.28^{c}	2.11 ± 0.19^{a}	198.6 ± 27.3^{a}
n4	26.11 ± 5.26^{ab}	1.23 ± 0.15^{ab}	117.25 ± 19.16^{bc}	0.31 ± 0.06^{b}	4.10 ± 1.74^{bc}	1.14 ± 0.26^{b}	177.8 ± 46.64^{a}
n5	21.58 ± 2.57^{b}	1.1 ± 0.17^{b}	95 ± 18.71^{c}	0.49 ± 0.03^{b}	5.73 ± 1.37^{ab}	1.88 ± 0.26^{a}	182.8 ± 34.14^{a}

there were no significant differences between the rhizosphere and bulk soils (F=1.2111, P=0.283) (Table S3). As depicted in Fig. 3, the archaeal communities displayed greater dispersion among latitudes, while with a relative aggregation between the rhizosphere and bulk soils, indicating dissimilarity among latitudes but greater similarity between the rhizosphere and bulk soils. The bacterial and fungal communities significantly differed across latitudes, locations, and interactions (Table S3), indicating that the bacterial and fungal communities were not similar across latitudinal gradients or between the rhizosphere and bulk soils.

High throughput sequencing was performed on rhizosphere and bulk soil samples from five latitudes of *C. odorata*. A total of 4 phyla, 6 classes, 14 orders, 15 families and 19 genera of archaea were identified; 25 phyla, 62 classes, 86 orders, 174 families and 455 genera of bacteria were identified; and 7 phyla, 24 classes, 72 orders, 106 families and 169 genera of fungi were identified. The bacterial diversity in the rhizosphere of *C. odorata* was greater than that in the rhizospheres of archaea and fungi. The main phyla are shown via percentage stacking diagrams (Fig. S1). The dominant archaeal phyla along the latitudinal gradient were *Thaumarchaeota* (40.5, 56.7, 68.2, 50.6 and 83.4%, respectively) and *Euryarchaeota* (52.0, 39.7, 14.5, 13.2 and 4.3%, respectively). The dominant bacterial phyla along the latitudinal gradient were *Proteobacteria* (33.6, 47.1, 33.6, 37.2 and 36.0%, respectively), *Actinobacteria* (21.0, 19.3, 24.8, 21.2 and 31.1%, respectively) and *Acidobacteria* (21.6, 16.3, 17.1, 21.8 and 14.1%, respectively). The dominant fungal phyla along the latitudinal gradient were *Ascomycota* (62.5, 68.2, 73.9, 76.3 and 77.3%, respectively) and *Basidiomycota* (32.9, 20.8, 21.8, 19.2 and 13.8%, respectively). The relative abundance of *Euryarchaeota* decreased with increasing latitude, whereas that of *Ascomycota* increased with increasing latitude.

Soil nutrients and their associations with dominant phyla

The comprehensive nutrient contents of n1 and n2 were high, and those of n4 and n5 were low (Table 1). The maximum values of SOM, TN, AN, TP, AP, and AK (except TK) were found in n1 or n2, and the minimum values were found in n4 or n5. TN and AN tended to decrease with increasing latitude, and there was no significant difference in AK content among the five latitudes (P<0.05).

Different letters in a single column indicate significant differences among latitudes (P<0.05). The n1–n5 represent sampling sites at latitudes of 22°46′ to 24°26′N.

The cumulative explanatory variables of archaeal RDA1 (59.08%) and RDA2 (0.91%) were 59.99%. Among these, AN (F=7.2, P=0.016) emerged as a significant factor influencing the dominant archaeal phyla (Fig. 4, Table S4). *Euryarchaeota* was significantly positively correlated with available N and total P, whereas *Thaumarchaeota* was significantly negatively correlated with available N (Table S5). The cumulative explanatory variable of bacterial RDA1 (42.01%) and RDA2 (28.83%) was 70.84%. Among these, TK (F=6.8, P=0.002), TN (F=6.7, P=0.004), and AK (F=4.1, P=0.024) were identified as significant factors influencing the dominant bacterial phyla (Fig. 4, Table S4). *Proteobacteria* was significantly positively correlated with total P, very significantly negatively correlated with total K and significantly positively

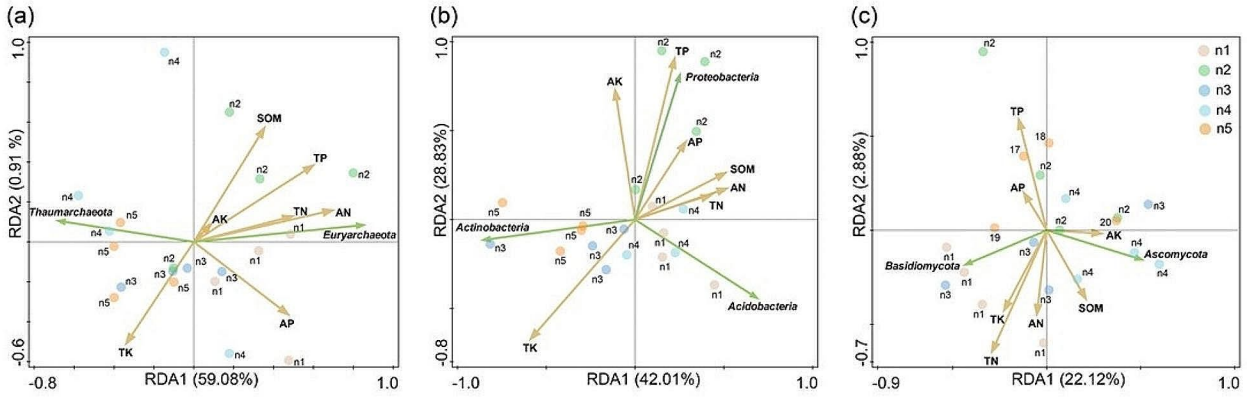

Fig. 4 Redundancy analysis (RDA) of the relationships between soil nutrients and the dominant phyla of archaea (**a**), bacteria (**b**) and fungi (**c**). The angle between the dominant phyla and the nutrient element is acute, the correlation is positive, and the obtuse angle is negative

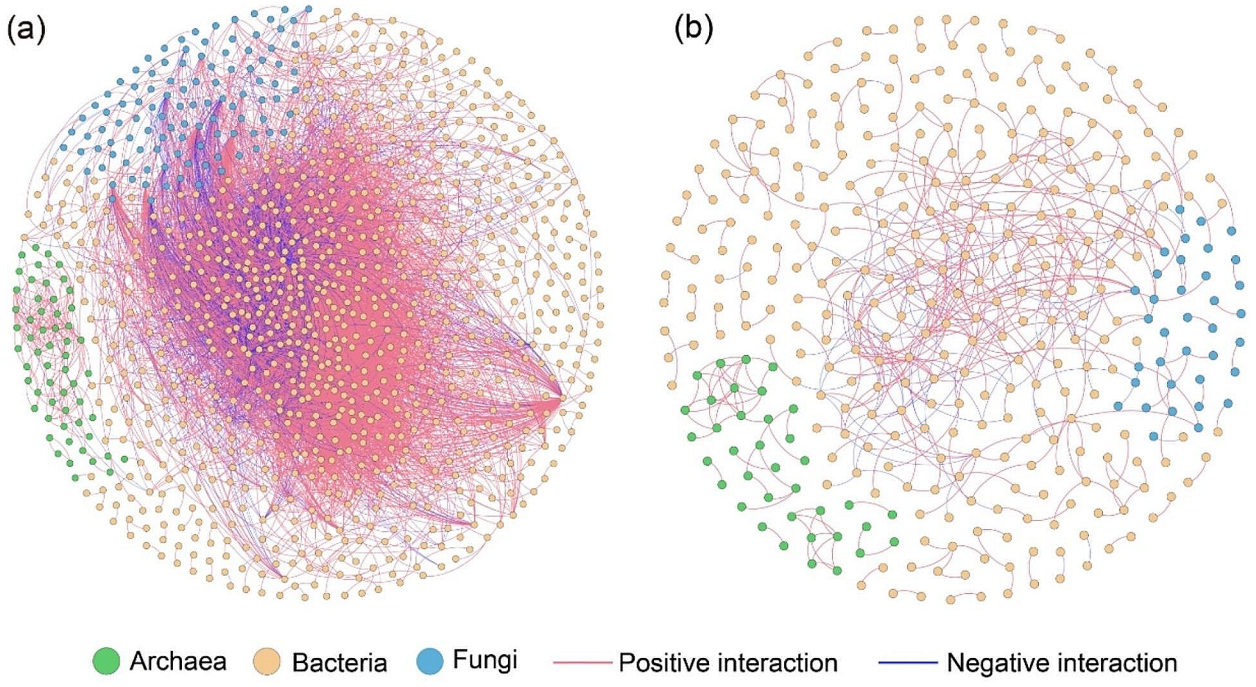

Fig. 5 Network analysis of bulk soil (**a**) and the rhizosphere (**b**). The connection indicates a strong and significant ($P < 0.001$) correlation; the nodes represent unique sequences in the datasets

correlated with available K. *Actinobacteria* was significantly negatively correlated with available N and significantly positively correlated with total K (Table S5). The cumulative explanatory variable of fungal RDA1 (22.12%) and RDA2 (2.88%) were 25.00%, and there was no significant correlation between the dominant phyla and soil nutrients (Fig. 4, Table S4).

Co-occurrence network

The co-occurrence networks of archaea, bacteria and fungi in the bulk soil presented greater density (Fig. 5; Table 2), and there were more nodes and edges in the bulk soil (1,031 nodes, 11,817 edges) than in the rhizosphere (377 nodes, 556 edges), which suggested that the complexity of the rhizosphere microbial networks was lower than that in the bulk soil. In contrast, the modularity of the rhizosphere microbial networks was greater than that of the bulk soil. In the bulk soil, the positive correlations between the edges accounted for 74.87%, and the negative correlations accounted for 25.13%; in the rhizosphere, the positive correlations between the edges accounted for 81.29%, and the negative correlations accounted for 18.71%. It can be concluded that the rhizosphere has a greater positive connection than does

Table 2 Topological properties of the co-occurrence networks of the rhizosphere and bulk soils

Location	Nodes	Edges	Correlation		Modularity	Number of Communities
			Postive	Negative		
Bulk soil	1031	11,817	74.87%	25.13%	0.832	100
Rhizosphere	377	556	81.29%	18.71%	1.106	102

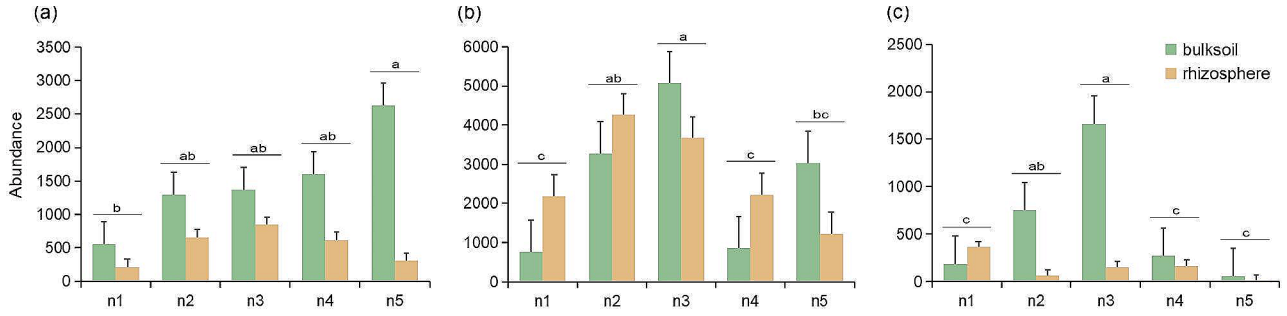

Fig. 6 Comparison of arbuscular mycorrhizae (**a**), plant pathogens (**b**) and soil saprotrophs (**c**) in the rhizosphere and bulk soils. n1–n5 represent sampling sites at latitudes of 22°46′ to 24°26′N. Lowercase letters indicate significant differences in functional fungal abundance among different latitudes on the basis of one-way ANOVA with LSD multiple comparisons ($P < 0.05$)

the bulk soil. The microbial network properties (node, edge, modularity) significantly differed between the rhizosphere and bulk soils, with no significant variation along latitudinal gradients and no discernible distribution pattern (Fig. S2, Table S6).

Fungal function prediction

For the fungal communities, FUNGuild identified 27 of 217 zOTUs as highly probable, including arbuscular mycorrhizae (13 zOTUs), plant pathogens (8 zOTUs) and soil saprotrophs (6 zOTUs). The presence of arbuscular mycorrhizae and soil saprotrophs significantly differed between rhizosphere and bulk soils but showed no significant variation along latitudinal gradients. Conversely, plant pathogens significantly differed along latitudinal gradients but did not significantly differ between rhizosphere and bulk soils (Fig. 6, Table S7). The abundance of arbuscular mycorrhizae in the bulk soil increased with latitude and was greater than that in the rhizosphere. The abundance of plant pathogens in the rhizosphere soil was greater than that in the bulk soil, except in n3 and n5. The abundance of soil saprotrophs in the bulk soil was generally greater than that in the rhizosphere, except in n1. The plant pathogens and soil saprotrophs in the rhizosphere and bulk soils did not exhibit latitudinal patterns.

Discussion

Alterations in soil microbial communities during the dispersal process of alien plants

The alpha diversity analysis revealed that the bacterial abundance was relatively high and that the archaeal and fungal abundances were relatively low in the rhizosphere and bulk soils, which was in accordance with previous findings that the number of soil microorganisms of different invasive plants was the highest in bacteria [37]. Chen et al. (2020) [38] proposed that the high diversity of bacteria in the rhizosphere provides plants with the opportunity to improve nutrient utilization efficiency and increase plant biomass through synergistic interactions between different microorganisms. The high diversity of bacterial communities may provide favourable conditions for the invasion of *C. odorata*. Additionally, the Shannon index of bacteria in the rhizosphere soil was generally lower than that in the bulk soil (Fig. 2). This observation contrasts with that of a previous study by Zhu et al. (2023) [39], who reported that the bacterial alpha diversity of the rhizosphere was greater than that of bulk soil. We speculated that this result may be caused by the allelopathic effects of *C. odorata.* The allelochemicals produced by invasive species can disrupt decomposition processes in soil communities when they are released into novel ecosystems [40]. Consequently, the release of allelopathic substances may hinder the growth and proliferation of soil bacteria in the rhizosphere. On the other hand, there were no significant differences observed in the archaeal and fungal communities between rhizosphere and bulk soils (Table S2), which does not support our first hypothesis. Compared with bacteria, archaea are less influenced by root exudates [41], and the fungal community composition is less sensitive to the rhizosphere environment than the bacterial community composition is [42]. Thus, we speculate that the minimal impact of allelopathy on archaeal and fungal communities results in insignificant differences in diversity between rhizosphere and bulk soil communities.

The β diversity results indicate significant differences in the archaeal community structure among latitudes, with dissimilar community structures observed. However,

there were no significant differences in community structure between rhizosphere and bulk soils, indicating high similarity. In contrast, bacterial and fungal communities significantly differ among latitudes and between rhizosphere and bulk soil structures, with relatively low similarity (Fig. 3, Table S3). Archaea may be actively involved in rhizosphere processes only under specific conditions (such as reduced oxygen and/or high CO or CO_2 pressures) [43]. Therefore, the archaeal communities in the rhizosphere and bulk soils were highly similar. There were significant differences in the structure of the bacterial and fungal communities between the rhizosphere and bulk soils, which was consistent with the findings of previous studies [44, 45]. Bacteria and fungi are soil organisms that are sensitive to invasive plants [46, 47]. The difference in the bacterial and fungal communities in the rhizosphere and bulk soil indicate that soil bacteria and fungi are sensitive to the invasion of *C. odorata*. Moreover, we speculated that *C. odorata* specifically selected for bacterial and fungal communities in the rhizosphere.

In our study, although the diversity and community structure of archaeal, bacterial, and fungal communities are influenced to some extent by latitudinal gradients, there is no clear pattern of latitudinal distribution. The observed influence of latitude on community diversity and structure is likely attributable to differences in soil nutrients or soil heterogeneity among the sampling sites. Studies have indicated that the latitudinal diversity gradient of soil bacterial communities from broad areas with different soil types may be significantly masked by pronounced soil heterogeneity [48]. In small-scale areas, soil heterogeneity or variations in soil nutrients may amplify the impact of latitude on soil microorganisms. Previous studies have reported that soil microbial community diversity increases or decreases with increasing latitude [11, 49]. These different results highlight the uncertainty in the latitudinal pattern of soil microorganisms and may indicate that there are specific patterns for different plants and ecosystems [39]. The latitudinal patterns of soil microbial biomass and community composition are highly dependent on both biotic and abiotic factors. Biotic factors such as pathogens, competitive interactions, mutualistic interactions, and abiotic factors such as climatic and soil properties [50]. In previous studies, microbes have been shown to more readily exhibit latitudinal patterns at larger scales, as climate plays an important role in shaping soil microbial communities [51]. In our study, the latitudinal range was concentrated in Pu' er city, and there was little difference in climate characteristics; therefore, observing distinct latitudinal patterns is more challenging. Simultaneously, plant invasion might alter latitudinal biodiversity patterns of their associated biotic communities [52], and the invasive plant *C. odorata* may also have caused this result.

Dominant environmental factors

In terms of the soil nutrients in n1–n5, the contents of SOM, TN, AN, AP, TP and TK at various latitudes were significantly different, except for AK, but there were no latitudinal patterns. The soil nutrient pool is a key factor determining the physiological ecology of soil organisms and plants [53]. The heterogeneity of soil conditions contributes to population differentiation, which in turn promotes the adaptation of invasive plants to novel environments [47]. Soil nutrient heterogeneity may increase the invasion ability of *C. odorata*.

Soil microorganisms interact with soil environmental factors in a complex and close relationship. Redundancy analysis revealed the relationships among the dominant phyla of archaea, bacteria, fungi, and soil environmental factors, identifying soil total potassium (TK), total nitrogen (TN), available nitrogen (AN), available phosphorus (AP), and available potassium (AK) as significant drivers influencing the soil microbial community structure. AN and TP were identified as important factors influencing the dominant phyla of archaea, whereas TK, TN, and AK were identified as important factors influencing the dominant phyla of bacteria, supporting our second hypothesis. Archaea play roles in nitrogen fixation and ammonia oxidation in soil [54, 55], bacteria degrade OM and cycle elements [56], and fungi act as primary decomposers, playing vital roles in nutrient cycling [57]. Archaea, bacteria, and fungi exhibit distinct functionalities and metabolic characteristics in soil ecosystems, hence their differential responses to soil nutrients. Previous studies have shown that the soil physicochemical factors that govern the oil microbial community structure vary across different ecosystems. In previous studies, the soil physicochemical factors that dominate the soil microbial community differed. For example, SOM, TN and pH are the main factors affecting the rhizosphere soil microbial community structure of *Zanthoxylum bungeanum* [58]. pH, TP and TK were the main factors affecting the composition and distribution of the dominant flora in the mixed forest of *Castanopsis hystrix* and *Pinus massoniana* [59]. pH and the N: P ratio are the best predictors of bacterial diversity in continental forest systems [12]. The microbial communities presented distinct nutrient preferences, which changed with the soil environment.

Cooccurrence network analysis of rhizosphere and bulk soil

In the natural environment, microorganisms prefer to form a complex network structure to coexist through various interactions rather than as independent individuals [55]. Currently, co-occurrence network analysis has been widely used to investigate the interactions among microorganisms and their relationships with the surrounding environment and to evaluate the complexity of

targeted communities. In this study, the results of the rhizosphere and bulk soil network analyses were as follows. The complexity of the rhizosphere microbial community network was lower than that of the bulk soil network, which was consistent with the findings of Liu et al. (2023) [60]. We believe that there are several reasons for the less complex microbial community networks in the rhizosphere. First, the time-consuming process of rhizosphere soil extraction could decrease the complexity of microbial networks [61]. Second, root exudates have been shown to attract specific microorganisms and influence the composition of rhizosphere microbiomes [62], thus reducing the complexity of rhizosphere microorganisms. In addition, studies have shown that the rhizosphere communities constitute a subset of soil communities and that bulk soil is a resource pool for the rhizosphere soil [18]. Thus, a less complex microbial community network in the rhizosphere was expected. The other result was that the rhizosphere networks had greater modularity and greater positive links than did the bulk soil networks, which was consistent with the findings of Li et al. (2021) [63]. The rhizosphere is a hotspot for microbial diversity, with richer and more distinct microbial communities active in the rhizosphere than in neighbouring bulk soil [64]. These active microbial communities enable the elements in the rhizosphere to circulate rapidly, and the rhizosphere network allocates more modules for more executive functions [65]. There were more positive links among the rhizosphere, indicating that more symbiotic and cooperative relationships occurred, which helps to maintain the resistance of rhizosphere microorganisms to environmental fluctuations and overcomes environmental stress [39], which is more beneficial for alien plants to invade.

Analysis of fungal main function

Zhang et al. (2019) [66] reported that invasive plants can affect the soil biotope through the root system, thereby increasing the influence of plant invasion on the abundance or biomass of certain components in the communities and increasing nutrient cycling, thus promoting the invasion of alien plants. Fungi are sensitive to invasive plants, and many fungi (e.g., mycorrhizal symbionts, plant pathogens, and saprotrophs) are more closely related to plants than other organisms are and play a key role in ecosystems [47]. This study revealed that the abundances of arbuscular mycorrhizae and soil saprotrophs in bulk soil were generally greater than those in the rhizosphere, which was similar to the results obtained after the invasion of bamboo by Li et al. (2022) [67]. However, studies have also shown that the abundance of arbuscular mycorrhizae and soil saprotrophs in bulk soil is generally lower than that in the rhizosphere [68]. The quality and quantity of organic matter substrate, nutrient availability, and amount of root secretions can contribute to such differences [69, 70]. The results of the abundance comparison of plant pathogens in rhizosphere and bulk soils were different from those of arbuscular mycorrhizae and soil saprophytes. While bulk soil is suitable for pathogen growth and survival, the rhizosphere is a playground and infection court for pathogens to establish parasitic relationships with plants [71]. As an alien plant, *C. odorata* can secrete allelopathic substances [26]. Some phenolic compounds in root secretions can trigger spore germination of fungal pathogens [72], which may result in a slightly greater abundance of pathogens in the rhizosphere.

The abundance of arbuscular mycorrhizae in the bulk soil increased with increasing latitude, whereas the distributions of plant pathogens and soil saprotrophs in the rhizosphere and bulk soils did not exhibit a latitudinal distribution. Unlike the results obtained by Hu et al. (2019) [73], our results do not follow the general latitudinal trend of increasing biodiversity from the poles to the tropics, which is consistent with the assertion that microbes do not follow the general latitudinal trend [74, 75]. It is possible that because of the short latitudinal gradient used in our study, the latitudinal patterns of different soil taxa were not significant. Accordingly, the variation in the abundance of fungal functional groups at different latitudes is most likely a specific response to soil nutrient resources and other biological environments. In this study, we conducted surveys exclusively in Pu' er city, which has a limited latitudinal scale, and we did not consider information such as temperature and humidity. Therefore, future research should simultaneously consider multiple abiotic and biotic factors across larger spatial scales to explore the mechanisms underlying latitude-driven variations in microbial communities.

Conclusion

This study elucidated the distribution patterns and influencing factors of archaea, bacteria, and fungi in rhizosphere and bulk soils along latitudinal gradients following the invasion of *C. odorata*. Differences in bacterial community diversity and structure, fungal community structure, and microbial network complexity between rhizosphere and bulk soils may be related to the root exudates of *C. odorata*. Compared with bulk soil, the rhizosphere microbial network exhibited greater symbiotic cooperation, which may be conducive to the invasion of *C. odorata*. The difference in soil nutrients among the sampling sites may have partially influenced the archaeal, bacterial, and fungal communities according to latitude. However, due to the relatively small latitudinal scale, a discernible latitudinal distribution pattern did not emerge. Furthermore, specific driving factors among bacterial, archaeal, and fungal communities were identified,

demonstrating distinct nutrient preferences among archaea, bacteria, and fungi. This finding also indicates the complex microbial response to soil nutrient elements following the invasion of *C. odorata*. These findings expand our understanding of the structure and diversity of rhizosphere and bulk soil microbial communities along a latitudinal gradient, providing scientific evidence for investigating the invasion mechanisms of *C. odorata*.

Supplementary Information

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Supplementary Material 1

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Not applicable.

Author contributions
All authors contributed to the study conception and design. Material preparation and data collection were prepared by Wen-jun Liu. Data analysis was performed by Ming-zhu Zhang and Wei-tao Li. The manuscript was written by Ming-zhu Zhang, Wei-tao Li, and Yu-long Zheng. All authors commented on previous versions of the manuscript and all authors read and approved the final manuscript.

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Data availability
The HiSeq sequence was deposited in the GenBank database of the National Center for Biotechnology Information (NCBI) with accession numbers PRJNA973797, PRJNA973801, and PRJNA973803.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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