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Variations of soil bacterial community structure and function under different habitats of *Tamarix ramosissima* Ledeb. in the upper reaches of the Tarim River, Northwest China

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Abstract: Diversity of soil microorganisms in different habitats of arid and semi-arid areas plays an important role in the soil texture and nutrient, promoting the growth of vegetation in those areas. To clarify the response of soil bacterial community diversity to the changes of environmental factors in different habitats, this study collected soil samples under the canopies of *Tamarix ramosissima* Ledeb. in oasis, transition zone, and desert habitats in the upper reaches of the Tarim River, Northwest China. High-throughput sequencing technology and PICRUSt2 software were used to explore the composition and function of soil bacterial communities in different habitats of *T. ramosissima*. The results showed that: (1) soil environmental factors under the canopy of *T. ramosissima* in the three habitats differed significantly, with soil moisture and nutrient conditions being better in the oasis; (2) Proteobacteria, Bacteroidetes, Firmicutes, Actinobacteria, and Gemmatimonadetes were the major bacterial communities in the three habitats; (3) soil bacterial community composition under the canopy of *T. ramosissima* varied greatly, and the richness was significantly different among the three habitats; (4) redundancy analysis indicated that soil water content and available phosphorous were the most important environmental factors influencing the composition of soil bacterial community; and (5) 6 primary functions and 21 secondary functions were obtained by PICRUSt2 function prediction, with metabolism being the most dominant function. This study revealed the response of soil bacterial community composition to habitat changes and their driving factors in the upper reaches of the Tarim River, which could improve the understanding of ecological sensitivity of soil microorganisms in arid and semi-arid areas, and provide a theoretical foundation for improving soil quality and ecological protection.

Keywords: high-throughput sequencing; soil bacterial community; environmental factors; function prediction; soil nutrients

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1 Introduction

Soil microorganisms, as a crucial link between above-ground and below-ground ecosystems, play a dominant role in soil nutrient conversion cycle, ecosystem stability, anti-interference, and sustainable resource utilization. They are key factors in maintaining soil health and soil quality (Zhao et al., 2020). Soil bacteria are the most numerous and diverse soil microorganisms in the soil ecosystem, performing crucial ecological functions, such as decomposition, mineralization, and promotion of soil material cycling and energy flow (Guo et al., 2020). Their activity and diversity reflect the stability of soil microbial communities and are closely related to stress response and resource availability (Sun et al., 2020). Because soil bacterial communities are highly responsive to changes in soil environmental factors, they become the key biological indicators reflecting the changes in soil environment quality and health (Chen et al., 2019).

There is a complex network of relationships among above-ground vegetation, soil environmental factors, and soil microorganisms. Soil microbial communities are significantly affected by soil chemical properties, especially soil pH, carbon, and nitrogen contents (Wang et al., 2022). Additionally, they are closely related to many other environmental factors, such as soil moisture and temperature, nutrients, vegetation types, and may also be affected by exogenous substances. Studies have shown that soil pH can directly or indirectly affect bacterial diversity through different ways, such as changing the utilization of nutrients by bacteria, the ability of physiological and metabolic activity, and establishing new inter-population competition relations (Zhang et al., 2017). Soil temperature changes affect the evaporation and movement of soil water, which in turn affects the access of soil microorganisms to water and nutrients (Frindte et al., 2019). The increase of soil water content within a certain scope can increase soil microorganism quantity and soil respiration intensity, and excessive moisture conditions can lower the soil permeability, resulting in a decline in the richness and biomass of soil microorganisms (Yang et al., 2016). Most studies have shown significantly positive correlations between soil properties and soil microorganisms, such as soil organic carbon, total nitrogen, and organic matter (Rousk et al., 2010; Liu et al., 2018). The influence of plants on soil microorganisms mainly changes in soil physical and chemical properties through root secretions and litter differences, regulates the composition and structure of soil microbial community, and plays an important role in the functional composition of soil bacteria (Landesman et al., 2014). Meanwhile, soil microorganisms can indirectly affect the growth and succession of plant communities by promoting the fixation of nitrogen and the dissolution of insoluble phosphorus and potassium (Hu et al., 2020).

Soil environmental conditions are heterogeneous in different landscapes. Oasis and desert are special geographical landscapes existing in arid areas. Oases are the ecosystems dominated by vegetation, their primary productivity is significantly higher than the surrounding environment, and they depend on external mountain surface and groundwater (Wang, 2000). Deserts are areas with little annual precipitation, lack of soil moisture, sparse vegetation, even large areas of bare land, and low ecosystem biological productivity. Desert-oasis transition is the zone between desert and oasis, and it is the ecological zone where desert system and oasis system interact and transform (Zhao et al., 2016). The transition zone has similar characteristics to the desert habitat, with scarce precipitation and large evaporation, significant resource-based water shortage, serious wind erosion and accumulation on the surface, and easy to form soil biological crust (Zhou et al., 2021). The transition zone also has some similar characteristics to oasis, which can retain a certain degree of fertility, so that some desert vegetation resistant to drought, salt and alkali, and wind erosion, and sand burial can grow and develop normally (Ma et al., 2023). The formation of desert-oasis transition zone is due to the gradient change of water and heat environmental factors from oasis to external desert, which leads to the transition characteristics of comprehensive landscape, including vegetation, soil, and landform (Mu et al., 2013). In summary, oasis, transition zone, and desert have significantly different environmental conditions, which might have different characteristics of soil bacterial communities.

Taklimakan Desert is an ecologically fragile area in Northwest China. It belongs to the warm

temperate continental climate. Precipitation is scarce, evaporation is strong, and diurnal and seasonal temperature difference is large. This area mainly dominated by desert plants such as *Tamarix ramosissima* Ledeb., *Nitraria tangutorum* Bobrov, *Alhagi camelorum* Fisch., *Phragmites communis* Trin., and *Karelinia caspica* (Pall.) Less. Desert vegetation is the critical element in maintaining the stability of deserts, oases, and transition zones. *T. ramosissima*, with its drought, salt, and barren tolerance, is an excellent species for windbreak and sand fixation in arid areas. It plays an important role in curbing ecological degradation and maintaining the stability of oasis ecosystems (Zheng et al., 2010; Xiao et al., 2021). Therefore, in this study, the soil under the canopy of *T. ramosissima* in desert, oasis, and transition zone in the upper reaches of the Tarim River were taken as the study material, the high-throughput sequencing technology was used to reveal the soil bacterial community structure and function in different habitats, aiming to provide scientific basis for the sustainable development of soil ecological function in the upper reaches of the Tarim River. The study tries to explore the following scientific questions: (1) whether there are differences in soil bacterial community characteristics, diversity, and functional genes under the canopy of *T. ramosissima* in different habitats? and (2) what are the main environmental factors determining the soil bacterial community under the canopy of *T. ramosissima* in different habitats?

2 Materials and methods

2.1 Study area

Study area is located in the desert-oasis transition zone of the Tarim River, Northwest China (39°30′–41°15′N, 79°40′–81°53′E; 1012 m a.s.l.). Precipitation is less than 50 mm, but evaporation can reach as high as 2550 mm. Annual mean temperature is 11°C, average annual sunshine duration is about 2814 h, and frost-free period is about 190–220 d. Soil types include mainly sandy, brownish desert, and saline soils (Meng et al., 2019).

2.2 Sample collection and processing

According to the distribution of naturally growing *T. ramosissima* in different habitats (oasis, transition zone, and desert; Fig. 1), we established 3 quadrats with the area of 20 m×20 m under similar conditions, totaling 9 quadrats (Zhang et al., 2023). The characteristics of *T. ramosissima* populations in different habitats are shown in Table 1. Soil samples in each quadrat were collected. Well-grown *T. ramosissima* samples with similar morphology were selected. The surface litter was removed at the position close to plants' roots, and surface layer of 0–20 cm soil was harvested with a soil auger and a sterile shovel sterilized with 75.00% alcohol. About 10 g of the collected soil samples were taken into sterile centrifuge tubes for the determination of soil microorganisms, and soil samples were placed at –280°C for deoxyribonucleic acid (DNA) extraction. In addition, the undisturbed soil samples were taken by ring knife for the determination of soil bulk density, and 0–20 cm soil was collected by sterile shovel. After removing plant roots, stones, and other impurities, we loaded a portion into an aluminum box for the determination of soil water content. The remaining soil samples were dried in a 2-mm sieve and put into a sterile sealed bag for the determination of soil physical and chemical properties.

Fig. 1 Landscape of different habitats of *Tamarix ramosissima* Ledeb. in the upper reaches of the Tarim River. (a), oasis; (b), transition zone; (c), desert.

Table 1 Community structure of *Tamarix ramosissima* Ledeb. in different habitats

Habitat type	Density (plants/hm²)	Height (cm)	Crown width (cm)	Coverage (%)
Oasis	183.33±58.57[b]	380.81±35.95[a]	398.47±57.47[a]	92.00±2.00[a]
Transition zone	383.33±92.80[a]	132.04±4.25[b]	190.63±14.01[b]	67.00±2.00[b]
Desert	191.33+30.14[b]	161.97±2.80[b]	202.41±12.78[b]	52.00±2.00[c]

Note: Different lowercase letters within the same column indicate significant differences at $P<0.05$ level. Mean±SE.

2.3 Measurement of soil environmental factors

We measured soil physical and chemical properties according to Bao (2000). The pH was determined by potentiometric method on a 1:5 soil:water ratio suspension (PHS−3C, Shanghai Yidian Scientific Instrument Co., Ltd., Shanghai, China). Electrical conductivity (EC) was determined by conductivity method (DDS-307, Shanghai Yidian Scientific Instrument Co., Ltd., Shanghai, China). Soil water content (SWC) was determined by drying method. Soil bulk density (BD) was determined using the ring knife method. Soil organic carbon (SOC) was determined by potassium dichromate volumetric method with external heating. Available phosphorus (AP) was determined by sodium bicarbonate leaching. Available nitrogen (AN) was determined by alkaline diffusion method. Total nitrogen (TN) was determined by Kjeldahl method. Total phosphorus (TP) was determined by molybdenum-antimony colorimetric method. Soil microbial biomass was referred from Wu et al. (2011). Microbial biomass nitrogen (MBN), microbial biomass phosphorus (MBP), and microbial biomass carbon (MBC) were determined by chloroform fumigation-extraction method.

2.4 Soil bacterial DNA extraction, polymerase chain reaction (PCR) amplification, and gene libraries

DNA from soil samples of different habitats was extracted by the MO BIO's PowerSoil DNA Isolation Kit (MO BIO Laboratories, Inc., Carlsbad, USA). The concentration of DNA was measured using a microplate reader (Synergy HTX, Gene Company Ltd., Beijing, China), and the quality of DNA was detected by 1.00% agarose gel electrophoresis.

For bacterial communities, full-length region of the bacterial 16S rDNA gene sequence was amplified using universal bacterial primers 27F (5′-AGRGTTTGATYNTGGCTCAG-3′) and 1492R (5′-TASGGHTACCTTGTTASGACTT-3′). PCR amplification was performed in a total reaction volume of 30.0 uL, containing 10.5 uL of nuclease-free water, 15.0 uL of KOD One^{TM} PCR Master Mix (Toyobo Co., Ltd., Osaka, Japan), 3.0 uL of barcode primer pairs, and 1.5 uL of genomic DNA. The reaction conditions for PCR were as follows: initial denaturation at 95°C for 2 min, 25 cycles of denaturation at 98°C for 10 s, annealing at 55°C for 30 s, extension at 72°C for 90 s; and a final extension at 72°C for 2 min. The PCR was amplified and the products were purified and quantified, homogenized to obtain the sequencing library, and the sequences of tagged genes were determined by PacBio Single Molecule Real-Time Sequencing technology (Biomarker Technology Co., Ltd., Beijing, China).

2.5 Processing of sequencing data

Raw amplicons were corrected using SMRT-Link v.8.0 software to obtain circular consensus sequencing (CCS) sequences, Lima v1.7.0 software was used to identify CCS sequences of different samples by barcode sequences, and UCHIME v.4.2 software was used to remove chimeras and to obtain high-quality CCS sequences. The obtained high quality sequences were clustered at a 97.00% similarity level using USEARCH v.10.0 software to obtain operational taxonomic units (OTUs). The OTUs were taxonomically identified and annotated using the bacterial SILVA (high quality ribosomal ribonucleic acid (RNA) databases) as a reference database, then the community composition of each sample at different levels (phylum, class, order, family, genus, and species) was calculated. Sample alpha diversity indices including Chao1 index, accumulated cyclone energy (ACE) index, Shannon index, and Simpson index were calculated by

the QIIME v.2.0 software. All sequencing raw data were deposited in Sequence Read Archive (SRA) of NCBI (National Centre for Biotechnology Information) database with the Bio Project ID PRJNA1123075.

2.6 Statistical analysis

SPSS v.26.0 software (IBM, Chicago, USA) was used to process and analyze the data of soil environmental factors and microbial data. One-way analysis of variance (ANOVA) and least significant difference (LSD) were selected to analyze and test the differences among habitats (P<0.05). The statistical results were shown as mean±standard error. Data processing, statistical analysis, and drawing were completed by Excel v.2022, Canoco v.5.0 (CanocoLab, Microsoft, Redmond, Washington DC, USA), and Origin v.2023 (OriginLab, Northampton, USA). We analyzed the effect size by LEfSe (linear discriminant analysis (LDA) effect size) according to the LDA score >4, which was used to identify significant differences by the biomarkers between groups. We applied principal coordinate analysis (PCoA) to analyze beta diversity based on the Binary-Jaccard distance. The correlation between soil microorganisms and environmental factors was analyzed using the Biomarker Microbial Diversity Analysis Platform (www.biocloud.net). This matrix was used to show the differences in microbial community structure between groups. Relative abundance of functional genes of samples was obtained by comparing the Kyoto encyclopedia of genes and genomes (KEGG) database information with Phylogenetic Investigation of Communities by Reconstruction of Unobserved States (PICRUSt2) software.

3 Results

3.1 Soil environmental factors

Soil environmental factors under the canopy of *T. ramosissima* in different habitats were analyzed by one-way ANOVA. Results showed that contents of SOC, TN, AN, and MBP in the oasis were significantly higher than those in the transition zone and desert (P<0.05; Table 2). Contents of TP and AP in transition zone were significantly lower than those in the oasis (P<0.05; Table 2). However, there was no significant difference in soil BD, pH, MBN, and MBC among the three habitats (P>0.05; Table 2).

Table 2 Characteristics of soil environmental factors under the canopy of *T. ramosissima* in different habitats

Soil environmental factor	Oasis	Transition zone	Desert
SWC (%)	32.00±1.00^{a}	22.00±3.00^{b}	1.00±0.00^{c}
BD (g/cm^3)	1.10±0.18^{a}	1.14±0.08^{a}	1.30±0.01^{a}
pH	8.74±0.08^{a}	8.29±0.28^{ab}	8.24±0.07^{b}
EC (μS/cm)	420.33±26.36^{c}	2396.67±129.14^{a}	1640.67±132.16^{b}
SOC (g/kg)	3.49±0.09^{a}	2.03±0.04^{b}	2.18±0.11^{b}
TP (g/kg)	0.61±0.01^{a}	0.54±0.01^{b}	0.57±0.02^{ab}
TN (g/kg)	0.27±0.02^{a}	0.08±0.01^{b}	0.07±0.01^{b}
AN (mg/kg)	8.48±0.89^{a}	4.12±0.24^{b}	5.07±0.31^{b}
AP (mg/kg)	1.34±0.01^{b}	0.87±0.07^{c}	1.91±0.11^{a}
MBN (mg/kg)	2.78±0.21^{a}	4.27±1.06^{a}	4.20±0.28^{a}
MBC (mg/kg)	49.36±10.49^{a}	44.02±1.44^{a}	54.35±6.23^{a}
MBP (mg/kg)	3.01±0.18^{a}	2.00±0.11^{b}	2.10±0.16^{b}

Note: SWC, soil water content; BD, bulk density; EC, electrical conductivity; SOC, soil organic carbon; TP, total phosphorus; TN, total nitrogen; AN, available nitrogen; AP, available phosphorus; MBN, microbial biomass nitrogen; MBC, microbial biomass carbon; MBP, microbial biomass phosphorus. Different lowercase letters within the same row indicate significant differences among the three habitats at P<0.05 level. Mean±SE. The abbreviations are the same in the following figures.

3.2 Soil bacterial community composition

By classifying and annotating the high-throughput sequencing results, we obtained 29 bacterial

phyla. For the convenience of observation, only 10 phyla with the highest relative abundance were displayed, and the other species were merged as others (Fig. 2). The relative abundance from high to low was Proteobacteria (21.00%–61.00%), Bacteroidetes (16.00%–69.00%), Actinobacteria (0.00%–11.00%), Firmicutes (1.00%–10.00%), Gemmatimonadetes (0.00%–6.00%), Patescibacteria (0.00%–5.00%), Planctomycetes (0.00%–7.00%), Verrucomicrobia (0.00%– 4.00%), Deinococcus-Thermus (0.00%–2.00%), and Acidobacteria (0.00%–2.00%). Proteobacteria and Bacteroidetes were the dominant phyla in each habitat.

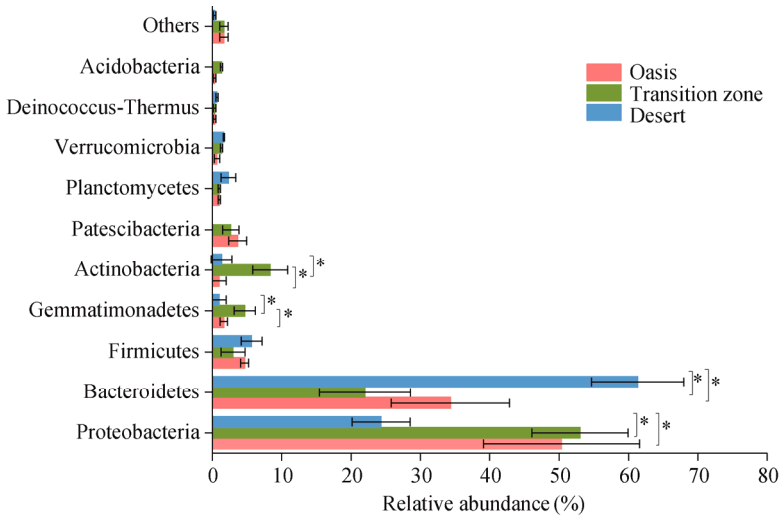

Fig. 2 Relative abundance of the first 10 phyla of soil bacterial community under the canopy of *T. ramosissima* in different habitats. Bars are standard errors. * indicates significant differences among the three habitats at $P<0.05$ level.

As known from the LEfSe evolutionary branching diagram (Fig. 3), a total of 24 bacterial taxa in the three habitats were significantly different, with 8 in the transition zone, 6 in the oasis, and 10 in the desert. The number of different species in the desert was higher than that in the oasis. With the decrease of water, the number of potential biomarker species increased. Bacteroidetes, Sphingomonadaceace, Hymenobacteraceae, Sphingomonadales, *Tunicatimoncs*, and *Pontibacter* were the significantly differentiated bacteria in the oasis. The bacterial communities with significant differences in the transition zone were Acidimicrobiia, Oceanospirillales, Actinomarinales, *uncultured_bacterium_o_Actinomarinales*, etc. Differential indicator bacteria in the desert are *Alifodinibius*, *Halofilum*, Balneolaceae, Saccharospirillaceae, Balneolales, Ectothiorhodospirales, Rhodovibrionales, and others. All of the above bacteria play an important role in the differences in community structure composition between soils of different habitats.

3.3 Soil bacterial diversity

As shown in Figure 4, there were significant differences in ACE and Chao1 indices among the three habitats ($P<0.05$). The ACE and Chao1 indices of soil bacteria in the oasis were significantly higher than those in the desert ($P<0.01$). The ACE index of soil bacteria in the oasis was significantly higher than that in the transition zone ($P<0.05$), but there was no significant difference in Simpson and Shannon indices among the three habitats ($P>0.05$).

Based on the Binary-Jaccard distance algorithm, we used PCoA to analysis soil bacterial community composition under the canopy of *T. ramosissima* in the three habitats (Fig. 5). The contribution rates of PC1 (principal coordinate) and PC2 were 43.46% and 19.79%, respectively. From Figure 5, it could be seen that the sampling points from the same habitat aggregated together, while the sampling points of different habitats were scattered. This result indicated that the structure and composition of soil bacterial community under the canopy of *T. ramosissima* in the same habitat were similar, while there were differences among different habitats.

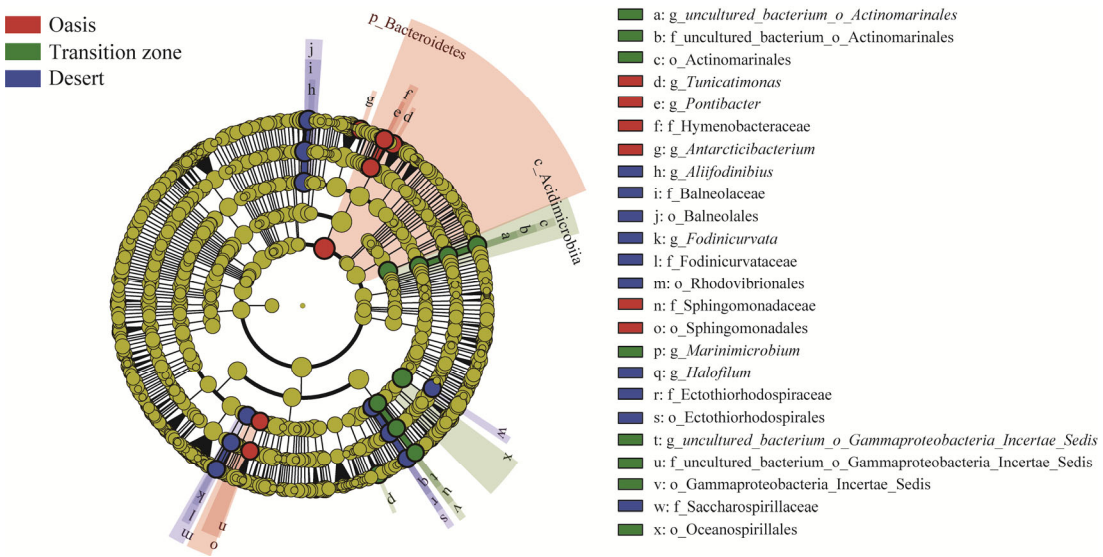

Fig. 3 Linear discriminant analysis (LDA) effect size (LEfSe) of soil bacterial community under the canopy of *T. ramosissima* in different habitats. We used LDA score >4 to identify significant differences based on biomarkers between groups. p, phylum; c, class; o, order; f, family; g, genus.

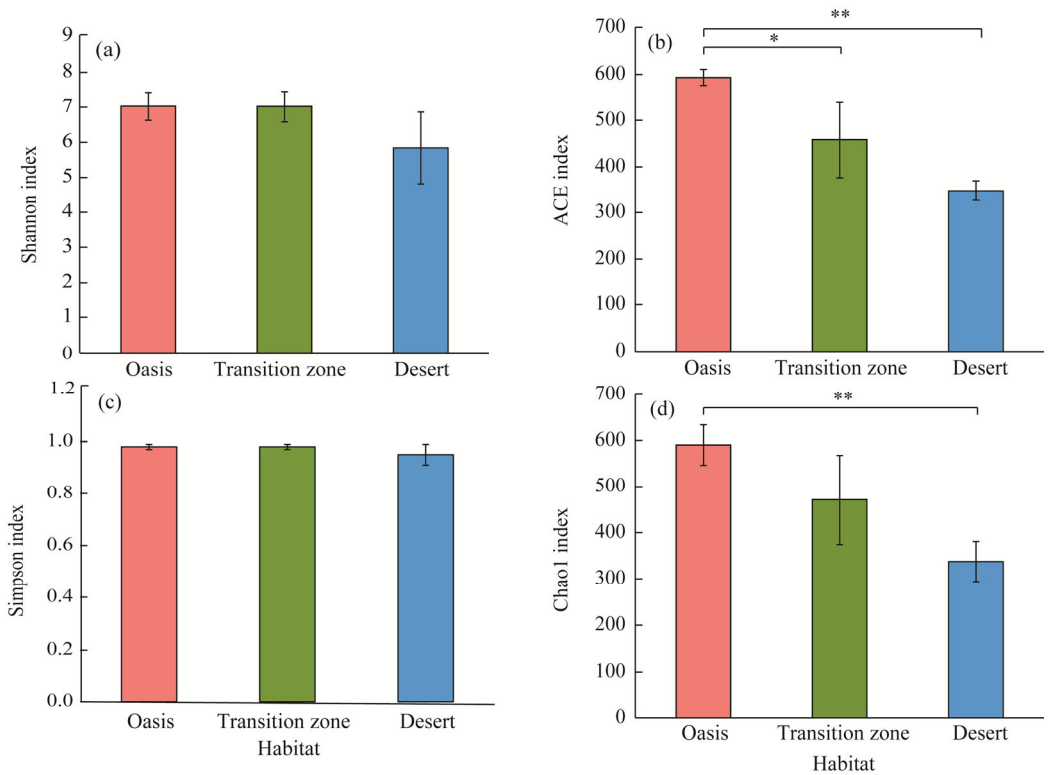

Fig. 4 Diversity and richness indices of soil bacterial community under the canopy of *T. ramosissima* in different habitats. (a), Shannon index; (b), ACE (accumulated cyclone energy) index; (c), Simpson index; (d), Chao1 index. Bars are standard errors. * indicates significant differences among the three habitats at $P<0.05$ level, and ** indicates significant differences among the three habitats at $P<0.01$ level.

3.4 Relationships between dominant soil bacteria and environmental factors

The relationships between the top 10 bacterial phyla in terms of phylum-level abundance and soil environmental factors are shown in Figure 6. The contribution rates of the first and second sorting

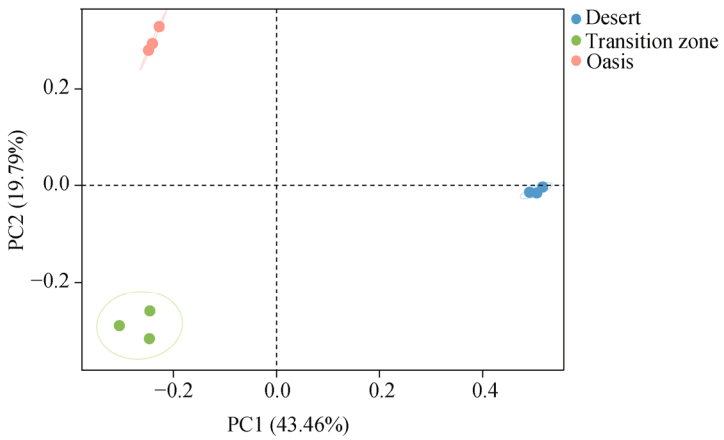

Fig. 5 Principal coordinate analysis (PCoA) of soil bacterial community under the canopy of *T. ramosissima* in different habitats. PC, principal coordinate.

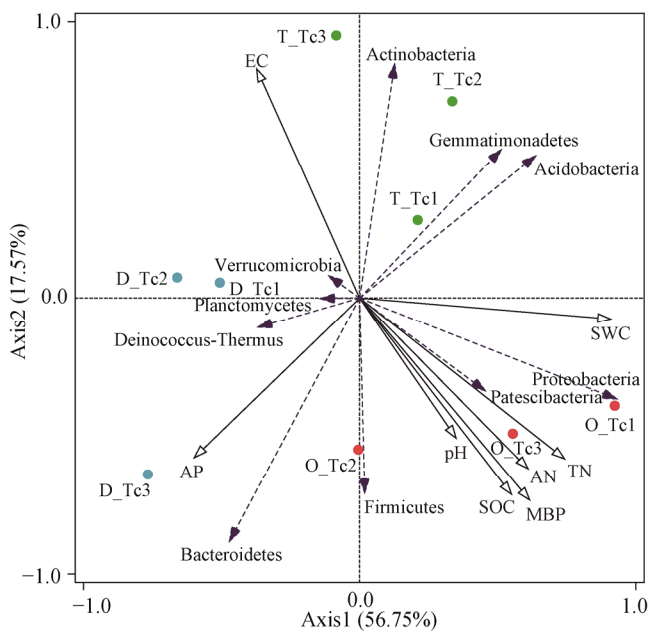

Fig. 6 Redundancy analysis (RDA) of phylum-level bacterial community and soil environmental factors. O_Tc, oasis; D_Tc, desert; T_Tc, transition zone.

axes were 56.75% and 17.57%, respectively, and the cumulative contribution rate of these two axes was 74.32%, which could effectively explain the relationship between bacterial community and environmental factor. The results showed that SWC, AP, and TN were the most critical environmental factors affecting soil bacterial community structure. SWC was positively correlated with TN, AN, MBP, SOC, and pH. AP was negatively correlated with EC and SWC. Effects of soil environmental factors on bacteria varied according to bacterial taxa. Planctomycetes and Acidobacteria were positively correlated with SWC. Bacteroidetes and Deinococcus-Thermus were positively correlated with AP, but negatively correlated with SOC, TN, and AN. Gemmatimonadetes and Acidobacteria were positively correlated with SWC and EC, but negatively correlated with AP, pH, and SOC.

Monte Carlo permutation test was used to assess the contribution of all environmental factors to the interpretation of soil bacterial community composition, and five soil indicators, i.e., SWC, AP, AN, EC, and TP, were selected. Based on the correlation analysis between environmental

factors and microbial taxa, we constructed a correlation network diagram, as shown in Figure 7. The complexity of the correlation network between soil microbial species and environmental factors in the oasis was the highest among the three habitats. Most bacterial genera were positively correlated with environmental factors, and AP and AN positively promoted every bacterial genus. There was no significant difference in the positive and negative correlation between bacterial genera and environmental factors in the transition zone. SWC and TP had more significant effects on the bacterial genus. Most bacterial genera in the desert were negatively correlated with SWC. In all three habitats, Proteobacteria showed significant effects in response to environmental factors, followed by Bacteroidetes.

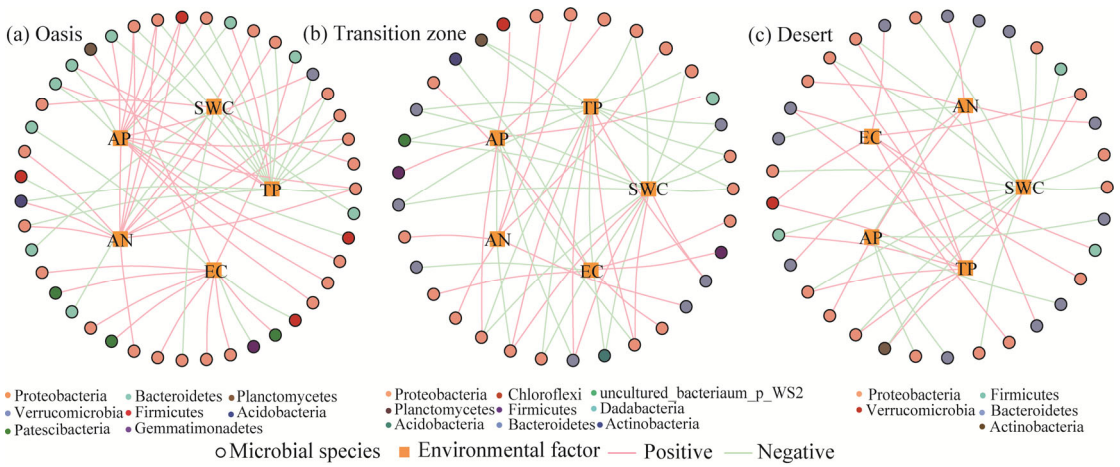

Fig. 7 Correlation network between soil microbial species and environmental factors in different habitats. (a), oasis; (b), transition zone; (c), desert.

3.5 Prediction of soil bacterial function

Based on the characteristic sequences of the 16S rDNA markers gene, we used PICRUSt2 software to predict the functions of soil bacterial OTUs under the canopy of *T. ramosissima* in different habitats. A total of 6 classes of primary metabolic functions were obtained, among which those with relative abundance greater than 1.00% were metabolism, genetic information processing, environmental information processing, cellular processes, human diseases, and organismal systems (Table 3). Except for two functions of genetic information processing and human diseases, the relative abundance of other functional genes was significantly different among the three habitats. The relative abundance of functional genes of metabolism and organismal systems in the oasis was significantly higher than those of the other two habitats (P<0.05), while the relative abundance of functional genes in environmental information processing and cellular processes was significantly lower (P<0.05).

Based on the secondary functions of KEGG database, we predicted 21 sub-functional layers from 6 primary functional layers of soil bacteria. Among them, there were 18 sub-functional layers with relative abundance above 0.10% (Fig. 8). Global and overview maps function genes were dominated with its relative abundance of 42.78%. The functional genes of the three habitats differed in the sub-functional layers. The abundance of membrane transport function genes in the transition zone was significantly higher than those of the other two habitats (P<0.05). In the desert, the relative abundance of functional genes of amino acid metabolism, nucleotide metabolism, and metabolism of the other amino acids was significantly higher, but those of metabolism and membrane transport, and metabolism of cofactors and vitamins were significantly lower than those of the other habitats (P<0.05).

Table 3 Characteristics of primary function of soil bacterial community under the canopy of *T. ramosissima* in different habitats

Soil bacterial function	Relative abundance (%)		
	Oasis	Transition zone	Desert
Metabolism	80.85[a]	79.45[b]	79.18[b]
Genetic information processing	7.23[a]	7.28[a]	7.27[a]
Environmental information processing	5.14[b]	5.94[a]	5.98[a]
Cellular processes	2.74[b]	3.42[a]	3.54[a]
Human diseases	2.65[a]	2.57[a]	2.66[a]
Organismal systems	1.39[a]	1.34[b]	1.37[ab]

Note: Different lowercase letters within the same row indicate significant differences among the three habitats at $P<0.05$ level.

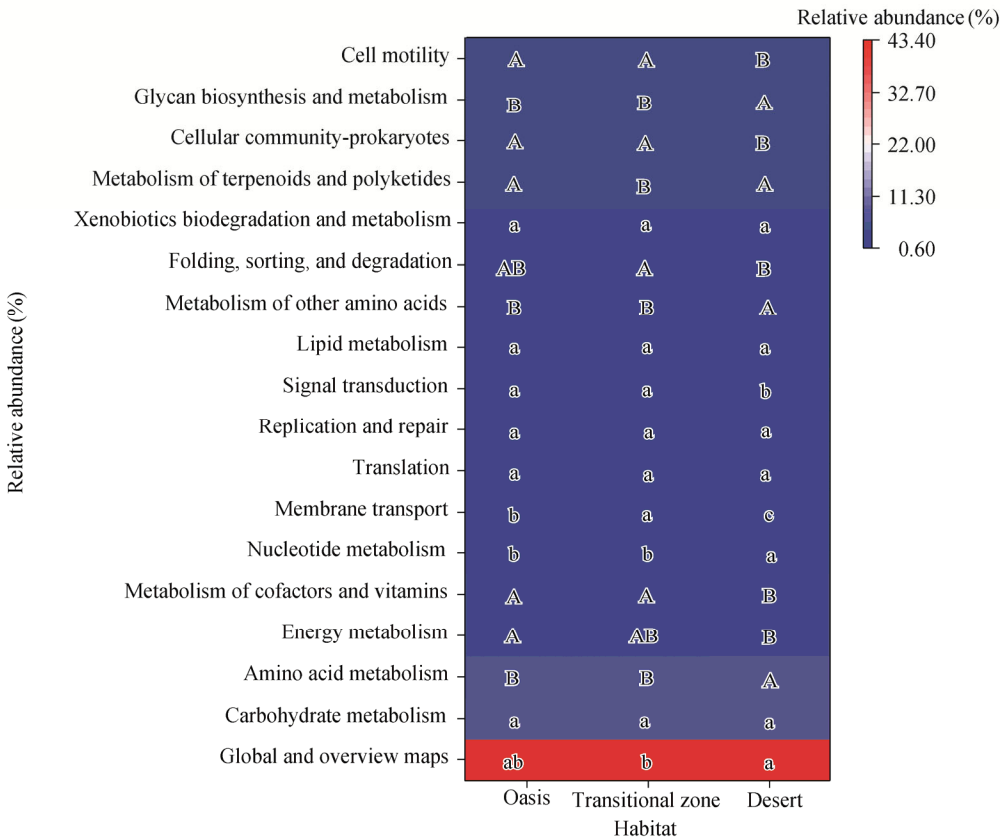

Fig. 8 Heatmap of soil bacterial function prediction in different habitats. Only the function with relative abundance of metabolic pathways greater than 0.10% was demonstrated. Different uppercase letters within the same row indicate significant differences among the three habitats at $P<0.01$ level, and different lowercase letters within the same row indicate significant differences among the three habitats at $P<0.05$ level.

4 Discussion

4.1 Soil bacterial community composition

Diversity and richness of soil bacteria under the canopy of *T. ramosissima* varied among different habitats. The Chao1 and ACE indices of soil bacterial communities in the desert were extremely significantly lower than those in the oasis ($P<0.01$), indicating that soil bacteria were very sensitive to changes in the micro-environment where they survived (Ma et al., 2020). Oasis owns adequate soil nutrients and better soil moisture conditions, which can provide a more suitable

living environment for soil bacteria and influence their growth and reproduction, thus increasing the bacterial community richness. However, the Shannon and Simpson indices of soil bacteria in the three habitats were not significantly different (P>0.05), which may be due to the fact that there was no significant change in soil pH among the three habitats. Previous studies have shown that soil pH was the main factor determining the diversity and composition of soil bacteria (Bahram et al., 2018; Liu et al., 2020). Beta diversity analyses showed that species diversity of soil bacterial communities varied more between different habitats than within the same habitat, which further indicated that the richness and relative proportion of soil microbial communities changed significantly in different habitats, but the dominant species were similar.

In this study, a total of 28 phyla, 71 classes, 153 orders, 237 families, and 397 genera were detected using sequencing technology. We found that the dominant soil bacterial phyla under the canopy of *T. ramosissima* in different habitats were Proteobacteria, Bacteroidetes, and Firmicutes, which was consistent with previous research in desert ecosystems (Bahadur et al., 2021). Proteobacteria distributes widely, and the strong nitrogen-fixing capacity and variable morphological and physiological properties give them a great competitive advantage in the ecological niche (Stevenson and Hallsworth, 2014). This result was also supported by the RDA analysis, which showed a significant positive correlation between soil TN and Proteobacteria abundance. Proteobacteria and Firmicutes reproduce via spores, the ultraviolet repair mechanism is complete, and the secondary anabolism ability is strong, adapting to the strong light and dry climate environment (Ren et al., 2018). There was no significant difference in the phyla composition of soil bacterial community under the canopy of *T. ramosissima* in different habitats in the upper reaches of the Tarim River, but there was a difference in the percentage of community abundance. The reason for this could be attributed to the discrepant soil nutrients in the three habitats, which led to the difference in microbial communities and abundance. The relative abundance of Bacteroidetes and Firmicutes in the desert was significantly higher than those of the other two habitats. Bacteroidetes and Firmicutes are involved in promoting organic matter decomposition and carbon cycling processes (Larsbrink and McKee, 2020; Gavande et al., 2021). Bacteroidetes are the main members of polysaccharide degradation pathway, capable of converting complex polysaccharides into utilizable compounds, and efficiently utilizing the polysaccharide compounds secreted by plant roots, thereby gaining greater competitiveness in drought and low-fertility environments (Gavande et al., 2021). Members of the Firmicutes are participating in biogeochemical cycles such as nitrogen utilization and stress response in desert soils (Lester et al., 2007; Goswami et al., 2014). Gemmatimonadetes are adapted to grow in soils with low water content and is difficult to survive in acidic soils. Salt-tolerant or halophilic characteristics make them suitable for growth and reproduction in soils with high salt content (Chen et al., 2022). These soil microorganisms distributed in arid and semi-arid deserts constantly adapt to the arid environment through natural selection under long-term stress of adversity, which is also an effective guarantee for the normal function of soil ecosystem.

4.2 Influence of environmental factors on soil bacteria

Numerous studies have shown that the abundance and community composition of soil microorganisms are closely related to the soil physical-chemical properties, such as pH, water content, and organic matter content (Cheng et al., 2020; Cui et al., 2020). In this study, based on RDA analysis, we found that SWC and AP were the most important soil environmental factors leading to the differences in the composition of soil bacterial communities under the canopy of *T. ramosissima* in different habitats, while pH was not the most important influencing factor, which was inconsistent with the conclusions of other studies (Zhao et al., 2019). The reason may be that the sampling point is located in the oasis-desert transition zone, and the soil pH ranges from 8.24 to 8.74, which is alkaline. The overall change in soil pH is slight, so the influence of pH is blurred. SWC as the key to maintain normal metabolism of microorganism, the effectiveness of change will cause the change of nutrient status, and then affect the soil microbial community diversity

(Wang et al., 2018). In this study, SWC in the oasis was significantly higher than those in the transition zone and desert, and the fact that both oasis soil bacterial diversity and abundance were significantly higher, which has been confirmed indirectly. Previous studies have found that microbial biomass and diversity increased with increasing soil moisture content, and the diversity of soil bacterial and fungal communities in arid and semi-arid areas showed a significantly positive correlation with soil moisture content when SWC was in the range of 0.00%–15.00% (Taniguchi et al., 2012). Soil phosphorus content was positively correlated with microbial biomass, and the death of microorganisms was able to significantly increase soil available phosphorus content (Jiang et al., 2021). In the desert, the content of available phosphorus was significantly higher than those in the oasis and transition zone. This result may be due to the high desert temperature, causing the death of a large number of temperature-intolerant strains and making the microbial community structure to form differences (Zhang et al., 2021). Meanwhile, phosphorus is easily converted to calcium phosphate and fixed by the soil under high saline environment. The microenvironment for microbial survival was damaged, leading to further changes in microbial community structure.

4.3 Prediction of soil bacterial functions

The impact of vegetation on the structure of soil bacterial communities further influences the functional composition of these bacteria (Jin et al., 2019; Liang et al., 2020). Three types of functional genes in the first functional layer, including metabolism, genetic information processing, and environmental information processing with high abundance, play important roles in plant growth. Especially, the relative abundance of metabolic function genes in the oasis accounted for more than 80.00%, which was the core function of bacteria. Previous studies have found that soil bacteria participate in the circulation and transformation of soil materials through metabolic activities, which in turn promote plant growth and increase crop yields. The role of nitrogen fixation and phosphorus solubilization is to increase the absorption of nitrogen and phosphorus nutrients by roots through metabolism (Yang et al., 2020). In the secondary functional layer, the relative abundance of membrane transport genes in the transition zone was significantly higher than those of the other two habitats. Studies have shown that membrane transport plays an important role in the transport of bacterial substances and the active uptake of nutrient (Zeng and Charkowski, 2021). Bacteria can selectively absorb metabolites secreted by plants by regulating membrane transport and establishing interaction with plants (Trivedi et al., 2020). These results indicate that soil bacterial communities in the transition zone have more potential to interact with plants when membrane transport is the main function. The relative abundance of functional genes for amino acid metabolism, nucleotide metabolism, and other amino acid metabolism in the desert was significantly higher than those of the other habitats. The reason is that the low nutrient content in the desert soil will accelerate the decomposition of organic matter in its humus layer. Meanwhile, the ability of carbohydrate, amino acid, and nucleotide metabolism will be enhanced, resulting in the increase of metabolic genes and corresponding functional microorganisms in the desert, which is important to maintain the nutrient availability required by plant growth and reflect the adaptability of soil microorganisms to stress and disturbed environment (Zhou et al., 2017). The activation of these functions enables soil bacteria to promote their own nutrient uptake and utilization in harsh environments such as desert. The prediction of soil bacterial function helps to verify the changes of soil bacterial community structure in different habitats and to clarify the important influence of environmental factors on soil microbial community function.

5 Conclusions

In this study, we investigated the differences in diversity and function of soil bacterial communities under the canopy of *T. ramosissima* in the oasis, desert-oasis transition zone, and desert habitats in the upper reaches of the Tarim River, Northwest China. We found that there were differences in the percentage of community abundance in different habitats. The alpha

diversity indices of soil bacteria showed significant differences, with the desert soils displayed the lowest diversity and richness indices. Environmental factors, i.e., SWC and available phosphorus content act as driving factors to shape the soil bacterial community structure, diversity, and functional differences. Through function prediction, we found 6 classes of primary functions and 21 classes of secondary functions, with metabolic function being the most crucial. The changes in the structure and function of soil bacteria reflected the variations in soil environmental conditions, and also indicated the adaptability of soil microorganisms to stressful and disturbed environments. These findings could deepen the understanding of ecological sensitivity of soil microorganisms in arid and semi-arid areas and advance the knowledge of bacterial ecology in desert environments.

Conflict of 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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Author contributions

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