



# Variation in Bacterial Community Structure in Rhizosphere and Bulk Soils of Different Halophytes in the Yellow River Delta

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Soil microorganisms play the important role in driving biogeochemical cycles. However, it is still unclear on soil microbial community characteristics and microbial driving mechanism in rhizosphere and bulk soils of different halophyte species. In this study, we analyzed bacterial communities in the rhizosphere and bulk soils of three typical halophytes in the Yellow River Delta, i.e., *Phragmites communis*, *Suaeda salsa*, and *Aeluropus sinensis*, by high-throughput sequencing. The contents of total carbon, total nitrogen, and available phosphorus in rhizosphere soils of the three halophytes were significantly higher than those in bulk soils, which suggested a nutrient enrichment effect of the rhizosphere. Rhizosphere soil bacterial  $\alpha$ -diversity of *P. communis* was higher than that in bulk soil, whereas bacterial  $\alpha$ -diversity in rhizosphere soil of *S. salsa* and *A. sinensis* was lower than those in bulk soil. The dominant bacterial phyla were *Proteobacteria*, *Actinobacteria*, *Chloroflexi*, and *Bacteroidetes*, which accounted for 31, 20.5, 16.3, and 10.3%, respectively. LDA effect size (LEfSe) analysis showed that the bacterial species with significant differences in expression abundance was obviously different in the rhizosphere and bulk soil of three halophytes. The principal component analysis (PCoA) showed that bacterial community composition was greatly different between rhizosphere and bulk soils of *P. communis* and *S. salsa*, while no difference in *A. sinensis*. Changed bacterial community composition was mainly ascribed to salinity in rhizosphere and bulk soils. Additionally, salinity was positively correlated with *Bacteroidetes* and negatively correlated with *Actinobacteria* and *Acidobacteria*. Our study clarified the variation in bacterial community structure between rhizosphere and bulk soils with soil physicochemical properties, which proved a biological reference to indicate the characteristics of saline and alkaline land.

**Keywords:** rhizosphere microorganisms, high-throughput sequencing, bacterial community diversity, halophytes, Yellow River Delta

## INTRODUCTION

Soil salinization is a global ecological and environmental problem, which seriously affects vegetation restoration and the sustainable development of regional ecosystems. Salinized soil can influence the composition and function of plant communities by inhibiting soil microbial activities and soil nutrients (Albdaiwi et al., 2019). In China, the area of saline-alkali land is about 99.13 million hectares (Zhu et al., 2018). The Yellow River Delta is the main distribution area of saline-alkali soil with high salinity and low land utilization (Xia et al., 2019).

Soil microorganisms respond quickly to the changing external soil environment, and bacterial community structure is generally considered to be an important indicator for evaluating soil nutrients (Chourasiya et al., 2017). In recent years, the use of microorganisms to improve the soil environment and promote the restoration of vegetation in saline soil has increasingly become a hot spot (Berendsen et al., 2012). There is a close relationship among plants, soil, and microorganisms, and they interact with each other (Yuan et al., 2016). Studies have found that soils with different types of salt, pH, soil texture, and nutrient have different microbial communities (Yamamoto et al., 2018). Plants can change soil physicochemical properties by releasing root exudates, shaping rhizosphere microbial communities (Raaijmakers et al., 2009); meanwhile, rhizosphere microorganisms would affect rhizosphere soil (Bakker et al., 2015). In addition, the types and quantities of root exudates released by different plants are different; therefore, different halophytes result in the differences in microbial community structure between rhizosphere and bulk soils (Ladygina and Hedlund, 2010).

Recent studies have reported the characteristics of microbial communities in forest and farmland ecosystems (Teurlincx et al., 2018; Liang et al., 2019; Shao et al., 2019; Liu et al., 2021) and research on microbial communities in saline-alkali lands should be paid more attention. Salinity is one of the main factors affecting soil microbial diversity and composition in saline-alkali areas (Zhang et al., 2018; Yang and Sun, 2020; Zhao et al., 2020). The vegetation in saline-alkali areas is dominated by halophytes, which have an important impact on soil microbial communities (Cao et al., 2014). Rathore et al. (2017) have reported that halophytes enhanced soil microbial activities and promoted ecosystem health. Yamamoto et al. (2018) studied bacterial communities in the rhizosphere, root inner layer, and blank soil of two halophytes (*Glax maritima* and *Salicornia europaea*) in saline-alkali land and found that soil bacterial community functions of different plant types were significantly different. Jing et al. (2018) showed that planting *Atriplex triangularis* and *Suaeda glauca* for 3 months changed rhizosphere soil properties and bacterial community. Additionally, the research of Tian et al. (2020) on the microbial communities in rhizospheres of plants in salinized soil in North Yinchuan showed that *Medicago sativa* and *Achnatherum splendens* significantly improved the functional diversity of soil microbial community and enzyme activity. These studies reflect the influence of plant species on the rhizosphere microbial

community. Soil microbial communities shape some unique salt-tolerant mechanisms adapting to long-term salinity stress for halophytes in saline-alkali land (Bell et al., 2015). Therefore, the study on rhizosphere soil microorganisms of different halophyte species can help us to further understand the salt tolerance of halophytes and their interaction with rhizosphere soil microorganisms and find some specific flora related to plant growth and soil improvement.

Halophytes have formed different salt tolerance strategies undergoing long-term salinity stress (Mansour and Salama, 2004). There were varying degrees in the connection between plants and soil due to different salt tolerance strategies (Li et al., 2021). Thus, we hypothesized whether the differences in the relationship between halophytes and soil could cause the heterogeneity of soil microorganisms around plant roots? In this study, we selected three different types of typical halophytes (salt-repellent plant—*Phragmites communis*, salt-accumulating plant—*Suaeda salsa*, and salt-secreting plant—*Aeluropus sinensis*) in the Yellow River Delta (1) to explore the heterogeneity of bacterial community structure and ecological function of different types of halophytes in the rhizosphere and bulk soils; (2) to detect the relationship of the bacterial community with soil physicochemical properties; (3) to clarify different salt tolerance strategies of halophytes impacts on rhizosphere soil microorganisms.

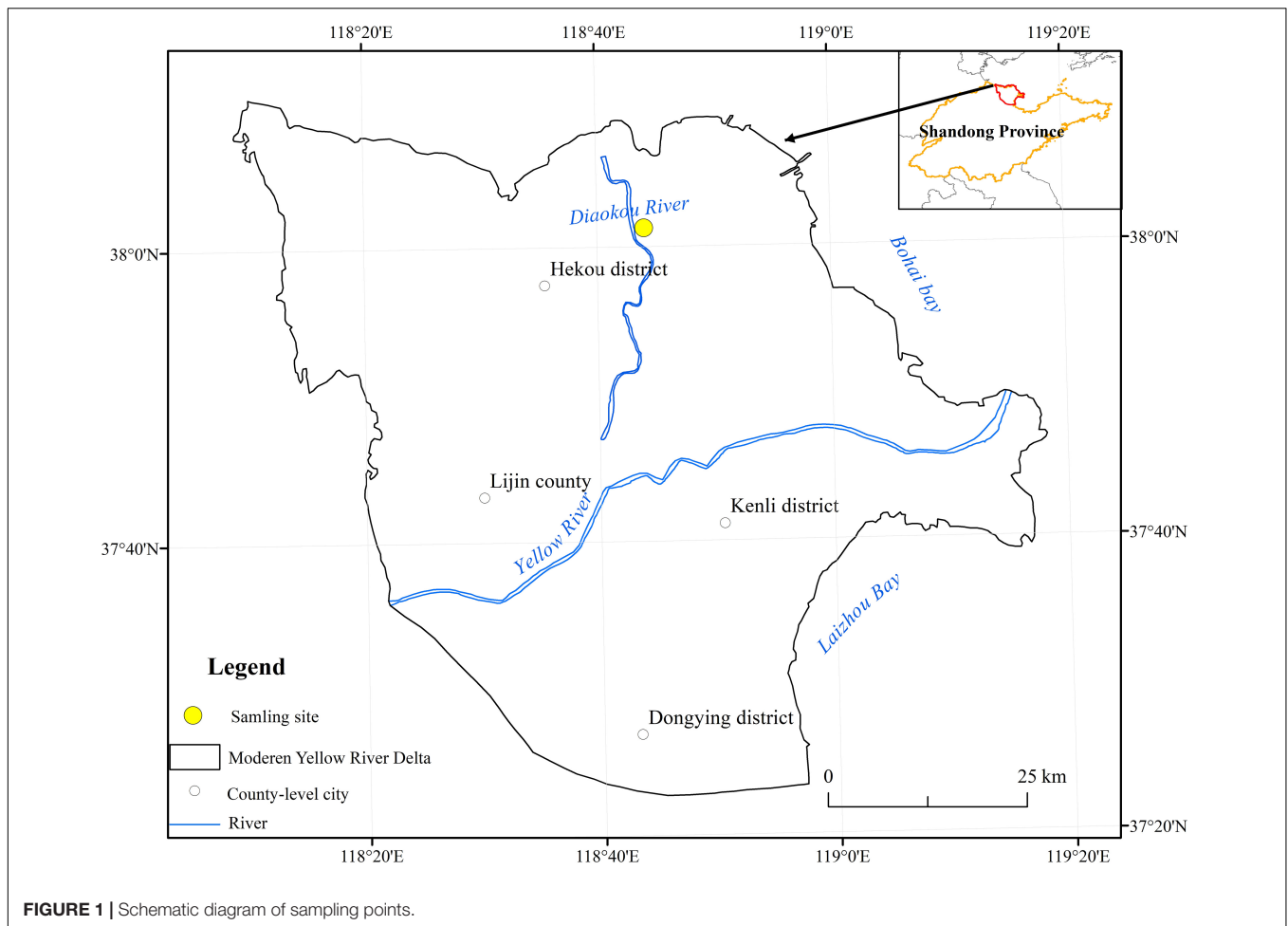
## MATERIALS AND METHODS

### Study Area

The study area is located in the Hekou District of Dongying City in the Yellow River Delta (37°35′–38°12′ N, 118°33′–119°20′ E) (Figure 1), with a semi humid continental monsoon climate. The annual average temperature is 12.1°C. The terrain is relatively flat, mostly sandy, and muddy soil, which is easy to compact and has poor ventilation. The dominant plants are *P. communis*, *S. salsa*, *A. sinensis*, and *Tamarix chinensis*, etc.

### Soil Sample Collection

In June 2020, three plant communities (*P. communis*, *S. salsa*, and *A. sinensis*) were scattered in 3 sampling areas, and each sample area was divided into 1 \* 1 m regional quadrats, randomly selected healthy plants in the quadrat, and shovel in the depth of 0–20 cm. Large pieces of soil without roots were shaken off and removed the soil around the roots as bulk soil. The soil attached to the root system (0–0.5 cm from the root) as the rhizosphere soil was carefully brushed, and the mixed roots in the rhizosphere soil were completely removed. A total of 18 soil samples were collected, and then, the samples of each sample point were divided into two parts: one was placed in a 50-ml sterilization centrifuge tube, placed in an ice box, brought back to the laboratory within 24 h, and frozen and dried at –80°C for soil microbial analysis (Wang W. C. et al., 2019); another portion were put into the ziplock bags with a written label, brought back to the laboratory, and dried naturally for the determination of soil physicochemical properties.



**FIGURE 1** | Schematic diagram of sampling points.

## Extraction of Total DNA From Soil and PCR Amplification of 16S rRNA Gene

Three repeated soils in the rhizosphere and bulk of different plants were all extracted with Omega's "Soil DNA Kit," primers 338F ACTCCTACGGGAGGCAGCAG and 806R: GGACTACHVGGGTWTCTAAT were used to amplify in the 16S V3-V4 region (Haas et al., 2011), the products were detected by 2% agarose gel electrophoresis, and purified by using AxyPrep DNA Gel Extraction Kit. The MiSeq PE300 platform of Illumina company (Shanghai Majorbio Bio-Pharm Technology Co., Ltd., China) was used for high-throughput sequencing. Qiime2 processed the original DNA data, and the obtained effective sequences were clustered by OTU for further analysis (PRJNA782205).

## Analysis of Soil Physicochemical Properties

Three repeated soils of rhizosphere and bulk of different halophytes were air-dried. The physicochemical properties of soil pH, salt ion concentration, organic carbon (OC), total carbon (TC), total nitrogen (TN), and available phosphorus (aP) were measured. Soil pH was measured by pH meter; soil salt was

measured by conductivity meter; OC was measured by potassium dichromate volumetric method (Ye et al., 2019), the TC and TN were measured by element analyzer, and the aP was measured by  $\text{NaHCO}_3$  extraction-molybdenum antimony anti-colorimetry (Wang et al., 2011).

## Data Analysis

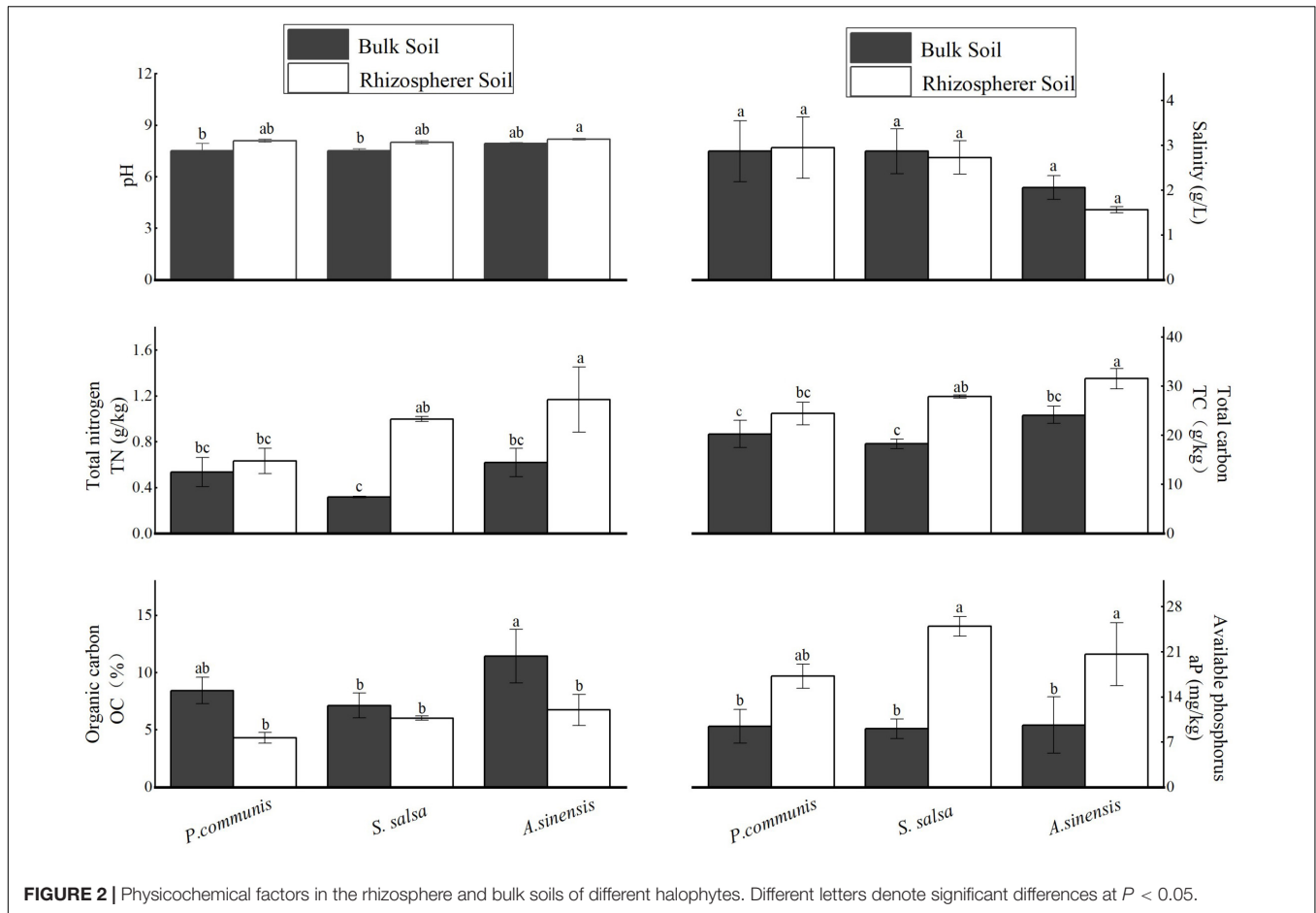
SPSS 23.0 was used for statistical analysis. CANOCO software was used to analyze the relationship between soil bacterial community diversity and soil physicochemical properties by RDA analysis. Bacterial community analyses (network analysis, LEfSe analysis, and PCoA) were carried out with the help of the platform.<sup>1</sup>

## RESULTS

### Soil Physicochemical Properties

The analysis of the physicochemical properties of the rhizosphere and bulk soils in different halophytes was shown in **Figure 2**. There were significant differences in soil nutrient contents.

<sup>1</sup><https://bioincloud.tech/#/>



**FIGURE 2 |** Physicochemical factors in the rhizosphere and bulk soils of different halophytes. Different letters denote significant differences at  $P < 0.05$ .

The contents of TN, TC, and aP in *S. salsa* and *A. sinensis* rhizosphere soils were significantly higher than those in bulk soils ( $p < 0.05$ ). The content of OC in rhizosphere soil of *A. sinensis* was significantly higher than that in bulk soil.

For the bulk soils of different halophytes, the OC content of *A. sinensis* was significantly higher than that of *S. salsa*. For rhizosphere soils of different halophytes, the TN and TC contents of *A. sinensis* were significantly higher than that of *S. salsa* and *P. communis*.

### α-Diversity Analysis

As shown in **Table 1**, the number of OTUs, Chao1 index, Shannon index, and faith in rhizosphere and bulk soils of the three halophytes had a similar change trend. The number of OTUs, Chao1 index, and Faith\_pd index in *A. sinensis* were significantly different ( $p < 0.05$ ). The number of OTUs, Chao1 index, and Faith\_pd index in *A. sinensis* rhizosphere soil were significantly lower than those in *P. communis* and *S. salsa* rhizosphere soil.

### Bacterial Community Structure

#### Relative Abundance Comparison

At the phylum level, the abundance of the top 10 bacterial phyla in the rhizosphere and bulk soils of *P. communis* and *S. salsa*

has changed (**Figure 3**). The relative abundance of *Proteobacteria* was the highest. The weighted heatmap (**Figure 4**) showed that *Bacteroidetes*, *Proteobacteria*, *Firmicutes*, and *Acidobacteria*, etc., in rhizosphere soil and *Chloroflexi*, *Actinobacteria*, and *Nitrospirae*, etc., in bulk soil were different among three different types of halophytes. In addition, the relative abundance of *Bacteroidetes* in *P. communis* rhizosphere soil was significantly higher than that in bulk soil; the relative abundance of *Planctomycetes* in *S. salsa* rhizosphere soil was significantly higher than that in bulk soil. The relative abundance of *Nitrospirae* in rhizosphere soil of *A. sinensis* was slightly lower than that in bulk soil.

At the genus level, the bacterial abundance of rhizosphere and bulk soils of three halophytes have changed, and the sum of the relative abundance of the top ten bacterial genera in bulk soils was all higher than their rhizosphere soils. According to the weighted heatmap, *Pelobacteriaceae*, *A4b*, *Hypomycobiaceae*, and *Acidimicrobiales*, etc., in rhizosphere soil and *Bacillus*, *Alphaproteobacteria*, etc., in bulk soil were different among three different types of halophytes.

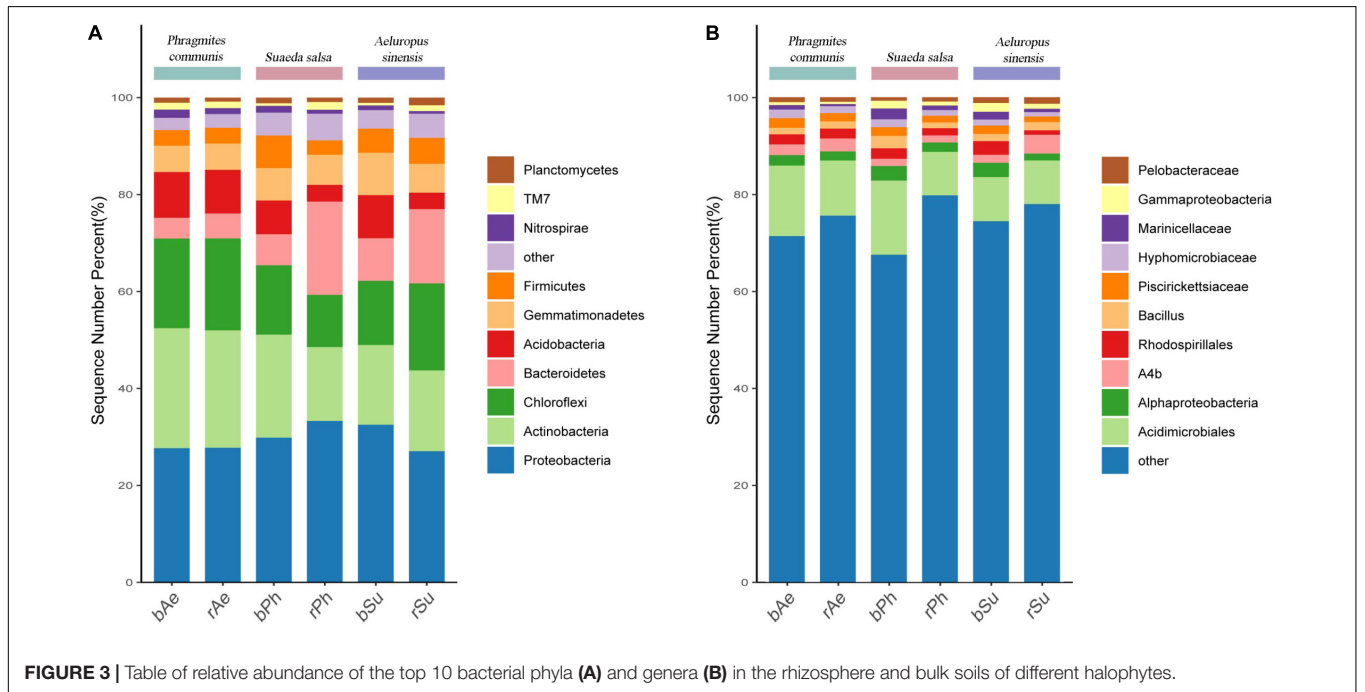
#### Comparison of Dominant Bacteria

In this study, the phyla of relative abundance (RA) > 10% were regarded as the dominant phyla (**Table 2** and **Figure 5**), including

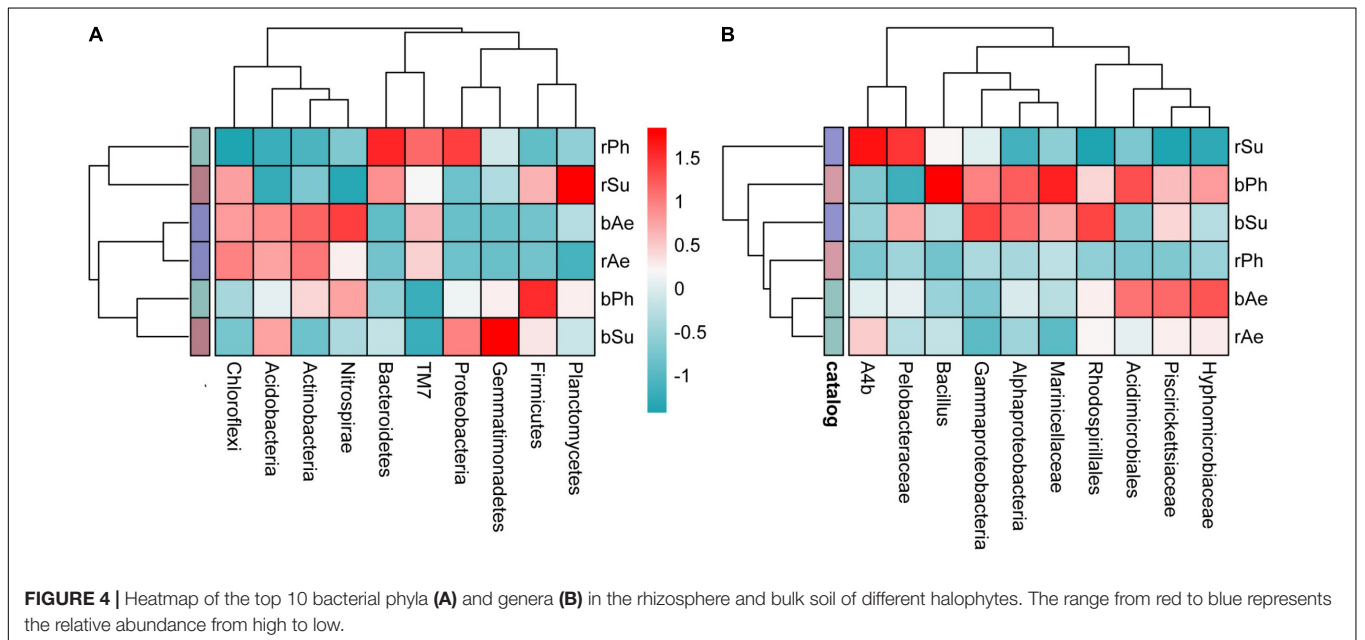
**TABLE 1** |  $\alpha$ -diversity in the rhizosphere and bulk soils of different halophytes.

Sample	OTUs	Chao1	Shannon	Faith_pd	Simpson
Bulk_Ph	1,122.3 ± 157.68ab	1,122.36 ± 157.69ab	9.01 ± 0.31a	106.85 ± 12.25a	0.994 ± 0a
Rhizosphere_Ph	1,253.7 ± 197.74a	1,253.92 ± 197.73a	9.04 ± 0.31a	110.06 ± 11.16a	0.994 ± 0a
Bulk_Su	1,156 ± 82.14ab	1,156.44 ± 82.3ab	9.3 ± 0.15a	101.76 ± 6.81ab	0.996 ± 0a
Rhizosphere_Su	1,059.67 ± 98.4ab	1,059.92 ± 98.2ab	9.29 ± 0.1a	101.33 ± 6.56ab	0.997 ± 0a
Bulk_Ae	1,201.33 ± 13.53ab	1,201.6 ± 13.47ab	9.21 ± 0.1a	102.79 ± 1.85ab	0.995 ± 0a
Rhizosphere_Ae	824 ± 88.71c	824.33 ± 88.52c	8.98 ± 0.2a	77.1 ± 5.69c	0.996 ± 0a

Ph, *Phragmites communis*; Su, *Suaeda salsa*; Ae, *Aeluropus sinensis*. Different letters denote significant differences at  $P < 0.05$ .



**FIGURE 3** | Table of relative abundance of the top 10 bacterial phyla (A) and genera (B) in the rhizosphere and bulk soils of different halophytes.



**FIGURE 4** | Heatmap of the top 10 bacterial phyla (A) and genera (B) in the rhizosphere and bulk soil of different halophytes. The range from red to blue represents the relative abundance from high to low.

**TABLE 2** | The dominant phyla in the rhizosphere and bulk soil of different halophytes.

Halophytes	Conditions	Dominant bacterial phylum
<i>P. communis</i>	Bulk soil	<i>Proteobacteria</i> , <i>chloroflexi</i> , <i>actinobacteria</i>
	Rhizosphere soil	<i>Proteobacteria</i> , <i>chloroflexi</i> , <i>actinobacteria</i> , <i>bacteroidetes</i>
<i>S. salsa</i>	Bulk soil	<i>Proteobacteria</i> , <i>actinobacteria</i> , <i>chloroflexi</i>
	Rhizosphere soil	<i>Proteobacteria</i> , <i>chloroflexi</i> , <i>actinobacteria</i> , <i>bacteroidetes</i>
<i>A. sinensis</i>	Bulk soil	<i>Proteobacteria</i> , <i>actinobacteria</i> , <i>chloroflexi</i>
	Rhizosphere soil	<i>Proteobacteria</i> , <i>actinobacteria</i> , <i>chloroflexi</i>

*Proteobacteria* (RA: 27–35%), *Actinobacteria* (RA: 11–25%), *Chloroflexi* (RA: 11–19%), and *Bacteroidetes* (RA: 4–20%). For *Bacteroidetes*, the relative abundance of the rhizosphere soil in *P. communis* showed significant changes, which was higher than that in bulk soil ( $p < 0.05$ ). The significant differences of the four dominant bacteria in the rhizosphere soil of the three halophytes were mainly between *A. sinensis* and *P. communis*. Results showed that the abundance of *Actinobacteria* and *Chloroflexi* in *A. sinensis* rhizosphere soil was significantly higher than those in *P. communis* rhizosphere soil, but the abundance of *Bacteroidetes* was significantly lower than that in *P. communis* rhizosphere soil.

### Analysis of Bacterial Symbiosis System

Symbiotic network analysis was carried out for bacterial species in the rhizosphere and bulk soil of three different halophytes (Figure 6), and the number of edges connected between all bacterial species and other nodes was calculated. There were 59 in rhizosphere soil (Figure 6A) and 42 in bulk soil (Figure 6B). The positive correlation connecting lines (95%) observed in rhizosphere soil was significantly more than the negative correlation (5%). *BRC1*, *Planctomycetes*, *OP11*, and *Verrucomicrobia* played a central role in the network analysis diagram (connectivity > 7), which were the key phylum in rhizosphere soil, but their abundance was relatively low. *Verrucomicrobia* and *BRC1* had 9 connecting lines, and the relative abundance was less than 1%. *Actinobacteria* with high relative abundance (RA > 15%) had only one connecting line in the network structure analysis. In bulk soil (Figure 6B), the positive correlation connecting line (57%) was more than the negative correlation (43%). *BRC1*, *Actinobacteria*, and *Thermi* (connecting line  $\geq 6$ ) had relatively high connectivity. In addition, there was 8 positive correlation connecting lines in *Planctomycetes* in rhizosphere soil, whereas the number of connecting lines was 0 in bulk soil.

### Significant Difference Analysis

The results of LEfSe analysis (Figure 7) showed that there were 76 distinct microbial between the rhizosphere and bulk soils of the three halophytes (LDA > 2). Significantly different bacteria between bulk and rhizosphere soil of *P. communis* were 6 and 12, which included *Gammaproteobacteria* (*Proteobacteria*),

*Burkholderiaceae* (*Proteobacteria*), *Flavobacteriaceae* (*Bacteroidetes*), and *Erythrobacteraceae* (*Bacteroidetes*), etc. The *S. salsa* were 7 and 17, including *Alteromonadales* (*Proteobacteria*), *Chromatiales* (*Proteobacteria*), *Cytophagaceae* (*Bacteroidetes*), *Rhodobacteraceae* (*Proteobacteria*), and *Geodermatophilaceae* (*Proteobacteria*), etc., and the *A. sinensis* were 10 and 26, including *Betaproteobacteria* (*Proteobacteria*), *Myxococcaceae* (*Proteobacteria*), *Alphaproteobacteria* (*Proteobacteria*), *Rubrobacteraceae* (*Proteobacteria*), and *Flavisolibacteria* (*Bacteroidetes*), etc. The bacteria with significant differences in the rhizosphere soil of *A. sinensis* were the most, and *Phragmites communis* were the least.

### Correlation Between Soil Bacterial Groups and Physicochemical Properties

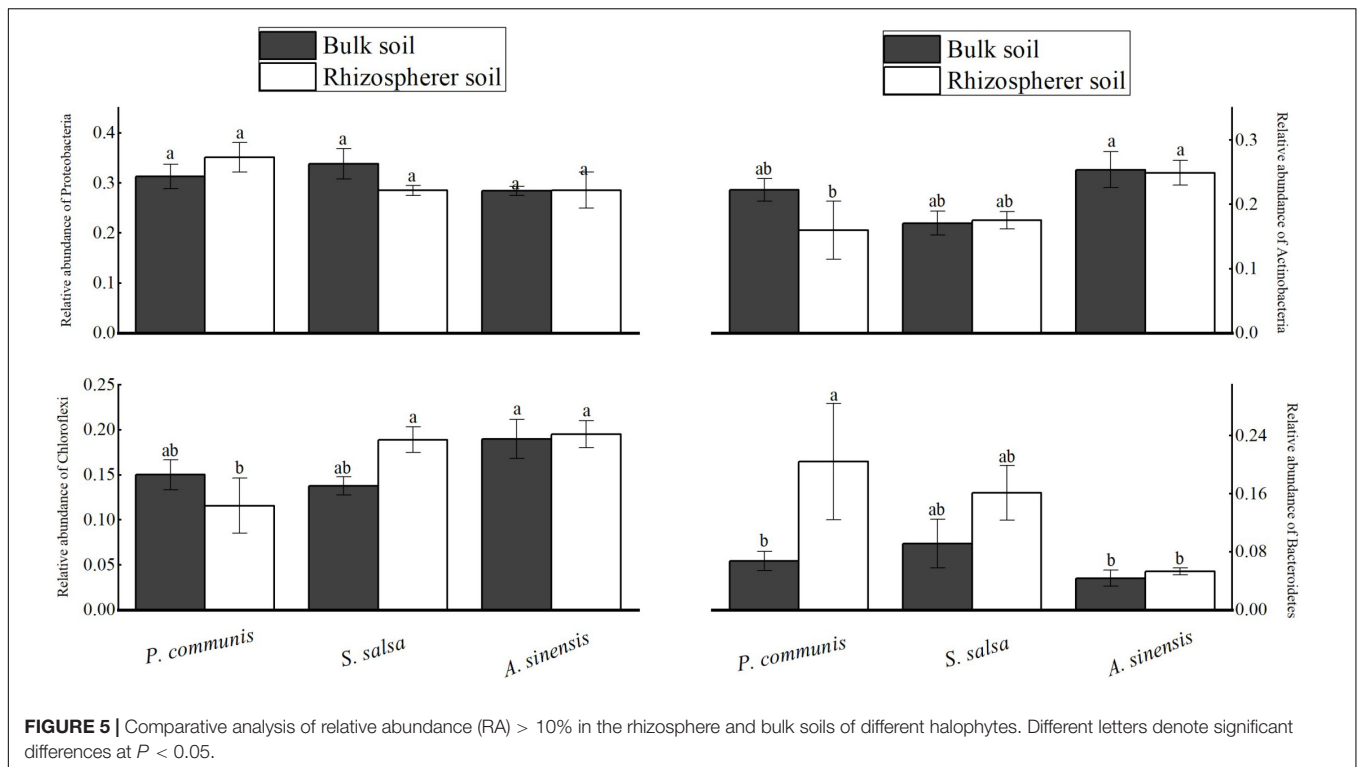
Based on Bray–Curtis similarity coefficient, the bacterial community composition of three halophytes was significantly different (Figure 8). The confidence ellipse of *P. communis* and *S. salsa* indicated that there was a great difference in the bacterial community structure between the rhizosphere and bulk soil in the two halophytes. The confidence ellipse of *A. sinensis* rhizosphere and bulk soil samples was clustered together, indicating that their composition was relatively similar.

At the OTU level, the first and second axes of RDA explained 21.63 and 20.19% of the variation in bacterial community composition, respectively (Figure 9). According to the length of rays, the bacterial community structure of the three halophytes was strongly affected by soil, salinity, and pH. The salinity was located in the first quadrant, with an obtuse angle with other environmental factors, which was negatively correlated with TN, TC, aP, OC, and pH. The pH located in the third quadrant, which had a positive correlation with OC, TN, TC, and aP. According to the position of the samples on the RDA diagram, the rhizosphere and bulk samples of *A. sinensis* were gathered together, and the nutrient content was relatively rich. Among the top eight phyla of relative abundance (RA > 2%), *Acidobacteria*, *Bacteroidetes*, and *Actinobacteria* had a great impact on the composition of the bacterial community. *Bacteroidetes* were located in the first quadrant, and *Acidobacteria* and *Actinobacteria* were located in the third quadrant. Salt was positively correlated with *Bacteroidetes* and negatively correlated with *Actinobacteria* and *Acidobacteria*. pH was positively correlated with *Actinomycetes* and negatively correlated with *Acidobacteria* and *Bacteroidetes*.

## DISCUSSION

### Characteristics of Physicochemical Properties in Rhizosphere and Bulk Soils of Different Halophytes

In saline soil, the root system of halophytes can affect the physicochemical properties of soil and the structure of the rhizosphere microbial community by regulating the salt content, forming a microenvironment that is conducive to plant growth and development (Lau and Lennon, 2012; Lareen et al., 2016). There are salt gland cells in the salt-secreting plant *A. sinensis*,



which can absorb soil salt and secrete the salt *in vitro* (Wu et al., 2020). The salt-accumulating plant *S. salsa* can absorb the salt from the soil and accumulate in the fleshy stems and leaves (Jia et al., 2021). Therefore, the salt content of *A. sinensis* and *S. salsa* was less in the rhizosphere than in bulk soil. The salt content in the rhizosphere of the salt-repellent plant *P. communis* was higher than that in bulk soil because its roots restrict the transport of  $\text{Na}^+$  to the ground and transport  $\text{Na}^+$  from the plant to the root soil (Peng et al., 2016).

Plant mucus secreted by plant roots, sloughed cells and tissues, and soluble products of broken cells contribute to the TC of plant rhizosphere soil (Ai et al., 2015), resulting in higher TC content of three plant rhizosphere soils than that in bulk soil. In addition, the sugar and amino acids secreted by plant roots will increase the availability of soil nitrogen and phosphorus (Smith, 2007), explaining higher content of TN and aP in rhizosphere soil than bulk soil. The results suggest that the root systems of the three halophytes can significantly increase soil carbon, nitrogen, and phosphorus content.

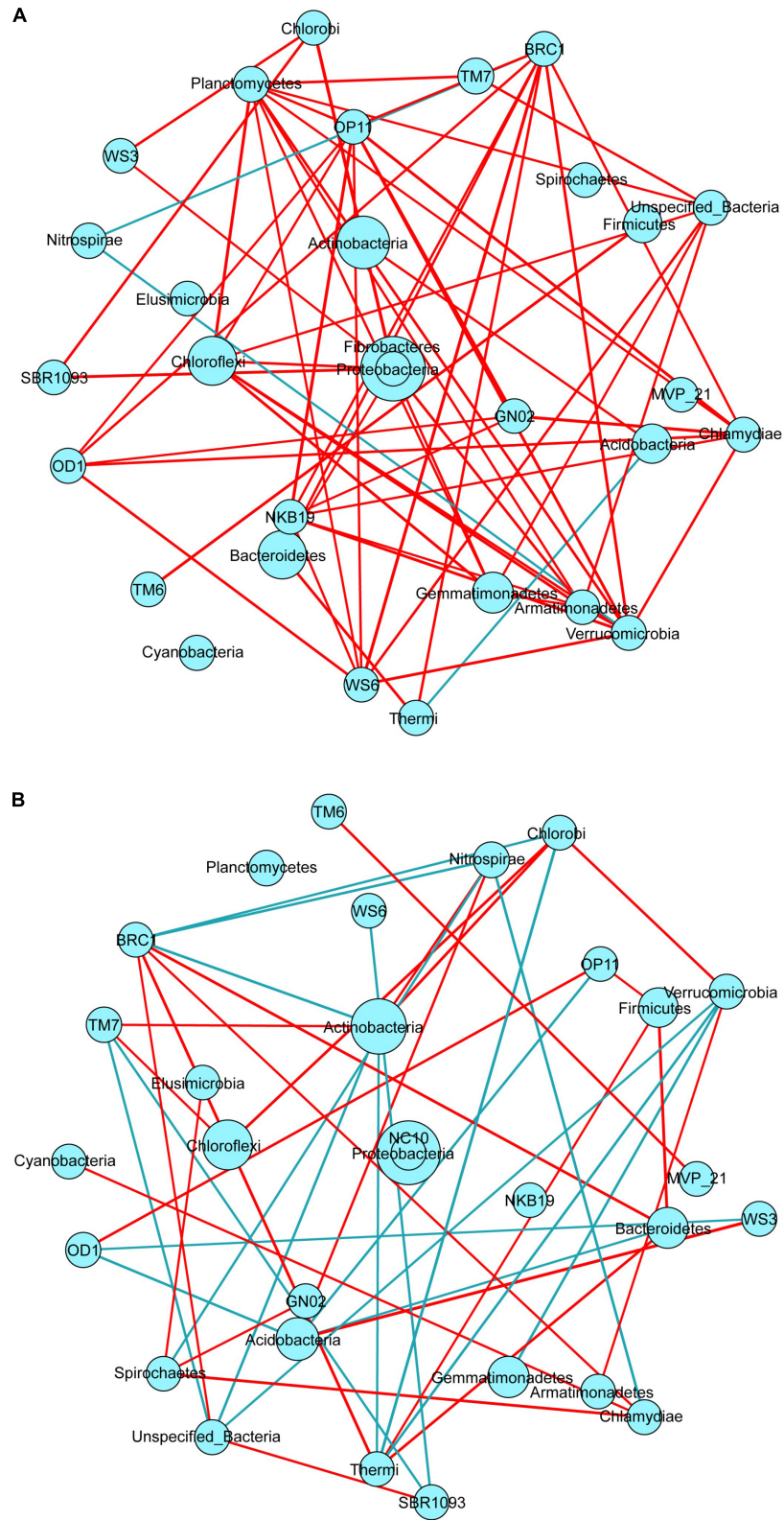
Among the three halophytes, OC content in *A. sinensis* rhizosphere was significantly lower than bulk soil, and it was not significant in the soil of *P. communis* and *S. salsa*. This result is similar to the determination results of rhizosphere and bulk soil organic carbon of *Amorpha fruticosa* by An et al. (2011) and *Agropyron cristatum* by Song et al. (2014). It may be caused by the high utilization rate of rhizosphere microorganisms.

High-quality soil is the basic condition to ensure plant growth and development. Soil salt content and pH have a great impact on microbial community structure and plant growth and development (Nacke et al., 2011). In this study, the salt content of the rhizosphere soil of the three plants was not significantly

different, but the salt content of rhizosphere soil in *A. sinensis* was relatively low, which was related to the fact that *A. sinensis* belongs to salt-secreting plants. In the three halophytes, the TN content of rhizosphere soil was different, which showed that *A. sinensis* is significantly higher than *P. communis*, which was the result of different rhizosphere precipitation caused by different halophytes. RDA also showed that *P. communis* could survive in soils with low carbon, nitrogen, and high salt content. For different plants, the types of organic acids secreted by roots are different, resulting in differences in the ability to compete with phosphate for adsorption sites (Chen et al., 2002). Therefore, the content of aP in rhizosphere soil of three halophytes was different. We found that the root system of *S. salsa* can improve the content of soil aP, and *A. sinensis* was more dependent on the content of nutrients in the soil than *P. communis* and *S. salsa*, which was consistent with the results of soil physicochemical properties. Therefore, *P. communis* and *S. salsa* have greater survival advantages in nutrient poor saline-alkali soil than *A. sinensis*.

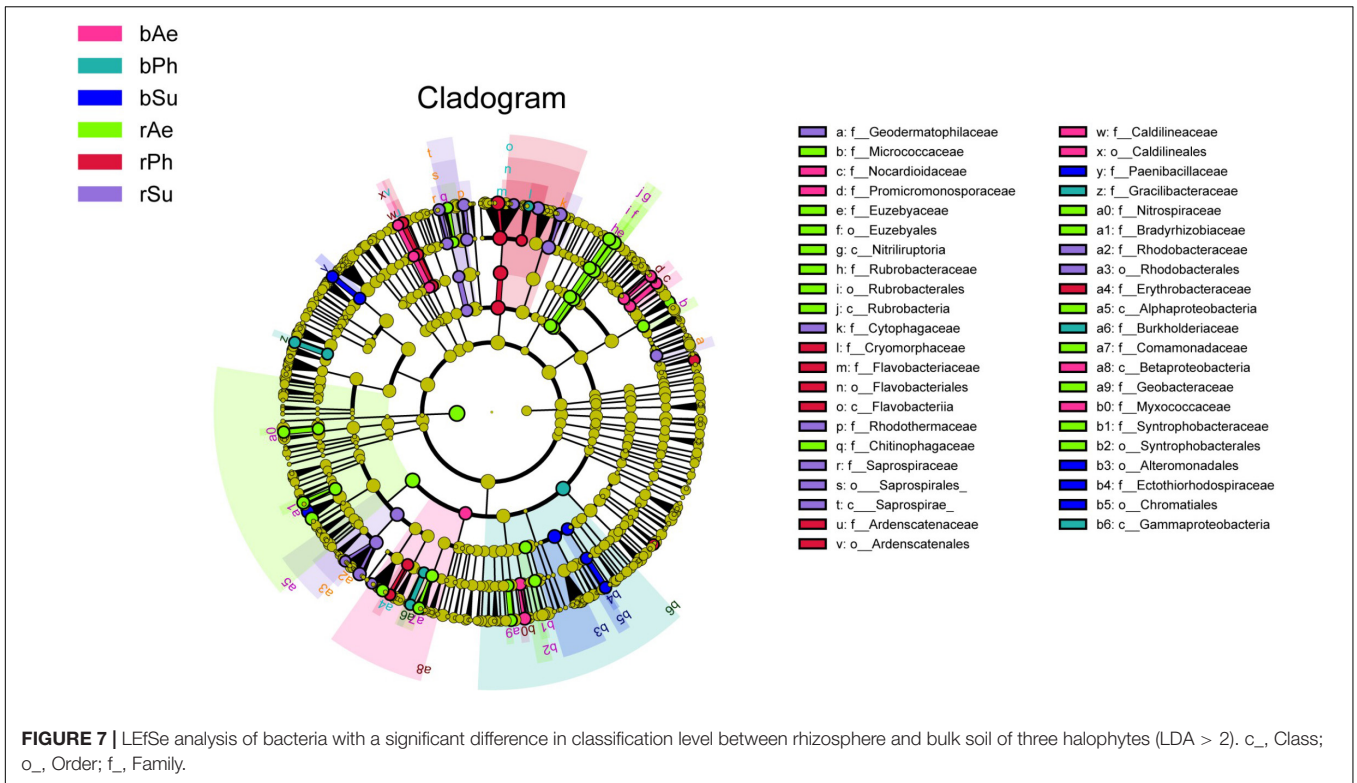
## Effects of Different Halophytes in the Rhizosphere and Bulk Soils on Bacterial Community Diversity

The RDA showed that soil salinity was the main factor affecting the characteristics of the bacterial community. Soil salinity was positively correlated with bacterial community  $\alpha$ -diversity, which was consistent with the results of Nie et al. (2009) in the Yellow River Delta. The results showed that mild salt stress promoted the survival and reproduction of salt tolerant and halophilic bacteria in the soil. In addition, the diversity and richness of bacterial community in *A. sinensis* rhizosphere soil were significantly lower



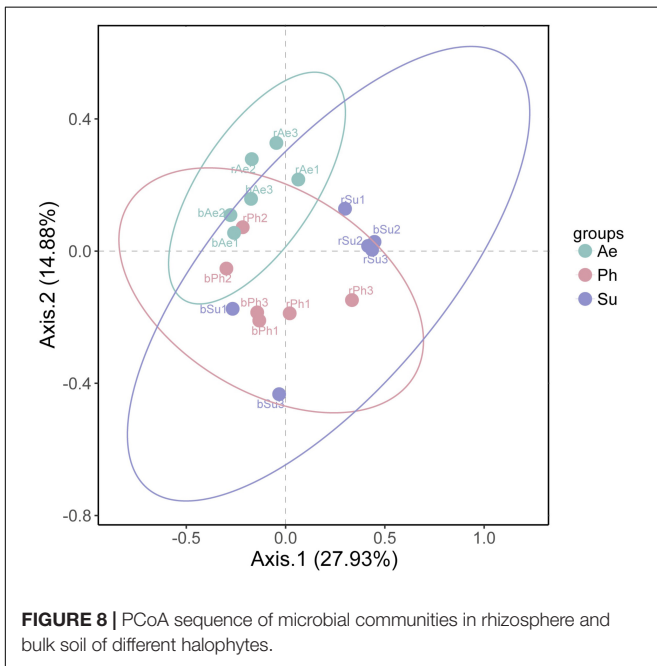
**FIGURE 6 |** Symbiotic network analysis of soil bacterial communities in the rhizosphere **(A)** and bulk **(B)** of three halophytes (correlation threshold > 0.5). Nodes in the network diagram represent bacterial gates, and the size of each node is in direct proportion to the relative abundance. The red connection line represents a positive correlation between bacteria, whereas the blue connection line represents a negative correlation between bacteria.





than that in bulk soil ( $p < 0.05$ ), and there was an obvious negative rhizosphere effect, which was related to the fact that *A. sinensis* belongs to salt-secreting plants. The salt content of rhizosphere soil was less than bulk soil due to the salt resistance mechanism of *A. sinensis*, decreasing rhizosphere soil bacterial community diversity. There was no significant difference in

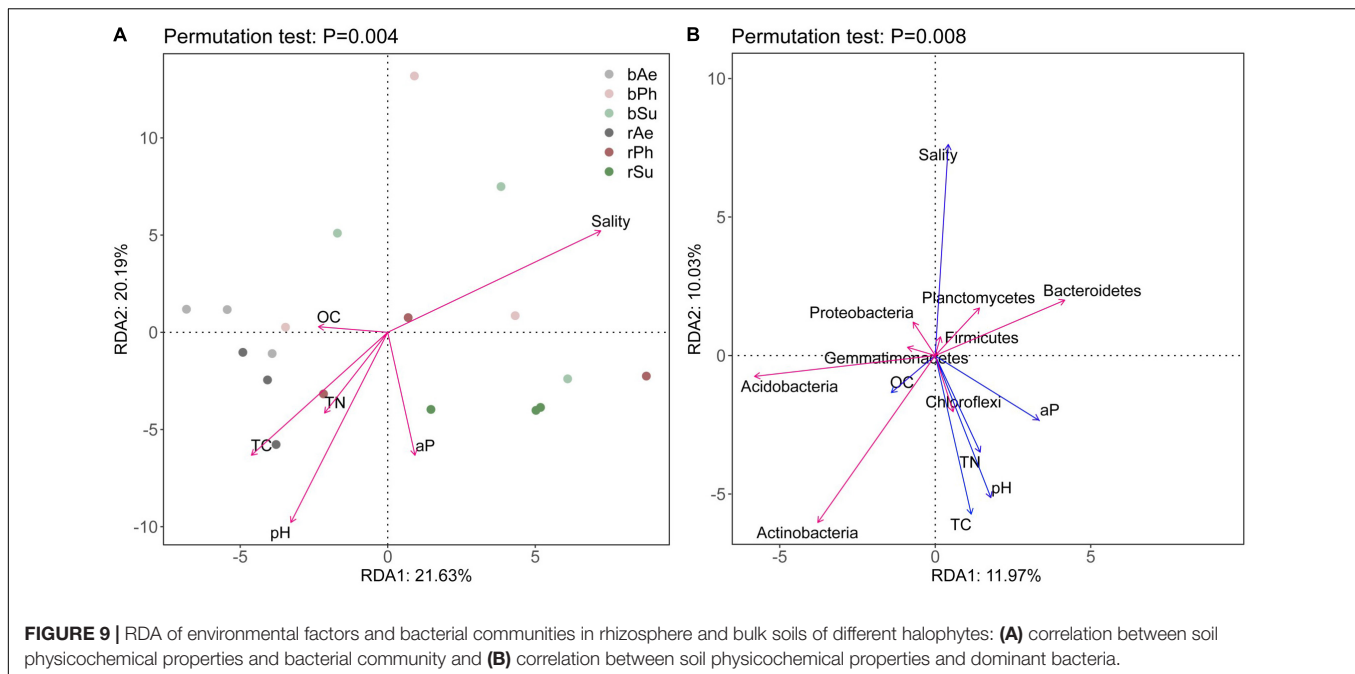
bacterial community diversity between rhizosphere and bulk soils of *P. communis*, *S. salsa*, but it was still consistent with the regular pattern of rhizosphere and bulk soil in *A. sinensis*, which further showed that the soil bacterial community in this area needed appropriate salt induction and stimulation to have higher diversity and richness.



In this study, the differences in bacterial diversity and richness of three halophytes rhizosphere soil showed that *P. communis* was significantly higher than *A. sinensis*, which was caused by the unique physiological process of different plants. Studies had shown that abscission and secretion were positively correlated with the growth of plant roots, the more vigorous the growth of plant roots, the more abscission and secretion in soil (Cao et al., 2017). Compared with the other two halophytes, the rhizome of *P. communis* is larger, sturdy, and well-developed, which makes the bacterial community in the rhizosphere soil of *P. communis* have higher diversity and richness.

### Effects of Rhizosphere and Bulk Soils of Different Halophytes on Bacterial Community Structure

In this study, the relative abundance of the *Proteobacteria* was significantly higher than that of other phyla, which included many nitrogen-fixing bacteria (Delmont et al., 2018). The relative abundance of *Proteobacteria* in the rhizosphere soil of the three halophytes did not change significantly compared with that in the bulk soil. This result was not in line with the research on the rhizosphere and bulk soil of *Lycium ruthenicum* by Li et al. (2018) and also was different from Wang X. T. et al. (2019)



on the rhizosphere effect of rice (*Orvaa sativa*) and wheat (*Triticum aestivwm*). Studies have shown that the changes in soil nitrogen content can cause differences in the signal molecules secreted by the different plant roots and then selected bacterial species. In particular, the higher nitrogen content in the soil will cause the nitrogen-fixing bacteria in *proteobacteria* to be replaced by non-nitrogen-fixing bacteria (Zheng et al., 2020). In this study, although the content of TN in *P. communis* rhizosphere soil was significantly lower than that of *A. sinensis*, there was no significant difference in *Proteobacteria*. This reflects that among the three halophytes, *P. communis* can survive under the condition of low nitrogen, and the low nitrogen microenvironment of the rhizosphere does not significantly inhibit the survival of *Proteobacteria*, which suggests that *P. communis* rhizosphere may contribute to the increase of the relative abundance of nitrogen-fixing bacteria in some soils. In addition, it also showed that although the nitrogen content in rhizosphere soil of *A. sinensis* is significantly higher than that in bulk soil, it was still at a low level, which should be related to the lack of nitrogen in this area.

Plant roots have a great influence on the construction of key bacterial species in the soil bacterial community. Compared with bulk soil, the rhizosphere soil bacterial community co-occurrence network had stronger connectivity and higher modularity, suggesting that plant rhizosphere soil had the ability to resist external environmental disturbance and recovery (Zhou et al., 2019). In the plant rhizosphere soil, there were many bacteria with low abundance with high network connectivity, such as *Planctomycetes*, *Verrucomicrobia*, and *OP11*. These bacteria have important ecological functions for the diversity of plant rhizosphere soil bacterial community, the stability of community structure, and the health of host plants (Nuccio et al., 2016). This result can provide theoretical guidance for the future selection of plant rhizosphere growth-promoting bacteria. By comparing

the rhizosphere and bulk soils of three halophytes, most of the bacteria with significant differences between the rhizosphere and bulk soils of three halophytes belong to *Proteobacteria*.

## CONCLUSION

Different types of halophytes had stronger effects on rhizosphere soil nutrients than on pH and salinity, and the rhizosphere soil nutrient content of different plant species was higher than that of bulk soil. However, their enrichment ability was different, and *A. sinensis* (salt-secreting) and *S. salsa* (salt-accumulating) had stronger rhizosphere nutrient accumulation ability than *P. communis* (salt-repellent). Plant species affected the diversity and richness of rhizosphere soil bacteria. Among the three halophytes, the diversity and richness of rhizosphere soil bacteria in *P. communis* and *S. salsa* were higher than that of *A. sinensis*. Different plant species made for the composition of dominant bacteria and significantly different microbial flora in rhizosphere soil and bulk soil. The number of significant differences bacteria in the expression abundance of *A. sinensis* rhizosphere soil was higher than that of *S. salsa* and *P. communis*, and the discovery of these significantly different microbial flora caused by plant species provided a basis for the excavation and utilization of specific microbial resources. Some low abundance phyla in plant rhizosphere soil were key phyla rather than high abundance dominant phyla, suggesting that attention should be paid attention to this kind of key phyla. Plant species can lead to differences in bacterial community structure. The bacterial community structure of *P. communis* and *S. salsa* in rhizosphere soil and bulk soil was quite different, while *A. sinensis* was not obvious, suggesting that *P. communis* and *S. salsa* had more obvious effects on the bacterial community structure of rhizosphere soil than *A. sinensis*. Soil salinity and pH were

the main factors affecting the bacterial community structure in the three types of halophytes. Salinity was positively correlated with bacterial community diversity, suggesting that moderate salt induction and excitation can promote the increase of bacterial diversity and richness in the rhizosphere soil of halophytes.

## DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: NCBI (accession: PRJNA782205).

## AUTHOR CONTRIBUTIONS

YZ was the executor of this experimental research, completed data analysis, and wrote the first draft of the manuscript. TL was

the designer and person in charge of the experimental project, guiding the experimental design, data analysis, thesis writing and modification, and fund support. PS guided data processing methods, experimental methods, and data sorting. JS supervised the experimental research process and fund support. WX and ZZ participated in sample determination experiments and data sorting. All authors contributed to the article and approved the submitted version.

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