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Microbial diversity in the saline-alkali soil of a coastal *Tamarix chinensis* woodland at Bohai Bay, China

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Abstract: Soil salinization or alkalization is a form of soil desertification. Coastal saline-alkali soil represents a type of desert and a key system in the network of ecosystems at the continent-ocean interface. *Tamarix chinensis* is a drought-tolerant plant that is widely distributed in the coastal saline-alkali soil of Bohai Bay, China. In this study, we used 454 pyrosequencing techniques to investigate the characteristics and distribution of the microbial diversity in coastal saline-alkali soil of the *T. chinensis* woodland at Bohai Bay. A total of 20,315 sequences were obtained, representing 19 known bacterial phyla and a large proportion of unclassified bacteria at the phylum level. Proteobacteria, Acidobacteria and Actinobacteria were the predominant phyla. The coverage of *T. chinensis* affected the microbial composition. At the phylum level, the relative abundance of γ-Proteobacteria and Bacteroidetes decreased whereas Actinobacteria increased with the increasing coverage of *T. chinensis*. At the genus level, the proportions of *Steroidobacter, Lechevalieria,* Gp3 and Gp4 decreased with the increase of the vegetation coverage whereas the proportion of *Nocardioides* increased. A cluster analysis showed that the existing *T. chinensis* changed the niches for the microorganisms in the coastal saline-alkali soil, which caused changes in the microbial community. The analysis also distinguished the microbial community structure of the marginal area from those of the dense area and sparse area. Furthermore, the results also indicated that the distance to the seashore line could also affect certain groups of soil bacteria in this coastal saline-alkali soil, such as the family Cryomorphaceae and class Flavobacteria, whose population decreased as the distance increased. In addition, the seawater and temperature could be the driving factors that affected the changes.

Keywords: coastal saline-alkali soil; *Tamarix chinensis*; bacteria; pyrosequencing

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Soil salinization or alkalization is a form of soil desertification. Coastal saline-alkali soil is a common form of soil salinization and alkalization, which represents a type of desert (Szabolcs, 1992; Thomas and Middleton, 1993). This typical arid land represents a key ecosystem at the continent–ocean interface (Carpentier et al., 2013) and has high continental and marine nutrient inputs due to a high microbial community turnover and high mineralization of organic matter. However, this ecosystem is ecologically and economically vulnerable (Zhu et al., 2012). It may be exposed to a variety of organic pollutants from oil and chemical spills (Wilms et al., 2006a, b;

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Kim et al., 2014). Coastal saline-alkali soil has high primary production rate and, in turn, intense heterotrophic activity (Wilms et al., 2006a). Previous studies suggested that such high microbial activity led to oxygen depletion within the first few millimeters of the sediments, below the prevailing anoxic condition (Graue et al., 2011). The microbial diversity of coastal saline-alkali soil was analyzed using culture-independent or cultivation-based methods. Proteobacteria and Bacteroidetes were the dominant phyla found from the surface to 20 cm depth in the sediment (Llobet-Brossa et al., 1998), and other studies showed that only Proteobacteria could be the dominant phylum in coastal saline-alkali soil (Kim et al., 2004; Köpke et al., 2005).

Tamarix is an Old World genus that has grown in the Mediterranean region since the Tertiary Period. The *Tamarix* genus is widely distributed in eastern and southern Asia, southern Europe, the Mediterranean, the Middle East and North Africa. The genus includes typical desert plants and contains approximately 54 species of shrubs and trees. Most of these species occur in salty, dry, or riparian habitats (Gaskin and Schaal, 2002). They adapted to saline soils by excreting the excessive salts out through foliar glands. As a consequence, they can promote soil de-salinization in their vicinity (Cao et al., 2011). *Tamarix chinensis* is native to China, Mongolia and Japan and is one of the dominant salt-tolerant plant species in the coastal saline-alkali soil of Bohai Bay, China (Gaskin and Schaal, 2002; Hou et al., 2012; Zhu et al., 2012). As an early riparian species with specific adaptations to flood and salt conditions, *T. chinensis* is a perennial shrub that grows along the coastal shores in the Yellow River Delta. This plant plays an important role in preventing soil erosion, regulating the microclimate and retaining coastal saline-alkali soil ecological stability in the region (Jiang et al., 2012).

To date, limited researches have been conducted on the microorganisms related to *Tamarix*. Phyllosphere bacterial populations were investigated and the results indicated that the geographical distance was the most important driving factor for the microbial community in the *Tamarix* phyllosphere (Finkel et al., 2012; Qvit-Raz et al., 2012). The differences in the microbial communities in the rhizosphere and non-rhizosphere of *Tamarix* were also investigated (Ma and Yin, 2009). Moreover, several studies showed that the extracts of *Tamarix* had antimicrobial activities (Sultanova et al., 2001; Saïdana et al., 2008; Ksouri et al., 2009; Lefahal et al., 2010). Regarding the soil microbial community in *Tamarix* woodlands, only one study surveyed the seasonal changes of the soil microbial communities in a *T. chinensis* community from the Yellow River Delta using phospholipid fatty acid (PLFA) methods (Cao et al., 2011). Therefore, it was interesting to investigate the microbial composition in coastal saline-alkali soil under the *Tamarix* woodland and the influence of the plants on the microorganisms in this ecosystem.

In this study, we attempted to investigate the characteristics and distribution of soil microbial diversity in the *T. chinensis* woodland in the coastal saline-alkali soil of Bohai Bay. The results, with a much higher resolution than that of PLFA, could provide the first insight into the microbial community in coastal saline-alkali soil of this study area and show the influence of tree cover on the soil microbial composition.

1 Materials and methods

1.1 Study area and sampling

Soil samples were mainly collected in November 2012 and the sampling site (37°05'N, 119°21'E) is located at Bohai Bay, China. Three sites were selected to represent dense, marginal and sparse tree coverages, with the coverages defined as high (>80%), intermediate (60%–80%) and low (<10%), respectively. Five soil cores in 5-cm diameter were randomly collected from each coverage type, and the upper 10 cm of the five cores were mixed and pooled in a gas-tight bottle. The else soil samples were collected in September 2012 from high vegetation coverage sites to assess seasonal variations. Samples were transported in an icebox and stored at −80°C in the laboratory before further analysis.

1.2 DNA extraction, Polymerase Chain Reaction (PCR) amplification and pyrosequencing

Before DNA extraction, the samples were sieved through a 2-mm mesh for thorough homogenization and to remove roots and plant detritus (Dong et al., 2013; Dhar et al., 2015). Genomic DNA was isolated from 1 to 1.25 g of mixed soil using the PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA). The extracted DNA was checked by 1% agarose gel, and the concentration was determined using a Nanodrop ND-1000 UV-Vis Spectrophotometer (Nano-Drop Technologies, Wilmington, DE). The eluted DNA was stored at –20°C.

The 16S rRNA gene fragments in appropriate size and sequence variability were amplified with primer 341F (CCTAYGGGRBGCASCAG) and a modified primer 806R (GGACTACNNGGG TATCTAAT) (Yu et al., 2005). By using these primers, the V1–V3 region of the 16S rRNA gene was amplified. Each PCR reaction contained 2 μL 10×buffer, 1.6 μL dNTP, 0.8 μL forward primer, 0.8 μL reverse primer and 0.8 μL l Pfu Taq DNA polymerase. Thermal cycling consisted of an initial denaturation at 94°C for 3 min, followed by 25 cycles of denaturation at 94°C for 30 s, annealing at 50°C for 30 s, an extension at 72°C for 30 s and a final extension of 10 min at 72°C.

Amplicons were purified using the AxyPrep DNA Gel Extraction Kit (Axygen). Concentrations of the amplicons were quantified by a TBS-380 system, and equal amount of the amplicons were mixed in a single tube. The emulsion PCR was carried out using techniques noted by Margulies et al. (2005), and sequencing was performed on a GS FLX Titanium System (454 Life Sciences, Roche Applied Science).

1.3 Phylogenetic assignment, alignment and clustering of 16S rRNA gene fragments

All reads were processed with mothur, according to the procedure described by Schloss et al. (2011). Sequences were depleted of barcodes and primers and then subjected to quality control. Short sequences with less than 200 base pairs and sequences with an ambiguous base or with homopolymer runs exceeding 6 bp were removed. Sequences were then denoised and the chimeras were removed (Roesch et al., 2007; McKenna et al., 2008). The remaining high quality reads were assigned to a reference taxonomy, the SILVA reference database (Pruesse et al., 2007), using the RDP naïve Bayesian rRNA classifier (confidence threshold, 80%). Operational taxonomic units (OTUs) were defined after the removal of singleton sequences, clustering at 3% divergence (97% similarity). This classification was used for all further downstream analyses on all taxonomic levels. Phylotypes were identified using Megablast and the representative sequence from each phylotype was aligned using the Ribosomal Database Project (RDP) (Cole et al., 2007).

1.4 Statistical analysis

Diversity and richness estimators were made at the 3% dissimilarity level with DOTUR (Roesch et al. 2007). A cluster analysis was performed using a hierarchical cluster analysis from the SPSS version 16 (SPSS, Inc., Chicago, IL).

2 Results

A total of 20,315 valid sequences were obtained through pyrosequencing assays (Table 1). A total

Table 1 Vegetation coverage, pyrosequencing reads, diversity and richness estimators of the three sites

Sample ID	Vegetation coverage (%)	Reads	Chao1 index	Observed Species index	Shannon index	Simpson index
MA	5	7,753	1,694	692.4	8.6665	0.9946
SA	72	2,260	1,141	570.0	8.3687	0.9944
DA-N	100	1,639	1,475	626.8	8.5141	0.9948
DA-S	100	8,663	1,607	693.6	8.7940	0.9962

Note: MA and SA indicate the marginal area and sparse area, respectively. DA-N and DA-S indicate the soil samples collected in November and September at the dense area, respectively.

of 1,639 sequences of each sample were selected to calculate those estimators based on the pyrosequencing reads numbers. The results indicated that the sample from SA (sparse area) had the lowest values in Chao1 and observed species index.

A total of 19 phyla and a large proportion of unclassified bacteria at the phylum level were detected in all samples (Fig. 1). Proteobacteria, Acidobacteria, and Actinobacteria were abundant (>15%). There were low proportions of some phyla and candidate divisions. The dominant bacterial phyla were similar in all samples, regardless the *T. chinensis* coverage level. The dominant soil bacterial phylum was Proteobacteria, with an abundance higher than 27.8%. The phylum was subdivided into α-, β-, δ-, and γ-Proteobacteria classes. Within these classes, the α-, β- and δ-Proteobacteria had similar proportions in the four samples, whereas the γ-Proteobacteria decreased in abundance as the vegetation coverage increased. The second most abundant phylum was Acidobacteria, with the highest abundance in the marginal area. The third most abundant phylum was Actinobacteria and its abundance increased with the increase of vegetation coverage. Bacteroidetes was the fourth most abundant phylum with the abundance decreased with the increase *T. chinensis* coverage. The other bacterial phyla also varied with the coverage level of *T. chinensis* (Fig. 1b). There were also several phyla found in specific areas. For example, the phyla Fibrobacteres and Tenericutes were only detected in the marginal area, and the candidate phylum OD1 was only detected in the dense area in November.

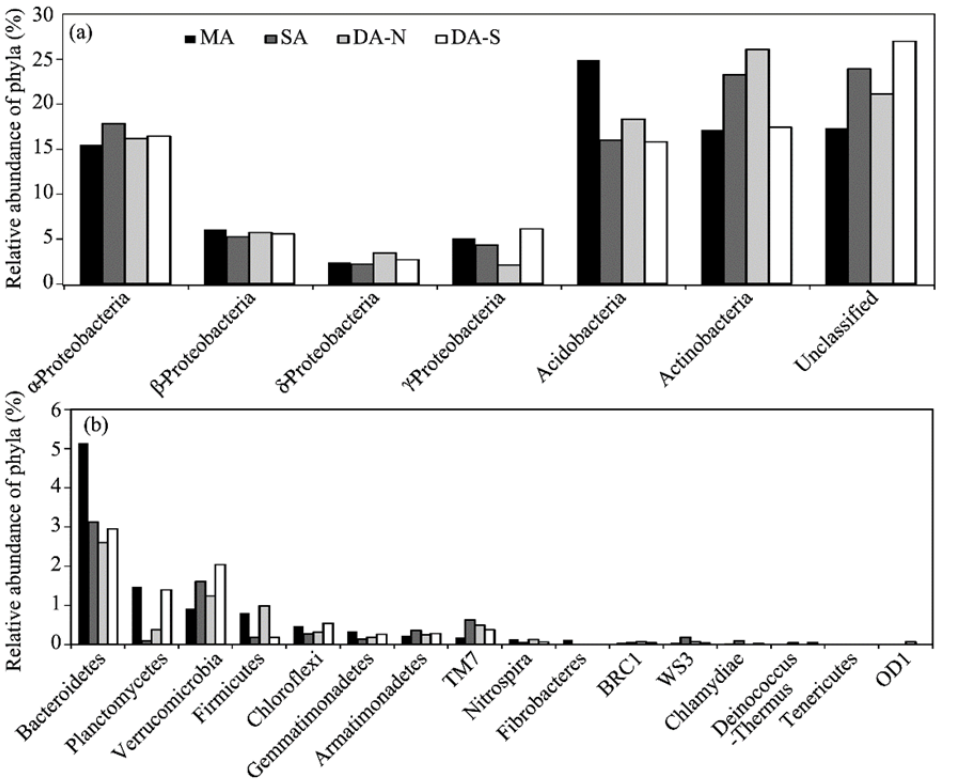

Fig. 1 Relative abundance of phyla and proteobacterial classes for each soil library

The number of genera was too large to present in one figure; therefore, only the genera with a relative abundance higher than 1% are shown in Fig. 2. The predominant classified genera were Gp4 and Gp6, which belonged to Acidobacteria and their relative abundances reached up to 15.3% and 7.8%, respectively. Some changes in the proportion of the classified genera also corresponded to the change in *T. chinensis* coverage within the same sampling date. For example, the proportion of Gp4, *Steroidobacter*, *Lechevalieria* and Gp3 decreased, whereas *Nocardioides* increased with the increase of the tree coverage.

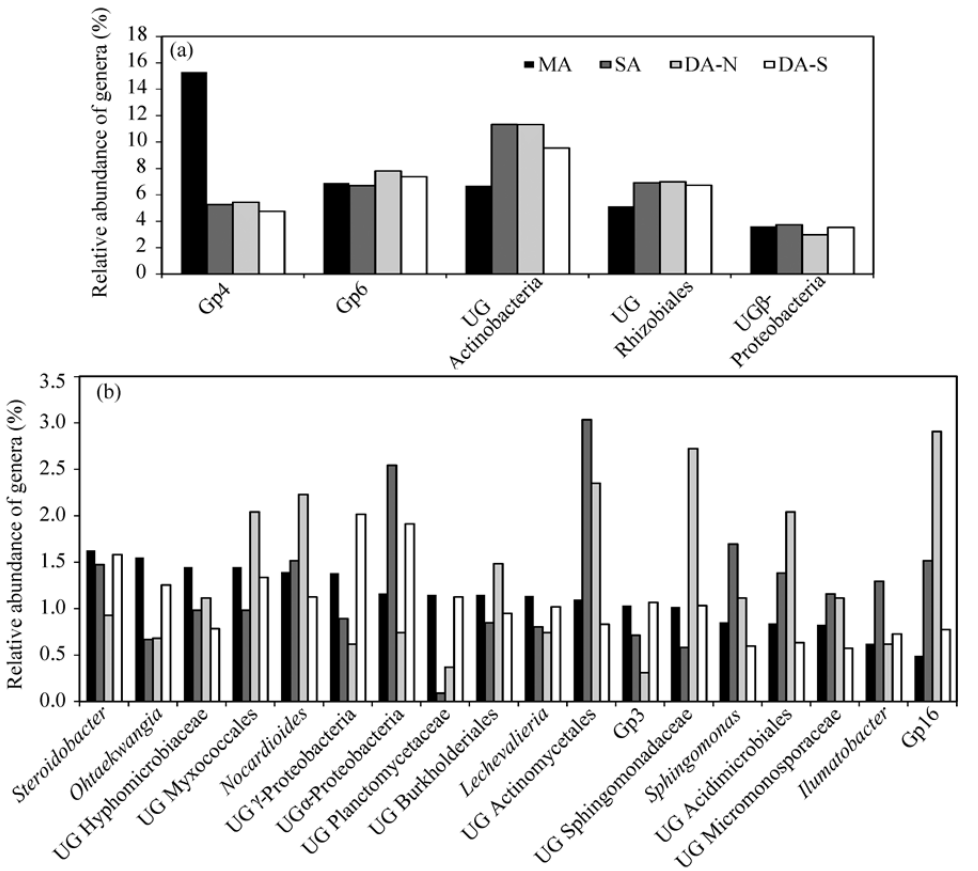

Fig. 2 Relative abundance of genera for each soil library. Only genera with more than 1% relative abundance are shown here. UG indicates an unclassified genus.

The results of the cluster analysis indicated that the vegetation coverage of *T. chinensis* had a strong effect on the bacterial composition (Fig. 3). The relative abundances at both the phylum and genus levels showed that the marginal area was different from the other sample sites. At the phylum level, the sparse and dense areas from the same sampling season were clustered together. However, at the genus level, the sparse and dense areas from different sampling season were clustered into the same groups.

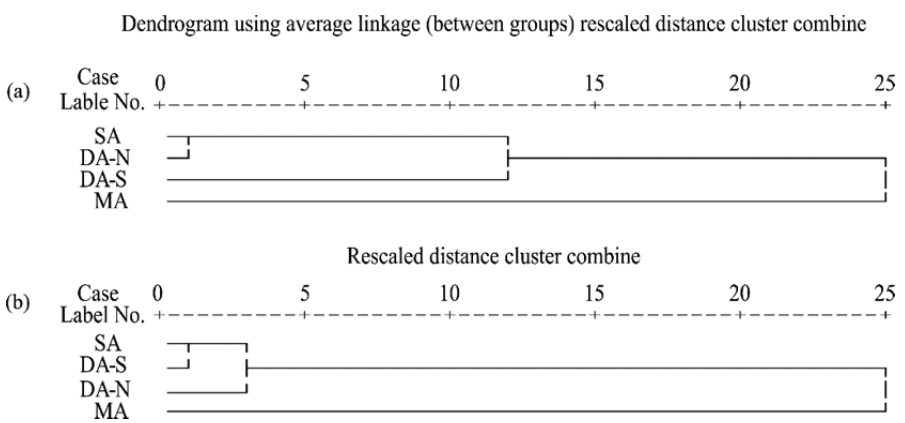

Fig. 3 Cluster analysis based on the relative abundances of (a) known phyla and (b) genera of known phyla

The functional community also shifted along with environmental change in this coastal saline-alkali soil. The results showed that the relative abundance of the family Cryomorphaceae and class Flavobacteria decreased with the increase of *T. chinensis* coverage (Fig. 4).

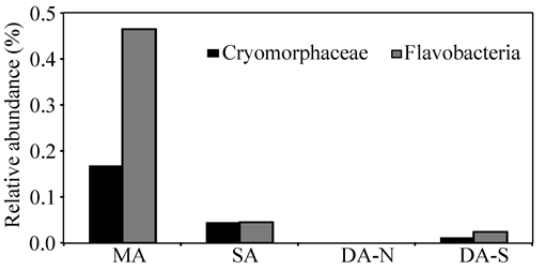

Fig. 4 Relative abundance of the family Cryomorphaceae and class Flavobacteria

3 Discussion

In this study, 454 pyrosequencing techniques were used to investigate the characteristics of soil microbial diversity in coastal saline-alkali soil under the *T. chinensis* woodland at Bohai Bay. Proteobacteria, Acidobacteria, and Actinobacteria were the dominant phyla. The relative abundance of Proteobacteria was stable in the different samples, which may be due to the arid environmental condition. The dominant phyla were widely distributed in the arid environment. Previous studies showed that Proteobacteria was always the dominant bacterial group in desert ecosystems and was ubiquitously distributed in deserts worldwide (Nagy et al., 2005; Chanal et al., 2006; Orlando et al., 2010; Saul-Tcherkas and Steinberger, 2011; Zhang et al., 2012). Meanwhile, studies using pyrosequencing and clone library methods showed that Proteobacteria could be the dominant phylum in coastal saline-alkali soil environments (Gray and Herwig, 1996; Urakawa et al., 1999; Kim et al., 2004, 2008). However, the dominant class of this phylum varied across locations (Bull et al., 2005). In addition to Proteobacteria, the predominant phyla Acidobacteria and Actinobacteria in this study were not predominant phyla in other coastal saline-alkali soil environments (Gray and Herwig, 1996; Urakawa et al., 1999; Kim et al., 2004; Kim et al., 2008). Members of these two phyla are commonly found in most types of soils. Actinobacteria was also widely distributed in desert ecosystems (Nagy et al., 2005; Chanal et al., 2006; Orlando et al., 2010; Saul-Tcherkas and Steinberger, 2011; Zhang et al., 2012). The abundance of this phylum always constituted a large percentage of the inhabitants of arid soils because it was highly resilient to low levels of soil moisture (Doroshenko et al., 2005). Acidobacteria represented, on average, 20% of the soil bacteria and was highly diverse and physiologically active *in situ*. Previous reports indicated members from this phylum had the ability to degrade a broad array of simple carbon compounds as well as plant and microbial polysaccharides including cellulose. This phylum was also well distributed in arid environments, especially in desert soils (Kuske et al., 2002). However, their individual functions and interactions with other higher taxa in soils are still unknown (Naether et al., 2012). In our study, the dominant classified genera were Gp4 and Gp6, which also belong to Acidobacteria. Although these genera were widely distributed in the soil, they were not well described yet (Zhang et al., 2011; Naether et al., 2012).

In addition to the dominant phyla, the Bacteroidetes, Planctomycetes, Verrucomicrobia and Firmicutes were also widely distributed in each sample. The relative abundances of these phyla were greater than 1%. Rare phyla, such as Chloroflexi, Gemmatimonadetes, Armatimonadetes and TM7, had abundances less than 1% and were also detected in all of the samples. However, no significant variation trends were found. Bacterial communities are known for their large contributions to several soil ecosystem functions, such as their key role in soil sustainability (Uroz et al., 2010). Our results provide the first insight into the characteristics of microbial diversity in coastal saline-alkali soil of the study area.

Plants living in coastal saline-alkali soil also affected the underground microbial composition. The cluster analysis results showed a tight relationship between bacterial community composition and *T. chinensis* coverage in this coastal saline-alkali soil. Previous studies showed that soil under the *Tamarix* woodland contained similar quantities of microorganisms in both coastal saline-alkali soil and the inland arid region, which indicated that the colonization of *Tamarix* provided stable growth conditions for microorganisms (Chen et al., 2008; Ma et al., 2008; Ma and Yin, 2009; Zhao et al., 2009). The microbial activity in coastal saline-alkali soil was higher than that of inland arid regions (Zhu et al., 2008; Zhao et al., 2009). There were no previous investigations regarding the effects of *Tamarix* on the underground microbial community composition. Our study provides the first insight into the relationship between the soil bacterial community composition and *T. chinensis*. The results showed that the relative abundance of γ-Proteobacteria and Bacteroidetes decreased with the increase of *T. chinensis* coverage, whereas the Actinobacteria increased with the increase of the coverage. The Fibrobacteres and Tenericutes were only detected in the marginal area, whereas OD1 was only detected in the dense area in November. A variation in the bacterial community also occurred at the genus level. The proportion of Gp4, *Steroidobacter*, *Lechevalieria*, and Gp3 decreased with the increasing in tree coverage, whereas *Nocardioides* increased with the increasing in tree cover. During the development of the *T. chinensis* woodland, the increase of some genera are highly likely linked to the abundance of *T. chinensis*.

The cluster analysis also revealed the effects of tree coverage on the soil bacteria composition. The marginal area was different from the other sites based on the relative abundance at the phylum or genus levels. The sparse and dense areas were close to each other, suggesting that the existence of *T. chinensis* changed the niches for the microorganisms in coastal saline-alkali soil and then distinguished the microbial community structure of the marginal area from that of the dense area and sparse area.

The results also indicated that the distance to the seashore line could also affect certain groups of soil bacteria in this coastal saline-alkali soil. For example, the relative abundance of the class Flavobacteria decreased with increasing distance from the seashore line, namely from the dense area to the sparse area, and then to the marginal area. Flavobacteria were the major decomposers of high-molecular-mass organic matter in sea water (Cottrell and Kirchman, 2000; Woyke et al., 2011). In the class Flavobacteria, the family Cryomorphaceae contains many species that play a crucial role in the carbon and energy fluxes in marine environments (Kirchman, 2002). Therefore, this trend of decreasing Flavobacteria might be due to the decreasing possibility of receiving large tides.

4 Conclusion

In this study, higher resolution of soil microbial community structure in coastal saline-alkali soil under the *T. chinensis* woodland at Bohai Bay were revealed. The results showed that, except 19 known bacterial phyla, a large proportion of unclassified bacteria at the phylum level were found. The dominant bacterial structure was likely due to the arid environmental conditions of the coastal saline-alkali soil. The existing of *T. chinensis* is also another important factor to change the soil microbial community, via changing the niches for the microorganisms in coastal saline-alkali soil. The third impact factor could be the distance to the seashore line, which could affect certain groups of soil bacteria in this saline-alkali soil.

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