Rhizobacterial communities of five co-occurring desert halophytes

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Background: Recently, researches have begun to investigate the microbial communities associated with halophytes. Both rhizobacterial community composition and the environmental drivers of community assembly have been addressed. However, few studies have explored the structure of rhizobacterial communities associated with halophytic plants that are co-occurring in arid, salinized areas. **Methods:** Five halophytes were selected for study: these co-occurred in saline soils in the Ebinur Lake Nature Reserve, located at the western margin of the Gurbantunggut Desert of Northwestern China. Halophyte-associated bacterial communities were sampled, and the bacterial 16S rDNA V3–V4 region amplified and sequenced using the Illumina Miseq platform. The bacterial community diversity and structure were compared between the rhizosphere and bulk soils, as well as among the rhizosphere samples. The effects of plant species identity and soil properties on the bacterial communities were also analyzed. **Results:** Significant differences were observed between the rhizosphere and bulk soil bacterial communities. Diversity was higher in the rhizosphere than in the bulk soils. Abundant taxonomic groups (from phylum to genus) in the rhizosphere were much more diverse than in bulk soils. Proteobacteria, Firmicutes, Actinobacteria, Bacteroidetes and Planctomycetes were the most abundant phyla in the rhizosphere, while Proteobacteria and Firmicutes were common in bulk soils. Overall, the bacterial community composition were not significantly differentiated between the bulk soils of the five plants, but community diversity and structure differed significantly in the rhizosphere. The diversity of H*alostachys caspica*, *Halocnemum strobilaceum* and *Kalidium foliatum* associated communities was lower than that of *Limonium gmelinii* and *Lycium ruthenicum* communities. Furthermore, the composition of H*alostachys caspica* and *Halocnemum strobilaceum* communities was very

different from that of *Limonium gmelinii* and *Lycium ruthenicum* communities. The diversity and community structure were influenced by soil EC, pH and nutrient content (TOC, SOM, TON and AP); of these, the effects of EC on bacterial community composition were less important than those of soil nutrients. **DISCUSSION:** Halophytic plant species played an important role in shaping associated rhizosphere bacterial communities. When salinity levels were constant, soil nutrients emerged as key factors structuring bacterial communities, while EC played only a minor role. Pairwise differences among the rhizobacterial communities associated with different plant species were not significant, despite some evidence of differentiation. Further studies involving more halophyte species, and individuals per species, are necessary to elucidate plant species identity effects on the rhizosphere for co-occurring halophytes.

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20 halophytes. Both rhizobacterial community composition and the environmental drivers of community assembly
21 have been addressed. However, few studies have explored the structure of rhizobacterial communities associated
22 with halophytic plants that are co-occurring in arid, salinized areas.

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24 Reserve, located at the western margin of the Gurbantunggut Desert of Northwestern China. Halophyte-
25 associated bacterial communities were sampled, and the bacterial 16S rDNA V3–V4 region amplified and
26 sequenced using the Illumina Miseq platform. The bacterial community diversity and structure were compared
27 between the rhizosphere and bulk soils, as well as among the rhizosphere samples. The effects of plant species
28 identity and soil properties on the bacterial communities were also analyzed.

29 **Results:** Significant differences were observed between the rhizosphere and bulk soil bacterial communities.
30 Diversity was higher in the rhizosphere than in the bulk soils. Abundant taxonomic groups (from phylum to
31 genus) in the rhizosphere were much more diverse than in bulk soils. Proteobacteria, Firmicutes, Actinobacteria,
32 Bacteroidetes and Planctomycetes were the most abundant phyla in the rhizosphere, while Proteobacteria and
33 Firmicutes were common in bulk soils. Overall, the bacterial community composition were not significantly
34 differentiated between the bulk soils of the five plants, but community diversity and structure differed
35 significantly in the rhizosphere. The diversity of H*alostachys caspica*, *Halocnemum strobilaceum* and *Kalidium*
36 *foliatum* associated communities was lower than that of *Limonium gmelinii* and *Lycium ruthenicum*
37 communities. Furthermore, the composition of H*alostachys caspica* and *Halocnemum strobilaceum*
38 communities was very different from that of *Limonium gmelinii* and *Lycium ruthenicum* communities. The
39 diversity and community structure were influenced by soil EC, pH and nutrient content (TOC, SOM, TON and
40 AP); of these, the effects of EC on bacterial community composition were less important than those of soil
41 nutrients.

42 **DISCUSSION:** Halophytic plant species played an important role in shaping associated rhizosphere bacterial
43 communities. When salinity levels were constant, soil nutrients emerged as key factors structuring bacterial
44 communities, while EC played only a minor role. Pairwise differences among the rhizobacterial communities
45 associated with different plant species were not significant, despite some evidence of differentiation. Further
46 studies involving more halophyte species, and individuals per species, are necessary to elucidate plant species
47 identity effects on the rhizosphere for co-occurring halophytes.

48

49   **INTRODUCTION**

50   Salinization is a serious land degradation problem, as high salinity limits plant growth. Salts may
51   accumulate in soils as a result of natural processes, such as mineral weathering, dust collection and precipitation,
52   or artificial processes, such as irrigation (Oosterbaan 1988); both may lead to saline soils that make it difficult
53   for plants to absorb moisture from the soil. Halophytes are salt-tolerant plants that can grow in areas with salt
54   (NaCl) concentrations higher than 400 mM (Flowers 2004; English & Colmer 2011). In saline soil environments,
55   halophytes play an important role in carbon sequestration, nutrient mineralization, nutrient cycling and
56   improvement of the micro-environment (Cao et al. 2014; Chaudhary et al. 2015), and may have great potential
57   to preserve ecosystems.

58   Salinity tolerance in halophytes is not solely due to physiological mechanisms and their genetic regulation
59   (Vasquez et al. 2005), but also to complex ecological processes within the plant rhizosphere and phyllosphere;
60   microorganisms inhabiting the roots and leaves of halophytes may significantly contribute to their salinity
61   tolerance (Ruppel et al. 2013). Many microorganisms have plant growth-promoting activities and confer salt
62   tolerance on halophytic plants (Nabti et al. 2007; Sgroy et al. 2009; Jha et al. 2012; Mapelli et al. 2013). Recent
63   studies of halophyte-associated microbial communities have addressed the ecological and environmental drivers
64   underlying community assembly and recruitment (Jha et al. 2012; Borruso et al. 2014; Marasco et al. 2016;
65   Chaudhary et al. 2017; Tian & Zhang 2017). These studies have revealed that bacterial communities in the
66   halophyte rhizosphere are distinctly different from those of non-halophytic plants, containing a larger proportion
67   of halophilic bacteria (Al-Mailem et al. 2010). Many halophilic bacteria have been identified or isolated from
68   halophyte roots, soils and desert habitats, including species belonging to the following genera: *Alkalimonas*,
69   *Bacillus*, *Brachybacterium*, *Brevibacterium,* *Cronobacter*, *Halobacillus*, *Halomonas*, *Marinococcus*,
70   *Methylibium*, *Nesterenkonia*, *Oceanobacillus*, *Staphylococcus*, *Stenotrophomonas*, *Virgibacillus* and
71   *Zhihengliuella* (Sgroy et al. 2009; Siddikee et al. 2010; Tang et al. 2011; Shi et al. 2012; Zhou et al. 2012;
72   Ramadoss et al. 2013; Borsodi et al. 2015; Zhao et al. 2016).

73   The diversity and composition of the rhizosphere bacterial community depends not only on the plant
74   species, but also on various soil parameters (Tian & Gao 2014; Rodriguez-Blanco et al. 2015; Pii et al. 2016;
75   Song et al. 2017). Different plant species, or even genotypes within species, tend to assemble distinct
76   rhizobacterial communities (Chaudhary et al. 2015). For example, in the rhizosphere of *Aster tripolium*,
77   Actinobacteria, Firmicutes and Proteobacteria are the most abundant bacterial phyla, and *Bacillus* the dominant
78   genus (Szymanska et al. 2016b). In contrast, Acidimicrobiales, Myxococcales and Sphingomonadales are
79   common in the rhizosphere of *Halimione portulacoides* and *Sarcocornia perennis* (Oliveira et al. 2014). The
80   *Puccinellia limosa* rhizosphere is dominated by *Halomonas* and *Nesterenkonia* species (Borsodi et al. 2015).
81   Similar rhizobacterial communities may be found in different environments when the same plant species is
82   present (Smalla et al. 2001; Berg & Smalla 2009). However, in certain environments, such as hypersaline soils,
83   plant species identity plays only a minor role compared to soil salinity in shaping microbial community structure
84   (Borruso et al. 2014); this result has been confirmed by studies of desert soils (Li et al. 2013). Overall, both plant
85   species identity and soil type can be important, depending on abiotic and biotic conditions (Berg & Smalla 2009).

86   While many studies have investigated the effects of plant species identity and various soil properties, as
87   well as other factors (i.e. temperature, geographical distance), on structuring microbial communities in the
88   rhizosphere, few studies have characterized the rhizobacterial communities associated with halophytic plants
89   found in arid, saline environments. In a Mediterranean salt marsh in Southeastern Spain, a study of eight

90   halophytes (*Asteriscus maritimus*, *Arthrocnenium macrostachyum*, *Frankenia corymbosa*, *Halimione*
91   *portulacoides*, *Limonium cossonianum*, *Limonium caesium*, *Lygeum spartum* and *Suaeda vera Forsskal*)
92   examined the soil microbiological and biochemical properties of the rhizosphere, revealing that soil microbial
93   activity and microbial-related soil properties, such as aggregate stability, were determined by the plant species.
94   However, the community composition of the microbes was not examined (Caravaca et al. 2005). Another study
95   recently compared the microbial communities associated with three dominant halophytes (*Aeluropus*, *Salicornia*
96   and *Suaeda*) in a coastal region of India (Chaudhary et al. 2015). To date, in halophytic species occurring in arid
97   desert environments, little is known regarding rhizobacterial community assembly and the relative contributions
98   of rhizosphere effects versus salinity to this process.
99   In this study, the bacterial communities associated with five halophytes (*Halocnemum strobilaceum*,
100   *Halostachys caspica*, *Limonium gmelinii*, *Lycium ruthenicum* and *Kalidium foliatum*) growing in arid, saline
101   environments were characterized. The diversity and structure of rhizosphere bacterial communities was
102   investigated using an Illumina MiSeq sequencing approach. The study goals were to: 1) compare the bacterial
103   communities of the rhizosphere with those found in bulk soil samples (i.e. non-rhizosphere samples), in order to
104   understand the effects of plant species identity on bacterial communities; 2) compare the rhizosphere community
105   composition of the five halophytic species so as to look for similarities across species; and, 3) evaluate the
106   relative contributions of plant species identity and soil salinity in structuring rhizosphere bacterial communities
107   in arid, saline habitats.

108   **MATERIALS & METHODS**

109   **Study area and sample collection**
110   Soil samples were collected from the Ebinur Lake Wetland, Xinjiang, China (44.595°N, 83.552°E) in July 2017,
111   following previously established protocols (Chaudhary et al. 2015; Edwards et al. 2015). The Ebinur Lake Nature
112   Reserve is located at the western margin of the Gurbantunggut Desert in Xinjiang, China. Conditions are windy
113   in the Reserve, which has a typical dry, continental climate, with an annual average precipitation of 105 mm and
114   evaporation of 1315 mm. Soils in the Reserve are highly salinized and alkalized, with an average electrical
115   conductivity (EC) of 5.41 mS/cm and pH of 8.77 in surface soils 0–10 cm deep; the mean soil water content is
116   7.19% (Zhang et al. 2014). As such, many halophytic species grow in this region. In this study, five co-occurring
117   halophytic plants species, four shrubs (*Halocnemum strobilaceum*, *Halostachys caspica*, *Lycium ruthenicum* and
118   *Kalidium foliatum*,) and one perennial herb (*Limonium gmelinii*), were selected for study.
119   Thirty samples were collected in total: 15 from the rhizosphere and 15 paired bulk soil samples. Each
120   rhizosphere sample came from a different plant; sampled individuals were distributed within a 1 km radius of
121   the GPS coordinates provided above (Fig S1). Three healthy individuals were randomly selected from each
122   species to be sampled. Plant roots were dug up using a shovel, in order to collect all roots to a depth of
123   approximately 35-45 cm. Excess soil was manually shaken from the roots, but any soil still attached after shaking
124   (a layer ~1 mm thick) was retained for study. Each root sample was immediately placed into a sterile flask with
125   30 ml of sterile Phosphate Buffered Saline (PBS) solution (137 mmol/L NaCl, 2.7 mmol/L KCl, 8.5
126   mmol/LNa$_2$HPO$_4$, 1.5 mmol/L KH$_2$PO$_4$, pH 7.3). Bulk soil samples were collected from sites 30-40 cm away
127   from the roots of a given plant; soils were collected to a depth of approximately 40 cm. About 100 g of fresh soil
128   from each sample was stored in a sterile plastic bag; these were immediately transported back to the lab on ice.
129   In the lab, the flasks containing root samples were stirred vigorously with sterile forceps to clean all the soil from
130   the root surfaces. This soil was then poured into a 50 ml sterile Falcon tube ready for DNA extraction.

Soil chemical analysis

Soil samples were dried in a hot air oven at 105℃ for 48 hours to determine the soil water content (SWC). After drying, samples were ground and sieved through 2 mm mesh. The electrical conductivity (EC) and pH were measured in a 1:2.5 (w:v) soil to water mix. The total organic carbon (TOC) and soil organic matter (SOM) were estimated using a spectrophotometer, after oxidizing soil samples with $K_2Cr_2O_4$ (Yang 1987). The total nitrogen (TON) was determined using the Kjeldahl method (Honda 1962). To measure available phosphorus (AP), samples were digested with $HClO_4$-H_2SO_4, and then the Mo-Sb colorimetric method was used for quantification (Agrochemistry Committee of the Chinese Soil Society 1983).

DNA extraction, amplification and sequencing

Rhizosphere samples were concentrated by pipetting 1 mL of the PBS/soil mix into a 2 mL sterile tube and centrifuging for 1 min at 10,000 g. The supernatant was discarded leaving only the soil fraction behind. About 0.2 g of soil (wet weight) from each bulk sample was transferred to a 2 mL sterile tube. Then, the total genomic DNA was extracted using an E.Z.N.A™ Mag-Bind Soil DNA Kit (OMEGA) following the manufacturer's instructions. DNA samples were inspected on a 1.0% agarose gel and quantified using a Nanodrop 2000 spectrophotometer (Nanodrop Technologies, Wilmington DE). The bacterial 16S rDNA V3–V4 region was amplified and sequenced for analysis. PCR products were visualized using electrophoresis on 1.5% agarose gels and purified using VAHTS™ DNA Clean Beads (Vazyme, Nanjing, China). Finally, about 10 ng of DNA from each sample was sequenced on the Illumina MiSeq platform by Sangon Technology Co., Ltd. (Shanghai, China). The sequence data has been submitted to the NCBI Sequence Read Archive database under accession number SRP129060.

Sequence preprocessing and OTU assignment

Quality control of raw sequencing data was conducted following Schmieder & Edwards (Schmieder & Edwards 2011). Ambiguous bases with Phred quality score < 20 at the end of a read and fragments containing Ns were trimmed. Reads with length < 200 nucleotides (nt) were removed, and the remaining reads truncated to 400-450 nt sequences. Chimeric sequences were identified with UCHIME (Edgar et al. 2011) and discarded (109–1397 chimeras per sample). The filtered sequences were then clustered into OTUs at a 97% similarity level. A representative sequence from each OTU was selected for both taxonomic annotation using the Ribosomal Database Project (RDP) classifier (Wang et al. 2007) and also to BLAST against the Silva and NCBI databases (Quast et al. 2013). OTUs with an RDP classification threshold below 0.8 or with identity and coverage lower than 90% were marked as unclassified. Singletons and sequences aligning to the mitochondria or chloroplast were removed (4–1450 reads per sample). Finally, the number of sequences in each sample was normalized by random resampling to the smallest sample size (n=35000) prior to calculation of species diversity indices (Shannon, Simpson, Chao1, ACE, and Good's coverage) using Mothur ver 1.30.1 (Schloss et al. 2009). OTU richness was calculated using the *vegan* package ver. 2.1-10 (Dixon 2003) in R ver. 3.2. Rarefaction analysis was implemented in Mothur 1.30.1 and a rarefaction curve produced in R. Using R, a species accumulation curve was also constructed (with the *vegan* package) and diagrams depicting bacterial community structure (composition and relative abundance) at multiple taxonomic ranks (phylum, class, order, family and genus) were generated.

Statistical analysis

One-way ANOVAs were used to test for differences in alpha diversity indices (OTU richness, Shannon diversity index and Good's coverage index) as well as soil physicochemical properties. A principal coordinates analysis

172   (PCoA) was performed on weighted UniFrac distances (using the *vegan* package) to compare community

173   composition among samples. A UPGMA tree depicting clustering relationships among samples was produced

174   based on Bray-Curtis beta diversity distance metrics. ANOSIM (999 permutations) and Adonis statistics,

175   available in the *vegan* package, were calculated to evaluate differences in rhizosphere community composition

176   among the five study species. Venn diagrams illustrating similarities/differences in OTU composition between

177   samples were produced with the *Venn-Diagram* package, ver. 1.6.16. Furthermore, STAMP 2.1.3 (Parks et al.

178   2014) and LEfSe 1.1.0 (Segata et al. 2011) were implemented to identify differentially abundant groups among

179   samples. Pearson's correlation coefficients were calculated between the community diversity and richness

180   indices and each soil property, and also among soil properties. Correspondence analysis (CA) was performed

181   using the *vegan* package to investigate links between community structure, soil properties and plant species.

182   **RESULTS**

183   **Soil properties**

184   The average soil water content (SWC) of bulk soils was 16.40 ± 4.57 %. The electrical conductance (EC) was

185   6.30 ± 1.21 mS/cm and pH 8.14 ± 0.27. The mean total organic carbon (TOC), soil organic matter (SOM), total

186   nitrogen (TON) and available phosphorus (AP) were 8.05 ± 4.15 g/kg, 13.87 ± 7.15 g/kg, 0.48 ± 0.23 g/kg and

187   0.82 ± 0.14 g/kg, respectively. *Halocnemum strobilaceum* and *Halostachys caspica* soils had higher EC and

188   lower TOC, SOM and TON compared to those of other species ($P < 0.05$). The AP content in *Halocnemum*

189   *strobilaceum* soils was significantly lower than for other species ($P < 0.05$) (Table 1).

190   **Bacterial community diversity**

191   In total, 1.83 Gb of raw sequence data was obtained from all samples; after quality controls, a total of 1.18 Gb

192   of clean sequence reads were available for further analysis. Good's coverage for all samples was higher than

193   0.98 (Table S1). Rarefaction curves stabilized as the number of sequences increased (Fig. S2), suggesting that

194   bacterial communities were reasonably well-characterized. Species accumulation curves nearly reached a

195   plateau, where the number of OTUs did not increase with sample size, indicating that the sample size was

196   sufficient for data analysis (Fig. S3). After removal of chimeras, plant sequences and singletons, a total of

197   1315341 reads were obtained from soil samples; these were grouped into 8087 OTUs. OTU richness was higher

198   in rhizosphere versus bulk soil samples ($P < 0.01$; Fig. 1). The number of OTUs identified in the rhizosphere of

199   each species ranged from a minimum of 2342 (for *Halocnemum strobilaceum*) to a maximum of 4602 (*Limonium*

200   *gmelinii*); within species, the number of OTUs present in all three replicates ranged from 317 to 729. In bulk soil

201   samples, the number of OTUs detected for each species ranged from 1108 to 3688, and between 94 and 220

202   OTUs were common to all three replicates within species (Table S1).

203   Bacterial community diversity was higher in the rhizosphere versus bulk soil samples (ANOVA $P < 0.01$)

204   (Fig. 1). Rhizobacterial diversity did not differ among *Halocnemum strobilaceum*, *Halostachys caspica* and

205   *Kalidium foliatum*, but was lower in these species than in *Limonium gmelinii* and *Lycium ruthenicum* ($P < 0.05$).

206   Diversity in *Lycium ruthenicum* bulk soil samples was higher than in the other four plant species ($P < 0.05$).

207   There were 1005, 1001, 677, 589 and 510 OTUs exclusive to the rhizobacterial communities associated with

208   *Halostachys caspica*, *Limonium gmelinii, Lycium ruthenicum*, *Kalidium foliatum*, and *Halocnemum*

209   *strobilaceum*, respectively; of these, 135, 187, 242, 88 and 63 OTUs, respectively, were found in all within-

210   species replicates. Comparing across species, 242 OTUs were identified in all bulk soil samples and 647 OTUs

211   in all rhizosphere samples; only 31 and 87 of these OTUs, respectively, were found in all three individuals of

212   each species (Fig. 2). Abundant OTUs (i.e., those accounting for $> 0.1\%$ of sequences) common to the

213   rhizospheres of all halophytes belonged to 16 genera, including *Acinetobacter*, *Aliifodinibius*, *Citrobacter*,
214   *Deferrisoma*, *Exiguobacterium*, *Gracilimonas*, *Halomonas*, *Marinobacter*, *Pseudomonas*, *Thioprofundum* and
215   others. Considering bulk soils, the most abundant OTUs came from four genera: *Acinetobacter*, *Citrobacter*,
216   *Exiguobacterium* and *Pseudomonas* (Fig. S4).

217   **Bacterial community structure**

218   A total of 36 phyla, 61 classes, 201 families and 617 genera were identified over all samples. In the bulk soil
219   samples, Proteobacteria and Firmicutes were the dominant phyla. Gammaproteobacteria and Bacilli were the
220   dominant classes, and *Acinetobacter*, *Bacillus*, *Citrobacter*, *Exiguobacterium* and *Pseudomonas* were the most
221   abundant genera (Fig. 3). In the rhizosphere samples, Acidobacteria, Actinobacteria, Bacteroidetes, Chloroflexi,
222   Firmicutes,Planctomycetes, Proteobacteriaand Verrucomicrobia were the most abundant phyla. Actinobacteria,
223   Bacilli,   Cytophagia,   Flavobacteriia,   Planctomycetia,   Sphingobacteriia,   Alphaproteobacteria,
224   Deltaproteobacteria and Gammaproteobacteriawere the most abundant classes. The most common genera
225   included *Acinetobacter*, *Aliifodinibius*, *Citrobacter*, *Deferrisoma*, *Exiguobacterium*, *Geminicoccus*, *Gp10*,
226   *Gracilimonas*, *Halomonas*, *Marinobacter*, *Pseudomonas* and *Thioprofundum*   (Fig. 3).

227   **Differences between rhizosphere and bulk soil samples**

228   The most abundant bacterial groups in bulk soil communities were less common in rhizosphere communities,
229   whereas some low abundance groups in the former were more common in the latter. At the phylum level, the
230   Firmicutes and Proteobacteria was relatively less abundant in the rhizosphere, especially in the case of Firmicutes
231   ($P < 0.001$), whereas the Acidobacteria, Actinobacteria, Bacteroidetes, Chloroflexi, Planctomycetes and
232   Verrucomicrobia were more abundant. A similar pattern was also observed at lower taxonomic ranks; however,
233   overall, there were more abundant groups in the rhizosphere. Comparing bulk soil, the following genera were
234   lower in abundance: *Acinetobacter*, *Citrobacter*, *Exiguobacterium*, *Halomonas* and *Pseudomonas*. Meanwhile,
235   *Aciditerrimonas*,   *Aliifodinibius*,   *Deferrisoma*,   *Fodinicurvata*,   *Geminicoccus*,   *Gp10*,   *Gracilimonas*,
236   *Marinobacter*, *Nitriliruptor*, *Planococcus* and *Thioprofundum* were more abundant in the rhizosphere samples
237   ($P < 0.01$) (Fig. 3).

238   Community composition differed significantly between rhizosphere and bulk soil samples (ANOSIM, R =
239   0.961, $P = 0.001$). A PCoA analysis illustrates these differences in community structure (Fig. 4a).   Rhizosphere
240   and bulk soil samples are separated on the first PCoA axis, which explained 82.33% of the variance. Bulk soil
241   samples clustered together, indicating a high degree of similarity among their bacterial communities. However,
242   rhizosphere samples were less tightly aggregated than bulk soil samples. Consistent with the PCoA results, the
243   UPGMA tree also distinguished rhizosphere communities from bulk soil communities (Fig. 4b).

244   **Community structure differences among the five halophytes**

245   Significant variation in community structure was observed among the five species' rhizospheres ($R^2 = 0.703$, P
246    $= 0.001$). However, pairwise differences between each species pair, though relatively large, were not significant
247   ($P > 0.05$) (Table 2). The rhizobacterial community of *Lycium ruthenicum* was most similar to that of *Limonium*
248   *gmelinii*. Meanwhile, the *Halocnemum strobilaceum* rhizobacterial community was most dissimilar to those of
249   other species. As determined by a LEfSe analysis, rhizobacterial community composition differed among the
250   five halophytes (Fig. 5). The genera *Gimesia* and *Pelagibius* were significantly more abundant in the *Lycium*
251   *ruthenicum* rhizosphere; *Albidovulum*, *Bauldia*, *Deferrisoma*, *Geminicoccus*, *Gp10* and *Thiohalomonas* were
252   more common in the *Limonium gmelinii* rhizosphere, *Citrobacter*, *Exiguobacterium*and *Pseudomonas* in the
253   *Halostachys caspica* rhizosphere, *Gracilimonas*, *Jiangella*, *Marinimicrobium*, *Planococcus* and*Pontibacter* in

254   the *Kalidium foliatum* rhizosphere, and *Fodinicurvata*, *Halomonas*, *Mesorhizobium* and *Salegentibacter* in the
255   *Halocnemum strobilaceum* rhizosphere.

256   In contrast, an Adonis analysis found no differences in community composition among bulk soil samples
257   from different species ($R^2 = 0.300$, $P = 0.413$). However, LEfSe analyses found differences in composition in
258   bulk soil communities for four out of the five species (Fig. 6). The bacterial community associated with *Lycium*
259   *ruthenicum* was relatively distinct from that of other species, mainly due to differences in the abundance of the
260   following families: Acidimicrobiaceae, Anaerolineaceae, Alteromonadaceae, Bacillaceae, Chromatiaceae,
261   Demequinaceae, Planctomycetaceae, Puniceicoccaceae, Rhodobiaceae and Sprospiraceae, . Meanwhile,
262   *Kalidium foliatum* communities were indistinguishable from those of the other four species.

263   **Correlations between bacterial diversity, community structure and soil properties**

264   Relationships between microbial community diversity and structure, and soil bio-chemical properties were
265   assessed with Pearson correlation coefficients and canonical correspondence analysis (CCA). The soil TOC,
266   TON and AP were all strongly positively correlated, while EC was negatively correlated with all other soil
267   variables except pH. Bacterial community diversity and richness were positively correlated with soil TON and
268   AP, but negatively correlated with EC (Table 3) The first canonical axis (CCA1) was negatively correlated with
269   EC, while the second canonical axis (CCA2) was positively correlated with SWC, but negatively correlated with
270   EC. The SWC, TOC, SOM, TON and AP were more important in determining the bacterial community
271   composition (as represented by longer arrows) than pH and EC, indicating that EC played only a minor role in
272   the shaping of community structure. Rhizosphere communities from *Lycium ruthenicum* and *Limonium gmelinii*
273   samples were positively associated with higher SWC, TON and AP. Meanwhile, *Halostachys caspica*
274   rhizosphere communities were positively correlated with EC, and *Halocnemum strobilaceum* communities
275   negatively correlated (Fig. 7a). Considering the bulk soil samples, CCA1 was positively correlated with EC and
276   negatively correlated with the TOC, TON and pH. The second axis (CCA2) was positively correlated with AP
277   and SWC. Apart from *Lycium ruthenicum,* the other species' samples were negatively correlated with SOM,
278   TON and AP, but positively correlated with EC. The TON, AP and pH had a stronger influence on community
279   structure than SOM or EC (Fig. 7b).

280   **DISCUSSION**

281   **Bacterial community structure in saline soils as compared to other environments**
282   Soil salinity has important effects on the distribution of plant communities, their composition and diversity (Xi
283   et al. 2016), and may also affect soil bacterial diversity and community structure (Fang et al. 2016; Pavloudi et
284   al. 2016). Plant communities in salinized habitats are dominated by halophytes, and the abundance and diversity
285   of associated microbial communities, in saline or hypersaline terrestrial environments, is usually low (Takekawa
286   et al. 2006; Jiang et al. 2007; Foti et al. 2008). In this study, bacterial communities were very low in richness
287   and diversity compared to documented communities in forests, grasslands and agricultural areas (Rampelotto
288   et al. 2013), maize crop soils (Garcia-Salamanca et al. 2013) and even other saline soils (Canfora et al. 2014);
289   however, metrics were consistent with those found in other "extreme" hypersaline soils in semiarid
290   Mediterranean regions (Canfora et al. 2015). The soils surrounding *Halocnemum strobilaceum* had the lowest
291   diversity and richness, perhaps as a result of the relatively high soil EC and low nutrient availability. Soils
292   associated with *Lycium ruthenicum* were the most diverse of all studied plant species. Considering that nutrient
293   availability in *Lycium ruthenicum*-associated soils was only mediocre, other factors (i.e., plant community

294   composition) likely affected the soil bacterial community (Ravit et al. 2003; Cao et al. 2014). Indeed, based on

295   field observations, the plant community surrounding focal *Lycium ruthenicum* individuals was more diverse and

296   had higher percent cover than for other species.

297   Bulk soil samples had similar, relatively simple bacterial communities. Only four genera, *Acinetobacter*,

298   *Citrobacter*, *Exiguobacterium* and *Pseudomonas*, were common, which differs from the bacterial communities

299   of saline soils in Inner Mongolia (Borruso et al. 2014) and the Shandong Peninsula coast (Tian & Zhang 2017).

300   Differences in community composition may be due to distinct climatic and/or soil properties among geographic

301   regions (Ben-David et al. 2011). However, the dominance of Bacilli (Firmicutes) and γ-proteobacteria in the

302   study region is consistent with previous studies (Tang et al. 2011; Borsodi et al. 2013), confirming that these

303   two taxa are important in saline or hypersaline environments. A low level of structural differentiation was also

304   found when comparing communities associated with different plant species, as determined by a LEfSe analysis.

305   The highest differentiation was observed between *Lycium ruthenicum* and the other species; in contrast,

306   *Kalidium foliatum* communities were indistinguishable from those of other species. This suggests that soil

307   bacterial communities are highly similar in arid environments, at least on a small geographic scale. Microhabitat

308   similarities may produce such similar bacterial communities, as low plant cover and a lack of plant litter are

309   common to arid environments.

310   **Bacterial community composition in the rhizosphere versus bulk soils**

311   Rhizosphere effects may be an important driving force shaping microbial communities and leading to

312   compositional differences between the rhizosphere and the bulk soils (Morgan & Whipps 2001). In this study,

313   bacterial communities differed between the rhizosphere and bulk soils, with higher community diversity and

314   richness in the rhizosphere, consistent with previous studies (Avis et al. 2008; Borruso et al. 2014; Edwards et

315   al. 2015; Chaudhary et al. 2017; Yang et al. 2017). Higher diversity may be a result of root exudates, which can

316   raise nutrient concentrations (Li et al. 2014). While soil properties were not measured exhaustively here, the soil

317   TOC and TON contents estimated in the rhizosphere of *Limonium gmelinii* and *Lycium ruthenicum* were

318   approximately 5-7 times higher than in the bulk soils. However, it should be noted that bulk soils may have

319   greater microbial richness than the rhizosphere in some cases (Shange et al. 2012; Carbonetto et al. 2014; Gomes

320   et al. 2014; Tian & Zhang 2017). These divergent results suggest that the soil type and plant species identity

321   have complex effects on bacterial communities, with the strength of their effects depending on abiotic and biotic

322   conditions (Berg & Smalla 2009).

323   In addition to diversity differences, the composition of bacterial communities also differed between the

324   rhizosphere and bulk soil samples, as revealed by PCoA and cluster analysis. Compared to bulk soils, the

325   rhizosphere communities had more groups with relative abundance > 1%, such as the following

326   phyla:Actinobacteria, Bacteroidetes, Firmicutes, Planctomycetes and Proteobacteria. Dominance by a greater

327   number of groups has also been reported in other saline ecosystems, both marine and terrestrial (Tang et al. 2011;

328   Marasco et al. 2013; Oliveira et al. 2014; Soussi et al. 2016). At the genus level, many genera were abundant in

329   the rhizosphere, for example *Acinetobacter*, *Bacillus*, *Citrobacter*, *Deferrisoma*, *Exiguobacterium*, *Haliea*,

330   *Halomonas*, *Marinimicrobium*, *Marinobacter*, *Methylohalomonas*, *Microbulbifer*, *Planococcus*, *Pseudomonas*

331   and *Thioprofundum* (Fig. 3, Fig. S5). Meanwhile, the richness of groups common in bulk soils (i.e. γ-

332   proteobacteria and Firmicutes) was reduced in the rhizosphere; for example, the abundance of Firmicutes was

333   about 80% lower. The low abundance of Firmicutes in the rhizosphere has been reported many times; see one

334   such case study in barley, where Firmicutes is almost excluded from the rhizosphere (Bulgarelli et al. 2015).

335 Although γ-proteobacteria were less abundant in the rhizosphere, as observed by a decrease in the number of
336 occurrences of *Acinetobacter*, *Citrobacter* and *Pseudomonas* species, γ-proteobacteria remained the most
337 abundant class, as found in many plant-associated bacterial communities (Mukhtar et al. 2017).
338   Shifts in bacterial community composition in bulk soils versus the rhizosphere may be the consequence of
339 active selection by plants (Kowalchuk et al. 2002). As many endophytes and bacteria colonizing root surfaces
340 have beneficial effects, such as nitrogen fixation, phytohormone production, nutrient supply and pathogen
341 suppression (Rosenblueth & Martinez-Romero 2006; Hardoim et al. 2008), they typically promote plant growth
342 and can alleviate salt stress in halophytes (Ali et al. 2015). Some *Microbulbifer* and *Planococcus* species have
343 the ability to degrade complex hydrocarbons (See-Too et al. 2017). Meanwhile, *Bacillus*, *Exiguobacterium*,
344 *Halomonas*, *Planococcus* and *Pseudomonas*can generate 1-aminocyclopropane-1- carboxylic acid (ACC)
345 deaminase to convert the ethylene precursor ACC into ammonia and α-ketobutyrate; this has the effect of
346 lowering the ethylene concentration within plant tissues, reducing its constraining effect on root elongation and
347 general plant growth (Siddikee et al. 2010). Moreover, some *Bacillus*, *Halomonas* and *Pseudomonas* species in
348 can produce indole-3-acetic acid (IAA) to confer salt tolerance (Tiwari et al. 2011). *Halomonas* species are able
349 to tolerate a wide set of abiotic stresses, and promote plant growth via IAA production, phosphate solubilization,
350 nitrogen fixation and more (Mapelli et al. 2013). In rhizobacterial communities, *Bacillus* and *Pseudomonas*
351 species are critically important for plant growth; these species have multiple functional activities, including
352 phosphate solubilization, phytopathogen inhibition (Prashar et al. 2014) and auxin production. Why these species
353 are less abundant in the rhizosphere (versus bulk soils) remains unclear. It could be caused by competition among
354 rhizobacteria, but this hypothesis needs verification. Moreover, the effects of many other common genera in the
355 rhizosphere (whether beneficial, harmful or neutral), as well their inter-relationships (mutualistic or competitive)
356 with plant growth promoting species, need further investigation.
357 **Differences among halophytes in rhizobacterial communities and relationship to soil properties**
358 A number of studies have demonstrated that microbial community composition is plant species specific
359 (Andreote et al. 2009; Poli et al. 2016), leading to unique rhizobacterial communities among species. Here, five
360 halophyte-associated rhizobacterial communities varied both in diversity (ANOVA $P < 0.01$) and structure
361 (Adonis $R^2 = 0.703$, $P = 0.001$). Rhizobacterial diversity was lower in *Halostachys caspica*, *Halocnemum*
362 *strobilaceum* and *Kalidium foliatum* than in *Limonium gmelinii* and *Lycium ruthenicum* ($P < 0.05$). While
363 community composition also seemed to vary, differences were not significant (Table 2). *Halomonas* was the
364 dominant genera in *Halocnemum strobilaceum* communities (32.4% of total abundance), a significantly higher
365 proportion than in the other plant-associated communities; this trend is consistent with previous studies (Al-
366 Mailem et al. 2010; Marasco et al. 2016), including of other halophytes (Borsodi et al. 2015). In the *Halostachys*
367 *caspica* rhizosphere, *Exiguobacterium* was the most common genus, followed by *Citrobacter*, *Acinetobacter*
368 and *Pseudomonas*. Meanwhile, in the *Kalidium foliatum* rhizosphere, *Halomonas, Exiguobacterium* and
369 *Gracilimonas* were most abundant. The rhizobacterial communities of *Limonium gmelinii* and *Lycium*
370 *ruthenicum* were highly similar (Adonis $R^2 = 0.324$, $P = 0.108$), perhaps as a result of similar soil properties.
371 The relatively high abundance of *Exiguobacterium* in the rhizosphere is unique to this study, suggesting that it
372 is potentially important in the study region, but this requires furtherinvestigation.
373   Furthermore, among replicates for a given plant species, only a small proportion of OTUs occurred in all
374 three. Interestingly, these shared OTUs were usually highly abundant overall, whereas OTUs that were found
375 only in one or two individuals were mostly rare OTUs (with a relative abundance less than five). Thus, bacterial

376 communities may have individual specificity, potentially influenced by a plant's genotype, age or health (Zhu et
377 al. 2013; Belimov et al. 2015). The OTUs found across all five plant species belong to 16 genera in total, and
378 some, such as *Deferrisoma*, *Exiguobacterium*, *Geminicoccus*, *Gracilimonas* and *Marinimicrobium*, were also
379 included in the taxa identified in the LEfSe. As successful colonizers of halophyte plants in saline-arid lands,
380 these may be good plant growth promotion rhizobacteria (PGPR) candidates.

381   Soil properties are also important determinants of soil microbial communities (Szymanska et al. 2016a;
382 Rathore et al. 2017). In particular, soil salinity is considered a primary environmental factor, directly or indirectly
383 driving the composition and diversity of prokaryotic communities (Marasco et al. 2016; Zhong et al. 2016). In
384 this study, soil EC had a positive influences on the bulk soil bacterial communities, and other soil factors also
385 shaped bacterial community composition. Soil nutrients (TON, TOC and AP) were most important for *Lycium*
386 *ruthenicum*. Similarly, a recent study found that variation in prokaryotic community structure was significantly
387 correlated with the TON and PO_4^{3-} concentration (Zhong et al. 2016). In the rhizosphere, EC was negatively
388 correlated with rhizobacterial community diversity and structure, though its influence on community structure
389 was only minor as revealed by the CCA. In contrast, the effects of soil nutrients, such as TOC, SOM, TON and
390 AP, were much stronger than those of EC or soil pH. The low diversity and compositional variation seen in
391 *Halostachys caspica* and *Halocnemum strobilaceum* rhizobacterial communities were negatively correlated with
392 soil TOC, SOM, TON and AP. These results imply that, when salinity levels are similar among habitats, the
393 influence of salinity on the rhizosphere microbial community structure is relatively weak. In these cases,
394 rhizobacterial community structure is more strongly influenced by the host plant identity and soil nutrient
395 content, whereas salinity has a minor effect.

396   Overall, variation in rhizobacterial community structure among the five study plant species was significant,
397 though pairwise differences did not reach significance despite the large number of OTUs that were unique to
398 each species. This may be explained by the relatively low total abundance of rare OTUs, as well as the low
399 proportion of shared OTUs in a given plant species. While abundant OTUs were shared across all five plant
400 species (and accounted for a large proportion of total richness in each), they differed in relative abundance. This
401 suggests that, in similar saline habitats, plants tend to select similar bacterial species to colonize roots, perhaps
402 as a consequence of adaptation to salinity stress; these species may act to promote plant growth or alleviate salt
403 stress. Coevolution between microorganisms and associated plant species has been addressed in leguminous
404 *Rhizobium* species (Wang et al. 2018). Community differences (especially in the richness of abundant groups)
405 may be closely related to differences in root exudates or plant litter between plant species (Chaudhary et al.
406 2015), as supported by the results here. However, the effects of other factors, such as ion concentration, and
407 interactions between microbiomes within a community (Chen et al. 2013; Poosakkannu et al. 2017) cannot be
408 excluded.

409 **CONCLUSIONS**

410   The present study investigated the composition and diversity of rhizobacterial communities in five co-
411 occurring halophytic species growing in salinized, arid desert soils within the Ebinur Lake Wetland Reserve in
412 Northwestern China. Significant differences were found between the rhizosphere and bulk soil communities,
413 both in diversity and bacterial composition. Diversity was higher in the rhizosphere than in the bulk soils.
414 Abundant taxonomic groups (from phylum to genus) in the rhizosphere were much more diverse than in bulk
415 soils. Actinobacteria, Bacteroidetes, Firmicutes, Planctomycetes and Proteobacteria were the most abundant

416 phyla in the rhizosphere, while Firmicutes and Proteobacteria were common in bulk soils. Comparing among
417 species, significant differences in rhizobacterial diversity and identity were observed. The diversity of
418 *Halostachys caspica*, *Halocnemum strobilaceum* and *Kalidium foliatum* associated communities was lower than
419 that of *Limonium gmelinii* and *Lycium ruthenicum* communities. Furthermore, the composition of *Halostachys*
420 *caspica* and *Halocnemum strobilaceum* communities was very different from that of *Limonium gmelinii* and
421 *Lycium ruthenicum* communities. Thus, plant species identity can have important effects on root-associated
422 bacterial communities. Diversity was positively correlated with soil nutrients, including TOC, SOM, TON and
423 AP, but negatively correlated with EC, though the effects of EC were much lower than those of soil nutrient
424 content. In conclusion, halophytic plant species played an important role in shaping associated rhizosphere
425 bacterial communities. Furthermore, when salinity levels were constant, soil nutrients emerged as key factors
426 structuring bacterial communities. These results provide insight into the nature of halophyte microbial
427 communities in arid regions, as well as the factors shaping these communities. However, pairwise differences
428 among the five rhizobacterial communities were not significant, despite some evidence for differentiation among
429 plant species. Further studies involving more halophyte species and individuals per species are necessary to
430 elucidate plant species identity effects on the rhizosphere for co-occurring halophytes.
431
432

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438

439 **ADDITIONAL INFORMATION AND DECLARATIONS**
440 **Fig. S1** Collection locations of soil samples used in the present study.
441 **Fig. S2** Rarefaction curves for bacterial OTUs, clustering at 97% sequence similarity. Error bars indicate
442 standard errors.
443 **Fig. S3** Species accumulation curves for soil samples. The horizontal bars within boxes represent the medians,
444 while the tops and bottoms of the boxes represent 75th and 25th quartiles, respectively. Plus signs (+) indicate
445 outliers.
446 **Fig. S4** Phylogeny and taxonomic classification of abundant OTUs shared among either rhizosphere or bulk soil
447 communities.
448 **Fig. S5** Relative abundance of common phyla and genera in bulk soil and rhizosphere bacterial communities.
449 **Table S1** Alpha diversity indices of bacterial communities in rhizosphere and bulk soil samples.
450
451

452 **TABLE CAPTIONS**
453 **Table 1** Soil characteristics of bulk soil samples from five halophytes.
454 **Table 2** Adonis analysis of bacterial community composition for bulk soil and rhizosphere samples.
455 **Table 3** Pearson correlation coefficients among soil chemical properties, and between soil properties and

456 community diversity.

457

458

459 **FIGURE LEGENDS**

460

461 **Fig. 1** Multiple comparisons of OTU richness (a) and α-diversity (Shannon's index) (b) between rhizospheric

462 and bulk soil bacterial communities, and among plant species within soil type. Within boxes, horizontal bars

463 indicate medians, while the tops and bottoms of boxes illustrate 75th and 25th quartiles, respectively. Small

464 circles represent outliers in bulk samples. G, B, J, S, Z indicate bulk soil samples from *Lycium ruthenicum*,

465 *Limonium gmelinii*, *Halocnemum strobilaceum*, *Halostachys caspica,* and *Kalidium foliatum*, respectively, while

466 GQ, BX, JM, SM and ZZ denote the corresponding rhizosphere samples from each species. Significance levels

467 (p values) are provided for among-species comparisons within soil type (bulk versus rhizosphere), as well as

468 between soil types.

469

470 **Fig. 2** Venn diagram showing the OTUs shared among different samples. a: rhizosphere samples, b: bulk soil

471 samples. Information on OTU numbers is provided as follows: the total number of OTUs detected across all

472 three replicates for each species (the number of OTUs shared among the three replicates).

473

474 **Fig. 3** Diagrams depicting community composition and relative abundance at different taxonomic levels. a:

475 phylum, b: class, and c: genus.

476

477 **Fig. 4** Principal coordinate analysis (PCoA) (a) and UPGMA clustering diagram (b) of soil samples. G, B, J, S

478 and Z represent bulk soil samples from *Lycium ruthenicum*, *Limonium gmelinii*, *Halocnemum strobilaceum*,

479 *Halostachys caspica* and *Kalidium foliatum*, respectively, while GQ, BX, JM, SM and ZZ represent rhizosphere

480 samples associated with these species.

481

482 **Fig. 5** LEfSe analysis at multiple taxonomic levels comparing rhizobacterial community composition for five

483 focal plant species. (a) Cladogram illustrating the taxonomic groups explaining the most variation among

484 rhizobacterial communities. Each ring represents a taxonomic level, with phylum (p), class (c), order (o), family

485 (f) and genus (g) emanating from the center to the periphery. Each circle is a taxonomic unit found in the dataset,

486 with circles or nodes shown in colors (other than yellow) indicating where a taxon was significantly more

487 abundant. (b) Histogram of the LDA scores computed for groups with differential abundance among the

488 rhizobacterial communities of the five plant species.

489

490 **Fig. 6** LEfSe analysis of bacterial community composition for bulk soil samples from four plant species. (a)

491 Cladogram illustrating the taxonomic groups that explain the most variation among the bacterial communities.

492 (b) Histogram of the LDA scores computed for groups with differential abundance among the bacterial

493 communities of the four plant species. *Kalidium foliatum*-associated communities did not form a separate group

494 (from other plant species' associated communities) and, therefore, these are absent from the cladogram and

495 histogram.

496

497   **Fig. 7** Canonical correspondence analysis (CCA) of the effect of soil properties on bacterial community structure
498   in the rhizosphere (a) and bulk soil samples (b). The soil properties are indicated with arrows, and include soil
499   pH, electrical conductivity (EC), total organic carbon (TOC), soil organic matter (SOM), total nitrogen (TON),
500   phosphorous (AP) and soil water content (SWC). The percentage of variation explained by each axis is provided.
501   GQ, BX, JM, SM and ZZ represent rhizosphere samples associated with *Lycium ruthenicum*, *Limonium gmelinii*,
502   *Halocnemum strobilaceum*, *Halostachys caspica* and *Kalidium foliatum*, respectively. G, B, J, S and Z represent
503   bulk soil samples from *Lycium ruthenicum*, *Limonium gmelinii*, *Halocnemum strobilaceum*, *Halostachys*
504   *caspica* and *Kalidium foliatum*, respectively.
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Figure 1

Multiple comparisons of OTU richness (a) and α-diversity (Shannon's index) (b) between rhizospheric and bulk soil bacterial communities, and among plant species within soil type.

Within boxes, horizontal bars indicate medians, while the tops and bottoms of boxes illustrate 75th and 25th quartiles, respectively. Small circles represent outliers in bulk samples. G, B, J, S, Z indicate bulk soil samples from *Lycium ruthenicum*, *Limonium gmelinii*, *Halocnemum strobilaceum*, *Halostachys caspica*, and *Kalidium foliatum*, respectively, while GQ, BX, JM, SM and ZZ denote the corresponding rhizosphere samples from each species. Significance levels (p values) are provided for among-species comparisons within soil type (bulk versus rhizosphere), as well as between soil types.

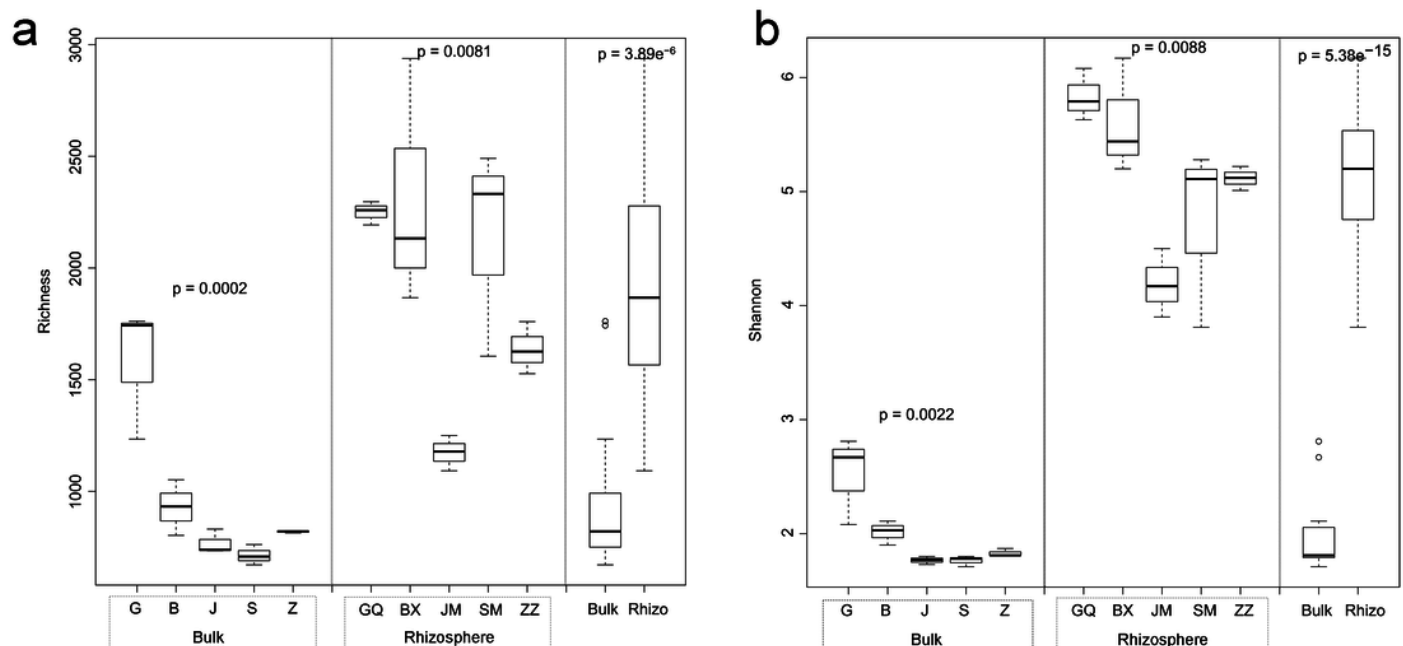



Figure 2

Venn diagram showing the OTUs shared among different samples.

a: rhizosphere samples, b: bulk soil samples. Information on OTU numbers is provided as follows: the total number of OTUs detected across all three replicates for each species (the number of OTUs shared among the three replicates).

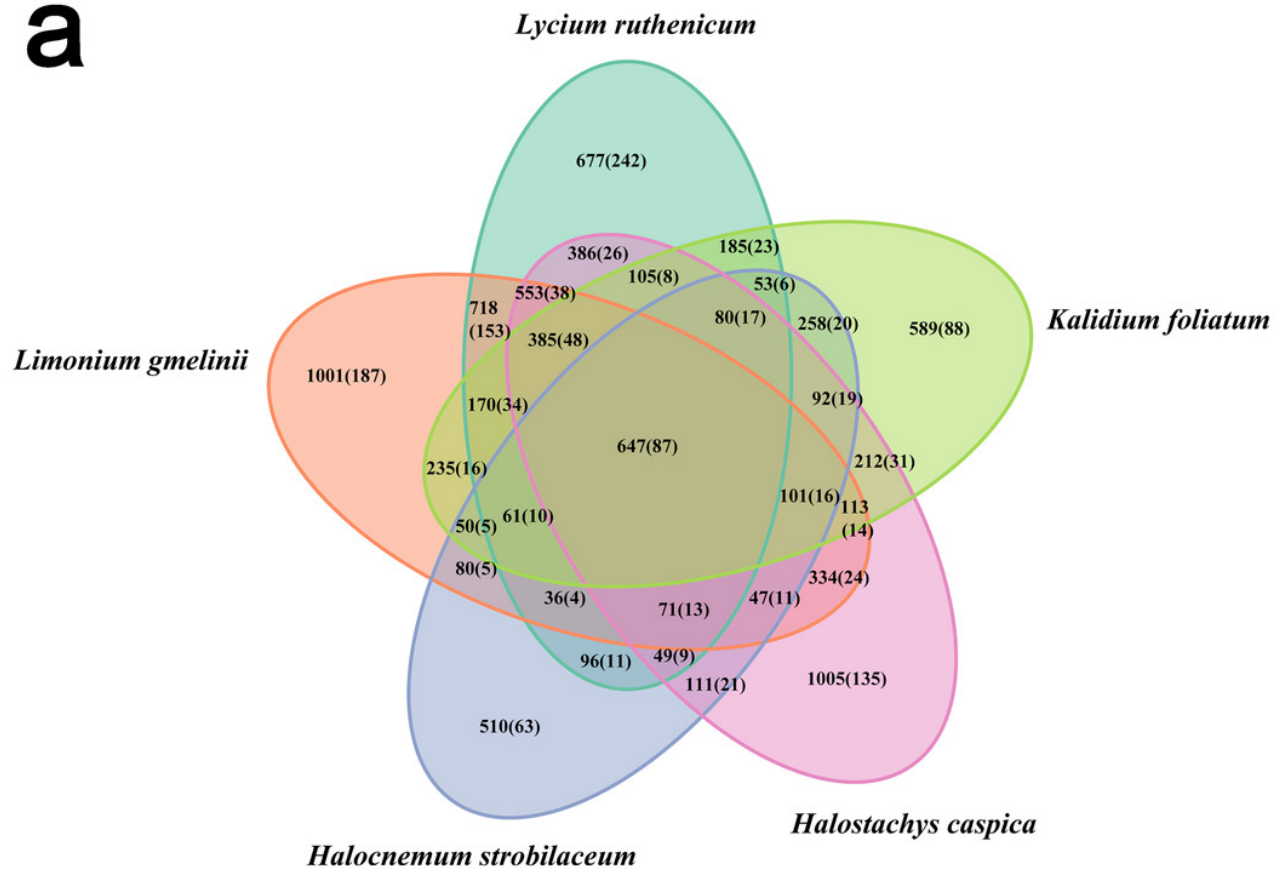
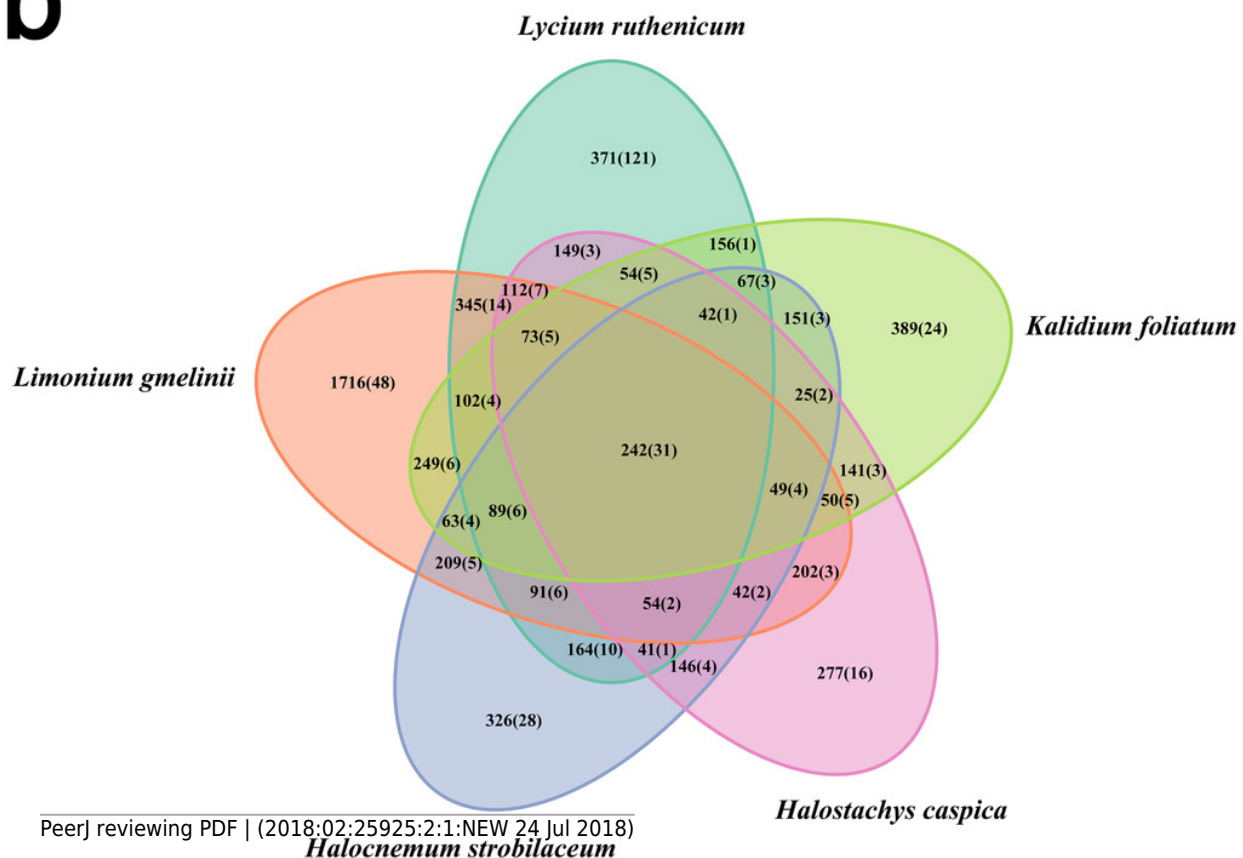



Figure 3

Diagrams depicting community composition and relative abundance at different taxonomic level.

a: phylum, b: class, c: genus. com/", 2.34.

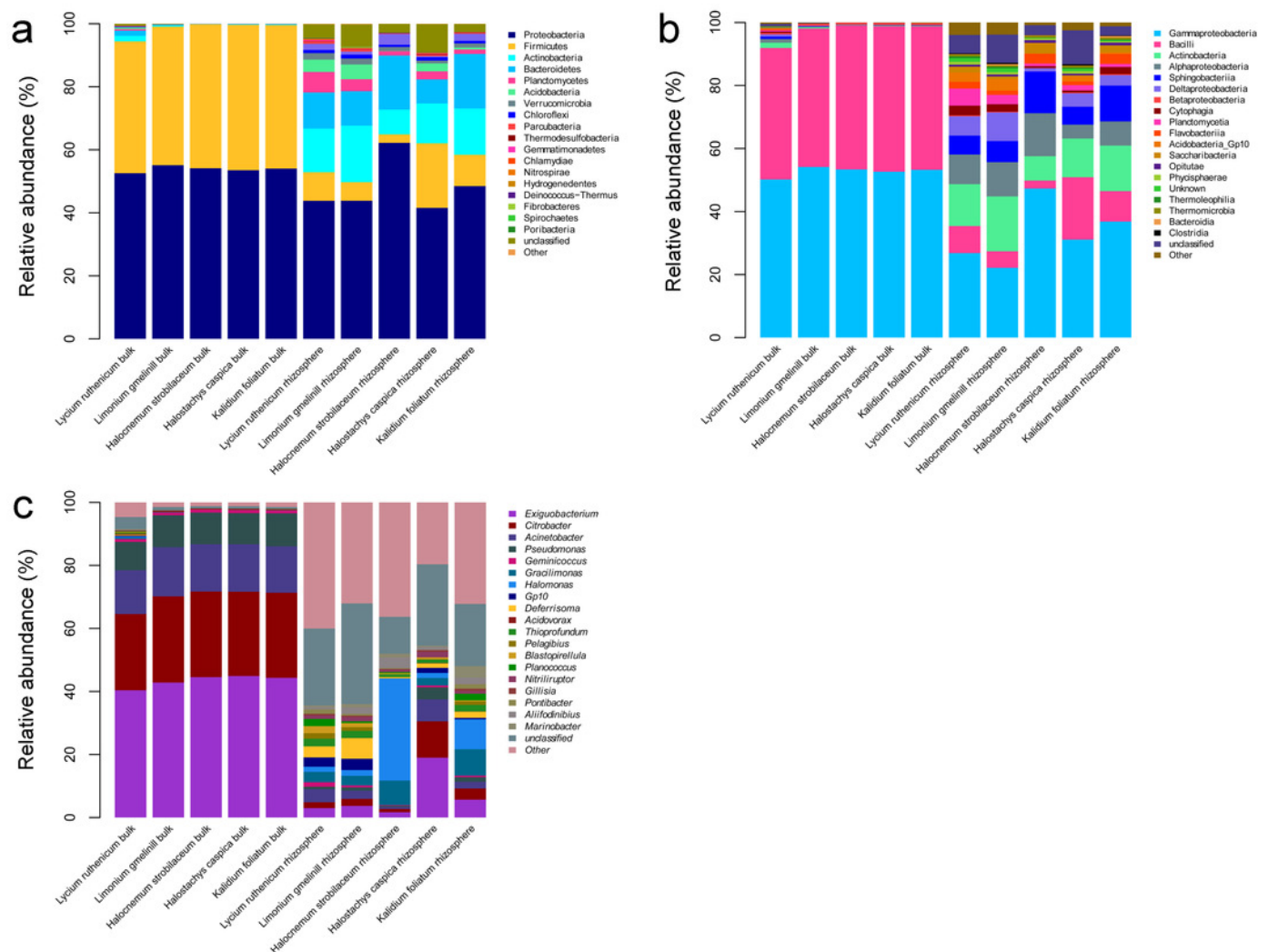



Figure 4

Principal coordinate analysis (PCoA) (a) and UPGMA clustering diagram (b) of soil samples

G, B, J, S and Z represent bulk soil samples from *Lycium ruthenicum*, *Limonium gmelinii*, *Halocnemum strobilaceum*, *Halostachys caspica* and *Kalidium foliatum*, respectively, while GQ, BX, JM, SM and ZZ represent rhizosphere samples associated with these species.

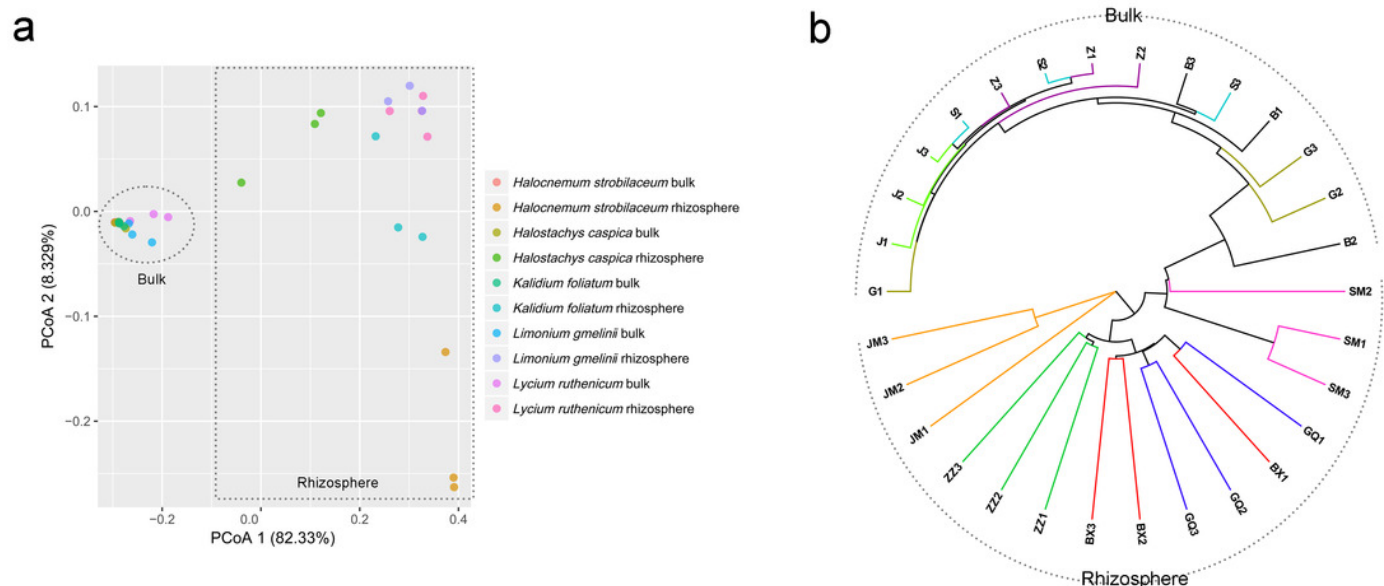



Figure 5

LEfSe analysis at multiple taxonomic levels comparing rhizobacterial community composition for five focal plant species.

(a) Cladogram illustrating the taxonomic groups explaining the most variation among rhizobacterial communities. Each ring represents a taxonomic level, with phylum (p), class (c), order (o), family (f) and genus (g) emanating from the center to the periphery. Each circle is a taxonomic unit found in the dataset, with circles or nodes shown in colors (other than yellow) indicating where a taxon was significantly more abundant. (b) Histogram of the LDA scores computed for groups with differential abundance among the rhizobacterial communities of the five plant species.

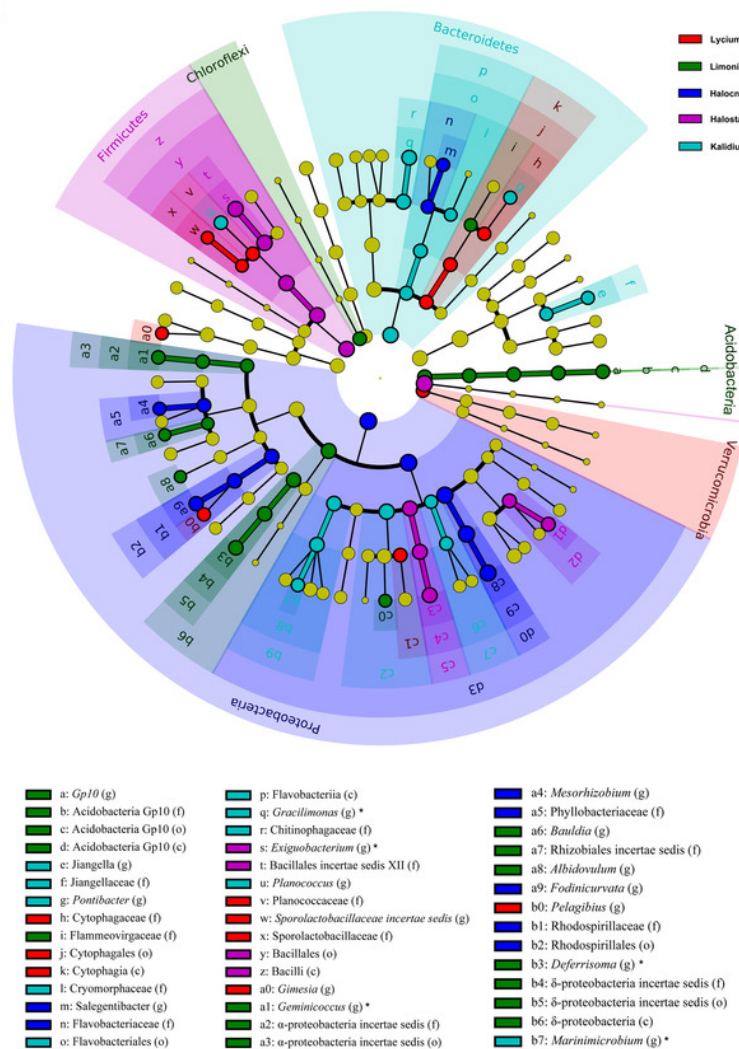
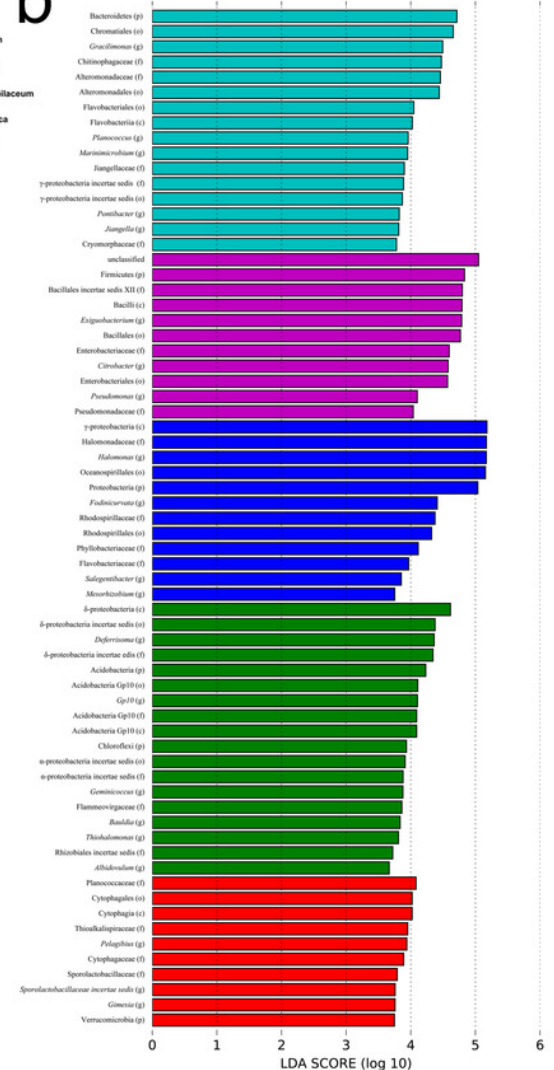



Figure 6

LEfSe analysis of bacterial community composition for bulk soil samples from four plant species.

(a) Cladogram illustrating the taxonomic groups that explain the most variation among the bacterial communities. (b) Histogram of the LDA scores computed for groups with differential abundance among the bacterial communities of the four plant species. *Kalidium foliatum*-associated communities did not form a separate group (from other plant species' associated communities) and, therefore, these are absent from the cladogram and histogram.

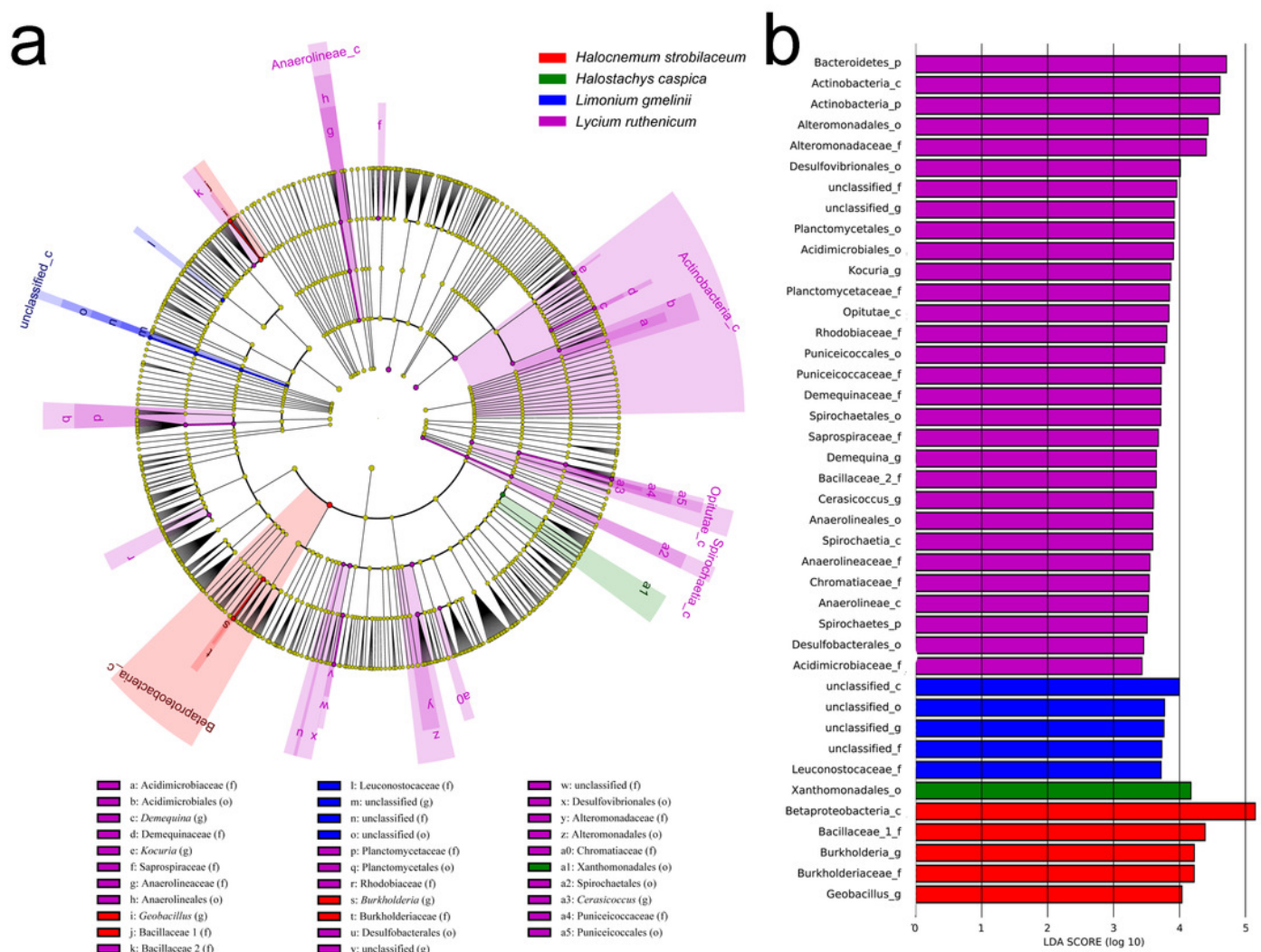
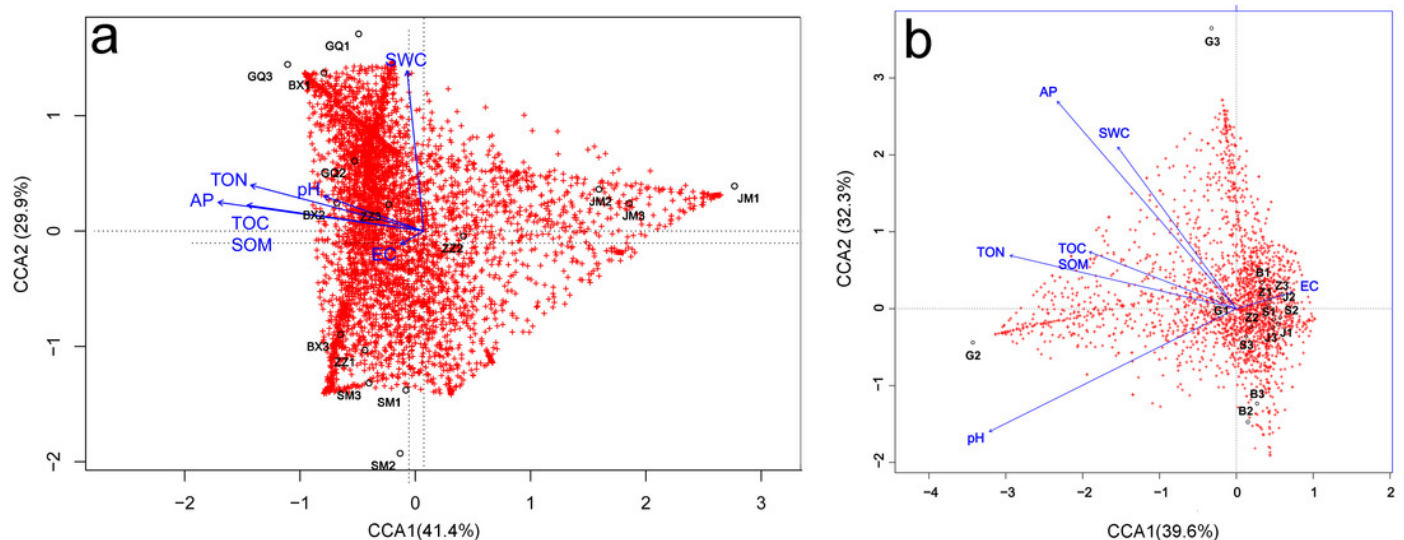



Figure 7

Canonical correspondence analysis (CCA) of the effect of soil properties on bacterial community structure in the rhizosphere (a) and bulk soil samples (b)

The soil properties are indicated with arrows, and include soil pH, electrical conductivity (EC), total organic carbon (TOC), soil organic matter (SOM), total nitrogen (TON), phosphorous (AP) and soil water content (SWC). The percentage of variation explained by each axis is provided. GQ, BX, JM, SM and ZZ represent rhizosphere samples associated with *Lycium ruthenicum*, *Limonium gmelinii*, *Halocnemum strobilaceum*, *Halostachys caspica* and *Kalidium foliatum*, respectively. G, B, J, S and Z represent bulk soil samples from *Lycium ruthenicum*, *Limonium gmelinii*, *Halocnemum strobilaceum*, *Halostachys caspica* and *Kalidium foliatum*, respectively.

Soil characteristics of bulk soil samples from five halophytes.

2 **Table 1** Soil characteristics of bulk soil samples from five halophytes.

	TOC (g/kg)	SOM (g/kg)	TON (g/kg)	AP (g/kg)	pH	EC (mS/cm)	SWC (%)
Lycium ruthenicum	9.14 ± 3.43a	15.75 ± 5.92a	0.58 ± 0.24a	0.89 ± 0.15a	8.23 ± 0.37	5.56 ± 1.26b	19.73 ± 2.18a
Limonium gmelinii	10.78 ± 1.60a	18.59 ± 2.77a	0.60 ± 0.10a	0.80 ± 0.08a	8.33 ± 0.24	6.61 ± 0.91ab	17.02 ± 3.51a
Kalidium foliatum	11.27 ± 5.66a	19.43 ± 9.76a	0.64 ± 0.25a	0.92 ± 0.08a	8.02 ± 0.25	5.65 ± 0.53b	16.45 ± 6.11a
Halostachys caspica	5.53 ± 0.95b	9.53 ± 1.63b	0.34 ± 0.03ab	0.82 ± 0.06a	8.05 ± 0.16	6.78 ± 1.42ab	10.42 ± 2.57b
Halocnemum strobilaceum	3.15 ± 1.09b	5.43 ± 1.88b	0.21 ± 0.02b	0.62 ± 0.06b	8.05 ± 0.30	7.14 ± 1.46a	17.71 ± 3.16a
mean	8.05 ± 4.15	13.87 ± 7.15	0.48 ± 0.23	0.82 ± 0.14	8.14 ± 0.27	6.30 ± 1.21	16.40 ± 4.57

3 Values are given as means (± standard error) (n = 3).

4 Different letters indicate significant differences among five halophytes at $P < 0.05$ level.

Adonis analysis of bacterial community composition for bulk soil and rhizosphere samples.

1   **Table 2** Adonis analysis of bacterial community composition for bulk soil and rhizosphere samples.

	Lycium ruthenicum	Limonium gmelinii	Halocnemum strobilaceum	Halostachys caspica	Kalidium foliatum
Lycium ruthenicum		0. 323(0.3)	0.399(0.199)	0.319(0.289)	0.367(0.089)
Limonium gmelinii	0. 324(0.108)		0.145(0.486)	0.042(0.894)	0.086(0.615)
Halocnemum strobilaceum	0.697(0.126)	0.718 (0.098)		0.096(0.605)	0.175(0.499)
Halostachys caspica	0.528(0.104)	0.513(0.11)	0.750(0.104)		0.016(0.904)
Kalidium foliatum	0.457(0.097)	0.504(0.102)	0.521(0.098)	0.574(0.114)	

2   data was shown in format of R^2 (P value); values below diagonal are for rhizosphere samples, and above diagonal for bulk samples.

Pearson correlation coefficients among soil chemical properties, and between soil properties and community diversity.

1   **Table 3** Pearson correlation coefficients among soil chemical properties, and between soil properties and

2   community diversity.

	TOC	TON	AP	SWC	pH	EC	OTU richness	Shannon index
TOC							0.446	0.484
TON	0.970***						0.549*	0.620*
AP	0.728**	0.761***					0.559*	0.609*
SWC	0.479*	0.476*	0.137				0.485	0.435
pH	0.420	0.467	0.151	0.301			0.504	0.459
EC	-0.211	-0.235	-0.126	-0.206	0.235		-0.093	-0.054

3   *   indicates significance level, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

4   EC: electrical conductivity, TOC: total organic carbon, SOM: soil organic matter, TON: total nitrogen, AP:

5   available phosphorous, SWC: soil water content.