

1       **Soil priming effects and involved microbial community along salt gradients**

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19 **Abstract**

20 Soil salinity mediates microorganisms and soil process, like soil organic carbon (SOC) cycling.  
21 Yet, how soil salinity affects SOC mineralization via shaping bacterial communities diversity and  
22 composition remains elusive. Therefore, soils were sampled along a salt gradient (salinity at 0.25%,  
23 0.58%, 0.75%, 1.00% and 2.64%) and incubated for 90 days to investigate i) SOC mineralization (i.e.  
24 soil priming effects induced by cottonseed meal, as substrate) and ii) responsible bacteria community,  
25 by using high throughput sequencing and natural abundance <sup>13</sup>C isotopes (to partition cottonseed meal  
26 derived CO<sub>2</sub> and soil derived CO<sub>2</sub>. We observed negative priming effect during first 28 days of  
27 incubation but turned to positive priming effect after day 56. Negative priming at the early stage might  
28 be due to the preferential utilization of cottonseed meal. The followed positive priming decreased with  
29 the increase of salinity, which might be caused by the decreased alpha diversity of microbial  
30 community in soil with high salinity. Specifically, soil pH and EC along salinity gradient were the  
31 dominant variables modulating the structure of microbial community and consequently SOC priming  
32 (estimated by distance-based multivariate analysis and path analysis). By adopting O2PLS, priming  
33 effects were linked with specific microbial taxa, e.g., Proteobacteria (*Luteimonas*, *Hoeflea* and  
34 *Stenotrophomonas*) were the core microbial genus that attributed to the substrate induced priming  
35 effects. Here, we highlight that the increase of salinity reduced the diversity of microbial community  
36 and shifted dominant microorganisms(*Actinobacteria* and *Proteobacteria* (*Luteimonas*, *Hoeflea* and  
37 *Stenotrophomonas*)) that determined SOC priming effects, which provides a theoretical basis for  
38 understanding of SOC dynamics and microbial drivers under salinity gradient.

39

40 Keywords: *Salt gradient, priming effects, bacterial community, core microorganisms*

## 41 **1. Introduction**

42 Soil salinization is an increasing environmental problem caused by natural and  
43 human activities in the arid and semi-arid area (Wichern et al., 2006). Salinization is  
44 often a major threat to crop productivity in agricultural land. Soil microorganisms suffer  
45 from osmotic stress. Soil salinity often cause microbial death or dormant. It was widely  
46 reported that the increased salinity decrease microbial biomass, enzymatic activity, and  
47 alpha diversity of microbial community (Laura, 1974; Pathak and Rao, 1998; Rietz and  
48 Haynes, 2003). Soil salinity is reported to the major determinants of composition,  
49 activity of microbial community (Kamble et al., 2014). Although salinity is reported to  
50 be a vital factor in influencing microorganisms in the arid and semi-arid area, limited  
51 studies investigated C processes (e.g. priming effect) driven by microbial community  
52 in salinity soils (Sardinha et al., 2003).

53 Soil organic carbon (SOC) is the largest pool (1500 Pg C) in the terrestrial carbon  
54 (C) cycle, and contains twice as much C as the atmosphere (Filley and Boutton, 2006;  
55 Wiesmeier et al., 2019). The input of substrate C can influence the output (i.e., CO<sub>2</sub>  
56 release) through a phenomenon called priming effect, which was firstly discovered by  
57 LÖhnis (1926). Substrate additions accelerate or decrease soil organic C mineralization,  
58 referred to positive or negative priming effects (Kuzyakov et al., 2000). The intensity  
59 of the priming effect affects the turnover of SOC and thus storage pool (Sullivan and  
60 Hart, 2013). Soil priming effects are affected by many biotic and abiotic factors  
61 (Lavelle, 1997; Martin W, 2019), to investigate abiotic and biotic mechanisms  
62 underlying SOC priming enhance strong understanding of the SOC cycling.

63 Soil priming effects is affected by soil fauna animals (Scheu and Parkinson, 1994),  
64 activities, diversity and composition of microbial community (Di Lonardo et al., 2017;  
65 Fontaine et al., 2011). The microbial decomposers are the major player in the  
66 decomposition process of added C sources. The addition of substrate, such as composts  
67 (Xun et al., 2016), animal sludges (Hartmann et al., 2015), sewage sludges (Su et al.,  
68 2017; Wagner and Raquel, 2011) and plant residues (Dai et al., 2017), generally

69 increases soil microbial biomass C and stimulates the microbial activities thus enhanced  
70 the loss of SOC (positive priming effects) (Fontaine et al., 2003; Bird et al., 2011; Li et  
71 al., 2018; Ali et al., 2019).

72 Concerning abiotic factors, the priming effect can be controlled by climate  
73 variables (Hagemann, 2008), and soil properties, like pH, EC, TN, etc (Blagodatskaya  
74 and Kuzyakov 2008; Luo et al., 2017). To understand how environmental and edaphic  
75 factors affect the processes of SOC mineralization, is important to estimate terrestrial  
76 C pool (Lehmann and Kleber, 2015). Although many studies have tested the effects of  
77 soil pH, SOC content, and other edaphic variables on soil priming effect, few study  
78 investigated soil priming effects in salinity soil (Asghar et al., 2012), especially linked  
79 with soil microbial community structure and their functions in C decomposition (Soina  
80 et al., 2018).

81 Thus, we sampled the soils along natural salinity gradients (0.25%, 0.58%, 0.75%,  
82 1.00%, 2.64% apart from total water-soluble salt). Based on these soils, we conducted  
83 a 90 days of indoor incubation applying C3 substrate of cottonseed meal ( $\delta^{13}\text{C}=-$   
84  $23.47\text{‰}$ ) to C4 soils with salt gradient ( $\delta^{13}\text{C}$  between  $-14.21\text{‰}$  and  $-16.01\text{‰}$ ), to  
85 investigate: 1) mineralization rate of cottonseed meal and induced soil priming effects  
86 along salt gradients; 2) diversity of microbial community in the soils with increased  
87 salinity, and 3) identify the bacteria taxa associated Soil priming. We hypothesized that  
88 i) soil microbial community diversity and composition will be different with the  
89 different in soil variables particularly pH and EC along salinity gradients, and ii) Soil  
90 C processes like priming effects will be regulated mainly by microbial community and  
91 especially the core microbial species. To clarify the priming effects and involved  
92 microbial groups would help us better understanding C sequestration potential and  
93 underlying mechanisms in saline soils.

94

## 95 **2. Materials and methods**

### 96 *2.1. Soil sampling and cottonseed meal production.*

97 The soil type was gray desert soil, which was collected from farmlands (82.90°  
98 longitude, 44.96° latitude) in **Xiao Yinpan town**, Bole City, Bortala, northern Xinjiang  
99 Uygur Autonomous Region, northwest China. The farmlands soil is naturally formed  
100 original saline-salinity soil and with a continuous 30 years planting of maize (C4 crop)  
101 and maize straw returning to soil for 7-8 year. **In September 2021, we determining the**  
102 **sampling area, and use the five-point sampling method to collecting non-rhizosphere**  
103 **soil. The soil samples were indoor air drying and hand-picked to remove visible other**  
104 **debris, animal and plant residues and then sieved at field moisture (<2mm) and**  
105 **subsequently adjusted to 40% of water holding capacity (WHC). Texture was**  
106 **determined by the pipette method without carbonate in all soil samples. They were then**  
107 **incubated at 25 °C for 7 days before starting the experiments, to allow any early**  
108 **sampling and sieving effects to subside.**

109 Cottonseed meal is a kind of reddish or yellow granular material obtained by  
110 pressing, leaching and other cottonseed. The cottonseed meal was purchased from the  
111 market and dried at 105 °C for 24 h indoor, then further pulverized by a ball mill and  
112 passed through < 2 mm sieve.

113

## 114 2.2. *Soil and substrate analyses*

115 EC and pH of soil and cottonseed meal were measured at a soil: water ratio of 1:5  
116 (weight/weight) (Bao, 2000). Air-dry soil (5 g, <2 mm) and 25 ml of deionised water  
117 were shaken together for 1 min and left to settle for 30 min, which was repeated once  
118 more before pH was determined with a pH electrode. Soil water-soluble salt was  
119 analyzed by weighted at a soil:water ratio of 1:5 (weight/weight). Air-dry soil (5 g, <1  
120 mm) and 25 ml of deionised water were shaken together for 30 min, filtration to obtain  
121 clear filtrate, using thermostat water bath to evaporate and weigh(Bao, 2000). Soil total  
122 carbon (TC), total nitrogen (TN) are collect soil to be tested was dried and ground  
123 through a 0.15mm screen, and a certain amount of treated soil sample was wrapped in

124 tin foil and placed in an element analyzer for determinatio (air-dried, milled <150  $\mu\text{m}$ )  
125 were determined by dry combustion (LECO CNS 2000, LECO Corporation, Michigan,  
126 USA). Soil microbial biomass C was determined by fumigation extraction (Vance et  
127 al., 1987; Wu et al., 1990). The  $\text{K}_2\text{SO}_4$  extractable organic C was determined using an  
128 organic carbon autoanalyser (Shimadzu, Analytical Sciences, Kyoto, Japan). Soil  
129 microbial biomass C ( $B_c$ ) was calculated from:  $B_c = 2.22 E_c$ , where  $E_c = [(\text{organic C}$   
130  $\text{extracted from fumigated soil}) \text{ minus } (\text{organic C extracted from non-fumigated soil})]$ .  
131 The natural  $\delta^{13}\text{C}$  (‰) abundance of the soils (air-dried, milled <200  $\mu\text{m}$ ) was  
132 determined using an elemental analyser-isotope ratio mass spectrometer (Sercon Ltd,  
133 Crewe, UK). All measurements are given on an oven-dry weight basis (o.d., 105 °C, 24  
134 h).

135 The  $\delta^{13}\text{C}$  (‰) abundance of the cottonseed meal (air-dried, milled <200  $\mu\text{m}$ ) was  
136 determined using an elemental analyser-isotope ratio mass spectrometer (Sercon Ltd,  
137 Crewe, UK). The main elemental composition of the substrate was determined using  
138 elemental analysis (Vario EL Cube, Hanau, Germany), with the samples combusted at  
139 1200 °C. Natural  $\delta^{13}\text{C}$  (‰) abundance ,the total carbon, total nitrogen contents and C/N  
140 of the cottonseed meal was presented in Table 1.

141

### 142 2.3. *Experimental design*

143 After pre-incubation, five soils with salinity gradient were thoroughly mixed with  
144 cottonseed meal at 20 mg C  $\text{g}^{-1}$  soil (d.w. basis), and incubated over 90 days following  
145 moisture adjustment to 40% of water-holding capacity (WHC) to investigate the  
146 substrate mineralization and priming effects. Each soil sample (40 g d.w. basis) was  
147 incubated in a 100 ml beaker inside a 1 L brown glass jar. Three jars with only water  
148 and NaOH were set as blank. All the jars were sealed with a rubber bung and incubated  
149 in a randomized block design at 25 °C for the 90 days of incubation. The NaOH vials  
150 were changed after 1, 3, 5, 7, 14, 28, 56 and 90 days for determination of evolved  $\text{CO}_2$

151 and  $^{13}\text{C}$ - $\text{CO}_2$  (‰). Meanwhile, soil biomass C,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , pH, EC, TC, TN and DNA  
152 extraction were measured at day 28.

153

#### 154 2.4. *Soil $\text{CO}_2$ -C and its isotopic composition*

155 Soil C evolved as  $\text{CO}_2$ -C in jars was measured by trapping  $\text{CO}_2$  in 1 M NaOH  
156 (20 ml) during soil incubation. After the NaOH (20 ml) trapping  $\text{CO}_2$  at different  
157 periods of soil incubation, 5 ml 1 M NaOH of each sample was mixed with 10 ml  
158 deionised water and titrated with 0.05 M standardised HCl by the TIM840 autotitrator  
159 (Radiometer Analytical, Villeurbanne Cedex, France). Meanwhile, the  $\delta^{13}\text{C}$  (‰) of  
160 trapped  $\text{CO}_2$ -C was precipitated, with 8 ml of the 1 M NaOH (20 ml) mixed with 8 ml  
161 1.5 M  $\text{BaCl}_2$  in vials (Aoyama et al., 2000). The  $\text{BaCO}_3$  precipitate was trapped on the  
162 glass fibre the filter, rinsed with deionised water several times, and dried overnight  
163 (80 °C), weighed (0.100-0.200 mg) into tin capsules, and analyzed for  $\delta^{13}\text{C}$  on an  
164 elemental analyzer-isotope ratio mass spectrometer (Sercon Ltd, Crewe, UK).

165

#### 166 2.5. *DNA exaction and sequencing*

167 The total soil DNA was extracted from 0.50 g of moist soil using a FastDNA Spin  
168 Kit (MP Biomedicals, Santa Ana, CA, USA) according to the manufacturer's protocol.  
169 The extracted DNA was dissolved in 50  $\mu\text{l}$  of TE buffer, quantified using a  
170 spectrophotometer and stored at  $-20$  °C until sequencing.

171 V3-V4 hypervariable regions of the bacterial 16S rRNA gene were amplified with  
172 primers 341F (5'-CCTAYGGRBGCASCAG-3') and 806R(5'-  
173 GGACTACHVGGGTWTCTAAT-3'). The PCR reactions were conducted with a  
174 thermocycler PCR system (GeneAmp 9700, ABI, USA) by using the following  
175 programs: 3 min of denaturation at 95 °C; followed by 27 cycles of 30 s at 95 °C, 30 s  
176 at 55 °C, and 45 s at 72 °C; and a final extension at 72 °C for 10 min with a thermocycler  
177 PCR system (GeneAmp9700, ABI, USA). PCR amplicons pooled from the triplicate  
178 reactions were purified using a QIAquick PCR purification kit (Qiagen, Shenzhen,

179 China), and quantified using a NanoDrop ND-1000 spectrophotometer (Thermo  
180 Scientific, Waltham, MA, USA). The PCR products were purified, mixed, and sent to  
181 Majorbio, Inc. (Shanghai, China) for sequencing based on the Illumina MiSeq platform.

182

## 183 2.6. Calculations

### 184 2.6.1. $CO_2$ - $\delta^{13}C$ emission

185 The mineralisation of cottonseed meal was separated from SOC mineralisation  
186 according to the change of stable isotopic composition ( $\delta^{13}C$ ) with time. The standard  
187 equation for determining  $\delta^{13}C$  (‰) is derived from:

$$188 \delta^{13}C \text{ (‰)} = [(R_{\text{sample}}/R_{\text{VPDB}}) - 1] \times 1000, \quad \text{Eqn. 1}$$

189 where  $R_{\text{sample}}$  is the mass ratio of  $^{13}C$  to  $^{12}C$  of each sample and  $R_{\text{VPDB}}$  is the  
190 international PDB(**Peedee Belemnite**) limestone standard. The labeled  $^{13}C$  (%) of  
191 cottonseed meal was then estimated from:

$$192 CO_2\text{-}^{13}C \text{ (‰)} = (\delta_{\text{treatment}} - \delta C4) / (\delta C3 - \delta C4), \quad \text{Eqn. 2}$$

193 where  $CO_2\text{-}^{13}C$  (%) is the proportion of evolved  $CO_2$  from C3 (cottonseed meal)  
194 matter,  $\delta_{\text{treatment}}$  is the  $\delta^{13}C$  (‰) in treatments of soil with cottonseed meal,  $\delta C4$  is the  
195  $\delta^{13}C$  (‰) in control soil and  $\delta C3$  is the  $\delta^{13}C$  (‰) from cottonseed meal. Thus, the  $CO_2\text{-}$   
196 C produced from cottonseed meal during the incubation was calculated from:

$$197 CO_2\text{-}^{13}C \text{ (}\mu\text{g g}^{-1} \text{ soil)} = CO_2\text{-}^{13}C \text{ (‰)} \times \text{total } CO_2\text{-}C \text{ (}\mu\text{g g}^{-1} \text{ soil)} / 100, \quad \text{Eqn. 3}$$

198  $CO_2$  from SOC was  $CO_2\text{-}^{13}C$  subtracted from total evolved  $CO_2\text{-}C$ . The absolute  
199 soil priming effect (or primed soil  $CO_2\text{-}C$ ) with the addition of cottonseed meal was  
200 calculated from:

$$201 \text{Primed soil } CO_2\text{-}C \text{ (}\mu\text{g C g}^{-1} \text{ soil)} = CO_2\text{-}C_{\text{treatment}} - CO_2\text{-}C_{\text{control}} \quad \text{Eqn. 4}$$

202 where  $CO_2\text{-}C_{\text{treatment}}$  is the non-isotopically labeled  $CO_2\text{-}C$  evolved from  
203 cottonseed meal amended soil,  $CO_2\text{-}C_{\text{control}}$  is non-isotopically labeled  $CO_2\text{-}C$  evolved  
204 from soil without cottonseed meal.

205

## 206 2.7. Statistics



207 The data of <sup>16</sup>S gene sequencing were processed using the Quantitative Insights  
208 Into Microbial Ecology (QIIME) 1.9.0-dev pipeline (Caporaso et al., 2010). In brief,  
209 Reads with less than length 200 bp and ambiguous bases were discarded. The sequences  
210 were then binned into operational taxonomic units (OTUs) by UCLUST (Edgar, 2010)  
211 based on 97% pairwise identity. Chimeric OTUs identified by USEARCH (Edgar et al.,  
212 2011) in QIIME were removed. The most abundant sequence from each OTU was  
213 selected to represent that OTU. Taxonomy was assigned to 16S OTUs against a subset  
214 of the Silva 104 database. The representative OTU sequences were aligned using  
215 PyNAST (Caporaso et al., 2010). We obtained between 64,425 and 89,989 clean\_reads  
216 per sample for all experimental samples.

217 To avoid potential bias caused by sequencing depth, all sample datasets were  
218 rarefied for the bacteria  $\alpha$ -diversity and  $\beta$ -diversity analyses. Faith's phylogenetic  
219 diversity was calculated to provide an integrated index of the phylogenetic breadth  
220 across taxonomic levels (Faith, 1992). To compare  $\beta$ -diversity between samples,  
221 principal coordinate analyses based on the unweighted and weighted UniFrac  
222 (Lozupone et al., 2007a) distances were calculated using the function 'pcoa' in the R  
223 package 'Ape'. Additionally, permutational multivariate analysis of variance  
224 (PERMANOVA) was carried out using the function 'adonis' in the R 'vegan' to  
225 measure effect size and significance on  $\beta$ -diversity. The variable influence projection  
226 (VIP) value was processed using the way of O2PLS analysis by the SIMCAP 14  
227 (Version 14.1.0.2047) (Wang et al., 2016). The y-matrix was defined as the  
228 environmental factors datasets and the x-matrix was defined as the microbial  
229 community on genus level dataset.

230 Data were logarithmically transformed and analyzed by ANOVA. All analyses  
231 were performed using SPSS software (13<sup>th</sup> edition). Pearson's correlation analyses were  
232 performed to assess the linear correlation among soil physio-chemical properties and  
233 microbial community. MULTIVARIATE analysis were operated to investigate  
234 interaction of salinity treatments on bacteria community parameters.

235

### 236 **3. Results**

#### 237 3.1. Soil physicochemical properties along salt gradients

238 The major soil physicochemical properties along salt gradients were presented  
239 (Table 1) and all of soil physicochemical properties has significant difference ( $P <$   
240  $0.05$ ). The total soluble salinity content in the soils ranged from 0.25% to 2.64% of  
241 salinity soils, soil salt gradients increasing gradually from salinity 1 samples to salinity  
242 5 samples. The pH and EC in soils ranged from 8.45 to 8.85 and from  $1.06 \text{ ms cm}^{-1}$  to  
243  $7.75 \text{ ms cm}^{-1}$ . Soil total C and N were increased with salinity, ranging from 3.16% to  
244 3.57%, and from 0.18% to 0.26%. The  $\delta^{13}\text{C}$  value for soils are between -14.21‰ and -  
245 16.01‰, which were relatively enriched compared to cottonseed meal (-23.47‰). This  
246 allowed separation of soil derived  $\text{CO}_2$  from total evolved  $\text{CO}_2$ , according to the classic  
247 mixed modeling.

248

#### 249 3.2. Total $\text{CO}_2$ evolution

250 During the whole 90 days of incubation, the cumulative  $\text{CO}_2$  evolved had  
251 similar trends, which the amount of  $\text{CO}_2$  increased with the incubation times (Fig. S1).  
252 The cumulative  $\text{CO}_2$  evolved increased more rapidly with the addition of cottonseed  
253 meal before 14 days, compared to non-amended soils. At 90 days of incubation. The  
254 cumulative  $\text{CO}_2$  evolved in the soil with the lowest salinity (Salinity 1) gave the lowest  
255  $\text{CO}_2$  emission ( $597 \mu\text{g C g}^{-1}$ ) in the non-amended soils (Fig. S1,  $P < 0.001$ ).

256

#### 257 3.3. Cottonseed derived $^{13}\text{CO}_2$ and soil priming effects

258 The total cumulative  $\text{CO}_2\text{-C}$  was divided three parts based the  $\delta^{13}\text{C}$  value,  
259 including basal soil-derived  $\text{CO}_2$ , cottonseed meal-derived  $\text{CO}_2$  and primed soil  $\text{CO}_2$   
260 (Fig.1). The cottonseed meal-derived  $\text{CO}_2$  had a significant contribution to the total  $\text{CO}_2$   
261 evolved during the early incubation period. The cottonseed meal-derived  $\text{CO}_2$  was  
262 significantly higher in Salinity 1, Salinity 2 and Salinity 3 than in Salinity 4 and Salinity

263 5 before 28 days incubation. Meanwhile, the soil priming effects was negative in all  
264 amended soil treatments before 28 days incubation and the direction of priming effect  
265 in most of soil samples turned into positive after 28 days. During the whole 90 days  
266 incubation, there was a negative correlation between cottonseed meal-derived CO<sub>2</sub> and  
267 primed soil CO<sub>2</sub> (Fig. 2).

268

#### 269 3.4. Bacterial diversity and community structure

270 The number of sequences ranged from 64,425 to 91,261 for per sample (average  
271 value of 80,602). About 27,990 OTUs in total were obtained under different five  
272 treatments. Bacterial community diversity was measured by a series of OTU-based  
273 analyses of alpha diversity including chao1 estimator, and observed\_species in the  
274 QIIME pipeline (Fig. 3). Chao1 diversity estimator and observed\_species was  
275 significantly different in treatments, being the highest in Salinity 1, followed by Salinity  
276 3, Salinity 2, Salinity 4 and Salinity 5 ( $P < 0.01$ ). In general, bacterial community  
277 diversity decreased with increasing salinity (Fig. 3).

278 The most abundant phylum in the soils and their correlation with salinity were  
279 shown in Fig. 4. Among them, Actinobacteria was the dominant taxa in all soils, with  
280 the abundance ranging from 50.07 % (Salinity 3) to 68.99 % (Salinity 4). The relative  
281 abundance of Bacteroidetes, Firmicutes, and Deinococcus-Thermus increased with  
282 the salinity, while Acidobacteria decreased with salinity degree.

283 Based on OTUs of five gradient salt treatments, the PCA analysis showed that  
284 treatments from Salinity 2 and Salinity 4 clustered together. Meanwhile, soil samples  
285 of Salinity 1, Salinity 3 and Salinity 5 distributed in the first, fourth and three quadrant,  
286 which indicated that these treatments had large environmental heterogeneity (Fig. S4).

287 In order to visualize the relationship between environmental factors and microbial  
288 community, *Canonical Correspondence Analysis* (CCA) was conducted, showing that  
289 NO<sub>3</sub><sup>-</sup>-N, EC and TC had a more obvious impact than other factors for microbial  
290 community (Fig. 3). Soil EC were positively correlated with pH, NH<sub>4</sub><sup>+</sup>-N, and

291 negatively correlated with TN, TC and MBC. Mantel test and Distance-based  
292 multivariate analysis showed the contribution rate of different environmental factors  
293 account for 78% of the variability of microbial communities (Table 2). The value of pH  
294 (31%) and EC (12%) had a strong influence on microbial community.

295

### 296 3.5. Relation between soil microbial community and C dynamics

297 Based on the O2PLS analysis, the variable influence projection (VIP) values of  
298 bacterial genus more than 1.00% were showed their contributions to C decomposition  
299 of cottonseed meal-derived C, basal soil-derived C, and primed soil C (Table 3). There  
300 were many microbial taxa positively correlating to soil primed CO<sub>2</sub>, for insatnce, genera  
301 of *Actinomarinales*, *Luteimonas*, *Nocardioides*, *Hoeflea*, *Intrasporangium*,  
302 *Nitrolancea*, *Pseudarthrobacter* and *Stenotrophomonas* had a positive correlation with  
303 primed CO<sub>2</sub>. In order to further to evaluate the relationship between soil properties, soil  
304 bacterial communities and C decomposition, we used the structural equation modeling  
305 (SEM) to suggest the direct and indirect impacts of salinity and microbial community  
306 on soil C decomposition (Fig. 7). The result showed that soil pH and EC had negative  
307 contribution to bacterial diversity, while bacterial diversity had a strong positive  
308 influence on the primed soil C (Fig. 5). For instance, salinity properties of EC had a  
309 directly negative influence on the bacterial diversity but positive influence on the  
310 primed soil C. Meanwhile, pH were negatively correlated with bacterial diversity and  
311 positively correlated with substrate derived C.

312

## 313 4. Discussion

### 314 4.1. Soil priming effects along salty gradients

315 Understanding soil C dynamics along salinity gradients is crucial to predict C  
316 sequestration in salty soils. In the early stage of the incubation, we observed that the  
317 cumulative substrate derived CO<sub>2</sub> in the soils with lower salinity was significantly  
318 higher than soils with higher salinity (Fig. 1), which can be possibly explained by that

319 high salinity inhibited microbial activity. Many studies have reported the influence of  
320 soil salinity on organic matter decomposition, mostly, the decomposition of organic  
321 matter are decreased by salinity (Wichern et al., 2006; Ghollarata and Raiesi, 2007;  
322 Tripathi et al., 2007; Setia et al., 2012). Yet, the response of microbial community to  
323 the increasing levels of salinity and consequent effects on soil priming effects remains  
324 largely unknown.

325 Here, we found soil priming effects was gradually changed from negative to  
326 positive priming effect (Fig. 1). The early pattern of the dynamics of the priming effect  
327 in this study was similar to other studies showing preferential utilization of labile C  
328 substance. The first phase of negative priming effects was likely to be caused by  
329 microbial assimilation of substrate. The soil microbes turned to use the new added  
330 substrate and thus used less of the original SOC. This was attributed to “preferential  
331 substrate utilization” (Perelo et al., 2005).

332 Soil microbial biomass-related growth predominating in the first phase were most  
333 likely to utilize SOC, leading to a positive priming effects after substrate was largely  
334 vanished. The magnitude of priming effects depends on soil microbial biomass size  
335 (Schneckenberger et al., 2008). It was found that the amount of added easily available  
336 organic C is beyond 50% of microbial biomass C (Blagodatskaya and Kuzyakov, 2008).  
337 Namely, the second phase of positive PEs probably was due to increased biomass size  
338 and enhanced demand on SOC. Secondly, C that was assimilated into microbial  
339 biomass in the first stage may also be mineralized in the second stage due to the  
340 turnover of microbial biomass (Shahbaz et al., 2017; Perelo et al., 2005).

341

#### 342 4.2. Microbial community along salt gradients

343 Previous studies concerning the impact of salinity on soil microbial community  
344 used different soils with a range of salt levels. In the present study we investigated the  
345 influence of soil salinity on microbial communities in soils from the closed area  
346 covering a range of salt content. Similarly, Rousk et al. (2011) also used agricultural

347 soils from the same area representing a range of soil salinity. Here, we found microbial  
348 diversity (alpha diversity) decreased with increasing salinity (Fig. 3). The negative  
349 impact on microbial diversity can be explained by that the accumulation of large  
350 amounts of salt in the soil raised the extracellular osmotic concentration (Rath and  
351 Rousk, 2015; Oren, 2011). The high osmotic pressures made it difficult for many  
352 microorganisms to adapt to and thus reduce their biological activity. The changes of  
353 soil microbial community structure were also explained by salinity (Herlemann et al.,  
354 2011; Campbell and Kirchman, 2013). We found that Bacteroidetes, Firmicutes,  
355 Acidobacteria and Deinococcus-Thermus were dominant in these soils (Fig. 4). These  
356 results are supported by previous findings that Firmicutes possess the high salinity  
357 resistance. Other studies also found that Bacteroidetes is dominant taxa in alkaline  
358 saline soil because of its resistant to salt (Valenzuela-Encinas et al., 2009; Keshri et al.,  
359 2013). Other study shows that the dominant phyla are Bacteroidetes and followed by  
360 Proteobacteria in the haloalkaline soil (Keshri et al., 2013). These results are consistent  
361 with the esuarine or marine environments, despite some studies suggest that soil salinity  
362 is not found to be a decisive factor for bacterial community and their growth (Rousk et  
363 al., 2011).

364 The difference of microbial community structure is affected by many soil variables,  
365 and pH and EC were the most important ones (Fig. 3; Table 2). Our results showed that  
366 the value of soil pH and EC would significantly affect the microbial community  
367 structure and the combined contribution rate of these two variables to microbial  
368 community was 43% (Table 2). At high levels of salt and alkaline arid condition, soil  
369 pH has been also shown to have a very powerful influence on the soil bacterial  
370 community structures (Bååth and Anderson, 2003; Fierer and Jackson, 2006; Rousk et  
371 al., 2010). Meanwhile, it is consequently unlikely that soil pH differences between the  
372 studied soils obscured the influence of salt (Rousk et al., 2011). Salinity has been  
373 identified as one of the most potent environmental factors that determine assembly of  
374 microbiome. Salinity has been regarded to play the vital role in shaping microbial

375 community in different ecosystem. This, despite the clear evidence from aquatic  
376 microbial ecology (Lozupone and Knight, 2007b), show a potential for salt to affect  
377 soil microbial communities apart from that of pH (Rath and Rousk, 2015).

378

#### 379 4.3. The core microbial taxa regulating C decomposition along salinity gradient

380 The correlation of microbial taxa and SOC decomposition (priming) were found  
381 according to the results of O2PLS and SEM (Table 3; Fig. 5). Here we showed that  
382 *Streptomyces* (Actinobacteria), *Glycomyces* (branch of Actinobacteria), *Agromyces*  
383 (branch of Actinobacteria), and *Sphingomonas* (branch of Proteobacteria) at the genus  
384 level were significantly correlated with the C process particularly primed soil-driven C.  
385 Most of these functional taxa belonged to Actinobacteria and Proteobacteria. In a recent  
386 study, Ren et al. (2018) found that Actinobacteria had negative impact on SOC  
387 mineralization across land-use change (Fierer et al., 2007; Goldfarb et al., 2011) and  
388 Proteobacteria drove the positive soil respiration (He et al., 2012; Stevenson et al.,  
389 2004), indicating the balance of soil C dynamics were largely regulated by these two  
390 phyla. We found similar result that *Streptomyces* (branch of Actinobacteria) had a  
391 negative correlation with primed soil CO<sub>2</sub>. Actinobacteria are able to grow  
392 preferentially on the C-rich refractory materials and relatively easily decompose the  
393 cellulose, lignocellulose (Khodadad et al., 2011), indicating these microorganisms  
394 preferentially use the C source that is used partially by others.

395 Although some studies suggest soil salinity may not be a vital factor for C  
396 decomposers (Rousk et al., 2011), the composition of microbial community are  
397 considered to play a decisive role in determining C dynamic processes in response to  
398 salt stress (Ramsey et al., 2005; Schimel et al., 2007; Nottingham et al., 2009). Here,  
399 SEM analysis showed that soil pH and EC in salted soils reduced microbial diversity  
400 and thus limited the utilization of SOC by microbial community, It was reported that  
401 high pH and salinity are the major determinants of soil microbial activity and  
402 community structure (Kamble et al., 2014).

403

## 404 **5. Conclusion**

405 Cotton meal is a kind of organic material with high nitrogen content, adding cotton  
406 meal in salinised soil can stimulate and promote the release of soil nutrients. The  
407 microorganisms mainly use the organic matter in the cotton meal in the pre-culture  
408 period, so the soil carbon excitation is negative excitation, Soil priming effect turned  
409 from negative to positive at the later stage of incubation (day 28), because  
410 microorganisms turned to decompose SOC from the labile substrate. With the increase  
411 of salinity, the diversity of microbial community decreased. Soil microbial community  
412 was mainly controlled by soil pH and EC. By O2PLS, we found Actinobacteria and  
413 Proteobacteria (*Luteimonas*, *Hoeflea* and *Stenotrophomonas*) dominant in these soils  
414 were the core microbial taxa that affecting the process of organic C mineralization,  
415 particularly soil primed CO<sub>2</sub>.

416

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420

## 421 **Data availability**

422 The datasets used and analysed during the current study available from the  
423 corresponding author on reasonable request.

424

## 425 **Author contributions**

426 K.W. conceptualized and conducted the experiment. H.Z. and D.C. conducted the  
427 data analysis and wrote the manuscript, conducted the indoor experiment. C.M. and  
428 Z.Z. assisted in conducting the experiment. All authors reviewed the manuscript. All  
429 authors contributed to the manuscript and approved the submitted version.

430



431 **Competing interests**

432 The authors declare no competing interests.

433

434 **Reference**

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**Table 1.** Soil samples and Cottonseed meal properties

	<b>Salinity 1</b>	<b>Salinity 2</b>	<b>Salinity 3</b>	<b>Salinity 4</b>	<b>Salinity 5</b>	<b>Cottonseed meal</b>
<b>Total C (%)</b>	3.38b	3.18c	3.16c	3.57a	3.35b	42.98
<b>Total N (%)</b>	0.18d	0.19d	0.20c	0.22b	0.26a	5.84
<b>C/N ratio</b>	18.32a	16.56b	15.71c	16.54b	12.94d	7.38
<b><math>\delta^{13}\text{C}</math> value (‰)</b>	-14.21a	-14.79c	-14.60b	-14.55b	-16.01d	-23.47
<b>pH (H<sub>2</sub>O)</b>	8.85a	8.45c	8.58b	8.59b	8.55b	7.63
<b>EC (dS m<sup>-1</sup>)</b>	1.06e	1.96c	1.28d	2.64b	7.75a	2.56
<b>Salinity (%)</b>	0.25e	0.58d	0.75c	1.00b	2.64a	ND

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669

670 **Table 2.** Mantel test and Distance-based multivariate analysis relevance and  
671 contribution rate between soil properties and bacterial community compositions.

	pH	EC	NO <sub>3</sub> <sup>-</sup> -N	NH <sub>4</sub> <sup>+</sup> -N	MBC	TN	TC
Correlation	0.74**	0.56**	0.36**	0.68**	0.31**	0.11	0.27
Contribution	0.31**	0.12**	0.05	0.04	0.16	0.03	0.07**

672 Note: \* p < 0.05, \*\* p < 0.01

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674

675 **Table 3.** The variable influence projection (VIP) value and Spearman's correlation  
 676 between the relative abundances of genera and C dynamic.

Phylum-Genus	VIP	Cottonseed meal CO <sub>2</sub> -C(μg g <sup>-1</sup> )	Primed soil CO <sub>2</sub> -C(μg g <sup>-1</sup> )	Basal soil CO <sub>2</sub> -C(μg g <sup>-1</sup> )
Actinobacteria-Actinomarinales	1.36		0.63**	
Proteobacteria-Luteimonas	1.31		0.80**	
Actinobacteria-Nocardioidea	1.30		0.54*	
Proteobacteria-Hoeflea	1.29		0.73**	
Actinobacteria-Streptomyces	1.27		-0.84**	
Actinobacteria-Glycomyces	1.26	0.63**		
Actinobacteria-Marmoricola	1.26	-0.52		
Proteobacteria-Nitrospira	1.23		0.59	
Actinobacteria-Intrasporangium	1.22		0.60*	
Actinobacteria-Agromyces	1.19			0.58*
Proteobacteria-Sphingomonas	1.18			0.65**
Actinobacteria-Myceligenans	1.16			
Chloroflexi-Nitrolancea	1.15		0.65**	
Actinobacteria-Pseudarthrobacter	1.06		0.62**	
Proteobacteria-Stenotrophomonas	1.00	-0.50	0.72**	

677 Note:\* p < 0.05, \*\* p < 0.01

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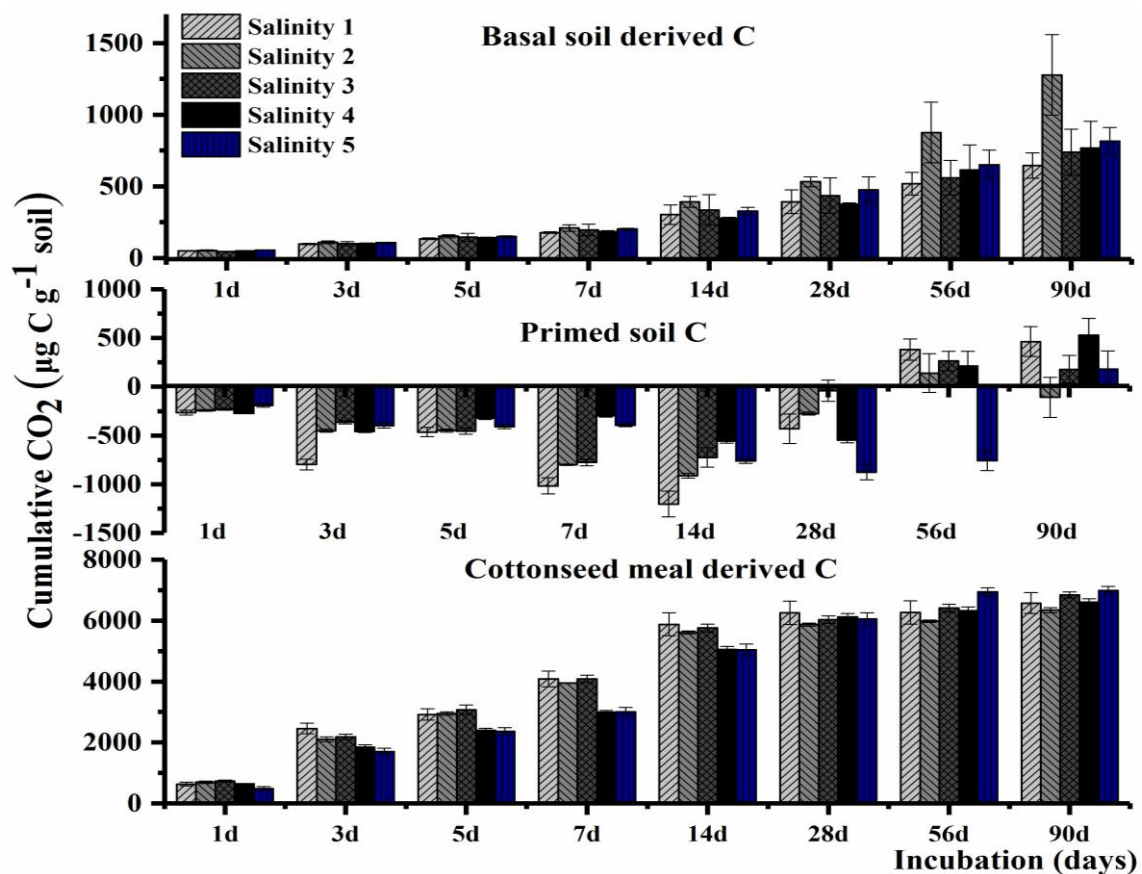
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**Fig. 1.** Partitioning of CO<sub>2</sub> evolution after addition of cottonseed meal in different five salinity soils. Cumulative CO<sub>2</sub> evolved from salinity soil of 0.25 % (a) , 0.58 % (b) , 0.75 % (c) , 1.00% (d) and 2.64% (e) . Error bars represent standard errors of the means (n = 3).

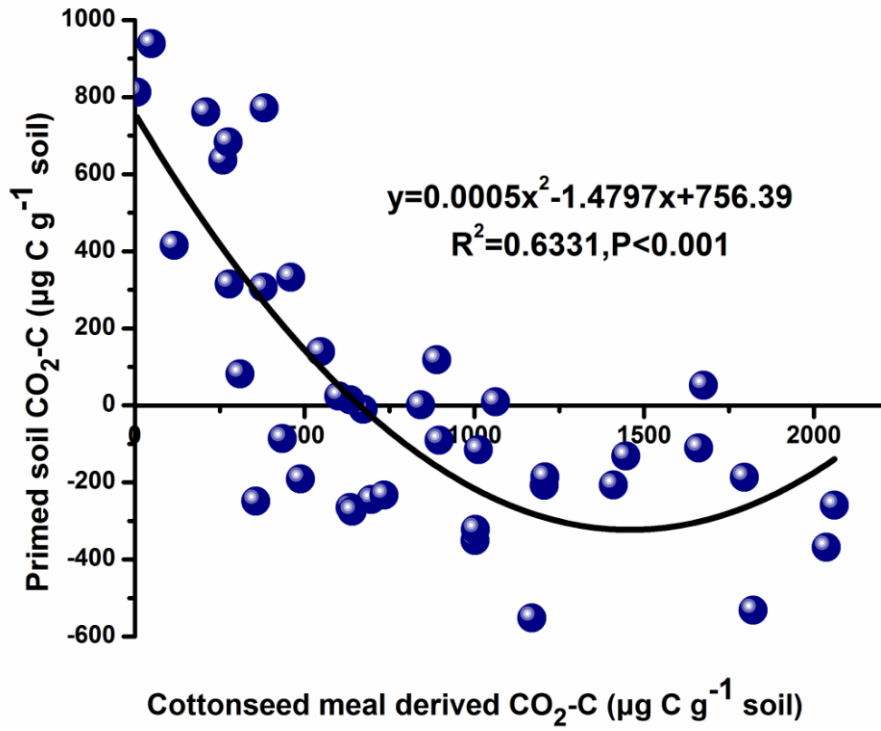
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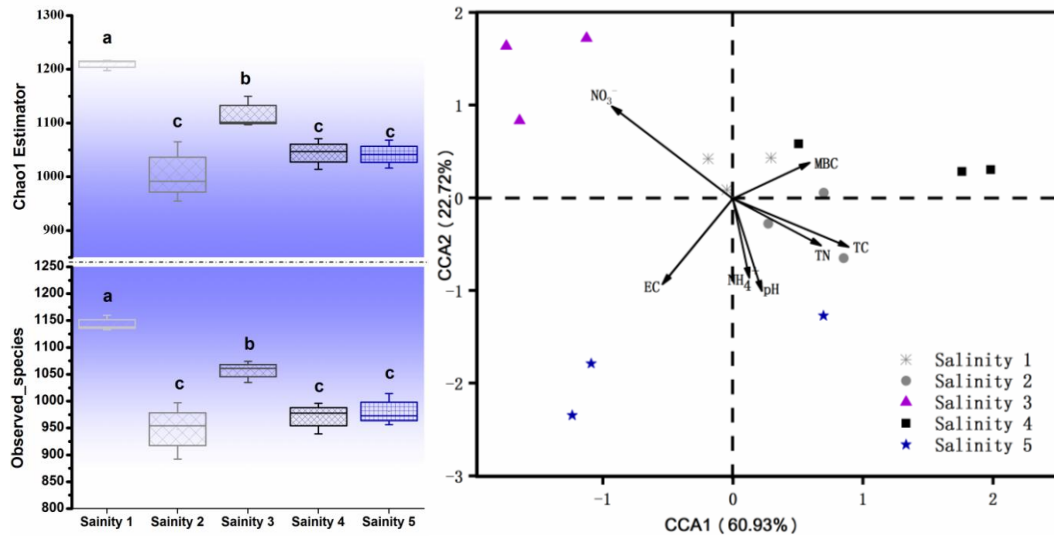
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**Fig. 2.** Correlation between primed soil mineralisation and cottonseed meal mineralisation following different five salinity soils during 90 days incubation



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708 **Fig. 3.** Microbial community alpha diversity (Chao1) observed\_species and beta  
 709 diversity. Within each panel, boxplot data refer to maximum date (top line), 99% (the  
 710 second line), mean (the third line), 1% (the fourth line) and minimum date (bottom line)  
 711 of the different treatments, with statistical significance ( $P < 0.05$ ).

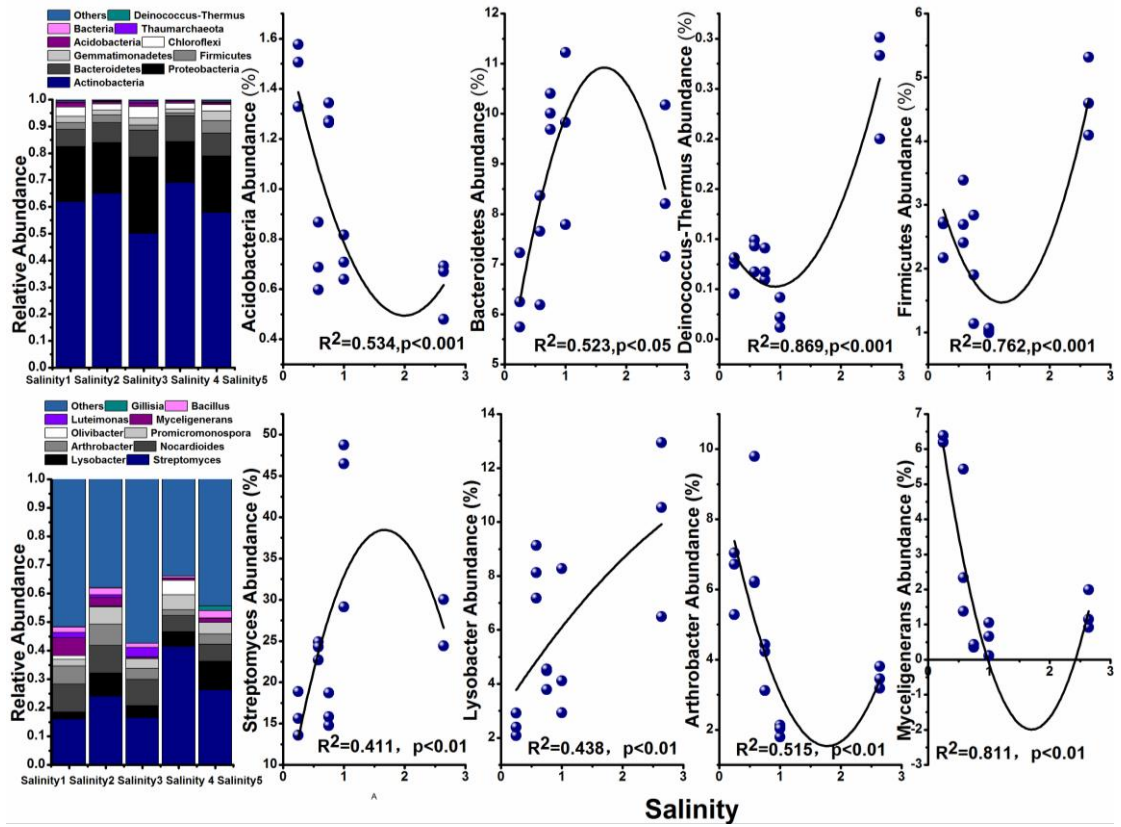
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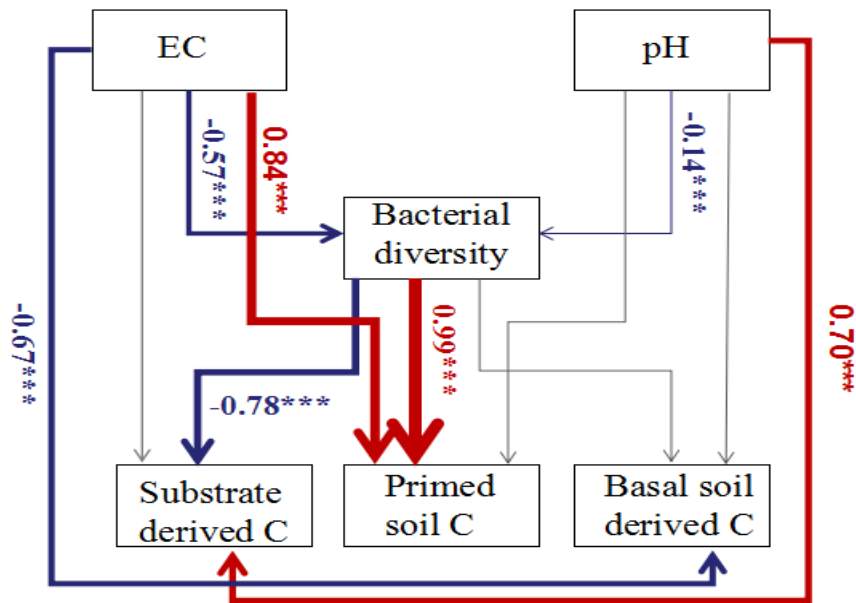
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**Fig. 4.** The top 10 of phylums and genes in bacterial community in soils with a gradient of salinity



$\chi^2 = 0.85, P = 0.65, GFI = 0.98, RMSEA < 0.001$

721

722 **Fig. 5.** Path analysis detecting the underlying causal relationships between soil salinity  
 723 physicochemical factors and microbial community composition of carbon dynamics in  
 724 the soil system. Red lines indicate positive relationships, while blue lines indicate  
 725 negative relationships. The width of arrows indicates the strength of significant  
 726 standardized path coefficients ( $P < 0.05$ ). Paths with non-significant coefficients are  
 727 presented as gray lines. \*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ; \* $P < 0.05$

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