Alteration of Nutrient Substrates and Absence of Seawater Due to Coastal Embankments Affects Soil Microbial Communities in Salt Marshes of Eastern China

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Abstract

Aims: Although the influence of coastal embankments on soil physicochemical properties and carbon (C) and nitrogen (N) cycling has been widely studied, the mechanisms of their effects on the soil microbial ecology are still poorly understood. Thus, the aim of this study was to investigate variations in soil bacterial and archaeal communities between natural and embanked saltmarshes, as well as the determinants that drive these variations.

Methods: 16S rRNA gene sequence analysis was performed to assess the impacts of embankments on the bacterial and archaeal communities of the invasive *Spartina alterniflora* Loisel., as well as native *Suaeda salsa* (L.) Pall. and *Phragmites australis* (Cav.) Trin. ex Steud. saltmarshes in the coastal China.

Results: Embankments significantly decreased the Simpson diversity index of the *S. alterniflora* saltmarsh, while increasing the OTU richness in the *P. australis* saltmarsh. Additionally, the bacterial and archaeal community compositions in the embanked *S. alterniflora* and *P. australis* saltmarshes were considerably modified. However, no variations were found between the bacterial and archaeal communities of the natural and embanked *S. salsa* saltmarshes.

Conclusions: These results were possibly because embankments decreased the soil nutrient substrates (e.g., soil organic C and N) dramatically in the *S. alterniflora* saltmarsh, while increased soil nutrient substrates significantly in the *P. australis* saltmarsh. However, embankments had a negligible effect on the soil nutrient substrates in the *S. salsa* saltmarsh. Moreover, embankments increased the abundance of Betaproteobacteria, and decreased the abundance of sulfur- and sodium-dependent bacteria due to the dramatic change in soil physicochemical properties.

1 Introduction

Coastal land reclamation through the establishment of coastal embankments has caused considerable ecological problems in natural coastal ecosystems. For instance, they have greatly threatened coastal habitats and biodiversity (particularly the soil microbial communities) and altered ecosystem processes and functions (particularly C and N cycling) (Dick and Osunkoya 2000; Ma et al. 2014; Yang et al. 2016). Soil bacteria are the most abundant and diverse group of soil microbes, with archaea also being numerically abundant (Buckley and Schmidt 2002; Fierer et al. 2007). Both play a crucial role in the transformation of soil nutrients and in the biogeochemical cycles (Nannipieri et al. 2003; Philippot et al. 2013; DeCrappeo et al. 2017; Gryta and Frac 2020). Moreover, bacteria and archaea are sensitive soil elements that can rapidly detect and react to various conditions and changes in the soil environment (Gryta and Frac 2020). Although the effects of coastal embankments on aboveground ecosystems have been widely studied, their potential advantages and risks to belowground ecosystems, particularly soil bacterial and archaeal communities, have not been fully estimated.

Soil nutrient substrates are one of the primary driving factors for bacterial and archaeal diversity, richness, and community composition (Peralta et al. 2013; Sun et al. 2021; Kuang et al. 2021). In

particular, soil organic C and N (SOC and SON, respectively) decomposition provides energy and nutrition for soil microorganisms; thus, soil C and N are overarching driving factors for the growth of soil bacteria and archaea (Zechmeister-Boltenstern et al. 2015; Yang et al. 2020). However, various bacterial and archaeal taxa respond differently to nutrient availability. For instance, copiotrophic bacteria (e.g., phylum Bacteroidetes) prefer nutrient-rich environments, as labile organic C and N (LOC and LON, respectively) inputs can significantly promote their growth (Fierer et al. 2007; Newton and McMahon 2011; Philippot et al. 2013). In contrast, because LOC and LON inputs have the opposite effect on oligotrophic bacteria (e.g., phylum Actinobacteria), these organisms prefer nutrient-poor environments (Podosokorskaya et al. 2013; Trivedi et al. 2013; Xie et al. 2014; Verzeaux et al. 2016). Additionally, high quality organic matter (e.g., with low C/N rate) has been reported to increase the relative abundance of archaea (e.g., phylum Crenarchaeota) (Bates et al. 2011). Coastal embankments can either increase, decrease, or have negligible effects on soil C and N sequestration, while shifting the availability of soil C and N by altering the inputs of plant residues in the soil (Laudicina et al. 2009; Cui et al. 2012; Wang et al. 2014). Therefore, the responses of soil bacterial and archaeal communities to coastal embankments may differ depending on the shifts in nutrient substrates caused by these structures.

Soil microbial communities are considerably influenced by biotic (e.g., the quantity and quality of plant materials) (Angel et al. 2010) and abiotic (e.g., climate, soil type, and soil physicochemical properties) factors (Bainard et al. 2016; Nguyen et al. 2018). Plant properties, such as the aboveground and belowground biomass, strongly affect soil bacteria and archaea (Brotosudarmo et al. 2014a; Li et al. 2015; Urbanová et al. 2015); the former influences the growth of photosynthetic bacteria (PSB) by affecting the amount of light that reaches the soil (He et al. 2012; Li et al. 2014a; Brotosudarmo et al. 2015), and the latter dictates the availability of C and N, in addition to providing unique environments for soil bacteria and archaea (Kuske et al. 2002; Urbanová et al. 2015). Soil physicochemical properties critically influence bacterial and archaeal communities (Yang et al. 2020; Sun et al. 2021; Zhang et al. 2021). For instance, soil pH can affect their community compositions, as the relative abundance of bacteria increases with increasing soil pH (Högberg et al. 2007; Peralta et al. 2013; Sun et al. 2021). Similarly, soil salinity restricts the growth of bacteria and archaea by limiting water availability (Rath and Rousk 2015; Zhang et al. 2021). Additionally, soil moisture is a vital driver of soil bacterial community composition, especially the proportion of aerobic and anaerobic bacteria, because it affects soil aeration conditions (Guo and Zhou 2020; Yang et al. 2020; Sun et al. 2021). Notably, the establishment of coastal embankments considerably shifts the net primary production and physicochemical properties of coastal wetland soils (Yang et al. 2016; Yang et al. 2019). Thus, the identification of biotic and abiotic factors that affect soil bacterial and archaeal communities in environments with coastal embankments may improve our understanding of how these structures have impacted bacterial and archaeal communities in soils.

China has been constructing increasingly intensive coastal embankments, with approximately 60% of the total length of its mainland coastline being enclosed by thousands of kilometers of embankments (Ma et al. 2014; Sun et al. 2015). The Jiangsu province has the highest abundance of coastal wetlands and embankments in Eastern China (Chung et al. 2004). Currently, a large portion of the natural coastal

wetlands in this region have been reclaimed by embankments (i.e., construction of dikes, seawalls, and barriers along the coastline), fishponds, farmlands, and urban lands (Liu 2018). The results of previous studies that have focused on the impacts of the conversion of coastal wetland to other land-use types on soil microbial communities are inconsistent (Xu et al. 2017; Li et al. 2019; Yang et al. 2019). For instance, studies have documented both an increase and decrease in bacterial abundance and diversity in the soil, especially the relative abundance of Proteobacteria, due to the conversion of coastal wetlands into farmlands (Xu et al. 2017; Li et al. 2019; Yang et al. 2019). These inconsistent results may be caused by multiple factors, such as differences in land reclamation history and intensity and land-use patterns following the establishment of coastal embankments (Yang et al. 2016). Additionally, it is difficult to distinguish between the effects of coastal embankments and subsequent land-use conversions (e.g., fishponds and agricultural and urban land) on soil microbial communities (Bai et al. 2013; Bu et al. 2015). Therefore, the impact of coastal embankments without associated land-use changes on soil bacterial and archaeal communities of coastal wetlands is still unknown. We hypothesized that the establishment of coastal embankments without land-use changes would shift the diversity and composition of bacterial and archaeal communities by changing the soil physicochemical properties and nutrient substrates. To verify our hypothesis, we compared the diversity and composition of bacterial and archaeal communities of embanked and adjacent unembanked *Spartina alterniflora* Loisel., *Suaeda salsa* (L.) Pall., and *Phragmites australis* (Cav.) Trin. ex Steud. salt marshes by extracting and sequencing their 16S rRNA genes; in addition, the plant biomass and soil properties (i.e., soil moisture, salinity, pH, SOC, LOC, water-soluble organic C (WSOC), SON, LON, and water-soluble organic N (WSON)) of embanked and adjacent unembanked *S. alterniflora*, *S. salsa*, and *P. australis* salt marshes along Jiangsu coasts were also compared. The aim of this study was to: (1) understand whether the establishment of coastal embankments without land-use changes influences the diversity and composition of bacterial and archaeal communities, and (2) if so, identify the factors that drive those variations.

2 Methods

2.1 Study sites

The study was conducted in coastal Yancheng (32°48'–34°29' N, 119°53'–121°18' E), Jiangsu province (Fig. 1). The mean annual temperature and precipitation of this region are 13.7–14.6°C and 980–1,070 mm, respectively (Wang and Liu 2005). The seawater salinity is approximately 30.9‰ (Yang et al. 2020). *S. alterniflora*, *S. salsa*, and *P. australis* salt marshes are the main vegetation types in coastal Jiangsu. *S. alterniflora* is an invasive perennial grass that was introduced in China from North America in 1979, while *S. salsa* and *P. australis* are native to coastal Jiangsu (An et al. 2007; Qin and Li 2012).

The coastal wetlands of Yancheng are an important stop on the migration route of shorebirds between East Asia and Australia. This is also the largest wintering area of the endangered Red-crowned Cranes (*Grus japonensis*) (Liu et al. 2010; Wang et al. 2019b). However, since its introduction, *S. alterniflora* has been outcompeting the native plants for resources such as space; therefore, some embankments have been constructed to control the expansion of *S. alterniflora* (Wang and Liu 2005; An et al. 2007; Qin and Li

2012; Wang et al. 2019a, b). These coastal embankments were covered with waterproof material, and the land-use in the embanked region did not change at the study sites.

2.2 Field sampling

In September 2016, four parallel transects (40 × 40 m) were constructed in embanked *S. alterniflora* (ESA), *S. salsa* (ESS), and *P. australis* (EPA) salt marshes and unembanked *S. alterniflora* (USA), *S. salsa* (USS), and *P. australis* (UPA) salt marshes (Fig. 1). We randomly selected three plots (2 × 2 m) in each transect, and soil samples were randomly collected from three points (5 cm diameter × 30 cm depth) in each plot. All soil samples from the same plots were mixed intensively to form the final soil sample. Finally, 24 soil samples (four replicates × six treatments) were obtained. All roots were removed from the soil samples and ground in the laboratory. The soil samples were divided into four subsamples. The first soil subsample was placed in an aluminum box to determine soil moisture. The second was air-dried, passed through a 1 mm sieve, and then used for the measurement of soil pH, salinity, SOC, and SON. The third was passed through a 2 mm sieve and preserved at 4°C, and then used for the determination of WSOC and WSON concentrations. The fourth soil subsample was passed through a 2 mm sieve and stored at – 80°C for use in molecular analyses.

Three quadrats (50 × 50 cm) were constructed at each transect to collect plant samples, including leaves, stems, litter, and roots. Roots were collected in each transect from three blocks of soil (10 cm length × 10 cm width × 30 cm depth), which were sifted through a 15 mm sieve. The aboveground biomass was calculated as the sum of the leaf, stem, and litter biomass and the belowground biomass was represented by the root biomass.

2.3 Soil and plant properties

Soil pH was determined in a 1:2.5 soil:water suspension using a pH meter, and the soil salinity was determined in a 1:5 soil:water suspension using a conductivity meter (Yang et al. 2016). The total inorganic C and N were obtained from 10 g of air-dried soil samples using 1 M HCl. Recalcitrant organic C (ROC) and recalcitrant organic N (RON) were measured using the acid hydrolysis method (Rovira and Vallejo 2002; Yang et al. 2016). The soil SOC, SON, ROC, and RON were determined using an Elementar Vario Micro CHNS analyzer (Elementar Analysensystem GmbH, Langenselbold, Germany). The LOC and LON were calculated using the following equations:

$$\text{LOC} = \text{SOC} - \text{ROC} \quad (1)$$

$$\text{LON} = \text{SON} - \text{RON} \quad (2)$$

The WSOC and WSON were determined following a previously established method (Cabrera and Beare 1993; Yu et al. 1994; Yang et al. 2016). In addition, the leaf, stem, litter, and root biomass were measured after oven-drying at 65°C.

2.4 DNA extraction and Polymerase Chain Reactions (PCR)

Total genomic DNA from samples was extracted using the Omega Bio-Tek E.Z.N.A. Soil DNA Extraction Kit (Omega Bio-Tek, Atlanta, USA) following the manufacturer's protocol. The DNA concentration and purity were monitored using 1% agarose gels. According to the concentration, DNA was diluted to 1 ng/ μ L using sterile water.

The 16S rRNA genes of distinct regions (V3-V4/16S) were amplified using the 338F primer (5'-ACTCCTACGGGAGGCAGCA-3') and 806R primer (5'-GGACTACHVGGGTWTCTAAT-3') (Fierer et al. 2005). All PCR reactions were carried out with 15 μ L of Phusion High-Fidelity PCR Master Mix (New England Biolabs, USA), 0.2 μ M of forward and reverse primers each, and approximately 10 ng template DNA. Thermal cycling consisted of initial denaturation at 98°C for 1 min, followed by 30 cycles of denaturation at 98°C for 10 s, annealing at 50°C for 30 s, and elongation at 72°C for 30 s. Finally, it was held at 72°C for 5 min.

2.5 Quantification and sequencing of PCR products

Equal volume of 1X loading buffer (containing SYBR™ Green) was mixed with PCR products and electrophoresed on 2% agarose gel for detection. The PCR products were mixed at equidensity ratios. Then, the PCR products were purified using the Qiagen Gel Extraction Kit, according to the manufacturer's instructions (Qiagen, Germany).

Sequencing libraries were generated using the TruSeq DNA PCR-Free Sample Preparation Kit (Illumina, San Diego, CA, USA) following the manufacturer's recommendations, and index codes were added. The library quality was assessed on the Qubit 2.0 Fluorometer (Thermo Scientific, CN) and Agilent Bioanalyzer 2100 system (Agilent, Santa Clara, CA, USA). Finally, the library was sequenced on an Illumina NovaSeq platform, and 250 bp paired-end reads were generated.

2.6 Data analysis

Paired-end reads were assigned to soil subsamples based on their unique barcodes and truncated by cutting off the barcode and primer sequences. Paired-end reads were merged using FLASH v.1.2.7 (Center for Computational Biology, Baltimore, MD, USA), when at least some of the reads overlapped the read generated from the opposite end of the same DNA fragment, and the splicing sequences were called raw tags (Magoč and Salzberg 2011). Quality filtering of raw tags was performed under specific filtering conditions to obtain high-quality clean tags according to the QIIME v.1.9.1 quality-controlled process (Caporaso et al. 2010; Bokulich et al. 2013). The tags were compared with the Silva database using the UCHIME algorithm to detect and remove chimera sequences (Edgar et al. 2011; Haas et al. 2011). Subsequently, effective tags were obtained.

Sequence analysis was performed using Uparse software v.7.0.1001 (Edgar 2013). Sequences with $\geq$ 97% similarity were assigned to the same optical transform unit (OTU). A representative sequence of each OTU was screened for further annotation. For each representative sequence, the Silva Database was used based on the Mothur algorithm to annotate taxonomic information (Quast et al. 2013). To study the phylogenetic relationship of different OTUs and the difference in the dominant species in different

samples, multiple sequence alignment was conducted using MUSCLE software v.3.8.31 (Edgar 2004). OTU abundance information was normalized using a standard with sequence number corresponding to the sample with the least sequences. Subsequent analyses of alpha and beta diversity were performed based on the normalized data output.

Indices were calculated with QIIME v.1.9.1 and displayed with R software v.2.15.3 (Caporaso et al. 2010). The Simpson index was used to assess community diversity, and principal coordinate analysis (PCoA) and analysis of similarities (ANOSIM) were performed to detect differences in community structure (beta diversity). Significant differences in the soil bacterial and archaeal communities between USA and ESA, USS and ESS, or UPA and EPA were evaluated by linear discriminant analysis (LDA) effect size (LEfSe) (Segata et al. 2011). Cladograms were made showing the differences in the microbial lineages between USA and ESA, ESS and ESS, or UPA and EPA with LDA values of 4 or higher.

2.7 Statistical analysis

The influence of environmental factors on the bacterial and archaeal community structures at the phylum, class, order, family, genus, and species levels was evaluated with redundancy analyses (RDA) using CANOCO v.5.0 (Wageningen University & Research, Wageningen, Netherlands). The Monte Carlo permutation test (499 permutations) was performed and statistical significance was set at 0.05. Statistical software SPSS 22.0 (IBM Corp, Armonk, New York, USA) was used to analyze the data. The impacts of coastal embankments on the plant biomass, soil physicochemical properties, Simpson index, OTU richness, and relative abundance of dominant bacteria and archaea in USA, ESA, USS, ESS, UPS, and EPS were evaluated using one-way ANOVA (analysis of variance). The relationships between soil bacterial and archaeal diversity and absolute abundance with plant biomass and soil properties were evaluated using Pearson's correlation analysis. In addition, structural equation modeling (SEM) was carried out to determine the direct and indirect effects of coastal embankments on parameters related to the soil bacterial and archaeal absolute abundance following the expectations of the a priori model (Fig. S1); the normality of all endogenous variables and the overall model was tested and verified. The normal-distribution-based maximum likelihood method was used for parameter estimation (Boldea and Magnus 2009). The best-fitting model was selected by sequentially removing non-significant paths ($p < 0.05$). The overall goodness-of-fit for the model was tested using the chi-squared test (χ^2) and the root-mean-square error of approximation (RMSEA; $0 \leq \text{RMSEA} \leq 0.05$) (Schermerle-Engel et al. 2003). The SEM was carried out using Amos 22.0 (IBM Corp, SPSS, New York, USA).

3 Results

3.1 Plant and soil properties

The aboveground, belowground, and total biomass of ESA were 57.511%, 57.901%, and 57.658% lower, respectively, than those of USA, while those of EPA were 59.126%, 175.560%, and 109.143% lower, respectively, than those of UPA (Table 1). Additionally, the belowground biomass was 21.739% lower in

ESS than in USS; however, there were no significant differences in the aboveground and total biomass between the ESS and USS (Table 1).

Table 1

Aboveground, belowground, and total biomass (mean $\pm$ SE, n = 4) in the unembanked and embanked *Spartina alterniflora*, *Suaeda salsa*, and *Phragmites australis* salt marshes. Different superscripted lower-case letters indicate statistical significance at $p < 0.05$ between the unembanked and embanked ranges in the same plant salt marshes.

Biomass (kg·m ⁻²)			
	Aboveground	Belowground	Total
USA	3.921 $\pm$ 0.320 ^a	2.373 $\pm$ 0.379 ^a	6.294 $\pm$ 0.175 ^a
ESA	1.666 $\pm$ 0.144 ^b	0.999 $\pm$ 0.199 ^b	2.665 $\pm$ 0.117 ^b
USS	0.302 $\pm$ 0.022 ^a	0.046 $\pm$ 0.001 ^a	0.348 $\pm$ 0.023 ^a
ESS	0.271 $\pm$ 0.010 ^a	0.036 $\pm$ 0.003 ^b	0.307 $\pm$ 0.012 ^a
UPA	1.304 $\pm$ 0.124 ^a	0.982 $\pm$ 0.224 ^a	2.286 $\pm$ 0.191 ^a
EPA	2.075 $\pm$ 0.315 ^b	2.706 $\pm$ 0.388 ^b	4.781 $\pm$ 0.686 ^b
USA: unembanked <i>S. alterniflora</i> salt marsh; ESA: embanked <i>S. alterniflora</i> salt marsh; USS: unembanked <i>S. salsa</i> salt marsh; ESS: embanked <i>S. salsa</i> salt marsh; UPA: unembanked <i>P. australis</i> salt marsh; EPA: embanked <i>P. australis</i> salt marsh.			

The soil moisture of ESA and ESS were significantly lower than those of USA and USS, while the soil moisture of EPA was significantly higher than that of UPA (Table 2). Additionally, the soil salinity was significantly lower in ESA, ESS, and EPA than in USA, USS, and UPA (Table 2).

Table 2

Soil physicochemical properties (a) and concentrations of soil total, labile, and water-soluble organic C (b), and N (c) (mean $\pm$ SE, n = 4) in the unembanked and embanked *S. alterniflora*, *S. salsa*, and *P. australis* salt marshes. Different superscripted lower-case letters indicate statistical significance at $p < 0.05$ between the unembanked and embanked ranges in the same plant salt marsh.

(a)	Moisture (%)	pH	Salinity (‰)	
USA	52.248 ± 2.876 ^a	8.382 ± 0.032 ^a	12.783 ± 0.455 ^a	
ESA	29.693 ± 1.542 ^b	9.148 ± 0.040 ^b	2.399 ± 0.137 ^b	
USS	27.617 ± 0.665 ^a	8.843 ± 0.034 ^a	5.858 ± 0.406 ^a	
ESS	25.245 ± 0.380 ^b	9.001 ± 0.023 ^b	4.880 ± 0.188 ^b	
UPA	25.545 ± 0.347 ^a	8.830 ± 0.035 ^a	4.164 ± 0.160 ^a	
EPA	33.601 ± 3.360 ^b	9.068 ± 0.057 ^b	1.737 ± 0.033 ^b	
(b)	SOC (g·kg ⁻¹)	LOC (g·kg ⁻¹)	WSOC (g·kg ⁻¹)	
USA	7.343 ± 0.738 ^a	1.418 ± 0.190 ^a	0.175 ± 0.009 ^a	
ESA	2.859 ± 0.405 ^b	0.651 ± 0.156 ^b	0.120 ± 0.006 ^a	
USS	2.520 ± 0.464 ^a	0.835 ± 0.274 ^a	0.075 ± 0.003 ^a	
ESS	1.814 ± 0.117 ^a	0.295 ± 0.060 ^a	0.076 ± 0.003 ^a	
UPA	3.432 ± 0.300 ^a	1.772 ± 0.185 ^a	0.032 ± 0.001 ^a	
EPA	4.938 ± 0.699 ^b	1.969 ± 0.228 ^a	0.043 ± 0.003 ^b	
(c)	SON (g·kg ⁻¹)	LON (g·kg ⁻¹)	WSON (g·kg ⁻¹)	C/N
USA	0.646 ± 0.062 ^a	0.347 ± 0.042 ^a	0.047 ± 0.001 ^a	11.308 ± 0.249 ^a
ESA	0.250 ± 0.036 ^b	0.135 ± 0.028 ^b	0.044 ± 0.001 ^a	11.496 ± 0.239 ^a
USS	0.271 ± 0.048 ^a	0.164 ± 0.038 ^a	0.054 ± 0.001 ^a	9.266 ± 0.200 ^a
ESS	0.206 ± 0.011 ^a	0.084 ± 0.008 ^a	0.053 ± 0.001 ^a	8.787 ± 0.149 ^a
UPA	0.232 ± 0.026 ^a	0.128 ± 0.022 ^a	0.053 ± 0.001 ^a	15.617 ± 1.176 ^a
EPA	0.382 ± 0.071 ^b	0.215 ± 0.058 ^a	0.052 ± 0.001 ^a	14.316 ± 1.022 ^a
USA: unembanked <i>S. alterniflora</i> salt marsh; ESA: embanked <i>S. alterniflora</i> salt marsh; USS: unembanked <i>S. salsa</i> salt marsh; ESS: embanked <i>S. salsa</i> salt marsh; UPA: unembanked <i>P. australis</i> salt marsh; EPA: embanked <i>P. australis</i> salt marsh. SOC, total organic C; LOC, labile organic C; WSOC, water-soluble organic C; SON, total organic N; LON, labile organic N; WSON, water-soluble organic N.				

The SOC, LOC, WSOC, SON, and LON concentrations of ESA were 61.065%, 54.090%, 31.429%, 61.300%, and 61.095% lower, respectively, than those of USA (Table 2). The SOC, WSOC, and SON were 43.881%, 34.375%, and 64.655% higher, respectively, in EPA than in UPA (Table 2). Additionally, there were no significant differences in the concentrations of SOC, LOC, WSOC, SON, LON, and WSON between the ESS and USS (Table 2).

3.2 Alpha diversity of bacterial and archaeal communities

The OTU richness in the EPA was significantly higher than that in the UPA, and the Simpson diversity index in the ESA was significantly lower than that in the USA ($p < 0.05$; Fig. 2). However, the OTU richness and the Simpson diversity index between the USS and ESS both were not significant ($p \geq 0.05$; Fig. 2). Furthermore, the Pearson's correlation analysis of all salt marshes revealed that the variations in Simpson diversity indices were significantly positively correlated with soil moisture, SOC, SON, and LON (Fig. S2).

3.3 Taxonomic composition of soil bacterial and archaeal communities

The USA had an abundance of Deltaproteobacteria (from class to order, within the phylum Proteobacteria) and Epsilonproteobacteria (from class to order, within the phylum Proteobacteria), while the ESA had an abundance of Actinobacteria (from phylum to order), Betaproteobacteria (within the phylum Proteobacteria), and the order Xanthomonadales (from order to family, within the class Gammaproteobacteria, phylum Proteobacteria) (Fig. 3). Moreover, the absolute abundances of the phylum Chlorobi, and classes Ignavibacteria, Chlorobia (within the phylum Chlorobi), and Chloroflexi (within the phylum Chloroflexi) were significantly higher in the ESA than those in the USA ($p < 0.05$), whereas the absolute abundances of the phylum Fusobacteria and the class Rhodothermia (within the phylum Bacteroidetes) were significantly lower in the ESA than in the USA (Fig. 4).

The ESS had a high occurrence of Gammaproteobacteria (from class to family, within the phylum Proteobacteria) and the order Burkholderiales (within the class Betaproteobacteria) (Fig. 3).

The family *Shewanellaceae* (from family to genus, within the order Alteromonadales, class Gammaproteobacteria) was abundant in the UPA, while the Betaproteobacteria (from class to order), the order Pseudomonadales (within the class Gammaproteobacteria), and the family *Chromatiaceae* were abundant in the EPA (Fig. 3). Additionally, the absolute abundance of class 4C0d-2 (within the phylum Cyanobacteria) was significantly lower in the EPA than in the UPA ($p < 0.05$; Fig. 4).

3.4 Beta diversity of soil bacterial and archaeal communities

Bray-Curtis dissimilarity indices indicated the variations in the bacterial and archaeal communities between the USA and ESA and between UPA and EPA were 65.620% ($p = 0.0230$) and 45.830% ($p = 0.0460$), respectively (Fig. 5). However, the variation in the bacterial and archaeal communities between the USS and ESS was not significant ($p \geq 0.05$; Fig. 5).

3.5 Controls on the soil bacterial communities

Ten environmental variables (i.e., soil moisture, pH, salinity, SOC, LOC, WSOC, SON, LON, WSON, and C/N) explained 23.500% and 28.000% of the total changes in the composition of soil bacterial and archaeal communities at the phylum and class levels, respectively (Fig. 6). The results of Monte Carlo permutation tests revealed that the variations at the phylum level were closely related to C/N ($F = 7.00$, $p = 0.002$) and WSON ($F = 3.10$, $p = 0.036$) (Fig. 6a), while those at the class level were closely associated with WSOC ($F = 7.10$, $p = 0.002$), C/N ($F = 3.70$, $p = 0.010$), and SON ($F = 2.60$, $p = 0.042$) (Fig. 6b).

The SEM and Pearson's analysis revealed that the absolute abundances of Deltaproteobacteria and Epsilonproteobacteria were significantly positively correlated with soil moisture (Figs. 7 and S3). Soil salinity had a significant negative correlation with the absolute abundance of Betaproteobacteria and a significantly positive correlation with the absolute abundance of Desulfobacterales (Figs. 7 and S3). The absolute abundances of Alteromonadales and Pseudomonadales were significantly positively correlated with SOC concentrations; the absolute abundance of Actinobacteria was significantly negatively correlated with SOC and WSON (Fig. 7 and S3). The absolute abundance of Bacteroidetes was significantly positively correlated with the soil LOC, SON, and C/N (Figs. 7 and S3). A significant negative correlation was found between the absolute abundances of Chlorobi, Ignavibacteria, Chloroflexi, and *Chromatiaceae* and aboveground biomass (Fig. S3).

4 Discussion

Our results showed that coastal embankments caused different responses to soil microbial diversity and community compositions in invasive *S. alterniflora*, as well as native *S. salsa* and *P. australis* salt marshes in the coastal wetlands of eastern China (Fig. 2). The establishment of coastal embankments significantly decreased the Simpson diversity index in the *S. alterniflora* salt marsh, while increasing the OTU richness in the *P. australis* salt marsh (Fig. 2). Interestingly, coastal embankments only slightly changed the microbial diversity and richness in the 0–30 cm soil layer of the *S. salsa* salt marsh ($p \geq 0.05$; Fig. 2). Soil nutrient substrates (e.g., SOC and SON) provide media for the growth of microbes and, as such, are critical drivers of soil bacterial and archaeal diversity and richness (Yu et al. 2019; Gao et al. 2020; Novoa et al. 2020; Yang et al. 2020). In this study, the soil bacterial and archaeal diversity were highly positively correlated with SOC, SON, and LON in soil (Fig. S2). The accumulation of nutrients in the soil is primarily determined by the quantity and quality of plant residue input into the soil (Fig. S2; Chantigny 2003; Belay-Tedla et al. 2008; Yang et al. 2016). As the establishment of coastal embankments can limit the growth of *S. alterniflora* by blocking seawater (Table 1; Fig. S2; Fierer and Jackson, 2006; Zhong et al. 2011; Zhao et al. 2020), the decreased plant biomass led to lower SOC, SON, and LON in the soil of the embanked *S. alterniflora* salt marsh, which ultimately decreased the diversity of the soil bacteria and archaea (Tables 1 and 2; Fig. S2; Yang et al. 2016; Yu et al. 2019). Conversely, the increased biomass of *P. australis* led to the increase of SOC and SON in the embanked *P. australis* salt marsh, which presumptively increased the OTU richness (Tables 1 and 2; Yang et al. 2020). In particular, coastal embankments had insignificant effects on SOC, LOC, WSOC, SON, LON, and WSON in the *S. salsa* salt

marsh, which explains the negligible impact of these structures on bacterial and archaeal diversity and richness in the *S. salsa* salt marsh (Fig. 2 and S2; Table 2). Soil moisture is a vital driver of soil bacterial and archaeal diversity (Guo and Zhou 2020; Yang et al. 2020; Sun et al. 2021). Previous studies have reported that the higher soil water availability in coastal zones is advantageous for the diversity of soil bacteria and archaea of these areas, which is consistent with the results of this study (Table S2; Gao et al. 2020; Novoa et al. 2020). The embankments stop seawater from reaching coastal wetlands, which decreased soil moisture in the *S. alterniflora* salt marsh, contributing to the lower diversity (Table 2). However, the probable presence of aquifers in embanked soil and rains can decrease the impact of embankments (Guo and Jiao 2007; Yang et al. 2016; Ma et al. 2019). In this study, the soil moisture increased in the embanked *P. australis* salt marsh, which might explain its higher OTU richness (Figs. 2 and S2; Table 2). In summary, our results indicated that the establishment of coastal embankments influenced the bacterial and archaeal diversity and richness in *S. alterniflora* and *P. australis* communities by shifting soil nutrient substrates and altering soil moisture (Tables 1 and 2; Fig. S2).

The establishment of coastal embankments drastically modified the composition of soil bacterial and archaeal communities in *S. alterniflora* and *P. australis* salt marshes (Fig. 5). PCoA and Bray-Curtis dissimilarity indices revealed that the soil bacterial and archaeal community compositions in the embanked *S. alterniflora* and *P. australis* salt marshes were clustered and distinct from those in unembanked *S. alterniflora* and *P. australis* salt marshes, respectively (Fig. 5). However, the variation in the soil bacterial and archaeal community compositions between the embanked and unembanked *S. salsa* communities was insignificant (Fig. 5). Additionally, SON, which represents available nutrients, vitally influenced the composition of the bacterial and archaeal communities among different plant communities (Figs. 6 and S4; Bates et al. 2011; Yang et al. 2020; Rasmussen et al. 2021). Thus, in this study, the decrease in SON in the *S. alterniflora* salt marsh following the establishment of coastal embankments caused differentiation of the bacterial and archaeal communities between the unembanked and embanked *S. alterniflora* salt marshes (Figs. 5, 6, and S4; Table 2). Additionally, the WSOC, which is the immediate energy source for bacteria and archaea, was the most direct driver of soil bacterial and archaeal community composition among different plant communities in the coastal wetlands, because the variations in soil bacterial and archaeal communities were intimately related to the WSOC at the class, order, family, and genus levels (Figs. 6 and S4; Orwin et al. 2016; Santonja et al. 2017; Yang et al. 2020). In this study, the higher concentrations of WSOC and SON in the embanked *P. australis* salt marsh influenced the differentiation of the bacterial and archaeal communities in the embanked and unembanked *P. australis* salt marshes (Figs. 5, 6, and S4; Table 2). Furthermore, the insignificant difference in soil nutrient substrates explained the inconspicuous differentiation of bacterial and archaeal communities between the unembanked and embanked *S. salsa* salt marshes (Figs. 5, 6, and S4; Table 2). Therefore, our results confirmed that the establishment of coastal embankments influences the soil bacterial and archaeal community composition by primarily altering the concentrations of nutrient substrates (Table 2; Liao et al. 2007; Yang et al. 2016).

In this study, the establishment of coastal embankments had a negligible effect on the archaeal relative abundance at the phylum, class, order, family, genus, and species levels (Table S1). As archaea are

extremophilic microorganisms, few environmental factors can have dramatic effects on their growth, which might explain these results (Bates et al. 2011; Ventosa and Haba 2011).

Some bacterial groups were directly affected by the absence of seawater owing to the coastal embankments. For instance, some classes within Proteobacteria, the most abundant phylum in the sediment along the coast of the Yellow Sea, were strongly impacted (Figs. 3, 4, 7, and S3; Lee et al. 2020; Yang et al. 2020). In this study, the growth of Betaproteobacteria, a dominant class within Proteobacteria, was stimulated in embanked *S. alterniflora* and *P. australis* salt marshes (Figs. 2, 3, and 4; Tables 1 and 2). Additionally, the absolute abundance of Burkholderiales, a dominant order within Betaproteobacteria, increased in embanked *S. salsa* and *P. australis* salt marshes (Figs. 2, 3, and 4; Tables 1 and 2). Baña et al. (2020) reported that members of Betaproteobacteria are rarely found in seawater. Indeed, in this study, the absolute abundance of Betaproteobacteria was negatively correlated with soil salinity (Figs. 7 and S3). Therefore, we speculate that coastal embankments significantly reduced the soil salinity by blocking seawater, which ultimately promoted the growth of members within Betaproteobacteria (Figs. 2, 3, and 4; Tables 1 and 2). Conversely, in this study, the growth of Deltaproteobacteria, also a dominant class within Proteobacteria, was limited in the embanked *S. alterniflora* salt marsh, especially the order Desulfobacterales (Figs. 3, 4, 7, and S3). Many members of Deltaproteobacteria are sulfate-reducing bacteria that usually use sulfate as an electron acceptor (Kuever et al. 2005), and seawater is an important source of sulfate in coastal wetlands (Figs. 7 and S3; Wang et al. 2019a; Zhou et al. 2009; Xia et al. 2015). *S. alterniflora* is highly capable of accumulating sulfate from seawater, which leads to high sulfur concentrations in the soil through biomass decomposition (Madureira et al. 1997; Otero et al. 2002; Zhou et al. 2009; Xia et al. 2015). Thus, Deltaproteobacteria are common in *S. alterniflora* salt marshes (Kuever et al. 2005; Wang et al. 2012; Yang et al. 2020). However, in this study, the coastal embankments limited the sulfate input from seawater into the coastal wetlands, which ultimately restricted the growth of Deltaproteobacteria in the embanked *S. alterniflora* salt marsh (Figs. 3, 4, 7, and S3). Similarly, Epsilonproteobacteria are also involved in sulfur cycling in the coastal wetlands (Zhou et al. 2009; Wang et al. 2012; Yang et al. 2020). In this study, the growth of Epsilonproteobacteria was also restricted in the embanked *S. alterniflora* salt marsh by the lower the sulfate input (Figs. 3, 4, 7, and S3; Zhou et al. 2009; Wang et al. 2019a; Yang et al. 2020). Moreover, most strains in the order Alteromonadales are aerobic, and coastal embankments could provide an aerobic environment favorable for their growth by decreasing the soil moisture in *S. salsa* saltmarsh (Table 2; Bowman and McMeekin 2005; Yang et al. 2020). This explains the higher absolute abundance of Alteromonadales in the embanked *S. salsa* salt marsh (Fig. 3). *Shewanella*, the most abundant genus in coastal wetlands, grows optimally in seawater media, as it requires sodium ions to grow (Bowman, 2005; Bowman and McMeekin, 2005). In the *P. australis* salt marsh, coastal embankments significantly decreased the soil salinity, which ultimately limited the growth of *Shewanella* (Fig. 3; Table 2). Therefore, the establishment of coastal embankments strongly influenced the growth of some bacterial strains by stopping seawater from reaching the plant communities and consequently changing the soil physicochemical properties.

The growth of some chemoorganotrophic bacteria, especially oligotrophic and copiotrophic bacteria, was influenced by the establishment of coastal embankments. Actinobacteria is a type of the oligotrophic

bacteria whose growth is restricted in a nutrient-rich soil environment (Pascault et al. 2013; Trivedi et al. 2013; Verzeaux et al. 2016; Yang et al. 2020). Decreased *S. alterniflora* biomass in the soil of the embanked salt marsh significantly reduced the availability of nutrients (e.g., SOC and WSON), which was beneficial for the growth of Actinobacteria, reducing its abundance in the embanked *S. alterniflora* sediment (Figs. 3 and S3; Tables 1 and 2). Conversely, Bacteroidetes, the second most abundant bacterial phylum in tidal mudflats and near-shore sediments, is copiotrophic and the accumulation of SON and LOC could enhance its growth (Figs. 7 & S3; Kim and Kwon 2010). Generally, members of Bacteroidetes are degraders of high-molecular-weight organic matter (Kirchman 2002; Kim and Kwon 2010), and prefer to grow in low-quality media (e.g., those with high C/N), which is consistent with the observations of this study (Figs. 7 and S3; Thomas et al. 2011; Forss et al. 2013; Yang et al. 2020). As such, the abundance of *S. alterniflora* residues could enhance the growth of Bacteroidetes, as these have lignin and lignocellulosic materials and are, therefore, of low quality (Ji et al. 2011; Yang et al. 2020). However, in this study, the concentrations of SON and LOC were lower in the embanked *S. alterniflora* salt marsh, which supplied less high-molecular-weight organic matter, and limited the growth of Rhodothermi, which is a dominant order within Bacteroidetes (Fig. 4; Table 2). Thus, our results suggest that the establishments of coastal embankments modified distribution of chemoorganotrophic bacteria by altering the concentrations of organic nutrients in the soil (e.g., SOC, SON, LOC, and WSON).

Photosynthetic bacteria are widely distributed in coastal sediments (Okubo et al. 2006; Idi et al. 2014). In this study, the amount of obligately phototrophic bacteria from Chlorobi and the class Chloroflexi (Garrrity et al. 2005; Hanada 2014) was significantly higher in the embanked *S. alterniflora* salt marsh (Fig. 4). The light-limiting effect of the dense vegetation of *S. alterniflora* directly restricts the growth of PSB (He et al. 2012; Li et al. 2014a; Brotosudarmo et al. 2015). Indeed, the absolute abundances of Chlorobi and the class Chloroflexi were significantly negatively correlated with the aboveground biomass of plants (Fig. S3). Thus, the higher occurrence of Chlorobi and the class Chloroflexi might have been caused by the increase in sunlight due to the lower aboveground biomass of plants in the embanked *S. alterniflora* salt marsh (Figs. 4 and S3; Table 1; Wang et al. 2012). In contrast, the dark environment provided by the increased aboveground biomass of plants might explain the lower absolute abundance of 4C0d-2, which are also obligately phototrophic bacteria, in the embanked *P. australis* salt marsh (Fig. 4; Table 1). Chromatiaceae, also known as phototrophic purple sulfur bacteria, are able to grow by photolithoautotrophic metabolism (Imhoff 2005). In this study, the growth of Chromatiaceae was negatively correlated with the aboveground biomass of plants (Fig. S3). Thus, the decrease in the aboveground biomass of *S. salsa* in the embanked salt marsh explained the increased occurrence of Chromatiaceae in this environment (Table 1; Fig. S3). However, Chromatiaceae is also capable of chemoorganoheterotrophic growth under dark eutrophic and anoxic conditions (Imhoff 2005). In the embanked *P. australis* salt marsh, the increased soil moisture and aboveground biomass created an anoxic and dark environment (Tables 1 and 2) which, together with an increased SOC and SON, stimulated the growth of Chromatiaceae (Table 2). Generally, the establishment of coastal embankments affects the growth of PSB by primarily altering the aboveground biomass of plants.

A wide variety of pathogenic bacteria target plant and animal species; in this study, the presence of coastal embankments stimulated the growth of some pathogenic bacteria (Fig. 3; Dengl and Jones 2001; Glazebrook 2005). Xanthomonadales includes several plant pathogens, especially those belonging to the family *Xanthomonadaceae* (Bayer-Santos et al. 2019). Xanthomonadales are aerobic and, in this study, their absolute abundance was significantly negatively correlated with soil salinity (Fig. 3; Bayer-Santos et al. 2019). Therefore, the decreased soil moisture and salinity of the embanked *S. alterniflora* salt marsh created aerobic and low salinity conditions that ultimately promoted the growth of Xanthomonadales, especially that of *Xanthomonadaceae* (Fig. 3; Table 2; Bayer-Santos et al. 2019). Pseudomonadales is composed of chemoorganotrophic and pathogenic species that affect humans, animals, and plants (Palleroni 2005; Peix et al. 2009). In this study, the absolute abundance of Pseudomonadales was positively correlated with SOC concentration (Figs. 3 and 7; Palleroni 2005; Peix et al. 2009). The increased growth of Pseudomonadales in the embanked *P. australis* salt marsh might be explained by the significant increase in SOC in this environment (Table 2). Therefore, changes in many environmental factors, including the soil nutrient substrates, soil moisture, and salinity following the establishment of coastal embankments might significantly alter the growth of pathogenic bacteria (Figs. 7 and S3; Hutchison et al. 2004; Goberna et al. 2011; Monaghan and Hutchison 2012; Rahube et al. 2014; Shaharoon et al. 2019). Currently, coastal embankments are still being constructed worldwide (Ma et al. 2014). However, potential opportunities and/or threats to soil microbial communities affected by coastal embankments are still poorly understood. This study provides evidence that coastal embankments can significantly modify soil bacterial communities (i.e., diversity and community composition) (Figs. 2, 3, 4, and 5). These changes were due to the significant alteration of soil nutrient substrates quantities (e.g., SOC, SON, and C/N), as well as the dramatic decrease in soil salinity and the change in soil moisture due to lack of seawater in regions with coastal embankments in coastal China (Figs. 6, 7, and S3; Table 2).

5 Conclusion

The purpose of this study was to investigate the variations in soil bacterial and archaeal communities following the establishment of coastal embankments, and to identify their driving factors in coastal China. Coastal embankments significantly decreased the bacterial diversity in the *S. alterniflora* salt marsh, while increasing their OTU richness in the *P. australis* salt marsh. Additionally, we found that the embankments modified the soil bacterial and archaeal community compositions in the *S. alterniflora* and *P. australis* salt marshes. However, the variations in the soil bacterial and archaeal diversity, richness, and community compositions between the embanked and unembanked *S. salsa* salt marshes were insignificant. These results were probably due to the drastic changes in the concentrations of nutrient substrates in the embanked *S. alterniflora* and *P. australis* salt marshes, which were not noted in the *S. salsa* salt marshes.

The coastal embankments had an insignificant effect on the soil archaea, presumably because archaea have a strong tolerance to physically or geochemically extreme conditions. In bacteria, an increased abundance of Betaproteobacteria, which is rare in coastal environments, and a decreased abundance of sulfur- and sodium-dependent bacteria (e.g., Deltaproteobacteria, Epsilonproteobacteria, and *Shewanella*)

were observed in the embanked *S. alterniflora* and *P. australis* salt marshes. The growth of Betaproteobacteria was promoted, while that of Deltaproteobacteria, Epsilonproteobacteria, and *Shewanella* were limited in embanked environments because the soil physicochemical properties (e.g., soil moisture and salinity) were altered by the lack of seawater in the salt marshes. The coastal embankments reduced plant biomass and the concentrations of SOC, LOC, SON, and LON in the *S. alterniflora* salt marsh, which ultimately decreased the absolute abundance of oligotrophic Rhodothermia (within Bacteroidetes) and increased that of copiotrophic Actinobacteria; the increased plant biomass and concentrations of SOC and SON caused by the coastal embankments stimulated the growth of Pseudomonadales in the embanked *P. australis* salt marsh. An increase in the absolute abundance of PSB (e.g., Chlorobi and Chloroflexi) was observed in the embanked *S. alterniflora* salt marsh, which was attributed to the increase in sunlight due to the decrease of the aboveground biomass of plants. Moreover, the embankments presumably stimulated the growth of some pathogenic bacteria (e.g., Xanthomonadales and Pseudomonadales) in the *S. alterniflora* and *P. australis* salt marshes by modifying the soil physicochemical properties or concentration of nutrient substrates. As the study area is the most important habitat of the endangered Red-crowned Crane, the increased abundance of pathogenic bacteria might damage the local coastal ecosystem.

In summary, this study clarified the effects of coastal embankments on the biogeochemical cycles and highlighted their potential hazards to ecosystems.

Abbreviations

ANOVA, analysis of variance; ANOSIM, analysis of similarities; C, Carbon; C/N, Carbon Nitrogen ratio; DNA, Deoxyribonucleic acid; EPA, Embanked *Phragmites australis* (Cav.) Trin. ex Steud.; ESA, Embanked *Spartina alternifolia* Loisel.; ESS, Embanked *Suaeda salsa* (Linn.) Pall.; LDA, Linear discriminant analysis; LEfSe, Linear discriminant analysis effect size; LOC, Labile organic carbon; LON, Labile organic nitrogen; N, Nitrogen; NMDS, Nonmetric multidimensional scaling; OTUs, Operational taxonomic units; PCoA, Principal coordinates analysis; PSB, Photosynthetic bacteria; QIIME, Quantitative insights into microbial ecology; qPCR, Quantitative polymerase chain reaction; RDA, Redundancy analysis; RMSEA, Root-mean-square error of approximation; RNA, Ribonucleic acid; ROC, Recalcitrant organic carbon; RON, Recalcitrant organic nitrogen; SEM, Structural equation modelling; Simpson, Simpson's diversity index; SOC, Soil organic carbon; SON, Soil organic nitrogen; UPA, Unembanked *Phragmites australis* (Cav.) Trin. ex Steud.; USA, Unembanked *Spartina alternifolia* Loisel.; USS, Unembanked *Suaeda salsa* (Linn.) Pall.; WSOC, Water-soluble organic carbon; WSON, Water-soluble organic nitrogen.

Declarations

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Figures

Figure 1

Location of the sampling site in Yancheng, Jiangsu, China. USA: unembanked *Spartina alterniflora* salt marsh; ESA: embanked *S. alterniflora* salt marsh; USS: unembanked *Suaeda salsa* salt marsh; ESS: embanked *S. salsa* salt marsh; UPA: unembanked *Phragmites australis* salt marsh; EPA: embanked *P. australis* salt marsh.

Figure 2

The OTU richness (a) and the Simpson diversity (b) in the unembanked and embanked *Spartina alterniflora*, *Suaeda salsa*, and *Phragmites australis* salt marshes (0 – 30 cm soil depth). SA: *S. alterniflora*; SS: *S. salsa*; PA: *P. australis*; USA = unembanked SA salt marsh; ESA = embanked SA salt marsh; USS = unembanked SS salt marsh; ESS = embanked SS salt marsh; UPA = unembanked PA salt marsh; EPA = embanked PA salt marsh.

Figure 3

Indicator bacterial and archaeal groups between the unembanked and embanked (a) *Spartina alterniflora*, (b) *Suaeda salsa*, and (c) *Phragmites australis* salt marshes with LDA > 4.

Figure 4

The absolute abundance of dominant bacteria in the unembanked and embanked *Spartina alterniflora*, *Suaeda salsa*, and *Phragmites australis* salt marshes. Different superscripted lower-case letters indicate $p < 0.05$ between the unembanked and embanked ranges in the same plant community.

Figure 5

Principal coordinates analysis (PCoA) (a), and nonmetric multidimensional scaling (NMDS) plot of bacterial Bray-Curtis dissimilarity between the unembanked and embanked SA (b), SS (c), and PA(d) salt marshes. Red stars represent USA, orange squares represent ESA, green diamonds represent USS, yellow triangles represent ESS, blue circles represent UPA, and purple rectangles represent EPA.

Figure 6

Redundancy analysis (RDA) diagram illustrating the relationship between the compositions of soil bacterial and archaeal salt marshes at the phylum (a) and class (b) level from different sampling sites under variable environments. Solid black arrows show soil bacterial and archaeal community composition; colored arrows show soil moisture, pH, salinity, total organic carbon (SOC), labile organic C (LOC), water-soluble organic C (WSOC), total organic nitrogen (SON), labile organic N (LON), water-soluble organic nitrogen (WSON), and carbon-nitrogen ratio (C/N).

Figure 7

Structural equation modeling (SEM) examining the effects of soil and plant properties on soil dominant bacteria. Continuous and dashed arrows indicate positive and negative relationships, respectively. Numbers adjacent to arrows are the effect size of the relationships (* < 0.05 , ** < 0.01 , *** < 0.001).

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