Plant Growth Modifications Due to Coastal Embankments Affect Soil Bacterial and Archaeal Communities Over the Growing Season in Salt Marshes of Eastern China

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Research Article

Keywords: Bacterial and archaeal diversity, ecosystem N cycles, high-throughput sequencing, soil bacterial and archaeal community composition, 16S rRNA gene.

Posted Date: January 3rd, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1204887/v1

Abstract

Aims: Although the influences of coastal embankments on physicochemical soil properties and carbon (C) and nitrogen (N) cycling have been widely studied, the mechanisms of their effects on soil microbial ecologies remain poorly understood. Thus, the aim of this study was to investigate variations in the diversity and composition of 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 native *Suaeda salsa*, *Phragmites australis*, and invasive *Spartina alterniflora* saltmarshes on the east coast of China.

Results: Embankments were found to significantly decrease the microbial diversity of the *S. alterniflora* salt marsh, while they increased the OTU richness of the *P. australis* salt marsh. Embankments modified the compositions of soil bacterial and archaeal communities in both the *S. alterniflora* and *P. australis* salt marshes. However, variations in the microbial diversity, richness, and community compositions between the native and embanked *S. salsa* salt marshes were insignificant.

Conclusions: These results were possibly because the embankment significantly altered soil nutrient substrate levels (e.g., soil organic C and N) by variations in plant residues and physiochemical soil properties in *S. alterniflora* and *P. australis* saltmarshes, whereas the embankment had no observable changes in the soil nutrient substrate and the plant residue in *S. salsa* saltmarsh. This study also elucidated the effects of coastal embankments on biogeochemical cycles, and highlighted their potential hazards to ecosystems.

1 Introduction

The reclamation coastal land through the establishment of embankments has caused considerable ecological problems in natural coastal ecosystems. For instance, they have greatly threatened coastal habitats and biodiversity (particularly 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 comprise the most abundant and diverse group of soil microbes, with archaea also being relatively abundant (Buckley and Schmidt 2002; Fierer et al. 2007a). Both play a crucial role in the transformation of soil nutrients and in 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 impacts 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 elucidated.

Soil nutrient substrates are one of the primary driving factors for bacterial and archaeal diversity and community compositions (Peralta et al. 2013; Kuang et al. 2021; Sun et al. 2021). In particular, the decomposition of soil organic C and N (SOC and SON, respectively) provide energy and nutrition for soil microorganisms; thus, they are overarching driving factors for the presence and support of soil bacteria and archaea (Zechmeister-Boltenstern et al. 2015; Yang et al. 2020). However, various bacterial and archaeal taxa respond differently to the availability of nutrients. 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. 2007a; Newton and McMahon 2011; Philippot et al. 2013).

In contrast, because LOC and LON inputs have negative effects on oligotrophic bacteria (e.g., Acidobacterium and some species of Actinobacteria) and can limit their growth, 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 ratios) has been reported to increase the abundance of archaea (e.g., phylum Crenarchaeota) (Bates et al. 2011; Cotrufo et al. 2019). Coastal embankments can increase, decrease, or have negligible effects on the availability of soil C and N by modifying the inputs of plant residues into the soil in diverse coastal wetlands (Laudicina et al. 2009; Cui et al. 2012; Wang et al. 2014).

Consequently, the responses of soil bacterial and archaeal communities to coastal embankments may differ contingent on the shifts of nutrient substrates.

Soil microbial communities are considerably influenced by biotic (e.g., the quantity and quality of plant materials) (Angel et al. 2010; Cotrufo et al. 2019) and abiotic (e.g., climate, soil type, and soil physicochemical properties) factors (Bainard et al. 2016; Nguyen et al. 2018). Plant properties, including residues (e.g., litter and roots) and aboveground (e.g., leaves, stems and litter) biomass, strongly affect soil bacteria and archaea (Brotosudarmo et al. 2015; Li et al. 2014a; Urbanová et al. 2015). The former dictates the availability of soil C and N, in addition to providing unique environments for soil bacteria and archaea (Kuske et al. 2002; Urbanová et al. 2015), whereas the latter influences the presence of photosynthetic bacteria (PSB) by affecting the extent of light that reaches the soil surface (He et al. 2012; Li et al. 2014b; Brotosudarmo 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 higher soil pH (Högberg et al. 2007; Peralta et al. 2013; Sun et al. 2021). Similarly, soil salinity restricts the presence of bacteria and archaea by limiting the availability of water (Rath and Rousk 2015; Zhang et al. 2021). Furthermore, soil moisture is a vital driver of soil bacterial community composition, particularly the proportion of aerobic and anaerobic bacteria, as 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 the coastal embankments impact bacterial and archaeal communities in soils.

China has been increasing the intensive construction of coastal embankments, with approximately 60% of the total length of its mainland coastline being enclosed by thousands of kilometers of these levees (Ma et al. 2014; Sun et al. 2015). Jiangsu province has the highest abundance of coastal wetlands and embankments in Eastern China (Chung et al. 2004). Currently, a large proportion 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 unban lands (Liu 2018).

The results of previous studies with a focus on the impacts of the conversion of coastal wetlands to other land-use types on soil microbial communities have been inconsistent (Xu et al. 2017; Li et al. 2019; Yang et al. 2019). For instance, they have documented both increases and decreases in bacterial abundance and diversity in the soil (especially the abundance of Proteobacteria) due to the conversion of coastal wetlands to 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 histories, intensities, 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, agricultural, and urban land) on soil microbial communities (Bai et al. 2013; Bu et al. 2015). Therefore, the impacts of coastal embankments without associated land-use changes on the diversity and compositions of soil microbial communities remain unknown. Moreover, our previous studies revealed that there were diverse responses to coastal embankments by soil C and N pools for distinct vegetation types, as they have variable effects on residue biomasses of specific plants (Feng et al. 2022).

Thus, we hypothesized that there would be different responses from microbial communities for diverse vegetation types (e.g., microbial community diversity and compositions) to coastal embankments, which was due to variations in the quantity and quality of soil nutrients. Further, we hypothesized that variations in soil physicochemical properties following the establishment of embankments would affect the diversity and compositions of microbial communities. To verify our hypothesis, we compared the diversity and compositions of soil bacterial and archaeal communities by extracting and sequencing their 16S RNA genes in embanked and adjacent unembanked *Spartina alterniflora* Loisel., *Suaeda salsa* (L.) Pall., and *Phragmites australis* (Cav.) Trin. ex Steud. salt marshes along the Jiangsu coastline.

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)) were measured. The aim of this study was to: (1) understand whether the establishment of coastal embankments without land-use changes influenced the diversity and compositions of bacterial and archaeal communities for various vegetation types, and if so, (2) identify the factors that drive these variations.

2 Methods

2.1 Study sites

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

The coastal wetlands of Yancheng are one of the important stops on the migration route of shorebirds between East Asia and Australia. This is also the largest wintering area of endangered Red-crowned Cranes (*Grus japonensis*) (Liu et al. 2010; Wang et al. 2019b). However, since its introduction, *S. alterniflora* has been outcompeting native plants for resources such as space; therefore, several embankments have been constructed to control its expansion (Wang and Liu 2005; An et al. 2007; Qin and Li 2012; Wang et al. 2019a, b). These coastal embankments were covered with a waterproof material, and the land-use of the embanked region did not change at the study sites.

2.2 Field sampling

In September 2016, four parallel transects (40 × 40 m) were established 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 (Ø 5 cm × 30 cm deep) in each plot. All the soil samples from the same transects of the same salt marsh were homogeneously mixed. Finally, 24 soil samples (four replicates × six treatments) were obtained. All visible plant litter, stones, and roots were removed to form the final soil samples, which were divided into four subsamples after thorough mixing.

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, 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 the analyses of the diversity and compositions of soil bacterial and archaeal communities.

Three quadrats (50 × 50 cm) were established at each transect to collect the 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 leaves, stems, and litter biomass, whereas the belowground biomass was represented by the root biomass.

2.3 Soil and plant properties

The soil pH was determined in a 1:2.5 soil:water suspension using a pH meter, whereas the soil salinity was measured in a 1:5 soil:water suspension with 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. The recalcitrant organic C (ROC) and recalcitrant organic N (RON) were quantified 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:

LOC = SOC – ROC (1)

LON = SON – RON (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)

The total genomic DNA of the 50 mg soil 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, the DNA was diluted to 1 ng/μL 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 conducted with 15 μL of the Phusion High-Fidelity PCR Master Mix (New England Biolabs, USA), 0.2 μM each of forward and reverse primers, and ~10 ng of 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 volumes of 1X loading buffer (containing SYBR^{TM} Green) were mixed with the PCR products and electrophoresed on a 2% agarose gel for detection. The PCR products were mixed at equidensity ratios. Subsequently, 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 a Qubit 2.0 Fluorometer (Thermo Scientific, CN) and Agilent Bioanalyzer 2100 system (Agilent, Santa Clara, CA, USA). Finally, the library was sequenced using an Illumina NovaSeq platform, and 250 bp paired-end reads were generated.

2.6 Data analysis

Paired-end reads were assigned to the 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; the splicing sequences were designated as raw tags (Magoč and Salzberg 2011). The 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 ≥ 97% similarity were assigned to the same optical transform unit (OTU). Representative sequences of each OTU were screened for further annotation. For each representative sequence, the Silva Database was used based on the Mothur algorithm to annotate the taxonomic data (Quast et al. 2013). To study the phylogenetic relationships of different OTUs and the variations in the dominant species of different samples, multiple sequence alignment was conducted using MUSCLE software v.3.8.31 (Edgar 2004). The OTU abundance data was normalized using a standard with sequence numbers that corresponded to the sample with the least number of sequences. The ensuing 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 via R software v.2.15.3 (Caporaso et al. 2010). The Simpson index was employed to assess community diversity, and principal coordinate analysis (PCoA) and analysis of similarities (ANOSIM) were performed to detect differences in community structures (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) and effect size (LEfSe) (Segata et al. 2011). Cladograms were created 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 influences of environmental factors (e.g., soil moisture, salinity, pH, LOC, ROC, WSOC, LON, RON, WSON, and C/N) on the bacterial and archaeal community structures at the phylum, class, order, family, genus, and species levels were evaluated using redundancy analyses (RDA) via CANOCO v.5.0 (Wageningen University & Research, Wageningen, Netherlands). The Monte Carlo permutation test (499 permutations) was performed, and the 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, physicochemical soil 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 the diversity and abundance of soil bacteria and archaea and the plant biomass and soil properties were evaluated using Pearson's correlation analysis. Furthermore, structural equation modeling (SEM) was performed to determine the direct and indirect effects of coastal embankments on parameters related to soil bacterial and archaeal 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 the sequential removal of 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; $0 \leq \text{RMSEA} \leq 0.05$) (Schermelleh-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 litter, root, aboveground, residue, and total biomass of ESA were 70.642%, 57.901%, 57.773%, 61.001%, and 57.822% respectively, which were significantly lower than those of USA (Tables 1 and S1). However, the root, residue, and total biomass of EPA were 175.490%, 143.828%, and 104.229%, respectively, which was higher than those of UPA (Table 1). Of note is that there was a negligible difference between the residue and total biomass of the unembanked and embanked *S. salsa* salt marshes (Table 1).

Table 1

Leaf, stem, litter, root, aboveground, and total biomass (mean ± 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/m²)						
	Leaf	Stem	Litter	Aboveground	Root	Residues	Total
USA	1.106±0.112	1.903±0.228	0.763±0.064	3.771±0.317	2.373±0.379	3.136±0.417	6.144±0.176
ESA	0.520±0.053	0.848±0.057	0.224±0.047	1.593±0.148	0.999±0.199	1.223±0.175	2.592±0.123
USS	0.031±0.008	0.199±0.010	0.040±0.005	0.270±0.018	0.046±0.001	0.086±0.005	0.316±0.019
ESS	0.033±0.002	0.144±0.009	0.062±0.005	0.239±0.009	0.036±0.003	0.098±0.006	0.275±0.011
UPA	0.179±0.028	0.943±0.093	0.154±0.026	1.276±0.120	0.982±0.224	1.136±0.212	2.258±0.184
EPA	0.209±0.066	1.632±0.237	0.065±0.006	1.906±0.285	2.706±0.388	2.771±0.391	4.612±0.660

USA: unembanked *S. alterniflora* salt marsh; ESA: embanked *S. alterniflora* salt marsh; USS: unembanked *S. salsa* salt marsh; ESS: embanked *S. salsa* salt marsh; UPA: unembanked *P. australis* salt marsh; EPA: embanked *P. australis* salt marsh.

Following the establishment of the embankments, the soil moisture decreased significantly in the *S. alterniflora* and *S. salsa* salt marshes, whereas it increased dramatically in the *P. australis* salt marsh. Moreover, the embankments significantly increased the soil pH, and reduced soil salinity in all vegetation salt marshes (Table 2). The SOC, LOC, WSOC, ROC, SON, LON, and RON concentrations of ESA were 61.043%, 54.014%, 31.250%, 62.728%, 61.085%, 61.383%, 59.306%, respectively, which was lower than those of USA (Table 2).

Table 2
Soil physicochemical properties (a) and concentrations of soil total, labile, water-soluble, and recalcitrant organic C (b), and N (c) (mean ± 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 (‰)	C/N	SOC (g·kg^{-1})	LOC (g·kg^{-1})
USA	52.248±2.876^{a}	8.382±0.032^{a}	12.783±0.455^{a}	11.309±0.249^{a}	7.344±0.738^{a}	1.420±0.190^{a}
ESA	29.693±1.542^{b}	9.148±0.040^{b}	2.399±0.137^{b}	11.499±0.239^{a}	2.861±0.405^{b}	0.653±0.156^{b}
USS	27.617±0.665^{a}	8.843±0.034^{a}	5.858±0.406^{a}	9.2669±0.200^{a}	2.520±0.464^{a}	0.835±0.274^{a}
ESS	25.245±0.380^{b}	9.001±0.023^{b}	4.880±0.188^{b}	8.7879±0.149^{a}	1.814±0.117^{a}	0.295±0.060^{a}
UPA	25.545±0.347^{a}	8.830±0.035^{a}	4.164±0.160^{a}	15.619±1.176^{a}	3.433±0.300^{a}	1.772±0.185^{a}
EPA	33.601±3.360^{b}	9.068±0.057^{b}	1.737±0.033^{b}	14.319±1.022^{a}	4.938±0.698^{a}	1.968±0.228^{a}
(b)	WSOC (g·kg^{-1})	ROC (g·kg^{-1})	SON (g·kg^{-1})	LON (g·kg^{-1})	WSON (g·kg^{-1})	RON (g·kg^{-1})
USA	0.176±0.009^{a}	5.924±0.575^{a}	0.645±0.062^{a}	0.347±0.042^{a}	0.047±0.001^{a}	0.317±0.022^{a}
ESA	0.121±0.006^{b}	2.208±0.257^{b}	0.251±0.036^{b}	0.134±0.027^{b}	0.044±0.002^{a}	0.129±0.010^{b}
USS	0.075±0.003^{a}	1.685±0.213^{a}	0.270±0.048^{a}	0.163±0.038^{a}	0.053±0.001^{a}	0.114±0.012^{a}
ESS	0.075±0.004^{a}	1.519±0.089^{a}	0.206±0.011^{a}	0.084±0.008^{a}	0.051±0.001^{a}	0.130±0.007^{a}
UPA	0.032±0.001^{a}	1.661±0.154^{a}	0.231±0.026^{a}	0.128±0.021^{a}	0.216±0.057^{a}	0.113±0.006^{a}
EPA	0.043±0.004^{b}	2.970±0.529^{b}	0.382±0.071^{a}	0.216±0.057^{a}	0.053±0.001^{a}	0.175±0.016^{b}

USA: unembanked *S. alterniflora* salt marsh; ESA: embanked *S. alterniflora* salt marsh; USS: unembanked *S. salsa* salt marsh; ESS: embanked *S. salsa* salt marsh; UPA: unembanked *P. australis* salt marsh; EPA: embanked *P. australis* salt marsh. SOC, total organic C; LOC, labile organic C; WSOC, water-soluble organic C; ROC, recalcitrant organic C; SON, total organic N; LON, labile organic N; WSON, water-soluble organic N; RON, recalcitrant organic N.

The WSOC, ROC, and RON were 34.375%, 78.808%, and 54.867%, respectively, which was higher in EPA than in UPA (Table 2). Further, there were no significant differences in the concentrations of SOC, LOC, WSOC, ROC, SON, LON, WSON, and RON between the ESS and USS (Table 2). However, it is worthy of note that the WSOC concentrations in both ESS and USS were significantly higher than those in UPA and EPA, while the WSON concentrations in both the ESS and USS were markedly higher than those in USA and ESA (Table S1). The top two concentrations of ROC and RON were observed in USA and EPA (Table S1).

3.2 Alpha diversity of bacterial and archaeal communities

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

3.3 Taxonomic composition of soil bacterial and archaeal communities

USA possessed 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 abundances of the phylum Chlorobi, and classes Ignavibacteria, Chlorobia (within the phylum Chlorobi), and Chloroflexi (within the phylum Chloroflexi) were significantly higher in ESA than those in USA ($p < 0.05$), whereas the abundances of the phylum Fusobacteria and the class Rhodothermia (within the phylum Bacteroidetes) were significantly lower in ESA than in USA (Fig. 4).

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 UPA, while the Betaproteobacteria (from class to order), the order Pseudomonadales (within the class Gammaproteobacteria), and the family *Chromatiaceae* were abundant in EPA (Fig. 3). Additionally, the abundance of class 4C0d-2 (within the phylum Cyanobacteria) was significantly lower in EPA than in UPA ($p < 0.05$; Fig. 4). Moreover, the highest abundance of Gammaproteobacteria was observed in ESS in contrast to USA, ESA, USS, UPA, and EPA (Table S3). The top two abundances of Deltaproteobacteria and Epsilonproteobacteria were observed in USA and EPA (Table S3).

3.4 Beta diversity of soil bacterial and archaeal communities

Bray-Curtis dissimilarity indices indicated variations in the bacterial and archaeal communities between USA and ESA and between UPA and EPA were 65.620% ($p = 0.0230$) and 45.830% ($p = 0.0460$), respectively (Fig. 5). However, variations in the bacterial and archaeal communities between USS and ESS were 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, ROC, LOC, WSOC, RON, LON, WSON, and C/N) explained 23.500% and 28.000% of the total changes in the compositions 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 RON ($F = 2.60$, $p = 0.042$) (Fig. 6b).

The SEM and Pearson's analysis revealed that the abundance of Gammaprotebacteria was highly correlated with the concentrations of RON, LOC, LON, and WSOC (Fig. 7). The abundances of Deltaproteobacteria, Betaproteobacteria, and Epsilonproteobacteria were significantly correlated with the concentrations of ROC and RON (Fig. 7). Moreover, soil salinity had a significant negative correlation with the abundance of Betaproteobacteria (Fig. 7). The abundance of Actinobacteria was significantly negatively correlated with the LON, WSON, and RON concentrations (Fig. 7). The abundance of Rhodothermi was significantly correlated with the ROC concentration (Fig. 7). Moreover, a significant negative correlation was found between the abundances of Chlorobi, Ignavibacteria, Chloroflexi, and *Chromatiaceae* and aboveground biomass (Table S4).

4 Discussion

The establishment of coastal embankments significantly decreased the Simpson diversity index in the *S. alterniflora* salt marsh, while they increased the OTU richness in the *P. australis* salt marsh (Fig. 2). Interestingly, coastal embankments altered the microbial diversity and richness only slightly 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 presence 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 the SOC, ROC, SON, LON, and RON in the soil (Table S2). The accumulation of nutrients in the soil is primarily determined by the quantity and quality of plant residue inputs (Chantigny 2003; Belay-Tedla et al. 2009; Yang et al. 2016). The low soil salinity (e.g., 2.399‰) of the embanked *S. alterniflora* salt marsh created difficulties for this plant to complete its life cycle. As the establishment of coastal embankments limited the growth of *S. alterniflora* (Tables 1 and S2; Fierer and Jackson 2006; Zhong et al. 2011; Zhao et al. 2020), the decrease in plant residue biomass led to lower SOC, ROC, SON, LON, and RON in the soil of the embanked *S. alterniflora* salt marsh, which ultimately diminished the diversity of the soil bacteria and archaea (Tables 1, 2 and S2; Yang et al. 2016; Yu et al. 2019).

Conversely, the lower soil salinity (e.g., 1.737‰) in the embanked salt marsh was more suitable for the growth of *P. australis* than the high soil salinity (e.g., 4.164‰) of the unembanked salt marsh (Table 1). The increased residue biomass of *P. australis* caused by the low soil salinity led to an increase in the SOC and SON of the embanked *P. australis* salt marsh, which presumptively increased the OTU richness (Tables 1 and 2; Yang et al. 2020). However, coastal embankments had insignificant

impacts on plant residues, as well as soil SOC, LOC, WSOC, SON, LON, and WSON in the *S. salsa* salt marsh, which explained the negligible impact of these structures on bacterial and archaeal diversity and richness in the *S. salsa* salt marsh (Fig. 2; 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 reported that the higher availability of soil water in coastal zones was advantageous for the diversity of soil bacteria and archaea in these areas, which was consistent with the results of this study (Table S2; Gao et al. 2020; Novoa et al. 2020). The embankments prevented seawater from reaching the coastal wetlands, which decreased the soil moisture of the *S. alterniflora* salt marsh, thereby contributing to lower diversity (Table 2). However, the probable presence of aquifers within the embanked soil and precipitation can decrease the impact of embankments (Guo and Jiao 2007; Yang et al. 2016; Ma et al. 2019).

In this study, the soil moisture was increased in the embanked *P. australis* salt marsh, which might have explained its higher OTU richness (Fig. 2; Table 2). Soil pH shows an excellent correlation with bacterial and archaeal diversity; however, in our study, an insignificant correlation was observed between the soil pH and bacterial and archaeal diversity (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, which was primarily determined by plant residues, and changes in soil moisture (Tables 1, 2 and 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 the unembanked *S. alterniflora* and *P. australis* salt marshes, respectively (Fig. 5). However, the variation in the compositions of soil bacterial and archaeal populations between the unembanked and embanked *S. salsa* communities was insignificant (Fig. 5).

The WSOC, which is the first to be rapidly utilized by bacteria and archaea, was the most direct driver of soil bacterial and archaeal community composition among the different plant communities in the coastal wetlands. This was because the variations in the soil bacterial and archaeal communities were intimately related to the WSOC at the class, order, family, and genus levels (Figs. 6 and S2; Orwin et al. 2016; Santonja et al. 2017; Yang et al. 2020). Additionally, RON, which represents available nutrients, vitally influenced the composition of the bacterial and archaeal communities among the different plant communities (Figs. 6 and S2; Bates et al. 2011; Yang et al. 2020; Rasmussen et al. 2021).

Thus, in this study, the decrease of WSOC and RON in the *S. alterniflora* salt marsh following the establishment of coastal embankments caused a differentiation in the bacterial and archaeal communities between the unembanked and embanked *S. alterniflora* salt marshes (Figs. 5, 6 and S2; Table 2). Additionally, the higher concentrations of WSOC and RON in the embanked *P. australis* salt marsh influenced the differentiation of the bacterial and archaeal communities between the unembanked and embanked *P. australis* salt marshes (Figs. 5, 6 and S2; 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 S2; Table 2). Besides, the microbial community composition was also primarily influenced by changes in the soil C/N ratio (Fig. 6). An increased C/N ratio typically suggests that soils are degraded due to the loss of C, which limits microbial growth (Pereira et al. 2021). However, in this study, embankments did not change the soil C/N ratio for all vegetation types; thus, they did not modify the microbial community composition by altering the soil C/N ratio (Table 2).

Consequently, our results confirmed that the establishment of coastal embankments influenced the soil bacterial and archaeal community composition primarily by altering the concentrations of nutrient substrates, which was determined significantly by plant residues (Fig. 7; Table 2; Liao et al. 2007; Yang et al. 2016). In this study, the establishment of coastal embankments had a negligible effect on the relative archaeal abundance at the phylum, class, order, family, genus, and species levels (Table S5).

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

Several chemoorganotrophic bacteria were significantly influenced following the establishment of embankments. The phylum proteobacteria has been described in marine and terrestrial ecosystems as an important component of biogeochemical cycles, and was the most abundant phylum in the sediment of coastal Yancheng (Fig. S3; Lee et al. 2020; Yang et al. 2020). In this study, the class Gammaproteobacteria was the most abundant, and its relative abundance was influenced markedly following the establishment of embankments (Figs. 3 and S3).

The coastal embankment dramatically simulated the presence of Gammaprotebacteria in *S. salsa* saltmarshes (Fig. 3). Moreover, the abundance of Gammaproteobacteria in the embanked *S. salsa* saltmarsh was much higher than those in the other saltmarshes (Fig. 3; Table S3). Gammaproteobacteria is classified as a copiotrophic bacterial taxon, which has the capacity to grow quickly by utilizing labile compounds, particularly dissolved organic matter (Wang et al. 2020; Figueroa et al. 2021; Tian et al. 2021). Previous studies reported that *S. salsa* litter had lower lignin concentrations than that of *S. alterniflora* and *P. australis*. A lower lignin concentration translated to a faster passive release of labile compounds from the *S. salsa* litter (Cui et al. 2019; Trevathan-Tackett et al. 2020).

In this study, we also observed that *S. salsa* saltmarshes possessed higher WSON concentrations than *S. alterniflora* saltmarshes, and higher WSOC concentrations than *P. australis* saltmarshes (Table S1). The high WSOC and WSON concentrations increased the presence of Gammaproteobacteria in the *S. salsa* saltmarsh (Cleveland et al. 2007; Han et al. 2021). Additionally, when the supply of dissolved organic matter is sufficient Gammaproteobacteria will grow better under stable water conditions (Figueroa et al. 2021). The coastal embankment blocked the tide water, which provided a stable water supply and further improved the presence of Gammaproteobacteria in the *S. salsa* saltmarsh.

The class of Deltaproteobacteria is frequent in coastal sediments, and has been described as a degrader of recalcitrant compounds (Fig. S3; Fierer et al. 2007b; Liu et al. 2018; Trevathan-Tackett et al. 2020). Previous studies reported that several species of Deltaproteobacteria can even be isolated from recalcitrant crude oil (Acosta-González et al. 2013; Liu et al. 2018). In this study, SEM analysis also verified that the abundance of Deltaproteobacteria was highly correlated with ROC and RON concentrations in the soil (Fig. 7). Since *S. alterniflora* and *P. australis* residues are rich in lignin and lignocellulosic materials, the coastal embankments altered the inputs of recalcitrant materials from plant residues in the *S. alterniflora* and *P. australis* saltmarshes, which ultimately changed the ROC and RON concentrations in the soil (Ji et al. 2011; Cui et al. 2019; Yang et al. 2020).

Therefore, the coastal embankments decreased the quantities of plant residues, and soil ROC and RON, which resulted in the reduced abundance of Deltaproteobacteria in the *S. alterniflora* saltmarsh. The coastal embankments increased the amount of plant residues, as well as soil ROC and RON, which led to an increase in the abundance of Deltaproteobacteria in the *P. australis* saltmarsh (Tables 2 and S3). Similar to Deltaproteobacteria, we found that the abundances of Epsilonproteobacteria and Rhodothermi were obviously correlated with the ROC and RON concentrations, which supported the notion that Epsilonproteobacteria and Rhodothermi can break down refractory organic matters (Kirchman 2002; Kim and Kwon 2010; Lormieres and Oger 2017).

Thus, the coastal embankments had similar influences on Epsilonproteobacteria and Rhodothermi as on Deltaproteobacteria (Fig. 7). Moreover, some Actinobacteria are oligotrophic bacteria whose growth is restricted in nutrient-rich soils (Pascault et al. 2013; Trivedi et al. 2013; Verzeaux et al. 2016; Yang et al. 2020). Decreased *S. alterniflora* biomass in the soil of embanked salt marshes severely reduced the availability of nutrients (e.g., SOC and WSON), which was beneficial for the presence of Actinobacteria, and reduced its abundance in the embanked *S. alterniflora* sediment (Fig. 3; Tables 1 and 2). Thus, our results suggested that the establishment of coastal embankments influenced the distribution of chemoorganotrophic bacteria, as they modified the soil nutrient substrates (e.g., SOC, ROC, RON, and WSON) by appreciably altering the organic material inputs from plants.

Coastal embankments also affected the presence of photosynthetic bacteria by influencing plant growth. Photosynthetic bacteria are widely distributed in coastal sediments (Okubo et al. 2006; Idi et al. 2014). In this study, the quantity of obligately phototrophic bacteria from the phylum Chlorobi and class Chloroflexi (Garrity 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 restricted the presence of PSB (He et al. 2012; Li et al. 2014b; Brotosudarmo et al. 2015).

Indeed, the abundances of the phylum Chlorobi and class Chloroflexi were significantly negatively correlated with the aboveground biomass of plants (Table S4). Thus, the higher occurrence of the phylum Chlorobi and class Chloroflexi might have been induced by the increased sunlight due to the lower aboveground biomass of plants in the embanked *S. alterniflora* salt marsh (Fig. 4; Tables 1 and S4; Wang et al. 2012). In contrast, the shade provided by the increased aboveground biomass of plants might explain the lower abundance of 4C0d-2, which are also obligately phototrophic bacteria in the embanked *P. australis* salt marsh (Fig. 4; Table 1).

Chromatiaceae, which is known as phototrophic purple sulfur bacteria, can grow via photolithoautotrophic metabolism (Imhoff 2005). In this study, the presence of Chromatiaceae was negatively correlated with the aboveground biomass of plants (Table S4). Thus, the decreased aboveground biomass of *S. salsa* in the embanked salt marsh explained the greater occurrence of Chromatiaceae in this environment (Tables 1 and S4). Generally, the establishment of coastal embankments affects the presence of PSB by primarily altering the aboveground biomass of plants.

Pathogenic bacteria target plant and animal species. In this study, the coastal embankments stimulated the presence of some pathogenic bacteria that most likely threatened plants, and even the health of the entire ecosystem (Dangl and Jones 2001; Glazebrook 2005). For example, Xanthomonadales are aerobic, and in this study, their abundance was significantly negatively correlated with soil salinity (Fig. 3; Bayer-Santos et al. 2019). The decreased soil moisture and salinity of the embanked *S. alterniflora* salt marsh created aerobic conditions with low salinity that ultimately promoted the presence of Xanthomonadales, particularly that of *Xanthomonadaceae* (Fig. 3; Table 2; Bayer-Santos et al. 2019).

Xanthomonadales includes several plant pathogens, especially those belonging to the family *Xanthomonadaceae* (Bayer-Santos et al. 2019). Therefore, coastal embankments showed limited *S. alterniflora* growth, and the increased presence Xanthomonadales would damage it even further. Pseudomonadales are chemoorganotrophic, and in this study, their abundance was positively correlated with the SOC concentration (Figs. 3 and 7; Palleroni 2005; Peix et al. 2009). The increased presence of Pseudomonadales in the embanked *P. australis* saltmarsh might be explained by the significant increase in SOC in this environment (Table 2). Pseudomonadales is pathogenic species that affect animals and plants (Palleroni 2005; Peix et al. 2009). Therefore, the increased Pseudomonadales in embanked *P. australis* saltmarsh not only harmed plants, but also had negative impacts on animal health. As the study area is the most important habitat of the endangered Red-crowned Crane, the increased abundance of pathogenic bacteria could put this species at risk.

Several bacterial groups were directly affected by the absence of seawater owing to the coastal embankments. In this study, the presence of Betaproteobacteria (a dominant class within Proteobacteria) was stimulated in the embanked regions for all vegetation types (Figs. 3 and 4; Tables 1 and 2). Additionally, in embanked regions, the abundance of Betaproteobacteria were more pronounced near to shore, rather than at more seaward locations (Table S3). Betaproteobacteria has been suggested to originate from freshwater or terrestrial ecosystems and is rarely found in seawater (Ruiz-González et al. 2015; Baña et al. 2020; Figueroa et al. 2021).

Indeed, in this study, the abundance of Betaproteobacteria was negatively correlated with soil salinity and positively related with the soil pH (Fig. 7). Therefore, we speculated that coastal embankments significantly reduced soil salinity and increased the pH by blocking seawater, which ultimately promoted the growth of Betaproteobacteria. However, Betaproteobacteria have been reported to be highly active in the decomposition of organic matter and can utilize fresh and labile substrates (Dai et al. 2021). Thus, more abundant Betaproteobacteria in the embanked regions might have given rise to losses in labile nutrients (Fig. 7). In conclusion, 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 physicochemical soil properties, and varying bacterial populations may cause changes in the composition of soil nutrients.

5 Conclusion

This study endeavored to investigate alterations in soil bacteria and archaea communities to infer the deterministic processes that drove these variations following the establishment of embankments in the saltmarshes of coastal China. Embankments significantly decreased soil microbial diversity in the *S. alterniflora* salt marsh, while increasing their OTU richness in the *P. australis* salt marsh. Embankments significantly modified the compositions of soil bacterial and archaeal communities in the *S. alterniflora* and *P. australis* salt marshes. However, variations in soil bacterial and archaeal diversity, richness, and community compositions between native and embanked *S. salsa* salt marshes were insignificant. These results were likely due to the drastic changes in the concentrations of soil nutrient substrates that were caused by the variations in plant residues and physiochemical soil properties in the embanked *S. alterniflora* and *P. australis* salt marshes, which were not noted in the *S. salsa* salt marshes. This study provides further insights toward a better understanding of the variations and driving patterns of soil microbial communities following the establishment of embankments, which elucidated the effects of coastal embankments on 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;

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

Acknowledgements

This study was supported by the National 973 Key Project of Basic Science Research (grant no. 2013CB430405), and the National Natural Science Foundation of China (grant no. 32071632). We would like to thank Hui Zhao for assistance with the fieldwork, and all of the members of the Dafeng Milu National Nature Reserve and Yancheng National Nature Reserve for supporting this work.

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Conflicts of interest: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Availability of data and material: The data that support the findings of this study are available on request from the corresponding author.

Authors' contributions: **Hongyu Feng**: Conceptualization, Software, Formal analysis, Data Curation, Writing – Original Draft. **Yajun Qiao**: Methodology, Investigation. **Lu Xia**: Conceptualization, Methodology, Software, Formal analysis, Data Curation, Writing – Original Draft, Writing – Review & Editing, Visualization**. Wen Yang**: Conceptualization, Methodology, Writing – Review & Editing, Project administration, Funding acquisition. **Yongqiang Zhao**: Resources, Investigation. **Nasreen Jeelani**: Writing – Review & Editing. **Shuqing An**: Conceptualization, Resources, Writing – Review & Editing, Project administration, Funding acquisition.

Code availability: Not applicable.

Ethics approval: Not applicable.

Consent to participate: All authors participated in this manuscript.

Consent for publication: All authors revised the manuscript critically and approved the final manuscript for publication.

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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.

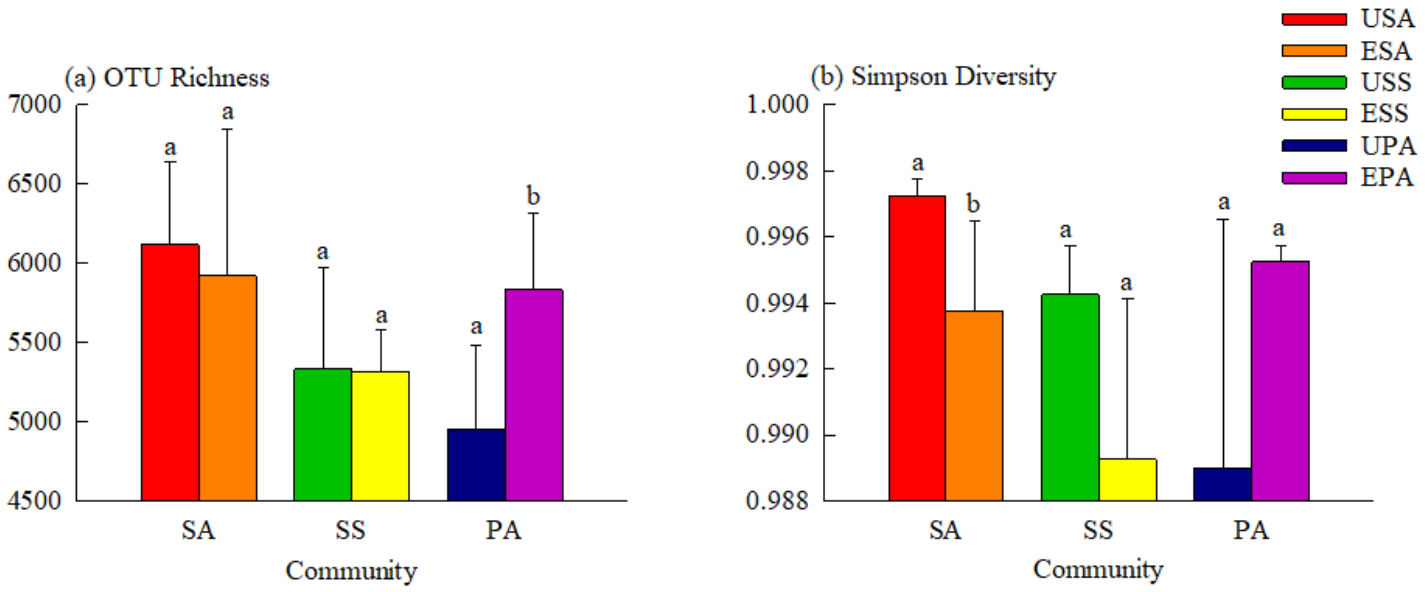

Figure 2

OTU richness (a) and 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

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.

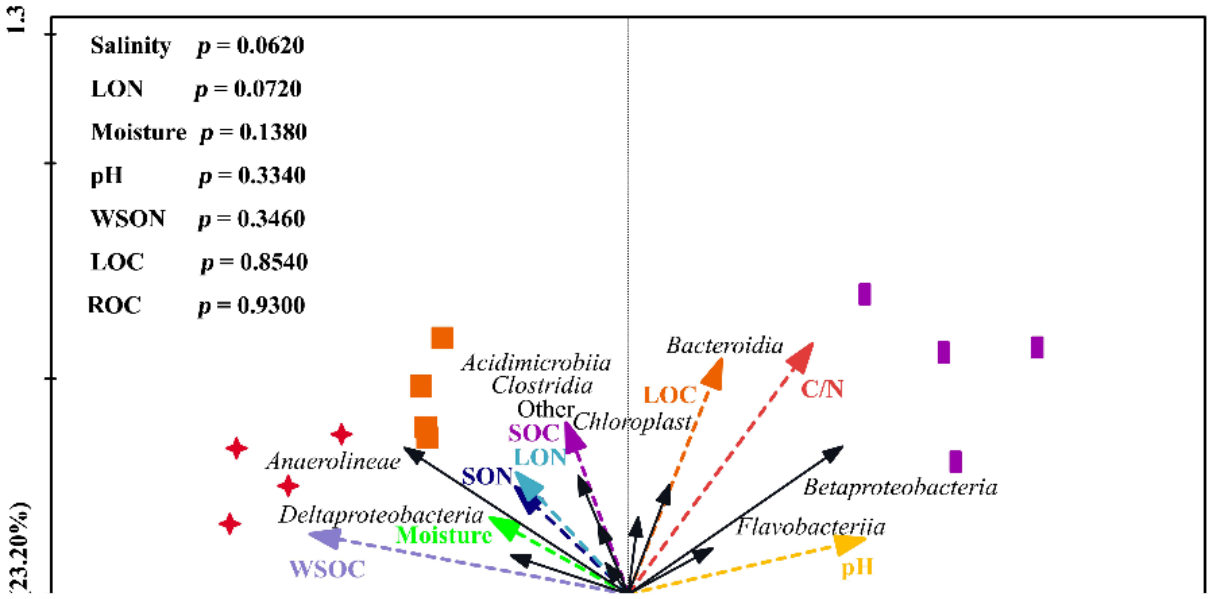

Figure 5

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

(a) Correlation analysis of physicochemical soil properties, root and litter biomass, and the concentrations of soil total, labile, recalcitrant and water-soluble organic C and N, as well as dominant bacteria at the phylum, class, and order levels. Pink indicates negative correlations, while purple indicates positive correlations. The darker the color, the stronger the correlation. **< 0.01 and *< 0.05. (b) 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). SOC, total organic C; LOC, labile organic C; WSOC, water-soluble organic C; ROC, recalcitrant organic C; SON, total organic N; LON, labile organic N; WSON, water-soluble organic N; RON, recalcitrant organic N.

Supplementary Files

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