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Soil bacterial community composition but not alpha diversity altered along a gradient of *Spartina alterniflora* invasion on the coast of Yellow Sea, China

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Introduction: *Spartina alterniflora* invasion may alter the characteristics and functions of the coastal wetland ecosystems. Previous studies have shown that invasion changes the biogeochemical processes and microbial diversity in marsh ecosystems; however, knowledge of the changes in bacterial communities and their function at different soil depths during invasion remains limited.

Methods: In the present study, we investigated *S. alterniflora* invasion on the dynamic changes of soil bacterial communities using Illumina MiSeq sequencing analyses of 16S rRNA at different soil depths (i.e., 0–10, 10–20, and 20–40 cm) during the invasive process (i.e., 1, 4, 7, and 12 years), as well as the potential correlations between soil physicochemical characteristics and enzyme activities.

Results: The invasion of *S. alterniflora* did not significantly affect soil bacterial alpha diversity or the functional profiles at the first and second levels of the Kyoto Encyclopedia of Genes and Genomes (KEGG). Furthermore, no significant changes were observed across different soil depths. However, the relative abundances of Chloroplast and Alphaproteobacteria increased from 3.03% and 5.05% in bare mudflat to 13.61% and 8.95% in the 12-year-old *S. alterniflora* invaded soil, respectively, whereas those of Deltaproteobacteria, Acidimicrobiia, and Bacilli decreased after *S. alterniflora* invasion for approximately 12 years. The relative abundances of soil bacteria varied with soil depth. Total phosphorus, carbon-to-nitrogen ratio, total carbon, and catalase activity were the key factors affecting soil bacterial community composition.

Discussion: The soil physicochemical characteristics changes caused by invasion may temporarily enhance soil fertility, they can lead to long-term wetland degradation through changed biological community and altered nutrient dynamics. This study provides a comprehensive understanding of the dynamic changes in bacterial communities, soil physicochemical characteristics, and enzyme activities during *S. alterniflora* invasion on coastal wetlands.

KEYWORDS

plant invasion, microbial community, coastal wetland, invasion age, biodiversity

1 Introduction

The invasion of alien plant species poses great threats to the biodiversity and function of the native ecosystem, which is considered the primary driving force for the changes in the invaded ecosystem (Zhang et al., 2021; Zhao et al., 2023) and can change soil biochemical characteristics, nutrient cycles, and microbial communities (Nirmala et al., 2023). Among them, *Spartina alterniflora* is a typical and common invasive species that has been introduced extensively because it can control natural erosion in coastal areas (Kim et al., 2023; Yang et al., 2023). The introduction of *S. alterniflora* in China began in 1979 and has quickly spread along the coasts, and subsequently became one of the beneficial species within coastal wetland ecosystems (Yang et al., 2016). Compared with other ecosystems, coastal wetlands typically have high productivity and offer valuable ecological services (Ge et al., 2020; Meng et al., 2020). Thus, it is essential to determine the impact of *S. alterniflora* invasion on soil characteristics to better understand the impact of invasion on coastal wetland ecosystems.

Soil microorganisms are of great significance in various processes within coastal wetland ecosystems, such as element cycles, information transmission, species distribution, and other biochemical processes (Thatoi et al., 2013; Hou et al., 2019; Ge et al., 2019), and microbial communities are sensitive to soil environmental alterations (Card and Quideau, 2010; Deng et al., 2016; An et al., 2020). Bacteria are considered one of the most abundant and diverse microbial communities that play pivotal roles in mediating soil biogeochemical cycles (Freedman and Zak, 2015; Jurburg et al., 2018; He et al., 2023). Understanding the conversion of soil bacterial communities provides a valuable link between plant invasion and soil development because it reveals the complex interactions between plants, soil, and microbes that drive ecosystem change. For instance, *S. alterniflora* invasion can change soil physicochemical characteristics, alter soil microbial community composition, and significantly affect some special functional bacteria related to nutrient cycles (Li et al., 2020; Lin et al., 2022). Therefore, understanding soil bacterial community and function succession after *S. alterniflora* invasion is fundamental for illustrating the relationship between *S. alterniflora* invasion and wetland ecosystem functions. Compared with the bare mudflat, the impact of *S. alterniflora* invasion on soil bacterial community composition and diversity was inconsistent; it significantly increased (Song et al., 2022) and decreased (Gao et al., 2019), and the changes in bacterial communities were time-dependent (Yang et al., 2019). Soil pH (Li et al., 2020), moisture (Nguyen et al., 2018), salinity (Guo et al., 2018), and nutrient substrates (Ling et al., 2017) play vital roles in driving the diversity of metabolic functions in coastal wetlands. In addition to these factors, the invasion age is an important driver of variation in soil microbial diversity (Zhang et al., 2020).

Plant invasion can alter soil microbial communities and the biogeochemical processes they mediate (Kao-Kniffin and Balser, 2008; Wang et al., 2023), thereby affecting nutrient cycling (Sokol et al., 2022; He et al., 2023). The deep root system of *S. alterniflora* releases exudates that can significantly alter the properties of deeper soil layers (Liao et al., 2007). The surface soil had higher soil organic carbon (SOC) and moisture content compared to deeper soil layers, and SOC storage initially decreased and then increased with increasing soil depth (Huang et al., 2022). Thus, the soil characteristics in deeper soil layers should also be considered (Nie et al., 2023), which may lead to a more precise explanation of these invasive effects. Although many studies have described the impact of *S. alterniflora* invasion on aboveground plant communities, soil characteristics, and functions (Davidson et al., 2018), little is known about its influence on soil physicochemical characteristics, enzyme activities, and bacterial communities at different soil depths during invasion.

The Jiangsu coastal zone is the largest *S. alterniflora* invasion region in China. Most of the natural areas is strictly protected and is rarely disturbed by human activities, making it an ideal research site. Our hypothesis posited that *S. alterniflora* invasion leads to alterations in soil bacterial communities, which, in turn, may be affected by varying soil characteristics and their respective depth profiles. The primary objectives of our study were as follows: (i) to evaluate the effects of *S. alterniflora* invasion on soil physicochemical characteristics and enzyme activities in different soil depths along the invasion age; (ii) to assess the alterations in soil bacterial community composition and function along the *S. alterniflora* invasion age; and (iii) to identify the main drivers that affect soil bacterial communities during the invasive process. Understanding this information is beneficial for improving the comprehension of the impact mechanism of *S. alterniflora* invasion and for accurately predicting the ecological influences.

2 Materials and methods

2.1 Study site and soil sampling

We carried out this experiment on the coast of Xiangshui County, Jiangsu Province, China (119.8875–119.8945°E, 34.4623–34.4647°N) (Figure 1). The climate type is transitional warm temperate–subtropical oceanic monsoon. The mean temperature and annual rainfall is 13.9°C and 929.0 mm, respectively. There is no other vascular plant except *S. alterniflora* in the selected coastal wetland. The soil type is coastal Solonchaks (initial developmental stage) by the World Reference Base for Soil Resources and Halosols by the Chinese Soil Taxonomy. Soil samples were collected from five different habitats: natural mudflat (without *S. alterniflora*) and 1-, 4-, 7-, and 12-year-old *S. alterniflora* invasive soil. These soil samples were collected after the tide has receded. Here, the invasion ages were differentiated by the fixed marks and by previous remote sensing image data similar to our previous studies (Ge et al., 2020).

All soil samples were taken in April 2023. At each of the five sampling habitats, three soil samples (approximately 50 m apart) were collected using 50-cm soil corers (diameter: 5 cm) and separated into three layers: surface soil layer (0–10 cm), middle soil layer (10–20 cm), and subsoil layer (20–40 cm). The soil samples were loaded into sterile Ziplock bags and taken to the laboratory using ice boxes. Soil samples from each habitat were processed as follows: three replicate samples from each habitat were individually homogenized and prepared for analysis. After the soil samples were well mixed, part of the soil was stored at 4°C to measure the enzyme activities, 10 g of the soil was stored at −80°C to analyze soil bacterial communities, and other soil samples were

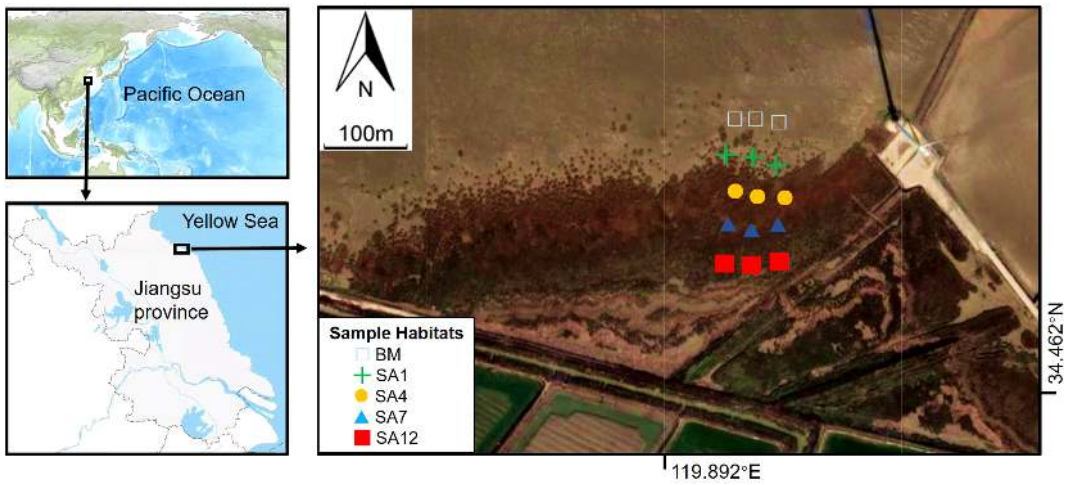


FIGURE 1
Map of the study area and soil sampling habitats. Notes: BM, bare mudflat; SA1, 1-year-old *S. alterniflora*; SA4, 4-year-old *S. alterniflora*; SA7, 7-year-old *S. alterniflora*; SA12, 12-year-old *S. alterniflora*.

air-dried and passed through a 2-mm sieve to separate roots, large particles of gravel, and litter to analyze the physicochemical characteristics in the laboratory.

2.2 Soil physicochemical characteristics

Soil moisture was determined by the oven-drying method at 105°C for 24 h. Soil salinity was calculated by determining electrical conductivity (EC); EC and pH were measured after a suspension of 5 g of soil and 25 mL of distilled water using a conductivity meter (Mettler-Toledo S230-B, Switzerland) and pH meter (Mettler-Toledo FE28, Switzerland), respectively. Total carbon (TC) and total nitrogen (TN) concentrations were determined by the CHNS elemental analyzer (Elementar Macrocube, Germany). SOC, total phosphorus (TP), and available phosphorus (AP) were determined with the methods of Avery and Bascomb (1982).

2.3 Soil enzyme activities

Catalase (CAT; EC 1.11.1.6), sucrase (SC; EC3.2.1.26), and urease (UE; EC 3.5.1.5) activities were measured according to the manufacturer's specifications. CAT was analyzed using H_2O_2 as the substrate and determined with a spectrophotometer (UV-2450, SHIMADZU) at 240 nm, and SC was determined with the substrate of sucrose and measured at 508 nm. UE was determined with the substrate of urea and measured at 578 nm.

2.4 DNA extraction and 16S rRNA gene sequencing

The total DNA was extracted from 0.5 g of soil (wet weight) using the PowerSoil®DNA Isolation Kit for soil (Mo Bio Laboratories, Inc., Carlsbad, CA, USA), according to the manufacturer's specifications. Then, the amount of extracted DNA was measured by a NanoDrop TM 2000 spectrophotometer (Thermo Scientific, USA) before polymerase chain reaction (PCR). PCR analysis was implemented to determine the 16S rRNA gene copy number of bacteria by the universal primers F515 (5′-GTGCCAGCMGCCGCGGTAA-3′) together with R907 (5′-CCGTCAATTCMTTTRAGTTT-3′) with the barcode. The PCR cycling parameters were set as follows: 98°C for 1 min, 30 cycles of 10 s at 98°C, 30 s at 50°C and 60 s at 72°C, and finally with an extension at 72°C for 5 min. The PCR products were confirmed with 2% agarose gel and then purified by the DNA Purification Kit (TIANGEN, China) before sequencing. The sequencing was carried out by the Illumina MiSeq platform (Shanghai Majorbio BioPharm Technology Company, China).

2.5 Statistical analysis

Two-way analysis of variance (ANOVA) followed by Tukey's tests was employed to identify the effect of *S. alterniflora* invasion ages on soil physicochemical characteristics, enzyme activities, and bacterial community richness and diversity indices in different soil depths. SIMPER was explored to detect the dissimilarity and the taxon contribution for the dissimilarity of bacterial community composition based on the data for the top 10 genera. Bacterial functional pathway modes within different soil samples were predicted with the PICRUSt database (Langille et al., 2013). The matrix of Pearson's correlations was calculated to find potential relationships among soil physicochemical characteristics, enzyme activities, and the relative abundances of the top 10 classes. The relationships between the potential environmental factors (averaged for each site by three samples) and the soil bacterial communities (top 10 classes) were analyzed by redundancy analysis (RDA). All these statistical analyses were conducted using the software R 4.2.1 (R Core Team, 2022) and PAST 4.03 (Hammer et al., 2001).

3 Results

3.1 Soil physicochemical characteristics

Soil physicochemical characteristics changed after the invasion of *S. alterniflora* and differed among the invasion ages (Table 1). Soil physicochemical characteristics showed a variety of trends during the invasion process. Soil moisture significantly increased with *S. alterniflora* invasion age in the surface soil (0–10 cm) ($p < 0.05$) and also significantly increased with soil depth in the bare mudflat and the *S. alterniflora*-invaded 1-year soil (Table 1). The surface soil pH significantly decreased in the 12-year-old *S. alterniflora* soil, and deeper soil (10–40 cm) pH first increased with *S. alterniflora* invasion age, with the highest value in the 7-year-old *S. alterniflora* soil, and then decreased in the 12-year-old *S. alterniflora* soil (Table 1). Soil pH was not significantly affected by the soil depth, except in the bare mudflat soil. Soil EC and AP concentrations first increased with *S. alterniflora* invasion age and then decreased in the 7-year-old *S. alterniflora* soil, but significantly increased in the 12-year-old *S. alterniflora* soil ($p < 0.05$, Table 1). Compared with the bare mudflat soil, TP dramatically decreased after the invasion of *S. alterniflora*, and the value was the lowest in the 3-year-old *S. alterniflora* soil. TP and AP were generally unaffected by the soil depth at the same invasion time. The TN dramatically increased with *S. alterniflora* invasion age (Table 1). TN significantly increased with soil depth in the 1- and 4-year-old *S. alterniflora* soils. SOC decreased after *S. alterniflora* invasion for 1 year and then increased progressively with invasion time. TC was not significantly affected by *S. alterniflora* invasion age or soil depth (Table 1). *S. alterniflora* invasion age significantly influenced the physicochemical characteristics, and soil depth had an evident impact on the physicochemical characteristics. The interaction between *S. alterniflora* invasion age and soil depth had a significant impact on soil physicochemical characteristics (Supplementary Table S1).

TABLE 1 Soil physicochemical characteristics in different soil depths along *S. alterniflora* invasion ages.

Soil characteristics	Soil depth (cm)	Sampling habitats				
		BM	SA1	SA4	SA7	SA12
Moisture (%)	0–10	0.22 ± 0.01f	0.23 ± 0.01ef	0.25 ± 0.02de	0.26 ± 0.02de	0.32 ± 0.02ab
	10–20	0.24 ± 0.02ef	0.24 ± 0.02ef	0.27 ± 0.02de	0.25 ± 0.01def	0.30 ± 0.03bc
	20–40	0.26 ± 0.01de	0.27 ± 0.06a	0.31 ± 0.04cd	0.25 ± 0.01de	0.34 ± 0.02a
pH	0–10	7.63 ± 0.01ab	7.42 ± 0.15cd	7.53 ± 0.04bc	7.73 ± 0.11ab	7.15 ± 0.22ef
	10–20	7.23 ± 0.09def	7.31 ± 0.14de	7.55 ± 0.12abc	7.65 ± 0.07ab	7.06 ± 0.07f
	20–40	7.27 ± 0.07de	7.59 ± 0.14abc	7.42 ± 0.13cd	7.74 ± 0.15a	7.27 ± 0.10de
EC	0–10	3.42 ± 0.09j	3.75 ± 0.15i	4.39 ± 0.12f	4.09 ± 0.05g	5.82 ± 0.09a
	10–20	3.25 ± 0.12j	3.72 ± 0.15i	4.67 ± 0.18e	3.79 ± 0.07hi	5.29 ± 0.04cd
	20–40	3.77 ± 0.12hi	5.48 ± 0.18bc	5.14 ± 0.19d	3.97 ± 0.12gh	5.69 ± 0.15ab
AP (mg/kg)	0–10	1.50 ± 0.07i	2.16 ± 0.22efgh	2.36 ± 0.19def	1.88 ± 0.20fghi	2.95 ± 0.22bc
	10–20	1.67 ± 0.16hi	1.75 ± 0.19ghi	2.47 ± 0.05cde	2.16 ± 0.21efgh	3.59 ± 0.20a
	20–40	1.93 ± 0.11fghi	2.80 ± 0.23cd	2.62 ± 0.11cde	2.22 ± 0.07efg	3.41 ± 0.26ab
TP (mg/kg)	0–10	8.94 ± 0.43a	7.84 ± 0.30bc	6.18 ± 0.29d	6.58 ± 0.25d	6.30 ± 0.46d
	10–20	8.50 ± 0.20ab	7.52 ± 0.24c	6.38 ± 0.21d	5.94 ± 0.15d	6.10 ± 0.31d
	20–40	8.68 ± 0.11a	6.63 ± 0.14d	8.09 ± 0.93b	5.91 ± 0.18d	6.23 ± 0.40d
TN (%)	0–10	1.01 ± 0.01f	1.25 ± 0.06e	1.27 ± 0.04de	1.29 ± 0.07cde	1.59 ± 0.05a
	10–20	1.00 ± 0.02f	1.41 ± 0.07bcd	1.45 ± 0.04ab	1.28 ± 0.07de	1.48 ± 0.06ab
	20–40	1.07 ± 0.04f	1.50 ± 0.05ab	1.54 ± 0.05ab	1.44 ± 0.04abc	1.53 ± 0.07ab
SOC (g/kg)	0–10	1.48 ± 0.05f	1.21 ± 0.04h	1.99 ± 0.06e	3.12 ± 0.10c	4.07 ± 0.10a
	10–20	1.27 ± 0.05gh	1.14 ± 0.07h	2.05 ± 0.03de	3.45 ± 0.08b	4.19 ± 0.03a
	20–40	1.41 ± 0.04fg	1.23 ± 0.07gh	2.21 ± 0.02d	3.53 ± 0.10b	4.21 ± 0.04a
TC (%)	0–10	0.58 ± 0.03a	0.62 ± 0.01a	0.64 ± 0.01a	0.62 ± 0.02a	0.65 ± 0.02a
	10–20	0.57 ± 0.03a	0.61 ± 0.04a	0.63 ± 0.02a	0.62 ± 0.03a	0.63 ± 0.04a
	20–40	0.60 ± 0.02a	0.62 ± 0.03a	0.63 ± 0.04a	0.60 ± 0.04a	0.65 ± 0.02a

Values are means ± SD ($n = 3$). Different letters indicate significant differences at the $\alpha = 0.05$ level between soil depths and *S. alterniflora* invasion ages. BM, bare mudflat; SA1, 1-year-old *S. alterniflora*; SA4, 4-year-old *S. alterniflora*; SA7, 7-year-old *S. alterniflora*; SA12, 12-year-old *S. alterniflora*.

3.2 Soil enzyme activities

Soil UE, SC, and CAT activities are presented in Figure 2. Compared to the bare mudflat, UE activity decreased at the *S. alterniflora* initial invasion stage, followed by a gradual increase with increasing invasion age, peaking in the 7-year-old *S. alterniflora* soil. It was significantly higher in the surface soil than in the subsoil. *S. alterniflora* invasion had no significant effect on the UE activity in the subsoil (20–40 cm). SC activity increased significantly with *S. alterniflora* invasion age, peaked in the 12-year-old *S. alterniflora* soil, and decreased with increasing soil depth. SC activity was the highest in the 12-year-old *S. alterniflora* surface soil. Soil CAT activity progressively increased after *S. alterniflora* invasion, peaking in the 4-year-old *S. alterniflora* soil, whereas no significant differences were observed among soil depths.

3.3 Soil bacterial alpha diversity

Chao1, ACE, Shannon, and Simpson values were measured to analyze bacterial community diversity (Table 2). In bare mudflat, Chao1 values were 1,406.7 ± 79.0 in the surface soil and 1,429.4 ± 195.9 in the subsoil, and invasive *S. alterniflora* substantially decreased the Chao1 values; they were 1,175.2 ± 191.9 in the surface soil and 1,090.9 ± 62.0 in the subsoil of 12-year-old *S. alterniflora*. Compared with bare mudflat, ACE values decreased with *S. alterniflora* invasion; they were 1,606.8 ± 202.0 and 1,593.7 ± 337.7 in bare mudflat surface soil and subsoil, respectively, and they were 1,372.0 ± 59.0 in the surface soil and 1,230.9 ± 127.6 in the subsoil of 12-year-old *S. alterniflora*. Shannon values were 5.6 ± 0.3 in the surface soil and 5.8 ± 0.3 in the subsoil of the bare mudflat. Invasive *S. alterniflora* did not significantly influence Shannon and Simpson values (Table 2). These results illustrate that *S. alterniflora* invasion did not significantly affect the soil bacterial alpha diversity.

3.4 Soil bacterial community structure and composition

The soil bacteria in the coastal wetland were mainly identified as the phylum Proteobacteria, Actinobacteria, Firmicutes, and Bacteroidetes (Figure 3). Proteobacteria was the main phylum in all bacterial communities and was dominated by Gammaproteobacteria (8.2%–14.3%), Deltaproteobacteria (8.0%–12.6%), and Alphaproteobacteria (5.1%–10.2%) (Figure 3). Compared with the bare mudflat, *S. alterniflora* invasion significantly increased the relative abundance of Chloroplast ($p<0.05$), and the relative abundance of Alphaproteobacteria increased by approximately twofold in the soil of 4-year-old *S. alterniflora* (Figure 3). The relative abundance of Chloroplast increased from 4.3% ± 1.5% and 0.7% ± 0.1% in the mudflat surface soil and deeper soil to 12.7% ± 4.5% and 22.8% ± 6.1% in the 7-year-old *S. alterniflora* surface soil and subsoil, respectively. In the subsoil, the relative abundance of Clostridia increased from 7.5% ± 2.5% in the bare mudflat to 12.7% ± 3.5% in 7-year-old *S. alterniflora* soils (Figure 3). However, *S. alterniflora* invasion substantially decreased the relative abundances of Acidimicrobiia. The relative abundance of Acidimicrobiia affiliated with Actinobacteria decreased from 11.0%–13.8% in the bare mudflat to 7.2%–10.1% in the 12-year-old *S. alterniflora* soil. The relative abundance of Bacilli affiliated with Firmicutes first increased with *S. alterniflora* invasion for 1 year, and then decreased by approximately 3.7-fold in the 7-year-old *S. alterniflora* soil (Figure 3). Chloroplast, Gammaproteobacteria, and Acidimicrobiia contributed 22.38%, 15.45%, and 13.56% of the total community difference, respectively, and they shared 51.38% of the total community difference (Table 3). The results of the 10 most abundant classes in each sample illustrated an evident variation in the soil bacterial community composition across different invasion ages of *S. alterniflora* (Supplementary Table S2). The relative abundances of the top 10 classes increased with invasion age, accounting for 69.8%, 72.6%, 74.0%, 72.3%, and 79.7% of the bacterial communities in the mudflats and 1-, 4-, 7-, and 12-year-old *S. alterniflora* soils, respectively (Supplementary Table S2).

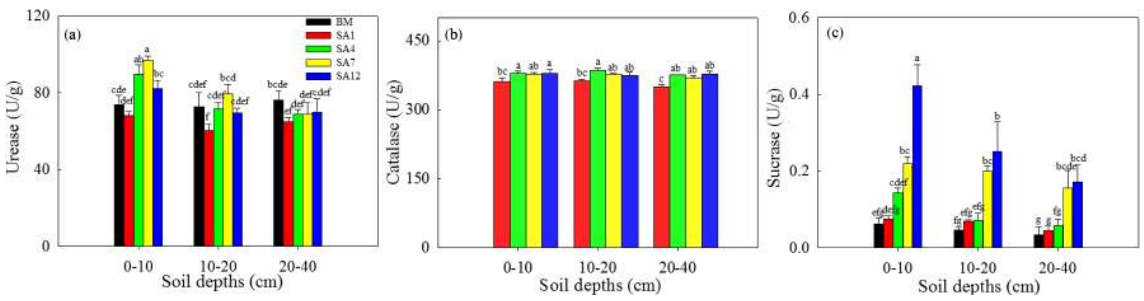


FIGURE 2
Soil enzyme activities in different soil depths along *S. alterniflora* invasion ages. **(a)** Urease; **(b)** catalase; **(c)** sucrase. Values are means ± SD. Different letters mean significant difference ($p < 0.05$) between soil depths and *S. alterniflora* invasion ages. BM, bare mudflat; SA1, 1-year-old *S. alterniflora*; SA4, 4-year-old *S. alterniflora*; SA7, 7-year-old *S. alterniflora*; SA12, 12-year-old *S. alterniflora*.

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TABLE 2 Alpha diversity indices of soil bacterial community of different soil depths in different sampling habitats.

Sampling habitats	Soil depth (cm)	Chao1	ACE	Shannon	Simpson
BM	0–10	1,406.7 ± 79.0abcd	1,606.8 ± 202.0a	5.59 ± 0.25ab	0.008 ± 0.002c
	10–20	1,424.2 ± 168.8a	1,420.7 ± 139.4a	5.59 ± 0.26a	0.008 ± 0.000c
	20–40	1,629.4 ± 195.9abcd	1,593.7 ± 337.7a	5.77 ± 0.25 ab	0.009 ± 0.001c
SA1	0–10	1,697.9 ± 249.3 abcd	1,632.1 ± 254.1a	6.09 ± 0.28 ab	0.007 ± 0.002bc
	10–20	1,578.2 ± 127.1 cd	1,603.1 ± 69.1a	4.85 ± 0.48 ab	0.014 ± 0.000bc
	20–40	12,933.2 ± 48.0 abcd	1,669.8 ± 250.9a	4.51 ± 1.05 ab	0.015 ± 0.001c
SA4	0–10	1,288.1 ± 282.8 abc	1,441.4 ± 135.5a	5.46 ± 0.54 ab	0.012 ± 0.008c
	10–20	1,320.4 ± 134.8 abcd	1,263.9 ± 32.4a	4.95 ± 0. 45 ab	0.017 ± 0.004bc
	20–40	1,220.4 ± 42.2 bcd	1,330.5 ± 147.3a	4.67 ± 1.07 ab	0.020 ± 0.009bc
SA7	0–10	1,492.3 ± 44.1 cd	1,546.8 ± 137.5a	5.42 ± 0.27 ab	0.024 ± 0.010a
	10–20	1,272.4 ± 105.4 ab	1,380.8 ± 50.6a	4.63 ± 0.40 ab	0.028 ± 0.020c
	20–40	1,217.1 ± 186.6 abcd	1,414.1 ± 84.5a	4. 46 ± 0.73 ab	0.067 ± 0.056c
SA12	0–10	1,175.2 ± 191.9 bcd	1,372.0 ± 59.0a	5.43 ± 0.05 ab	0.023 ± 0.021bc
	10–20	1,184.2 ± 29. 1 bcd	1,290.9 ± 103.3a	5.38 ± 0.24b	0.111 ± 0.006ab
	20–40	1,090.8 ± 62.0 d	1,230.9 ± 127.6a	5.55 ± 0.24 ab	0.009 ± 0.003c

Values are means ± SD (n = 3). Different letters indicate significant differences at the α = 0.05 level between soil depths and *S. alterniflora* invasion ages. BM, bare mudflat; SA1, 1-year-old *S. alterniflora*; SA4, 4-year-old *S. alterniflora*; SA7, 7-year-old *S. alterniflora*; SA12, 12-year-old *S. alterniflora*.

3.5 Relationships among soil physicochemical characteristics, enzyme activity, and bacterial communities

Pearson's correlation analysis of soil bacterial communities with soil physicochemical characteristics and enzyme activities is shown in Figure 4. The results showed that moisture was significantly and positively correlated with EC, TC, TN, C/N, SOC, AP, and SC in the surface soils (correlation coefficients ranging from 0.67 to 0.93); it also had positive relationships with EC, TC, and AP in the subsoil (correlation coefficients ranging from 0.62 to 0.89). EC had a significantly positive association with TC, TN, C/N, and AP in both the surface soil and subsoil (correlation coefficients ranging from 0.62 to 0.92). EC was positively correlated with SOC and SC in the surface soil (r = 0.85 and 0.94) and CAT in the subsoil (r = 0.64). In addition, TP was negatively correlated with AP, CAT, UE, and SC in the surface soil (correlation coefficients ranging from 0.64 to 0.83), while it was negatively correlated with AP, CAT), UE, and SC in the subsoil (r = 0.55, 0.96, and 0.61, respectively). The results showed that Alphaproteobacteria was significantly and negatively correlated with pH, while positively correlated with TN in the surface soil. Bacilli was significantly and negatively correlated with TP (r = −0.58), and Deltaproteobacteria was positively correlated with TP (r = 0.52). Gammaproteobacteria had a significantly negative correlation with C/N in the surface soil (Figure 4A). Bacilli had negative relationships with moisture, EC, TC, C/N, SOC, AP, CAT, and SC in the middle soil, while being positively correlated with TP. Chloroplast had positive relationships with pH and CAT, while being negatively correlated with TP in the middle soil (Figure 4B). Deltaproteobacteria had a significantly negative

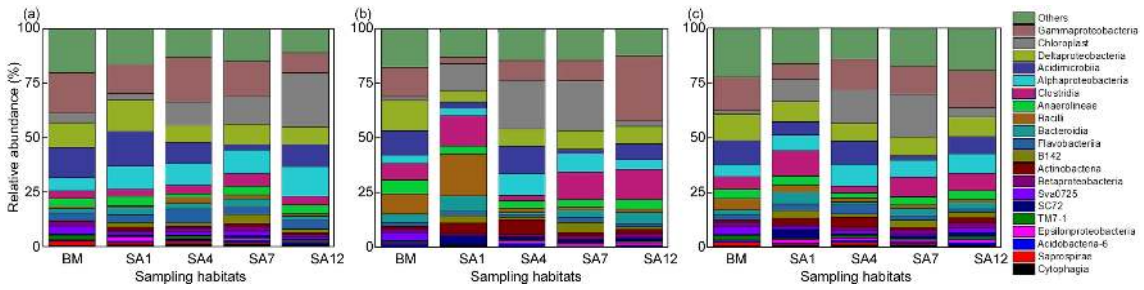


FIGURE 3
The relative abundance of soil bacterial community composition. **(a)** 0–10 cm; **(b)** 10–20 cm; **(c)** 20–40 cm. Those with a relative abundance of less than 1% were grouped as others. BM, bare mudflat; SA1, 1-year-old *S. alterniflora*; SA4, 4-year-old *S. alterniflora*; SA7, 7-year-old *S. alterniflora*; SA12, 12-year-old *S. alterniflora*.

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TABLE 3 Dissimilarity percentages (SIMPER) with the taxon contributions based on *S. alterniflora* invasion age (overall average dissimilarity = 38.72).

Taxon	Average dissimilarity	Contribution %	Cumulative %
Chloroplast	8.666	22.38	22.38
Gammaproteobacteria	5.982	15.45	37.83
Acidimicrobiia	5.249	13.56	51.38
Clostridia	4.276	11.04	62.43
Alphaproteobacteria	3.332	8.605	71.03
Deltaproteobacteria	3.268	8.441	79.47
Bacilli	3.043	7.858	87.33
Bacteroidia	1.871	4.832	92.16
Flavobacteriia	1.63	4.209	96.37
Anaerolineae	1.404	3.626	100

correlation with TC, C/N, and CAT, while being positively correlated with UE in the subsoil (Figure 4C).

The correlation indices among the soil physicochemical characteristics, enzyme activity, and relative abundances of bacterial communities also varied with soil depth (Figure 4). For instance, pH was negatively associated with Alphaproteobacteria (r = 0.52) in the surface soil, but positively correlated with Chloroplast (r = 0.61) in the subsoil. Deltaproteobacteria were positively correlated with TP (r = 0.52) in the surface soil but negatively correlated with TC (r = 0.52), C/N (r = 0.57), and CAT (r = 0.53) in the subsoil. UE was significantly positively correlated with Bacilli (r = 0.64) and negatively correlated with Acidimicrobiia (r = 0.59) in the surface soil. In comparison, in the subsoil, UE was positively correlated with Anaerolineae (r = 0.54) and Deltaproteobacteria (r = 0.60). The SC was positively correlated with Chloroplast (r = 0.59) in the surface soil and negatively correlated with Bacilli (r = 0.61) in the subsoil.

Soil characteristics had different relationships with bacterial communities. RDA illustrated the relationships between soil physicochemical characteristics, enzyme activity, and bacterial community composition. Soil characteristics in the first and second RDA dimensions accounted for 62.45% of the total variance in bacterial community structure (Figure 5). The RDA results clearly revealed that alterations in the soil bacterial community composition at the class level were most strongly associated with soil TP (Figure 5).

3.6 Predicted functions of bacterial colonies

PICRUSt was employed to analyze the functional content of bacterial colonies in *S. alterniflora* invasion soil of different ages. However, no significant differences were observed among the five groups at KEGG level 1 and KEGG level 2 ($p > 0.05$) (Figure 6).

4 Discussion

4.1 Variations of soil characteristics along the invasion chronosequence

Previous studies have shown that plant invasion can significantly change soil physicochemical characteristics (e.g., soil salinity, pH, and moisture) (Yuan et al., 2015); however, the effects are not constant (Souza-Alonso et al., 2015). In this study, soil moisture changed in an orderly manner and increased in the surface soil (0–10 cm) with the increasing age of invasion (Table 1). The increase in soil moisture following the invasion of *S. alterniflora* can be attributed to its extensive root system, which enhances water retention capacity in the soil. Additionally, the dense canopy formed by *S. alterniflora* reduced evaporation rates, further contributing to higher soil moisture. Yang et al. (2020) also found that soil moisture increased significantly after the invasion of *S. alter*niflora. Soil pH varies with the invasion of *S. alterniflora* and may increase (Gao et al., 2017), decrease (Yang et al., 2019; Zhang et al., 2020; Lin et al., 2021), or not be altered (Huang et al., 2016) by *S. alterniflora* invasion, which may be attributed to soil types and invasion history (Carey et al., 2015). In our study, pH significantly decreased in the surface soil after *S. alterniflora* invasion for approximately 12 years, whereas it significantly increased in the middle and subsoil layers after *S. alterniflora* invasion for approximately 7 years, and then decreased or remained unaffected after *S. alterniflora* invasion for approximately 12 years (Table 1). The soil physicochemical characteristics at different soil depths also showed inconsistent responses during invasion (Gao et al., 2017; Zhang et al., 2020).

The spatial and temporal distribution of phosphorus is a key index for assessing the risk, productivity, and function of wetland ecosystems (Cui et al., 2019). In this study, 12-year-old *S. alterniflora* invasion significantly enhanced the AP concentration (Table 1). This may be due to microbial decomposers related to *S. alterniflora* roots (Wang et al., 2021). The TN concentration increased with *S. alterniflora* invasion age, and there was no significant difference among soil depths (Table 1), which is in accordance with other coastal wetlands (Qi et al., 2019; Lin et al., 2021; Zhang et al., 2023). This may illustrate that *S. alterniflora* invasion plays a critical role in the soil nitrogen cycle. *S. alterniflora* can increase nitrogen distribution during photosynthesis and, thus, stimulate carbon and nutrient accumulation in the soil (Wang et al., 2018; Chen et al., 2018; Hou et al., 2019; Ge et al., 2020). Zhang et al. (2020) reported that *S. alterniflora* invasion increased SOC linearly with invasion age. SOC decreased at the initial invasion age of *S. alterniflora* and then increased with increasing invasion age at any soil depth (Table 1). The biodegradable carbon in *S. alterniflora* litter had a higher litter decomposition rate and induced more SOC (Huang et al., 2022; Liu et al., 2022). However, *S. alterniflora* invasion had no significant effect on TC (Table 1). This may be related to the invasion age, as plant invasion age is also a crucial element in determining the supply of nutrients in the soil (Souza-Alonso et al., 2015; Yang et al., 2023).

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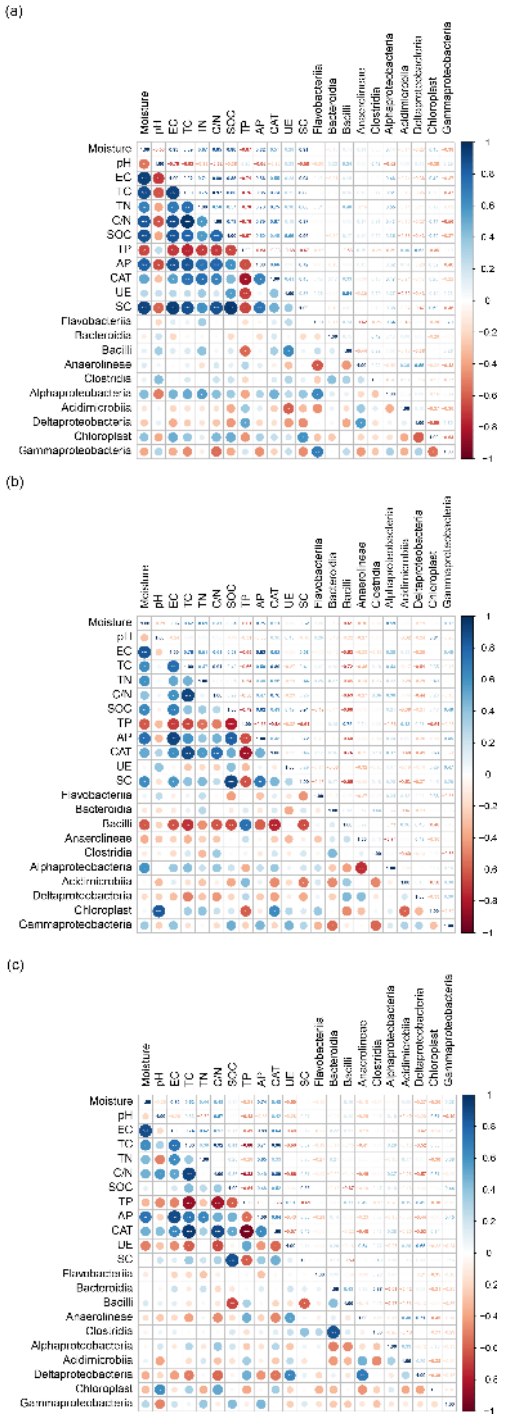


FIGURE 4
Pearson correlation analyses between soil physicochemical characteristics and the relative abundances of major bacterial class. **(a)** 0–10 cm; **(b)** 10–20 cm; **(c)** 20–40 cm. The color of the circle depends on the direction of the correlation (blue = positive; red = negative). The size of the circle is proportional to the *r* value. *p*-values in white are significant (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). EC, electrical conductivity; TC, total carbon; TN, total nitrogen; C/N, carbon-to-nitrogen ratio; SOC, soil organic carbon; TP, total phosphorus; AP, available phosphorus; CAT, catalase; UE, urease; SC, sucrase.

4.2 Bacterial succession along the invasion ages and soil depth

Alterations in the diversity of soil bacterial communities are closely correlated with the multifunctionalities of the ecosystem (Jing et al., 2015). Compared to the bare mudflats, *S. alterniflora* invasion significantly increased soil bacterial abundance and diversity (Yang et al., 2016; Rodríguez-Caballero et al., 2017; Yang et al., 2019; Lin et al., 2022). Interestingly, alpha diversity indices (Chao1, ACE, and Shannon) were not greatly affected by *S. alterniflora* invasion in

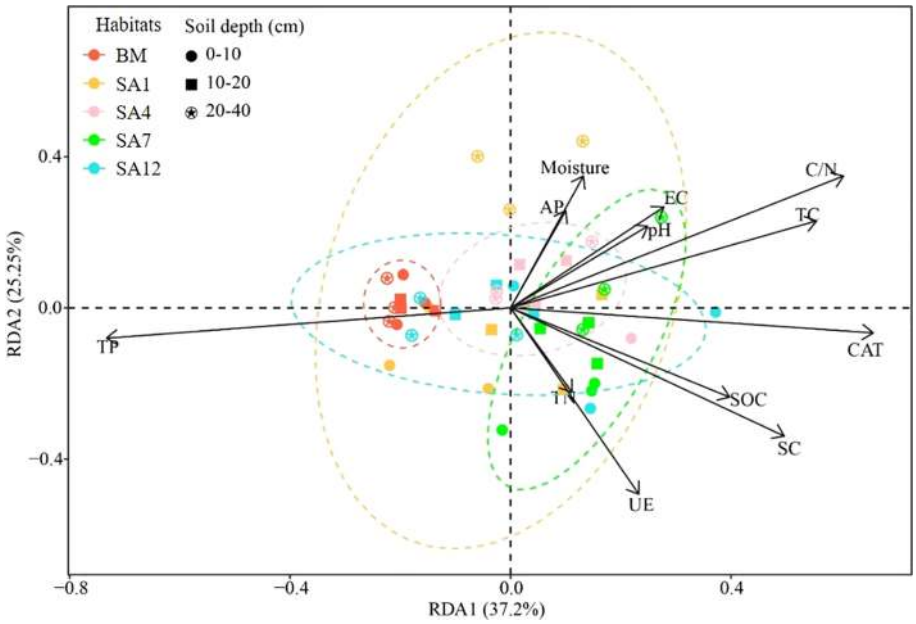


FIGURE 5
Relationships between soil physicochemical characteristics and bacterial community in different soil depths indicated by RDA ordination plots for the first two dimensions. The extent of correlations between soil characteristics and RDA axes is represented by the length and angle of arrows (soil characteristic vectors). BM, bare mudflat; SA1, 1-year-old *S. alterniflora*; SA4, 4-year-old *S. alterniflora*; SA7, 7-year-old *S. alterniflora*; SA12, 12-year-old *S. alterniflora*.

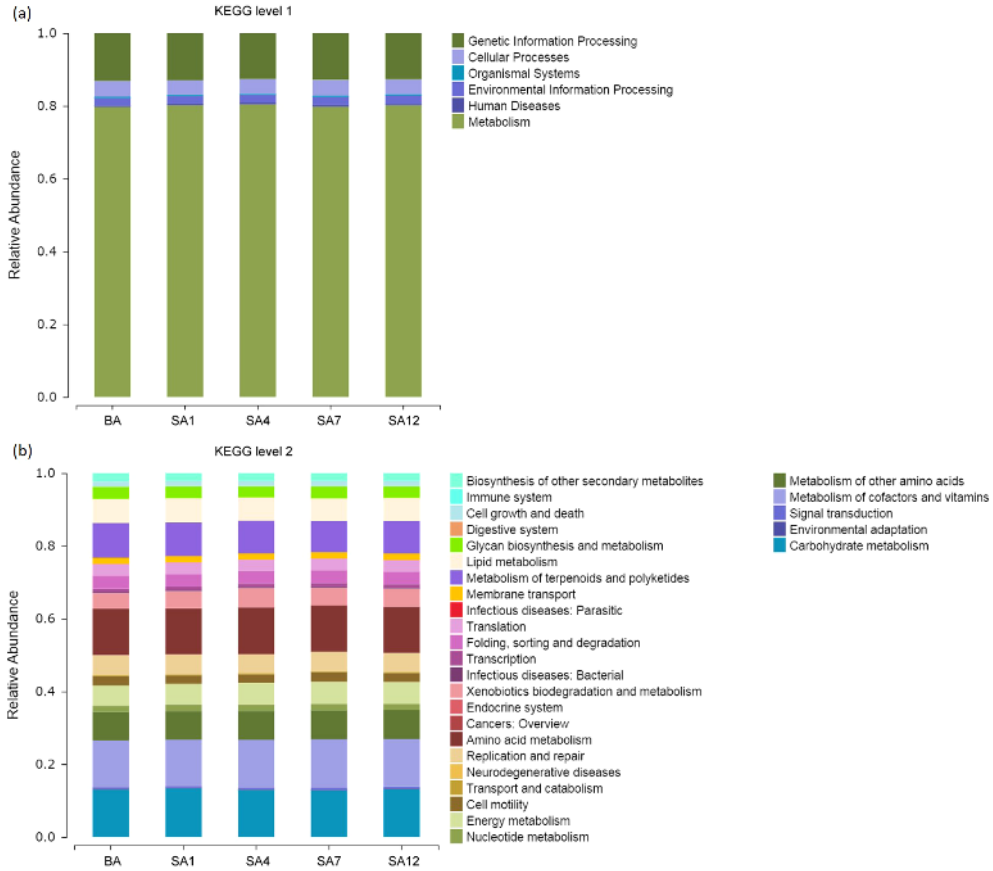


FIGURE 6
The different functional categories predicted by PICRUSt for the bacterial colonies. **(a)** KEGG levels 1; **(b)** KEGG levels 2. BM, bare mudflat; SA1, 1-year-old *S. alterniflora*; SA4, 4-year-old *S. alterniflora*; SA7, 7-year-old *S. alterniflora*; SA12, 12-year-old *S. alterniflora*.

this study (Table 2), suggesting that *S. alterniflora* invasion had no significant effect on soil bacterial alpha diversity. Soil bacterial diversity has varied in different studies. Other researchers have found that the Shannon index decreased after *S. alterniflora* invasion (Gao et al., 2019; Li et al., 2020). Carey et al. (2015) showed that there was a minor response in bacterial community composition and diversity after 5–6 years of *Aegilops triuncialis* and *Euphorbia caput-medusae* invasion in field experiments, although the soil characteristics changed. This discrepancy may be explained by the invasion stage (Liu et al., 2017), soil C and N contents, nutrient availability (Lin et al., 2022), and climatic conditions (Li et al., 2020). Soil microorganisms play crucial roles in maintaining the balance and stability of essential processes of nutrient cycling of soil; thus, the stable microbial structures and functions in soil are beneficial for the stability of coastal wetland ecosystems (Ali and Xie, 2020).

Compared to the bare mudflat, the relative abundances of Flavobacteriia and Bacteroidia, which are affiliated with Bacteroidetes, were higher in *S. alterniflora* invasive soil (Figure 3). Bacteroidetes are ubiquitous in anaerobic environments (Xu et al., 2017) and are generally considered as functional groups for decomposing complex organic compounds (Fernandez-Gomez et al., 2013). Moreover, *S. alterniflora* litter contained more recalcitrant substances, such as lignocellulosic and lignin materials (Zhang et al., 2010), which increased the relative abundance of Bacteroidetes, thus enhancing the degradation of *S. alterniflora* residues and promoting the accumulation of TN in the soil (Table 1). Likewise, Lin et al. (2022) reported that the relative abundances of Bacteroidetes and Firmicutes commonly increased as the invasion age of *S. alterniflora* increased. Proteobacteria was the predominant phylum in all soil bacterial communities in the wetland ecosystem (Figure 3) and has been broadly recognized in other studies (Liu et al., 2017; Lin et al., 2022). Among Proteobacteria, Gamma- and Delta-Proteobacteria were the two primary classes, which is in line with other reports (Zheng et al., 2019; Lin et al., 2022). Anaerolineae can respire multiple carbon compounds (Hug et al., 2013) and increased after *S. alterniflora* invasion of a salt marsh in China (Yang et al., 2020). However, this disagrees with our study, and we found that the relative abundance of Anaerolineae decreased after *S. alterniflora* invasion (Supplementary Table S2). The decrease in the relative abundance of Anaerolineae after *S. alterniflora* invasion may be due to changes in soil redox conditions. As *S. alterniflora* increased soil aeration through its dense root system, the soil became more aerobic, which was less favorable for anaerobic bacteria like Anaerolineae (Li et al., 2020; Dai et al., 2024). The relative abundances of the top 10 classes increased progressively with *S. alterniflora* invasion age (Supplementary Table S2). SOC accumulation in the invaded wetlands, along with invasion age, was beneficial for increasing the relative abundance of bacteria (Liu et al., 2017). Although soil bacterial alpha diversity was not significantly altered with the soil depth (Table 2), the relative abundance of Gammaproteobacteria, Alphaproteobacteria, Chloroplast, Clostridia, and Bacilli altered with soil depth (Figure 3). As the physicochemical characteristics of the deep soil layer changed (Table 1), the bacterial community composition can alter with the changed environmental characteristics (Song et al., 2022). In addition to the observed changes in soil bacterial community composition, the invasion of *S. alterniflora* also significantly impacts the beta diversity of bacterial communities. Beta diversity, which reflects the variation in community composition among different sites, is often altered by plant invasions due to changes in environmental conditions and resource availability (Zhang et al., 2020; Yang et al., 2016). In the context of *S. alterniflora* invasion, previous studies have shown that the beta diversity of soil bacterial communities tends to increase with the progression of invasion, likely due to the enhanced heterogeneity in soil physicochemical properties and the introduction of new organic substrates from plant litter (Yang et al., 2016; Rodríguez-Caballero et al., 2017).

4.3 Effects of soil characteristics on bacterial community composition

Soil physicochemical characteristics are widely recognized as one of the key driving elements affecting soil bacterial community composition and structure (Nguyen et al., 2018; Rath et al., 2019). In this study, we found that pH, TP, TN, CAT, and UE were the predominant factors influencing the relative abundance of bacteria in the surface soil (Figure 4A). Likewise, TP, TN, and pH are vital environmental factors that regulate the sediment bacterial community structure after *S. alterniflora* invasion (Song et al., 2022). pH was significantly negatively correlated with Alphaproteobacteria in the surface soil, but positively correlated with Chloroplast in deep soil (Figure 4). The results suggested that Alphaproteobacteria may thrive in more neutral conditions, which aligns with previous studies showing that Alphaproteobacteria are often abundant in low-pH environments. pH is an important factor affecting soil bacterial community composition in various soil types (Lauber et al., 2009; Tripathi et al., 2012; Ding et al., 2017). UE catalyzes the hydrolysis of carbon–nitrogen bonds between some amides and urea (Madejón et al., 2001) and is thus closely related to organic matter turnover and transformations (Baddam et al., 2016). UE activity gradually increased with *S. alterniflora* invasion age and peaked in the 7-year-old *S. alterniflora* soil (Figure 2). UE activity was significantly positively correlated with Bacilli, Anaerolineae, and Deltaproteobacteria, and negatively correlated with Acidimicrobiia (Figure 4). RDA illustrated that changes in the soil bacterial community composition were closely related to soil TP, C/N, TC, and CAT (Figure 5). P is the primary limiting factor of microbial growth (Sun et al., 2019; Wang et al., 2021). Likewise, TC and TN play major roles in the regulation of bacterial community structure in coastal wetlands (Lin et al., 2022).

The observed shifts in bacterial community composition, particularly the increased abundance of Chloroplast and Alphaproteobacteria, may be driven by root exudates from *S. alterniflora*, which can alter soil nutrient availability and pH (Zeleke et al., 2013). These exudates often contain organic compounds that selectively promote the growth of certain bacterial groups while inhibiting others. Over the long term, such changes in bacterial communities could enhance nutrient cycling and organic matter decomposition, potentially leading to increased soil fertility (Wang et al., 2024). However, they may also disrupt the balance of native microbial communities, affecting overall ecosystem stability and function. Here, we found that *S. alterniflora* invasion significantly altered soil properties such as pH, moisture, and nutrient availability, which, in turn, shaped the structure and function of bacterial

communities. For instance, the increase in soil moisture and EC likely created more favorable conditions for certain bacterial taxa, such as Gammaproteobacteria and Deltaproteobacteria, which were known for their roles in nutrient cycling and organic matter decomposition. Additionally, changes in SOC and TP content may influence microbial metabolic pathways, as indicated by shifts in bacterial functional groups (Xu et al., 2025). These interconnected changes suggested that *S. alterniflora* invasion not only affects individual soil parameters but also restructured the soil microbiome in ways that can have cascading effects on ecosystem processes.

Our findings revealed that *S. alterniflora* invasion significantly impacted soil properties and microbial communities in coastal wetlands, with implications for conservation and management. The invasion altered soil physicochemical characteristics, increasing soil moisture, SOC, EC, and AP, among others. While these changes may temporarily enhance soil fertility, they can lead to long-term wetland degradation through changed biological community and altered nutrient dynamics. Management efforts should prioritize early detection and control of *S. alterniflora*, especially in areas with intact native plant communities. Additionally, shifts in microbial community composition, such as increased abundance of Chloroplast and Alphaproteobacteria, highlight *S. alterniflora's* potential to disrupt ecosystem functions through changes in nutrient cycling. To counteract these effects, management strategies should be taken to control *S. alterniflora*, such as biological control agents, or promote native plants to support diverse and stable microbial communities. Moreover, our results emphasized the importance of considering soil depth in assessing invasion impacts, as deeper soil layers may respond differently compared to surface soils.

5 Conclusions

The present study illustrated that *S. alterniflora* invasion had no significant impact on soil bacterial alpha diversity but shifted the bacterial community composition, and the bacterial community composition changed with soil depths. TP, TC, C/N, and CAT were the primary limiting factors for bacterial community composition. The invasion of *S. alterniflora* modified the soil physicochemical characteristics at different soil depths, particularly by increasing soil moisture, EC, AP, and TN. However, characteristics at all soil depths showed unstable responses during the invasion process. Compared with the bare mudflat, UE activity first decreased and then increased with *S. alterniflora* invasion age. CAT and SC activity gradually increased with the invasion age of *S. alterniflora*. The 7-year-old *S. alterniflora* invasive soil had a better nutrient status. These results provide a comprehensive understanding of the effects of *S. alterniflora* invasion on coastal wetland ecosystems.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

LY: Data curation, Investigation, Validation, Writing – original draft, Writing – review & editing. YP: Data curation, Investigation, Writing – original draft. SW: Data curation, Formal analysis, Visualization, Writing – original draft. CR: Data curation, Investigation, Writing – original draft. HD: Data curation, Project administration, Writing – original draft. HL: Software, Supervision, Writing – original draft. BG: Conceptualization, Formal analysis, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2025.1531902/full#supplementary-material

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