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REGULAR ARTICLE

Exotic *Spartina alterniflora* Loisel. Invasion significantly shifts soil bacterial communities with the successional gradient of saltmarsh in eastern China

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Abstract

Aims The effects of invasive plants on soil carbon (C) and nitrogen (N) cycling are widely documented, while the mechanisms of their influences on the microbial ecology of soil remain unknown. Therefore, the objective of this study was to explore variations in soil bacterial communities following plant invasion, and the mechanisms that drive these changes.

Methods An invasive perennial herb, *Spartina alterniflora* Loisel., was examined via 16S rRNA genetic sequencing analyses, to assess the impacts of plant invasion on soil bacterial communities compared to bare flat and native *Suaeda salsa* (L.) Pall., *Scirpus mariqueter* Tang et Wang, and *Phragmites australis* (Cav.) Trin. ex Steud. communities in the coastal zone of China.

Results *S. alterniflora* invasion significantly increased soil bacterial abundance, species richness, and diversity for soil bacterial communities compared with native communities. *S. alterniflora* soil revealed a unique bacterial community composition, and possessed the highest relative abundance of chemo-lithoautotrophic bacteria, photoautotrophic bacteria (e.g., Chloroflexi, and Anaerolineae), and saprophytic and copiotrophic bacteria (e.g., Bacteroidetes) among the plant communities.

Conclusions Our results demonstrated that invasive *S. alterniflora* significantly altered soil bacterial

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abundance, diversity, and community composition through increases in nutrient substrate levels and altering soil physiochemical properties. Subsequently, the modification of soil bacterial communities, especially increased relative abundances of Chloroflexi, Anaerolineae, and Bacteroidetes following *S. alterniflora* invasion can enhance the degradation of recalcitrant *S. alterniflora* materials, while inducing the accumulation of soil organic C and N. These changes further potentially impacted ecosystem C and N cycles in the coastal zone of China.

Keywords Bacterial diversity · ecosystem C and N cycles · high-throughput sequencing · plant invasion · soil bacterial community composition · 16S rRNA gene

Abbreviations

ACE	Abundance-based coverage estimator
ANOVA	One-way analysis of variance
BF	Bare flat
C	Carbon
Chao1	Chao's species richness estimator
C:N ratio	Carbon: Nitrogen ratio
LDA	Linear discriminant analysis
LEfSe	Linear discriminant analysis effect size
N	Nitrogen
OTUs	Operational taxonomic units
PA	*Phragmites australis* (Cav.) Trin. ex Steud.
PCoA	Principal coordinates analysis
QIIME	Quantitative insights into microbial ecology
qPCR	Quantitative polymerase chain reaction
RDA	Redundancy analysis
RDP	Ribosomal database project
SA	*Spartina alternifolia* Loisel.
Shannon	Shannon's diversity index
Simpson	Simpson's diversity index
SM	*Scirpus mariqueter* Tang et Wang
SOC	Soil organic carbon
SOM	Soil organic matter
SON	Soil organic nitrogen
SS	*Suaeda salsa* (Linn.) Pall
WSOC	Water-soluble organic carbon

Introduction

Invasive plant species comprise an important component of global environmental change, the proliferation of which are mediated by anthropogenic activities (Szymura et al. 2018). Over 13,000 plant species have been successfully naturalized on the global scale, where many have become invasive (Divíšek et al. 2018). Plant invasion has been reported to threaten biodiversity and natural habitats worldwide (Bazzichetto et al. 2018; Divíšek et al. 2018), while profoundly altering species composition, native ecosystem processes (Lazzaro et al. 2018), and functionality (Fahey et al. 2018). For instance, numerous studies have documented that plant invasion can impact the carbon (C) and nitrogen (N) cycling of local ecosystems (Liao et al. 2008; Portier et al. 2019). This is due to alterations in the quantity and quality of plant residues (i.e., litter and roots) that enter the soil (Liao et al. 2008), soil nutrient resorption efficiencies (Sardans et al. 2017), litter decomposition rates (Frank et al. 2018), soil physicochemical properties (Yang et al. 2013), and microbial communities (Gaggini et al. 2018). Among microbial communities, soil bacteria are the most abundant and diverse types of microorganisms found in soils (Gans et al. 2005). It has been estimated that 1 g of soil contains up to 1 billion bacterial cells, comprising tens of thousands of microbial taxa (Ding et al. 2016). Soil bacteria play critical ecological roles in the transformation of soil nutrients and driving of biogeochemical (e.g., C and N) cycles (DeCrappeo et al. 2017). Therefore, appraising the impact of plant invasion on the bacterial communities of soils, and their responses, is critical toward more clearly elucidating the influences that invasive plants have on ecosystem C and N cycles. These aspects have not been widely reported as yet (Rodríguez-Caballero et al. 2017).

Soil nutrient substrates are considered to be overarching driving factors for soil bacterial communities (Orwin et al. 2016; Santonja et al. 2017), as they provide inorganic and organic substrates for soil bacteria (Yu et al. 2019). Typically, soil bacterial communities with higher organic matter inputs, combined with richly available nutrients are more remarkably abundant in contrast to fungal communities (Högberg et al. 2003; Yang et al. 2016). However, the responses of various bacterial community taxa to the availability of nutrients can differ (Francioli et al. 2016). For instance, Proteobacteria and Bacteroidetes grow rapidly, preferentially utilize labile C sources in nutrient-rich environments and are considered as copiotrophic phyla (Fierer et al. 2007; Verzeaux et al. 2016). Conversely, Acidobacteria, Nitrospirae, and Gemmatimonadetes are oligotrophic phyla that have the

capacity to degrade more recalcitrant C sources and prefer nutrient-poor environments (Trivedi et al. 2013; Verzeaux et al. 2016). Invasive plant species have been reported to either increase (Tamura and Tharayil 2014; Yang et al. 2017), decrease (Portier et al. 2019), or have negligible effects (Hughes et al. 2006) on the sequestration of soil C and N, while modifying availability of soil C and N by altering the inputs of plant residues into the soil (Yang et al. 2013). The responses of bacterial communities in soils to plant invasion may vary significantly, due to the diverse modification of soil C and N levels and nutrient availability subsequent to the invasion of particular plant species.

Soil bacterial communities are significantly influenced by biotic (e.g., plant properties) (Angel et al. 2010), and abiotic (e.g., climate, geographic distance, soil type, and soil physicochemical properties) factors (Bainard et al. 2016; Nguyen et al. 2018). Steinauer et al. (2016) reported that the high diversity of plant communities and biomass can promote soil microbial abundance and diversity as the result of substantial available resources from root exudates and litter residues. The physicochemical properties of soils have been widely regarded as one of the most crucial driving factors for soil bacterial communities (Bainard et al. 2016; Nguyen et al. 2018; Rath et al. 2019). For instance, soil pH is considered to be the most important factor for determining the alteration of soil bacterial diversity and community composition, at both local and regional scales (Rousk et al. 2010; Bainard et al. 2016). Notably, in wetlands, soil salinity is the primary factor that drives soil bacterial communities (Rath et al. 2019). Morrissey et al. (2014) demonstrated that soil salinity was strongly related to the structures of bacterial communities and microbial decomposition rates in tidal wetlands, ranging from fresh to low salinity environments. Soil moisture has been widely reported to influence soil bacterial communities by altering water stress and indirectly impacting soil C and N availability (Bainard et al. 2016; Banerjee et al. 2016; Keet et al. 2019). Generally, high moisture in soils is conducive to bacterial flourishing (Nakamura et al. 2003). Previous studies have revealed that plant invasion significantly shifted the net primary production (Stefanowicz et al. 2016), and physicochemical properties of soils (e.g., soil salinity, pH, and moisture) (Yuan et al. 2015) in native ecosystems. Thus, the identification of biotic and abiotic factors that affect soil bacterial communities following the establishment of invasive plant species, may contribute to an improved comprehension of how they impact bacterial communities in soils.

Spartina alterniflora Loisel. is a typical invasive perennial C_4 grass that reproduces primarily through rhizomes (Negrin et al. 2019), which was introduced to the coastal salt marshes of Eastern China from the Atlantic coast of North America in 1979 for erosion control. Subsequently, *S. alterniflora* has expanded rapidly across the Eastern coast of China, from Tianjin (in the north) to Beihai (in the south), through the invasion of bare flat, and/or the replacement of native plants (e.g., *Suaeda salsa* (L.) Pall., *Scirpus mariqueter* Tang et Wang, and *Phragmites australis* (Cav.) Trin. ex Steud.) (Yang et al. 2016, 2019). The Jiangsu coast has become the greatest *S. alterniflora* distribution area in China (Yang et al. 2013). Previous investigations conveyed that *S. alterniflora* had a greater net primary production, higher net photosynthetic rate, longer growing season, and lower litter decomposition rate in contrast to native plants (Liao et al. 2007). Consequently, the invasion of *S. alterniflora* has significantly altered the C and N cycling of ecosystems (Liao et al. 2007), particularly soil organic C and N sequestration (Yang et al. 2013, 2017; He et al. 2019), and greenhouse gases emissions (Gao et al. 2019). Further *S. alterniflora* has been reported to alter the microbial communities of soils (Yang et al. 2016), particularly the specific microbial taxa that are associated with sulfate reducing processes (Zeleke et al. 2013), and dissimilatory nitrate reduction processes (Gao et al. 2019). However, the impacts of *S. alterniflora* invasion on soil bacterial abundance, diversity, and community composition in contrast to primary native plants remain uncertain. We hypothesized that *S. alterniflora* invasion might alter bacterial abundance, diversity, and community composition by modifying the quantity or quality of plant residues, as well as the nutrient substrate levels and physicochemical properties of soils. To test this hypothesis, the Illumina MiSeq sequencing of bacterial 16S rRNA gene and quantitative polymerase chain reaction (qPCR) was undertaken, to analyze variations in soil bacterial abundance, diversity, and community composition. Soil moisture, pH, salinity, soil organic carbon (SOC), water-soluble organic carbon (WSOC), and soil organic nitrogen (SON) concentrations were also examined in an invasive nine-year-old *S. alterniflora* community, and compared with the bare flat and native C_3 plant

(i.e., *S. salsa*, *S. mariqueter*, and *P. australis*) communities with a successional gradient of coastal marshes in Eastern China.

Materials and methods

Study site

This study was conducted in the core region of the Jiangsu Yancheng Wetland National Nature Reserve for Rare Birds, in China (32°36′51″–34°28′32″N and 119°51′25″–121°5′47″E) (Yang et al. 2017). This reserve, which is the most extensive coastal wetland reserve in China, consists of aggrading mudflats with a mean annual temperature of 13.8 °C, precipitation of 1000 mm, and sea water salinity of 30.9‰ (Yang et al. 2013, 2016). *S. alterniflora* was intentionally introduced to the bare flat of this reserve in 1983 and became widely dispersed over the ensuing three decades, forming large areas of *S. alterniflora* salt marshes. The bare flat and *S. alterniflora* salt marshes are located in the lower and middle regions of the intertidal zone, respectively (Fig. 1; Yuan et al. 2015). The seaward invasion region of *S. alterniflora* was the bare flat that was devoid of vegetation prior to the invasion of *S. alterniflora* (Fig. 1; Yang et al. 2013, 2016). Since the bare flat provided an empty niche with no native plants competed with *S. alterniflora*, and *S. alterniflora* preferentially invaded this area of the reserve (Fig. 1; Yang et al. 2013, 2016). The native C_3 halophytes are *S. salsa*, *S. mariqueter*, and *P. australis*, where *S. salsa* and *S. mariqueter* salt marshes are located within the irregularly flooded high intertidal zone (Fig. 1; Yuan et al. 2015). *P. australis* salt marshes are situated within the seldomly flooded supralittoral zone (Fig. 1; Yuan et al. 2015). There is little overlap in the distribution of these salt marshes.

Field sampling

In December 2015, four parallel transects within the Jiangsu Yancheng reserve (each 5 km long × 50 m wide) were selected. The order of vegetation communities in each transect from sea to land was bare flat (i.e., control, no vegetation), *S. alterniflora* community, *S. salsa* community, *S. mariqueter*, and *P. australis* communities (Fig. 1). For each vegetation community we had a sampling site per transect, and there were 5 sampling sites in each transect. The sampling sites replaced by *S. alterniflora* communities had been the bare flat nine years earlier (Yang et al. 2019). At each sampling site of each transect, three 2 m × 2 m plots were established, and three soil cores (5 cm diameter × 30 cm depth) were randomly collected within each plot. All soil cores derived from each sampling site of each transect were thoroughly mixed to yield a final soil sample. Ultimately, we obtained 20 soil samples (4 replicates × 5 treatments). In the laboratory, the samples were gently crumbled, and all visible roots were removed. Each soil sample was divided into four portions: The initial soil subsample was used to measure soil moisture content (Yang et al. 2013). The second soil subsample was air-dried and sifted through a 1-mm sieve for the determination of soil pH, salinity, SOC, and SON. The third soil subsample was sifted through a 2-mm sieve and stored at 4 °C for the measurement of the WSOC concentration. The final subsample was sifted through a 2-mm sieve and immediately stored at −80 °C for DNA extraction.

Soil physicochemical analysis

The soil subsamples were weighed and oven-dried at 105 °C for 24 h to a constant weight for soil moisture determination. The pH of a 1:2.5 soil:water suspension was determined using a pH meter. The soil salinity was measured in a 1:5 soil:water suspension with a conductivity meter (Yang et al. 2013). Approximately 10 g of dried soil subsamples were treated with 1 M HCl at room temperature for 24 h to eliminate the total inorganic C and N. Subsequently, the SOC and SON concentrations were analyzed using a Vario Micro CHNS analyzer (Elementar Analysensysteme GmbH, Germany). The WSOC was determined according to a previously described method (Yang et al. 2016).

DNA extraction and quantification of 16S rRNA gene abundance

Microbial DNA was extracted from frozen soil samples (equivalent of 0.5 g dry weight soil) using the Power Soil DNA kit (MoBio Laboratories, Solana Beach, CA, USA) according to the manufacturer's

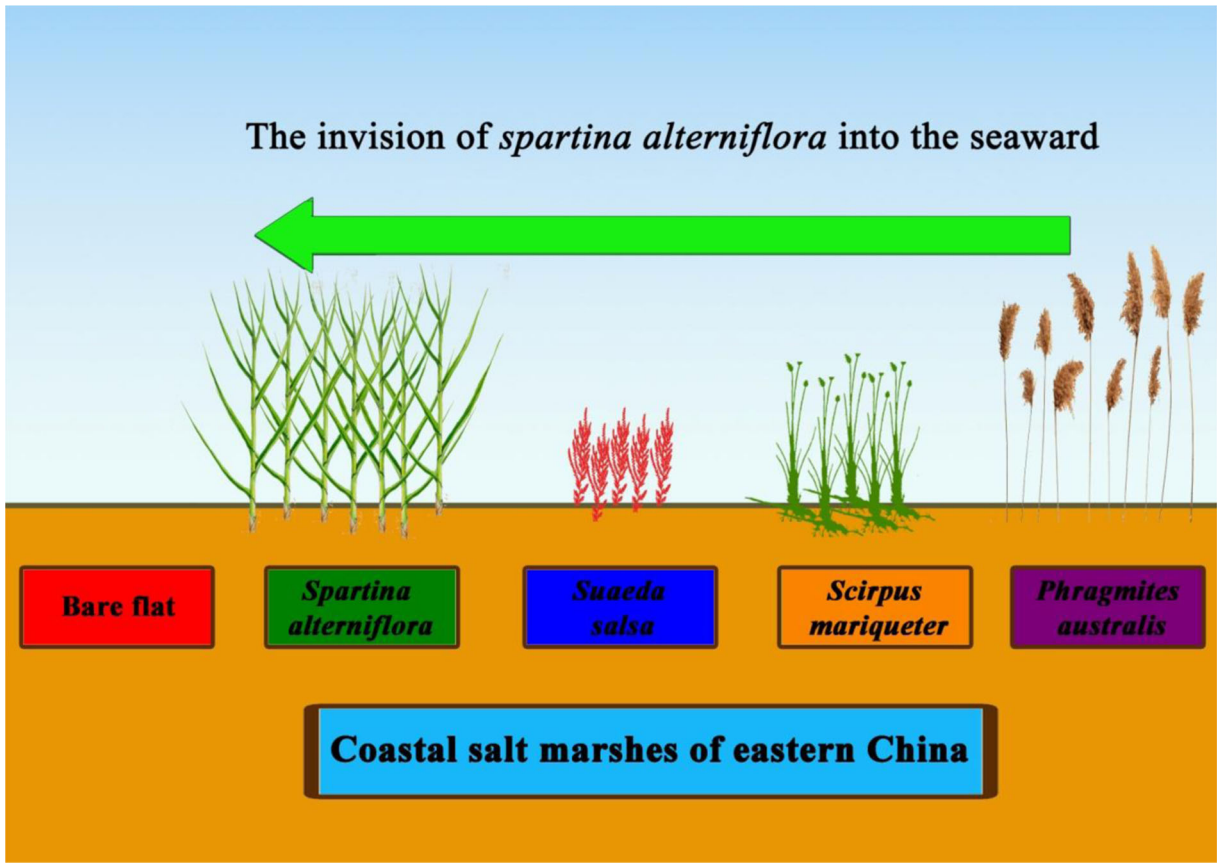

Fig. 1 Vegetation succession types in the Jiangsu Yancheng Wetland National Nature Reserve for Rare Birds of China, from sea to inland including bare flat, *S. alterniflora*, *S. salsa*, *S. mariqueter*, and *P. australis* communities. The seaward invaded region of *S. alterniflora* was originally bare flat that was devoid of vegetation

protocol. The abundance of soil bacteria was quantified via the qPCR analysis of the V3 + V4 regions of the 16S rRNA gene with the 338F primer (5′-ACTCCTACGGGAGGCAGCA-3′) and 806R primer (5′- GGACTACHVGGGTWTCTAAT-3′) (Fierer et al. 2005). The DNA template was diluted five times prior to amplification. A reaction volume of 25 μl included 12.5 μl of SYBR Green qPCR Master Mix (2 X) (Applied Biosystems), 2 μl of template DNA, 0.5 μl of 10 μM forward and reverse primers, and 9.5 μl of ddH_2O. The 16S rRNA gene was amplified using an ABI 7500 real-time PCR system (Applied Biosystems, Foster City, CA, USA). The cycling conditions were as follows: 10 min at 95 °C and 40 cycles of 15 s at 95 °C, and 1 min at 60 °C. All real-time PCR reactions were run in triplicate on the DNA extracted from each soil sample. The 16S rRNA copy number was calculated using the formula described by Sun et al. (2015).

16S rRNA amplification for Illumina MiSeq sequencing

The V3 + V4 regions of the bacterial 16S rRNA gene were amplified via PCR, which was performed using the 338F primer (5′- ACTCCTACGGGAGGCAGCA-3′) and 806R primer (5′-GGACTACHVGGGTW TCTAAT-3′) (Mori et al. 2013; Wang et al. 2018). The PCR reactions were conducted using an ABI GeneAmp® 9700 PCR System (Applied Biosystems, Foster City, USA), under the following program: 95 °C for 3 min; 27 cycles of 95 °C for 30 s, 55 °C for 30 s, 72 °C for 45 s, and 72 °C for 10 min. The PCR reactions were performed in triplicate in a 20 μl volume that contained 2 μl of 10 × buffer, 2 μl of 2.5 mM dNTPs, 0.8 μl forward primer (5 μM), 0.8 μl reverse primer (5 μM), 0.2 μl recombinant Taq polymerase, 0.2 μl bovine serum albumin, 1.25 μl of template DNA (10 ng), and

12.75 μl of ddH_2O. The amplicons were visualized on a 2% agarose gel and the bands were excised and purified using the AxyPrep DNA Gel Extraction kit (Axygen Biosciences, Union City, CA, USA) according to the manufacturer's instructions, and then quantified using QuantiFluor-ST (Promega, Madison, WI, USA). The purified amplicons were pooled in equimolar ratios and subjected to paired-end sequencing (2 × 300), which was performed with the Illumina MiSeq PE300 platform (Majorbio Bio-Pharm Technology Co., Ltd., Shanghai, China).

Pyrosequence data analysis

Sequences from the Illumina MiSeq platform were processed using the Quantitative Insights Into Microbial Ecology (QIIME; v. 1.8.0) software package (Caporaso et al. 2010). Raw FASTQ files were demultiplexed, quality-filtered by Trimmomatic v. 0.32 (Bolger et al. 2014), and merged by FLASH under the following standards: (a) low quality regions of sequence reads, i.e., an average quality value of <20 over a 50 bp sliding window, and sequences containing homopolymer regions (>6 bp) were removed from the paired-end sequence read files (Bolger et al. 2014); (b) The primers were closely matched, allowing for two mismatches of nucleotide sequences, and reads containing ambiguous bases were eliminated; (c) Sequences with an overlap longer than 10 bp were merged on the basis of their overlap sequence. A total of 1,022,685 reads were obtained from 20 samples using Illumina MiSeq sequencing. To obtain an equivalent sequencing depth for downstream analyses, the minimum number of reads (i.e., 38,352) in all of the subsets from each sample was randomly selected, using the Mothur program (v. 1.30.2), which ultimately yielded 767,040 reads from the 20 soil samples. The subsampled sequences were grouped by operational taxonomic units (OTUs) at 97% similarity levels using UPARSE v. 7.1 (Edgar 2013). A total of 64,749 OTUs were obtained from the 20 soil samples. The OTU richness (the total number of measured OTUs), Chao's species richness estimator (Chao1), abundance-based coverage estimator (ACE), Shannon's and Simpson's diversity indices (i.e., Shannon and Simpson), rarefaction curves for OTUs and Shannon-Wiener curves were calculated to compare soil bacterial community richness and diversity using the Mothur program v. 1.30.1 (Schloss et al. 2009). The taxonomic classifications of phylum, class, family, and genus were assigned using a Ribosomal Database Project (RDP) Bayesian classifier v. 2.2 (Wang et al. 2007). Subsequently, the tags were compared to the bacterial 16S rRNA Silva reference database v. 119 to detect chimeric sequences (Cole et al. 2009). Principal coordinates analysis (PCoA) of the OTUs data was performed using R software v. 3.2.2 (McMurdie and Holmes 2013). The Bray-Curtis similarity index was calculated using the OTU reads, and hierarchical clustering was determined from a β-diversity distance matrix using the QIIME software package v. 1.8.0 (Bokulich et al. 2013). Linear discriminant analysis (LDA) effect size (LEfSe) was employed to identify the potential statistically significant taxa of the soil bacterial communities between the different treatments using LEfSe (Segata et al. 2011). A cladogram showing the phylogenetic distribution of microbial lineages associated with the five types of plant communities with LDA values of 4 or higher was determined by LEfSe using R software v. 3.2.2.

Statistical analysis

The data were analyzed using SPSS v.19 software (SPSS Inc., Chicago, IL, USA). One-way analysis of variance (ANOVA) was used to evaluate the statistical significance of the effects of plant communities on the soil physicochemical properties, OTU richness, bacterial community richness, and diversity indices, relative abundance of dominant bacterial phylum, class, family, and genus, and the abundances of total bacteria based on 16S rRNA copy numbers. The significance of differences between group means was evaluated with Tukey's honest significant difference test at $P < 0.05$. Redundancy analysis (RDA) was conducted to assess the relative effects of environmental variables on soil bacteria composition at the phylum and class levels using CANOCO software for Windows 4.5. Those variables that were statistically significant with $P < 0.05$ of RDA were evaluated by the Monte Carlo permutation test (499 permutations). We used Pearson's correlation analysis to evaluate the relationships of soil bacterial abundance, diversity, and community composition with soil properties at the phyla level.

Results

Soil physicochemical characteristics

Soil moisture and salinity were significantly higher, whereas the pH was significantly lower in the *S. alterniflora* soil in contrast to bare flat, *S. salsa*, *S. mariqueter*, and *P. australis* soils (Table 1). SOC and SON concentrations were highest in the *S. alterniflora* soil, followed by *S. salsa*, *S. mariqueter*, *P. australis*, and bare flat soils (Table 1). The WSOC concentration in the *S. alterniflora* soil was significantly higher than that of the bare flat, *S. salsa*, *S. mariqueter*, and *P. australis* soils (Table 1).

Soil bacterial abundance and community diversity

The soil bacterial abundance was evaluated using the qPCR amplification of 16S rRNA gene. The 16S rRNA gene copy numbers were 3.14×10^7 copies/g for bare flat, 2.77×10^{10} copies/g for *S. alterniflora*, 1.77×10^8 copies/g for *S. salsa*, 1.98×10^8 copies/g for *S. mariqueter*, and 2.40×10^7 copies/g for *P. australis* soils (Fig. S1). *S. alterniflora* invasion significantly affected ($P < 0.01$) soil bacterial abundance (Fig. S1). The total bacterial abundance was significantly higher for the *S. alterniflora* soil than for the bare flat, *S. salsa*, *S. mariqueter*, and *P. australis* soils, with no statistical differences observed between these last four communities (Fig. S1).

The OTU richness, and species richness indices (i.e., ACE and Chao1) of the *S. alterniflora* soil were significantly higher than that of the bare flat, *S. salsa*, *S. mariqueter*, and *P. australis* soils (Table 2). Meanwhile, the *S. alterniflora* soil exhibited the steepest rarefaction curve with the highest taxon richness (Fig. S2a). Further, the Shannon diversity index was highest and Simpson diversity index was lowest in the *S. alterniflora* soil (Table 2). The Shannon-Wiener curves approached a plateau at less than 10,000 reads per sample (Fig. S2b), which also revealed that the highest diversity of bacterial communities was found in the *S. alterniflora* soil (Fig. S2b). The coverage of each sample ranged from 96.68 to 97.99% among the plant communities (Table 2).

Taxonomic composition of soil bacterial communities

At the phylum level, the soil bacterial communities were dominated by Proteobacteria (45.43% – 53.00%), Chloroflexi (5.46% – 14.48%), Bacteroidetes (3.59% – 13.67%), Firmicutes (2.03% – 10.84%), Acidobacteria (2.60% – 8.17%), Nitrospirae (0.78% – 5.45%), and Actinobacteria (1.66% – 5.06%) across all soil samples (Fig. 2). Other bacterial taxa had lower relative abundances (Fig. 2). Proteobacteria was the most dominant phylum in all of the communities (Fig. 2). The relative abundances of Chloroflexi, Bacteroidetes, Chlorobil, Latescibacteria, and Spirochaetae were highest in the *S. alterniflora* soil among the plant communities (Fig. 2). The highest relative abundances of Proteobacteria and Cyanobacteria in the bare flat soil were significantly higher than those in the *S. alterniflora*, *S. salsa*, *S. mariqueter*, and *P. australis* soils (Fig. 2). The relative abundances of Acidobacteria and Gemmatimonadetes

Table 1 Physicochemical characteristics of soils (0–30 cm depth) (mean ± SE, $n = 4$) in the bare flat, *S. alterniflora*, *S. salsa*, *S. mariqueter*, and *P. australis* communities in the coastal salt marshes of Eastern China

Community	Moisture (%)	pH	Salinity (%)	SOC (g kg^{-1})	WSOC (mg kg^{-1})	SON (g kg^{-1})
Bare flat	28.00 ± 1.11^{d}	8.38 ± 0.03^{b}	0.59 ± 0.01^{b}	0.85 ± 0.10^{d}	37.78 ± 4.77^{b}	0.08 ± 0.02^{d}
S. alterniflora	83.02 ± 2.64^{a}	7.65 ± 0.04^{c}	1.73 ± 0.20^{a}	14.23 ± 1.10^{a}	76.24 ± 7.97^{a}	0.84 ± 0.06^{a}
S. salsa	37.24 ± 0.79^{b}	8.96 ± 0.05^{a}	0.24 ± 0.02^{c}	6.33 ± 0.71^{b}	26.53 ± 3.47^{b}	0.38 ± 0.03^{b}
S. mariqueter	33.60 ± 1.43^{b}	8.90 ± 0.07^{a}	0.16 ± 0.01^{c}	6.77 ± 0.40^{b}	42.68 ± 7.85^{b}	0.40 ± 0.03^{b}
P. australis	31.76 ± 0.51^{cd}	9.01 ± 0.04^{a}	0.18 ± 0.02^{c}	3.05 ± 0.21^{c}	38.91 ± 6.68^{b}	0.21 ± 0.02^{c}
Source of variation						
Community	**	**	**	***	*	**

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (One-way ANOVA). Different superscript lower case letters indicate statistically significant differences at the $\alpha = 0.05$ level among the plant communities, using Tukey's honestly significant difference test. SOC: soil organic carbon; WSOC: soil water-soluble organic carbon; SON: soil organic nitrogen

Table 2 Number of sequences analyzed, and observed bacterial community richness and diversity indices (mean ± SE, n = 4) for the bare flat, *S. alterniflora*, *S. salsa*, *S. mariqueter*, and *P. australis* soils obtained for clustering at a 97% identity

Community	Reads	OTU richness	Richness estimators		Diversity indices		Coverage
			Ace	Chao1	Shannon	Simpson	
Bare flat	38,352	3240 ± 195^{b}	3801 ± 285^{b}	3797 ± 299^{b}	6.48 ± 0.13^{b}	0.0077 ± 0.0016^{ab}	0.9799 ± 0.0024^{a}
S. alterniflora	38,352	4091 ± 79^{a}	5289 ± 93^{a}	5344 ± 102^{a}	7.00 ± 0.12^{a}	0.0044 ± 0.0013^{b}	0.9668 ± 0.0005^{b}
S. salsa	38,352	3018 ± 108^{b}	3877 ± 144^{b}	3857 ± 161^{b}	6.36 ± 0.15^{b}	0.0069 ± 0.0011^{ab}	0.9761 ± 0.0009^{a}
S. mariqueter	38,352	2818 ± 204^{b}	3605 ± 273^{b}	3586 ± 262^{b}	6.35 ± 0.10^{b}	0.0068 ± 0.0010^{ab}	0.9782 ± 0.0019^{a}
P. australis	38,352	3021 ± 63^{b}	3718 ± 87^{b}	3694 ± 84^{b}	6.37 ± 0.09^{b}	0.0094 ± 0.0020^{a}	0.9786 ± 0.0007^{a}
Source of variation							
Community		*	*	*	**	n.s.	***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s.: not significant (One-way ANOVA). Different superscript lower case letters indicate statistically significant differences at the $\alpha = 0.05$ level among the plant communities, using Tukey's honestly significant difference test. Reads are the high-quality sequences after filtering and normalization; Richness estimators, diversity indices and coverage were calculated using the Mothur program. OTU richness: the total number of measured operational taxonomic units (OTUs)

in the *S. salsa* soil were significantly higher than those in the *S. alterniflora*, *S. mariqueter*, *P. australis*, and bare flat soils (Fig. 2). The relative abundances of Actinobacteria and Firmicutes were most abundant in the *S. mariqueter* and *P. australis* soils, respectively (Fig. 2).

At the class level, the relative abundances of ε-proteobacteria, Anaerolineae, Flavobacteriia, Bacteroidia, Spirochaetes, Clostridia, Chlorobia, Chloroflexi_unclassified, and Chloroflexi_uncultured were highest in the *S. alterniflora* soil among the plant communities (Table 3). The relative abundances of γ-proteobacteria, δ-proteobacteria, Sphingobacteriia, and Cyanobacteria in the bare flat soil were significantly higher than those in the other communities (Table 3). The relative abundances of α-proteobacteria and Nitrospira in the *S. salsa, S. mariqueter* and *P. australis* soils were significantly higher than those in the *S. alterniflora* and bare flat soils (Table 3). Additionally, the *S. salsa* soil exhibited higher relative abundances of Acidobacteria and Gemmatimonadetes, in contrast to the other communities (Table 3). The highest relative abundances of Actinobacteria and Bacilli were found in the *S. mariqueter* and *P. australis* soils among the plant communities, respectively (Table 3).

At the family level, the *S. alterniflora* soil revealed higher relative abundances of Anaerolineaceae, Desulfobacteraceae, Helicobacteraceae, Rhodobacteraceae, Psychromonadaceae, Spirochaetaceae, and Desulfarculaceae compared to the *S. salsa*, *S. mariqueter*, *P. australis*, and bare flat soils (Table S1). The relative abundance of Rhodospirillaceae was highest in the *S. salsa* soil, whereas the highest relative abundance of Bacillaceae, Chromatiaceae and Streptococcaceae were observed in the *P. australis* soil among the plant communities (Table S1).

At the genus level, the relative abundances of *Psychromonas* and *Sulfurovum* were most abundant in the *S. alterniflora* soil (Table S2). The relative abundances of *Bacillus* and *Lactococcus* were most highly represented in the *P. australis* soil (Table S2). The highest relative abundance of the *marine benthic group* was found in the bare flat soil, while the lowest relative abundance of the *terrestrial group* was observed in the *S. alterniflora* and bare flat soils (Table S2).

Bacterial groups with statistical differences

LEfSe was employed to identify potentially discriminating taxa among the plant communities (Figs. 3 and S3). We combined the LDA values of five types of plant communities to determine their differences with other bacterial groups (Fig. 3). When the results of the cladogram and the LDA values were combined, there were seven groups of bacteria enriched in the *S. alterniflora* soil, namely, Chloroflexi (e.g., Anaerolineae, Anaerolineales and Anaerolineaceae), Bacteroidetes (from phylum to class), Flavobacteria (from class to family; within Bacteroidetes), Alteromonadales (within γ-proteobacteria), Psychromonadaceae (within

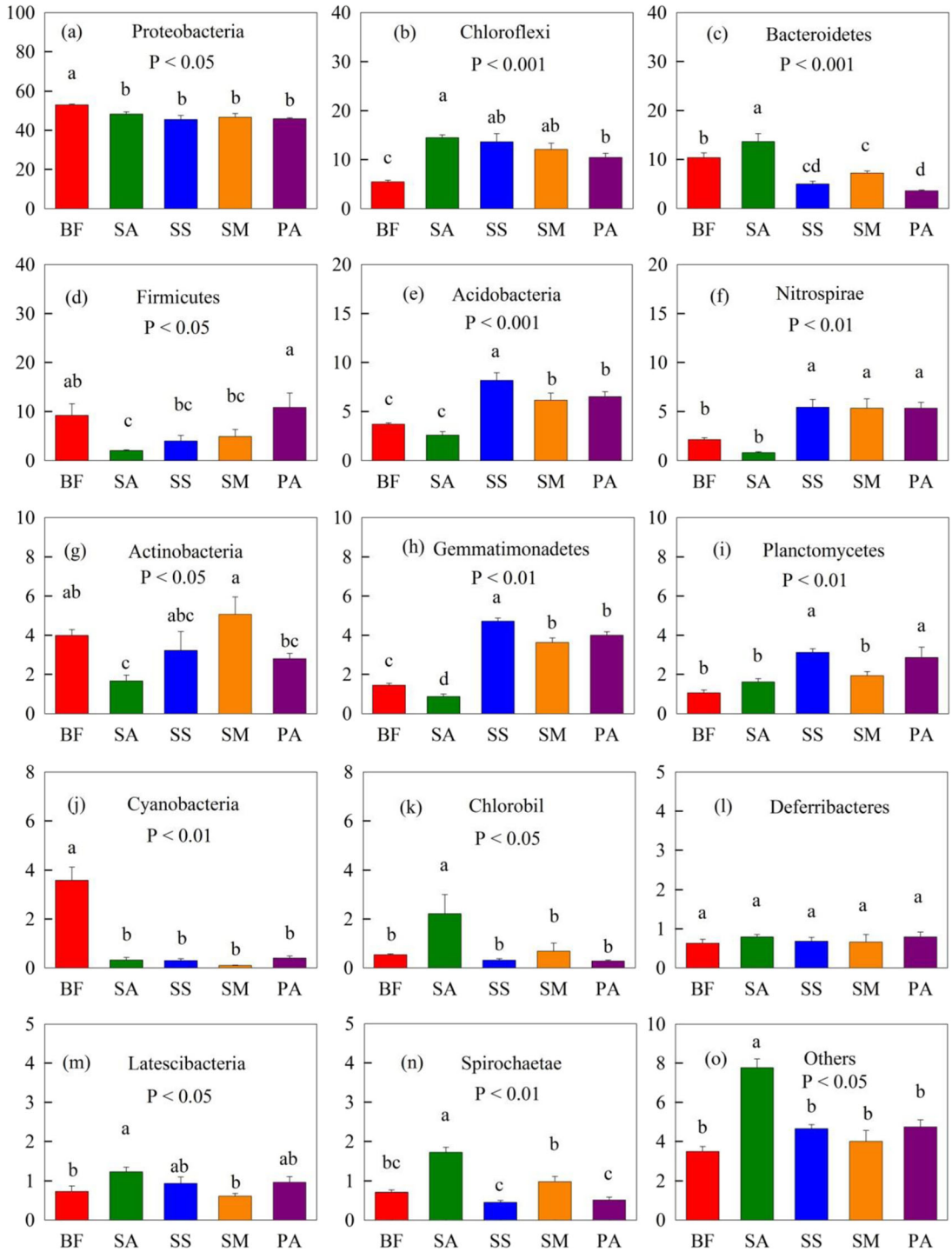

Fig. 2 Relative abundance (% of individual taxonomic groups) of the dominant bacterial phyla (mean ± SE, n = 4) present in the microbial communities of the bare flat, *S. alterniflora*, *S. salsa*, *S. mariqueter*, and *P. australi* soils (0–30 cm depth). Different letters indicate statistically significant differences at the $\alpha = 0.05$ level among the plant communities, using Tukey's honestly significant difference test in the One-way ANOVA. BF = bare flat; SA = *Spartina alterniflora*; SS = *Suaeda salsa*; SM = *Scirpus mariqueter*; and PA = *Phragmites australis*

Table 3 Relative abundances (% of individual taxonomic groups) of the dominant bacterial classes (mean ± SE, n = 4) present in the microbial communities of the bare flat, *S. alterniflora*, *S. salsa*, *S. mariqueter*, and *P. australis* soils (0–30 cm depth)

Class	Community					Source of variation
	Bare flat	*S. alterniflora*	*S. salsa*	*S. mariqueter*	*P. australis*	Community
δ-proteobacteria	20.52 ± 0.72^{a}	17.40 ± 1.07^{b}	16.60 ± 1.35^{b}	16.29 ± 0.71^{b}	17.66 ± 0.38^{b}	*
γ-proteobacteria	22.44 ± 0.31^{a}	16.13 ± 1.40^{b}	12.03 ± 0.42^{c}	12.00 ± 0.69^{c}	13.92 ± 0.32^{bc}	**
α-proteobacteria	3.86 ± 0.31^{d}	7.13 ± 0.85^{c}	13.27 ± 0.46^{a}	13.40 ± 0.41^{a}	8.86 ± 0.17^{b}	**
β-proteobacteria	2.19 ± 0.16^{ab}	1.26 ± 0.11^{bc}	0.85 ± 0.11^{c}	2.46 ± 0.67^{a}	1.50 ± 0.15^{abc}	*
ε-proteobacteria	1.77 ± 0.29^{b}	6.07 ± 1.10^{a}	0.63 ± 0.11^{b}	0.98 ± 0.40^{b}	0.49 ± 0.12^{b}	**
Anaerolineae	3.26 ± 0.35^{c}	10.69 ± 0.77^{a}	7.92 ± 1.53^{ab}	7.30 ± 1.54^{ab}	4.89 ± 0.70^{bc}	**
Bacilli	8.90 ± 2.41^{ab}	0.63 ± 0.10^{c}	3.87 ± 1.12^{bc}	4.48 ± 1.38^{bc}	10.61 ± 2.89^{a}	*
Acidobacteria	3.70 ± 0.16^{c}	2.60 ± 0.34^{c}	8.17 ± 0.77^{a}	6.17 ± 0.69^{b}	6.51 ± 0.48^{b}	***
Nitrospira	2.13 ± 0.19^{b}	0.78 ± 0.10^{b}	5.45 ± 0.79^{a}	5.34 ± 0.96^{a}	5.35 ± 0.61^{a}	**
Actinobacteria	3.99 ± 0.30^{ab}	1.66 ± 0.3^{c}	3.22 ± 0.96^{abc}	5.06 ± 0.89^{a}	2.80 ± 0.26^{bc}	*
Gemmatimonadetes	1.44 ± 0.10^{c}	0.86 ± 0.13^{d}	4.72 ± 0.16^{a}	3.62 ± 0.24^{b}	4.00 ± 0.18^{b}	**
Flavobacteriia	4.43 ± 0.62^{a}	5.09 ± 0.78^{a}	0.42 ± 0.07^{b}	0.83 ± 0.21^{b}	0.47 ± 0.08^{b}	**
Sphingobacteriia	2.33 ± 0.07^{a}	1.40 ± 0.32^{b}	1.22 ± 0.09^{b}	1.08 ± 0.12^{b}	1.03 ± 0.07^{b}	**
Bacteroidia	0.68 ± 0.06^{b}	2.53 ± 0.28^{a}	0.38 ± 0.02^{b}	1.33 ± 0.19^{a}	0.28 ± 0.02^{b}	**
Cyanobacteria	3.58 ± 0.54^{a}	0.32 ± 0.11^{b}	0.30 ± 0.08^{b}	0.10 ± 0.01^{b}	0.40 ± 0.09^{b}	**
Spirochaetes	0.71 ± 0.06^{bc}	1.72 ± 0.13^{a}	0.45 ± 0.05^{c}	0.98 ± 0.13^{b}	0.51 ± 0.07^{c}	**
Clostridia	0.27 ± 0.03^{bc}	1.40 ± 0.16^{a}	0.09 ± 0.02^{c}	0.37 ± 0.07^{b}	0.22 ± 0.04^{bc}	**
Deferribacteres	0.62 ± 0.10^{a}	0.80 ± 0.06^{a}	0.68 ± 0.10^{a}	0.66 ± 0.19^{a}	0.79 ± 0.12^{a}	n.s.
Chloroflexi_unclassified	0.27 ± 0.02^{b}	0.72 ± 0.17^{a}	0.44 ± 0.04^{b}	0.45 ± 0.04^{b}	0.35 ± 0.01^{b}	**
Chloroflexi_uncultured	0.61 ± 0.05^{b}	1.16 ± 0.13^{a}	0.07 ± 0.03^{c}	0.12 ± 0.09^{c}	0.06 ± 0.02^{c}	**
Chlorobia	0.04 ± 0.01^{b}	1.30 ± 0.83^{a}	0.02 ± 0.01^{b}	0.04 ± 0.02^{b}	0.02 ± 0.01^{b}	*
Others	12.26 ± 0.68^{b}	18.35 ± 0.43^{a}	19.20 ± 0.38^{a}	16.94 ± 1.20^{a}	19.28 ± 1.82^{a}	*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s.: not significant (One-way ANOVA). Different superscript lower case letters indicate statistically significant differences at the $\alpha = 0.05$ level among the plant communities, using Tukey's honestly significant difference test

Alteromonadales), ε-proteobacteria (e.g., Campylobacterales and Helicobacteraceae), and Desulfobacteraceae (within δ-proteobacteria) (Figs. 3 and S3).

The bacterial taxa enriched in the bare flat soil included proteobacteria, γ-proteobacteria (e.g., Xanthomonadales and Pseudomonadales), Firmicutes, Bacilli (from class to family; within Firmicutes), Lactobacillales (an order within Bacilli), Streptococcaceae (a family within Lactobacillales), the marine benthic group, Desulfobacterales (an order within δ-proteobacteria), Cyanobacteria (from phylum to family), and Actinobacteria (from phylum to class) (Figs. 3 and S3). The bacterial communities of the *S. salsa* soil were enriched with α-proteobacteria (e.g., Rhoodospirillales and Rhodospirillaceae), Acidobacteria (from phylum to class), Nitrospirae (from phylum to genus), Gemmatimonadetes (from phylum to class), Chromatiales (from order to family; within γ-proteobacteria), the terrestrial group, and Planctomycetes (Figs. 3 and S3). The *S. mariqueter* soil was abundant in α-proteobacteria (e.g., Rhodospirillales, Rhodospirillaceae and Rhodobacterales), Actinobacteria (from phylum to class), and Acidimicrobiales (an order within Actinobacteria) (Figs. 3 and S3). The bacterial taxa enriching the *P. australis* soil were Firmicutes, Bacilli (from class to family; within Firmicutes), Lactobacillales (an order within Bacilli), Streptococcaceae (a family within Lactobacillales), *Lactococcus* (a genus within Streptococcaceae), Nitrospirae (from phylum to genus), and Chromatiales (from order to family; within γ-proteobacteria) (Figs. 3 and S3).

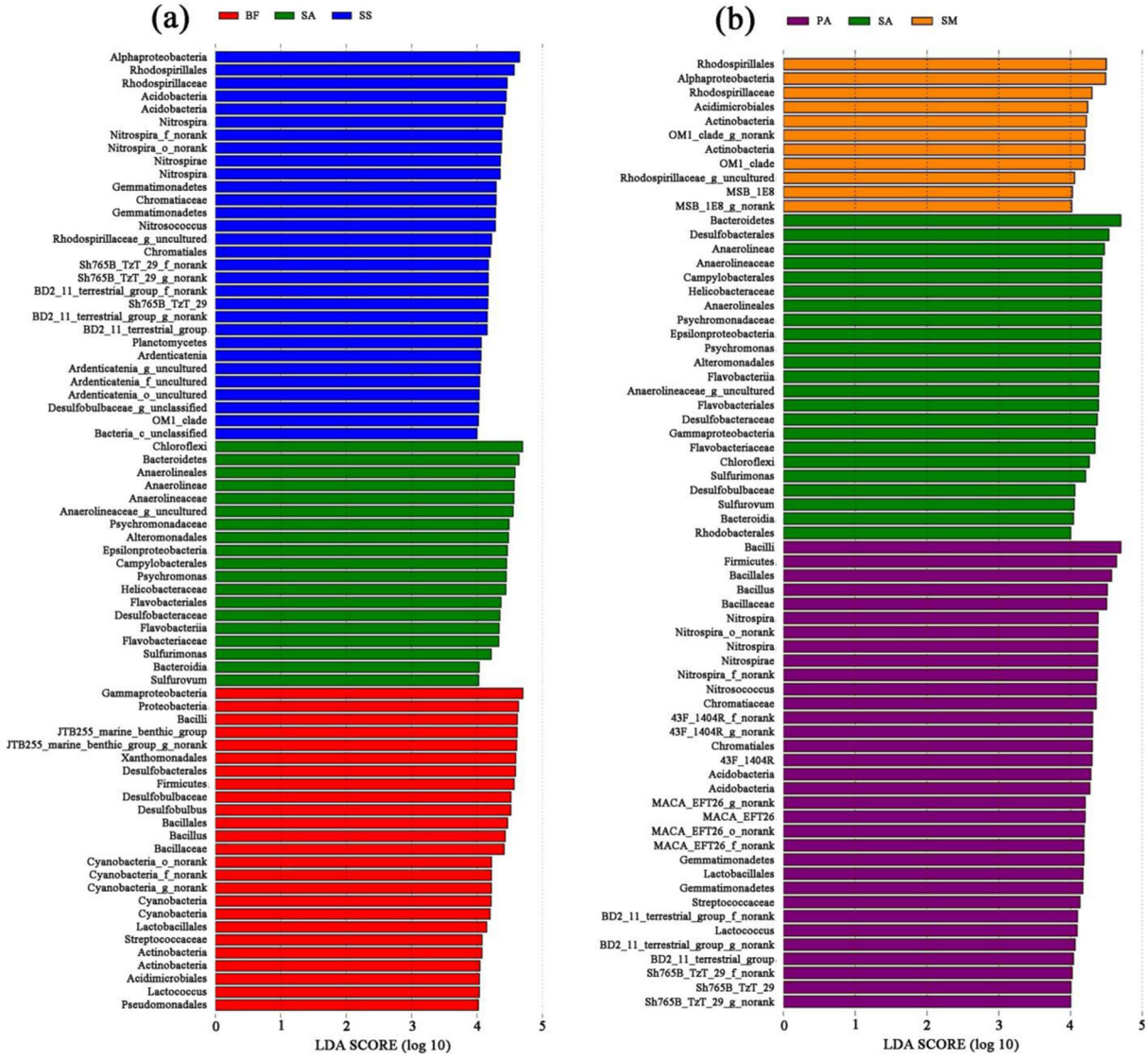

Fig. 3 Indicator microbial groups within the five types of communities with LDA values higher than 4. See Fig. 2 for abbreviations

Beta diversity of soil bacterial communities

At the OTUs level, the results of PCoA and the Bray-Curtis similarity indices analyses revealed that the different soil locations of *S. alterniflora* communities were clustered and distinct from the other soil types (Fig. 4), which indicated that the *S. alterniflora* soil contained unique bacterial communities. The different locations of bare flat soils were also clustered and distinct from those of the other soils (Fig. 4a). In contrast, the different locations of the *S. salsa*, *S. mariqueter*, and *P. australis* soils were close together, demonstrating that their bacterial community composition was similar (Fig. 4a). The composition of bacterial communities in the *S. alterniflora* and bare flat soils were more similar to each other, than those of the *S. salsa*, *S. mariqueter*, and *P. australis* soils (Fig. 4b).

Important driving factors for soil bacterial communities

Six environmental variables (i.e., soil moisture, pH, salinity, SOC, WSOC, and SON) explained 71.7% and 77.0% of the total changes in the composition of soil bacterial communities at the phylum and class levels, respectively (Fig. 5). The results of Monte Carlo permutation tests ($P < 0.05$) revealed that variations in the

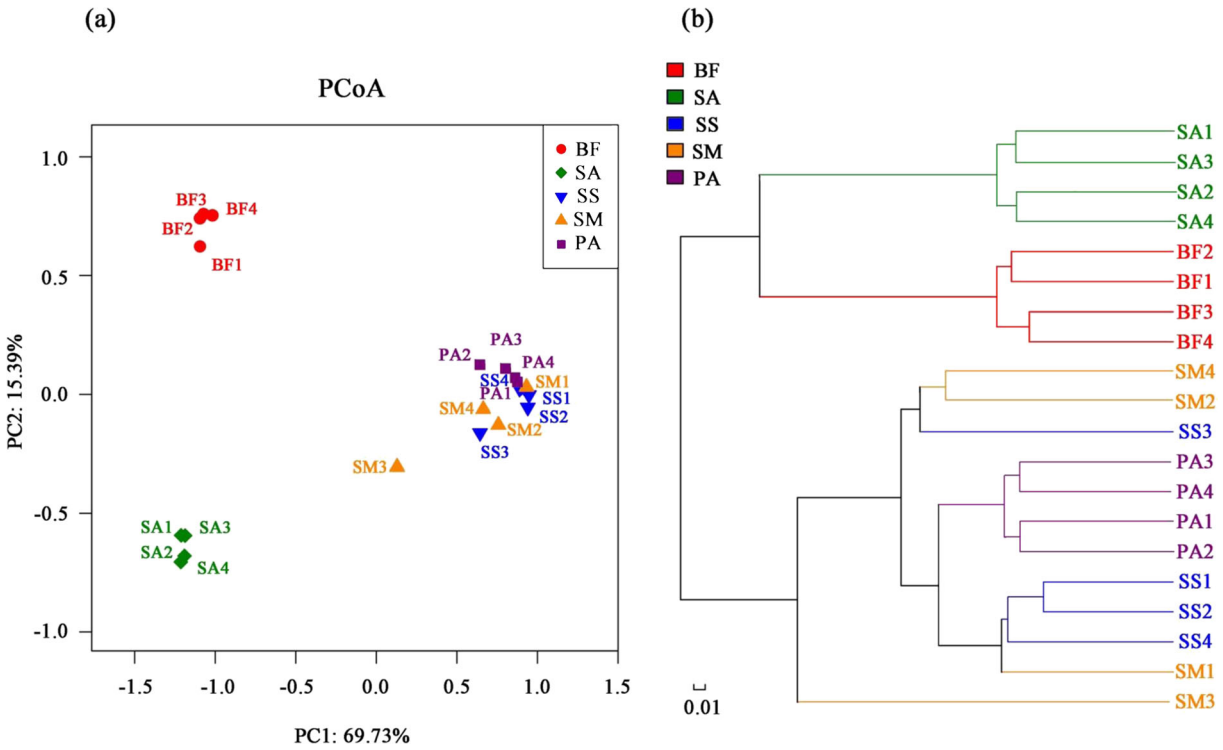

Fig. 4 (a) Principal coordinates analysis (PCoA) and (b) Clustering of samples. Bray-Curtis similarity index was calculated using OTU reads, and hierarchical clustering was calculated using the β-diversity distance matrix with QIIME. See Fig. 2 for abbreviations

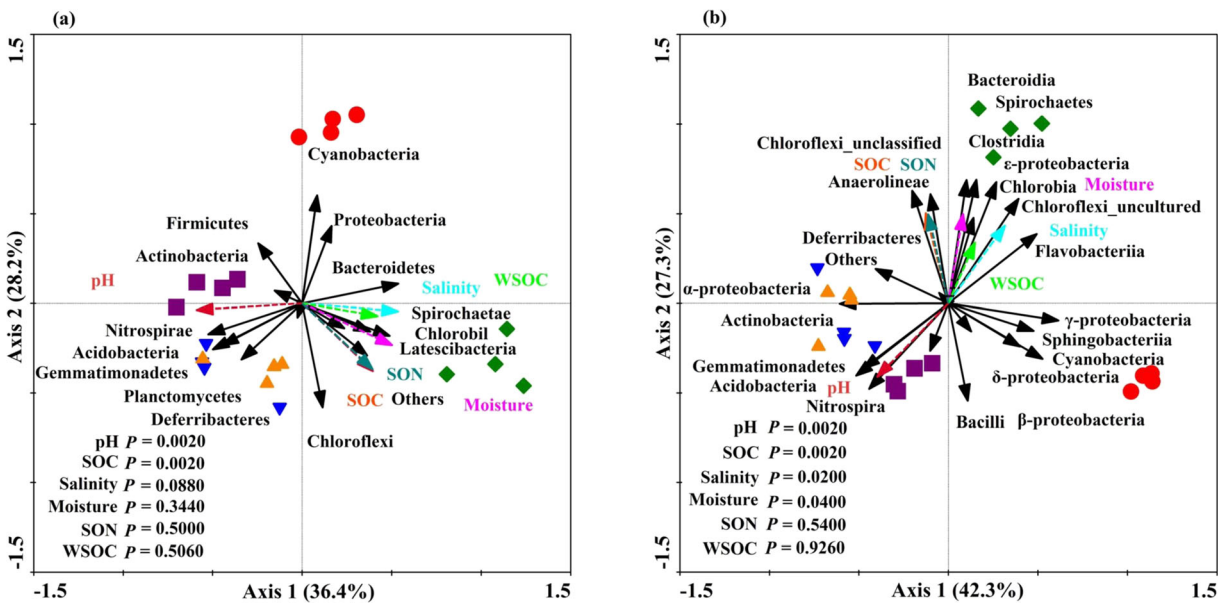

Fig. 5 Redundancy analysis (RDA) diagram illustrating the relationships between the compositions of soil bacterial communities at the phylum-level (a) and class-level (b) from different sampling sites under variable environments. Explanatory variables are shown via different arrows: soil bacterial community composition by solid black arrows; and the variables of soil physiochemical properties by colored arrows: soil moisture, pH, salinity, soil organic carbon (SOC), soil water-soluble organic carbon (WSOC), and soil organic nitrogen (SON). Red circles represent bare flat soil, green diamonds represent *S. alterniflora* soil, blue triangles represent *S. salsa* soil, orange triangles represent *S. mariqueter* soil, and purple squares represent *P. australis* soil

composition of soil bacterial communities at the phylum level were closely related to pH ($F = 9.69$, $P = 0.002$) and SOC ($F = 12.11$, $P = 0.002$) (Fig. 5a). However, changes in the composition of soil bacterial communities at the class level were intimately associated with soil pH ($F = 8.75$, $P = 0.002$), SOC ($F = 17.11$, $P = 0.002$), salinity ($F = 3.19$, $P = 0.020$), and soil moisture ($F = 2.73$, $P = 0.040$) (Fig. 5b). The most significant variations (36.4% and 42.3%), were explained by the total variation in the composition of soil bacterial communities in Axis 1 (Fig. 5). Axis 2 explained 28.2% and 27.3% of the total variations of the composition of soil bacterial communities at the phylum and class levels, respectively (Fig. 5). Pearson's correlation analysis revealed that variations in the bacterial community abundance (as determined by the 16S rRNA gene copy number), OTU richness, Ace, Chao1 and Shannon were highly correlated with soil moisture, WSOC, SOC, and SON (Table S3). The relative abundance of *Bacteroidetes* was strongly associated with WSOC, soil moisture and salinity (Table S3). Further, the relative abundances of Chloroflexi and Chlorobil were highly correlated to SOC, SON, and soil moisture (Table S3). The relative abundances of Acidobacteria, Nitrospirae, and Gemmatimonadetes had negative correlation with WSOC, soil moisture, and salinity (Table S3).

Discussion

Invasion by *Spartina alterniflora* significantly altered the abundance and diversity of soil bacteria in the coastal zone of Eastern China (Fig. S1; Table 2). In this study, the most enriched total bacterial abundance, the highest OTU richness, species richness (i.e., ACE and Chao1), and diversity (the highest Shannon and the lowest Simpson indices, respectively) of bacterial communities were observed in the *S. alterniflora* soil (Fig. S1; Table 2). This indicated that *S. alterniflora* invasion greatly enhanced the abundance of soil bacteria, as well as the richness and diversity of soil bacterial communities, in contrast to the bare flat and native plant communities. These results further demonstrated that plant invasion can shift the abundance and diversity of soil bacteria (Piper et al. 2015; Rodríguez-Caballero et al. 2017; Xiang et al. 2018). Soil nutrient substrates (e.g., WSOC, SOC, and SON) have been reported to serve as the critical drivers of soil bacterial abundance and diversity (Orwin et al. 2016; Santonja et al. 2017), as they provide vast quantities of available nutrients to stimulate the growth of soil bacteria, which results in higher bacterial abundance and diversity, in contrast to fungal communities (Yu et al. 2019). Numerous investigations have revealed that *S. alterniflora* invasion markedly enhanced WSOC, SOC, and SON levels by increasing plant residue inputs compared to native plant communities (Liao et al. 2007; Yang et al. 2013, 2017), which was consistent with the observations of this study (Table 1). Thus, the significantly increased soil bacterial abundance and diversity following *S. alterniflora* invasion were primarily derived from the highest WSOC, SOC, and SON levels (Fig. S1; Tables 1 and 2), which provided the most enriched nutrient substrates for the proliferation of bacteria (Yu et al. 2019). This hypothesis was supported by Pearson's correlation analysis, which showed that the abundance and diversity (except for the Simpson index) of soil bacteria were closely correlated with SOC, SON, and WSOC (Table S3). Additionally, soil bacterial communities are profoundly affected by the physicochemical properties of soils (Bainard et al. 2016; Nguyen et al. 2018). Soil moisture has been considered to be a crucial factor that mediates soil bacterial communities (Banerjee et al. 2016; Keet et al. 2019). Nakamura et al. (2003) concluded that high soil moisture was beneficial for the growth of bacteria. In this study, the highest soil moisture was observed in the *S. alterniflora* soil, as it was subjected to frequent inundation by semidiurnal tides (Table 1; Yuan et al. 2015), which likely facilitated bacterial growth (Nakamura et al. 2003), and ultimately promoted soil bacterial abundance and diversity (Fig. S1; Table 2). Salinity is considered to be an important determinant of bacterial communities in saline soils and aquatic systems (Gao et al. 2015). High salinity can alter the osmotic potential of soils, leading to decreased microbial biomass and alterations in microbiome profiles (Chowdhury et al. 2011; Kamble et al. 2014). Xi et al. (2014) confirmed that increased soil salinity can restrict the growth of heterotrophic bacteria. In this study, the greatest soil salinity was observed in the *S. alterniflora* soil among the plant communities (Table 1), which corresponded to the highest soil bacterial abundance and diversity (Fig. S1; Table 2). We deduced that the promotional effects of increased SOC, SON, WSOC, and soil moisture on bacterial

growth likely offset the inhibitory effects of high soil salinity on bacterial growth in the *S. alterniflora* soil (Table 1). This ultimately increased soil bacterial abundance and diversity following *S. alterniflora* invasion (Fig. S1; Table 2).

S. alterniflora invasion not only significantly altered soil bacterial abundance and diversity (Fig. S1; Table 2), but also modified the composition of soil bacterial communities in contrast to the bare flat, *S. salsa*, *S. mariqueter*, and *P. australis* soils (Tables 3, S1, and S2; Figs. 2, 3, and S3). PCoA and Bray-Curtis similarity indices revealed that different soil locations of *S. alterniflora* communities were clustered and distinct from other plant communities (Fig. 4), which confirmed that *S. alterniflora* soil contained a unique bacterial community composition. In this study, RDA analyses clearly indicated that variations in the composition of soil bacterial communities at the phylum and class levels were the most intimately related to soil pH (Fig. 5), which further verified that soil pH was an overarching driving factor for changes in the composition of soil bacterial communities (Rousk et al. 2010; Bainard et al. 2016). In addition, the composition of soil bacterial communities was highly associated with SOC, soil salinity, and moisture (Fig. 5). These results were supported by earlier studies, which showed that SOC (Lange et al. 2015; Bainard et al. 2016), soil salinity (Rath et al. 2019), and moisture (Banerjee et al. 2016; Keet et al. 2019) appeared to be the primary drivers for the composition of soil bacterial communities.

Proteobacteria was the predominant phylum across all plant communities (Fig. 2), while there was significant variability at the class level among the plant communities (Table 3). Specifically, ε-Proteobacteria was the most enriched in the *S. alterniflora* soil; δ- and γ-proteobacteria were most highly represented in the bare flat soil; and α-proteobacteria was most prevalent in the *S. mariqueter* and *S. salsa* soils (Table 3). *S. alterniflora* is a typical intertidal plant that invaded the middle regions of the intertidal zone in the coastal wetlands of Eastern China (Yuan et al. 2015). Intertidal sediments in China have been shown to be abundant in ε-proteobacteria (Wang et al. 2012), which was supported by our finding that the *S. alterniflora* soil was most enriched with this Proteobacteria (Table 3). This was likely due to the high relative abundance of ε-proteobacteria, which occurs more at oxic and anoxic interfaces, such as exists in these intertidal zones (Wang et al. 2012). ε-Proteobacteria are sulfur-oxidizing, nitrate-reducing chemo-lithoautotrophic bacteria that are unable to utilize most organic compounds for growth. However, they are capable of CO_2 fixation, which may contribute to the sulfur cycle in different environments (Lormières and Oger 2017). Wang et al. (2019) documented that *S. alterniflora* invasion increased soil sulfur storage compared to native plant communities in coastal China. It was reasoned that the increased sulfur storage in *S. alterniflora* soil may have been associated with the higher relative abundance of ε-proteobacteria. It was reported that marine sediments are enriched in δ- and γ-proteobacteria, which are involved in sulfate reduction under anaerobic conditions (Wang et al. 2012). In this study, the bare flat soil was the closest to the Yellow Sea of all the plant communities (Yang et al. 2017). Although the bare flat is a transition zone between the ocean and land (Yang et al. 2013), we speculated that the composition of its bacterial communities was similar to that of marine sediments (Table 3; Wang et al. 2012), since it is affected by semidiurnal tidal cycles (Yang et al. 2013). We also found that α-proteobacteria was the most enriched in *S. mariqueter* and *S. salsa* soils (Table 3). This may be explained by the preference of α-proteobacteria for habitats with very low nutrient levels (Vaz-Moreira et al. 2017). In this study, SOC, WSOC, and SON were lower in the *S. mariqueter* and *S. salsa* soils than in the *S. alterniflora* soil (Table 1), which provided the lower-nutrient environment that was conducive for the growth of α-proteobacteria. Moreover, α-Proteobacteria has been shown to be enriched in freshwater sediments (Wang et al. 2012). In this study, *S. salsa* and *S. mariqueter* salt marshes grew in high intertidal zones (Yuan et al. 2015; Yang et al. 2019), which were closer to land and possessed lower soil salinity, relative to the bare flat and *S. alterniflora* soils (Table 1). Thus, the most enriched α-proteobacteria in the *S. mariqueter* and *S. salsa* soils could be primarily attributed to lower nutrient substrate levels and soil salinity (Tables 1 and 3).

S. alterniflora soil possessed a unique bacterial community composition relative to native plant communities (Fig. 4), and had the highest relative abundance, not only of chemo-lithoautotrophic bacteria (e.g., ε-proteobacteria, Campylobacterales, Helicobacteraceae and Sulfurovum), but also of photoautotrophic bacteria (e.g., Chloroflexi, Anaerolineae, Anaerolineales and Anaerolineaceae) among the plant communities (Tables 3, S1, and S2; Figs. 2, 3, and S3). Chloroflexi

is frequently found in anoxic environments (Daquiado et al. 2016). In this study, the high moisture content of *S. alterniflora* soil provided the most favorable anoxic environment for the growth of Chloroflexi (Table 1), as was evidenced by our finding that the relative abundance of Chloroflexi was closely related to soil moisture (Table S3). Additionally, Chloroflexi can survive on cellular compounds that are released from dead biomass and metabolites (Xie et al. 2014; Cheng et al. 2017). It may be surmised that a large quantity of *S. alterniflora* materials entering the soil (Yang et al. 2013, 2017) generated additional dead biomass and metabolites, which ultimately produced more cellular compounds that promoted the survival of Chloroflexi. Generally, Chloroflexi plays a critical role in the degradation of organic matter and/or polysaccharides (Podosokorskaya et al. 2013; Xie et al. 2014). The Anaerolineae class of Chloroflexi has the capacity to degrade carbohydrates in conjunction with hydrogenotrophic methanogens (Cheng et al. 2017). Therefore, we extrapolated that the highest relative abundance of Chloroflexi and Anaerolineae in the *S. alterniflora* soil could enhance the accumulation of SOC and SON by accelerating the degradation of plant residues and/or organic matter in the coastal zone of Eastern China (Tables 3; Figs. 2, 3, and S3) (Liao et al. 2007; Yang et al. 2017).

LEfSe and ANOVA analyses revealed the significant enrichment of Bacteroidetes in the *S. alterniflora* soil, relative to the bare flat, *S. salsa*, *S. mariqueter*, and *P. australis* soils (Figs. 2, 3, and S3). Bacteroidetes are prevalent in anaerobic environments (Xu et al. 2017) and are considered as saprophytic and copiotrophic bacteria (Fierer et al. 2007; Wang et al. 2012; Lin et al. 2017) that are fast-growing and require labile C sources (Verzeaux et al. 2016). Many investigations in the literature have reported that *S. alterniflora* communities exhibit higher net primary production (Liao et al. 2007), and greater above- and below-ground biomass than native species (Yang et al. 2013). Significant *S. alterniflora* residue inputs into the soil greatly increased the nutrient substrate levels that promoted the growth of Bacteroidetes in copiotrophic environments (Table 1; Figs. 2, 3, and S3; Yang et al. 2013). Bacteroidetes were shown to degrade complex and polymeric organic matter (Thomas et al. 2011; Forss et al. 2013), while hydrolyzing polysaccharides such as cellulose and starch (Semrau 2011; Xu et al. 2017). *S. alterniflora* residues have been reported to contain more recalcitrant substances (e.g., lignin and lignocellulosic materials), and lower quality (e.g., higher C/N ratio of litter and roots) than native plants (Yang et al. 2019). It may be presumed that the increased relative abundance of Bacteroidetes following *S. alterniflora* invasion can enhance the degradation of refractory *S. alterniflora* residues, while promoting SOC and SON sequestration (Table 1; Figs. 2, 3, and S3). Interestingly, the lowest relative abundances of Acidobacteria, Actinobacteria, Nitrospirae, as well as Gemmatimonadetes were observed in the *S. alterniflora* soil among the plant communities under study (Fig. 2). Generally, Acidobacteria, Actinobacteria, Nitrospirae, and Gemmatimonadetes are considered as slow growing oligotrophic groups that thrive in soils with a low availability of resources (Pascault et al. 2013; Trivedi et al. 2013; Verzeaux et al. 2016). It was deduced that the greatly decreased relative abundances of Acidobacteria, Actinobacteria, Nitrospirae, and Gemmatimonadetes in the *S. alterniflora* soil likely resulted from the highest soil nutrient substrate levels, which provided a copiotrophic environment that restricted the growth of these oligotrophic bacteria (Table 1; Fig. 2). Currently, *S. alterniflora* is predicted to continue its rapid expansion in the future through competitive substitution in bare flat, native plant communities (e.g., *S. salsa*, *S. mariqueter*, and *P. australis*), and to dominate in the coastal zone of Eastern China (Zhang et al. 2017; Yang et al. 2019). However, potential opportunities and/or risks to belowground ecosystems, particularly soil microbial communities affected by *S. alterniflora* invasion remain poorly understood. This study demonstrated that *S. alterniflora* invasion can significantly shift soil bacterial communities (i.e., abundance, diversity and community composition) (Tables 2, 3, S1 and S2; Figs. 2, 3, S1 and S3). The mechanisms for the changes in soil bacterial communities were primarily derived from the effects of substantially increased soil nutrient substrates levels (e.g., SOC, SON, and WSOC), and the significant alteration of soil physicochemical properties (e.g., soil pH, moisture, and salinity) following *S. alterniflora* invasion in the coastal zone of Eastern China (Table 1 and S3; Fig. 5; Santonja et al. 2017; Rath et al. 2019).

Conclusions

This study comprised an attempt to investigate the alterations in soil bacterial communities and infer the

deterministic processes driving these variations along with *S. alterniflora* invasion in the coastal zone of Eastern China. We found that *S. alterniflora* invasion increased soil bacterial abundance and diversity in comparison with bare flat, and native plant communities. The highest relative abundance of chemolithoautotrophic bacteria (e.g., ε-proteobacteria, Campylobacterales, Helicobacteraceae, and Sulfurovum), photoautotrophic bacteria (e.g., Chloroflexi, Anaerolineae, Anaerolineales, and Anaerolineaceae), and saprophytic and copiotrophic bacteria (e.g., Bacteroidetes), as well as the lowest relative abundances of Acidobacteria, Actinobacteria, Nitrospirae, and Gemmatimonadetes were observed in the *S. alterniflora* soil. The increased relative abundances of Chloroflexi, Anaerolineae, and Bacteroidetes following *S. alterniflora* invasion presumably enhanced the degradation of refractory *S. alterniflora* residues, and accelerated the sequestration of SOC and SON. The shifts in soil bacterial communities following *S. alterniflora* invasion were driven primarily by variations in soil nutrient substrates and physicochemical properties (e.g., soil pH, moisture, and salinity). Our study provides further information to understand the variations and driving patterns of soil bacterial communities following plant invasion, which is helpful toward in clarifying the mechanisms that underlie the impacts of plant invasion on ecosystem C and N cycles.

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