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Short communication

Alterations in soil bacterial community in relation to *Spartina alterniflora* Loisel. invasion chronosequence in the eastern Chinese coastal wetlands

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ABSTRACT

In order to better understand the variations in soil bacterial community and associated drivers following plant invasion, we investigated changes in soil bacterial community along with 9-, 13-, 20- and 23-year-old *Spartina alterniflora* Loisel. (SA) invasion in comparison with bare flat (BF) in the eastern Chinese coastal wetlands, based on analyses of quantitative polymerase chain reaction (qPCR) and Illumina MiSeq DNA sequencing of 16S rRNA gene. The SA invasion significantly elevated soil bacterial abundance and diversity relative to BF, with the highest levels in 9-year-old SA soil, which gradually decreased with SA invasion from 9 to 23 years. The abundance of copiotrophic *Proteobacteria*, *β-proteobacteria*, and *Bacteroidetes* generally diminished along with SA invasion chronosequence. While, changes in abundance of oligotrophic *Chloroflexi*, *Acidobacteria*, *Nitrospirae* and *Planctomycetes* exhibited opposite trends. Our data suggest that soil nutrient substrates, and physiochemical properties (soil pH and/or moisture) primarily drive the shifts in soil bacterial abundance, diversity, and community composition along with SA invasion chronosequence in the costal wetlands of eastern China. Overall, soil bacterial abundance and diversity peaked in 9-year-old SA community, with soil bacterial community composition changing from copiotrophic to oligotrophic groups along with SA invasion chronosequence.

1. Introduction

Plant invasion, a primary driving force of global change (Carey et al., 2017), has been widely confirmed to threaten native biodiversity (Craig et al., 2015), by affecting ecosystem structure (Bray et al., 2017), processes and functions (Craig et al., 2015). Multiple studies have documented that plant invasion can alter carbon (C) and nitrogen (N) cycling of local ecosystem through modifying the quantity and quality of litter and root, nutrient use efficiency, soil properties and microclimate, and soil microbial community structure (Castro-Díez et al., 2014; Tamura and Tharayil, 2014; Carey et al., 2017; Rodríguez-Caballero et al., 2017). Among soil microbial community, soil bacteria are considered to be one of the richest and the most diversity groups of microbes, which play pivotal roles in participating soil organic matter (SOM) decomposition, and regulating soil C and N cycling (Jurburg et al., 2018). Consequently, appraising the responses of soil bacterial community to plant invasion have an essential implications for better understanding the impact mechanism of plant invasion on ecosystem C and N cycles.

Nutrient substrates (Ramirez et al., 2010; Ling et al., 2017), soil pH (Bainard et al., 2016), salinity (Guo et al., 2018), moisture (Nguyen et al., 2018), and plant community cover (Bainard et al., 2016) are one of the vital ecological drivers for soil bacterial abundance, diversity, and community composition. In particular, soil C and N are overarching factors for soil bacteria which rely on soil organic C and N decomposition to obtain energy (Yang et al., 2018). For example, *Chloroflexi*, *Nitrospirae*, and *Planctomycetes* prefer to survive in nutrient-poor conditions with slower growth rates, and to use recalcitrant C substrates (Fierer et al., 2007; Nie et al., 2018). On the contrary, *Proteobacteria* and *Bacteroidetes* favor nutrient-rich conditions and labile C materials

Abbreviations: ANOVA, One-way analysis of variance; BF, Bare flat; C, Carbon; N, Nitrogen; qPCR, Quantitative polymerase chain reaction; RDA, Redundancy analysis; SA, *Spartina alterniflora* Loisel.; 9SA, 9-year-old *Spartina alterniflora* Loisel.; 13SA, 13-year-old *Spartina alterniflora* Loisel.; 20SA, 20-year-old *Spartina alterniflora* Loisel.; 23SA, 23-year-old *Spartina alterniflora* Loisel.; SOC, Soil organic carbon; SOM, Soil organic matter; SON, Soil organic nitrogen; WSOC, Water-soluble organic carbon

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(Fierer et al., 2007; Philippot et al., 2013). Meanwhile, soil pH greatly affects diversity and community composition of soil bacteria in biomes and regions scales (Nie et al., 2018). Gao et al. (2015) found that soil salinity revealed an inhibitory impacting on most bacterial groups in quantity, but exerted little impact on bacterial diversity. Additionally, the alterations in soil moisture are widely accepted to impact soil microbial amount and the structure of community due to water stress (Bainard et al., 2016). Thus, influence of plant invasion on soil bacterial community may differ due to diverse variations in driving factors of bacterial communities as influenced by plant invasion.

Spartina alterniflora Loisel. (SA) is a perennial herb and was introduced from North America to China coast for beach and bank protection in 1979 (An et al., 2007). Currently, SA has quickly expanded along the China's coast and occupies 112,000 ha tidal flats and salt marshes (An et al., 2007). SA invasion has been reported to greatly alter soil organic C and N sequestration (Cheng et al., 2008; Yang et al., 2017), soil physicochemical properties (Yang et al., 2013, 2016), and total soil microbial biomass (Yang et al., 2016). Nevertheless, it is not clear to us regarding the alterations in soil bacterial community along with SA invasion chronosequences. We hypothesized that SA invasion could modify soil bacterial abundance, diversity, as well as community composition through shifting soil nutrient substrates, and physicochemical properties. To test this hypothesis, the variations in soil bacterial abundance, diversity, and community composition based on quantitative polymerase chain reaction (qPCR) and Illumina MiSeq DNA sequencing of bacterial 16S rRNA gene were measured. We also examined soil physicochemical properties, the levels of various soil C and N, plant biomass in 9-, 13-, 20-, 23-year-old SA communities and adjacent bare flat (BF) land in the eastern Chinese coastal wetlands.

2. Materials and methods

2.1. Experimental area and sampling

This study was carried out in the core area of Jiangsu Yancheng Wetland National Nature Reserve, China (32°36′51″–34°28′32″N and 119°51′25″–121°5′47″E; Fig. S1). The mean annual temperature and precipitation of this reserve are 13.6 °C and 1024 mm, respectively. SA was introduced to this reserve in 1983, and formed extensive SA community with mudflats aggrading (Fig. S1; Yang et al., 2017). The seaward invasion region of SA is the BF before SA invasion, and there is no vegetation cover in the BF (Yang et al., 2013, 2017).

The historical records and Landsat Thematic Mapper satellite images were analysed to identify the different SA invasion times in the sampling region. This chronosequence from seaward to landward included BF and SA communities which invaded in 2006 (9-year-old *Spartina alterniflora* Loisel.; 9SA), 2002 (13-year-old *Spartina alterniflora* Loisel.; 13SA), 1995 (20-year-old *Spartina alterniflora* Loisel.; 20SA), and 1992 (23-year-old *Spartina alterniflora* Loisel.; 23SA) (Fig. S1). In December 2015, four parallel transects were selected following the chronosequence (T1–T4; Fig. S1). Each transect is approximately 2 km long, the distance between adjacent transects is approximately 200 m. In every transect, five locations included the BF, 9SA, 13SA, 20SA and 23SA communities (Fig. S1). We randomly chose three 2 m × 2 m plots in each location. There was only SA cover and no other plants distribution in all plots of SA community. SA completely covered all SA plots due to its great invasiveness and expansion capability. We randomly collected three soil cores (diameter × depth, 0.05 m × 0.3 m) from each plot. Subsequently, soil samples from each transect location were thoroughly mixed to yield a final soil sample, and resulting in a total of 20 samples (4 replications × 5 communities). We randomly established three 0.5 m × 0.5 m quadrats to gather litter on the ground, and dug three soil blocks (0.15 m long × 0.15 m wide × 0.3 m deep) to gather root materials in each community of each transect.

2.2. Plant and soil properties analysis

Specific methods of collecting roots from soil blocks were described by Yang et al. (2017). All plant samples were cleaned and dried using oven at 65 °C for 48 h to constant weight to examine litter as well as root biomass. Soil which was placed in aluminum boxes and dried using oven at 105 °C for over 24 h until constant weight to measure moisture content. Plant and animal debris in soil samples was eliminated, and soil samples were sufficiently mixed and divided into three subsamples. The first soil subsample was air-dried and sifted using a 1 mm sieve for determination of soil salinity, pH, soil organic carbon (SOC), and soil organic nitrogen (SON). The second soil subsample was sifted using a 2 mm sieve and preserved at 4 °C for measurement of water-soluble organic carbon (WSOC) concentration. The third soil subsample was sifted using a 2 mm sieve and preserved at −80 °C for molecular analyses. Soil pH was analyzed in a 1:2.5 soil/water suspension using a digital pH meter. Soil salinity was determined in a 1:5 soil/water suspension (Yang et al., 2013). Soil inorganic C and N (i.e., carbonate) in soil samples were removed through the addition of 1 M HCl (Cheng et al. 2008), and then SOC and SON concentrations were measured using a CN elemental analyzer (Vario Micro CHNS analyzer, Germany). WSOC was determined in full accordance with previously described methods and steps (Yang et al., 2013).

2.3. Molecular analyses

DNA was extracted from 0.5 g soil samples using the PowerSoil DNA isolation kit (MoBio Laboratories, USA). Soil bacterial abundance was quantified by qPCR of 16S rRNA gene (Nguyen et al., 2018). The 16S rRNA gene was amplified on an ABI 7500 real-time PCR system (Applied Biosystems, USA). Template DNA was diluted five times before amplification. The total reaction volume was 25 μL which contained 12.5 μL SYBR Green qPCR Master Mix (2 x), 2 μL of template DNA, 0.5 μL of 10 μM primer pair 338F (5′-barcode-ACTCCTACGGGAGGCAGCA-3′) and 806 R (5′-GGACTACHVGGGTWTCTAAT-3′), and 9.5 μL ddH_20. The cycling conditions were as follows: 10 min at 95 °C, subsequently 40 cycles at 95 °C for 15 s and 1 min at 60 °C. The standard curves were obtained as described (Di et al. 2010). 16S rRNA gene copy number was calculated using the formula which was described by Sun et al. (2015).

Soil bacterial diversity and community composition were measured by 16S rRNA amplicon sequencing. The V3 + V4 regions of the bacterial 16S rRNA gene were amplified from bacterial genomic DNA using a pair of bacterial PCR primers, 338F and 806R. The cycling conditions were as follows: 3 min at 95 °C (an initial denaturation), then 27 cycles of 95 °C for 30 s, 55 °C for 30 s, and extension at 72 °C for 45 s, followed by a last step of 72 °C for 10 min (Hong et al., 2015). Following amplification, PCR products were electrophoresed in agarose gel (2%). PCR products from each sample were purified using the AxyPrep DNA Gel Extraction kit (Axygen, USA), then quantified using QuantiFluor-ST (Promega, USA). Purified amplicons were pooled in equimolar ratios and subjected to paired-end sequencing (2 × 300) on an Illumina MiSeq PE300 platform (Hong et al., 2015). Sequences from this platform were processed using the QIIME software package, and the specific processing methods were according to the description of Wang et al. (2018). The trimmed sequences were grouped into operational taxonomic units (OTUs) at 97% similarity levels using UPARSE. Soil bacterial diversity was estimated through the numbers of OTUs, Chao's species richness estimator (Chao), abundance-based coverage estimator (ACE) and Shannon indices using the Mothur program. Taxonomic classification in the phylum and class levels was carried out using the RDP Bayesian classifier. The relative abundance of each phylum and class was calculated by comparing the number of sequences classified as the phylum and class to the total number of rDNA gene sequences detected per sample.

2.4. Statistical analysis

One-way analysis of variance (ANOVA) was applied to evaluate the effects of SA invasion time on soil and plant properties, 16S rRNA gene copy number, OTUs, bacterial community diversity indices, relative abundance of dominant bacterial phylum and class with the SPSS 22 statistical software. The relationships between the soil bacterial community composition at phyla-level and soil and plant properties were analysed with redundancy analysis (RDA) using CANOCO 4.5 software. The statistical significance of RDA was tested using Monte Carlo permutation tests (499 permutations; $P < 0.05$). Pearson's correlation analysis was performed to correlate soil bacterial microbial abundance, diversity, and the relative abundance of the dominant bacterial phyla with the soil and plant properties.

3. Results

3.1. Soil bacterial abundance and diversity

Total bacterial abundance (i.e., 16S rRNA gene copy number) of SA soils increased 34–869 fold compared with that of BF soil (Fig. S2). The total bacterial abundance constantly declined along with SA invasion between 9 and 23 years (Fig. S2). A total of 1,032,935 reads and 75,843 OTUs were get from 20 soil samples by Illumina MiSeq DNA sequencing. To compare alpha diversity indices, we normalized the number of sequences for each sample to 38,352 reads (Table 1), which yielded 767,040 reads and 70,186 OTUs. The numbers of OTUs were highest in 9SA soil among the communities (Table 1). 9SA soil showed the highest ACE and Chao estimators, followed by 13SA, 20SA, 23SA and BF soils (Table 1). Shannon diversity index constantly declined along with SA invasion chronosequence (Table 1).

3.2. Taxonomic composition of soil bacterial community

The most dominant phylum was *Proteobacteria* among the communities, which accounted for 40.0–53.0% of total bacterial community composition (Fig. 1). The BF, 9SA, and 13SA soils exhibited higher abundance of *Proteobacteria* in comparison with 20SA and 23SA soils (Fig. 1). The abundance of *Chloroflexi*, *Acidobacteria*, *Nitrospirae*, *Gemmatimonadetes*, and *Planctomycetes* gradually increased, while the abundance of *Bacteroidetes* and *Chlorobil* progressively decreased along with SA invasion from 9 to 23 years (Fig. 1). The BF soil displayed higher abundance of *Firmicutes* and *Cyanobacteria* in comparison with SA soils (Fig. 1). At class level, the abundance of *ε-proteobacteria*, *Bacteroidia*, *Clostridia* and *Chlorobia* were highest in 9SA soil (Table S2). The abundance of *γ-proteobacteria*, *β-proteobacteria* and *Sphingobacteriia* progressively decreased, and the abundance of *Anaerolineae* gradually increased along with SA invasion chronosequence (Table S2). The abundance of *Flavobacteriia* in the BF and 9SA soils was higher than that in 13SA, 20SA and 23SA soils (Table S2).

3.3. Linking bacterial community to soil and plant properties

Eight variables of soil and plant properties that were present in the ordination explained 80.6% of the total variability in soil bacterial community at phyla-level (Fig. 2). The variations in soil bacterial community were highly related to pH ($F = 19.20$, $P = 0.0020$), SON ($F = 7.22$, $P = 0.0060$), SOC ($F = 4.29$, $P = 0.0060$), and WSOC ($F = 3.48$, $P = 0.0460$) (Fig. 2). The pearson's correlation analysis revealed that variations in 16S rRNA gene copy number, Ace, Chao and Shannon were highly associated with soil moisture, SOC, WSOC, SON, litter and root biomass (Table S3). The abundance of *Chloroflexi*, *Acidobacteria, Nitrospirae, Gemmatimonadetes* and *Planctomycetes* was negatively correlated with soil pH (Table S3).

4. Discussion

The SA invasion greatly affected soil bacterial abundance and diversity along with invasion chronosequence (Table 1 and Fig. S2). The highest 16S rRNA gene copy number, OTUs, Ace, Chao, and Shannon indices of bacterial communities were found in 9SA soil (Table 1; Fig. S2), suggesting that soil bacterial abundance and diversity were highest in 9SA soil. This finding was similar to our previous study showing that soil total microbial biomass attained the richest state in invaded 10-year-old SA community through phospholipid fatty acids analysis (Yang et al., 2016). Soil nutrient substrates (e.g., SOC, WSOC, and SON), particularly WSOC can directly provide available labile C and a source of energy for soil microbial growth as well as metabolism (Rodríguez-Caballero et al., 2017). Soil bacterial abundance and diversity constantly declined along with SA invasion from 9 to 23 years (Table 1 and Fig. S2); this may be mainly due to gradually decreased supply of soil nutrient substrates (Table S1) which would restrict bacterial metabolism and growth. The deduction was supported by our finding that abundance and diversity of soil bacteria were highly associated with SOC, WSOC, SON, and biomass of litter as well as root (Table S3). Additionally, it is widely reported that soil moisture has a great effect on soil bacteria (Bainard et al., 2016; Nguyen et al., 2018), and higher soil moisture may favor bacteria growth (Nakamura et al., 2003). Consequently, the greatest bacterial abundance and diversity in 9SA soil may be partly attributable to the high soil moisture, which greatly promoted bacterial growth (Tables 1, S1 and Fig. S2). In this study, soil bacterial abundance and diversity among the communities was not affected by soil pH (Table S3). This phenomenon may be explained by the previous finding that soil pH is a vital factor in determination of bacterial community composition (Lauber et al., 2009; Bainard et al., 2016) rather than abundance (Guo et al., 2018). Interestingly, soil salinity showed little related to soil bacterial abundance (Table S3), which might be explained by the small variation in soil salinity along

Table 1
Number of sequences analysed, observed soil bacterial community richness and diversity indices (mean ± SE, n = 4) following *Spartina alterniflora* Loisel. invasion in the eastern Chinese coastal wetlands obtained for clustering at 97% similarity levels.

Community	Reads	OTUs	ACE	Chao	Shannon	Coverage (%)
Bare flat	38,352	3240 ± 195^{b}	3801 ± 285^{c}	3797 ± 299^{c}	6.48 ± 0.13^{c}	97.99 ± 0.24^{a}
Spartina alterniflora Loisel.						
9 years	38,352	4091 ± 79^{a}	5289 ± 93^{a}	5344 ± 102^{a}	7.00 ± 0.12^{a}	96.68 ± 0.05^{c}
13 years	38,352	3635 ± 82^{b}	4811 ± 96^{ab}	4862 ± 112^{ab}	6.85 ± 0.07^{ab}	96.95 ± 0.08^{bc}
20 years	38,352	3312 ± 72^{b}	4327 ± 82^{bc}	4319 ± 69^{bc}	6.72 ± 0.03^{abc}	97.32 ± 0.05^{b}
23 years	38,352	3269 ± 193^{b}	4323 ± 313^{bc}	4296 ± 320^{bc}	6.67 ± 0.11^{bc}	97.29 ± 0.24^{b}
Source of variation						
Invasion time		**	*	**	*	**

Different superscript lower case letters indicate statistically significant differences at the $\alpha = 0.05$ level across *Spartina alterniflora* Loisel. invasion chronosequence. Reads are the high-quality sequences after filtering and normalization; The richness estimators (Ace and Chao), diversity indices (Shannon), and coverage were calculated using the MOTHUR program.

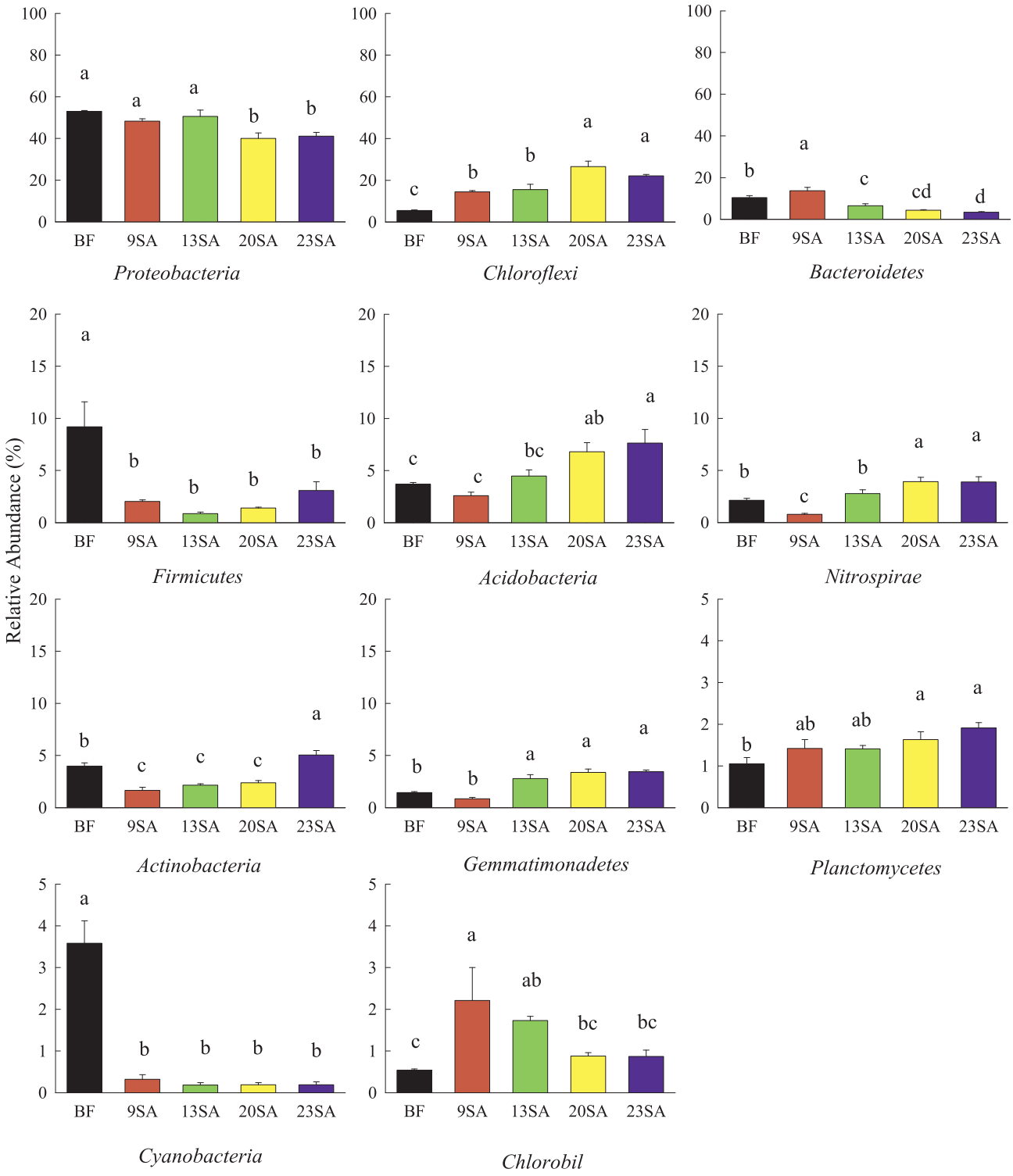

Fig. 1. The relative abundance (% of individual taxonomic group) of the dominant bacterial phyla (mean ± SE, n = 4) present in soil microbial community following *Spartina alterniflora* Loisel. invasion in the eastern Chinese coastal wetlands. Different letters indicate statistically significant differences at α = 0.05 level across *Spartina alterniflora* Loisel. invasion chronosequence. Bare flat = BF; 9SA = 9-year-old *Spartina alterniflora* Loisel.; 13SA = 13-year-old *Spartina alterniflora* Loisel.; 20SA = 20-year-old *Spartina alterniflora* Loisel.; 23SA = 23-year-old *Spartina alterniflora* Loisel..

with SA invasion from 9 to 23 years (Table S1). Thus, soil bacterial abundance and diversity were highest in 9SA soil (Table 1 and Fig. S2), may be the result of the greatest nutrient substrates and the highest soil moisture, rather than soil pH and salinity across the invasion chronosequence (Table S1).

The SA invasion shifted soil bacterial community composition across the invasion chronosequence (Table S2; Fig. 1). Generally, *Proteobacteria*, especially the *β-proteobacteria*, are considered as copiotrophic soil bacteria (Wang et al., 2017), which are fast growing and favor by nutrient-rich conditions (Fierer et al., 2007; Philippot et al., 2013). Thus, decreased abundance of *Proteobacteria* and *β-proteobacteria* along with SA invasion chronosequence may be caused by generally decreasing supply of nutrient substrates that limited the growth of *Proteobacteria* and *β-proteobacteria* (Tables S1 and S2; Fig. 1). Wang

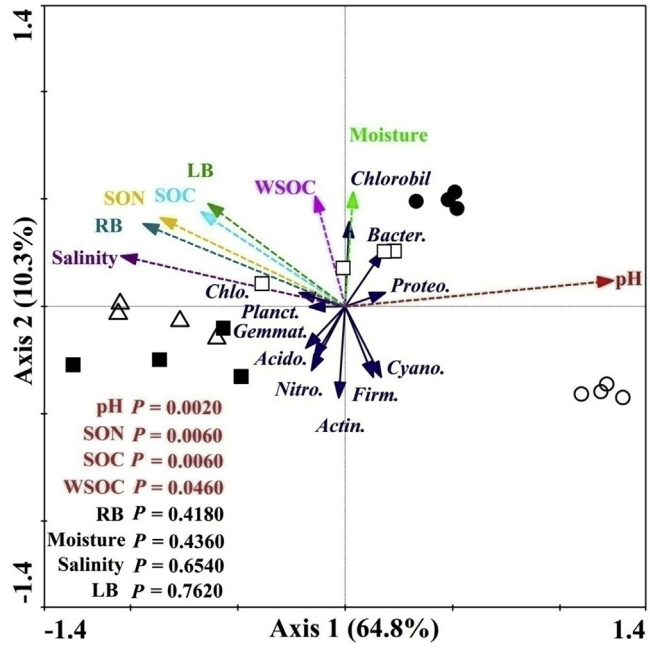

Fig. 2. Redundancy analysis (RDA) diagram illustrating the relationship between the soil bacterial community at phyla-level from different sampling sites and environmental variables. The explanatory variables are showed by different arrows: soil bacterial community by blue solid arrows: *Proteobacteria* (*Proteo.*); *Chloroflexi* (*Chlo.*); *Bacteroidetes* (*Bacter.*); *Firmicutes* (*Firm.*); *Acidobacteria* (*Acido.*); *Nitrospirae* (*Nitro.*); *Actinobacteria* (*Actin.*); *Gemmatimonadetes* (*Gemmat.*); *Planctomycetes*(*Planct.*); *Cyanobacteria* (*Cyano.*); *Chlorobil*; and the variables of soil and plant properties by colored arrow: soil moisture, pH, salinity, soil organic carbon (SOC), soil water-soluble organic carbon (WSOC), soil organic nitrogen (SON), litter biomass (LB) and root biomass (RB). Open circles represent bare flat soil, Filled circles represent 9SA soil, open square represent 13SA soil, open triangles represent 20SA soil, Filled square represent 23SA soil. See Fig. 1 for abbreviations.

et al. (2012) reported that marine sediment is most enriched in γ-*proteobacteria*, which are highly associated with sulfate reduction under anaerobic conditions. The BF soil showed the biggest γ-*proteobacteria* abundance (Table S2), probably because bacterial community composition of this locale was more similar to that of marine sediment compared to SA soils (Wang et al., 2012) since the BF is closest to the Yellow Sea and deeply affected by semidiurnal tidal cycles (Yang et al., 2013).

Generally, *Bacteroidetes* are recognized as copiotrophic and saprophytic bacteria (Fierer et al., 2007), which prefer to anaerobic environments (Xu et al., 2017). In our experiments, the abundance of *Bacteroidetes* progressively declined along with SA invasion from 9 to 23 years (Fig. 1). One possible explanation of this result is that soil C availability (i.e., WSOC) progressively decreased due to diminishing litter entering the soil, and finally limited *Bacteroidetes* growth following SA invasion (Tables S1; Fig. 1). Additionally, soil moisture progressively decreased from 83.02% to 40.45% along with SA invasion chronosequence (Table S1), and progressively reduced soil moisture is unfavourable for *Bacteroidetes* growth (Xu et al., 2017). It is reported that *Bacteroidetes* play the vital role in hydrolysis of polysaccharides (Semrau, 2011), and degrade high polymer SOM (Thomas et al., 2011). Yang et al. (2017) demonstrated that soil C decay rate constantly declined along with SA invasion chronosequence due to lower litter decomposition (Yang et al., 2013). It is presumed that gradually declining *Bacteroidetes* abundance may decrease decomposition of recalcitrant SA residues and soil old C along with invasion chronosequence, and affect soil C turnover and accumulation (Fig. 1; Yang et al., 2017).

Interestingly, the abundance of *Chloroflexi* (from phylum to class), *Acidobacteria* (from phylum to class), *Nitrospirae* (from phylum to class), *Gemmatimonadetes* (from phylum to class), and *Planctomycetes* progressively raised along with SA invasion chronosequence (Table S2; Fig. 1). *Chloroflexi*, *Acidobacteria*, *Nitrospirae*, and *Planctomycetes* are described as an oligotrophic groups which favor nutrient-poor conditions with slower growth rates (Fierer et al., 2007; Ling et al., 2017; Nie et al., 2018). Increased abundance of *Chloroflexi*, *Acidobacteria*, *Nitrospirae* and *Planctomycetes* may be partly attribute to gradually decreasing soil nutrient substrates along with SA invasion chronosequence (Tables S1 and S2; Fig. 1). Furthermore, the abundance of *Acidobacteria* (Jones et al., 2009), *Gemmatimonadetes* (Wang et al., 2017) as well as *Planctomycetes* (Miranda et al., 2018) have been showed to be negatively correlated with pH, which were consistent with our pearson's correlation analysis (Table S3). It is deduced that gradually decreasing soil pH along with invasion chronosequence (Table S1) may be propitious to the growth of *Acidobacteria*, *Gemmatimonadetes* and *Planctomycetes*, and impelled them to increase along with SA invasion chronosequence (Table S2; Fig. 1). Generally, our studies revealed that the total variations of soil bacterial community composition along with SA invasion chronosequence were highly related to soil pH and nutrient substrates (i.e., SOC, WSOC, and SON) (Fig. 2). This finding further demonstrated that soil pH and nutrient substrates were one of the crucial drivers of the changes in community composition of soil bacteria (Lauber et al., 2009; Ling et al., 2017).

5. Conclusions

This study emphasized the variations of soil bacterial community following SA invasion chronosequence. The data manifest that soil bacterial abundance and diversity were highest in 9SA soil, which progressively declined from 9 to 23 years. The abundance of copiotrophic bacterial groups constantly decreased, whereas oligotrophic bacterial groups gradually raised along with SA invasion chronosequence. The detected alterations in soil bacterial community may be a result of the alterations in soil nutrient substrates, and physiochemical properties along with SA invasion from short- to long-term in the eastern Chinese coastal wetlands. This may have consequences on ecosystem processes, particularly soil C and N decomposition and accumulation. Overall, this study provides valuable insights regarding better understanding of variations as well as driving patterns of soil bacterial communities that was influenced by exotic plant invasion.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2018.11.009.

References

An, S., Gu, B., Zhou, C., Wang, Z., Deng, Z., Zhi, Y., Li, H., Chen, L., Yu, D., Liu, Y., 2007. *Spartina* invasion in China: implications for invasive species management and future research. Weed Res. 47, 183–191.

Bainard, L.D., Hamel, C., Gan, Y.T., 2016. Edaphic properties override the influence of crops on the composition of the soil bacterial community in a semiarid agroecosystem. Appl. Soil Ecol. 105, 160–168.

Bray, S.R., Hoyt, A.M., Yang, Z.J., Arthur, M.A., 2017. Non-native liana, Euonymus fortunei, associated with increased soil nutrients, unique bacterial communities, and faster decomposition rate. Plant Ecol. 218, 329–343.

Carey, C.J., Blankinship, J.C., Eviner, V.T., Malmstrom, C.M., Hart, S.C., 2017. Invasive plants decrease microbial capacity to nitrify and denitrify compared to native

California grassland communities. Biol. Invasions 19, 2941–2957.
Castro-Díez, P., Godoy, O., Alonso, A., Gallardo, A., Saldaña, A., 2014. What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. Ecol. Lett. 17, 1–12.
Cheng, X.L., Chen, J.Q., Luo, Y.Q., Henderson, R., An, S.Q., Zhang, Q.F., Chen, J.K., Li, B., 2008. Assessing the effects of short-term *Spartina alterniflora* invasion on labile and recalcitrant C and N pools by means of soil fractionation and stable C and N isotopes. Geoderma 145, 177–184.
Craig, M.E., Pearson, S.M., Fraterrigo, J.M., 2015. Grass invasion effects on forest soil carbon depend on landscape-level land use patterns. Ecology 96, 2265–2279.
Di, H.J., Cameron, K.C., Shen, J.P., Winefield, C.S., O'Callaghan, M., Bowatte, S., He, J.Z., 2010. Ammonia-oxidizing bacteria and archaea grow under contrasting soil nitrogen conditions. FEMS Microbiol. Ecol. 72, 386–394.
Fierer, N., Bradford, M.A., Jackson, R.B., 2007. Toward an ecological classification of soil bacteria. Ecology 88, 1354–1364.
Gao, Y.C., Wang, J.N., Guo, S.H., Hu, Y.L., Li, T.T., Mao, R., Zeng, D.H., 2015. Effects of salinization and crude oil contamination on soil bacterial community structure in the Yellow River Delta region, China. Appl. Soil Ecol. 86, 165–173.
Guo, X.P., Lu, D.P., Niu, Z.S., Feng, J.N., Chen, Y.R., Tou, F.Y., Liu, M., Yang, Y., 2018. Bacterial community structure in response to environmental impacts in the intertidal sediments along the Yangtze Estuary, China. Mar. Pollut. Bull. 126, 141–149.
Hong, C., Si, Y.X., Xing, Y., Li, Y., 2015. Illumina MiSeq sequencing investigation on the contrasting soil bacterial community structures in different iron mining areas. Environ. Sci. Pollut. R. 22, 10788–10799.
Jones, R.T., Robeson, M.S., Lauber, C.L., Hamady, M., Knight, R., Fierer, N., 2009. A comprehensive survey of soil acidobacterial diversity using pyrosequencing and clone library analyses. ISME J. 3, 442–453.
Jurburg, S.D., Natal-da-Luz, T., Raimundo, J., Morais, P.V., Sousa, J.P., Elsas, J.D., Salles, J.F., 2018. Bacterial communities in soil become sensitive to drought under intensive grazing. Sci. Total Environ. 618, 1638–1646.
Lauber, C.L., Hamady, M., Knight, R., Fierer, N., 2009. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. Appl. Environ. Microbiol. 75, 5111–5120.
Ling, N., Chen, D.M., Guo, H., Wei, J.X., Bai, Y.F., Shen, Q.R., Hu, S.J., 2017. Differential responses of soil bacterial communities to long-term N and P inputs in a semi-arid steppe. Geoderma 292, 25–33.
Miranda, A.R.L., Mendes, L.W., Rocha, S.M.B., Brink, P.J.V., Bezerra, W.M., Melo, V.M.M., Antunes, J.E.L., Araujo, A.S.F., 2018. Responses of soil bacterial community after seventh yearly applications of composted tannery sludge. Geoderma 318, 1–8.
Nakamura, A., Tun, C.C., Asakawa, S., Kimura, M., 2003. Microbial community responsible for the decomposition of rice straw in a paddy field: estimation by phospholipid fatty acid analysis. Biol. Fert. Soils 38, 288–295.
Nguyen, L.T.T., Osanai, Y., Lai, K., Anderson, I.C., Bange, M.P., Tissue, D.T., Singh, B.K., 2018. Responses of the soil microbial community to nitrogen fertilizer regimes and historical exposure to extreme weather events: Flooding or prolonged-drought. Soil Biol. Biochem. 118, 227–236.
Nie, Y.X., Wang, M.C., Zhang, W., Ni, Z., Hashidoko, Y., Shen, W.J., 2018. Ammonium nitrogen content is a dominant predictor of bacterial community composition in an acidic forest soil with exogenous nitrogen enrichment. Sci. Total Environ. 624, 407–415.
Philippot, L., Raaijmakers, J.M., Lemanceau, P., van der Putten, W.H., 2013. Going back to the roots: the microbial ecology of the rhizosphere. Nat. Rev. Microbiol. 11, 789–799.
Ramirez, K.S., Lauber, C.L., Knight, R., Bradford, M.A., Fierer, N., 2010. Consistent effects of nitrogen fertilization on soil bacterial communities in contrasting systems. Ecology 91, 3463–3470.
Rodríguez-Caballero, Caravaca, F., Alguacil, M.M., Fernández-López, M., Fernández-González, A.J., Roldán, A., 2017. Striking alterations in the soil bacterial community structure and functioning of the biological N cycle induced by *Pennisetum setaceum* invasion in a semiarid environment. Soil Biol. Biochem. 109, 176–187.
Semrau, J.D., 2011. Current knowledge of microbial community structures in landfills and its cover soils. Appl. Microbiol. Biot. 89, 961–969.
Sun, R.B., Zhang, X.X., Guo, X.S., Wang, D.Z., Chu, H.Y., 2015. Bacterial diversity in soils subjected to long-term chemical fertilization can be more stably maintained with the addition of livestock manure than wheat straw. Soil Biol. Biochem. 88, 9–18.
Tamura, M., Tharayil, N., 2014. Plant litter chemistry and microbial priming regulate the accrual, composition and stability of soil carbon in invaded ecosystems. New Phytol. 203, 110–124.
Thomas, F., Hehemann, J.H., Rebuffet, E., Czjzek, M., Michel, G., 2011. Environmental and gut bacteroidetes: the food connection. Front. Microbiol. 2, 1–16.
Wang, J.C., Song, Y., Ma, T.F., Raza, W., Li, J., Howland, J.G., Huang, Q.W., Shen, Q.R., 2017. Impacts of inorganic and organic fertilization treatments on bacterial and fungal communities in a paddy soil. Appl. Soil Ecol. 112, 42–50.
Wang, R.Q., Xiao, Y.P., Lv, F.J., Hu, L.Y., Wei, L.G., Yuan, Z.Q., Lin, H.X., 2018. Bacterial community structure and functional potential of rhizosphere soils as influenced by nitrogen addition and bacterial wilt disease under continuous sesame cropping. Appl. Soil Ecol. 125, 117–127.
Wang, Y., Sheng, H.F., He, Y., Wu, J.Y., Jiang, Y.X., Tam, N.F.Y., Zhou, H.W., 2012. Comparison of the levels of bacterial diversity in freshwater, intertidal wetland, and marine sediments by using millions of illumina tags. Appl. Environ. Microb. 78, 8264–8271.
Xu, S., Lu, W.J., Liu, Y.T., Ming, Z.Y., Liu, Y.J., Meng, R.H., Wang, H.T., 2017. Structure and diversity of bacterial communities in two large sanitary landfills in China as revealed by high-throughput sequencing (MiSeq). Waste Manage. 63, 41–48.
Yang, W., Jeelani, N., Leng, X., Cheng, X.L., An, S., 2016. *Spartina alterniflora* invasion alters soil microbial community composition and microbial respiration following invasion chronosequence in a coastal wetland of China. Sci. Rep. 6, 26880.
Yang, W., Zhao, H., Chen, X.L., Yin, S.L., Cheng, X.L., An, X.Q., 2013. Consequences of short-term C_4 plant *Spartina alterniflora* invasions for soil organic carbon dynamics in a coastal wetland of Eastern China. Ecol. Eng. 61, 50–57.
Yang, W., Zhao, H., Leng, X., Cheng, X.L., An, S.Q., 2017. Soil organic carbon and nitrogen dynamics following *Spartina alterniflora* invasion in a coastal wetland of eastern China. Catena 156, 281–289.
Yang, Y., Dou, Y.X., An, S.S., 2018. Testing association between soil bacterial diversity and soil carbon storage on the Loess Plateau. Sci. Total Environ. 626, 48–58.