



The Invasion of *Alternanthera philoxeroides* Increased Soil Organic Carbon in a River and a Constructed Wetland With Different Mechanisms

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Edited by:

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Specialty section:

This article was submitted to
Population and Evolutionary
Dynamics,
a section of the journal
Frontiers in Ecology and Evolution

Received: 20 June 2020

Accepted: 22 September 2020

Published: 06 November 2020

Citation:

Yang R, Li K, Fang J, Quan Q, Zhang C and Liu J (2020) The Invasion of *Alternanthera philoxeroides* Increased Soil Organic Carbon in a River and a Constructed Wetland With Different Mechanisms. *Front. Ecol. Evol.* 8:574528. doi: 10.3389/fevo.2020.574528

Wetlands have been considered as a vital reservoir of global carbon and are vulnerable to plant invasion. However, the influence mechanism of plant invasion on soil organic carbon (SOC) in wetlands remains unclear. In this study, we investigated SOC, soil physicochemical properties, and soil microbes in the invaded and non-invaded sites in Xinxue River and Xinxue River Constructed Wetland to research the effects of *Alternanthera philoxeroides* invasion on SOC and explore the related mechanisms. The invasion of *A. philoxeroides* increased SOC content and density in both the river and the constructed wetland. SOC in the two types of wetlands was positively correlated with moisture content and negatively correlated with bulk density, dissolved oxygen, water temperature, soil temperature, and pH. The invasion decreased the dissolved oxygen in the river and the soil temperature in the constructed wetland which might be the explanation for the increase of SOC in the two types of wetlands. In the river, the decrease of dissolved oxygen caused by plant invasion could alter the microbial community and limit the decomposition of SOC by microbes, which was confirmed by the increase of microbial α diversity indices and the correlations between soil microbial community in the river and dissolved oxygen showed by RDA analysis. The invasion of *A. philoxeroides* significantly shifted the soil microbial community in the constructed wetland. Redundancy analysis showed that the variation of soil microbial community structure in the constructed wetland could be mainly explained by soil pH and soil temperature. The decrease of soil temperature in the constructed wetland might inhibit microbial activities and result in the accumulation of SOC. In addition, the indicator species reflecting soil microbial community shifted by plant invasion were highly correlated with SOC, suggesting that the variation of indicator species between invaded sites and non-invaded sites might be another reason for the difference in SOC. The study indicates that *A. philoxeroides* invasion might increase the carbon storage in rivers and constructed wetlands with different mechanisms.

Keywords: *Alternanthera philoxeroides*, invasion, river, constructed wetland, soil organic carbon, dissolved oxygen, soil temperature, microbial community

INTRODUCTION

As a vital reservoir of carbon, wetlands can offset partial release of carbon dioxide into the atmosphere (Dixon and Krankina, 1995; Mitsch et al., 2013; Nag et al., 2019). The carbon sequestration function of wetland soil plays an important role in mitigating global climate change (Nag et al., 2017; Zhao et al., 2017). According to the Convention on Wetlands signed in 1971, wetlands could be divided into natural wetlands and constructed wetlands (Hawkins and Smith, 1983; Ramsar Convention Secretariat, 2004). Rivers are an example of typical natural wetlands, and a constructed wetland is a combination of water, plants, and substrates, which is modeled on natural wetlands (Hui et al., 2009; Zhang et al., 2009). Rivers and constructed wetlands are important carbon reservoirs (Zhang L. et al., 2015; Reddy et al., 2016). The increase of exotic plant invasion in wetlands, which threatens ecological functions, is gaining increasing attention in ecology research (van der Putten et al., 2007; Seebens et al., 2017; Vaz et al., 2019). Invasive plants can affect the carbon cycle of wetlands' ecosystems, but the mechanisms remain unclear (McKinley and Blair, 2008; Jin et al., 2017; Bobul'ská et al., 2019; Qi et al., 2019).

Plant invasion has direct and indirect effects on the soil organic carbon (SOC) storage of wetlands. Plant invasion can directly affect SOC storage attributed to the high net primary productivity of invasive plants (Burke et al., 1998; Ehrenfeld, 2003; Tamura and Tharayil, 2014). Plant invasion may also affect SOC via the root exudation and litter decomposition (Craig et al., 2015). Plant invasion could indirectly impact SOC storage by altering soil physicochemical properties (Yang et al., 2017; Qi et al., 2019; Yang, 2019). A study by Yang (2019) demonstrated that *Spartina alterniflora* invasion not only directly increased SOC content, but also indirectly affected SOC through mediating the effects of soil moisture content. Moreover, the decrease of soil temperature could also enhance SOC storage (Yang, 2019).

The indirect effect also includes the impact of plant invasion on microorganisms. Microorganisms, as natural decomposers, directly play a part in the carbon cycle of wetlands (Huang et al., 2014). Dramatic shifts in soil nutrient content caused by plant invasion could alter the richness and diversity of soil microbial communities (Lorenzo et al., 2010; Yang et al., 2013; Lazzaro et al., 2014). Fontaine et al. (2003) reported that when soil nutrient availability highly increased, the microbial decomposition of fresh organic matter increased while the microbial decomposition of soil organic matter decreased, resulting in SOC accumulation. In addition, the change of soil physicochemical properties such as pH and temperature caused by plant invasion can indirectly affect SOC storage by affecting microbial activities (Bainard et al., 2016; Nguyen et al., 2018). The carbon storage of wetlands was affected by certain microbes such as Betaproteobacteria and Planctomycetacia (Xin and Qin, 2019). The carbon metabolic rate could be altered by the variation of the microbial community. For example, the abundance of heterotrophic bacteria such as Bacteroidetes was increased with *Spartina alterniflora* invasion, which increased microbial respiration and resulted in the decrease of SOC (Song et al., 2020). Therefore, the indirect effect of plant invasion

on SOC storage in wetlands is the key part of the influence mechanism of plant invasion on SOC (Zhang G. et al., 2019; Zhang P. et al., 2020; Yang et al., 2020).

Alternanthera philoxeroides (Mart.) Griseb., a species native to South America, is widely distributed in Oceania, South America, North America, Africa, and many other countries and regions (Telesnicki et al., 2011). In the 1930s, it was first introduced, widely planted and disseminated as feed in South China. In 2003, it was listed in the first batch of invasive alien species in China by the State Environmental Protection Administration of China (Pang et al., 2007). At present, *A. philoxeroides* is mainly distributed in low altitude, relatively warm, and humid climate areas east of 97°E and south of 44°N in China (Pang et al., 2007).

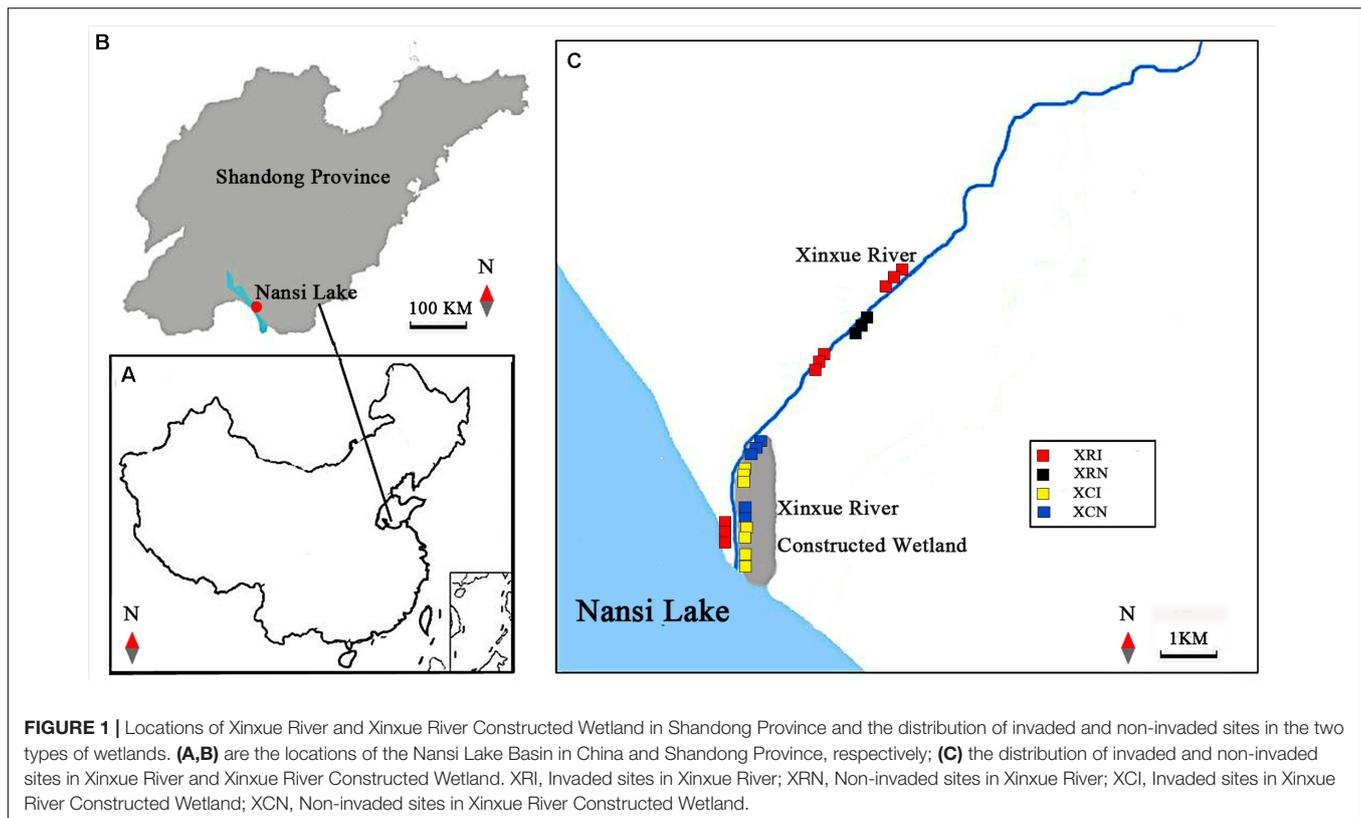
To explore the influence mechanism of plant invasion on SOC in rivers and constructed wetlands, we chose Nansi Lake Basin, where the invasion was serious, as the research site. We hypothesized that *A. philoxeroides* invasion could increase SOC storage by altering soil physicochemical properties and the soil microbial community. To test this hypothesis, we examined the SOC content and density, compared the soil physicochemical properties and soil microbial community composition in the invaded sites and non-invaded sites in Xinxue River (XR) and Xinxue River Constructed Wetland (XC) in 2018. We also analyzed the correlations between SOC, soil physicochemical properties and soil microorganisms. This study is of great significance to understand the impact of the invasion of *A. philoxeroides* and other similar invasive plants on the wetland carbon stock.

MATERIALS AND METHODS

Study Area and Field Sampling

This study was conducted in the second largest freshwater lake in Huaihe River Basin, Nansi Lake, Shandong Province, China (116°34'–117°21'E, 34°27'–35°20'N). Nansi Lake, the largest freshwater lake in North China, serves as an important hub for water transfer and storage in the East Route of the South-to-North Water Transfer Project in China (Wu et al., 2010). Xinxue River (XR) is one of the principal inflow rivers of Nansi Lake. The Xinxue River Constructed Wetland (XC) was built in 2007 and is located on the southern bank of Xinxue River.

In July 2018, soil samples for physicochemical properties analyses and microbial samples in surface soil for microbial analyses were collected in the sediments in XR and XC (**Figure 1**). To explore the effects of *A. philoxeroides* invasion on SOC in wetlands, samples in non-invaded sites were assumed to substitute for the samples in the pre-invasion condition, and this experimental design was consistent with Chen et al. (2018). In XR, nine invaded sites were sampled uniformly and randomly throughout the river. And due to the less non-invaded places in the middle and lower reaches of XR, we only chose three non-invaded sites in the upstream to collect soil samples and microbial samples. In XC, we chose seven invaded sites and five non-invaded sites to collect soil and microbial samples. All collected samples were labeled in sealed bags. Soil samples were stored at 4°C and analyzed in 48 h (Fang et al., 2019; Boscutti et al., 2020;



Zhang P. et al., 2020). Microbial samples were stored at -80°C before microbial sequencing.

Laboratory Analyses

Soil samples were air-dried at room temperature ($\sim 25^{\circ}\text{C}$) and then sieved by a 0.15 mm sieve. Soil samples (0.05–0.3 g, accurate to 0.0001 g) were added into hard glass tubes and mixed with 10.00 mL potassium dichromate-sulfuric acid solution (0.4 mol L^{-1}). The glass tubes were inserted into the wire cage and then heated in the oil bath at $170\text{--}180^{\circ}\text{C}$ for 5 min. The liquid and soil residue in the tube was transferred to a 250 mL triangular bottle, the tube and funnel were washed with distilled water, and the washing liquid was poured into the triangular bottle. Three drops of o-phenanthroline indicator were added into the triangular bottle, the residual K_2CrO_7 was titrated by 0.2 mol L^{-1} ferrous sulfate solution. The titration was finished when the solution changed from orange to blue-green and then to brown-red. About 0.2 g of SiO_2 was selected as blank control, and about 0.2 g of the standard soil GBW 07413a (ASA-2) was selected as the standard control. The volume of consumed ferrous sulfate was recorded and substituted into the following formula:

$$OM = \frac{c \times (V_0 - V) \times 0.003 \times 1.724 \times 1.10}{m} \times 1000$$

OM: mass fraction of soil organic matter (g kg^{-1}); V_0 : standard solution volume of ferrous sulfate consumed by blank experiment (mL); V : standard solution volume of ferrous sulfate consumed by sample determination (mL); c : concentration of

ferrous sulfate standard solution (mol L^{-1}); m : weight of the drying sample (g); 0.003: the mass of 1/4 mmol of carbon (g mmol^{-1}); 1.724: conversion factor of organic carbon to organic matter; 1.10: oxidation correction coefficient; 1,000: conversion factor from g to kg.

SOC content and density were calculated by the formulae:

$$SOC = OM \div 1.724$$

$$SOCD = SOC \times \text{bulk density}$$

SOC: mass fraction of soil organic carbon (g kg^{-1}); SOCD: mass fraction of soil organic carbon per unit volume (kg m^{-3}); bulk density: weight of soil per unit volume (g cm^{-3}) (Rudiyanto, Minasny and Setiawan, 2016). The content of soil organic matter was determined by potassium dichromate oxidation method, referring to the determination of soil organic matter in the Agricultural Industry Standard of the People's Republic of China published in 2006.

The pH of soil was obtained by using the determination of pH in soil (NY/T 1377-2007). The bulk density and moisture content were determined by using the ring knife method (Li and Zheng, 2019).

Microbial Analyses

The diversity and richness of the soil microbial samples in the invaded sites and non-invaded sites in XR and XC were analyzed by 16S rRNA amplicon sequencing. First, a

rapid CTAB DNA isolation technique was used to extract DNA in microbial samples (Stewart and Via, 1993). The 515F (5'-GTGCCAGCMGCCGCGTAA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') primers were used for the amplification of the microbial (bacterial and archaeal) 16S rRNA V4 fragments (Wu et al., 2016). The truseq DNA PCR free sample preparation kit (Illumina, San Diego, CA, United States) was used to construct the sequencing library and add tags. Quantitation and detection of the constructed library were carried out utilizing a Qubit Fluorescence Quantitative Analyzer (Thermo Fisher Scientific) and an Agilent 2100 Biological Analyzer (Agilent Technologies, Palo Alto, CA, United States). Based on the Illumina HiSeq sequencing platform, the library which met the standard was sequenced to get raw data (Jiao et al., 2016). Splicing, filtering, quality control, and chimeric filtering were carried out to get effective tags (Caporaso et al., 2010). The effective tags with similarities greater than 97% were clustered into Operational Taxonomic Units (OTUs), and the representative sequences of OTUs were annotated to obtain the community composition of microbial samples.

Statistical Analyses

All statistical analyses of soil properties were performed using SPSS software (version 21.0), R (v4.0.1), Canoco 4.5, and Origin 2017. A two-way analysis of variance (ANOVA) was used to analyze the effects of plant invasion, wetland types, and their interactions on SOC and other soil physicochemical properties. One-way ANOVA was performed to analyze the differences in the effects of plant invasion on SOC and other soil physicochemical properties in the river and the constructed wetland, and it was also conducted when the interaction effects were significant in the two-way ANOVA (Nitao, 1989; Qi et al., 2019; Yang

et al., 2020). Spearman correlation analyses were conducted in R (v4.0.1) to study the relationships between SOC and other soil physicochemical properties. The microbial data analysis was performed by QIIME, R (v4.0.1), and Galaxy platform¹. The microbial α diversity indices including richness indices (Chao1, ACE) and diversity indices (Shannon, Simpson), were calculated using QIIME (Zhang H. et al., 2020). Redundancy analysis (RDA) was conducted in Canoco 4.5 for the relationships between soil properties and microbial composition at the phyla-level. Monte Carlo permutation test (999 permutations) was used to test the statistical significance of the variables of RDA at the 0.05 level (Zhang G. et al., 2020). The differences in microbial composition between invaded sites and non-invaded sites were analyzed and visualized by linear discriminant analysis effect size (LEfSe) using Galaxy platform (Liu et al., 2018). Spearman correlation analyses of SOC and other soil physicochemical properties with indicator species were also carried out in R (v4.0.1).

Accession Number

The raw sequencing data have been submitted to NCBI Sequence Read Archive (SRA) with the Accession Number of SRP267962².

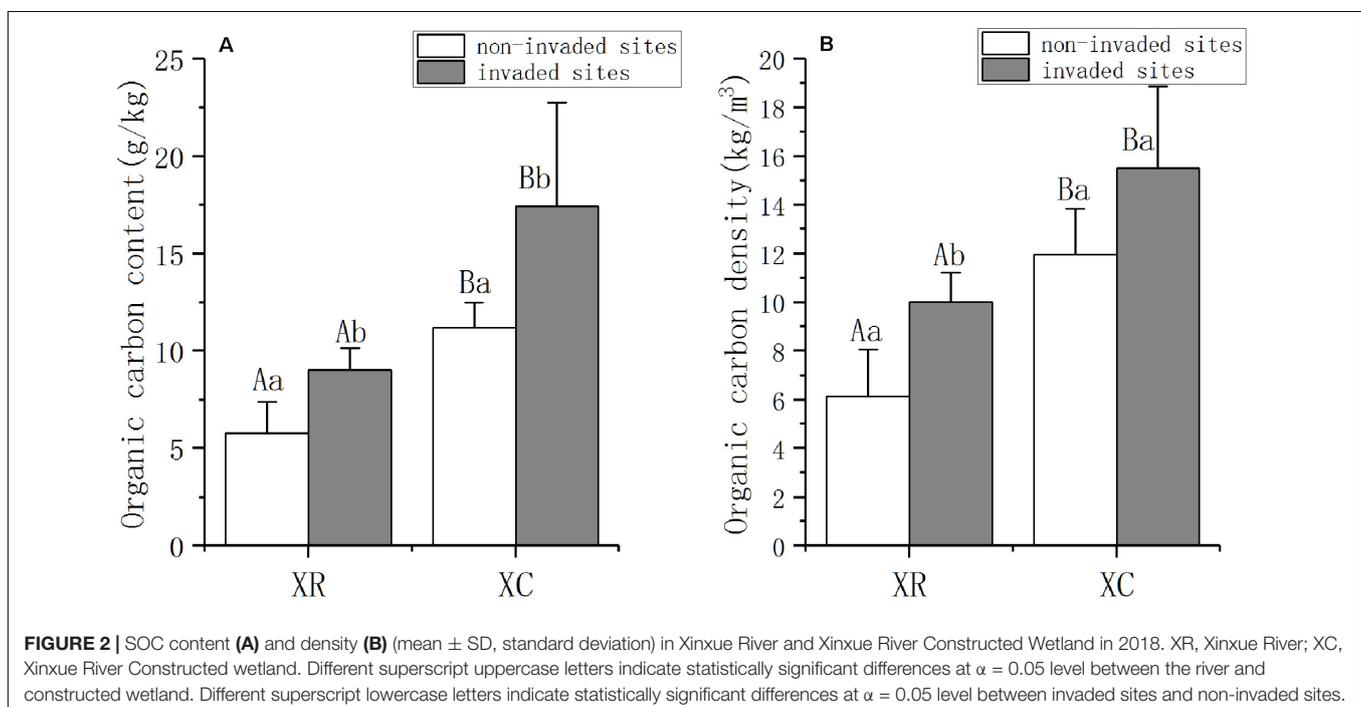
RESULTS

Effects of *A. philoxeroides* Invasion on SOC Content and Density

A. philoxeroides invasion strongly affected SOC in the two types of wetlands (Figure 2). SOC content was significantly higher

¹<http://huttenhower.sph.harvard.edu/galaxy/>

²<https://www.ncbi.nlm.nih.gov/sra/?term=SRP267962>



in invaded sites than in non-invaded sites both in XR and XC ($P_{XR} = 0.003$, $P_{XC} = 0.029$, **Figure 2A**). In XR, the SOC density in invaded sites (XRI) was 63% higher than that in non-invaded sites (XRN) ($P = 0.002$, **Figure 2B**), while the density of SOC in the invaded sites (XCI) was 30% higher than that in non-invaded sites (XCN) in XC (**Figure 2B**). The content of SOC in XC was 93% higher than that in XR in both invaded sites and non-invaded sites (**Figure 2A**). SOC density in XCI was 55% higher than that in XRI ($P < 0.0001$, **Figure 2B**), while in the non-invaded sites, SOC density in XCN was 94% higher than that in XRN ($P = 0.006$, **Figure 2B**).

Soil Physicochemical Properties and the Relationships Between SOC and Soil Physicochemical Properties

In XR, dissolved oxygen in invaded sites was significantly lower than that in non-invaded sites (**Table 1**). Water temperature and soil temperature in invaded sites in XC were significantly lower than those in non-invaded sites (**Table 1**). In the invaded sites in the two types of wetlands, soil moisture content in XRI was significantly lower than that in XCI (**Table 1**), while bulk density, dissolved oxygen, water temperature, soil temperature, and pH in XRI were significantly higher than those in XCI (**Table 1**). However, there was no significant difference in moisture content and bulk density in the non-invaded sites in the two types of wetlands (**Table 1**). Spearman correlation analysis showed that SOC content was significantly positively correlated with moisture content, but significantly negatively related to bulk density, dissolved oxygen, water temperature, soil temperature, and pH (**Figure 3**). The correlations of SOC density were basically the same with SOC content, except for bulk density.

Soil Microbial Community and the Relationships Between Soil Microbial Community and Soil Properties

Proteobacteria was the most dominant phylum among all the studied sites, which accounted for 46.4–54.4% of total bacterial community composition (**Figure 4**). Chloroflexi, Bacteroidetes, Acidobacteria, Gemmatimonadetes, Actinobacteria, and Verrucomicrobia were also abundant phyla. Euryarchaeota,

Bathyarchaeota, and Elusimicrobia were important Archaea in the studied area.

The microbial diversity indices (Shannon and Simpson) were significantly lower in XRN than in XRI and XCN (**Table 2**). The microbial richness indices (Chao1 and ACE) and observed species were also lower in XRN than in XRI and XCN, but there was no significant difference between invaded sites and non-invaded sites in the two types of wetlands. Based on Spearman correlation analysis, the microbial diversity indices had significantly positive correlations with the content and density of SOC and significantly negative correlations with dissolved oxygen, water temperature, and soil temperature.

The relationships between microbial community structure and soil properties in the invaded sites and non-invaded sites in the two types of wetlands were revealed by the Redundancy analysis (RDA) (**Figure 5**). The first two axes explained 34.1% of the total variation in soil microbial community at the phyla-level (**Figure 5**). The soil microbial community was significantly correlated with dissolved oxygen ($P < 0.05$), dissolved oxygen explained 19.4% of the variation in the microbial community structure. Meanwhile, there was a clear separation between XR (XRI, XRN) and XC (XCI, XCN). SOC showed a positive relation with the samples in XR, but a negative relation with the samples in XC.

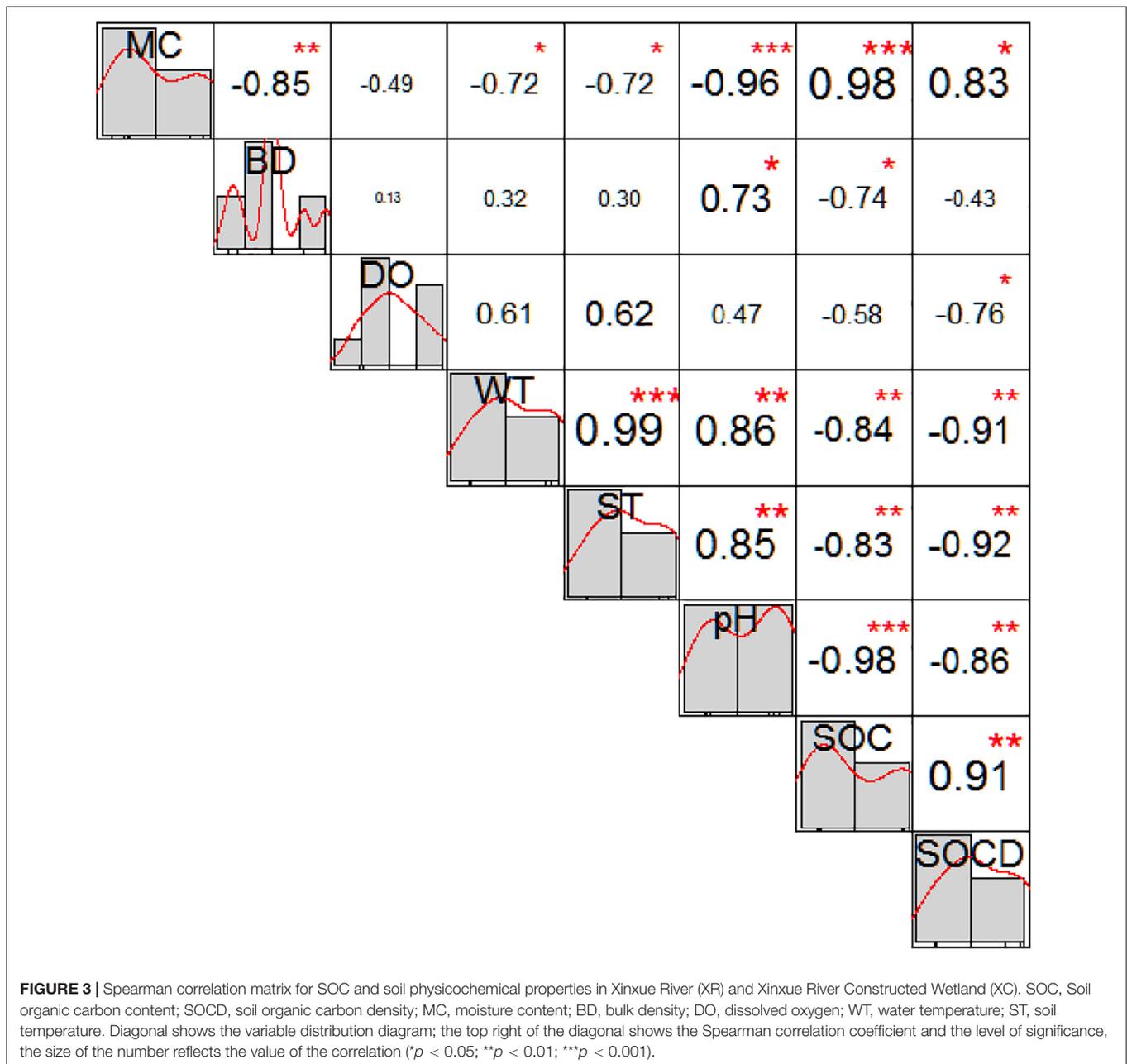
The RDA results of XR and XC were shown in **Figures 6A,B**, respectively. In XR, the first two axes explained about 63.1% of the total variation (**Figure 6A**). The microbial community significantly correlated with bulk density and dissolved oxygen. They respectively explained 23% and 20.5% of the total variation of microbial community structure. The first two axes in XC explained about 53.4% of the total variation (**Figure 6B**). Microbial community significantly correlated with pH and soil temperature. They respectively explained 19.8 and 15.6% of the total variation in microbial community structure.

We quantified the indicator species reflecting soil microbial community shifted by plant invasion in XR and XC (**Figure 7**). In XR, phylum Gemmatimonadetes was enriched in invaded sites (**Figure 7A**). And 12 bacterial groups were abundant in non-invaded sites of XR, such as the phyla Proteobacteria and Verrucomicrobia. For Proteobacteria, the orders Xanthomonadales and Cellvibrionales, family

TABLE 1 | Soil physicochemical properties (mean, SD) in Xinxue River (XR) and Xinxue River Constructed Wetland (XC).

Invasion		Moisture content (%)	Bulk density (g/cm ³)	Dissolved oxygen (mg/L)	Water temperature (°C)	Soil temperature (°C)	pH
XR	Invaded sites (XRI)	38.93 (8.42) ^{Aa}	1.13 (0.20) ^{Aa}	7.65 (3.67) ^{Aa}	30.38 (1.86) ^{Aa}	30.28 (1.17) ^{Aa}	7.67 (0.40) ^{Aa}
	Non-invaded sites (XRN)	37.72 (0.62) ^{Aa}	1.06 (0.06) ^{Aa}	12.7 (2.34) ^{Ab}	31.5 (1.30) ^{Aa}	31.70 (0.26) ^{Aa}	7.42 (0.11) ^{Aa}
XC	Invaded sites (XCI)	59.93 (17.27) ^{Ba}	0.93 (0.16) ^{Ba}	4.39 (2.77) ^{Ba}	26.77 (2.54) ^{Ba}	26.70 (2.89) ^{Ba}	6.81 (0.21) ^{Ba}
	Non-invaded sites (XCN)	46.23 (7.91) ^{Aa}	1.07 (0.12) ^{Aa}	4.87 (2.10) ^{Ba}	27.68 (0.94) ^{Bb}	27.56 (1.62) ^{Bb}	7.15 (0.16) ^{Ba}
Source of variation							
Wetland types		8.485**	1.709	17.082***	19.103***	21.131***	19.408***
Invasion		2.169	0.244	4.268	1.429	1.848	0.117
Wetland types * Invasion		1.52	2.082	2.903	0.016	0.112	5.332*

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Different superscript uppercase letters indicate statistically significant differences at $\alpha = 0.05$ level between river and constructed wetland. Different superscript lowercase letters indicate statistically significant differences at $\alpha = 0.05$ level between invaded sites and non-invaded sites.



Xanthomonadaceae, genera *Denitratisoma* and *Arenimonas* within the class Gammaproteobacteria and family Haliangiaceae within the class Deltaproteobacteria were more abundant in non-invaded sites than in invaded sites. For Verrucomicrobia, the relative abundance of the class Verrucomicrobiae, the family Rubritaleaceae, and the genus *Luteolibacter* were higher in XRN than in XRI. In XC, five bacteria lineages were higher in invaded sites than in non-invaded sites, including class Bacilli, families Planococcaceae, Microbacteriaceae, and Sandaracinaceae, and genus *Geothermobacter*. However, the relative abundance of family unidentified_Solibacterales and genus *Bryobacter* within the order Solibacterales, family unidentified_Acidobacteriales within the order Acidobacteriales, genus *Sphingomonas* within

the phylum Bacteroidetes, and genus *Terrimonas* within the phylum Proteobacteria were higher in XCN than in XCI (Figure 7B).

Spearman correlation analysis showed that the indicator species were highly related with soil properties in XR and XC (Figure 8). In XR, the relative abundance of Gemmatimonadetes enriched in invaded sites had positive correlations with SOC content and density, but negative correlations with dissolved oxygen and soil temperature (Figure 8A). In XR, the species showed negative correlations with SOC content and density and positive correlations with dissolved oxygen and soil temperature, which were more abundant in non-invaded sites than in invaded sites. In XC, the indicator species in invaded sites positively

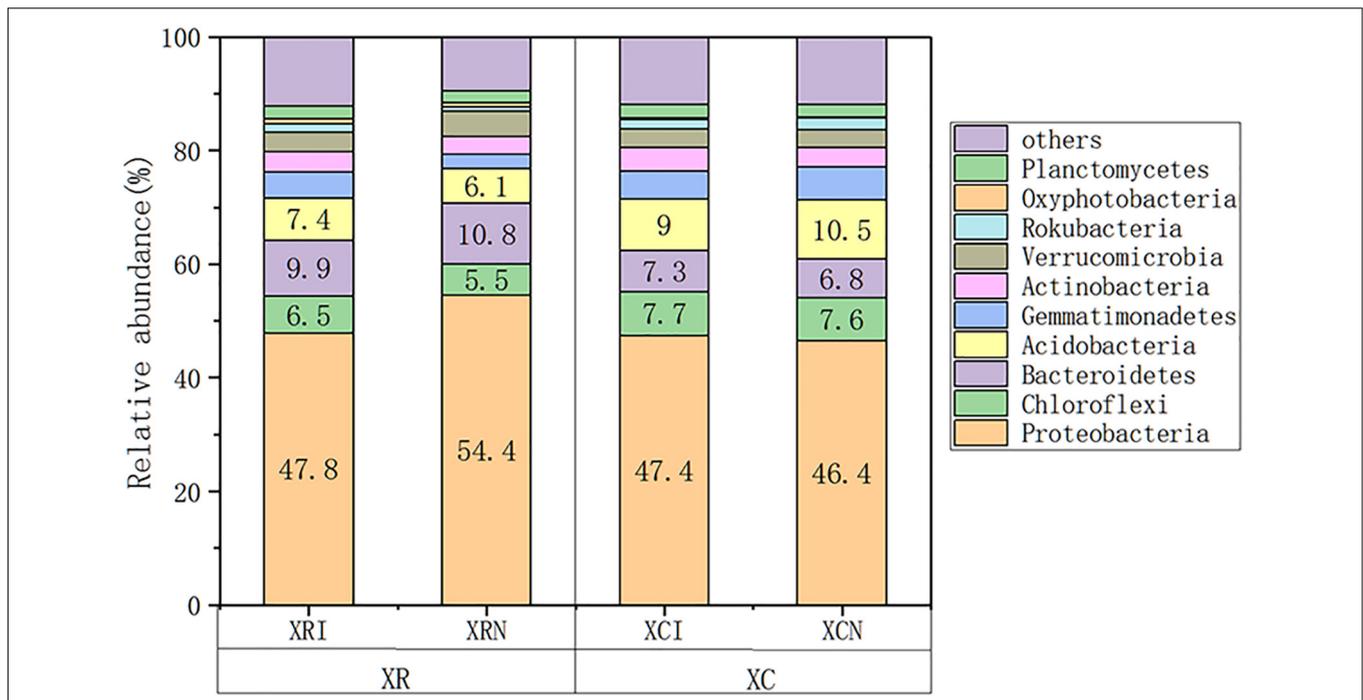


FIGURE 4 | Relative abundance of soil microbial species at invaded sites and non-invaded sites in the two types of wetlands. XRI, Xinxue River invaded sites; XRN, Xinxue River non-invaded sites; XCI, Xinxue River Constructed Wetland invaded sites; XCN, Xinxue River Constructed Wetland non-invaded sites.

TABLE 2 | Alpha Diversity analysis index of invaded sites and non-invaded sites of two types of wetlands.

	Invasion	Observed species	Shannon	Simpson	chao1	ACE	OTU
XR	XRI	6,712	10.6639 ^{Aa}	0.998 ^{Aa}	7322.27	7570.56	74,497
	XRN	6,282	10.3193 ^{Ab}	0.997 ^{Ab}	7137.45	7408.21	78,456
XC	XCI	6,373	10.7483 ^{Aa}	0.998 ^{Aa}	7152.02	7369.87	76,416
	XCN	6,511	10.7834 ^{Ba}	0.998 ^{Ba}	7442.08	7666.01	75,775

Different superscript uppercase letters indicate statistically significant differences at $\alpha = 0.05$ level between river and constructed wetland. Different superscript lowercase letters indicate statistically significant differences at $\alpha = 0.05$ level between invaded sites and non-invaded sites. XRI, Xinxue River invaded sites; XRN, Xinxue River non-invaded sites; XCI, Xinxue River Constructed Wetland invaded sites; XCN, Xinxue River Constructed Wetland non-invaded sites.

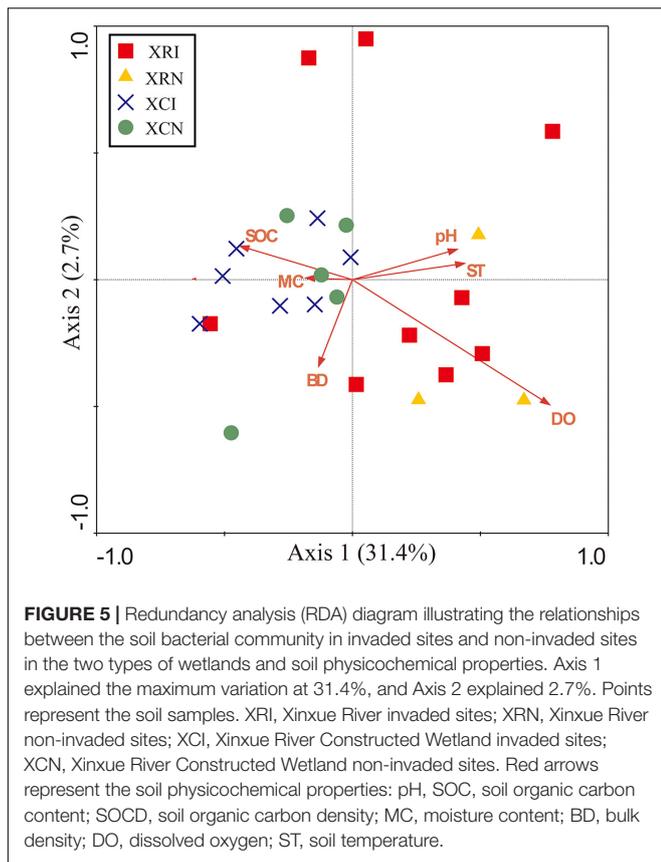
correlated with SOC content and density, but negatively correlated with pH. And the indicator species in non-invaded sites of XC showed negative correlations with the content and density of SOC and moisture content, and positive correlations with pH and bulk density (Figure 8B).

DISCUSSION

Previous studies demonstrated that plant invasion greatly impacts the soil carbon cycle (Ehrenfeld, 2003; Drenovsky and Batten, 2007; Tamura and Tharayil, 2014), but the influence mechanism of plant invasion on SOC in wetlands remains unclear. In our study, in both the river and the constructed wetland, *A. philoxeroides*-invaded sites had higher SOC content and density than non-invaded sites. Our result showed that the plant invasion could increase the content of SOC, which was consistent with previous studies (He et al., 2019; Zhang G. et al., 2019). Invasive plants with high net primary productivity

could increase the content of SOC through root exudation and litter decomposition (Craig et al., 2015; Zhou et al., 2015). When the soil nutrients increased, microbes decomposed the fresh organic matter instead of soil organic matter, resulting in the accumulation of SOC (Fontaine et al., 2003). It might be an explanation for the increase of SOC in the river and the constructed wetland with *A. philoxeroides* invasion.

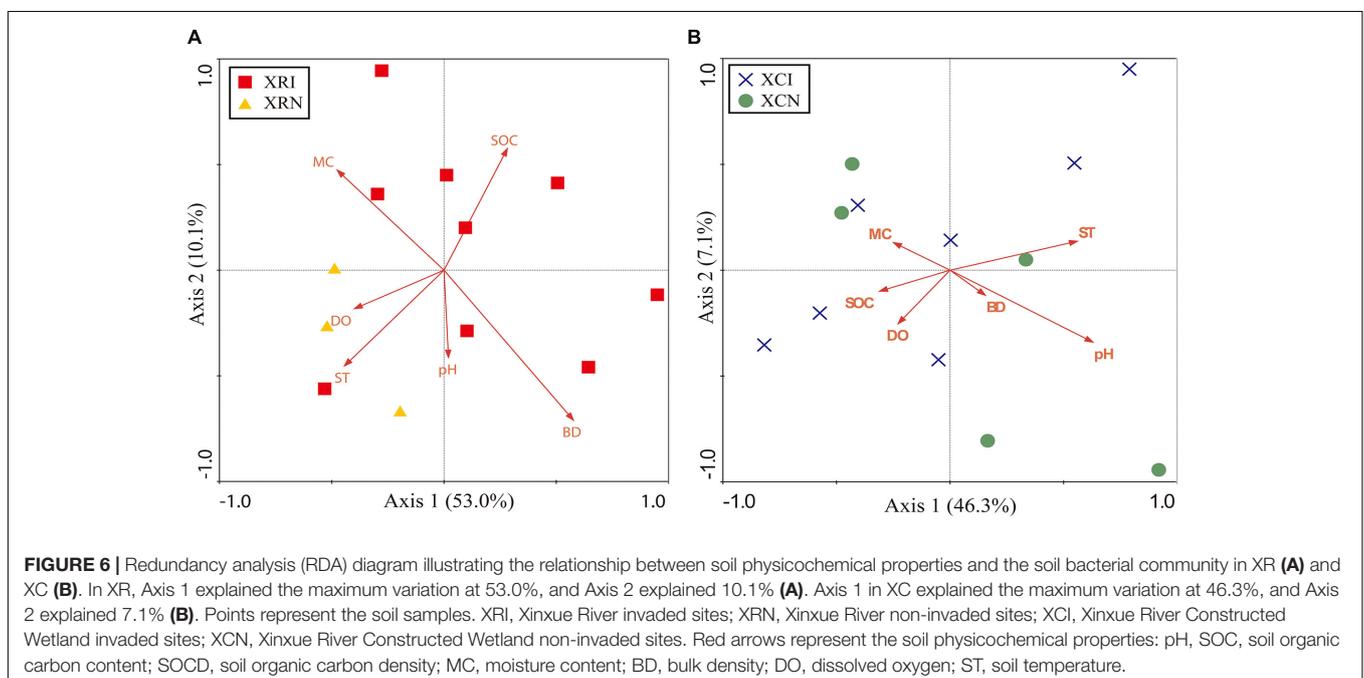
Plant invasion can indirectly affect the carbon cycle by changing soil physicochemical properties including moisture content, pH, bulk density, dissolved oxygen, and temperature (Huang et al., 2014; Qi et al., 2019; Yang, 2019). In our study, the positive correlations between SOC and moisture content and the negative correlations between SOC and bulk density, dissolved oxygen, water temperature, soil temperature, and pH (Figure 3) conformed with the results of Qi et al. (2019). The effect of *A. philoxeroides* invasion on the storage of SOC might be related to the alternation of different physicochemical properties in the river and the constructed wetland. In the river, dissolved oxygen was significantly decreased in invaded sites.



The negative correlation of SOC with this reduced dissolved oxygen could partially explain the higher content of SOC in invaded sites. A previous study reported that dissolved oxygen

could be taken up by microbes for microbial activities (Higashino et al., 2008). The consumption of dissolved oxygen in invaded sites in the river might be due to the increase of the activities and reproduction of microorganisms, which was confirmed by the fact that invaded sites had a higher richness of microbes than non-invaded sites. The decreased dissolved oxygen with plant invasion in the river correlated with the alteration of the microbial community (Figure 6A), which might limit the consumption of SOC by aerobic heterotrophic microorganisms such as Betaproteobacteria (Zhang Y. et al., 2015), and might indirectly result in the accumulation of SOC. Hence, we inferred that in the river invaded by plants, dissolved oxygen might be the dominant factor affecting the consumption of SOC by altering microbial respiration and composition. However, plant invasion in the constructed wetland altered different soil properties. The significant decrease of soil and water temperature might be due to the shielding effect of invasive plants on the water surface (Wang et al., 2009). Lower temperatures might inhibit microbial growth and even alter soil microbial community structure (Supramaniam et al., 2016). In the constructed wetland, soil temperature was related in the variation of microbial community structure (Figure 6B), which could be a reason for the difference in SOC between invaded sites and non-invaded sites. In the river and the constructed wetland, *A. philoxeroides* invasion could change different soil properties including dissolved oxygen and temperature to affect the storage of SOC indirectly.

Plant invasion can affect soil microorganisms, which act as one of the main factors of SOC formation (Bradford et al., 2013). The root exudates of invasive plants are an important carbon source for soil microbes (Craig et al., 2015). A previous study has shown that plant invasion could elevate soil microbial abundance and diversity (Yang et al., 2019). In our study, *A. philoxeroides*-invaded sites in the river had higher microbial



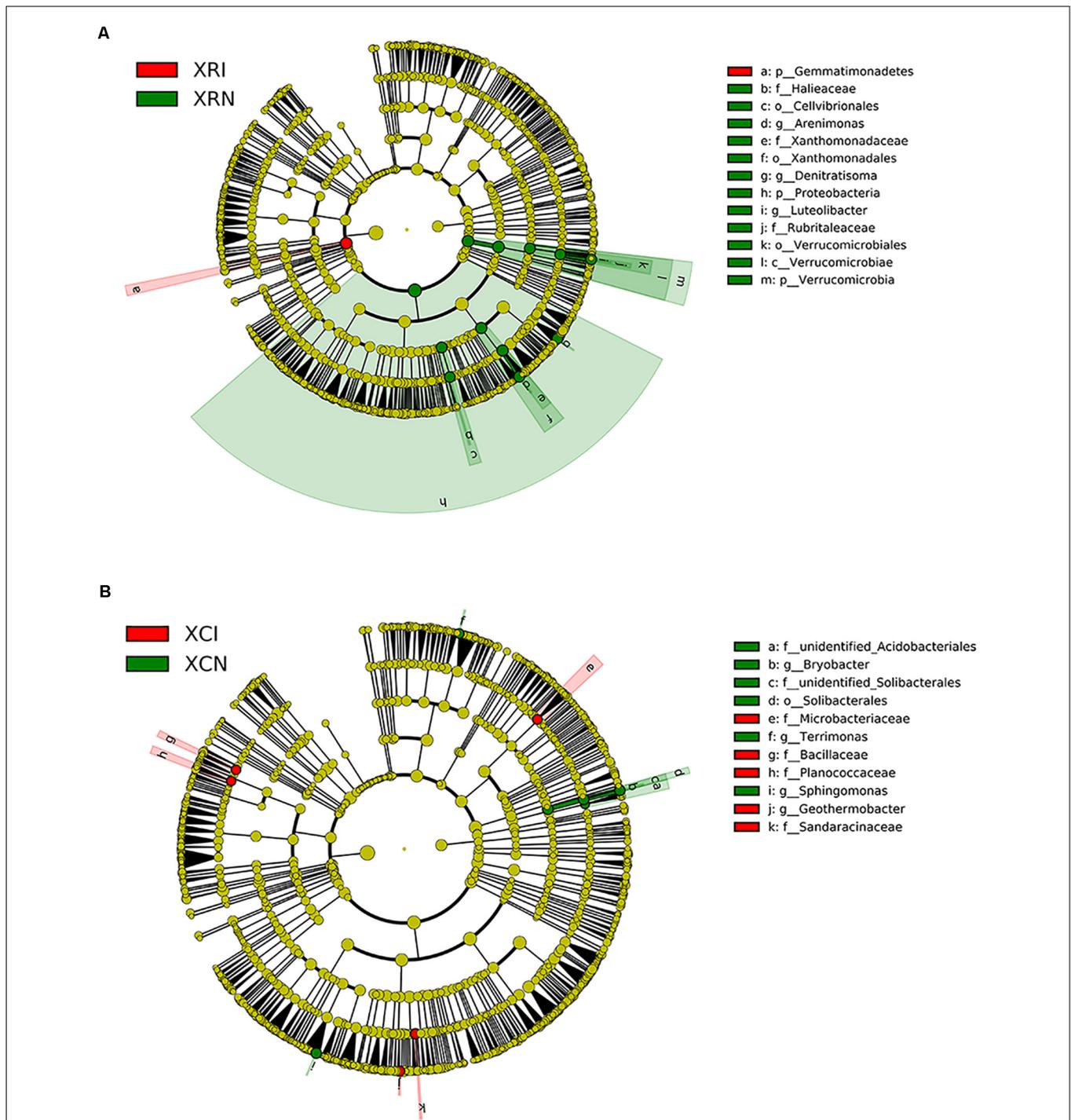
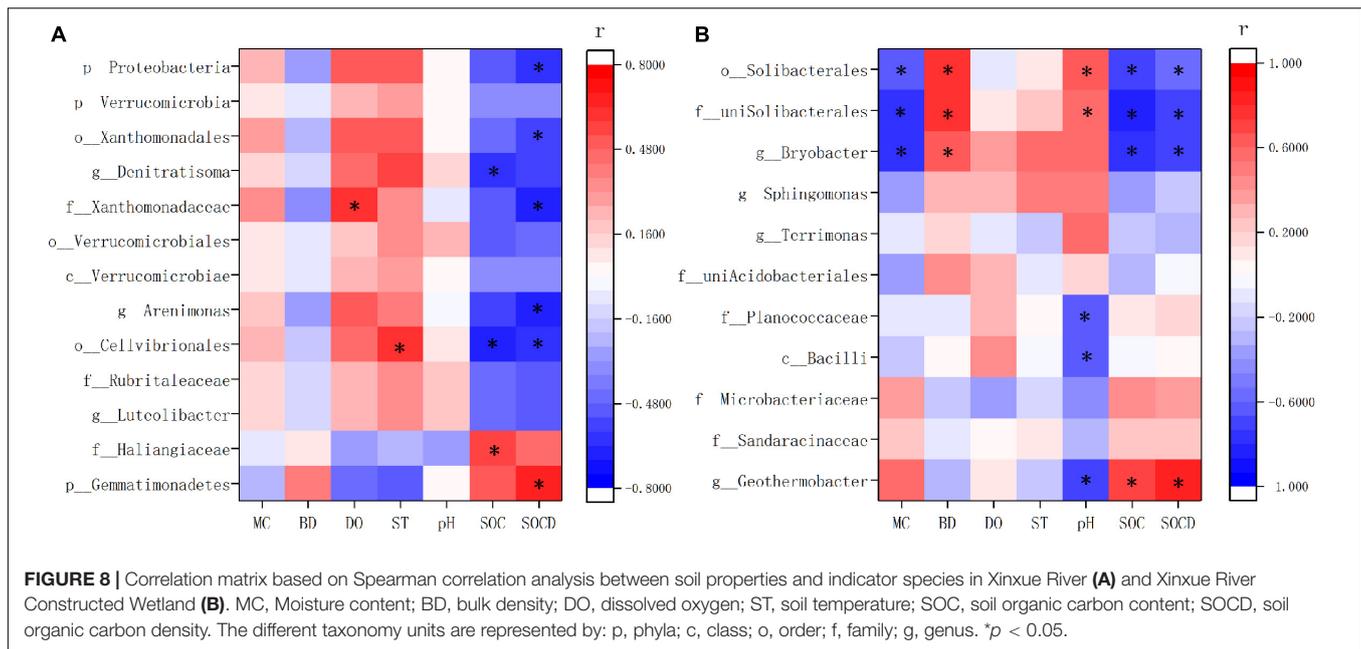


FIGURE 7 | The differences in microbial lineages between invaded sites and non-invaded sites analyzed by linear discriminant analysis effect size (LEfSe) in Xinxue River **(A)** and Xinxue River Constructed Wetland **(B)**. The cladogram shows the lineages with linear discriminant analysis score higher than 2.0. The different taxonomy units are represented by rings with different diameters. Yellow nodes show no significant difference in invaded sites and non-invaded sites, while red means the higher units in invaded sites and green means the higher units in non-invaded sites. XRI, Xinxue River invaded sites; XRN, Xinxue River non-invaded sites; XCI, Xinxue River Constructed Wetland invaded sites; XCN, Xinxue River Constructed Wetland non-invaded sites.

diversity indices (Shannon and Simpson) than the non-invaded sites, which might be due to the plant invasion. But there was no difference in the microbial diversity in the constructed wetland.

The stable microbial diversity indices in the constructed wetland might be because of the compensation from other microbial groups for some microbial variations or the limited impacts of



plant invasion on microbial α diversity indices (Custer and van Diepen, 2020). The result of LEfSe showed that the microbial community structure in the river and the constructed wetland was significantly different between the invaded and non-invaded sites (Figure 7). The microbial community structure might be changed by plant invasion. In our study area, the indicator species in *A. philoxeroides*-invaded sites and non-invaded sites showed positive and negative correlations with SOC. Phylum Gemmatimonadetes, reported to be capable of photosynthetic reaction, served as the indicator species in invaded sites of river (Zeng et al., 2014). The indicator species in non-invaded sites of the river including classes Gammaproteobacteria and Deltaproteobacteria, and family Rubritaleaceae could degrade polysaccharides (Martinez-Garcia et al., 2012; Desta et al., 2014; Rosenberg et al., 2014). By querying KEGG³, the indicator species in invaded sites of the constructed wetland have M00169, M00345, and M00579 metabolic pathways of carbon fixation. However, the indicator species in non-invaded sites including order Acidobacteriales, genera Sphingomonas and Terrimonas have been reported to be able to degrade cellulose and other polysaccharides (Desta et al., 2014; Rosenberg et al., 2014). Order Solibacterales could participate in the mineralization of phosphorus (Bergkemper et al., 2016). The indicator species might be an important factor for the increase of SOC caused by plant invasion.

Furthermore, the results indicate that plant invasion might have a greater impact on SOC in the river than in the constructed wetland. This might be because rivers are vulnerable to plant invasion and constructed wetlands have higher SOC content and density than rivers. The lower content and density of SOC in rivers might be due to physicochemical properties, water velocities, and vegetation coverage (Braskerud, 2001;

Cao et al., 2015). Moreover, the positive correlation between SOC and dissolved oxygen in the constructed wetland was different from the river and other studies (Cao et al., 2015), which might be because the roots of invasive plants import root exudates and oxygen into the soil. However, the degrees of plant invasion in the river and the constructed wetland are not experimentally controlled, and the lack of data before and after the plant invasion of the same area is also a limitation of this study. More experimental studies are needed to validate the influence mechanisms of plant invasion on SOC.

CONCLUSION

The study found that the invasion of *A. philoxeroides* significantly increased SOC content and density in both the river and the constructed wetland. SOC in the two types of wetlands had positive correlation with moisture content and negative correlations with bulk density, dissolved oxygen, water temperature, soil temperature, and pH. The invasion decreased the dissolved oxygen in the river and the soil temperature in the constructed wetland. It is possible that the alternation of different soil properties in the two types of wetlands with plant invasion resulted in the difference in SOC. With plant invasion, the decrease of dissolved oxygen in the river might alter the microbial community and limit the decomposition of organic carbon by microbes. The increase of microbial α diversity indices and the correlations between soil microbial community in the river and dissolved oxygen verified the effect of plant invasion on SOC. In the constructed wetland, plant invasion only changed the microbial community structure. And RDA analysis showed that the variation in soil microbial community structure in the constructed wetland could be mainly explained by pH and soil temperature. We suggest that the decrease of

³<https://www.genome.jp/kegg/kegg2.html>

soil and water temperature in the constructed wetland might inhibit the microbial growth and reduce microbial respiration. Furthermore, the variation in indicator species caused by plant invasion might be related to the difference in SOC, as confirmed by their correlations. This study is of great significance to understand the impact of the invasion of *A. philoxeroides* and other similar invasive plants on the wetland carbon stock, and provides a foundation for further research on the relationship between global change and plant invasion.

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in the online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://www.ncbi.nlm.nih.gov/>, SRP267962.

ETHICS STATEMENT

The sample collection in this study was approved by the Management Committee of the Xinxue River Constructed Wetland.

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AUTHOR CONTRIBUTIONS

KL, RY, and JL: conception and design of study, analysis and interpretation of data. KL and RY: acquisition of data. RY and JL: drafting the manuscript. JF, KL, JL, CZ, and QQ: revising the manuscript critically for important intellectual content. RY, KL, JF, QQ, CZ, and JL: approval of the version of the manuscript to be published. All authors contributed to the article and approved the submitted version.

FUNDING

This study was supported by the Major Science and Technology Program for Water Pollution Control and Treatment (No. 2017ZX07101003), the National Natural Science Foundation of China (No. 32071523), the Natural Science Foundation of Shaanxi Province (No. 2019JLP-26), and the Natural Science Foundation of Shandong Province (No. ZR2017MC013).

ACKNOWLEDGMENTS

We would like to thank Lifei Wang for English language editing.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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