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Impacts of *Spartina alterniflora* invasion on C-cycling functional genes and microbial communities in salt marsh wetlands during cold season

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Abstract

Background The invasiveness of *Spartina alterniflora* Loisel. into the estuarine coastal wetlands has impacted the stability of soil organic carbon, as well as the functional genes of soil microorganisms. However, the mechanisms by which *S. alterniflora* invasion affects soil organic carbon, especially at the micro-level, is still unclear. Therefore, this study compared the differences in soil carbon cycling (C-cycling) functional genes between invaded and native areas during the cold season, as well as the changes in microbial communities involved in differential functional genes' expression.

Results Our results showed that in salt marsh wetlands dominated by *Suaeda salsa* (L.) Pall., invasion by *S. alterniflora* negatively impacts soil microbial biomass carbon (MBC) and reduces the diversity of C-cycling functional genes. The invasion species significantly increased the relative abundance of carbon fixation genes, while decreasing the relative abundance of carbon degradation genes. Additionally, the differential genes-expressing microbial communities exhibited notable differences across groups. At the class level, both generalist taxa (e.g., Gammaproteobacteria, Deltaproteobacteria) and specialist taxa (e.g., Nitrospiria, Flavobacteriia) collectively influenced the abundance of C-cycling functional genes. Correlation and hierarchical partitioning analyses revealed that the increased soil carbon fixation capacity was closely associated with increased soil organic carbon (SOC) and decreased MBC, whereas the decline in soil carbon degradation capacity was linked to higher soil electrical conductivity (EC) and a lower C:P ratio.

Conclusions Our study filled a gap in research during the cold season and revealed that the invasion of *S. alterniflora* significantly impacts both soil C-cycling functional genes and their expressing microbial communities, thereby potentially affecting the soil organic carbon of salt marsh wetland ecosystems.

Keywords C degradation functional genes, C fixation functional genes, Microbial communities, Plant invasion, *Spartina alterniflora*, Salt marsh wetland

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Introduction

Salt marsh wetlands serve as critical links between marine and terrestrial ecosystems, possessing high productivity and ecological service value. They play an essential role in the biogeochemical cycling processes of coastal zones (Murray et al. 2014; Tang et al. 2018). While salt marsh wetlands only account for 4.3% of the global wetland area, they contribute 46.9% of the carbon storage in marine sediments, making them an important blue carbon sink on Earth (Mcleod et al. 2011). Currently, biological invasion is one of the greatest threats to salt marsh wetlands habitats. *Spartina alterniflora*, a common invasive species in the estuarine coastal wetlands of China, was introduced for natural erosion control. This exotic cordgrass has rapidly established and competed with native species, such as *Suaeda salsa* and *Phragmites australis* (Meng et al. 2020; Lin et al. 2021; Gao et al. 2022), leading to a sharp decline in native species abundance, and even complete replacement in some areas (Zhang et al. 2017). As a C4 plant, *S. alterniflora* has a longer growing season and a higher net photosynthetic rate than C3 plants like *S. salsa*. Changes in aboveground vegetation communities affect soil organic matter inputs, which, in turn, alter soil nutrient fluxes and biogeochemical cycles, disrupting the carbon balance within the ecosystem (Meng et al. 2020; Lin et al. 2021). Therefore, understanding how *S. alterniflora* invasion influences soil C-cycling in salt marsh wetland ecosystems is crucial for predicting changes in wetland soil organic carbon.

Soil organic carbon is one of the most important nutrients in soil, playing a crucial role in maintaining the health of soil ecosystems. The dynamics of the soil organic carbon pool are closely linked to plant invasions (Lal 2018). Studies have shown that the invasion of *S. alterniflora* affects the accumulation and turnover of SOC in wetlands (Tian et al. 2023). Soil microbes are one of the main drivers of organic carbon changes (Schimel and Schaeffer 2012), with evidence suggesting that microbes contribute more than 50% to the soil organic carbon pool (Liang et al. 2017). The invasion of *S. alterniflora* can influence soil organic carbon by altering soil microbial community diversity and composition (Lin et al. 2021), complexity, and the richness of key taxa (Chen et al. 2021; Fan et al. 2021). Gao et al. (2022) indicated that *S. alterniflora* invasion changes the bacterial community composition across the entire soil profile, significantly reduces microbial network stability, and decouples the relationship between microbes and the carbon pool. These findings highlight the indispensable role of microbes in soil carbon cycling (Cui et al. 2021; Wei et al. 2021; Zhang et al. 2021).

Soil microorganisms primarily promote the storage and stability of SOC through processes such as inorganic carbon fixation, organic carbon transformation, and interactions with plants and soil and regulate the decomposition of soil organic matter by degrading plant and microbial biomass residues and through soil priming effects (Wu et al. 2024). Microorganisms containing C-cycling genes participate in the carbon cycle through the expression of genes that encode relevant enzymes, thereby regulating soil carbon storage. Consequently, the diversity and abundance of microbial functional genes can explain variations in C-cycling (Dong et al. 2020; Ma et al. 2021). Research has shown that in salt marsh wetlands dominated by *P. australis*, the invasion of *S. alterniflora* enhances carbon metabolism; but in mangrove ecosystems, *S. alterniflora* invasion alters microbial functional traits related to nutrient cycling, potentially reducing the carbon sequestration capacity (Dai et al. 2024). Changes in microbial communities and carbon-related functional genes caused by plant invasions are closely linked to the dynamics of SOC. Moreover, microbial functional traits may not always align with shifts in taxonomic diversity (Kuzyakov et al. 2009). Therefore, examining microbial functional characteristics is essential for understanding the mechanisms by which microorganisms drive soil carbon cycling, especially given our limited knowledge of underground microbial communities in invaded ecosystems. In addition, current researches primarily focused on the changes in SOC and its driving factors during the growing season of *S. alterniflora*, with limited attention given to the cold season. While soil organic matter and microbial activity in the cold season are influenced by climatic conditions and plant dormancy or semi-dormancy, microbial activity and metabolic patterns continue to affect the decomposition and accumulation of soil organic carbon (Kuffner et al. 2012). Moreover, microbial communities and functional characteristics are subject to seasonal variations (Koranda et al. 2013). Therefore, exploring the mechanisms behind changes in SOC during the cold season is crucial for gaining a more comprehensive understanding of ecosystem carbon storage capacity and is significant for revealing soil quality changes under different climatic conditions.

This study employed metagenomic methods to compare the characteristics of microbial functional genes involved in C-cycling in the soils of *S. alterniflora*-invaded and native vegetation areas in a salt marsh wetland ecosystem, as well as the changes in the associated microbial communities. We selected the Xihu Harbor salt marsh wetland in Xiangshan County, Ningbo City as the research site. The study elucidated the abundance and changing trends of functional genes involved in soil carbon cycling, reflecting the microbial potential for soil organic carbon decomposition and fixation during clod

season. The research objectives are: (1) to investigate the impacts of *S. alterniflora* invasion on soil C-cycling functional genes, (2) to analyze the microbial taxa and their changing trends of differentially expressed genes, and (3) to identify the driving factors behind changes in soil C-cycling functional genes in salt marsh wetland soil. The findings from this study will enhance our understanding of the mechanisms by which *S. alterniflora* invasion affects soil carbon cycle functional genes and associated microbial communities, thereby providing valuable insights into the broader impacts of *S. alterniflora* on soil C cycling in salt marsh wetland ecosystems.

Materials and methods

Site description and soil sampling

This study was conducted in the Xihu Harbor, Xiangshan County, Ningbo Province in southeastern China. This site has subtropical monsoon climate, a mean annual temperature of 17–18 ℃, a mean precipitation of 1300–1500 mm, most of which occurs in summer. We collected soils from five locations along the western shoreline of Xihu Harbor in December 2023, about 500 m between each location. Each location had two community types, *S. alterniflora* (Invasion) and dominant indigenous plants (Native). This area was initially a habitat for *S. salsa*, but is currently affected by the invasion of *S. alterniflora*, with a clear contrast between native vegetation and invasive vegetation. Additional file 1: Table S1 shows the sampling information in detail.

At each of the five sampling locations, we randomly laid out 2 m × 2 m quadrats for each vegetation communities. The topsoil (0–20 cm) samples were collected by an auger (5 cm diameter). The vegetation root system was densely distributed and soil microbial activity was high within this depth. Five cores were collected using the five-point sampling method and pooled to form a composite sample in each community type, resulting in a total of ten samples (two types of plant community × five replicates). Each composite soil sample was divided into two portions, and one was immediately used to determine the dissolved organic carbon (DOC) and microbial biomass carbon (MBC), and then air-dried to determine the remaining soil properties, while the other was stored at −80 ℃ prior to DNA extraction.

Soil properties analyses

Soil samples were assessed for bulk density (BD) (cutting ring method, 100 cm^3), electric conductivity (DDSJ-308F electric conductometer), soil pH (Sartorius PB-10 pH meter). Total nitrogen (TN) was measured with a Kjeldahl nitrogen tester (Komy 1995). Total phosphorus (TP) was digested by perchloric acid and measured colorimetrically using a UV-1900i. SOC was determined with potassium dichromate-concentrated sulfuric acid oxidation method. DOC was determined by TOC-V CPH total C analyzer (Shimadzu Scientific Instruments, Kyoto, Japan), and permanganate oxidizable organic carbon (POXC) was assayed by oxidation of 333 mM $KMnO_4$ (Blair et al. 1995). MBC was assayed by chloroform fumigation. Labile organic carbon (LOC) was calculated by the sum of POXC, MBC and DOC, recalcitrant organic carbon (ROC) was counted by SOC minus LOC (Zhang et al. 2022), and the top 20 cm SOC storage (SOCS, kg m^{-2}) was estimated by the following formula (Xia et al. 2021):

$$SOCS = \frac{SOC \times BD \times D}{100}$$

where SOC is the SOC concentration (g kg^{-1}), BD is the bulk density (g cm^{-3}), and D is thickness of the sampled layer (20 cm).

DNA extraction and sequencing

Soil DNA was extracted using the QIAamp® Fast DNA Stool Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. The quality and concentration of DNA samples were assessed by agarose gel electrophoresis and NanoDrop2000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA) respectively. DNA was fragmented by S220 Focused-ultrasonicators (Covaris, USA) and cleaned up by Agencourt AMPure XP beads (Beckman Coulter Co., USA). The libraries were constructed using TruSeq Nano DNA LT Sample Prepararion Kit (Illumina, San Diego, CA, USA) according to the manufacturer' s instructions. The shotgun metagenome sequencing was conducted by OE Biotech Co., Ltd. (Shanghai, China). Paired-end reads were generated on an IIumina Novaseq 6000 2 × 150 bp platform.

Raw data in the fastq format were trimmed and filtered using fastp (v 0.20.1) (Chen et al. 2018). Metagenome assembly was conducted using MEGAHIT (Li et al. 2015a) after obtaining valid reads. We used gaps inside scaffold as breakpoints to interrupt the scaffold into new contigs (Scaftig), and these new Scaftigs with length > 500 bp were retained. Open reading frames (ORF) prediction of assembled scaffolds using prodigal (Hyatt et al. 2010) was performed and translated into amino acid sequences. MMSeqs was used to build the non-redundant gene sets for all predicted genes. The clustering parameters were 95% identity and 90% coverage, and the longest gene was selected as a representative sequence of each gene set. Clean reads of each sample were aligned against the non-redundant gene set (95% identity) using salmon, and the abundant information of the gene in the corresponding sample

was counted. Diamond was conducted to blast predicted genes against the non-redundant protein sequences database of NCBI-NR with the parameters (e-value of $1e^{-5}$) in the blastp mode (Buchfink et al. 2015). The Kyoto Encyclopedia of Genes and Genomes (KEGG) annotation was conducted using diamond against the database with an e-value of $1e^{-5}$. The taxonomy of the species was obtained as a result of the corresponding taxonomy database of the NR Library, and the abundance of the species was calculated using the corresponding abundance of the genes. To construct abundance profiles at the corresponding taxonomic levels, we performed abundance statistics at each taxonomic level.

Statistical analysis

Statistical analyses were conducted in the R (v. 4.3.2). Difference analyses were performed by paired *t*-test or Wilcoxon test, based on normality and Shapiro–Wilk test results. Principal coordinate analysis (PCoA) based on Bray–Curtis dissimilarity was performed to explore the similarities and differences in the gene composition for different treatment groups using the 'vegan' R package, and the permutational multivariate analysis of variance (PERMANOVA) to assess the effects of *S. alterniflora* invasion on C-cycling genes and associated functional communities. We also calculated Spearman coefficients for determining the links between environmental variables, the relative abundance of microbial functional genes and associated functional communities. Heatmaps were made using the 'pheatmap' package. Mantel test was calculated using the mantel function from the 'ecodist' package. Finally, we used a hierarchical partitioning to estimate the importance of each environmental variable and how well they explained the microbial functional genes. Hierarchical partitioning was performed by 'rdacca.hp' package, which calculates the variable importance from all subset models, leading to an unordered assessment of importance (Lai et al. 2022).

Results

Soil properties

Plant invasion affected soil properties (Fig. 1; Additional file 1: Table S2). Invasion significantly increased soil electrical conductivity ($P<0.05$). The concentrations of SOC, DOC and ROC were significantly increased after invasion ($P<0.001$; $P<0.01$), but LOC was not affected

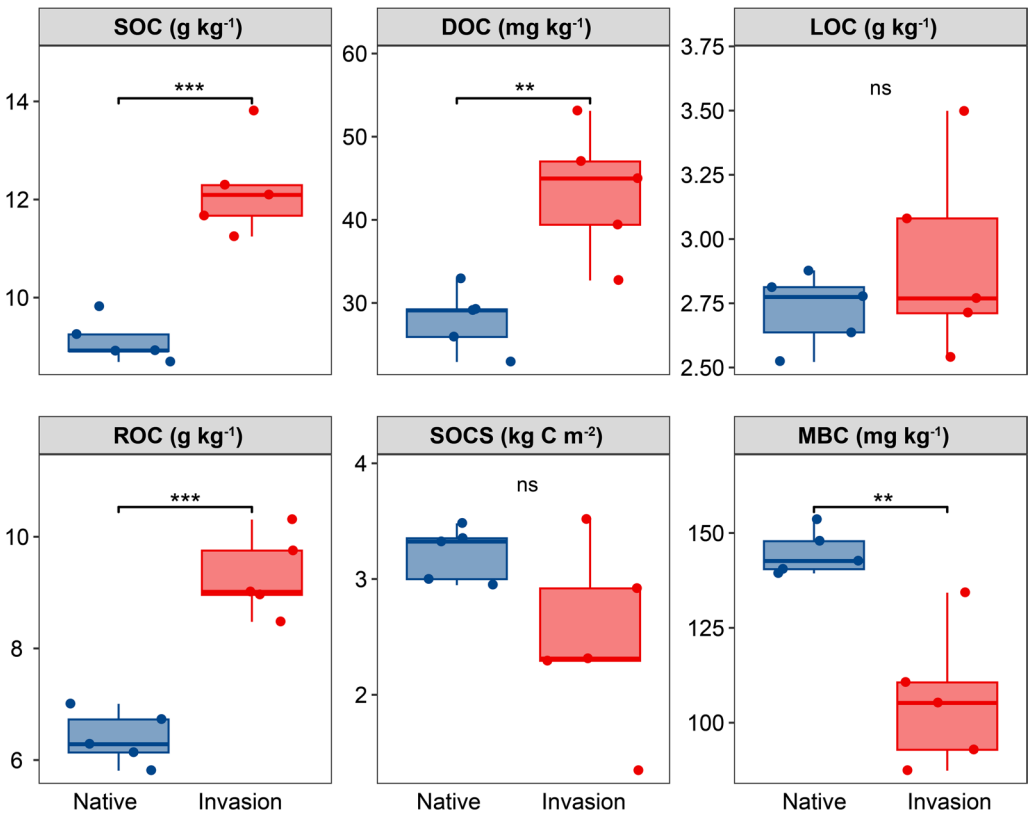


Fig. 1 Effects of *S. alterniflora* invasion on soil C-related properties ($n=5$). SOC: soil organic carbon; DOC: dissolved organic carbon; ROC: recalcitrant organic carbon; LOC: labile organic carbon; SOCS: soil organic carbon storage; MBC, microbial biomass carbon. Asterisks denote significant correlation (*$P<0.05$, **$P<0.01$, ***$P<0.001$, and same below)

(Fig. 1). Soil microbial biomass carbon was significantly decreased after invasion ($P < 0.01$), but there was no significant change in soil organic carbon storage.

The composition of C-cycling functional genes

The study focused on functional genes involved in the two pathways of carbon fixation and decomposition metabolism (Additional file 2: Table S3). Microbial diversity results showed that the Shannon index of functional genes in native vegetation plots was significantly higher than that in invasive plots (Additional file 1: Fig. S1). PCoA analysis indicated significant differences in the relative abundance of soil carbon cycle functional genes (carbon fixation and decomposition metabolism pathways) between invasion and native group ($P < 0.05$) (Fig. 2a). Statistical analyses were conducted separately for the two pathways, and regardless of whether they were native or invasive plots, the abundance of carbon fixation functional genes was generally higher than that of carbon degradation functional genes (Fig. 2b). In addition, invasion significantly increased the relative abundance of carbon fixation functional genes, but the abundance of functional genes involved in carbon degradation significantly decreased ($P < 0.05$) (Fig. 2b).

Common carbon fixation pathways include: the Calvin-Benson-Bassham (CBB) cycle, the micro-aerobic reductive tricarboxylic acid (rTCA) cycle, the 3-hydroxypropionate (3HP) bicycle, the 3-hydroxypropionate/4-hydroxybutyrate (3HP4HB) cycle, the dicarboxylate/4-hydroxybutyrate (DC4HP) cycle, and the anaerobic Wood-Ljungdahl (WL) pathway (Ward and Shih 2019). All these pathways were detected in this study. We conducted statistical analysis on these 6 pathways and found that in the invasion group, the rTCA, WL, and DC4HP pathways showed a significant upward trend, while the remaining pathways did not show significant changes. Microbial functional genes degrade starch, cellulose, hemicellulose, chitin, lignin, and pectin by secreting various enzymes. Analysis revealed that the invasion of *S. alterniflora* did not have a significant impact on each carbon degradation pathway (Fig. 2c).

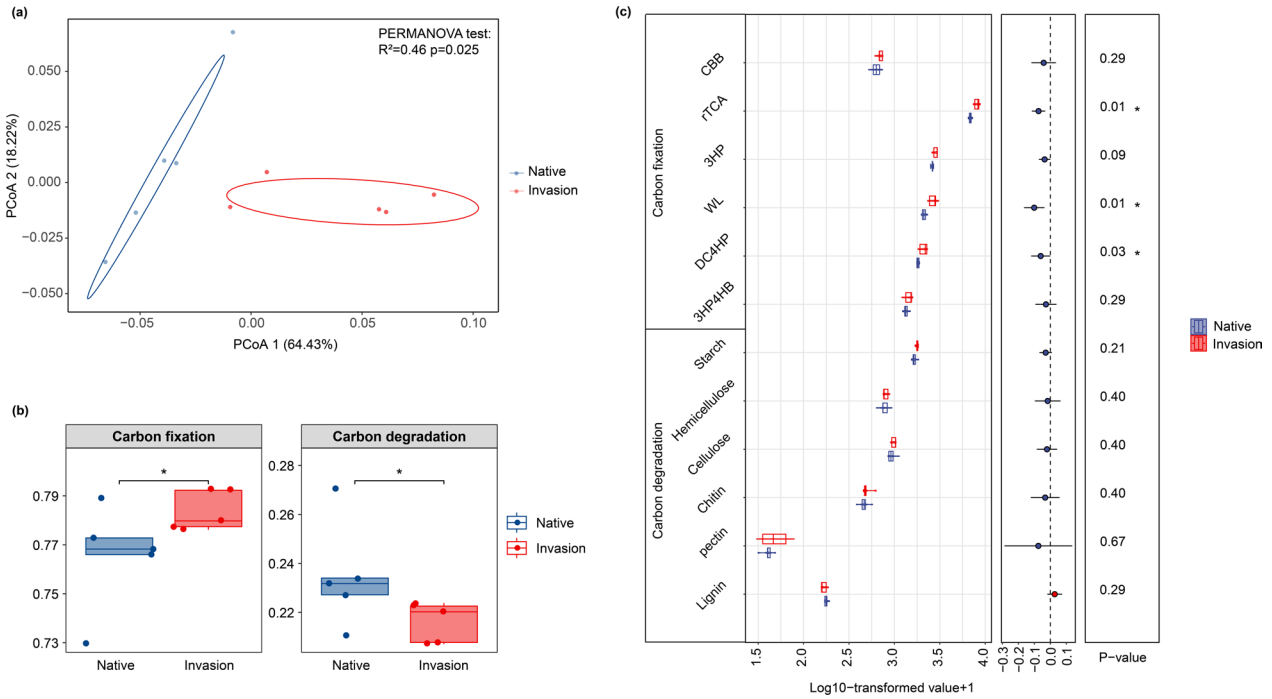


Fig. 2 **a** Principal coordinate analysis (PCoA) of the composition of C-cycling genes based on Bray–Curtis distances. The variations explained by PCoA 1 and PCoA 2 are shown as percent values along the axes. A permutational multivariate analysis of variance (PERMANOVA) was used to determine the significant effect of *S. alterniflora* invasion on the C-cycling genes. **b** Box plots show the effects of *S. alterniflora* invasion on the relative abundance of carbon fixation and carbon degradation functional genes. **c** Comparison of functional genes of different pathways of carbon fixation and carbon degradation in response to the invasion of *S. alterniflora*. The box plot on the left indicates the mean relative abundance of each pathway in the different groups, the middle graph shows the 95% confidence interval with the error line, and the right graph is *P*-value of the difference between the two sample groups

Relative abundance of functional genes involved in carbon fixation and carbon degradation

Statistical analysis was conducted on individual functional genes involved in carbon fixation and degradation to understand their intergroup variations (Additional file 3: Table S4), resulting in 29 functional genes with significant differences between groups (Fig. 3). Among the functional genes encoding carbon fixation, there were significant changes in the functions of 5 pathways (Fig. 3a). In the rTCA pathway, invasion significantly increased the relative abundance of *por* ($P<0.01$), significantly increased the relative abundance of *pta* ($P<0.05$), but significantly reduced the relative abundance of *sucD* and *sucC* ($P<0.01$). In the 3HP pathway, invasion significantly decreased the relative abundance of *mcl*, *mcmA2*, *accB* ($P<0.05$), and significantly decreased the relative abundance of *MCEE*, *mch* ($P<0.01$), wherein *mcmA2* and *MCEE* were simultaneously involved in the 3HP4HB pathway. In the WL pathway, *cooS*, *acsB*, *metF*, and *fdhA* showed a significant increase in relative abundance in the invaded group ($P<0.05$), *fdhB* showed a highly significant increase ($P<0.01$). In the DC4HP3 pathway, invasion highly significantly reduced the relative abundance of *ACAT* ($P<0.01$), which was also involved in the 3HP4HB pathway.

The differential functional genes of carbon degradation pathways are shown in Fig. 3b. We sorted them from easily degradable carbon to recalcitrant carbon, and all five types of substances in the figure, except for starch, belong to hard-to-degrade organic matter. The analysis results showed that the relative abundance of *treS* and *malZ* involved in starch degradation significantly increased ($P<0.05$) in the native vegetation community, while the relative abundance of *pulA*, *malQ*, and *PYG* significantly decreased ($P<0.05$); the relative abundance of *xynD* involved in hemicellulose degradation significantly increased ($P<0.05$); the relative abundance of *endoglucanase* and *CBH2* involved in cellulose degradation significantly increased ($P<0.05$), and the relative abundance of *bglB* and *bgaB* highly significantly increased ($P<0.01$); the relative abundance of *nagA* and *pultative chitinase* involved in chitin degradation significantly increased ($P<0.05$).

Taxonomic assignments of differential functional genes involved in carbon fixation and carbon degradation

The study identified the microbial taxa involved in expressing significantly different functional genes at the class level from taxonomic annotations. PCoA and PERMANOVA analyses found significant differences ($P<0.05$) in the related microbial taxa between native and invaded sites (Additional file 1: Fig. S2). The top 15 classes of microbes were visualized (Fig. 4), indicating that the class-level microbes carrying carbon fixation and degradation differential functional genes were basically similar, and they were mainly bacteria. The dominant taxa carrying these functional genes were mainly Gammaproteobacteria, Deltaproteobacteria, Alphaproteobacteria. In the carbon fixation groups, invasion significantly increased the abundance of Deltaproteobacteria and Desulfobacteria ($P<0.05$), highly significantly increased the abundance of Gammaproteobacteria and Desulfobulbia ($P<0.01$), highly significantly reduced the abundance of Alphaproteobacteria and Polyangia ($P<0.01$), and significantly reduced the abundance of Actinomycetes, Myxococcia, Acidimicrobiia ($P<0.05$). At the taxonomic unit level of functional genes related to carbon degradation, the trend of microbial changes was basically similar to that of carbon fixation pathways (Additional file 4: Table S5). Notably, in the carbon fixation pathway, Nitrospiria, Desulfuromonadia, and Terriglobia were unique microbial groups, among which Nitrospiria and Desulfuromonadia showed an increasing trend in the invasion group. Gemmatimonadetes, Flavobacteriia, and Cytophagia were unique microbes in the carbon degradation pathway, among which Flavobacteriia and Cytophagia exhibited a decreasing trend in the invasion group.

Relationship between differential functional genes, associated functional community, and environmental factors

The interrelationships between soil properties and differential C-cycling functional genes, as well as their associated microorganisms, are shown in Additional file 1: Fig. S3, S4, and Table S6.

Specifically, in the carbon fixation pathway, EC was significantly negatively correlated with *sucC*, Actinomycetes, Acidimicrobiia, and Terriglobia ($P<0.05$). Soil water content (SWC) was highly positively correlated with *por* and *fdhB* ($P<0.01$), significantly negatively correlated with *MCEE*, *ACAT*, and *acr* ($P<0.05$), and significantly positively correlated with Gammaproteobacteria ($P<0.05$) and highly negatively correlated with Actinomycetes and Polyangia ($P<0.01$). SOC, DOC, and ROC were highly positively correlated with *por* ($P<0.01$), while their relationships with *mch*, *ACTA*, and *acr* were just the opposite. Gammaproteobacteria was highly positively correlated with SOC, DOC, and ROC ($P<0.01$), significantly negatively correlated with MBC ($P<0.05$), and Alphaproteobacteria, Actinoycetes, Polyangia and Acidimicrobiia was highly positively correlated with MBC ($P<0.01$).

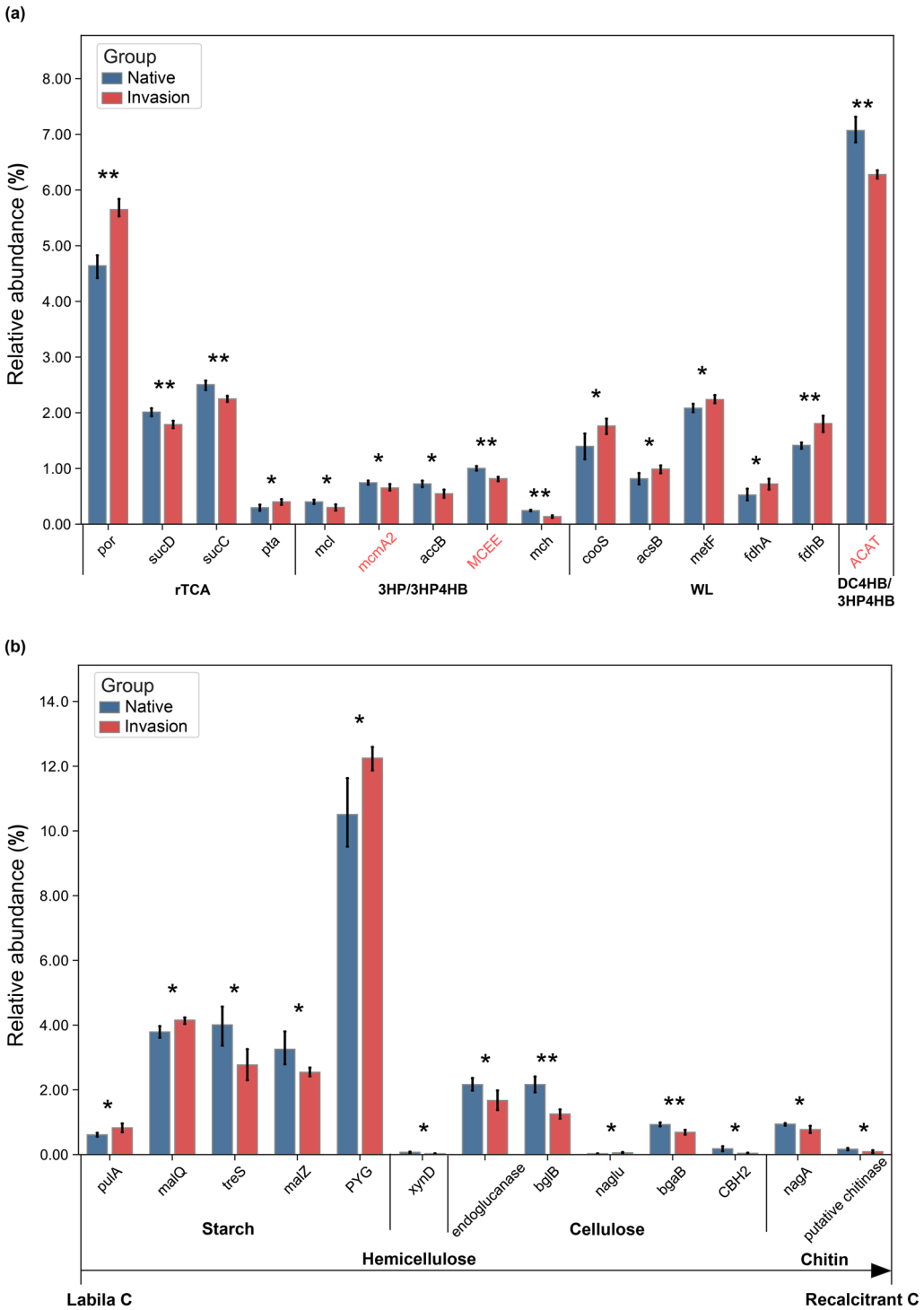


Fig. 3 Relative abundances of significantly different genes between groups responsible for microbial **a** carbon fixation, and **b** carbon degradation in soils of *S. alterniflora* and native vegetation communities. The red-letter genes indicate that they participate in both pathways simultaneously

In the carbon degradation pathway, EC was significantly positively correlated with *PYG* ($P<0.05$), and significantly negatively correlated with *treS*, *xynD*, and *CBH2* ($P<0.05$). It was also significantly positively correlated with Gammaproteobacteria ($P<0.05$), while Actinomycetes showed the opposite trend.

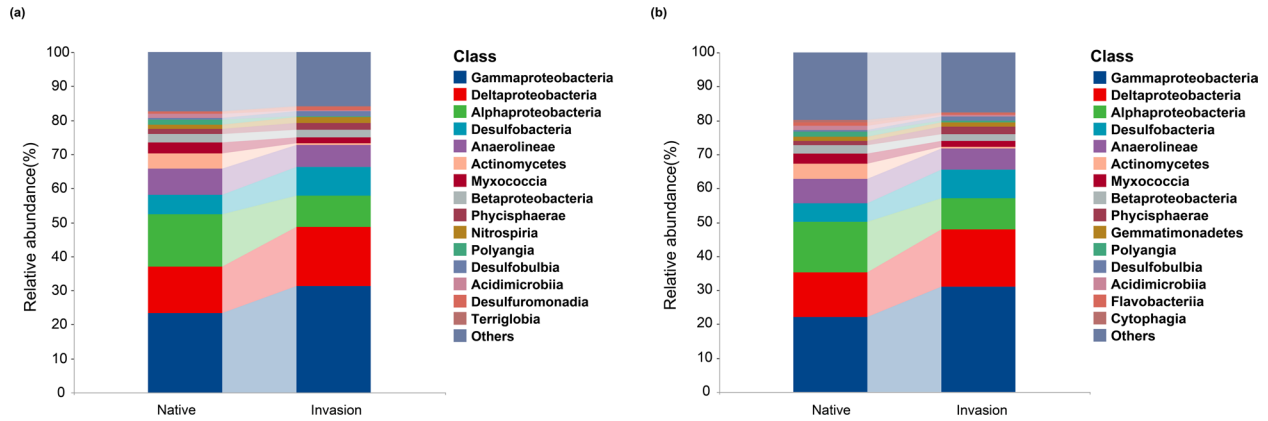


Fig. 4 Changes in the relative abundance of taxonomic assignments differential genes for **a** carbon fixation and **b** carbon degradation at the class level in soil with two vegetation taxa

SWC was highly significantly positively correlated with *pulA* ($P<0.01$), highly significantly negatively correlated with *xynD* ($P<0.01$), significantly negatively correlated with *bglB* and *CBH2* ($P<0.05$), significantly positively correlated with Gammaproteobacteria ($P<0.05$), and highly significantly negatively correlated with Actinomycetes and Polyangia ($P<0.01$). *MalQ* and *naglu* were significantly or highly significantly positively correlated with SOC, DOC, and ROC, while *bglB*, *bagB*, and *CBH2* were significantly or highly significantly negatively correlated ($P<0.05$; $P<0.01$). Gammaproteobacteria was significantly or highly significantly positively correlated with SOC, DOC, and ROC, and significantly negatively correlated with MBC, while Actinoycetes and Polyangia showed the opposite trend ($P<0.05$; $P<0.01$).

Mantel analysis indicated that the differential functional genes related to soil carbon fixation and their expressing communities were significantly correlated with SWC, SOC, DOC, ROC, SOCS, MBC, C:N ratio, and C:P ratio. The differential functional genes related to soil carbon degradation and their expressing communities were significantly correlated with EC, SOC, DOC, ROC, MBC, and C:P ratio.

Hierarchical partitioning to estimate the importance of each environmental variable (Fig. 5). We mainly selected environmental factors that were significantly correlated with C-cycling functional genes for analysis (Mantel test), and found that in the carbon fixation pathway, the selected environmental factors explained 87% of the variation in the carbon fixation functional genes, with MBC and SOC being the top two influencing factors, explaining 19.18% and 12.57%, respectively. In the carbon degradation pathway, the selected environmental factors explained 67% of the variation in the carbon degradation functional genes,

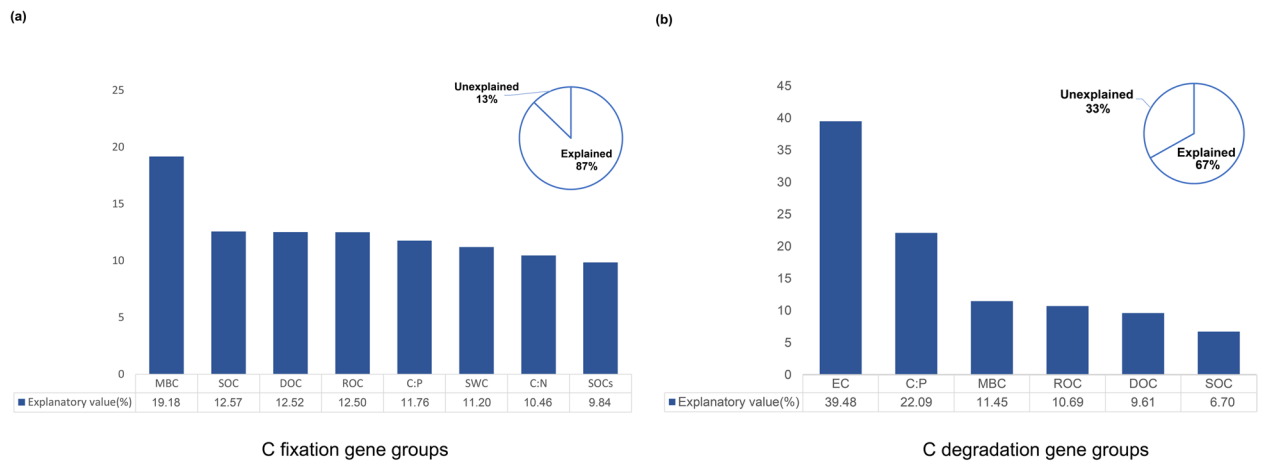


Fig. 5 Hierarchical partitioning to estimate the importance of each environmental variable, **a** carbon fixation gene groups, **b** carbon degradation gene groups

with EC and C:P ratio being the main influencing factors, explaining 39.48% and 22.09%, respectively.

Discussion

Effects of *S. alterniflora* invasion on C-cycling genes

Soil organic matter is an essential component of soil and a significant carbon reservoir in the global carbon cycle. The balance between carbon input and output in the underground environment determines the stock of organic carbon in soil, where substrate type plays a key role in shaping soil organic carbon (Ma et al. 2017). Previous studies have indicated that plant invasions can reduce soil nutrient reserves (Wang et al. 2019; Yang et al. 2021). In this study, the invasion of *S. alterniflora* significantly reduced the MBC concentration, but the concentrations of SOC, DOC, and ROC significantly increased (Fig. 1). The observed trend in SOC changes aligns with the results of Liu et al (2017a) concerning the growing season, but contrasts with findings by Tian et al. (2023). This difference appears to be primarily driven by vegetation type, a trend also been reported by Xia et al. (2021). Lin et al. (2021) demonstrated that *S. alterniflora* can increase the carbon content both during the warm and winter seasons. These findings suggested that, despite reduced microbial activity and weaker root system activities during winter, the invasion of *S. alterniflora* still increased the concentration of organic carbon in salt marsh wetland soil. Notably, although the concentration of SOC significantly increased in invasion group, the SOCS in the native vegetation showed an increasing trend compared to the invasion group (Fig. 1). One of the contributing factors to this increased in SOC could be the higher biomass of *S. alterniflora* compared to *S. salsa* (Zhang et al. 2019). However, carbon sequestration is influenced by litter quality, microbial biomass, microbial diversity and soil water oxygen conditions. Firstly, the relatively low litter mass of *S. alterniflora* affects organic carbon storage (Liao et al. 2008). Secondly, the invasion of *S. alterniflora* increases soil moisture, and is more limited by oxygen supply than *S. salsa*, which inhibited microbial activity and reduced microbial biomass (Poret-Peterson et al. 2007). Additionally, the invasion significantly decreased the Shannon index of C-cycling functional genes (Additional file 1: Fig. S1), which is important because functional gene diversity plays a crucial role in mediating multiple nutrient cycles in terrestrial ecosystems (Liu et al. 2023). These changes have the potential to affect the stock of organic carbon. There was evidence suggesting that after the invasion of *S. alterniflora* into salt marsh wetlands, soil organic carbon content follows a pattern of initial increase followed by a decrease, with a turning point around 20 years (Gao et al. 2022; Tang et al. 2012; Zhang et al. 2017). Therefore, although SOCS have not changed significantly, the reduction of soil MBC (one of the important parameters of soil active nutrient pool) and diversity could negatively impact the decomposition and transformation of organic matter. This may hinder the long-term accumulation of organic carbon.

The soil carbon cycle primarily involves several processes, including carbon fixation (the conversion of CO_2 into organic matter), carbon degradation (the decomposition of organic matter), and methane metabolism (methane production and oxidation) (Liu et al. 2017b). Research has mainly focused on the first two processes. The accumulation of soil organic carbon is mainly through the input of above-ground and below-ground biomass (such as fallen leaves and root exudates), along with fixation and transformation by soil microorganisms. The continuous synthesis and accumulation of organic carbon by microorganisms increases the abundance of soil carbon fixation functional genes (Schmidt et al. 2011). However, in cases where the stock of SOC is insufficient, microbial carbon fixation activity will also be increased (Yuan et al. 2025; Zhao et al. 2018). In this study, the lack of invasive group SOCS may stimulate microorganisms to enhance carbon fixation, thereby increasing the abundance of carbon fixation genes and promoting the microbial transformation and utilization of SOC in the soil. This result aligns with previous research findings (Wang et al. 2022). Among the six organic carbon fixation pathways, microaerobic/anaerobic rTCA is an important pathway for microorganisms to fix CO_2 and synthesize organic compounds, and it is more active in environments with abundant carbon sources (Fuchs 2011; Hua et al. 2018). The invasion group exhibited higher concentrations of SOC and DOC, which provided more carbon to microorganisms, thus promoting the expression and abundance of rTCA pathway-related functional genes, among which the *por* and *pta* significantly increased. The WL pathway relies on anaerobic microorganisms for the reduction of CO_2 and the production of organic compounds (Weiss et al. 2016). Invasion significantly increased SWC (Additional file 1: Table S2), which reduced soil porosity (Li et al. 2018), creating an anaerobic environment that enhanced the carbon fixation efficiency of the WL pathway. Furthermore, the higher EC implies that the dissolved salts in the soil provide more electron donors and acceptors. A study pointed out that the WL pathway increases with sediment salinity (Fang et al. 2022), which could also explain its heightened activity in invasion group. In this study, the expression of functional genes such as *cooS*, *fdhA*, and *fdhB* from the WL pathway was significantly increased. Research has showed that microbes may adopt energy-conserving strategies, such as rTCA cycle and

WL pathways, for carbon fixation under oligotrophic conditions (Jiang et al. 2022). Our results indicated that both the rTCA cycle and WL pathways were significantly enhanced in the invasion group, suggesting that the invasion has induced an oligotrophic state in the soil, thereby necessitating increased carbon fixation to augment organic carbon levels in the soil. The anaerobic DC4HB activity increased after the invasion, possibly due to the higher SWC and DOC (Wang et al. 2022). For carbon degradation functional genes, their relative abundance was significantly increased in the native group. This could be attributed to the sufficient organic carbon in the soil of the native plots to meet the microbial utilization and decomposition. Meanwhile, the C:N ratio of *S. alterniflora* litter is higher than that of *S. salsa*, and a lower C:N ratio in litter typically accelerates the decomposition process (Liao et al. 2008; Zhang et al. 2014). This difference may also influence the expression of functional genes related to mineralization. As shown in Fig. 3b, the functional genes involved in starch degradation (*PYG*, *malQ*, *pulA*) significantly increased in the invasion group, while those involved in cellulose and lignin degradation (*xynD*, *bagB*, *bglB*) significantly decreased.

Effects of *S. alterniflora* invasion on microbial communities that express differential genes

Microorganisms are the main drivers of biogeochemical cycles. In this study, we investigated microorganisms expressing differential functional genes involved in carbon fixation and degradation in both invaded and native groups. The results showed that *S. alterniflora* invasion significantly impacted microbial taxa associated with carbon fixation and degradation. At the class level, most microorganisms in both pathways were similar (Fig. 4a and b), suggesting that these dominant microbial taxa may be generalists that mainly perform most ecological functions in their habitats. Consistent with previous studies, Gammaproteobacteria, Deltaproteobacteria, Alphaproteobacteria (Proteobacteria), and Desulfobacteria (Thermodesulfobacteriota) were among the most widely distributed microbial groups in salt marsh wetlands, which is because they play an important role in the degradation and absorption of organic matter, as well as the biogeochemical cycling of elements (Lin et al. 2021; Zhang et al. 2020). The significant intergroup variations highlighted that differences in soil properties and substrate availability are key factors in shaping microbial communities. In microbial communities expressing carbon fixation, we found Nitrospiria, Desulfuromonadia, and Terriglobia to be specific microbial groups. Notably, Nitrospiria has been identified as a key microorganism involved in carbon fixation under anoxic conditions (Overholt et al. 2022). The relative abundance of Nitrospiria and Desulfuromonadia was higher in the invaded group, suggesting that the invasion benefits the reproduction of certain carbon-fixing microorganisms, thereby enhancing carbon fixation. Among the microbial communities expressing carbon degradation, Gemmatimonadetes, Flavobacteriia, Cytophagia were observed as specific bacterial groups. Both Flavobacteriia and Cytophagia have been recognized for their critical role in the mineralization of recalcitrant macromolecules (Kolton et al. 2013). They showed an increasing trend in native group, which could contribute to the observed increase in soil carbon degradation functional gene abundance. Although these specific microorganisms may be low in abundance and habitat-specific, both abundant and rare microbial communities play crucial ecological functions within a habitat (Huber et al. 2007). Additionally, an individual strain can perform multiple ecological functions, underscoring the need for further analysis of functional microbial taxa, especially at the species level.

Factors driving C-cycling functional genes and microbial communities under *S. alterniflora* invasion

Environmental factors are the primary drivers shaping functional microbial communities. The results of this study indicated that the majority of microbes expressing differential functional genes were affected by SWC. The invasion of *S. alterniflora* significantly altered SWC (Additional file 1: Table S2), directly affecting microbial water utilization (Additional file 1: Fig. S4), indirectly impacting microbial functions and processes (Zhang et al. 2018; Huang et al. 2021). This is consistent with Davidson and Janssens (2006), who emphasized the critical role of soil water in the carbon cycle. In addition, SOC, DOC, ROC, and MBC were found to significantly influence microbial communities expressing soil C-cycle differential functional genes. SOC provides a stable, long-term carbon source and habitat for microorganisms. DOC, as an unstable C, offers a readily available carbon source and active compounds, promoting microbial metabolism. ROC has high stability and can be stored in the soil for extended periods. Invasion altered SOC and impacted the microbial community. From the results, it is known that the correlation between soil carbon components such as DOC and microorganisms is exactly opposite to that presented by MBC. Specifically, the majority of Gammaproteobacteria and Deltaproteobacteria are nutrient-rich microorganisms, capable of efficiently utilizing the organic carbon resources in the soil (Goldfarb et al. 2011). However, they showed a negative correlation with MBC. This suggested that, despite the invasion increasing the relative abundance of some anaerobic microorganisms, overall

microbial activity may be hindered by environmental condition and interspecies competition.

According to hierarchical partitioning and variation partitioning, the environmental factors influencing the functional genes of carbon fixation and degradation differ (Fig. 5). In the carbon fixation pathway, MBC and SOC were the top factors affecting the abundance of functional genes, with MBC being a biological factor and SOC a non-biological factor. This highlighted that both biological and non-biological factors play significant roles in the carbon fixation pathway. As a metabolic product and substrate of microorganisms, MBC plays a crucial role in microbial assimilation and dissimilation processes (Liao et al. 2023). *Por* significantly increased in *S. alterniflora* vegetation communities and showed a negative correlation with MBC, while the increase in SOC provided an abundant carbon sources for soil microorganisms, thereby promoting its expression (Additional file 1: Fig. S3); this gene is essential for the metabolic activities of anaerobic microorganisms. This suggested that the invasion creates anaerobic conditions that reduce MBC levels, but some anaerobic microorganisms fully utilized substrates (increased SOC) to improve carbon fixation efficiency, enabling them to better maintain their metabolism processes. This finding is consistent with other studies that have highlighted the importance of MBC and SOC as key environmental factors influencing soil biological characteristics, including the abundance of soil microorganisms and C-cycling functional genes (Li et al. 2015b; Yang et al. 2023). In carbon degradation pathways, EC and C:P ratio were the main influencing factors of functional genes. Soil water and salt content jointly affect EC. Following the invasion of *S. alterniflora*, EC significantly increased, and the excessive accumulation of salt ions inhibit soil microbial activity, leading to a reduction in the expression of soil carbon degradation functional genes (*treS*, *xynD*, *endoglucanase*, and *CBH2*). This finding aligns with the results of Rath and Rousk (2015), who pointed out that soil salinity is one of the powerful environmental factors affecting soil microorganisms, with increasing salt concentration inhibiting soil respiration. Similarly, another study also demonstrated that soil salinity can influence the decomposition and transformation of soil organic carbon (Brinson et al. 1981). Furthermore, consistent with previous research, there was a close relationship between C:P stoichiometric characteristics and the abundance of genes related to C-cycling (Luo et al. 2020). However, the relationship between soil carbon degradation functional genes and C:P ratio in the context of *S. alterniflora* invasion requires further investigation.

Finally, we summarize the main research findings in Fig. 6. The conceptual diagram illustrates that the increase

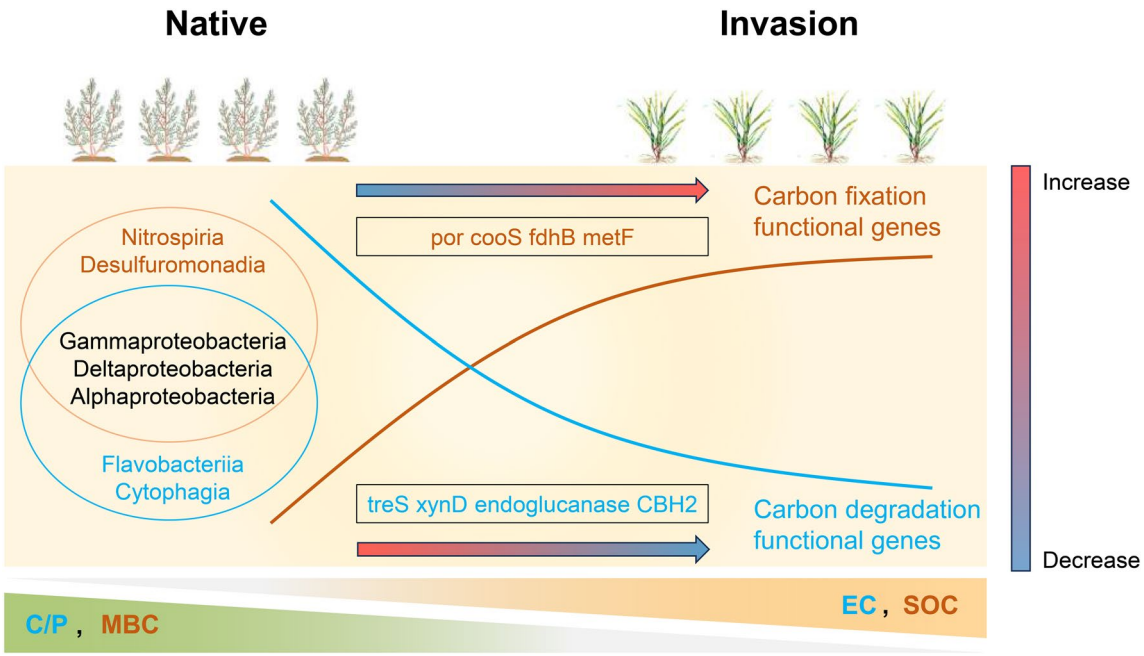


Fig. 6 A summary diagram showing the response of functional genes involved in carbon fixation (CF) and carbon degradation (CD) to the invasion of *S. alterniflora*. The brown curve represents the trend of CF functional genes and the blue curve represents the trend of CD functional genes. Similarly, all brown words are related to CF functional genes, and blue words are related to CD functional genes

in soil carbon fixation capacity following the invasion of *S. alterniflora* was closely related to the increase in SOC and the decrease in MBC. Conversely, the reduction in soil carbon degradation capacity was closely associated with the increase in soil EC and the decrease in C:P ratio. Furthermore, changes in co-occurring microbes (Gammaproteobacteria, Deltaproteobacteria and Alphaproteobacteria) with high relative abundance at class level, as well as unique microbes (carbon fixation: Nitrospiria, Desulfuromonadia; carbon degradation: Flavobacteriia, Cytophagia) with low relative abundance, collectively influenced the expression of soil carbon cycle genes. However, it is important to note that this analysis only reflects the potential functions of microorganisms and does not provide direct evidence of their actual activity. Given that various ecological processes are profoundly influenced by the composition, structure, and functional genes of soil microorganisms, future studies should integrate research on both functional genes and the taxonomic levels of soil microorganisms to enhance our understanding of how microbial structure and function regulate the ecological processes of soil carbon cycling in salt marsh wetlands. Additionally, considering the negative impacts of *S. alterniflora* invasion on soil MBC and the diversity of carbon cycling functional genes, long-term research will be indispensable for a comprehensive assessment of these impacts.

Conclusion

This study used metagenomic data to investigate alterations in soil microbial functional genes and their determinants in *S. salsa*-dominated salt marshes due to the invasion of *S. alterniflora*. The results revealed that, during the cold season, the invasion generally exerts negative impact on soil MBC and the diversity of C-cycling functional genes. At the functional gene level, the invasion enhanced the soil's carbon fixation potential while inhibiting its carbon degradation capacity. Both widely prevalent dominant microbes and unique microbes contributed to these observed differences. Moreover, the increased soil carbon fixation capability was closely associated with elevated SOC levels and reduced MBC, while the diminished carbon degradation was linked to increased soil EC and decreased C:P ratio. In summary, the invasion of *S. alterniflora* not only altered the soil environment in salt marsh ecosystem but also disrupted the C-cycling processes. This study provides novel insights into the effects of *S. alterniflora* invasion on soil carbon storage, particularly during the cold season, contributing to the growing body of research on microbial function in salt marshes and emphasizing the importance of controlling *S. alterniflora* invasion to enhance blue carbon storage in wetland ecosystems. These results can inform environmental management and decision-making related to the protection and restoration of salt marsh wetlands.

Supplementary Information

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Additional file 1
Additional file 2
Additional file 3
Additional file 4

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Author contributions
Experimental design, investigation, data curation, writing-original draft: XLZ; experiments conducted and data collection: QJW and JXF; methodology, investigation, data curation: SHZ, FZ, and YZ; supervision, revised, review and discussion: BM, QZ, XDY, and SXX.

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Availability of data and material
The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
All authors agreed and approved the manuscript for publication in Ecological Processes.

Competing interests
The authors declare that they have no competing interests.

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