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***Spartina alterniflora* invasion controls organic carbon stocks in coastal marsh and mangrove soils across tropics and subtropics**

Running title: *S. alterniflora* controls on SOC stocks

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Abstract: Coastal wetlands are among the most productive ecosystems and store large amounts of organic carbon (C) – the so termed “blue carbon”. However, wetlands in the tropics and subtropics have been invaded by smooth cordgrass (*Spartina alterniflora*) affecting storage of blue C. To understand how *S. alterniflora* affects SOC stocks, sources, stability, and their spatial distribution, we sampled soils along a 2500 km coastal transect encompassing tropical to subtropical climate zones. This included 216 samplings within three coastal wetland types: a marsh (*Phragmites australis*) and two mangroves (*Kandelia candel* and *Avicennia marina*). Using $\delta^{13}\text{C}$, C: nitrogen (N) ratios and lignin biomarker composition we traced changes in the sources, stability and storage of SOC in response to *S. alterniflora* invasion. The contribution of *S. alterniflora*-derived C up to 40 cm accounts for 5.6%, 23% and 12% in the *P. australis*, *K. candel* and *A. marina* communities, respectively, with a corresponding change in SOC storage of +3.5, -14 and -3.9 t C ha⁻¹. SOC storage did not follow the trend in aboveground biomass from the native to invasive species, or with vegetation types and invasion duration (7–15 years). SOC storage decreased with increasing mean annual precipitation (1000–1900 mm) and temperature (15.3–23.4 °C). Edaphic variables in *P. australis* marshes remained stable after *S. alterniflora* invasion and so, their effects on SOC content were absent. In mangrove wetlands, however, electrical conductivity, total N and phosphorus, pH and active silicon were the main factors controlling SOC stocks. Mangrove wetlands were most strongly impacted by *S. alterniflora* invasion and efforts are needed to focus

on restoring native vegetation. By understanding the mechanisms and consequences of invasion by *S. alterniflora*, changes in blue C sequestration can be predicted to optimize storage can be developed.

KEYWORDS: blue carbon, soil organic carbon storage, $\delta^{13}\text{C}$, lignin biomarkers, *Spartina alterniflora*, exotic species invasion, mangrove ecosystems, coastal wetlands

1 INTRODUCTION

Coastal wetlands play a critical role in storing carbon (C), referred to as ‘blue carbon’ (Macreadie et al., 2019), which provides significant promise for climate change mitigation (Duarte et al., 2013). Coastal wetlands are, however, one of the most vulnerable ecosystems as they are sensitive to climate and environmental change. The expansion of invasive plant species is a result of, and contributes to, these changes (Davidson et al., 2018).

Of particular interest is the invasion of *Spartina alterniflora*, also known as smooth cordgrass or *Sporobolus alterniflorus*, which has superior traits of high tolerance to flooding and saline conditions, a long growing season, high net photosynthetic efficiency, and a large specific leaf area index (Liu et al., 2020). This perennial C4 grass was introduced in 1979 to intertidal wetlands of China from its native range, the United States, to stabilize soil and protect the coastline (Bernik et al., 2016). Since then, *S. alterniflora* has been widely distributed over 340 km² of eastern coastal wetlands from Liaoning in Northeast China to Guangxi Province in the south. Invasion by *S. alternifolia* has become one of the most important ecological problems in central-south China. The *S. alterniflora* distribution covers 92.4% of the total area in the tropical and subtropical coastal wetlands (Lu and Zhang, 2013). *S. alterniflora* invasions not only replace the local species and threaten the biodiversity in native ecosystems (Didham et al., 2005), but also alter ecosystem

processes related to C stock (Hopkinson et al., 2012) through changing C inputs and quality of net primary production, root system distribution and rhizodeposition (Seliskar et al., 2002), and nutrient cycling (Ehrenfeld, 2003).

Over the last decade, many studies have addressed the *S. alterniflora* invasion induced changes of soil organic carbon (SOC) storage compared to native communities, including a decrease (Stevens et al., 2006; Kelleway et al., 2017), increase (Zhang et al., 2010; Wolkovich et al., 2010; Yang et al., 2017) or negligible effects (Liao et al., 2018a; Chen et al., 2017). Furthermore, the temporal changes in SOC storage remain poorly understood (Osland et al., 2012; Kelleway et al., 2016). Previous studies mainly focused on native species including *Phragmites australis* (Emery et al., 2014; Zhang et al., 2017), *Cyperus malaccensis* (Sridhar et al., 2010; Jin et al., 2017), *Suaeda salsa* (Yuan et al., 2015; Yang et al., 2016), and *Scirpus mariqueter* (Cheng et al., 2008; Schwarz et al., 2011), while studies on *S. alterniflora* invasion in mangrove forests are scarce. Mangroves occupy only 0.5% of the global coastal area, however, they contribute 10–15% to coastal sediment C storage and export 10–11% of the particulate terrestrial C to the ocean (Alongi, 2014). Consequently, it is imperative to better understand how *S. alterniflora* invasion influences the biogeochemical cycle of C in coastal ecosystems.

Coastal wetlands are subject to a complex series of interactions between overflowing, salinity, alternating oxidative-reductive conditions, high pH, N overloading, sea-level rise, tidal action and changes to plant communities including the invasion by *S. alterniflora*, with these interactions influencing SOC dynamics (Breithaupt et al., 2014; Hinson et al., 2019). Many studies (Williams et al., 2015; Stagg et al., 2017) only investigate one or some fundamental factors that control SOC dynamics. However, *S. alterniflora* invasion is dependent upon a complex series of responses from coastal wetlands (Osland et al., 2018; Yang, 2019a). Factors influencing this invasion may include (i) Climate factors: global precipitation and temperature affect coverage distribution and NPP of *S. alterniflora*. Jobbágy and Jackson (2000) showed that climate was the most important factor controlling SOC dynamics in surface layers, while texture was the dominant factor in the deep soil. Hinson et al. (2019) concluded that latitude and precipitation explained ~46% of the variance in SOC storage for wetlands on the West Coast and Gulf Coast of the USA; (ii) Soil properties:

few quantitative relationships describe the effects of edaphic variables as altered by *S. alterniflora* on SOC storage (e.g., Grüneberg et al., 2013; Yuan et al., 2015; Liu et al., 2017); and (iii) quantity and quality (or chemical composition) of plant litter: vegetation communities had differences in litters and root exudates, directly affecting the quality and quantity of organic C input, and finally deciding the C accumulation in soils. Until now, very few studies have evaluated how changes to multiple contributing factors such as the plant community, climate, and soil physicochemical and biogeochemical properties regulate SOC storage, and what are the essential differences in the three native communities (i.e., *P. australis*, *Kandelia candel* and *Avicennia marina*) following *S. alterniflora* invasion (Luo et al., 2017; Yang, 2019a).

The isotopic signature associated with C inputs from *S. alterniflora* (C4 plant) differ from native plants with are C3. The average values of $\delta^{13}\text{C}$ for C4 plants and C3 plants were about -11‰ and -27‰ , respectively (Waring and Maricle, 2012). After the plant litter is incorporated into soil, differences in redox conditions, soil development, and the degree and type of microbial decomposition of SOC may significantly alter the $\delta^{13}\text{C}$ values (Werth and Kuzyakov, 2010). Therefore, $\delta^{13}\text{C}$ values reflect the combined effects of the plant residues and consecutive isotopic fractionation processes, which provide evidence of SOC source and turnover (Guillaume et al., 2015; Xia et al., 2021).

The C:N ratio of the organic matter can also provide valuable information. While C is lost as CO_2 or CH_4 during microbial transformation processes (Whiting and Chanton, 1993), N is mostly retained in soils progressively decreasing C:N ratio. Thus, C:N ratios are widely used as proxies for assessing the degree of SOC decomposition and loss (Drollinger et al., 2019), i.e., a lower C:N ratio generally implies a higher degree of SOC decomposition (Davis et al., 2003). The C:N ratio can be used to indicate SOC sources. A low C:N ratio (5–8) usually indicate aquagenic organic matter sources (Redfield, 1963), while a high C:N ratio (> 15) can indicate organic matter from terrestrial sources (Meyers, 1994).

Biomarkers can provide further information on the SOM sources. Lignin, is one of the most recalcitrant C forms derived from plant residues and has been widely used as a biomarker. Lignin is composed of a suite of single-ring phenol compounds, including vanillyl (V), syringyl (S), and

cinnamyl (C). Their abundances and monomer ratios, including S/V, C/V and acid-to-aldehyde (Ad-to-Al), are quantitative indicators of the molecular composition, stability and source of plant-derived C in soils (Shafi et al., 2004; Thevenot et al., 2010). While previous studies have employed $\delta^{13}\text{C}$ and C:N ratios (Kusumaningtyas et al., 2019; Sasmito et al., 2020), few studies have combined the indices to evaluate the turnover of SOC, especially for coastal wetlands with *S. alterniflora* invasion. Therefore, the $\delta^{13}\text{C}$ signature, C:N ratio and lignin biomarkers are powerful tools to elucidate the sources, stability, mixing and transformations of SOC in terrestrial and aquatic ecosystems.

To cover the broad regions that have been invaded by *S. alterniflora*, we selected 27 paired sampling sites at 9 locations from 8 independent coastal wetlands along China's coastline covering both subtropical and tropical climate zones. The objectives of this study were: (i) to quantify the changes in SOC storage using a chronosequence approach varying from 7–15 years in nine locations with native species in response to *S. alterniflora* invasion; (ii) to identify whether and how exotic *S. alterniflora* invasion influences SOC sources and stability based on the C:N ratio, $\delta^{13}\text{C}$ signature and lignin biomarkers; (iii) to investigate the response of the vertical distribution of SOC, proportion of *S. alterniflora*-derived organic C, and C budgets following *S. alterniflora* invasion; and (iv) to clarify the joint effects of environmental factors and soil properties on SOC stocks in response to *S. alterniflora* invasion.

2 MATERIALS AND METHODS

2.1 Site description

To better understand the comprehensive mechanisms of SOC storage, budgets, sources and stability in response to *S. alterniflora* invasion, a range of statistical methods were used to analyze the main factors that control SOC turnover. We selected 9 locations with a total of 27 paired sampling sites from the 8 independent coastal wetlands covering subtropical and tropical climate zones (Figure 1), including Chongming Island (CI), Hengsha Island (HI), Yueqing Bay (YB), the Minjiang River Estuary (ME), Jiulong River Estuary (JE), Zhangjiang River Estuary (ZE1 and ZE2), Zhanjiang (ZJ) and Beihai (BH). The native species that are dominant at these sites included

P. australis, and mangrove species *K. candel* and *A. marina*. Each native species grew in the 3 independent locations, and has been invaded by adjacent C4 *S. alterniflora*. The native species *P. australis* is native to CI, HI, ME; *K. candel* is native to YB, JE, ZE1; and *A. marina* is native to ZE2, ZJ, BH. Detailed information of the sampling sites is shown in Table S1.

2.2 Sample collection

Three independent replicate sites were selected and sampled in June-August 2015 for each location, resulting in a total of 27 paired sampling sites. Each site had two community types (i.e., a paired site comparison), one dominated by native species (*P. australis* (grass), *K. candel* (mangrove), *A. marina* (mangrove)), and the other had a significant population of the invasive *S. alterniflora*. Using historical records to confirm the native species composition at each site, we established that *S. alterniflora* completely outcompeted *P. australis*. For the native mangrove sites, the invasion had begun along the margin and empty within the mangrove community, and it was currently spreading its cover by all the mangrove community. The time of invasion by *S. alterniflora* ranged from 7 to 15 years, while the native species had been growing at these sites for more than 30 years.

Firstly, we randomly selected vegetation plot (square 10 m × 10 m), and then chose one small subplot (1 m × 0.6 m) in the middle of vegetation plot. Samples were collected at 0–10, 10–20, 20–30 and 30–40 cm depth intervals using an auger, and three sub-samples in one subplot were collected to form one composite sample per layer (Wang et al., 2019), resulting in a total of 216 samples (nine sampling locations × three replicates × two communities × four sampling depths). The aboveground biomass of grasses was collected from 1 m² square in the center of vegetation plot (10 m × 10 m). The mangrove aboveground biomass was calculated by an empirical formula based on diameter at the breast height, vertical height and density of mangrove trees (Table S1; Tam et al., 1995). Visible stones and root residues were removed before grinding and analysis. The samples were divided into two parts, one was stored frozen in the laboratory, and the other part was stored air-dried in the dark.

2.3 Laboratory analyses

Bulk density (BD, g cm^{-3}) was determined using the cutting ring method (100 cm^3). Samples were assessed for salinity (EC, $\mu\text{S cm}^{-1}$) (DDS-307 salinity meter, Boqu Scientific Instruments, Shanghai, China), and pH (Orion Scientific Instruments, Minnesota, USA). Particle size distribution (%) was measured using a Master Sizer 2000 Laser Particle Size Analyzer (Malvern Scientific Instruments, Suffolk, UK).

Samples (about 0.50 g dry weight) were acidified with 1.0 M HCl (20 mL) to remove carbonates, and then washed 3–4 times with distilled water to remove residual acid. Soil organic carbon (SOC, g kg^{-1}) and total nitrogen (TN, g kg^{-1}) were measured with a Vario EL III Elemental Analyzer (Elementar Scientific Instruments, Hanau, Germany). Dissolved organic carbon (DOC, mg kg^{-1}) was extracted with deionized water (1: 5 ratio) and measured using a TOC-V CPH total C analyzer (Shimadzu Scientific Instruments, Kyoto, Japan). Microbial biomass carbon (MBC, mg kg^{-1}) was assayed using the fumigation-extraction and extracts measured on the TOC-V analyzer (Vance et al., 1987). Labile organic carbon (LOC, g kg^{-1}) was oxidized with 0.33 M KMnO_4 and determined using a colorimetric method. The stable carbon isotope signatures ($\delta^{13}\text{C}$ ratios) were measured using an elemental analyzer-continuous flow isotope ratio-mass spectrometer (Finnegan MAT253, Thermo Scientific, Waltham, MA, USA).

For total phosphorus (TP, g kg^{-1}) analyses, 1.00 g soil was first digested by 5 mL 12.4 M perchloric-acid and measured colorimetrically on a UV-2450 spectrophotometer (Shimadzu Scientific Instruments, Kyoto, Japan). For active iron (Fe_{Ac} , mg g^{-1}), aluminum (Al_{Ac} , mg g^{-1}), and silicon (Si_{Ac} , mg g^{-1}), 1.00 g soil was extracted (m:v = 1:50 ratio) by oxalic acid-ammonium oxalate solution (mol/mol = 4/5), and measured colorimetrically using 1,10-phenanthroline monohydrate, chromeazurol, molybdenum blue methods, respectively, on a UV-1800 spectrophotometer (Shimadzu Scientific Instruments, Kyoto, Japan).

For lignin phenol analysis, samples (about 1.00 g) were extracted with 1.00 g copper oxide (CuO), 0.10 g ammonium iron (II) sulfate [$\text{Fe}(\text{NH}_4)_2(\text{SO}_4)_2 \cdot 6\text{H}_2\text{O}$] and 15 mL of nitrogen (N_2)-purged NaOH solution (2 mmol L^{-1}) in Teflon-lined bombs. Then all bombs were flushed with N_2 in the headspace for 10 min and heated at 150°C for 2.5 h in an oven. The lignin oxidation

products (LOPs) were derivatized with N, O-bis-(trimethylsilyl) trifluoroacetamide (BSTFA) and pyridine at 70°C for 3 h to yield trimethylsilyl (TMS) derivatives, and were quantified using internal standards (i.e., trans-Cinnamic acid) on an Agilent 7890B/7010B TQ GC-MS system (Agilent, USA) using a DB-5MS column (Xia et al. 2020a).

2.4 Calculations and statistical analyses

Data sets were checked for homogeneity and normality before analysis. The results were expressed with the mean $\pm$ standard deviation. One-way analysis of variance (ANOVA) was used to compare the significance ($p < 0.05$) of aboveground dry biomass of native and invasive species with Tukey's test by SPSS ver.21.0. Pearson correlation analysis, redundancy analysis (RDA) and meta-analysis were performed by using SPSS ver.21.0, Graphpad, Canoco 5.0 and R statistic software, respectively.

Changes in SOC content caused by *S. alterniflora* invasion (ΔSOC , g kg⁻¹) were estimated using the following formula:

$$\Delta\text{SOC} = \text{SOC}_{\text{Invasive}} - \text{SOC}_{\text{Native}}$$

where $\text{SOC}_{\text{Invasive}}$ and $\text{SOC}_{\text{Native}}$ are the soil organic carbon contents (g kg⁻¹) in invasive and native communities, respectively.

SOC storage (SOCS) was calculated as:

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

where SOC is soil organic carbon content (g kg⁻¹), BD is bulk density (g cm⁻³), and D is the thickness of sampled layer (cm).

We estimated the changes in SOCS (ΔSOCS , kg C m⁻²) caused by *S. alterniflora* invasion using the following formula:

$$\Delta\text{SOCS} = \text{SOCS}_{\text{Invasive}} - \text{SOCS}_{\text{Native}}$$

where $\text{SOCS}_{\text{Invasive}}$ and $\text{SOCS}_{\text{Native}}$ are the soil organic carbon storage (kg C m⁻²) in invasive and native communities, respectively.

The proportion of C4 *S. alterniflora*-derived SOC (f , %) in *P. australis* and mangrove (*K. candel* and *A. marina*) communities was calculated using a two end-member stable isotope mass

balance equation (Werth and Kuzyakov, 2010):

$$f = \frac{\delta^{13}C_{mix} - \delta^{13}C_{old}}{\delta^{13}C_{new} - \delta^{13}C_{old}} \times 100\%$$

where $\delta^{13}C_{mix}$ is the average $\delta^{13}C$ -SOC from sites with invasive *S. alterniflora*, $\delta^{13}C_{old}$ is the average $\delta^{13}C$ -SOC in native *P. australis* and mangrove (*K. candel* and *A. marina*) communities, and $\delta^{13}C_{new}$ is the average $\delta^{13}C$ of *S. alterniflora* plant materials, which is the $\delta^{13}C$ value of leaves, litter and roots, being an average of -13.4‰ (Cheng et al., 2006; Yang et al., 2016).

Gains = Current SOC storage of invasive communities $\times f$

Retained SOC storage = Current SOC storage of invasive communities – Gains

Losses = Retained SOC storage – Current SOC storage of native communities

C budget = Current SOC storage of invasive communities – native communities

3 RESULTS

3.1 SOC content and storage following invasion by *S. alterniflora*

The average SOC content in the native *P. australis* community was equivalent to the invasive *S. alterniflora* community, and the average Δ SOC content was overall close to zero in four soil layers. However, the average SOC content in the native mangrove *K. candel* community was higher than that of the community with the invasive *S. alterniflora*, with a mean Δ SOC content of -3.61 – -1.66 g kg⁻¹. Similar to the *K. candel* community, the average SOC content in the native mangrove *A. marina* community was also slightly higher than that of the community with the invasive *S. alterniflora*, and the mean Δ SOC content was positive in the upper soil layer (0–10 cm) but negative in sub-layers (10–40 cm). The average SOC content decreased with depth in general at all sampling sites, irrespective of community composition (Figure 2). The SOC content largely varied (Figure S1), but the Δ SOC content overall had similar trends for the same native species in independent coastal wetlands under *S. alterniflora* invasions (Figure S2).

The average SOC storage in 0–40 cm in the native *P. australis* community (7.1 kg C m⁻²) was slightly lower ($p > 0.05$) than that of the community with the invasive *S. alterniflora* (7.5 kg C m⁻²). The average SOC storage in the native *K. candel* (5.4 kg C m⁻²) and *A. marina* (5.0 kg C m⁻²)

mangroves were larger than ($p < 0.05$) those of the corresponding *S. alterniflora* community (4.0 and 4.6 kg C m⁻²). The losses in SOC storage at depths of 0–40 cm were 0.06, 2.3 and 0.96 kg C m⁻², and the proportions of *S. alterniflora*-derived C were 5.6%, 23% and 12% in the native *P. australis*, *K. candel* and *A. marina* communities. Thus, the budget for SOC storage was +3.5, -14 and -3.9 t C ha⁻¹ following *S. alterniflora* invasion into *P. australis*, *K. candel* and *A. marina* communities, respectively (Table 1; Figure 4c). The average SOC storage had irregular patterns with the sampling depth in both native *P. australis* and its corresponding invasive *S. alterniflora* community, while the average SOC storage decreased with soil depth in the mangrove communities and their adjacent invasive *S. alterniflora* community (Figure 3). For independent coastal wetlands, the SOC storage varied greatly (Figure S3), but Δ SOC storage had a consistent trend for the same native species following *S. alterniflora* invasion (Figure S4).

3.2 Native and invasive vegetation biomass

The aboveground biomass of *P. australis* was 26% lower than that of the community with the invasive *S. alterniflora* ($p > 0.05$). The *S. alterniflora* communities currently occupy areas in the margins of the mangrove communities and in the empty spaces within the mangrove communities, with the aboveground biomass of *K. candel* and *A. marina* being 4.7 and 20 times that of invasive *S. alterniflora*, respectively ($p < 0.05$; Figure S5).

3.3 Changes in $\delta^{13}\text{C}$ values and C:N ratios

The average $\delta^{13}\text{C}$ of SOC in soil under the native *P. australis* (C3 plant; $\delta^{13}\text{C} = -23.2\text{‰}$) community became ^{13}C -enriched following *S. alterniflora* (C4 plant; $\delta^{13}\text{C} = -22.5\text{‰}$) invasion ($p > 0.05$). The average $\delta^{13}\text{C}$ of SOC in soil under *K. candel* (C3 plant) and *A. marina* (C3 plant) mangrove communities were -25.3‰ and -24.6‰, respectively, and significantly ^{13}C -enriched 2.9‰ and 1.5‰ compared to their corresponding *S. alterniflora* invasion with a mean of -22.4‰ and -23.1‰ ($p < 0.05$; Figure 4a).

The average soil C:N ratios in the *P. australis* community (11–19) were not significantly ($p > 0.05$) lower than that of the community with the invasive *S. alterniflora* (7.1–21), while the soil

C:N ratios in the native *K. candel* (8.3–13) and *A. marina* (8.0–12) community decreased slightly ($p > 0.05$) following *S. alterniflora* invasion, ranging from 8.2–15, 5.6–10, respectively. The soil C:N ratios in the *P. australis* communities were higher than those of the mangrove communities, regardless of whether the native communities were invaded by *S. alterniflora* (Figure 4b).

3.4 Lignin biomarker composition

The content of plant-derived lignin phenols in soils (Table S2) show a significant relationship ($p < 0.01$) with SOC content in both native and invasive communities (Figure 4d). C/V and S/V decreased in the *P. australis* community but increased in the mangrove forests (dominated by *K. candel* and *A. marina*) following *S. alterniflora* invasion, especially for C/V. The (Ad/Al)_V and (Ad/Al)_S in the *P. australis* community decreased following *S. alterniflora* invasion. In contrast, (Ad/Al)_V and (Ad/Al)_S in the mangrove forests increased after *S. alterniflora* invasion, especially for (Ad/Al)_S. The values of lignin monomers (C/V, S/V, (Ad/Al)_V, (Ad/Al)_S) in the *P. australis* community decreased while an increase was observed in the mangrove community following invasion by *S. alterniflora*. This increase was more evident in the *K. candel* than the *A. marina* community (Figure 5).

4 DISCUSSION

4.1 Effects of plant biological traits and invasion duration on SOC stocks

S. alterniflora has several advantageous eco-physiological traits over many native species. These traits have enabled it to replace co-occurring native species, especially grasses, in the saltmarshes along the eastern coast of China. *S. alterniflora* has higher net primary production (NPP) and litter yield than native *P. australis* (Yang et al., 2016), altering plant C input to soils (Kelleway et al., 2017). C sequestration in soils was also limited by litter quality and decomposition under ecosystems (Fierer et al., 2005). Liao et al. (2008b) reported that the decomposition rate of *S. alterniflora* litter, particularly the belowground root residues, was slower than that of *P. australis* litter due to the lower litter quality (i.e., higher C:N ratio) of *S. alterniflora* (Duan et al., 2018). Respiration of roots and microorganisms is another important factor

influencing C stocks. Bu et al. (2015) have verified that CO₂ efflux from soil and microbial biomass in the *S. alterniflora* stands was higher than that of native *P. australis* stands in the Yangtze River estuary, but ANPP and SOC were higher in the *S. alterniflora* stands than that of ecosystems with native species. Our results have confirmed that the aboveground biomass of invasive *S. alterniflora* was larger than native *P. australis* (Figure S5), and SOC storage in the *S. alterniflora* community was 3.2% higher than that of *P. australis* community ($p > 0.05$; Table 1). This indicated that increased NPP and slower decomposition of biomass derived from *S. alterniflora* outweighed the invasion-induced C loss, confirmed by increased CO₂ efflux from soil in comparison with *P. australis* (Van Kleunen et al., 2010).

While the positive effect of *S. alterniflora* on SOC stocks has been well documented in grass marshes (e.g., He et al., 2019; Yang, 2019b), there is a paucity of studies that investigate the effects of *S. alterniflora* invasion in mangrove communities (e.g., Giri and Long, 2014; Sun et al., 2019). Although the ANPP of *S. alterniflora* varies from 1000 to 1500 g m⁻² year⁻¹, and can be as high as 4000 g m⁻² year⁻¹ under optimal conditions (Kirwan et al., 2009), the ANPP of *S. alterniflora* was much lower than that of mangrove (*K. candel* and *A. marina*; Figure S5). The SOC storage in mangroves decreased by 26% and 7.8% (respectively) following *S. alterniflora* invasion (Figure 3), consistent with other studies on mangrove community encroachment (e.g., Osland et al., 2013; Lunstrum and Chen, 2014). Soils or sediments tend to efficiently sequester organic C in mangrove forests, which is attributed to the morphological structure of mangroves and their widespread roots (Krauss, 2003). Litter from mangroves consists of leaves, branches, standing and fallen main stems. The unique tree structure and complex aerial root systems (e.g., prop roots, pneumatophores) across mangrove species result in greater biomass than grasses, and these specific structures are more effective for trapping organic-rich sediments (Kristensen et al., 2008). The litter from above- and below-ground components in mangrove forests tend to have greater recalcitrant C compounds (e.g., lignin, tannins, cutin, suberin and waxes) and are more difficult to decompose than grass litter (Chanda et al., 2015). Therefore, high rates of organic C burial in mangrove forests are attributed primarily to the production, accumulation, burial and decomposition of aerals and roots. Thus, invasion by *S. alterniflora* can lower the SOC storage.

The decrease in aboveground biomass of *K. candel* was much lower than that of *A. marina* (Figure S5), but the decrease in SOC storage in the *K. candel* community was much larger than that of the *A. marina* community following *S. alterniflora* invasion (Figure S3 & Figure S4). Consequently, the net SOC storage is dependent not only on the apparent NPP and litters, but largely on how much of the apparent NPP and litters eventually enters the soil, how organic matter is eventually formed and transferred to different soil depths.

S. alterniflora invasion has been shown to gradually increase the aboveground and belowground biomass in invaded ecosystems, achieving a steady increase after 8 years (Yu et al., 2014). The impacts of *S. alterniflora* invasion on SOC dynamics across a chronosequence, however, are not fully understood. There were linearly negative or positive relationships between the SOC stock and duration of *S. alterniflora* invasion, and most studies have focused on grass-dominated marsh and tidal flats. In contrast, short-term invasion of *S. alterniflora* did not alter SOC stocks (Tong et al., 2011). Liu et al. (2017) reported that *S. alterniflora* invasion increased the SOC storage with depth and years since invasion in saltmarsh (including mudflat, *Suaeda salsa*, and grass flat). The highest proportion of *S. alterniflora*-derived C have been reported 17 years after invasion, with decreased decay rate of old C and the increased mean residence time following 20 years in bare flat land (Yang et al., 2017). We, however, observed no relationships between changes in SOC storage and the time since *S. alterniflora* invasion up to 40 cm in depth across three native communities (Figure 6a & Figure S6). Whether the effects of *S. alterniflora* invasion on SOC storage are positive or negative depend on the specific soil depth, invasion chronosequence and native species. On the contrary, many salt marshes were encroached by mangrove forest with climate change (e.g., sea-level rise) (Osland et al., 2012). Many studies (Lunstrum and Chen, 2014; Yando et al., 2016) considered that SOC storage can increase with encroachment over a longer period, driven by rapid increases in aboveground biomass and large belowground stocks (i.e., inclusive of root and non-root C) (Kelleway et al., 2016).

4.2 Response of SOC stocks to regional climate factors and climate change

Contrasting climate factors, soil properties and biological traits have long been the basis of

predicting changes in SOC stocks. However, at small regional scales or controlled experiments, where climatic and soil properties are uniform, *S. alterniflora* invasion influences the quantity and quality of organic C inputs into soils. These variables cause plant-soil feedback to regulate local SOC cycling and stocks. Climate is generally regarded as the dominant factor controlling SOC stocks, and often explains the largest proportion of SOC variation at large regional or global scales (Kurganova et al., 2014; 2015; Fellman et al., 2017; Spivak et al., 2019).

We calculated Δ SOC storage between adjacent native and invasive communities in order to fully eliminate the differences in background (i.e., native species, soil properties, etc.), retaining the straddling climate factors across subtropical and tropical climate zones. A negative relationship between Δ SOC storage at depths of 0–40 cm and MAT (Figure 6b) was detected, which is supported by other studies from large regional to global estimates (Jobbágy and Jackson, 2000). The increases in SOC storage with decreasing temperature and precipitation are attributed to the dependence upon the decreased rate of SOM decomposition (Chmura et al., 2003; Davidson and Janssens, 2006; Qiu et al., 2018). Stronger negative relationships with depth were observed in the 0–30 cm soil layer (Figure S7), while the effects of MAT on SOC storage was not evident in the 30–40 cm soil layer (Figure S7). The effects of temperature on SOC storage also diminished with soil depth (Yang et al., 2010; Liu et al., 2012), while some studies indicated that temperature had greater effects on SOC storage through its effect on stabilizing SOC at soil depths greater than 1 m (Yang et al., 2019a; Lin et al., 2018). The biogeochemical processes influencing SOC turnover in the top 30 cm have been largely related to biological processes following the invasion by *S. alterniflora* (Craft et al., 2003). Biological activity decreases with depth due to the lower density of roots and lack of litter input when depths exceed 30 cm. These results indicated that climatic effects may be mediated by biological processes. Similar to the effect of MAT, negative relationships between Δ SOC storage and MAP were also observed at depths of 0–40 cm (Figure 6b), with the relationship being stronger in the 0–30 cm layer compared to the 30–40 cm soil layer (Figure S7). Coastal wetlands have a predominantly anaerobic environment that is often affected by tidal action and rising sea levels. In our study, the effects of MAT on SOC storage were therefore a greater influence than MAP, and overwhelmed the relationship with MAP.

On a century or millennium scale, temperature and precipitation depending on latitude and longitude control the distribution of marshes and mangroves in coastal wetlands (Cavanaugh et al., 2019). Contrary to the process of *S. alterniflora* invading mangroves, increased temperature and sea level rise have caused the expansion of mangrove forests into saltmarshes with global warming (Saintilan et al., 2013; Cavanaugh et al., 2019). Mangroves expand their range to higher latitudes and encroach salt marsh vegetation with declining freeze events (Cavanaugh et al., 2014). Other studies also suggest that mangrove encroachment enhances SOC storage (e.g., Yando et al., 2016; Kelleway et al., 2017). In turn, blue C storage in mangrove forests will decrease following *S. alterniflora* invasion under climate warming. Moreover, some marshes will be permanently lost, but not converted to mangroves with intensified climate change, thus the organic C storage will decline further.

4.3 Effects of edaphic variables and confounding factors on SOC dynamics

Climate and vegetation C input regulate the transformation rate of SOC storage from one to another capacity. However, whether SOC can be stably preserved or the potential of SOC storage is determined by soil physical and chemical properties (Luo and Viscarra-Rossel, 2020). The effects of soil properties on SOC dynamics in response to *S. alterniflora* invasion have received increasing attention (e.g., Ruiz Sinoga et al., 2012; Yang, 2019a). Zhang et al. (2011) has demonstrated that SOC content in a single *P. australis* community was lower than in a community with a mixed *P. australis* and *S. alterniflora* population. This was attributed to the differences in vegetation type and salinity, whereas higher microbial activity was detected in the *P. australis* community, leading to greater litter and SOC mineralization. Zhang et al. (2008) reported significant alterations of soil properties, including TN, TP, cation exchange capacity (CEC), MBC and MBN following invasion of mangrove wetlands by *S. alterniflora*, resulting in lower SOC storage. Wang et al. (2016) has shown that *S. alterniflora* invasion in a mangrove forest has led to significant decreases in TP, MBC, MBN, and activities of acid phosphatase with an increase in pH, potentially causing a decrease in SOC content. These studies showed the SOC content increased in marshes but decreased in mangrove forests following *S. alterniflora* invasion, and

these were consistent with our results (Figure 2 & Figure 3), which were attributed to the differences in soil properties.

In our study, the native species were invaded marginally, adjacently, and internally. We considered the soil properties are similar before *S. alterniflora* invasion, and these soil properties in native communities will change with the invasion chronosequence, thus indirectly impacting SOC turnover and stocks. We used *RDA* approach and Pearson correlation analysis to describe the effects of soil properties on SOC content in the native (*P. australis*, *K. candel* and *A. marina*) and adjacent invasive (*S. alterniflora*) communities at a broad regional scale (Figure 7; Figure S8 & Figure S9). Clay and sand contents, pH and TN were the primary factors controlling SOC contents in native *P. australis* and corresponding *S. alterniflora* communities in marsh wetlands (Figure 8). The NPP of *S. alterniflora* was higher, and the litter decomposition rate was lower than that of *P. australis* (Zedler and Kercher, 2004; Zhang et al., 2014). *S. alterniflora* invasion made a slight contribution to SOC sequestration in the marsh wetlands as it had a higher proportion of recalcitrant organic C (ROC) and lower proportion of LOC and mineralizable C per unit SOC (Yang et al., 2013). Therefore, the increased SOC stocks following invasion by *S. alterniflora* into *P. australis* communities resulted from increased net photosynthetic rate, biomass, litter quality and decomposition, and decreased SOC mineralization.

Edaphic variables were important in controlling SOC content after mangrove (*K. candel* and *A. marina*) was invaded by *S. alterniflora* (Figure 7). Factors including TN, pH, Si_{Ac} were of particular importance. Sand was negatively related to SOC content in the *A. marina* community (Figure S8). SOC stocks in the *K. candel* community was greater than in the *A. marina* community (Figure 3), this being attributed to fine-grained sediment which controls SOC storage (Bai et al., 2016). Our results highlighted the importance of sediment type to SOC storage, as indicated by the positive relationships with TN, Fe_{Ac}, and clay (Figure S8). Therefore, the positive effect of fine soil fractions on stabilizing soil C may be via mineral protection of SOM (Desjardins et al., 2006). SOC content was mainly affected by EC, WC, sand and TN in the *S. alterniflora*-invaded *K. candel* community, while EC, pH, TN and TP were the main factors in the *S. alterniflora*-invaded *A. marina* community. Moreover, the C sequestration rate was controlled by the recalcitrant

character of organic materials in wetlands (Bernal and Mitsch, 2013). Compared to marsh, fringe mangroves are within or close to the estuary. Therefore, mangroves have frequent anaerobic conditions derived from daily tidal inundation with limited soil respiration, thus lowering C losses. Therefore, the decreased SOC stocks in mangrove wetlands compared to marsh wetlands following *S. alterniflora* invasion were attributed to a greater NPP of mangrove (Hutchison et al., 2013), lower salinity (Saintilan et al., 2013), more recalcitrant organic substances (Barreto et al., 2016), decreased enzyme activities and microbial diversity (Morrissey et al., 2014), and extended anaerobic conditions. These mechanisms are site-specific and dependent on coastal hydro-geomorphology settings, which explains the substantial variations in organic C burial rates, C density and C stocks in independent wetlands (Twilley et al., 2018).

4.4 Identification of SOC sources and stability by coupling $\delta^{13}\text{C}$, C:N ratios and lignin biomarkers

When vegetation species composition changes from C3 to C4 plants, or vice versa, $\delta^{13}\text{C}$ of SOM can be used to identify the sources and to quantify the proportions of organic C derived from residues and rhizodeposition derived from the C3 to C4 vegetation communities (Werth and Kuzyakov, 2010; Sasmito et al., 2020). Our data revealed only a slight increase ($p > 0.05$) in $\delta^{13}\text{C}$ values in native *P. australis* after invasion of *S. alterniflora* community. This lack of strong increase in $\delta^{13}\text{C}$ could be explained by the fact that *P. australis* is predominantly C3 but can switch to the C4 photosynthetic pathway under more extreme environments (Srivastava et al., 2014), and the duration of invasion by *S. alterniflora* (i.e., 12–13 years) is relatively short, where the *P. australis* monoculture has been the dominant community for over 30 years in the coastal wetlands. However, the average $\delta^{13}\text{C}$ values in mangrove forests (dominated by *K. candel* and *A. marina*, both C3 only) significantly increased following *S. alterniflora* invasion ($p < 0.05$; Figure 4a), which is attributed to the C4 photosynthetic pathway of *S. alterniflora* (Antonielli et al., 2002). Based on the mixing model, the proportion of *S. alterniflora*-derived C in *P. australis* community was 5.6% in the 0–40 cm layer (Table 1). A similar result has been previously reported by Cheng et al. (2006), where *S. alterniflora*-derived C contributed of 5.1% (0–5 cm) and 9.5–11% (20–40

cm) in the Yangtze River estuary, while Zhang et al. (2010) showed a contribution of 11–19% (0–10 cm) in the Wanggang estuarine wetland. The proportions of *S. alterniflora*-derived C in *K. candel* and *A. marina* community were 23% and 12%, respectively, which were higher than that of *P. australis* community (Table 1). These results illustrated that SOC turnover rate in mangroves was faster than that of marsh after *S. alterniflora* invasion, and verified SOC storage decreased to a greater extent in the mangrove compared to marsh communities.

Based on a data-assimilation approach and controlled experiments, a negative relationship was observed between the SOC decomposition rate and the corresponding C:N ratio (Jiang et al., 2013; Xu et al., 2016). Generally, herbaceous C4 plants (i.e., *S. alterniflora*) have higher C:N ratios than C3 plants (i.e., *P. australis*) because the latter have more *Rubisco* proteins, and the proteins are beneficial to improve photosynthetic efficiency (Still et al., 2003). The higher photosynthetic efficiency and production potentially provide greater residual biomass inputs to soil or sediment. The soil C:N ratio in the *S. alterniflora* community was higher than that of *P. australis* (Figure 4b), suggesting large amounts of recalcitrant litter inputs from *S. alterniflora* with a greater resistance to mineralization (Yang et al., 2009). Thus, SOC storage in the *S. alterniflora* community was higher than that of the *P. australis* community (Figure 3). The C:N ratios in mangrove forests slightly decreased after invasion by *S. alterniflora* because of the differences in C:N ratios between grass and woody organic materials.

The soil C:N ratios gradually decreased from subtropical to tropical zones in coastal wetlands (Figure 4b), to some extent, implying the decrease in the SOC stability. This is consistent with SOC storage of *P. australis* > *K. candel* > *A. marina* whether it was invaded or not. The C:N ratio may indirectly indicate the SOC sources. Algae in aquatic environments typically have a very narrow C:N ratio ranging from 5 to 8, and vascular plants in terrestrial ecosystems have a C:N ratio >15 (Meyers, 1994). The C:N ratios in soils suggest a mixture of terrestrial and aquagenic or marine sources, and the soils or sediments in coastal wetlands were increasingly affected by marine sources with increasing tropical conditions. Thus, it is not sufficient to use the C:N ratio as a single indicator of SOC stability because the soil C:N ratios depends on many processes and can be affected by various C and N sources.

Lignin is one of the most abundant components of higher plants in terrestrial ecosystems and represents an important part of plant-derived C from biomass residues into soils (Xia et al., 2020b). Lignin is somewhat recalcitrant due to its nonhydrolyzable C-C and C-O-C bonds and the richness of aromatic structures (Crow et al., 2009). Significant relationships ($p < 0.01$) between lignin and SOC contents in all sampling sites were observed (Figure 4d). The Ad-to-Al ratios of V and S units increase with the increase in lignin decomposition. V monomers of lignin are more stable than S and C monomers, thus increases in C/V and S/V imply enhanced lignin decomposition (Bahri et al., 2006). Both monomer ratios (C/V, S/V) and Ad-to-Al ratios ((Ad/Al)_V, (Ad/Al)_S) decreased in the *P. australis* community, but increased in mangroves after invasion by *S. alterniflora*, and the increase was more evident in the *K. candel* community (Figure 5). Consequently, lignin in the *P. australis* community was more degraded than in the *S. alterniflora* community. In contrast, lignin in the mangrove communities was more stable than in the *S. alterniflora* community, which is consistent with the increase in SOC storage in the marsh and decrease in the mangrove communities following *S. alterniflora* invasion.

The C- and S- to-V ratios can also be used as source indicators being able to distinguish grasses from mangrove (Thevenot et al., 2010). Given the C/V and S/V ratios with boundaries of different sources (Jex et al., 2014), the sources of lignin phenols in the grass marsh are derived from non-woody angiosperm tissues (A_{nw}). While the sources in mangroves are derived from the complex of massive woody angiosperm (A_w) and non-woody angiosperm (A_{nw}), the quantity of lignin sources derived from leaves and grasses increase in mangroves following *S. alterniflora* invasion (Figure 9).

4.5 Implications for wetland C management and control of *S. alterniflora* invasion

The complexity of coastal ecosystems restricts the accurate prediction of SOC storage and the determination of key factors involved in SOC storage. We are aware that despite 216 samplings on 9 sites in native ecosystems regarding changes in SOC storage following *S. alterniflora* invasion may be uncertain. However, we believe that our model provides reliable results because the qualitative data combining $\delta^{13}C$, C:N ratios and lignin biomarker composition confirmed our

sample authenticity and validity (Figure 10). The involvement of further sampling sites in other wetland ecosystems will provide more details and definite statements to SOC storage on a larger regional or continental scale.

As an exotic species, *S. alterniflora* has positive effects on native ecosystems, such as higher levels of primary production, protection from storms, and maintenance of elevation; but this species also poses significant threats (i.e., biodiversity change) (Gedan et al., 2010). Both *S. alterniflora* and *P. australis* are aggressive species in China and the USA, respectively. Each species is mutually considered as invasive species, thus, long-term investigations of native and invasive species in global scale are required.

Although the positive and negative effects of *S. alterniflora* on SOC storage in marsh and mangrove wetland had been verified, the behavior and quantity of SOC stocks in different wetlands varied extensively. This SOC variability between wetlands result from the morphology and biology of species, invasion years, tidal action, and edaphic variables (e.g., pH, EC, fertility, and redox potential) (Yando et al., 2016; Kelleway et al., 2017; Twilley et al., 2018). Globally, organic C burial rates in mangrove forests have an average of $2.7 \pm 0.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, which is about 20 times larger than that of terrestrial forest ecosystems (Breithaupt et al., 2012). However, studies have estimated that mangrove deforestation causes the emission of $0.007\text{--}0.03 \text{ Pg CO}_2 \text{ y}^{-1}$ (Hamilton and Friess, 2018). Therefore, mangrove forests rank among the most C-rich forests, which can be increased by selecting high C-density species for afforestation and by increasing the area of mangrove.

Mangroves cover approximately $137,600 \text{ km}^2$ of coastline distributed across around 118 countries; with 39% found in Asia, 20% in Latin America and the Caribbean, 20% in Africa, 12% in Oceania, 8.4% in North America, and 0.70% in other regions (Bunting et al., 2018). The area of mangrove forest in China is about 22,025 ha (less than 50% of the mangrove area of 48,266 ha in 1950s) while the potential mangrove habitat is 58,848 ha (24% of the historical area 250,000 ha) (Liu et al., 2014). The global rate of mangrove loss has, however, reduced between the late 20th and early 21st century, from ~2% to <0.4% per year (Friess et al., 2019). *S. alterniflora* is more tolerant to increased salinity and flooding stresses than native species, therefore, its competitive

advantage will increase with sea level rise (Hanson et al., 2016). Mangroves not only ease the greenhouse effect, but also stabilize shorelines and decrease the effects of natural disasters, including those of tsunamis and hurricanes (Saderne et al., 2018). Undeniably, knowledge and information gained will aid policy and environmental management decisions concerning the restoration of mangrove forests facing the increasingly threats from invasion by *S. alterniflora*.

5 CONCLUSIONS

Coastal wetlands have been identified as critical C reservoirs, which have been affected by the invasion of *S. alterniflora*. Changes in SOC storage in native ecosystems were not completely consistent with the difference in aboveground net primary productivity (NPP) of native and invasive species nor the years since invasion (7–15 years). Increasing temperature from North to South over the 2500 km transect decreased SOC storage with the effects being evident in the surface soil layers (0–30 cm) but diminished in the deeper layers. Invasion by *S. alterniflora* increased SOC storage in *P. australis* marsh by 3.5 t C ha⁻¹, while substantial losses –14 and –3.9 t C ha⁻¹ were observed in native *K. candel* and *A. marina* communities, respectively. The proportions of *S. alterniflora*-derived C across the three communities were 5.6%, 23% and 12%. The increased SOC stocks in marsh was due to the increased NPP, higher C:N ratio and lower mineralization of C derived from *S. alterniflora*. The depleted SOC stocks in mangrove wetlands following invasion were attributed to decreased NPP, higher salinity, lower recalcitrant organic inputs, increased enzyme activities and microbial diversity from speculation, and alternative wet-dry conditions. SOC stocks were regulated mainly by the joint effects of climate, plant biological traits and edaphic variables in the coastal wetlands. This study has implications for better understanding the mechanisms driving C sequestration potential in coastal marsh and mangrove wetlands undergoing exotic *S. alterniflora* invasion worldwide. The control of *S. alterniflora* invasion into mangrove communities will provide significant advantages to blue C storage in these systems. Results from this study can facilitate environmental management and policy decisions concerning the restoration of mangrove forests facing the increasingly serious *S. alterniflora* invasion worldwide.

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CONFLICT OF INTEREST

All authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that supports this study are available in the Supplementary materials, and they could contact with the corresponding author.

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Figure Captions

FIGURE 1 Sampling locations and plant communities in the coastal wetlands along the 2500 km coastline extending from tropical regions in southern China to the subtropical Yangtze delta. 54 sites with total 216 samplings were chosen with 8 independent wetland types and 9 sampling locations, including Chongming Island, Hengsha Island, Yueqing Bay, Minjiang River Estuary, Jiulong River Estuary, Zhangjiang River Estuary, Zhanjiang and Beihai. Each location has two community types, one type is native species only (dominated by *P. australis*, *K. candel* or *A. marina*), and the other adjacent population was invaded by *S. alterniflora*.

FIGURE 2 Comparison of soil organic carbon (SOC) content under native and invasive vegetation types in the coastal wetlands depending on soil depth. The change in SOC (Δ SOC)

content was calculated as the difference between invasive and native vegetation types. The results are expressed as the means $\pm$ standard deviation ($n = 9$). The color code is red for *P. australis*, green for *K. candel*, blue for *A. marina*, and black for *S. alterniflora*. The abbreviations bottom in colors are independent wetlands, including CI: Chongming Island, HI: Hengsha Island, YB: Yueqing Bay, ME: Minjiang River Estuary, JE: Jiulong River Estuary, ZE1: Zhangjiang River Estuary 1, ZE2: Zhangjiang River Estuary 2, ZJ: Zhanjiang and BH: Beihai.

FIGURE 3 Comparison of cumulative soil organic carbon (SOC) storage from the surface to the given depths (expressed as the means $\pm$ SD, $n = 9$) between native and invasive vegetation types in the coastal wetlands. The change in SOC (Δ SOC) storage was calculated as the difference in SOC storage between invasive and native vegetation types. The color code is red for *P. australis*, green for *K. candel*, blue for *A. marina*, and black for *S. alterniflora*. The abbreviations bottom in colors are independent wetlands, including CI: Chongming Island, HI: Hengsha Island, YB: Yueqing Bay, ME: Minjiang River Estuary, JE: Jiulong River Estuary, ZE1: Zhangjiang River Estuary 1, ZE2: Zhangjiang River Estuary 2, ZJ: Zhanjiang and BH: Beihai.

FIGURE 4 Comparisons in stable C isotope composition of SOC ($\delta^{13}\text{C}_{\text{SOC}}$) (a), C:N molar ratio (b), the calculated proportion of SOC from the C4 plant *S. alterniflora* (c), and the relationship between lignin and SOC content (d) in the coastal wetlands under native (*P. australis*, *K. candel*, and *A. marina*) and invasive (*S. alterniflora*) communities. The color code is red for *P. australis*,

green for *K. candel*, blue for *A. marina*, and black for *S. alterniflora*. Values for each parameter marked with * were significantly different ($p < 0.05$) between native and invasive communities using t-test. The numbers above the boxes represent the order of outliers in all data, and each dot represents one outlier.

FIGURE 5 Compositions of lignin biomarker monomers across soil depths under native (*P. australis*, *K. candel*, and *A. marina*) and invasive (*S. alterniflora*) communities in the coastal wetlands. C/V (a) and S/V (b) represent the cinnamyl- or syringyl-to-vanillyl ratios. (Ad/Al)_V (c) and (Ad/Al)_S (d) represent the acid-to-aldehyde ratios of vanillyl and syringyl units. The color code is red for *P. australis*, green for *K. candel*, blue for *A. marina*, and black for *S. alterniflora*. Values for each parameter marked with * were significantly different ($p < 0.05$) between native and invasive communities using t-test. The numbers above the boxes represent the order of outliers in all data, and each dot represents one outlier.

FIGURE 6 Relationships between changes in SOC storage at depths of 0–40 cm (Δ SOC) and duration of invasion by *S. alterniflora* (a), and between Δ SOC and mean annual precipitation (MAP) or mean annual temperature (MAT) (b). The dashed line represents the absence of SOC changes (Δ SOC storage being zero). Square, diamond and triangle represent *P. australis*, *K. candel* and *A. marina*, respectively.

FIGURE 7 Redundancy analysis (RDA) of soil organic carbon fractions and soil physio-chemical properties in the coastal wetlands with native and invasive communities. a, b, and c represent native species of *P. australis*, *K. candel*, and *A. marina*, respectively, while A, B and C represent invasive species that *S. alterniflora* is replacing *P. australis*, *K. candel*, and *A. marina*. Abbreviations: SOC, soil organic carbon; LOC, labile organic carbon; DOC, dissolved organic carbon; MBC, microbial biomass carbon; TN, total nitrogen; TP, total phosphorus; EC, electrical conductance; WC, water content; Fe_{Ac}, active iron; Si_{Ac}, active silicon. The sampling sites in figures are wetland name abbreviations (see Fig. 2) + species initials.

FIGURE 8 Relative importance of biogeochemical soil properties for SOC fractions under native (*P. australis*, *K. candel* and *A. marina*) and invasive (*S. alterniflora*) communities in the coastal wetlands across a 2500 km climate gradient. Abbreviations: TN, total nitrogen; TP, total phosphorus; EC, electrical conductance; WC, water content; Fe_{Ac}, active iron; Si_{Ac}, active silicon.

FIGURE 9 Scatter plot of S/V vs. C/V based on SOC-standardized lignin monomer composition data of all sampling sites (a) and end-member values of S/V and C/V for selected plants (b). The end-member figure includes woody angiosperm tissue, non-woody angiosperm tissue, woody gymnosperm tissue (G_w), and non-woody gymnosperm. S/V and C/V represent the syringyl- and cinnamyl-to-vanillyl ratios. The scatter plots in the range of the thin dashed lines represent sources from non-woody angiosperm tissue.

FIGURE 10 Schematic model of various factors of SOC storage at depths up to 40 cm depth in coastal wetlands. Red color denotes *P. australis*, green color is *K. candel*, blue color is *A. marina*, and black color is *S. alterniflora*. The different black dashed lines represent corresponding invasive *S. alterniflora* communities in relative to *P. australis*, *K. candel* and *A. marina*. C:N ratios represent the soil organic carbon to total nitrogen ratios, S/V and C/V represent the syringyl- and cinnamyl-to-vanillyl ratios, and $(Ad/Al)_{V/S}$ represent the acid-to-aldehyde ratios of vanillyl or syringyl units.

TABLE 1 Carbon budgets in the coastal wetlands under the native *Phragmites australis*, *Kandelia candel*, and *Avicennia marina* communities in response to invasive *Spartina alterniflora* community

Native species	Current SOC storage (kg C m ⁻²)		Proportion of <i>S. alterniflora</i> -derived C (f, %)	Gains (kg C m ⁻²)	Retained SOC storage (kg C m ⁻²)		
	Native	Invasive				Losses (kg C m ⁻²)	C budget (t C ha ⁻¹)
<i>Phragmites australis</i>	7.1±1.3 (a)	7.5±1.1 (a)	5.6±19%	0.41	7.0	-0.06	3.5
	5.4±0.64	4.0±0.77					
<i>Kandelia candel</i>	(a)	(b)	23±15%	0.93	3.1	-2.3	-14
	5.0±0.94	4.6±0.91					
<i>Avicennia marina</i>	(a)	(b)	12±10%	0.57	4.1	-0.96	-3.9

Note: Paired sample t-test was used to compared the significance ($p < 0.05$) of current SOC storage between native and invasive community.

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