Responses of coastal sediment organic and inorganic carbon to habitat modification across a wide latitudinal range in

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A B S T R A C T

Coastal wetlands are important to the global carbon (C) budget and climate regulation. Plant invasion and aquaculture reclamation have drastically transformed China's coastal wetlands, but knowledge of the effects on sediment carbon remains limited. We sampled top layer sediments (0–20 cm) in 21 coastal wetlands in southeastern China across the tropical-subtropical climate gradient, that have experienced the same sequence of habitat transformation from native mudflats (MFs) to *Spartina alterniflora* marshes (SAs) then to aquaculture ponds (APs). We measured the sediment carbon contents and ancillary physicochemical parameters. Landscape change from MFs to SAs increased sediment organic carbon (SOC) but decreased sediment inorganic carbon (SIC) content, whereas conversion of SAs to APs resulted in the opposite changes. Based on stepwise regression analysis, ammonium concentration and particle size distribution were the common factors that affected changes in SOC between habitat types, whereas for SIC it was ammonium and chloride concentrations. Habitat change affected SOC to a larger degree than SIC. Overall, invasion of MFs by SAs 38 increased total carbon storage in the top sediment by 22%, or 6.6×10^6 g C ha⁻¹; 39 conversion of SAs to APs decreased it by 9.7%, or 3.5×10^6 g C ha⁻¹. Our results showed the differential effects of different habitat modification scenarios on the sediment carbon pools and help assess how landscape-scale change affects terrestrial carbon budget and emission in the context of global climate change.

Keywords: Sediment organic carbon (SOC); Sediment inorganic carbon (SIC); Coastal

wetland; Invasive plants; Aquaculture reclamation; Carbon storage

1. Introduction

Coastal wetlands, including mudflats, salt marshes and mangroves, are among the most productive ecosystems that are highly efficient in sequestering and storing carbon to mitigate climate change (Bertram et al., 2021; Macreadie et al., 2021; Xu et al., 2022; Zhang et al., 2021a). Despite covering just 0.2% of the Earth's surface, coastal 50 wetlands globally store at least 44.6 Tg C yr⁻¹ (Chmura et al., 2003), contributing 50% of carbon burial into the sediment (Duarte et al., 2013). However, plant invasion and 52 reclamation increasingly modify the ecological properties of coastal wetlands (Bu et al., 2015; Davidson et al., 2018; Sun et al., 2015), and are estimated to have caused degradation or habitat loss in 50% of the world's coastal wetlands (Barbier et al., 2011; Yang and Yang, 2020). These habitat modifications can greatly alter the hydrological conditions, redox environment, nutrient cycles, sediment properties, biodiversity and overall ecosystem structure (Andreetta et al., 2016; Dick and Osunkoya, 2000; Lin et al., 2022; Liu et al., 2022; Piper et al., 2015), thereby affecting the wetlands' carbon capture and storage capacities (Bu et al., 2015).

60 Coastal wetlands in China cover approximately 5.80×10^6 ha in 2014 (Sun et al., 2015), which have been profoundly changed by *Spartina alterniflora* invasion (An et al., 2007). As a way to control the spread of *S. alterniflora* and increase land use for food production, some of the *S. alterniflora* marshes were subsequently cleared and converted into aquaculture ponds (Duan et al., 2020). Today, there is an estimated total 65 area of 5.46 \times 10⁴ ha of *S. alterniflora* marshes (Liu et al., 2018) and 1.56 \times 10⁶ ha of aquaculture ponds (Duan et al., 2020), representing over a quarter of the native wetland area. Such a vast extent of landscape modification can have significant ramifications on sediment carbon content, but most research to-date has been focused on the effects on sediment organic carbon (SOC) at the local scale (Bu et al., 2015; Liu et al., 2021; Xiang et al., 2015; Xu et al., 2022; Wan et al., 2018; Wang et al., 2021), while little is known about how sediment inorganic carbon (SIC) will respond to *S. alterniflora* invasion and reclamation (Yang and Yang, 2020; Zhu et al., 2020), or how habitat modification affects wetland SOC and SIC pools across the wider geographical and environmental gradients. This knowledge gap leads to uncertainties in the assessment of regional and global wetland carbon budget and its feedback on climate.

To fill this knowledge gap, three habitat types (native mudflats, *S. alterniflora* 77 marshes and aquaculture ponds) from 21 coastal wetlands spanning 20°42′ N to 31°51′ N in mainland China were investigated to gain insights into the effects of habitat modifications on sediment carbon contents. The primary objectives were to investigate the responses of SOC and SIC pools to *S. alterniflora* invasion and aquaculture reclamation, and to evaluate the main environmental factors influencing the SOC and SIC contents in impacted coastal wetlands across the tropical-subtropical gradient in southeastern China. The results will improve our understanding of how landscape modifications affect the coastal wetland carbon cycle at the national scale.

2. Materials and methods

2.1. Study areas and sediment sampling

Three habitat types were selected at each location: native mudflats (MFs), marshes with invasive *S. alterniflora* (SAs) and reclaimed aquaculture ponds (APs) (Yang et al., 2022). Field sampling was conducted between December 2019 and January 2020. At each location, three independent replicate plots were selected for MFs (or SAs), and the upper 0–20 cm sediments were collected using a steel corer (1.5 m length, 5 cm internal diameter). For APs, independent replicate ponds were selected at each location. Within each pond, a transect extending ~30 m from the bank to the center was used for sampling at three sites at 10 m intervals. As a result, a total of 189 sediment samples 105 (21 sampling sites \times 3 habitat types \times 3 plots (or ponds)) collected. All sediment 106 samples were stored at 4 °C until analyses in the laboratory.

2.2. Sediment physicochemical analyses

2.3. Analysis of carbon contents

Plant residues and stones were removed from the sediment samples before total carbon (TC) and sediment organic carbon (SOC) measurements. A subsample (~50 g fresh sediment) was freeze-dried, homogenized and ground to fine powder, and then sifted through a 2-mm mesh for carbon content analysis (Yang et al., 2022a, 2022b). Approximately 1 g of the freeze-dried sample was analyzed with a combustion analyzer (Elementar Vario MAX CN, Germany) for TC. To measure SOC, approximately 3 g of freeze-dried sample was screened, weighed, and extracted in 1 M hydrochloric acid 128 (HCl) solution for 24 hr to remove the inorganic carbon, then oven-dried at 60° C (Liu

et al., 2017; Yang et al., 2022), and subsequently analyzed with the combustion analyzer (Elementar Vario MAX CN, Germany). The content of sediment inorganic carbon (SIC) was calculated as the difference between the TC and SOC (Zhu et al., 2020). Sediment carbon storage at 0–20 cm depth per hectare was calculated from the measured carbon content and bulk density as (Wang et al., 2018; Zhu et al., 2020):

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$$
C_{\text{storage}} = C_{\text{content}} \times BD \times 20
$$
 (Eq. 1)

135 where C_{storage} is the carbon storage of TC, SOC or SIC at the 0–20 cm depth ($\times 10^6$ g C 136 ha⁻¹), C_{content} is the carbon content of TC, SOC or SIC (g kg⁻¹), and BD is the bulk 137 density (g cm⁻³).

2.4. Statistical analysis

One-way analysis of variance (ANOVA) was conducted to test for significant differences between habitat types for SOC, SIC and sediment physicochemical properties, using the SPSS version 22.0 (IBM, Armonk, NY, USA). Spearman correlation analysis was conducted to examine the relationships between SOC, SIC and different sediment physicochemical variables, using corrplot and Hmisc packages in R software (Version 4.1.0). The main variables influencing sediment SOC (or SIC) content were evaluated by a stepwise regression analysis, and the results were plotted using OriginPro 2021. The weighted response ratios (RR++) were calculated to assess the responses of SOC and SIC to habitat modification, following Hedges et al. (1999) 148 and Tan et al. (2019). All results were considered significant at $p \le 0.05$ and were 149 presented as mean \pm 1 standard error.

150 **3. Results**

151 *3.1. SOC content across habitat types*

Across all sampling sites, the SOC content varied in the range of $1.87-9.35 \text{ g kg}^{-1}$ 153 in MFs, 5.96–22.78 g kg⁻¹ in SAs, and 4.13–21.56 g kg⁻¹ in APs (Figure 2a). SOC 154 content (10.02 \pm 0.54) was the highest in SAs (10.48 \pm 0.95 g kg⁻¹), followed by APs (8.48 \pm 0.86 g kg⁻¹) and MFs (6.40 \pm 0.43 g kg⁻¹) (Figure 2b). Based on the analysis of 156 weighted RR, conversion of MFs to SAs increased SOC content significantly by 70.9%, 157 but conversion of SAs to APs decreased SOC content by 15.3% (Figure 3a). 158 *3.2. SIC content across habitat types* SIC content varied significantly in the range of $0.28-12.25$ g kg⁻¹ (Figure 4a) 160 across habitat types (p <0.05). SIC content was the highest in MFs (5.63 \pm 0.49 g kg⁻¹), followed by APs $(4.63 \pm 0.72 \text{ g kg}^{-1})$ and SAs $(3.66 \pm 0.50 \text{ g kg}^{-1})$ (Figure 4b). Based 162 on the analysis of weighted RR, conversion of MFs to SAs decreased SIC content 163 significantly by 33.6% (Figure 3b), but conversion of SAs to APs increased SIC content 164 by 26.9% (Figure 3b).

165 *3.3. Total carbon storage across habitat types*

166 Total C storage (TC_{storage}) in the top 0-20 cm sediment for the different habitat 167 types is shown in Figure 5. Across all sampling sites, TC_{storage} was the highest in SAs 168 $(36.36 \pm 1.57 \times 10^6 \text{ g C ha}^{-1})$, followed by APs $(32.85 \pm 1.59 \times 10^6 \text{ g C ha}^{-1})$ and MFs 169 (29.77 \pm 0.75 \times 10⁶ g C ha⁻¹) (Figure 5). TC_{storage} increased by 22.1% following the 170 conversion of MFs to SAs, but decreased by 9.7% when SAs were converted to APs. 171 SOC_{storage} was significantly higher than SIC_{storage} (p <0.05) and it accounted for 172 56.4–74.1 % of TC_{storage} (Figure 5).

173 *3.4. Environmental control of sediment carbon contents*

174 Spearman correlation analysis showed that in the case of MFs-to-SAs conversion, 175 SOC content was correlated positively with SWC, NH₄⁺-N and S_{clay} (p <0.01 or p <0.001) 176 and negatively with BD and $S_{sand} (p<0.01)$ or $p<0.001$) (Figure 6a). SIC content was 177 correlated positively with S_{clav} and S_{silt} ($p<0.01$ or $p<0.001$) and negatively with salinity, 178 NH_4^+ -N and $S_{\text{sand}}(p<0.01 \text{ or } p<0.001)$ (Figure 6a). 179 In the case of SAs-to-APs conversion, SOC content was correlated positively with 180 NH₄⁺-N, Cl⁻, S_{clay} and $S_{\text{silt}}(p<0.01 \text{ or } p<0.001)$ and negatively with pH, SO_4^2 and S_{sand} 181 (p <0.01 or p <0.001) (Figure 6b). SIC content was correlated positively with S_{silt}

182 (p <0.001) and negatively with salinity, NH₄⁺-N, Cl⁻, SO₄²⁻ and S_{sand} (p <0.01 or p <0.001)

183 (Figure 6b).

184 Based on stepwise multiple regression analysis, NH₄⁺-N and pH were the main 185 drivers of SOC change in the case of MFs-to-SAs conversion, while SIC was mostly 186 influenced by NH_4^+ -N, sediment clay content, salinity and Cl⁻ (Table 1). Changes in 187 NH₄⁺-N, SO₄² and pH explained 43% of the variation in SOC in the case of 188 SAs-to-APs conversion, while SIC was strongly affected by Cl⁻, NH₄⁺-N, NO₃⁻-N and 189 SO_4^2 ⁻ (Table 1).

- 190 **4. Discussion**
- 191 *4.1. Habitat modification effect on sediment organic carbon*

Although previous studies have evidenced that *S. alterniflora* invasion significantly affected SOC content in vegetated wetlands in China (Li et al., 2009; Xiang et al., 2015; Yang et al., 2017a; Zhang et al., 2021b), its effects on native mudflats were less clear. Here, based on data from 21 coastal sites across the tropical-subtropical gradient in China, we found that SOC content in the top 0-20 cm SAs was significantly higher than that in MFs (Figure 2), representing an increase of 70.9% when native mudflats were converted to *S. alterniflora* marshes (Figure 3a).

The size of SOC pool in sediment is determined by the balance between organic carbon inputs (autochthonous and allochthonous sources) and outputs (e.g., decomposition, leaching, removal, etc.) (Amundson, 2001; Hou et al., 2018; Schlesinger and Bernhardt, 2013). The continuous river flow and periodic tidal flushing in native mudflats would increase sediment erosion, reduce or dilute SOC and minimize SOC accumulation in the sediment. Invasion by *S. alterniflora* could mitigate sediment erosion by weakening water flow with aboveground biomass and stabilizing the sediment with roots; it would also introduce more photosynthetically fixed carbon into the sediment (Xiang et al., 2015; Yang et al., 2016; Zhang et al., 2010). We found 208 that NH₄⁺-N content in the SAs (24.0 g kg^{-1}) was higher than that in the MFs (13.3 g kg^{-1} (Figure 6a), likely reflecting the results of nutrient remineralization and retention by the marsh vegetation (Liao et al., 2007; Yang and Guo, 2018). This higher level 211 NH₄⁺-N would support higher organic carbon production by plants and microbes (Pastore et al., 2017; Xie et al., 2019; Wang et al., 2013), which would explain its

213 significant and positive correlation with SOC content $(p<0.01;$ Figure 6a).

Compared to coastal marshes, the deeper and stagnant nature of aquaculture pond water would favor the development of anoxic condition within the sediment (Tan et al., 2020; Yang et al., 2022b), which is expected to slow down the decomposition of unconsumed feed and animal wastes and allow more organic matter to accumulate in the sediment. However, we found that SOC in aquaculture ponds was significantly lower than that in *S. alterniflora* marshes (*p*<0.001; Figure 2b). In the aquaculture ponds, organic carbon mainly came as external supply of feed, but most of which would be converted to farmed animal biomass and be harvested from the ponds. In contrast, organic carbon was mainly produced internally via photosynthesis in the marshes, most of which would remain in the system (not harvested); hence, SOC was able to accumulate to a higher level over time.

4.2. Habitat modification effect on sediment inorganic carbon

SIC plays an important role in C sequestration, especially in coastal 227 saline–alkaline areas (Zhu et al., 2020), but few studies have investigated the effect of 228 plant invasions and aquaculture reclamation on SIC in coastal wetland (Yang and Yang, 2020; Zhu et al., 2020). Here we showed that native mudflats had higher SIC than *S. alterniflora* marshes (Figure 4b). The SIC pool consists mainly of carbonates, which include lithogenic inorganic carbon (LIC) and pedogenic inorganic carbon (PIC). LIC is derived from the parent sediment material, which is conserved in unweathered sediments (Wu et al., 2009; Yang and Yang, 2020). PIC is formed by direct precipitation

of carbonate parent material (Eq. 2) (Wu et al., 2009; Yang and Yang, 2020) or weathering of calcium silicate (Eq. 3) (Lal and Kimble, 2000; Emmerich, 2003; Wu et al., 2009):

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2HCO3 + Ca2+ \rightarrow CaCO3 + H2O + CO2
$$
\n
$$
CaSiO3 + 2H2O + CO2 \rightarrow H4SiO4 + CaCO3
$$
\n(Eq. 2)

The processes can be driven by microbes in saline sediments (Dupraz et al., 2004; Kremer et al., 2008; Schlager, 2003), especially photosynthetic microbes (Zhu and Dittrich, 2016). Dense vegetation in the marshes would have competed against benthic autotrophs for nutrients and light, therefore decreased biological precipitation of PIC when the mudflats were invaded by *S. alterniflora*.

The increase in SIC following conversion of *Spartina* marshes to aquaculture ponds might be related to management practices. For example, addition of fertilizer in 245 the form of NH₄HCO₃ would have favored carbonate precipitation, as has been shown in the conversion of coastal marshes to croplands (Zhu et al., 2020). Also, liming was used by some farmers to disinfect the ponds prior to stocking (Pouil et al., 2019; Yang 248 et al., 2022b), which would have increased sediment Ca^{2+} concentration and promoted SIC formation.

4.3. Implications for sediment carbon storage and emission

In the literature, the response of coastal sediment C storage to landscape change varied markedly. Zhu et al. (2020) found that conversion of coastal marshes to 253 croplands decreased total C storage $(TC_{storage})$ in the top sediment $(0-15 \text{ cm})$ by 254 21–52%. Wang et al. (2019) showed that $TC_{storage}$ increased by 8% following the conversion of *Phragmites australis* marshes to *S. alterniflora* marshes, while 256 conversion of mangrove marshes to *S. alterniflora* marshes decreased TC_{storage} by 18%. Xia et al. (2021) reported that *S. alterniflora* invasion decreased SOC storage in mangrove marshes dominated by *Kandelia obovata* and *Avicennia marina* but it had no effect in *P. australis* saltmarshes across the tropical and subtropical regions of coastal China. Conversely, Xu et al. (2022) found that *S. alterniflora* invasion had no significant effect on SOC storage in vegetated native wetlands in coastal China. The highly variable and at times conflicting observations suggest that the response of sediment C storage may depend on the local environmental conditions as well as the scenario of habitat change. To attain a better understanding of the topic, we sampled 21 coastal wetlands that spanned a broad geographical and climate gradient, and that have undergone the same sequence of transformation, i.e., from mudflats to *S. alterniflora* marshes then to aquaculture ponds.

Spartina alterniflora was introduced to China over 4 decades ago to restore coastal vegetation, provide biofuel material, protect and stabilize shoreline (Zhang et al., 2017), but it has since spread rapidly throughout China's coasts (An et al., 2007). While invasion of mudflats by *S. alterniflora* has negative impacts on coastal flora and fauna (Chen et al., 2004; Li et al., 2009), based on our findings, it also significantly increased 273 TC_{storage} by 22.1% in the top 0–20 cm sediment (Figure 5); along with the above-ground biomass and deeper root mass, this represents a large increase in 'fixed' carbon in the land. In the context of carbon capture and climate mitigation, this may be viewed as an unintended benefit of *S. alterniflora* invasion.

As a measure to control the spread of *S. alterniflora* and to support coastal aquaculture, increasingly more *Spartina* marshes are being cleared and converted to aquaculture ponds (Duan et al., 2021). Based on our data, such habitat modification 280 would decrease TC_{storage} by 9.7% (Figure 5). As the coastal aquaculture sector in China continues to expand (Ren et al., 2019), conversion of *Spartina* marshes to aquaculture ponds would release a vast amount of stored carbon from the marsh sediment, adding to 283 the overall climate footprint of the aquaculture operation (Yuan et al., 2019). Sediment carbon includes both SOC and SIC; interestingly, SOC and SIC responded very differently to habitat modifications (Figure 3). Conversion of mudflats to *Spartina* marshes increased SOC but decreased SIC; the opposite occurred when *Spartina* marshes were converted to aquaculture ponds (Figure 3). Because SOC and SIC likely have different chemical reactivity and susceptibility to microbial actions, the different directions of change would affect the overall carbon dynamics in the sediment. For example, some of the SOC could be metabolized by microbes under anoxic 291 condition into CH₄, which has a stronger warming effect than $CO₂$ (Gao et al., 2018; 292 Tong et al., 2012; Xiang et al., 2015; Yang et al., 2017b). Therefore, the higher TC_{storage} as well as higher proportion of SOC in marshes and aquaculture ponds make them potentially stronger hotspots than mudflats to drive further warming.

5. Conclusions and recommendations

The coastal landscape of China has undergone significant transformation over the

past several decades. We showed that the sequence of change from native mudflats to *Spartina* marshes to aquaculture ponds has resulted in significant changes to the sediment C pool. Overall, invasion of mudflats by *S. alterniflora* increased C storage in 300 the top sediment by 6.6×10^6 g C ha⁻¹, which may help mitigate climate warming. On the other hand, conversion of *Spartina* marshes to aquaculture ponds decreased the 302 sediment C storage by 3.5×10^6 g C ha⁻¹, which needs to be taken into account when assessing the climate impact of the expanding coastal aquaculture sector.

Plant invasions and aquaculture reclamation affect not only sediment physicochemical properties, but also various sediment microfauna. Novel methods such as isotopic tracing can be used to quantify the microfauna's contribution to sediment C pool, its stability and turnover. Likewise, process measurements such as microbial metabolism will help understand and predict changes to the dynamics and fate of sediment carbon. In this study, we estimated the landscape-scale change in sediment carbon storage in response to habitat modifications. Our findings can be coupled with GIS and process-based data to hind- and fore-cast landscape-scale change in coastal sediment carbon dynamics and emission.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this 317 paper.

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Regression equations for sediment organic carbon (SOC) and sediment inorganic carbon (SIC) contents as functions of sediment Regression equations for sediment organic carbon (SOC) and sediment inorganic carbon (SIC) contents as functions of sediment \overline{c}

Table 1

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 \overline{a}

Figure 2. (a) surface sediment SOC content across three wetland habitat types for the 21 sampling sites, and (b) boxplots of surface sediment SOC content for the three wetland habitat types. MFs, SAs and APs represent mud flats, *S. alterniflora* marshes and aquaculture ponds, respectively. Different lowercase letters above the bars indicate significant differences between wetland habitat types (p <0.05). Error bars respectively. Different lowercase letters above the bars indicate significant differences between wetland habitat types (*p*<0.05). Error bars SOC content for the three wetland habitat types. MFs, SAs and APs represent mud flats, S. alterniflora marshes and aquaculture ponds, Figure 2. (a) surface sediment SOC content across three wetland habitat types for the 21 sampling sites, and (b) boxplots of surface sediment represent standard error ($n = 63$). represent standard error $(n = 63)$. \circ $\sqrt{2}$ $\overline{7}$ ∞

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12 aquaculture bonds. Bars represent the RR++ values and 95% CIs (
$$
n = 63
$$
). The asterisks (*) indicate significance at $p < 0.05$.

Figure 4. (a) surface sediment SIC content across three wetland habitat types for the 21 sampling sites, and (b) boxplots of surface **Figure 4.** (a) surface sediment SIC content across three wetland habitat types for the 21 sampling sites, and (b) boxplots of surface sediment SIC content for the three wetland habitat types. MFs, SAs and APs represent mud flats, S. alterniflora marshes and aquaculture sediment SIC content for the three wetland habitat types. MFs, SAs and APs represent mud flats, *S. alterniflora* marshes and aquaculture ponds, respectively. Different lowercase letters above the bars indicate significant differences between wetland habitat types (*p*<0.05). ponds, respectively. Different lowercase letters above the bars indicate significant differences between wetland habitat types (p<0.05). 16 14 15

Error bars represent standard error $(n = 63)$. Error bars represent standard error $(n = 63)$. 17

Figure 5. Sediment storage of total C, sediment organic carbon (SOC), and sediment inorganic carbon (SIC) at 0-20 cm depth for the three wetland habitat types. MFs, SAs and APs represent mud flats, *S. alterniflora* marshes and 22 aquaculture ponds, respectively. Error bars represent standard error $(n = 63)$.

Figure 6. Correlation matrix for the different habitat modification scenarios: (a) conversion of MFs to SAs; (b) conversion of SAs to APs. Colors of the circle segments indicate the direction of correlation (blue = positive; red = negative); size of the colored segment is proportional to the *r* value (between -1 and 1). Asterisks within each circle indicate level of significance (**p* < 0.05; ***p* < 0.01; ****p* < 0.001). SWC, BD, Sclay, Sslit, Ssand, SOC and SIC represent sediment water content, bulk density, clay content, silt content, sandy content, organic carbon and inorganic Figure 6. Correlation matrix for the different habitat modification scenarios: (a) conversion of MFs to SAs; (b) conversion of SAs to APs. Colors of the circle segments indicate the direction of correlation (blue = positive; red = negative); size of the colored segment is proportional to Sslit, Ssand, SOC and SIC represent sediment water content, bulk density, clay content, silt content, sandy content, organic carbon and inorganic the *r* value (between -1 and 1). Asterisks within each circle indicate level of significance (*p < 0.05; **p < 0.01; **p < 0.001). SWC, BD, Sclay, carbon, respectively carbon, respectively 24 26 25 27 28

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Supporting Information

Responses of coastal sediment organic and inorganic carbon to

habitat modification across a wide latitudinal range in southeastern China

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S1

Supporting Information Summary

No. of pages: 4 No. of tables: 1

- **Page S3:** Table S1. Fitting parameters of the first order kinetics for soil organic carbon
- mineralization in surface soil (0–20 cm) from three wetland habitat types across the
- different coastal sites in China.

29 **Table S1** Surface soil physico-chemical properties across the three wetland habitat types.

30 MFs, SAs and APs represent mud flats, *S. alterniflora* marshes and aquaculture ponds,

31 respectively.

132 Lowercase letters within the same column indicate significant differences at $p \le 0.05$ between three

33 wetland habitat types. Data are after Yang et al. (2022) for reference and review only. See main text for

explanation of the abbreviations. 34

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