

1 **Storage, patterns and influencing factors for soil organic carbon in coastal wetlands of**  
2 **China**

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4 **Running title:** Controls on SOC stocks in coastal wetlands

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6 Shaopan Xia<sup>1,2</sup>, Zhaoliang Song<sup>2,3\*</sup>, Lukas Van Zwieten<sup>4</sup>, Laodong Guo<sup>5</sup>, Changxun Yu<sup>6</sup>, Weiqi Wang<sup>7</sup>,  
7 Qiang Li<sup>2</sup>, Iain P. Hartley<sup>8</sup>, Yuanhe Yang<sup>9</sup>, Hongyan Liu<sup>10</sup>, Yidong Wang<sup>11</sup>, Xiangbin Ran<sup>12</sup>, Congqiang Liu<sup>2,3</sup>,  
8 Hailong Wang<sup>13,14</sup>

9  
10 1 Institute of Resource, Ecosystem and Environment of Agriculture, College of Resources and Environmental Sciences,  
11 Nanjing Agricultural University, Nanjing 210095, China

12 2 School of Earth System Science, Institute of Surface-Earth System Science, Tianjin Key Laboratory of Earth Critical Zone  
13 Science and Sustainable Development in Bohai Rim, Tianjin University, Tianjin 300072, China

14 3 Haihe Laboratory of Sustainable Chemical Transformations, Tianjin 300192, China

15 4 Wollongbar Primary Industries Institute, NSW Department of Primary Industries, Australia

16 5 School of Freshwater Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI 53204, USA

17 6 Department of Biology and Environmental Science, Linnaeus University, 39231 Kalmar, Sweden

18 7 Key Laboratory of Humid Subtropical Eco-Geographical Process, Ministry of Education, Fujian Normal University, Fuzhou,  
19 China

20 8 Geography, College of Life and Environmental Sciences, University of Exeter, Rennes Drive, Exeter EX4 4RJ, UK

21 9 State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, 100093  
22 Beijing, China

23 10 College of Urban and Environmental Sciences, Peking University, Peking 100871, China

24 11 Tianjin Key Laboratory of Water Resources and Environment, Tianjin Normal University, Tianjin 300387, China

25 12 First Institute of Oceanography, Ministry of Natural Resources, No. 6 Xianxialing Road, Qingdao 266061, China

26 13 School of Environment and Chemical Engineering, Foshan University, Foshan, Guangdong, 528000, China

27 14 School of Environmental and Resource Sciences, Zhejiang A&F University, Hangzhou, Zhejiang, 311300, China

28 \*Correspondence: [zhaoliang.song@tju.edu.cn](mailto:zhaoliang.song@tju.edu.cn) Telephone: +086-15202264081

29 Address: School of Earth System Science, Tianjin University, Tianjin 300072, China

30 **Abstract:** Soil organic carbon (SOC) in coastal wetlands, also known as ‘blue C’, is an essential  
31 component of the global C cycles. To gain a detailed insight into blue C storage and controlling  
32 factors, we studied 142 sites across ca. 5000 km of coastal wetlands, covering temperate,  
33 subtropical and tropical climates in China. The wetlands represented 6 vegetation types  
34 (*Phragmites australis*, mixed of *P. australis* and *Suaeda*, single *Suaeda*, *Spartina alterniflora*,  
35 mangrove (*Kandelia obovata* and *Avicennia marina*), tidal flat) and 3 vegetation types invaded  
36 by *S. alterniflora* (*P. australis*, *K. obovata*, *A. marina*). Our results revealed large spatial  
37 heterogeneity in SOC density of the top 1-meter ranging 40–200 Mg C ha<sup>-1</sup>, with higher values  
38 in mid-latitude regions (25–30° N) compared to those in both low- (20° N) and high- latitude  
39 (38–40° N) regions. Vegetation type influenced SOC density, with *P. australis* and *S.*  
40 *alterniflora* having the largest SOC density, followed by mangrove, mixed *P. australis* and  
41 *Suaeda*, single *Suaeda* and tidal flat. SOC density increased by 6.25 Mg ha<sup>-1</sup> following *S.*  
42 *alterniflora* invasion into *P. australis* community, but decreased by 28.56 and 8.17 Mg ha<sup>-1</sup>  
43 following invasion into *K. obovata* and *A. marina* communities. Based on field measurements  
44 and published literature, we calculated a total inventory of 57 × 10<sup>6</sup> Mg C in the top 1-meter soil  
45 across China’s coastal wetlands. Edaphic variables controlled SOC content, with soil chemical  
46 properties explaining the largest variance in SOC content. Climate did not control SOC content,  
47 but had a strong interactive effect with edaphic variables. Plant biomass and quality traits were  
48 a minor contributor in regulating SOC content, highlighting the importance of quantity and  
49 quality of OC inputs and the balance between production and degradation within the coastal  
50 wetlands. These findings provide new insights into blue C stabilization mechanisms and  
51 sequestration capacity in coastal wetlands.

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53 **Keywords:** Blue carbon, salt marsh, mangrove, vegetation type, plant invasion, coastal  
54 wetlands, climate change

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## 59 **1 Introduction**

60 Global wetlands, represent 6–8% of the world’s land surface area, and store approximately  
61 20–30% of the terrestrial soil carbon (C) pool (estimated to contain 2500 Pg C) (Lal, 2008;  
62 Nahlik and Fennessy, 2016). Specifically, coastal wetlands which occupy only <0.3% of the  
63 ocean surface contribute approximately 47% of the total organic carbon (OC) buried in marine  
64 sediments, with an estimated OC accumulation rate of 0.07–0.22 Pg C year<sup>-1</sup> globally  
65 (Hopkinson et al., 2012; Duarte et al., 2013). Coastal wetlands are characterized by high  
66 primary productivity, deposition rate, C burial rate and low methane (CH<sub>4</sub>) emissions, and thus  
67 play an important role in land-ocean ecosystem structure and function (Serrano et al., 2019).  
68 Therefore, enhancing the capacity of wetlands to sequester OC is an important component of  
69 the global effort to mitigate CO<sub>2</sub> entering the atmosphere contributing to climate change.

70 Although wetlands function as important C sinks, coastal wetlands are less studied than  
71 those of uplands (i.e., cropland, grassland, and forest) due to the challenges posed by  
72 hydrological conditions (i.e., Yang et al., 2007; Xu et al., 2018). Thus, it is important to study  
73 C stocks at different spatial scales to allow the assessment of C sequestration and fixation.  
74 Given the complexity in the biogeochemistry and ecology of coastal wetlands, there is high  
75 variability in the quantity and rate of OC buried in underlying soils, depending on geographic  
76 settings, vegetation composition, exotic plant invasion and wetland type (e.g., saltmarsh,  
77 estuary) across the coastal wetlands (Atwood et al., 2017; Hayes et al., 2017; Osland et al.,  
78 2018; Rovai et al., 2018; Xia et al., 2021b). However, most studies on coastal wetland C stocks  
79 and sequestration mechanisms have been focused on sites characterized by high C density  
80 (Whitaker et al., 2015), a single vegetation type (Gao et al., 2019) or single wetland type (Yan  
81 et al., 2008), and sites strongly disturbed by human activities (Kirwan and Megonigal, 2013),  
82 or wetlands with *Spartina alterniflora* invasion (Gao et al., 2020). On the other hand, studies  
83 focused on a national scale are based on comprehensive meta-analysis using a dataset compiled  
84 from published literature rather than field measurements (Xiao et al., 2019). In addition, how  
85 different are the SOC density in coastal wetlands with inland wetlands, is not fully clear. Such  
86 comparison would strengthen researchers' cognition of the contribution of coastal wetland C  
87 storage. Although these existing works are key to understanding the role of coastal wetland C

88 cycles, it is still difficult to accurately quantify the C stocks and processes controlling these  
89 stocks due to the paucity in field data to validate models (i.e., soil physico-chemical properties,  
90 climate, and vegetation biomass). In addition, data variability among sites likely resulted from  
91 differences in methods/protocols and the limited number of sampling locations (Meng et al.,  
92 2019; Hinson et al., 2017). The deficiency and regional bias of studies from China's coastal  
93 wetlands have limited the reliable estimation of their capability as regional and global C sinks  
94 (e.g., Jiao et al., 2018; Liu et al., 2014; Fu et al., 2021). Therefore, it is necessary to measure  
95 these variabilities in climate, vegetation and soil conditions to quantify soil organic carbon  
96 (SOC) stocks and their uncertainties in coastal wetlands across local and global scales.

97 To better contribute to achieving carbon neutralization, understanding how the soil C pools  
98 and their specific stability in coastal wetlands respond to environmental conditions are  
99 important for climate change mitigation and sustainable wetland management (Davidson and  
100 Janssens, 2006; Lal, 2004; Han et al., 2020). The predominant factors driving SOC dynamics  
101 include climate, plant biological traits, and soil properties (Dungait et al., 2012; Lehmann and  
102 Kleber, 2015; Luo et al., 2017). Firstly, climatic variables such as precipitation and temperature  
103 are usually considered to be critical (Carvalhais et al., 2014) because of their direct effect on  
104 organic C inputs via plant CO<sub>2</sub> assimilation, and output via microbial aerobic and anaerobic  
105 respiration. However, the effects of precipitation and temperature on net OC accumulation are  
106 highly variable (e.g., Chen et al., 2013; Wang et al., 2020; Luo et al., 2020) with different  
107 responses in topsoil and subsoil (Hicks Pries et al., 2017; Melillo et al., 2017; Zhou et al., 2018),  
108 including increase, decrease and no change. For example, coastal peat swamp systems are  
109 usually C sinks with higher primary productivity and lower CO<sub>2</sub> release because long-term  
110 water supersaturation and low temperature in the systems are not favorable for microbial  
111 activities and subsequent SOC mineralization (Bernal and Mitsch 2012; Friberg et al., 2003).

112 Secondly, plant C input is the determinant factor of soil C stocks although higher biomass  
113 production may not necessarily result in higher litter C input (Gao et al., 2019). In addition to  
114 biomass or litter quantity, litter quality is another important factor regulating organic C stability  
115 and preservation (Osland et al., 2018; Bahadori et al., 2021). The vegetation diversity, including  
116 native grasses *Phragmites australis*, *Suaeda*, *Acorus calamus*, invasive grasses *Spartina*

117 *alterniflora*, and mangrove *Kandelia obovata*, *Avicennia marina*, *Ceriops tagal*, *Bruguiera*  
118 *sexangular*, can also regulate the quality of C inputs into wetland soils (Yang et al., 2019; Xia  
119 et al., 2021a; Fu et al., 2021). The influence of vegetation communities and in particular changes  
120 in vegetation composition (i.e., native vs. invasive species or grasses vs. mangrove) on SOC  
121 remains relatively unstudied in these wetland systems.

122 Thirdly, although climatic and biological factors (e.g., plant C inputs) could regulate the  
123 magnitude or rate of apparent SOC shifting from one status to another, the final SOC stock  
124 capacity of soil is generally controlled by the physicochemical properties of soil (Luo and  
125 Raphael, 2020). Increasing evidence has shown that soil geochemistry and physical structure  
126 provides a physicochemical barrier to microbial accessibility of SOC (Sun et al., 2019, Duan et  
127 al., 2020). The physicochemical environment also regulates the supply of water, oxygen,  
128 nutrients, and other resources, which are necessary for microbial communities to utilize SOC,  
129 as well as for plant C assimilation and deposition as detritus or rhizodeposits (Luo and Raphael,  
130 2020). The stabilization of organic carbon in soil has been shown to vary significantly because  
131 of physical stabilization mechanism, chemical stabilization mechanism, and biochemical  
132 protection mechanism (Feng et al., 2013; Sui et al., 2021). However, large field datasets  
133 showing spatial heterogeneity of edaphic variables in coastal wetlands remain scarce, which  
134 perpetuates the extensive uncertainties about the patterns of SOC stocks and the main  
135 controlling factors. It is thus critical to understand the extent to which soil properties and  
136 processes regulate SOC stabilization and stocks in different field scenes.

137 The climatic, biotic, and edaphic factors often interact with each other and collectively  
138 regulate SOC dynamics through different processes and mechanisms (Zhang et al., 2002; Yang  
139 et al., 2019). However, most previous studies have focused on a single independent factor, with  
140 few quantitatively analyzing the relative effects on SOC stocks based on large scale field data.  
141 Studies focusing on the effects of a single factor on SOC dynamics may lead to uncertainties in  
142 the outcomes (Meng et al., 2019; Tangen et al., 2020). In addition to topsoil layers (e.g., 0–30  
143 cm), deeper soil layers (below 30 cm) could store more organic C than the topsoil layers (Meng  
144 et al., 2019). This motivated us to extend our soil sampling to 100 cm to better understand the  
145 deep soil C stocks. Such information can provide new insights into mechanisms underpinning

146 SOC dynamics, which are essential for predicting SOC stocks as well as understanding  
147 feedback loops from global environmental change (Belyea et al., 2004).

148 In the present study, we attempted to sample wetlands across broad regions that include  
149 almost all coastal wetlands of China, covering temperate, subtropical and tropical climate zones.  
150 Our objectives were to: (1) systematically quantify the SOC content and density in China's  
151 coastal wetlands and their interrelationship with the location of wetlands, vegetation type,  
152 invasion species, and climatic zone; (2) estimate the total inventory of SOC sequestration and  
153 regional variability across China's coastal wetlands and compare SOC density with inland  
154 wetlands; (3) explore climatic, biological, and edaphic drivers of the distribution and dynamics  
155 of SOC contents and stocks. We hypothesized that (1) SOC contents and densities were largely  
156 affected by vegetation type, invasion species, and climatic factors; (2) SOC densities greatly  
157 varied among different coastal wetlands and were lower than that of inland wetlands; and (3)  
158 SOC dynamics were interactively controlled by climate, plant biological traits and edaphic  
159 variables, and the effects of edaphic variables override climate and plant inputs on SOC stocks.  
160 This study provides crucial information for understanding the contribution of coastal wetlands  
161 in China to the global C cycles, and will allow for the optimization of wetland management  
162 strategies and policy decisions at the national scale.

163

## 164 **2 Materials and methods**

### 165 2.1 Study areas

166 We selected 142 representative wetland sampling sites along China's coast line from  
167 Liaoning to Hainan Province (108°–122°E, 20°–40°N) covering temperate, subtropical and  
168 tropical climate zones (Figure 1). The sampled wetlands include Liao River Delta (LRD),  
169 Duliujian River (DLJR), Nandagang wetland (NDG), Yellow River Estuary (YRE), Linhong  
170 River Estuary (LRE), Sheyang River Estuary (SRE), Doulong Harbor (DH), Dafeng Wetland  
171 (DW), Qidong Wetland (QW), Wanggang wetland (WGW), Yancheng Wetland (YCW),  
172 Chongming Island (CI), Hengsha Island (HI), Yueqing Bay (YB), Minjiang River Estuary  
173 (MRE), Jiulong River Estuary (JRE), Zhangjiang River Estuary (ZRE), Zhanjing (ZJ), Beihai  
174 (BH), Dongzhai Bay (DB), Qinglan Harbor (QH), Xinying Harbor (XH), Sanya Bay (SYB),

175 Sibi Bay (SBB), Xinyang Bay (XB), Tielu Harbor (TH), Danzhou (DZ) and Lingao (LG) (Table  
176 1). The mean annual precipitation (MAP) and mean annual temperature (MAT) ranged from  
177 551.6 to 1871 mm and from 8.40 to 23.4°C, respectively. The dominant native species at these  
178 sites include *Phragmites australis*, *Suaeda glauca*, *Suaeda salsa*, *Spartina alterniflora*,  
179 *Kandelia obovata*, *Avicennia marina*, *Aeluropus littoralis*, *Sonneratia apetala*, *Rhizophora*  
180 *stylosa*, *Aegiceras corniculatum* (Table 1).

181

## 182 2.2 Experimental design, vegetation survey and sample collection

183 Field surveys and soil samples were conducted during the plant's growing seasons from  
184 June to August in 2015–2019. To provide the required spatial heterogeneity, we selected  
185 representative wetlands in each coastal city or province with several sampling sites in each  
186 independent wetland (Table 1). Based on the plant biogeography and dominant vegetation, we  
187 categorized all the sampling sites into six vegetation types, including *P. australis*, *Suaeda*, *P.*  
188 *australis* + *Suaeda*, *S. alterniflora*, mangrove, and tidal flat. Three invasive vegetation types  
189 (occurred at sites CI, HI, YB, MRE, JRE, ZRE, ZJ and BH): *P. australis* invaded by *S.*  
190 *alterniflora*, *K. obovata* invaded by *S. alterniflora*, *A. marina* invaded by *S. alterniflora*. Using  
191 historical records on the native species composition at each site, we have established that  
192 invasive *S. alterniflora* completely outcompeted native *P. australis*. For the native mangrove  
193 sites, the invasion had begun along the margin and sparsely populated zones within the  
194 mangrove community with the invasion spreading. The invasion by *S. alterniflora* occurred  
195 from 7 to 15 years ago, while the native species had been growing at these sites for more than  
196 30 years (Wang et al., 2019). Specifically, the sites with native species were relatively close to  
197 their corresponding invaded sites, and we considered SOC contents and soil properties are  
198 similar before *S. alterniflora* invasion in paired sites. The vegetation biomasses are shown in  
199 Table S1 (our field survey), Table S2 (Yang et al., 2016) and Table S3 (Wang et al., 2019).

200 Each independent soil was homogenized from three subsamples (within a distance of 20–  
201 50 m), and we dispersedly collected several samples from each independent wetland. Samples  
202 (from sites LRD, DLJR, NDG and YRE) were collected with an auger at the depths of 0–10,  
203 10–20, 20–30, 30–40, 40–60, 60–80, and 80–100 cm, including a total of 28 sites with 196

204 samples, while samples (CI, HI, YB, MRE, JRE, ZRE, ZJ and BH) were collected at the depths  
205 of 0–10, 10–20, 20–30, and 30–40 cm, including a total of 54 sites with 216 samples. The SOC  
206 contents and densities at 60 sites in Jiangsu Province (LRE, SRE, DH, DW, QW, WGW, YCW)  
207 and Hainan Province (DB, QH, XH, QH, SYB, SBB, XB, TH, DZ, LG) were obtained from  
208 published literature. Together, a total of 142 sites were ultimately obtained. Field samples were  
209 divided into two parts. One part was freeze-dried for measuring microbial biomass carbon  
210 (MBC), dissolved organic carbon (DOC) and lignin phenols. The other part was air-dried at  
211 room temperature in the shade. After removal of the visible stones and root residues, the air-  
212 dried soils were gently ground into fine powder, and sieved through a 2 mm and 0.15 mm  
213 stainless steel screen to measure soil physico-chemical properties.

214

## 215 2.3 Measurements of soil physico-chemical parameters

### 216 2.3.1 Analysis of soil physical parameters

217 Soil bulk density (BD,  $\text{g cm}^{-3}$ ) was measured using the cutting ring method ( $100 \text{ cm}^3$ ).  
218 Soil water content (SWC, %) was determined by drying soil samples at  $105^\circ\text{C}$  to constant  
219 weight. Soil grain size, defined as clay ( $< 2 \mu\text{m}$ ), silt ( $2\text{--}20 \mu\text{m}$ ) and sand ( $>20 \mu\text{m}$ ), were  
220 measured by a Mastersizer (3000, Malvern Instruments, Malvern, UK) (Lu, 2000).

### 221 2.3.2 Analysis of soil chemical parameters

222 Soil pH and electrical conductance (EC,  $\mu\text{S cm}^{-1}$ ) were determined using a pH meter and  
223 DDS-307 conductivity analyzer (at a soil to water ratio (w:v) of 1:5; Leici company, Shanghai)  
224 (Lu, 2000). DOC ( $\text{mg kg}^{-1}$ ) was extracted with deionized water (w:v = 1:5 ratio), and MBC ( $\text{mg}$   
225  $\text{kg}^{-1}$ ) was extracted using the chloroform-fumigation method (Vance et al., 1987), and then  
226 measured using a TOC- $V_{\text{CPH}}$  analyzer (Shimadzu, Japan). Labile organic carbon (LOC,  $\text{g kg}^{-1}$ )  
227 was extracted with 2.5 M  $\text{H}_2\text{SO}_4$  and measured by the colorimetric method using a UV-Vis  
228 spectrophotometer (UV-2600, Daojin company, Japan; Rovira and Ramón Vallejo, 2007). For  
229 total phosphorus (TP,  $\text{g kg}^{-1}$ ) analyses, about 0.03 g soil was melted with lithium metaborate at  
230  $950^\circ\text{C}$  for 0.5 h, then dissolved by 4% (v/v)  $\text{HNO}_3$ , and measured by the colorimetric method  
231 using a UV-Vis spectrophotometer (Ru et al., 2018).

232 For SOC determination, 0.50 g soil was acidified with 20 mL HCl (1.0 M) for 24 h to



233 remove carbonates, and then washed 3–4 times with distilled water until neutral condition. The  
234 total OC and total nitrogen (TN) of the samples were measured using an Elementar Vario EL  
235 III (Elementar Analysensysteme, GmnH, Germany).

### 236 2.3.3 Analysis of plant-derived lignin phenols

237 For the determination of plant-derived lignin phenols in soil, 1.00 g soil, 1.00 g copper  
238 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  
239 ( $\text{N}_2$ )-purged NaOH (2 mmol  $\text{L}^{-1}$ ) were combined in Teflon-lined bombs. The bombs were  
240 flushed with  $\text{N}_2$  for about 10 min and heated to 150°C for 2.5 h in an oven. The lignin oxidation  
241 products (LOPs) were derivatized with N, O-bis-(trimethylsilyl) trifluoroacetamide (BSTFA)  
242 and pyridine at 70°C for 3 h to yield trimethylsilyl (TMS) derivatives, and were quantified using  
243 internal standards (i.e., trans-Cinnamic acid) on an Agilent 7890B-7010B TQ GC-MS system  
244 (Agilent, USA), with separation of derivatized lignin phenols using a DB-5MS column (30 m  
245  $\times$  0.25 m  $\times$  0.25  $\mu\text{m}$ ) (Xia et al., 2021a). Vanillyl, syringyl and cinnamyl (VSC) phenols were  
246 summed to represent lignin in soils, and lignin content ( $\Lambda_8$ ) was normalized to the OC content  
247 to reflect its relative abundance.

248

### 249 2.4 Statistical calculation and analysis

250 Data were checked for homogeneity of variance and normality before comprehensive  
251 analysis. If not, we then performed logarithmic transformation on the data. To utilize and take  
252 advantage of all SOC measurements, we used a generalized boosted linear model to obtain the  
253 missing data of individual soil properties for a few samples based on the “mice” package by *R*  
254 software ([www.r-project.org](http://www.r-project.org)). Data were compared the statistical significance ( $p < 0.05$ ) using  
255 a one-way analysis of variance (*ANOVA*). The heatmap of Pearson correlation coefficients was  
256 conducted by “ggplot2” package within *R* software. Regression prediction analysis was  
257 conducted on the “randomForest” package based on a classification tree to explore the relative  
258 influence on SOC contents and density. Data were graphed using Origin 10.0. Variance  
259 partitioning analysis (VPA) was conducted using *R* software with the ‘vegan’ package to  
260 quantify the explanations of categories of different factors for SOC content and their  
261 interactions. The stepwise multiple regression (*SMR*) model was conducted by SPSS 21.0 to

262 assess the variances in SOC content and density explained by different environmental factors.

263 In this study, we sampled a total of 88 soil profiles, 28 profiles with depths of 0–100 cm  
264 (LRD, DLJR, NDG and YRE) and 60 profiles with depths of 0–40 cm (CI, HI, YB, MRE, JRE,  
265 ZRE, ZJ and BH). For the 28 profiles with depths of 0–100 cm, we randomly selected 14  
266 profiles as group 1 from the given 28 profiles to build a linear regression equation between the  
267 measured SOC density in the 0–40 cm layer and measured SOC density in the 40–60 cm layer  
268 ( $p < 0.001$ ; Figure S1A). According to the modeled equation obtained from group 1, we used  
269 the measured SOC density in the 0–40 cm layer (group 2) to calculate the predicted SOC density  
270 in the 40–60 cm layer of group 2. The differences between the measured density in the 40–60  
271 cm layer (group 2) and the predicted SOC density in the same layer (group 2) were tested using  
272 a paired-sample *t*-test ( $p < 0.001$ ; Figure S1B) (Li et al., 2019). Therefore, we consider that the  
273 method of the prediction model is reasonable and effective.

274 Given that, we then established a linear regression equation between the measured SOC  
275 density in the 0–40 cm layer and measured SOC density in the 40–60 cm layer based on 28  
276 profiles (group 1 + group 2; Figure S1C). The measured SOC density in the 0–40 cm layer  
277 (including sites CI, HI, YB, MRE, JRE, ZRE, ZJ and BH) was used to predict the unknown  
278 SOC density in the 40–60 cm layer (CI, HI, YB, MRE, JRE, ZRE, ZJ and BH) based on the  
279 prediction model ( $y = 0.35x + 3.35$ ;  $R^2 = 0.73$ ,  $p < 0.001$ ). Similarly, we used the measured  
280 SOC density in the 0–60 cm and 0–80 cm layers to calculate the predicted SOC density in the  
281 60–80 cm (Figure S2) and 80–100 cm (Figure S3) layers, respectively ( $p < 0.001$ ). Thus, the 28  
282 soil profiles were used to predict the SOC density in the 40–100 cm layer of 60 soil profiles.  
283 For the obtained SOC contents from published literature, we firstly used the formula (Figure 2)  
284 to get soil bulk density and then to calculate the SOC density. Similarly, we used the known  
285 SOC density to predict the unknown SOC density with corresponding soil layers based on the  
286 prediction method.

287 Calculations of SOC density at national scales in coastal wetlands are obtained primarily  
288 in line with four patterns: independent wetlands, vegetation types, invasion types, and climate  
289 zones (temperate, subtropical, tropical). We calculated SOC density ( $SOC_D$ ) for each soil layer  
290 as follows (Xiao et al., 2019):

291 
$$SOC_D = \frac{SOC \times BD \times D}{100} \times 10 \quad (1)$$

292 where  $SOC_D$  is SOC density (Mg C ha<sup>-1</sup>), SOC represents SOC content (g kg<sup>-1</sup>), BD is bulk  
293 density (g cm<sup>-3</sup>), and D is soil thickness (cm).

294 The current SOC sequestration stock was calculated with the following equation:

295 
$$SOCS = Area \times SOC_D \quad (2)$$

296 where SOCS, Area (Table 1) and  $SOC_D$  are SOC sequestration, soil area and SOC density,  
297 respectively.

298 The total inventory of SOC was calculated as follows:

299 
$$TI_{soc} = SOCS_{p1} + SOCS_{p2} + \dots \dots SOCS_{pn}$$

300 where  $TI_{SOC}$  represents a total inventory of SOC in the top 1-meter across China's coastal  
301 wetlands,  $SOCS_{pn}$  represents the current SOC sequestration stock in each coastal province of  
302 China.

303

### 304 **3 Results**

#### 305 3.1 Relationship between bulk density and soil organic carbon

306 We established a database with 412 measurements of SOC content and paired bulk density.  
307 SOC contents ranged from 0.63 to 36.7 g kg<sup>-1</sup>, and bulk density was in the range of 0.45–1.87  
308 g cm<sup>-3</sup>, demonstrating large variability of organic C and physical properties in the coastal  
309 wetlands. There was an empirical relationship between measured SOC content and bulk density  
310 in the form of  $y = -0.47 \ln(x) + 2.24$  ( $R^2 = 0.72$ ;  $p < 0.001$ ) (Figure 2).

311

#### 312 3.2 Vertical and geographic SOC content distributions

313 The large standard deviations for vegetation types reflect the wide distribution of  
314 vegetation and diversity of wetlands in coastal regions. SOC contents overall decreased with  
315 soil depth within the 0–40 cm layer (Figure 3). The wetlands had large spatial differences in  
316 SOC contents, with the highest SOC content in the Minjiang River Estuary ( $23.0 \pm 3.94$  g kg<sup>-1</sup>)  
317 <sup>1</sup>), and the lowest SOC content in the Yellow River Estuary ( $3.93 \pm 1.94$  g kg<sup>-1</sup>). Different  
318 sampling sites within the same wetland also displayed some differences in SOC contents  
319 (Figure 3A). When grouped by vegetation types, *S. alterniflora* ( $16.6 \pm 4.86$  g kg<sup>-1</sup>) had the

320 highest SOC content, and tidal flat ( $4.03 \pm 1.76 \text{ g kg}^{-1}$ ) had the lowest SOC content (Figure 3B).  
321 When grouped by invasion types, the average SOC content in the native *P. australis* ( $\Delta\text{SOC} =$   
322  $-0.51 \text{ g kg}^{-1}$ ;  $p > 0.05$ ), *K. obovata* ( $\Delta\text{SOC} = -2.76 \text{ g kg}^{-1}$ ;  $p < 0.01$ ) and *A. marina* ( $\Delta\text{SOC} = -$   
323  $0.87 \text{ g kg}^{-1}$ ;  $p < 0.01$ ) communities decreased sharply following *S. alterniflora* invasion (Figure  
324 3C). The measured SOC content was highest in subtropical zones ( $17.4\text{--}20.2 \text{ g kg}^{-1}$ ), which are  
325  $38.5\text{--}68.9\%$  and  $96.2\text{--}155\%$  higher than those in tropical ( $10.3\text{--}14.6 \text{ g kg}^{-1}$ ) and temperate  
326 zones ( $6.85\text{--}10.3 \text{ g kg}^{-1}$ ), respectively (Figure 3D).

327

### 328 3.3 Comparisons in SOC storage between wetlands or vegetation types

329 SOC density varied broadly within soil profiles depending on the independent wetland,  
330 vegetation type, invasion type, and climatic zone. Different spatial patterns of SOC density for  
331 independent wetlands were observed between  $20^{\circ}\text{N}$  and  $40^{\circ}\text{N}$ , with relatively higher SOC  
332 densities in mid-latitude regions compared to high- and low- latitude regions. The Yellow River  
333 Estuary had the lowest SOC densities ( $28.5\text{--}51.7 \text{ Mg C ha}^{-1}$ ), whereas the Hengsha Island had  
334 the highest SOC density ( $176\text{--}202 \text{ Mg C ha}^{-1}$ ) (Figure 4A).

335 When grouped by vegetation type, soils with *P. australis* community had the highest OC  
336 density ( $127 \text{ Mg C ha}^{-1}$ ), being about two times higher than tidal flat ( $59.5 \text{ Mg C ha}^{-1}$ ), followed  
337 by *S. alterniflora* > mangrove > *P. australis* + *Suaeda* > *Suaeda* > tidal flat (Figure 4B). The  
338 average SOC storage in the native *P. australis* community slightly increased following *S.*  
339 *alterniflora* invasion, but in the mangrove community, it markedly decreased compared to the  
340 corresponding *S. alterniflora* community, especially in the *K. obovata* community (Figure 4C).  
341 We found that wetland SOC density was much higher in subtropical zones than those in the  
342 temperate and tropical zones, while the SOC density was similar between the temperate and  
343 tropical zones (Figure 4D).

344 Across the soil profiles, SOC density decreased with depth in the 0–40 cm layer, but  
345 displayed no significant decrease in the 40–100 cm layer. This suggests that SOC is more  
346 reactive or labile in topsoil than in subsoil/deeper soil, probably related to the root system  
347 distribution and rhizodeposits in soil profile. In the past, the IPCC (2003) recommended a soil  
348 depth of 30 cm for the assessment of SOC density in response to global climate change.

349 However, we found that only 40% of the organic C was stored in the top 30 cm, and the majority  
350 of the soil C stocks was partitioned in the 30–100 cm layer regardless of the location of wetland,  
351 types of vegetation, vegetation invasion, and climate-zone (Figure 4), suggesting that the deeper  
352 OC should be also considered in OC stock assessment.

353

#### 354 3.4 Correlations between environmental variables and SOC content under different scenarios

355 For independent wetlands, the Pearson correlations showed that SOC contents were largely  
356 different and were significantly correlated to various edaphic variables (Figure 5A), suggesting  
357 a large spatial heterogeneity of soil properties for the location of each coastal wetland. For the  
358 three climatic zones, the significant differences between SOC content and edaphic variables  
359 were BD, clay and MBC (Figure 5B). Both TN and BD were the common factors affecting  
360 SOC content for soils with different vegetation, while the other soil parameters were a variant  
361 for each vegetation type (Figure 5C). We found that the correlations between SOC content and  
362 edaphic variables were strongly altered following *S. alterniflora* invasion of native species (*P.*  
363 *australis*, *K. obovata*, *A. marina*). For example, the particle size composition (clay, silt and sand)  
364 was significantly correlated to SOC content for soils with *S. alterniflora* vegetation, but not for  
365 *P. australis* vegetation (Figure 5D). The correlations between climatic factors (MAT and MAP)  
366 and SOC density was best described using a cubic function, and the relationships in 0–40 cm  
367 layer were more prominent than in 40–100 layer (Figure 6).

368

#### 369 3.5 Environmental controls on SOC content and density

370 We conducted variance partitioning analysis (VPA) using two categories (soil properties  
371 and climate), soil properties solely explained 29% of the variance, and climate only explained  
372 3% of the variance for SOC content, while soil properties and climate had the largest interactive  
373 effects (42%; Figure 7A). Then, the results of the VPA using three categories (soil chemical  
374 properties, physical properties and climate) showed that soil chemical properties were the most  
375 important variable explaining SOC content (59% of the variation), while soil physical  
376 properties (15%) only accounted for a small proportion (Figure 7B).

377 In determining the relative importance of soil factors on SOC content and density, random

378 forest analysis was carried out and the results demonstrated edaphic variables were in the order  
379 TN > BD > TP > (Ad/Al)<sub>v</sub> > MBC > pH > SWC > EC > DOC > clay > silt > sand > S/V >  
380 (Ad/Al)<sub>s</sub> ( $p < 0.05$ ; Figure 8A), while for SOC density followed the order of TN > EC > SWC >  
381 MBC > TP > DOC > pH > sand > silt > sand > (Ad/Al)<sub>v</sub> ( $p < 0.05$ ; Figure 8B). However,  $\Lambda_8$   
382 (reflecting plant C inputs into soil) was not a significant factor influencing SOC content and  
383 density.

384 Stepwise multiple regression analysis was used to assess the combined effects of soil  
385 physical, chemical properties, biological traits (i.e., plant-derived lignin phenols) and climatic  
386 factors on SOC content. The extracted factors explained more than 90% of the variation in the  
387 SOC content. For the extracted parameters based on these analyses of different classification  
388 basis, soil chemical properties were the dominant factor controlling SOC content, followed by  
389 soil physical properties. Biological traits were a minor contributor to regulating SOC content,  
390 and MAP and MAT only exerted effects under specific regions with a large latitude span (Table  
391 2).

392

## 393 **4 Discussion**

### 394 4.1 SOC inventories in China's coastal wetlands

395 Our dataset here represents the most comprehensive assessment of measured organic C  
396 density and sequestration inventory of coastal wetlands in China. Our study utilized 100 cm as  
397 an ideal sampling depth to identify the SOC density and sequestration stock (Howard et al.,  
398 2017), thereby capturing both the more dynamic organic C in the surface soil and the more  
399 stable C stocks in the subsoil. Previous studies have demonstrated that SOC density varied  
400 widely depending on wetland types (Xiao et al., 2019) and locations (Nahlik and Fennessy,  
401 2016), with higher C stocks under lower temperature and anaerobic conditions (Lee et al., 2018).  
402 As such, we have carried out a more detailed division of coastal wetlands, including the location  
403 of independent wetland, vegetation composition, invasion type and climatic zone, to more  
404 accurately quantify the C stocks in coastal wetlands of China.

405 We found a wide range of SOC densities, ranging from about 40 to 200 Mg C ha<sup>-1</sup>. VPA  
406 results likely showed that the diversity of precipitation and temperature in different climatic

407 regions (temperate, subtropical and tropical) contributed to these substantial variations on long  
408 time-scales (Figure 7; Osland et al., 2018). The results showed that the Yellow River Estuary  
409 had the lowest SOC content and density across the national scale. This system had the highest  
410 sand content reinforcing the notion that grain size plays an important role  
411 in aggregate stabilization and C sequestration capacity in global coastal wetlands (Yu et al.,  
412 2021). The differing contribution of autochthonous vs. allochthonous C inputs is also likely to  
413 vary spatially because of differences in local hydrological conditions, wetland management and  
414 vegetation in the catchment (Saintilan et al., 2013). Autochthonous inputs mainly include plant  
415 aboveground litter, root residues and their secretions, primary and secondary products of  
416 phytoplankton and benthos; while allochthonous inputs mainly include particulate organic  
417 carbon (POC) and dissolved organic carbon (DOC) carried by the processes of tidal inundation,  
418 surface runoff and groundwater (Saintilan et al., 2013; Xia et al., 2021a). This highlights the  
419 importance of both broad and small spatial-scale data in understanding differences in C stocks  
420 under natural scenarios and estimating regional wetland C stocks. The soil C densities of coastal  
421 wetlands in China were basically close to the values ( $93.7 \text{ Mg ha}^{-1}$ ) reported by Xiao et al.  
422 (2019), but lower than those reported for coastal wetlands in USA ( $300 \text{ Mg ha}^{-1}$ ) (Nahlik and  
423 Fennessy, 2016) are higher than ours.

424

## 425 4.2 Factors affecting SOC distribution patterns

### 426 4.2.1 Climatic influences

427 Temperature and moisture control net primary productivity which influences inputs  
428 (detritus and rhizodeposits) of OC, as well as SOC decomposition (Jobbágy and Jackson, 2010).  
429 Hiltunen et al. (2013) have reported that temperature is the primary factor affecting the  
430 accumulation and decomposition of SOC in wetlands of Central Finland. Increased temperature  
431 stimulates the loss of organic C pools, especially in high latitudes (Clair et al., 2002; Inglett et  
432 al., 2012), thus stressing the risk of SOC loss under a warming climate (Bond-Lamberty and  
433 Thomson, 2010). SOC density in tropical zones (i.e., Zhanjiang and Beihai) was generally lower  
434 than that in subtropical areas (Figure 4D), most likely due to higher rates of SOC decomposition  
435 in the former. The difference of SOC density of each layer in subsoil (40–100 cm) is much

436 lower than that in topsoil (0–40 cm), we assumed that SOC density in the subsoil is relatively  
437 more stable compared to topsoil across the three climate zones. However, Li et al. (2020)  
438 demonstrated that SOC in subsoil in forest ecosystems is likely to be more vulnerable than in  
439 topsoil under rising temperatures, and this phenomenon was primarily controlled by climate  
440 and soil C quality. We consider that changing climate will have different effects on SOC stocks  
441 based on whether the soils are from upland and wetland. The availability of water (i.e., high  
442 water content or shallow water table) in soils can be strongly affected by hydrological dynamics  
443 and soil porosity, which may largely restrict oxygen availability for microbes to utilize SOC  
444 and soil thermal regimes (Luo et al., 2020). As such, the response of the soil C pool to  
445 temperature in wetlands is also influenced by abiotic processes of soil itself, including water  
446 availability, nutrient input, and oxygen supply (Olefeldt and Roulet, 2012). The VPA showed  
447 soil properties and climate had the largest interactive effects (42%; Figure 7A). This further  
448 revealed that other physical and chemical factors, such as temperature, could also affect the  
449 mineralization of OC pools by microorganisms (Villa and Bernal, 2018).

450 High precipitation and temperature are usually coupled with high plant productivity (Beer  
451 et al., 2010), thus influencing plant C inputs into soil, which interacts with inundation periods  
452 and depths. In addition, climate can have a direct effect on soil texture, chemical properties and  
453 mineralogy, which are closely linked with SOC turnover (Luo et al., 2017). A recent study  
454 focusing on the main driving factors controlling C cycling suggested that soil properties (e.g.,  
455 soil clay content and C:N ratio) rather than climate control the vertical variations of SOC,  
456 microbial biomass carbon, and microbial metabolic quotient (Sun et al., 2020). In other words,  
457 the sensitivity of SOC dynamics to climate variability may be buffered by changes in primary  
458 productivity and soil properties. Our results demonstrate the importance of the interactions  
459 between climate, soil, and the amounts and quality of C input (Figure 7; Figure S4). Because  
460 of the complex processes involved in forming organic C under different climate conditions,  
461 further studies on the trade-off or net effect between primary productivity and soil C  
462 decomposition are justified (Bradford et al., 2016). However, to fully consider the influence of  
463 all factors on SOC dynamics, previous studies often incorporate climate factors with plant  
464 biomass as well as soil properties into one model, which will overestimate the impact of climate



465 on SOC dynamics. This clearly needs further attention and warrants in-depth studies (i.e.,  
466 geological and tidal information) in the future.

467

#### 468 4.2.2 Vegetation composition and exotic plant invasion

469 The quantity and quality of C inputs are strongly affected by vegetation type, which is  
470 predominantly controlled by climatic conditions and interacts with soil conditions (Beer et al.,  
471 2010; Luo et al., 2017). Different plant communities can influence OC sequestration rates  
472 within each vegetation type (Mitsch et al., 2013; Villa and Mitsch, 2015). Researchers often  
473 take it for granted that SOC stocks are high under vegetation communities with high net primary  
474 productivity (NPP). While it is established that NPP influences C inputs into soil, its effect on  
475 SOC stock, particularly in deeper soil layers, is minimal (Figure 4). In other words, it may  
476 largely depend on how much biomass ends up in soils, transformation pathways to SOM,  
477 priming effects and transportation to deeper soil layers. Thus, NPP may not be a useful indicator  
478 of C inputs, especially in deeper soil layers (Xiao et al., 2019). Subsoils may be subject to  
479 greater environmental controls than topsoil, including water logging and anoxic conditions.  
480 These environmental conditions may result in more complex SOC stabilization processes and  
481 a divergent behavior in the decomposer community (Keiluweit et al., 2017), lessening the  
482 influence of NPP on SOC stock in deeper soil layers. Therefore, the difference in SOC stocks  
483 in subsoil among vegetation types was less than that in topsoil (Figure 4). The relatively minor  
484 role of plant C inputs ( $\Lambda_8; p > 0.05$ ) in determining the spatial distribution of SOC content and  
485 density (Figure 8), however, does not signify less important factor for local C management.  
486 Under similar climatic and edaphic conditions, as the mixed vegetation of *P. australis* and  
487 *Suaeda*, *Suaeda* alone had lower NPP (Figure 9), thus lower inputs of SOC compared to other  
488 vegetation types.

489 The influence of plant C inputs is straightforward as C influx to soil directly determines  
490 OC content. The quality of C inputs (e.g., lignin, C:N, and lignin: N) influences OC utilization  
491 by microorganisms and their utilization strategies (Bending et al., 2002; Cotrufo et al., 2013).  
492 This in turn controls the composition, preservation, and distribution of SOC pools and their  
493 decomposability as a cohort (Prescott, 2010; Raich and Tufekciogul, 2000). SOC content and

494 density in woody mangrove (*K. obovata* and *A. marina*) sharply decreased following the  
495 herbaceous *S. alterniflora* invasion (Figure 3C & 4C). Litters from above- and below-ground  
496 components in mangrove forests tend to have greater recalcitrant C compounds (e.g., lignin,  
497 tannins, cutin, suberin, and waxes) and are more difficult to decompose than those from invasive  
498 *S. alterniflora* (Chanda et al., 2015). More importantly, soils or sediments tend to efficiently  
499 sequester organic C in mangrove forests, which is attributed to the morphological structure of  
500 mangroves and their widespread density and distribution of roots (Krauss et al., 2003). The  
501 unique tree structure and complex aerial root systems (e.g., prop roots and pneumatophores)  
502 across mangrove species could result in greater biomasses than grasses, and these specific root  
503 structures are more effective for trapping organic-rich sediments (Kristensen et al., 2008). For  
504 two herbaceous plants, SOC density in native *P. australis* community slightly increased  
505 following *S. alterniflora* invasion (Figure 4C). We mainly attributed this result to the following  
506 three reasons: (i) the decomposition rate of *S. alterniflora* litter, particularly the belowground  
507 root residues, was slower than that of *P. australis* litter due to the lower litter quality (i.e., higher  
508 C:N ratio) of *S. alterniflora* (Liao et al., 2008; Duan et al., 2018); (ii) the biomass of *S.*  
509 *alterniflora* was higher than that of *P. australis* (Wang et al., 2019); (iii) *S. alterniflora* grew  
510 closer to the coast and estuary in comparison to *P. australis*.

511 However, the SOC density in wetlands predominantly vegetated by mangroves (e.g.,  
512 southern China from south-central Zhejiang to Hainan Province) is not the largest despite  
513 having the highest biomass and the percent of recalcitrant C components (Xia et al., 2021b).  
514 The net SOC density is dependent not only on the apparent NPP and litters (Figure 9), but  
515 largely on how much of the apparent NPP and litters eventually enters the soil, and how SOC  
516 is eventually preserved and stabilized in environments. In addition, plant/litterfall lateral export  
517 or import via tidal water also might be the key process to influencing SOC accumulation.

518

#### 519 4.2.3 Soil properties

520 The stabilization mechanisms of SOC have been intensively discussed with respect to (i)  
521 physical protection by aggregates associated with minerals, (ii) the nature of recalcitrant  
522 compounds of SOC, and (iii) refractory biological components (such as microbial residual

523 carbon), and cementation of physicochemical function and biological substances (Cui et al.,  
524 2014; Throckmorton et al., 2015; Sarker et al., 2018). These SOC stabilization mechanisms  
525 have been demonstrated in uplands to increase C sequestration (Fujisaki et al., 2018; Wang et  
526 al., 2015; Poeplau et al., 2017; Luo et al., 2017; Sarker et al., 2018). Less attention, however,  
527 has been paid to understanding the mechanisms of soil C stabilization in coastal wetlands at  
528 large regional scale, and investigations on the relative influence of individual soil properties  
529 remain scarce.

530 VPA showed that soil chemical properties were more important than physical properties  
531 in controlling SOC content (Figure 7B). Also, stepwise multiple regression analysis showed  
532 that the quality of C fractions and nutrients are the most important factors for SOC content  
533 (Table S4 & S5). However, increasing evidence suggests that physical protection plays an  
534 important role in the preservation of SOC and chemical make-up is less important in uplands  
535 (Ekschmitt et al., 2008; Kleber et al., 2011; Guo et al., 2018). We attributed these differences in  
536 preservation to (i) OC with recalcitrant compounds is decomposable in uplands at the time scale  
537 from years to decades (Fontaine et al., 2007; Schmidt et al., 2011), and (ii) coastal wetlands are  
538 in the intertidal zones or permanently flooded environments.

539 In detail, we found clay is an important parameter influencing SOC content in tidal flats,  
540 and this is consistent with studies of Lehmann et al. (2007) and Dungait et al. (2012), showing  
541 that clay content is an important factor in controlling SOC dynamics in salt marshes. For the *K.*  
542 *obovata* community, SOC content significantly decreased following *S. alterniflora* invasion,  
543 and C/V was the most important parameter controlling SOC content (Table S4). High contents  
544 of plant-derived lignin phenols were found in mangrove soils (Supplementary original data).  
545 Recalcitrant organic C was reported to be a major proportion of SOC in an estuarine ecosystem  
546 in southern China (Lian et al., 2018). In the *A. marina* community, silt content is considered as  
547 a pivotal parameter, and this is also consistent with the study of Xiong et al. (2018) showing  
548 that SOC content was primarily controlled by the proportion of finer soil particles in a mangrove  
549 ecosystem. For *S. alterniflora* community, both  $(Ad/Al)_v$  and  $(Ad/Al)_s$  were important factors  
550 controlling SOC content, and suggested SOC molecular composition exerted important roles in  
551 protecting from decomposition. Sun et al. (2019) have reported that the simpler OC molecular

552 structure (higher ratio of alkyl C to O-alkyl C and lower aromaticity) of *S. alterniflora* soils  
553 hindered the accumulation of SOC compared with mangrove. Therefore, intrinsic SOC  
554 stabilization such as chemical protection possibly plays a significant role in controlling SOC  
555 dynamics and turnover.

556 One study reported that organo-mineral association was the major mechanism of SOC  
557 stabilization in salt marshes, recalcitrant C (as indicated by relatively high aromaticity and low  
558 mineral OC) in mangrove soil contributes to SOC stabilization (Sun et al., 2019). Future studies  
559 should strengthen the understanding of the role of mineral (i.e., iron, aluminum, calcium  
560 compounds) association in SOC stabilization, and help quantifying the relative importance of  
561 mineral association vs. chemical protection in SOC stabilization in coastal ecosystems at large-  
562 regional scales.

563

#### 564 4.3 Comparisons of SOC density in coastal wetlands with inland wetlands

565 Based on the geographic locations, hydrological conditions and salinity, researchers often  
566 categorized the wetlands as: river, coastal, lake and marsh (Figure 10; State Forestry  
567 Administration, 2015). SOC density of these wetland types generally decreased in the order of  
568 marsh > lake > river > coastal. Marsh wetlands store the most C, and are mainly distributed in  
569 the northeast China and Qing-Tibetan Plateau regions, most likely reflecting high litter  
570 inputs/preservation, cool temperatures and relatively anaerobic conditions which minimize C  
571 mineralization and favor C accumulation (Lin et al., 2013). Lakes also promote C accumulation  
572 because they are mostly closed basins that stabilize C and transport little C from surrounding  
573 environments (Euliss et al., 2014; Pennock et al., 2010). By contrast, river wetlands are ‘neutral  
574 pipes’ for C accumulation that merely convey landward C to oceans, and mostly accept  
575 particulate organic carbon and dissolved organic carbon from upstream (Cole et al., 2007;  
576 Aufdenkampe et al., 2011). Compared to inland wetlands, coastal wetlands are adjacent to the  
577 landward and ocean. Plant productivity is usually low under saline conditions and long-term  
578 flooded environments with high water-level. Mild climatic conditions enhance the  
579 decomposition of OC thus limiting the potential for C storage, because coastal wetlands would  
580 be exposed to air at low tide and subjected to alternating wet-dry environment (Moinet et al.,

581 2018), even though, they are generally believed to have the highest C store among terrestrial  
582 ecosystem worldwide (Lu et al., 2017). Coastal wetlands are open ecosystems, and the different  
583 roles of inland and coastal wetlands in C accumulation are interesting and need further study.  
584 Wetland types (marsh, lake, coastal, and river) were examined to gain a better understanding of  
585 their roles in contributing to SOC sequestration.

586

#### 587 4.4 Implications for blue C management in coastal wetlands

588 Coastal wetlands are open ecosystems at the land and ocean interface, which are more  
589 prone to be influenced by anthropogenic activities, rising sea-level, hydrogeological conditions,  
590 and river runoff (Rogers et al., 2014; Meng et al., 2017). The multifunctional and complex roles  
591 of organic C in these systems remain largely unstudied, in particular relating to the storage, and  
592 factors controlling the storage of blue C. Marsh wetlands are mainly distributed in inland  
593 regions (Northeast China and Qing-Tibetan Plateau), and contain the largest C pool. However,  
594 the coastal regions are at greater risk of being utilized for agricultural and industrial purposes,  
595 thus resulting in accelerated decomposition and release of stored organic C (O'Connor et al.,  
596 2019). Therefore, salt marshes (such as Liao River Delta) are one of the primary focuses for  
597 wetland C managements in China. The salinity, redox state and nutrient content (particularly  
598 TN and TP) of the wetlands can be affected by climate change and anthropogenic activities  
599 including development, tillage, drainage. Treating these variables as a constant may result in  
600 poor quantification of SOC stocks (Table S4). Eutrophication and pollution are the main  
601 problems threatening ecological health of river and lake wetlands (Beaulieu et al., 2019).  
602 Comprehensive protection measures are needed to strengthen supervision and administration  
603 of environmental protection in river and lake basins, and to reduce the discharge of pollutants  
604 from industrial and domestic wastewaters, thus maintaining the environmental status and C  
605 budgets of river and lake wetlands (Xiao et al., 2019). Additionally, land use change and  
606 intensity (i.e., coastal wetland restoration, harvest of wetland macrophytes, and frequency of  
607 tides) should be fully considered, which may significantly affect SOC stabilization processes  
608 and thus SOC stocks in managed areas. If these processes are fully addressed, improved  
609 predictions as well as increased blue C accumulation are possible, providing significant

610 opportunities to contribute to climate change mitigation.

611

#### 612 4.5 Uncertainties in C sequestration and outlooks

613 While our study provides a vast and comprehensive dataset of SOC stocks and their  
614 controlling factors in wetlands across climate gradient, vegetation composition and invasion  
615 types, there are still limitations and uncertainties in the datasets and assessment. Firstly, most  
616 of China's coastal wetland area data were taken from literature, and current data sources are  
617 derived from the national soil census (Zheng et al., 2013), local investigation reports (Ding et  
618 al., 2004), and remote sensing data (Ma et al., 2015). The above data used for calculating C  
619 sequestration in wetlands are inconsistent in data acquisition. Secondly, although our sampling  
620 sites in coastal wetlands were representative and decentralized, more sampling sites could be  
621 added to further strengthen the statistical significance. Thirdly, there are diverse types with a  
622 large amount of different dominant plants (Figure 10), even within the same wetland in the  
623 whole coastal wetlands, the categorization was based on our investigations and subjectivity  
624 (Table 1). Fourthly, depths of wetland soils varied significantly and there are several examples  
625 from our data showing that sampling even to 100 cm may not truly represent the C storage  
626 potential of these systems. However, data for soil depths were unavailable in some sites. Due  
627 to the lack of these reliable data, we used the existing soil C stocks (0–100 cm) to predict other  
628 sites (40–100 cm). The model estimation methods might over- or under- estimate C stocks in  
629 China's coastal wetlands. Although our results of C stocks here were obtained based on  
630 multisource data, new calculations here are effective to reflect the whole picture of organic C  
631 distributions at a national scale.

632

### 633 **5 Conclusions**

634 Coastal wetlands play an important role in C sequestration, and at the same time they are  
635 sensitive to climate change and anthropogenic disturbances. Although high precipitation and  
636 temperature conditions usually result in high plant productivity and thus higher C inputs into  
637 soil, wetland SOC density are not simply correlated with MAT and MAP. Changes in SOC  
638 density under vegetation communities were not completely consistent with NPP. This was

639 attributed to differences in SOC decomposition/preservation, litter inputs, and the quality of  
640 SOC. We calculated a total inventory of  $57 \times 10^6$  Mg C in the top 1-meter soil in coastal wetlands  
641 of China. Edaphic variables solely override climate control of SOC content, chemical make-up  
642 (i.e., the nature of recalcitrant compounds) plays more important role in the preservation of  
643 SOC than physical protection. Soil chemical properties exert strong interactive effects with  
644 climate. Plant biological traits were a minor contributor in regulating SOC content. Random  
645 forest analysis results showed that the relative importance of predictor variables was in the order  
646 of TN > BD > TP > (Ad/Al)<sub>v</sub> > MBC > pH > SWC > EC > DOC > Clay > Silt > and > S/V >  $\Delta_8$   
647 for SOC contents, and with the order of TN > EC > SWC > MBC > TP > DOC > pH > Sand >  
648 Silt > Clay > (Ad/Al)<sub>v</sub> for SOC density. Knowledge and information gained have important  
649 implications for understanding mechanisms in SOC stabilization and sequestration capability,  
650 and will aid policy and decisions concerning vegetation cover and environmental management,  
651 thus contributing to global efforts to mitigate climate change.

652

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659

### 660 **Conflict of interest**

661 All authors declare no conflict of interests.

662

### 663 **Data availability statement**

664 The data that support this study are available in the Supplementary materials, and the  
665 supplementary original data would be open access for researchers in figshare webpage  
666 [https://figshare.com/articles/dataset/Supplementary\\_original\\_data\\_for\\_Storage\\_patterns\\_and\\_influencing\\_factors\\_for\\_soil\\_organic\\_carbon\\_in\\_coastal\\_wetlands\\_of\\_China\\_/20180450](https://figshare.com/articles/dataset/Supplementary_original_data_for_Storage_patterns_and_influencing_factors_for_soil_organic_carbon_in_coastal_wetlands_of_China_/20180450).  
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1020 **Figure Captions**

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1023 **FIGURE 1** Distributions of sampling locations along the temperate-subtropical-tropical  
1024 climate zone in China's coastal wetlands, including 108 sampling sites from Liaoning Province  
1025 (the north) to Hainan Province (the far south). Circles represent sites with our concurrent field  
1026 and lab measurements, triangles denote sites or samples compiled with data from literature, and  
1027 diamonds represent those with data extrapolated from similar wetlands.

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1031 **FIGURE 2** Relationships between soil organic carbon (SOC) content and bulk density (BD) in  
1032 China's coastal wetlands. Data presented here included 412 paired SOC content and bulk  
1033 density measurements for different layers in filed samples, including 0–100 cm layer in LRD,  
1034 DLJR, NDG and YRE, and 0–40 cm layer in CI, HI, YB, MRE, JRE, ZRE, ZJ and BH. The  
1035 formula was modeled from the paired data points of all samples in the light blue region. The  
1036 formulas of different colors were modeled from the paired data points of different soil layers.  
1037 A logarithmic line model is used to estimate the bulk density for soils without the measured  
1038 data.

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1042 **FIGURE 3** Vertical distributions of SOC contents (mean  $\pm$  SD) in the top 0–40 cm profile  
1043 based on sampling location (A), vegetation type (B), invasion type (C; *P. australis* invaded by  
1044 *S. alterniflora*, *K. obovate* invaded by *S. alterniflora*, *A. marina* invaded by *S. alterniflora*) and  
1045 climatic zone (D).

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1049 **FIGURE 4** Vertical distributions of SOC density (mean  $\pm$  SD) in the 0–100 cm profile based  
1050 on sampling location (A), vegetation type (B), invasion type with invasive species *S.*  
1051 *alterniflora* (C) and climatic zone (D). All the data analyzed were collected from our field  
1052 survey and lab measurements.

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1056 **FIGURE 5** Pearson correlations between soil parameters and SOC content in independent  
1057 wetlands (A), climate zones (B), vegetation types (C), and invasion types (D). Abbreviations:  
1058 SOC, soil organic carbon; TN, total nitrogen; MBC, microbial biomass carbon; DOC, dissolved  
1059 organic carbon; TP, total phosphorus; EC, electrical conductance; SWC, soil water content; BD,  
1060 bulk density; S/V, the syringyl-to-vanillyl ratio; C/V, the cinnamyl-to-vanillyl ratio; (Ad/Al)<sub>v</sub>,  
1061 the acid-to-aldehyde ratio of vanillyl unit; (Ad/Al)<sub>s</sub>, the acid-to-aldehyde ratio of syringyl unit;  
1062  $\Lambda_8$ , organic carbon (OC)-normalized concentration of lignin phenols (V+S+C).

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1066 **FIGURE 6** Relationships between MAT ( $^{\circ}$ C) and SOC density in the 0–40 cm (A) and 40–100  
1067 cm (B) profiles, and between MAP (mm) and SOC density in the 0–40 cm (C) and 40–100 cm  
1068 (D) profiles.

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1072 **FIGURE 7** Variance partitioning analysis (VPA) for SOC contents in China's coastal wetlands.  
1073 Soil chemical properties here include MBC, DOC, TN, TP, pH, and EC; Soil physical properties  
1074 include SWC, BD, and particle size composition (clay, silt and sand); Climate include MAT and  
1075 MAP. The numbers in the circles indicate the explained values, residuals represent unexplained  
1076 value.

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1079 **FIGURE 8** The relative importance of predictor variables from the regression prediction  
1080 analysis using random forest of the changes to SOC content (A) and density (B). The relative  
1081 influence of three categories of variables are calculated as the sum of the relative importance  
1082 of individual variables in each variable group (i.e., soil chemical properties, soil physical  
1083 properties, and lignin reflecting litter input and composition). Soil chemical properties here  
1084 include DOC, TP, pH, EC and MBC; Soil physical properties include BD, SWC, clay, silt and  
1085 sand; and plant traits include lignin content  $\Lambda_8$ , S/V, C/V, (Ad/Al)<sub>v</sub>, and (Ad/Al)<sub>s</sub>. Red columns  
1086 indicate that variables have significant differences ( $p < 0.05$ ) in SOC contents.

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1090 **FIGURE 9** Vegetation composition and distributions in terms of tidal actions, and aboveground  
1091 biomass with SOC density depending on each vegetation type. Green histograms represent the  
1092 relative size of aboveground biomass of a given vegetation. Blue histograms represent the  
1093 relative size of SOC density vegetated corresponding plants in the top 0–40 cm, and pink  
1094 histograms are SOC densities in the 40–100 cm layer.

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1098 **FIGURE 10** Schematic showing the distributions of SOC density among different wetland  
1099 types in the critical wetland zone. There are four wetland types (i.e., lake, river, coastal, and  
1100 marsh) integrated with our field measurements and regional characteristics. The SOC density  
1101 in top 1 m of lake, river and marsh wetlands are derived from Xiao et al. (2019).

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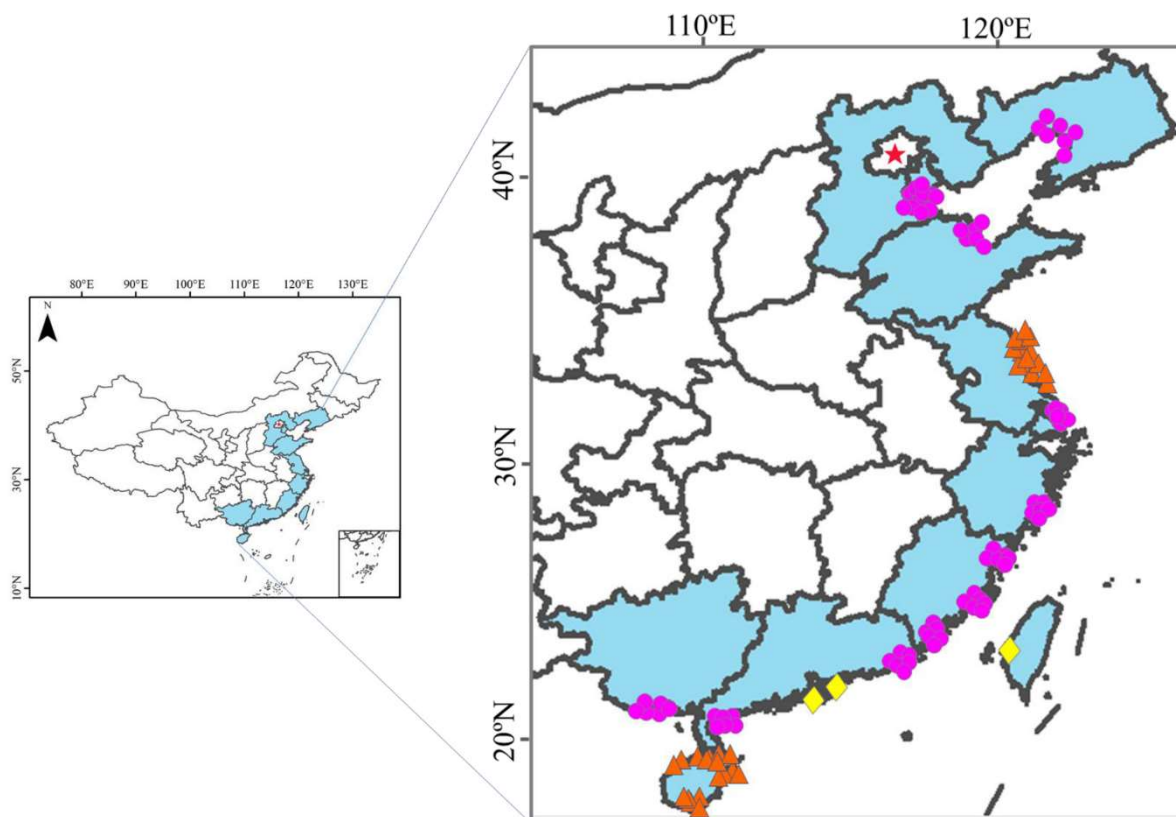
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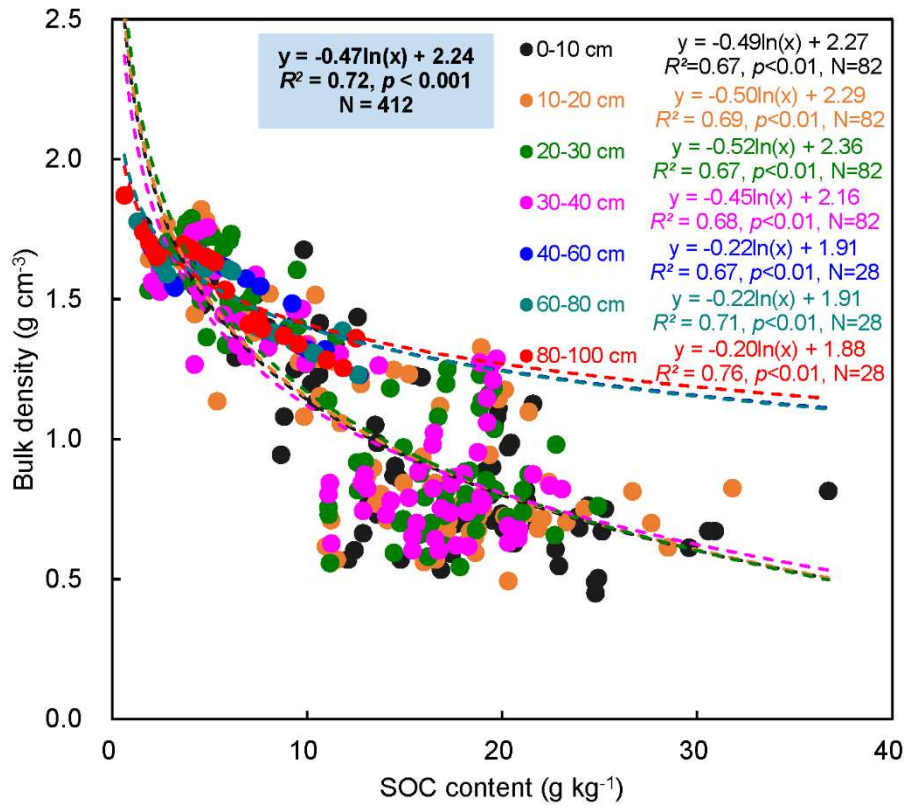
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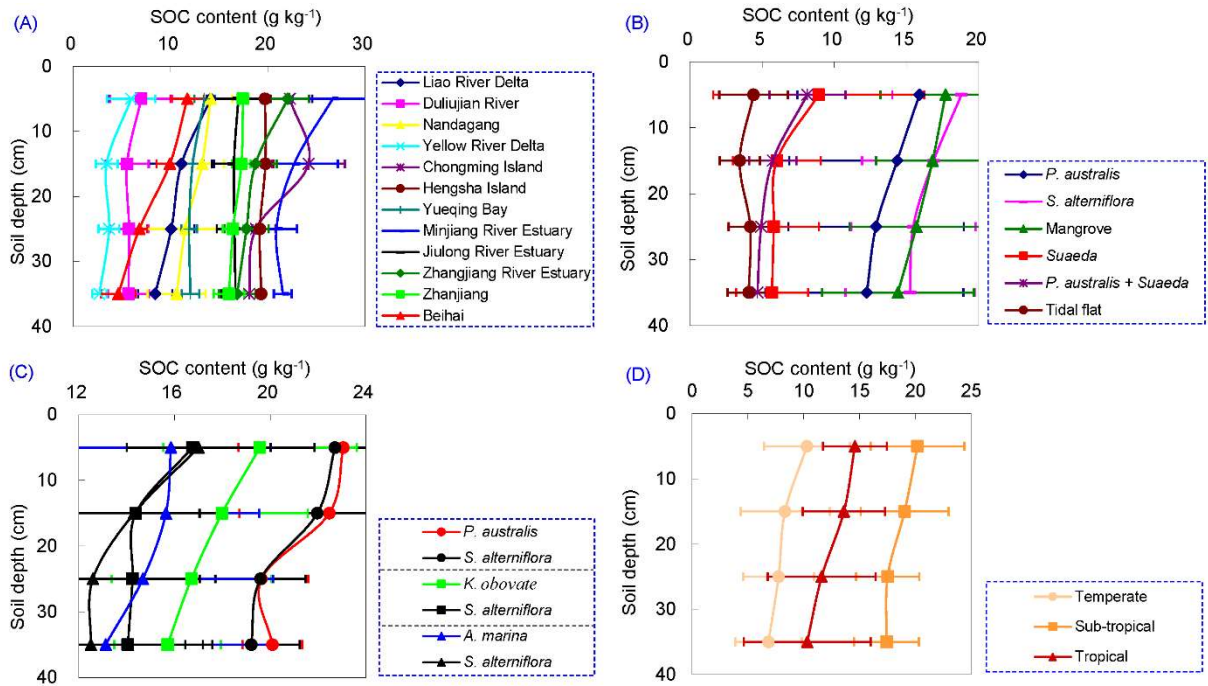
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1125 Figure 2



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1142 Figure 3



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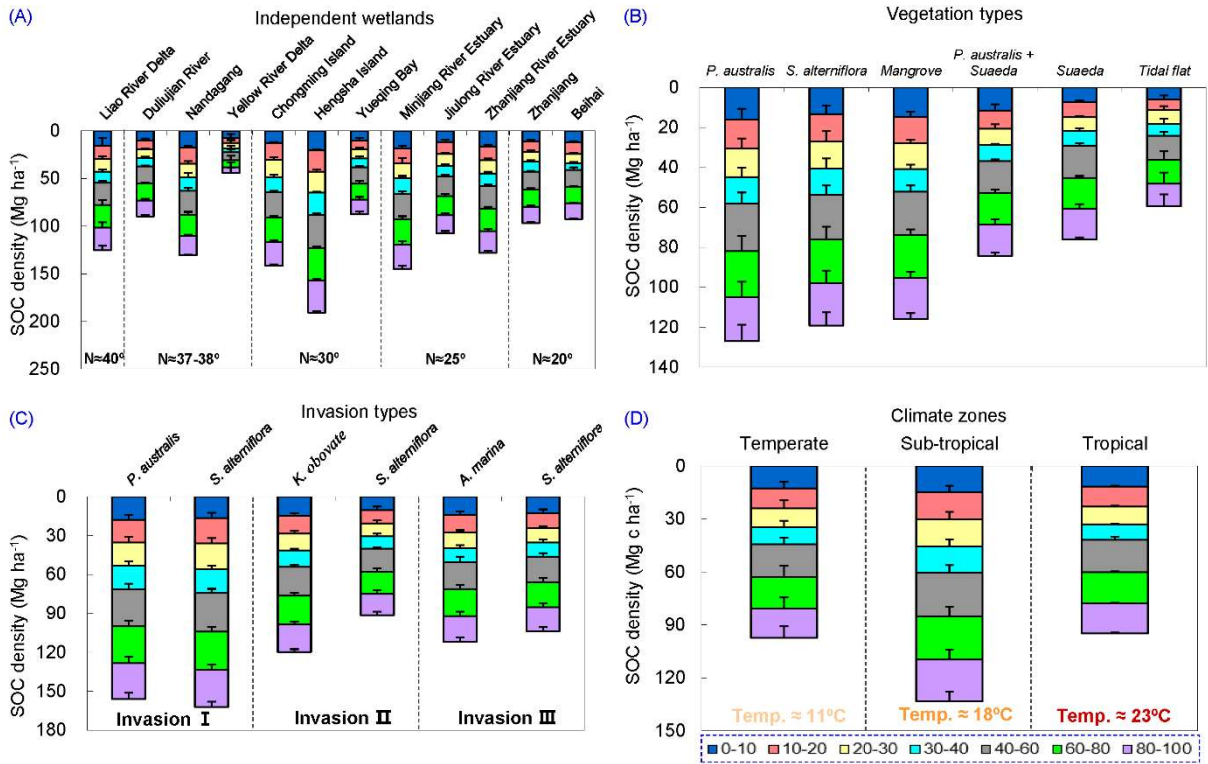
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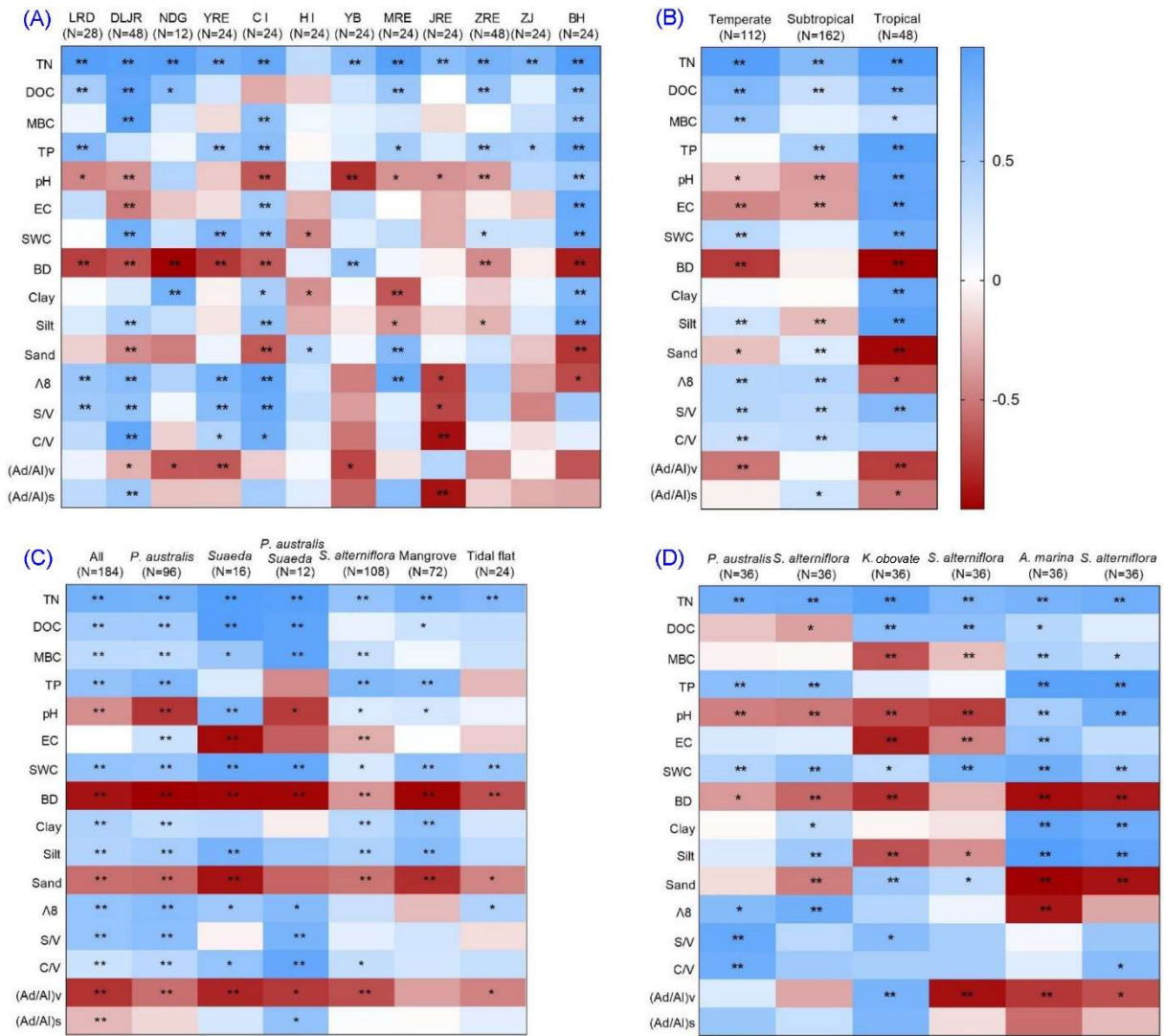
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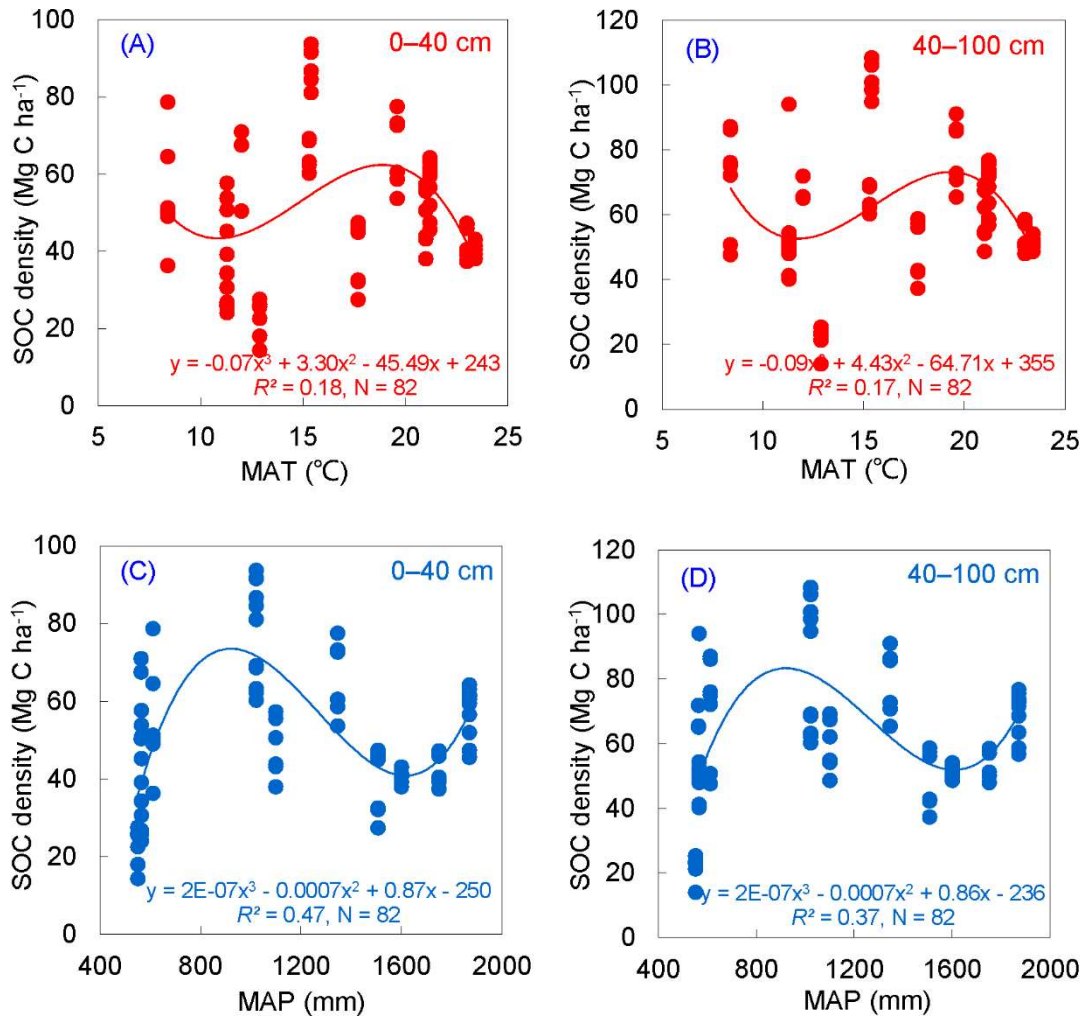
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1179 Figure 5



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1192 Figure 6



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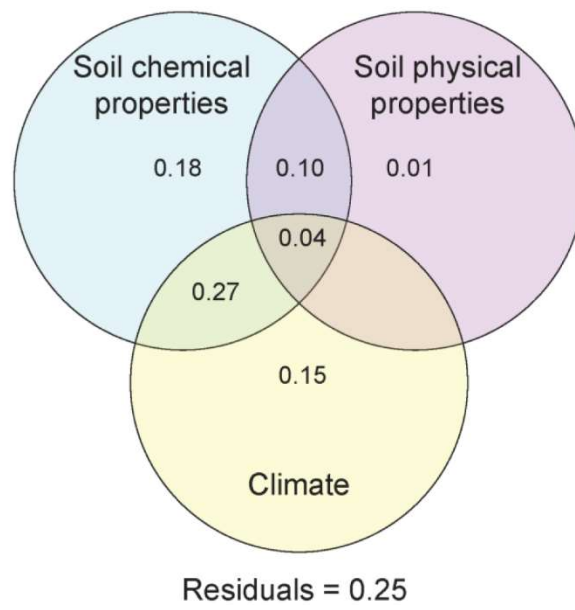
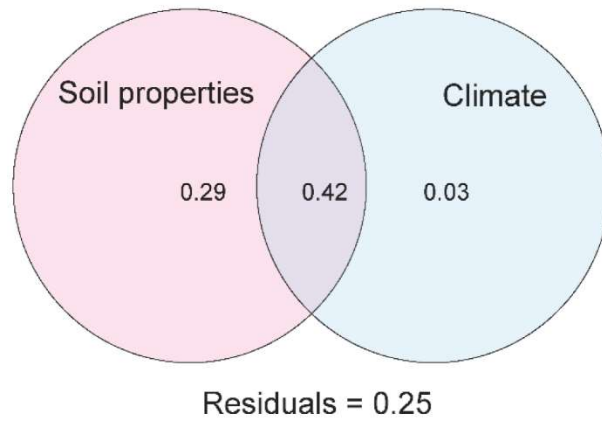
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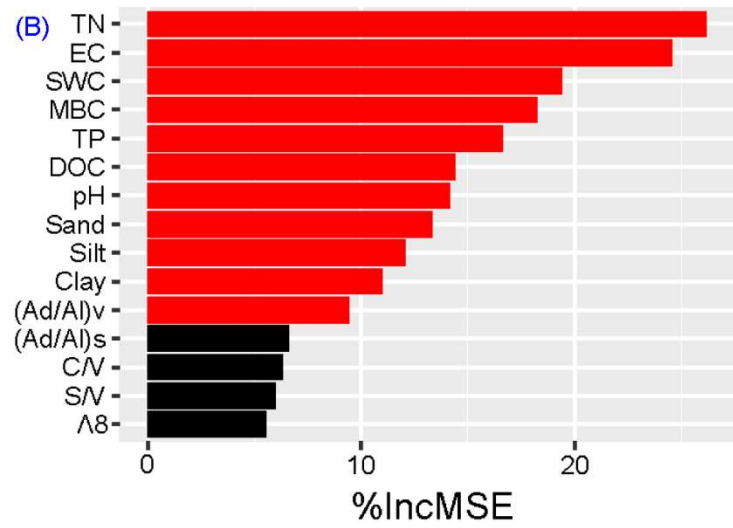
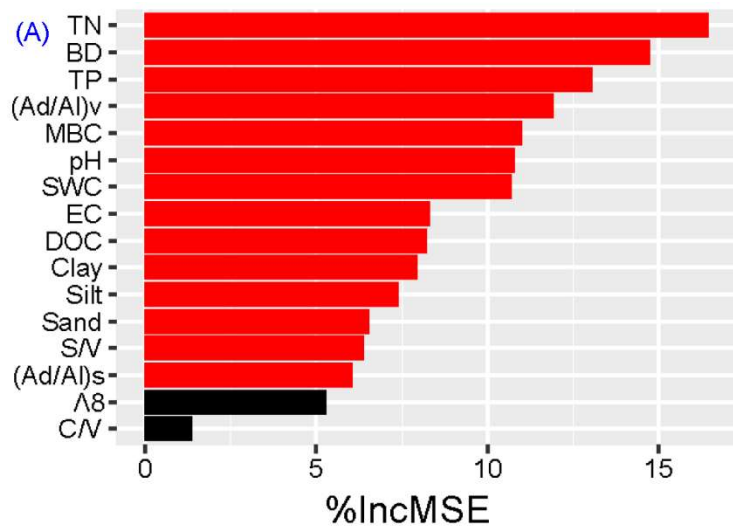


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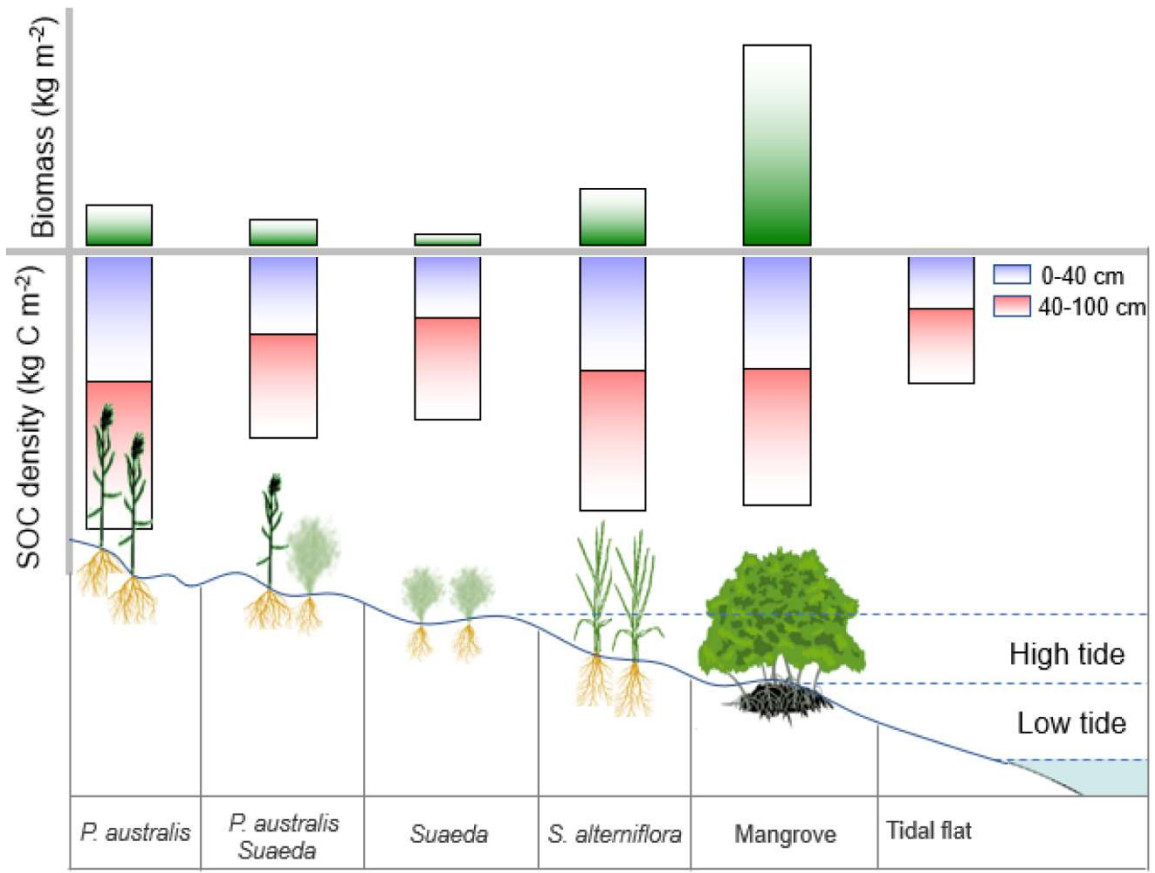
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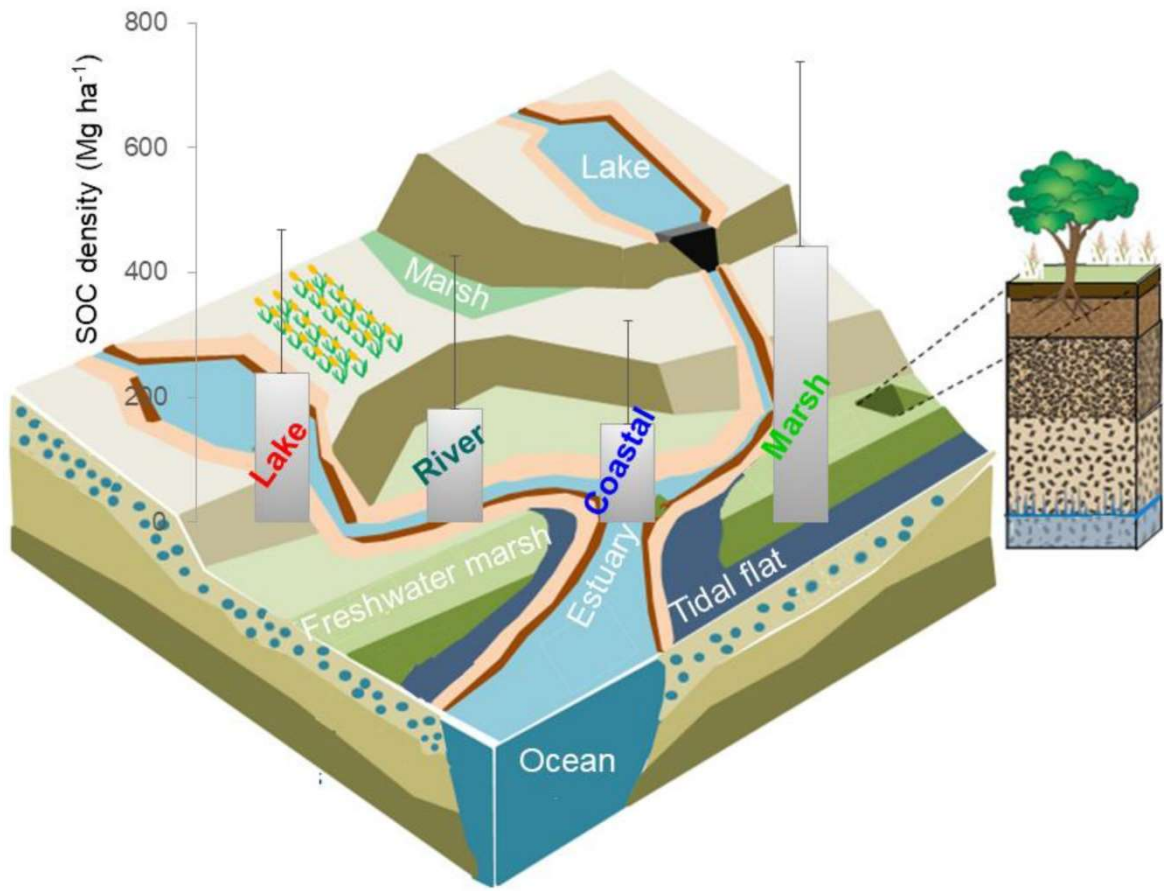
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1232 Figure 9



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1248 Figure 10



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**Table 1** Summary of SOC sequestration capacity in coastal wetlands of China synthesized from sampled soil cores and literature data

Province/ city	Area of coastal wetlands (10 <sup>3</sup> ha) <sup>a</sup>	Soil depth (cm)	SOC stock (Mg ha <sup>-1</sup> )	Representative wetlands	SOC sequestration (10 <sup>6</sup> Mg)	Main plants	The number of samples (sites × layers)	References
Liaoning	97.47	0–40	54.34±12.51	Liao River Delta (LRD)	5.30±1.22	<i>P. australis</i> , <i>S. glauca</i> , <i>S. salsa</i> , Tidal flat	49 (7 × 7)	This study
		40–100	70.77±14.59		6.90±1.42			
Tianjin	18.97	0–40	37.45±11.33	Duliujian River (DLJR)	0.71±0.21	<i>P. australis</i> , <i>S. glauca</i> , <i>S. salsa</i> , Tidal flat	84 (12 × 7)	This study
		40–100	52.40±13.21		0.99±0.25			
Hebei	18.65	0–40	63.01±9.00	Nandagang wetland (NDG)	1.18±0.17	<i>P. australis</i> , <i>S. glauca</i> , <i>S. salsa</i> , Tidal flat	21 (3 × 7)	This study
		40–100	67.58±3.11		1.26±0.06			
Shandong	76.34	0–40	22.43±4.74	Yellow River Estuary (YRE)	1.71±0.36	<i>P. australis</i> , <i>S. glauca</i> , <i>S. salsa</i> , <i>S. alterniflora</i> , Tidal flat	42 (6 × 7)	This study
		40–100	21.77±3.67		1.66±0.28			
Jiangsu	52.88	0–100	47.61±21.97	Wanggang Wetland (WGW), Yancheng Wetland (YCW), Dafeng Wetland (DW)	2.52±1.16	<i>P. australis</i> , <i>S. salsa</i> , <i>S. alterniflora</i> , <i>A. littoralis</i>	22 sites	Gao et al., 2016; Liu et al., 2017; Zang, 2019; Yang, 2019; Yang et al., 2016; Fu et al., 2021
Shanghai	71.25	0–40	76.40±12.50	Chongming Island (CI), Hengsha Island (HI)	5.44±0.89	<i>P. australis</i> , <i>S. alterniflora</i>	84 (12 × 7)	This study
		40–100	89.85±13.43		6.40±0.96			
Zhejiang	29.51	0–40	38.49±7.93	Yueqing Bay (YB)	1.14±0.23	<i>K. obovate</i> , <i>S. alterniflora</i>	42 (6 × 7)	This study
		40–100	49.16±8.51		1.45±0.25			
Fujian	34.23	0–40	57.51±9.46	Minjiang River Estuary (MRE), Jiulong River Estuary (JRE), Zhangjiang River Estuary (ZRE)	1.97±0.32	<i>P. australis</i> , <i>S. alterniflora</i> , <i>K. obovate</i> , <i>A. marina</i> ,	168 (24 × 7)	This study
		40–100	69.57±10.16		2.38±0.35			
Guangdong	49.37	0–40	42.94±3.95	Zhanjiang (ZJ)	2.12±0.20	<i>A. marina</i> , <i>S. alterniflora</i>	42 (6 × 7)	This study
		40–100	53.94±4.24		2.66±0.21			
Guangxi	81.88	0–40	40.91±1.86	Beihai (BH)	3.35±0.15	<i>A. marina</i> ,	42	This study

		40–100	51.76±2.00		4.24±0.16	<i>S. alterniflora</i>	(6 × 7)	
Hainan	10.23	0–100	315.21±248.5 8	Dongzhai Bay (DB), Qinglan Harbor (QH), Xinying Harbor (XB), Sanya Bay (SYB), Sibi Bay (SBB), Xinyang Bay (XB), Tielu Harbor (TH), Danzhou (DZ), Lingao (LG)	3.22±2.54	<i>S. apetala</i> , <i>K. obovate</i> , <i>R. stylosa</i> , <i>A. marina</i> , <i>A. corniculatum</i> , <i>B. sexangular</i> , <i>C. tagal</i> , <i>B. gymnorrhiza</i>	38 sites	Gao et al., 2019; Wang et al., 2019; Huang et al., 2017; Xiong et al., 2018; Xin et al., 2014; Lin et al., 2015; Gao et al., 2018; Fu et al., 2021
Hong Kong <sup>b</sup>	0.11	0–100	110.90±5.30 ~ 160.3±21.00	—	0.09±0.01	—	—	Fu et al., 2021
Macao <sup>b</sup>	0.01	0–100	110.90±5.30 ~ 160.30±21.00	—	0.00±0.00	—	—	Fu et al., 2021
Taiwan <sup>c</sup>	20.35	0–100	135.80±25.90 ~ 192.00±23.80	—	0.13±0.02	—	—	Fu et al., 2021

1265 <sup>a</sup>The data of area of coastal wetlands in each Province of China along coastlines was originated from Mao et al. (2020);

1266 <sup>b</sup>SOC stocks Hong Kong and Macao was substituted by the data of Pearl River Estuary;

1267 <sup>c</sup>SOC stocks in Taiwan was substituted by the data of Fujian, Guangdong, Guangxi and Hainan.

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**Table 2** Stepwise multiple regression analysis between SOC contents and environmental factors

Classification basis		Regression equation	$R^2$	$p$ value	Std. error of the estimate	$N$	Extracted parameters
Vegetation types	<i>P. australis</i>	$Y = -21.53 + 7.85\text{TN} + 0.02\text{MAP} + 0.01\text{MBC} - 0.02\text{DOC} - 0.15\text{SWC} + 7.34\text{TP} + 1.41\text{pH} - 4.53(\text{Ad/Al})_v$	0.98	<0.001	1.31	96	TN, MAP, MBC, DOC, SWC, TP, pH, (Ad/Al) <sub>v</sub>
	<i>Suaeda</i>	$Y = 0.07 + 7.97\text{TN}$	0.98	<0.001	0.62	16	TN
	<i>P. australis</i> , <i>Suaeda</i>	$Y = -2.39 + 11.86\text{TN}$	0.92	<0.001	0.61	12	TN
	<i>S. alterniflora</i>	$Y = 30.20 - 47.59(\text{Ad/Al})_v + 11.13\text{TN} - 0.68\text{MAT} - 0.11\Lambda_8 - 0.001\text{EC} + 0.02\text{DOC}$	0.91	<0.001	1.64	108	(Ad/Al) <sub>v</sub> , TN, MAT, $\Lambda_8$ , EC, DOC
	Mangrove	$Y = 24.55 - 15.22\text{BD} - 0.001\text{EC} + 0.02\text{DOC} + 0.20\text{SWC}$	0.96	<0.001	1.08	72	BD, EC, DOC, SWC
	Tidal flat	$Y = 7.79 + 7.43\text{TN} + 0.10\text{Clay} - 0.70\text{MAT} - 0.02\text{DOC}$	0.83	<0.001	0.81	24	TN, Clay, MAT, DOC
Invasion types	<i>P. australis</i>	$Y = 19.75 + 6.97\text{TN} - 0.22\text{SWC}$	0.91	<0.001	1.26	36	TN, SWC
	<i>S. alterniflora</i>	$Y = -14.68 + 11.41\text{TN} + 1.69\text{pH} + 0.21\text{Sand} + 0.02\text{DOC}$	0.98	<0.001	0.73	36	TN, pH, Sand, DOC
	<i>K. obovate</i>	$Y = 2.97 + 9.07\text{TN} + 3.52\text{C/V}$	0.98	<0.001	0.61	36	TN, C/V
	<i>S. alterniflora</i>	$Y = 49.14 - 150.56(\text{Ad/Al})_v + 27.25(\text{Ad/Al})_s$	0.89	<0.001	1.32	36	(Ad/Al) <sub>v</sub> , (Ad/Al) <sub>s</sub>
	<i>A. marina</i>	$Y = 52.35 + 0.24\text{SWC} - 2.21\text{MAT} + 4.02\text{TP} + 0.37\text{pH} - 2.87\text{BD}$	0.99	<0.001	0.23	36	SWC, MAT, TP, pH, BD
	<i>S. alterniflora</i>	$Y = 14.75 - 7.17\text{BD} + 9.78\text{TP}$	0.95	<0.001	1.15	36	BD, TP
Climate zone	Temperate	$Y = 4.88 + 8.17\text{TN} + 0.004\text{MBC} - 0.07\text{SWC} - 2.35\text{BD}$	0.95	<0.001	1.11	112	TN, BD, MBC, SWC, BD
	Subtropical	$Y = 5.57 + 8.78\text{TN} + 5.70\text{BD} + 0.005\text{MBC} + 0.03\text{DOC} - 0.001\text{EC} - 22.18(\text{Ad/Al})_v$	0.90	<0.001	1.47	168	TN, BD, MBC, DOC, EC, (Ad/Al) <sub>v</sub>
	Tropical	$Y = 3.71 + 4.23\text{TN} - 4.03\text{BD} + 0.07\text{SWC} + 0.64\text{pH}$	0.99	<0.001	0.41	48	TN, BD, SWC, pH