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1 Losses and destabilization of soil organic carbon stocks in coastal wetlands converted
2 into aquaculture ponds

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32 **Abstract**

33 Coastal-wetlands play a crucial role as carbon (C) reservoirs on Earth due to their C pool
34 composition and functional sink, making them significant for mitigating global climate change.
35 However, due to the development and utilization of wetland resources, many wetlands have been
36 transformed into other land-use types. The current study focuses on the alterations in soil organic-C
37 (SOC) in coastal-wetlands following reclamation into aquaculture ponds. We conducted sampling at
38 11 different coastal-wetlands along the tropical to temperate regions of the China coast. Each site
39 included two community types, one with solely native species (*Suaeda salsa*, *Phragmites australis*
40 and Mangroves) and the other with an adjacent reclaimed aquaculture pond. Across these 11
41 locations we compared SOC stock, active OC fractions, and soil physicochemical properties
42 between coastal wetlands and aquaculture ponds. We observed that different soil uses, sampling
43 sites, and their interaction had significant effects on SOC and its stock ($p<0.05$). Reclamation
44 significantly declined SOC concentration at depths of 0-15cm and 15-30cm by 35.5% and 30.3%,
45 respectively, and also decreased SOC stock at 0-15cm and 15-30cm depths by 29.1% and 37.9%,
46 respectively. Similar trends were evident for SOC stock, labile organic-C (LOC), dissolved
47 organic-C (DOC) and microbial biomass organic-C (MBC) concentrations ($p<0.05$), indicating soil
48 C-destabilization and losses from soil following conversion. Soils in aquaculture ponds exhibited
49 higher bulk density (BD) (11.3%) and lower levels of salinity (61.0%), soil water content (SWC)
50 (11.7%), total nitrogen (TN) concentration (23.8%) and available-nitrogen concentration (37.7%)
51 ($p<0.05$) than coastal-wetlands. Redundancy-analysis revealed that pH, BD and TN concentration
52 were the key variables most linked with temporal variations in SOC fractions and stock between
53 two land use types. This study provides a theoretical basis for the rational utilization and
54 management of wetland resources, the achievement of an environment-friendly society, and the
55 preservation of multiple service functions within wetland ecosystems.

56

57 **Keywords:** soil organic carbon (SOC), coastal wetland, reclaimed aquaculture pond, active OC
58 fractions

1. Introduction

Coastal wetlands, serving as crucial transitional ecosystems between terrestrial and marine ecosystems (Hao et al., 2024), play a vital role in promoting siltation and tidal prevention, protecting dykes, and providing habitats for saline plants and animals (Osland et al., 2022; Xia et al., 2022). Despite covering only 0.3% of the oceans, they contribute approximately 47% of the total organic carbon burial in marine sediments, with the global rate of organic carbon (C) accumulation estimated to be between 0.07-0.22 Pg C yr⁻¹ (Hopkinson et al., 2012; Duarte et al., 2013). Consequently, compared to inland wetlands, coastal wetlands exhibit higher rates of C deposition and possess stronger C sequestration capacity (Mao et al., 2015; Yang et al., 2022a), storing more C per unit area (Zhu et al., 2020; Zhang et al., 2021), and offering greater potential for mitigating the greenhouse effect (Hu et al., 2020; Tan et al., 2020; Gong et al., 2023).

Due to a combination of factors such as the geographical advantages of wetlands and the delayed recognition of their ecological functions, wetlands have historically been prioritized for development and utilization (Xu et al., 2020; Hong et al., 2021; Tan et al., 2022). Unfortunately, global wetlands have experienced 50% decline within a century, primarily due to their conversion for agriculture and other purposes (Bridgham et al., 2006; Davidson & Finlayson, 2019; Wang et al., 2021). In China, the coastal aquaculture industry has flourished since the 1990s (Yang et al., 2022a). Over the past few decades, growing demand for food and economic benefits has fueled the rapid expansion of coastal aquaculture, leading to intense competition for land use (Yao, 2013; Troell et al., 2016). Consequently, a substantial portion of China's coastal wetlands, estimated to be 15,632.64 km² in 2017, accounting for 41.10% of the total area of the low-lying coastal zone (below 17 m), has been widely reclaimed for aquaculture ponds (Duan et al., 2020). This reclamation process involves removing existing vegetation and converting dikes into steep slopes (Yang et al., 2022b), altering the original habitat conditions and transforming natural wetlands into artificial wetlands with increased anthropogenic disturbances (Kashaigili et al., 2008; Hu et al., 2009). These

changes inevitably affect the spatial and temporal distribution of runoff, wetland vegetation, and various biogeochemical properties such as soil cation exchange capacity (CEC), pH, water status, bulk density, and nutrient concentration (Tan et al., 2022; Yang et al., 2022a; Zhang et al., 2023).

To date, most research has focused on analyzing soil physicochemical properties and nutrients, including carbon (C), nitrogen (N), and phosphorus (P) concentrations (Bai et al., 2013; Macreadie et al., 2013; Wang et al., 2014; Bu et al., 2015; Wan et al., 2018), as well as carbon emissions (Yang et al., 2017; Yang et al., 2022a), in individual estuarine or coastal wetlands. Additionally, previous studies focusing on broader scales have relied on datasets compiled from published literature with integrated meta-analysis, rather than field measurements (Xiao et al., 2019; Xia et al., 2022). For instance, Tan et al. (2020) conducted a global meta-analysis exploring the effects of various land use and land cover change (LULCC) types, including aquaculture ponds, on CO₂, CH₄, and N₂O emissions from natural coastal wetlands, riparian wetlands, and peatlands. Notably, due to sensitivity to plants and microbial activities, the active OC from the total SOC pool, which includes labile organic carbon (LOC), microbial biomass organic carbon (MBC) and dissolved organic carbon (DOC), is highly susceptible to oxidation and decomposition (Wang et al., 2019; Lin et al., 2022). Therefore, distinguishing the active OC fraction from the total SOC pool is crucial for assessing the impact of coastal wetland reclamation on soil C dynamics. Furthermore, since active OC provides a substrate for microbial activity and is a primary source of CO₂ and CH₄ produced by microbes, proper management of this active OC pool is critical for mitigating global climate change and increasing SOC stock (Wang et al., 2019). However, there is still limited research on exploring SOC pools and how OC stock respond to reclamation for aquaculture across broader geographic and environmental gradients. In this study, we aimed to investigate (i) changes in soil total OC stock and active OC fractions (i.e., LOC, MBC, and DOC), and (ii) the relationships between these changes in SOC pools and other key soil physicochemical traits by comparing 22 pairs of wetland sites with nearby reclaimed ponds across 11 coastal wetland areas in China.

110 2. Materials and methods

111 2.1 Study region

112 We selected 11 locations with a total of 22 paired sampling plots, each consisting of one wetland
113 plot and one nearby reclaimed pond, across 11 independent coastal wetlands spanning tropical to
114 temperate climate zones in China (Fig. 1). These locations include the Liaohe River Estuary (S1),
115 Yellow River Estuary (S2), Yancheng (S3), Yangtze River Estuary (S4), Hangzhou Bay (S5),
116 Minjiang River Estuary (S6), Jiulong River Estuary (S7), Zhangjiang River Estuary (S8), Zhenzhu
117 Bay (S9), Zhanjiang (S10), and Dongzhai port (S11). Relevant sampling site information is outlined
118 in Table 1. At each site, we collected samples from two different community types: the native
119 species community, consisting of *Suaeda salsa*, *Phragmites australis*, and Mangroves (*Aegiceras*
120 *corniculatum*, *Kandelia candel*, *Bruguiera gymnorhiza*), and the adjacent reclaimed aquaculture
121 pond. The native species *Suaeda salsa* is native to S1 and S2; *Phragmites australis* is native to
122 S3~S6; and Mangrove is native to S7~S11. Historical records were used to confirm the native
123 species composition of each site and to identify the ponds from which the native species were
124 converted.

125 2.2 Experimental design and sampling

126 We randomly selected five vegetation plot (10 m × 10 m square) in each site and land-use, and then
127 chose one small subplot (1 m × 0.6 m) in the middle of the vegetation plot. Soil samples (0-15 cm
128 and 15-30 cm depth layers) were collected from each of the 11 selected sites at five replicated
129 quadrats from October to November 2018 using a soil drilling sampler with a 9 cm diameter. A total
130 of 220 samples (11 sampling sites × 2 community types × 2 soil layers × 5 replicate quadrats) were
131 collected and immediately stored in sterile bags in ice coolers before transportation to the laboratory.
132 Soil samples were subsequently homogenized, sieved through a 2 mm mesh to remove gravel,
133 organic debris, and plant residues, and then separated into two equal proportions. One proportion
134 was air-dried at room temperature and passed through a 0.25 mm sieve for physical and chemical

135 analysis. The second proportion was stored at 4 °C for SOC fraction analyses.

136 2.3 Sample analysis

137 Soil pH was measured with a pH meter (Starter 300, Parsippany, USA), and salinity was measured
138 using a 2265FS EC Meter (Spectrum Technologies Inc., Paxinos, USA). Bulk density (BD) was
139 measured from three additional 5 × 3 cm cores from each site. Soil water content (SWC) was
140 measured using the gravimetric method (Lu, 2000). Soil total N (TN) concentration was determined
141 using an elemental analyzer (Elementar Vario MAX, Elementar Scientific Instruments, Hanau,
142 Germany). Soil total P (TP) concentration was determined after digestion of the soil with
143 HClO₄-H₂SO₄ acid (Lu, 2000). Soil available N (AN) concentration was determined by the alkaline
144 hydrolysis diffusion method and extracted using 40 mL of 2.0 mol·L⁻¹ KCl. Soil available P (AP)
145 concentration was determined by the diffusion method with the Mehlich III using a San++
146 continuous flow analyzer (Lu, 2000). The ratios of C:N, C:P, N:P, and AN:AP (in mass basis) in soil
147 were also calculated.

148 We analyzed the concentration of SOC and labile organic C (LOC) of the air-dried, finely
149 ground soils, and that of microbial biomass organic C (MBC) and dissolved organic C (DOC) of
150 fresh soils. SOC concentration was determined using an elemental analyzer (Elementar Vario MAX,
151 Elementar Scientific Instruments, Hanau, Germany) and, soil LOC concentration was determined
152 using the 333 mM KMnO₄ digestion method (Chung et al., 2010; Xu et al., 2011), in which soil
153 slurry (soil to distilled water w/v ratio of 1:5) was shaken at 300 rpm and 25 °C for 30 min,
154 centrifuged at 10,000 rpm for 20 min, and then filtered through a decarbonized 0.45-μm filter. MBC
155 concentration was determined using the fumigation–extraction method (Vance et al., 1987; Fang et
156 al., 2020). Briefly, 10 g fresh soil samples were extracted by 0.5 M K₂SO₄ (1 h shaking). A paired
157 10 g fresh-soil sample was fumigated with alcohol-free chloroform in a desiccator for 24 h in the
158 dark at 22 °C, and the fumigated soils were extracted by the 0.5 M K₂SO₄ solution (1 h shake). The
159 extracts from non-fumigated and fumigated soils were filtered through glass-fiber filter papers. Soil

DOC concentration was determined using a total organic C analyzer (TOC-V, Shimadzu Scientific Instruments, Kyoto, Japan), following extraction using deionized water (1:5 w/v). The SOC stock at the depths of 0-15 cm or 15-30 cm was estimated following the approach of Mishra et al. (2010):

$$SOC_{stock} = SOC_{concentration} \times BD \times 15 \times 10$$

where SOC_{stock} is the soil organic carbon stock at depths of 0-15 cm or 15-30 cm ($t\ C\ km^{-2}$), $SOC_{concentration}$ is soil organic carbon concentration ($g\ kg^{-1}$), BD is the bulk density ($g\ cm^{-3}$).

2.4 Statistical analyses

SPSS version 22.0 (IBM, Armonk, NY, USA) statistical analysis software were used to carry out the measured data, and Origin version 2022 (OriginLab Corp., Northampton, MA, USA) software was used for plotting. The data were reported as the mean \pm standard error (SE) for five replicates. Before the analysis of variance (ANOVA), all datasets were tested for normality (Shapiro-Wilk's test) and homoscedasticity (Bartlett-test). Unless stated otherwise, the main effects of treatment were compared using the least significant differences at 5%. Two-way analysis of variance (ANOVA) was used to analyze the effects of treatment and site in SOC and active OC fractions, and SOC stock across 11 sampling sites. We chosen to use a two-way ANOVA with sites as fixed factor and non a mixed model with site as random factor to can detect possible interactions between the land use (treatment) and site given the great gradient of sites with different native vegetation. We performed an independent sample t tests to test the differences in other soil studied variables between coastal wetlands and aquaculture ponds using $p < 0.05$ as the cutoff for statistical significance. The associations between SOC fractions, stock and soil physicochemical properties between the coastal wetlands and aquaculture ponds were tested using Pearson's correlation coefficients in the "corrplot" R packages (version 4.0.3; R Core Team, 2020). Redundancy analysis (RDA) was used to analyze the potential physicochemical factors affecting SOC fractions and stock between the coastal wetlands and aquaculture ponds.

185

186 **3. Results**187 *3.1 Soil physicochemical variables*

188 Significant variations were observed in mean soil BD (Fig. 2a), salinity (Fig. 2c), SWC (Fig. 2d),
 189 TN (Fig. 2e), AN (Fig. 2f), C:N (Fig. 2i), C:P (Fig. 2j), N:P (Fig. 2k) and AN:AP (Fig. 2l) between
 190 coastal wetlands and aquaculture ponds, while no significant variations were found in mean soil pH
 191 (Fig. 2b), TP (Fig. 2g) and AP (Fig. 2h) at 0-30 cm depth (Table S1). Compared to the coastal
 192 wetlands, soil BD and pH were higher in the aquaculture ponds by 11.3% ($p < 0.05$) and 3.28% ($p >$
 193 0.05), respectively. Additionally, significant decreases in soil salinity, SWC, TN and AN were
 194 observed in the aquaculture ponds, by 61.01%, 11.7%, 23.8% and 37.7%, respectively ($p < 0.05$).
 195 Similar trends were evident for C:N, C:P, N:P and AN:AP levels after coastal wetlands reclamation
 196 ($p < 0.05$).

197 *3.2 Variation in SOC concentration across coastal wetlands and aquaculture ponds*

198 There were significant effects of treatment and site on SOC concentration at 0-15 cm layer ($p <$
 199 0.001) and 15-30 cm layer ($p < 0.001$), and a treatment \times site interaction for SOC concentration at
 200 0-15 cm layer ($p < 0.01$) and 15-30 cm layer ($p < 0.05$) (Fig. 3a). Across 11 sampling sites, SOC
 201 concentration ranged from 6.40-31.8 g kg⁻¹ at the 0-15 cm depth and 4.90-26.5 g kg⁻¹ at the 15-30
 202 cm depth coastal wetlands. In aquaculture ponds, SOC concentration ranged from 5.14-17.59 g kg⁻¹
 203 at the 0-15 cm depth and 3.55-18.1 g kg⁻¹ at the 15-30 cm depth. In general, reclamation of coastal
 204 wetlands into aquaculture ponds significantly declined SOC concentration at 0-15 cm and 15-30 cm
 205 depth by 35.5% and 30.3%, respectively ($p < 0.05$). Across 11 sampling sites, SOC concentration of
 206 coastal wetlands was the highest in S10 (29.1 ± 1.57 g kg⁻¹) and the lowest in S4 (5.77 ± 0.32 g
 207 kg⁻¹), while SOC concentration of aquaculture ponds was the highest in S8 (17.7 ± 0.49 g kg⁻¹) and
 208 the lowest in S1 (4.34 ± 0.38 g kg⁻¹) (Fig. 3b).

209

210 3.3 Variation in SOC stock across coastal wetlands and aquaculture ponds

211 Overall, there were main effects of treatment and site on SOC stock at the 0-15 cm layer ($p < 0.001$)
212 and the 15-30 cm layer ($p < 0.001$). Moreover, there was a treatment \times site interaction for SOC
213 stock at the 0-15 cm layer ($p < 0.01$) and the 15-30 cm layer ($p < 0.05$) (Fig. 4). Across 11 sampling
214 sites, SOC stock at the 0-15 cm depth ranged from 1230.50 to 3357.07 t C km⁻² (mean = 2367 t C
215 km⁻²) in coastal wetlands and from 10898.98 to 22654.61 t C km⁻² (mean = 1754 t C km⁻²) in
216 aquaculture ponds. At the 15-30 cm depth, SOC stock ranged from 927.95 to 3013.33 t C km⁻²
217 (mean = 2107 t C km⁻²) in coastal wetlands and from 8076.87 to 23832.64 t C km⁻² (mean = 1738 t
218 C km⁻²) in aquaculture ponds. In summary, the conversion of coastal wetlands to aquaculture ponds
219 significantly decreased the SOC stock by 29.13% at the 0-15 cm depth and by 37.89% at the 15-30
220 cm depth ($p < 0.05$).

221 3.4 Variation in active OC fractions concentrations across coastal wetlands and aquaculture ponds

222 There were significant differences in concentrations of soil LOC (Fig. 5a, Fig. S1), MBC (Fig. 5b,
223 Fig. S2), and DOC (Fig. 5c, Fig. S3) between coastal wetlands and aquaculture ponds. Compared to
224 the coastal wetlands, soil LOC concentration was found to be 33.49% lower in aquaculture ponds (p
225 < 0.05). Similarly, a significantly lower (25.2%) soil MBC concentration was observed in
226 aquaculture ponds compared to coastal wetlands ($p < 0.05$). However, soil DOC concentration was
227 15.8% higher in the aquaculture ponds than in coastal wetlands ($p < 0.05$).

228 3.5 Environmental drivers of SOC stock and fractions

229 The SOC concentration had a positive correlation with SOC stock ($r = 0.82$), LOC ($r = 0.84$), SWC
230 ($r = 0.68$), C:N ($r = 0.67$) and C:P ($r = 0.61$) ($p < 0.01$), and a negative correlation with pH ($r =$
231 -0.57), BD ($r = -0.73$) and DOC ($r = -0.39$) ($p < 0.01$) (Fig. 6). A negative correlation between soil
232 MBC concentration and pH ($r = 0.17$, $p < 0.05$) was also evident. Moreover, DOC concentration
233 was negatively correlated with AP ($r = -0.25$) and N:P ($r = -0.18$) ($p < 0.05$).

234 Correlations between environmental variables and SOC fractions, stock were also examined

235 using redundancy analysis (RDA) (Fig. 7). Based on the results of RDA, the first two RDA axes
236 explained 56.5% of the variance in total cumulative species. Notably, pH (explaining 51.7% of
237 variations, $p < 0.01$), BD (15.1%, $p < 0.01$) and TN (11.4%, $p < 0.01$) were the variables that
238 explained most of the temporal variations in SOC fractions concentration and stock. In addition,
239 variances were significantly explained by C:N (10.6%, $p < 0.01$), AN:AP (2.8, $p < 0.01$), salinity
240 (2.2%, $p < 0.01$), N:P (2%, $p < 0.01$), SWC (1.4%, $p < 0.01$), AN (1.1%, $p < 0.05$), and C:P (0.9%, p
241 < 0.05).

242 *3.6 Collectively changes in SOC pools and driving factors*

243 After reclamation, the SOC concentration and stock showed a decreasing trend (Fig. 8).
244 Additionally, compared to the coastal wetlands, soil LOC and MBC decreased, while DOC
245 increased in the aquaculture ponds. Notably, soil pH and BD were identified as key factors
246 controlling SOC stock and fractions. Higher soil pH and BD contributed to a decrease in SOC
247 concentration, whereas soil DOC concentration tended to increase.

248 **4. Discussion**

249 *4.1 Effects of land-use change on soil physical and chemical properties*

250 Changes in land use alter the soil microenvironment, inevitably affecting soil physical and chemical
251 properties such as, soil water content, bulk density, electrical conductivity, and pH (Spohn et al.,
252 2013; Tan et al., 2022). Previous studies have found that unsuitable utilization, irrational scale of
253 development in economical use, and unscientific management methods can lead to soil fertility
254 decline, land degradation, and soil erosion (Tan et al., 2022).

255

256 We found that the bulk density of the soil both above and below the cultivated wetland pond
257 increased significantly ($p < 0.05$). Natural vegetation, that is very dense in these natural wetlands,
258 maintains soil pore and soil aggregate formation, improving soil texture and maintaining a low bulk
259 density (Li et al., 2023a). Thus, its removal and change into an aquaculture pond were affected by

human disturbance, management measures, and cover removal. In these new conditions, the mechanical structure of the soil was partially disrupted, resulting in an increase in bulk density. Following wetland reclamation for aquaculture ponds, there was a variable decrease in soil salinity. This decrease can be attributed to the higher initial levels of soil salinization in coastal areas, the cultivation of salt-tolerant vegetation, and irregular freshwater recharge during aquaculture operations (Jin et al., 2012; Yang et al., 2015). In general, the conversion of *Phragmites australis* and mangrove wetlands into aquaculture ponds led to an increase in soil pH. Lin & Lin (2022) revealed that bait input during the aquaculture process could significantly increase soil sulfide, resulting from sulfate (SO_4^{2-}) reduction with high organic loading (Canfield et al., 1993; Lv et al., 2018). This sulfate reduction may be the main reason for the increase in pH in the aquaculture ponds after reclamation. The change from a *Suaeda salsa* natural wetland to a pond did not imply a change in soil pH, thus, the change of soil pH with conversion depends on the type of original natural wetland vegetation type (Zhang et al., 2008). This study observed a consistent decrease in soil pH from the wetlands of the Liaohe River Estuary to Dongzhai Port, following a north-to-south gradient. This decrease corresponds to a decline in soil alkalinity and an increase in acidity, aligning with the typical pattern of changes in soil acidity and alkalinity along latitudinal gradients.

As an important characterization parameter of soil fertility level and property status, soil nutrients can directly or indirectly affect ecological indicators such as SOC, C fractions, and C pool stability. Previous studies have found that diverse factors influence soil nutrient concentrations, including vegetation type, soil depth, climatic conditions, and management practices (Tu et al., 2017). In this study, soil TN concentration of the whole profile (0-30 cm) significantly decreased ($p < 0.05$) after mangrove wetlands reclamation, and the study showed that SOC and TN concentration were high in areas with high biomass (Tian et al., 2010). Mangroves are usually tall and densely covered, grow vigorously, and accumulate abundant biomass in subtropical and tropical climates. However, after being transformed into aquaculture ponds, soil TN was lost due to vegetation

removal, human turning, water change, and other activities. The mean soil AN concentration in the upper and lower layers showed that aquaculture ponds had higher AN levels than *Suaeda salsa* wetlands, while *Phragmites australis* and mangrove wetlands had higher AN levels than aquaculture ponds. This was mainly due to the fact that *Suaeda salsa* were shorter and had less biomass than *Phragmites australis* and mangrove, with this low biomass being associated with low soil AN concentration (Tian et al., 2010). Thus, the AN concentration increased in aquaculture ponds when they are replaced by a farming activity due to the presence of artificial baiting, animal residues, and feces during the farming activity (Jobbágy & Jackson, 2001). There was no significant change in soil TP concentration before and after wetlands reclamation ($p < 0.05$), possibly because phosphorus bait feed can artificially supplement soil P in aquaculture ponds.

4.2 Effects of land-use change on soil organic carbon

SOC is of great importance in coastal wetland ecosystems, and small fluctuations in its concentration or composition can profoundly impact wetland cycling of C, potential sequestration of C, and stability of C pools (DeGryze et al., 2004). Land use change, as a direct and influential form of human intervention, has long-term effects on the biogeochemical cycle of soil. It drives changes in physical and chemical properties and nutrient conditions of the soil by altering above-ground vegetation types, affecting the decomposition and transformation processes of SOC and ultimately impacting the stock of wetland SOC (Blair et al., 1995; Chmura et al., 2003).

The results of this study showed a decrease in the average SOC concentration of *Suaeda salsa*, *Phragmites australis*, and mangrove wetlands after reclamation, consistent with previous observations. This decline can be attributed to the decomposition of litter and residues from above-ground vegetation, root rot of underground plants, and secretion discharge, which serve as the primary sources of SOC input in wetland soil (Zhang et al., 2010), and all of which are greatly reduced after wetland reclamation. Moreover, frequent river and tidal effects on natural coastal

312 wetlands can bring a large amount of suspended organic matter, which also contributes to increases
313 in SOC input to natural wetland soil to a certain extent (Li et al., 2023b). Nonetheless, the
314 conversion of these wetlands into aquaculture ponds resulted in a decrease in SOC input due to
315 activities like cover removal and anthropogenic disturbance. Additionally, irregular water cover,
316 aeration, and drainage in aquaculture ponds contribute to SOC loss. The within-site comparative
317 analysis revealed no significant alteration in SOC concentration before and after the reclamation of
318 *Suaeda salsa* wetlands ($p > 0.05$). This lack of change can be attributed to the shorter height, lower
319 biomass, reduced apoptosis, and plant residues of *Suaeda salsa* compared to *Phragmites australis*
320 and mangrove species, resulting in lower SOC concentration and stock in the soil.

321

322 The effect of wetland reclamation on SOC concentration and stock in aquaculture ponds is not
323 only related to the drop of litter and root exudates inputs due to changes in cover condition, but is
324 also closely related to changes of soil physicochemical properties and nutrient conditions associated
325 with the wetland reclamation (Spaccini & Piccolo, 2013). In this study, SOC was positively
326 correlated with SWC ($p < 0.01$). Soil water status will change the turnover process of SOC by
327 affecting life activities such as soil microbial enzyme activity and metabolism, thus leading to
328 changes in SOC concentration and stock (Laiho et al., 2004). When the ambient water is sufficient
329 but allows air penetration, the microbial activity and metabolic rate increase, leading to enhanced
330 decomposition and mineralization of SOC and a subsequent decrease in its concentration and stock.
331 However, as water levels increase, the oxygen supply in soil diminishes, which stresses the growth
332 and reproduction of soil microorganisms. This results in a slower decomposition and transformation
333 rate of SOC, leading to an increase in its concentration and stock (Xia et al., 2022). In addition, soil
334 SOC was significantly negatively correlated with bulk density and pH ($p < 0.01$) (Fig. 8). The RDA
335 results also confirmed that one of the main reasons for the SOC decrease after *Phragmites australis*
336 and mangrove wetlands reclamation was the increase of soil bulk density and pH. Soil bulk weight
337 is the most effective parameter for predicting changes in soil structure and function; generally, the

richer the organic matter, the more granular structure, the lower the degree of soil compactness, the greater the porosity, and the smaller the bulk weight. Soil pH stimulates or inhibits microbial growth and reproduction by influencing enzyme activity and community composition of soil microorganisms, thereby accelerating or attenuating the rate of SOC degradation to a certain degree, and altering the SOC concentration and stock (Li et al., 2023a). Moreover, SOC was significantly and positively correlated with TN, AN, and AP concentration ($p < 0.05$). Soil N and P are vital nutrients in wetland ecosystems, and soil microorganisms will stimulate a variety of complex metabolic activities to obtain their optimal C/N/P ratios for growth and reproduction, thus affecting the input and output pathways of SOC concentration and stock (Li et al., 2023b; Zhou et al., 2023). Notably, in this study, there was no consistent pattern in the influence of different climatic zones or geospatial distributions on SOC stock, similar to the findings of Xia et al. (2022). Although climate can regulate the magnitude or rate of SOC transfer from one status to another, the SOC stock is usually controlled by soil physico-chemical properties (Gao et al., 2019; Luo et al., 2021; Xia et al., 2022). In other words, soil variables were completely beyond the control of climate on SOC stock.

4.3 Effects of land-use change on soil active OC fractions

Soil LOC is a very active part of SOC with simple structure, poor stability and fast turnover rate, which can provide energy for the life activities of soil microorganisms in a short time (Zhang et al., 2011). Our findings revealed decreased soil LOC concentration after reclamation of mangrove wetlands, while no significant changes were observed after reclamation of *Suaeda salsa* and *Phragmites australis* wetlands. This can be attributed to variations in the quantity and quality of organic matter introduced into the soil through different vegetation, affecting the population size and functional structure of soil microorganisms to varying degrees (Thorburn et al., 2012). However, the factors influencing soil LOC are not solely responsible, as they represent the combined effects of multiple factors. Additionally, these factors may have promoting or counteracting impacts, resulting in generally insignificant differences in soil LOC concentration

363 after the reclamation of *Suaeda salsa* and *Phragmites australis* wetlands. The correlation analysis
364 results showed that soil LOC was significantly positively correlated with SWC and SOC ($p < 0.01$).
365 Plant residues, particularly lignin fragments, were identified as the primary source of soil LOC and
366 were sensitive to changes in the surrounding environment (Datta et al., 2010). Moreover, SOC and
367 LOC were often in dynamic equilibrium and could be transformed into each other to a certain extent
368 (Hagedorn et al., 2000; Prommer et al., 2020). Therefore, habitats with high SOC concentration and
369 stock typically exhibit higher soil LOC concentration.

370

371 Soil MBC plays an essential role in wetland ecosystems' active OC components which can
372 reflect soil microbial activity and characterize soil structure and function (Lin et al., 2022). This
373 study found no significant changes in soil MBC concentration in the whole profile after the
374 reclamation of the *Suaeda salsa* and mangrove wetlands, while there was a significant overall
375 decrease in soil MBC concentration after the reclamation of *Phragmites australis* wetlands. This
376 can be related to the differences in the amount and type of deadfall entering the soil on soil MBC
377 concentration. After reclamation, although the aboveground vegetation was removed, the presence
378 of farm biomass residues, excreta, and artificially added bait fertilizers provided microbial sources
379 to the soil, resulting in the replenishment of the soil MBC concentration (Jangid et al., 2008). This
380 study observed a vertical decrease in average soil MBC concentration with increasing soil layer
381 depth. This can be attributed to the higher accumulation of organic matter, such as decaying plant
382 material and residues, in the upper layer compared to the lower layer. Additionally, influenced by
383 root distribution, the upper layer exhibits greater root aggregation and secretion, providing richer
384 nutrients sources for soil microorganisms to decompose and utilize. Moreover, the upper layer
385 benefits from better hydrothermal conditions and air permeability, creating a more favorable
386 environment for the growth and reproduction of soil microorganisms.

387

388 Soil DOC concentration is highly active and readily soluble in water (Ibrahim et al., 2021). It is

389 produced through the decomposition of organic matter by soil microorganisms, and can in turn act
390 on soil microorganisms to provide energy for their life activities (Lin et al., 2012; Han et al., 2012).
391 The results showed that, in general, the average concentration of soil DOC in both the upper and
392 lower soil layers increased after reclamation of the *Suaeda salsa* and *Phragmites australis* wetlands.
393 Moreover, the reclamation of wetlands for aquaculture ponds had a greater impact on the DOC
394 concentration and stock in the lower soil layer than the upper soil layer. Previous studies have found
395 that aboveground vegetation litter, underground root exudates and humus are the primary input
396 sources of soil DOC. In contrast, soil microbial mineralization into CO₂ or leaching with water is
397 the main forms of output. Dead branches, rotten leaves, plant roots, and other substances introduce
398 DOC to natural wetlands. Perennial tides and rivers can partially wash away the soil, resulting in
399 DOC loss. Furthermore, we observed that soil DOC was more sensitive to precipitation and showed
400 a decreasing trend with increasing rainfall along the studied climate gradient, consistent with
401 previous studies (Borken et al., 2008). This was also one of the reasons for the low DOC
402 concentration in mangrove wetland soil in areas with abundant precipitation. However, after
403 reclamation into aquaculture ponds, a relatively closed environment was established, reducing water
404 flow and diminishing erosion. In addition, the sampling time in this study was in the late stage of
405 aquaculture, when farmers would take intermittent drainage measures to facilitate fishing.
406 Meanwhile, it has been shown that structural and qualitative variations in organic matter input to the
407 soil can also lead to large differences in the chemical composition and properties of DOC (Kalbitz
408 et al., 2007). The chemical composition of DOC greatly influences its adsorption and retention
409 capacity within soils. In general, substances with larger volume, larger specific surface area, and
410 lower mobility are more prone to being trapped by soils and binding to mineral surface adsorption
411 sites (Gu et al., 1994). Correlation analysis showed that soil DOC concentration was positively
412 correlated with pH and BD ($p < 0.05$). Soil pH primarily influences the composition of microbial
413 communities and enzyme activity within soils. It can promote or inhibit the metabolic activities of
414 different bacteria, subsequently affecting soil organic matter degradation rates and transformation

415 processes of soil DOC. As the soil BD increases, the soil becomes more compact and more likely to
416 trap DOC, making it less susceptible to loss and leading to an increase in concentration (Wang et
417 al., 2017). In summary the reduction in SOC stock following the conversion of coastal wetland to
418 aquaculture ponds can be attributed to several factors. Among them to:

419 -Vegetation removal, which disrupts the natural carbon sequestration processes and reduces the
420 input of organic matter to soil.

421 -The construction of aquaculture ponds involves significant soil disturbance, including the
422 alteration of soil structure and the removal of the topsoil layer, which contains a high concentration
423 of organic carbon,, and moreover the change in soil physicochemical properties such as: soilpH, bulk
424 density, wàter status and bulk density.

425 -Anthropogenic disturbances such as the addition of feed and chemicals, that futher disrupt soi
426 microbial activity, affecting carbon cycling processes

427 -Hydrological Changes: The conversion alters the natural hydrology of wetlands, affecting the
428 water table and soil moisture content, which are critical factors for maintaining high SOC levels in
429 wetland soils.

430 ***4.4 Implications for wetland C management***

431 Coastal wetlands provide a wide range of economic and ecosystem services and play a crucial role
432 in carbon sequestration (Macreadie et al., 2013; Hao et al., 2024). Our study clearly shows the
433 significant loss of carbon caused by the conversion of coastal wetlands to aquaculture ponds,
434 thereby affecting the carbon-sink capacity of wetlands. Duan et al. (2020) reported, by analyzing
435 Landsat 8 images of 2017, that human-reclaimed ponds in China's coastal area covered a total
436 surface of 15,633 km². Given our mean estimation of a loss of 983 t C km² in the 0-30 cm of soil by
437 conversion, we can estimate that approximately 15,352t of carbon has been lost in this process. This
438 is equivalent to 0.56 Gt of CO₂. Considering that in 2022 the total CO₂ emitted by human activities
439 globally was 36.8 Gt (International Energy Agency), the wetland to pond conversion in China over

440 the last decades is equivalent to 1.52% of current annual human CO₂ emissions.

441 There is an urgent need for specific initiatives and actions that encourage the sustainable
442 management and conservation of coastal wetlands to maintain the stability of soil carbon pools and
443 long-term carbon sequestration potential, and to minimize the continuation of reclamation for
444 agricultural needs and economic benefits (Bu et al., 2015). Additionally, the targets of the
445 Kunming-Montreal Global Biodiversity Framework (KM-GBF) call for the reduction of losses in
446 areas of high biodiversity importance to near zero by 2030 (Joly, 2022). Therefore, there is an
447 urgent need to find a balance between economic development and ecological protection while
448 safeguarding the livelihoods of coastal residents. Encouraging the sustainable management and
449 protection of coastal wetlands is critical (Bu et al., 2015; Fu et al., 2024). Assessing the restoration
450 potential of these lands requires a better understanding of current land use, the objectives of the
451 communities that own and manage the land, and acceptable alternative livelihood options.

452

453 **5. Conclusions**

454 Wetland conversion, sampling sites, and their interaction significantly affected SOC concentration
455 and its stock. Specifically, the reclamation of coastal wetlands into aquaculture ponds resulted in a
456 significant mean decrease in SOC concentration at depths of 0-15 cm and 15-30 cm by 35.5% and
457 30.3%, respectively ($p < 0.05$), as well as a decrease in SOC stock, LOC, and MBC concentrations
458 ($p < 0.05$). In contrast, soil DOC concentration was found to be 15.8% higher in aquaculture ponds
459 compared to coastal wetlands ($p < 0.05$). Furthermore, soils in aquaculture ponds had significantly
460 higher bulk density (11.3%) and lower salinity (61.0%), SWC (11.7%), total nitrogen concentration
461 (23.8%), and available nitrogen concentration (37.7%) compared to coastal wetlands ($p < 0.05$).
462 Redundancy analysis indicated that pH, bulk density, and total nitrogen concentration explained
463 most of the temporal variations in SOC fractions and stock between two community types. Our
464 results clearly showed that the conversion from wetland to ponds destabilizes SOC and, by reducing

465 organic matter inputs, strongly decreases soil C stock. But these effects significantly depends on the
466 natural vegetation removed during wetland conversion. The extent of SOC loss is closely related to
467 the biomass of natural vegetation; the greater the biomass removed, the more substantial the SOC
468 loss after conversion.

469

470

471 **Declaration of competing interest** The authors declare no competing interests.

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473 **References**

474 Bai, J., Xiao, R., Zhang, K., Gao, H., Cui, B., & Liu, X. (2013). Soil organic carbon as affected by
475 land use in young and old reclaimed regions of a coastal estuary wetland, China. *Soil Use and*
476 *Management*, 29(1), 57-64.

477 Blair, G. J., Lefroy, R. D., & Lisle, L. (1995). Soil carbon fractions based on their degree of
478 oxidation, and the development of a carbon management index for agricultural systems.
479 *Australian Journal of Agricultural Research*, 46(7), 1459-1466.

480 Borken, W., Ahrens, B., Schulz, C., & Zimmermann, L. (2011). Site-to-site variability and temporal
481 trends of DOC concentrations and fluxes in temperate forest soils. *Global Change Biology*,
482 17(7), 2428-2443.

483 Bridgman, S. D., Megonigal, J. P., Keller, J. K., Bliss, N. B., & Trettin, C. (2006). The carbon
484 balance of North American wetlands. *Wetlands*, 26(4), 889-916.

485 Bu, N. S., Qu, J. F., Li, G., Zhao, B., Zhang, R. J., & Fang, C. M. (2015). Reclamation of coastal
486 salt marshes promoted carbon loss from previously-sequestered soil carbon pool. *Ecological*
487 *Engineering*, 81, 335-339.

488 Canfield, D. E., Thamdrup, B., & Hansen, J. W. (1993). The anaerobic degradation of organic
489 matter in Danish coastal sediments: iron reduction, manganese reduction, and sulfate reduction.
490 *Geochimica et Cosmochimica Acta*, 57(16), 3867-3883.

491 Chmura, G. L., Anisfeld, S. C., Cahoon, D. R., & Lynch, J. C. (2003). Global carbon sequestration
 492 in tidal, saline wetland soils. *Global Biogeochemical Cycles*, 17(4), 1111.

493 Chung, H., Ngo, K. J., Plante, A., & Six, J. (2010). Evidence for carbon saturation in a highly
 494 structured and organic-matter-rich soil. *Soil Science Society of America Journal*, 74(1),
 495 130-138.

496 Datta, S. P., Rattan, R. K., & Chandra, S. (2010). Labile soil organic carbon, soil fertility, and crop
 497 productivity as influenced by manure and mineral fertilizers in the tropics. *Journal of Plant*
 498 *Nutrition and Soil Science*, 173(5), 715-726.

499 Davidson, N. C., & Finlayson, C. M. (2019). Updating global coastal wetland areas presented in
 500 Davidson and Finlayson (2018). *Marine and Freshwater Research*, 70(8), 1195-1200.

501 DeGryze, S., Six, J., Paustian, K., Morris, S. J., Paul, E. A., & Merckx, R. (2004). Soil organic
 502 carbon pool changes following land-use conversions. *Global Change Biology*, 10(7),
 503 1120-1132.

504 Duan, Y., Li, X., Zhang, L., Chen, D., & Ji, H. (2020). Mapping national-scale aquaculture ponds
 505 based on the Google Earth Engine in the Chinese coastal zone. *Aquaculture*, 520, 734666.

506 Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I., & Marbà, N. (2013). The role of coastal
 507 plant communities for climate change mitigation and adaptation. *Nature Climate Change*,
 508 3(11): 961-968.

509 Elser, J. J., Fagan, W. F., Denno, R. F., Dobberfuhl, D. R., Folarin, A., Huberty, A., Interlandi, S. S.,
 510 Kilham, S., McCauley, E., Schulz, K. L., Siemann, E. H., & Sterner, R. W. (2000). Nutritional
 511 constraints in terrestrial and freshwater food webs. *Nature*, 408(6812), 578-580.

512 Fang, Y., Singh, B.P., Collins, D., Armstrong, R., Van Zwieten, L., & Tavakkoli, E. (2020). Nutrient
 513 stoichiometry and labile carbon content of organic amendments control microbial biomass and
 514 carbon-use efficiency in a poorly structured sodic-subsoil. *Biology and Fertility of Soils*, 56,
 515 219-233.

516 Fu, C., Steckbauer, A., Mann, H., & Duarte, C. M. (2024). Achieving the Kunming–Montreal
 517 global biodiversity targets for blue carbon ecosystems. *Nature Reviews Earth & Environment*,
 518 5, 538-552.

519 Gao, Y., Zhou, J., Wang, L., Guo, J., Feng, J., Wu, H., & Lin, G. (2019). Distribution patterns and
 520 controlling factors for the soil organic carbon in four mangrove forests of China. *Global*
 521 *Ecology and Conservation*, 17, e00575.

522 Gong, W., Duan, X., Sun, Y., Zhang, Y., Ji, P., Tong, X., Qiu, Z., & Liu, T. (2023). Multi-scenario
 523 simulation of land use/cover change and carbon storage assessment in Hainan coastal zone
 524 from perspective of free trade port construction. *Journal of Cleaner Production*, 385, 135630.

525 Gu, B., Schmitt, J., Chen, Z., Liang, L., & McCarthy, J. F. (1994). Adsorption and desorption of
 526 natural organic matter on iron oxide: mechanisms and models. *Environmental Science &*
 527 *Technology*, 28(1), 38-46.

528 Hagedorn, F., Kaiser, K., Feyen, H., & Schleppi, P. (2000). Effects of redox conditions and flow
 529 processes on the mobility of dissolved organic carbon and nitrogen in a forest soil (Vol. 29, No.
 530 1, pp. 288-297). American Society of Agronomy, Crop Science Society of America, and Soil
 531 Science Society of America.

532 Han, L., Sun, K., Yang, Y., Xia, X., Li, F., Yang, Z., & Xing, B. (2020). Biochar's stability and
 533 effect on the content, composition and turnover of soil organic carbon. *Geoderma*, 364,
 534 114184.

535 Hao, Q., Song, Z., Zhang, X., He, D., Guo, L., van Zwieten, L., Yu, C., Wang, Y., Wang, W., Fang,
 536 Y., Fang, Y., Liu, C & Wang, H. (2024). Organic blue carbon sequestration in vegetated
 537 coastal wetlands: Processes and influencing factors. *Earth-Science Reviews*, 255, 04853.

538 Hopkinson, C. S., Cai, W. J., & Hu, X. (2012). Carbon sequestration in wetland dominated coastal
 539 systems—a global sink of rapidly diminishing magnitude. *Current Opinion in Environmental*
 540 *Sustainability*, 4(2), 186-194.

541 Hong, C., Burney, J. A., Pongratz, J., Nabel, J. E., Mueller, N. D., Jackson, R. B., & Davis, S. J.
 542 (2021). Global and regional drivers of land-use emissions in 1961–2017. *Nature*, 589(7843),
 543 554-561.

544 Howe, A. J., Rodríguez, J. F., & Saco, P. M. (2009). Surface evolution and carbon sequestration in
 545 disturbed and undisturbed wetland soils of the Hunter estuary, southeast Australia. *Estuarine,
 546 Coastal and Shelf Science*, 84(1), 75-83.

547 Hu, M., Sardans, J., Yang, X., Peñuelas, J., & Tong, C. (2020). Patterns and environmental drivers
 548 of greenhouse gas fluxes in the coastal wetlands of China: A systematic review and synthesis.
 549 *Environmental Research*, 186, 109576.

550 Hu, W., Shao, M., Wang, Q., Fan, J., & Horton, R. (2009). Temporal changes of soil hydraulic
 551 properties under different land uses. *Geoderma*, 149(3-4), 355-366.

552 Ibrahim, M. M., Zhang, H., Guo, L., Chen, Y., Heiling, M., Zhou, B., & Mao, Y. (2021). Biochar
 553 interaction with chemical fertilizer regulates soil organic carbon mineralization and the
 554 abundance of key C-cycling-related bacteria in rhizosphere soil. *European Journal of Soil
 555 Biology*, 106, 103350.

556 International Energy Agency. <https://www.iea.org/reports/co2-emissions-in-2022>. Purchased
 557 3/4/2024.

558 Jangid, K., Williams, M. A., Franzluebbers, A. J., Sanderlin, J. S., Reeves, J. H., Jenkins, M. B.,
 559 Endale Dinku. M., Coleman D. C., & Whitman, W. B. (2008). Relative impacts of land-use,
 560 management intensity and fertilization upon soil microbial community structure in agricultural
 561 systems. *Soil Biology and Biochemistry*, 40(11), 2843-2853.

562 Jin, X., Huang, J., & Zhou, Y. (2012). Impact of coastal wetland cultivation on microbial biomass,
 563 ammonia-oxidizing bacteria, gross N transformation and N₂O and NO potential production.
 564 *Biology and Fertility of Soils*, 48, 363-369.

565 Jobbágy, G. E., & Jackson, R. B. (2001). The distribution of soil nutrients with depth: Global
 566 patterns and the imprint of plants. *Biogeochemistry*, 53(1):51-77.

567 Joly, C. A. (2022). The Kunming-Montréal global biodiversity framework. *Biota Neotropica*, 22(4),
568 e2022e001.

569 Kalbitz, K., Meyer, A., Yang, R., & Gerstberger, P. (2007). Response of dissolved organic matter in
570 the forest floor to long-term manipulation of litter and throughfall inputs. *Biogeochemistry*, 86,
571 301-318.

572 Kasper, M., Buchan, G. D., Mentler, A., & Blum, W. E. H. (2009). Influence of soil tillage systems
573 on aggregate stability and the distribution of C and N in different aggregate fractions. *Soil and*
574 *Tillage Research*, 105(2), 192-199.

575 Laiho, R., Laine, J., Trettin, C. C., & Finér, L. (2004). Scots pine litter decomposition along
576 drainage succession and soil nutrient gradients in peatland forests, and the effects of
577 inter-annual weather variation. *Soil Biology and Biochemistry*, 36(7), 1095-1109.

578 Li, Q., Song, Z., Xia, S., Kuzyakov, Y., Yu, C., Fang, Y., Chen, J., Wang, Y., Shi, Y., Luo, Y., Li,
579 Y., Chen, J., Wang, W., Zhang, J., Fu, X., Vancov, T., Van Zwieten, L., Liu, C., & Wang, H.
580 (2023a). Microbial necromass, lignin, and glycoproteins for determining and optimizing blue
581 carbon formation. *Environmental Science & Technology*, 58(1), 468-479.

582 Li, Y., Fu, C., Hu, J., Zeng, L., Tu, C., & Luo, Y. (2023b). Soil carbon, nitrogen, and phosphorus
583 stoichiometry and fractions in blue carbon ecosystems: implications for carbon accumulation
584 in allochthonous-dominated habitats. *Environmental Science & Technology*, 57(14),
585 5913-5923.

586 Lin, G., & Lin, X. (2022). Bait input altered microbial community structure and increased
587 greenhouse gases production in coastal wetland sediment. *Water Research*, 218, 118520.

588 Lin, S., Wang, W., Sardans, J., Lan, X., Fang, Y., Singh, B. P., Xu, X., Wiesmeier, M., Tariq, A.,
589 Zeng, F., Alrefaei, A. F., & Penuelas, J. (2022). Effects of slag and biochar amendments on
590 microorganisms and fractions of soil organic carbon during flooding in a paddy field after two
591 years in southeastern China. *Science of the Total Environment*, 824, 153783.

592 Lin, Y., Munroe, P., Joseph, S., Henderson, R., & Ziolkowski, A. (2012). Water extractable organic
593 carbon in untreated and chemical treated biochars. *Chemosphere*, 87, 151–157.

594 Lu, R. K. (2000). Analysis Methods of Soil Science and Agricultural Chemistry. Agriculture
595 Science and Technology Press, Beijing, China.

596 Luo, Z., Viscarra-Rossel, R. A., & Qian, T. (2021). Similar importance of edaphic and climatic
597 factors for controlling soil organic carbon stocks of the world. *Biogeosciences*, 18(6),
598 2063-2073.

599 Lv, X., Yu, P., Mao, W., & Li, Y. (2018). Vertical variations in bacterial community composition
600 and environmental factors in the culture pond sediment of sea cucumber *Apostichopus*
601 *japonicus*. *Journal of Coastal Research*, 84, 69-76.

602 Macreadie, P. I., Hughes, A. R., & Kimbro, D. L. (2013). Loss of ‘blue carbon’ from coastal salt
603 marshes following habitat disturbance. *PloS One*, 8(7), e69244.

604 Mao, D. H., Wang, Z. M., Li, L., Miao, Z. H., Ma, W. H., Song, C. C., Ren, C. Y., & Jia, M. M.
605 (2015). Soil organic carbon in the Sanjiang Plain of China: storage, distribution and controlling
606 factors. *Biogeosciences*, 12(6), 1635-1645.

607 Mishra, U., Ussiri, D. A., & Lal, R. (2010). Tillage effects on soil organic carbon storage and
608 dynamics in Corn Belt of Ohio USA. *Soil and Tillage Research*, 107(2), 88-96.

609 Osland, M. J., Chivoiu, B., Enwright, N. M., Thorne, K. M., Guntenspergen, G. R., Grace, J. B.,
610 Dale, L. L., Brooks, W., Herold, N., Day, J. W., Sklar, F. H., & Swarzenzki, C. M. (2022).
611 Migration and transformation of coastal wetlands in response to rising seas. *Science Advances*,
612 8(26), eabo5174.

613 Prommer, J., Walker, T. W., Wanek, W., Braun, J., Zezula, D., Hu, Y., Hofhansl, F., & Richter, A.
614 (2020). Increased microbial growth, biomass, and turnover drive soil organic carbon
615 accumulation at higher plant diversity. *Global Change Biology*, 26(2), 669-681.

616 Schuster, L., Taillardat, P., Macreadie, P. I., & Malerba, M. E. (2024). Freshwater wetland
617 restoration and conservation are long-term natural climate solutions. *Science of the Total*
618 *Environment*, 922, 171218.

619 Spaccini, R., & Piccolo, A. (2013). Effects of field managements for soil organic matter
620 stabilization on water-stable aggregate distribution and aggregate stability in three agricultural
621 soils. *Journal of Geochemical Exploration*, 129, 45-51.

622 Spohn, M., Babka, B., & Giani, L. (2013). Changes in soil organic matter quality during
623 sea-influenced marsh soil development at the North Sea coast. *Catena*, 107, 110-117.

624 Tan, L., Ge, Z., Ji, Y., Lai, D. Y., Temmerman, S., Li, S., Li, X., & Tang, J. (2022). Land use and
625 land cover changes in coastal and inland wetlands cause soil carbon and nitrogen loss. *Global*
626 *Ecology and Biogeography*, 31(12), 2541-2563.

627 Tan, L., Ge, Z., Zhou, X., Li, S., Li, X., & Tang, J. (2020). Conversion of coastal wetlands, riparian
628 wetlands, and peatlands increases greenhouse gas emissions: A global meta-analysis. *Global*
629 *Change Biology*, 26(3), 1638-1653.

630 Thorburn, P. J., Meier, E. A., Collins, K., & Robertson, F. A. (2012). Changes in soil carbon
631 sequestration, fractionation and soil fertility in response to sugarcane residue retention are
632 site-specific. *Soil and Tillage Research*, 120, 99-111.

633 Tian, H., Chen, G., Zhang, C., Melillo, J. M., & Hall, C. A. (2010). Pattern and variation of C: N: P
634 ratios in China's soils: a synthesis of observational data. *Biogeochemistry*, 98, 139-151.

635 Troell, M., Kautsky, N., Beveridge, M., Henriksson, P., Primavera, J., Rönnbäck, P., Folke, C.
636 (2013). Aquaculture. In: Levin, S.A. (Ed.), *Encyclopedia of Biodiversity*, second ed. Academic
637 Press, Waltham, pp. 189-201.

638 Tu, J., Wang, B., McGrouther, K., Wang, H., Ma, T., Qiao, J., & Wu, L. (2017). Soil quality
639 assessment under different *Paulownia fortunei* plantations in mid-subtropical China. *Journal of*
640 *Soils and Sediments*, 17, 2371-2382.

641 Vance, E.D., Brookes, P.C., & Jenkinson, D.S. (1987). An extraction method for measuring soil
642 microbial biomass C. *Soil Biology and Biochemistry*, 19, 703-707.

643 Wan, S., Mou, X., & Liu, X. (2018). Effects of reclamation on soil carbon and nitrogen in coastal
644 wetlands of Liaohe River Delta, China. *Chinese Geographical Science*, 28, 443-455.

645 Wang, C., Tong, C., Chambers, L. G., & Liu, X. (2017). Identifying the salinity thresholds that
646 impact greenhouse gas production in subtropical tidal freshwater marsh soils. *Wetlands*, 37,
647 559-571.

648 Wang, W., Sardans, J., Wang, C., Zeng, C., Tong, C., Chen, G., Huang, J., Pan, H., Peguero, G.,
649 Vallicrosa, H., & Peñuelas, J. (2019). The response of stocks of C, N, and P to plant invasion
650 in the coastal wetlands of China. *Global Change Biology*, 25(2), 733-743.

651 Wang, W., Sardans, J., Zeng, C., Zhong, C., Li, Y., & Peñuelas, J. (2014). Responses of soil
652 nutrient concentrations and stoichiometry to different human land uses in a subtropical tidal
653 wetland. *Geoderma*, 232, 459-470.

654 Wang, X., Xiao, X., Xu, X., Zou, Z., Chen, B., Qin, Y., Zhang, X., Dong, J., Liu, D., Pan, L., & Li,
655 B. (2021). Rebound in China's coastal wetlands following conservation and restoration.
656 *Nature Sustainability*, 4(12), 1076-1083.

657 Wolaver, T. G., & Spurrier, J. D. (1988). Carbon transport between a euhaline vegetated marsh in
658 South Carolina and the adjacent tidal creek: contributions via tidal inundation, runoff and
659 seepage. *Marine Ecology Progress Series*, 42(1):53-62.

660 Xia, S., Song, Z., Van Zwieten, L., Guo, L., Yu, C., Wang, W., Li, Q., Hartley, I. P., Yang, Y., Liu,
661 H., Wang, Y., Ran, X., Liu, C., & Wang, H. (2022). Storage, patterns and influencing factors
662 for soil organic carbon in coastal wetlands of China. *Global Change Biology*, 28(20),
663 6065-6085.

664 Xiao, D., Deng, L., Kim, D. G., Huang, C., & Tian, K. (2019). Carbon budgets of wetland
665 ecosystems in China. *Global Change Biology*, 25(6), 2061-2076.

666 Xu, M., Lou, Y., Sun, X., Wang, W., Baniyamuddin, M., & Zhao, K. (2011). Soil organic carbon
667 active fractions as early indicators for total carbon change under straw incorporation. *Biology*
668 & *Fertility of Soils*, 47, 745-752.

669 Xu, X., Chen, M., Yang, G., Jiang, B., & Zhang, J. (2020). Wetland ecosystem services research: A
670 critical review. *Global Ecology and Conservation*, 22, e01027.

671 Yang, P., Bastviken, D., Jin, B. S., Mou, X. J., Tong, C., & Yao, Y. (2017). Effects of coastal marsh
672 conversion to shrimp aquaculture ponds on CH₄ and N₂O emissions. *Estuarine, Coastal and*
673 *Shelf Science*, 199, 125-131.

674 Yang, P., He, Q., Huang, J., & Tong, C. (2015). Fluxes of greenhouse gases at two different
675 aquaculture ponds in the coastal zone of southeastern China. *Atmospheric Environment*, 115,
676 269-277.

677 Yang, P., Zhang, L., Lai, D. Y., Yang, H., Tan, L., Luo, L., Tong, c., Hiong, Y., Zhu, W., & Tang,
678 K. W. (2022a). Landscape change affects soil organic carbon mineralization and greenhouse
679 gas production in coastal wetlands. *Global Biogeochemical Cycles*, 36(12), e2022GB007469.

680 Yang, P., Tang, K. W., Tong, C., Lai, D. Y., Zhang, L., Lin, X., Yang, H., Tan, L., Zhang, Y. Hong,
681 Y., Tang, C., & Lin, Y. (2022b). Conversion of coastal wetland to aquaculture ponds decreased
682 N₂O emission: Evidence from a multi-year field study. *Water Research*, 227, 119326.

683 Yao, H. (2013). Characterizing landuse changes in 1990-2010 in the coastal zone of Nantong,
684 Jiangsu province, China. *Ocean Coast Management*, 71, 108-115.

685 Zhang, G., Bai, J., Zhao, Q., Jia, J., Wang, X., Wang, W., & Wang, X. (2021). Soil carbon storage
686 and carbon sources under different *Spartina alterniflora* invasion periods in a salt marsh
687 ecosystem. *Catena*, 196, 104831.

688 Zhang, K., Delgado-Baquerizo, M., Zhu, Y. G., & Chu, H. (2020). Space is more important than
689 season when shaping soil microbial communities at a large spatial scale. *Msystems*, 5(3),
690 10-1128.

691 Zhang, M., Zhang, X., Liang, W., Jiang, Y., Dai, G., Wang, X., & Han, S. (2011). Distribution of
692 soil organic carbon fractions along the altitudinal gradient in Changbai Mountain, China.
693 *Pedosphere*, 21(5), 615-620.

694 Zhang, T., Song, B., Han, G., Zhao, H., Hu, Q., Zhao, Y., & Liu, H. (2023). Effects of coastal
695 wetland reclamation on soil organic carbon, total nitrogen, and total phosphorus in China: a
696 meta-analysis. *Land Degradation & Development*, 34(11), 3340-3349.

697 Zhang, Y., Ding, W., Luo, J., & Donnison, A. (2010). Changes in soil organic carbon dynamics in
698 an Eastern Chinese coastal wetland following invasion by a C₄ plant *Spartina alterniflora*. *Soil*
699 *Biology and Biochemistry*, 42(10), 1712-1720.

700 Zhou, J., Zhang, J., Chen, Y., Qin, G., Cui, B., Lu, Z., Wu, J., Huang, X., Thapa, P., Li, H., & Wang,
701 F. (2023). Blue carbon gain by plant invasion in saltmarsh overcompensated carbon loss by
702 land reclamation. *Carbon Research*, 2(1), 39.

703 Zhu, Y., Wang, Y., Guo, C., Xue, D., Li, J., Chen, Q., Song, Z., Lou, Y., Kuzyakov, Y., Wang, Z
704 & Jones, D. L. (2020). Conversion of coastal marshes to croplands decreases organic carbon
705 but increases inorganic carbon in saline soils. *Land Degradation & Development*, 31(9),
706 1099-1109.

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Table 1. Sampling sites description. The reclamation years of aquaculture ponds at each sampling site were obtained by remote sensing image interpretation, literature review and field investigation. Soil samples were collected at depths of 0-15 cm and 15-30 cm.

Sampling sites abbreviation	Location of sampling sites	Geographic location	Wetland types before reclamation	Years of breeding ponds
Liaoh River Estuary (S1)	Lujia Town, Shuangtaizi District, Panjin City, Liaoning Province	N40°41'~41°27' E121°30'~122°30'	<i>Suaeda salsa</i>	Around 40 years
Yellow River Estuary (S2)	Kenli District, Dongying City, Shandong Province	N37°40'~38°10' E118°41'~119°16'	<i>Suaeda salsa</i>	Around 15 years
Yancheng (S3)	Sheyang County, Yancheng City, Jiangsu Province	N32°48'~34°29' E119°53'~121°18'	<i>Phragmites australis</i>	Around 20 years
Yangtze River Estuary (S4)	Chongming Island, Chongming District, Shanghai City	N31°25'~31°38' E121°50'~122°5'	<i>Phragmites australis</i>	Around 30 years
Hangzhou Bay (S5)	Cixi City, Zhejiang Province	N30°17'~30°20' E121°5'~121°10'	<i>Phragmites australis</i>	Around 30 years
Minjiang River Estuary (S6)	Tantou Town, Changle District, Fuzhou City, Fujian Province	N26°00'~26°03' E119°34'~119°40'	<i>Phragmites australis</i>	Around 30 years
Jiulong River Estuary (S7)	Fugong Town, Longhai District, Zhangjiang City, Fujian Province	N24°23'~24°27' E117°54'~117°56'	Mangroves (<i>Aegiceras corniculatum</i>)	Around 20 years
Zhangjiang River Estuary (S8)	Dongxia Town, Yunxiao County, Zhangjiang City, Fujian Province	N24°23'33"~24°27' E117°23'~117°32'	Mangroves (<i>Kandelia candel</i>)	Around 40 years
Zhenzhu Bay (S9)	Fangcheng District, Fangchenggang City, Guangxi Province	N21°31'~21°37' E108°00'~108°16'	Mangroves (<i>Aegiceras corniculatum</i>)	Around 20 years
Zhanjiang (S10)	Gaoqiao Town, Lianjiang City, Guangdong Province	N21°9'~21°34' E109°44'~109°56'	Mangroves (<i>Bruguiera</i>)	Around 20 years

			<i>gymnorhiza</i>)	
Dongzhai port	Yanfeng Town, Haikou City,	N19°51'~20°1'	Mangroves	
(S11)	Hainan Province	E110°32'~110°37'	(<i>Bruguiera</i>	Around 20 years
			<i>gymnorhiza</i>)	

Figure captions

Figure 1. Sampling sites and plant communities of tropical to temperate regions of the China coast were sampled at 11 dependent wetland types and 11 sampling sites, including Liaohe River Estuary (S1), Yellow River Estuary (S2), Yancheng (S3), Yangtze River Estuary (S4), Hangzhou Bay (S5), Minjiang River Estuary (S6), Jiulong River Estuary (S7), Zhangjiang River Estuary (S8), Zhenzhu Bay (S9), Zhanjiang (S10), and Dongzhai Port (S11), with a total of 220 samples. Each site had two community types, one with only native species (*Suaeda salsa*, *Phragmites australis*, and Mangroves) and the other with reclaimed aquaculture ponds. Soil samples were collected at depths of 0-15 cm and 15-30 cm.

Figure 2. Physicochemical characterization at 0-30 cm depth for the coastal wetlands and aquaculture ponds across the 11 sampling sites. Properties measured include soil bulk density (BD; a), pH (b), salinity (c), soil water content (SWC; d), total nitrogen (TN; e), available nitrogen (AN; f), total phosphorus (TP; g), available phosphorus (AP; h), C:N ratio (i), C:P ratio (j), N:P ratio (k), and AN:AP ratio (l). Data represent means and standard errors (n=110). Different letters indicate significant differences between coastal wetlands and aquaculture ponds ($p < 0.05$).

Figure 3. (a) Variations at 0-15 cm and 15-30 cm depth of SOC concentration after converting wetlands into aquaculture ponds across 11 sampling sites, shown in the left-side histogram, and corresponding boxplots on the right. Two-way ANOVA of the effects of land use (treatment) and site on SOC concentration are shown in the upper left corner of figure. (b) Distribution at 0-30 cm depth of SOC after coastal wetlands reclamation into aquaculture ponds across 11 sampling sites. Data represent means and standard errors (n=55). Different letters indicate significant differences between coastal wetlands and aquaculture ponds ($p < 0.05$).

Figure 4. Variations at 0-15 cm and 15-30 cm depth of SOC stock after converting wetlands into aquaculture ponds across the 11 sampling sites, shown in the left-side histogram, and corresponding boxplots on the right. Two-way ANOVA of the effects of land use (treatment) and site on SOC stock are shown in the upper left corner of figure. Data represent means and standard errors (n=55). Different letters indicate significant differences between coastal wetlands and aquaculture ponds ($p < 0.05$).

Figure 5. Boxplots of soil labile organic carbon (LOC; a), microbial biomass organic carbon (MBC; b), dissolved organic carbon (DOC; c) at 0-30 cm depth across coastal wetlands and aquaculture ponds. Data represent means and standard errors (n=110). Different letters indicate significant differences between coastal wetlands and aquaculture ponds ($p < 0.05$).

Figure 6. Pearson correlation analysis between SOC fractions and stock, and environmental variables at 0-30 cm depth across coastal wetlands and aquaculture ponds (n=110). SOC, soil organic carbon; LOC, labile organic carbon; MBC, microbial biomass organic carbon; DOC, dissolved organic carbon; BD, bulk density; SWC, soil water content; TN, total nitrogen; AN, available nitrogen; TP, total phosphorus; AP, available phosphorus. * and ** indicate significant correlations at $p < 0.05$ and 0.01, respectively.

Figure 7. Results of redundancy analysis (RDA), based on SOC fractions and stock, and environmental variables, using a Monte Carlo permutation test ($p < 0.05$). When the angles between the response and explanatory variables are acute, it represents a positive correlation between the

two variables; while obtuse angles represent a negative correlation. The pie chart shows the percentage of the variance of SOC fractions and stock explained by the different variables. SOC, soil organic carbon; LOC, labile organic carbon; MBC, microbial biomass organic carbon; DOC, dissolved organic carbon; BD, bulk density; SWC, soil water content; TN, total nitrogen; AN, available nitrogen; TP, total phosphorus; AP, available phosphorus.

Figure 8. Conceptual diagram illustrating the effects of reclamation into aquaculture ponds on SOC and active OC fractions along the tropical to temperate regions of the China coast. SOC, soil organic carbon; LOC, labile organic carbon; MBC, microbial biomass organic carbon; DOC, dissolved organic carbon; BD, bulk density.