Landscape Change Affects Soil Organic Carbon Mineralization
and Greenhouse Gas Production in Coastal Wetlands

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Abstract

Plant invasion and aquaculture activities have drastically modified the landscape of coastal wetlands in many countries, but their impacts on soil organic carbon (SOC) mineralization and greenhouse gas production remain poorly understood. We measured SOC mineralization rate and soil CO$_2$ and CH$_4$ production rates in three habitat types from 21 coastal sites across the tropical and subtropical zones in China: native mudflats (MFs), Spartina alterniflora marshes (SAs) and aquaculture ponds (APs). Landscape change from MFs to SAs or APs increased total and labile fraction of SOC, as well as carbon mineralization rate and greenhouse gas production, but there were no discernible differences in SOC source-sink dynamics between SAs and APs. SOC mineralization rate was highest in SAs (20.4 μg g$^{-1}$ d$^{-1}$), followed by APs (16.9 μg g$^{-1}$ d$^{-1}$) and MFs (11.9 μg g$^{-1}$ d$^{-1}$), with CO$_2$ as the dominant by-product. Bioavailable SOC was less than 2% and was turned over within 60 days in all three habitat types. Proliferation of S. alterniflora marshes and expansion of aquaculture pond construction had resulted in a net increase in soil CO$_2$-eq production of 0.4–4.3 Tg yr$^{-1}$ in the last three decades. Future studies will benefit from better census and monitoring of coastal habitats in China, complementary in situ measurements of greenhouse gas emissions, and more sampling in the southern provinces to improve spatial resolution.

Plain Language Summary

Wetlands are one of the largest reservoirs of soil carbon and play importance role in the global terrestrial biogenic carbon cycle. Coastal wetlands are major sinks for carbon due to high sedimentation rate and burial of
organic matter. However, landscape modifications due to invasive vegetation and aquaculture activities have profoundly impacted the carbon source-sink dynamics in coastal wetlands. We compared the soil organic carbon turnover and greenhouse gas (CO$_2$ and CH$_4$) production between native mudflat, *Spartina* marshes and aquaculture ponds in five coastal provinces across the tropical-subtropical gradient in China. Landscape modification of native mudflats increased soil carbon mineralization rate and greenhouse gas production, predominantly as CO$_2$, and the effect was consistent across the large geographical and climate gradients. Our results provide a better insight into the carbon dynamics in impacted wetlands across a large geographical range.
<table>
<thead>
<tr>
<th>54</th>
<th><strong>List of abbreviations:</strong></th>
<th>55</th>
<th>APs: Aquaculture ponds</th>
<th>BD: Soil Bulk Density</th>
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</thead>
<tbody>
<tr>
<td>56</td>
<td><strong>CO₂:</strong> Carbon Dioxide</td>
<td>56</td>
<td><strong>CH₄:</strong> Methane</td>
<td></td>
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<tr>
<td>57</td>
<td><strong>C₀:</strong> Bioavailable SOC</td>
<td>57</td>
<td><strong>DOC:</strong> Dissolved Organic Carbon</td>
<td></td>
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<tr>
<td>58</td>
<td><strong>DON:</strong> Dissolved Organic Nitrogen</td>
<td>58</td>
<td><strong>EF:</strong> Environmental Factors</td>
<td></td>
</tr>
<tr>
<td>59</td>
<td><strong>MBC:</strong> Microbial Biomass Carbon</td>
<td>59</td>
<td><strong>MFs:</strong> Mud flat</td>
<td></td>
</tr>
<tr>
<td>60</td>
<td><strong>MBN:</strong> Microbial Biomass Nitrogen</td>
<td>60</td>
<td><strong>SAs:</strong> <em>Spartina alterniflora</em> marshes</td>
<td></td>
</tr>
<tr>
<td>61</td>
<td><strong>Sal:</strong> Soil Salinity</td>
<td>61</td>
<td><strong>SOCM:</strong> SOC Mineralization Rate</td>
<td></td>
</tr>
<tr>
<td>62</td>
<td><strong>SOC:</strong> Soil Organic Carbon</td>
<td>62</td>
<td><strong>Soil C:N:</strong> Total Carbon: Total Nitrogen</td>
<td></td>
</tr>
<tr>
<td>63</td>
<td><strong>ΣSOCM:</strong> Cumulative anaerobic SOC Mineralization</td>
<td></td>
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<tr>
<td>64</td>
<td><strong>s(RR++):</strong> Standard error of RR++</td>
<td>64</td>
<td><strong>SPS:</strong> Soil Particle Size</td>
<td></td>
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<tr>
<td>65</td>
<td><strong>SWC:</strong> Soil Water Content</td>
<td>65</td>
<td><strong>RR:</strong> Response Ratio</td>
<td></td>
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<tr>
<td>66</td>
<td><strong>RR++:</strong> Weighted Response Ratio</td>
<td>66</td>
<td><strong>TC:</strong> Total Carbon</td>
<td></td>
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<tr>
<td>67</td>
<td><strong>TN:</strong> Total Nitrogen</td>
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1. Introduction

Wetlands are considered to be among the most productive but vulnerable ecosystems (Kirwan & Megonigal, 2013; Su et al., 2021; Wen et al., 2019). Despite covering just 4–6 % of the total land area, wetlands hold approximately 450 Pg of the global soil carbon, representing 25–30 % of the terrestrial biosphere carbon pool (Kayranli et al., 2010). Coastal wetlands are a crucial sink in the global carbon cycle due to high sedimentation rate and burial of organic matter (Drake et al., 2015; Packalen et al., 2014; Zhang et al., 2021a), and it is estimated that coastal wetlands globally store at least 53.7 Tg C yr\(^{-1}\) (Wang et al., 2021). However, wetland habitats have been impacted around the world, and despite international initiative to protect these habitats (e.g. Ramsar Convention on Wetlands), wetland degradation and loss rate remains high in Asia (Davidson, 2014), potentially altering the land’s carbon source-sink dynamics over different time and spatial scales (Mitsch et al., 2013).

Plant invasion and land-use change are two major threats to the world's coastal wetlands (Sun et al., 2015; Walker and Smith, 1997; Zhu et al., 2020). Invasive plant species may alter the soil microbial community compositions and dynamics, above- and below-ground carbon pools, primary productivity, and nutrient and carbon mineralization rates (Piper et al., 2015; Yuan et al., 2019; Zhang et al., 2010). Land-use change can modify hydrology, nutrient cycles, soil properties and overall ecosystem structure (Andreetta et al., 2016; Dick & Osunkoya, 2000; Gao et al., 2019). Increasing range shift by exotic species and coastal development will intensify these threats, potentially changing the dynamics of soil
organic carbon (SOC) and subsequent production of greenhouse gases such as carbon dioxide (CO$_2$) and methane (CH$_4$) (Gao et al., 2018a; Yang et al., 2017), and their feedback effect on climate is a major concern.

China accounts for about 4.2% of the global wetland area, and despite the conservation effort, wetlands still disappear at a rate close to 1% per year (Meng et al., 2017). Coastal wetlands in mainland China cover an estimated area of 5.79 M ha across its southern and eastern seabords, and invasion by *Spartina alterniflora* and land-use change for aquaculture have profoundly changed this coastal landscape (Duan et al., 2020; Ren et al., 2019; Sun et al., 2015). For example, *S. alterniflora* was first introduced into China in 1982 and by 2015, *S. alterniflora* marshes had covered 54,600 ha (Mao et al., 2019). Similarly, it has been estimated that coastal aquaculture ponds in China grew from 6,000 km$^2$ to ~10,000 km$^2$ in the past three decades (Duan et al., 2021). To-date, most of the research has been focused on changes to wetland ecosystem at the local scale, in terms of SOC (Gao et al., 2016), soil composition (Wang et al., 2019) and stability (Yang et al., 2016; Zhang et al., 2021b) and related carbon emissions (Gao et al., 2018b; Tan et al., 2020; Yang et al., 2017), but they do not allow for a fuller comparison of the SOC and greenhouse gas dynamics in impacted coastal wetlands across the wider geographical and environmental gradients. There has been only one study that compared SOC and plant biomass compositions (C, N and P) from eight coastal locations invaded by *S. alterniflora*, but it did not examine greenhouse gas production (Wang et al., 2019). Also, many of the coastal wetland areas in China have been converted into aquaculture ponds, which were
not included in the earlier study (Wang et al., 2019).

In order to generate a more comprehensive understanding of the biogeochemical consequences of habitat modification in coastal wetlands, we systematically studied 21 coastal wetland areas spanning 20°42’ N to 31°51’ N in mainland China. We hypothesized that soil organic carbon content and carbon mineralization rate would increase when mudflats were converted into marshes due to organic input from marsh vegetation, which could also lead to higher greenhouse gas production. We expected the soil properties to change in the opposite direction when marsh vegetation was removed to create aquaculture ponds. We further hypothesized that landscape modification dominated over other local environmental factors in affecting soil properties and greenhouse gas production across the broad latitudinal range.

To test these hypotheses, we sampled three habitat types at each location: native mudflats, mudflats that were converted into marshes by invasive *S. alterniflora*, and aquaculture ponds that were created from *S. alterniflora* marshes. We compared the soil physicochemical properties, SOC, carbon mineralization rate, and soil CO₂ and CH₄ production rates. The results will improve our understanding of the changes to soil characteristics in coastal wetlands as results of *S. alterniflora* invasion and aquaculture activities, the consequent carbon turnover and greenhouse gas production, and the related environmental drivers.

2. Methods
2.1. Study Area

Field sampling campaigns were conducted in five Chinese provinces including Shanghai (SH), Zhejiang (ZJ), Fujian (FJ), Guangdong (GD), and Guangxi (GX) (Figure 1). The large latitudinal and longitudinal ranges (20°42′ N to 31°51′ N; 109°11′ E to 122°11′ E) covered a tropical-to-subtropical climate gradient. The annual average temperature range was 11.0–23.0 °C and precipitation range was 1000–2200 mm across the five provinces. Their coastal wetlands combined cover about 2.58 × 10^6 ha, or 44.5 % of the total coastal wetlands in China (Sun et al., 2015), and they all have been impacted by *S. alterniflora* invasion or construction of aquaculture ponds. There was approximately 334 km^2 of *S. alterniflora* marshes (Liu et al., 2018) and 5309 km^2 of aquaculture ponds (Duan et al., 2020) along the coastal zone of the five provinces, representing 61.2% and 36.9% of the total areas of *S. alterniflora* marshes and aquaculture ponds, respectively, in China.

2.2. Soil Sampling

Field sampling was conducted in December 2019 and January 2020 at 21 sites across the five provinces, with two sites in SH, six in ZJ, nine in FJ, three in GD and one in GX (Figure 1). At each site, triplicate surface soil samples (top 20 cm) were collected from the three habitats (mud flat, *S. alterniflora* marshes and aquaculture ponds) using a steel corer (1.5 m length; 5 cm internal diameter) and transferred into ziplock bags; a total of 189 soil samples were collected (21 sampling sites × 3 habitats × 3 plots). All soil samples were transported in a chilled cooler to the laboratory, where they were stored at 4 °C until processing.
2.3. Analyses of Soil Physicochemical Properties.

In the laboratory, a subsample of the soil was freeze-dried, homogenized and then ground to a fine powder for measuring pH, salinity, soil particle size, inorganic nitrogen, Cl⁻, SO₄²⁻, total carbon (TC), total nitrogen (TN) and soil organic carbon (SOC). Soil pH was measured by an Orion 868 pH meter (Thermo Fisher Scientific, Cambridge, Massachusetts, USA; a 1:2.5 soil/distilled water mixture) with a measurement precision of ±1.0%. Soil salinity was measured by a Eutech Instruments-Salt6 salinity meter (Thermo Fisher Scientific, San Francisco, California, USA; a 1:5 soil/distilled water mixture) with a measurement precision of ±1.0%. A subsample was treated with the deflocculant hexametaphosphate and then analyzed for particle size based on laser diffraction (Mastersizer 2000, Malvern Instruments, Malvern, UK). Soil particle size (SPS) was calculated on a volume basis using the Malvern proprietary software. Soil inorganic nitrogen species (NH₄⁺-N and NO₃⁻-N) were extracted by 2 M KCl (Gao et al., 2019; Yin et al., 2017) and quantified by a flow injection analyzer (Skalar Analytical SAN⁺⁺, Netherlands) (Yang et al., 2021). The detection limit and relative standard deviation (RSD) for inorganic nitrogen were 0.6 μg L⁻¹ and ≤3.0% in 24 hr, respectively. Soil Cl⁻ and SO₄²⁻ contents were determined according to Chen & Sun (2020). Soil TC and TN were determined using a combustion analyzer (Elementar Vario MAX CN, ELEMENTAR, Hanau, Frankfurt, Germany) with a measurement precision of ±2.0%. Soil water content (SWC) and bulk density (BD) were determined after drying fresh soil at 105 °C for 48 h (Percival & Lindsay, 1997; Yin et al., 2019).
SOC was measured according to Liu et al. (2017). Briefly, 3 g of air-dried sample was
screened, weighed and extracted in 1 M hydrochloric acid (HCl) solution for 24 h, then
oven-dried at 60 °C. Afterward, SOC was determined by a combustion analyzer
(Elementar Vario MAX CN, ELEMENTAR, Hanau, Frankfurt, Germany) based on
standard procedures. The microbial biomass carbon (MBC) and nitrogen (MBN) contents
were measured using the chloroform fumigation extraction method (Templer et al., 2003;
Vance et al., 1987). Briefly, two portions of 10 g soil sample were fumigated with
ethanol-free CHCl₃ for 24 h; two additional 10 g samples were not fumigated (Wang et al.,
2011). All samples were then extracted in 0.5 M K₂SO₄ solution. Afterwards, the soil
extracts were analyzed for total dissolved organic carbon (DOC) and total dissolved
organic nitrogen (DON) using a TOC analyzer (Shimadzu TOC-VCPH/CPN, Kyoto, Japan)
with a measurement precision of ±2.0% and a flow injection analyzer (Skalar Analytical
SAN⁺⁺, Netherlands) with a measurement precision of ±3.0%, respectively. Soil MBC and
MBN contents were calculated from the differences in extractable DOC and DON
between fumigated and unfumigated samples, using a $K_{EC}$ (correction factor) of 0.38 for
MBC and 0.54 for MBN (Li et al., 2010; Vance et al., 1987).

2.4. Soil Organic Carbon Mineralization Incubation Experiment

The rates of anaerobic mineralization of SOC into CO₂ and CH₄ were determined
according to Kane et al. (2013) and Luo et al. (2019b). Briefly, approximately 30 g of
fresh soil sample was put into a 200 mL glass incubation bottle (in triplicate);
deoxygenated in situ water was then added in 1:1 v/v to make a slurry with 160 mL
headspace. All incubation bottles were flushed with pure N\textsubscript{2} gas for 5–8 min to create an anoxic condition (Vizza et al., 2017; Wassmann et al., 1998), then sealed with a silicone rubber and incubated for 60 days at *in situ* temperature. On Days 1, 3, 7, 14, 21, 30, 45 and 60, each bottle was shaken on a rotary shaker for 0.5 h at 200 rpm min\textsuperscript{-1} to drive CO\textsubscript{2} and CH\textsubscript{4} into the headspace (Luo et al., 2019a); 5 mL of the headspace gas sample was then withdrawn with a syringe and 5 mL of pure N\textsubscript{2} gas was added back to maintain the pressure (Yang et al., 2019). The extracted gas samples were analyzed for CH\textsubscript{4} and CO\textsubscript{2} on a gas chromatograph equipped with a flame ionization detector (FID) (GC-2010, Shimadzu, Japan). Three CH\textsubscript{4} (or CO\textsubscript{2}) gas standards, namely 1.96 (490.5), 8.25 (1003.4), and 100.3 (3090.3) ppm, were used in the calibration. The detection limits for CH\textsubscript{4} and CO\textsubscript{2} were 0.3 ppm and 1.0 ppm, respectively, and the measurement reproducibility was ≦ 2.0% and ≦ 3.0%, respectively. The measured CO\textsubscript{2} and CH\textsubscript{4} concentrations were corrected for pH, headspace volume, pressure and temperature (Ye et al., 2012), and was corrected for the dilution effect from the added N\textsubscript{2} gas (Tong et al., 2010). SOC mineralization rate [SOCM; $\mu$g C g\textsuperscript{-1} (dry weight) day\textsuperscript{-1}] was estimated from the combined CO\textsubscript{2} and CH\textsubscript{4} produced per gram of dry soil over time. Soil dry weight was calculated from the sample wet weight and its water content (see section 2.3). The cumulative mineralization of SOC over the 60 days of incubation (ΣSOBCM) was fitted to a first-order kinetic equation to derive the mineralization rate constant ($k$; d\textsuperscript{-1}) (Cooper et al., 2011; Hyvonen et al., 2005):

$$\Sigma\text{SOCM} = C_0 \times [1 - exp(-kt)]$$

Eq.(1)
where $\Sigma_{SOCM}$ is the cumulative amount of CO$_2$–C and CH$_4$–C mineralized from SOC ($\mu$g C g$^{-1}$), $C_0$ is the initial bioavailable SOC ($\mu$g C g$^{-1}$), and $t$ is the incubation time (d).

2.5. Calculation of $\Delta$EF, $\Delta$ΣSOCM and $\Delta$SOC Mineralization Parameters

To explore the synchronous responses of various environmental and soil parameters to habitat modification as results of plant invasion and aquaculture pond creation, we examined the rates of change of environmental factors ($\Delta$EF), cumulative SOC mineralization ($\Delta$ΣSOCM), and SOC mineralization parameters [$\Delta C_0$, $\Delta k$, and $\Delta(C_0/SOC)$], which were calculated as follows:

\[
\Delta EF = \frac{(EF_A - EF_B)}{EF_B} \quad \text{Eq. (2)}
\]

\[
\Delta \Sigma_{SOCM} = \frac{(\Sigma_{SOCM_A} - \Sigma_{SOCM_B})}{\Sigma_{SOCM_B}} \quad \text{Eq. (3)}
\]

\[
\Delta C_0 = \frac{C_{0A} - C_{0B}}{C_{0B}} \quad \text{Eq. (4)}
\]

\[
\Delta k = \frac{(k_A - k_B)}{k_B} \quad \text{Eq. (5)}
\]

\[
\Delta(C_0 / SOC) = \frac{[(C_0 / SOC)_A - (C_0 / SOC)_B]}{(C_0 / SOC)_B} \quad \text{Eq. (6)}
\]

where the subscripts B and A denote before and after habitat modification, respectively.

The relationships between $\Delta$ΣSOCM (or $\Delta$SOC mineralization parameters) and $\Delta$EF were further examined to reveal the key EF affecting SOC mineralization in the different habitats.

2.6. Calculation of Response Ratio and Weighted Response Ratio
The response ratio (RR) was calculated to assess the responses of SOCM, ΣSOCM, \( C_0 \) and \( k \) to habitat modification, following Hedges et al. (1999), Luo et al. (2006) and Tan et al. (2019). A total of 21 sites with data for treatment groups (habitats after modification) and control groups (habitats before modification) were used to calculate the natural logarithm of RR (lnRR):

\[
\text{Eq.(7)} \quad \ln \text{RR} = \ln \left( \frac{\bar{X}_T}{\bar{X}_C} \right) = \ln(\bar{X}_T) - \ln(\bar{X}_C)
\]

where the subscripts T and C denote treatment and control groups, respectively; \( X \) denotes the mean value of the parameter (SOCM, ΣSOCM, \( C_0 \) or \( k \)). The variance (\( v \)) was calculated as:

\[
\text{Eq.(8)} \quad v = \frac{S_T^2}{n_T \bar{X}_T^2} + \frac{S_C^2}{n_C \bar{X}_C^2}
\]

where \( n \) denotes the sample size and \( S \) the standard deviation.

We also calculated a weighted response ratio (RR++) from individual RR\(_{ij}\) (\( i = 1, 2, 3, \ldots, m \); \( j = 1, 2, 3, \ldots, y_i \)) pairwise comparison between treatment and control groups:

\[
\text{Eq.(9)} \quad \text{RR}^{++} = \frac{\sum_{j=1}^{m} \sum_{j=1}^{y_j} w_{ij} \text{RR}_{ij}}{\sum_{j=1}^{m} \sum_{j=1}^{y_j} w_{ij}}
\]

where \( m \) is the number of groups (different habitat types), \( y_i \) is the number of comparisons in the \( i \)th group, and \( w_{ij} \) is the weighting factor. \( w_{ij} \) and the standard error (s(RR++)) were calculated as follows:

\[
\text{Eq.(10)} \quad w_{ij} = \frac{1}{v}
\]
The 95% confidence interval (95% CI) for the log response ratio was estimated as:

\[
95\% \text{ CI} = \text{RR}_{++} \pm 1.96 \times s(\text{RR}_{++})
\]

If the 95% CI did not overlap with zero, the response of the concerned variable to habitat modification was considered significant.

### 2.7. Statistical Analysis.

All data were tested for normality and homogeneity of variance. Significant differences in environmental factors, SOC, ΣSOCM and SOC mineralization parameters \([ΔC_0, Δk, \text{ and } Δ(C_0/\text{SOC})]\) among habitat types were tested by analysis of variance (ANOVA) followed by pairwise comparisons. Pearson correlation analysis was used to examine the relationships between ΣSOCM (or SOC mineralization parameters) and environmental variables. Redundancy analysis (RDA) was performed to determine which ΔEF best explained the variability in ΔSOCM [or ΔC_0, Δk and Δ(C_0/SOC)]; input parameters for the analysis include ΔpH, Δsalinity, ΔSWC, ΔBD, ΔNH_4^+-N, ΔNO_3^-N, ΔCl^-, ΔSO_4^{2-}, ΔC:N, ΔSOC, ΔMBC, ΔMBN and ΔSPS. ANOVA and Pearson correlation analysis were done in SPSS 17.0 (SPSS Inc., USA); RDA was done in CANOCO 5.0 for Windows (Microcomputer Power, Ithaca, USA). All results were considered significant at \(p < 0.05\) and were summarized as mean ± 1 standard error, unless otherwise stated. Sampling site map, statistical plots and conceptual diagrams were produced using ArcGIS 10.2 (ESRI Inc., Redlands, CA, USA), OriginPro 9.0 (OriginLab Corp. USA) and EDraw Max.
version 7.3 (EdrawSoft, Hong Kong, China), respectively.

3. Results

3.1. Soil Properties Across Habitat Types.

The soil physicochemical properties were shown in Figure 2. There were no significant differences in mean soil pH (Figure 2a), salinity (Figure 2b), bulk density (Figure 2d), Cl$^-$ (Figure 2e), MBC (Figure 2h), soil C:N (Figure 2i) or soil particle size (Figs 2j-l) among the three habitat types ($p > 0.05$), but there were significant differences for the other parameters. Soil SO$_4^{2-}$ (Figure 2f) were higher in aquaculture ponds (APs) than in mud flats (MFs) and $S.$ alterniflora marshes (SAs) ($p < 0.05$ or $< 0.01$). Soil water content was higher in SAs and APs than in MFs ($p < 0.05$; Figure 2c). SOC (Figure 2g) was higher in SAs, followed by APs and MFs ($p < 0.01$).

3.2. Soil Organic Carbon Mineralization (SOCM) Rate

Across all sampling sites, the rate of CO$_2$ production from anaerobic SOC mineralization averaged 11.9 ± 1.6 $\mu$g g$^{-1}$ d$^{-1}$ in MFs, 20.4 ± 2.1 $\mu$g g$^{-1}$ d$^{-1}$ in SAs, and 16.9 ± 2.3 $\mu$g g$^{-1}$ d$^{-1}$ in APs (Figure 3a). Overall, CO$_2$ production rate decreased significantly among the three habitats in the order of SAs > APs > MFs ($p<0.01$). The rate of CH$_4$ production from SOC mineralization averaged 5.0 ± 1.4 ng g$^{-1}$ d$^{-1}$ in the MFs, 25.8 ± 2.8 ng g$^{-1}$ d$^{-1}$ in SAs, and 14.3 ± 1.3 ng g$^{-1}$ d$^{-1}$ in the APs (Figure 3b). Like CO$_2$, CH$_4$ production rate decreased significantly among the three habitats in the order of SAs > APs > MFs ($p<0.01$).
The SOCM rates for the different wetland habitat types are shown in Figure 4 and Figure S1. Because CO$_2$ production rates were 1000-fold higher than CH$_4$ production rates on a per mass basis, the SOCM rates were mainly driven by mineralization of SOC into CO$_2$. Across all sampling sites, the mean SOCM rates varied in the range of 3.9–20.5 μg g$^{-1}$ d$^{-1}$ for MFs, 7.2–38.2 μg g$^{-1}$ d$^{-1}$ for SAs, and 6.6–30.0 μg g$^{-1}$ d$^{-1}$ for APs (Figure 4a). The measured rates peaked on the 3rd day in all habitat types, then steadily decreased toward the end of the incubation (Figure 4a). The SOCM rate was significantly higher in SAs (20.4 ± 2.1 μg g$^{-1}$ d$^{-1}$), followed by APs (16.9 ± 2.4 μg g$^{-1}$ d$^{-1}$) and MFs (11.9 ± 1.7 μg g$^{-1}$ d$^{-1}$) ($p<0.05$ or $<0.01$) (Figure 4b).

3.3. Cumulative Soil Organic Carbon Mineralization ($\Sigma$SOCM)

$\Sigma$SOCM during the 60-d incubation period for the different wetland habitat types is shown in Figure 5 and Figure S2. $\Sigma$SOCM across all sampling sites was 35.5–186.9 μg g$^{-1}$ in MFs, 59.2–284.0 μg g$^{-1}$ in SAs, and 49.8–271.4 μg g$^{-1}$ in APs (Figure S2). $\Sigma$SOCM increased initially but then approached a plateau toward the end of the incubation, and the values increasingly diverged from one another among the three habitat types (Figure 5a) and there were significant differences among the three habitats ($p<0.05$ or $<0.01$) (Figure 5b). The mean $\Sigma$SOCM was highest in SAs (111.5 ± 12.6 μg g$^{-1}$), followed by APs (90.0 ± 12.8 μg g$^{-1}$) and MFs (65.2 ± 9.0 μg g$^{-1}$). At the end of the 60-day incubation, the mean $\Sigma$SOCM$_{final}$ was 95.0, 163.0 and 135.0 μg g$^{-1}$ for MFs, SAs and APs, respectively (Table 1).

3.4. First-Order Kinetic Model for Carbon Mineralization.
To better compare the mineralization processes across the wetland habitat types, the data were fitted to a first-order kinetic model. The values of the fitting parameters $C_0$ (initial bioavailable SOC) and $k$ (mineralization rate constant) are listed in Table 1 and Table S1. Across all the sampling sites, $C_0$ varied in the range of 48.1–252.3 μg g$^{-1}$ for MFs, 80.2–373.2 μg g$^{-1}$ for SAs, and 67.8–365.7 μg g$^{-1}$ for APs (Table S1). The mean $C_0$ was highest in SAs (152.3 μg g$^{-1}$), followed by APs (125.6 μg g$^{-1}$) and MFs (88.8 μg g$^{-1}$) (Table 1). MFs had a higher mean $k$ but lower $C_0$/SOC than the other two habitats (Table 1). The $\Sigma$SOCM$_{\text{final}}$/C$_0$ values varied by less than 0.5% among the three habitats (Table 1). The goodness of fit values (Adj. $R^2$) of the equations were all better than 0.94 (Table 1).

3.5. Response of Carbon Mineralization Parameters to Habitat Modification.

The Weighted response ratios (RR$_{++}$) of SOCM, $\Sigma$SOCM, $C_0$ and $k$ are shown in Figure 6. Conversion of MFs to SAs significantly ($p<0.05$) increased SOCM by 43.4% (range 21.9–61.1 %; Figure 6a), $\Sigma$SOCM by 40.4% (range 21.9–48.4 %; Figure 6b) and $C_0$ by 47.9% (Figure 6c). However, conversion of SAs to APs significantly ($p<0.05$) decreased SOCM by 22.2% (range 8.9–30.4 %; Figure 6a), $\Sigma$SOCM by 21.8% (range 16.0–31.5 %; Figure 6b), and $C_0$ by 24.5% (Figure 6c). Moreover, MF-to-SA and SA-to-AP conversions significantly increased $k$ by 3.2% and 2.9%, respectively ($p<0.05$) (Figure 6d).


Based on redundancy analysis (RDA), changes in EF ($\Delta$EF) presented in the ordination explained 69.0% of the variability in $\Delta$$\Sigma$SOCM, $\Delta$C$_0$, $\Delta$k, and $\Delta$(C$_0$/SOC) in the case of MF-to-SA conversion (Figure 7a), and 64.1% in the case of SA-to-AP conversion (Figure
Overall, ΔSOC was the most important driver of ΔΣSOCM in both scenarios of habitat modification, explaining 45.5% of the variability when MFs were converted to SAs (Figure 7a), and 37.2% when SAs were converted to APs (Figure 7b). Interestingly, ∆NH₄⁺-N was only a minor factor (4.8%) in MFs-to-SAs conversion, but it became the second main driver (16.2%) in SAs-to-APs conversion; ∆SO₄²⁻ played a slightly larger role in the latter scenario (6.4% vs. 8.5%). The correlation coefficients between changes in ΣSOCM, C₀, k and C₀/SOC and the different environmental variables for the different cases of habitat modification are shown in Table 2.

4. Discussion

4.1. Comparison of Soil Properties Among Habitat Types

Previous studies have shown that the soil physicochemical properties are sensitive to environmental changes and anthropogenic disturbances (e.g., Gao et al., 2019; Mueller et al., 2016; Wang et al., 2019). In the present study, we assessed the response of soil properties to habitat modification in impacted coastal wetlands in China. Among the variables examined, only soil SOC and SO₄²⁻ differed significantly among the three habitat types. The soil SO₄²⁻ in APs was about twice the concentration in MFs and SAs (Figure 2f). Similar results were reported earlier that soil SO₄²⁻ in the aquaculture ponds was 3–5 times higher than the natural saltmarsh (Gao et al., 2019). While SO₄²⁻ in the soil could be converted to H₂S by sulfate reducing bacteria under anaerobic condition and be lost from the system, the much larger volume of saltwater in APs might be able to replenish SO₄²⁻ more quickly, thereby maintaining a higher SO₄²⁻ concentration in the soil.
Additional SO$_4^{2-}$ may have also originated from aquaculture feeds and pond disinfectants (Feng, 2014; Zou et al., 2022).

Contrary to the expectation that use of feeds would increase the soil carbon content in aquaculture ponds, we found SOC in APs was significantly lower than SAs (Figure 2g). The results could be primarily attributed to higher productivity of the marsh vegetation leading to larger inputs of plant litter and root exudates into the soil (Mueller et al., 2016; Xia et al., 2021), which were eliminated when the vegetation was removed to create the aquaculture ponds. By comparison, SOC in the mudflats was the lowest likely due to the lack of autochthonous or allochthonous carbon inputs.

4.2. Production of Carbon Greenhouse Gases Among Habitat Types

Organic carbon in waterlogged soil is mineralized primarily via anaerobic microbial metabolism (e.g., Hopfensperger et al., 2014; Kostka et al., 2002), with CO$_2$ as the main by-product (e.g., Gribsholt & Kristensen, 2003; Kim et al., 2015; Luo et al., 2019b). This is consistent with our observations that CO$_2$ production rates were 1000-fold higher than CH$_4$ production rates on a per mass basis (Figure 3). Similar to earlier observations (Boulogne et al., 2016; Keller et al., 2015; Kim et al., 2015), it appeared that the bacterial communities required about three days to acclimate to the experimental condition before they reached maximum SOC mineralization rates, after which the rates decreased as labile organic carbon became depleted (Figure 4a).

It is worth noting that CO$_2$ and CH$_4$ production in our study was measured by incubation of slurries, which may not reflect the dynamic condition in situ where river flow and
periodic tidal flushing would change the soil conditions (Wells et al., 2018) and affect CO$_2$ and CH$_4$ production. Therefore, future research may consider *in situ* measurements using tracer technique, without the need for incubation, to give more accurate gas production rates.

### 4.3. Responses of Soil Carbon Turnover to Habitat Modification

The differences in SOC mineralization rate and cumulative SOC mineralization among the three habitat types (Figs. 4b and 5b) followed the differences in their SOC content (Figure 2g), showing that *S. alterniflora* invasion and aquaculture operation both increased labile soil organic substrates and subsequent mineralization activities relative to the native mudflats. Nevertheless, based on the first-order kinetic model, $C_0$/SOC was all under 0.02 (Table 1), meaning that < 2% of the soil organic carbon was bioavailable to microbes (labile to semi-labile), and the vast majority might be considered as refractory for longer-term burial. Our data also suggest that all bioavailable carbon was mineralized within 60 days, and the value of $\Sigma$SOCM$_{final}/C_0$ being slightly higher than 1 may be indicative of inherent uncertainty in deriving $C_0$ from curve fitting, or labile $C_0$ facilitating mineralization of some of the refractory carbon (i.e., priming effect; Guenet et al., 2010).

Based on our incubation experiments, the CO$_2$ production rate averaged 1.6 g C kg$^{-1}$ yr$^{-1}$ across the coastal wetlands in our study. Assuming this represented the labile fraction of carbon deposition, the corresponding potential burial of refractory carbon would be ~8.4 g C kg$^{-1}$ yr$^{-1}$. Given the measured soil bulk density of 1300 kg m$^{-3}$ and a median sediment accretion rate of ~3.4 cm yr$^{-1}$ in coastal marshes in China (Wang et al., 2006), the
estimated carbon burial rate would be \( \sim 370 \text{ g C m}^{-2} \text{ yr}^{-1} \). This is comparable to the estimated mean carbon accumulation rate \( (\sim 200 \text{ g C m}^{-2} \text{ yr}^{-1}) \) for tidal wetlands in China in a recent study (Wang et al., 2021; their Fig. 2).

Because habitat types affect both carbon deposition (as indicated by SOC and \( C_0 \) data) and carbon mineralization (\( \Sigma \text{SOCM} \)), we may derive a ‘Habitat Ratio’ using data from Figure 2 and Table 1 to compare their overall carbon source-sink dynamics (Table 3). Comparison of the Habitat Ratio between SAs and APs showed that the former had higher organic carbon deposition, bioavailable carbon and cumulative C mineralization, but all by a similar extent (20–21%); therefore, the soil carbon source-sink dynamics did not appear to be different between the two habitat types. On the other hand, SAs had 50% higher SOC than MFs but 71–72% higher bioavailable carbon and carbon mineralization, suggesting that SAs functioned as more concentrated stocks of labile soil organic carbon and stronger net carbon emission sources relative to MFs. This is consistent with others’ observations showing an increase in labile organic carbon fraction in \( S. \text{alterniflora} \) soil with time (Cui et al., 2021), but it contradicts another study suggesting that \( S. \text{alterniflora} \) invasion of mudflat decreased the labile organic carbon pool in the soil (Yang et al., 2013). The differences could be due to the fact that Yang et al. (2013) measured carbon mineralization under aerobic condition, which did not represent the water-logged, low-oxygen condition of the soil and which would have suppressed methanogenesis and underestimated the labile carbon turn-over. APs had 25% higher SOC, but 41–42% higher bioavailable carbon and carbon mineralization than MFs, reflecting the high amounts of
sedimented labile organics from excess feeds and biological productivity in the ponds (Yang et al., 2022).

4.4. Implications for Coastal Biogeochemistry

Continuous land development and land use change has drastically altered the coastal landscape of China (Cui et al., 2016; Meng et al., 2017). Based on our findings, conversion of mudflats to Sparitina marshes increased soil organic carbon mineralization, but conversion of Spartina marshes to aquaculture ponds decreased soil organic carbon mineralization (Figure 8)—This was consistent across all sites over a large latitudinal range, independent of differences in local geography, land management practices or climate conditions. In both land change scenarios, soil organic carbon was the overwhelming factor (37.2–45.5 %) that determined the mineralization activity.

The invasive S. alterniflora was introduced to China originally to protect mudflats against erosion, and it has proliferated along the coast since (An et al., 2007). Meanwhile, increasing food demand has led to rapid expansion of coastal aquaculture in China (Ren et al., 2019). While on-the-ground census data are rare, scientists used remote sensing methods to estimate the historical change in areal coverage by S. alterniflora marshes (Mao et al., 2019) and coastal aquaculture ponds (Duan et al., 2021) in the recent decades. Combining these literature data with our measured habitat-specific soil CO$_2$ and CH$_4$ production potentials, we calculated the total CO$_2$-eq production in the 20 cm topsoil, considering CH$_4$ has 45 times the 100-year warming potential as CO$_2$ (Neubauer & Megonigal, 2015); we further assessed landscape change effect by estimating the net
increase in soil CO$_2$-eq production relative to native mudflats. Our calculations suggest that total soil CO$_2$-eq production increased 12-fold as *S. alterniflora* marshes spread along China’s coast, whereas the expanding aquaculture activities increased total soil CO$_2$-eq production ~1.6 fold during the past three decades (Figure 9). The estimated land coverage by coastal aquaculture ponds was an order of magnitude larger than *S. alterniflora* marshes; consequently, the net increase in soil CO$_2$-eq production relative to native mudflats was largely driven by the large-scale conversion of coastal land to aquaculture ponds (Figure 9). Nevertheless, the total area of coastal aquaculture ponds appeared to have plateaued in recent years and therefore the contribution of soil CO$_2$-eq production from coastal aquaculture is expected to remain stable at ~4.3 Tg yr$^{-1}$. Meanwhile, if *S. alterniflora* marsh expansion continues along the trajectory, it is expected to cause further net increase in soil CO$_2$-eq production to ~0.7 Tg yr$^{-1}$ by end of this decade.

5. Conclusions and recommendations

The coastal mudflat habitats of China have undergone drastic changes in the recent decades due to the spread of the invasive *S. alterniflora* and conversion to aquaculture ponds. We showed that these land use change increased the total and labile fractions of soil organic carbon, carbon mineralization rate as well as greenhouse gas production relative to the native mudflats, and the effects were consistent across a wide latitudinal range and climate gradient (Figure 8). As the areal coverage of *S. alterniflora* marshes and coastal aquaculture ponds continue to increase, we may expect a net increase in carbon
greenhouse gas production and emission along the coast. This study provides a better insight into assessing the effects of land use and land cover change (LULCC) on coastal wetland carbon biogeochemical cycle process and land surface greenhouse gas emission across a large geographical range.

Several recommendations should be considered in future study: 1) Accurate census and monitoring of coastal habitats including small-hold aquaculture ponds is much needed in China and it will improve our assessment of landscape change effects on coastal carbon and greenhouse gas dynamics. 2) While we measured greenhouse gas production in soils, the actual emissions to the atmosphere could be further modulated by in situ physical (e.g., water turbulence, wind) and biological factors (e.g., consumption by microbes). Measurements of in situ emissions from the different habitats, using methods such as flux chambers, will be valuable. 3) Lastly, most of our sampling sites were concentrated in the northeastern part of the coast. Additional sampling in the southern provinces would allow data analysis based on a finer spatial resolution.

**Conflict of Interest**

The authors declare no conflicts of interest relevant to this study.

**Data Availability Statement**

The data used in this study are available in the Mendeley research data repository: Yang et al. (2022), Ancillary variables, SOC mineralization parameters, and carbon greenhouse gases production potential in impacted coastal wetlands across a wide latitudinal range in China, Mendeley Data, V1 (https://doi.org/10.17632/3r2827w6f4.1).
Acknowledgements

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Zhang, W. S., Li, H. P., Xiao, Q. T., & Li, X. Y. (2021c). Urban rivers are hotspots of riverine greenhouse gas (N₂O, CH₄, CO₂) emissions in the mixed-landscape chaohu


Figure captions

**Figure 1.** Locations of the study areas and 21 sampling sites across the coastal regions in southeastern China. Three wetland habitat types were investigated including mud flat (MFs), *S. alterniflora* marshes (SAs) and aquaculture ponds (APs).

**Figure 2.** Surface soil physicochemical properties across the three wetland habitat types (mean + SE; n = 63). MFs, SAs and APs represent mud flats, *S. alterniflora* marshes and aquaculture ponds, respectively. Different letters above the bars indicate significant differences (p<0.05).

**Figure 3.** Box plots of CO\textsubscript{2} and CH\textsubscript{4} production rates in surface soil for the three wetland habitat types, measured by incubation experiments (n = 63). MFs, SAs and APs represent mud flats, *S. alterniflora* marshes and aquaculture ponds, respectively. Different letters above the boxes indicate significant differences (p < 0.05).

**Figure 4.** (a) SOC mineralization rate in surface soil for the three wetland habitat types, measured by incubation experiments (mean ± SE; n = 63). (b) Boxplots of SOC mineralization rates for the three wetland habitat types; different letters above the boxes indicate significant differences (p < 0.05). MFs, SAs and APs represent mud flats, *S. alterniflora* marshes and aquaculture ponds, respectively.

**Figure 5.** (a) Cumulative SOC mineralization in surface soil over the 60-d incubation period for the three wetland habitat types (mean ± SE; n = 63). (b) Boxplots of cumulative SOC mineralization for the three wetland habitat types; different letters above the bars indicate significant differences (p < 0.05). MFs, SAs and APs represent mud flats, *S. alterniflora* marshes and aquaculture ponds, respectively.

**Figure 6.** Weighted response ratios (RR\textsuperscript{++}) of (a) SOC mineralization rate, (b) cumulative SOC mineralization (ΣSOCM), (c) initial SOC (*C*\textsubscript{0}) and (d) mineralization rate constant (*k*) for the different habitat modification scenarios: MFs → SAs represents conversion of mudflats to *S. alterniflora* marshes; SAs → APs represents conversion of *S. alterniflora* marshes to aquaculture ponds. Bars represent the RR\textsuperscript{++} values and 95% CIs (n = 63). Effects of habitat modifications were significant at p < 0.05 in all cases.
Figure 7. Redundancy analysis (RDA) biplots of the relationship between $\Delta \Sigma \text{SOCM}$, $\Delta C_0$, $\Delta k$, and $\Delta (C_0/SOC)$, and $\Delta \text{EF}$ (environment factors) for the different habitat modification scenarios: (a) conversion of mud flats to $S. \ alterniflora$ marshes; (b) conversion of $S. \ alterniflora$ marshes to aquaculture ponds. The pie charts show the percentages of variance in $\Delta \Sigma \text{SOCM}$ explained by the different variables. List of abbreviations is provided in the text.

Figure 8. A schematic illustration of landscape change effects on soil organic carbon mineralization and carbon emission in impacted coastal wetlands across a wide latitudinal range in China.

Figure 9. Changes in coastal landscape and related soil CO$_2$-eq production in China: (a) $S. \ alterniflora$ marsh area (from Mao et al., 2019), estimated marsh soil CO$_2$-eq production and net increase relative to native mudflats; (b) coastal aquaculture pond area (from Duan et al., 2021), estimated pond soil CO$_2$-eq production and net increase relative to native mudflats. See text (section 4.4) for explanation.
Table 1

Fitting parameters of the first order kinetics and \( C_0 \)/SOC values for SOC mineralization in surface soil (0–20 cm) across the three wetland habitat types.

<table>
<thead>
<tr>
<th>Habitat types</th>
<th>( \Sigma\text{SOCM}_{\text{final}} ) (( \mu g ) g(^{-1}))</th>
<th>Fitting parameters</th>
<th>( \Sigma\text{SOCM}_{\text{final}}/C_0 )</th>
<th>( C_0/\text{SOC} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mud flat</td>
<td>95.0</td>
<td>88.8</td>
<td>0.127</td>
<td>0.94</td>
</tr>
<tr>
<td>S. alterniflora marshes</td>
<td>162.9</td>
<td>152.3</td>
<td>0.127</td>
<td>0.95</td>
</tr>
<tr>
<td>Aquaculture ponds</td>
<td>135.0</td>
<td>125.6</td>
<td>0.126</td>
<td>0.95</td>
</tr>
</tbody>
</table>
Table 2
Pearson correlation coefficients between changes in ΣSOCM, $C_0$, $k$ and $C_0$/SOC, and different environmental variables in surface soil (0–20 cm) for the different habitat change scenarios: conversion of mudflat to *S. alterniflora* marshes, and conversion of *S. alterniflora* marshes to aquaculture ponds. SOC, MBC and MBN represent soil organic carbon, microbial biomass carbon and microbial biomass nitrogen, respectively. Significant correlations are indicated by the symbols * ($p < 0.05$) and ** ($p < 0.01$).

<table>
<thead>
<tr>
<th>Environmental variables</th>
<th>Conversion of mud flat to <em>S. alterniflora</em> marshes</th>
<th>Conversion of <em>S. alterniflora</em> marshes to aquaculture ponds</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\Delta$ΣSOCM</td>
<td>$\Delta C_0$</td>
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<tr>
<td>pH</td>
<td>-0.165</td>
<td>-0.155</td>
</tr>
<tr>
<td>Soil salinity</td>
<td>-0.036</td>
<td>-0.024</td>
</tr>
<tr>
<td>Soil water content</td>
<td>0.139</td>
<td>0.147</td>
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<tr>
<td>Soil bulk density</td>
<td><strong>-0.285</strong></td>
<td><strong>-0.293</strong></td>
</tr>
<tr>
<td>NH$_4^+$-N</td>
<td><strong>0.441</strong></td>
<td><strong>0.451</strong></td>
</tr>
<tr>
<td>NO$_3^-$-N</td>
<td>0.057</td>
<td>0.061</td>
</tr>
<tr>
<td>Soil C:N</td>
<td>-0.114</td>
<td>-0.131</td>
</tr>
<tr>
<td>Cl$^-$</td>
<td>-0.024</td>
<td>-0.020</td>
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<tr>
<td>SO$_4^{2-}$</td>
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<td>0.034</td>
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<tr>
<td>SOC</td>
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<td><strong>0.739</strong></td>
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<td>MBC</td>
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<td>Soil sandy content</td>
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Table 3
Habitat Ratio for SOC, $C_0$ and $\Sigma$SOCM, based on data from Fig. 2 and Table 1. MFs, SAs and APs represent mud flats, *S. alterniflora* marshes and aquaculture ponds, respectively.

<table>
<thead>
<tr>
<th></th>
<th>SAs : APs : MFs</th>
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<tr>
<td>SOC</td>
<td>1.50 : 1.25 : 1</td>
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<tr>
<td>$C_0$</td>
<td>1.72 : 1.41 : 1</td>
</tr>
<tr>
<td>$\Sigma$SOCM</td>
<td>1.71 : 1.42 : 1</td>
</tr>
</tbody>
</table>
Figure 1. Locations of the study areas and 21 sampling sites across the coastal regions in southeastern China. Three wetland habitat types were investigated including mud flat (MFs), *S. alterniflora* marshes (SAs) and aquaculture ponds (APs).
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<table>
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<tr>
<th>Incubation period (d)</th>
<th>Mud flat</th>
<th>S. alterniflora marshes</th>
<th>Aquaculture ponds</th>
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<tr>
<td>MFs</td>
<td>SAs</td>
<td>APs</td>
<td></td>
</tr>
<tr>
<td>0.91 ± 0.18</td>
<td>1.82 ± 0.15</td>
<td>3.65 ± 0.23</td>
<td></td>
</tr>
</tbody>
</table>

**Figure 4.** (a) SOC mineralization rate in surface soil for the three wetland habitat types, measured by incubation experiments (mean ± SE; n = 63). (b) Boxplots of SOC mineralization rates for the three wetland habitat types; different letters above the boxes indicate significant differences (p < 0.05). MFs, SAs and APs represent mud flats, *S. alterniflora* marshes and aquaculture ponds, respectively.
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Supporting Information

Landscape Change Affects Soil Organic Carbon Mineralization and Greenhouse Gas Production in Coastal Wetlands

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No. of pages: 3    No. of tables: 1

Page S3: Table S1. Fitting parameters of the first order kinetics for soil organic carbon mineralization in surface soil (0–20 cm) from three wetland habitat types across the different coastal sites in China.
<table>
<thead>
<tr>
<th>Province</th>
<th>Site</th>
<th>Mud flat</th>
<th>S. alterniflora marshes</th>
<th>Aquaculture ponds</th>
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<td>Zhejiang</td>
<td>Shanghai</td>
<td>59.708</td>
<td>0.234</td>
<td>82.214</td>
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<td></td>
<td>Chongming Island</td>
<td>59.708</td>
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<td>51.653</td>
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<td>0.185</td>
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<td></td>
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<td>Aquaculture ponds</td>
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</table>

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

Landscape Change Affects Soil Organic Carbon Mineralization and Greenhouse Gas Production in Coastal Wetlands

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Supporting Information Summary

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Page S3: Figure S1. Soil organic carbon mineralization rate in surface soil (0–20 cm) from three wetland habitat types across the different coastal sites in China.

Page S4: Figure S2. Cumulative mineralization of soil organic carbon in surface soil (0–20 cm) from three wetland habitat types across the different coastal sites in China.
Figure S1. Soil organic carbon mineralization rates in surface soil (0–20 cm) from three wetland habitat types across different coastal sites in China.
Figure S2. Cumulative mineralization of soil organic carbon in surface soil (0–20 cm) from three wetland habitat types across different coastal sites in China.