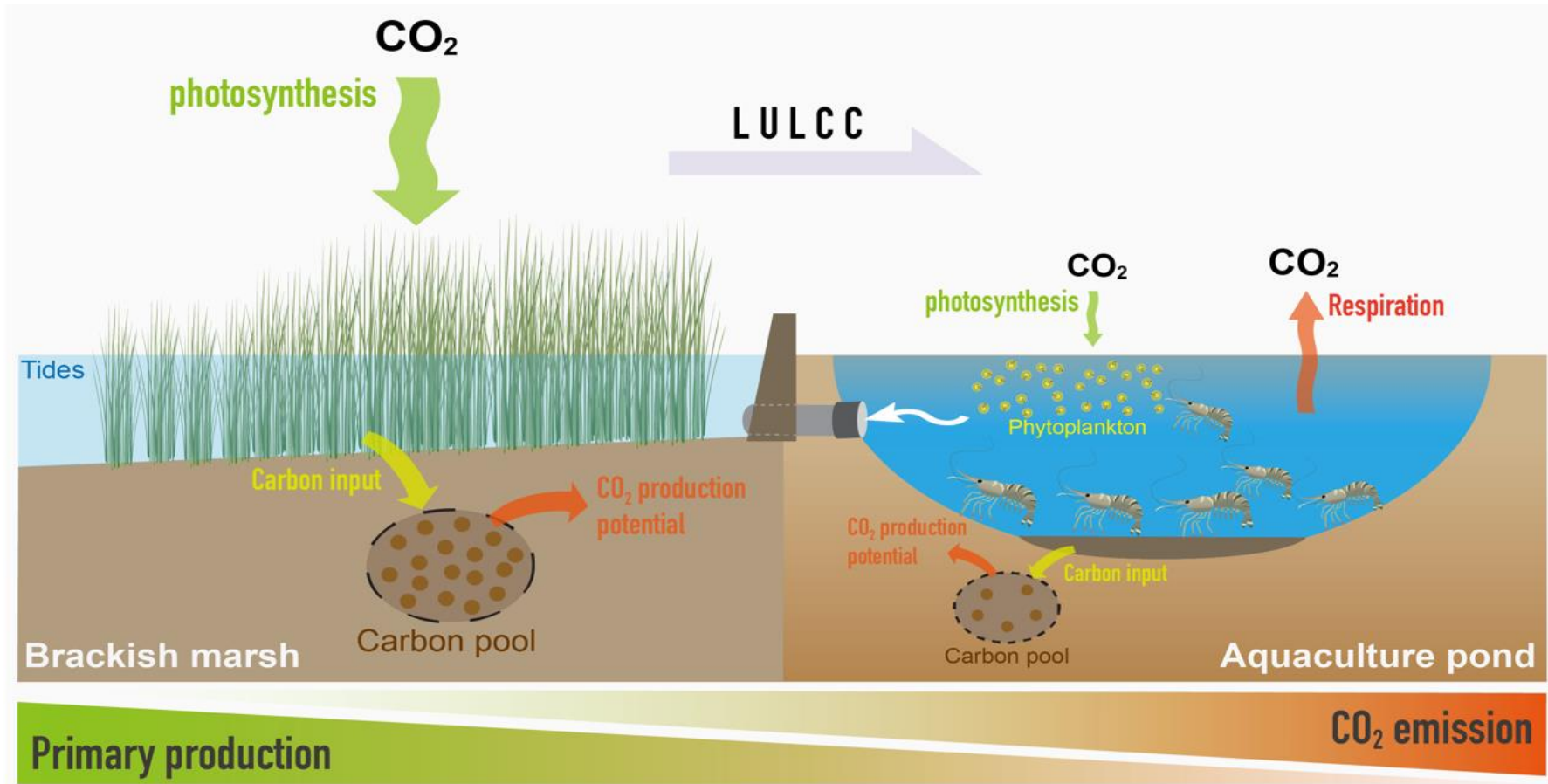


1 **Graphical Abstract**

2

1 **HIGHLIGHTS**

- 2 ● Converting coastal marsh to aquaculture ponds increased CO₂ emission by 101%
- 3 ● Sediment anaerobic CO₂ production potential decreased by 69% after conversion
- 4 ● Marsh vegetation played a key role in CO₂ uptake and sequestration
- 5 ● Sediment temperature was a main physical driver in CO₂ seasonal dynamics

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2 **Effects of conversion of coastal marshes to aquaculture ponds on**
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4 **sediment anaerobic CO₂ production and emission in a subtropical**
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6 **estuary of China**
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ABSTRACT

The extensive conversion of carbon-rich coastal wetland to aquaculture ponds in the Asian Pacific region has caused significant changes to the sediment properties and carbon cycling. Using field sampling and incubation experiments, the sediment anaerobic CO₂ production and CO₂ emission flux were compared between a brackish marsh and the nearby constructed aquaculture ponds in the Min River Estuary in southeastern China over a three-year period. Marsh sediment had a higher total carbon and lower C:N ratio than aquaculture pond sediment, suggesting the importance of marsh vegetation in supplying labile organic carbon to the sediment. Conversion to aquaculture ponds significantly decreased sediment anaerobic CO₂ production rates by 69.2% compared to the brackish marsh, but increased CO₂ emission, turning the CO₂ sink (-490.8 ± 42.0 mg m⁻² h⁻¹ in brackish marsh) into a source (6.2 ± 3.9 mg m⁻² h⁻¹ in aquaculture pond). Clipping the marsh vegetation resulted in the highest CO₂ emission flux (382.6 ± 46.7 mg m⁻² h⁻¹), highlighting the critical role of marsh vegetation in capturing and sequestering carbon. Sediment anaerobic CO₂ production and CO₂ uptake (in brackish marsh) and emission (in aquaculture ponds) were highest in the summer, followed by autumn, spring and winter. Redundancy analysis and structural equation modeling showed that the changes of sediment temperature, salinity and total carbon content accounted for more than 50% of the variance in CO₂ production and emission. Overall, the results indicate that vegetation clearing was the main cause of change in CO₂ production and emission in the land conversion, and marsh replantation should be a

1
2 primary strategy to mitigate the climate impact of the aquaculture sector.
3

4 **Keywords:** Organic carbon decomposition; Carbon dioxide (CO₂) fluxes; Habitat
5 alteration; Coastal wetland; Aquaculture ponds
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1. Introduction

Global climate change due to increased emission of greenhouse gases (GHGs) is one of the most pressing environmental issues of our time. Carbon dioxide (CO₂) accounts for nearly 60% of the total atmospheric radiative forcing (IPCC, 2014; Le Quéré et al., 2018). In 2021, the atmospheric CO₂ concentration reached a new peak value of 415.7 ppm. (World Meteorological Organization, 2022). Despite the small areal coverage of marine vegetated habitats such as salt marshes, mangroves and seagrass beds— about 0.2% of the ocean surface, they have disproportionate influence on the global carbon cycle, contributing ~50% of the annual carbon burial into the sediment (Duarte et al., 2013). Due to the high primary productivity and organic matter burial and anaerobic soil condition, coastal wetlands sequester atmospheric CO₂ at a rate ≥ 10 times higher than terrestrial forests (Mcleod et al., 2011; Mitsch et al., 2013; Tan et al., 2020). As such, even small disturbances to these coastal habitats may have a strong feedback on global carbon emission and climate warming (IPCC, 2014; Yao et al., 2021).

Land-use and land-cover change (LULCC) is now the second largest anthropogenic cause of GHG emissions, trailing only fossil fuel combustion (Friedlingstein et al., 2020; IPCC, 2014). More than 16% of the coastal wetlands around the globe have been impacted by LULCC (Hong et al., 2021; Murray et al., 2019), with an estimated annual loss rate of 0.2–5.0 % (Davidson and Finlayson, 2019). Along with a rapidly growing population, aquaculture plays a significant role in improving nutritional status and food security, promoting ocean and marine resource sustainability and socioeconomic development, all

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2 of which can help achieve the 2030 United Nations Sustainable Development goals
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4 (Ottinger et al., 2016; Suweis et al., 2015). In China, more than 11,163 km² of the natural
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6 coastal wetlands has been cleared for development since the 1950s, most of which was for
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8 the construction of earthen aquaculture ponds (Meng et al., 2017; Ren et al., 2019). The
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10 total area of aquaculture ponds converted from coastal wetlands in China was
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12 approximately 8,629 km² in 2021 (Duan et al., 2021; Wang et al., 2023).
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18 This extensive habitat transformation removes the vegetation and converts free-flowing
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20 water to standing water (He et al., 2021; Yang et al., 2022a), and the addition of animal
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22 wastes and excess feeds from aquaculture is expected to enhance carbon mineralization in
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24 the sediment (Naskar et al., 2020; Ye et al., 2022). Within the anoxic, organic-rich sediment,
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26 microbial production of methane (CH₄) is a main concern due to its high warming potential
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28 (Beaulieu et al., 2019; Sepulveda-Jauregui et al., 2018). Studies have shown that converted
29
30 aquaculture ponds have higher CH₄ emission than the natural wetlands (Tan et al., 2020;
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32 Yang et al., 2022a), which could be partly explained by an increase in ebullition as the main
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34 CH₄ transport pathway (Yang et al., 2022a). In inundated sediment, CO₂ production by
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36 anaerobic respiration using various electron acceptors usually precedes methanogenesis
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38 along the Redox cascade (Gruca-Rokosz et al., 2011; Xing et al., 2005). Indeed, CO₂ efflux
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40 from sediment is estimated to be orders of magnitude higher than CH₄ efflux in eutrophic
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42 inland habitats (Gruca-Rokosz and Tomaszek, 2015; Xing et al., 2005) and coastal wetlands
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44 (Barroso et al., 2022; Hsieh et al., 2021; Magenheimer et al., 1996). Unlike CH₄, the
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46 transport of the highly soluble CO₂ is primarily through diffusion rather than ebullition, and
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2 it can be recaptured by photoautotrophs, possibly leading to uncoupling between sediment
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5 CO₂ production and net emission to air.
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7 As earthen pond aquaculture continues to expand and intensify along the coast of China
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10 (Duan et al., 2021; Ren et al. 2019; Yang et al., 2022b) and elsewhere in SE Asia (Luo et
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12 al., 2022), it is necessary to investigate the effects of LULCC on sediment CO₂ production
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14 and emission in coastal wetlands over a longer period and in a higher temporal resolution.
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16 Such data will help scientists estimate more accurately the CO₂ budget and emission in
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18 impacted wetlands, and the feedback on climate along the rapidly changing coastal
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20 landscape (Hopkinson et al., 2012; Pendleton et al., 2012). Ideally, one should monitor the
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22 change throughout the process of land conversion. Unfortunately, historical environmental
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24 data and routine monitoring is lacking for many of the converted aquaculture ponds. To
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26 circumvent this problem, in this study we compared the sediment anaerobic CO₂ production,
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28 CO₂ emission fluxes and associated physicochemical factors between a brackish marsh and
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30 an area that had been converted to aquaculture ponds, in the Min River estuary of
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32 southeastern China, with high-frequency sampling over a three-year period. To gain an
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34 insight into the effect of vegetation clearing—a standard practice when constructing earthen
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36 ponds—on CO₂ emission, we included a treatment where we clipped the aboveground
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38 shoots in the marsh. We aimed to evaluate the effects of converting coastal marshes to
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40 aquaculture ponds on sediment CO₂ production and emission, and to identify key
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42 physicochemical factors that drive the response of CO₂ to land conversion.
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57 **2. Materials and methods**

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2.1. Study area

The Shanyutan wetland (26°00'36" to 26°03'42"N, 119°34'12" to 119°40'40"E) in the Min River estuary, Fujian, in southeastern China (Figure 1) is influenced by a subtropical monsoonal climate, with a mean annual air temperature of ca. 19.6 °C and a mean annual precipitation of 139 cm (Yang et al., 2022a). Salt water of 4.2±2.5 ‰ average salinity inundates the wetland via semidiurnal tides of 2.5–6.0 m (Tong et al., 2018). The dominant vegetation here includes the native *Cyperus malaccensis* and *Phragmites australis*, and the invasive *Spartina alterniflora*. Over the past decades, extensive areas of *C. malaccensis* and *S. alterniflora* marshes have been converted to earthen aquaculture ponds for food production, mostly shrimp (*Litopenaeus vannamei*) (Yang et al., 2022b).

The size of the aquaculture ponds in the region ranges from 1.2 to 3.0 ha, with a mean water depth of ~1.5 m. The period of shrimp farming is from June to November and the stocking density is 150–250 postlarvae m⁻². The shrimp are fed pellets (5000 kg ha⁻¹) daily at 08:00 a.m. and 4:00 p.m. local time. There is no water exchange during the farming period (Yang et al., 2022b).

A brackish *C. malaccensis* marsh and three converted aquaculture ponds nearby were selected for the study (Figure 1). Between April 2019 and January 2020, sampling and incubation experiments were carried out monthly for a total 10 times. Subject to Covid-19-related travel restrictions and staff availability, CO₂ fluxes from the brackish marsh and aquaculture ponds were measured between April 2019 and December 2021 for a total of 36 times during the three-year period.

1
2 *2.2. Collection and analysis of sediment*
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4 Three permanent quadrats (1 m × 1 m) two meters apart were established within *C.*
5 *malaccensis* marsh for the collection of sediment and porewater samples. 15-cm long
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7 sediment cores were collected in each quadrat using a steel cylinder (5 cm in diameter). For
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9 the aquaculture ponds, triplicate 15-cm long sediment cores were randomly collected within
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11 each pond. Sediment samples were stored at 4 °C in the dark until analysis. During each
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13 sampling campaign, sediment temperature (T_s) and electrical conductivity (EC) were
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15 measured *in situ* using a portable meter (2265FS, Spectrum Technologies, USA).
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24 In the laboratory, sediment pH (sediment-to-water ratio of 1:2.5 w/v) and salinity
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26 (sediment-to-water ratio of 1:5 w/v) were measured with a pH meter (Orion 868, USA) and
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28 a salinity meter (Eutech Instruments- Salt6, USA), respectively. A subsample of the
29
30 sediment was freeze-dried and ground in a ball mill after the removal of plant roots for the
31
32 measurement of sediment total carbon (STC) and sediment total nitrogen (STN), using an
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34 elemental analyser (Elementar Vario MAX CN, Germany).
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40 *2.3. Collection and analysis of sediment porewater*
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43 To collect porewater from the marsh sediment, a series of PVC porewater samplers (5
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45 cm inner diameter) were installed within each aforementioned quadrat in the marsh; each
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47 sampler extended 15 cm into the sediment and 5 cm above the sediment surface, with the
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49 top opening covered by a 0.2- μ m nylon membrane screen (BiotransTM) ([Tong et al., 2018](#)).
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54 To collect porewater from the aquaculture pond sediment, 15-cm long sediment cores
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56 were collected at three randomly sites in each pond using a steel cylinder sampler (5 cm
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2 inner diameter); the sediment porewater was then extracted by centrifugation at 4,000 rpm
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5 for 10 min (Hereaus Omnifuge 2000 RS) (Matos et al., 2016).
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8 Approximately 50 mL of each porewater sample was filtered through a 0.45- μ m filter
9
10 (Biotrans™ nylon membranes) within 24 h of collection. The filtrates were stored at 4 °C
11
12 for further measurement within one week. Each porewater filtrate was split into four
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14 portions for measuring SO_4^{2-} , Cl^- , NH_4^+ -N and NO_3^- -N. SO_4^{2-} and Cl^- concentrations were
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16 measured with a Dionex 2100 ion chromatograph (Thermo Fisher Scientific, Sunnyvale,
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18 California, USA); NH_4^+ -N and NO_3^- -N concentrations were measured with a flow injection
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20 analyzer (Skalar Analytical SAN⁺⁺, Netherlands).
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26 27 *2.4. Measurement of sediment anaerobic CO₂ production*

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29 The sediment anaerobic CO₂ production was determined by incubation according to Liu
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31 et al. (2019) and Wang et al. (2017). Approximately 50 g of fresh sediment and 50 mL of
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33 *in situ* water were added to a 200-mL incubation bottle; the slurry was then purged with N₂
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35 gas for 5–8 min to displace the oxygen. The bottles were sealed with a silicone rubber
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37 stopper and incubated at *in situ* sediment temperature with agitation (175 rpm) for 12 days.
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5 mL of headspace sample was extracted from each incubation bottle every four days to
measure CO₂ (total 4 times); 5 mL of N₂ gas was added back to balance the pressure. CO₂
concentrations of the extracted gas samples were determined on a gas chromatograph (GC-
2014, Shimadzu, Kyoto, Japan) equipped with a flame ionization detector (FID). Sediment
anaerobic CO₂ production [$\mu\text{g CO}_2 \text{ g}^{-1}$ (dry weight) d^{-1}] was calculated from the linear rate
of increase in headspace CO₂ concentration over time (Liu et al., 2019; Yang et al., 2022b).

2.5. CO₂ flux measurements

Repeated measurements of CO₂ fluxes were made between April 2019 and December 2021. Triplicate plots (1 m × 1 m) were set up in the marsh to measure CO₂ flux using static chambers (100 cm height × 35 cm width × 35 cm length) made of transparent plexiglass (Yuan et al., 2015; Tong et al., 2010). The top of each chamber had an electric fan installed inside to mix the headspace during measurements; a permanently installed bottom collar with a water-filled channel (30 cm height, 35 cm width, 35 cm length) was inserted 20 cm into the sediment. To assess the effect of marsh vegetation on CO₂ flux, we established additional plots nearby where the plant shoots were clipped and sealed with petroleum jelly to prevent gaseous exchange through the stems (Kelker and Chanton, 1997; Tong et al., 2012; Yang et al., 2022a).

In each aquaculture pond, CO₂ flux across the water-air interface was measured with a floating chamber (Natchimuthu et al., 2017). The floating chamber covering an area of 0.1 m² and a volume of 5.2 L was made from a polyethylene basin (plexiglas®) with an electric fan installed inside, and was fitted with Styrofoam on the side for floatation. We covered the outside of the floating chamber with reflective aluminum foil to minimize internal heating by sunlight.

During each sampling campaign, headspace samples from the chambers were drawn into aluminum-foil gas sample bags (Dalian Delin Gas Packing Co., Ltd., China) at 15-minute intervals over a 45-min period at each sampling site. CO₂ concentration of the collected gas samples were determined within 48 h on a gas chromatograph (GC-2014,

1 Shimadzu, Kyoto, Japan) equipped with FID. The flux of CO₂ (mg CO₂ m⁻² h⁻¹) was
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4 calculated from rate of increase in headspace CO₂ concentration over time; the results were
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7 then extrapolated to the annual cumulative CO₂ emission (*CE*) as:
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$$10 \quad CE = \sum MFi \times Di \times 24 \quad (\text{Eq.1})$$

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12 where *MFi* is the CO₂ flux at the *i*th month of the year (mg CO₂ m⁻² h⁻¹) and *Di* is the number
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14 of days in that month; CO₂ fluxes for unobserved months were estimated as the average
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18 fluxes of the observed months in the same season.
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21 *2.6. Statistical analysis*

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24 Differences in physicochemical factors (i.e., *Ts*, sediment salinity, sediment pH, STC,
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26 STN, concentrations of SO₄²⁻, Cl⁻, NH₄⁺-N and NO₃⁻-N in porewater), anaerobic CO₂
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28 production and CO₂ fluxes between habitats (brackish marsh and aquaculture ponds) and
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30 between seasons were tested by one-way analysis of variance (ANOVA) using SPSS
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32 version 25.0 software (SPSS Inc., Chicago, IL, USA). The change rates of CO₂ production
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37 (ΔP_{CO_2}), CO₂ fluxes (ΔF_{CO_2}) and physicochemical factors (i.e., ΔT_s , $\Delta \text{Salinity}$, ΔpH , ΔSTC ,
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39 ΔSTN , ΔSO_4^{2-} , ΔCl^- , $\Delta \text{NH}_4^+\text{-N}$ and $\Delta \text{NO}_3^-\text{-N}$) between the two habitats can reflect the
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42 synchronous responses of CO₂ dynamics and environmental factors to land conversion.
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45 Redundancy analysis (RDA) was performed to explore the relative influence of the change
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47 rates of different physicochemical factors on ΔP_{CO_2} and ΔF_{CO_2} using CANOCO 5.0
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49 software (Microcomputer Power, Ithaca, NY, USA). To further examine the direct and
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52 indirect effect of the different physicochemical factors on ΔP_{CO_2} and ΔF_{CO_2} , a partial least
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55 square structural equation modeling (PLS-SEM) analysis was performed in R V3.5.3 (R
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2 Foundation for Statistical Computing, 2013) with the ‘semPLS’ package. Briefly, the
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4 physicochemical factors were successively entered into the PLS-SEM in descending order
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7 by relative influence of each physicochemical factor from the RDA results, until the model
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9 cannot achieve significance. Then we test the PLS-SEM with different paths among the
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11 selected variables following a reasonable and conceptual assumption regarding variable
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13 dependencies, and the final model with the minimum Akaike’s information criterion (AIC)
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15 was obtained. AIC was generally calculated for the simple regression model and the
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17 segmented linear regression model to assess fit of the models. Maximum-likelihood
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19 estimation was used to obtain the path coefficients, and the χ^2 goodness-of-fit test, degrees
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21 of freedom, p value (Chi-square) and AIC were used to evaluate the model (Šimová et al.,
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23 2019; Tan et al., 2022). All data were presented as mean \pm standard error (SE), unless
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25 otherwise stated. In all statistical tests, a significance level of $p < 0.05$ was used.
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3. Results

3.1. Physicochemical characteristics of sediment and porewater

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41 The physicochemical characteristics of the sediments and porewaters are shown in
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43 [Figure S1](#). The sediments in both habitats were brackish (mean salinity $< 10\text{‰}$) and slightly
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45 acidic (pH < 7). The porewater SO_4^{2-} and Cl^- concentrations were both lower than the
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47 typical values in seawater, and the average sediment C:N molar ratio was ~ 16 in the marsh
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49 and ~ 21 in the aquaculture ponds, substantially higher than the Redfield ratio.
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55 Compared to the brackish marsh, the aquaculture ponds had significantly lower
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57 sediment T_S , salinity, STC and STN, as well as lower concentrations of porewater Cl^- , NO_3^-
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2 -N and $\text{NH}_4^+\text{-N}$ ($p < 0.01$ or < 0.05 ; [Figures S1a, b, e, g and h](#)), while the differences in
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4 sediment pH and porewater SO_4^{2-} concentration were insignificant ($p > 0.05$; [Figures S1c,](#)
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7 [d, f and i](#)).

10 3.2. Sediment anaerobic CO_2 production

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12 The sediment anaerobic CO_2 production in the marsh averaged $606.7 \pm 117.1 \text{ ug g}^{-1} \text{ d}^{-1}$
13 (range 116.4–990.9 $\text{ug g}^{-1} \text{ d}^{-1}$), which was significantly higher than that in the aquaculture
14
15 ponds ($186.7 \pm 38.2 \text{ ug g}^{-1} \text{ d}^{-1}$; range 42.2–373.8 $\text{ug g}^{-1} \text{ d}^{-1}$) ($p < 0.01$; [Figure 2a](#)). Both
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17
18 habitats showed the same seasonal differences in the sediment anaerobic CO_2 production,
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21 with significantly higher rates in the summer, followed by autumn, spring and winter
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24 (Figure 2b). The sediment carbon turnover rate, calculated as the ratio of anaerobic CO_2
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27 production rate to STC, was $3\% \text{ d}^{-1}$ in the marsh and $1.2\% \text{ d}^{-1}$ in the aquaculture ponds.
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31 3.3. CO_2 emission fluxes

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33 The brackish marsh acted as a CO_2 sink during the whole study period, with the CO_2
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35 flux ranging from -992.9 to -74.4 $\text{mg m}^{-2} \text{ h}^{-1}$ and averaging $-490.8 \pm 42.0 \text{ mg m}^{-2} \text{ h}^{-1}$ ([Figure](#)
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38 [3a](#)). The net CO_2 uptake was highest in the summer, followed by autumn and winter, and
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41 lowest in spring ([Figure 3c](#)). Conversely, the clipped marsh acted as a strong source of CO_2
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44 throughout the study; the CO_2 flux ranged from 35.6 to 1277.9 $\text{mg m}^{-2} \text{ h}^{-1}$ and averaged
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47 $382.6 \pm 46.7 \text{ mg m}^{-2} \text{ h}^{-1}$ ([Figure 3a](#)), and was the highest in the summer ([Figure 3d](#)). The
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50 CO_2 flux from the aquaculture ponds varied between -19.0 and 77.9 $\text{mg m}^{-2} \text{ h}^{-1}$, and it
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53 averaged $6.2 \pm 3.9 \text{ mg m}^{-2} \text{ h}^{-1}$ ([Figure 3b](#)). The ponds acted as a CO_2 source in spring and
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55
56 summer, and as a sink in winter ([Figure 3e](#)).

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2 Overall, the CO₂ flux was significantly different among the three habitats and was
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4 highest in the clipped marsh, followed by the aquaculture ponds, then the untreated marsh
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6 ($p < 0.05$). Extrapolating our measurements to a full year, the annual cumulative CO₂ flux
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8 from the marsh was -1037.7 to -2124.5 g CO₂ m⁻² per year, whereas the aquaculture ponds
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10 emitted a total of -16.9 to 61.8 g CO₂ m⁻² per year. In comparison, the clipped marsh
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12 released a total of 1015.3–1897.7 g CO₂ m⁻² per year (Figure 4).
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18 3.4. Environmental drivers of CO₂ production and flux 19

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21 According to redundancy analysis (RDA), the environmental factors explained 75.5%
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23 of the variances in ΔF_{CO_2} and ΔP_{CO_2} among all data (Figure 5). Δ salinity, ΔT_s , Δ STC and
24
25 Δ Cl⁻ together accounted for 80% relative influence (Figure 5). ΔT_s and Δ STC were
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27 positively correlated with ΔF_{CO_2} and ΔP_{CO_2} , while Δ salinity and Δ Cl⁻ were negatively
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29 correlated with ΔF_{CO_2} and weakly to ΔP_{CO_2} . Based on the structural equation model (SEM),
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31 ΔT_s had a direct positive effect on both ΔF_{CO_2} and ΔP_{CO_2} . Δ Cl⁻ negatively affected ΔF_{CO_2}
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33 directly and indirectly via ΔP_{CO_2} . Δ STC had a positive effect on ΔF_{CO_2} by way of ΔP_{CO_2}
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35 (Figure 6). Overall, ΔT_s had the largest total effect compared to Δ Cl⁻ and Δ STC (Figure 6).
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43 We also conducted RDA and SEM analyses for the different habitats: The
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45 environmental factors explained 79.3% (marsh) and 76.8% (aquaculture ponds) of the
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47 variances in ΔF_{CO_2} and ΔP_{CO_2} (Figure S2). Δ Cl⁻ had the largest relative influence in the
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49 marsh (61.4%), whereas in the aquaculture ponds it was ΔT_s (61.1%) (Figure S2). SEM
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51 analysis showed that ΔT_s had the largest total effect, negatively in the marsh and positively
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53 in the aquaculture ponds (Figure S3).
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4. Discussion

The rapid growth and intensification of aquaculture worldwide has raised concerns of its environmental impacts including GHG emissions (Yuan et al., 2019). In China, the coastal land area converted for aquaculture use increased rapidly in the past three decades (Duan et al., 2021). To assess the related climate footprint, some researchers focused on GHG emissions due to feeds, fertilizers and energy consumption (Xu et al., 2022); others compared the aquaculture system types, cultivated species, environmental conditions and management practices (Bhattacharyya et al., 2013; Zhang et al., 2022). While those studies provide valuable information on the status quo of the aquaculture systems, they do not illustrate the systematic change in GHG dynamics caused by the land use change, especially for earthen aquaculture ponds that were constructed by clearing the coastal marshes.

Vegetated coastal wetlands play a key role in capturing and sequestering carbon into the sediment (Chmura et al., 2003; Duarte et al., 2013; Kirwan and Mudd, 2012). Based on our cumulative CO₂ flux estimates (Figure 4), the brackish marsh had an annual CO₂ uptake of 282–579 g C m⁻² yr⁻¹, which is quite comparable to the estimated sediment carbon burial rate for coastal salt marshes in China (218 g C m⁻² yr⁻¹; Meng et al., 2019). The conversion of a vegetated marsh to aquaculture ponds would remove this carbon burial capacity and also alter the sediment characteristics and GHG dynamics (Yang et al., 2022a, 2022c).

4.1. Effects of land use change on sediment and porewater characteristics

The aquaculture ponds were insulated from the tidal flushing by the warmer and saltier estuarine water, as reflected by the lower T_s , salinity and Cl⁻¹ in the pond sediment and

1 porewater relative to the marsh (Figure S1). Moreover, management practices often aim to
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4 maintain a stable physicochemical condition within the ponds to improve production.
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7 Despite the regular application of feeds and deposition of animal wastes, the pond sediment
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10 and porewater were less organic (STC, STN) and nutrient rich (NO_3^- -N, NH_4^+ -N) than the
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13 marsh (Figure S1), suggesting that tidal input and deposition by vegetation of organics and
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16 nutrients was more important in this ecosystem.

17 18 *4.2. Effects of land use change on sediment anaerobic CO₂ production*

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21 The measured sediment anaerobic CO₂ production rate in the marsh sediment was > 2
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24 times that in the aquaculture ponds (Figure 2). While SEM highlighted the strong effects of
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27 T_s and STC on sediment CO₂ production (Figure 6), T_s and STC differed by only 33% and
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30 19%, respectively, between the marsh and the aquaculture ponds (Figure S1), and together
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33 they explained less than 40% of the variance in CO₂ production (Figure 5). Therefore, they
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36 were inadequate in explaining the difference in CO₂ production. Additionally, brackish
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39 marsh was supposed to have lower CO₂ production because higher sediment salinity may
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42 inhibit microbial metabolism (Chamber et al., 2013; Neubauer et al., 2013). However,
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45 salinity had only a weak influence on CO₂ production in SEM (Fig. 6). We speculate that
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47
48 the marsh vegetation released labile autochthonous organics and tidal flow also introduced
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51 more labile allochthonous organics into the marsh sediment, which together increased
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54 microbial respiration (Yang et al., 2022d). This is supported by the fact that the C:N ratio
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57 of the marsh sediment (~16) was lower than that of the aquaculture pond sediment (~21).
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60 The aquaculture operation may have also decreased sediment microbial diversity and
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1
2 microbial network complexity, resulting in lower overall microbial activity in the pond
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4 sediment (Yang et al., 2022c).
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7 4.3. Effects of land use change on CO₂ flux 8 9

10 The marsh overall acted as a net CO₂ sink (Figure 3a) despite its high sediment CO₂
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12 production rate (Figure 2). This suggests that carbon uptake by the marsh vegetation more
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14 than balanced the sediment CO₂ output, resulting in a net carbon burial (Duarte et al., 2013).
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16 The magnitude of this carbon sink was largest in the summer (Figure 3c), reflecting the
17
18 higher photosynthetic activity due to the higher temperature and light intensity.
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24 The important role of the vegetation in recycling the CO₂ from the sediment is further
25
26 illustrated by the clipped marsh treatment: By clipping the above-ground biomass, the
27
28 marsh became a strong CO₂ emitter (Figures 3a,d), likely fuelled by the high microbial CO₂
29
30 production, especially during the warmer months (Figure 2). Therefore, removal of marsh
31
32 vegetation for the construction of aquaculture ponds may result in an initial surge of 873.4
33
34 mg CO₂ m⁻² h⁻¹ emission until the sediment carbon stock became depleted or removed.
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40 The aquaculture ponds acted as a CO₂ emitter for much of the time (Figure 3b),
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42 especially in spring and summer when shrimp farming activity was the most intense (Figure
43
44 3e). Therefore, respiration by shrimp and microbes might significantly contribute to CO₂
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46 emission. This is consistent with previous studies highlighting the GHG output from
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48 earthen aquaculture ponds (Yuan et al., 2019; Zhang et al., 2019). Based on the average
49
50 CO₂ flux measurements, land use change from a marsh to aquaculture ponds would lead to
51
52 a net increase of 497 mg CO₂ m⁻² h⁻¹ output from the land (in addition to the initial surge
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1
2 due to removal of vegetation, as discussed above). This is also consistent with previous
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4 studies showing that LULCC increases CO₂ emission (Kauffman et al., 2018; Sasmito et
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6 al., 2019; Tan et al., 2020).
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10 A recent mesocosm study has shown that the presence of coastal vegetation would
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12 mediate the response of sediment labile organics, microbial community and CO₂ emission
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14 to salinity change, such that higher salinity increased CO₂ emission from vegetated habitat
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16 but decreased CO₂ emission from non-vegetated habitat (Chen et al., 2022). Consistent with
17
18 these earlier observations, during the three-year period of our study, the highest annual
19
20 cumulative CO₂ uptake (brackish marsh) and emission (aquaculture ponds) occurred in
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22 2019, followed by 2020 and 2021 (Figs. 3 and 4), which corresponded to the interannual
23
24 decline in precipitation recorded by a local weather station: 1807 mm in 2019, 1516 mm in
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26 2020 and 1439 mm in 2021. A higher precipitation would have lowered the *in situ* salinity
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28 and led to a higher net CO₂ uptake in a vegetated habitat (e.g., marsh) and higher net CO₂
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30 emission in a non-vegetated habitat (e.g. aquaculture ponds).
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40 In addition to CO₂, organic-rich anoxic sediment also produces CH₄, which is a much
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42 stronger greenhouse gas than CO₂ (Bastviken et al., 2008; Li et al., 2020; Rosentreter et al.,
43
44 2018). In an earlier companion study, the CH₄ fluxes from the brackish marsh and the
45
46 aquaculture ponds were measured respectively at 1.3 and 17.4 mg CH₄ m⁻² h⁻¹, for a net
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48 increase of 16.1 mg CH₄ m⁻² h⁻¹ emission due to the land conversion (Yang et al. 2022a).
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51 Considering that the global warming potential (GWP) of CH₄ is 28 times that of CO₂ on a
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53 100-year time horizon (IPCC, 2014), the total increase in carbon-equivalent emission due
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2 to the land use change would be $\sim 948 \text{ mg CO}_2\text{-eq m}^{-2} \text{ h}^{-1}$, with 52% in the form of CO_2 gas
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4 (Table 1). While some study has suggested that conversion of coastal marsh to aquaculture
5
6 ponds affects mainly CH_4 rather than CO_2 (Tan et al., 2020), in the case of the Shanyutan
7
8 wetland, the effect on CO_2 emission was equally important and should be taken into account
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10 when assessing the climate impact of LULCC in this region.
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15 *4.4. Recommendations and environmental implications*

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18 Several improvements can be considered in future study. Firstly, we only measured
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20 anaerobic CO_2 production in the sediment, but aerobic metabolism can occur in the water
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22 column, during ebbing tides in the marsh as well as non-culture period in the aquaculture
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24 ponds, which should be included in the total CO_2 production (Kauffman et al., 2018;
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26 Lovelock et al., 2017; Yang et al., 2018). Due to logistical constraints, gas fluxes were only
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28 measured during the daytime, but CO_2 output is expected to increase at night when
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30 photosynthesis stops, and our CO_2 fluxes may have been underestimated as a result.
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32 Installation of automated gas loggers on site may circumvent this problem. Some shrimp
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34 farmers drain the ponds and remove the top sediment during the non-farming period, which
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36 would change the carbon dynamics drastically (Kauffman et al., 2018; Sasmito et al., 2019).
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38 Comparison of aquaculture ponds with different management practices will shed light on
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40 this issue. While newly converted aquaculture ponds are expected to generate high income
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42 for the first 5–10 years, productivity often falls off afterward and the ponds are then
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44 neglected (Bosma et al., 2012; Cameron et al., 2019); however, these ponds may continue
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46 to produce and emit GHGs for a further period of time, and such ‘legacy’ climate effect also
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2 needs to be accounted for. Lastly, our clipped marsh treatment revealed the critical role of
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4 vegetation in carbon capture and burial, and therefore reverting unused ponds to vegetated
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6 marsh and wetland reforestation could be a sound strategy to offset the climate footprint of
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8 the aquaculture sector.
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11 12 **5. Conclusions**

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16 This multi-year field study showed that conversion of brackish marsh to aquaculture
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18 ponds strongly influenced the system's CO₂ dynamics in the Shanyutan wetland. Land
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20 conversion significantly decreased the sediment anaerobic CO₂ production, but increased
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22 CO₂ emission notably, turning the system net heterotrophic. Much of the effect may be
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24 attributed to the removal of marsh vegetation, with sediment temperature as additional key
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26 physical driving factor. The climate impact due to the net increase in CO₂ emission was on-
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28 par with the increase in CH₄ emission reported earlier, and therefore should be accounted
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30 for when assessing the climate impact of land use change.
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38 39 **Declaration of competing interest**

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41
42 The authors declare that they have no known competing financial interests or personal
43
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46

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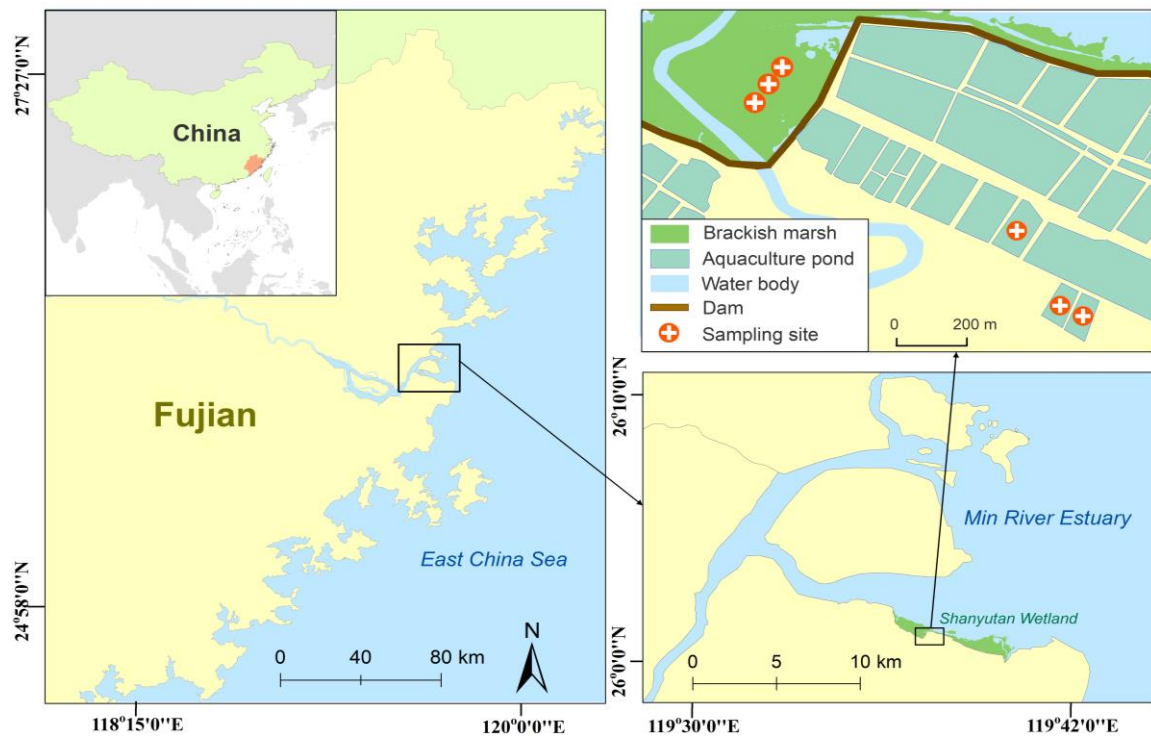
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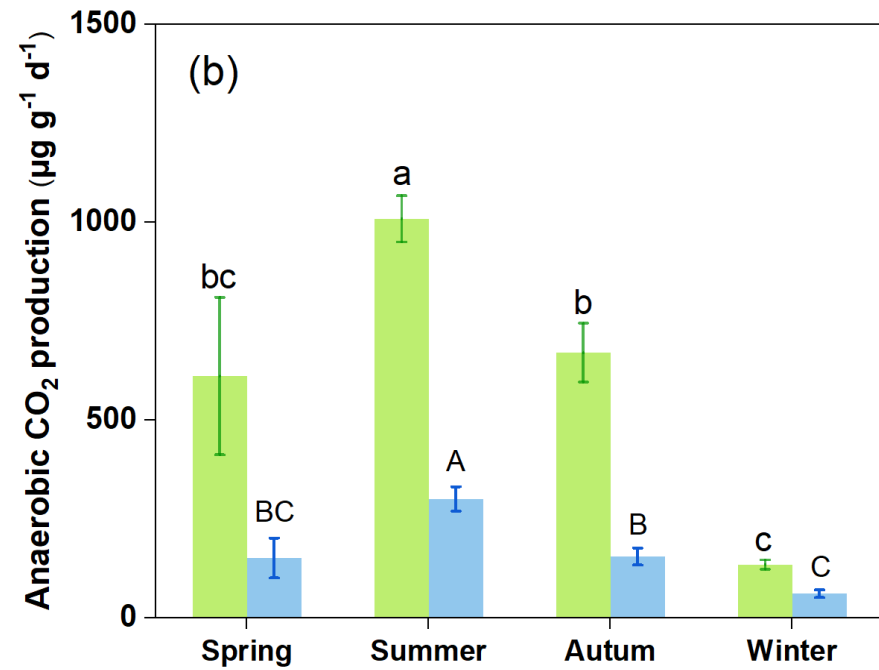
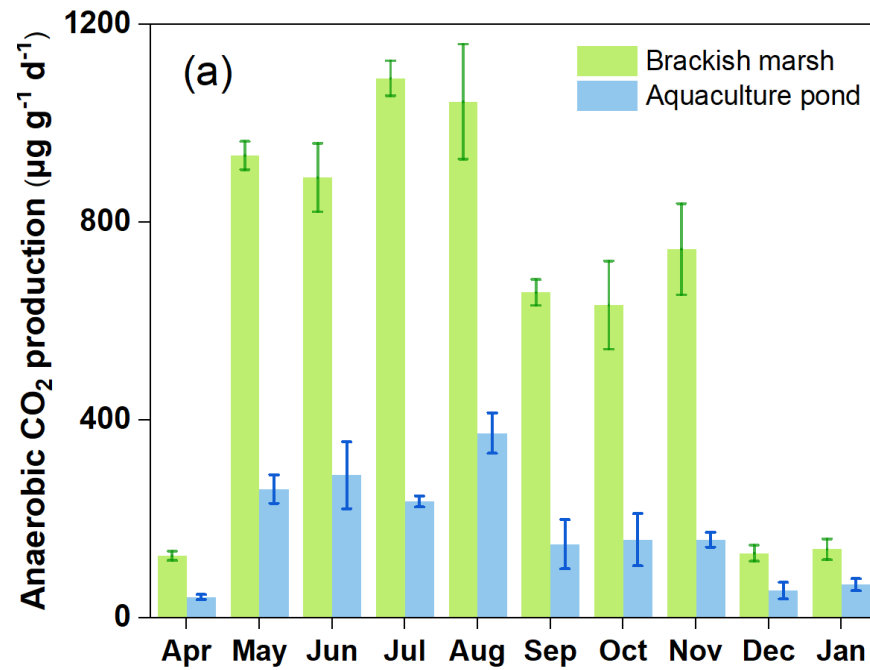
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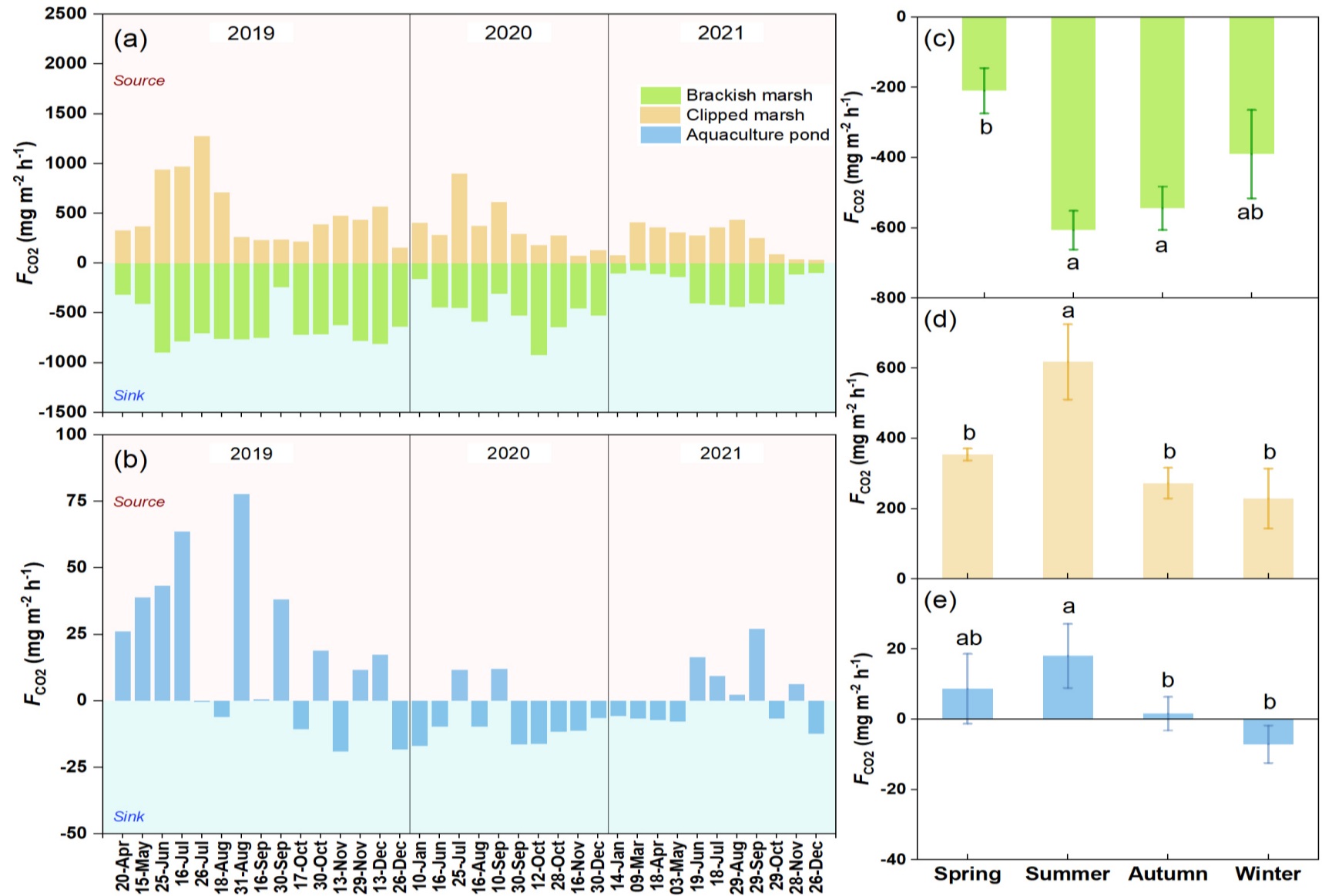
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2 **Figure 1.** The location of the sampling sites in the brackish marsh and aquaculture

3 ponds in Shanyutan Wetland within the Min River Estuary.



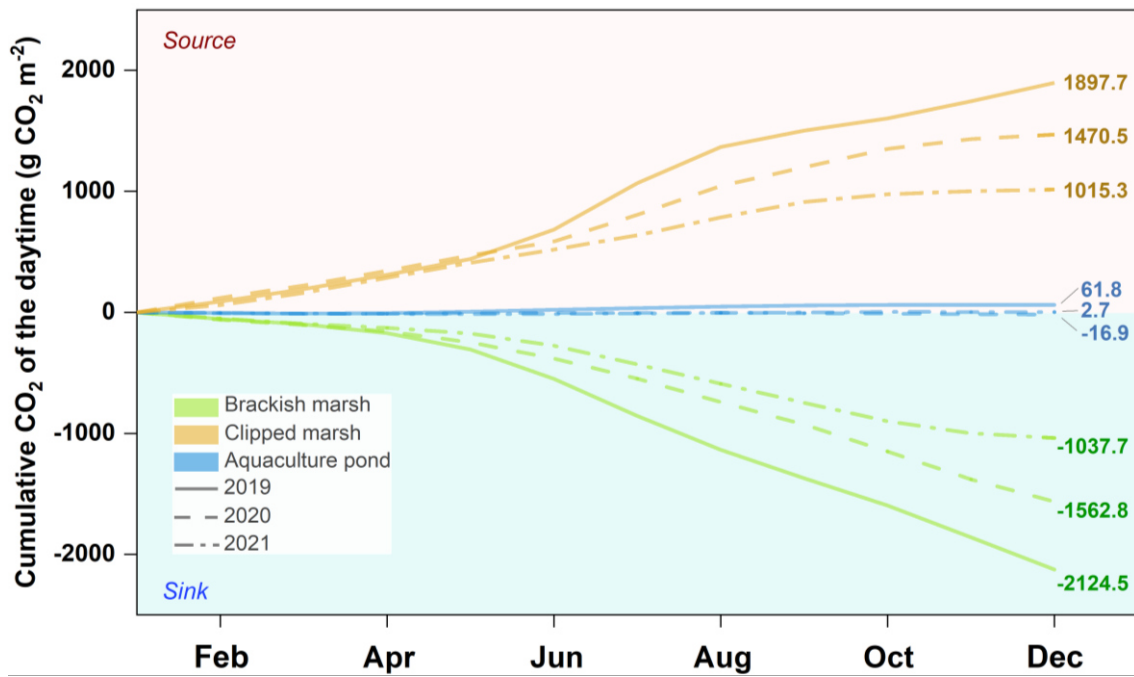
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 5 **Figure 2.** Monthly (a) and seasonal (b) variations of sediment CO₂ production potential (mean ± S.E.) between brackish marsh and
 6 aquaculture ponds. Different lowercase and uppercase letters indicate significant differences of sediment CO₂ production potential across
 7 four seasons in brackish marsh and aquaculture ponds, respectively.



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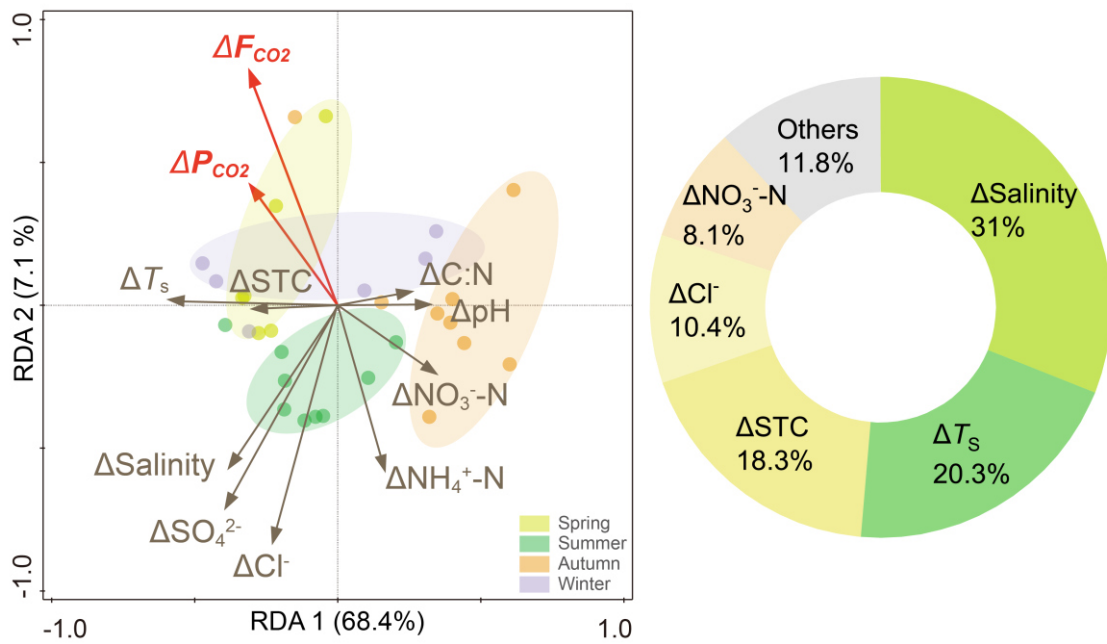
9 **Figure 3.** Monthly (a, b) and seasonal (c, d, e) variations of CO₂ flux (mean ± S.E.) among brackish marsh, clipped marsh and

10 aquaculture ponds. Different letters indicate significant differences of sediment CO₂ production potential across four seasons.



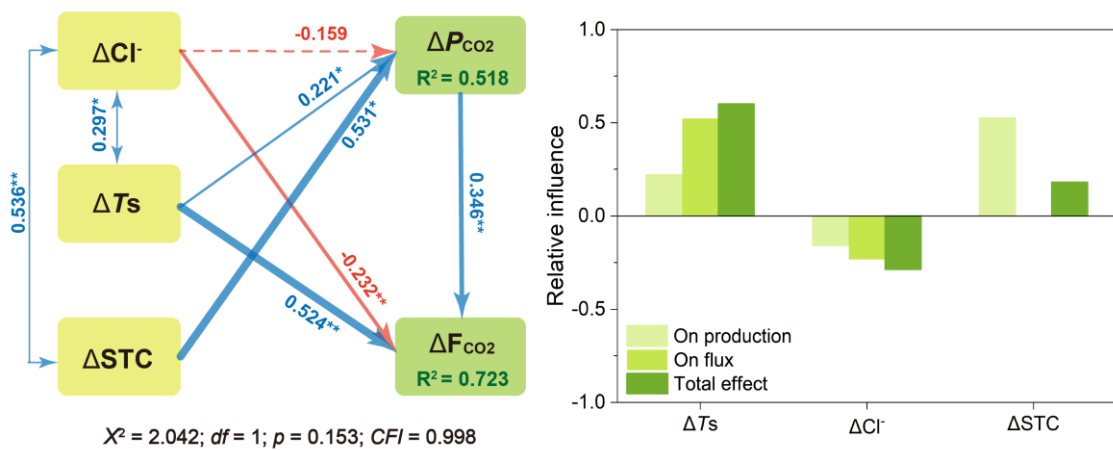
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12 **Figure 4.** Cumulative CO₂ fluxes among brackish marsh, clipped marsh and
 13 aquaculture ponds during the measurement period.



14

15 **Figure 5.** Redundancy analysis (RDA) of the relationship between the change rate of
 16 CO_2 production potential (ΔP_{CO_2}) as well as fluxes (ΔF_{CO_2}) and the change rate of
 17 environmental factors after land conversion. The pie charts show the percentages of
 18 relative influence of environmental factors on ΔF_{CO_2} and ΔP_{CO_2} .



19

20 **Figure 6.** Partial least square structural equation modeling (PLS-SEM) of the change
 21 rate of CO₂ production potential (ΔP_{CO_2}) and fluxes (ΔF_{CO_2}) response to the change rate
 22 of environmental factors caused by land conversion. Boxes indicate measured variables
 23 used in the model. The solid blue and red arrows indicate significant positive and
 24 negative effects, respectively, and the dotted arrow indicates insignificant effect on the
 25 dependent variable. Numbers adjacent to arrows are standardized path coefficients,
 26 indicating the effect size of the relationship. R^2 represents the variance explained for
 27 target variables. * $p < 0.05$; ** $p < 0.01$.

1 **Table 1**

2 The global warming potential and carbon emission of brackish marsh, clipped marsh and aquaculture ponds.

Habitat type	CO₂ flux (mg CO₂ m⁻² h⁻¹)	CH₄ flux* (mg CH₄ m⁻² h⁻¹)	C emission (mg C m⁻² h⁻¹)	GWP (mg CO₂-eq m⁻² h⁻¹)
Brackish marsh	-490.8	1.3	-11.1	-453.3
Clipped marsh	382.6	0.3	8.7	391.3
Aquaculture ponds	6.2	17.4	1.2	493.4

3 *Data was from [Yang et al. \(2022a\)](#). Global warming potential (GWP, mg CO₂-eq m⁻² h⁻¹) from CO₂ and CH₄ fluxes was calculated. The radiative forcing
4 constant of CH₄ is 28 times relative to CO₂ equivalent at the 100-year time horizon ([IPCC 2014](#)).

1 **Supporting Information**

2 **Effects of conversion of coastal marshes to aquaculture ponds on**
3 **sediment anaerobic CO₂ production and emission in a subtropical**
4 **estuary of China**

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24 **Supporting Information Summary**

25 **No. of pages: 7 No. of method description: 1 No. of figures: 3**

26 **No. of tables: 0**

27 **Page S3:** Measurement of CO₂ concentration.

28 **Page S4:** Figure S1. Boxplots of (a) sediment temperature (T_s); (b) sediment salinity; (c)
29 sediment pH; (d) sediment total carbon (STC) content; (e) sediment total nitrogen (STN)
30 content; (f) porewater SO₄²⁻ concentration; (g) porewater Cl⁻ concentration; (h)
31 porewater NO₃⁻-N concentration; (i) porewater NH₄⁺-N concentration in brackish marsh
32 and aquaculture ponds. * and ** indicate significant differences between summer and
33 winter at levels of $p < 0.05$ and $p < 0.01$, respectively. Data are after Yang *et al.* [2022a,
34 2022b] for reference and review only.

35 **Page S5:** Figure S2. Redundancy analysis (RDA) of the relationship between CO₂ fluxes
36 (F_{CO_2}) (and CO₂ production potential, P_{CO_2}) and environmental factors between brackish
37 marsh (a) and aquaculture ponds (b). The pie charts show the percentages of relative
38 influence of environmental factors on F_{CO_2} and P_{CO_2} .

39 **Page S6:** Figure S3. Partial least square structural equation modeling (PLS-SEM) of the
40 effect of environmental factors on CO₂ fluxes and CO₂ production potential among
41 brackish marsh (a) and aquaculture ponds (b). Boxes indicate measured variables entered
42 in the model. The solid blue and red arrows indicate significant positive and negative
43 effects, respectively, and the dotted arrows indicate insignificant effects on dependent
44 variables. Numbers adjacent to arrows are standardized path coefficients, indicating the
45 effect size of the relationship. R² represents the variance explained for target variables.
46 * $p < 0.05$; ** $p < 0.01$.

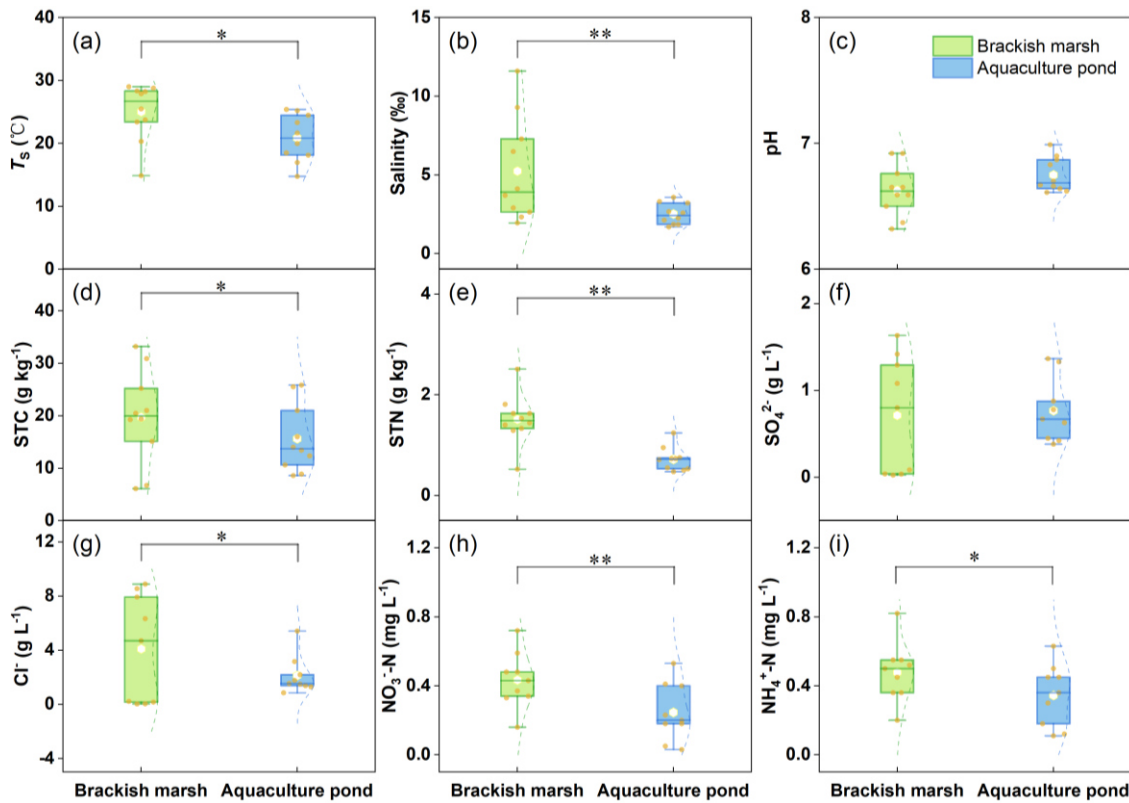
47 **Method description**

48 Measurement of CO₂ concentration

49 CO₂ concentrations were measured using a gas chromatograph (GC-2014,
50 Shimadzu, Japan) equipped with a flame ionization detector (FID); The column and
51 detector temperatures were set at 45°C and 280 °C, respectively; The flow rate of
52 nitrogen (the carrier gas) was set at 30 mL min⁻¹, while the flow rate of air and H₂ for
53 the FID were set at 400- and 40-mL min⁻¹, respectively. The gas chromatograph system
54 was Nanjing Special Gas Co., Ltd (low standard CO₂ = 395 ppm; high standard CO₂ =
55 3090 ppm). The mean analytical precision of individual measurements was 5%.

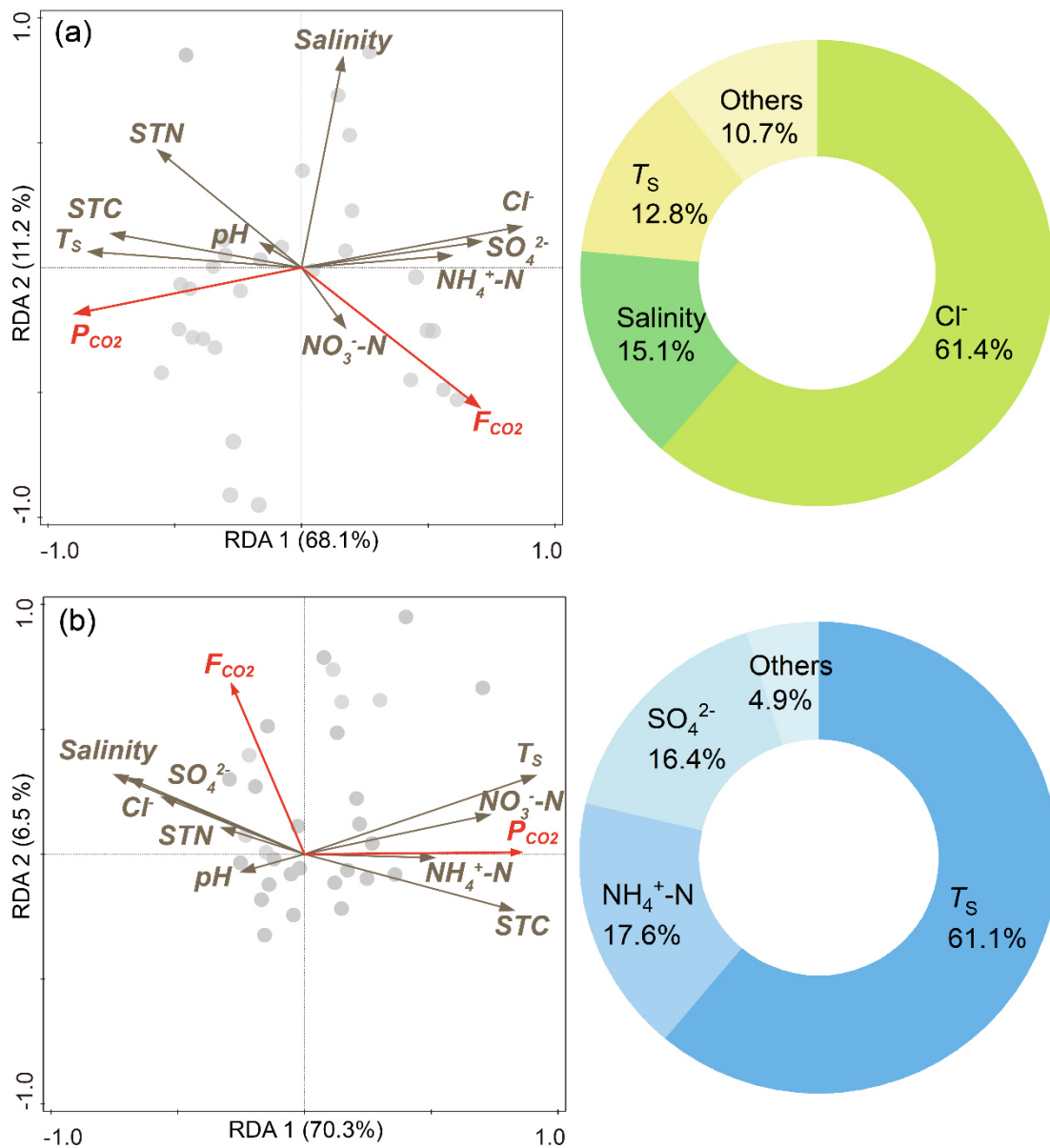
56 The CO₂ emission flux was calculated using a linear regression of the changes in
57 the gas concentrations inside the chamber and the measured time, base area, chamber
58 volume, and the molar volume of CO₂ at ambient temperature ([Hirota et al., 2004](#); [Helton
59 et al., 2014](#)). Similarly, a linear regression was also used for calculation of CO₂
60 production rate ([Liu et al., 2019](#); [Wang et al., 2017](#)).

61 The minimum detectable concentration difference of CO₂ was ±1.0 ppmv, which
62 was calculated uses replicates of standards. All CO₂ emission fluxes and production rates
63 were above the minimum detectable concentration difference. We excluded the fluxes
64 and production rates with poor linear relationships (i.e., $r^2 < 0.90$) from further analysis.
65 The majority of flux measurements had regression coefficients of $r^2 > 0.90$.



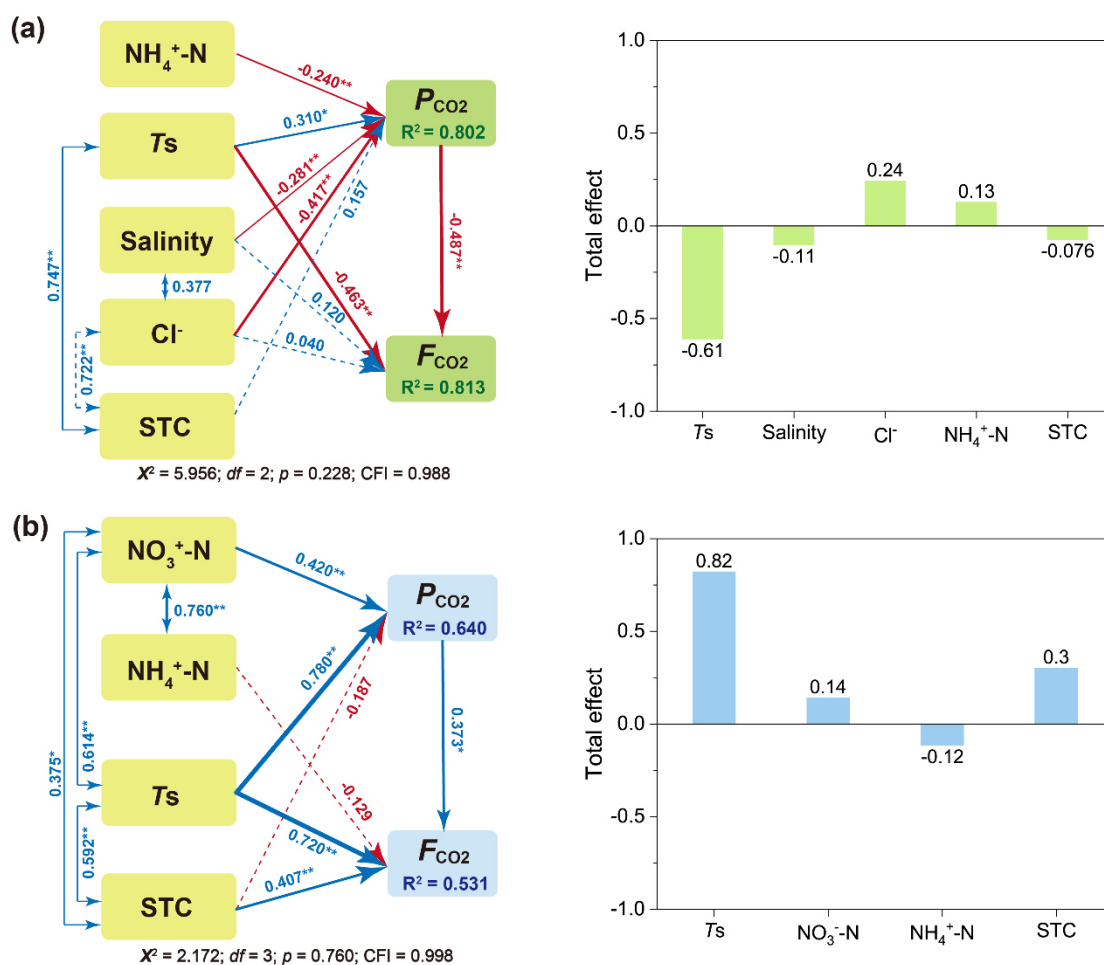
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67 **Figure S1.** Boxplots of (a) sediment temperature (T_s); (b) sediment salinity; (c) sediment
 68 pH; (d) sediment total carbon (STC) content; (e) sediment total nitrogen (STN) content;
 69 (f) porewater SO_4^{2-} concentration; (g) porewater Cl^- concentration; (h) porewater NO_3^- -
 70 N concentration; (i) porewater NH_4^+ -N concentration in brackish marsh and aquaculture
 71 ponds. * and ** indicate significant differences between summer and winter at levels of
 72 $p < 0.05$ and $p < 0.01$, respectively. Data are after [Yang et al. \[2022a, 2022b\]](#) for reference
 73 and review only.



74

75 **Figure S2.** Redundancy analysis (RDA) of the relationship between CO_2 fluxes (F_{CO_2})
 76 (and CO_2 production potential, P_{CO_2}) and environmental factors between brackish marsh
 77 (a) and aquaculture ponds (b). The pie charts show the percentages of relative influence
 78 of environmental factors on F_{CO_2} and P_{CO_2} .



79

80 **Figure S3.** Partial least square structural equation modeling (PLS-SEM) of the effect of
 81 environmental factors on CO_2 fluxes and CO_2 production potential among brackish
 82 marsh (a) and aquaculture ponds (b). Boxes indicate measured variables entered in the
 83 model. The solid blue and red arrows indicate significant positive and negative effects,
 84 respectively, and the dotted arrows indicate insignificant effects on dependent variables.
 85 Numbers adjacent to arrows are standardized path coefficients, indicating the effect size
 86 of the relationship. R^2 represents the variance explained for target variables. * $p < 0.05$;
 87 ** $p < 0.01$.

88 **Reference**

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102 and N₂O and soil concentrations of C, N and P across 26 paddy fields in southeastern
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