

1 ***Spartina alterniflora* invasion controls organic carbon stocks in coastal marsh and**
2 **mangrove soils across tropics and subtropics**

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4 **Running title: *S. alterniflora* controls on SOC stocks**

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60 **Abstract:** Coastal wetlands are among the most productive ecosystems and store large amounts
61 of organic carbon (C) – the so termed “blue carbon”. However, wetlands in the tropics and
62 subtropics have been invaded by smooth cordgrass (*Spartina alterniflora*) affecting storage of
63 blue C. To understand how *S. alterniflora* affects SOC stocks, sources, stability, and their
64 spatial distribution, we sampled soils along a 2500 km coastal transect encompassing tropical
65 to subtropical climate zones. This included 216 samplings within three coastal wetland types:
66 a marsh (*Phragmites australis*) and two mangroves (*Kandelia candel* and *Avicennia marina*).
67 Using $\delta^{13}\text{C}$, C: nitrogen (N) ratios and lignin biomarker composition we traced changes in the
68 sources, stability and storage of SOC in response to *S. alterniflora* invasion. The contribution
69 of *S. alterniflora*-derived C up to 40 cm accounts for 5.6%, 23% and 12% in the *P. australis*,
70 *K. candel* and *A. marina* communities, respectively, with a corresponding change in SOC
71 storage of +3.5, -14 and -3.9 t C ha⁻¹. SOC storage did not follow the trend in aboveground
72 biomass from the native to invasive species, or with vegetation types and invasion duration (7–
73 15 years). SOC storage decreased with increasing mean annual precipitation (1000–1900 mm)
74 and temperature (15.3–23.4 °C). Edaphic variables in *P. australis* marshes remained stable
75 after *S. alterniflora* invasion and so, their effects on SOC content were absent. In mangrove
76 wetlands, however, electrical conductivity, total N and phosphorus, pH and active silicon were
77 the main factors controlling SOC stocks. Mangrove wetlands were most strongly impacted by
78 *S. alterniflora* invasion and efforts are needed to focus on restoring native vegetation. By
79 understanding the mechanisms and consequences of invasion by *S. alterniflora*, changes in
80 blue C sequestration can be predicted to optimize storage can be developed.

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82 **KEYWORDS:** blue carbon, soil organic carbon storage, $\delta^{13}\text{C}$, lignin biomarkers, *Spartina*
83 *alterniflora*, exotic species invasion, mangrove ecosystems, coastal wetlands

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89 1 INTRODUCTION

90 Coastal wetlands play a critical role in storing carbon (C), referred to as ‘blue carbon’
91 (Macreadie et al., 2019), which provides significant promise for climate change mitigation
92 (Duarte et al., 2013). Coastal wetlands are, however, one of the most vulnerable ecosystems as
93 they are sensitive to climate and environmental change. The expansion of invasive plant species
94 is a result of, and contributes to, these changes (Davidson et al., 2018).

95 Of particular interest is the invasion of *Spartina alterniflora*, also known as smooth
96 cordgrass or *Sporobolus alterniflorus*, which has superior traits of high tolerance to flooding
97 and saline conditions, a long growing season, high net photosynthetic efficiency, and a large
98 specific leaf area index (Liu et al., 2020). This perennial C4 grass was introduced in 1979 to
99 intertidal wetlands of China from its native range, the United States, to stabilize soil and protect
100 the coastline (Bernik et al., 2016). Since then, *S. alterniflora* has been widely distributed over
101 340 km² of eastern coastal wetlands from Liaoning in Northeast China to Guangxi Province in
102 the south. Invasion by *S. alternifolia* has become one of the most important ecological problems
103 in central-south China. The *S. alterniflora* distribution covers 92.4% of the total area in the
104 tropical and subtropical coastal wetlands (Lu and Zhang, 2013). *S. alterniflora* invasions not
105 only replace the local species and threaten the biodiversity in native ecosystems (Didham et al.,
106 2005), but also alter ecosystem processes related to C stock (Hopkinson et al., 2012) through
107 changing C inputs and quality of net primary production, root system distribution and
108 rhizodeposition (Seliskar et al., 2002), and nutrient cycling (Ehrenfeld, 2003).

109 Over the last decade, many studies have addressed the *S. alterniflora* invasion induced
110 changes of soil organic carbon (SOC) storage compared to native communities, including a
111 decrease (Stevens et al., 2006; Kelleway et al., 2017), increase (Zhang et al., 2010; Wolkovich
112 et al., 2010; Yang et al., 2017) or negligible effects (Liao et al., 2018a; Chen et al., 2017).
113 Furthermore, the temporal changes in SOC storage remain poorly understood (Osland et al.,
114 2012; Kelleway et al., 2016). Previous studies mainly focused on native species including
115 *Phragmites australis* (Emery et al., 2014; Zhang et al., 2017), *Cyperus malaccensis* (Sridhar et
116 al., 2010; Jin et al., 2017), *Suaeda salsa* (Yuan et al., 2015; Yang et al., 2016), and *Scirpus*
117 *mariqueter* (Cheng et al., 2008; Schwarz et al., 2011), while studies on *S. alterniflora* invasion

118 in mangrove forests are scarce. Mangroves occupy only 0.5% of the global coastal area,
119 however, they contribute 10–15% to coastal sediment C storage and export 10–11% of the
120 particulate terrestrial C to the ocean (Alongi, 2014). Consequently, it is imperative to better
121 understand how *S. alterniflora* invasion influences the biogeochemical cycle of C in coastal
122 ecosystems.

123 Coastal wetlands are subject to a complex series of interactions between overflowing,
124 salinity, alternating oxidative-reductive conditions, high pH, N overloading, sea-level rise, tidal
125 action and changes to plant communities including the invasion by *S. alterniflora*, with these
126 interactions influencing SOC dynamics (Breithaupt et al., 2014; Hinson et al., 2019). Many
127 studies (Williams et al., 2015; Stagg et al., 2017) only investigate one or some fundamental
128 factors that control SOC dynamics. However, *S. alterniflora* invasion is dependent upon a
129 complex series of responses from coastal wetlands (Osland et al., 2018; Yang, 2019a). Factors
130 influencing this invasion may include (i) Climate factors: global precipitation and temperature
131 affect coverage distribution and NPP of *S. alterniflora*. Jobbágy and Jackson (2000) showed
132 that climate was the most important factor controlling SOC dynamics in surface layers, while
133 texture was the dominant factor in the deep soil. Hinson et al. (2019) concluded that latitude
134 and precipitation explained ~46% of the variance in SOC storage for wetlands on the West
135 Coast and Gulf Coast of the USA; (ii) Soil properties: few quantitative relationships describe
136 the effects of edaphic variables as altered by *S. alterniflora* on SOC storage (e.g., Grüneberg et
137 al., 2013; Yuan et al., 2015; Liu et al., 2017); and (iii) quantity and quality (or chemical
138 composition) of plant litter: vegetation communities had differences in litters and root exudates,
139 directly affecting the quality and quantity of organic C input, and finally deciding the C
140 accumulation in soils. Until now, very few studies have evaluated how changes to multiple
141 contributing factors such as the plant community, climate, and soil physicochemical and
142 biogeochemical properties regulate SOC storage, and what are the essential differences in the
143 three native communities (i.e., *P. australis*, *Kandelia candel* and *Avicennia marina*) following
144 *S. alterniflora* invasion (Luo et al., 2017; Yang, 2019a).

145 The isotopic signature associated with C inputs from *S. alterniflora* (C4 plant) differ from
146 native plants with are C3. The average values of $\delta^{13}\text{C}$ for C4 plants and C3 plants were about

147 -11‰ and -27‰ , respectively (Waring and Maricle, 2012). After the plant litter is
148 incorporated into soil, differences in redox conditions, soil development, and the degree and
149 type of microbial decomposition of SOC may significantly alter the $\delta^{13}\text{C}$ values (Werth and
150 Kuzyakov, 2010). Therefore, $\delta^{13}\text{C}$ values reflect the combined effects of the plant residues and
151 consecutive isotopic fractionation processes, which provide evidence of SOC source and
152 turnover (Guillaume et al., 2015; Xia et al., 2021).

153 The C:N ratio of the organic matter can also provide valuable information. While C is lost
154 as CO_2 or CH_4 during microbial transformation processes (Whiting and Chanton, 1993), N is
155 mostly retained in soils progressively decreasing C:N ratio. Thus, C:N ratios are widely used
156 as proxies for assessing the degree of SOC decomposition and loss (Drollinger et al., 2019),
157 i.e., a lower C:N ratio generally implies a higher degree of SOC decomposition (Davis et al.,
158 2003). The C:N ratio can be used to indicate SOC sources. A low C:N ratio (5–8) usually
159 indicate aquatic organic matter sources (Redfield, 1963), while a high C:N ratio (> 15) can
160 indicate organic matter from terrestrial sources (Meyers, 1994).

161 Biomarkers can provide further information on the SOM sources. Lignin, is one of the most
162 recalcitrant C forms derived from plant residues and has been widely used as a biomarker.
163 Lignin is composed of a suite of single-ring phenol compounds, including vanillyl (V), syringyl
164 (S), and cinnamyl (C). Their abundances and monomer ratios, including S/V, C/V and acid-to-
165 aldehyde (Ad-to-Al), are quantitative indicators of the molecular composition, stability and
166 source of plant-derived C in soils (Shafi et al., 2004; Thevenot et al., 2010). While previous
167 studies have employed $\delta^{13}\text{C}$ and C:N ratios (Kusumaningtyas et al., 2019; Sasmito et al., 2020),
168 few studies have combined the indices to evaluate the turnover of SOC, especially for coastal
169 wetlands with *S. alterniflora* invasion. Therefore, the $\delta^{13}\text{C}$ signature, C:N ratio and lignin
170 biomarkers are powerful tools to elucidate the sources, stability, mixing and transformations of
171 SOC in terrestrial and aquatic ecosystems.

172 To cover the broad regions that have been invaded by *S. alterniflora*, we selected 27 paired
173 sampling sites at 9 locations from 8 independent coastal wetlands along China's coastline
174 covering both subtropical and tropical climate zones. The objectives of this study were: (i) to
175 quantify the changes in SOC storage using a chronosequence approach varying from 7–15

176 years in nine locations with native species in response to *S. alterniflora* invasion; (ii) to identify
177 whether and how exotic *S. alterniflora* invasion influences SOC sources and stability based on
178 the C:N ratio, $\delta^{13}\text{C}$ signature and lignin biomarkers; (iii) to investigate the response of the
179 vertical distribution of SOC, proportion of *S. alterniflora*-derived organic C, and C budgets
180 following *S. alterniflora* invasion; and (iv) to clarify the joint effects of environmental factors
181 and soil properties on SOC stocks in response to *S. alterniflora* invasion.

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183 **2 MATERIALS AND METHODS**

184 **2.1 Site description**

185 To better understand the comprehensive mechanisms of SOC storage, budgets, sources and
186 stability in response to *S. alterniflora* invasion, a range of statistical methods were used to
187 analyze the main factors that control SOC turnover. We selected 9 locations with a total of 27
188 paired sampling sites from the 8 independent coastal wetlands covering subtropical and tropical
189 climate zones ([Figure 1](#)), including Chongming Island (CI), Hengsha Island (HI), Yueqing Bay
190 (YB), the Minjiang River Estuary (ME), Jiulong River Estuary (JE), Zhangjiang River Estuary
191 (ZE1 and ZE2), Zhanjiang (ZJ) and Beihai (BH). The native species that are dominant at these
192 sites included *P. australis*, and mangrove species *K. candel* and *A. marina*. Each native species
193 grew in the 3 independent locations, and has been invaded by adjacent C4 *S. alterniflora*. The
194 native species *P. australis* is native to CI, HI, ME; *K. candel* is native to YB, JE, ZE1; and *A.*
195 *marina* is native to ZE2, ZJ, BH. Detailed information of the sampling sites is shown in [Table](#)
196 [S1](#).

197

198 **2.2 Sample collection**

199 Three independent replicate sites were selected and sampled in June-August 2015 for each
200 location, resulting in a total of 27 paired sampling sites. Each site had two community types
201 (i.e., a paired site comparison), one dominated by native species (*P. australis* (grass), *K. candel*
202 (mangrove), *A. marina* (mangrove)), and the other had a significant population of the invasive
203 *S. alterniflora*. Using historical records to confirm the native species composition at each site,
204 we established that *S. alterniflora* completely outcompeted *P. australis*. For the native

205 mangrove sites, the invasion had begun along the margin and empty within the mangrove
206 community, and it was currently spreading its cover by all the mangrove community. The time
207 of invasion by *S. alterniflora* ranged from 7 to 15 years, while the native species had been
208 growing at these sites for more than 30 years.

209 Firstly, we randomly selected vegetation plot (square 10 m × 10 m), and then chose one
210 small subplot (1 m × 0.6 m) in the middle of vegetation plot. Samples were collected at 0–10,
211 10–20, 20–30 and 30–40 cm depth intervals using an auger, and three sub-samples in one
212 subplot were collected to form one composite sample per layer (Wang et al., 2019), resulting
213 in a total of 216 samples (nine sampling locations × three replicates × two communities × four
214 sampling depths). The aboveground biomass of grasses was collected from 1 m² square in the
215 center of vegetation plot (10 m × 10 m). The mangrove aboveground biomass was calculated
216 by an empirical formula based on diameter at the breast height, vertical height and density of
217 mangrove trees (Table S1; Tam et al., 1995). Visible stones and root residues were removed
218 before grinding and analysis. The samples were divided into two parts, one was stored frozen
219 in the laboratory, and the other part was stored air-dried in the dark.

220

221 **2.3 Laboratory analyses**

222 Bulk density (BD, g cm⁻³) was determined using the cutting ring method (100 cm³). Samples
223 were assessed for salinity (EC, μS cm⁻¹) (DDS-307 salinity meter, Boqu Scientific Instruments,
224 Shanghai, China), and pH (Orion Scientific Instruments, Minnesota, USA). Particle size
225 distribution (%) was measured using a Master Sizer 2000 Laser Particle Size Analyzer
226 (Malvern Scientific Instruments, Suffolk, UK).

227 Samples (about 0.50 g dry weight) were acidified with 1.0 M HCl (20 mL) to remove
228 carbonates, and then washed 3–4 times with distilled water to remove residual acid. Soil
229 organic carbon (SOC, g kg⁻¹) and total nitrogen (TN, g kg⁻¹) were measured with a Vario EL
230 III Elemental Analyzer (Elementar Scientific Instruments, Hanau, Germany). Dissolved
231 organic carbon (DOC, mg kg⁻¹) was extracted with deionized water (1: 5 ratio) and measured
232 using a TOC-V CPH total C analyzer (Shimadzu Scientific Instruments, Kyoto, Japan).
233 Microbial biomass carbon (MBC, mg kg⁻¹) was assayed using the fumigation-extraction and

234 extracts measured on the TOC-V analyzer (Vance et al., 1987). Labile organic carbon (LOC, g
235 kg⁻¹) was oxidized with 0.33 M KMnO₄ and determined using a colorimetric method. The
236 stable carbon isotope signatures (δ¹³C ratios) were measured using an elemental analyzer-
237 continuous flow isotope ratio-mass spectrometer (Finnegan MAT253, Thermo Scientific,
238 Waltham, MA, USA).

239 For total phosphorus (TP, g kg⁻¹) analyses, 1.00 g soil was first digested by 5 mL 12.4 M
240 perchloric-acid and measured colorimetrically on a UV-2450 spectrophotometer (Shimadzu
241 Scientific Instruments, Kyoto, Japan). For active iron (Fe_{Ac}, mg g⁻¹), aluminum (Al_{Ac}, mg g⁻¹),
242 and silicon (Si_{Ac}, mg g⁻¹), 1.00 g soil was extracted (m:v = 1:50 ratio) by oxalic acid-ammonium
243 oxalate solution (mol/mol = 4/5), and measured colorimetrically using 1,10-phenanthroline
244 monohydrate, chromeazurol, molybdenum blue methods, respectively, on a UV-1800
245 spectrophotometer (Shimadzu Scientific Instruments, Kyoto, Japan).

246 For lignin phenol analysis, samples (about 1.00 g) were extracted with 1.00 g copper oxide
247 (CuO), 0.10 g ammonium iron (II) sulfate [Fe(NH₄)₂(SO₄)₂·6H₂O] and 15 mL of nitrogen (N₂)-
248 purged NaOH solution (2 mmol L⁻¹) in Teflon-lined bombs. Then all bombs were flushed with
249 N₂ in the headspace for 10 min and heated at 150°C for 2.5 h in an oven. The lignin oxidation
250 products (LOPs) were derivatized with N, O-bis-(trimethylsilyl) trifluoroacetamide (BSTFA)
251 and pyridine at 70°C for 3 h to yield trimethylsilyl (TMS) derivatives, and were quantified
252 using internal standards (i.e., trans-Cinnamic acid) on an Agilent 7890B/7010B TQ GC-MS
253 system (Agilent, USA) using a DB-5MS column (Xia et al. 2020a).

254

255 **2.4 Calculations and statistical analyses**

256 Data sets were checked for homogeneity and normality before analysis. The results were
257 expressed with the mean ± standard deviation. One-way analysis of variance (ANOVA) was
258 used to compare the significance ($p < 0.05$) of aboveground dry biomass of native and invasive
259 species with Tukey's test by SPSS ver.21.0. Pearson correlation analysis, redundancy analysis
260 (RDA) and meta-analysis were performed by using SPSS ver.21.0, Graphpad, Canoco 5.0 and
261 R statistic software, respectively.

262 Changes in SOC content caused by *S. alterniflora* invasion (ΔSOC, g kg⁻¹) were estimated

263 using the following formula:

$$264 \quad \Delta SOC = SOC_{Invasive} - SOC_{Native}$$

265 where $SOC_{Invasive}$ and SOC_{Native} are the soil organic carbon contents (g kg^{-1}) in invasive
266 and native communities, respectively.

267 SOC storage (SOCS) was calculated as:

$$268 \quad SOCS = \frac{SOC \times BD \times D}{100}$$

269 where SOC is soil organic carbon content (g kg^{-1}), BD is bulk density (g cm^{-3}), and D is the
270 thickness of sampled layer (cm).

271 We estimated the changes in SOCS ($\Delta SOCS$, kg C m^{-2}) caused by *S. alterniflora* invasion
272 using the following formula:

$$273 \quad \Delta SOCS = SOCS_{Invasive} - SOCS_{Native}$$

274 where $SOCS_{Invasive}$ and $SOCS_{Native}$ are the soil organic carbon storage (kg C m^{-2}) in
275 invasive and native communities, respectively.

276 The proportion of C4 *S. alterniflora*-derived SOC (f , %) in *P. australis* and mangrove (*K.*
277 *candel* and *A. marina*) communities was calculated using a two end-member stable isotope
278 mass balance equation (Werth and Kuzyakov, 2010):

$$279 \quad f = \frac{\delta^{13}C_{mix} - \delta^{13}C_{old}}{\delta^{13}C_{new} - \delta^{13}C_{old}} \times 100\%$$

280 where $\delta^{13}C_{mix}$ is the average $\delta^{13}C$ -SOC from sites with invasive *S. alterniflora*, $\delta^{13}C_{old}$ is the
281 average $\delta^{13}C$ -SOC in native *P. australis* and mangrove (*K. candel* and *A. marina*) communities,
282 and $\delta^{13}C_{new}$ is the average $\delta^{13}C$ of *S. alterniflora* plant materials, which is the $\delta^{13}C$ value of
283 leaves, litter and roots, being an average of -13.4‰ (Cheng et al., 2006; Yang et al., 2016).

$$284 \quad \text{Gains} = \text{Current SOC storage of invasive communities} \times f$$

$$285 \quad \text{Retained SOC storage} = \text{Current SOC storage of invasive communities} - \text{Gains}$$

$$286 \quad \text{Losses} = \text{Retained SOC storage} - \text{Current SOC storage of native communities}$$

$$287 \quad \text{C budget} = \text{Current SOC storage of invasive communities} - \text{native communities}$$

288

289 **3 RESULTS**

290 **3.1 SOC content and storage following invasion by *S. alterniflora***

291 The average SOC content in the native *P. australis* community was equivalent to the invasive
292 *S. alterniflora* community, and the average Δ SOC content was overall close to zero in four soil
293 layers. However, the average SOC content in the native mangrove *K. candel* community was
294 higher than that of the community with the invasive *S. alterniflora*, with a mean Δ SOC content
295 of $-3.61 - -1.66 \text{ g kg}^{-1}$. Similar to the *K. candel* community, the average SOC content in the
296 native mangrove *A. marina* community was also slightly higher than that of the community
297 with the invasive *S. alterniflora*, and the mean Δ SOC content was positive in the upper soil
298 layer (0–10 cm) but negative in sub-layers (10–40 cm). The average SOC content decreased
299 with depth in general at all sampling sites, irrespective of community composition (Figure 2).
300 The SOC content largely varied (Figure S1), but the Δ SOC content overall had similar trends
301 for the same native species in independent coastal wetlands under *S. alterniflora* invasions
302 (Figure S2).

303 The average SOC storage in 0–40 cm in the native *P. australis* community (7.1 kg C m^{-2})
304 was slightly lower ($p > 0.05$) than that of the community with the invasive *S. alterniflora* (7.5
305 kg C m^{-2}). The average SOC storage in the native *K. candel* (5.4 kg C m^{-2}) and *A. marina* (5.0
306 kg C m^{-2}) mangroves were larger than ($p < 0.05$) those of the corresponding *S. alterniflora*
307 community (4.0 and 4.6 kg C m^{-2}). The losses in SOC storage at depths of 0–40 cm were 0.06 ,
308 2.3 and 0.96 kg C m^{-2} , and the proportions of *S. alterniflora*-derived C were 5.6% , 23% and
309 12% in the native *P. australis*, *K. candel* and *A. marina* communities. Thus, the budget for SOC
310 storage was $+3.5$, -14 and -3.9 t C ha^{-1} following *S. alterniflora* invasion into *P. australis*, *K.*
311 *candel* and *A. marina* communities, respectively (Table 1; Figure 4c). The average SOC storage
312 had irregular patterns with the sampling depth in both native *P. australis* and its corresponding
313 invasive *S. alterniflora* community, while the average SOC storage decreased with soil depth
314 in the mangrove communities and their adjacent invasive *S. alterniflora* community (Figure 3).
315 For independent coastal wetlands, the SOC storage varied greatly (Figure S3), but Δ SOC
316 storage had a consistent trend for the same native species following *S. alterniflora* invasion
317 (Figure S4).

318

319 **3.2 Native and invasive vegetation biomass**

320 The aboveground biomass of *P. australis* was 26% lower than that of the community with
321 the invasive *S. alterniflora* ($p > 0.05$). The *S. alterniflora* communities currently occupy areas
322 in the margins of the mangrove communities and in the empty spaces within the mangrove
323 communities, with the aboveground biomass of *K. candel* and *A. marina* being 4.7 and 20 times
324 that of invasive *S. alterniflora*, respectively ($p < 0.05$; [Figure S5](#)).

325

326 **3.3 Changes in $\delta^{13}\text{C}$ values and C:N ratios**

327 The average $\delta^{13}\text{C}$ of SOC in soil under the native *P. australis* (C3 plant; $\delta^{13}\text{C} = -23.2\text{‰}$)
328 community became ^{13}C -enriched following *S. alterniflora* (C4 plant; $\delta^{13}\text{C} = -22.5\text{‰}$) invasion
329 ($p > 0.05$). The average $\delta^{13}\text{C}$ of SOC in soil under *K. candel* (C3 plant) and *A. marina* (C3
330 plant) mangrove communities were -25.3‰ and -24.6‰ , respectively, and significantly ^{13}C -
331 enriched 2.9‰ and 1.5‰ compared to their corresponding *S. alterniflora* invasion with a mean
332 of -22.4‰ and -23.1‰ ($p < 0.05$; [Figure 4a](#)).

333 The average soil C:N ratios in the *P. australis* community (11–19) were not significantly ($p >$
334 0.05) lower than that of the community with the invasive *S. alterniflora* (7.1–21), while the soil
335 C:N ratios in the native *K. candel* (8.3–13) and *A. marina* (8.0–12) community decreased
336 slightly ($p > 0.05$) following *S. alterniflora* invasion, ranging from 8.2–15, 5.6–10, respectively.
337 The soil C:N ratios in the *P. australis* communities were higher than those of the mangrove
338 communities, regardless of whether the native communities were invaded by *S. alterniflora*
339 ([Figure 4b](#)).

340

341 **3.4 Lignin biomarker composition**

342 The content of plant-derived lignin phenols in soils ([Table S2](#)) show a significant relationship
343 ($p < 0.01$) with SOC content in both native and invasive communities ([Figure 4d](#)). C/V and
344 S/V decreased in the *P. australis* community but increased in the mangrove forests (dominated
345 by *K. candel* and *A. marina*) following *S. alterniflora* invasion, especially for C/V. The
346 $(\text{Ad/Al})_v$ and $(\text{Ad/Al})_s$ in the *P. australis* community decreased following *S. alterniflora*
347 invasion. In contrast, $(\text{Ad/Al})_v$ and $(\text{Ad/Al})_s$ in the mangrove forests increased after *S.*
348 *alterniflora* invasion, especially for $(\text{Ad/Al})_s$. The values of lignin monomers (C/V, S/V,

349 (Ad/Al)_v, (Ad/Al)_s) in the *P. australis* community decreased while an increase was observed
350 in the mangrove community following invasion by *S. alterniflora*. This increase was more
351 evident in the *K. candel* than the *A. marina* community (Figure 5).

352

353 4 DISCUSSION

354 4.1 Effects of plant biological traits and invasion duration on SOC stocks

355 *S. alterniflora* has several advantageous eco-physiological traits over many native species.
356 These traits have enabled it to replace co-occurring native species, especially grasses, in the
357 saltmarshes along the eastern coast of China. *S. alterniflora* has higher net primary production
358 (NPP) and litter yield than native *P. australis* (Yang et al., 2016), altering plant C input to soils
359 (Kelleway et al., 2017). C sequestration in soils was also limited by litter quality and
360 decomposition under ecosystems (Fierer et al., 2005). Liao et al. (2008b) reported that the
361 decomposition rate of *S. alterniflora* litter, particularly the belowground root residues, was
362 slower than that of *P. australis* litter due to the lower litter quality (i.e., higher C:N ratio) of *S.*
363 *alterniflora* (Duan et al., 2018). Respiration of roots and microorganisms is another important
364 factor influencing C stocks. Bu et al. (2015) have verified that CO₂ efflux from soil and
365 microbial biomass in the *S. alterniflora* stands was higher than that of native *P. australis* stands
366 in the Yangtze River estuary, but ANPP and SOC were higher in the *S. alterniflora* stands than
367 that of ecosystems with native species. Our results have confirmed that the aboveground
368 biomass of invasive *S. alterniflora* was larger than native *P. australis* (Figure S5), and SOC
369 storage in the *S. alterniflora* community was 3.2% higher than that of *P. australis* community
370 ($p > 0.05$; Table 1). This indicated that increased NPP and slower decomposition of biomass
371 derived from *S. alterniflora* outweighed the invasion-induced C loss, confirmed by increased
372 CO₂ efflux from soil in comparison with *P. australis* (Van Kleunen et al., 2010).

373 While the positive effect of *S. alterniflora* on SOC stocks has been well documented in grass
374 marshes (e.g., He et al., 2019; Yang, 2019b), there is a paucity of studies that investigate the
375 effects of *S. alterniflora* invasion in mangrove communities (e.g., Giri and Long, 2014; Sun et
376 al., 2019). Although the ANPP of *S. alterniflora* varies from 1000 to 1500 g m⁻² year⁻¹, and can
377 be as high as 4000 g m⁻² year⁻¹ under optimal conditions (Kirwan et al., 2009), the ANPP of *S.*

378 *alterniflora* was much lower than that of mangrove (*K. candel* and *A. marina*; [Figure S5](#)). The
379 SOC storage in mangroves decreased by 26% and 7.8% (respectively) following *S. alterniflora*
380 invasion ([Figure 3](#)), consistent with other studies on mangrove community encroachment (e.g.,
381 [Osland et al., 2013](#); [Lunstrum and Chen, 2014](#)). Soils or sediments tend to efficiently sequester
382 organic C in mangrove forests, which is attributed to the morphological structure of mangroves
383 and their widespread roots ([Krauss, 2003](#)). Litter from mangroves consists of leaves, branches,
384 standing and fallen main stems. The unique tree structure and complex aerial root systems (e.g.,
385 prop roots, pneumatophores) across mangrove species result in greater biomass than grasses,
386 and these specific structures are more effective for trapping organic-rich sediments ([Kristensen
et al., 2008](#)). The litter from above- and below-ground components in mangrove forests tend to
387 have greater recalcitrant C compounds (e.g., lignin, tannins, cutin, suberin and waxes) and are
388 more difficult to decompose than grass litter ([Chanda et al., 2015](#)). Therefore, high rates of
389 organic C burial in mangrove forests are attributed primarily to the production, accumulation,
390 burial and decomposition of aerals and roots. Thus, invasion by *S. alterniflora* can lower the
391 SOC storage. The decrease in aboveground biomass of *K. candel* was much lower than that of
392 *A. marina* ([Figure S5](#)), but the decrease in SOC storage in the *K. candel* community was much
393 larger than that of the *A. marina* community following *S. alterniflora* invasion ([Figure S3 &
Figure S4](#)). Consequently, the net SOC storage is dependent not only on the apparent NPP and
394 litters, but largely on how much of the apparent NPP and litters eventually enters the soil, how
395 organic matter is eventually formed and transferred to different soil depths.

398 *S. alterniflora* invasion has been shown to gradually increase the aboveground and
399 belowground biomass in invaded ecosystems, achieving a steady increase after 8 years ([Yu et
al., 2014](#)). The impacts of *S. alterniflora* invasion on SOC dynamics across a chronosequence,
400 however, are not fully understood. There were linearly negative or positive relationships
401 between the SOC stock and duration of *S. alterniflora* invasion, and most studies have focused
402 on grass-dominated marsh and tidal flats. In contrast, short-term invasion of *S. alterniflora* did
403 not alter SOC stocks ([Tong et al., 2011](#)). Liu et al. (2017) reported that *S. alterniflora* invasion
404 increased the SOC storage with depth and years since invasion in saltmarsh (including mudflat,
405 *Suaeda salsa*, and grass flat). The highest proportion of *S. alterniflora*-derived C have been
406

407 reported 17 years after invasion, with decreased decay rate of old C and the increased mean
408 residence time following 20 years in bare flat land (Yang et al., 2017). We, however, observed
409 no relationships between changes in SOC storage and the time since *S. alterniflora* invasion up
410 to 40 cm in depth across three native communities (Figure 6a & Figure S6). Whether the effects
411 of *S. alterniflora* invasion on SOC storage are positive or negative depend on the specific soil
412 depth, invasion chronosequence and native species. On the contrary, many salt marshes were
413 encroached by mangrove forest with climate change (e.g., sea-level rise) (Osland et al., 2012).
414 Many studies (Lunstrum and Chen, 2014; Yando et al., 2016) considered that SOC storage can
415 increase with encroachment over a longer period, driven by rapid increases in aboveground
416 biomass and large belowground stocks (i.e., inclusive of root and non-root C) (Kelleway et al.,
417 2016).

418

419 **4.2 Response of SOC stocks to regional climate factors and climate change**

420 Contrasting climate factors, soil properties and biological traits have long been the basis of
421 predicting changes in SOC stocks. However, at small regional scales or controlled experiments,
422 where climatic and soil properties are uniform, *S. alterniflora* invasion influences the quantity
423 and quality of organic C inputs into soils. These variables cause plant-soil feedback to regulate
424 local SOC cycling and stocks. Climate is generally regarded as the dominant factor controlling
425 SOC stocks, and often explains the largest proportion of SOC variation at large regional or
426 global scales (Kurganova et al., 2014; 2015; Fellman et al., 2017; Spivak et al., 2019).

427 We calculated Δ SOC storage between adjacent native and invasive communities in order to
428 fully eliminate the differences in background (i.e., native species, soil properties, etc.),
429 retaining the straddling climate factors across subtropical and tropical climate zones. A
430 negative relationship between Δ SOC storage at depths of 0–40 cm and MAT (Figure 6b) was
431 detected, which is supported by other studies from large regional to global estimates (Jobbágy
432 and Jackson, 2000). The increases in SOC storage with decreasing temperature and
433 precipitation are attributed to the dependence upon the decreased rate of SOM decomposition
434 (Chmura et al., 2003; Davidson and Janssens, 2006; Qiu et al., 2018). Stronger negative
435 relationships with depth were observed in the 0–30 cm soil layer (Figure S7), while the effects

436 of MAT on SOC storage was not evident in the 30–40 cm soil layer (Figure S7). The effects of
437 temperature on SOC storage also diminished with soil depth (Yang et al., 2010; Liu et al., 2012),
438 while some studies indicated that temperature had greater effects on SOC storage through its
439 effect on stabilizing SOC at soil depths greater than 1 m (Yang et al., 2019a; Lin et al., 2018).
440 The biogeochemical processes influencing SOC turnover in the top 30 cm have been largely
441 related to biological processes following the invasion by *S. alterniflora* (Craft et al., 2003).
442 Biological activity decreases with depth due to the lower density of roots and lack of litter input
443 when depths exceed 30 cm. These results indicated that climatic effects may be mediated by
444 biological processes. Similar to the effect of MAT, negative relationships between Δ SOC
445 storage and MAP were also observed at depths of 0–40 cm (Figure 6b), with the relationship
446 being stronger in the 0–30 cm layer compared to the 30–40 cm soil layer (Figure S7). Coastal
447 wetlands have a predominantly anaerobic environment that is often affected by tidal action and
448 rising sea levels. In our study, the effects of MAT on SOC storage were therefore a greater
449 influence than MAP, and overwhelmed the relationship with MAP.

450 On a century or millennium scale, temperature and precipitation depending on latitude and
451 longitude control the distribution of marshes and mangroves in coastal wetlands (Cavanaugh
452 et al., 2019). Contrary to the process of *S. alterniflora* invading mangroves, increased
453 temperature and sea level rise have caused the expansion of mangrove forests into saltmarshes
454 with global warming (Saintilan et al., 2013; Cavanaugh et al., 2019). Mangroves expand their
455 range to higher latitudes and encroach salt marsh vegetation with declining freeze events
456 (Cavanaugh et al., 2014). Other studies also suggest that mangrove encroachment enhances
457 SOC storage (e.g., Yando et al., 2016; Kelleway et al., 2017). In turn, blue C storage in
458 mangrove forests will decrease following *S. alterniflora* invasion under climate warming.
459 Moreover, some marshes will be permanently lost, but not converted to mangroves with
460 intensified climate change, thus the organic C storage will decline further.

461

462 **4.3 Effects of edaphic variables and confounding factors on SOC dynamics**

463 Climate and vegetation C input regulate the transformation rate of SOC storage from one to
464 another capacity. However, whether SOC can be stably preserved or the potential of SOC

465 storage is determined by soil physical and chemical properties (Luo and Viscarra-Rossel, 2020).
466 The effects of soil properties on SOC dynamics in response to *S. alterniflora* invasion have
467 received increasing attention (e.g., Ruiz Sinoga et al., 2012; Yang, 2019a). Zhang et al. (2011)
468 has demonstrated that SOC content in a single *P. australis* community was lower than in a
469 community with a mixed *P. australis* and *S. alterniflora* population. This was attributed to the
470 differences in vegetation type and salinity, whereas higher microbial activity was detected in
471 the *P. australis* community, leading to greater litter and SOC mineralization. Zhang et al. (2008)
472 reported significant alterations of soil properties, including TN, TP, cation exchange capacity
473 (CEC), MBC and MBN following invasion of mangrove wetlands by *S. alterniflora*, resulting
474 in lower SOC storage. Wang et al. (2016) has shown that *S. alterniflora* invasion in a mangrove
475 forest has led to significant decreases in TP, MBC, MBN, and activities of acid phosphatase
476 with an increase in pH, potentially causing a decrease in SOC content. These studies showed
477 the SOC content increased in marshes but decreased in mangrove forests following *S.*
478 *alterniflora* invasion, and these were consistent with our results (Figure 2 & Figure 3), which
479 were attributed to the differences in soil properties.

480 In our study, the native species were invaded marginally, adjacently, and internally. We
481 considered the soil properties are similar before *S. alterniflora* invasion, and these soil
482 properties in native communities will change with the invasion chronosequence, thus indirectly
483 impacting SOC turnover and stocks. We used *RDA* approach and Pearson correlation analysis
484 to describe the effects of soil properties on SOC content in the native (*P. australis*, *K. candel*
485 and *A. marina*) and adjacent invasive (*S. alterniflora*) communities at a broad regional scale
486 (Figure 7; Figure S8 & Figure S9). Clay and sand contents, pH and TN were the primary factors
487 controlling SOC contents in native *P. australis* and corresponding *S. alterniflora* communities
488 in marsh wetlands (Figure 8). The NPP of *S. alterniflora* was higher, and the litter
489 decomposition rate was lower than that of *P. australis* (Zedler and Kercher, 2004; Zhang et al.,
490 2014). *S. alterniflora* invasion made a slight contribution to SOC sequestration in the marsh
491 wetlands as it had a higher proportion of recalcitrant organic C (ROC) and lower proportion of
492 LOC and mineralizable C per unit SOC (Yang et al., 2013). Therefore, the increased SOC
493 stocks following invasion by *S. alterniflora* into *P. australis* communities resulted from

494 increased net photosynthetic rate, biomass, litter quality and decomposition, and decreased
495 SOC mineralization.

496 Edaphic variables were important in controlling SOC content after mangrove (*K. candel* and
497 *A. marina*) was invaded by *S. alterniflora* (Figure 7). Factors including TN, pH, Si_{Ac} were of
498 particular importance. Sand was negatively related to SOC content in the *A. marina* community
499 (Figure S8). SOC stocks in the *K. candel* community was greater than in the *A. marina*
500 community (Figure 3), this being attributed to fine-grained sediment which controls SOC
501 storage (Bai et al., 2016). Our results highlighted the importance of sediment type to SOC
502 storage, as indicated by the positive relationships with TN, Fe_{Ac}, and clay (Figure S8).
503 Therefore, the positive effect of fine soil fractions on stabilizing soil C may be via mineral
504 protection of SOM (Desjardins et al., 2006). SOC content was mainly affected by EC, WC,
505 sand and TN in the *S. alterniflora*-invaded *K. candel* community, while EC, pH, TN and TP
506 were the main factors in the *S. alterniflora*-invaded *A. marina* community. Moreover, the C
507 sequestration rate was controlled by the recalcitrant character of organic materials in wetlands
508 (Bernal and Mitsch, 2013). Compared to marsh, fringe mangroves are within or close to the
509 estuary. Therefore, mangroves have frequent anaerobic conditions derived from daily tidal
510 inundation with limited soil respiration, thus lowering C losses. Therefore, the decreased SOC
511 stocks in mangrove wetlands compared to marsh wetlands following *S. alterniflora* invasion
512 were attributed to a greater NPP of mangrove (Hutchison et al., 2013), lower salinity (Saintilan
513 et al., 2013), more recalcitrant organic substances (Barreto et al., 2016), decreased enzyme
514 activities and microbial diversity (Morrissey et al., 2014), and extended anaerobic conditions.
515 These mechanisms are site-specific and dependent on coastal hydro-geomorphology settings,
516 which explains the substantial variations in organic C burial rates, C density and C stocks in
517 independent wetlands (Twilley et al., 2018).

518

519 **4.4 Identification of SOC sources and stability by coupling $\delta^{13}\text{C}$, C:N ratios and lignin** 520 **biomarkers**

521 When vegetation species composition changes from C3 to C4 plants, or vice versa, $\delta^{13}\text{C}$ of
522 SOM can be used to identify the sources and to quantify the proportions of organic C derived

523 from residues and rhizodeposition derived from the C3 to C4 vegetation communities (Werth
524 and Kuzyakov, 2010; Sasmito et al., 2020). Our data revealed only a slight increase ($p > 0.05$)
525 in $\delta^{13}\text{C}$ values in native *P. australis* after invasion of *S. alterniflora* community. This lack of
526 strong increase in $\delta^{13}\text{C}$ could be explained by the fact that *P. australis* is predominantly C3 but
527 can switch to the C4 photosynthetic pathway under more extreme environments (Srivastava et
528 al., 2014), and the duration of invasion by *S. alterniflora* (i.e., 12–13 years) is relatively short,
529 where the *P. australis* monoculture has been the dominant community for over 30 years in the
530 coastal wetlands. However, the average $\delta^{13}\text{C}$ values in mangrove forests (dominated by *K.*
531 *candel* and *A. marina*, both C3 only) significantly increased following *S. alterniflora* invasion
532 ($p < 0.05$; Figure 4a), which is attributed to the C4 photosynthetic pathway of *S. alterniflora*
533 (Antonielli et al., 2002). Based on the mixing model, the proportion of *S. alterniflora*-derived
534 C in *P. australis* community was 5.6% in the 0–40 cm layer (Table 1). A similar result has been
535 previously reported by Cheng et al. (2006), where *S. alterniflora*-derived C contributed of 5.1%
536 (0–5 cm) and 9.5–11% (20–40 cm) in the Yangtze River estuary, while Zhang et al. (2010)
537 showed a contribution of 11–19% (0–10 cm) in the Wanggang estuarine wetland. The
538 proportions of *S. alterniflora*-derived C in *K. candel* and *A. marina* community were 23% and
539 12%, respectively, which were higher than that of *P. australis* community (Table 1). These
540 results illustrated that SOC turnover rate in mangroves was faster than that of marsh after *S.*
541 *alterniflora* invasion, and verified SOC storage decreased to a greater extent in the mangrove
542 compared to marsh communities.

543 Based on a data-assimilation approach and controlled experiments, a negative relationship
544 was observed between the SOC decomposition rate and the corresponding C:N ratio (Jiang et
545 al., 2013; Xu et al., 2016). Generally, herbaceous C4 plants (i.e., *S. alterniflora*) have higher
546 C:N ratios than C3 plants (i.e., *P. australis*) because the latter have more *Rubisco* proteins, and
547 the proteins are beneficial to improve photosynthetic efficiency (Still et al., 2003). The higher
548 photosynthetic efficiency and production potentially provide greater residual biomass inputs to
549 soil or sediment. The soil C:N ratio in the *S. alterniflora* community was higher than that of *P.*
550 *australis* (Figure 4b), suggesting large amounts of recalcitrant litter inputs from *S. alterniflora*
551 with a greater resistance to mineralization (Yang et al., 2009). Thus, SOC storage in the *S.*

552 *alterniflora* community was higher than that of the *P. australis* community (Figure 3). The C:N
553 ratios in mangrove forests slightly decreased after invasion by *S. alterniflora* because of the
554 differences in C:N ratios between grass and woody organic materials.

555 The soil C:N ratios gradually decreased from subtropical to tropical zones in coastal
556 wetlands (Figure 4b), to some extent, implying the decrease in the SOC stability. This is
557 consistent with SOC storage of *P. australis* > *K. candel* > *A. marina* whether it was invaded or
558 not. The C:N ratio may indirectly indicate the SOC sources. Algae in aquatic environments
559 typically have a very narrow C:N ratio ranging from 5 to 8, and vascular plants in terrestrial
560 ecosystems have a C:N ratio >15 (Meyers, 1994). The C:N ratios in soils suggest a mixture of
561 terrestrial and aquagenic or marine sources, and the soils or sediments in coastal wetlands were
562 increasingly affected by marine sources with increasing tropical conditions. Thus, it is not
563 sufficient to use the C:N ratio as a single indicator of SOC stability because the soil C:N ratios
564 depends on many processes and can be affected by various C and N sources.

565 Lignin is one of the most abundant components of higher plants in terrestrial ecosystems and
566 represents an important part of plant-derived C from biomass residues into soils (Xia et al.,
567 2020b). Lignin is somewhat recalcitrant due to its nonhydrolyzable C-C and C-O-C bonds and
568 the richness of aromatic structures (Crow et al., 2009). Significant relationships ($p < 0.01$)
569 between lignin and SOC contents in all sampling sites were observed (Figure 4d). The Ad-to-
570 Al ratios of V and S units increase with the increase in lignin decomposition. V monomers of
571 lignin are more stable than S and C monomers, thus increases in C/V and S/V imply enhanced
572 lignin decomposition (Bahri et al., 2006). Both monomer ratios (C/V, S/V) and Ad-to-Al ratios
573 ((Ad/Al)_V, (Ad/Al)_S) decreased in the *P. australis* community, but increased in mangroves after
574 invasion by *S. alterniflora*, and the increase was more evident in the *K. candel* community
575 (Figure 5). Consequently, lignin in the *P. australis* community was more degraded than in the
576 *S. alterniflora* community. In contrast, lignin in the mangrove communities was more stable
577 than in the *S. alterniflora* community, which is consistent with the increase in SOC storage in
578 the marsh and decrease in the mangrove communities following *S. alterniflora* invasion.

579 The C- and S- to-V ratios can also be used as source indicators being able to distinguish
580 grasses from mangrove (Thevenot et al., 2010). Given the C/V and S/V ratios with boundaries

581 of different sources (Jex et al., 2014), the sources of lignin phenols in the grass marsh are
582 derived from non-woody angiosperm tissues (A_{nw}). While the sources in mangroves are derived
583 from the complex of massive woody angiosperm (A_w) and non-woody angiosperm (A_{nw}), the
584 quantity of lignin sources derived from leaves and grasses increase in mangroves following *S.*
585 *alterniflora* invasion (Figure 9).

586

587 **4.5 Implications for wetland C management and control of *S. alterniflora* invasion**

588 The complexity of coastal ecosystems restricts the accurate prediction of SOC storage and
589 the determination of key factors involved in SOC storage. We are aware that despite 216
590 samplings on 9 sites in native ecosystems regarding changes in SOC storage following *S.*
591 *alterniflora* invasion may be uncertain. However, we believe that our model provides reliable
592 results because the qualitative data combining $\delta^{13}C$, C:N ratios and lignin biomarker
593 composition confirmed our sample authenticity and validity (Figure 10). The involvement of
594 further sampling sites in other wetland ecosystems will provide more details and definite
595 statements to SOC storage on a larger regional or continental scale.

596 As an exotic species, *S. alterniflora* has positive effects on native ecosystems, such as higher
597 levels of primary production, protection from storms, and maintenance of elevation; but this
598 species also poses significant threats (i.e., biodiversity change) (Gedan et al., 2010). Both *S.*
599 *alterniflora* and *P. australis* are aggressive species in China and the USA, respectively. Each
600 species is mutually considered as invasive species, thus, long-term investigations of native and
601 invasive species in global scale are required.

602 Although the positive and negative effects of *S. alterniflora* on SOC storage in marsh and
603 mangrove wetland had been verified, the behavior and quantity of SOC stocks in different
604 wetlands varied extensively. This SOC variability between wetlands result from the
605 morphology and biology of species, invasion years, tidal action, and edaphic variables (e.g.,
606 pH, EC, fertility, and redox potential) (Yando et al., 2016; Kelleway et al., 2017; Twilley et al.,
607 2018). Globally, organic C burial rates in mangrove forests have an average of 2.7 ± 0.7 Mg C
608 $ha^{-1} yr^{-1}$, which is about 20 times larger than that of terrestrial forest ecosystems (Breithaupt et
609 al., 2012). However, studies have estimated that mangrove deforestation causes the emission

610 of 0.007–0.03 Pg CO₂ y⁻¹ (Hamilton and Friess, 2018). Therefore, mangrove forests rank
611 among the most C-rich forests, which can be increased by selecting high C-density species for
612 afforestation and by increasing the area of mangrove.

613 Mangroves cover approximately 137,600 km² of coastline distributed across around 118
614 countries; with 39% found in Asia, 20% in Latin America and the Caribbean, 20% in Africa,
615 12% in Oceania, 8.4% in North America, and 0.70% in other regions (Bunting et al., 2018).
616 The area of mangrove forest in China is about 22,025 ha (less than 50% of the mangrove area
617 of 48,266 ha in 1950s) while the potential mangrove habitat is 58,848 ha (24% of the historical
618 area 250,000 ha) (Liu et al., 2014). The global rate of mangrove loss has, however, reduced
619 between the late 20th and early 21st century, from ~2% to <0.4% per year (Friess et al., 2019).
620 *S. alterniflora* is more tolerant to increased salinity and flooding stresses than native species,
621 therefore, its competitive advantage will increase with sea level rise (Hanson et al., 2016).
622 Mangroves not only ease the greenhouse effect, but also stabilize shorelines and decrease the
623 effects of natural disasters, including those of tsunamis and hurricanes (Saderne et al., 2018).
624 Undeniably, knowledge and information gained will aid policy and environmental management
625 decisions concerning the restoration of mangrove forests facing the increasingly threats from
626 invasion by *S. alterniflora*.

627

628 **5 CONCLUSIONS**

629 Coastal wetlands have been identified as critical C reservoirs, which have been affected by
630 the invasion of *S. alterniflora*. Changes in SOC storage in native ecosystems were not
631 completely consistent with the difference in aboveground net primary productivity (NPP) of
632 native and invasive species nor the years since invasion (7–15 years). Increasing temperature
633 from North to South over the 2500 km transect decreased SOC storage with the effects being
634 evident in the surface soil layers (0–30 cm) but diminished in the deeper layers. Invasion by *S.*
635 *alterniflora* increased SOC storage in *P. australis* marsh by 3.5 t C ha⁻¹, while substantial losses
636 –14 and –3.9 t C ha⁻¹ were observed in native *K. candel* and *A. marina* communities,
637 respectively. The proportions of *S. alterniflora*-derived C across the three communities were
638 5.6%, 23% and 12%. The increased SOC stocks in marsh was due to the increased NPP, higher

639 C:N ratio and lower mineralization of C derived from *S. alterniflora*. The depleted SOC stocks
640 in mangrove wetlands following invasion were attributed to decreased NPP, higher salinity,
641 lower recalcitrant organic inputs, increased enzyme activities and microbial diversity from
642 speculation, and alternative wet-dry conditions. SOC stocks were regulated mainly by the joint
643 effects of climate, plant biological traits and edaphic variables in the coastal wetlands. This
644 study has implications for better understanding the mechanisms driving C sequestration
645 potential in coastal marsh and mangrove wetlands undergoing exotic *S. alterniflora* invasion
646 worldwide. The control of *S. alterniflora* invasion into mangrove communities will provide
647 significant advantages to blue C storage in these systems. Results from this study can facilitate
648 environmental management and policy decisions concerning the restoration of mangrove
649 forests facing the increasingly serious *S. alterniflora* invasion worldwide.

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652

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658

659

660 **CONFLICT OF INTEREST**

661 All authors declare no conflict of interests.

662

663

664 **DATA AVAILABILITY STATEMENT**

665 The data that supports this study are available in the Supplementary materials, and they could
666 contact with the corresponding author.

667

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1060 **TABLE 1** Carbon budgets in the coastal wetlands under the native *Phragmites australis*, *Kandelia candel*,
 1061 and *Avicennia marina* communities in response to invasive *Spartina alterniflora* community

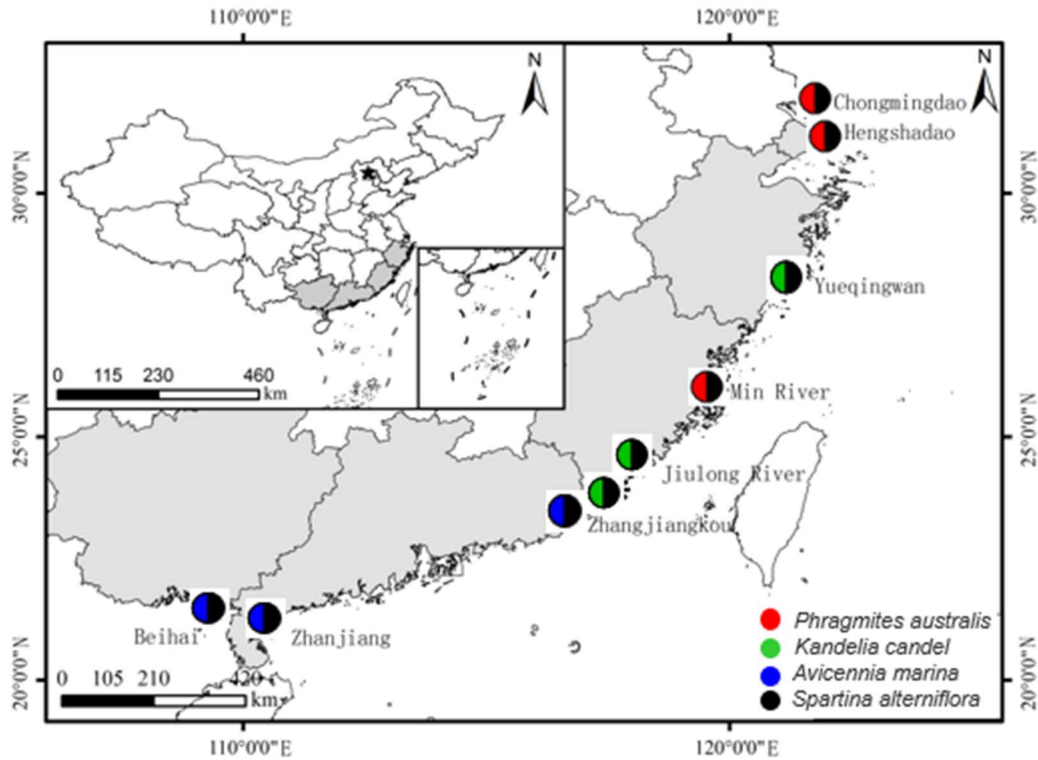
Native species	Current SOC storage (kg C m ⁻²)		Proportion of <i>S. alterniflora</i> - derived C (f, %)	Gains (kg C m ⁻²)	Retained SOC storage (kg C m ⁻²)		C budget (t C ha ⁻¹)
	Native	Invasive			Losses (kg C m ⁻²)		
<i>Phragmites australis</i>	7.1±1.3 (a)	7.5±1.1 (a)	5.6±19%	0.41	7.0	-0.06	3.5
<i>Kandelia candel</i>	5.4±0.64 (a)	4.0±0.77 (b)	23±15%	0.93	3.1	-2.3	-14
<i>Avicennia marina</i>	5.0±0.94 (a)	4.6±0.91 (b)	12±10%	0.57	4.1	-0.96	-3.9

1062 Note: Paired sample t-test was used to compared the significance ($p < 0.05$) of current SOC storage between native and invasive
 1063 community.

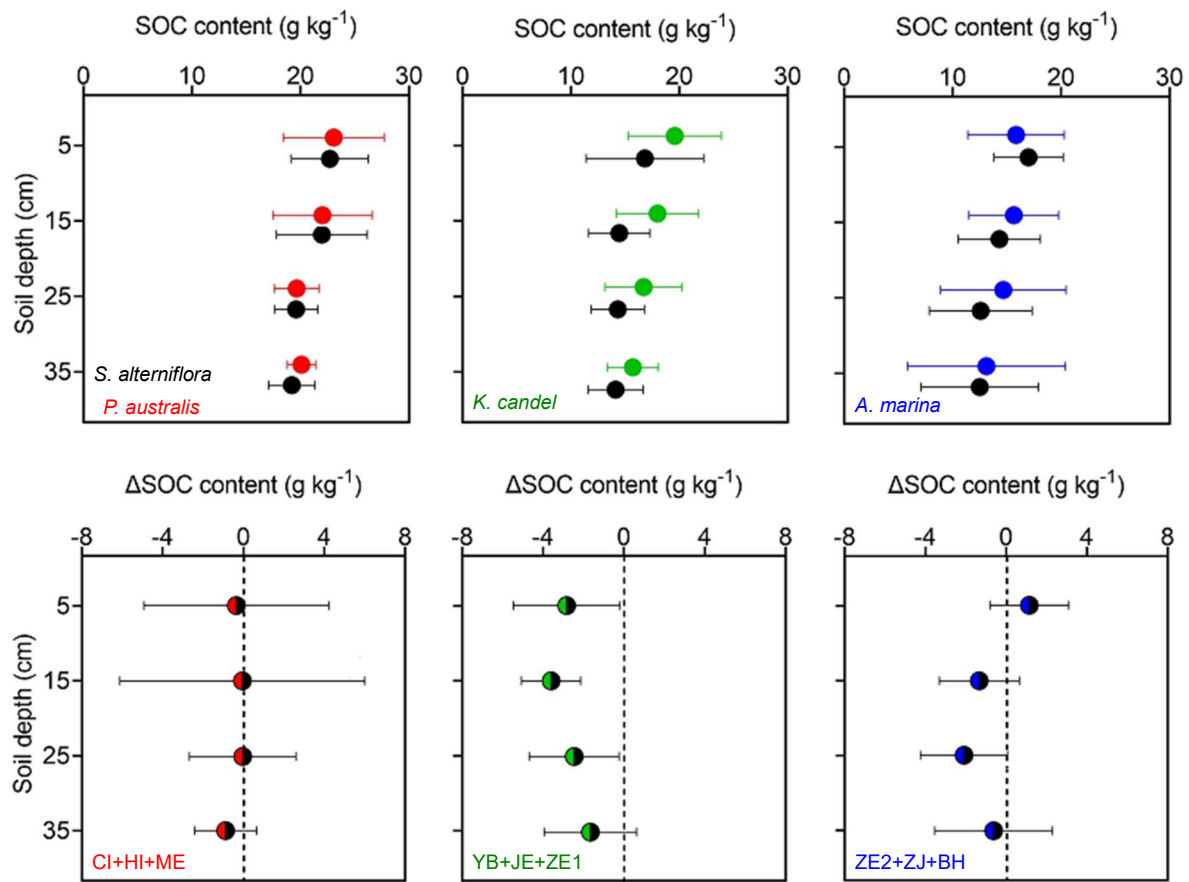
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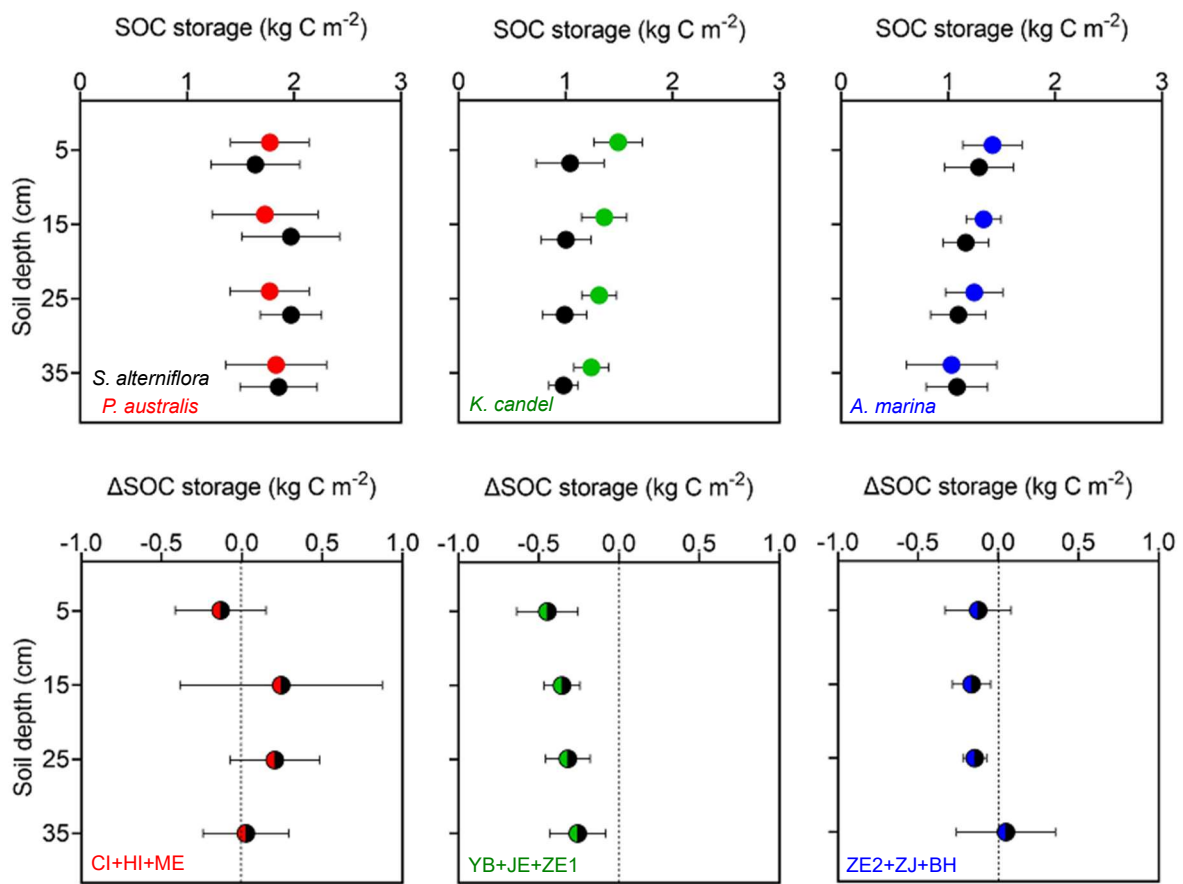
Figures and Figure Captions



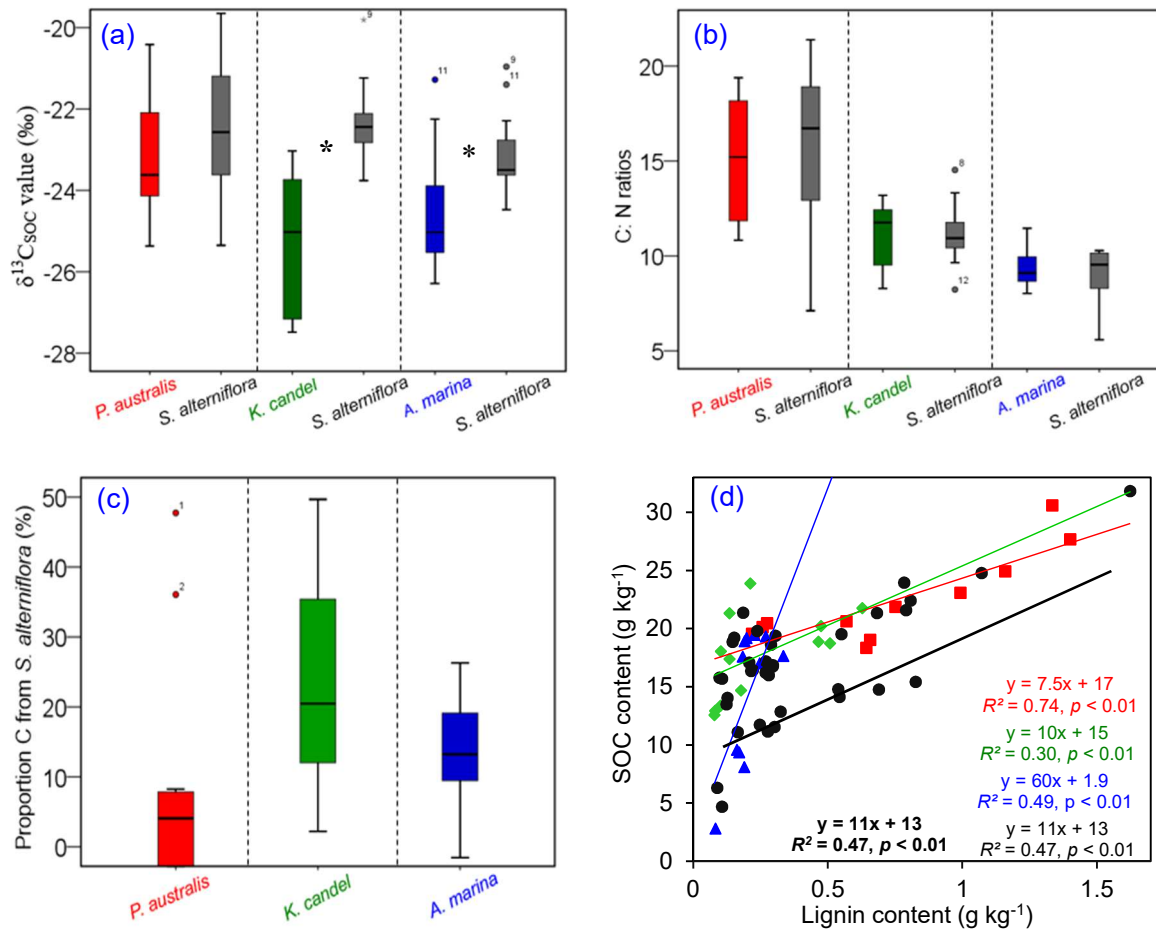
1069 **Figure 1** Sampling locations and plant communities in the coastal wetlands along the 2500 km
1070 coastline extending from tropical regions in southern China to the subtropical Yangtze delta.
1071 54 sites with total 216 samplings were chosen with 8 independent wetland types and 9 sampling
1072 locations, including Chongming Island, Hengsha Island, Yueqing Bay, Minjiang River Estuary,
1073 Jiulong River Estuary, Zhangjiang River Estuary, Zhanjiang and Beihai. Each location has two
1074 community types, one type is native species only (dominated by *P. australis*, *K. candel* or *A.*
1075 *marina*), and the other adjacent population was invaded by *S. alterniflora*.
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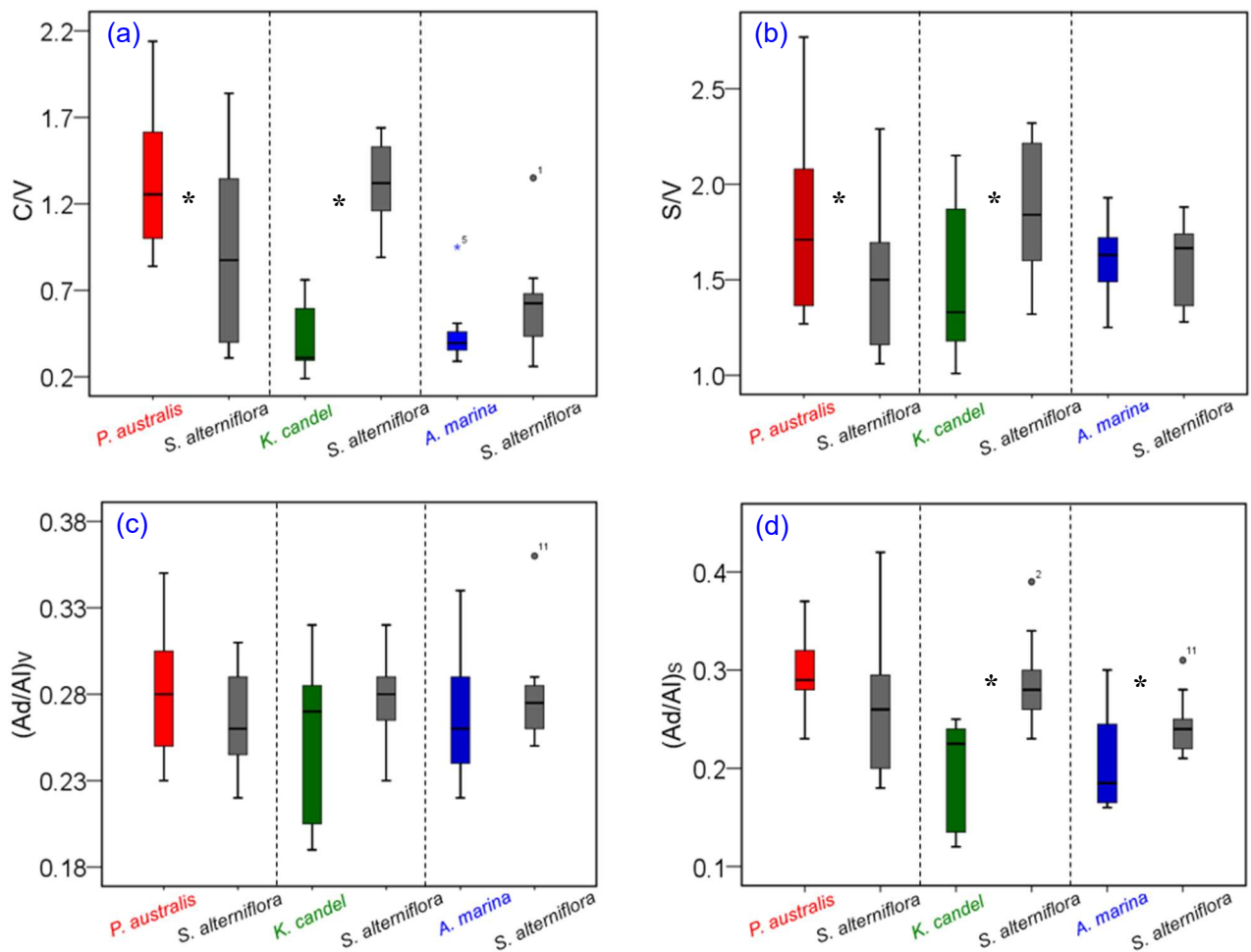
1078 **Figure 2** Comparison of soil organic carbon (SOC) content under native and invasive
 1079 vegetation types in the coastal wetlands depending on soil depth. The change in SOC (Δ SOC)
 1080 content was calculated as the difference between invasive and native vegetation types. The
 1081 results are expressed as the means \pm standard deviation ($n = 9$). The color code is red for *P.*
 1082 *australis*, green for *K. candel*, blue for *A. marina*, and black for *S. alterniflora*. The
 1083 abbreviations bottom in colors are independent wetlands, including CI: Chongming Island, HI:
 1084 Hengsha Island, YB: Yueqing Bay, ME: Minjiang River Estuary, JE: Jiulong River Estuary,
 1085 ZE1: Zhangjiang River Estuary 1, ZE2: Zhangjiang River Estuary 2, ZJ: Zhanjiang and BH:
 1086 Beihai.
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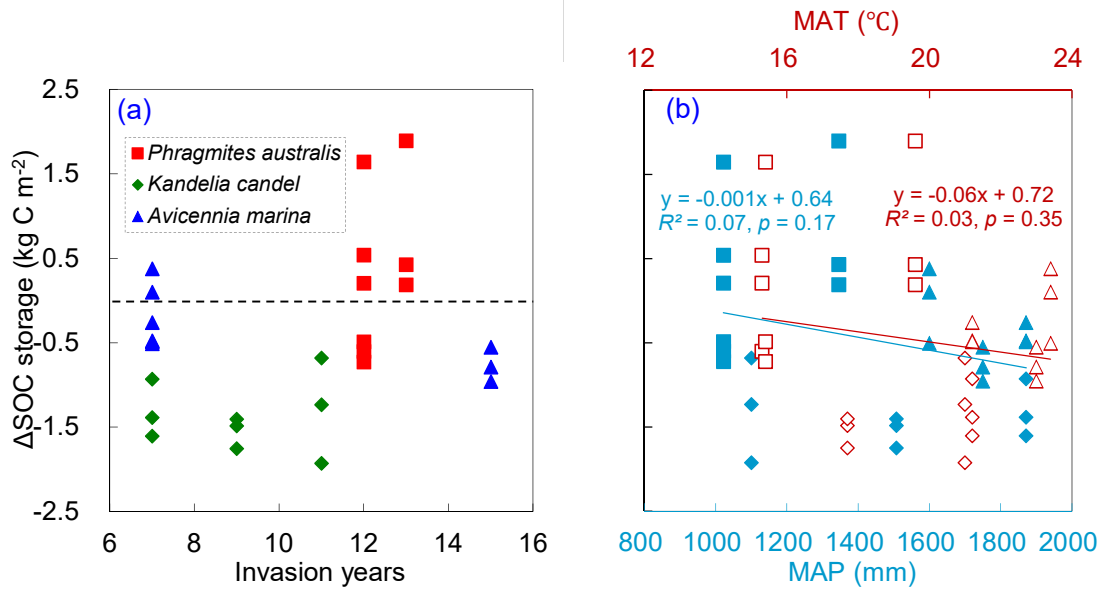
1089 **Figure 3** Comparison of cumulative soil organic carbon (SOC) storage from the surface to the
 1090 given depths (expressed as the means \pm SD, $n = 9$) between native and invasive vegetation
 1091 types in the coastal wetlands. The change in SOC (Δ SOC) storage was calculated as the
 1092 difference in SOC storage between invasive and native vegetation types. The color code is red
 1093 for *P. australis*, green for *K. candel*, blue for *A. marina*, and black for *S. alterniflora*. The
 1094 abbreviations bottom in colors are independent wetlands, including CI: Chongming Island, HI:
 1095 Hengsha Island, YB: Yueqing Bay, ME: Minjiang River Estuary, JE: Jiulong River Estuary,
 1096 ZE1: Zhangjiang River Estuary 1, ZE2: Zhangjiang River Estuary 2, ZJ: Zhanjiang and BH:
 1097 Beihai.
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1100 **Figure 4** Comparisons in stable C isotope composition of SOC ($\delta^{13}\text{C}_{\text{SOC}}$) (a), C:N molar ratio
 1101 (b), the calculated proportion of SOC from the C4 plant *S. alterniflora* (c), and the relationship
 1102 between lignin and SOC content (d) in the coastal wetlands under native (*P. australis*, *K. candell*,
 1103 and *A. marina*) and invasive (*S. alterniflora*) communities. The color code is red for *P. australis*,
 1104 green for *K. candell*, blue for *A. marina*, and black for *S. alterniflora*. Values for each parameter
 1105 marked with * were significantly different ($p < 0.05$) between native and invasive communities
 1106 using t-test. The numbers above the boxes represent the order of outliers in all data, and each
 1107 dot represents one outlier.
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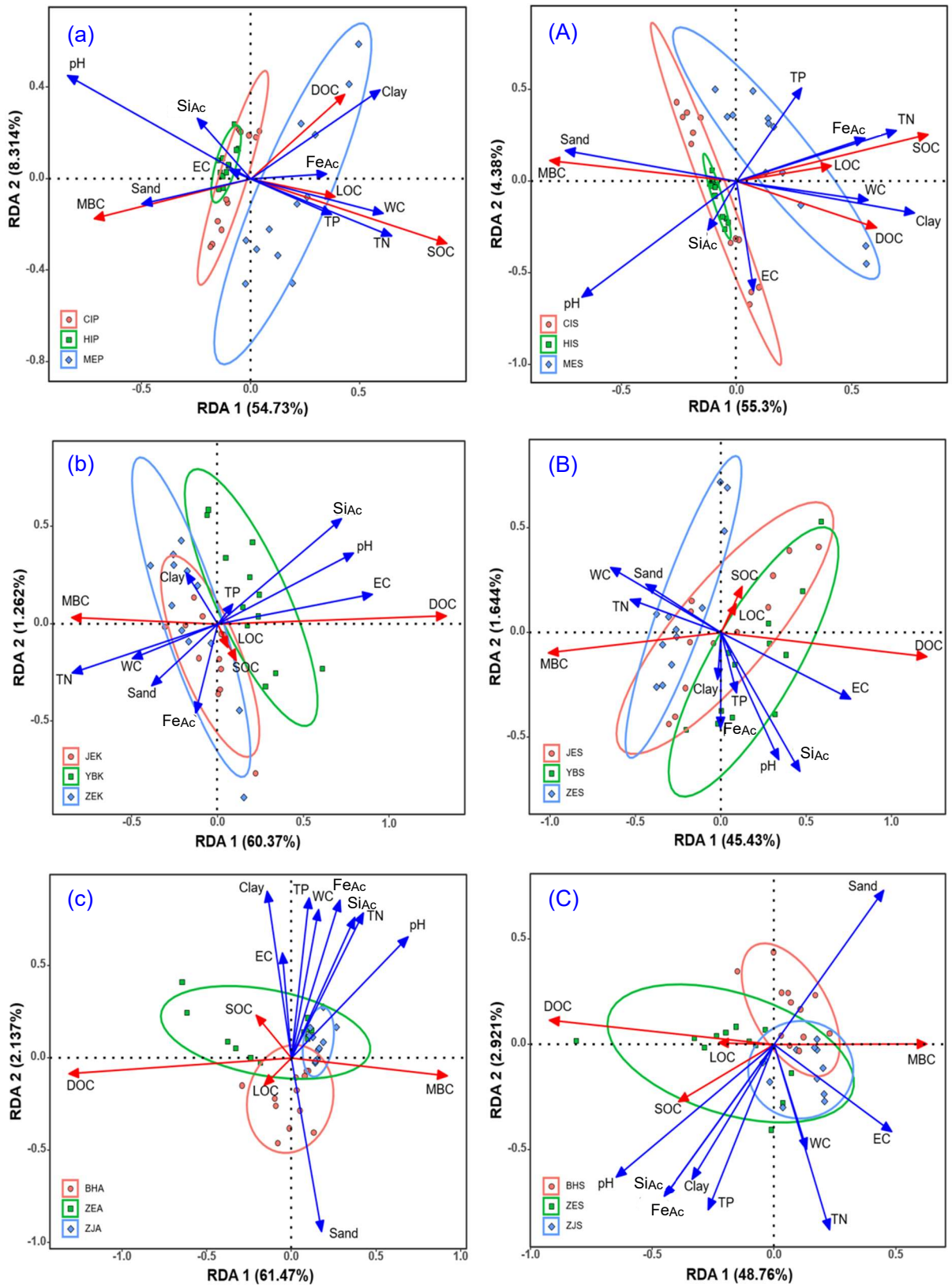
1110 **Figure 5** Compositions of lignin biomarker monomers across soil depths under native (*P.*
 1111 *australis*, *K. candel*, and *A. marina*) and invasive (*S. alterniflora*) communities in the coastal
 1112 wetlands. C/V (a) and S/V (b) represent the cinnamyl- or syringyl-to-vanillyl ratios. (Ad/Al)_v
 1113 (c) and (Ad/Al)_s (d) represent the acid-to-aldehyde ratios of vanillyl and syringyl units. The
 1114 color code is red for *P. australis*, green for *K. candel*, blue for *A. marina*, and black for *S.*
 1115 *alterniflora*. Values for each parameter marked with * were significantly different ($p < 0.05$)
 1116 between native and invasive communities using t-test. The numbers above the boxes represent
 1117 the order of outliers in all data, and each dot represents one outlier.
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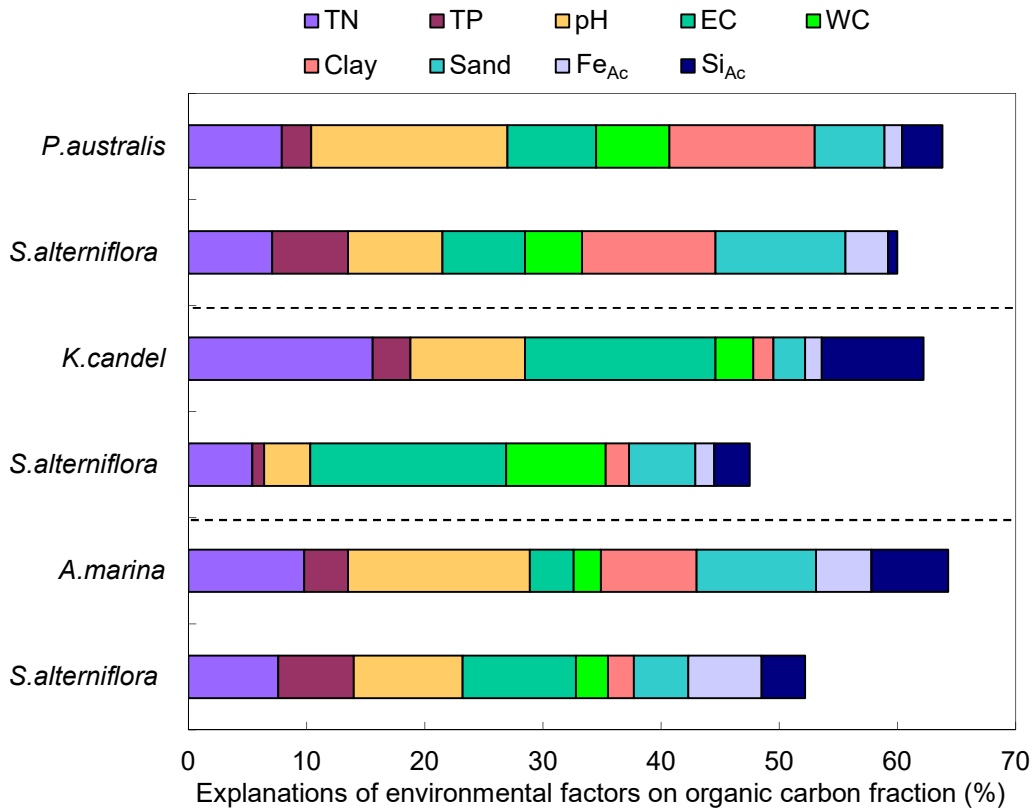
1121 **Figure 6** Relationships between changes in SOC storage at depths of 0–40 cm (Δ SOC) and
 1122 duration of invasion by *S. alterniflora* (a), and between Δ SOC and mean annual precipitation
 1123 (MAP) or mean annual temperature (MAT) (b). The dashed line represents the absence of SOC
 1124 changes (Δ SOC storage being zero). Square, diamond and triangle represent *P. australis*, *K.*
 1125 *candel* and *A. marina*, respectively.

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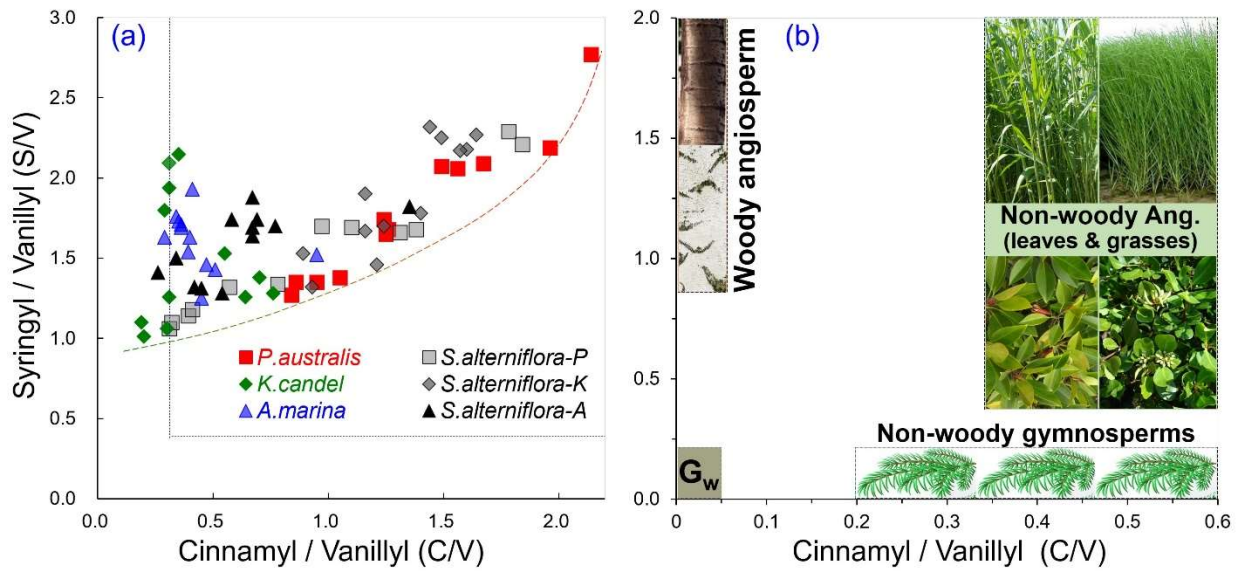
1128 **Figure 7** Redundancy analysis (RDA) of soil organic carbon fractions and soil physio-chemical

1129 properties in the coastal wetlands with native and invasive communities. a, b, and c represent
1130 native species of *P. australis*, *K. candel*, and *A. marina*, respectively, while A, B and C represent
1131 invasive species that *S. alterniflora* is replacing *P. australis*, *K. candel*, and *A. marina*.
1132 Abbreviations: SOC, soil organic carbon; LOC, labile organic carbon; DOC, dissolved organic
1133 carbon; MBC, microbial biomass carbon; TN, total nitrogen; TP, total phosphorus; EC,
1134 electrical conductance; WC, water content; Fe_{Ac}, active iron; Si_{Ac}, active silicon. The sampling
1135 sites in figures are wetland name abbreviations (see Fig. 2) + species initials.
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1138 **Figure 8** Relative importance of biogeochemical soil properties for SOC fractions under native
 1139 (*P. australis*, *K. candel* and *A. marina*) and invasive (*S. alterniflora*) communities in the coastal
 1140 wetlands across a 2500 km climate gradient. Abbreviations: TN, total nitrogen; TP, total
 1141 phosphorus; EC, electrical conductance; WC, water content; Fe_{Ac}, active iron; Si_{Ac}, active
 1142 silicon.
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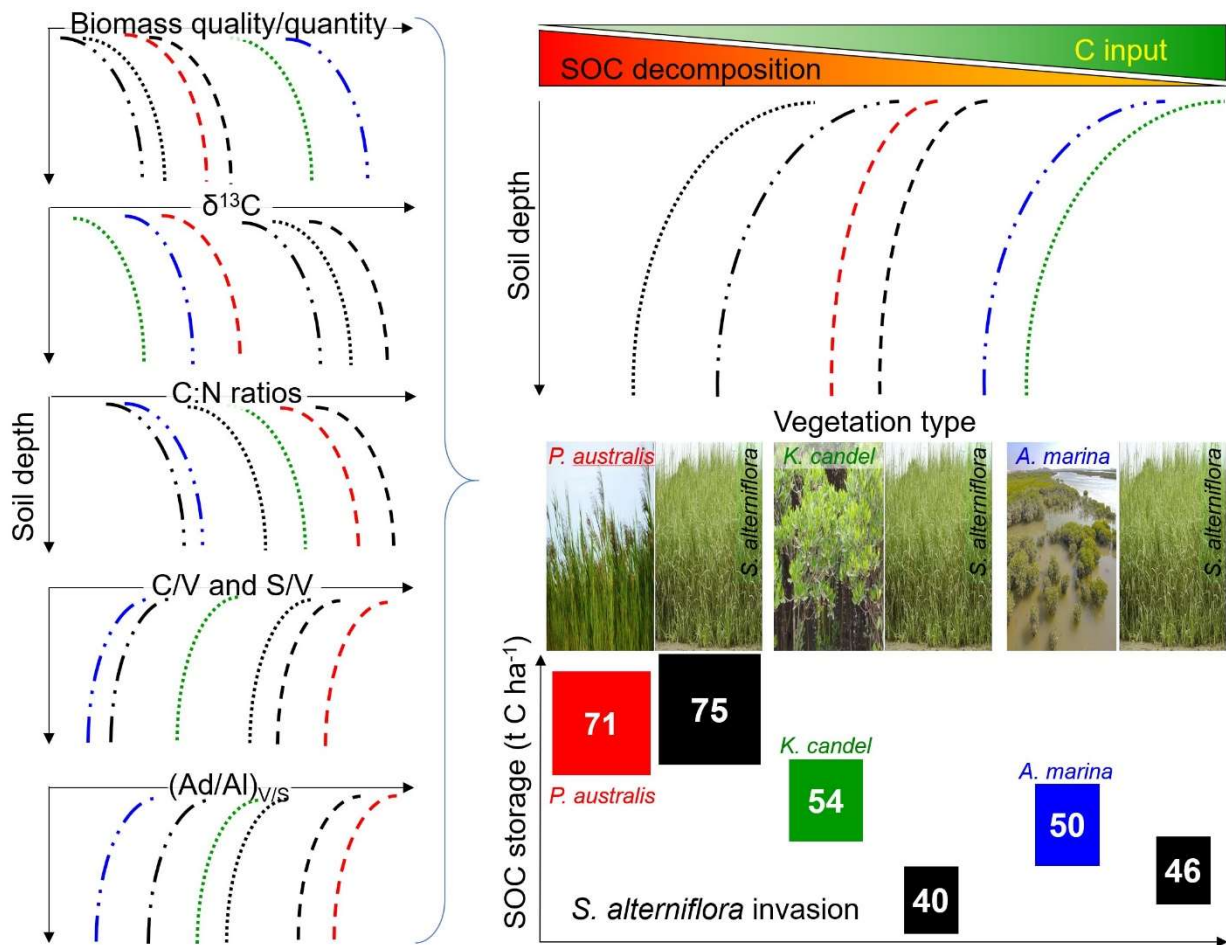
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1146 **Figure 9** Scatter plot of S/V vs. C/V based on SOC-standardized lignin monomer composition
1147 data of all sampling sites (a) and end-member values of S/V and C/V for selected plants (b).
1148 The end-member figure includes woody angiosperm tissue, non-woody angiosperm tissue,
1149 woody gymnosperm tissue (G_w), and non-woody gymnosperm. S/V and C/V represent the
1150 syringyl- and cinnamyl-to-vanillyl ratios. The scatter plots in the range of the thin dashed lines
1151 represent sources from non-woody angiosperm tissue.

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1155 **Figure 10** Schematic model of various factors of SOC storage at depths up to 40 cm depth in
 1156 coastal wetlands. Red color denotes *P. australis*, green color is *K. candel*, blue color is *A.*
 1157 *marina*, and black color is *S. alterniflora*. The different black dashed lines represent
 1158 corresponding invasive *S. alterniflora* communities in relative to *P. australis*, *K. candel* and *A.*
 1159 *marina*. C:N ratios represent the soil organic carbon to total nitrogen ratios, S/V and C/V
 1160 represent the syringyl- and cinnamyl-to-vanillyl ratios, and $(\text{Ad/Al})_{\text{V/S}}$ represent the acid-to-
 1161 aldehyde ratios of vanillyl or syringyl units.

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