Zhou *et al. Carbon Research* (2023) 2:39
https://doi.org/10.1007/s44246-023-00070-4

Carbon Research

ORIGINAL ARTICLE

Open Access

Blue carbon gain by plant invasion in saltmarsh overcompensated carbon loss by land reclamation

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Abstract

Saltmarsh is a major contributor to global blue carbon (C) sink. However, plant invasion and anthropic activities have greatly altered its distribution and its blue C function in the last decades. We used remote sensing and data synthesis to investigate how the four decades of plant invasion and land reclamation affect the spatiotemporal variation of blue C in Yancheng saltmarshes, the largest coastal ecosystem in eastern China. We revealed that the invasion of exotic cordgrass, *Spartina alterniflora*, greatly increased the regional blue C storage, mainly by the seaward expansion of cordgrass in mudflats and its high ecosystem C stock. The iconic *Suaeda salsa* "Red Beach" marshes shrank by 90%, mainly due to reed occupation by the native reed, *Phragmites australis*. *Phragmites australis* marsh area was greatly occupied by reclamation, but well offset by its intrusion into *Suaeda salsa*. The blue C gain by cordgrass invasion overcompensated C loss due to land reclamation and the loss of "Red Beach". Our findings highlight that coastal blue C is greatly regulated by vegetation coverage, and the seaward cordgrass invasion can benefit the saltmarsh C sequestration. Such a similar process may apply in other regions of the world, with potentially large implications for blue C sinks.

Highlights

- *Spartina alterniflora* marshes had high carbon sink capacity.
- The spatiotemporal dynamics of plant cover in Yancheng saltmarshes were attributed to the *Spartina alterniflora* invasion into mudflats and anthropogenic activity.
- The blue carbon gain by *Spartina alterniflora* invasion overcompensated carbon loss due to land reclamation and the loss of "Red Beach".

Keywords Saltmarshes, Carbon sequestration, Spatiotemporal dynamics, Saltmarsh cover change, *Spartina alterniflora* invasion

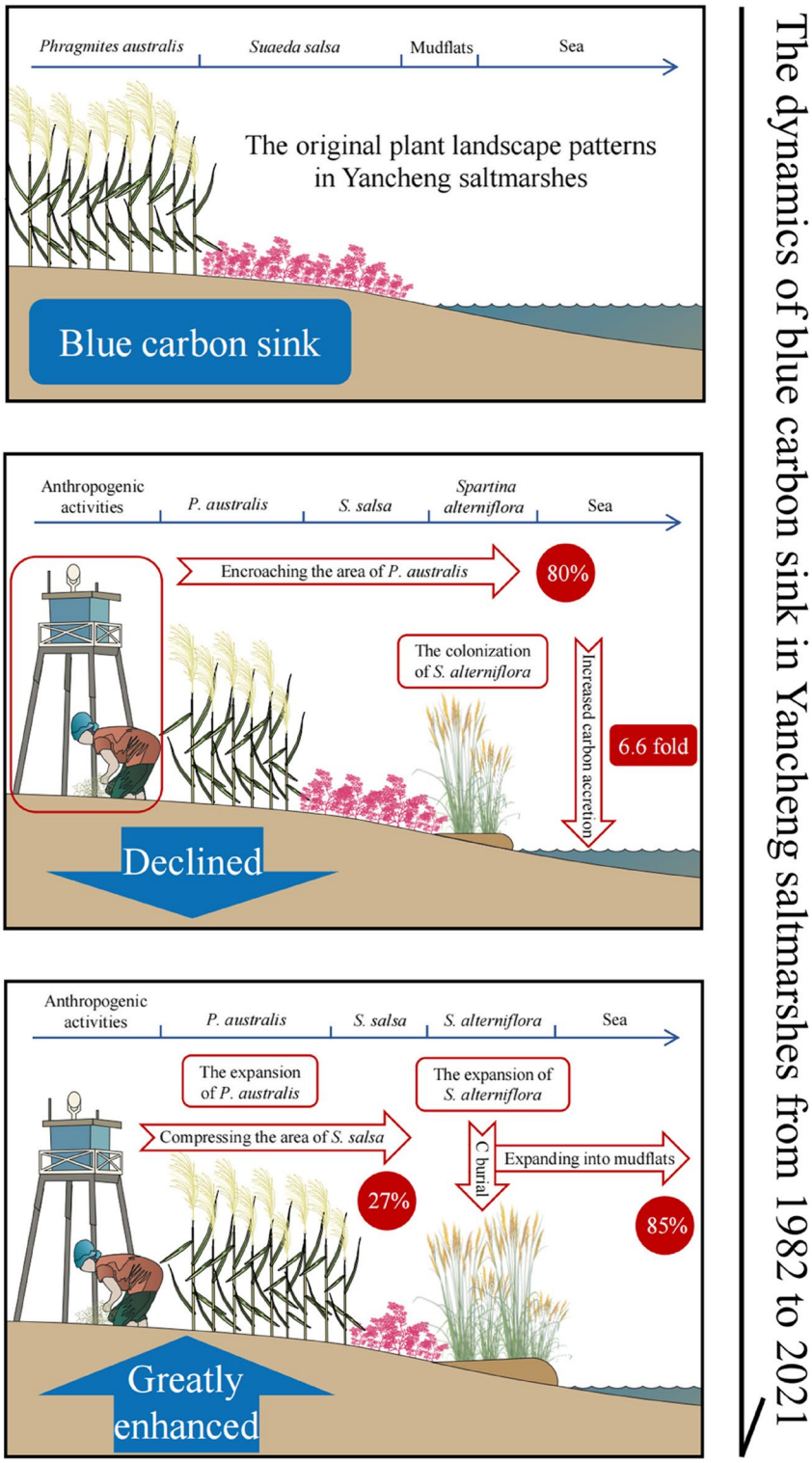
Handling editor: Hailong Wang.

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Graphical Abstract



1 Introduction

Coastal wetlands, also known as blue carbon (C) ecosystems, consist of a wide variety of saltmarshes, mangrove forests, and seagrass meadows. Although these ecosystems occupy a relatively small fraction of the earth's surface, they play a disproportionately large role in global C cycling (Milton et al. 2018; Najjar et al. 2018). In the coastal ecosystem of China, saltmarsh is the most prominent wetland type, widely distributed across the entire coastline of China (Cao et al. 2013; Wang et al. 2023). Previous studies on saltmarshes in China suggested that the total soil C stock amounted to 7.5 ± 0.6 Tg, and the average carbon accumulation rate (CAR) reached 201 g C m^{-2} yr^{-1} – much higher than the global average (168 g C m^{-2} yr^{-1}) (Fu et al. 2021; Macreadie et al. 2019; Wang et al. 2019), highlighting coastal wetlands of China as an important C pool in global C budget (Wang et al. 2021a, b).

Unfortunately, over recent decades, the landscape of saltmarshes in China has been undergoing rapid changes, mainly due to species invasion and land use changes (Osland et al. 2018; Wang et al. 2022a, b, 2021a). All these processes strongly modified the distribution and composition of saltmarshes, with potentially far-reaching impact on coastal C stock due to the variable C sequestration capacity of different marsh types. For instance, *Spartina alterniflora* (*S. alterniflora*), an exotic marsh type, is aggressively invading the coastal mudflats of China (Mao et al. 2019). This marsh type is characterized by high biomass and large dense roots that may contribute to coastal C sink (Dan et al. 2015; Huang et al. 2018). For example, previous studies conducted in the Yellow River Delta, Yancheng, and Jiuduansha saltmarshes have indicated that the expansion of *S. alterniflora* led to an increase in soil organic carbon (SOC) storage (Huang et al. 2015; Liao et al. 2007; Zhang et al. 2018). In contrast, *Suaeda salsa* (*S. salsa*), a native marsh type, is steadily replaced by *Phragmites australis* (*P. australis*) in some areas due to soil desalination, a process that may undermine regional C sink (Wang et al. 2022a, b). The vegetation transition was in strong agreement with the desalination trend, which was attributed to the colonization of *S. alterniflora* at the low-elevation mudflats increased sediment deposition and decreased the salt inundation from seawater (Hughes et al. 2019; Liu et al. 2007; Redfield 1972; Zhou et al. 2015). As a result, the decreasing salinity of the habitat made *S. salsa* less competitive, and its living area was primarily occupied by *P. australis* (Wang et al. 2022a, b). This effect caused the expansion of *P. australis* seaward, continuously outcompeting and replacing *S. salsa* (Li et al. 2021; Wang et al. 2022a, b). This long-distance interaction may undermine regional C sink potential and require careful management of saltmarshes to sustain their ecological and C sequestration functions.

Coastal land reclamation has become a common global practice, with China leading the way in massive land reclamation initiatives. The demand for coastal reclamation in China has risen significantly over the years, driven mainly by economic growth (Ma et al. 2014). China has reclaimed around 11,162 km^2 of land between 1979 to 2014 (Meng et al. 2017), while losing approximately 22,000 km^2 of coastal wetlands since 1949 (Sengupta et al. 2018). Land reclamation poses a risk of greatly decreasing the previously sequestered and stored C pools of saltmarshes (Bu et al. 2015). Coastal reclamation is often implemented to satisfy the increasing demand for agricultural land. However, studies have shown that converting salt marshes into croplands can lead to a significant decline in SOC pools over a period of decades (Fernandez et al. 2010; Iost et al. 2007). Such land use conversion causes roughly 0.15–1.02 Pg yr^{-1} of CO_2 released from coastal ecosystems (Pendleton et al. 2012).

These emerging phenomena observed in coastal wetlands call for a re-assessment of the blue C sink in China. However, current knowledge on the spatiotemporal distribution of major marsh types in China remains fragmented (Meng et al. 2019), posing obstacles for accurate assessment of coastal C pool, especially on a regional-scale. Here we systematically evaluated the spatiotemporal dynamics of marsh types and the associated C stock change in Yancheng, the largest saltmarsh ecosystem in China that has been heavily impacted due to the invasion of *S. alterniflora* and land reclamation, and have experienced significant uncertainties in their blue C sink capacity (Li et al. 2023). Specifically, we (1) mapped changes in marsh types between 1982 and 2021 using Remote Sensing; (2) examined the dynamics of C stock and CAR associated with different marsh types by meta-analysis; and (3) evaluated the blue C sink capacity following the long-term trajectory of marsh cover change across the study region. We anticipate that the insights generated from this study will update the current understanding of coastal C sink in China, and the study may also serve as a template for exploring C stock change in other coastal regions of the world, where vegetation shift is underway.

2 Methods and materials

2.1 Study area

The Yancheng Natural Reserve (32°34′-34°28′N, 119°27′-121°16′E), located in central to northern Jiangsu Province, is the largest continuous coastal wetland in China. Its core area is situated between Xinyanggang and Doulonggang estuaries. This region is dominated by a subtropical monsoon climate with a mean annual air temperature of 14.9 °C and mean annual precipitation of 1,010 mm. The study area represents an intertidal silt-muddy coastal saltmarsh

landscape subject to irregular semidiurnal tides (Wang et al. 2022a, b). With little anthropogenic disturbance in this region, the vegetation retains the original ecological succession sequence of the coastal zone. From sea to land, the sequence was: mudflat, *S. alterniflora*, *S. salsa*, and *P. australis* (Gao et al. 2012, 2016; Liu et al. 2007; Xu 2015; Zang 2019). The obtained sampling sites are shown in Fig. 1. The sampling sites were primarily in Sheyang county and Dafeng city, with the rest in the core areas of the Yancheng Natural Reserve.

2.2 Saltmarsh classification

We generated 8 time-series coastal vegetation maps between 1982 and 2021 using cloud-free Landsat images (30 by 30 m, Landsat 5–8) downloaded from the National Aeronautics and Space Administration (https://www.nasa.gov/) and GS Cloud website (http://www.gscloud.cn/). All maps were created using supervised classification with human–computer interaction, and each map includes six coastal landcover types, referring to mudflat, *S. alterniflora*, *S. salsa*, *P. australis*, water, and human land use. Specifically,

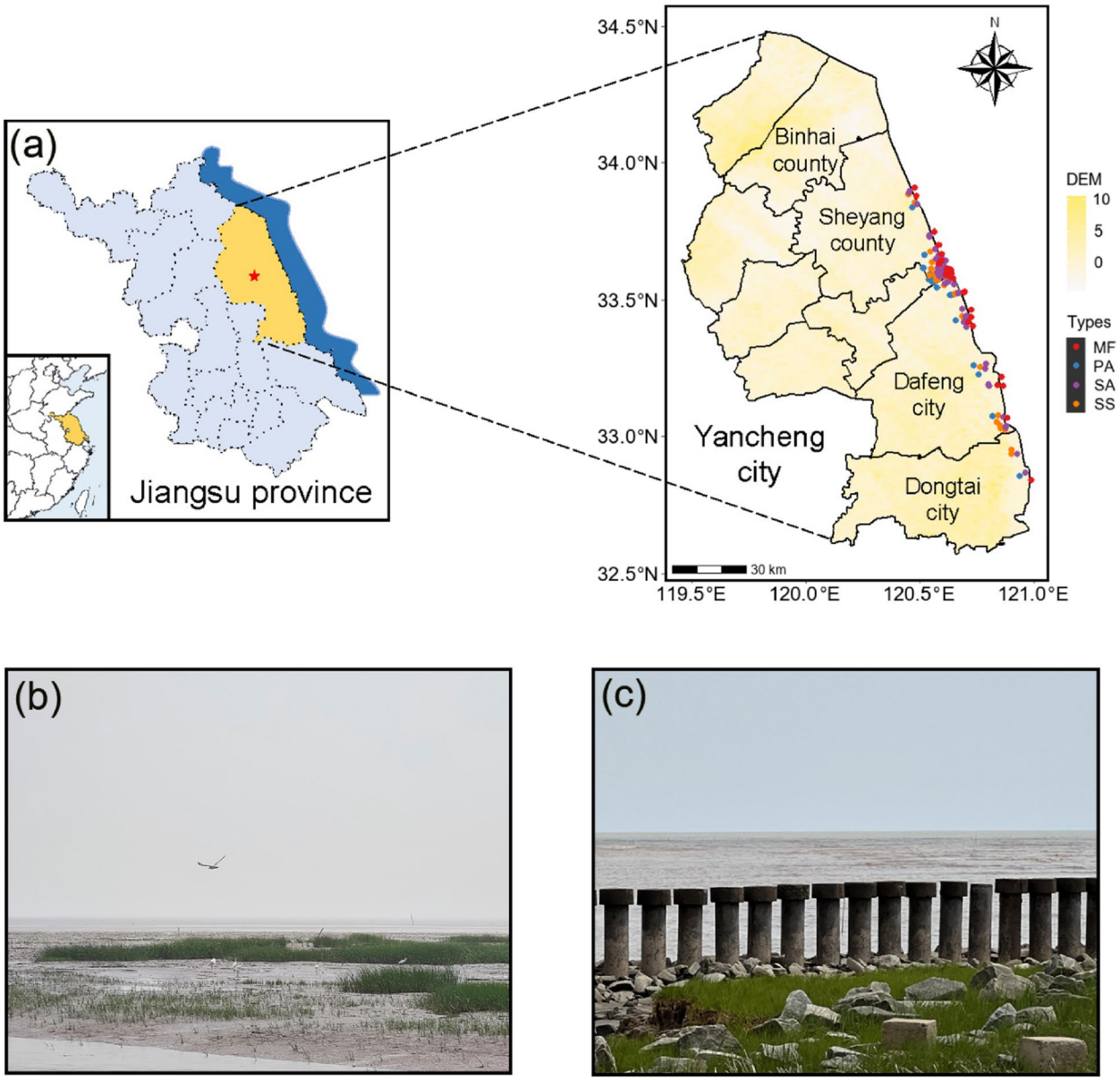


Fig. 1 The specific position of data collection points and the habitat status in Yancheng saltmarshes, where (**a**) the location of the sampling sites with different marsh types in Yancheng city, Jiangsu Province, China. MF was mudflat, PA was *P. australis*, SA was *S. alterniflora*, and SS was *S. salsa*, (**b**) the natural saltmarsh habitat with *S. alterniflora* expanding into mudflats, and (**c**) the saltmarsh habitat with dike construction that inhibited the *S. alterniflora* expansion

we acquired all clear-sky Landsat images during low tide between July and November – the low-growth season when inter-vegetation contrast is maximized for optimal spectral separation between classes (Wang et al. 2022a, b). We validated the resulting maps using visual interpretation and high-resolution aerial images based on published in situ studies of saltmarshes, and then computed the overall classification accuracy and Kappa coefficient associated with each map for accuracy assessment. During the processes, 70% of samples were used for model training and the remaining 30% of samples for assessing accuracy.

2.3 Data acquisition and processing

We carried out a literature search in 2021 for articles concerning the C cycling of Yancheng saltmarshes (mainly concentrated on articles from 2008 to 2020) in Web of Science (https://www.webofscience.com/wos) and China National Knowledge Infrastructure (CNKI, https://www.cnki.net) employing the following string: (coastal wetland OR tidal marsh OR saltmarsh OR tidal flat) AND Yancheng AND carbon. Ultimately, we completed our search on January 1, 2022, with 106 papers. The original data was obtained directly from the table, and the graphs were digitally extracted using GetData Graph Digitizer 2.26.

We analyzed soil bulk density (BD) data from all studies selected, and for those without BD measurements, we computed the BD data from the SOC measurements using the empirical equation below:

$$OC = 0.04 \times LOI + 0.0025 \times LOI^2 \quad (1)$$

$$BD = 1/\left[LOI/k_1 + (1 - LOI)/k_2\right] \quad (2)$$

where OC was the content of organic carbon (%), LOI was the loss of ignition (%), BD was the bulk density (g cm^{-3}), and k_1 and k_2 were the self-packing densities of the pure organic and inorganic components (Craft et al. 1991; Morris et al. 2016).

Most of our data analysis was performed in R 4.1.2 (R Core Team 2021). The permutation test was used to verify the differences among the C stock, CAR, total C storage, and C burial amount of Yancheng saltmarshes, mostly using the R package '*RVAideMemoire*' (Hervé, 2021). The general linear and generalized additive models were constructed to fit the relationship of the variables by using the R package '*mgcv*' (Wood 2011). The regulatory factors of C pools in Yancheng saltmarshes were discussed through the structural equation model (SEM), using the R package '*piecewiseSEM*' (Lefcheck 2016).

2.4 Calculation of C stock and C burial

The plant C stock per unit area was calculated by multiplying the biomass per unit area by the plant C content as shown in the equation below:

$$\text{Plant C stock per unit area (g C m}^{-2}) = \text{Plant biomass (g m}^{-2}) \times \text{C contents in plant (\%)} \quad (3)$$

$$\text{Plant C storage (Mg C)} = \text{Plant C stock per unit area (Mg C ha}^{-1}) \times \text{area (ha)} \quad (4)$$

SOC stock was determined by SOC content and soil depth in a particular region. Therefore, it is necessary to calculate SOC content within 0–1 m soil depth after sampling at intervals (n is the total number of soil intervals), and then obtain the C stock (Mg C ha^{-1}) through area multiplication and unit transformation.

$$\text{C density (g cm}^{-3}) = \text{Bulk density (g cm}^{-3}) \times \text{C content (\%)}/100 \quad (5)$$

$$\text{C stock in single soil depth (g cm}^{-2}) = \text{Soil C density (g cm}^{-3}) \times \text{Soil depth (cm)} \quad (6)$$

$$\text{C stock per unit area (g cm}^{-2}) = \sum_{i=1}^{n} \text{C stock in depth}_i \left(\text{g cm}^{-2}\right) \quad (7)$$

$$\text{SOC storage (Mg C)} = \text{SOC stock per unit area (Mg C ha}^{-1}) \times \text{area (ha)} \quad (8)$$

The content of radionuclides in sediments has been widely used to determine the age of sediments in estuaries, coastal wetlands, and continental shelf regions, reveal depositional processes and trace biogeochemical sources (Bellucci et al. 2007; Xia et al. 2016). From the measurement of radionuclides, soil accretion rate (SAR) is obtained, and the CAR in coastal wetlands is usually calculated by SAR and C density. The annual C burial is equal to CAR multiplied by area.

$$\text{CAR (g C m}^{-2}\text{ yr}^{-1}) = \text{C density (g cm}^{-3}) \times \text{SAR (mm yr}^{-1})/10000 \quad (9)$$

$$\text{C burial (g C yr}^{-1}) = \text{CAR (g C m}^{-2}\text{ yr}^{-1}) \times \text{area (m}^2) \quad (10)$$

We combined remote sensing with data synthesis to determine the C sequestration of different vegetations and the distribution dynamics in Yancheng saltmarshes from 1982 to 2021. This way, we were able to clarify the C storage and C burial in the Yancheng area over a broad spatiotemporal scale, and predict the direction and

magnitude of future C stock changes across the study region. The complete procedure is illustrated in Fig. S1.

3 Results

3.1 Changes of Yancheng saltmarsh area

The distribution of different marsh types in Yancheng between 1982 and 2021 was mapped in time-series (Fig. 2a), with an overall classification accuracy between 87 and 98%, and Kappa Coefficient between 0.82 and 0.90 (Table S1). From 1982 to 2021, the total area of Yancheng saltmarsh decreased by 43.09 km^2 (Table 1, Fig. 2c). The net loss was mainly induced by the reduction of *S. salsa*, which reduced from 411.8 km^2 to 43.11 km^2 (net loss of 90%). While the area of *S. salsa* underwent a dramatic decrease, that of *S. alterniflora* significantly increased by 287.5 km^2 over an expansive period of 40 years. The area occupied by *P. australis* also increased from 164.9 km^2 to 203.1 km^2.

Table 1 The area of Yancheng saltmarsh covered by different vegetation types, and the net change of carbon storage over the past four decades. PA was *P. australis*, SA was *S. alterniflora*, and SS was *S. salsa*

Year	Area of salt marshes (km^2)				Total regional carbon storage (Gg C)
	PA	SA	SS	Total	
1982	164.9	0.067	411.8	576.8	3151
1987	117.0	0.680	425.2	542.9	2910
1992	124.0	12.44	327.5	464.0	2545
2002	102.4	136.6	215.2	454.2	2695
2007	115.2	131.3	168.0	414.5	2505
2012	138.3	175.5	147.6	461.4	2858
2017	174.2	223.0	90.5	487.7	3133
2021	203.1	287.5	43.11	533.7	3529
Net change	38.16	287.5	-368.7	-43.09	377.3

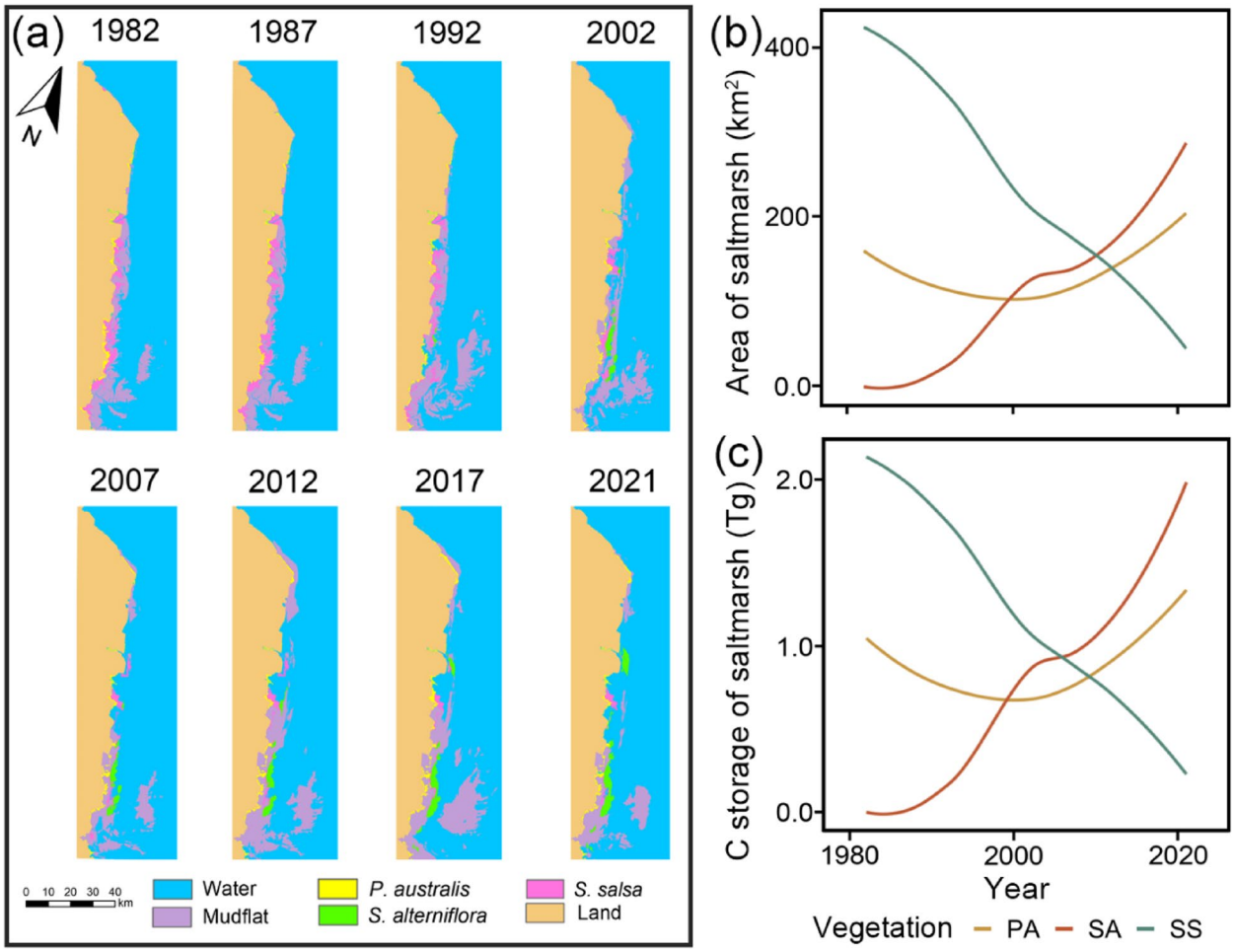


Fig. 2 The dynamics of saltmarshes in Yancheng, in which (**a**) the map of Yancheng saltmarsh with different types from 1982 to 2021, (**b**) the variations in the area of Yancheng saltmarsh over recent four decades, and (**c**) the dynamics of total C storage in Yancheng saltmarsh covering with different vegetation types

Further analysis found that the massive loss of the *S. salsa* marsh area was transformed to *P. australis* marsh, land reclamation, and non-vegetated mudflats, which accounted for 27%, 25%, and 39%, respectively (Table S2). The vastly increased *S. alterniflora* marsh was mainly attributed to its colonization in mudflats (about 85%), with a small proportion invading the native saltmarshes. In terms of *P. australis* marsh, land reclamation occupied its area of 49.88 km^2, accounting for 80% of the net reduction. However, the rapid expansion of *P. australis* in *S. salsa* marsh made up for its loss by land reclamation, and achieved a net increase.

3.2 The C stock and CAR

We analyzed marsh-specific plant biomass per unit area, and identified significant differences among marsh types ($P < 0.05$). Specifically, *S. alterniflora* marsh has the highest plant biomass per unit area, followed by *P. australis*, and *S. salsa* (Fig. 3a). However, the C content in plant tissues showed different patterns. The aboveground C content of *S. salsa* was significantly lower than that of the other two marshes, while the belowground C content of *S. alterniflora* was significantly lower than the other two types (Fig. 3a; $P < 0.05$). The plant C stock per unit area measured for different marsh types followed the order of *S. alterniflora* (1270 ± 122.0 g C m^{-2}) > *P. australis* (789.4 ± 74.55 g C m^{-2}) > *S. salsa* (98.29 ± 6.79 g C m^{-2}) (Fig. 3b; $P < 0.05$).

At the 0–100 cm soil depth, no significant difference was found in SOC stock among marsh types (Fig. 4a; $P > 0.05$). However, the SOC stock per unit area at different soil depths showed distinct patterns. Particularly, at the 0–20 cm soil depth, the SOC stock in *S. alterniflora* was significantly higher than that in *P. australis* and *S. salsa*, while at the 50–100 cm soil depth, the SOC stock in *P. australis* was significantly higher than that in the other two marsh types (Fig. 4b, d; $P < 0.05$). However, at 20–50 cm soil depth, no significant difference was detected among marsh types (Fig. 4c; $P > 0.05$).

The regulators of plant biomass and SOC stock at the 0–20 cm and 20–50 cm soil depths were explored by SEM. The results showed that aboveground biomass (AGB) was mainly affected by pH, total potassium (TK), plant height, and coverage, while belowground biomass (BGB) was regulated by NO_3^-, NH_4^+, and

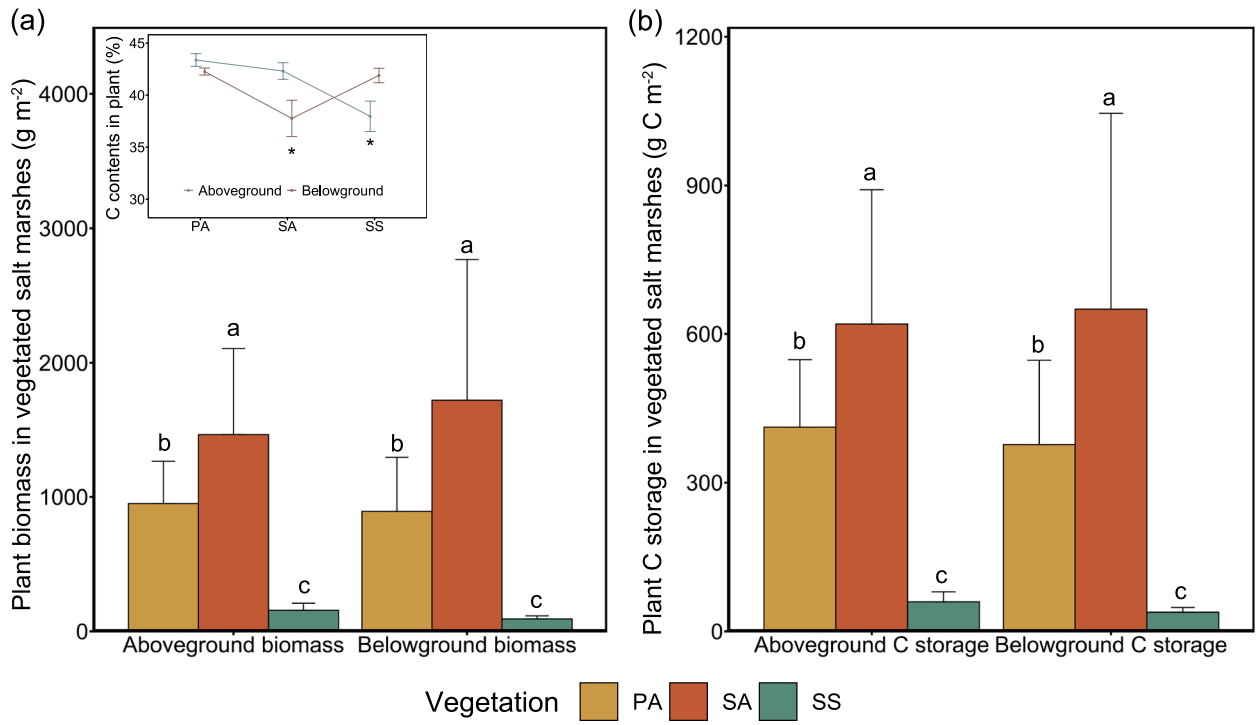


Fig. 3 The plant C of Yancheng saltmarsh, in which (**a**) the plant biomass and its C contents of vegetated saltmarshes in Yancheng, and (**b**) the plant C storage per unit area in Yancheng saltmarshes with different vegetations. PA was *P. australis*, SA was *S. alterniflora*, and SS was *S. salsa*. AGB was above-ground biomass, BGB was below-ground biomass, AGC stock was above-ground C stock, and BGC stock was below-ground C stock. The asterisks indicated significantly lower C contents than the other two vegetations, and the different lowercase letters indicated significant differences among saltmarshes types (permutation test; $P < 0.05$)

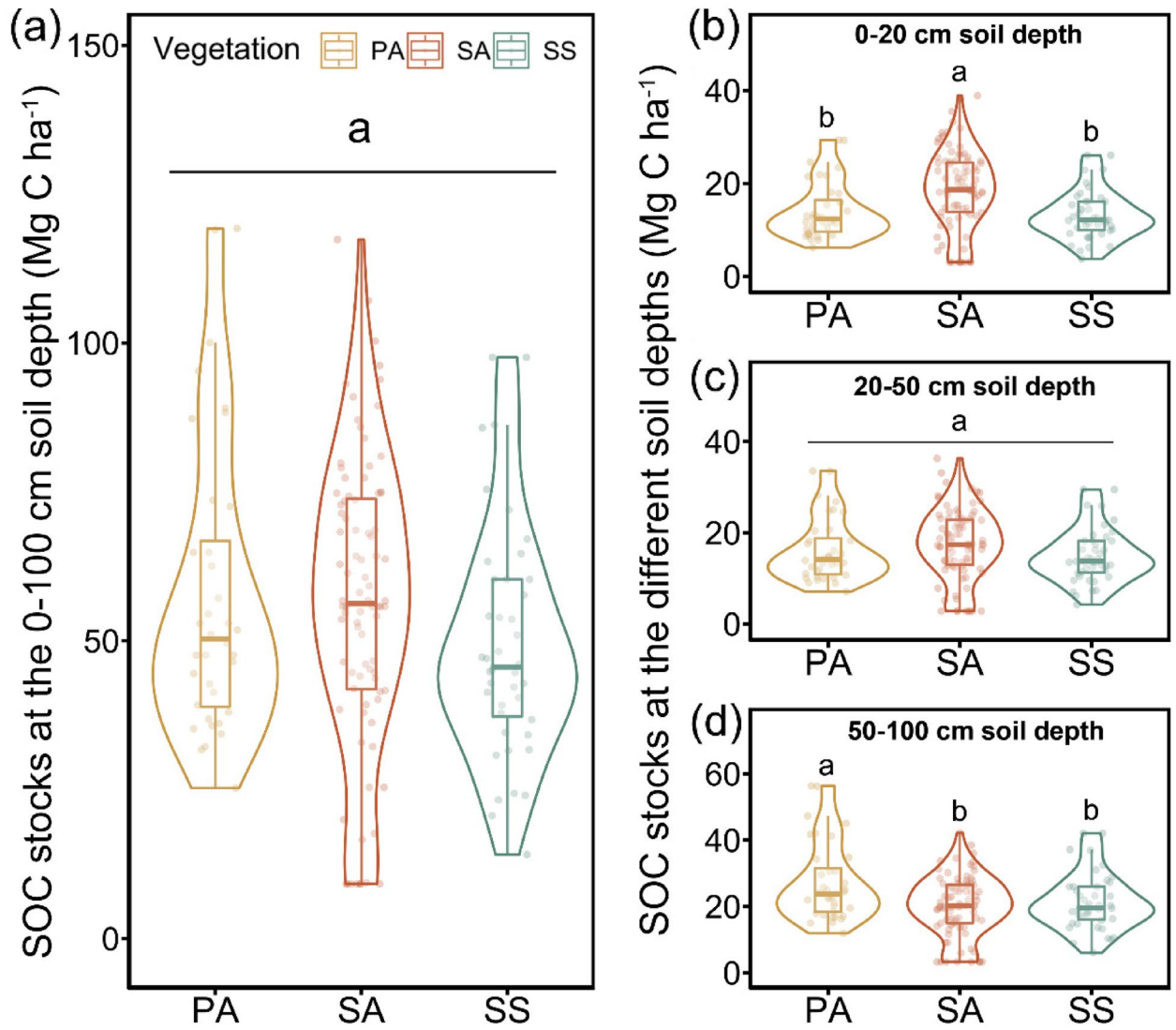


Fig. 4 The SOC storage covered different vegetations in Yancheng saltmarsh, in which (**a**) the C storage at the 0–100 cm soil depth, (**b**) the C storage at the 0–20 cm soil depth, (**c**) the C storage at the 20–50 cm soil depth, and (**d**) the C storage at the 50–100 cm soil depth. PA was *P. australis*, SA was *S. alterniflora*, and SS was *S. salsa*. The different lowercase letters indicated significant differences among saltmarshes types (permutation test; $P < 0.05$)

plant coverage (Fig. S2a; $P > 0.05$). The main regulatory factors of SOC stock were soil water content (SWC), dissolved organic carbon (DOC), the ratio of carbon to nitrogen (C/N), available phosphorous (AP), AGB, and carbonate (CO_3^{2-}) at the 0–20 cm soil depth (Fig. S2b; $P > 0.05$), but BGB, DOC, and pH influenced the SOC stock at the 20–50 soil depth (Fig. S2c; $P > 0.05$).

Both C density and CAR of *S. alterniflora* were significantly higher than that of *P. australis* and *S. salsa* (Table 2; $P < 0.05$). Specifically, the CAR was 242.2 ± 11.26 g C m^{-2} yr^{-1} in *S. alterniflora*, followed by 108.5 ± 5.00 g C m^{-2} yr^{-1} in *S. salsa*, and 94.77 ± 7.80 g C m^{-2} yr^{-1} in *P. australis* (Table 2).

Table 2 The soil C density (extracted from reported articles, which were mostly focused on surface soil) and CAR (carbon accumulation rate) of Yancheng saltmarsh with different vegetation coverings, where PA was *P. australis*, SA was *S. alterniflora*, and SS was *S. salsa*. Different superscript lowercases within a row indicated significant differences among vegetation types at $P < 0.05$. The values were means ± SE (The original data of soil C density were sourced from Bao et al. 2016; Fu et al. 2021; Liu et al. 2010, 2013; Qi et al. 2019; Zang 2019)

Types	C density (mg C cm^{-3})	CAR (g C m^{-2} yr^{-1})
PA	4.8 ± 0.1^{b}	94.77 ± 7.80^{b}
SA	8.4 ± 0.2^{a}	242.2 ± 11.27^{a}
SS	5.3 ± 0.06^{b}	108.5 ± 5.00^{b}

3.3 Dynamics of C storage and C burial

Over the 40 years succession, the total area of saltmarsh in Yancheng decreased by 43.09 km^2, while the total C storage and C burial increased from 3152 to 3529 Gg, and from 60.35 Gg yr^{-1} to 93.57 Gg yr^{-1}, respectively (Fig. 5a). Among them, the total soil C storage, plant C storage, and the C burial increased by 17.98 Gg, 359.0 Gg, and 33.22 Gg yr^{-1}, respectively (Fig. 5b, c, d). The proportion of the plant C pool in the total C pool also increased from 5 to 15%, owing to drastic rise in plant C storage induced largely by *S. alterniflora* expansion (increased by 210.2%).

3.4 Effects of *S. alterniflora* expansion

The area of *S. alterniflora* tremendously expanded from 1982 to 2021 (Fig. 6a), and the total plant C storage and C

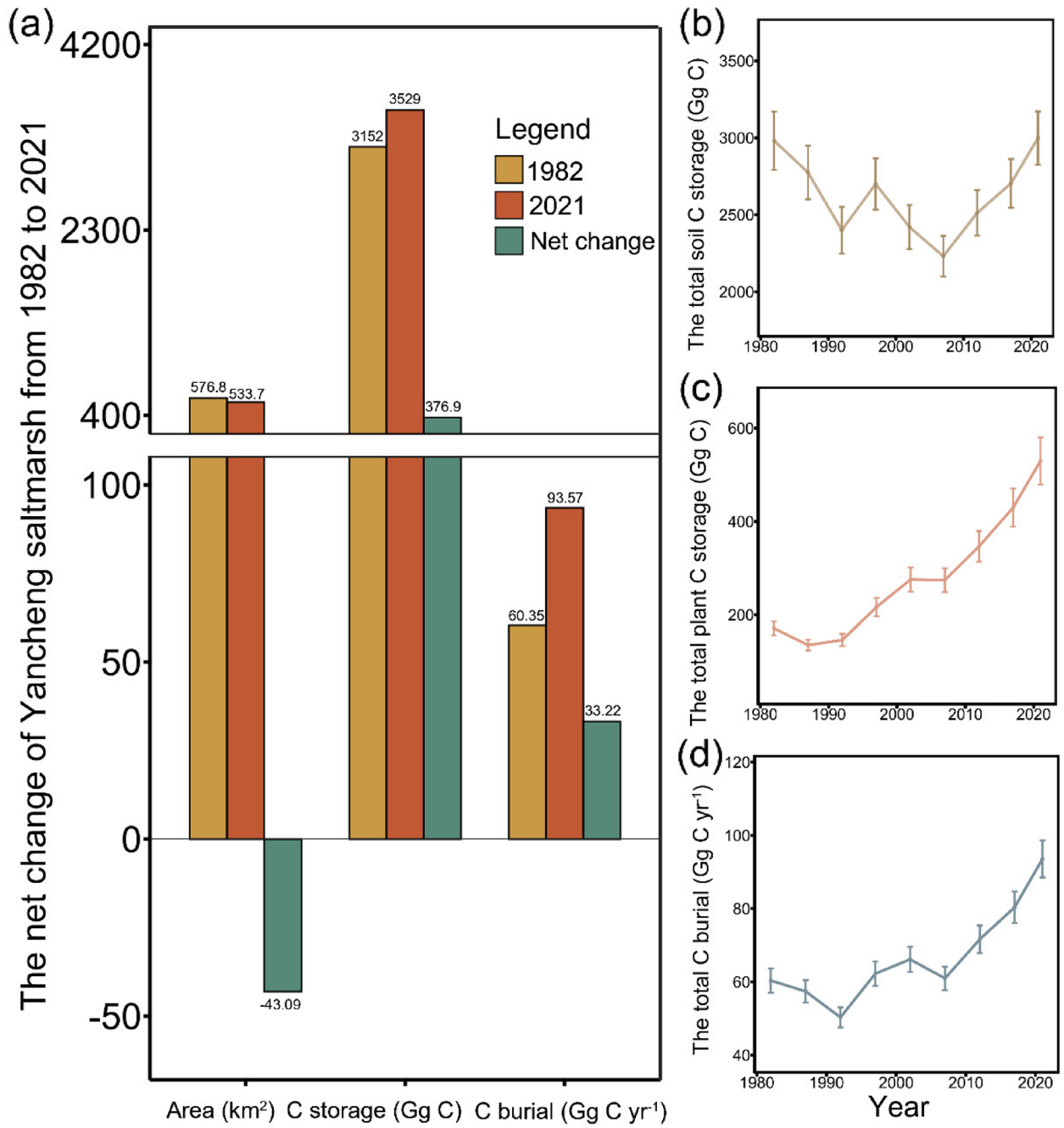


Fig. 5 The net changes of area and C sequestration in Yancheng saltmarsh, in which (**a**) the net exchanges of the total area, total C storage, and total C burial over the last 40 years, (**b**) the dynamics of total soil C storage from 1982 to 2021, (**c**) the dynamics of total plant C storage from 1982 to 2021, and (**d**) the dynamics of C burial from 1982 to 2021

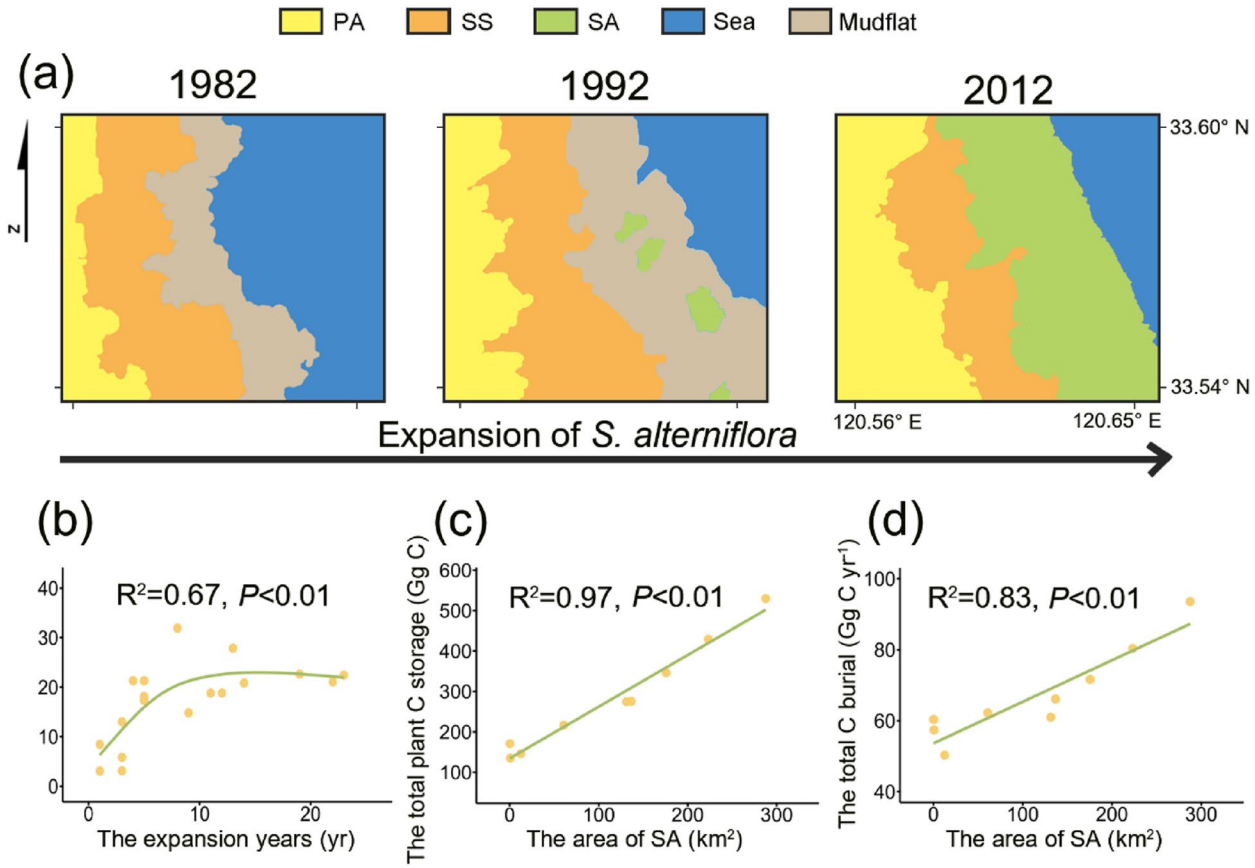


Fig. 6 The map of *S. alterniflora* expansion and its influence on C storage and C burial, in which (**a**) the expansive trend of *S. alterniflora* revised from the remote-sensing image in 1982, 1992 and 2012, (**b**) the relationship between the soil C storage at the 0–20 cm soil depth and the expansion year of *S. alterniflora*, (**c**) the relationship between the total plant C storage in Yancheng saltmarsh and the area of *S. alterniflora*, and (**d**) the relationship between the total C burial rate in Yancheng saltmarsh and the area of *S. alterniflora*

burial also greatly increased (Fig. 5c, d). The linear regression results proved that the elevated plant C storage and C burial were positively correlated with the expansion of *S. alterniflora* (Fig. 6c, d; $P < 0.01$). *S. alterniflora* expansion also promoted surface SOC stock, but the relationship was not linear. The generalized additive model suggested that the SOC storage in areas colonized by *S. alterniflora* increased rapidly in the first few years, and peaked at the 10th year of *S. alterniflora* establishment (Fig. 6b; $P < 0.01$), after which the SOC storage remained relatively stable over time. In addition, the SOC at peak storage was 4.86 times higher than that at the beginning of propagation, showing the contribution of *S. alterniflora* to C sequestration.

4 Discussion

4.1 Changes of Yancheng saltmarsh area

Saltmarshes are sensitive to anthropogenic activities, especially coastal reclamation, affecting the distribution of saltmarshes directly or indirectly (Chen et al. 2022). From 1982 to 2021, changes in the area of Yancheng saltmarshes showed a "U-shape" tendency that first fell and then rose (Fig. S3). The total area of Yancheng saltmarshes reached 533.7 km^2 in 2021, basically returning to the level of the 1980s. The total area did not change much, but the area of different marsh types altered considerably, mainly due to the effects of the anthropogenic reclamation and the conversion of mudflat to *S. alterniflora* saltmarsh.

From 1985 to 2010, about 7552 km^2 of coastal wetlands were lost in mainland China caused by reclamation, and the shoreline was therefore vastly altered (Liu et al. 2020). Similarly, the total area of Yancheng saltmarsh experienced a sharp decrease from 1982 to 2007, dropping by 28.14%, from 576.8 km^2 to 414.5 km^2. In the 1980s and early 1990s, conversion to aquaculture ponds became the dominant driver of reclamation, especially in northern China (Wang et al. 2020). During late 1990s to 2010s, urban, industrial, and port expansions were the main driving forces of reclamation, and the reclamation projects reached a maximum in 2009 (Gu et al.

2018). Anthropogenic reclamation activities pushed the coastline regression (Fig. S4), which directly decreased the area of *P. australis* by 38% till the 2010s. The decline continued until the government implemented protection policies to conserve and restore coastal wetlands in 2009 (Tang et al. 2009).

S. alterniflora invasion is an important issue in the coastal regions of China, and previous studies usually indicated that *S. alterniflora* outcompetes native marshes, and then spreads to areas unsuitable for most native plants (Nie et al. 2022). However, our time-series remote sensing analyses suggested that mudflat was the predominant habitat colonized by *S. alterniflora* in the region. The establishment and expansion of *S. alterniflora* at the low-elevation mudflats can modify water flow, increase sediment deposition, and promote the desalinization of high-elevation saltmarshes, thus influencing the interspecific competition between *P. australis* and *S. salsa* (Wang et al. 2022a, b; Zhou et al. 2015). As a result, decreased soil salinity enables the seaward movement of *P. australis*, leading to the displacement of *S. salsa* marshes over time, while the *S. alterniflora* remains stable and expands into mudflats (Tang et al. 2022; Wang et al. 2022a, b; Yang et al. 2016). This encroachment of land reclamation on the landward and *S. alterniflora* expansion on the seaward have kept the total saltmarsh area stable over the past several decades. However, there has been a significant shift in the distribution of plant communities in saltmarshes, with a considerable reduction in the area occupied by *S. salsa* due to the transition to *P. australis* through interspecific competition (Li et al. 2021). Therefore, our study further proved that *S. alterniflora* did not directly invade the area where native plants grew from the landscape scale, but indirectly exacerbated interspecific competition among native plants by transforming the mudflats into *S. alterniflora* marsh.

Besides the competition between *P. australis* and *S. salsa* that expedited the decline of *S. salsa* marsh area, climate change and anthropogenic reclamation were vital to *S. salsa* marsh shrinking (Kirwan and Mudd 2012). When sea-level rise exceeds the C deposition in sediments, sub-tidal saltmarshes will gradually degrade to unvegetated mudflats (Saintilan 2021; Törnqvist et al. 2019). Meanwhile, dams built with cement along the coastline inhibit the landward migration of saltmarshes, further leading to the loss of saltmarsh area. Anthropogenic reclamation, such as shipping, fishing, and tourism, greatly influences on the distribution of saltmarshes (Poppe and Rybczyk 2021). The temporal reduction of saltmarshes showed a trend similar to that in reclamation areas in southern Hangzhou Bay, indicating that saltmarshes loss was closely related to reclamation activities (Chen et al. 2022). Our results also demonstrated that more than half of the *S. salsa* marsh area has degraded to non-vegetated mudflats and encroached by anthropogenic reclamation (Table S2).

4.2 The C stocks and CAR

Halophytes directly contribute to the C cycle in the saltmarsh ecosystem because they are major OC producers (Wang et al. 2022a, b). In this study, we found that AGB and BGB in *S. alterniflora* were far higher than those in *P. australis* and *S. salsa*, consistent with previous observations that *S. alterniflora* had higher plant biomass than other types of saltmarshes (Zhou et al. 2015). The SEM results showed that the biomass was mainly regulated by vegetation characteristics (plant height and coverage) and soil physicochemical properties (pH, TK, NH_4^+, etc.). On the one hand, *S. alterniflora* was a C4 plant, while *P. australis* and *S. salsa* were C3 plants. Generally, C4 plants had higher photosynthetic efficiency than C3 plants (Shang et al. 2014; Zhou et al. 2007). On the other hand, the higher plant height and coverage (Liao et al. 2007; Zuo et al. 2012), the more vital propagation ability (Li et al. 2009; Zhao et al. 2020), and the longer growing season of *S. alterniflora* (Tang et al. 2022) contributed to its accumulation of plant C and expansion of living space. *S. alterniflora* was competitively superior to the native species in terms of nutrient uptake and utilization efficiency, and the competitive advantages enabled its C acquisition and storage (Li et al. 2021; Xie et al. 2019). From the proportion of plant C pool to the total C pool (Table S3), the vegetation types were differentiated in the plant C sequestration capacity. *S. alterniflora* owned the most extraordinary capacity in plant C sequestration, and it was 1.52- and 9.42-fold of *P. australis* and *S. salsa*, which supported the potential of *S. alterniflora* in plant C stabilization.

As the largest OC pool in saltmarshes, soil C cycling is complex and variable (Diao et al. 2020; Spencer et al. 2016). Elsey-Quirk et al. (2011) found that SOC stock was the central part of total C stock in saltmarsh ecosystem, which was also consistent with our findings. In our findings, SOC stock accounted for more than 80% of the total C stock in the vegetated saltmarshes, and it was up to 98% in *S. salsa* saltmarshes. There was no significant difference in SOC stock among different vegetations. However, for different soil depths, we found that the SOC stock of *S. alterniflora* at the 0–20 cm soil depth was higher than that of other vegetated saltmarshes, while it was significantly lower than that of *P. australis* at the 50–100 cm soil depth. We speculated that such a result was related to the distribution of plant roots in different vegetations. *S. alterniflora* has sufficiently proliferated roots distributed mainly in the surface soil layer, especially in the

0–20 cm depth, occasionally extending to 50–100 cm belowground (Cheng et al. 2006; Liu et al. 2017). In addition, the SOC stock in the newly developed *S. alterniflora* saltmarshes was similar to the mudflat (Liu et al. 2017; Wang and Wall 2010), indicating that the SOC increment in *S. alterniflora* saltmarshes took time to accumulate. Thus, the significantly lower SOC stock in *S. alterniflora* saltmarshes than that of *P. australis* saltmarshes in the deeper soil depth was partly owing to the short duration of *S. alterniflora* colonization.

The soil C stock in saltmarshes is mainly due to the rapid accumulation of OC-rich sediments and conditions that promote the preservation of OC (Miller et al. 2022; Xia et al. 2021a, b). It was estimated that the introduction of *S. alterniflora* increased the CAR seven-fold more than adjacent mudflats (Huang et al. 2018). In this study, the CAR of *S. alterniflora* was more than twice as much as the *P. australis* and *S. salsa* saltmarshes, further corroborating its strong C accumulation capability. First, *S. alterniflora* has higher plant biomass and litter yield than native plants, boosting plant C input to soils (Gao et al. 2016; Yang et al. 2016). Second, the several advantageous traits of *S. alterniflora*, such as densely growing canopies and roots, are beneficial for attenuating waves and maintaining sedimentation, thus sequestrating more C (Koch et al. 2009; Yang 2019). Third, the litter decomposition rate of *S. alterniflora*, particularly the root residues, was much slower than that of *P. australis* litter due to its lower litter quality (i.e., higher C: N ratio) (Duan et al. 2018). The increased C input, C sequestration, and slower litter decomposition derived from *S. alterniflora* reduced the C turnover in saltmarshes and promoted C accumulation (Xia et al. 2021a, b).

4.3 Expansion of *S. alterniflora*

S. alterniflora originated from the east coast of North America and the Gulf of Mexico (Cheng et al. 2006). The strong adaptability and tolerance of *S. alterniflora*, together with intentional introduction and plantation, enable it to be widely distributed in saltmarshes of different geographical and climatic regions (Zuo et al. 2012). As a typical halophyte, it is strongly tolerant to salinity and flooding (Daehler and Strong 1996). Since its introduction in 1979, *S. alterniflora* has been continuously expanding in the coastal areas of China (Mao et al. 2019; Zhang et al. 2017).

The expansion of *S. alterniflora* significantly altered C cycling in saltmarshes. The unique traits of *S. alterniflora*, such as high primary productivity, enriched nutrient utilization efficiency, and strong C captivate capacity, make it efficient in fixing C in both biomass and soils to strengthen coastal C sink (Choi and Wang 2004; Kaštovská and Šantrůčková, 2007; Kirwan and Mudd 2012; Tang et al. 2022). We found that, compared to native marsh types (*P. australis* and *S. salsa*), *S. alterniflora* possessed greater surface soil C stock, plant C stock, and CAR. In addition, the promotion on surface SOC stock showed a cumulative effect along with the *S. alterniflora* colonization duration and peaked in the 10th year (the peak increased the SOC stock by almost five times compared with the early stage). To summarize, the blue C sequestration capacity in Yancheng saltmarshes was enhanced along with the expansion of *S. alterniflora*.

The area of *S. alterniflora* had expanded by 287.5 km^2 in Yancheng from 1982 to 2021. Along with the expansion of *S. alterniflora*, the proportion of *S. alterniflora* in the total area of Yancheng saltmarshes continuously increased (Fig. S5), resulting in strengthened C storage and C burial. The strongly positive relationships of the total plant C storage and C burial with the area of *S. alterniflora* confirmed that *S. alterniflora* drove the C sequestration in Yancheng saltmarshes over temporal scales, especially in the aspect of plant C storage and C burial (Fig. 6c, d). Greater CAR is usually associated with greater SOC stock, but the relationship is not always true in reality. The total SOC storage was correlated with the total area of Yancheng saltmarshes rather than the area of *S. alterniflora* (Fig. S6a, b) because no significant differences existed in the SOC stock (0–100 cm) among different vegetations. The increment of SOC stock requires a continuous high CAR for some time (Ouyang and Lee 2020). Thus, the future SOC stock of *S. alterniflora* would be more extensive than that of the other two native plants under such a great CAR. *S. alterniflora* is prospected to play an increasingly essential role as a C sink for its continuous expansion and promoting SOC storage.

The expansion of *S. alterniflora* in mudflats not only resulted in a substantial enhancement of the blue C sinks in saltmarshes but also initiated a succession of plant communities that altered the original saltmarsh ecosystems' blue C sinks. (Liu et al. 2017; Nie et al. 2022). The establishment of *S. alterniflora* at the low-elevation mudflats enhanced the accumulation of organic matter and increased the sediment elevation due to the strong ability to capture fine-grained sediments. This led to progressively shorter inundation and lower seawater input to the landward *P. australis* and *S. salsa* marshes, altering their plant communities (Redfield 1972; Wang et al. 2022a, b). The halophyte *S. salsa* was strongly dependent on the tidally driven episodic accumulation of salt, which killed its competitors (Cheng et al. 2006; Tang et al. 2022). The adaptability and preference of different halophytes to salt altered the competition between *P. australis* and *S. salsa*

(Cao et al. 2022; Yan et al. 2022; Zhao et al. 1999), resulting in the modification of plant structure in Yancheng saltmarshes after *S. alterniflora* invasion (Fig. S7). Consequently, the desalination trend made it more competitive, causing it to migrate seaward and compress the *S. salsa* zone. The substitution of *S. salsa* by *P. australis* was also helpful in strengthening the blue C sinks in saltmarshes because *P. australis* had a significantly higher capacity in plant C stock than *S. salsa* (Wang et al. 2022a, b). This vegetation transition has critical implications for the long-term C sequestration potential of saltmarshes and their ability to act as natural C sinks. Further studies are necessary to understand the underlying mechanisms driving these plant community successions and their implications for coastal ecosystem management.

4.4 Implication

Our study provided novel insights into the succession of plant landscape patterns and the saltmarsh C sequestration in coastal wetlands of China. The colonization of *S. alterniflora* mainly occupied the non-vegetated mudflats (Mao et al. 2019). The shrinking zone of native *S. salsa* was not caused by direct competition of exotic *S. alterniflora*, but by the occupation of native *P. australis,* which was indirectly driven by the promoted soil sedimentation of *S. alterniflora* expansion to mudflats (Wang et al. 2022a, b).

The widespread and rapid expansion of *S. alterniflora* to mudflats along the coast of China promoted primary productivity and plant C inputs (Li et al. 2009; Liao et al. 2007), and slowed water flow that accelerated sediment accumulation (Liu et al. 2017), favoring C storage and C accumulation. *S. alterniflora* saltmarshes had 2.8- and 6.6-fold more total C stock and CAR than mudflats, respectively (Table S4). China has 5,300 km^2 of mudflats (Wang et al. 2021a, b). There is a tremendous potential to increase the blue C sink in these mudflats. *S. alterniflora* has been regarded as an invasive species in China and human intervention has been implemented to avoid its broader expansion. However, *S. alterniflora* colonization also strengthened C sequestration, prevented the beaches from erosion, and did not compete with native species directly. Follow-up studies are needed to explore whether the carbon sequestration potential of *S. alterniflora* should be exploited to reach China's carbon–neutral goal.

Developing environmental management strategies to balance the negative impacts of *S. alterniflora* and its strong capacity for C sequestration to attain carbon neutrality is a complex challenge. Firstly, it is needed to comprehensively reassess the invasive behavior of *S. alterniflora* by considering its capacity for blue C sinks and its adverse environmental impacts. Additionally, it may be beneficial to explore methods for utilizing the carbon captured by *S. alterniflora* in a sustainable way, such as through bioenergy production or carbon storage. Collaborative efforts, involving scientists, policymakers, and local communities, may be needed to develop efficient and sustainable management strategies that balance the benefits of C sequestration with the protection of native ecosystems. The adoption of such strategies will require significant investment in research, monitoring, and management efforts, but will ultimately be essential for the attainment of carbon neutrality and the protection of our environment.

5 Conclusion

This study systematically analyzed the SOC stock, the plant C stock, and the soil C accumulation rate associated with decades of marsh cover change in Yancheng, China. We found that *S. alterniflora* had an exceptionally high C sink capacity in its soil surface C storage, plant C storage, and C burial. In addition, the expansion of *S. alterniflora* contributed to an increase in the surface (0–20 cm) SOC stock, which had a cumulative effect with incrementing expansion years, and tended to be stable after peaking at the 10^{th} year. Although Yancheng saltmarsh's total area reduced by 43.09 km^2 over the past four decades, the total C storage and C burial were strengthened to different degrees due to the high C sequestration of *S. alterniflora*. The colonization of *S. alterniflora* in mudflats increased the saltmarsh area and promoted carbon accumulation, therefore facilitating the expansion of the native *P. australis*. Largely expanded *P. australis* led to massive shrinkage of the *S. salsa* marsh area, which also offset the compressed living zone by land reclamation. The direct and indirect carbon gain by *S. alterniflora* invasion overcompensated carbon stock loss due to land reclamation and the areal loss of carbon-dense marsh of *S. salsa* to the marsh of *P. australis*, a species with a lower carbon accumulation rate (from 108.5 ± 5.00 g C m^{-2} yr^{-1} to 94.77 ± 7.80 g C m^{-2} yr^{-1}). Our findings provide a theoretical basis for the C neutrality of Yancheng saltmarshes. The spatiotemporal assessment on the C sequestration of Yancheng saltmarshes is of great significance for better understanding of the blue C ecosystems of China.

Abbreviations

AGB	Aboveground biomass
AP	Available phosphorous
BD	Bulk density
BGB	Belowground biomass
C	Carbon
C/N	Carbon–nitrogen ratio
CAR	Carbon accretion rate
CNKI	China National Knowledge Infrastructure
CO_3^{2-}	Carbonate
DOC	Dissolved organic carbon

LOI	Loss of ignition
MF	Mudflats
PA	*Phragmites australis*
SA	*Spartina alterniflora*
SEM	Structural equation model
SS	*Suaeda salsa*
SOC	Soil organic carbon
SWC	Soil water content
TK	Total potassium

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1007/s44246-023-00070-4.

Additional file 1: Table S1. Overall accuracy and Kappa index of supervised classification from 1985 to 2019. **Table S2.** The transformation of different marsh types and land reclamations between 1987 and 2021, where the total was the net change of land cover. **Table S3.** The soil C storage at the 0–100 cm soil depth and plant C storage per unit area, and their proportion to total C storage. **Table S4.** A brief comparison of *S. alterniflora* and mudflats, in the aspect of soil C stock, plant C stock, and CAR. **Fig. S1.** The flow chart of data analysis and remote sensing used to calculate the dynamics of C sequestration in Yancheng saltmarsh. **Fig. S2.** Factors in manipulating the C storage, in which (a) the indicators regulating plant biomass, (b) the indicators regulating C storage at the 0–20 cm soil depth, and (c) the indicators regulating C storage at the 20–50 cm soil depth. **Fig. S3.** The variation of total area in Yancheng saltmarsh along with time series. **Fig. S4.** The changes in coastlines under anthropogenic reclamation. **Fig. S5.** The proportion of different vegetation to the total area of Yancheng saltmarsh with time series. **Fig. S6.** The regulations of soil C storage, in which (a) the relationships between the total SOC storage in Yancheng saltmarsh and the total area of Yancheng saltmarsh, (b) the relationships between the total SOC storage in Yancheng saltmarsh and the area of *S. alterniflora* in Yancheng, and(c) the correlation of C accumulation rate and surface SOC stock. **Fig. S7.** The niches of different vegetations on the salt gradient and the consequences of *S. alterniflora* invasion on the saltmarsh vegetation successions.

Additional file 2. Appendix dataset.

Authors' contributions

Wang Faming and Zhou Jinge designed this study. Zhou Jinge, Wang Faming, and Zhang Jingfan discussed analysis methods. Zhou Jinge collected the data, conducted the analysis, and drafted the manuscript. Chen Yaping and Wang Faming edited this manuscript. All authors discussed the results and contributed to writing the manuscript. The authors read and approved the final manuscript.

Funding

This study was funded by the National Natural Science Foundation of China (U2106209, 31870463, 32011530164, 31670621, 32171594), the CAS Project for Young Scientists in Basic Research (YSBR-037), the CAS Youth Innovation Promotion Association (2021347), ANSO collaborative research (ANSO-CR-KP-2022–11), Guangdong Basic and Applied Basic Research Foundation (2021B1515020011), Science and Technology Planning Project of Guangdong Province (2021B1212110004), the National Forestry and Grassland Administration Youth Talent Support Program (2020BJ003), and the National Key Research Program of China (2021YFC3100402).

Availability of data and materials

The data and code that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Competing interests

The authors declare no competing interests.

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Received: 30 March 2023 Revised: 6 September 2023 Accepted: 12 September 2023
Published online: 23 October 2023

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