

RESEARCH ARTICLE

Restoration of native saltmarshes enhances carbon sequestration and mitigates warming effects following *Spartina alterniflora* removal

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Abstract

1. The rapid expansion of exotic *Spartina alterniflora* has significantly threatened native coastal ecosystems' structure and function, prompting global control efforts. Consequently, native saltmarshes restoration has emerged as a nature-based solution following invasive species removal. However, given that *S. alterniflora* is a high-carbon invasive species, the impacts of native saltmarshes restoration on coastal blue carbon benefits following its removal remain uncertain.
2. Here, we quantified atmospheric carbon uptake and organic carbon storage among restored native saltmarshes (*Phragmites australis* and *Bolboschoenoplectus marigueter* communities), unrestored bare mudflat following *S. alterniflora* removal and uncontrolled *S. alterniflora* communities to assess whether native saltmarshes can compensate for the carbon sinks and the climate effects after invasive species eradication.
3. The results showed that *S. alterniflora* removal drastically reduced carbon sink, with unrestored mudflat transitioning to a carbon source. While restored native saltmarshes showed lower atmospheric carbon uptake compared to pre-eradication *S. alterniflora* levels, they exhibited significantly enhanced carbon sequestration relative to unrestored mudflats. Additionally, the organic carbon density of soil (0–50 cm) and vegetation in restored sites exceeded unrestored areas by >1.4 times, recovering >70% of the carbon storage observed in *S. alterniflora* communities.
4. Sustained global warming potentials (SGWP) analysis over a 100-year timescale revealed that without post-eradication vegetation restoration, saltmarsh could shift from climate cooling to warming effects. Native saltmarsh restoration effectively mitigated this transition, demonstrating substantial climate change mitigation potential.
5. *Synthesis and applications.* Our findings not only reveal that native saltmarsh restoration is a blue carbon-friendly ecological restoration approach following *S. alterniflora*

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removal, but also highlight the critical trade-offs between carbon losses from invasive species removal and the carbon offset achieved through restoring native vegetation, providing actionable guidance for coastal management. These insights are particularly valuable for regions facing similar invasive species challenges, informing the development of integrated strategies that maximize carbon compensation while enhancing coastal sustainability and climate resilience. Future restoration programmes should prioritise multifunctional outcomes that simultaneously address biodiversity conservation and climate mitigation objectives.

KEYWORDS

climate change, coastal blue carbon, ecological restoration, ecosystem carbon fluxes, invasive species, organic carbon storage, saltmarshes

1 | INTRODUCTION

Saltmarshes are distributed globally, except in Antarctica, and are primarily located in large river deltas and estuaries, playing crucial roles in enhancing resilience, biodiversity, livelihoods and climate mitigation, significantly contributing to the global blue carbon sink (Macreadie et al., 2021).

Despite their ecological importance, saltmarshes have experienced a concerning global decline with a rate of 0.28% year⁻¹ from 2000 to 2019 (Campbell et al., 2022). Additionally, *Spartina alterniflora*—a global coastal invader and powerful ecosystem engineer—has aggressively invaded across global coastlines (Ning et al., 2021), including the Pacific coast of North America; European shorelines (England, France, the Netherlands and Spain); Oceania (Australia, New Zealand and Tasmania) and East Asia (particularly China) (Idaszkin & Bortolus, 2011; Kennedy et al., 2017; Kerr et al., 2016; Ren et al., 2021). Through its dominance in intertidal zones, *S. alterniflora* has emerged as a severe threat to coastal ecosystems worldwide (Stokstad, 2023).

To curb the degradation of global ecosystems, the United Nations proposed the UN's Decade on Ecosystem Restoration (2021–2030), aligning with global initiatives like the Sustainable Development Goals and the Global Biodiversity Framework (Mason et al., 2023). The IPCC Sixth Assessment Report specifically emphasizes the role of wetland restoration in strengthening ecosystem resilience and sustainability in the face of climate change (Masson-Delmotte et al., 2021). Given the significant blue carbon sink potential, the conservation and restoration of saltmarshes have gained global prominence and have been positioned as valuable coastal nature-based climate solutions (Mason et al., 2023).

Globally, diverse *S. alterniflora* removal methods (e.g., mowing, flooding herbicides and combined methods) (Kleinhenz et al., 2016; Major et al., 2003; Smith & Lee, 2015; Yuan et al., 2011) and native vegetation restoration have been implemented in regions, such as North America (Washington, British Columbia), Europe (England, France), Australia (New South Wales) and East Asia (China) (Holsman et al., 2010; Kriwoken & Hedge, 2000; Yang et al., 2020). In 2023, China initiated a large-scale control plan aiming to remove

90% of *S. alterniflora* by 2025 to protect coastal ecological security, which is by far the largest action plan for wetland invasive species control in China and even in the world (Stokstad, 2023). By 2019, *S. alterniflora* had been distributed across all coastal provinces in China, meaning that 55,409 ha of *S. alterniflora* would be removed, accounting for approximately 43.5% of saltmarsh vegetation (Hu et al., 2021). However, as a C₄ species, *S. alterniflora* exhibits high net photosynthetic efficiency and high net primary productivity through its specialized C₄ photosynthetic pathway (Cheng et al., 2006). These physiological adaptations enable *S. alterniflora* to have superior carbon sequestration capacity compared to C₃ plants, significantly enhancing the carbon sink potential of invaded mudflats (Zhou et al., 2023). As a result, removing *S. alterniflora* on a large scale will significantly alter saltmarsh' distribution and composition. Consequently, the coastal zone's blue carbon capacities may be further affected. What are the potential impacts of such large-scale management of *S. alterniflora* on saltmarsh' carbon sequestration, and how to balance the negative effects of *S. alterniflora* and maintain or boost blue carbon capacities of saltmarshes, is a crucial concern for the recovery and function improvement of saltmarshes alongside *S. alterniflora* control, both in China as well as in other global regions where *S. alterniflora* removal methods are being implemented, along with and native vegetation restoration.

Integrating saltmarsh restoration targets into broader nature-based climate solutions could provide an opportunity to reverse biodiversity decline and replenish carbon sinks lost due to *S. alterniflora* removal. However, current research has predominantly focused on understanding the invasion dynamic (Neira et al., 2007; Xu et al., 2022) or ecological restoration outcomes (Duggan-Edwards et al., 2020; Wood et al., 2017). Few studies have revealed the combined effects of *S. alterniflora* eradication and saltmarsh restoration on carbon sequestration capacity, as well as whether subsequent restoration of native vegetation can effectively compensate for potential carbon loss—a critical gap our research addresses. Here, we specifically determined how atmosphere-ecosystem carbon fluxes and plant-soil carbon density vary between different treatments: (i) areas subjected to restoration of native plants, (ii) areas subjected that had not been

restored after *S. alterniflora* eliminated and (iii) areas with invasive *S. alterniflora*. We expected blue carbon capacity in restoration and non-restoration marshes to be influenced by the interplay between plant traits and edaphic properties. These findings provide a comprehensive understanding of blue carbon functional dynamics following *S. alterniflora* removal and native vegetation restoration in degraded saltmarsh ecosystems, offering critical insights for global coastal wetland management strategies.

2 | MATERIALS AND METHODS

2.1 | Study sites description

S. alterniflora was introduced in China during the 1970s to achieve coastline protection. Since then, it has spread extensively across eastern coastal wetlands in China (Figure 1a), posing a predominant

ecological issue in central-south China (Xu et al., 2022). With nationwide *S. alterniflora* elimination and coastal wetland restoration, Wenzhou in Zhejiang Province focuses on restoring saltmarshes to the north and a combination of saltmarshes and mangroves to the south (Figure 1a).

The study site is located in a saltmarsh at the eastern end of Chongming Island (31°25'N–31°38'N, 121°50'E–122°05'E) in the Yangtze River estuary, China. This area serves as a vital stopover site for migratory birds along the East Asian-Australasian Flyway and is one of the earliest areas for large-scale *S. alterniflora* management in China. In recent decades, it has experienced a serious invasion of *S. alterniflora*, which has threatened bird habitats and biodiversity. To address the degradation of native saltmarshes, ecological restoration projects were initiated in 2013. Removal measures included physical (e.g., involving harvesting and waterlogging) and chemical (herbicides) measures were used to control the invasive *S. alterniflora* (Zhao et al., 2020). Subsequently, in-situ native saltmarsh species

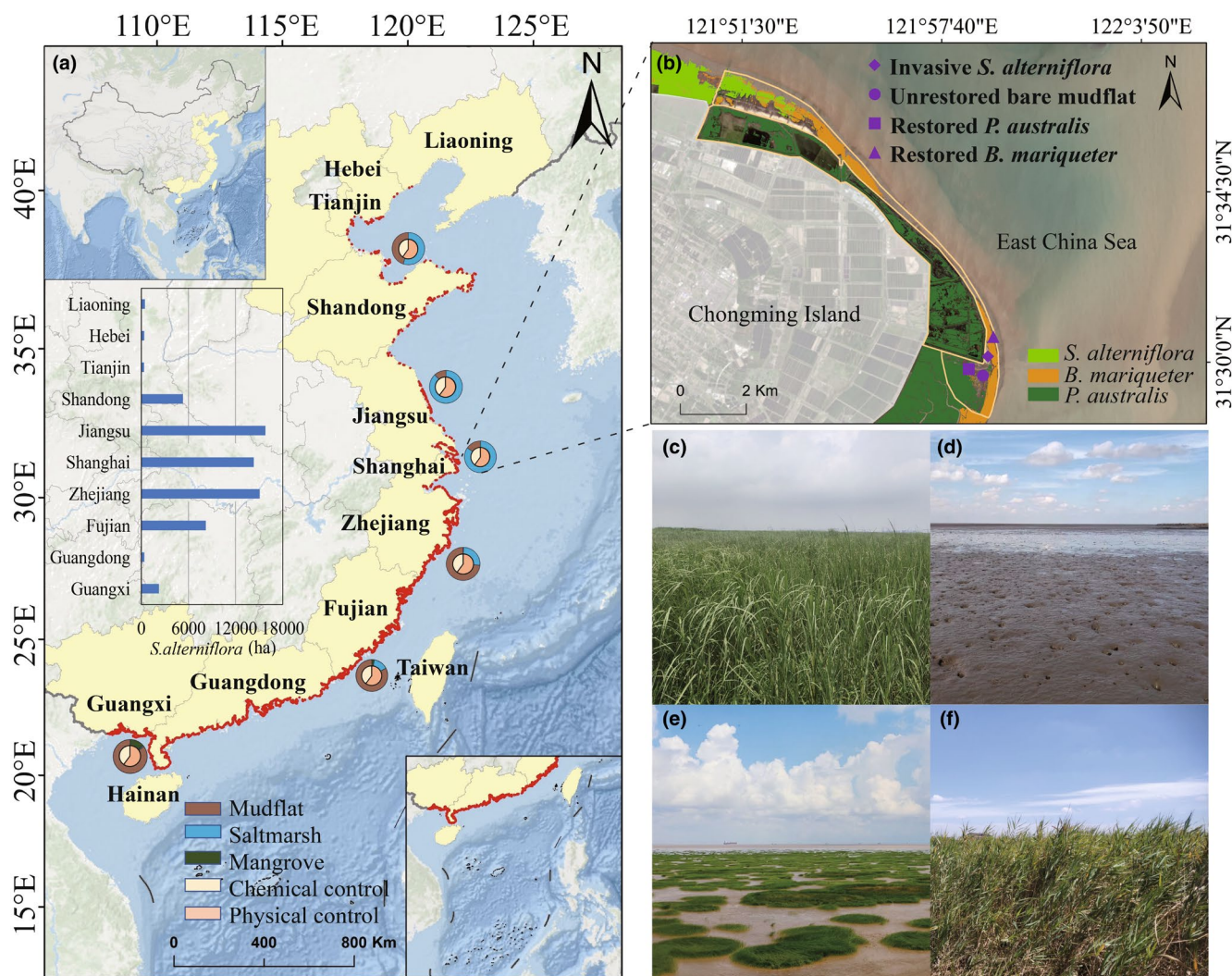


FIGURE 1 Illustration of the study area and sample sites including: (a) coastal wetlands distribution and management of *Spartina alterniflora* in China, (b) ecological restoration area and sample sites in the Chongming Dongtan, photos of invasive *S. alterniflora* (c), unrestored bare mudflat (d), restored native saltmarshes (*Bolboschoenoplectus marigueter* and *Phragmites australis*) (e, f).

B. mariqueter and *P. australis* were recovered following *S. alterniflora* removal, beginning in 2015 (Yuan et al., 2022). *B. mariqueter* was a typical pioneer species distributed in low tidal flats and generally grew to a height of 30–90 cm with dense tufting, while *P. australis*, grew in high tidal flats and can reach up to 4 m in height with a more expansive growth habit.

Sampling areas were established in *S. alterniflora* community, unrestored bare mudflat following *S. alterniflora* removal, restored *P. australis* and *B. mariqueter* (Figure 1b). The permit for sample collection was issued by the Shanghai Chongming Dongtan National Nature Reserve (permit number [2025]151). The sampling did not require ethics approval.

2.2 | Ecosystem carbon fluxes measurements

In March 2021, three independent replicate vegetation quadrats (2 m × 2 m, spaced 5 m apart) were randomly established in the above sampling areas and three replicate plots within each quadrat (nine replicates per habitat type), representing 6 years post-restoration.

To assess the carbon flux variations, real-time and automated in-situ measurements of CO₂ and CH₄ fluxes were conducted monthly from April 2021 to March 2022, using an Ultraportable GHG Analyser (Los Gatos Research, Inc., CA, USA). Measurements were conducted between 9:00 and 15:30 on sunny days within a 2-day period to minimize diurnal variations and maintain consistent environmental conditions. Before data collection, comprehensive in-situ leak testing was conducted and strict low-interference deployment procedures were followed to minimize external disturbances. The carbon fluxes were monitored and calculated using the linear rate of gas concentration change over time, as described by Song et al. (2020) and Yang et al. (2020).

To evaluate the potential contribution of gaseous carbon balance to climate change, the sustained global warming potential (SGWP) was calculated using a 100-year horizon. Daytime/nighttime SGWP was calculated using monthly averaged thresholds of photosynthetically active radiation (PAR < 10 μmol m⁻² s⁻¹ for nighttime) to refine. SGWP was calculated as follows Yang et al. (2020):

$$\text{SGWP} = \text{FCO}_2 + \text{FCH}_4 \times 45, \quad (1)$$

where FCO₂ and FCH₄ are flux per unit mass of CO₂ (μg CO₂ m⁻² s⁻¹) and CH₄ (μg CH₄ m⁻² s⁻¹), respectively.

2.3 | Organic carbon analyses

In September 2021, soil samples were collected using a stainless-steel sampler to assess variations in organic carbon density across the above sites. Each sample was segmented into 10-cm intervals up to a top 50-cm depth. Simultaneously, above-ground and below-ground plant parts within a 50 cm depth were harvested and

oven-dried at 65°C to a constant weight. Organic carbon and total nitrogen content were determined using a Vario elemental analyser (Elementar, Germany). Bulk density was calculated from the dried sample mass and its original volume.

Soil organic carbon (SOC) density from each soil core was calculated as follows:

$$\text{SOC}_{\text{org},5} = \sum_{j=1}^5 \text{SOC}_j \times \text{BD}_j \times D_j \times 10^4, \quad (2)$$

$$\text{SOC}_{\text{density}} = \text{SOC}_{\text{org},i} \times S_i \times 10^{-2}, \quad (3)$$

where SOC_{org,5} is SOC content of 0–50 cm depth marshes soil (g m⁻²), SOC_j is mean SOC content of the soil layer *j* (%), BD_j is bulk density of the soil layer *j* (g cm⁻³), D_j is the thickness of soil layer *j* (cm); S_i is per unit area in each survey area (ha), SOC_{density} is SOC stock per unit area (Mg Cha⁻¹) of sediments.

Vegetation organic carbon (VOC) density from each plants part was calculated as follows:

$$\text{VOC}_a = \text{VC}_{\text{aorg},i} \times \text{VB}_i \times S_i \times 10^{-2}, \quad (4)$$

$$\text{VOC}_b = \text{VC}_{\text{borg},i} \times \text{VB}_i \times S_i \times 10^{-2}, \quad (5)$$

$$\text{VOC}_{\text{density}} = \text{VOC}_a + \text{VOC}_b, \quad (6)$$

where VOC_a or VOC_b is organic carbon stock of above-ground and below-ground parts of plants (%), VC_{aorg,i} or VC_{borg,i} is mean organic carbon content of above-ground and below-ground parts (%), VB_i is biomass of above-ground or below-ground parts of plants (g m⁻²), S_i is per unit area of vegetation in each survey area (ha), VOC_{density} is total carbon stock per unit area (Mg Cha⁻¹) of vegetation.

2.4 | Measurement of plant and key environmental characteristics

Leaf chlorophyll concentration (Chl) was measured using a Soil Plant Analysis Development-502 meter (Yang et al., 2017), with five leaves randomly collected per site (15 leaves per quadrat) and the entire leaf area was measured and averaged across all leaves sampled. In addition, the normalized difference vegetation index (NDVI) was derived monthly from Sentinel-2 Multi-Spectral Instrument (MSI) Level-2A surface reflectance data. All satellite imagery processing was performed using the Google Earth Engine (GEE) platform (Gorelick et al., 2017). Sentinel-2 data provides multispectral images at 10-m spatial resolution with a 4/5-day revisit frequency and images are available through the Copernicus Data Space Ecosystem (<https://dataspace.copernicus.eu/>).

Soil water content (SWC) was determined by the mass ratio of moist soil to dry soil. Temperature (T) was measured using Decagon sensors (Decagon EC-5, USA), pH was determined using a Soilstik meter (Soilstik, Spectrum, USA) and salinity (SAL) of overlying water was gauged using a salinity meter (AZ8371, China).

2.5 | Statistical analyses

Data analysis was performed using SPSS 23 (SPSS Inc., Chicago, IL, USA), with graphical representations generated through SigmaPlot (version 14.0, California, USA) and R version 4.1.3 (R Core Team, 2023). Mean and standard error were calculated for all parameters. Differences in carbon fluxes and carbon density were evaluated using one-way analysis of variance (ANOVA) with Tukey's honest significant difference test. In addition, we performed an aggregated boosted tree (ABT) analysis to assess relative importance of plant characteristics and soil properties on carbon fluxes in sampling areas (De'ath, 2007). Correlation analyses were conducted to explore the relationships between fluxes and environmental variables, using Spearman's correlation coefficient, representing the resulting correlation matrix through a correlation plot (Wei & Simko, 2021). Finally, a Redundancy (RDA) analysis was used to examine the relationships between soil and vegetation carbon density and environmental variables. The significance threshold was set at $p < 0.05$.

3 | RESULTS

3.1 | Dynamics of ecosystem carbon fluxes in restored native saltmarshes following *S. alterniflora* removal

The study revealed significant differences in ecosystem CO_2 and CH_4 fluxes among invasive *S. alterniflora*, unrestored bare mudflat and restored native saltmarshes. Compared to exotic *S. alterniflora*, atmospheric net CO_2 uptake of restored native saltmarshes (*P. australis* and *B. maritima*) declined, with a reduction of 35.6% and 77.4%, respectively (Figure 1a, Table 1). Nevertheless, with the highest CO_2 uptake by net ecosystem carbon exchange (NEE) in *S. alterniflora* community, its ecosystem CO_2 release by ecosystem respiration (ER) also became higher (Figure 1b). Correspondingly, CO_2 release by ER in restored native saltmarshes (*P. australis* and *B. maritima*) also decreased, with a decrease of 23% and 71.33%, respectively, compared to *S. alterniflora* community (Figure 2b; Table 1). Furthermore, net CO_2 absorption increased from April to September as enhanced photosynthetic activity, which exceeded potential ER. Subsequently, net CO_2 uptake declined as plant greenness diminished during senescence. When ER overshadowed ecosystem CO_2 uptake during dormancy as most vegetation was inactive, plant respiration dominated (Figure 2a). In contrast, unrestored bare mudflat exhibited minor CO_2 release throughout the year ($p < 0.05$, Table 1).

Further, restoration of native saltmarshes notably reduced cumulative CH_4 emissions by 65.2% and 87.5% in restored *P. australis* and *B. maritima* ($p < 0.05$, Table 1), respectively, compared to *S. alterniflora* community (Figure 2c,d). Compared to CO_2 fluxes, low CH_4 emissions were consistent throughout the year but increased significantly across the plants' maturity and senescence (Figure 2c,d).

Overall, neither restored *P. australis* nor *B. maritima* fully compensates for the loss of atmospheric carbon absorption caused by

TABLE 1 Estimated annual mean carbon fluxes and sustained global warming potential (SGWP) and carbon stocks for restored native saltmarshes following *Spartina alterniflora* removal.

Restoration types	Daytime			Nighttime			Carbon stocks		
	CO_2 fluxes (NEE) ($\text{Mg C ha}^{-1} \text{ year}^{-1}$)	CH_4 fluxes ($\text{Mg C ha}^{-1} \text{ year}^{-1}$)	SGWP ($\text{Mg C-eq ha}^{-1} \text{ year}^{-1}$)	CO_2 fluxes (ER) ($\text{Mg C ha}^{-1} \text{ year}^{-1}$)	CH_4 fluxes ($\text{Mg C ha}^{-1} \text{ year}^{-1}$)	SGWP ($\text{Mg C-eq ha}^{-1} \text{ year}^{-1}$)	Vegetation (Mg C ha^{-1})	Soil (Mg C ha^{-1})	
<i>S. alterniflora</i> community	-30.83 ± 3.71 a	0.49 ± 0.07 a	-26.20 ± 2.62 a	16.22 ± 1.64 a	0.63 ± 0.15 a	25.37 ± 3.79 a	15.49 ± 1.05 a	48.85 ± 2.81 a	
Unrestored bare mudflat	0.79 ± 0.03 d	0.003 ± 0.001 c	0.83 ± 0.05 d	1.19 ± 0.13 d	0.008 ± 0.006 c	1.28 ± 0.23 d	—	31.57 ± 0.78 b	
Restored <i>P. australis</i>	-19.85 ± 1.20 b	0.17 ± 0.02 b	-19.42 ± 1.58 b	12.48 ± 0.35 b	0.22 ± 0.02 b	15.09 ± 0.06 b	14.57 ± 1.52 a	38.87 ± 0.64 ab	
Restored <i>B. maritima</i>	-6.97 ± 1.26 c	0.07 ± 0.01 c	-6.66 ± 1.43 c	4.65 ± 0.28 c	0.07 ± 0.03 bc	5.40 ± 0.71 c	2.34 ± 0.07 b	43.17 ± 1.13 ab	

Note: Values in the table are shown as means $\pm$ SE ($n = 9$). Different lowercase letters indicate significant differences under above restorations within the same carbon budgets at $p < 0.05$.

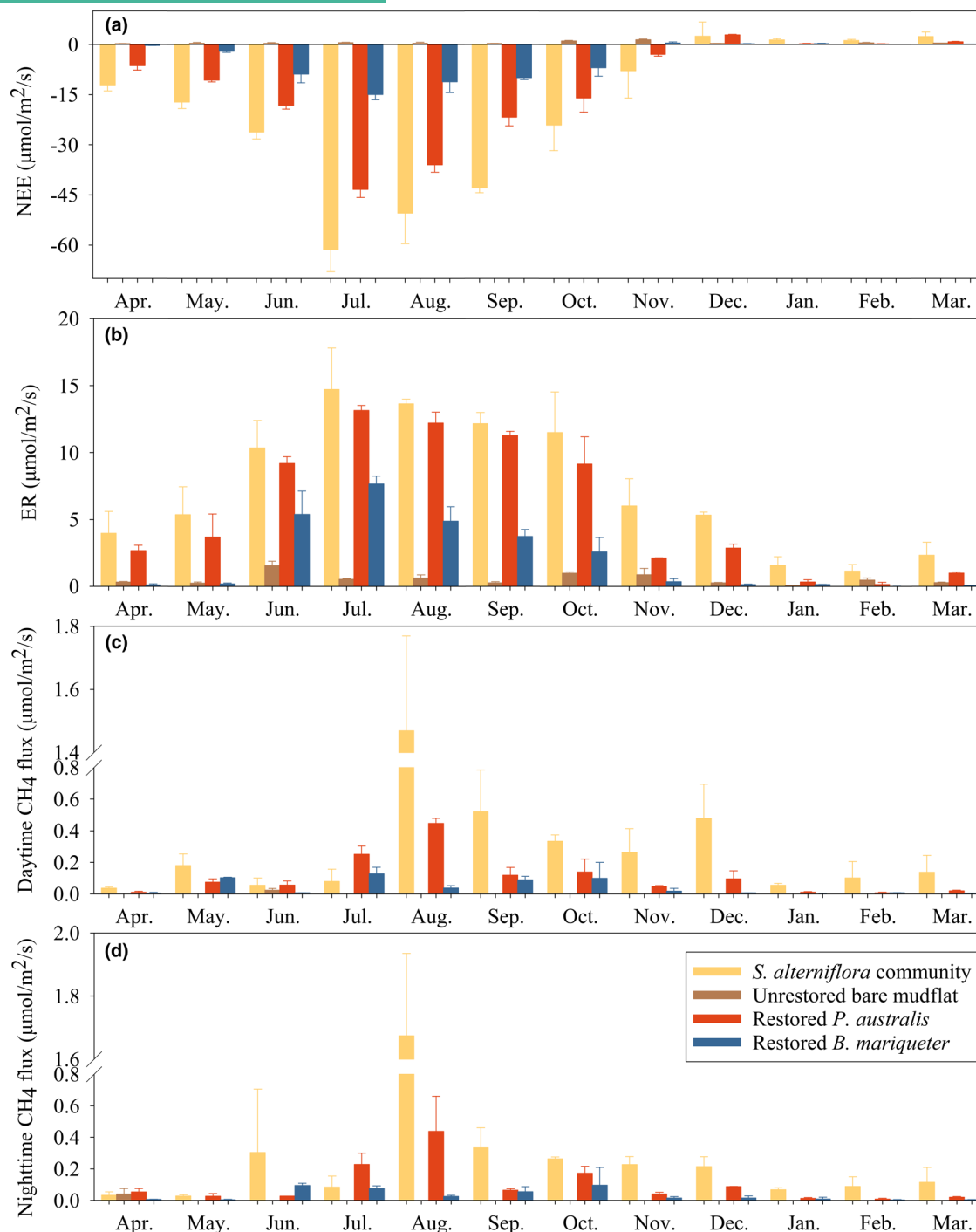


FIGURE 2 Seasonal variations of carbon fluxes (mean $\pm$ SE) under different restoration scenarios.

eliminating *S. alterniflora*. However, native saltmarshes restoration again contributed significantly to the atmospheric net carbon sink when compared to unrestored bare mudflat (Table 1).

3.2 | The SGWP in restored native saltmarshes following *S. alterniflora* removal

The estimated annual SGWP was -0.83 , 2.11 , -4.33 and $-1.26 \text{ MgCha}^{-1} \text{ year}^{-1}$ in the *S. alterniflora* community, unrestored

bare mudflat, restored *P. australis* and restored *B. maritima* community, respectively (Table 1). Both the highest cooling effect during daytime and warming potential during nighttime were observed in *S. alterniflora* community (Figure 3). Eventually, the weak cooling effect was observed in the *S. alterniflora* marshes due to excessive CH_4 emissions and increased ecosystem respiration (ER) (Table 1). On the other hand, unrestored bare mudflat exerted a warming effect throughout the year (Figure 3; Table 1). This indicates that restored native saltmarshes effectively resisted warming potential, particularly during vegetation growing seasons (Figure 3a; Table 1).

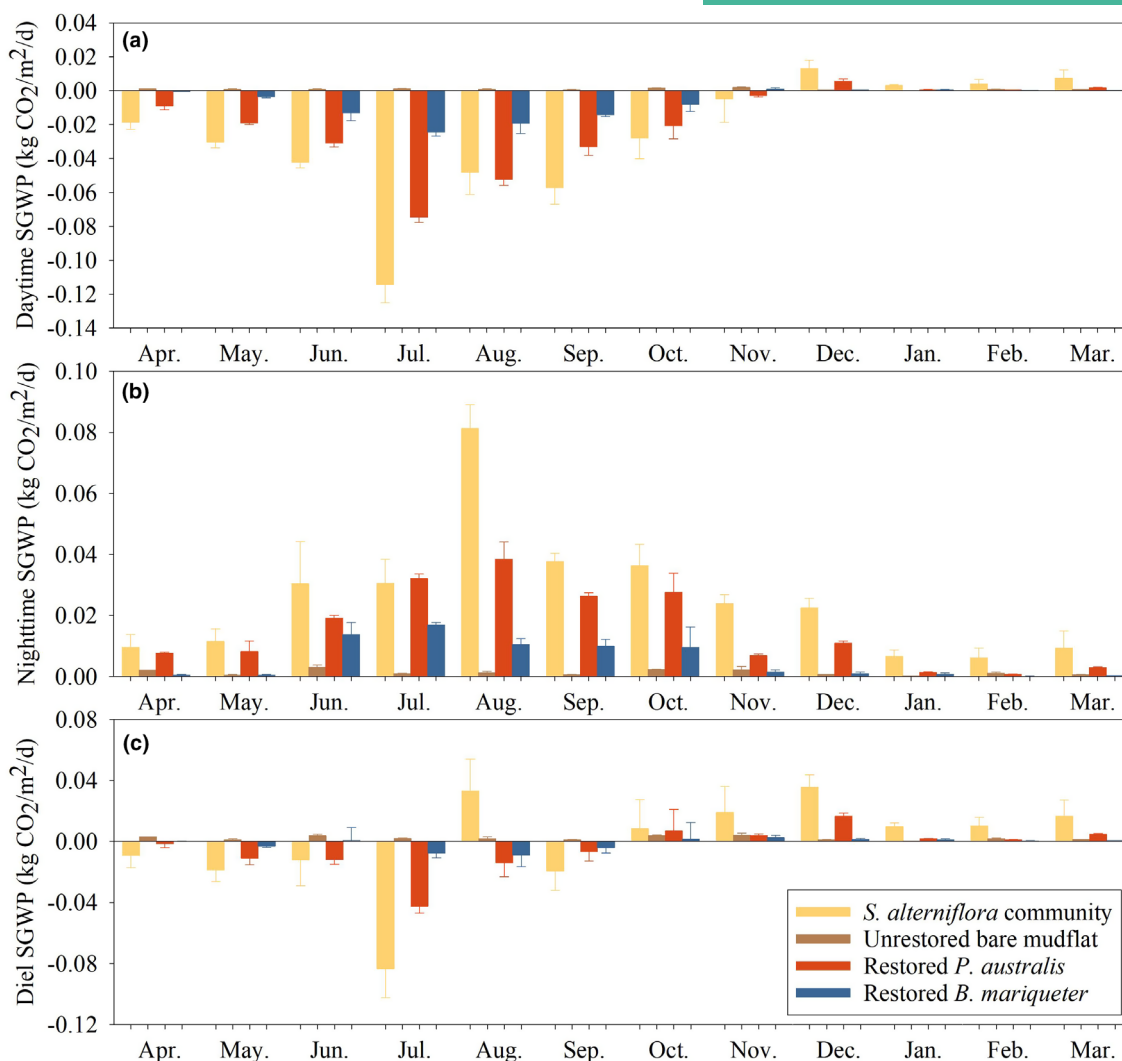


FIGURE 3 The variations of sustained global warming potential SGWP (mean $\pm$ SE) under different restoration scenarios throughout the seasonal cycle.

3.3 | Changes of organic carbon density in vegetation restoration and unrestored wetlands following *S. alterniflora* removal

Our results showed that the *S. alterniflora* community exhibited the highest total organic carbon density (64.36 Mg Cha⁻¹). In contrast, unrestored bare mudflat initially showed a decline in carbon density (31.57 Mg Cha⁻¹) following *S. alterniflora* removal, but subsequently showed recovery after native vegetation restoration (Figure 5). For restored native saltmarshes (*P. australis* and *B. maritima*), the values were estimated as 53.44 Mg Cha⁻¹ and 45.52 Mg Cha⁻¹, respectively, which were higher than unrestored bare mudflat but lower than the *S. alterniflora* community (Table 1).

Unrestored bare mudflat experienced a substantial 35.39% reduction in SOC density and almost an entire loss in VOC density following *S. alterniflora* removal (Figure 4). While in restored native saltmarshes (*P. australis* and *B. maritima*), SOC density at 50 cm depth notably increased by 1.23 times and 1.37 times compared to unrestored bare mudflat and achieved 79.55% and 88.35% that

of *S. alterniflora* community, respectively. Remarkably, restored *P. australis* community exhibited higher VOC density than restored *B. maritima* due to increased biomass ($p < 0.05$, Figure 4), which, respectively, recovered to 94.06% and 15.17% that of *S. alterniflora* community (Table 1).

3.4 | Factors influencing the response of blue carbon capacities to ecological restoration

ABT models revealed that NEE in restored marshes was significantly influenced by plant characteristics (Figure 5a), which enhanced ecosystem net CO₂ uptake with the increase of Chl, NDVI and AGB (Figure 6). While NDVI and AGB were primary predictors of ecosystem CH₄ exchange (Figure 5b). Cumulative CH₄ emissions were positively correlated with NDVI, AGB and T, while negatively correlated with SAL (Figure 6). Moreover, RDA analysis revealed that organic carbon density was significantly affected by AGB, SWC and bulk density, contributing up to 92.60% of the total explanatory rate (Figure 7).

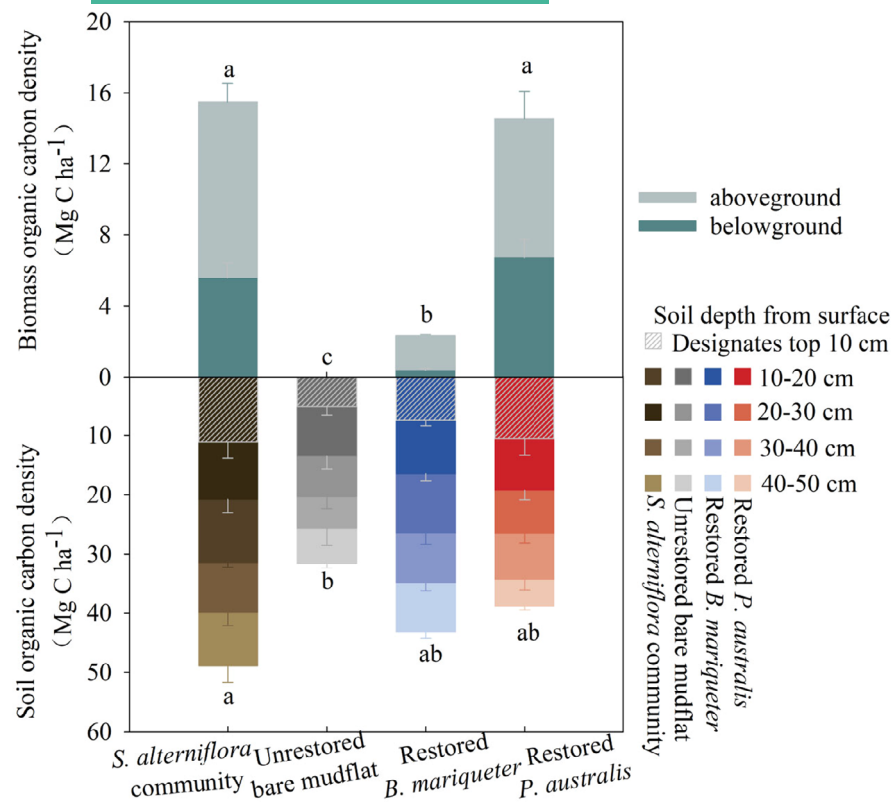
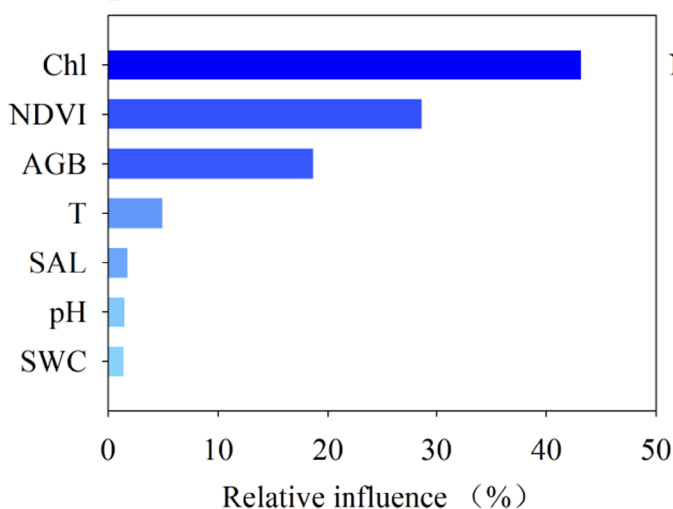


FIGURE 4 Mean organic carbon density to a depth of 50 cm in response to native saltmarsh restoration following *S. alterniflora* removal. Different lowercase letters indicate significant differences among different restorations within the same carbon density at $p < 0.05$. Vertical bars denote standard errors of mean values ($n = 9$).

(a) CO₂ fluxes



(b) CH₄ fluxes

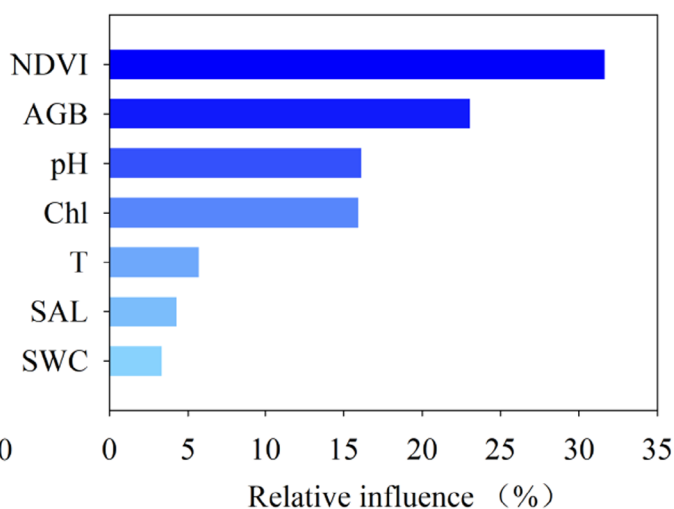


FIGURE 5 Aggregated boosted tree (ABT) analysis of relative influence of edaphic variables and plant biological traits on ecosystem CO₂ (a) and CH₄ (b) fluxes in above-mentioned restoration wetlands following *S. alterniflora* elimination. AGB, above-ground biomass; Chl, leaf chlorophyll concentration; NDVI, normalized difference vegetation index; SAL, salinity; SWC, soil water content; T, temperature.

4 | DISCUSSION

4.1 | Native saltmarshes restoration can maximize CO₂ uptake and reduce CH₄ emissions following *S. alterniflora* removal

Integrated management of invasive *S. alterniflora* control, ecosystem restoration and carbon sequestration enhancement presents a

significant challenge for global coastal zone management. In practice, the choice of restoration strategy will be coupled with other significant socio-ecological gains and may be directed by other objectives than solely achieving carbon benefits, such as enhancing biodiversity and/or protecting native species (Qi & Chmura, 2023). Biological invasion has been shown to cause a series of serious damages to native ecosystems (Ning et al., 2021). As a consequence, attitudes and actions toward *S. alterniflora* tend to favour controlling or even

FIGURE 6 Spearman correlation coefficients between edaphic variables and plant biological traits and ecosystem carbon fluxes change in above-mentioned restoration wetlands following *S. alterniflora* elimination. The figure shows a correlation plot, with the upper diagonal indicating the correlation ellipses, with colours as shown in the figure legend. The lower half shows the Spearman correlation coefficient values with the same colour legend. Significance levels are represented as follows: ** $p < 0.01$; * $p < 0.05$. AGB, above-ground biomass; Chl, leaf chlorophyll concentration; NDVI, normalized difference vegetation index; SAL, salinity; SWC, soil water content; T, temperature.

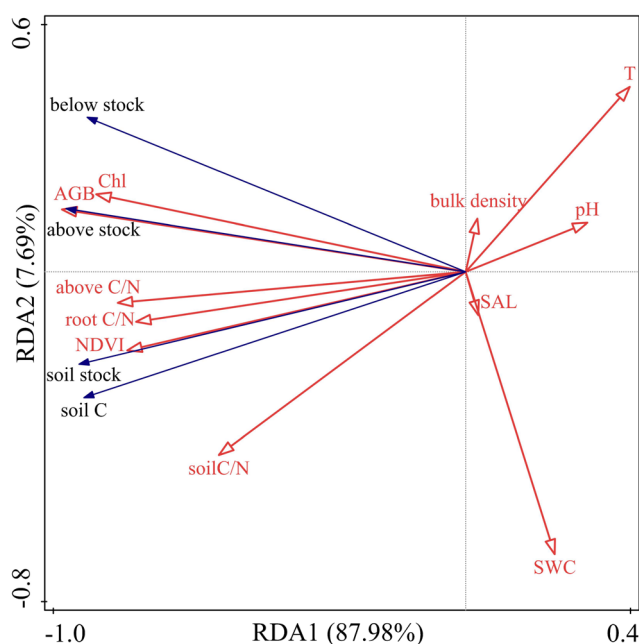
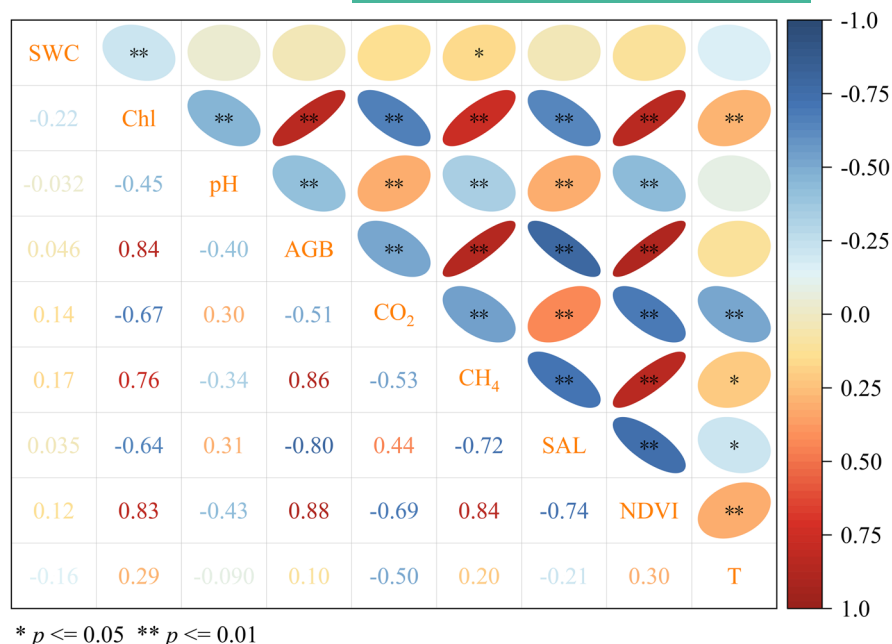


FIGURE 7 Redundancy analysis (RDA) of organic carbon stocks and physicochemical properties at 0–10 cm soil depth in response to native saltmarshes restoration following *S. alterniflora* removal. AGB, above-ground biomass; Chl, leaf chlorophyll concentration; NDVI, normalized difference vegetation index; SAL, salinity; SWC, soil water content; T, temperature.

complete eradication (Zhao et al., 2023), which could in turn potentially risk the saltmarsh' carbon absorption ability. Meta-analyses indicated that restored wetlands could reach a level comparable to natural wetlands approximately 5–25 years following restoration (Liu, Fagherazzi, et al., 2024). Our research examined the carbon balance in the sixth year following restoration. We found that native saltmarshes restoration not only significantly displayed annual CO₂

uptake compared to unrestored bare mudflat, but also provided additional effects by weakening high CH₄ emissions caused by invasions, which would be an additional benefit to their contribution to bird habitat and biodiversity.

The change in vegetation types shifted carbon flux dynamics in coastal wetlands through distinct physiological and phenological controls (Guo et al., 2025). Our results indicated that Chl concentration and vegetation coverage were the primary factors influencing ecosystem CO₂ fluxes through photosynthetic capacity, while vegetation coverage and biomass mainly regulated CH₄ emissions through plant-mediated CH₄ transport (Figures 5 and 6; Table S1). This suggests that vegetation characteristics can buffer the sensitivity of ecosystem-scale carbon flux dynamics to soil factor variability during plant community succession. Invasive *S. alterniflora* has several advantageous ecophysiological traits, such as a longer growing season, higher net photosynthetic efficiency and greater specific leaf area index compared to native saltmarshes (Bernik et al., 2016). These traits enhance photosynthetic carbon uptake, outweigh respiratory carbon release and ultimately dominate carbon dynamics (Table 1). In contrast, unrestored bare mudflat functioned as a weak carbon source, with CO₂ exchange primarily driven by soil respiration. Restoration of native saltmarshes following *S. alterniflora* removal significantly altered carbon flux patterns by modifying plant physiological traits that regulate CO₂ and CH₄ exchange (Table S1). Consequently, selecting native species with higher photosynthetic capacity and larger canopy structures could substantially enhance ecosystem-level CO₂ uptake during saltmarsh restoration. Our results showed that restored *P. australis* had 2.18 times greater CO₂ uptake than restored *B. maritima*, largely due to its superior photosynthetic capacity at a broader canopy scale (Figure 2; Table S1). Moreover, the sources of CH₄ production substrates and the efficiency of this pathway can vary between species (Vázquez-Lule & Vargas, 2021). In bare tidal flats,

CH₄ was mainly produced by obligate acetotrophic methanogens (Xiang et al., 2015), which suppressed CH₄ formation with increased sulphate input and lack of plant conduction from deeper soil to the atmosphere. While in *S. alterniflora* marshes, despite sulphate-accumulation-suppressed CH₄ production, facultative methanogens may circumvent competition by utilizing non-competitive substrates (i.e., trimethylamine) (Yuan et al., 2015), which still stimulated more CH₄ emissions (Figure 2c,d). Compared to *S. alterniflora*, native saltmarshes produce CH₄ through competitive substrate utilization, which is usually inhibited by sulphates in coastal wetlands.

4.2 | Native saltmarsh restoration provides a substantial pathway for climate warming mitigation

Meanwhile, our study highlighted the importance of comprehensive greenhouse gas (CO₂ and CH₄) emissions accounting in evaluating the climate benefits of wetland restoration. Although CH₄ emissions were relatively lower compared to the magnitude of net CO₂ uptake, CH₄ has higher global warming potentials than CO₂ over a 100-year timescale (Zhang et al., 2023). Excessive CH₄ emissions may partially offset the initial cooling effects through CO₂ uptake in wetland ecosystems, a pattern observed consistently in both coastal saltmarsh and mangrove ecosystems (Peng et al., 2021; Rosentreter et al., 2018). In this study, the SGWP₋₁₀₀ revealed that while CH₄ emissions from invasive *S. alterniflora* greatly offset the cooling effect of CO₂ uptake, the ecosystem still maintains a net potential cooling effect (Table 1). However, unmanaged eradication without subsequent restoration not only leads to the loss of coastal carbon sinks but also contributes to a potential warming effect, thereby exacerbating global warming. In contrast, restored native saltmarshes showed significant radiative cooling, indicating their value for long-term climate mitigation benefits.

These findings emphasize that subsequent native vegetation recovery following *S. alterniflora* removal is essential for maintaining coastal wetlands as effective carbon sinks and achieving meaningful climate mitigation. Strategically optimized wetland restoration that enhances climate-regulating negative feedback could make meaningful contributions to achieving the Paris Agreement's temperature targets.

4.3 | Response of organic carbon storage to *S. alterniflora* eradication and native vegetation restoration

Plant invaders generally increase blue carbon storage by intensifying biomass, elevating deposits and monopolizing mudflats into carbon-rich vegetated habitats (Zhou et al., 2023). The removal of *S. alterniflora* not only reduced photosynthetic carbon input but also exposed previously sequestered soil carbon to oxidative conditions, which may potentially accelerate microbial remineralization

and carbon loss (Zhu et al., 2024). This mechanistic understanding explains the observed lower SOC accumulation in unrestored bare mudflat with limited plant-derived organic matter input and external sediment interception (Figure 4). The results in this study showed distinct changes in SOC dynamics following *S. alterniflora* removal. Unrestored bare mudflat exhibited significant SOC decline (~56% reduction in 0–10 cm layer) 6 years post-removal. In contrast, sites restored with native vegetation (*B. maritima* or *P. australis*) showed significant SOC recovery (0.44–1.05 times increase in topsoil carbon stocks), underscoring the critical importance of immediate revegetation. Beyond simply increasing plant biomass carbon and litter production (Luo et al., 2017), these restored ecosystems facilitate: (i) enhanced trapping of particulate organic matter, (ii) improved sediment deposition and (iii) the development of biogeomorphic feedbacks that collectively regulate carbon cycling processes (Temming et al., 2022). These common interactions among vegetation, soil physicochemical properties and microtopography with native marshes restoration regulate long-term carbon sequestration.

We also found that two native species exhibited fundamentally different carbon storage strategies. *B. maritima*, as a pioneer species, has low-growing morphology (height: 30–90 cm) and fragile stem structure that promotes rapid incorporation of plant residue into surface soils. Combined with frequent tidal inundation, these characteristics create persistent anaerobic conditions that strongly suppress microbial mineralization (Table S1), resulting in exceptional carbon preservation efficiency. On the other hand, *P. australis* produced greater plant biomass (1.49–2.01 kg m⁻²). Its standing dead culms during dormancy (November to March) limit direct plant residue carbon input. Furthermore, reduced inundation frequency and higher canopy elevation in its habitat create more oxidized soil conditions that enhance decomposition rates (Guo et al., 2025). These results suggest two key management strategies for optimizing carbon storage in coastal wetland restoration: (i) targeted selection of vegetation species based on their carbon sequestration potential and (ii) implementation of microtopographic engineering to enhance soil carbon preservation. Such integrated approaches could significantly improve the carbon storage function of restored wetlands.

The restoration strategy of native plant replacement following invasive species removal proved particularly effective for carbon storage rehabilitation, achieving 71%–83% of the carbon storage observed in *S. alterniflora* marshes within 6 years. While native species exhibited lower carbon sequestration ability than *S. alterniflora*, their rapid establishment and complementary carbon preservation mechanisms effectively compensated for this difference.

4.4 | Implications for balancing blue carbon benefits with native ecosystems protection

Coastal zone management following *S. alterniflora* removal presents a critical global challenge: balancing invasive species management

with blue carbon conservation. Our study provides the comprehensive quantification of carbon sequestration trade-offs when replacing high-carbon invasive *S. alterniflora* with native vegetation. Through mechanistic analysis, we demonstrate that native plant restoration can effectively: (i) restore >70% of the carbon stocks observed in invasive *S. alterniflora* marshes within 6 years, (ii) enhance long-term carbon storage through optimized species composition (e.g., selecting plant species with high biomass and primary productivity) and (iii) reduce CH₄ emissions by >60% compared to invaded ecosystems. These findings establish native plant restoration as a viable nature-based solution for maintaining coastal carbon sinks while restoring ecological integrity.

The restoration framework developed in this study has broad applicability to coastal wetlands worldwide facing similar challenges in invasive species management and blue carbon conservation. Notably, quite a range of mangrove ecosystems is also increasingly threatened by *S. alterniflora* encroachment. While mature mangroves possess greater biomass (standing stock: 78.8–211.4 MgCha⁻¹) (Liu, Chen, et al., 2024) than invasive *S. alterniflora* (14.4–16.5 MgCha⁻¹), mangroves only grow in tropical and subtropical coastal zones due to temperature limitations. Saltmarshes are widely distributed, but it is challenging to completely compensate for the carbon loss caused by the removal of *S. alterniflora* solely by restoring the same area of saltmarshes. Based on our results (Table 1), an additional 1.9 ha of restored *P. australis* or 6.2 ha of restored *B. maritima* would be required to match the pre-clearance atmospheric carbon sink of *S. alterniflora* per hectare. To address these challenges, we propose a three-pronged approach: (i) mixed or integrative approaches, such as combining native revegetation with invasive plant biomass conversion, implementing phased restoration to maintain continuous carbon uptake and developing species mixtures that optimise carbon-biodiversity trade-offs; (ii) multi-objective management framework includes biodiversity conservation, carbon sequestration enhancement and coastal resilience and (iii) integrated policy includes developing invasive species-carbon accounting protocols, establishing transnational blue carbon credit mechanisms and creating adaptive management guidelines for different ecoregions. By bridging science and policy, this integration would facilitate transnational collaboration and advance the practical application of nature-based solutions (NbS) for coastal sustainability and climate mitigation.

5 | CONCLUSIONS

In conclusion, this study revealed that while *S. alterniflora* invasion enhances short-term carbon sequestration, its replacement with native vegetation presents a sustainable pathway for coastal ecosystem management by achieving multiple ecological objectives. Through comprehensive comparison, native saltmarsh restoration following invasive species removal can recover over 70% of initial carbon stocks within 6 years while simultaneously restoring critical ecosystem functions, for example, providing habitat and coastal protection. The restored native communities not only reestablish atmospheric carbon sinks (2.18–6.98 MgCha⁻¹ annual carbon uptake) but also provide significant

climate mitigation benefits through combined CO₂ uptake and substantial CH₄ emission reductions (65%–88% lower than invaded stands). To address the residual carbon deficit, we emphasize the necessity of implementing scaled restoration efforts using spatial compensation approaches (1.9–6.2 times the area ratio, depending on the species) complemented by innovative biomass conversion strategies. These findings demonstrated coastal saltmarsh restoration as a nature-based solution that strategically integrates carbon sequestration targets with biodiversity conservation and climate resilience imperatives. These integrated restoration approaches should be prioritized and advocated in global blue carbon initiatives and climate policy frameworks, as they represent a scientifically grounded, ecologically balanced strategy for addressing the interconnected challenges of climate change mitigation and ecosystem degradation in coastal zones worldwide.

AUTHOR CONTRIBUTIONS

Lin Yuan, Dong Wang, Hualei Yang and Fabio A. Labra conceived the ideas and designed methodology; Dong Wang and Hualei Yang collected the data; Dong Wang and Yuekai Hu analysed the data; Dong Wang, Lin Yuan, Hualei Yang, Fabio A. Labra, Zhiyuan Zhao and Wenzong Zhou led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Data available via Zenodo. Research data Repository. <https://doi.org/10.5281/zenodo.13956795> (Wang et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Edaphic variables and plant characteristics under different restoration scenarios in invaded wetlands following *Spartina alterniflora* removal.

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