



RESEARCH ARTICLE

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Plant community, geomorphology, and macrobenthos as drivers of spatial variations in soil carbon and nitrogen in a coastal shoal

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Abstract

Coastal salt marsh wetlands are crucial reservoirs of soil carbon (C) and nitrogen (N). However, the effects of plant type, geomorphology, and macrobenthos on spatial variations in soil C and N in coastal wetlands remain unclear. In this study, the spatial distribution of soil C and N components was investigated in a coastal wetland (Jiuduansha Shoal) in the Yangtze Estuary, and plant type distribution, plant biomass, soil properties, and macrobenthos species and biomass along the geomorphological gradient were measured. The results showed that the amounts and stocks of soil total C, soil organic C, soil total N, and soil microbial biomass C and N at the *Spartina alterniflora* (SA) and *Phragmites australis* (PA) sites were significantly higher than those at the bare mudflat (BM) sites. The soil and microorganism C and N variables showed a remarkable increasing trend from low- to high-elevation sites. The abundance of macrobenthos at the *Scirpus mariqueter* site was the highest among the plant communities and was significantly higher than that at the *Zizania latifolia* (ZL) and BM sites. The air-free dry weight (AFDW) of macrobenthos in the PA community was the highest among the communities. The variability in soil C and N was mainly sensitive to plant biomass, soil water content, bulk density, macrobenthos AFDW, particle size, electrical conductivity, and nutrient levels. We suggest that the synergetic effects of biotic and abiotic factors in the intertidal environment need to be fully considered in assessing and managing the C and N pools of coastal salt marshes in East China.

Keywords Coastal wetlands, Blue carbon, Spatial heterogeneity, Marsh plants, Macrobenthos

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1 Introduction

Coastal wetlands are recognized as “Blue Carbon” ecosystems owing to the strong accumulation rate of carbon (C) and nitrogen (N) through biological and sedimentary pathways (Bernal et al. 2012, Lovelock et al. 2019). In the ecosystems, soil organic C (SOC) pool plays a pivotal role in global C cycling (Olefeldt et al. 2016), because a minor change in SOC pool could provoke dramatical fluctuations in the C exchange between atmosphere and land (Davidson et al. 2006). SOC mainly consists of labile and stable fractions, and the labile components of easily oxidizable carbon and microbial biomass carbon (SMBC) are considered early indicators of SOC variation (Zhang et al. 2007).

The predominant factors influencing wetland soil C and N dynamics include climatic conditions, plant biological traits, and soil properties (Luo et al. 2017). Interactions between temperature and rainfall directly affect plant CO₂ assimilation and soil microbial activity, which further affect soil C and N stocks (Carvalhais et al. 2014). Wetland plants play key roles in organic matter input and N uptake (Pennings et al. 2001). Therefore, different vegetation types significantly influence soil C and N dynamics by altering soil biogeochemical processes in wetlands (Meng et al. 2020), typically under anaerobic conditions (Wang et al. 2019).

Coastal wetlands are regularly flooded by tidal water, and plant communities are arranged in topographic zonation patterns (Moffett et al. 2012). Tidal flooding and flat elevations have been identified as the primary factors that determine plant survival and community development. Wetland plants can assimilate N directly from soil, groundwater, and N-fixing microorganisms, which probably influence the soil N content and distribution (Vineis 2022). Additionally, variations in edaphic properties along the topographic gradient regulate soil C and N contents and its allocation in the inorganic particles and microbes (Luo et al. 2021).

Macrobenthos in the coastal wetlands are the key animal groups regulating the soil profile and features. Macrobenthos are one of the main decomposers in tidal wetland ecosystems, influencing soil C and N processes (Danovaro et al. 2002). The bioturbation activity of macrobenthos can enhance material exchange between sediments and the overlying tidal water (Bang et al. 2019, Guimond et al. 2020), exerting a significant influence on ecosystem biogeochemical processes (Chen et al. 2021).

Although the interaction between vegetation, edaphic and hydrological conditions, and benthic animals might regulate wetland biogeochemical processes (Zhang et al. 2002, Yang 2019), previous studies have only focused on a single independent factor influencing soil C and N dynamics (Meng et al. 2019, Tangen et al. 2020). In the

present study, we investigated the spatial distribution of soil C and N content and stocks as well as the C and N content of microbial biomass in a coastal wetland in the Yangtze Estuary of East China. The field survey area covered the dominant vegetation types and elevation gradients, and macrobenthos communities were investigated. Plant type distribution, plant biomass, soil properties, and macrobenthos species and biomass along the geomorphological gradient were also measured. The main objectives of this study were (1) to discern the synergistic effects of vegetation types, topographical features, and macrobenthos on soil C and N components and (2) to identify the key soil variables in relation to soil C and N contents and stocks. The results of this study will provide useful information to support management plans for wetland C and N pools to enhance the ecological capabilities of coastal wetlands in the Yangtze Estuary.

2 Materials and methods

2.1 Study area

The study area is located in the Jiuduansha Shoal (also the Jiuduansha Shoal National Nature Reserve, 31°03′–31°17′N, 121°46′–122°15′E) in the Yangtze Estuary (Fig. 1). The Jiuduansha Shoal is among the youngest shoals in the Yangtze Estuary and originated in the 1950s as a result of continuous sedimentary accretion owing to sediment transportation with Yangtze River runoff. The Jiuduansha Shoal has a subtropical monsoon climate, with an average temperature of 17.3 °C and an annual precipitation of 1,145 mm (Tang et al. 2011; Hu et al. 2016). Since 2000, the Jiuduansha Shoal has undergone notable evolution owing to revegetation engineering (Cheng et al. 2020). Currently, the highest elevation reaches approximately 4–4.5 m based on the local Wusong datum. Tidal movement in the wetland is characterized by mixed semi-diurnal and semilunar patterns, and the maximum and average tidal ranges were recorded at 4.62 m and 2.67 m, respectively, based on the local Wusong datum (Qiao et al. 2012). The low tidal flats (<~2.5 m) are unvegetated mudflats, the middle tidal flats (~2.5–3.0 m) are dominated by the native pioneering species *Scirpus mariqueter* and *S. triqueter*, and the high tidal flats (>~3.0 m) are dominated by *Phragmites australis*, *Spartina alterniflora*, and *Zizania latifolia* (Huang et al. 2007, Lin et al. 2015). Spatially, the dominant plant species are distributed along gradients corresponding to the elevation of the intertidal wetland.

2.2 Field sampling

In the autumn (September) and winter (December) seasons of 2022, we collected soil, plant, and macrobenthos samples from seven transects (S1–S7) in the intertidal areas. Four sampling points were selected for

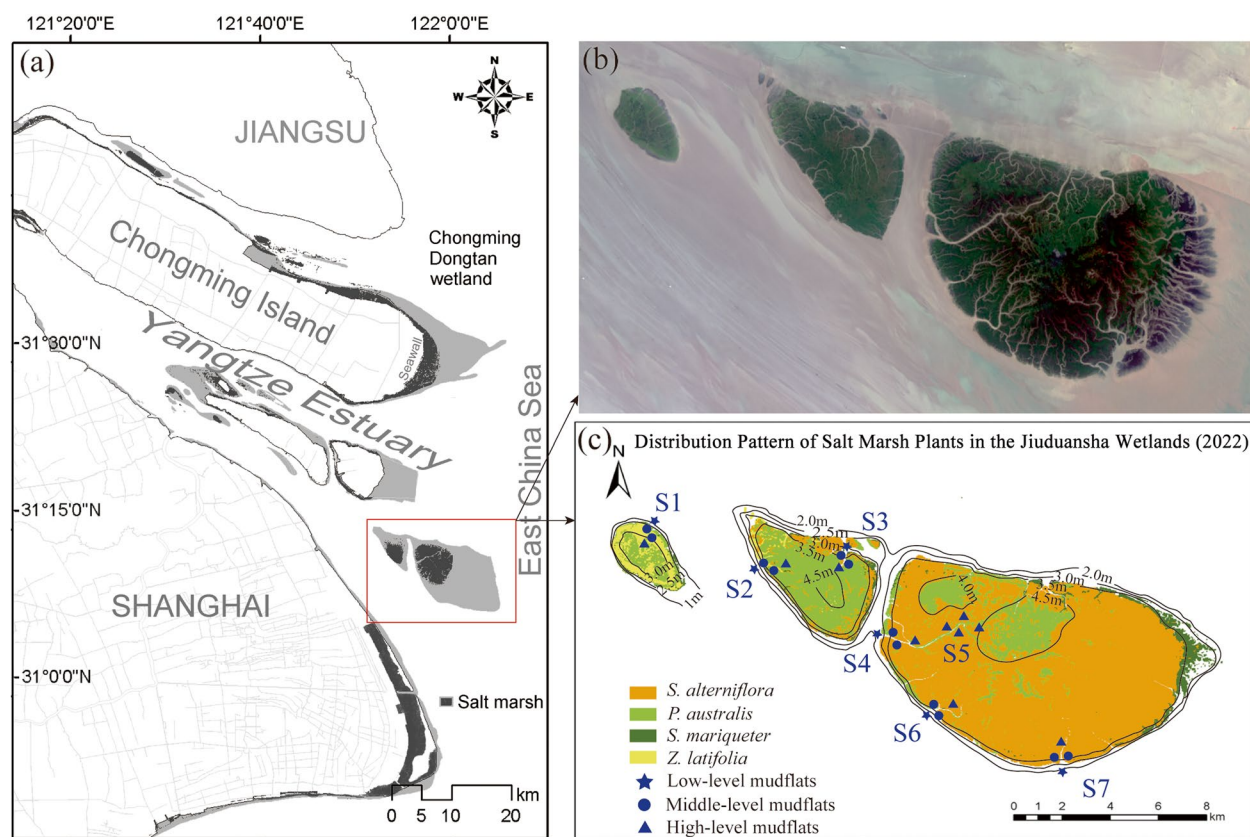


Fig. 1 Location of the Yangtze Estuary (a) and Jiuduansha Shoal (b). S1–S7 (c) indicate the sampling transects in the wetland within vegetation types along the flat elevation

each transect based on various elevation gradients and vegetation types (Fig. 1). Different sampling points were established based on elevation grouping of high-level mudflats (HM), middle-level mudflats (MM), and low-level mudflats (LM) and in the vegetation type groups of the *P. australis* community (PA), *S. alterniflora* community (SA), *Z. latifolia* community (ZL), *S. mariqueter* community (SM), and bare mudflats (BM). Soil and vegetation samples were collected at each point on six replicate quadrat samples (soil bulk: 0.25 m × 0.25 m × 0.30 m; plant: 0.50 m × 0.50 m). Parallel soil bulk samples (0.25 m × 0.25 m × 0.30 m) were collected for investigating the macrobenthos community. After field sampling, the soil and vegetation samples were immediately transported to the laboratory and stored at 4 °C until subsequent analysis.

2.3 Measurement of plant biomass

Aboveground plant organs were harvested from each sampling plot. The plant materials were cleaned and oven-dried at 60 °C until constant weight to obtain aboveground biomass. This is because it is quite difficult to sift out the huge root systems of marsh plants and

accurately determine the belowground plant biomass. We calculated the root biomass of the PA, SA (similar to that of *Z. latifolia*), and SM communities using root:shoot ratios of 69.3%, 60.1%, and 45%, respectively, based on a previous careful investigation of belowground biomass of marsh plants in the Yangtze Estuary (Xie et al. 2020; Li et al. 2022).

2.4 Measurement of macrobenthos

Macrobenthos were collected from the soil bulk samples using 10 mm mesh sieves (Huang et al. 2021). In the laboratory, all the macrobenthos were preserved in 75% ethanol, and then enumerated and identified at the taxonomic level based on the local and national macrobenthos atlases. All macrobenthos samples were incinerated at 600 °C in a muffle furnace to obtain the ash-free dry weight (AFDW).

The abundance and AFDW of macrobenthos were calculated as follows:

$$B = b/S \quad (1)$$

$$D = N/S \quad (2)$$

where, b is the dry weight (g) of the sampled individuals of the species, excluding ash; B is AFDW (g m^{-2}); N is the number of macrobenthic individuals sampled; S is the sampling plot area (m^2); and D is the abundance (ind. m^{-2}).

2.5 Measurement of soil C and N

The soil samples were air-dried and sieved through a 2 mm sieve, and twigs, roots, and stones were removed from the dried sample. Soil total carbon (STC) and soil total nitrogen (STN) (g kg^{-1}) were directly measured using an elemental analyzer (Vario EL III; Elementar, Germany). A portion of the dried samples was subjected to acid washing with 3 mol L^{-1} HCl and shaken for 24 h to centrifugation, and then rinsed with enough water (Gradient; Merck Millipore, Darmstadt, Germany) to remove carbonates. An elemental analyzer (Vario EL III; Elementar, Germany) was used to measure SOC content (g kg^{-1}) (Xue et al. 2020).

Soil C and N stocks (Mg ha^{-1}) were calculated as follows:

$$\text{stock} = \frac{\text{content} \times BD \times H}{100} \times 10 \quad (3)$$

where H is soil thickness (30 cm) and BD is bulk density (g cm^{-3}).

A part of the fresh soil samples was immediately freeze-dried, and then sieved to 0.6 mm and stored at 4 °C. Soil microbial biomass C (SMBC) and N (SMBN) were measured using the chloroform fumigation extraction method (Brookes et al. 1982; Ross 1990). The C and N were extracted with 0.5 mol L^{-1} K_2SO_4 from both fumigated and non-fumigated samples and measured using an elemental analyzer (Elementar Vario EL III CHNOS; Elementar Analysensysteme GmbH). A conversion factor of 0.38 (Lu 2000) was used to convert extractable C (the difference in C between the fumigated and non-fumigated samples) to SMBC. A KEC factor of 0.54 (Wu et al. 2005) was used to convert the extractable N (the difference in N between the fumigated and non-fumigated samples) to SMBN.

2.6 Measurement of soil variables

Sediment water content (SWC) and electrical conductivity (EC) were measured using a soil triparameter instrument (Spectrum 2265FS; USA). Sediment bulk density (BD) was measured using the cutting ring method. The sediment particle size (PS) was analyzed using a Laser Particle Size Analyzer (LS13 320; Beckman Coulter, USA). The pH was measured using the electrode method (soil:water ratio: 2.5:1) (Hernández et al. 2023). Alkaline

hydrolytic nitrogen (AN) was determined using the alkaline hydrolysis diffusion method (Liu et al. 2022). Available phosphorus (AP) and potassium (AK) were measured using a soil fertilizer nutrient quick measuring instrument (HM-TYB; Hengmei Electronic Technology Co., Ltd., China). This assessment followed the neutrality or calcareous soil universal extract-colorimetric method outlined in NY/T 1848–2010 (Guo et al. 2022). Total phosphorus (TP) was measured using NaOH melting molybdenum–antimony antichromogenic UV spectrophotometry (Wang et al. 2010).

2.7 Data analysis

The measurement data were calculated as the mean of the replicates with standard errors ($\text{mean} \pm \text{S.E.}$). One-way analysis of variance (ANOVA) and least significant difference were used to assess the differences in soil C and N amounts and stocks, plant biomass, macrobenthos abundance and biomass, and soil physicochemical properties among the various elevations and vegetation types. Pearson correlation and redundancy (RDA) analyses were used to test the relationship between soil C and N variables (SOC, STC, STN, SMBC, and SMBN) and environmental factors. The ANOVA analysis was performed using SPSS 25.0 (SPSS Inc.). The RDA was performed using CANOCO 5.0 (Microsoft, USA).

3 Results

3.1 Spatial patterns of C and N

The STC, SOC, and STN contents and stocks at the SA sites were significantly higher than those at the BM sites ($p < 0.05$), whereas the differences among the vegetated sites were not significant (Fig. 2a–c). The highest levels of SOC ($5.03 \pm 0.25 \text{ g kg}^{-1}$) and STC ($14.00 \pm 0.15 \text{ g kg}^{-1}$) and the consequent C and N stocks ($18.23 \pm 0.90 \text{ Mg ha}^{-1}$ and $50.27 \pm 0.87 \text{ Mg ha}^{-1}$ for SOC and STC, respectively) were observed at the SA sites. The highest STN content ($0.58 \pm 0.021 \text{ g kg}^{-1}$) and stock ($2.13 \pm 0.075 \text{ Mg ha}^{-1}$) were observed at the PA sites. The SMBC and SMBN amounts at the vegetated sites were on average higher by 23.64% and 37.03%, respectively, than those at the BM sites, with the SA sites having a significantly high value.

All soil and microorganism C and N variables showed a remarkably increasing trend from the LM sites to the HM sites. At the HM sites, the soil and microorganism C variables were on average 1.12 and 1.28 times higher, respectively, than those at the MM and LM sites ($p < 0.05$, Fig. 2d–f). At the HM sites, the soil and microorganism N variables were on average 1.31 and 1.48 times higher, respectively, than those at the MM and LM sites ($p < 0.05$, Fig. 2d–f).

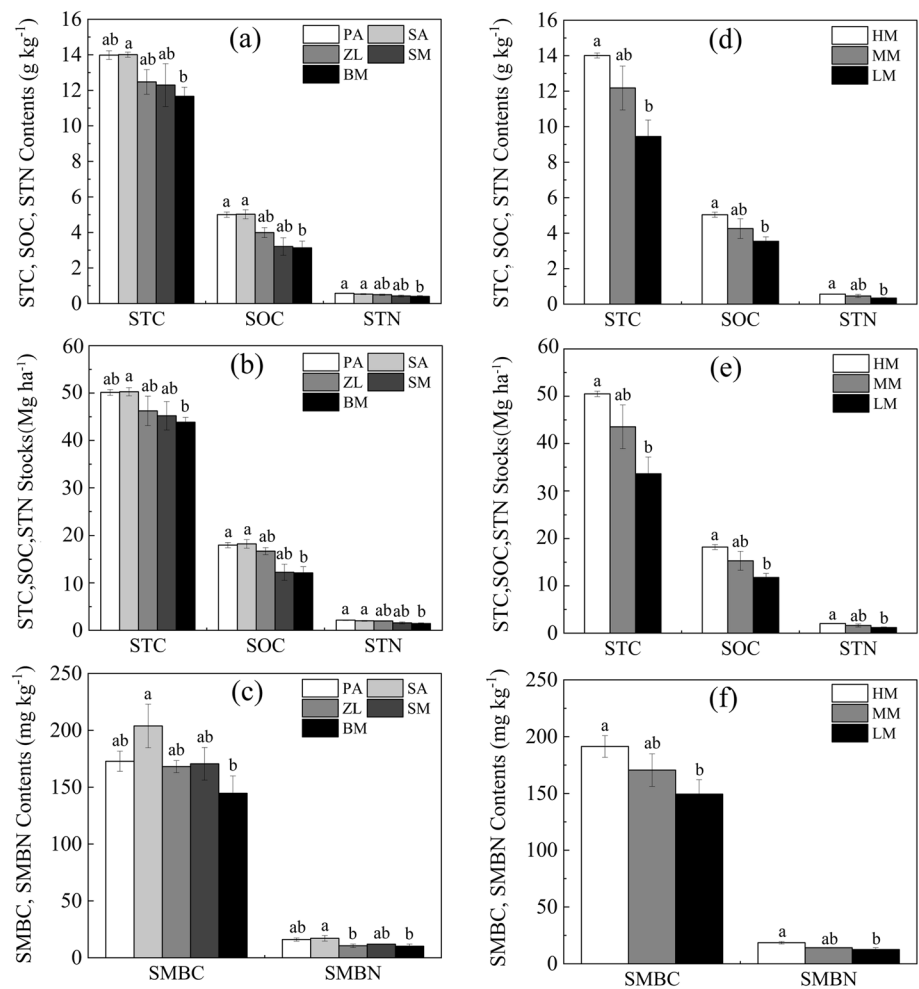


Fig. 2 Spatial variations in STC, SOC, and STN contents and stocks, as well as SMBC and SMBN amounts at different elevations (a, b, c) and vegetation zones (e, d, f) in the Jiuduansha Shoal. Different letters indicate significant differences at the $p < 0.05$ level among sampling sites. PA, *Phragmites australis*; SA, *Spartina alterniflora*; SM, *Scirpus mariqueter*; ZL, *Zizania latifolia*; BM, bare mudflats; HM, high-level mudflats; MM, middle-level mudflats; LM, low-level mudflats

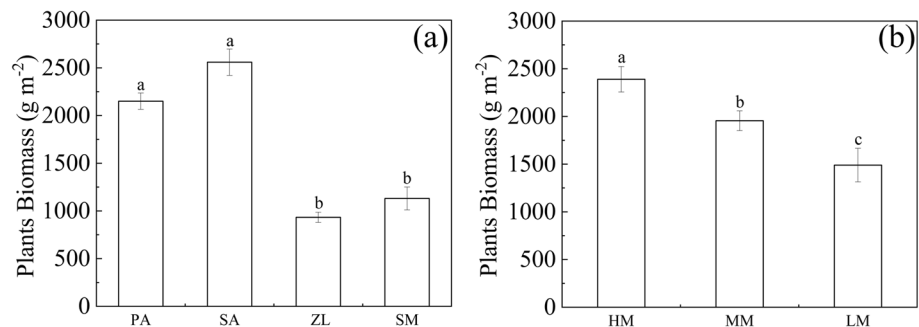


Fig. 3 Differences in plants biomass (PB) at different vegetation zones (a) and elevations (b) in the Jiuduansha Shoal. Vertical bars denote the standard error of the mean and different lowercase letters above the bars indicate significant differences at the $p < 0.05$ level among sampling sites. PA, *Phragmites australis*; SA, *Spartina alterniflora*; SM, *Scirpus mariqueter*; ZL, *Zizania latifolia*; BM, bare mudflats; HM, high-level mudflats; MM, middle-level mudflats; LM, low-level mudflats

3.2 Vegetation biomass

As shown in Fig. 3a, the plant biomasses at the SA and PA sites (Poaceae species) were significantly higher than that at the SM sites (Cyperaceae species). The highest and lowest plant biomass values were found at the SA ($2558.97 \pm 137.58 \text{ g m}^{-2}$) and ZL ($933.12 \pm 53.58 \text{ g m}^{-2}$) communities. The plant biomass at the SA sites was on average 2.26 and 2.74 times higher than that at the SM and ZL sites, respectively. The plant biomass at the PA sites was on average 1.90 and 2.30 times higher than that at the SM and ZL sites, respectively.

Plant biomass showed a notable increasing trend with increasing elevation. At the HM sites, the plant biomass was on average 1.22 and 1.60 times higher than that at the MM and LM sites, respectively ($p < 0.05$, Fig. 3b).

3.3 Macrobenthos community

3.3.1 Spatial distribution of macrobenthos

Thirty-two macrobenthos species from seven classes were identified at the survey sites, including Anolpa, Polychaeta, Gastropoda, Bivalvia, Malacostraca, Osteichthyes, and Insecta. The predominant classes in the Jiuduansha Shoal were Gastropoda and Malacostraca (Table 3 in Appendix). The abundance of macrobenthos at the SM sites ($358.24 \pm 17.54 \text{ ind m}^{-2}$) was the highest among the communities (Fig. 4a), and significantly higher than

that at the ZL and BM sites ($p < 0.05$). The macrobenthos abundance at the BM sites ($205.03 \pm 16.20 \text{ ind m}^{-2}$) was lower by 30.73% on average than that at the PA, SA, and ZL sites.

As shown in Fig. 4b and Table 3 in Appendix, six macrobenthos classes were collected from the PA communities, with *Ellobium chinense*, *Assimineea* sp., and *Assimineea latericea* accounting for the highest percentage (32%). Six classes were recorded in the SA communities, with *Assimineea* sp., *A. latericea*, *Assimineea violacea*, *Glauconome chinensis*, and *Ilyoplax deschampsii* accounting for the highest percentage (29%). Four classes were present in the SM communities, with *Assimineea* sp., *A. latericea*, and *Onchidium reevesii* accounting for the highest percentage (44%). Four classes were collected in the ZL communities, with *Assimineea* sp., *A. latericea*, *A. violacea*, and *Cerithidea sinensis* accounting for the highest percentage (38%). Four classes were recorded in the BM communities, with *Assimineea* sp., *A. latericea*, and *G. chinensis* accounting for the highest percentage (45%).

The abundance of macrobenthos at the HM sites ($318.53 \pm 44.77 \text{ ind m}^{-2}$) was the highest among the elevation levels and was significantly higher than that at the LM sites ($p < 0.05$, Fig. 4c and d). As listed in Table 3 in Appendix, seven macrobenthos classes were present at the HM sites, with *Ellobium chinense* and *Assimineea* sp.

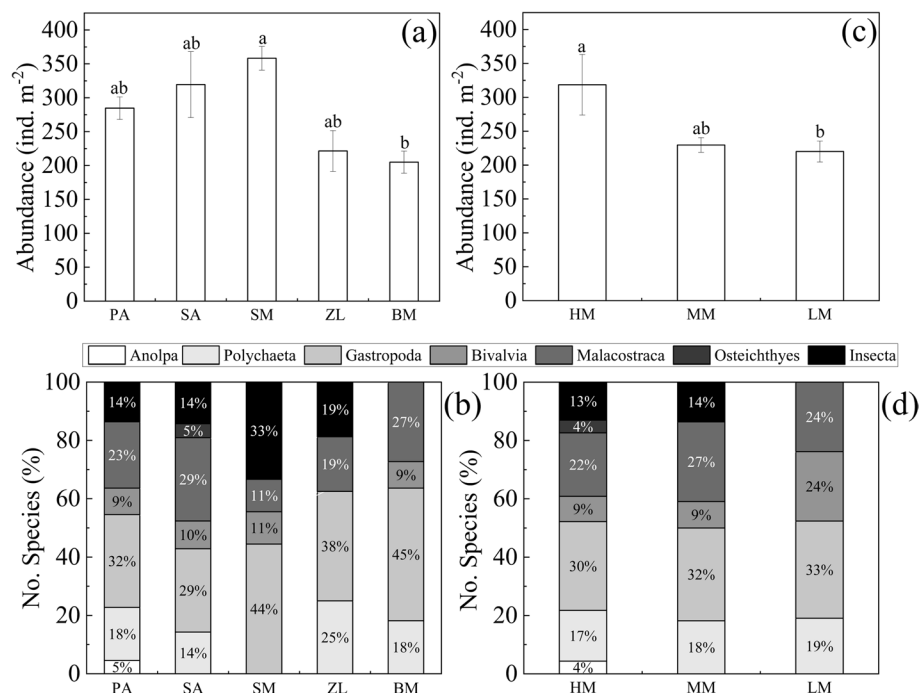


Fig. 4 Differences in abundance (a, c) and species composition (b, d) at different elevations and vegetation zones in the Jiuduansha Shoal. Vertical bars denote the standard error of the mean and different lowercase letters above the bars indicate significant differences at the $p < 0.05$ level among sampling sites. PA, *Phragmites australis*; SA, *Spartina alterniflora*; SM, *Scirpus mariqueter*; ZL, *Zizania latifolia*; BM, bare mudflats; HM, high-level mudflats; MM, middle-level mudflats; LM, low-level mudflats

accounting for the highest percentage (30%). Five classes were recorded at the MM sites, with *Assimineea* sp., *A. latericea*, and *O. reevesii* accounting for the highest percentage (32%). Four classes were present at the LM sites, with *Stenothyra glabra* and *Assimineea* sp. accounting for the highest percentage (33%).

3.3.2 Macrobenthos biomass

The AFDW of macrobenthos in the PA community ($26.23 \pm 3.44 \text{ g m}^{-2}$) was the highest among all communities, with Malacostraca being the largest contributor. The variance analysis indicated that the AFDW in the PA community was significantly higher than that in the BM sites ($p < 0.05$), whereas the AFDW of the SA, ZL, and SM communities was not significantly different ($p > 0.05$) (Fig. 5a). The AFDW in BM sites ($10.32 \pm 1.70 \text{ g m}^{-2}$) was lower than that in the SA, ZL, and SM zones (22.80 ± 3.12 , 17.74 ± 4.69 , and $20.24 \pm 3.01 \text{ g m}^{-2}$, respectively). In SA, SM, ZL, and BM, Polychaeta was the largest contributor across communities (Fig. 5b).

The AFDW of macrobenthos in the HM sites ($23.86 \pm 3.54 \text{ g m}^{-2}$) was the highest among all elevations; Malacostraca (*Chironomus neglectum* and *Orisarma neglectum*) was the largest contributor to the total biomass across all HM sites (Fig. 5c and d, Table 3

in Appendix). The AFDW of macrobenthos in the LM sites ($12.38 \pm 2.76 \text{ g m}^{-2}$) was the lowest among elevations, with Malacostraca (*Philyra pisum* and *O. neglectum*) being the largest contributor to the total biomass across all LM sites (Fig. 5c and d, Table 3 in Appendix). The results indicated that AFDW at the HM sites was significantly higher than that in the LM sites ($p < 0.05$). The AFDW of macrobenthos in the MM sites ($18.08 \pm 2.02 \text{ g m}^{-2}$) was not significantly different from that of the other elevations ($p > 0.05$), Malacostraca (*O. neglectum*, *Orisarma sinense*, and *Helice tientsinensis*) was the largest contributor to the total biomass across all MM sites (Fig. 5c and d, Table 3 in Appendix).

3.4 Soil variables

The soil physical and chemical variables of the different vegetation types are listed in Table 1. Sediment BD at the PA sites was significantly lower than that at the other vegetation zones ($p < 0.05$). The EC at the SA sites were significantly lower than that at the PA sites ($p < 0.05$). The PS and AK values at the ZL sites were significantly lower than those in the other vegetation zones ($p < 0.05$). At the SA sites, AP was significantly higher than that in the other vegetation zones ($p < 0.05$). However, significant

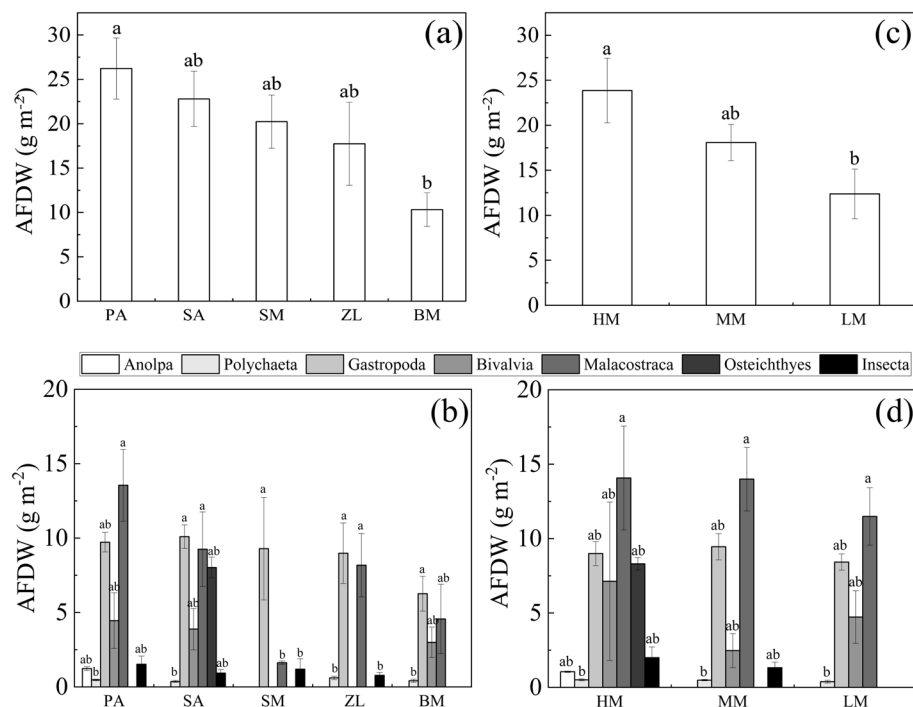


Fig. 5 Differences of macrobenthos AFDW (a, c) and species of macrobenthos AFDW (b, d) abundance. Changes in macrobenthos AFDW (c) and different species of macrobenthos AFDW (d) in various elevations of the Jiuduansha Shoal. Different letters indicate significant differences at the $p < 0.05$ level among sampling sites. PA, *Phragmites australis*; SA, *Spartina alterniflora*; SM, *Scirpus mariqueter*; ZL, *Zizania latifolia*; BM, bare mudflats; HM, high-level mudflats; MM, middle-level mudflats; LM, low-level mudflats

Table 1 Characteristics of soil physicochemical variables in the Jiuduansha shoals (mean ± S.E.) within various plant communities. PA was *P. australis*; SA was *S. alterniflora*; SM was *S. maritima*; ZL was *Z. latifolia*

Items	PA	SA	ZL	SM
BD (g cm ⁻³)	1.18 ± 0.008 ^b	1.22 ± 0.009 ^a	1.20 ± 0.024 ^a	1.27 ± 0.013 ^a
SWC (%)	59.28 ± 2.31 ^a	66.05 ± 2.32 ^a	81.43 ± 12.51 ^a	85.20 ± 1.80 ^a
EC (m s ⁻¹)	1682.28 ± 81.93 ^b	2072.80 ± 92.24 ^a	1874.80 ± 82.89 ^{ab}	1495.00 ± 90.00 ^{ab}
pH	7.87 ± 0.029 ^a	7.89 ± 0.025 ^a	7.78 ± 0.04 ^a	7.78 ± 0.025 ^a
PS (μm)	38.71 ± 1.21 ^a	33.06 ± 1.37 ^{ab}	29.44 ± 3.02 ^b	41.01 ± 3.31 ^a
AP (mg kg ⁻¹)	37.67 ± 1.49 ^b	43.66 ± 2.82 ^a	41.75 ± 1.48 ^{ab}	35.92 ± 0.51 ^{ab}
AK (mg kg ⁻¹)	281.39 ± 7.56 ^a	294.48 ± 14.46 ^a	227.76 ± 11.46 ^b	237.44 ± 10.29 ^a
TP (g kg ⁻¹)	0.025 ± 0.00 ^a	0.023 ± 0.00 ^a	0.024 ± 0.00 ^a	0.023 ± 0.00 ^a
AN (mg kg ⁻¹)	25.31 ± 1.36 ^a	24.09 ± 1.71 ^a	29.49 ± 1.03 ^a	16.60 ± 2.61 ^a

BD was soil bulk density, SWC was soil water content, EC was electrical conductivity, PS was particle size, AP was available phosphorus, AK was available potassium, TP was total phosphorus, AN was alkaline hydrolytic nitrogen. Different letters indicate significant differences ($p < 0.05$)

Table 2 Characteristics of soil physicochemical variables in the Jiuduansha shoals (mean ± S.E.) within various elevation levels. HM was high-level mudflats, MM was middle-level mudflats, and LM was low-level mudflats

Items	HM	MM	LM
BD (g cm ⁻³)	1.20 ± 0.01 ^b	1.21 ± 0.02 ^{ab}	1.23 ± 0.01 ^a
SWC (%)	64.08 ± 1.84 ^a	85.74 ± 4.18 ^a	91.02 ± 8.24 ^a
EC (m s ⁻¹)	1846.99 ± 65.10 ^{ab}	1811.50 ± 81.87 ^b	2157.28 ± 77.90 ^a
pH	7.89 ± 0.02 ^a	7.78 ± 0.06 ^a	7.79 ± 0.03 ^a
PS (μm)	35.53 ± 0.93 ^a	31.06 ± 3.11 ^a	34.33 ± 1.12 ^a
AP (mg kg ⁻¹)	40.52 ± 1.54 ^a	39.75 ± 1.58 ^{ab}	32.42 ± 2.12 ^b
AK (mg kg ⁻¹)	277.95 ± 7.92 ^a	252.86 ± 12.94 ^a	267.98 ± 8.49 ^a
TP (g kg ⁻¹)	0.024 ± 0.00023 ^a	0.024 ± 0.00074 ^a	0.025 ± 0.00041 ^a
AN (mg kg ⁻¹)	24.39 ± 1.07 ^{ab}	26.05 ± 3.37 ^a	18.83 ± 1.65 ^b

BD was soil bulk density, SWC was soil water content, EC was electrical conductivity, PS was particle size, AP was available phosphorus, AK was available potassium, TP was total phosphorus, AN was alkaline hydrolytic nitrogen. Different letters indicate significant differences ($p < 0.05$)

differences in SWC, pH, TP, or AN were absent among the vegetation types.

The soil physicochemical variables at different elevations are listed in Table 2. Sediment BD at the LM sites was significantly lower than that at the HM sites ($p < 0.05$). The EC at the LM sites was significantly lower than that at the MM sites ($p < 0.05$). At the HM sites, AP was significantly lower than that at the LM sites ($p < 0.05$) and at the MM sites, AN was significantly lower than that at the LM sites ($p < 0.05$). However, SWC, pH, PS, AK, and TP showed no significant differences between the elevation levels.

3.5 Main factors affecting soil C and N

Results of the Pearson correlation analysis (Fig. 6a) showed that SOC content and stock were significantly and positively correlated with PB, AFDW, SWC, AK, and AN and negatively correlated with BD, PS, and EC

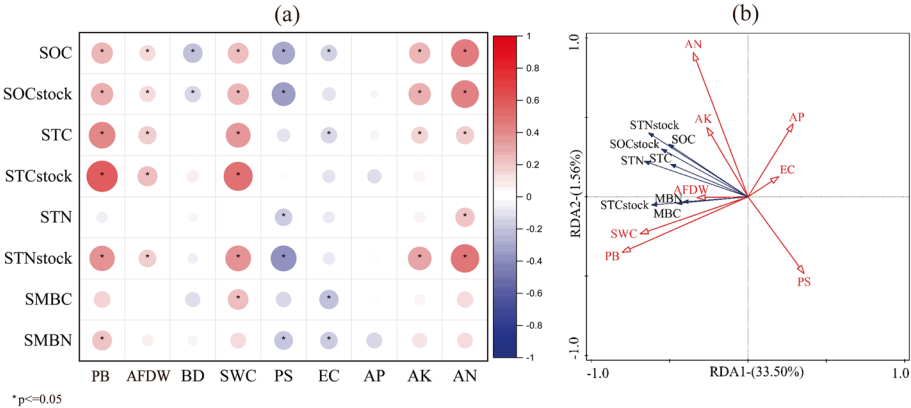


Fig. 6 Pearson correlation (a) and redundancy analysis (RDA) (b) between soil C and N components and influencing factors. AFDW, macrobenthos biomass; BD, bulk density; EC, electrical conductivity; SWC, soil water content; PS, particle size; AP, available phosphorus; AK, available potassium; AN, alkaline hydrolytic nitrogen

($p < 0.05$). The STC content and stock were significantly and positively correlated with PB, AFDW, and SWC and negatively correlated with EC ($p < 0.05$). The STC content was significantly and positively correlated with AK and AN ($p < 0.05$). The STN content was significantly and positively correlated with AN, whereas significantly and negatively correlated with PS ($p < 0.05$). The STN stock was significantly and positively correlated with PB, AFDW, SWC, AK, and AN, whereas significantly and negatively correlated with PS ($p < 0.05$). The SMBC content was significantly and positively correlated with SWC and significantly and negatively correlated with EC ($p < 0.05$). The SMBN content was significantly and positively correlated with PB and significantly negatively correlated with EC and PS ($p < 0.05$).

Based on the RDA results, SWC, PB, and AN exhibited a significantly positive influence on SOC, STC, and STN contents and stocks, and SMBC and SMBN amounts (Fig. 6b). Significant negative effects of PS, AP, and EC were observed on soil and microbial C and N variables.

4 Discussion

4.1 Effects of vegetation types on soil C and N

In the coastal wetlands of the Yangtze Estuary (including the Jiuduansha Shoal), the PA and SA communities mainly grow in high-level mudflats, the SM and ZL communities are distributed in middle-level mudflats, and few vegetation communities grow in low-level mudflats owing to differences in ecological niches of different species (Pan et al. 2014, Zhang et al. 2015). Significant differences were observed in soil C and N amounts and stocks between the vegetated marshes and bare mudflats. Previous studies have demonstrated the crucial role of marsh vegetation in enhancing soil C and N stocks in surface soil layers (Wolkovich et al. 2010).

Our research showed that SA communities exhibited higher plant biomass than the other vegetation types, which is consistent with previous findings (Zhou et al. 2015). *Spartina alterniflora* is an invasive species, originally from East America, that displays superior competitiveness against native salt marsh plants along the coast of China in terms of nutrient uptake and utilization efficiency (Li et al. 2009, Qiu et al. 2023). The strong invasive characteristics can also be attributed to the large root systems of SA communities, which can alter the physical and chemical properties of the soil (Wan et al. 2020, He et al. 2021a). The advantageous traits of SA, such as dense canopies and roots with strong wave attenuation and sedimentation capturing ability, might result in increased C and N retention compared to local plants such as SM (Chen et al. 2005b; Yang 2019). In contrast, the native SM community, as the pioneer species on the coast, exhibited a significantly lower plant biomass than

the other communities. Owing to their low-level canopy structure and prolonged inundation, the C sequestration capacity of SM communities is restricted under conditions of external stress and reduced sediment deposition (Cheng et al. 2006, Qian et al. 2019). Furthermore, SMBC and SMBN were positively correlated with plant biomass, SOC, and STN (Fig. 5), which is consistent with results of previous studies demonstrating that increased SMBC and SMBN resulted from concomitant increases in fresh organic material input and sequestration of SOC and STN (Haynes 2000, Liao et al. 2008).

The results of RDA indicated a significant positive correlation between PB and the soil C and N components (Fig. 6), revealed that the increase in PB promoted the contents of STC, STN, and SMBN as well as STC and SOC stocks. Previously, Miao et al. (2019) presented that the aboveground plant biomass and litter amount exhibited a stronger correlation with SOC. Vegetation types also exhibit differing capacities for soil C and N sequestration, as evidenced by variations in the contents and stocks of STC, SOC, and STN, with the *Spartina* community showing the highest contents. This result is consistent with the findings of the previous researches (Cheng et al. 2006; Zhou et al. 2023).

4.2 Effects of topography on soil C and N

There was considerable spatial heterogeneity in the distribution of soil C and N components in the Jiuduansha Shoal, which decreased significantly from high- to low-elevation mudflats (Fig. 2). The relatively higher soil C and N contents and stocks at high elevations than that in low-elevation sites can be attributed to greater plant productivity (Hu et al. 2019). Moreover, high-elevation marsh soils have the most advanced root structures, which can protect the soil from erosion and are more conducive to microbial biomass accumulation, thus leading to an increase in the accumulation of soil C and N (Lennon et al. 2012; Jing et al. 2020). On low-lying flats, continuous tidal inundation and wave currents limit vegetation growth. These areas tend to be eroded by strong tidal flooding, which hinders the accumulation of nutrient-rich soil particles (Saint-Laurent et al. 2014).

Along flat elevations, variations in soil physicochemical properties were identified to influence soil C and N dynamics, mainly because of microbial activity and mineralization processes (He et al. 2021b). Both the Pearson correlation and RDA results showed that SWC was positively correlated with SOC, STC, and STN contents and stocks (Fig. 6). Under high SWC conditions, the anoxic decomposition of soil organic matter tends to be inhibited, resulting in decreased C and N return rates (Zhao et al. 2016). Higher soil moisture resulted in lower BD, which was negatively correlated with SOC content and

stock (Fig. 6a and b). This is probably because SOC can be mobilized in porous spaces within the soil matrix (Anh et al. 2014).

Furthermore, the correlations between soil AK and AN and soil C and N contents and stocks were significantly positive (Fig. 6). The nutrients AP, AK, and AN can be directly utilized by plants for growth (Tian et al. 2021). Sufficient soil nutrients also provide material support for the metabolic activities of soil microorganisms (Philipot et al. 2024). In the present study, both the Pearson's correlation test and RDA results showed that SMBC and SMBN were significantly related to the soil properties SWC, PS, and EC (Fig. 6a and b), which is in line with finding of previous studies (Esperschütz et al. 2013). A previous study also found a strong relationship between soil physicochemical properties, SMBC, and SMBN (Zhang et al. 2016).

4.3 Effects of macrobenthos on soil C and N

Macrobenthos in coastal wetlands serve as both a source and sink of C and N of terrestrial origin (Fig. 7). Macrobenthos residues are buried in sediments and become a source of organic matter (McLeod et al. 2009, Pardo et al. 2023). Additionally, macrobenthos regulate soil C and N dynamics not only by converting organic matter (e.g., vegetation litter) into sediments, but also by accumulating C and N within their bodies (e.g., shell carbon) as a potent C and N sink into sediments (Barnes 2017; Van der Schatte Olivier et al. 2020). In the present study, we analyzed the AFDW of macrobenthos in different

habitats, indicating the potential organic matter input into the wetland soil during the animal life cycle.

In coastal habitats, vegetation type and geomorphology are the most important factors determining the distribution of various macrobenthos species (Chen et al. 2005a, 2009). In the Jiuduansha Shoal, there was a comparable difference in macrobenthos abundance and species number among the habitats (Fig. 4a and b), and the macrobenthos enrichment level in the vegetated marsh was significantly higher than that at the BM sites. The abundance of macrobenthos in the SM communities was the highest among the communities, and mollusks (Gastropoda and Bivalvia) were the dominant species (Fig. 4b). This could be attributed to the complex geomorphological structure of the SM communities, which provides a suitable underground environment, and the intricate root structure of the vegetation, which offers ample living space for macrobenthos (Capehart et al. 1989, Ricklefs 1993). Macrobenthos in the BM included a few species with low abundance, and the dominant species were gastropods (Fig. 4b). Under frequent tidal currents, the drastic perturbation of low-lying mudflats inhibits the massive proliferation of macrobenthos (Lv et al. 2016).

Another vital process by which macrobenthos affect soil C and N dynamics is their burrowing activity. Bio-turbation due to macrobenthos regulates C and N turnover as well as the diversity and structure of microbial communities in intertidal wetlands, which also directly influences sedimentary processes through organic matter metabolism coupled with aerobic respiration and

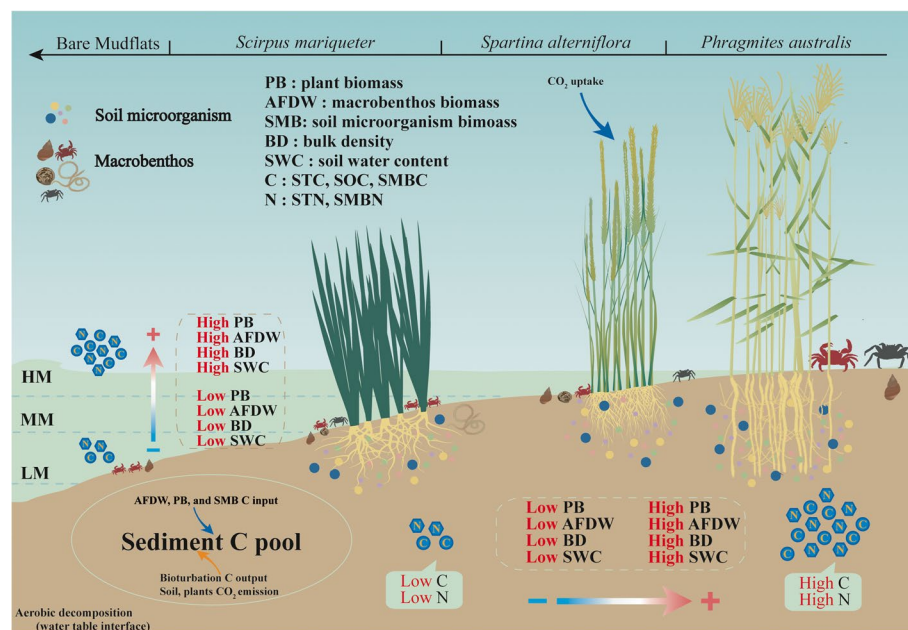


Fig. 7 Mechanism framework on roles of plant community, geomorphology, and macrobenthos in spatial variations of soil C and N in coastal shoal

metabolic excretions (Furukawa 2005). Bioturbation is a key factor in the microbial remineralization of deposited SOC and greenhouse gas emissions in wetlands (Cameron et al. 2019; Thomson et al. 2019). Thus, frequent perturbation by macrobenthos favors the mixing of sediments at different soil depths and increases the oxygen content around caves, significantly stimulating microbial decomposition pathways (Kristensen 2008). A previous study showed that macrobenthos (e.g., worms, snails, and crabs) increased the mineralization of organic matter in the sediment and promoted the decomposition of soil C and N, thus changing the characteristics of the C and N budget and resulting in the loss of stored organic matter (Nie et al. 2021).

A previous study showed that N_2 -fixation by microorganisms in bioturbated sediments may be a vital process leading to N input into ecosystems (Bertics et al. 2010). Macrobenthos can increase denitrification rates by up to 400% through their activities (e.g., feeding, burrowing, and bioturbation) (Gilbert et al. 1998; Howe et al. 2004). However, some studies have reported that sediments bioturbated by macrobenthos could be both a source of fixed N and a loss owing to stimulated denitrification (Laverock et al. 2011). Overall, the relationship between macrobenthos organisms and C and N pools in sediments is complex. Macrobenthic composition, biomass, and organic matter distribution in sediments are interdependent (Zaborska et al. 2018). Further investigations on the interaction between wetland soil C and N turnover and storage and macrobenthos behavior and life cycle are needed to understand the role of soil animals in influencing soil C and N dynamics.

5 Conclusions

The spatial distributions of soil C and N components were investigated in a coastal wetland in the Yangtze Estuary. Furthermore, the roles of plant type, plant biomass, tidal table, soil properties, and macrobenthos in variations in soil C and N contents and stocks were explored. The results showed that the STC, SOC, and STN contents and stocks at the SA and PA sites were significantly higher than those at the BM sites. The mean values of SMBC and SMBN in the vegetated sites were significantly higher than those of the BM sites. All soil and microorganism C and N variables showed a remarkably increasing trend from the LM to the HM sites. The abundance of macrobenthos at the SM sites and the AFDW of macrobenthos in the PA community was the highest among all communities. The soil C and N in the salt marsh was positively correlated to PB, SWC, macrobenthos AFDW, Ak and AN, while PS, BD and EC had a negative effect. Our results provide a scientific basis for assessing the C and N sequestration

potential of coastal salt marshes in East China with synergetic effects of biotic and abiotic factors, also supporting the management of the C and N pools.

Appendix

Table 3 Community character of the benthic macroinvertebrates in the Jiuduansha shoals (mean±S.E.)

Zones	Phyla	Class	Species	Biomass(g/m ²)	Density(ind./m ²)
High tidal	Nemertea	Anolpa	<i>Cerebratulus</i> sp.	2.16±0.47	40.00±8.00
			<i>Tylorhynchus heterochaetus</i>	0.65±0.28	33.33±12.50
			<i>Dentineptyx glabra</i>	0.76±0.44	34.09±12.61
			<i>Heteromastus filiformis</i>	0.72±0.37	24.00±8.00
	Mollusca	Gastropoda	<i>Noto-mastus latericeus</i>	0.50±0.20	33.33±14.43
			<i>Ellobium chinense</i>	1.07±0.43	47.50±14.19
			<i>Assimineia</i> sp.	2.61±1.93	69.33±5.29
			<i>Assimineia latericea</i>	12.15±5.36	41.43±15.28
			<i>Assimineia violacea</i>	8.91±2.72	31.88±11.31
			<i>Cerithiopsis largillierii</i>	7.07±1.70	16.00±8.00
			<i>Cerithidea sinensis</i>	18.02±3.35	26.66±5.33
			<i>Neritina violacea</i>	10.37±0.49	26.66±5.33
		Bivalvia	<i>Corbicula fluminea</i>	17.66±0.95	32.00±16.00
			<i>Glaucanome chinensis</i>	3.33±3.17	85.33±23.25
	Arthropoda	Malacostraca	<i>Orchestia platensis</i>	0.48±0.60	50.00±5.00
			<i>Uca arcuata</i>	10.03±1.04	29.33±5.89
			<i>Ilyoplax des-champsi</i>	1.73±1.24	61.08±35.12
			<i>Chironomus neglectum</i>	83.91±29.60	31.67±11.44

Zones	Phyla	Class	Species	Biomass(g/ m ²)	Density(ind./ m ²)	Zones	Phyla	Class	Species	Biomass(g/ m ²)	Density(ind./ m ²)	
Middle tidal	Chor- date	Osteich- thyes	<i>Orisarma neglectum</i>	56.92±11.50	27.78±8.33	Low tidal		Insecta	<i>Helice tientsin- ensis</i>	43.55±4.50	20.00±4.00	
			<i>Orisarma sinense</i>	38.45±4.32	17.78±1.78				<i>Larva of Lepidop- tera</i>	0.49±0.029	17.60±3.92	
			<i>Perioph- thalmus canton- ensis</i>	96.26±4.26	24.00±8.00				<i>Coleoptera</i>	0.56±0.024	16.00±3.58	
		Insecta	<i>Larva of Lepidop- tera</i>	0.82±0.083	17.60±3.92				<i>Diptera larvae</i>	0.66±0.081	25.85±6.15	
			<i>Coleoptera</i>	0.78±0.11	21.33±8.68				Poly- chaeta	<i>Tylor- rhynchus hetero- chaetus</i>	0.39±0.020	16.00±0.00
			<i>Diptera larvae</i>	2.77±4.82	81.25±53.13					<i>Den- tineptyts glabra</i>	0.36±0.090	24.00±8.00
	Annelida	Poly- chaeta	<i>Tylor- rhynchus hetero- chaetus</i>	0.57±0.13	17.78±1.78		<i>Het- eromastus filiformis</i>	0.25±0.038		20.00±4.00		
			<i>Den- tineptyts glabra</i>	1.02±0.11	24.00±3.02		<i>Noto- mastus latericeus</i>	0.34±0.18		33.33±14.43		
			<i>Het- eromastus filiformis</i>	0.42±0.16	21.33±5.33		Mollusca	Gastrop- oda		<i>Stenothyra glabra</i>	0.59±0.12	43.75±17.68
			<i>Noto- mastus latericeus</i>	0.31±0.15	18.67±7.05					<i>Ellobium chinense</i>	0.89±0.015	40.00±8.00
			Gastrop- oda	<i>Ellobium chinense</i>	1.13±0.23				29.71±4.17	<i>Assimineia sp.</i>	1.82±0.22	73.89±7.58
				<i>Assimineia sp.</i>	3.12±2.23			71.89±5.33	<i>Assimineia latericea</i>	7.60±1.38	40.00±17.48	
		<i>Assimineia latericea</i>		10.57±3.76	39.29±13.36	<i>Assimineia violacea</i>		5.95±1.89	21.33±5.33			
		<i>Assimineia violacea</i>		10.45±3.70	21.33±1.48	<i>Cerith- ideopsis largillierti</i>		4.68±0.64	16.00±1.50			
		<i>Cerith- ideopsis largillierti</i>		5.00±0.96	18.67±7.06	Bivalvia	<i>Cerithidea sinensis</i>	16.16±5.56	35.00±13.69			
		<i>Cerithidea sinensis</i>		12.67±1.27	18.00±2.00		<i>Corbicula fluminea</i>	15.43±3.36	25.00±5.00			
		<i>Onchid- ium reevesii</i>	15.24±1.79	37.33±14.11	<i>Mactra veneri- formis</i>		34.27±6.06	24.00±8.00				
		Bivalvia	<i>Moerella iridescens</i>	0.49±0.70	56.00±8.00		<i>Moerella iridescens</i>	25.12±7.89	64.00±16.00			
			<i>Glauco- nome chinensis</i>	2.47±1.15	48.00±16.00		<i>Glauco- nome chinensis</i>	3.37±2.51	164.58±99.12			
			Arthrop- oda	Malacos- traca	<i>Orchestia platensis</i>		0.49±0.075	40.00±8.00	<i>Sinono- vacula constricta</i>	8.04±0.83	17.50±1.50	
					<i>Uca arcuata</i>	6.55±0.43	13.33±2.67	Arthrop- oda	Malacos- traca	<i>Coro- phium volutur</i>	0.65±0.13	12.00±4.00
					<i>Ilyoplax des- champsii</i>	1.71±1.12	59.38±37.64			<i>Spha- eroma sinensis</i>	0.58±0.065	24.00±8.00
					<i>Orisarma neglectum</i>	54.50±7.78	37.50±14.43			<i>Ilyoplax des- champsii</i>	1.44±0.17	76.61±42.79
		<i>Orisarma sinense</i>			33.75±3.23	22.67±2.38						

Zones	Phyla	Class	Species	Biomass(g/ m ²)	Density(ind./ m ²)
			<i>Philyra pisum</i>	40.00±1.90	27.78±8.33
			<i>Orisarma neglectum</i>	50.11±3.21	20.00±12.00

Acknowledgements

This study is funded by the National Key R&D Program of China (2023YFC0113104 and 2023YFC3208500), the National Natural Science Foundation of China (U2040204 and 42141016), the grants from Shanghai Municipal Science and Technology Commission (22dz1209600), the Jiangsu Key Laboratory of Coast Ocean Resources Development and Environmental Security, Hohai University (Grant No. JSCE202301), and the Project of the Zhejiang Water Conservancy Bureau (RB2414). We thank the support of Elsevier Language Editing Services (Elsevier B.V.) for revising the language of this paper.

Authors' contributions

Qing Lyu: Conceptualization, Methodology, Investigation, Formal analysis, Writing—review & editing. Ke Zhou: Investigation, Formal analysis. Shi-Xian Liu: Investigation, Formal analysis. Hai-Feng Cheng: Investigation, Formal analysis. Wei Zhang: Investigation, Formal analysis. Yuan Tian: Investigation, Formal analysis. Ke-Hua Zhu: Investigation, Formal analysis. Hua-Yu Chen: Investigation, Formal analysis. Zeng-Feng Li: Investigation, Formal analysis. Zeng Zhou: Writing—review & editing. Zhen-Ming Ge: Conceptualization, Methodology, Investigation, Formal analysis, Writing—review & editing. All authors have perused and consented to the final version of the manuscript.

Funding

This study is funded by the National Key R&D Program of China (2023YFC3208500 and 2023YFC0113104), the National Natural Science Foundation of China (U2040204 and 42141016), the grants from Shanghai Municipal Science and Technology Commission (22dz1209600), the Jiangsu Key Laboratory of Coast Ocean Resources Development and Environmental Security, Hohai University (Grant No. JSCE202301), and the Project of the Zhejiang Water Conservancy Bureau (RB2414).

Data availability

Raster data will be available under request.

Declarations

Competing interests

The authors have no competing interests to declare that are relevant to the content of this article.

Received: 15 August 2024 Revised: 2 December 2024 Accepted: 4 December 2024
Published online: 23 December 2024

References

Anh PTQ, Gomi T, MacDonald LH, Mizugaki S, Khoa PV, Furuichi T (2014) Linkages among land use, macronutrient levels, and soil erosion in northern Vietnam: A plot-scale study. *Geoderma* 232:352–362

Bang JH, Lee EJ (2019) Differences in crab burrowing and halophyte growth by habitat types in a Korean salt marsh. *Ecol Ind* 98:599–607

Barnes DK (2017) Polar zoobenthos blue carbon storage increases with sea ice losses, because across-shelf growth gains from longer algal blooms outweigh ice scour mortality in the shallows *Glob. Glob Change Biol* 23:5083–5091

Bernal B, Mitsch WJ (2012) Comparing carbon sequestration in temperate freshwater wetland communities. *Glob Change Biol* 18:1636–1647

Bertics VJ, Sohm JA, Treude T, Chow CET, Capone DG, Fuhrman JA, Ziebis W (2010) Burrowing deeper into benthic nitrogen cycling: the impact

of bioturbation on nitrogen fixation coupled to sulfate reduction. *Mar Ecol Prog Ser* 409:1–15

Brookes P, Powelson D, Jenkinson D (1982) Measurement of microbial biomass phosphorus in soil. *Soil Biol Biochem* 14:319–329

Cameron C, Hutley LB, Friess DA, Munksgaard NC (2019) Hydroperiod, soil moisture and bioturbation are critical drivers of greenhouse gas fluxes and vary as a function of landuse change in mangroves of Sulawesi. *Indonesia Sci Total Environ* 654:365–377

Capehart AA, Hackney CT (1989) The potential role of roots and rhizomes in structuring salt-marsh benthic communities. *Estuaries* 12:119–122

Carvalhois N, Forkel M, Khomik M, Bellarby J, Jung M, Migliavacca M, Mu MQ, Saatchi S, Santoro M, Thurner M, Weber U, Ahrens B, Beer C, Cescatti A, Randerson JT, Reichstein M (2014) Global covariation of carbon turnover times with climate in terrestrial ecosystems. *Nature* 514:213–7

Chen Z, Fu C, Wang H, Li B, Wu J, Chen J (2005a) Effects of *Spartina alterniflora* invasions on the benthic macro-invertebrates community at Dongtan of Chongming salt marsh, the Yangtze River estuary. *Wetland Sci* 3:1–7

Chen Z, Li B, Chen J (2005b) Some growth characteristics and relative competitive ability of invasive *Spartina alterniflora* and native *Scirpus mariqueter*. *Biodiversity Sci* 13:130

Chen ZB, Guo L, Jin BS, Wu JH, Zheng GH (2009) Effect of the exotic plant on macrobenthos communities in salt marshes of the Yangtze River Estuary. *China Estuarine Coastal Shelf Sci* 82:265–272

Chen XX, Wiesmeier M, Sardans J, Van Zwieten L, Fang YY, Gargallo-Garriga A, Chen YY, Chen SY, Zeng CS, Peñuelas J, Wang WQ (2021) Effects of crabs on greenhouse gas emissions, soil nutrients, and stoichiometry in a subtropical estuarine wetland. *Biol Fertil Soils* 57:131–144

Cheng HF, Xin P, Liu J, Gu FF, Wang W, Han L (2020) Morphological evolution and dynamic mechanics of the Jiuduansha Shoal (China) during 1959–2018. *Adv Water Sci* 31:491–501

Cheng XL, Luo YQ, Chen JQ, Lin GH, Chen JK, Li B (2006) Short-term C4 plant invasions change the soil carbon in C3 plant-dominated tidal wetlands on a growing estuarine Island. *Soil Biol Biochem* 38:3380–3386

Danovaro R, Gambi C, Mirto S (2002) Meiofaunal production and energy transfer efficiency in a seagrass bed in the western Mediterranean. *Mar Ecol Prog Ser* 234:95–104

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440:165–173

Esperschütz J, Zimmermann C, Dümig A, Welzl G, Buegger F, Elmer M, Munch JC, Schlöter M (2013) Dynamics of microbial communities during decomposition of litter from pioneering plants in initial soil ecosystems. *Biogeosciences* 10:5115–5124

Furukawa Y (2005) Biogeochemical consequences of infaunal activities. Interactions between Macro- and Microorganisms in Marine Sediments, American Geophysical Union, Washington 60:159–177

Gilbert F, Stora G, Bonin P (1998) Influence of bioturbation on denitrification activity in Mediterranean coastal sediments: an in situ experimental approach. *Mar Ecol Prog Ser* 163:99–107

Guimond JA, Seyffert AL, Moffett KB, Michael HA (2020) A physical-biogeochemical mechanism for negative feedback between marsh crabs and carbon storage. *Environ Res Lett* 15(3):034024

Guo S, Liu X, Tang J (2022) Enhanced degradation of petroleum hydrocarbons by immobilizing multiple bacteria on wheat bran biochar and its effect on greenhouse gas emission in saline-alkali soil. *Chemosphere* 286(Pt 2):131663

Haynes RJ (2000) Labile organic matter as an indicator of organic matter quality in arable and pastoral soils in New Zealand. *Soil Biol Biochem* 32:211–219

He C, Wang X, Wang D, Zhao Z, Wang F, Cheng L, Feng H, Zhang P (2021) Impact of *Spartina alterniflora* invasion on soil bacterial community and associated greenhouse gas emission in the Jiuduansha wetland of China. *Appl Soil Ecol* 168:104168

He CQ, Cheng LY, Wang DY, Zhao ZZ, Wang ZY, Wang FF, Wang XX, Zhang P, Chen XP, Liu XY (2021) *Spartina alterniflora* raised soil sulfide content by regulating sulfur cycle-associated bacteria in the Jiuduansha Wetland of China. *Plant Soil* 469:107–121

Hernández TD, Slater BK, Shaffer JM, Basta N (2023) Comparison of methods for determining organic carbon content of urban soils in Central Ohio. *Geoderma Region* 34:e00680

- Howe RL, Rees AP, Widdicombe S (2004) The impact of two species of bioturbating shrimp (*Callinassa subterranea* and *Upogebia deltaura*) on sediment denitrification. *J Mar Biol Assoc UK* 84:629–632
- Hu Y, Wang L, Fu XH, Yan JF, Wu JH, Tsang YF, Le YQ, Sun Y (2016) Salinity and nutrient contents of tidal water affects soil respiration and carbon sequestration of high and low tidal flats of Jiuduansha wetlands in different ways. *Sci Total Environ* 565:637–648
- Hu C, Li F, Xie YH, Deng ZM, Hou ZY, Li X (2019) Spatial distribution and stoichiometry of soil carbon, nitrogen and phosphorus along an elevation gradient in a wetland in China. *Eur J Soil Sci* 70:1128–1140
- Huang H, Zhang L (2007) A study of the population dynamics of *Spartina alterniflora* at Jiuduansha shoals, Shanghai. *China Ecol Eng* 29:164–172
- Huang Y, Li Y, Chen Q, Huang Y, Tian J, Cai M, Huang Y, Jiao Y, Yang Y, Du X, Liu Z, Zhao Y (2021) Effects of reclamation methods and habitats on macrobenthic communities and ecological health in estuarine coastal wetlands. *Mar Pollut Bull* 168:112420
- Jing X, Chen X, Fang J, Ji C, Shen H, Zheng C, Zhu B (2020) Soil microbial carbon and nutrient constraints are driven more by climate and soil physicochemical properties than by nutrient addition in forest ecosystems. *Soil Biol Biochem* 141:107657
- Kristensen E (2008) Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. *J Sea Res* 59:30–43
- Laverock B, Gilbert JA, Tait K, Osborn AM, Widdicombe S (2011) Bioturbation: impact on the marine nitrogen cycle. *Biochem Soc Trans* 39:315–320
- Lennon JT, Aanderud ZT, Lehmkuhl BK, Schoolmaster DR (2012) Mapping the niche space of soil microorganisms using taxonomy and traits. *Ecology* 93:1867–1879
- Li B, Liao CH, Zhang XD, Chen HL, Wang Q, Chen ZY, Gan XJ, Wu JH, Zhao B, Ma ZJ, Cheng XL, Jiang LF, Chen JK (2009) Invasions in the Yangtze River estuary, China: An overview of current status and ecosystem effects. *Ecol Eng* 35:511–520
- Li Y-L, Ge Z-M, Xie L-N, Li S-H, Tan L-S (2022) Effects of waterlogging and salinity increase on CO₂ efflux in soil from coastal marshes. *Appl Soil Ecol: a Section Agricul Ecosyst Environ* 170:104268
- Liao JD, Boutton TW (2008) Soil microbial biomass response to woody plant invasion of grassland. *Soil Biol Biochem* 40:1207–1216
- Lin WP, Chen GS, Guo PP, Zhu WQ, Zhang DH (2015) Remote-Sensed monitoring of dominant plant species distribution and dynamics at Jiuduansha Wetland in Shanghai. *China Remote Sensing* 7:10227–10241
- Liu C, Zhuang J, Wang J, Fan G, Feng M, Zhang S (2022) Soil bacterial communities of three types of plants from ecological restoration areas and plant-growth promotional benefits of *Microbacterium invictum* (strain X-18). *Front Microbiol* 13:926037
- Lovelock CE, Duarte CM (2019) Dimensions of Blue Carbon and emerging perspectives. *Biol Lett* 15:20180781
- Lu RK (2000) Soil agrochemistry and analytical methods. China Agricultural Science and Technology Press, Beijing
- Luo ZK, Feng WT, Luo YQ, Baldock J, Wang EL (2017) Soil organic carbon dynamics jointly controlled by climate, carbon inputs, soil properties and soil carbon fractions. *Glob Change Biol* 23:4430–4439
- Luo ZK, Viscarra-Rossel RA, Qian T (2021) Similar importance of edaphic and climatic factors for controlling soil organic carbon stocks of the world. *Biogeosciences* 18:2063–2073
- Lv WW, Liu ZQ, Yang Y, Huang YH, Fan B, Jiang QC, Zhao YL (2016) Loss and self-restoration of macrobenthic diversity in reclamation habitats of estuarine islands in Yangtze Estuary. *China Mar Pollut Bull* 103:128–136
- McLeod RJ, Wing SR (2009) Strong pathways for incorporation of terrestrially derived organic matter into benthic communities. *Estuar Coast Shelf Sci* 82:645–653
- Meng W, Feagin RA, Innocenti RA, Hu B, He M, Li H (2020) Invasion and ecological effects of exotic smooth cordgrass in China. *Ecol Eng* 143:105670
- Meng WQ, Feagin RA, Hu BB, He MX, Li HY (2019) The spatial distribution of blue carbon in the coastal wetlands of China. *Estuar Coast Shelf Sci* 222:13–20
- Miao R, Ma J, Liu Y, Liu Y, Yang Z, Guo M (2019) Variability of aboveground litter inputs alters soil carbon and nitrogen in a coniferous-broadleaf mixed forest of central China. *Forests* 10(2):188
- Moffett KB, Gorelick SM, McLaren RG, Sudicky AE (2012) Salt marsh ecohydrological zonation due to heterogeneous vegetation-groundwater-surface water interactions. *Water Resour Res* 48(2):W02516
- Nie L, Li Y, Hou Y, Di L, Xi M, Yu Z (2021) Dynamics of organic carbon under bioturbation by mud crabs (*Macrophthalmus japonicus*) and clamworms (*Perinereis aibuhitensis*) in an estuary ecosystem. *J Exp Mar Biol Ecol* 534:151474
- Olefeldt D, Goswami S, Grosse G, Hayes D, Hugelius G, Kuhry P, McGuire AD, Romanovsky VE, Sannel ABK, Schuur EAG, Turetsky MR (2016) Circumpolar distribution and carbon storage of thermokarst landscapes. *Nat Commun* 7:13043
- Pan Y, Xie YH, Deng ZM, Tang Y, Pan DD (2014) High water level impedes the adaptation of to deep burial: Responses of biomass allocation and root morphology. *Sci Rep* 4:5612
- Pardo JC, Poste AE, Frigstad H, Quintana CO, Trannum HC (2023) The interplay between terrestrial organic matter and benthic macrofauna: Framework, synthesis, and perspectives. *Ecosphere* 14(5):e4492
- Pennings SC, Bertness MD (2001) Salt Marsh Communities Marine Community Ecology 11:289–316
- Philippot L, Chenu C, Kappler A, Rillig MC, Fierer N (2024) The interplay between microbial communities and soil properties. *Nat Rev Microbiol* 22:226–239
- Qian L, Yan J, Hu Y, Gao L, Wu P, Wang L (2019) Spatial distribution patterns of annual soil carbon accumulation and carbon storage in the Jiuduansha wetland of the Yangtze River estuary. *Environ Monit Assess* 191(12):750
- Qiao JL, Wang L, Tang YS, Hu YH, Jia JW (2012) Distribution and characteristics of total petroleum hydrocarbons in Jiuduansha tidal wetland and their potential impact on soil microbial respiration. *J Environ Sci Health Part A Toxic Hazard Subst Environ Eng* 47:319–325
- Qiu S, Wang Z, Xu J, Cui E, Yan L (2023) Influence of vegetation dynamics on soil organic carbon and its fractions in a coastal wetland. *Ecosyst Health Sustain* 9:0016
- Ricklefs, R. E. a. S., D. (eds.). Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, paper \$27.95. 414 pp. ISBN: 0-226-71823-9. *Journal of evolutionary biology*. 1993; 7:635–636.
- Ross D (1990) Measurements of microbial biomass C and N in grassland soils by fumigation-incubation procedures: influence of inoculum size and the control. *Soil Biol Biochem* 22:289–294
- Saint-Laurent D, Gervais-Beaulac V, Berthelot JS (2014) Variability of soil properties in different flood-risk zones and link with hydroclimatic changes (Southern Quebec, Canada). *Geoderma* 214:80–90
- Tang YS, Wang L, Jia JW, Fu XH, Le YQ, Chen XZ, Sun Y (2011) Response of soil microbial community in Jiuduansha wetland to different successional stages and its implications for soil microbial respiration and carbon turnover. *Soil Biol Biochem* 43:638–646
- Tangen BA, Bansal S (2020) Soil organic carbon stocks and sequestration rates of inland, freshwater wetlands: Sources of variability and uncertainty. *Sci Total Environ* 749:141444
- Thomson ACG, Trevathan-Tackett SM, Maher DT, Ralph PJ, Macreadie PI (2019) Bioturbator-stimulated loss of seagrass sediment carbon stocks. *Limnol Oceanogr* 64:342–356
- Tian H, Qiao J, Zhu Y, Jia X, Shao M (2021) Vertical distribution of soil available phosphorus and soil available potassium in the critical zone on the Loess Plateau, China. *Sci Rep* 11(1):3159
- Van der Schatte Olivier A, Jones L, Vay LL, Christie M, Wilson J, Malham S (2020) A global review of the ecosystem services provided by bivalve aquaculture. *Rev Aquacult* 12:3–25
- Vineis JH (2022) Nutrient influence on microbial structure and function within salt marsh sediments. Northeastern University ProQuest Dissertations & Theses, Boston, 2022:217
- Wan S, Liu XT, Mou XJ, Zhao YQ (2020) Comparison of carbon, nitrogen, and sulfur in coastal wetlands dominated by native and invasive plants in the Yancheng National Nature Reserve China. *Chin Geograph Sci* 30:202–216
- Wang F, Lu X, Sanders CJ, Tang JW (2019) Tidal wetland resilience to sea level rise increases their carbon sequestration capacity in United States. *Nat Commun* 10(1):5434
- Wang LA, Yin CQ, Wang WD, Shan BQ (2010) Phosphatase activity along soil C and P gradients in a reed-dominated wetland of North China. *Wetlands* 30:649–655
- Wolkovich EM, Lipson DA, Virginia RA, Cottingham KL, Bolger DT (2010) Grass invasion causes rapid increases in ecosystem carbon and nitrogen storage in a semiarid shrubland. *Glob Change Biol* 16:1351–1365

- Wu J, Brookes PC (2005) The proportional mineralisation of microbial biomass and organic matter caused by air-drying and rewetting of a grassland soil. *Soil Biol Biochem* 37:507–515
- Xie LN, Ge ZM, Li YL, Li SH, Tan LS, Li XZ (2020) Effects of waterlogging and increased salinity on microbial communities and extracellular enzyme activity in native and exotic marsh vegetation soils. *Soil Sci Soc Am J* 84:82–98
- Xue L, Jiang J, Li X, Yan Z, Zhang Q, Ge Z, Tian B, Craft C (2020) Salinity affects topsoil organic carbon concentrations through regulating vegetation structure and productivity. *J Geophys Res: Biogeosci* 125:e2019JG005217
- Yang RM (2019) Interacting effects of plant invasion, climate, and soils on soil organic carbon storage in coastal wetlands. *J Geophys Res Biogeosci* 124:2554–2564
- Zaborska A, Włodarska-Kowalczyk M, Legeżyńska J, Jankowska E, Winogradow A, Deja K (2018) Sedimentary organic matter sources, benthic consumption and burial in west Spitsbergen fjords – Signs of maturing of Arctic fjordic systems? *J Mar Syst* 180:112–123
- Zhang LQ, Yuan L, Huang HM (2015) Coastal wetlands in the Changjiang estuary. Springer International Publishing, pp 137–159
- Zhang Y, Li C, Trettin CC, Li H, Sun G (2002) An integrated model of soil, hydrology, and vegetation for carbon dynamics in wetland ecosystems. *Glob Biogeochem Cycles* 16(4):9–1
- Zhang JB, Song CC, Wang SM (2007) Dynamics of soil organic carbon and its fractions after abandonment of cultivated wetlands in northeast China. *Soil Tillage Res* 96:350–360
- Zhang C, Nie S, Liang J, Zeng GM, Wu HP, Hua SS, Liu JY, Yuan YJ, Xiao HB, Deng LJ, Xiang HY (2016) Effects of heavy metals and soil physicochemical properties on wetland soil microbial biomass and bacterial community structure. *Sci Total Environ* 557:785–790
- Zhao QQ, Bai JH, Liu Q, Lu QQ, Gao ZQ, Wang JJ (2016) Spatial and seasonal variations of soil carbon and nitrogen content and stock in a tidal salt marsh with *Tamarix chinensis*. *China Wetlands* 36:S145–S152
- Zhou CF, Zhao H, Sun ZY, Zhou LX, Fang C, Xiao Y, Deng ZF, Zhi YB, Zhao YQ, An SQ (2015) The invasion of *Spartina alterniflora* alters carbon dynamics in China's Yancheng Natural Reserve. *Clean-Soil Air Water* 43:159–165
- Zhou J, Zhang J, Chen Y, Qin G, Cui B, Lu Z, Wu J, Huang X, Thapa P, Li H (2023) Blue carbon gain by plant invasion in saltmarsh overcompensated carbon loss by land reclamation. *Carbon Res* 2:39