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Coastal conversion alters topsoil C, N and P stocks and stoichiometric balances in subtropical coastal wetlands

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Highlights:

- ◆ Coastal conversion substantially increases topsoil C, N, and P concentrations.
- ◆ Conversion from mudflats would enhance topsoil C stocks, but from marshes do not.
- ◆ Lower N:P ratio in cropland soils shows more P than N retention in soil.
- ◆ Converted croplands and ponds show more homogeneous distribution of C, N, and P.
- ◆ Coastal conversion alters topsoil C, N and P stocks and stoichiometric balances.

Abstract:

The extensive conversion of coastal wetlands into agricultural and aquaculture areas has significant repercussions on soil nutrient balance. However, how coastal conversion specifically influences the dynamics and stoichiometry of topsoil carbon (C), nitrogen (N), and phosphorus (P) remains limited due to the considerable spatial variability and a lack of comprehensive field data. Here, we investigated the concentration and distribution of total C (TC), N (TN) and P (TP), along with their stoichiometric balance in four distinct coastal landscapes, including natural marshes and mudflats, as well as converted agricultural croplands and aquaculture ponds. The results revealed that converted croplands and ponds exhibited a substantial increase in soil C, N and P concentrations, particularly in comparison to mudflats. Furthermore, converting mudflats into croplands or ponds can enhance topsoil C stocks, whereas converting from marshes may not change or even lose stored C. Cropland soils exhibited considerably higher levels of available N ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$) and available P compared to those in natural marshes and mudflats. The distribution of soil TC, TN, and TP demonstrated greater spatial heterogeneity in natural marshes and mudflats, while the converted areas were more uniform and became hotspots for N and P accumulation. Coastal conversion altered soil C:N:P stoichiometry, with cropland soils exhibiting a lower N:P ratio (2.9 ± 1.1), indicating that long-term application of N and P fertilizers could decrease the N:P ratio, as P is more retained in the soil than N. Furthermore, it was observed that the dynamics of C, N and P, as well as their stoichiometry, are closely linked to soil physicochemical properties, especially soil organic matter and texture. These findings highlight that coastal conversion and associated management practices markedly affected soil C, N and P dynamics, leading to a reshaping of their stoichiometric balances, particularly in the topsoil layer.

Keywords: topsoil; C, N and P dynamics; land use change; coastal wetlands

1. Introduction

Coastal wetlands, serving as dynamic transition zones between terrestrial and marine ecosystems, provide diverse and productive habitats (Ma et al., 2014; Wang et al., 2021). Their crucial roles in coastal defense, biodiversity support, and nutrient balance maintain render them indispensable for the health of both natural systems and human communities (Hu et al., 2024; Karstens et al., 2016). Unfortunately, these vital ecosystems have historically experienced continuous and substantial losses due to human disturbances and global environmental changes. On one hand, urbanization, agriculture, and infrastructure development frequently encroach upon coastal wetlands, directly destroying them or converting these areas into residential, industrial, or agricultural lands (Cui et al., 2021). Additionally, global environmental changes, particularly rising sea levels and coastal erosion, significantly threaten these wetlands with loss and degradation (Schuerch et al., 2018; Spencer et al., 2016). In China, factors such as land reclamation, coastal erosion, and sea level rise have contributed to a nearly 51% reduction in coastal wetland areas between 1984 and 2012 on a national scale (Gu et al., 2018; Sun et al., 2015; Wang et al., 2021). This leads to the displacement of native vegetation, accelerated degradation, and intensified fragmentation of wetlands, thereby adversely affecting their primary productivity, nutrient balance, and overall ecosystem functions (Rodríguez et al., 2017; Schuerch et al., 2018). The ongoing conversion and degradation of these ecosystems highlight the urgent need for focused and effective conservation and restoration efforts to enhance the resilience of coastal wetlands in the face of global changes.

Soil carbon (C), nitrogen (N), and phosphorus (P) are essential elements crucial for sustaining plant growth, microbial activity, and overall ecosystem health, particularly in the topsoil layer (Smal et al., 2019; Zhang et al., 2022). The topsoil, being the uppermost layer of soil where most plant roots reside, plays a vital role in soil fertility, nutrient cycling, and supporting diverse plant and microbial communities (Chirinda et al., 2014; Liu et al., 2020). However, the conversion and degradation of coastal wetlands can significantly affect the dynamics of soil C, N, and P, yet the specific impacts remain unclear (Karstens et al., 2016; Wang et al., 2018; Zhang et al., 2023). Typically, converting coastal wetlands to other uses, such as agriculture or aquaculture, can disturb or remove soil organic matter, thus reducing the soil's capacity to store C and nutrients (Yu et al., 2016). Conversely, a recent nationwide study indicated that although soil organic C notably decreased following coastal reclamation, total N and total P saw significant increases, primarily within the 0-40 cm soil layers (Zhang et al., 2023). However, some studies, such as that by Xu et al. (2018), did not observe significant changes in soil C, N, and P dynamics or their C:N:P stoichiometry even after 63 years of coastal reclamation. These findings highlight that the effects of conversion and degradation on soil C, N, and P concentrations, as well as their stoichiometric characteristics in coastal wetlands—particularly in the topsoil layer—are still contentious and require further research. Specifically, the conversion to cropland and ponds involves distinctly different environmental processes, and their impacts on coastal nutrient balance have been largely overlooked, presenting considerable uncertainties.

China has approximately 18,400 km of coastline and around 5.8 million hectares of coastal wetlands. Since the early 1980s, due to extensive infrastructure development, land reclamation, and various environmental changes, China's coastal wetlands have experienced severe loss, degradation, and fragmentation on regional to national scales (Hu et al., 2024; Jiang et al., 2015; Sun et al., 2015). However, the interaction between coastal conversion and topsoil nutrient dynamics has rarely been

evaluated. In this study, our objectives were to (1) quantify the concentrations and stoichiometry of topsoil C, N, and P resulting from coastal conversion and degradation, (2) evaluate the distribution patterns and heterogeneity of topsoil C, N and P, and (3) investigate the driving factors affecting soil C, N and P dynamics.

2. Materials and methods

2.1. Site description

The Min River estuarine wetland, located on the southeast coast of China, is characterized by a subtropical monsoon climate, with an average annual temperature of 15°C and precipitation of 1350 mm. This coastal wetland is experiencing significant challenges due to both human disturbances (such as aquaculture reclamation and dam construction) and natural factors (tidal erosion and typhoon), leading to substantial loss, degradation, and fragmentation. Land use in this area is broadly categorized into two types: natural landscapes, consisting of marshes and mudflats, and human-converted areas, comprising ponds and croplands. A dam distinctly separates the marshes and mudflats from the ponds and croplands. The natural tidal marshes in this region, subject to twice-daily tidal ebb and flow (Hu et al., 2023a), host vegetation uniquely adapted to the saline environment. These marshes are dominated by *Kandelia obovata*, *Phragmites australis*, and *Cyperus malaccensis*.

Adjacent to the sea, the mudflats, interspersed with salt marshes, are characterized by their flat, muddy surfaces. These surfaces are exposed during low tide and submerged at high tide, consisting mainly of fine-grained sediment such as mud or silt. The ponds in this area, initially reclaimed from marshes in the early 2000s for aquaculture purposes (shrimp farming), have undergone restoration efforts to mitigate soil degradation and preserve bird habitats. As a result, many of these aquaculture ponds are now undergoing natural restoration (Hu et al., 2023b). The croplands, converted from marshes in the 1970s, are predominantly used for growing vegetables and rice, involving the application of N and P fertilizers. A more comprehensive description of the region can be found in Hu et al. (2023a).

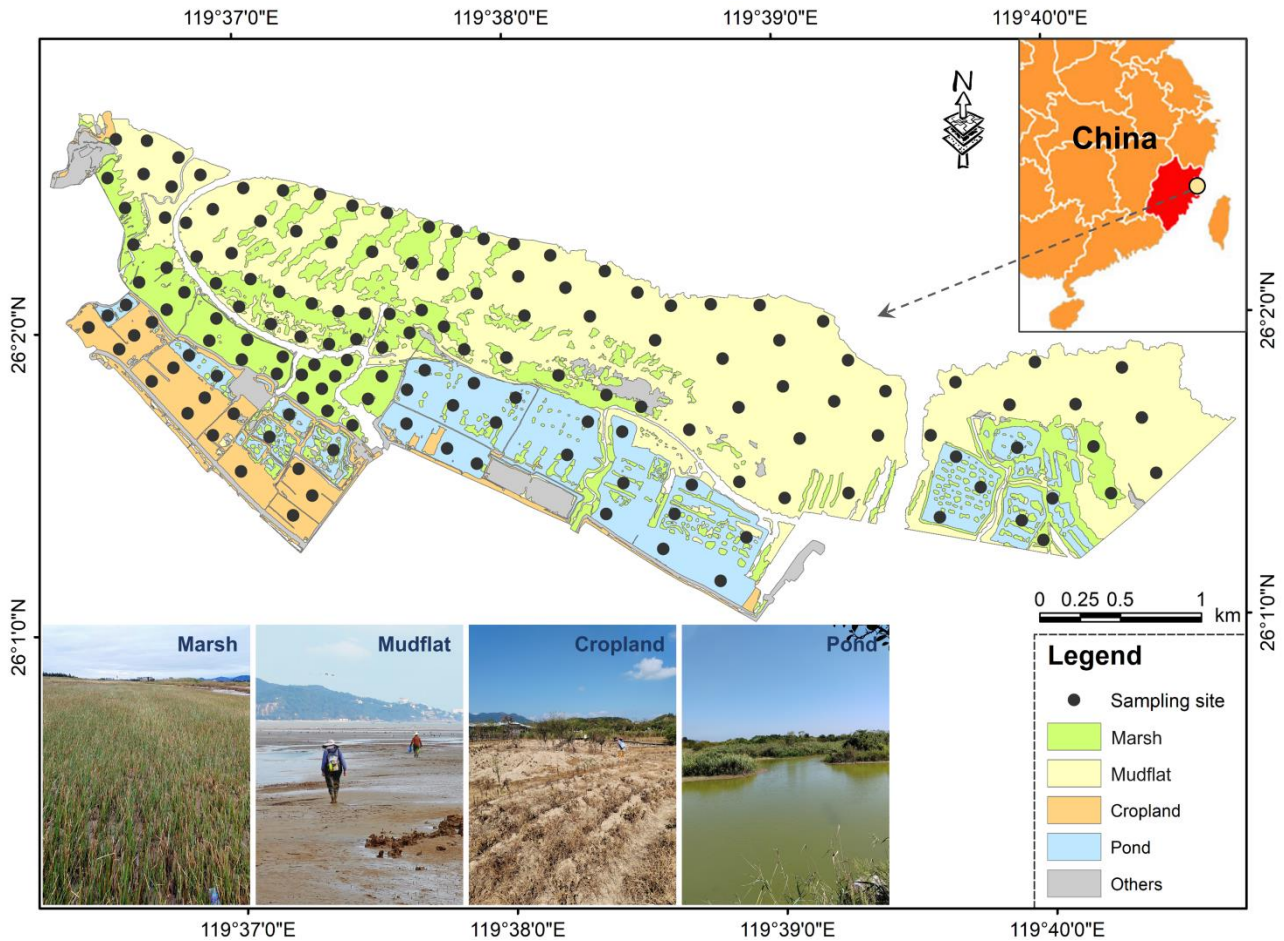


Fig S1. Sampling sites (black dots) and main landscapes in the Min River estuary, southeastern China.

2.2. Soil sampling and analysis

The sampling process was conducted from September to December 2022, utilizing high-resolution spatial sampling techniques. A total of 153 soil samples were collected, comprising 69 from marshes, 38 from mudflats, 33 from ponds, and 13 from croplands. At each site, a 1 m × 1 m quadrat was established, and 2 to 3 topsoil (20 cm) samples were randomly collected and subsequently mixed to represent a single composite sample. These samples were then placed in zip-lock bags and transported to the laboratory for further processing. Once air drying, any roots and stones were removed, and the samples were ground and sieved for analysis of soil C, N, P concentrations, as well as other physicochemical properties.

Soil total C (TC) and total N (TN) concentrations were determined using an elemental analyzer (Elementar, Frankfurt, Germany). Soil total P (TP) concentration was determined using a flow injection analyzer (Skalar Analytical SAN++, Lachat, Netherland) after digestion by $\text{HClO}_4\text{-H}_2\text{SO}_4$. Soil available N, including ammonium and nitrate, was extracted by 2M KCl and analyzed by a flow injection analyzer (Skalar Analytical SAN++, Lachat, Netherland). Available P (AP) concentration was measured following a 0.5M NaHCO_3 extraction (Olsen and Sommers, 1982). Soil organic matter (SOM) was determined using the loss-on-ignition method. Soil moisture was calculated based on the loss of water to constant weight at 105°C, while bulk density was calculated as the ratio of dry soil weight to its volume. Electrical conductivity (EC) was measured using a portable conductivity meter (2265FS, USA). Soil pH was measured using a pH meter with a soil-to-water ratio of 2.5:1. Salinity was measured using a salinity meter (Oakton Instruments, Springfield, USA). Additionally, soil

particle size distribution was analyzed using a particle-size analyzer (Mastersizer 2000, Malvern, UK). We classified soil textures according with the United States Department of Agriculture classification criteria, that includes: clay, clay loam, loam, silty clay, silty clay loam, silt loam, silt, sandy clay, sandy clay loam, sandy loam, loamy sand, and sand textures.

2.3. Statistical analyses

The stoichiometry of soil C, N, and P across all sites was calculated in terms of molar ratios (atomic ratio) by converting their concentrations from g kg^{-1} to units of mol kg^{-1} . To visualize the spatial variability of these elements, Kriging interpolation was employed using the Geostatistical Analyst extension tool in ArcGIS 10.2 software. A one-way analysis of variance (ANOVA) was conducted to assess differences in soil C, N, and P concentrations and their associated physicochemical properties across different sites. The Mantel test was applied to investigate the relationships between the dynamics of soil C, N, and P and selected physicochemical properties, using the “*vegan*” R package. Pearson correlations were used to assess the relationship between various soil properties and were visualized with a heatmap. Furthermore, the Random Forest model was utilized to investigate the relative importance of environmental factors on changes in soil C, N, and P, using soil C, N, and P concentrations as response variables and soil physicochemical properties as explanatory variables using the *randomForest* R package. In addition, we calculated soil C, N and P stocks in different coastal landscapes based on their concentration, bulk density and soil layer height (20 cm). To assess the effects of soil physicochemical variables on TC, TN, and TP simultaneously, we conducted a Redundancy Analysis (RDA) using the CCA (González et al., 2008), *corrplot* (Wei T and V, 2021), and *vegan* (Oksanen, 2010) packages within the R platform. Subsequently, we analyzed the differences in the scores of the first two axes of the RDA for soil samples from distinct sites. This was achieved using a one-way ANOVA with a Bonferroni post hoc test, to identify significant spatial differences between these site score sets within the 2D space of the RDA. For these analyses, we utilized Statistica 8.0 (StatSoft Inc., Tucson, OK, USA).

3. Results

3.1. Soil physicochemical properties

Soil physicochemical properties across various coastal landscapes are displayed in Table 1. Notably, the cropland sites exhibit considerably lower soil pH, electrical conductivity, and salinity compared to marshes, mudflats, and ponds ($p < 0.05$). Soil bulk density is typically lower in marshes and higher in croplands, while the trend for soil moisture is the opposite. Marshes and ponds feature markedly higher concentrations of soil organic matter than the mudflats ($p < 0.05$). Additionally, there is a clear link between soil particle size and coastal landscape types, with marshes and ponds predominantly composed of clay and silt, whereas mudflats and croplands are mostly sandy (Fig. 1). These observations indicate a discernible impact of coastal conversion on soil physicochemical properties, leading to reduced soil pH, salinity, and moisture, as well as changes in the distribution of soil particle sizes.

Table 1. Changes in soil physicochemical properties across different coastal landscapes

Properties	Coastal landscape				CV	p
	Marsh	Mudflat	Pond	Cropland		

pH	6.3±0.5b	6.9±0.4a	6.1±0.6b	5.6±0.4c	9.7	<0.001
Electrical conductivity (mS cm ⁻³)	8.7±2.4a	9.8±1.9a	6.0±2.5b	0.4±0.3c	44.2	<0.001
Salinity (‰)	5.5±1.5a	4.2±1.7b	4.3±2.4b	1.2±0.3c	46.3	<0.001
Bulk density (g cm ⁻³)	0.9±0.2c	1.1±0.3b	1.1±0.2b	1.4±0.1a	24.4	<0.001
Moisture (%)	68.9±18.8a	52.8±25.4b	52.6±16.6b	11.8±7.9c	44.3	<0.001
Organic matter (g kg ⁻¹)	9.6±3.6a	6.6±4.5b	10.7±3.2a	8.0±1.7ab	43.5	<0.001

The presented values are expressed as mean ± standard deviation. Different letters indicate statistically significant differences among various coastal landscapes ($p < 0.05$, ANOVA).

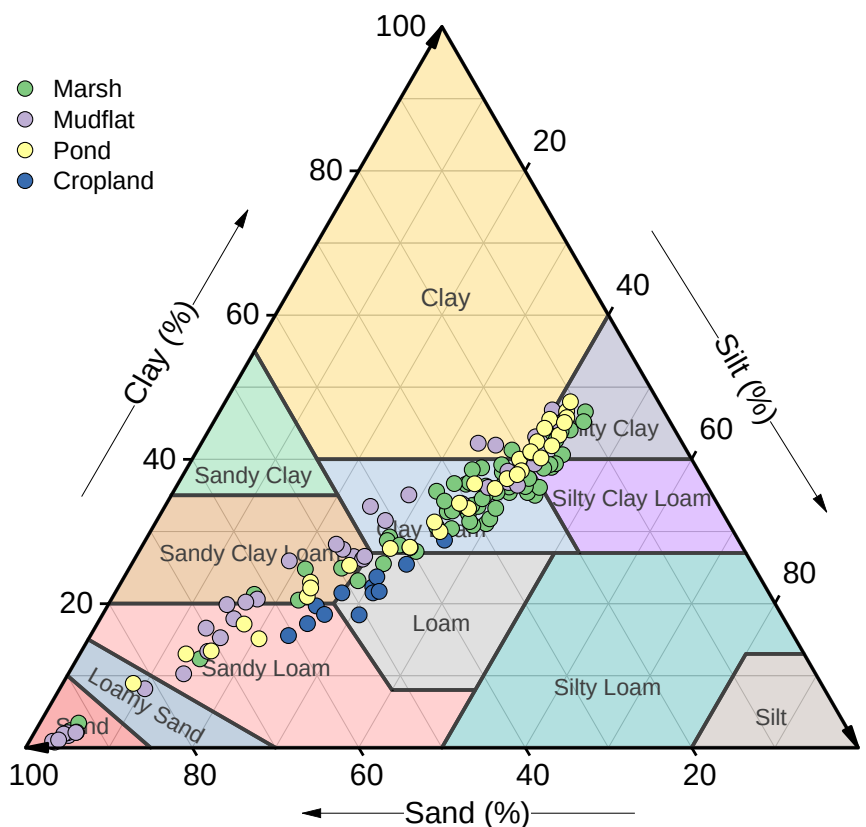


Fig. 1. Soil particle size distribution across different coastal landscapes.

3.2. Soil C, N and P concentrations and stocks

The concentrations of TC, TN, and TP varied from 0.7 g kg⁻¹ to 31.4 g kg⁻¹ (mean 10.5 ± 5.5 g kg⁻¹), from 0.1 g kg⁻¹ to 2.8 g kg⁻¹ (mean 1.0 ± 0.5 g kg⁻¹), and from 0.1 g kg⁻¹ to 2.2 g kg⁻¹ (mean 0.6 ± 0.3 g kg⁻¹) across different coastal landscapes, respectively (Fig. 2). Converted ponds exhibited considerably higher TC and TN concentrations compared to mudflats ($p < 0.05$). Furthermore, cropland soils have notably higher TN concentrations than mudflats. In terms of soil TP, croplands showed higher levels than other landscapes, while mudflats had the lowest. Croplands and ponds recorded the higher TC stocks than mudflats (13.1±8.2 Mg ha⁻¹). Comparatively, cropland soils experienced dramatic increases in soil TN (TP) stocks, rising by 97% (234%), 176% (341%) and 49% (146%) compared to marsh, mudflat, and pond soils, respectively. In summary, coastal conversion

has markedly elevated the levels of C, N and P in soils across diverse coastal landscapes, especially in croplands. From the perspective of soil C storage, whereas the conversion of mudflats to cropland or ponds can enhance the storage of topsoil C, but the conversion from marshes may not affect or could even result in the loss of stored C.

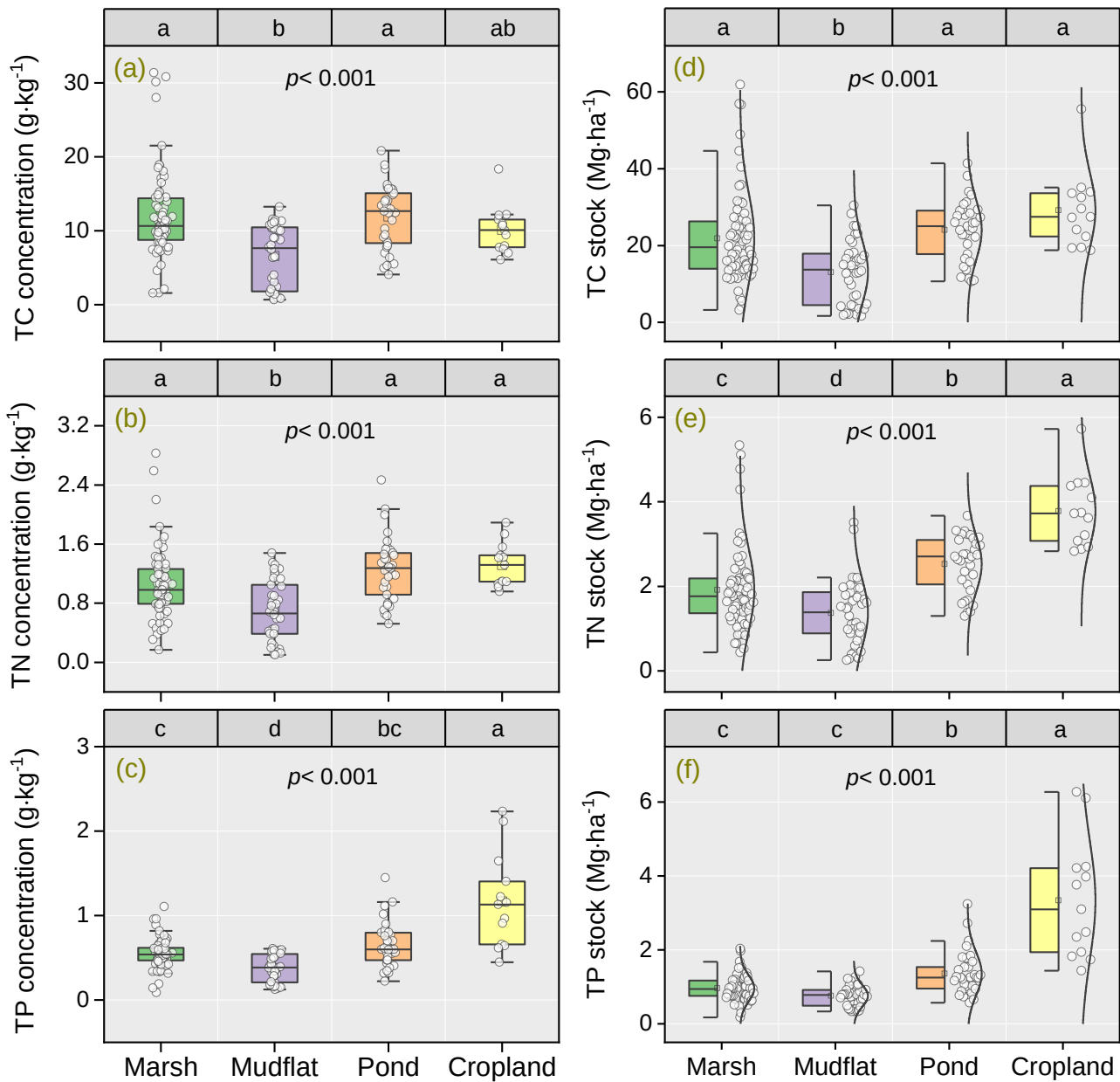


Fig. 2. Variations of topsoil TC, TN, and TP concentrations and storage across diverse coastal landscapes. TC, total carbon; TN, total nitrogen; TP, total phosphorus. Different letters indicate significant differences among various coastal landscapes ($p < 0.05$, ANOVA).

3.3. Available N and P dynamics

The concentration of soil $\text{NH}_4^+\text{-N}$ varied across different coastal landscapes, ranging from 0.2 mg kg^{-1} to 10.5 mg kg^{-1} . It is notably higher in croplands ($5.9 \pm 2.2 \text{ mg kg}^{-1}$) and ponds ($4.7 \pm 2.2 \text{ mg kg}^{-1}$) compared to marshes ($3.5 \pm 1.4 \text{ mg kg}^{-1}$) and mudflats ($3.4 \pm 1.2 \text{ mg kg}^{-1}$) (Fig. 3; $p < 0.05$). Soil concentrations of $\text{NO}_3^-\text{-N}$ and AP were significantly elevated in cropland soils, with the lowest values recorded in mudflats. Additionally, the $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, and AP stocks in cropland soils were

considerably higher than in other landscapes ($p < 0.05$), although they displayed notable spatial heterogeneity. Overall, soil management in croplands has substantially enhanced the levels and storages of available N and P.

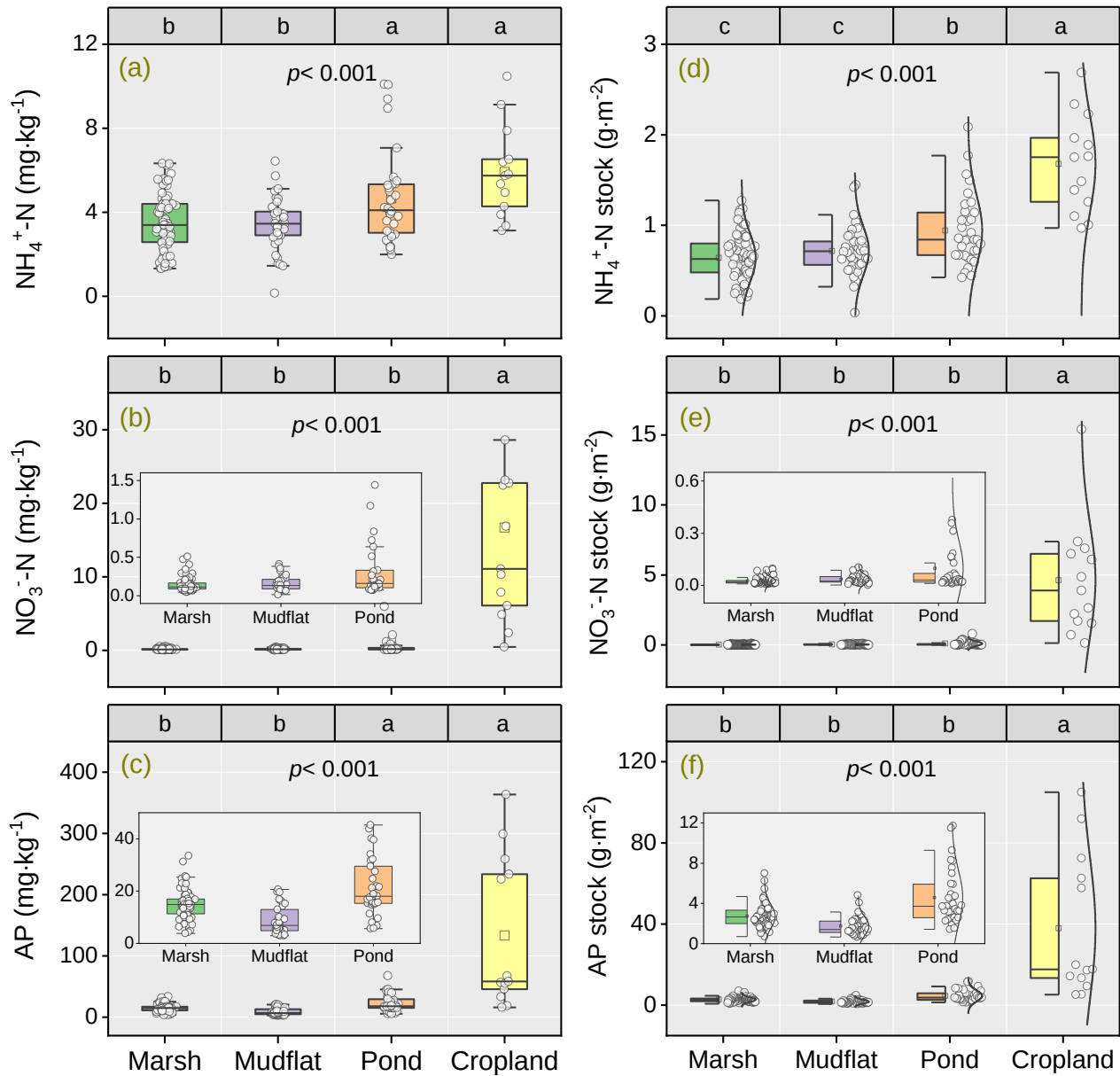


Fig. 3. Dynamics of soil $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, and AP concentrations and storages in different coastal landscapes. Different letters indicate significant differences among various coastal landscapes ($p < 0.05$, ANOVA).

3.4. Spatial distribution of soil C, N and P

The concentrations of soil TC, TN, and TP exhibited substantial spatial variability, with coefficient of variation (CV) of 52.6%, 47.2% and 54.7%, respectively (Fig. 4). Notably, high concentrations of TC and its hotspots were predominantly observed in marshes and ponds, significantly exceeding those in mudflats and croplands. Among these, mudflats presented the greatest spatial heterogeneity in TC, with a CV of 63.8%. Generally, soil TN, TP, and $\text{NH}_4^+\text{-N}$ concentrations have similar overall spatial patterns, showing higher values in croplands and ponds. The concentrations of $\text{NO}_3^-\text{-N}$ and AP in the soil demonstrated pronounced spatial variability, with CVs of 392.8% and 193.6%, respectively. The hotspots for these nutrients were primarily found in croplands. Overall, the dynamics of soil C, N,

and P along coastal areas are intricately associated with landscape types. Natural marshes exhibited a notably higher distribution of TC, while converted areas like croplands and ponds are identified as hotspots for N and P concentrations.

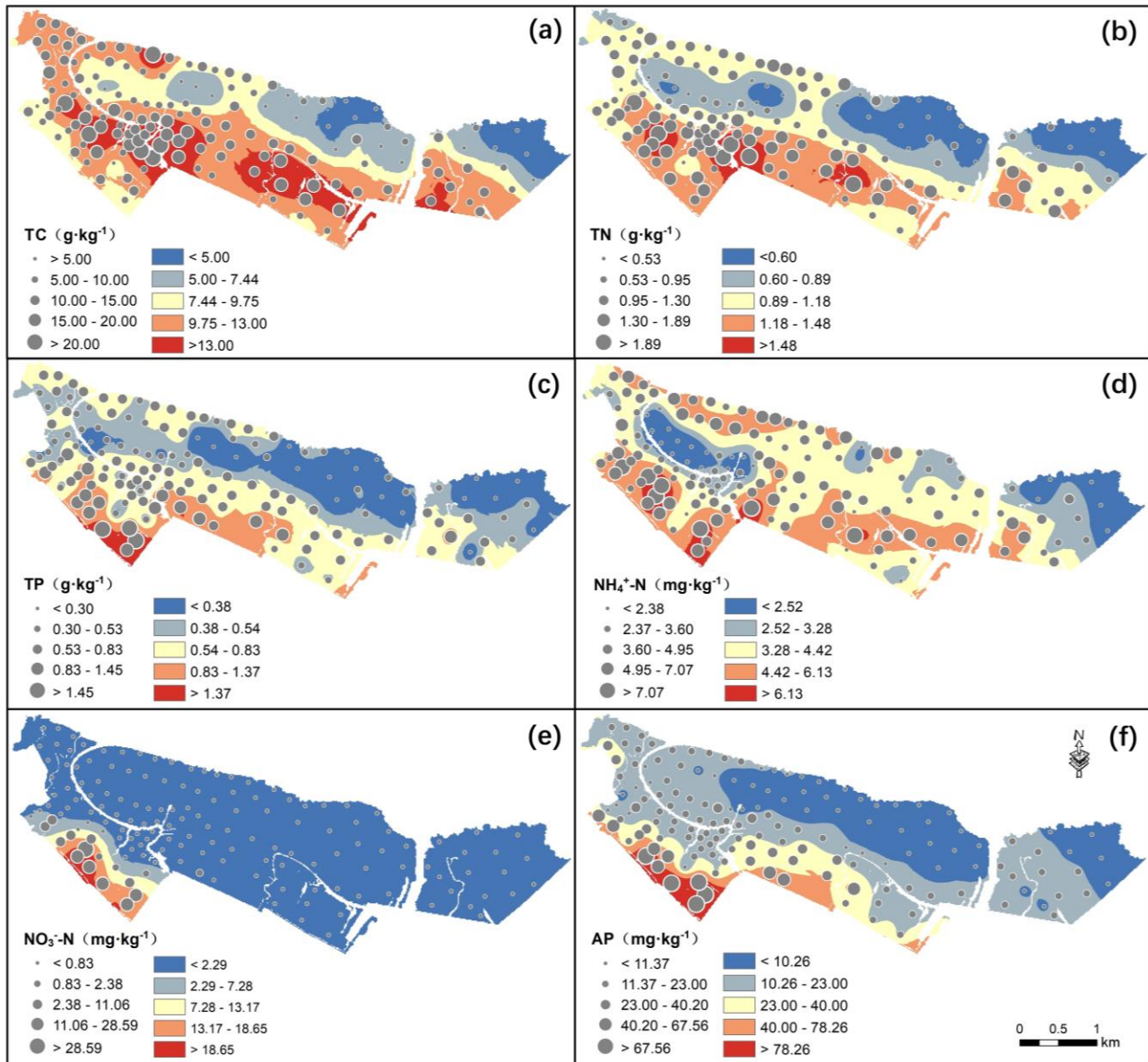


Fig. 4. Spatial distribution of soil TC, TN, TP, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$ and AP concentrations in the Min River estuarine wetland. TC, total carbon; TN, total nitrogen; TP, total phosphorus, $\text{NH}_4^+\text{-N}$, ammonium; $\text{NO}_3^-\text{-N}$, nitrate; AP, available phosphorus.

3.5. Soil C:N:P stoichiometry and distribution under different coastal landscapes

Soil C: N: P stoichiometry exhibited marked variations across different coastal landscapes (Fig. 5). The ranges for the C:N, C:P, and N:P ratios in soils were 4.2 to 28.3, 7.1 to 235.7, and 1.3 to 23.3, respectively, with corresponding CVs of 30.3%, 55.5%, and 50.2%. Marsh soils stood out, showing elevated C:N and C:P ratios with averages of 13.4 ± 3.5 and 57.5 ± 26.2 , respectively, which were notably higher than those found in other areas ($p < 0.05$). In contrast, cropland soils presented the lowest values for these ratios. The N:P ratios in cropland soils were particularly lower, averaging 2.9 ± 1.1 , further emphasizing the stoichiometric distinction among the coastal landscapes. The spatial

distribution of soil C:N and C:P ratios exhibited a consistent pattern, with marshes exhibiting significantly higher values than other environments. These ratios peaked primarily in marsh sites, indicating these sites as critical hotspots for such stoichiometric measures. Conversely, the soil N:P ratio distribution was more uniform, with the lowest values consistently found in cropland soils, suggesting a different nutrient dynamic in agricultural areas compared to natural coastal landscapes.

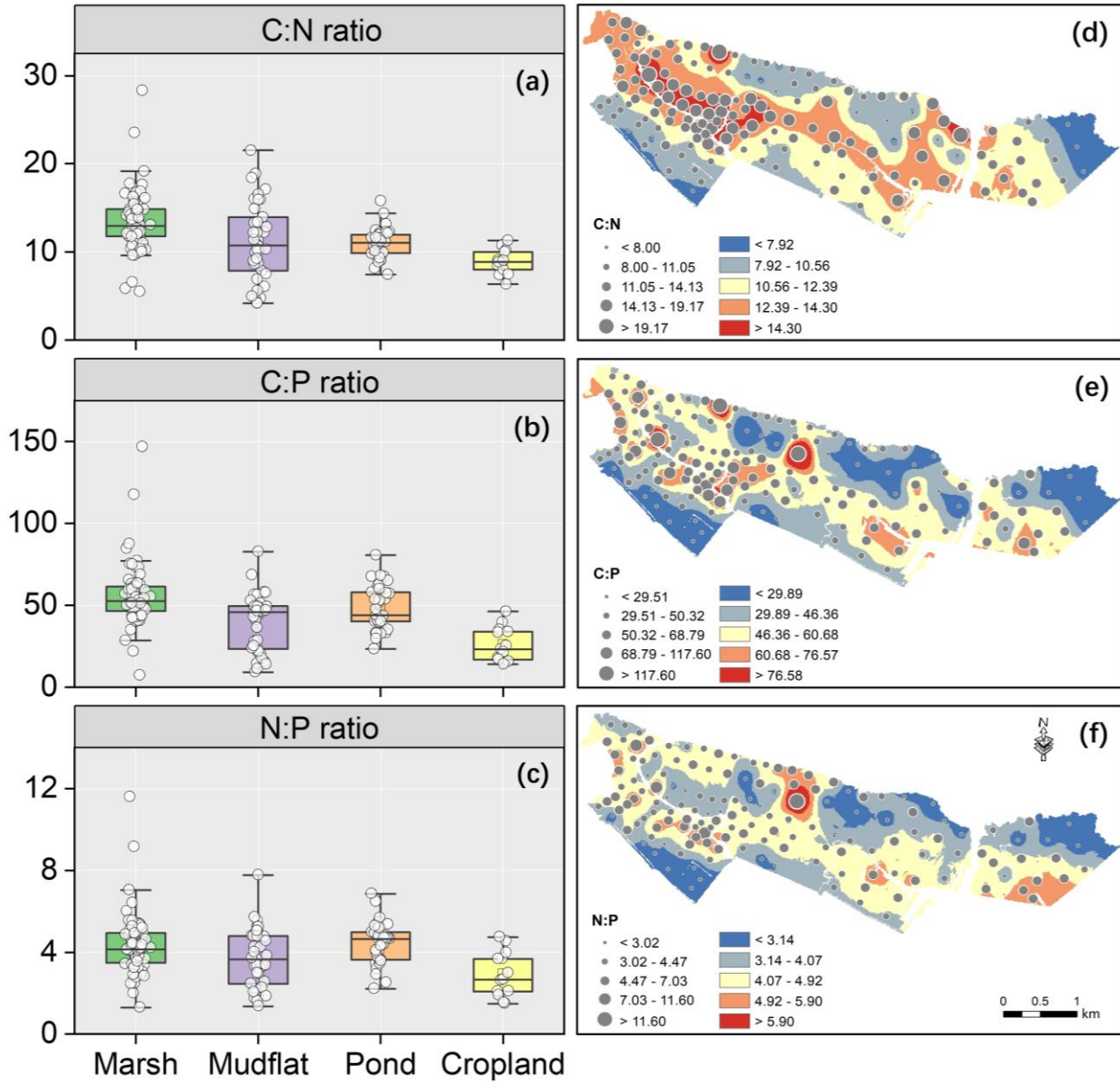


Fig. 5. Stoichiometric characteristics of soil C: N: P and their distributions in under different coastal landscapes.

3.6. Factors influencing the dynamics of C, N, and P

The study revealed strong correlations between TC concentrations and various factors such as SOM, pH, particle size, and salinity (Fig. 6). Similarly, soil TN concentrations were influenced by pH, SOM, particle size, and $\text{NH}_4^+\text{-N}$ concentrations. Soil TP concentrations were primarily affected by pH, salinity, SOM, bulk density, N availability, particle size, and AP concentrations. Heatmap analysis illustrated a negative correlation between soil pH and EC with the concentrations of $\text{NO}_3^-\text{-N}$, $\text{NH}_4^+\text{-N}$, and AP. Salinity was found to positively correlate with soil C:N, C:P, and N:P ratios, as well as SOM concentrations, while showing a negative correlation with $\text{NO}_3^-\text{-N}$ and AP concentrations.

Conversely, soil bulk density negatively correlated with soil C:N and C:P ratios, and SOM, but positively with NO_3^- -N and AP concentrations. Soil water content showed opposite trends. Additionally, the distribution of soil clay and silt was positively correlated with C:N, C:P, and N:P ratios, whereas sand displayed negative correlations. The Random Forest analysis identified soil organic matter, pH, and particle size distribution as the key soil parameters associated with the dynamics of soil C, N, and P. These findings indicate that a combination of soil physicochemical properties and nutrient status is key to understanding the variation in soil C, N, P dynamics across different coastal landscapes.

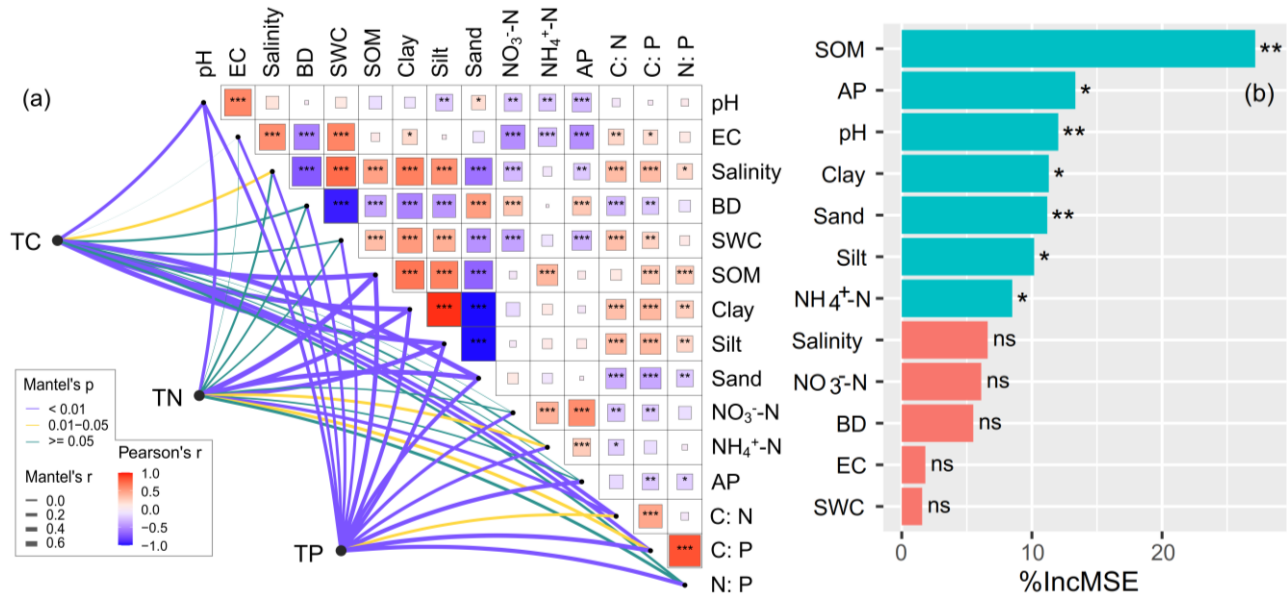


Fig. 6. Relationships between soil TC, TN, TP and soil physicochemical properties based on Mantel test (a) and the importance scores (%) of different factors estimated by the random forest model (b). The importance of each predictor is measured by the increment in Mean Squared Error (MSE) of each predictor. TC, total carbon; TN, total nitrogen; TP, total phosphorus; EC, electrical conductivity; BD, bulk density; SWC, soil water content; SOM, soil organic matter; AP, available phosphorus.

The RDA revealed that variables such as NH_4^+ -N, NO_3^- -N, AP, salinity, SWC, pH, EC, SOM, and clay content collectively accounted for 71% of the total variance in TC, TN, and TP (Fig. 7). The most determinant factors were soil NH_4^+ -N and AP concentrations ($F=96.2$, $P<0.0001$ and $F=63$, $P<0.0001$, respectively), followed by SOM ($F=101$, $P<0.0001$), pH ($F=30.9$, $P<0.0001$), and salinity ($F=49.1$, $P<0.0001$), mostly consistent with previous analyses. The case scores from different sites were distinctly separated along the first RDA axis, while the case scores from croplands were differentiated from the other three sites along the second RDA axis.

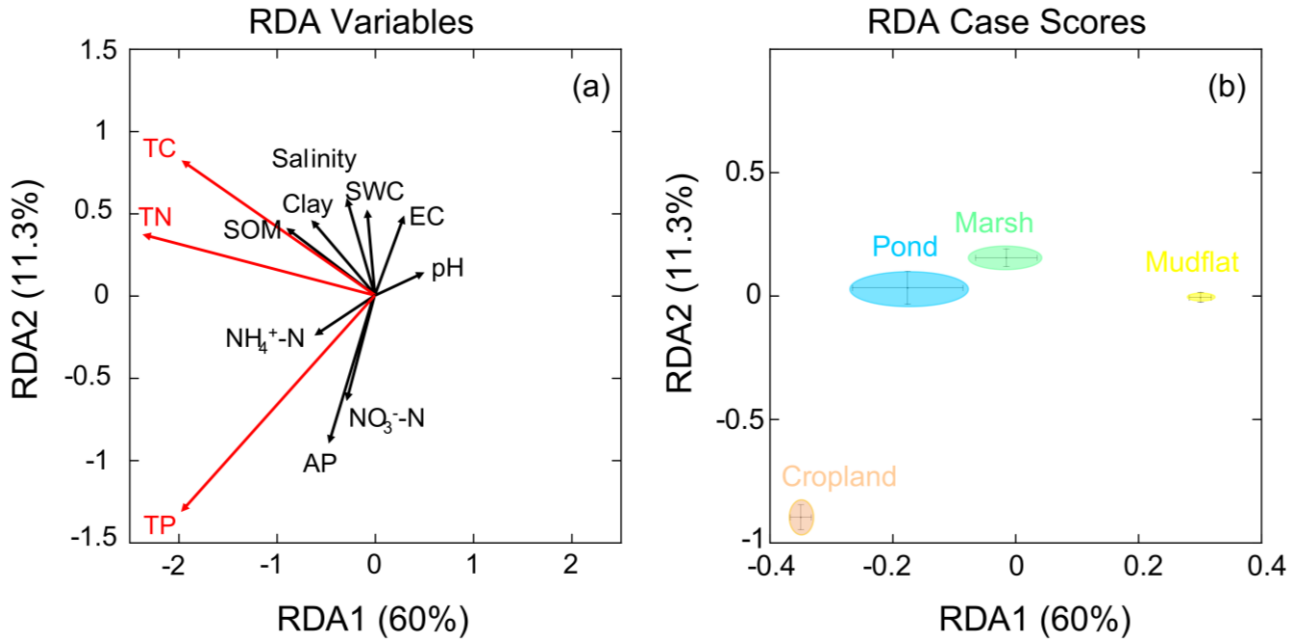


Fig. 7. Redundancy analyses with NH₄⁺-N, NO₃⁻-N, AP, Salinity, SWC, pH, EC, SOM and Clay as constraining (independent) variables and TC, TN and TP as dependent variables (a). The mean $\pm$ confidence interval (95%) of the cases scores if the two main RDA axes of different site (croplands, ponds, marshes and mudflats) are showed (b). TC, total carbon; TN, total nitrogen; TP, total phosphorus; EC, electrical conductivity; BD, bulk density; SWC, soil water content; SOM, soil organic matter; AP, soil available phosphorus.

4. Discussion

4.1. Soil C, N and P concentrations and stocks following coastal conversion

While numerous studies have been conducted on the dynamics of soil C, N, and P in response to land-use changes in terrestrial ecosystems, the results often present considerable uncertainties (Beillouin et al., 2022; Buruso et al., 2023; Li et al., 2020; Zheng et al., 2021). Moreover, there is a notable scarcity of research specifically targeting coastal conversion (Hu et al., 2024). In natural sites, the average TC concentrations varied significantly, ranging from 6.6 g kg⁻¹ in coastal mudflats to 12.1 g kg⁻¹ in marshes, with an overall mean of 10.1 g kg⁻¹ (Fig. 2). These observed concentrations were comparable to those found in the Liaohe estuary (12.6 g kg⁻¹), yet markedly lower than those in the Yangtze River estuary (23.2 g kg⁻¹), and higher than in the Yellow River estuary (4.7 g kg⁻¹) (Xia et al., 2022). The variations in soil C concentrations across these regions can be attributed to diverse factors such as distinct climatic conditions and dominant vegetation, as well as unique soil types and sedimentation histories. For instance, the coastal wetland in this study, situated in a subtropical zone, benefits from higher temperatures that foster vigorous plant growth and result in an increased input of organic matter (Hu et al., 2020b). Conversely, the wetland at the Yellow River estuary, located in a temperate zone, experiences lower average temperatures which contribute to a slower rate of organic matter decomposition. Furthermore, marshes exhibit higher soil C concentrations than mudflats, primarily due to the abundant plant biomass that directly contributes to soil organic matter accumulation (Xia et al., 2023). The anaerobic or anoxic environments in these marshes also effectively inhibit microbial decomposition of organic matter, thereby further enhancing soil C concentration (Lu et al., 2023). This is confirmed by a substantial positive correlation observed between soil C concentrations and organic matter (Fig. 6).

In the coastal soils, TN concentrations varied from 0.7 g kg⁻¹ in mudflats to 1.1 g kg⁻¹ in marshes, averaging 0.9 g kg⁻¹ overall. Similarly, TP concentrations ranged from 0.4 g kg⁻¹ in mudflats to 0.6 g kg⁻¹ in marshes, with a mean of 0.5 g kg⁻¹. These values closely align with those observed in the Yellow River estuary, where both TN and TP were recorded at 0.7 g kg⁻¹, but they were lower than the concentrations in the Yangtze River estuary, which were 1.9 g kg⁻¹ for TN and 1.0 g kg⁻¹ for TP (Xia et al., 2022). In coastal wetlands, N and P frequently act as limiting nutrients, critically influencing primary productivity and nutrient cycling (Sundareshwar et al., 2003). The lower N and P concentrations observed in these coastal wetlands indicate on one hand that vigorous plant growth increases the absorption of soil nutrients and/or that potential N and P availability is naturally low, as evidenced by the observed low concentrations of available N and P (Fig. 3). Moreover, soil N and P concentrations in marshes are generally higher than those in mudflats. This difference may be attributed to the combined effects of various ecological processes. In marshes, plants absorb and accumulate nutrients for growth and return them to the soil upon decomposition, leading to a progressive build-up of organic matter rich in N and P (Spohn and Berg, 2023). Additionally, vegetation stabilizes the soil, thereby mitigating erosion and the consequent loss of nutrient-rich sediments, while root systems foster microbial activities that further enhance nutrient cycling (Henneron et al., 2020; Tang et al., 2021). Vegetated areas also act as natural traps for nutrient-rich sediments carried by tidewater, thereby enriching the soil. Together, these factors create a nutrient-richer environment in vegetated marshes compared to the typically nutrient-scarce conditions found in mudflats. These scenarios are corroborated by the markedly higher organic matter concentration in marsh soils (Fig. 1), alongside a significant positive correlation between soil organic matter and TC concentration (Fig. 6a).

The reclamation of coastal wetlands for agriculture and aquaculture has significantly altered the concentrations and stocks of C, N, and P in the topsoil. In particular, ponds that were previously used for aquaculture show higher soil C concentrations than natural mudflats, mainly due to factors related to their historical usage and current ecological dynamics (Hu et al., 2023b). The elevated initial C levels in these ponds are often a legacy of their previous aquaculture period, where substantial organic matter was accumulated from uneaten feed, feces, and other biological wastes (Yuan et al., 2021). As these ponds recover, this organic accumulation, along with contributions from bird droppings and plant residue, continues to enhance the soil C concentration (Yang et al., 2022). Additionally, the enclosed nature of these ponds reduces erosion and promote more stable sedimentation, further fostering conditions that favor the preservation and build-up of organic C in the soil. In addition, N concentrations in cropland soil are typically higher than those in mudflats, while P concentrations significantly surpass those found in both marsh and mudflat soils. This disparity is largely due to agricultural practices such as tilling, crop rotation, and the application of fertilizers or compost, all of which significantly contribute to nutrient enrichment (Zheng et al., 2021). Additionally, the decomposition of plant residues left in fields after harvesting also increases the nutrient pool. Cropland soils, characterized by better drainage and aeration, facilitate microbial activities that efficiently convert organic forms of N and P into inorganic, making these nutrients more readily available (Gramlich et al., 2018; Yang and Norton, 2019). In contrast, the saturated soil conditions of wetlands lead to slower decomposition rates owing to limited oxygen availability, thereby resulting in lower levels of these nutrients (Lu et al., 2023; Mueller et al., 2017). Additionally, the stocks of soil C, N, and P follow a similar pattern. Compared to mudflats, converted cropland or ponds lead to an increase in topsoil C stocks, while this effect is not observed in marshes.

The RDA, along with other statistical analyses, indicated that $\text{NH}_4^+\text{-N}$, AP, SOM, pH, and clay are the soil variables most closely associated with soil TC, TN, and TP (Figs. 6-7). It also revealed that mudflats possess soils with higher pH and lower values of SOM. In contrast, marsh soils exhibit higher SOM levels and proportionally higher TC values relative to TN and TP. Ponds have proportional TN values in relation to TC and TP. Cropland soils, however, display the highest absolute values of available-N and -P, with proportionally higher TP values. This data suggests that the distinct management practices of ponds and especially croplands effectively reshape soil conditions. Long-term application of N and P fertilizers in croplands tends to increase nutrient concentrations. However, P, being the most immobile and prone to retention in the soil through salt precipitation and adsorption processes, tends to accumulate at high levels in non-plant-available forms in intensively fertilized croplands (Hu et al., 2023a; Lambers, 2022; Peñuelas and Sardans, 2022). Similarly, in ponds, the substantial accumulation of fish and shrimp waste leads to higher levels of TC, TN, and TP, but with a higher proportional amount of TN compared to other natural sites, aligning with the widely observed high N concentrations in animal feces (Ghojoghi et al., 2023; Yang et al., 2022; Yuan et al., 2021).

4.2. Land uses and soil managements cause C:N:P stoichiometry imbalance

Ecological stoichiometry, which focuses on the balance of key chemical elements like C, N, and P, is crucial for understanding the nutrient needs and limitations of various organisms, as well as for assessing ecosystem responses to environmental changes (Cleveland and Liptzin, 2007; Isles, 2020; Peñuelas and Sardans, 2022). In our study, the average soil C:N:P ratios for natural wetlands were found to be 52.8:4.3:1 (Fig. 5). These ratios are lower than the global scale ratios of 186:13:1 reported by Cleveland and Liptzin (2007), yet they align closely with the average ratios of 60:5:1 observed in China on a national scale (Tian et al., 2010). This variation in these ratios can be partially attributed to differences in ecosystem types, decomposition rates, vegetation diversity, and specific environmental conditions, such as nutrient loadings and hydrological dynamics. For instance, Cleveland and Liptzin (2007) focused on forest and grassland ecosystems, which typically have a higher C concentration due to the abundance of C-rich plant materials, including trees. In contrast, the water-saturated and anaerobic conditions prevalent in wetlands facilitate the enhanced cycling and enrichment of N and P, resulting in comparatively lower C:N:P ratios (Baldwin and Mitchell, 2012; Hu et al., 2020a). Therefore, the soil C:N:P ratios in wetland ecosystems exhibit significant differences when compared to those in terrestrial ecosystems like forests and grasslands. Our data offer a valuable contribution to the understanding of global soil nutrient balances, enriching the existing body of knowledge with specific insights into wetland soil dynamics.

In the present study, we observed that C:N:P ratios were typically higher in natural sites (52.8:4.3:1) than in converted sites (42.1:4:1), particularly in cropland sites (25.9:2.9:1). This variation is understandable given the distinct environmental conditions of these ecosystems. Wetlands, characterized by their waterlogged conditions, foster anaerobic environments that significantly slow down the decomposition process of organic matter (Mueller et al., 2017). This leads to an accumulation of C-rich plant materials, which decompose more slowly compared to the plant and animal residues typically found in cropland soils. Moreover, the anaerobic conditions in wetlands restrict the processes of N and P mineralization, thereby reducing the relative availability of these nutrients compared to C (Fellman and D'Amore, 2007). In contrast, cropland soils are usually well-aerated and subjected to agricultural practices like fertilization, which receives additions of N and P-rich substances (Gramlich et al., 2018; Ma et al., 2022). These practices alter the soil nutrient

composition, resulting in a lower C:N ratio compared to natural landscapes. These observations further corroborate the notion that organic-rich topsoil, characterized by its dynamic interactions between organisms and the environment and its well-regulated C:N:P ratios, can effectively indicate the nutrient status of soil during soil development (Tian et al., 2010).

In addition, our study highlighted that the soil N:P ratio in cropland soils (2.9 ± 1.1) was significantly lower compared to marshes (4.3 ± 1.5), mudflats (4.2 ± 3.5), and ponds (4.4 ± 1.0). This observation is typical in cropland regions subjected to long-term P fertilization, where a substantial portion of the applied P either precipitates or is strongly adsorbed, resulting in an increase in TP stocks without a corresponding rise in plant-available P. The N cycle within soil is dynamic and complex, encompassing processes such as mineralization, nitrification, and denitrification, which contribute to N loss through leaching, gaseous emissions, and other pathways (Henneron et al., 2020; Zhang et al., 2020). The rapid absorption of N by fast-growing crops leading to a rapid depletion of available N in the soil. When crops are harvested, the N accumulated within them is removed from the soil system, thereby reducing the soil's N storage (Zhang et al., 2021). This dynamic also highlights the significant role of soil P concentration in influencing the C:P and N:P ratios. Phosphorus in the soil is typically found in mineral forms, which are stable and not easily lost through gaseous pathways as N (Hu et al., 2023b). Moreover, the extended and intensive use of N fertilizers in cropland systems can create a relative surplus of other nutrients, including P, thereby contributing to the reduced N:P ratio and an imbalance between N and P (Peñuelas and Sardans, 2022). These findings indicate that long-term application of N and P fertilizers tends to lower the soil N:P ratio, as N is rapidly utilized and lost in significant quantities, while P remains more stable and is retained more effectively in the soil.

4.3. Spatial patterns of soil C, N, and P concentrations and C:N:P ratios

Land use changes, such as deforestation, urbanization, or conversion to agriculture, can profoundly impact the spatial distribution of soil C, N, and P, along with their stoichiometry, due to alterations in vegetation cover, soil management, and environmental interactions (Li et al., 2020; Tian et al., 2010; Zhang et al., 2023). In our study, the concentrations of soil TC, TN, and TP across various coastal landscapes exhibited substantial spatial heterogeneity, with coefficient of variation (CV) of 52.6%, 47.2% and 54.7%, respectively (Fig. 4). Notably, high concentrations of TC and its hotspots were predominantly observed in marshes and ponds, significantly exceeding those in mudflats and croplands. Among these, the spatial heterogeneity of TC in mudflats was the greatest (CV 63.8%), while it was the least in cropland (CV 31.6%). These results are consistent with the size of the area that occupied the four sites in 2D plot with the two first axes of the RDA analyses, where we can observe that the two managed ecosystems have lower distribution surface than the two natural ecosystems. Mudflats, dynamic environments influenced by tidal actions, riverine inputs, and wave activities, exhibit greatly varied sediment deposition (Redzuan and Underwood, 2020; Sasmito et al., 2020). This leads to uneven distribution of organic matter, and consequently, C concentration can vary significantly across different areas of the mudflat. In contrast, croplands typically undergo uniform agricultural practices aimed at optimizing soil conditions for crop growth, resulting in more homogenized soil properties, including C concentration.

Generally, soil TN, TP, and $\text{NH}_4^+\text{-N}$ concentrations across different landscapes exhibit similar spatial patterns, with natural sites showing higher overall CV than converted sites. Further, converted sites, particularly croplands, exhibit significantly more hotspots and peaks in N and P distribution. This is mainly attributed to the concentrated application of N and P fertilizers in these areas, which can result in a lasting impact on nutrient accumulation and current distribution patterns (Ma et al.,

2022; Yang and Norton, 2019). In contrast, natural marshes and mudflats tend to show relatively low and uniform distributions of soil $\text{NH}_3\text{-N}$ and AP, while ponds and croplands demonstrate high spatial heterogeneity, with CVs of 207.9% and 60.1% for ponds, and 94.9% and 92.3% for croplands, respectively. This alteration in nutrient dynamics also impacts the stoichiometric distribution of soil C, N, and P in different coastal landscapes. The average CVs for soil C:N and C:P ratios are 30.3% and 55.5%, respectively, with the highest variability observed in mudflats (40.0% and 81.9%). The dynamic nature of mudflats, including their flooding and draining cycles, significantly influences the distribution and decomposition of organic matter and nutrients (Sasmito et al., 2020). Additionally, the higher C concentration in mudflats versus the higher N and P concentration in croplands also contributes to this stoichiometric imbalance. The soil N:P ratio also displays significant spatial heterogeneity (50.2%), with less internal spatial variation in croplands and ponds, which is mainly attributable to human management practices (Fig. 8).

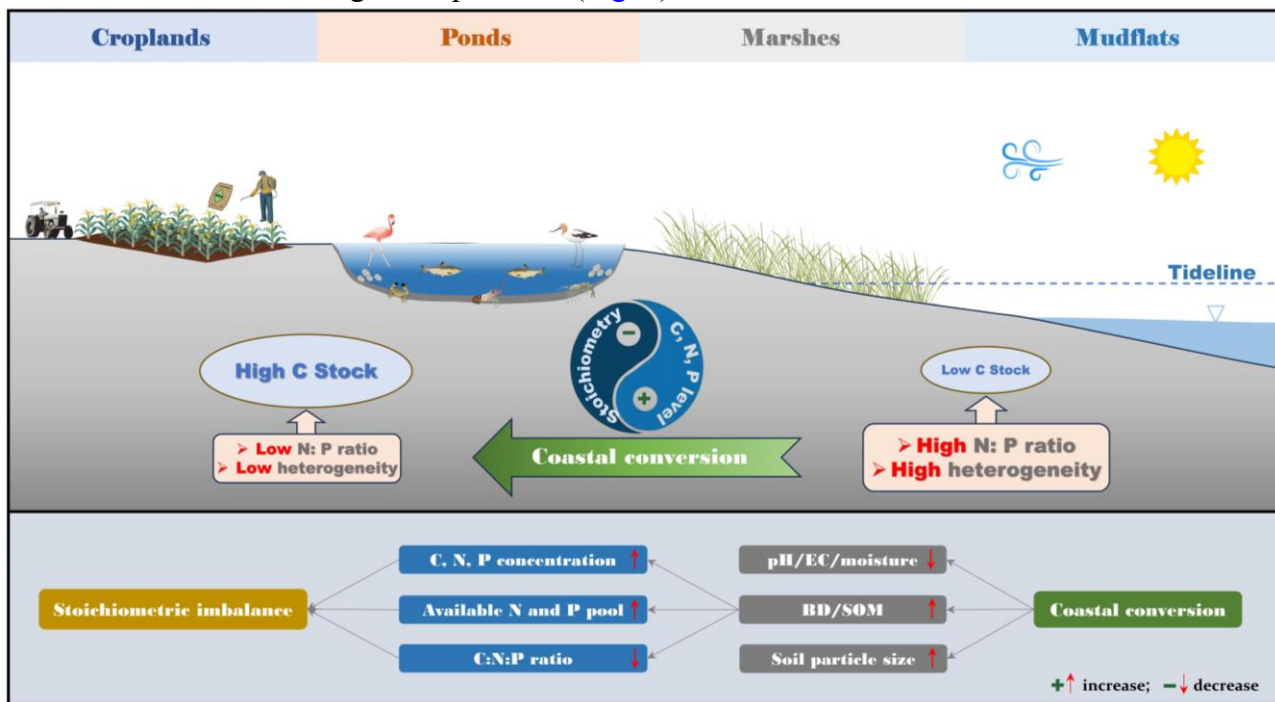


Fig. 8. The conceptual framework showing the effects of coastal conversion on soil C, N and P dynamics and stoichiometric balances. C, carbon; N, nitrogen; P, phosphorus; EC, electrical conductivity; BD, bulk density; SOM, soil organic matter.

5. Conclusions

This study provides valuable insights into the potential effects of coastal conversion on nutrient cycling by examining the dynamics of soil C, N, and P, as well as their stoichiometric relationships. The results demonstrate a significant correlation between soil nutrient dynamics and land use practices in coastal regions. Specifically, natural mudflats displayed lowest total C stocks, while converted areas such as croplands and ponds serve as hotspots for C, N and P concentration. This emphasizes the nutrient shifts resulting from coastal conversion, highlighting that the conversion of mudflats into cropland or ponds can enhance topsoil C stocks, whereas converting marshes may not significantly impact or might even decrease C stocks. The study also points out imbalances in C:N:P ratios, indicating that the prolonged use of N and P fertilizers in croplands tends to lower the soil N:P ratio due to the rapid consumption of N while P remains more stable and accumulates in the soil. In

addition, natural marshes and mudflats exhibit greater spatial heterogeneity compared to the more uniform soil properties of converted croplands and ponds, likely a result of consistent agricultural practices. These insights reveal that coastal land conversion alters topsoil C, N and P stocks and stoichiometric balances. Conversion from mudflats to croplands or ponds increases soil C stocks relative to marshes, and converted croplands exhibit higher levels of available N and P compared to ponds. Future research should broaden its focus to encompass a wider range of coastal ecosystems and landscapes, providing a more comprehensive understanding of soil nutrient dynamics and their implications at both regional and global scales.

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References

- Baldwin, D.S., Mitchell, A.M., 2012. Impact of sulfate pollution on anaerobic biogeochemical cycles in a wetland sediment. *Water Res.* 46, 965-974.
- Beillouin, D., Cardinael, R., Berre, D., Boyer, A., Corbeels, M., Fallot, A., Feder, F., Demenois, J., 2022. A global overview of studies about land management, land-use change, and climate change effects on soil organic carbon. *Global Change Biol.* 28, 1690-1702.
- Buruso, F.H., Zenebe Adimassu, Sibali., L.L., 2023. Effects of land use/land cover changes on soil properties in Rib watershed, Ethiopia. *Catena* 224 106977.
- Chirinda, N., Elsgaard, L., Thomsen, I.K., Heckrath, G., Olesen, J.E.J.C., 2014. Carbon dynamics in topsoil and subsoil along a cultivated toposequence. *Catena* 120, 20-28.
- Cleveland, C.C., Liptzin, D., 2007. C:N:P stoichiometry in soil: is there a “Redfield ratio” for the microbial biomass? *Biogeochemistry* 85(3), 235-252.
- Cui, L., Li, G., Chen, Y., Li, L., 2021. Response of landscape evolution to human disturbances in the coastal wetlands in Northern Jiangsu Province, China. *Remote Sens.* 13, 2030.
- Fellman, J.B., D’Amore, D.V., 2007. Nitrogen and phosphorus mineralization in three wetland types in southeast Alaska, USA. *Wetlands* 27(1), 44-53.
- Ghojoghi, A., Ghorbani, R., Patimar, R., Salmanmahiny, A., Naddafí, R., Fazel, A., Jardine, T.D., 2023. The fate of nitrogen in the Zarin-Gol River receiving trout farm effluent. *Sci. Rep.* 13, 21762.
- González, I., Déjean, S., Martin, P.G.P., Baccini, A., 2008. CCA: An R package to extend canonical correlation analysis. *J. Stat. Softw.* 23, 1-14.
- Gramlich, A., Stoll, S., Stamm, C., Walter, T., Prasuhn, V., 2018. Effects of artificial land drainage on hydrology, nutrient and pesticide fluxes from agricultural fields – A review. *Agr. Ecosyst. Environ.* 266, 84-99.
- Gu, J., Luo, M., Zhang, X., Christakos, G., Agustí, S., Duarte, C.M., Wu, J., 2018. Losses of salt marsh in China: Trends, threats and management. *Estuar. Coast. Shelf S.* 214, 98-109.
- Henneron, L., Kardol, P., Wardle, D.A., Camille, C., Fontaine, S., 2020. Rhizosphere control of soil nitrogen cycling: a key component of plant economic strategies. *New Phytol.* 228, 1269-1282.
- Hu, M., Le, Y., Sardans, J., Yan, R., Zhong, Y., Sun, D., Tong, C., Peñuelas, J., 2023a. Moderate salinity improves the

- availability of soil P by regulating P-cycling microbial communities in coastal wetlands. *Global Change Biol.* 29, 276-288.
- Hu, M., Peñuelas, J., Sardans, J., Yang, X., Tong, C., Zou, S., Cao, W., 2020a. Shifts in microbial-biomass C:N:P stoichiometry and bacterial community composition in subtropical estuarine tidal marshes along a gradient of freshwater–oligohaline water. *Ecosystems* 23, 1265–1280.
- Hu, M., Sardans, J., Le, Y., Yan, R., Peñuelas, J., 2023b. Coastal wetland conversion to aquaculture pond reduced soil P availability by altering P fractions, phosphatase activity, and associated microbial properties. *Chemosphere* 311, 137083.
- Hu, M., Sardans, J., Yang, X., Peñuelas, J., Tong, C., 2020b. Patterns and environmental drivers of greenhouse gas fluxes in the coastal wetlands of China: A systematic review and synthesis. *Environ. Res.* 186, 109576.
- Hu, M., Yan, R., Ni, R., Wu, H., 2024. Coastal degradation regulates the availability and diffusion kinetics of phosphorus at the sediment-water interface: Mechanisms and environmental implications. *Water Res.* 250, 121086.
- Isles, P.D.F., 2020. The misuse of ratios in ecological stoichiometry. *Ecology* 101, e03153.
- Jiang, T., Pan, J.-F., Pu, X., Wang, B., Pan, J.-J., 2015. Current status of coastal wetlands in China: Degradation, restoration, and future management. *Estuar. Coast. Shelf S.* 164, 265-275.
- Karstens, S., Buczko, U., Jurasinski, G., Peticzka, R., Glatzel, S., 2016. Impact of adjacent land use on coastal wetland sediments. *Sci. Total Environ.* 550, 337-348.
- Lambers, H., 2022. Phosphorus acquisition and utilization in plants. *Annu. Rev. Plant Biol.* 73, 17-42.
- Li, H., Zhu, H., Qiu, L., Wei, X., Liu, B., Shao, M., 2020. Response of soil OC, N and P to land-use change and erosion in the black soil region of the Northeast China. *Agr. Ecosyst. Environ.* 302, 107081.
- Liu, Y., Ma, W., Kou, D., Niu, X., Wang, T.-Y., Chen, Y., Chen, D., Zhu, X., Zhao, M., Hao, B., Zhang, J., Yang, Y., Hu, H., 2020. A comparison of patterns of microbial C : N : P stoichiometry between topsoil and subsoil along an aridity gradient. *Biogeosciences* 17, 2009-2019.
- Lu, Z., Xiao, K., Wang, F., Wang, Y., Yu, Q., Chen, N., 2023. Salt marsh invasion reduces recalcitrant organic carbon pool while increases lateral export of dissolved inorganic carbon in a subtropical mangrove wetland. *Geoderma* 437, 116573.
- Ma, P., Nan, S., Yang, X., Qin, Y., Ma, T., Li, X.-l., Yu, Y., Bodner, G., 2022. Macroaggregation is promoted more effectively by organic than inorganic fertilizers in farmland ecosystems of China—A meta-analysis. *Soil Till. Res.* 221, 105394.
- Ma, Z., Melville, D.S., Liu, J., Chen, Y., Yang, H., Ren, W., Zhang, Z., Piersma, T., Li, B., 2014. Rethinking China's new great wall. *Science* 346, 912- 914.
- Mueller, P., Schile-Beers, L.M., Mozdzer, T.J., Chmura, G.L., Dinter, T.G.V., Kuzyakov, Y., de Groot, A.V., Esselink, P., Smit, C., D'Alpaos, A., Ibáñez, C., Lazarus, M., Neumeier, U., Johnson, B.J., Baldwin, A.H., Yarwood, S.A., Montemayor, D.I., Yang, Z., Wu, J., Jensen, K., Nolte, S., 2017. Global-change effects on early-stage decomposition processes in tidal wetlands-implications from a global survey using standardized litter. *Biogeosciences* 15, 3189-3202.
- Oksanen, J., 2010 <http://vegan.r-forge.r-project.org/>, 2010.
- Olsen, S.R., Sommers, L.E., 1982. Phosphorus. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), *Methods of Soil Analysis*, 2nd ed. Agronomy Series No. 9, Part 2 Soil Science Society of America, Inc., Madison, WI, pp. 403–430.
- Peñuelas, J., Sardans, J., 2022. The global nitrogen-phosphorus imbalance. *Science* 375(6578), 266-267.
- Redzuan, N.S., Underwood, G.J.C., 2020. Movement of Microphytobenthos and Sediment Between Mudflats and Salt Marsh During Spring Tides. *Front. Mar. Sci.* 7, 496.
- Rodríguez, J.F., Saco, P.M., Sandi, S.G., Saintilan, N., Riccardi, G.A., 2017. Potential increase in coastal wetland vulnerability to sea-level rise suggested by considering hydrodynamic attenuation effects. *Nat. Commun.* 8, 16094.
- Sasmito, S.D., Kuzyakov, Y., Lubis, A.A., Murdiyarso, D., Hutley, L.B., Bachri, S., Friess, D.A., Martius, C., Borchard,

- N., 2020. Organic carbon burial and sources in soils of coastal mudflat and mangrove ecosystems. *Catena* 187, 104414.
- Schuerch, M., Spencer, T., Temmerman, S., Kirwan, M.L., Wolff, C., Lincke, D., McOwen, C.J., Pickering, M.D., Reef, R., Vafeidis, A.T., Hinkel, J., Nicholls, R.J., Brown, S., 2018. Future response of global coastal wetlands to sea-level rise. *Nature* 561, 231-234.
- Smal, H., Ligęza, S., Pranagal, J., Urban, D., Pietruczyk-Popławska, D., 2019. Changes in the stocks of soil organic carbon, total nitrogen and phosphorus following afforestation of post-arable soils: A chronosequence study. *Forest Ecol. Manag.* 451, 117536.
- Spencer, T., Schuerch, M., Nicholls, R.J., Hinkel, J., Lincke, D., Vafeidis, A.T., Reef, R., McFadden, L., Brown, S., 2016. Global coastal wetland change under sea-level rise and related stresses: The DIVA Wetland Change Model. *Global Planet. Change* 139, 15-30.
- Spohn, M., Berg, B., 2023. Import and release of nutrients during the first five years of plant litter decomposition. *Soil Biol. Biochem.* 176, 108878.
- Sun, Z.G., Sun, W.L., Tong, C., Zeng, C.S., Yu, X., Mou, X.J., 2015. China's coastal wetlands: Conservation history, implementation efforts, existing issues and strategies for future improvement. *Environ. Int.* 79, 25-41.
- Sundareshwar, P.V., Morris, J.T., Koepfler, E., Fornwalt, B., 2003. Phosphorus limitation of coastal ecosystem processes. *Science* 299, 563-565.
- Tang, C., Liu, Y., Li, Z., Guo, L., Xu, A., Zhao, J., 2021. Effectiveness of vegetation cover pattern on regulating soil erosion and runoff generation in red soil environment, southern China. *Ecol. Indic.* 129, 107956.
- Tian, H., Chen, G., Zhang, C., Melillo, J.M., Hall, C.A.S., 2010. Pattern and variation of C:N:P ratios in China's soils: a synthesis of observational data. *Biogeochemistry* 98(1), 139-151.
- Wang, W., Sardans, J., Wang, C., Zeng, C., Tong, C., Chen, G., Huang, J., Pan, H., Peguero, G., Vallicrosa, H., Peñuelas, J., 2018. The response of stocks of C, N, and P to plant invasion in the coastal wetlands of China. *Global Change Biol.* 25, 733-743.
- Wang, X., Xiao, X., Xu, X., Zou, Z., Chen, B., Qin, Y., Zhang, X.Z., Dong, J., Liu, D., Pan, L., Li, B., 2021. Rebound in China's coastal wetlands following conservation and restoration. *Nat. Sustain.* 4, 1076-1083.
- Wei T, V, S., 2021. R package 'corrplot': Visualization of a Correlation Matrix. (Version 0.92). <https://github.com/taiyun/corrplot>.
- Xia, S., Song, Z., van Zwieten, L., Guo, L., Yu, C., Wang, W., Li, Q., Hartley, I.P., Yang, Y., Liu, H., Wang, Y., Ran, X., Liu, C., Wang, H., 2022. Storage, patterns and influencing factors for soil organic carbon in coastal wetlands of China. *Global Change Biol.* 28, 6065-6085.
- Xia, S., Song, Z., Wang, W., Fan, Y., Guo, L., van Zwieten, L., Hartley, I.P., Fang, Y., Wang, Y., Zhang, Z., Liu, C.-Q., Wang, H., 2023. Patterns and determinants of plant-derived lignin phenols in coastal wetlands: Implications for organic C accumulation. *Funct. Ecol.* 37, 1067-1081.
- Xu, C., Pu, L., Li, J., Zhu, M., 2018. Effect of reclamation on C, N, and P stoichiometry in soil and soil aggregates of a coastal wetland in eastern China. *J. Soil Sediment* 19, 1215-1225.
- Yang, O., Norton, J.M., 2019. Short-term nitrogen fertilization affects microbial community composition and nitrogen mineralization functions in an agricultural soil. *Appl. Environ. Microb.* 86, e02278-02219.
- Yang, P., Zhang, L., Lai, D.Y.F., Yang, H., Tan, L., Luo, L., Tong, C., Hong, Y., Zhu, W., Tang, K.W., 2022. Landscape change affects soil organic carbon mineralization and greenhouse gas production in coastal wetlands. *Global Biogeochem. Cy.* 36, e2022GB007469.
- Yu, J., Zhan, C., Li, Y., Zhou, D., Fu, Y., Chu, X., Xing, Q., Han, G., Wang, G., Guan, B., Wang, Q., 2016. Distribution of carbon, nitrogen and phosphorus in coastal wetland soil related land use in the Modern Yellow River Delta. *Sci. Rep.* 6, 37940.
- Yuan, J., Liu, D., Xiang, J., He, T., Kang, H., Ding, W., 2021. Methane and nitrous oxide have separated production zones

- and distinct emission pathways in freshwater aquaculture ponds. *Water Res.* 190, 116739.
- Zhang, H., Ouyang, Z., Jiang, P., Li, M., Zhao, X., 2022. Spatial distribution patterns and influencing factors of soil carbon, phosphorus, and C:P ratio on farmlands in southeastern China. *Catena* 216, 106409.
- Zhang, T.H.L., Song, B., Han, G., Zhao, H., Hu, Q., Zhao, Y., Liu, H., 2023. Effects of coastal wetland reclamation on soil organic carbon, total nitrogen, and total phosphorus in China: A meta-analysis. *Land Degrad. Dev.* 34, 3340-3349.
- Zhang, X., Ward, B.B., Sigman, D.M., 2020. Global nitrogen cycle: Critical enzymes, organisms, and processes for nitrogen budgets and dynamics. *Chem. Rev.* 120, 5308–5351.
- Zhang, X., Zou, T., Lassaletta, L., Mueller, N.D., Tubiello, F.N., Lisk, M.D., Lu, C., Conant, R.T., Dorich, C.D., Gerber, J.S., Tian, H., Bruulsema, T.W., Maaz, T.M., Nishina, K., Boudirsky, B.L., Popp, A., Bouwman, L., Beusen, A.H.W., Chang, J., Havlík, P., Leclère, D., Canadell, J.G., Jackson, R.B., Heffer, P., Wanner, N.S., Zhang, W., Davidson, E.A., 2021. Quantification of global and national nitrogen budgets for crop production. *Nature Food* 2, 529-540.
- Zheng, S., Xia, Y.-h., Hu, Y., Chen, X., Rui, Y., Gunina, A., He, X., Ge, T., Wu, J., Su, Y., Kuzyakov, Y., 2021. Stoichiometry of carbon, nitrogen, and phosphorus in soil: Effects of agricultural land use and climate at a continental scale. *Soil Till. Res.* 209, 104903.