Latitudinal responses of wetland soil nitrogen pools to plant invasion and subsequent aquaculture reclamation along the southeastern coast of China

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A B S T R A C T

The impact of invasive species and land use change on soil nitrogen pools in coastal wetlands has been reported at local scale, but uncertainty persists for regional pattern due to geographical variability and limited field data. This study measured the top soil (upper 20 cm) organic nitrogen (SON), inorganic nitrogen (SIN) and total nitrogen (STN) concentrations and stocks across 21 coastal wetland sites in China (20°42′N−31°51′ N) that had undergone the same sequence of transformation from mudflats (MFs) to invasive *Spartina alterniflora* marshes (SAs) then to earthen aquaculture ponds (APs). Results showed that the conversion of MF to SA significantly increased SON and SIN concentrations and stocks by 37.7–86.1%, but subsequent conversion to APs significantly decreased them by 13.5–34.6%. SON/SIN ratio decreased upon invasion by *S. alterniflora* and it had a negative effect on STN accumulation, whereas conversion of SAs to APs showed the opposite trends. The change rates of SON, SIN and STN stocks showed clear decreasing trends with increasing latitude in the MF-to-SA conversion scenario, reflecting the strong influence of environmental temperatures, but weaker or insignificant trends were observed in the SA-to-AP conversion scenario, likely because of mitigating anthropogenic activities in aquaculture ponds. Our findings can be used to inform strategies to control invasive species and reduce the greenhouse gas nitrous oxide (N_2O) emissions, and support global N model for climate change in response to habitat modifications in coastal wetlands.

Keywords: Soil organic nitrogen (SON); Soil inorganic nitrogen (SIN); Exotic invasive

plants; Aquaculture reclamation

1. Introduction

Coastal wetlands consist of mudflats, salt marshes, mangroves or seagrass beds (Duarte et al., 2013; Mcleod et al., 2011), and they are important carbon and nitrogen pools (Reddy and DeLaune, 2008; Xu et al., 2020) thanks to their high primary productivity, high sediment accretion rate, and low decomposition rate (Mcleod et al., 2011; Neubauer and Megonigal, 2021; Xu et al., 2020). Land-use change and exotic species invasion have impacted coastal wetlands world-wide (Murray et al., 2019; Tan et al., 2022; Wang et al., 2023a). During the past century, over 21% natural coastal wetlands have been lost or degraded globally as a result of land use change to support population growth and economic development (Davidson and Finlyson, 2018; Han et al., 2014; Fluet-Chouinard et al., 2023). Alteration of plant community through invasion or de-vegetation would change the primary production and the rate of organic deposition into the soil (Ge et al., 2015; Wang et al., 2023b), while corresponding changes to the soil microbial community would affect organic remineralization rate (Bahram et al., 2022; Yang et al., 2022a; Yang et al., 2023). Land conversion to aquaculture ponds also changes soil particle size and creates a continuously water-logged environment, and the aquaculture operation itself may introduce additional disturbances to soil chemistry, e.g. by adding fertilizer and organic wastes (Kauffman et al., 2018; Yang et al., 2021).

Many coastal areas in China have undergone a sequence of habitat modification, with native mudflats being invaded by *S. alterniflora* and subsequent clearing of *S. alterniflora* marshes to create earthen aquaculture ponds (Li et al., 2022; Liu et al., 2018;

Wang et al., 2023c). This provides a unique opportunity to examine the sequential effect of landscape modification on ecological vulnerability (Zang et al., 2017) and soil biogeochemistry. Earlier studies showed that landscape transformation may impact the organic and inorganic pools of the soil differently, and that the soil greenhouse gas production and emission may respond in an unexpected way. For example, invasion of mudflats by *S. alterniflora* has been shown to increase soil organic carbon concentration but decrease inorganic carbon concentration, whereas subsequent removal of *S. alterniflora* to create aquaculture ponds caused the opposite changes (Duan et al., 2023; Yang et al., 2022a; Hong et al., 2023). Similar changes were also observed in soil organic carbon mineralization rate (Yang et al., 2022a; Hong et al., 2023).

However, most previous studies were focused on the impact of landscape transformation on carbon pools, while little information was available on the change in soil nitrogen (N) pools. Soil N pool is dominated by organic N (> 90%) (Schulten and Schnitzer, 1997), and there is a dynamic exchange between the organic and inorganic pools (Reddy and DeLaune 2008; Schulten and Schnitzer, 1997), the latter of which fuels primary production and emission of N_2O, which is a more powerful greenhouse gas than carbon dioxide and methane (Xu et al., 2022a; Xu et al., 2022b). Therefore, landscape modification may change the fractions of soil N pools and regional greenhouse effect. An earlier study along the southeast coast of China found that soil organic nitrogen (SON) increased after invasion of mudflats by *S. alterniflora* but decreased when the *Spartina* marshes were converted to aquaculture ponds, primarily due to changing organic matter input (Lin et al., 2023). These findings were in line with the changes in soil inorganic nitrogen (SIN) (Yang et al., 2023). Moreover, invasion of *S. alterniflora* was reported to increase SIN stock by enhancing litter decomposition (Smyth et al. 2012), soil N mineralization (Feng et al., 2023) and the uptake of dissolved inorganic N (i.e. NH_4^+-N and NO_3^--N) from tidal subsidies (Peng et al. 2011), which further increased the plant's invasion ability. Invasion of mudflat by *S. alterniflora* can also alter sediment N_2O production potential by changing N substrate availability and abundance of ammonia oxidizers (Yang et al., 2023).

Many studies have been conducted at the local scale, and the regional and latitudinal response patterns of soil N to habitat modification are still unclear. It is therefore of interest to investigate the stocks of soil N pool, their environmental drivers, and how their proportionalities are changed by habitat modification along a broad geographical range. For this, we systematically studied 21 coastal wetland areas across the tropical and subtropical zones in south-eastern China. We compared the SON and SIN pools and various physiochemical variables in three habitat types: native mudflats, *S. alterniflora* marshes and earthen aquaculture ponds, to explore the common effect patterns of habitat modification on the soil N pool across the different latitudes. We hypothesized that (1) invasion of native mudflats by *S. alterniflora* would increase soil N concentrations and stocks due to enhanced organic matter input from marsh plants; (2) when *S. alterniflora* marshes were removed to create aquaculture ponds, the soil N pools would change in the opposite direction.

2. Materials and methods

2.1. Study area, soil sampling and analysis

This study was a part of a larger research campaign between December 2019 and January 2022 that aimed at understanding the effects of landscape transformation on coastal wetland ecology and biogeochemistry in southeastern China. Sampling campaign was conducted in five provinces along the Chinese coastline including Shanghai, Zhejiang, Fujian, Guangdong and Guangxi, with a total of 21 sampling sites (Fig. 1). Descriptions of the wetland areas, local climate and history of habitat modification (mudflats to *S. alterniflora* marshes, then to earthen aquaculture ponds) can be found in (Hong et al., 2023; Lin et al., 2023; Yang et al., 2022a and 2023).

Previous studies have suggested that soil properties in the top 30 cm are most sensitive to management practices associated with LULCC (Eid et al., 2019; Hennings et al., 2021). Surface soil (0−20 cm) samples were collected in each plot using a steel soil corer (5 cm internal diameter), for a total of 189 soil samples (21 sampling sites * 3 habitats * 3 plots). All soil samples were transported to the laboratory in a cooler and stored at 4℃ until processing. Detailed methods for the analyses of soil pH, salinity, particle size distribution, water content (SWC), bulk density (SBD), porewater Cl^- and SO_4^{2-}, total carbon, and microbial genetic diversity are described in Support Information. The data on soil physiochemical properties are given in Table S1. In this study, we focused on the analysis of soil N among the different habitat types and the relations with various environmental factors.

In the laboratory, roots and gravel were removed from each fresh soil sample. Afterward, a subsample was air-dried, finely ground (< 0.149 mm) and used for measuring soil total N (STN) with a Vario MAX CN analyzer (Elementar Scientific Instruments, Germany) (Lin et al., 2023; Xia et al., 2021). Another subsample was extracted with 2 M KCl solution for nitrate-N (NO_3^--N) and ammonium-N (NH_4^+-N) (Gao et al., 2019), and the concentrations of NO_3^--N and NH_4^+-N in the extracts were quantified using SAN^{++} Continuous Flow Analyzer (Skalar, Netherlands). Soil inorganic N (SIN) was the sum of soil NO_3^--N and NH_4^+-N, and soil organic N (SON) was calculated as the difference between STN and SIN. Soil N stocks (t N ha^{-1}) were calculated by multiplying SBD (g cm^{-3}) by the different N factions (SON, SIN and STN) scaled to the soil depth interval (cm)

2.2. Statistical analysis

The Kolmogorov–Smirnov and Levene's tests were used to confirm that all the data groups met the assumptions of normality and homogeneity of variances, respectively. One-way analysis of variance (1 way-ANOVA) with Tukey's HSD test was used to test the differences between habitat types in soil N fractions (SON, SIN and STN) and environmental variables including pH, salinity, SWC, SBD, clay, silt, sand, porewater Cl^- and SO_4^{2-} concentrations, C:N ratio, Chao1 index and Shannon index of microbial diversity.

To account for anthropogenic management practices (e.g. fertilization and irrigation) and spatial heterogeneity of environmental condition (e.g. temperature, rainfall), we used response ratio (RR) and weighted RR (RR_{++}) to quantify the effect of habitat modification on different variables (Hedges et al., 1999; Tan et al., 2023a). RR and RR_{++} are commonly used in ecological meta-analysis to assess heterogeneity of each paired data set (representing sampling sites) and obtain an overall estimate. Here, RR was defined as the natural logarithm of the ratio of the N factions or environmental variables in the modified habitat to the paired original habitat. RR_{++} was calculated from the individual RR pairwise comparison between the modified habitat and original habitat (Hedges et al., 1999).

Spearman correlation analysis, redundancy analysis (RDA) and structural equation model (SEM) were performed to test the relationship between the RR of N stocks and environmental variables, and identify the key factors to drive the change in soil N stocks. Spearman correlation analysis was performed in R (version 4.1.0) using corrplot and Hmisc packages. RDA was conducted in CANOCO 5.0 (Microcomputer Power, Ithaca, USA). SEM was constructed in R with the lavaan package using the method of Tan et al. (2022) and (2023b). All data were presented in mean ± standard error (SE), unless otherwise stated. In all statistical tests, a significance level of $p < 0.05$ was used.

3. Results

3.1. Soil nitrogen concentrations in different habitat types

SON concentration varied across all sampling sites and habitat types: 257.9−1407.9

mg kg^{-1} in MF, 596.3−2672.7 mg kg^{-1} in SA, and 472.4−2501.5 mg kg^{-1} in AP (Fig. 2a). The mean SON concentration was highest in SA (1075.3 ± 53.3 mg kg^{-1}), followed by AP (930.5 ± 94.8 mg kg^{-1}) and MF (780.6 ± 94.1 mg kg^{-1}) (Fig. 2b). Therefore, conversion of MF to SA increased SON concentration by 37.7% ($p < 0.05$), whereas conversion of SA to AP decreased SON concentration by 13.5% ($p < 0.05$).

SIN concentration ranged 4.2−27.7 mg kg^{-1} in MF, 10.1−50.6 mg kg^{-1} in SA, and 5.7−31.5 mg kg^{-1} in AP (Fig. 2c). The mean SIN concentration was highest in SA (25.8 ± 2.3 mg kg^{-1}), followed by AP (18.5 ± 1.9 mg kg^{-1}) and MF (14.6 ± 1.4 mg kg^{-1}) (Fig. 2d). Conversion of MF to SA increased SIN concentration by 77.3% ($p < 0.05$), but conversion of SA to AP decreased SIN concentration by 28.2% ($p < 0.05$).

3.2. Response of soil N stocks to habitat modification

SON, SIN and STN stocks were all highest in SA, followed by AP and MF (Table 1). SON accounted for over 97% of the STN stock, whereas NH_4^+-N accounted for about 92% of the SIN stock in all habitat types. Based on the weighted response ratio (RR_{++}) for the sequence of habitat modification, conversion of MF to SA significantly increased SON, SIN and STN stocks by 38.6%, 86.1% and 39.5% (percentage change of mean difference), respectively. In contrast, conversion of SA to AP significantly decreased SON, SIN and STN stocks by 17.6%, 34.6% and 18.0%, respectively (Fig. 3).

There was a latitudinal gradient in the response of soil N stocks to habitat modification: The response ratio (RR) of SON, SIN and STN stocks all decreased significantly with increasing latitude in the MF-to-SA conversion scenario, while significant negative trends were observed for SON and STN stocks in the SA-to-AP conversion scenario (Fig. 4). Similar patterns were also found in the soil N stocks in all habitat types at the province level (Table S2).

When we considered the relative proportions of SON and SIN, the SON/SIN ratio decreased by 15.5% when MFs were converted to SAs, but increased by 36.4% when SAs were converted to APs (Fig. 5a). The response ratio (RR) of STN correlated negatively to RR of SON/SIN ratio for MF-to-SA conversion (Fig. 5b), but positively for SA-to-AP conversion (Fig. 5c).

3.3. Environmental control of soil N stock responses

According to redundancy analysis (RDA), salinity, Cl^- and Chao1 index and clay together explained 63.7% of the variations in RR of the soil N stocks when MFs were converted to SAs (Fig. 6a). Based on the structural equation model (SEM), salinity and Cl^- had positive direct and indirect effects on RR of SIN and STN stocks (Fig. 7a). Clay had a positive effect on RR of SON (direct) and STN (indirect) stocks (Fig. 7a). Chao1 index had a negative effect on RR of SON (direct) and STN (indirect) stocks (Fig. 7a).

For the conversion of SAs to APs, RDA showed that SWC, clay, sand and pH together explained 67.5% of variations in RR of the soil N stocks (Fig. 6b). Based on SEM, SWC and clay had positive and direct effect on RR of SON and SIN stocks, and indirect effect on RR of STN stock (Fig. 7b). pH affected RR of SIN stock positively and directly (Fig. 7b). Sand had a negative direct effect on RR of SON and SIN stocks and an indirect effect on STN stock (Fig. 7b).

4. Discussion

4.1. Soil N response to conversion of mudflat to Spartina marsh

The results of this study, which included 21 sampling sites, revealed that conversion of mudflats to *S. alterniflora* marshes increased SON and SIN concentrations and stocks by 37.7–86.1% based on the percentage change of mean difference (Fig. 2 and Fig.3). These results supported our first hypothesis. This might be attributed to the higher productivity, input of plant litters and root exudates in marshes than in unvegetated mudflats (Mcleod et al., 2011; Neubauer and Megonigal, 2021; Tong et al., 2011; Fig. 8a and 8b). The invasive *S. alterniflora* is also efficient in trapping organic- and nitrogen-rich particles from terrestrial runoff and tidal input, thanks to its high shoot density and well-developed underground root system (Hsieh et al., 2021; Li et al., 2021), which would also increase the STN stock in the topsoil (Fig. 8b).

In this study, SON was the dominant fraction of STN (Table 1) and the response patterns of SON and STN to habitat modification were almost the same (Fig. 3). Since the soil bulk density was statistically the same between habitat types (Table S1), the changes of N stock were primarily driven by changes in N concentration.

Chao1 index and Shannon index in SAs were significantly higher than in MFs (Table S1) and showed a significantly negative relationship with SON stock in the RDA and SEM results (Fig.6 and Fig. 7). This suggests more diverse microbe communities decomposing SON in SAs, potentially increasing SIN concentration and stock as seen in our data (Fig. 3). In addition, the shade provided by plant canopies and water absorption by ground litter may prevent soil surface evaporation and increase the retention of salt water from tidal inundation (Kadiri et al., 2011), as indicated by the higher soil salinity and SWC in SAs (Table S1), which would add additional exogenous N to the soil and explain the positive correlation in RR between SIN stock and salinity (Fig. S1b). The elevated SIN including NO_3^--N and NH_4^+-N could in turn fuel N_2O production, as has been shown in our companion study (Yang et al., 2023).

When we examined the relative proportions of the different N fractions, we found that the SON/SIN ratio decreased significantly after habitat modification, owing to a greater rise in SIN than in SON (Fig. 3 and Fig. 5a). Interestingly, RR of STN was negatively correlated with RR of SON/SIN ratio (Fig. 5b), suggesting that SIN availability was key in supporting the growth and spread of *S. alterniflora*, which in turn elevated the total soil N concentration (Feng et al., 2023; Sardans et al., 2017).

4.2. Soil N response to conversion of Spartina marsh to aquaculture pond

Based on the change rate of weighted response ratio, SON, SIN and STN concentrations and stocks decreased by 13.5–34.6% when SAs were converted to APs, which supported our second hypothesis (Fig. 2 and Fig.3). This at first glance may seem counter-intuitive because aquaculture operation is often thought to cause heavy eutrophication (Burford et al., 2003), but similar decrease in soil organic carbon concentration has been observed (Hong et al., 2023). When constructing the aquaculture ponds, farmers remove the vegetation and the organic-rich topsoil. Most of the coastal aquaculture ponds in our study are for farming shrimp that have a relatively low feed conversion ratio (i.e. high efficiency to utilize feed), and therefore only a small amount of organic waste would be added to the soil (Yang et al., 2021; Fig. 8c). Additionally, the common practice of draining and drying out the ponds would cause additional loss of soil N in APs (Kauffman et al., 2018; Sasmito et al., 2019; Fig. 8c).

Conversion of SAs to APs increased the SON/SIN ratio significantly, and the RR of SON/SIN correlated positively with RR of STN (Fig. 5a and 5c), indicating that soil N pool in APs was mainly controlled by SON dynamics. Unlike SAs, SIN had minor effect on ecosystem productivity and SON accumulation, due to the absence of vegetation in APs. SWC and clay both had a positive effect on SIN and SON (Fig 7b), likely because of better retention of N in porewater and N adsorption onto fine particle surfaces (Daugherty et al., 2019; Fissore et al., 2009; Hennings et al., 2021). Conversely, higher sand concentration would increase soil porosity and lower N retention, as suggested by the negative effect by sand in the SEM analysis (Fig 7b).

4.3. Latitudinal patterns of soil N response to habitat modifications

We found clear latitudinal gradients in soil N responses to habitat modifications (Fig. 4). With increasing latitude, RRs of SON, SIN and STN stock decreased in the MF-to-SA conversion scenario, likely reflecting the effect of temperature. Across the sampling sites in this study, the mean annual temperature decreased linearly with increasing latitude (Fig. S2). Temperature has well-documented influences on plant growth and N mineralization (Fissore et al., 2009; Liu et al., 2017; Tao et al., 2018). The higher temperatures and longer growing seasons at the lower latitudes would result in higher plant productivity and hence organic N input to the soil, and subsequent mineralization of SON would then release SIN (Fissore et al., 2009; Liu et al., 2017; Tao et al., 2018).

Although similar latitudinal gradients were observed for SON and STN in the SA-to-AP conversion scenario, the relationships were weaker, and the trend for SIN was not significant (Fig. 4). This might be due to the fact that the aquaculture pond soil was more strongly subject to anthropogenic activities, which weakened the influence by environmental temperature (latitude). Notably, for reducing the impact of heterogeneity and improving the overall evaluation of response of soil N pools to APs conversion, it is worthy and necessary to conduct larger spatial scale field-based investigation.

4.4. Implications for land management

Many studies reported that *S. alterniflora* has distinct traits such as higher nutrient utilization efficiency (He et al., 2023; Liao et al., 2007) and longer growth period (Xu et al., 2020) that allow it to out-compete native plants, leading to a decline in biodiversity and other ecosystem services of coastal wetlands (Duan et al., 2020; Ge et al. 2015). In this study, we discovered that SIN had a positive influence on soil N accumulation in *S. alterniflora* marshes, which is consistent with the results of Xu et al. (2020). Therefore, reducing nutrient loading in coastal water will be key to mitigating *S. alterniflora* invasion and proliferation.

Our previous research showed that ammonia oxidation was the overall rate-limiting step in N_2O production in these habitats, which had a strong positive correlation with abundance of ammonia-oxidizing archaea (AOA) *amoA* and NH_4^+-N concentration in the soil (Yang et al., 2022b and 2023). SAs have the largest N_2O production potential due to the higher NH_4^+-N concentration than MFs and APs (Table 1, Table S2 and Fig. 4). Considering the latitudinal gradient in STN and SON response to habitat modification that we found in this study (Fig. 4), converting *S. alterniflora* marshes to aquaculture ponds, especially in low-latitude coastal areas, could be an effective strategy for achieving multiple benefits such as controlling invasive species, boosting food production and reducing soil N_2O emission, with a low N loss caused by reclamation.

To prevent further N loss from aquaculture ponds after reclamation, native aquatic vegetation can be replanted in the ponds (Buhmann and Papenbrock, 2013; Tan et al., 2023b). The vegetation will not only increase organic matter input to the soil, it may also filter out the excess nutrients and other contaminants in the pond water, oxygenate the water via photosynthesis, and provide additional food to the farmed animals (Buhmann and Papenbrock, 2013; Tan et al., 2023b).

5. Conclusions and recommendations

We investigated the effect of coastal habitat modification on soil N across 21 sampling sites along the southeast coast of China. Our result showed that soil organic and inorganic N increased significantly when mudflats were invaded by *S. alterniflora*, but decreased when *S. alterniflora* marshes were subsequently cleared to create aquaculture ponds. The relative proportions of SON and SIN changed in opposite directions between the two land conversion scenarios, indicating the effects of marsh vegetation (present or absent) and environmental conditions in the different habitat types. By comparing the latitudinal patterns across all 21 sites, we also deduced the relative influence of environmental temperature and anthropogenic activities on soil N change in response to habitat modification. Our findings can be used to support land-use policy, invasive species control and the development of strategies to mitigate N_2O emissions. The dataset could also support improving the accuracy of global N model forecasting for climate change in response to habitat modification in coastal wetlands.

Some improvements can be considered in future study: (a) Multiple land-use types often co-exist in the coastal region, such as paddy field, dry farmland and reclaimed marshland, most of them have been converted from natural wetlands. Building on this study, it will be of interest to investigate the response of soil N pool to the other land conversion scenarios. (b) The N concentration and stock in deeper soil (> 20 cm) have not been measured, but which will be needed to understand the long-term N sequestration at the selected sites. (c) Lastly, coastal habitat modification is not limited to the southeastern part of China. Additional sampling in the northern provinces would allow for a more complete spatial coverage.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this

paper.

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Table 1

SON, SIN and STN stocks in mud flats, *S. alterniflora* marshes and aquaculture ponds.

Habitat type	**SON stock (t N ha^{-1})**	**SIN stock (kg N ha^{-1})**		**STN stock (t N ha^{-1})**
		NH_4^+-N	**NO_3^--N**	
Mud flat	1.941 ± 0.063	32.148 ± 3.427	3.143 ± 0.168	1.978 ± 0.063
***S. alterniflora* marsh**	2.691 ± 0.128	62.458 ± 6.221	4.672 ± 0.423	2.760 ± 0.130
Aquaculture pond	2.217 ± 0.130	39.491 ± 3.945	3.594 ± 0.267	2.262 ± 0.130

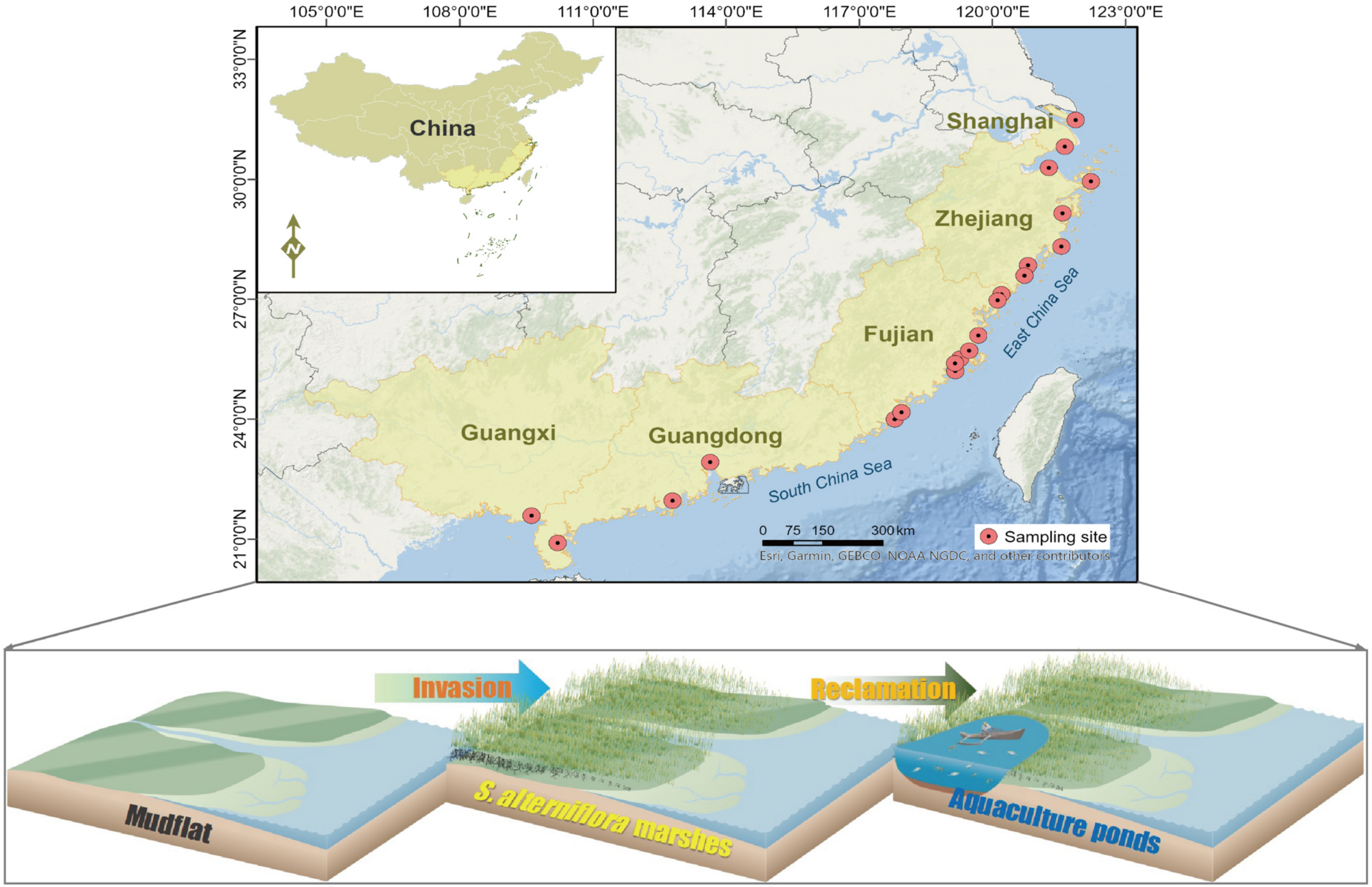

Figure 1 Locations of the 21 sampling sites across the coastal regions in southeastern China. Three wetland habitat types were investigated including native mud flat (*MF*), *S. alterniflora* marsh (*SA*) and aquaculture pond (*AP*).

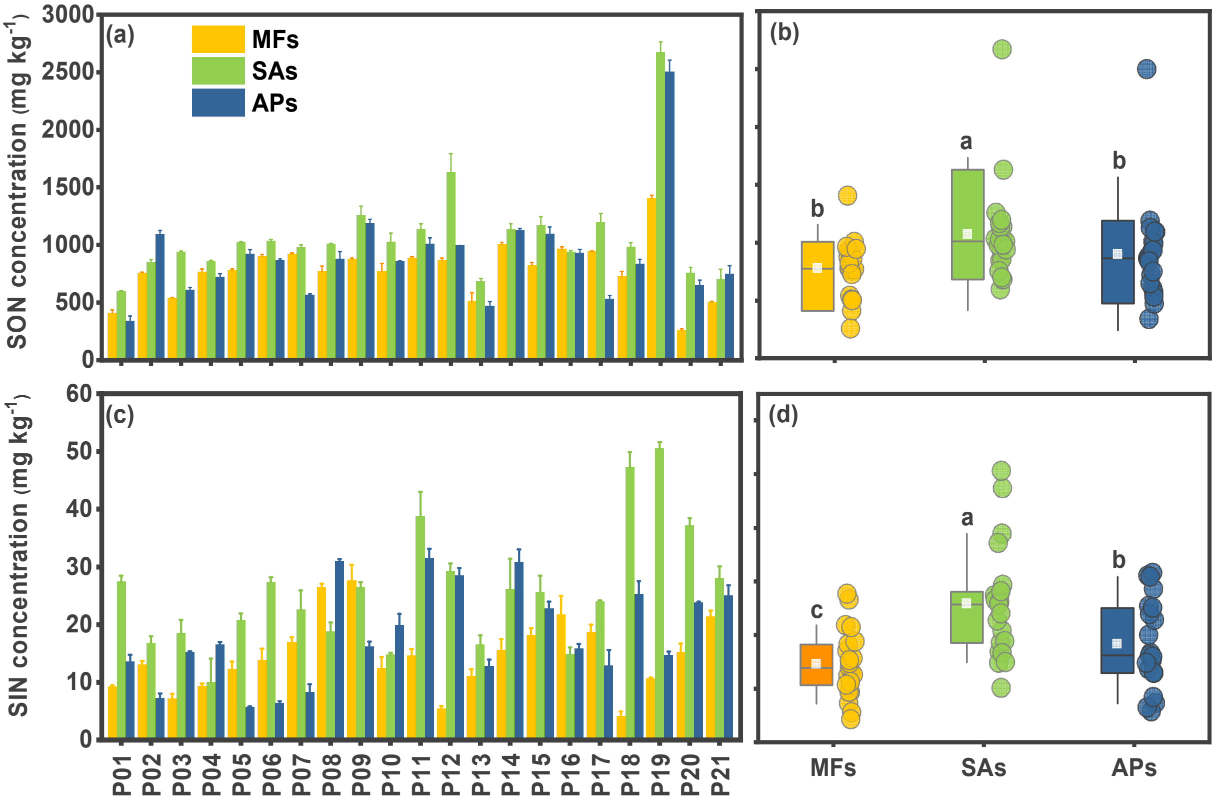

Figure 2 Surface soil organic nitrogen (a) and inorganic nitrogen (c) concentrations (mean + S.E.) in the three habitat types at the 21 sampling sites, and the corresponding boxplots (b and d). MFs, SAs and APs represent mud flats, *S. alterniflora* marshes and aquaculture ponds, respectively. Different lowercase letters above the boxplots within each panel indicate significant differences between habitat types (p<0.05).

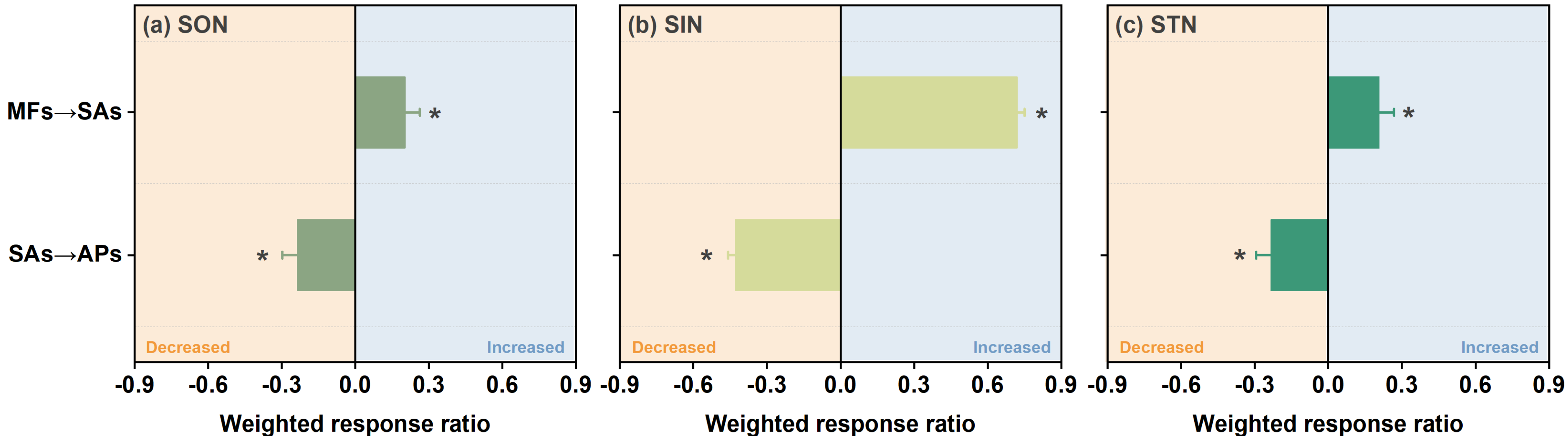

Figure 3 Weighted response ratios (RR_{++}) of SON (a), SIN (b) and STN (c) stocks in the upper 20 cm soil for the different habitat modification scenarios: MFs → SAs represents conversion of mudflats to *S. alterniflora* marshes; SAs → APs represents conversion of *S. alterniflora* marshes to aquaculture ponds. Bars represent the RR_{++} values and 95% CIs (n = 21 sampling sites). Asterisks indicate significantly different from zero (p<0.05).

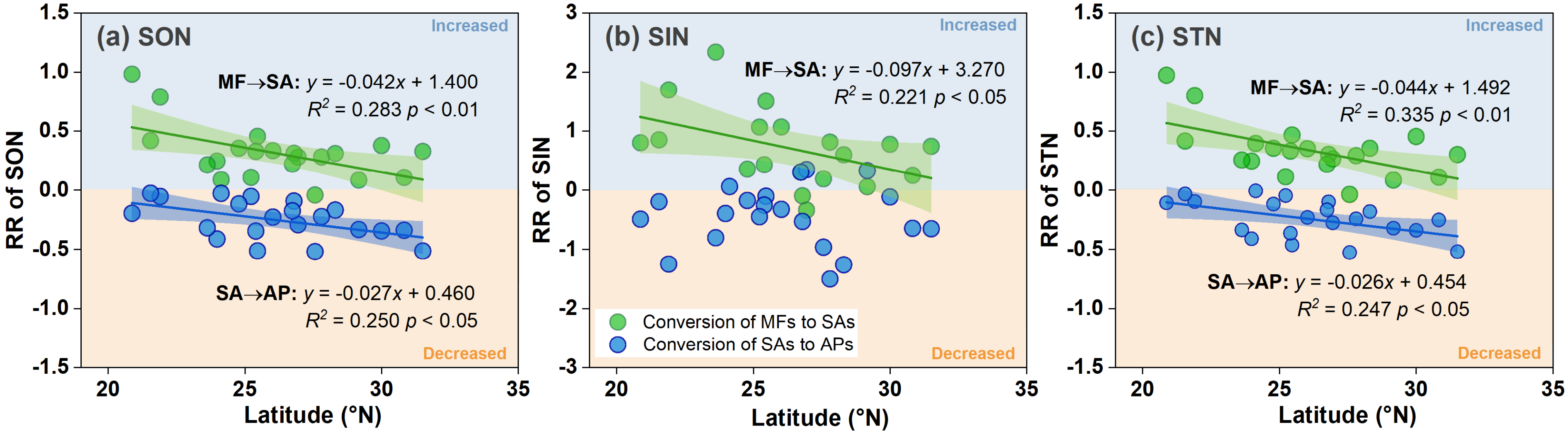

Figure 4 Latitude gradients in the response ratio (RR) of SON (a), SIN (b) and STN (c) stocks in the upper 20 cm for the different habitat modification scenarios: MFs → SAs represents conversion of mudflats to *S. alterniflora* marshes; SAs → APs represents conversion of *S. alterniflora* marshes to aquaculture ponds.

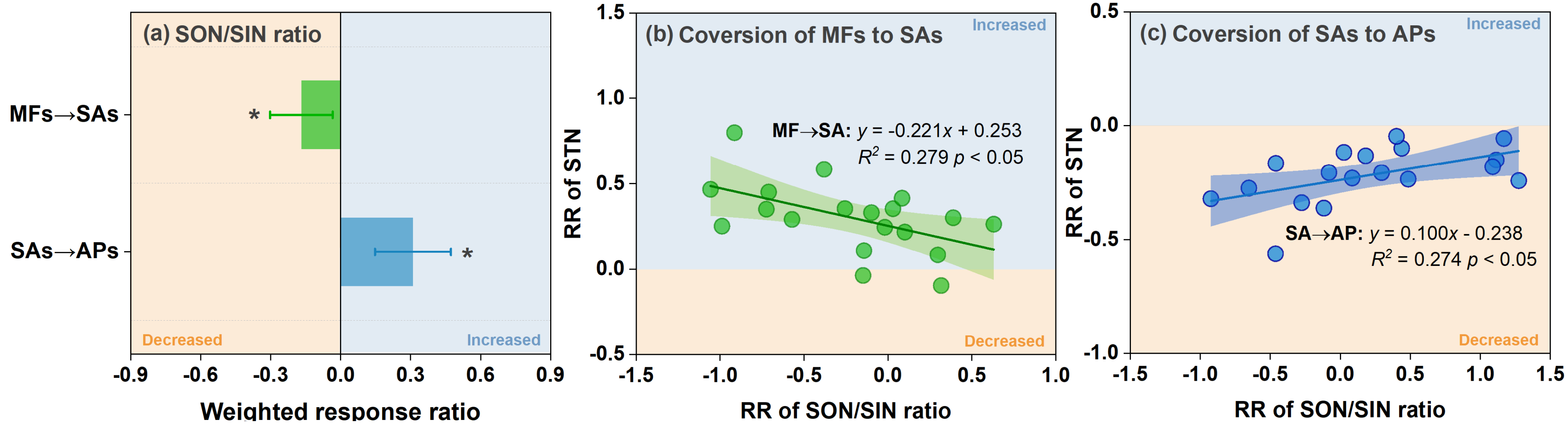

Figure 5 Weighted response ratios (RR_{++}) of SON/SIN ratio in the two habitat modification scenarios (a); bars represent the RR_{++} values and 95% CIs (n = 21 sampling sites). Asterisks indicate significant change from zero (p<0.05). Linear regressions of RR of SON/SIN ratio against RR of STN for converting mudflats to *S. alterniflora* marshes (b) and converting *S. alterniflora* marshes to aquaculture ponds (c).

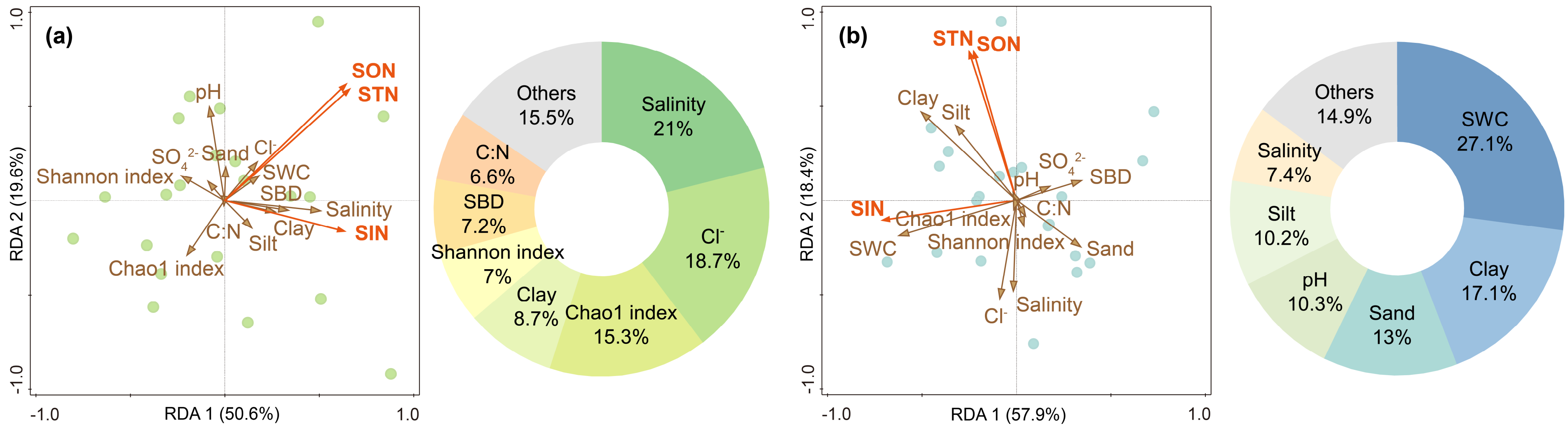

Figure 6 Redundancy analysis (RDA) of the relationship between the RR of SON, SIN and STN stocks, and the RR of environmental factors, for converting mudflats to *S. alterniflora* marshes (a) and converting *S. alterniflora* marshes to aquaculture ponds (b). The pie charts show the percentages of relative influence of the different environmental factors.

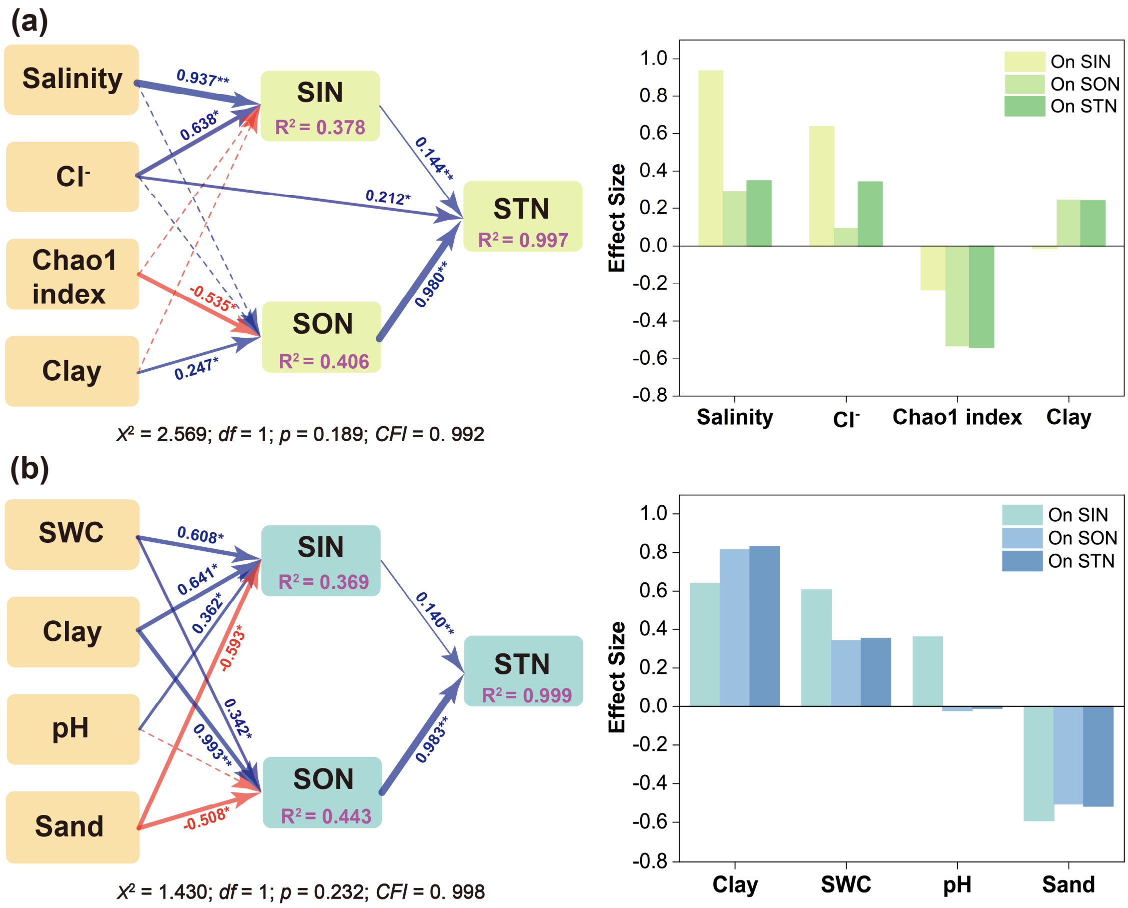

Figure 7 Partial least square structural equation modeling (PLS-SEM) of the RR of SON, SIN and STN stocks response to the RR of environmental factors, for converting mudflats to *S. alterniflora* marshes (a) and converting *S. alterniflora* marshes to aquaculture ponds (b). Boxes indicate measured variables used in the model. Solid blue and red arrows indicate significant positive and negative effects, respectively; dotted arrow indicates insignificant effect on the dependent variable. Numbers adjacent to arrows are standardized path coefficients, indicating the effect size of the relationship. R^2 represents the variance explained for target variables. * $p < 0.05$; ** $p < 0.01$.

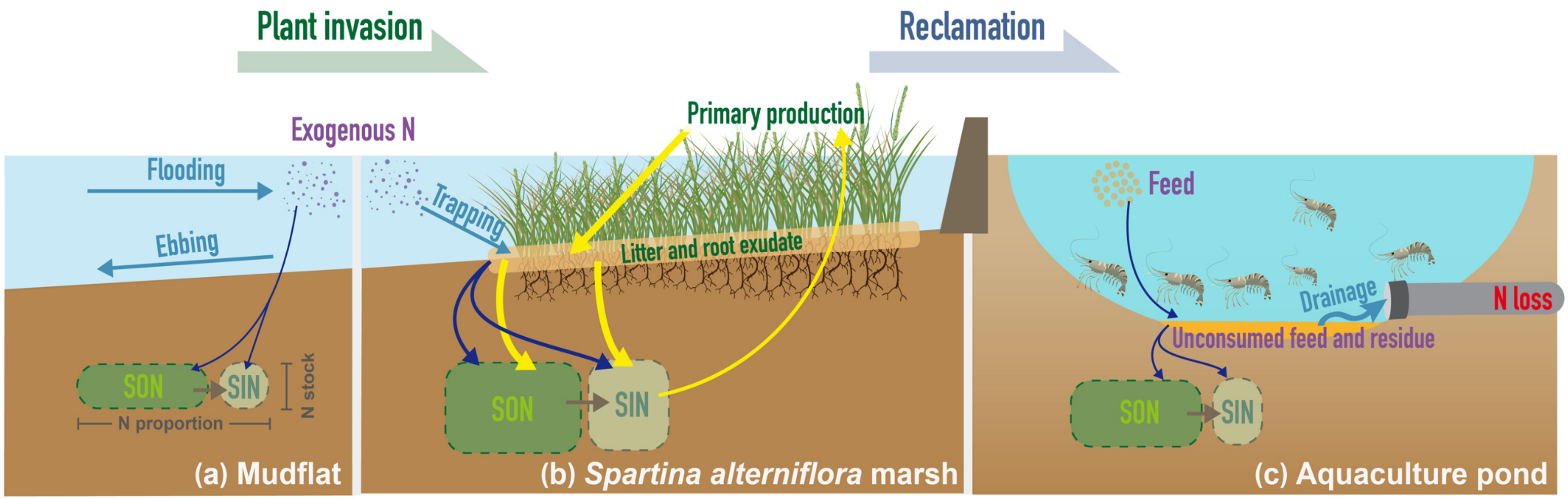

Figure 8 Conceptual diagram of the response of soil nitrogen (N) stocks to habitat modifications. Yellow and blue arrows indicate the allocation of autochthonous and allochthonous N sources, respectively. The lengths of the N boxes represent their relative proportions within each habitat; the heights of the N boxes represent their relative stock between habitats.

Supporting Information

Latitudinal responses of wetland soil nitrogen pools to plant invasion and subsequent aquaculture reclamation along the southeastern coast of China

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Supporting Information Summary

No. of pages: 6 No. of method description: 1 No. of figures: 2 No. of tables: 2

Materials and methods

Measurement of environmental variables

In the laboratory, the soil samples were freeze-dried, homogenized and then ground into a fine powder for physicochemical analyses. Briefly, soil pH was measured with a pH meter (Orion 868 pH meter, USA; soil-to-water ratio 1:2.5 w/v), salinity (as NaCl) with a salinity meter (Eutech Instruments-Salt6, USA; soil-to-water ratio 1:5 w/v) and particle size distribution with a Master Sizer 2000 Laser Particle Size Analyzer (Malvern Instruments, UK). Gravimetric soil water content (SWC) and bulk density (SBD) were measured based on the measurements of the wet and dried weight and the given soil volume. After filtering through a 0.45-μm filter (BiotransTM nylon membranes), Cl- and SO42- concentrations of soil porewater were determined with a Dionex 2100 ion Chromatograph (Thermo Fisher Scientific, Sunnyvale, California, USA). C:N is the ratio of soil total carbon content to STN.

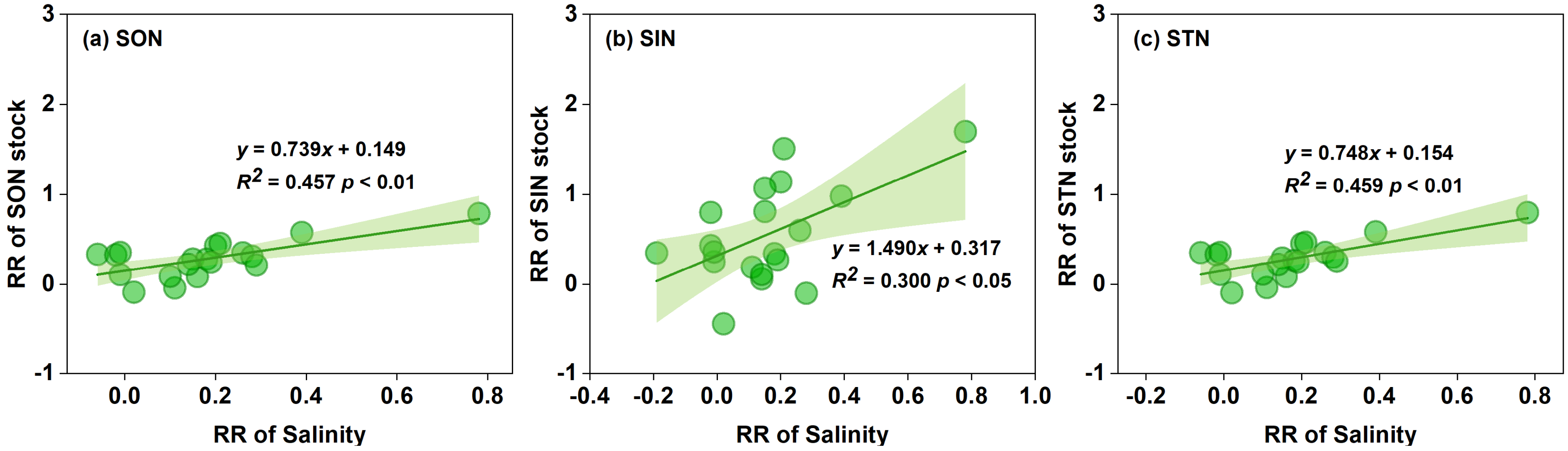

Figure S1. Linear regression between RR of salinity and RR of soil organic N (SON), inorganic N (SIN) and total N (STN) stocks for the conversion of MFs to SAs.

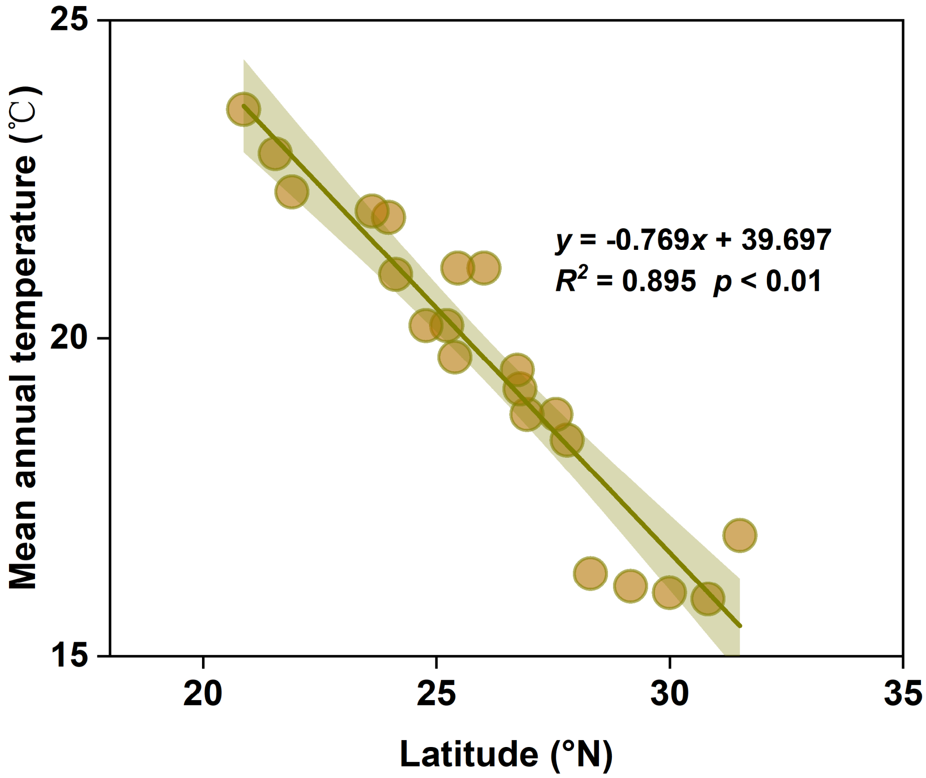

Figure S2. Linear regression between latitude and mean annual temperature.

Table S1 Surface soil physicochemical properties across the three habitat types: mud flat (MF), *S. alterniflora* marshes (SA) and aquaculture ponds (AP).

Properties	**Habitat types**		
	MF	**SA**	**AP**
pH	7.99±0.06**a**	7.95±0.06**a**	7.82±0.06**a**
Salinity (‰)	3.96±0.20**a**	4.54±0.23**a**	4.21±0.31**a**
SWC (%)	43.05±1.33**b**	47.12±1.38**a**	47.78±1.70**a**
SBD (g cm^{-3})	1.29±0.02**a**	1.26±0.02**a**	1.25±0.03**a**
Cl^- (mg L^{-1})	36.84±2.15**b**	40.94±2.23**a**	37.75±3.43**b**
SO_4^{2-} (mg L^{-1})	8.90±0.63**b**	9.13±0.50**b**	17.48±1.40**a**
C:N ratio	36.84±2.15**b**	40.94±2.23**a**	37.75±3.43**b**
Clay (%)	10.41±0.47**a**	10.94±0.49**a**	10.50±0.57**a**
Silt (%)	54.07±2.29**a**	52.67±2.41**bc**	50.14±2.56**c**
Sandy (%)	35.53±2.69**b**	36.38±2.86**b**	39.35±3.06**a**
Chao1 index	6075.38±158.74**b**	7253.20±194.57**a**	6380.57±195.18**b**
Shannon index	7.75±0.18**b**	8.92±0.22**a**	8.88±0.13**a**

Different lowercase letters along the same row indicate significant differences at $p < 0.05$ between habitat types. Data are taken from Yang et al. (2022) for reference and review only. See main text for explanation of the abbreviations.

Table S2 The concentration and stock of NH_4^+-N and NO_3^--N among mud flat (MF), *S. alterniflora* marshes (SA) and aquaculture ponds (AP) across five provinces.

Habitats	Province	NH_4^+-N concentration (mg kg^{-1})	NO_3^--N concentration (mg kg^{-1})	NH_4^+-N stock (kg ha^{-1})	NO_3^--N stock (kg ha^{-1})
MF	Shanghai	10.04±1.65	1.11±0.25	26.33±3.84	2.92±0.60
	Zhejiang	13.02±2.76	1.36±0.10	49.81±10.36	3.38±0.83
	Fujian	14.98±2.19	1.22±0.06	46.45±3.28	2.66±0.03
	Guangdong	8.90±3.09	1.12±0.15	25.14±12.12	3.22±1.32
	Guangxi	19.93±1.07	1.48±0.05	61.73±12.81	4.55±0.57
SA	Shanghai	20.34±4.58	1.80±0.73	55.50±15.02	4.95±2.20
	Zhejiang	18.10±2.23	1.59±0.20	44.82±2.39	3.57±0.03
	Fujian	22.27±2.38	1.80±0.27	43.97±13.00	2.93±0.14
	Guangdong	42.64±3.64	2.39±0.55	115.53±5.87	6.48±0.98
	Guangxi	26.61±2.07	1.47±0.10	89.25±12.04	4.94±0.58
AP	Shanghai	9.10±3.48	1.31±0.29	27.59±9.91	4.04±1.01
	Zhejiang	12.23±3.80	1.66±0.38	36.00±23.59	6.26±0.77
	Fujian	19.77±2.35	1.50±0.18	35.21±1.83	3.00±0.49
	Guangdong	20.09±3.29	1.19±0.03	51.14±15.71	3.03±0.38
	Guangxi	24.11±1.73	0.92±0.08	74.69±19.41	2.80±0.26

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