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Saltmarsh reclamation enhances plant species richness and reduces soil macrofaunal biomass by regulating soil properties through elevation

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Globally, saltmarsh reclamation results in significant losses of coastal wetlands. However, the impacts on above- and below-ground biodiversity and the underlying mechanisms remain poorly understood. We hypothesized that saltmarsh reclamation differently affects plant and soil macrofaunal communities by regulating soil properties through elevation. To test this, we surveyed 36 plots in Sheyang County, eastern China and used t-tests, redundancy analysis, and structural equation modeling to examine differences and the direct/indirect effects of elevation and soil physico-chemical properties on plant and soil macrofaunal diversity. Results showed that plant species richness in reclaimed areas was significantly higher than that in saltmarshes, whereas the total and average biomass of soil macrofauna exhibited an inverse pattern. Plant species richness positively associated with elevation but negatively correlated with soil available phosphorus (AP) and electrical conductivity (EC). The total and average biomass of soil macrofauna positively correlated with soil ammonium nitrogen (AN), total nitrogen (TN), total potassium (TK), and inversely related to total phosphorus (TP), elevation, mud content (SMC). Elevation indirectly increased plant species richness via soil water content (SWC), total carbon (TC), AN, and nitrate nitrogen (NN), but decreased it through bulk density (BD). For soil macrofauna, elevation indirectly reduced total biomass via SWC, TC, and AN, while indirectly increasing it through available potassium (AK). These findings elucidate the mechanisms driving above- and below-ground biodiversity changes following saltmarsh reclamation, providing a comprehensive understanding of these ecological alterations.

KEYWORDS

above- and below-ground biodiversity, aquaculture ponds, coastal wetland, invasive *Spartina alterniflora*, plant colonization, structural equation modeling

1 Introduction

Coastal wetlands play crucial roles in preserving biodiversity, purifying water, offering flood defense, sequestering carbon, fostering tourism, and providing recreational opportunities (Barbier et al., 2008; Temmerman et al., 2013). Yet, land reclamation has emerged as a pivotal factor resulting in the global decline of coastal wetlands, precipitating habitat destruction, biodiversity loss, and ecosystem functions degradation (Gedan et al., 2009; Sun et al., 2015; Sengupta et al., 2023). Globally, approximately 78% of major coastal cities have reclaimed a cumulative of 2.53×10^5 ha of additional land during the 21st Century, with particular prominence in East Asia (Sengupta et al., 2023). China ranks among the countries with the largest coastal wetland reclaimed area in the world. Between 1950 and 2014, China witnessed the loss of 8.01×10^6 ha (58%) of its coastal wetlands, with reclamation and infrastructure construction accounting for 70–82% of the total disappearance (Sun et al., 2015). Despite numerous studies have investigated the alterations in biodiversity patterns resulting from coastal wetland reclamation (Yu et al., 2016; Wang et al., 2021; Ge et al., 2021b), the specific mechanisms driving changes in above- and below-ground biodiversity remain unclear.

Coastal saltmarshes are wetland ecosystems covered by salt-tolerant herbaceous or low-shrub vegetation at the land and sea interface (Silliman, 2014). Saltmarshes are among the most productive vegetation types within coastal wetlands (Loreau et al., 2001; Lotze et al., 2006; Bauer et al., 2013; Tilman et al., 2017). Although saltmarsh reclamation has delivered considerable social and economic benefits to coastal areas, it has simultaneously precipitated the degradation of saltmarsh ecosystems by disrupting hydrological conditions and soil properties (Sengupta et al., 2023). Consequently, biodiversity patterns have been compelled to adapt to these altered environments (Liu et al., 2016; Day et al., 2021). Typically, in coastal wetlands, soil moisture and salinity are the primary factors governing the directions and processes of saltmarsh evolution (Zhang et al., 2013a; Pan et al., 2018). When saltmarshes are converted into aquaculture ponds, the increased elevation of pond embankment, resulting in decreased seawater, soil moisture, pH, salinity, as well as increased soil bulk density and nutrient levels (Cui et al., 2016; Xie et al., 2017; Cao et al., 2018). Moreover, saltmarsh reclamation can lead to significant alterations in land use types and landscape dynamics within coastal zones, thereby exerting a substantial influence on the ecological balance and biodiversity in these regions (Goeldner, 1999; Wu et al., 2018). However, additional research is imperative to comprehensively understand the implications of the variations of elevation and soil properties on both above- and below-ground biodiversity.

Saltmarsh reclamation exerts a profound influence on the composition and diversity of plant communities by modifying the elevation and soil properties (Cui et al., 2016; Xie et al., 2017; Cao et al., 2018). Elevation serves as a critical environmental constraint within coastal wetlands. Higher elevations can reduce tidal currents, flooding frequency, and salinity levels (Silvestri et al., 2005), which in turn influences the spatial distribution of saltmarshes (Balke

et al., 2016). Furthermore, alterations in elevation can lead to variations in soil physical-chemical properties, reflecting the effects of seawater leaching over a spatio-temporal sequence (Walker et al., 2010). After reclamation, due to the decreased seawater inundation, saltmarshes with few species experienced significant reduction. Consequently, the soil has transitioned towards drier conditions and improved in quality, facilitating the rapid expansion of xerophytic plant communities (Li et al., 2014; Yu et al., 2016). Moreover, certain plant species can establish themselves in these new habitats through seed dispersal (Visscher et al., 2023). Notably, weeds exhibit remarkable adaptability to their surroundings and are typically widely distributed (Marshall et al., 2003), thereby contributing to increased plant species richness. Research has shown that soil organic carbon, texture and nutrients mainly influence the occurrence and establishment of plants (Gaston et al., 2001; Korres et al., 2017). However, the specific mechanisms by which saltmarsh reclamation impacts plant communities through altering soil properties have not been extensively investigated.

In addition to plant communities, soil macrofauna, as a key component of underground biodiversity, are also significantly affected by land reclamation. Soil macrofauna is an integral component of coastal saltmarsh ecosystems, actively engaging in processes such as energy flow, decomposition, and nutrient cycling (Ricardo et al., 2012; Lv et al., 2019; Xue et al., 2019). Extensive research indicates that saltmarsh reclamation can significantly alter the composition and diversity of soil macrofaunal communities (Salgado et al., 2007; Ryu et al., 2011; Ricardo et al., 2012). Additionally, soil macrofaunal communities are known to exhibit strong correlations with various soil properties (Chao et al., 2012; Ge et al., 2021b), and their assemblages are closely linked to the specific combinations of abiotic factors present in tidal flats (Ryu et al., 2011). The elevation, serving as a comprehensive indicator of environmental conditions, tends to increase with saltmarsh reclamation, thereby substantially affecting the composition, diversity, and biomass of macrofaunal communities (Salgado et al., 2007). The collective influence of soil properties, including moisture, organic matter content, nutrient availability, and grain size, shapes the distribution and diversity of soil macrofaunal communities (Ayuke, 2010; Zhang et al., 2021a; Li et al., 2022). Particularly, soil nutrients are frequently affected by transportation through water flow and human activities associated with reclamation efforts (Bannert et al., 2011; Xie et al., 2017). Current research on coastal wetland reclamation has not thoroughly examined the specific case of saltmarshes being converted into aquaculture ponds. Furthermore, it has not investigated the subsequent alterations in both above- and below-ground biodiversity over several decades, nor has it explored the intricate mechanisms underlying these transformations. Additionally, there is a limited body of research addressing the direct and indirect effects of elevation and soil properties on both plant and soil macrofaunal communities following saltmarsh reclamation.

Jiangsu Province, encompassing a quarter of China's total coastal wetlands (Xie et al., 2012), featured extensive saltmarshes over 300 km² by the year 2000 (Sun et al., 2023). These saltmarshes

were primarily characterized by invasive *Spartina alterniflora* (*S. alterniflora*), and native *Phragmites australis* (*P. australis*) and *Suaeda* spp (Ge et al., 2015; Tian et al., 2016). The cumulative loss of saltmarshes induced by reclamation from 2001 to 2020, reached 249.6 km² (Sun et al., 2023). We formulate the hypothesis that the transformation of saltmarshes into aquaculture ponds will change land use types and landscape patterns, which, in turn, will alter elevation. This increased elevation can significantly mitigate the impacts of tidal flooding, thereby reducing soil leaching. These changes in environmental conditions directly influence soil physico-chemical properties, including fertility, acidity, alkalinity,

and permeability. Consequently, these soil properties directly affect plant and soil macrofaunal communities, while elevation indirectly influences them through these soil properties. To validate this hypothesis, we conducted an investigation across 36 plots distributed in two regions within Sheyang coastal wetland, which encompass both saltmarshes and reclaimed areas (Figure 1). Prior to reclamation, these regions were predominantly saltmarsh ecosystems (Supplementary Figure 1). The landward sides were subsequently transformed into aquaculture ponds, experiencing similar levels of human disturbance. Our aim to address three key questions: 1) What are the impacts of saltmarsh reclamation on

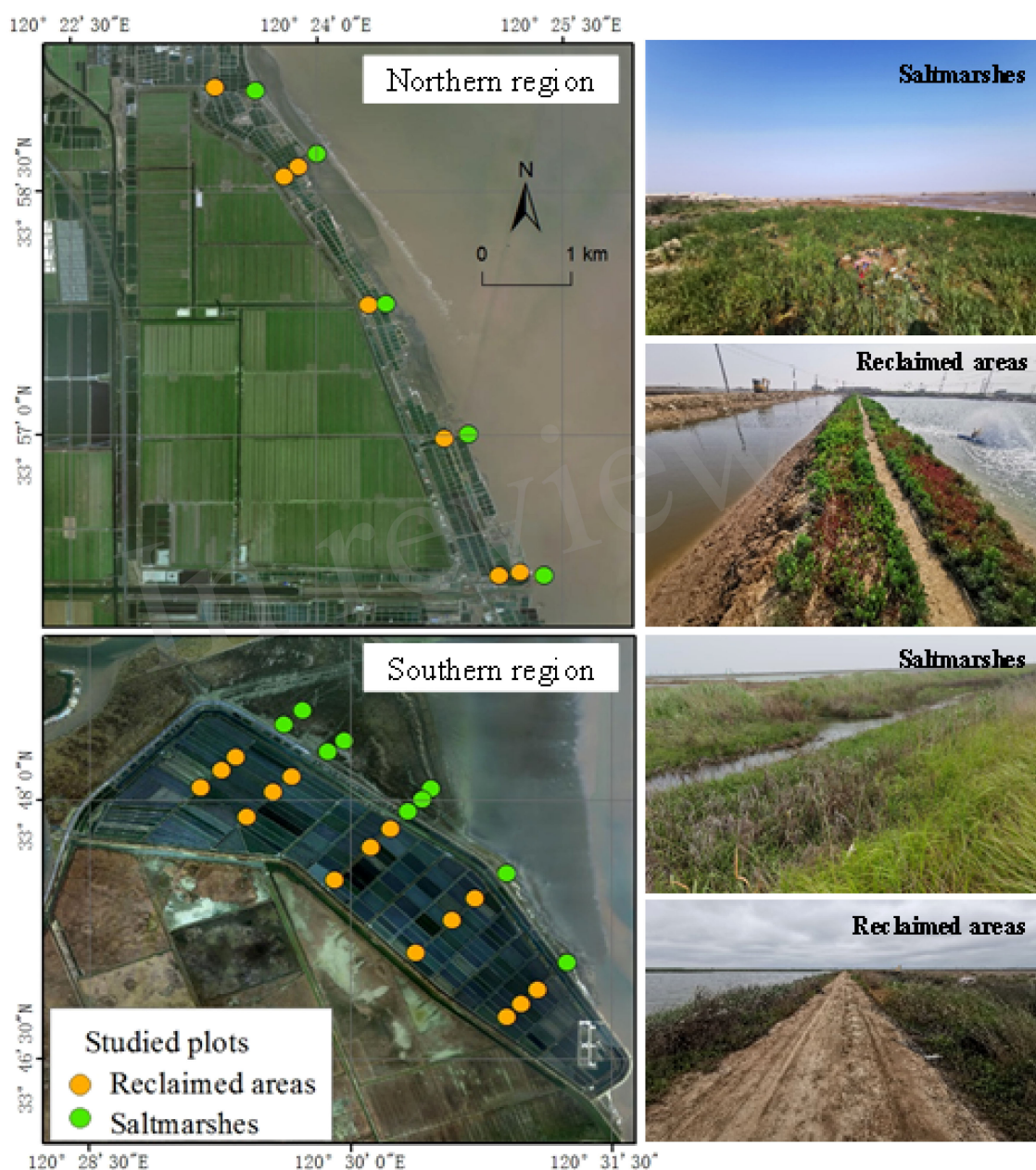


FIGURE 1

The geographical distribution of the 36 studied plots across the northern and southern regions of Sheyang, Jiangsu Province, eastern China, encompassing both saltmarshes and reclaimed areas.

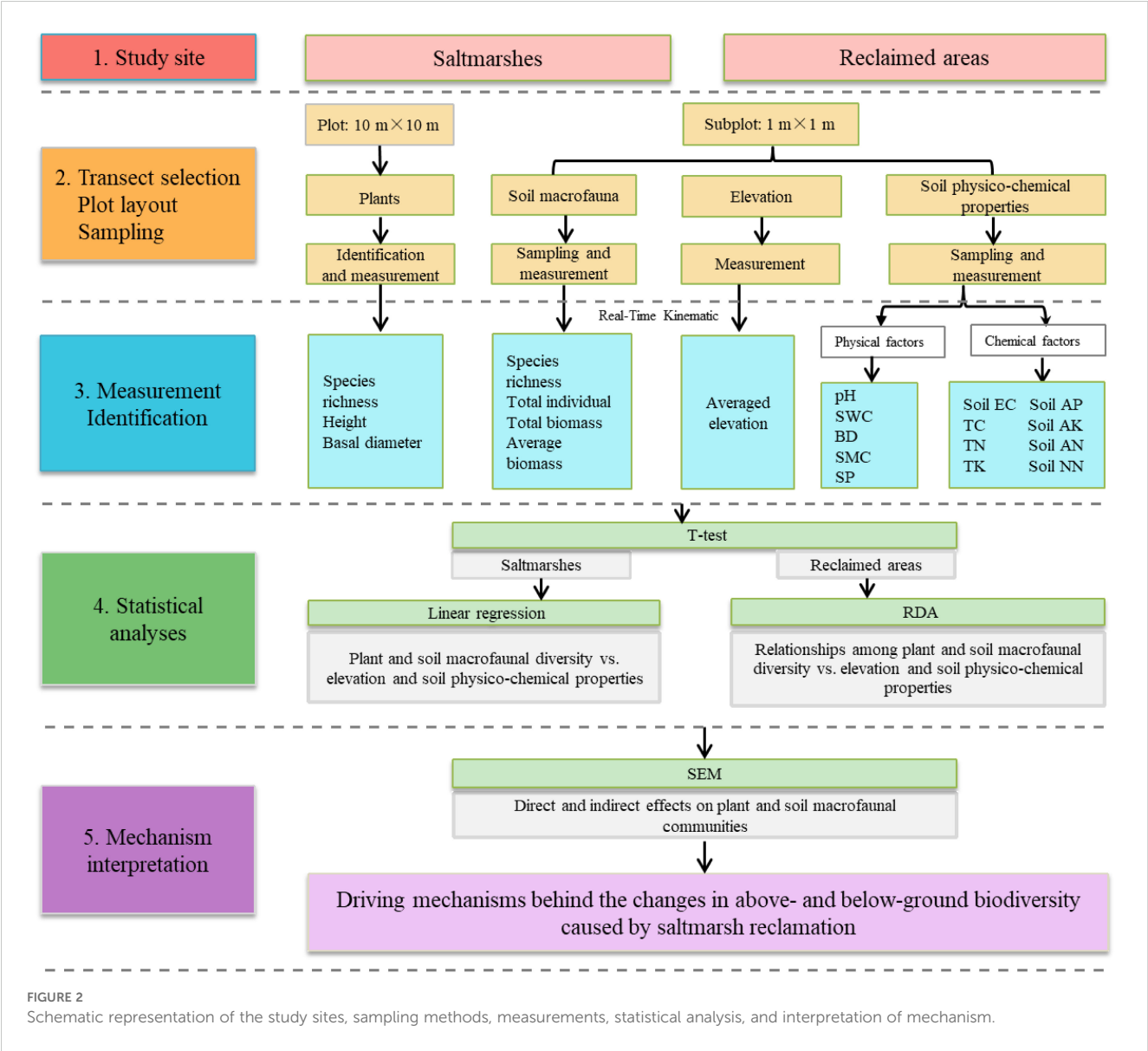
plant and soil macrofaunal communities? 2) How do soil physico-chemical properties change in response to saltmarsh reclamation? 3) How does elevation indirectly influence plant and soil macrofaunal communities by regulating soil physico-chemical properties post-saltmarsh reclamation? Our research aims to provide valuable theoretical insights for predicting variations in both plant and soil macrofauna biodiversity resulting from saltmarsh reclamation.

2 Materials and methods

2.1 Study site

Sheyang County, located within the coordinates 33°31'12"N to 34°07'15"N and 119°55'48"E to 120°34'47"E, is situated in Jiangsu

Province, eastern China (Figure 1). This area experiences a typical subtropical monsoon climate, characterized by cool summers and warm winters. The mean annual temperature is 14 °C, with a mean annual precipitation of 1,000 mm. Over recent years, sediment deposition in mudflat provides suitable space for saltmarshes plants to grow. The dominant saltmarsh species were *P. australis* and *Suaeda* spp. before the invasion of *Spartina alterniflora*, which has gradually replaced the native saltmarsh species. Reclamation activities have been conducted in the vicinity of the Sheyang estuary to create aquaculture ponds. The southern region of the estuary was reclaimed in 2005, resulting in an enclosed area of approximately 6.1 km². The northern region was reclaimed in 2006, covering about 1.5 km². The construction of pond embankment directly resulted in the isolation of saltmarshes and a reduction in mudflats. The schematic processes of the samplings, measurements, statistical analysis, and mechanism interpretation of our study were showed in Figure 2.



2.2 Transect selection, plot layout, and sampling

From May to June 2023, we conducted a comprehensive survey and established 10 transects in the northern and southern regions of the Sheyang estuary (Figure 1). We selected these regions to expand the number of plots, given their comparable reclaimed history and the presence of saltmarshes and reclaimed areas. Our analysis of these measured variables revealed no significant differences between the northern and southern regions (Supplementary Table 5). In general, numerous studies have shown that random or stratified-random sampling methods are commonly used in biodiversity assessments (Singh and Mangat, 1996; Martino et al., 2018). In our study, we selected the transect sampling method because it captures subtle variations in both flora and fauna from saltmarshes to reclaimed areas, while also incorporating elements of randomness and representativeness (Ge et al., 2019, 2021b). These transects were strategically positioned to run perpendicular to the coastlines, with spacing intervals varying from 0.5 to 1.9 km. Within each transect, we randomly selected 3 to 6 replicate sites in both saltmarsh and reclaimed areas, ensuring a separation distance of 30 to 500 m between them. In total, 36 sampling sites were identified (Supplementary Table 1). At each site, we delineated plant plots of approximately 10 m × 10 m. The number of sampling plots in the southern and northern regions is indeed directly proportional to their respective areas (Supplementary Table 1; Supplementary Figure 3). We meticulously identified all existing plant species, documenting their names, dominance-aggregation, coverage, height, and basal diameter. Additionally, we calculated the dominance of plant species using the following equation (Supplementary Table 3): $\text{dominance} = (\text{relative height} + \text{relative coverage} + \text{relative frequency})/3$.

To assess elevation, soil physico-chemical properties, and soil macrofauna, we randomly established three 1 m × 1 m subplots within each plot. Due to the minimal variations in slope, the consistent slope types in both saltmarshes and reclaimed areas, and the uniform environmental factors across these two regions, we did not consider slope and slope type in our study. We individually measured the elevation of each subplot using Real-Time Kinematic (RTK) technology and subsequently computed the average for each plot. Soil samples were taken using a metallic corer (20 cm depth and 7.5 cm in diameter) from the 0–20 cm soil layer (immediately below the litter layer) within each subplot and then combined. Soil sampling was collected on sunny days with no recorded rain in the preceding three days. For macrofauna collection, we randomly gathered quantitative soil samples measuring 25 cm × 25 cm × 30 cm near the center of each subplot and combined them. Soil macrofauna found on the sample surface were picked up using forceps within 48 hours and preserved in 75% alcohol (Wong et al., 2016). Soil macrofauna was collected using a 2 mm seawater sieve, preserved in 75% alcohol, and stored in plastic bottles. The samples were then transported to the lab for detailed identification, enumeration, and comprehensive analysis of the soil macrofaunal community's abundance, species diversity, and biomass.

2.3 Soil macrofauna identification

The examination of soil macrofauna was conducted by Qingdao Guomao Environmental Testing Co., Ltd., a professional testing agency, following the implementation standards GB 17378-2007 and GB/T 12763-2007. They used a ZOOM645 stereomicroscope and a BM2000 biological microscope for the identification of soil macrofauna, followed by precise weighing. Before weighing, the specimens were placed on absorbent paper to eliminate surface moisture, and any tubes, hermit crab shells, body camouflage, or other attachments to macrofauna were carefully removed. Refining the identification of species to the lowest taxonomic unit, typically at the genus or species level. The weighing procedure was carried out using an electronic balance boasting a sensitivity of 0.0001 g (JA2003). For tube-dwelling macrofauna, the tubes were first removed before weighing. Hermit crabs were weighed without their shells, while mollusks were generally weighed with their shells, which were then dried. For large or numerous mollusks, the shells and flesh were weighed separately. Filter paper was used to remove surface moisture from the macrofauna. Additionally, separate measurements of flesh and ash weight were obtained for shellfish. Counting methods included considering only the head of easily breakable annelids or segmented organisms, and excluding dead shells for mollusca. In instances where large sample sizes were involved, a portion of the sample was weighted for conversion.

2.4 Soil physico-chemical properties measurement

For each sampling plot, we comprehensively measured 14 key soil physico-chemical properties, including soil pH (pH), soil water content (SWC), bulk density (BD), soil mud content (SMC), soil porosity (SP), soil electrical conductivity (soil EC), total carbon (TC), total nitrogen (TN), total phosphorus contents (TP), total potassium (TK), soil available phosphorus (soil AP), soil available potassium (soil AK), soil ammonium nitrogen (soil AN), and soil nitrate nitrogen (soil NN). These edaphic parameters are widely recognized as crucial factors influencing the distribution patterns of plants and soil macrofauna within coastal wetlands (Ge et al., 2021b). Soil pH was determined using a pH meter. SWC was assessed by comparing soil quality before and after drying. BD was determined using the ring knife method. SMC was measured post-washing with water and subsequent drying. SP was calculated based on bulk density and specific gravity, with specific gravity measured using a pycnometer. Soil EC was measured at a minimum of five locations within each plot using a portable WET Sensor (WET-2, England). TC and TN were analyzed using inductively coupled plasma optical emission spectrometry (Spectro Analytical Instruments) following pressure digestion (HNO₃ digestion). TP and TK were determined using the phosphorus vanadium molybdate yellow colorimetric method and flame photometer method after high-temperature digestion (NaOH digestion). Soil AP was assessed using the sodium bicarbonate extracted-

molybdenum antimony colorimetric method (Spark, Tecan, Switzerland). Soil AK was detected using the ammonium acetate extraction flame photometer method (XP, BWB, England). Soil AN and Soil NN were measured using the indophenol blue colorimetric method and dual-wavelength ultraviolet spectrophotometry following KCl extraction.

2.5 Statistical analyses

Initially, we utilized linear regression to investigate the impact of elevation on soil physico-chemical properties. Simultaneously, we conducted principal components analysis (PCA) on elevation and soil physico-chemical properties to identify significant correlations among them. Subsequently, we employed *t*-test to assess the differences of plant and soil macrofaunal diversity, elevation, and soil physico-chemical properties between saltmarshes and reclaimed areas. Furthermore, we performed redundancy analysis (RDA) to examine the relationships among plant and soil macrofaunal diversity, elevation, and soil physico-chemical properties, aiming to identify potential factors influencing plant and soil macrofaunal communities. RDA was performed using the “vegan” package in R software.

Finally, we used structural equation modeling (SEM) to disentangle causal pathways through which elevation and soil physico-chemical properties directly and indirectly affect plant and soil macrofaunal diversity. SEM was fitted using the “sem” package in R software, considering all possible pathways among the explanatory variables, simplifying initial models based on selected models by eliminating nonsignificant pathways. For SEM, we estimated direct and indirect effects as standardized path coefficients, enabling comparisons among predictor variables. The fit of SEM was evaluated using Chi-square (χ^2), Comparative fit index (CFI), Tucker–Lewis index (TLI) and Root mean square error of approximation (RMSEA). A satisfactory SEM was deemed when $P > 0.05$ for the χ^2 test, CFI > 0.9 , TLI > 0.9 , and RMSEA < 0.05 .

Before conducting statistical analyses, we assessed the normality of elevation and soil physico-chemical properties using Shapiro–Wilk test (Supplementary Table 2). To ensure symmetry and linearity, numerical predictors underwent log-transformed.

Statistical significance was determined at $P < 0.05$. All statistical analyses were conducted in R version 4.3.1 (R Core Team, 2021).

3 Results

3.1 Variations in the composition of plant and soil macrofaunal communities between saltmarshes and reclaimed areas

In total, 17 plant species were identified across saltmarshes and reclaimed areas, belonging to 15 genera and 11 families (Supplementary Table 3). Notably, *Spartina alterniflora* was the sole species detected in the saltmarshes. The reclaimed areas harbored 17 plant species, with the most prevalent ones being *Phragmites australis*, *Suaeda*, *Artemisia capillaris*, *Avena fatua*, and *Euphorbia esula*. A *t*-test indicated a statistically significant increase in plant species richness in the reclaimed areas compared with the saltmarshes ($t = 8.40$, $P < 0.0001$). However, no statistically significant differences were observed in plant height ($t = 0.01$, $P = 0.99$) and basal diameter ($t = 0.87$, $P = 0.39$) between saltmarshes and reclaimed areas (Table 1; Figure 3A).

In total, 33 soil macrofaunal species were identified across saltmarshes and reclaimed areas, belonging to 4 phyla, 30 genera and 32 families (Supplementary Table 4). In saltmarshes, a total of 180 soil macrofaunal individuals were gathered, which were categorized into 23 species, 3 phyla, 21 families, and 21 genera. The phyla represented were Mollusca (10 species, accounting for 43%), Annelida (7 species, 30%), and Arthropoda (6 species, 26%). The dominant species (individuals $\geq 5\%$) were *Assiminea latericea*, *Cerithidea largillierti*, *Umbonium thomasi*, *Neanthes japonica*, *Orchomene breviceps*, accounting for 76% of the total individuals. Frequently encountered species (number of plots occurring ≥ 6) were *Neanthes japonica*, *Assiminea latericea*, *Cerithidea largillierti*, *Potamocorbula laevis*. The average weight of soil macrofauna ranged from 0.001 to 1.40 g, with the three heaviest species being *Glauconome primeana*, *Cerithidea largillierti*, and *Umbonium thomasi* (Supplementary Table 4).

In reclaimed areas, a total of 123 soil macrofaunal individuals were collected, representing 15 species, 3 phyla, 14 families, and 13

TABLE 1 The *t*-test of plant and soil macrofaunal diversity between saltmarshes and reclaimed areas.

Variables	<i>df</i>	<i>t</i>	<i>P</i> -value	Mean of saltmarshes	Mean of reclaimed areas
Plant height [cm]	28.42	0.01	0.99	4.26	4.26
Plant basal diameter [mm]	33.99	0.87	0.39	2.17	2.29
Plant species richness	32.06	8.40	<0.0001	1.33	4.81
Soil macrofaunal species richness	30.26	−0.38	0.70	0.52	0.45
Soil macrofaunal total individual	29.703	−0.16	0.87	1.24	1.18
Soil macrofaunal total biomass [mg]	33.71	−2.56	<0.05	−0.57	−3.13
Soil macrofaunal average biomass [mg]	33.94	−3.21	<0.01	−1.81	−4.30

All variables were log-transformed. Significance at $P < 0.05$ is highlighted in bold. *df*, degree of freedom.

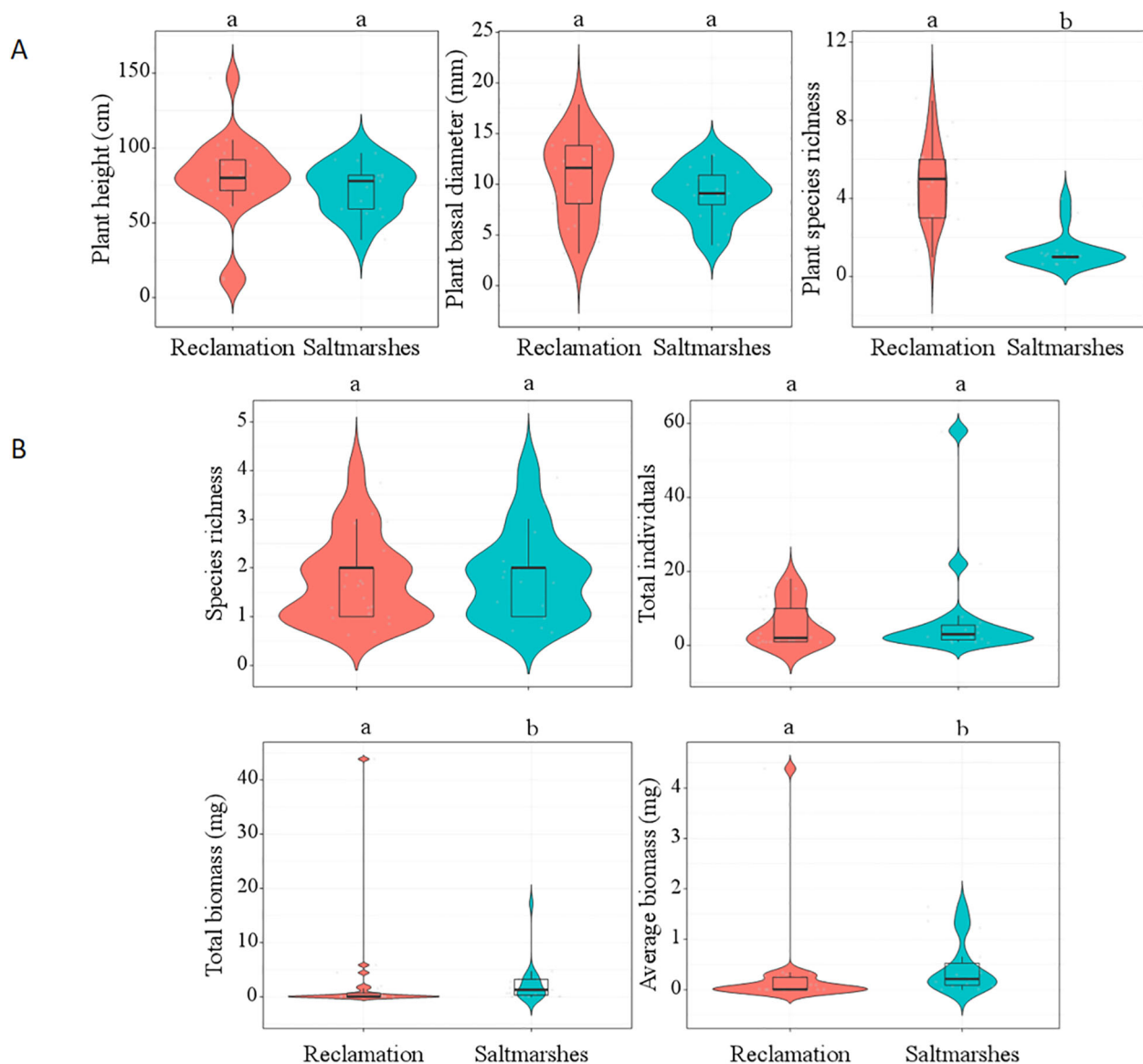


FIGURE 3

The t-test of plant diversity and soil macrofaunal diversity between saltmarshes and reclaimed areas. Different letters indicate significant differences between saltmarshes and reclaimed areas ($P < 0.05$). (A) Plant diversity; (B) soil macrofaunal diversity.

genera (Supplementary Table 4). The phyla present were Arthropoda (9 species, 69%), Mollusca (4 species, 31%), and Annelida (2 species, 13%). The dominant species were *Neanthes succinea*, *Assimineia latericea*, *Porcellio* sp., *Corophium sinense*, which collectively accounted for 75.6% of the individuals. The species most frequently encountered were *Assimineia latericea* and *Porcellio* sp. The average biomass of soil macrofauna ranged from 0.001 to 8.56 g, with the two heaviest species being *Scapharca subcrenata* and *Macrophthalmus japonicus*. The t-test revealed that the total and average biomass of soil macrofauna in reclaimed areas were significantly lower compared to those in saltmarshes ($t = -2.56$, $P = 0.02$; $t = -3.21$, $P < 0.01$). Soil macrofaunal total biomass in reclaimed area reduced to 1%. Nonetheless, there were no significant differences in the total individual ($t = -0.16$, $P = 0.87$)

and species richness ($t = 0.70$, $P = 0.52$) between saltmarshes and reclaimed areas (Table 1; Figure 3B).

3.2 Variations in elevation and soil physico-chemical properties between saltmarshes and reclaimed areas

The t-test showed that SWC, SP, soil EC, TC, soil AK, and soil AN were significantly higher in saltmarshes compared with reclaimed areas ($P < 0.05$), while elevation (E) and BD were significantly lower in saltmarshes than that in reclaimed areas ($P < 0.05$). No significant differences were observed in soil pH, SMC, TN, TP, TK, soil AP, and soil NN between saltmarshes and

TABLE 2 The t-test of elevation and soil physico-chemical properties between saltmarshes and reclaimed areas.

Environmental factors	df	t	P-value	Mean of saltmarshes	Mean of reclaimed areas
E [m]	31.95	6.34	<0.001	1.79	2.11
Soil pH [pH]	23.56	1.34	0.19	8.09	8.24
SWC [%]	19.75	-3.61	<0.01	37.42	23.69
BD [g·cm ⁻³]	27.86	2.10	<0.05	0.97	1.17
SMC [%]	16.19	1.35	0.20	88.59	95.58
SP [%]	20.59	-2.09	<0.05	40.38	32.76
Soil EC [μS·cm ⁻¹]	21.13	-2.29	<0.05	7912.53	4857.09
TC [g·kg ⁻¹]	17.18	-3.16	<0.01	24.47	18.18
TN [g·kg ⁻¹]	20.11	-1.42	0.17	0.97	0.83
TP [g·kg ⁻¹]	32.24	0.06	0.95	0.81	0.81
TK [g·kg ⁻¹]	17.31	-0.73	0.47	20.81	20.05
Soil AP [mg·kg ⁻¹]	23.54	-1.81	0.08	4.14	3.65
Soil AK [mg·kg ⁻¹]	16.53	-2.81	<0.05	778.05	507.69
Soil AN [mg·kg ⁻¹]	16.37	-2.81	<0.05	6.86	4.02
Soil NN [mg·kg ⁻¹]	33.78	0.52	0.61	1.91	2.25

E, elevation; SWC, soil water content; BD, bulk density; SMC, soil mud content; SP, soil porosity; Soil EC, soil electrical conductivity; TC, total carbon; TN, total nitrogen; TP, total phosphorus; TK, total potassium; Soil AP, soil available phosphorus; Soil AK, soil available potassium; Soil AN, soil ammonium nitrogen; Soil NN, soil nitrate nitrogen. Significance at $P < 0.05$ is highlighted in bold. *df*, degree of freedom.

reclaimed areas ($P > 0.05$) (Table 2). The first two PCA axes accounted for 59.3% of the variance in elevation and soil physico-chemical properties (Figure 4). PC1 represented the axis of soil salinity, nutrition and moisture, characterized by higher SWC, SP, soil EC, TC, TN, soil AK, and soil AN, along with lower soil pH and BD. PC2 indicated the axis related to soil phosphorus, with higher TP and soil AP (Supplementary Table 6). The PCA biplot depicted that with increasing elevation, soil pH and BD increased, whereas SP, SWC, soil AK, soil EC, and soil AN decreased (Figure 4; Supplementary Figure 2; Supplementary Figure 6).

3.3 Effects of elevation and soil physico-chemical properties on plant and soil macrofaunal communities

The RDA elucidated the intricate relationships among plant and soil macrofaunal communities, elevation, and soil physico-chemical properties in saltmarshes and reclaimed areas (Figure 5). The eigenvectors of RDA1 and RDA2 explained 43.45% and 22.71% of the variance in plant and soil macrofaunal communities, respectively. Plant species richness increased with E, and decreased with soil AP and soil EC. Plant basal diameter increased with soil AP. Plant height increased with soil AN, TK, TN, SP, SWC, and TC. The species richness, total individual, total biomass, and average biomass of soil macrofauna increased with soil AN, TN, TK, SP, SWC, TC, soil NN, soil AK, and soil EC, but decreased with TP, E, SWC, pH, and BD (Figure 5).

3.4 Elevation affects plant species richness and soil macrofaunal biomass by regulating soil physico-chemical properties

The best-fitted SEMs demonstrated a strong fit to the data, explaining 96%, 80%, and 75% of the variations in plant species richness, total and average biomass of soil macrofauna, respectively (Figure 6). Although elevation did not directly impact plant species richness and soil macrofaunal biomass, it exerted indirect effects by regulating soil physico-chemical properties (Figure 6; Supplementary Table 7). Specifically, elevation positively influenced plant species richness indirectly through SWC, TC, soil AN, and soil NN, while it negatively affected plant species richness via BD. Elevation indirectly decreased soil macrofaunal total biomass by affecting SWC, TC, and soil AN, but it indirectly increased soil macrofaunal total biomass through soil AK. Additionally, elevation indirectly reduced the average biomass of soil macrofauna by affecting TC and soil AN (Supplementary Table 7).

4 Discussion

4.1 Effects of saltmarsh reclamation on plant and soil macrofaunal communities

Our findings indicate that saltmarsh reclamation significantly increased plant species richness while reducing soil macrofaunal biomass within coastal wetlands. The transformation of saltmarshes

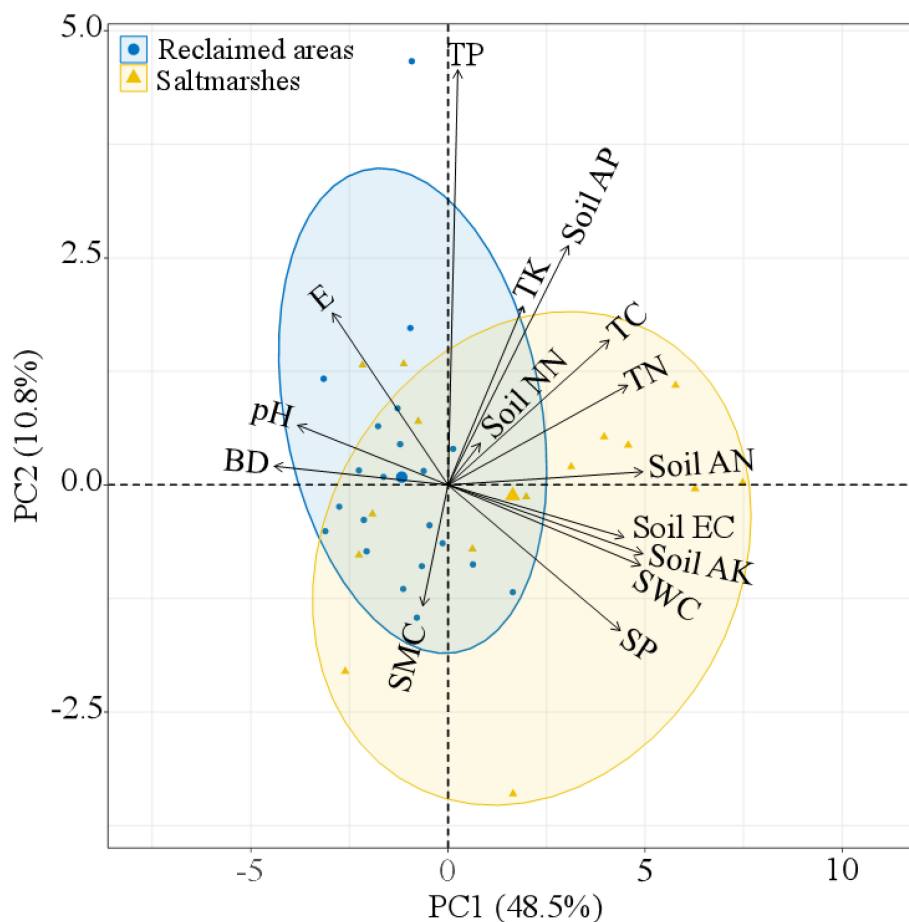


FIGURE 4

PCA biplot of elevation and soil physico-chemical properties in saltmarshes and reclaimed areas. E, elevation; SWC, soil water content; BD, bulk density; SMC, soil mud content; SP, soil porosity; Soil EC, soil electrical conductivity; TC, total carbon; TN, total nitrogen; TP, total phosphorus; TK, total potassium; Soil AP, soil available phosphorus; Soil AK, soil available potassium; Soil AN, soil ammonium nitrogen; Soil NN, soil nitrate nitrogen. The yellow ellipse represents saltmarshes, while the blue ellipse denotes reclaimed areas.

into aquaculture ponds primarily influenced land use types and landscape patterns, notably by raising elevation, which altered hydrological conditions and ecological processes (Portnoy and Giblin, 1997; Huang et al., 2021; Naser, 2022). Additionally, saltmarsh reclamation has resulted in long-term changes to soil physico-chemical properties (Li et al., 2014; Xie et al., 2017; Ge et al., 2021a). Specifically, with the increase in terrain elevation, BD and freshwater rose, while SWC, SP, soil EC, TC, soil AN, soil NN, and seawater decreased (Supplementary Figure 6). These changes are attributed to reduced seawater leaching effects, relatively stable salinity and prolonged destabilization (Walker et al., 2010; Chan et al., 2016). Additionally, it is part of the physical-biological feedbacks within ecogeomorphology (Murray et al., 2008). For example, plant growth can significantly modify sediment dynamics (Horstman et al., 2015); conversely, plant growth is also constrained by factors such as sedimentation rate, inundation duration, and salinity, which are influenced by morphological changes (Lovelock et al., 2015).

Saltmarsh reclamation indirectly promotes the establishment and growth of 17 plant species that are tolerant to salt and water,

while partially inhibiting the competitive species *S. alterniflora*. Previous studies have also indicated that saltmarsh reclamation mainly contributes to shifts in plant diversity within coastal wetlands (Li et al., 2014; Allan et al., 2015; Cao et al., 2018) and facilitates the introduction of non-native plant species through various invasive pathways (Zhang and Shao, 2013b). *S. alterniflora* is the only species left in saltmarshes. About 20 years ago, the dominant saltmarsh species were *P. australis* and *Suaeda* spp. The suitable habitat for *P. australis* and *Suaeda* spp. has been reclaimed, and *S. alterniflora* is highly competitive in lower tidal flat, so *S. alterniflora* has gradually replaced the native saltmarsh species (Netto and Lana, 1999). Soil physico-chemical properties can directly affect plant diversity. For example, plant species richness positively correlated with TN, and negatively correlated with SWC, BD, TC, soil AP, soil EC, and soil AN (Figure 5; Supplementary Figure 4). Especially, optimal salinity levels can promote plant growth, whereas exceeding the tolerance threshold may hinder it (Coletti et al., 2017; Parihar et al., 2015). In reclaimed areas, lower soil EC and SWC often lead to the proliferation of more salt-sensitive and drought-resistant plants (Supplementary Table 1).

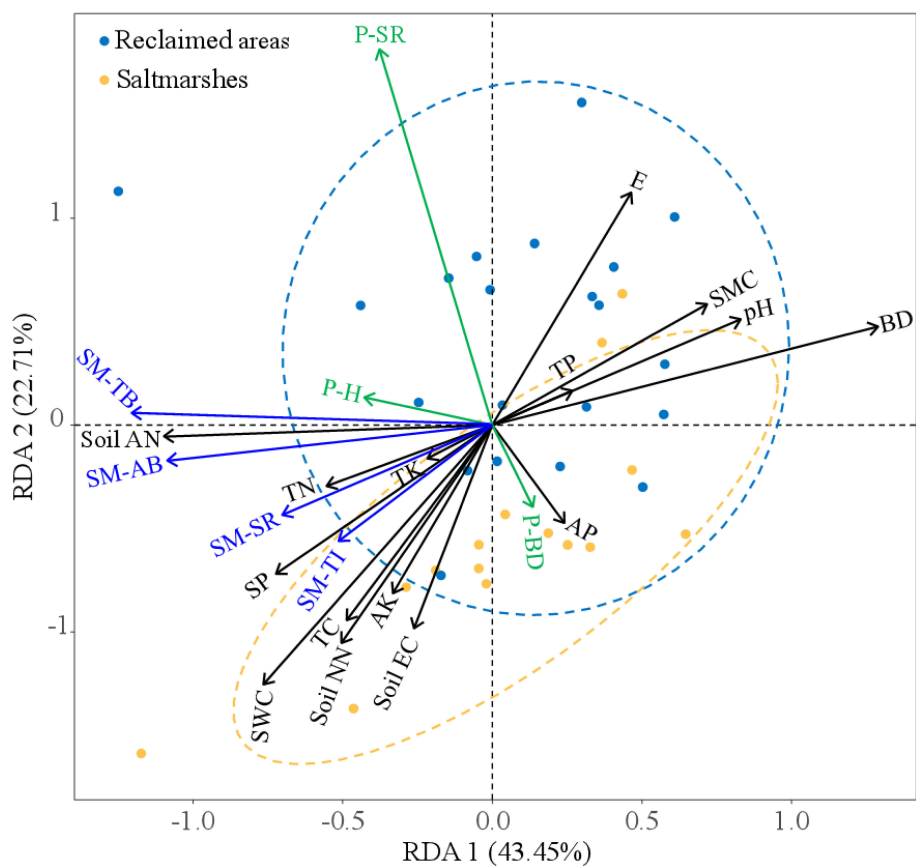


FIGURE 5 RDA biplot illustrating the relationships among soil properties (black), plant diversity (green), and soil macrofaunal diversity (blue) in saltmarshes and reclaimed areas. P-H, plant height; P-BD, plant basal diameter; P-SR, soil macrofaunal species richness; SM-TI, soil macrofaunal total individual; SM-SR, soil macrofaunal species richness; SM-TB, soil macrofaunal total biomass; SM-AB, soil macrofaunal average biomass. The introduction of abbreviated soil physico-chemical properties can be found in Figure 4.

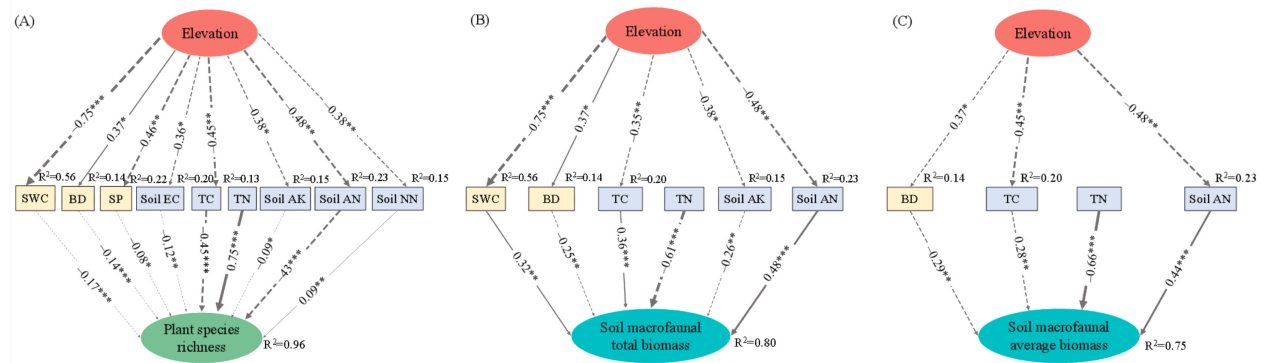


FIGURE 6 The best-fitted structural equation model explains that elevation indirectly influences plant species richness and soil macrofaunal biomass through soil physico-chemical properties. Notes: Solid and dashed lines represent significant positive and negative paths, respectively (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). The standardized regression coefficients are shown for each path, and the width of lines reflects the relative values of standardized path coefficient. R^2 indicates the total variation in a dependent variable that is explained by the combined independent variables. All variables were log-transformed. An introduction to the abbreviated soil physico-chemical properties is shown in Figure 4. (A) Plant species richness; (B) Soil macrofaunal total biomass; (C) Soil macrofaunal average biomass.

Additionally, seed germination and seedling growth are influenced by hydrological dynamics, flooding frequency, and sedimentary processes, all of which can impede successful plant establishment (Bouma et al., 2014; Coletti et al., 2017). These results can be explained by plant-soil feedback, where plants alter soil biological and abiotic properties in their growth environment, and the changed soils subsequently affect the fitness of plants (Bever, 1994).

Saltmarsh reclamation has led to a decrease in both the total and average biomass of soil macrofauna. This change is attributed to the presence of distinct soil macrofaunal species in both saltmarshes and reclaimed areas, each exhibiting different biomass levels (Supplementary Table 4). Soil macrofaunal biomass positively correlated with SWC, TC, and soil AN, while showing negative correlations with BD, TN, and soil AK (Figure 5; Supplementary Figure 5). These correlations highlight how soil properties can directly influence the survival and reproduction of soil macrofauna (Ge et al., 2021a). Studies have shown that sediment characteristics, tidal levels, salinity, and elevation collectively impact the establishment and persistence of macrofaunal communities in saltmarshes (Ysebaert and Herman, 2002; Chao et al., 2012; Xue et al., 2019). Following saltmarsh reclamation, many soil macrofaunal communities were lost due to their inability to adapt to the new environments characterized by drier conditions and lower salinity (Wang et al., 2021). Changes in food sources, breeding habitats, and shelters for soil macrofauna also influenced their composition and biodiversity (Ge et al., 2021b; Wang et al., 2010). Conversely, several studies have indicated that reclamation negatively impacts the species richness, abundance, biomass, diversity, and community succession of soil macrofauna (Koo et al., 2008; Wu et al., 2021; Naser, 2022). We observed a reduction in the abundance of Gastropoda, Bivalvia, and Polychaeta groups with limited mobility, while highly active Malacostraca increased in reclaimed areas. Additionally, Insecta larvae were found in reclaimed areas but not in saltmarshes. This aligns with findings that reclamation alters community structure, significantly decreasing the number of larger crustaceans, which are gradually replaced by mollusks and annelids (Huang et al., 2021).

Soil moisture (SWC), nutrients (TN, TK, TC, TP, soil AN, soil NN, and soil AK), salinity (soil EC and pH), and soil physical structure (BD and SP) significantly influence soil macrofaunal communities. These soil properties are also related to the growth, reproduction, and distribution of soil macrofauna (Pandey and Thiruchitrambalam, 2019; Ge et al., 2021b). Soil nutrients are essential for primary productivity and thus play a critical role in food availability for macrofaunal communities (Ge et al., 2021b). Similarly, studies have shown that soil macrofauna are significantly affected by a combination of salinity, soil particle size, and elevation (Ysebaert and Herman, 2002), as well as by soil moisture (Ge et al., 2021a) and clay content (Li et al., 2020). Soil macrofaunal diversity positively correlated with salinity, pH, and larger soil particle diameter, while negatively correlating with TN and TP (Huang et al., 2021). We also found that certain phyla, such as Chaetognatha, Annelida, Mollusca, and Arthropoda, are better adapted to high-salinity soils near the coast.

4.2 Saltmarsh reclamation indirectly influences plant and soil macrofaunal communities by regulating soil properties through elevation

Saltmarsh reclamation plays a pivotal role in shaping both plant and soil macrofaunal communities by regulating soil properties through changes in elevation. The SEMs revealed that soil AN, soil AK, SWC, and TC negatively correlated with elevation, while BD positively correlated with it. These factors, acting as environmental filters, influencing plant and soil macrofaunal diversity. This suggested that elevation-driven changes in soil compaction and hydrology act as habitat filters, selectively excluding taxa with specific physiological tolerances. Elevation is often regarded as a comprehensive indicator of regional environmental conditions (Yuan and Lu, 2003), as it affects sediment composition, flooding conditions, and soil physico-chemical properties along the elevation gradient (Zhang et al., 2021b). The influence of seawater and tidal effects on saltmarshes and soil macrofauna diminishes with increasing elevation (Salgado et al., 2007; Ge et al., 2021b). Many studies investigating the relationship between soil macrofauna and environmental factors frequently utilize elevation gradients, which have long been recognized as critical determinants of ecosystem dynamics and biodiversity (Carey et al., 2015; Yang et al., 2016).

Plant communities in coastal wetlands display a zonal distribution along the elevation gradient. Erosion caused by seawater decreases with rising elevation, leading to diminished environmental stressors and creating more favorable habitats for plant growth, thereby increasing plant abundance (Boorman, 2003). Elevation and plant distribution represent a typical bidirectional feedback process. On one hand, changes in elevation significantly influence the growth and succession of plants, leading to variations in inundation duration and frequency, which affect their long-term adaptation. Consequently, different plant species thrive within their optimal elevation ranges (Keddy, 2010). On the other hand, plant growth can promote sediment accumulation, ultimately resulting in an increase in elevation. Meanwhile, plant distribution is primarily influenced by biotic factors such as competition and environmental filtering (Lambers et al., 2019). Furthermore, soil macrofaunal diversity transitions from saltmarshes to reclaimed areas, characterized by a shift from swimming benthic organisms to burrowing and attached species (Yuan and Lu, 2003).

Soil moisture, nutrients, and salinity significantly impact plant and soil macrofaunal communities, particularly through alterations in elevation during saltmarsh reclamation. Research has shown that salinity and elevation collectively affect soil macrofauna (Ysebaert and Herman, 2002). Additionally, changes in elevation influence flooding duration and soil properties, leading to zonation in the composition and abundance of soil macrofauna in Gulf of Mexico and Brazilian saltmarshes (Netto and Lana, 1999; Mouton and Felder, 2007; Compton et al., 2013; Dewenter et al., 2023). Saltmarshes at lower elevations near seawater often exhibit higher diversity and density of soil macrofauna, while both abundance and diversity tend to decrease with increasing elevation (Zhang et al.,

2021b). To effectively mitigate the impacts of saltmarsh reclamation, a comprehensive approach to assessment and management throughout the reclamation processes is essential. This should include a thorough consideration of both above- and below-ground organisms, as well as soil physico-chemical properties. Meanwhile, slope and slope types may significantly impact biodiversity during saltmarsh reclamation (Khan et al., 2013; Huang et al., 2015). Future studies should take these factors into account. Additionally, rising sea levels driven by climate change could alter land use types and landscape patterns in coastal wetlands. As a result, these changes may lead to modifications in elevation and soil properties, subsequently affecting both above- and below-ground biodiversity (Vo et al., 2014).

It should be noted that our findings reflect the ecological conditions within the first two decades following reclamation. Longer-term effects of saltmarsh conversion, particularly those involving successional changes beyond 20 years, require further investigation. In our study, while the number of sampling plots may not be sufficient to fully capture the overall patterns of plant and soil macrofaunal diversity, our results are robust enough to detect several statistically significant trends. This suggests that our selected plots are adequate for identifying the “reclamation effects.” Consequently, our findings highlight the significant role that elevation and soil physico-chemical properties play in influencing both above- and below-ground biodiversity. Further in-depth research is needed to determine whether our conceptual insights can be broadly applied to other coastal ecosystems.

5 Conclusions

Saltmarsh reclamation has led to notable alterations in the elevation and soil physico-chemical properties of coastal wetlands, profoundly affecting both above- and below-ground biodiversity in plant and soil macrofaunal communities. Notably, saltmarsh reclamation has enhanced plant species richness from 1 to 17, resulting in a 99% decrease in soil macrofaunal total biomass, by regulating soil properties through elevated changes. Specifically, soil moisture, nutrients, and salinity are the primary factors influencing plant species richness and soil macrofaunal biomass. Elevation had an indirect positive effect on plant species richness via SWC, TC, soil AN, and soil NN, and an indirect negative effect through BD. Furthermore, elevation indirectly decreased soil macrofaunal total biomass through SWC, TC, and soil AN, but indirectly increased it through soil AK. Our study highlights the underlying mechanisms driving variations in above- and below-ground biodiversity resulting from saltmarsh reclamation. Future studies should establish long-term monitoring of both plant and soil macrofaunal community succession following reclamation and compare the effects of different reclamation methods. Besides, implementing effective management strategies, such as elevation control, preserve tidal creeks in reclaimed areas, establishing priority conservation zones for soil macrofauna in low-elevation

areas should be emphasized. These findings can be applied to investigate the impacts of coastal wetland reclamation on both above- and below-ground biodiversity, particularly regarding how variations in land use and landscape interact with elevation on a larger scale.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author/s.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

GZ: Writing – original draft, Funding acquisition, Conceptualization, Investigation. SW: Writing – original draft, Funding acquisition, Conceptualization, Investigation. MX: Conceptualization, Funding acquisition, Supervision, Writing – review & editing. HH: Writing – original draft, Methodology, Investigation, Writing – review & editing. JH: Conceptualization, Writing – review & editing, Investigation. JG: Writing – review & editing, Methodology, Investigation. ZC: Investigation, Methodology, Writing – review & editing. JZ: Writing – review & editing, Conceptualization, Methodology.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2025.1633852/full#supplementary-material>

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