

Mechanisms Underlying the Impacts of *Alternanthera philoxeroides* Invasion on Surface Soil Organic Carbon in the Hongze Lake Wetland: Direct Priming Effects and Phosphorus Limitation influencing Indirect Pathways

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Research Article

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Abstract:

Background and Aims: Alien plant invasion can alter wetland soil organic carbon (SOC), but pathways remain unclear. We examined how *Alternanthera philoxeroides* invasion affects herbaceous communities, soil properties, and SOC in the Hongze Lake lakeshore wetland, and identified direct and indirect pathways.

Methods: In May 2025, we established 11 sampling sites with nine quadrats each (99 total). We measured plant diversity, biomass, soil nutrients, soil physicochemical properties, and SOC. We used linear mixed models with spatial correction (PCNM), partial correlation, and structural equation modeling (SEM).

Results: Invasion reduced species number from 42 to 33 (21.4%). After spatial correction, Shannon and Simpson indices increased, while Margalef decreased. SOC in 0–40 cm decreased by 34.9%, and nitrate nitrogen declined in both 0–20 and 20–40 cm layers. Although available phosphorus (AP) did not differ significantly between groups, SEM showed that relative abundance of *A. philoxeroides* (Pi) negatively affected AP ($\beta = -0.285$), AP positively predicted SOC ($\beta = 0.655$), and the indirect effect was -0.187 . Pi also directly reduced SOC ($\beta = -0.199$). The bulk density pathway was non-significant ($p = 0.065$).

Conclusion: *Alternanthera philoxeroides* invasion reduced SOC mainly via direct priming of native organic matter by root exudates and indirectly by depleting AP, aggravating phosphorus (P) limitation and promoting phosphatase-mediated co-metabolism. These findings inform carbon-pool management in freshwater lake wetlands.

Keywords

Alternanthera philoxeroides; Soil organic carbon; Herbaceous plant species diversity; Soil available phosphorus; Soil bulk density; Hongze Lake Wetland

1. Research Background

Economic globalization has intensified cross-border species exchange, and China is one of the most severely affected countries by invasive alien plant species. *Alternanthera philoxeroides* (alligator weed), a perennial herb native to South America (Garcia-Franco et al. 2015), has caused serious ecological and economic damage due to its strong invasiveness.

In addition to natural succession, *A. philoxeroides* has attained dominance in many plant communities, sometimes forming single-species stands (Du et al. 2022). Studies in China reported 30-36% disappearance of native species under its invasion (Krug and Sosa 2019). Given its trend of northward expansion (Wu et al. 2024), Hongze Lake is facing sustained invasion pressure.

Invasive plants profoundly influence wetland soil organic carbon (SOC) pools by altering vegetation, soil properties, and microbial processes. Effects vary among species and habitats, showing increases (*A. philoxeroides*; Yang et al. 2020), decreases (*Spartina alterniflora*; Lin et al. 2023), or no effect (*Phragmites communis*; Windham and Lathrop 1999).

The mechanisms involve three pathways. (1) Altered carbon inputs: invaders change litter and root exudate quantity, potentially increasing (Oelofse et al. 2016) or decreasing (Li et al. 2024) SOC. (2) Changes in soil properties: invaders modify pH, nutrients, and enzyme activities, affecting SOC stability (Mahlobo et al. 2025). (3) Nutrient limitation: competitive uptake intensifies phosphorus (P) limitation, inducing microbial phosphatase secretion and SOC mineralization via co-metabolism (Vilà et al. 2011).

Plant diversity exhibits bidirectional feedback with wetland SOC (Liu et al. 2024), with global analyses showing positive richness-carbon correlations (Li et al. 2025). Regulation occurs via direct input (litter/root exudates (Pisani et al. 2016)) and indirect pathways (soil pH, moisture, bulk density (Spohn et al. 2025; Thakur et al. 2017; Wright et al. 2017)). Several theories explain invasion effects on diversity: driver-passenger (Zhang et al. 2024), competitive exclusion (Paine et al. 2008) and environmental filtering (Kraft et al. 2015). Dominance-evenness compensation means no single diversity index fully captures invasion impacts, necessitating multi-dimensional assessment (Dostál et al. 2013).

This study investigated *A. philoxeroides* effects on herbaceous diversity, soil nutrients, and SOC in Hongze Lake. Previous studies (Suseela et al. 2016; Wang et al. 2019) revealed multiple mechanisms but rarely addressed Hongze Lake or controlled spatial autocorrelation (Siesa et al. 2011). Using linear mixed models and structural equation models with spatial correction, we addressed three questions: (1) Does *A. philoxeroides* invasion reduce SOC by altering surface soil nutrients? (2) Does invasion reduce SOC

- 65 directly via diversity/biomass reduction or indirectly via soil properties? (3) Do diversity and nutrients
- 66 independently contribute to SOC variation under invasion?

2. Study Area and Methods

2.1 Study Area

The Hongze Lake wetland is located at the junction of Suqian and Huai'an Cities, Jiangsu Province (33°18'27"N, 118°42'36"E) (Huang et al. 2024). As one of China's five largest freshwater lakes, the area has a typical monsoon climate with annual mean temperature 14.8 °C and annual precipitation approximately 926 mm (Liu et al. 2011).

2.2 Sample Collection and Experimental Design

2.2.1 Sampling Site Layout

In May 2025, 12 sampling points were deployed at equal intervals along the lake's shoreline. At each point, nine 10 × 10 m quadrats were established parallel to the shoreline (5 m from water's edge, ≥10 m apart), with three 1 × 1 m subplots per quadrat. One point (hzh11) was excluded due to anthropogenic disturbance, leaving 11 points and 99 quadrats for analysis (Fig. 1).

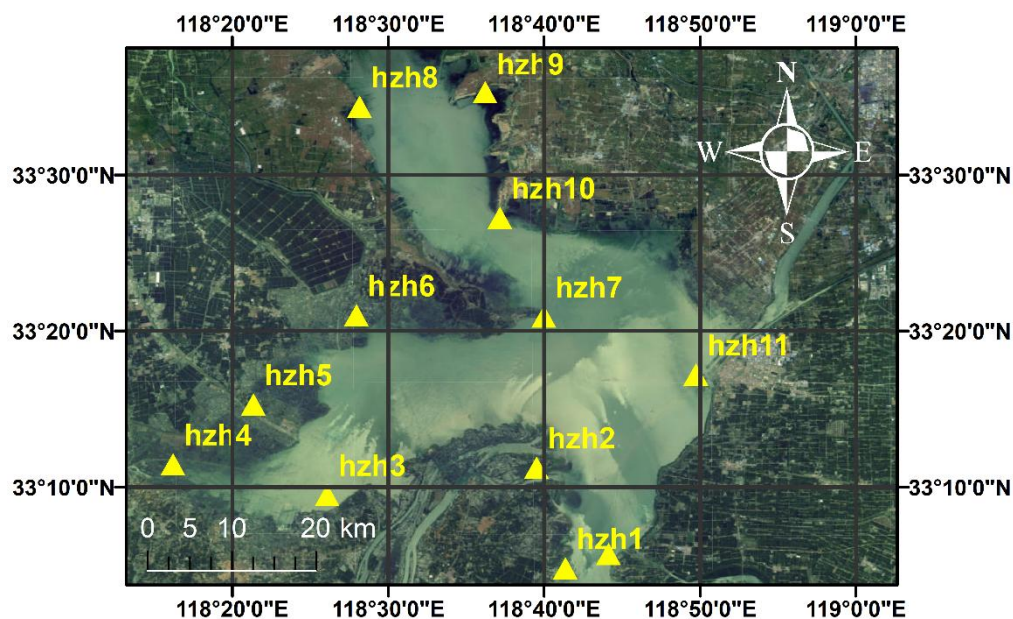


Fig. 1 Locations of the 11 sampling points (black dots) along the shoreline of Hongze Lake. Base map source: GS (2025) 1508.

2.2.2 Classification of Invasion Intensity of Invasive Plants

Invasion intensity was characterized by the relative abundance (P_i) of *A. philoxeroides* within each quadrat. Quadrats were classified as non-invaded ($P_i = 0$) or invaded ($P_i > 0$) (Wang et al. 2018). Sample sizes: non-invaded $n=52$, invaded $n=47$. The relative abundance (P_i) was calculated as:

$$P_i = \frac{n_i}{N} \times 100\% \quad (1)$$

where n_i is the number of *A. philoxeroides* individuals and N is the total number of individuals of all species in the quadrat.

2.2.3 Sample Collection and Plant Survey

Soil samples were collected from 0–20 cm and 20–40 cm layers within each sub-quadrat. One undisturbed core per layer was extracted with a 100 cm³ cutting ring for bulk density determination. Remaining soil was homogenized, sieved (2 mm), and divided into portions: one frozen at –20 °C for available nutrients, and one air-dried for physicochemical property analysis. Roots and litter were manually removed prior to analysis.

2.2.4 Measurement of Soil Indicators

Soil pH was determined potentiometrically at a soil:water ratio of 1:2.5 (w/v) using a calibrated pH meter (Shashikant et al. 2021), whereas soil water content was measured gravimetrically by oven-drying fresh soil at 105 °C to constant mass (Shashikant et al. 2021). Bulk density was determined using a cutting ring of known volume at a depth of 0–40 cm, with dry mass obtained after oven-drying at 105 °C to constant mass (Zeng et al. 2024). Total carbon (TC) and total nitrogen (TN) were quantified using an elemental analyzer (Vario EL III, Elementar, Germany) after air-dried soil was ground and passed through a 0.25 mm sieve (Wang et al. 2025). Total phosphorus (TP) was determined by NaOH alkali fusion at 720 °C for 30 min, followed by molybdenum-antimony anti-colorimetric method (Zhang et al. 2023). The ammonium nitrogen (NH₄⁺-N) was measured colorimetrically by the indophenol blue method at 625 nm (Ahmad et al. 2025), and NO₃⁻-N was assayed by dual-wavelength UV spectrophotometry at 220 and 275 nm (Zang et al. 2025). Available phosphorus was determined by the Olsen method, using 0.5 mol L⁻¹ NaHCO₃ (pH 8.5) at a soil : solution ratio of 1:20 for 30 min, followed by colorimetric determination (Zhang et al. 2022), and SOC was quantified by the Walkley–Black dichromate oxidation method with external heating at 170 °C for 5 min (Sofa et al. 2023).

2.2.5 Measurement and Calculation of Plant Indicators

Aboveground and belowground biomass were harvested from 1 × 1 m quadrats, oven-dried at 65 °C to constant weight, and weighed (Assiri et al. 2023).

α -diversity was quantified using the Shannon-Wiener (H), Margalef (R), Simpson (D), and Pielou

(E) indices (Asnakew et al. 2025; Chai et al. 2015; Pongsirijinda et al. 2025; Zhang et al. 2025), along with importance value (IV) (Zhang et al. 2025) and occurrence rate (Chu et al. 2007). The key indices were calculated as:

$$IV = \frac{\text{relative frequency} + \text{relative abundance} + \text{relative coverage}}{3} \quad (2)$$

$$R = \frac{S - 1}{\ln N} \quad (3)$$

$$H = - \sum_{i=1}^S P_i \times \ln P_i \quad (4)$$

$$D = 1 - \sum_{i=1}^S (P_i) \quad (5)$$

$$E = \frac{H}{\ln S} \quad (6)$$

$$f_i = \frac{F_i}{n} \quad (7)$$

where S is total species number, N total individuals, P_i proportion of species i, F_i number of quadrats containing species i, and n total quadrats.

2.3 Calculation and Statistical Analysis

All analyses were performed in R (v4.5.2), with significance at $p < 0.05$. Linear mixed models (LMMs) were constructed with data transformations applied as needed to satisfy normality (Shapiro-Wilk) and homoscedasticity (Breusch-Pagan) assumptions. Principal coordinates of neighbour matrices (PCNM) eigenvectors derived from sampling site coordinates were included as spatial predictors to control spatial autocorrelation. Fixed effects were tested using F-tests (Satterthwaite df) followed by Tukey's post hoc comparisons. Variance explained by invasion and spatial factors was quantified via marginal R^2 and hierarchical partitioning (glmm.hp). Generalized linear mixed models were used when analysis of variance (ANOVA) assumptions were not met.

Partial correlation analysis, treating plots as fixed factors, was used to examine variable associations after removing environmental heterogeneity. Pearson correlations were computed on residual matrices, with p-values adjusted by false discovery rate (FDR) ($p < 0.05$). To avoid ecologically meaningless but statistically significant correlations, a threshold of $|r| > 0.25$ was applied.

Structural equation models (SEM) were constructed using lavaan, incorporating Pi, SOC, bulk density, pH, and available phosphorus. Variables were standardized and checked for collinearity (variance inflation factor (VIF) < 5). Model fit was evaluated using χ^2 , comparative fit index (CFI), root mean square error of approximation (RMSEA), and standardized root mean square residual (SRMR). Indirect effects and 95% confidence intervals (CIs) were estimated by bootstrap (1000 resamples).

Boxplots show median, interquartile range (IQR), range, and raw points; bar charts show mean + SD; SEM path coefficients are standardized (β). Significance: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. And LMMs included spatial correction (PCNM) and Tukey's post-hoc tests; partial correlations used FDR-adjusted residuals; SEM indirect effects via bootstrap (1000 iterations). Key abbreviations used in figures and tables are: soil organic carbon (SOC), total carbon (TC), available phosphorus (AP), bulk density (BD), TN, TP (total phosphorus), nitrate nitrogen (NO_3^- -N), ammonium nitrogen (NH_4^+ -N), soil inorganic carbon (SIC), and relative abundance of *A. philoxeroides* (Pi). Detailed descriptions of all analytical procedures are provided above.

Additional quantitative details supporting the Results are provided in the Online Resource 1. Online Resource 1 Table R1 reports the proportional changes between non-invaded and invaded groups for species, genera, families, and soil variables (0–40 cm TC, SOC, and AP). Supplementary Table S2 summarizes the percentage of variance in 0–40 cm SOC and 0–20 cm and 20–40 cm NO_3^- -N explained by invasion and PCNM spatial variables. Supplementary Table S3 presents the relative increase in SOC and TC in the 0–20 cm layer compared with the 20–40 cm layer. These tables are cited in the Results section where the corresponding analyses are described.

3. Result

3.1 Species diversity and biomass of herbaceous plants along the shoreline of Hongze Lake wetland under different invasion intensities of *A. philoxeroides*

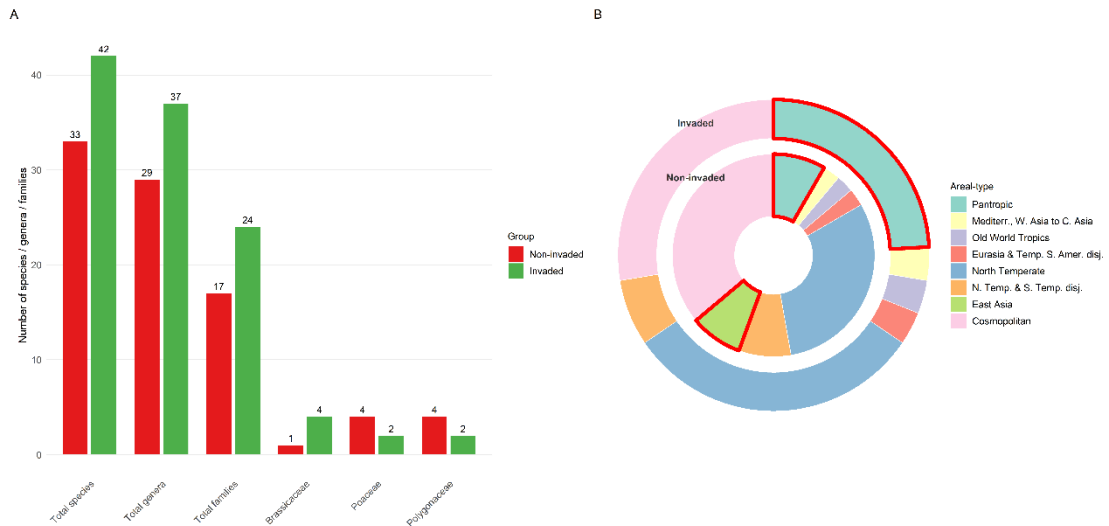
A total of 51 herbaceous species belonging to 42 genera and 23 families were recorded. Invasion reduced species numbers from 42 to 33 (21.4%), with genera and families reduced by 21.6% and 29.2%, respectively (Online Resource 1). In terms of floral composition, the number of pan tropical genera has increased, while the number of East Asian genera has disappeared (Fig. 2). After LMM correction, Shannon and Simpson indices were significantly higher in invaded than non-invaded group ($p < 0.05$); Margalef was significantly lower ($p < 0.05$) in non-invaded group; Pielou showed no significant difference ($p > 0.05$; Fig. 3). Aboveground, belowground, and total biomass showed no significant differences between groups ($p > 0.05$; Fig. 4).

Table 1 Overall species frequency and occurrence rate of herbaceous plants along the shore of the Hongze Lake wetland

Species designation	Frequency	Appearance rate
<i>Alternanthera philoxeroides</i>	47	0.47
<i>Cirsium arvense</i>	39	0.39
<i>Humulus scandens</i>	36	0.36
<i>Calystegia hederacea</i>	33	0.33
<i>Artemisia argyi</i>	26	0.26
<i>Geranium carolinianum</i>	26	0.26
<i>Cayratia japonica</i>	20	0.20
<i>Avena fatua</i>	19	0.19
<i>Brassica juncea</i>	17	0.17
<i>Galium aparine</i>	16	0.16

Table 2 Comparison of the occurrence rates of herbaceous plant species between the non-invaded and invaded groups in the Hongze Lake wetland.

Invaded group		Non-invaded group	
Species designation	Appearance rate	Species designation	Appearance rate
<i>Alternanthera philoxeroides</i>	1.00	<i>Cirsium arvense</i>	0.42
<i>Cirsium arvense</i>	0.36	<i>Humulus scandens</i>	0.40
<i>Geranium carolinianum</i>	0.36	<i>Calystegia hederacea</i>	0.35
<i>Calystegia hederacea</i>	0.32	<i>Cayratia japonica</i>	0.29
<i>Humulus scandens</i>	0.32	<i>Brassica juncea</i>	0.27
<i>Artemisia argyi</i>	0.28	<i>Euphorbia helioscopia</i>	0.25
<i>Avena fatua</i>	0.19	<i>Artemisia argyi</i>	0.25
<i>Artemisia lavandulifolia</i>	0.19	<i>Taraxacum mongolicum</i>	0.25
<i>Bolboschoenus planiculmis</i>	0.17	<i>Hemisteptia lyrata</i>	0.19
<i>Galium spurium</i>	0.17	<i>Avena fatua</i>	0.19



Note: (A) Numbers of families, genera, and species, along with specific family-level changes for selected families (*Brassicaceae*, *Poaceae*, *Polygonaceae*). Values above bars indicate total counts; red and green bars represent non-invaded and invaded groups, respectively. (B) Floristic composition of genera by areal-type, with the inner ring showing non-invaded and the outer ring showing invaded groups. Red outlines highlight major shifts, including an increase in Pantropic elements and the disappearance of East Asian elements in invaded areas. Color codes as per legend.

Fig. 2 Herbaceous community composition and genus areal-types in non-invaded and invaded groups

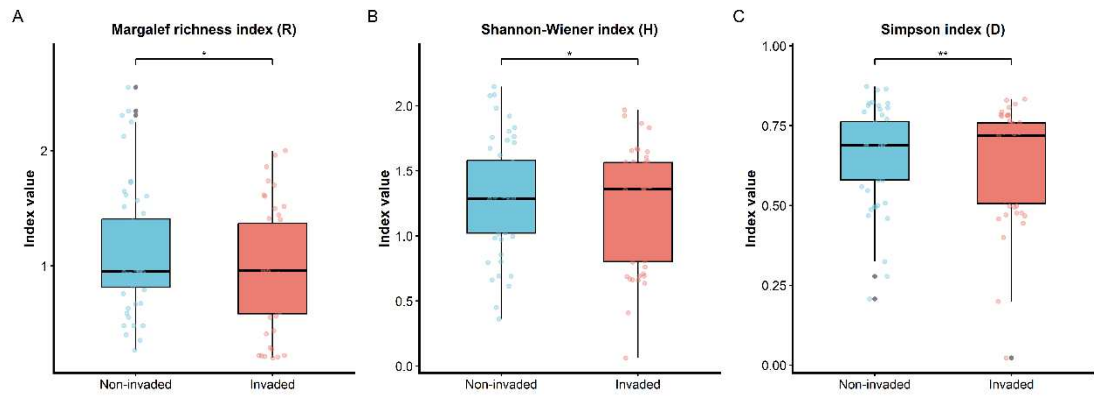
Table 3 Importance values of herbaceous plant species in the non-invaded and invaded groups in the Hongze Lake wetland

Invaded group		Non-invaded group	
Species name	IV	Species name	IV
<i>Alternanthera philoxeroides</i>	55.68	<i>Cirsium arvense</i>	23.08
<i>Geranium carolinianum</i>	17.45	<i>Humulus scandens</i>	20.85
<i>Cirsium arvense</i>	16.56	<i>Cayratia japonica</i>	14.47
<i>Bolboschoenus planiculmis</i>	14.56	<i>Calystegia hederacea</i>	14.45
<i>Artemisia argyi</i>	14.02	<i>Artemisia argyi</i>	12.14
<i>Humulus scandens</i>	13.50	<i>Euphorbia helioscopia</i>	11.65
<i>Calystegia hederacea</i>	12.80	<i>Brassica juncea</i>	10.71
<i>Avena fatua</i>	8.41	<i>Taraxacum mongolicum</i>	10.62
<i>Artemisia lavandulifolia</i>	7.99	<i>Avena fatua</i>	9.02
<i>Galium spurium</i>	7.52	<i>Ophiopogon japonicus</i>	8.72

Table 4 Species diversity indices and biomass of herbaceous plants in different groups in Hongze

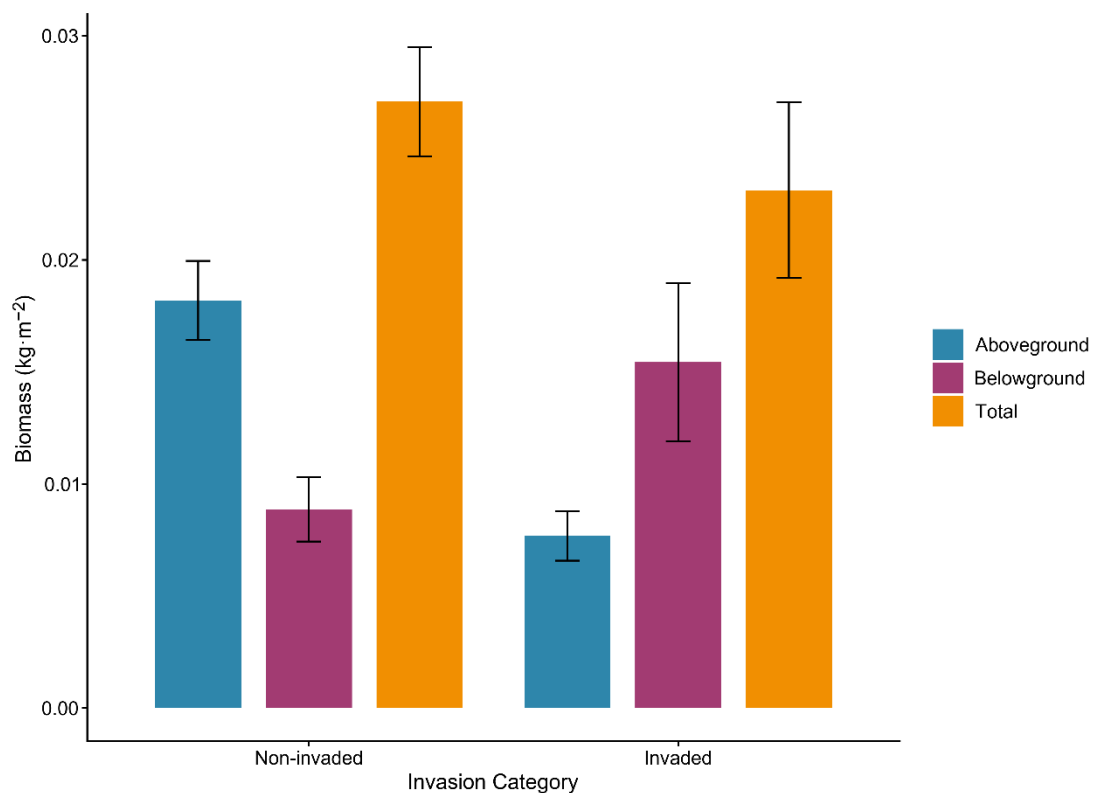
Lake wetland		
Metric	Groups	Mean $\pm$ SD
Shannon-Wiener (H)	Overall	1.27 $\pm$ 0.43
	Non-invaded group	1.30 $\pm$ 0.42 b
	Invaded group	1.23 $\pm$ 0.44 a
Margalef (R)	Overall	1.05 $\pm$ 0.53
	Non-invaded group	1.12 $\pm$ 0.54 a
	Invaded group	0.99 $\pm$ 0.52 b
Simpson (D)	Overall	0.65 $\pm$ 0.16
	Non-invaded group	0.66 $\pm$ 0.15 b
	Invaded group	0.64 $\pm$ 0.17 a
Pielou (E)	Overall	0.85 $\pm$ 0.15
	Non-invaded group	0.84 $\pm$ 0.12 a
	Invaded group	0.86 $\pm$ 0.18 a
Aboveground biomass (kg·m ⁻²)	Overall	0.13 $\pm$ 0.01
	Non-invaded group	0.18 $\pm$ 0.02 a
	Invaded group	0.08 $\pm$ 0.01 a
Belowground biomass (kg·m ⁻²)	Overall	0.12 $\pm$ 0.02
	Non-invaded group	0.09 $\pm$ 0.01 a
	Invaded group	0.15 $\pm$ 0.04 a
Total biomass (kg·m ⁻²)	Overall	0.25 $\pm$ 0.02
	Non-invaded group	0.27 $\pm$ 0.02 a
	Invaded group	0.23 $\pm$ 0.04 a

Note: Values are means $\pm$ SD. Different superscript letters within a row indicate significant differences between groups ($p < 0.05$) based on LMM with spatial correction (see Methods). For Shannon and Simpson, the raw mean order is opposite to the letter order due to spatial correction (Simpson's paradox); letters denote LMM-adjusted differences. Sample sizes: non-invaded n=52, invaded n=47.



Note: median and IQR; whiskers: range; points: raw data. Asterisks indicate significant differences after LMM with spatial correction (*, $p < 0.05$; **, $p < 0.01$; see Methods). Raw medians may show opposite trends due to spatial heterogeneity (Simpson's paradox).

Fig. 3 Boxplots of A- Margalef richness index (R), B- Shannon-Wiener index (H), and C- Simpson index (D) for non-invaded and invaded groups



Note: No significant differences were found (LMM, $p > 0.05$; see Methods).

Fig. 4 Aboveground, belowground, and total biomass (mean + SD) of herbaceous plants in non-invaded (n=52) and invaded (n=47) groups.

222 3.2 Basic Physicochemical Properties of Soil along the Shoreline of Hongze Lake Wetland under
223 Different Invasion Intensities of *A. philoxeroides*
224 Soil pH, moisture, and bulk density showed no significant differences between invaded and non-
225 invaded groups (Table 5; $p > 0.05$).

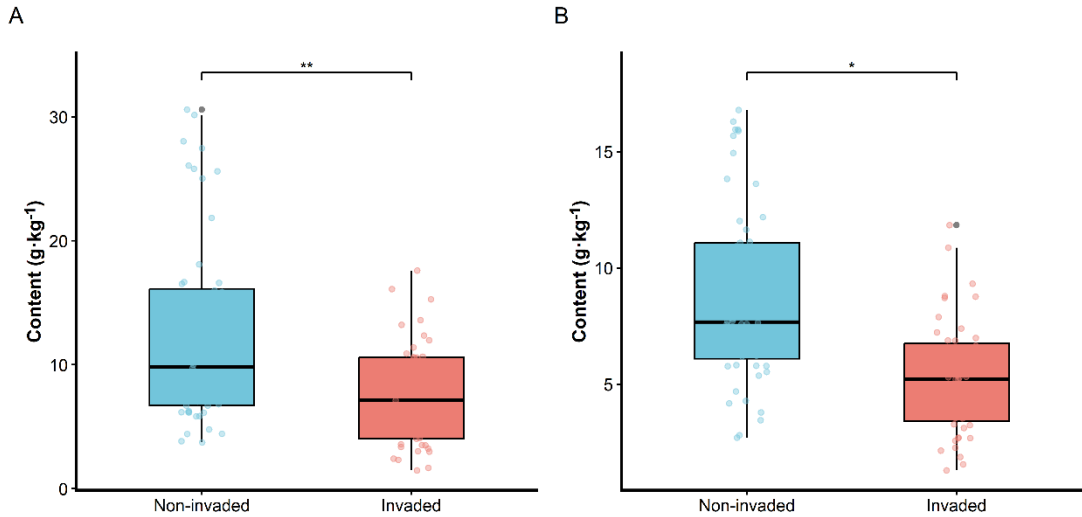
Table 5. Soil physicochemical properties and nutrient availability

Indicator	Soil layer	Total	Non-invaded group	Invaded group
TN ($\text{g}\cdot\text{kg}^{-1}$)	0-20 cm	0.69 ± 0.37	0.85 ± 0.37 a	0.53 ± 0.29 a
	20-40 cm	0.62 ± 0.33	0.78 ± 0.31 a	0.44 ± 0.25 a
	0-40 cm	0.66 ± 0.34	0.81 ± 0.32 a	0.48 ± 0.26 a
$\text{NH}_4^+\text{-N}$ ($\text{mg}\cdot\text{kg}^{-1}$)	0-20 cm	1.65 ± 2.05	1.81 ± 2.32 a	1.47 ± 1.70 a
	20-40 cm	1.50 ± 2.49	1.65 ± 3.58 a	1.33 ± 2.03 a
	0-40 cm	1.57 ± 2.25	1.73 ± 2.75 a	1.40 ± 1.53 a
$\text{NO}_3^-\text{-N}$ ($\text{mg}\cdot\text{kg}^{-1}$)	0-20 cm	2.96 ± 1.85	3.31 ± 2.19 a	2.57 ± 1.30 b
	20-40 cm	2.87 ± 1.96	3.19 ± 2.21 a	2.52 ± 1.58 b
	0-40 cm	2.91 ± 1.84	3.25 ± 2.14 a	2.54 ± 1.37 a
TP ($\text{g}\cdot\text{kg}^{-1}$)	0-20 cm	0.48 ± 0.26	0.49 ± 0.27 a	0.46 ± 0.25 a
	20-40 cm	0.46 ± 0.25	0.47 ± 0.23 a	0.45 ± 0.27 a
	0-40 cm	0.47 ± 0.25	0.48 ± 0.24 a	0.45 ± 0.25 a
AP ($\text{mg}\cdot\text{kg}^{-1}$)	0-20 cm	13.10 ± 17.58	17.79 ± 20.78 a	7.91 ± 11.26 a
	20-40 cm	10.98 ± 13.56	14.84 ± 15.86 a	6.71 ± 8.79 a
	0-40 cm	12.06 ± 15.25	16.34 ± 17.95 a	7.31 ± 9.71 a
SIC ($\text{g}\cdot\text{kg}^{-1}$)	0-20 cm	3.36 ± 4.50	3.80 ± 4.83 a	2.87 ± 4.11 a
	20-40 cm	2.63 ± 3.86	3.35 ± 4.50 a	1.82 ± 2.82 a
	0-40 cm	3.04 ± 3.74	3.69 ± 4.64 a	2.32 ± 2.24 a
pH	0-20 cm	7.85 ± 0.25	7.84 ± 0.18 a	7.86 ± 0.31 a
	20-40 cm	7.88 ± 0.21	7.85 ± 0.18 a	7.88 ± 0.28 a
	0-40 cm	7.86 ± 0.23	7.85 ± 0.17 a	7.91 ± 0.24 a
Gravimetric water content ($\text{g}\cdot\text{kg}^{-1}$)	0-20 cm	117.01 ± 51.81	110.30 ± 30.06 a	124.44 ± 67.89 a
	20-40 cm	123.31 ± 58.52	114.82 ± 38.32 a	132.71 ± 74.13 a
	0-40 cm	120.15 ± 52.60	112.77 ± 30.99 a	128.32 ± 68.56 a
Soil bulk density ($\text{g}\cdot\text{cm}^{-3}$)	0-20 cm	1.03 ± 0.14	0.99 ± 0.08 a	1.08 ± 0.18 a
	20-40 cm	1.02 ± 0.17	0.98 ± 0.15 a	1.07 ± 0.18 a
	0-40 cm	1.03 ± 0.14	0.98 ± 0.09 a	1.08 ± 0.16 a

Note: Values are means $\pm$ SD. Different letters in a row indicate significant differences between groups (LMM, $p < 0.05$; see Methods). All comparisons were non-significant ($p > 0.05$). Sample sizes: non-invaded $n=52$, invaded $n=47$.

231 3.3 Soil Nutrient Availability along the Shoreline of Hongze Lake Wetland under Different Invasion
232 Intensities of *A. philoxeroides*

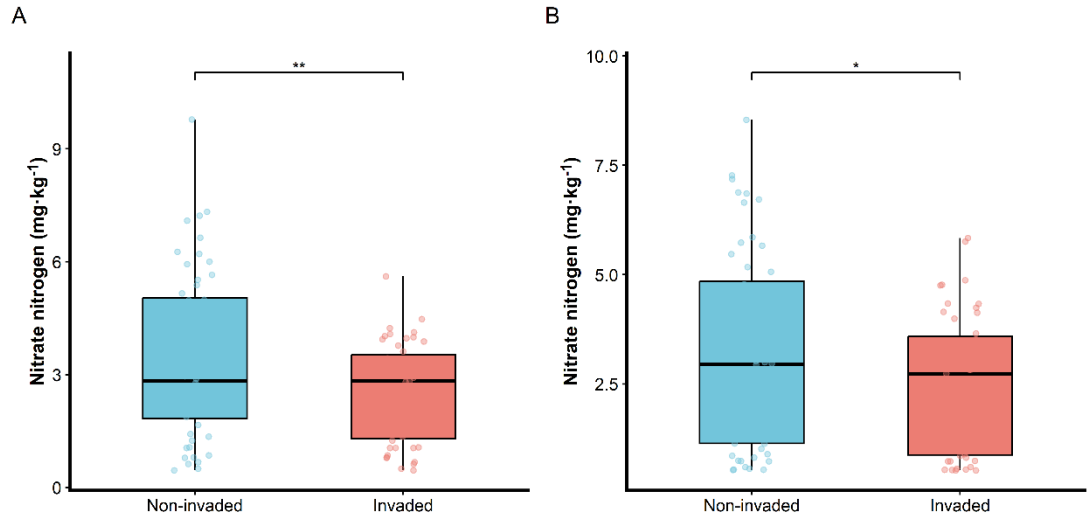
233 Total carbon ranged from 1.18 to 33.00 g·kg⁻¹; SOC ranged 0.98–22.43 g·kg⁻¹. Both TC and SOC
234 showed surface enrichment, with 0–20 cm contents 23.6% and 21.7% higher than 20–40 cm, respectively
235 (Online Resource 1). In the 0–40 cm layer, TC and SOC decreased by 34.4% and 34.9%, respectively, in
236 invaded relative to non-invaded groups ($p < 0.05$; Online Resource 1). Variance partitioning showed that
237 invasion independently explained 2.83% of SOC variation, while PCNM spatial variables explained
238 23.51% (Online Resource 1).



Note: median and IQR; whiskers: range; points: raw data. Asterisks indicate significant differences (LMM, $p < 0.05$; see Methods).

Fig. 5 Boxplots of (A) total carbon (TC) and (B) soil organic carbon (SOC) in the 0–40 cm layer for non-invaded (n=52) and invaded (n=47) groups.

Total nitrogen, $\text{NH}_4^+\text{-N}$, TP, and SIC showed no significant between non-invaded and invaded groups ($p > 0.05$; Table 5). The nitrate nitrogen ($\text{NO}_3^-\text{-N}$) decreased significantly in invaded groups in both 0–20 cm and 20–40 cm layers ($p < 0.05$; Fig. 6). Invasion independently explained 1.83% and 0.51% of $\text{NO}_3^-\text{-N}$ variation in these layers, respectively (Online Resource 1). Available phosphorus (AP) showed no significant between-group difference ($p > 0.05$), but declined by 55.3% in invaded groups (Online Resource 1). Partial correlation revealed significant positive AP-SOC association ($r = 0.429$, $p < 0.05$), suggesting AP may influence invasion effects on SOC. Only $\text{NO}_3^-\text{-N}$ showed significant between-group differences; AP, though non-significant in LMM, correlated with SOC and may influence invasion effects.

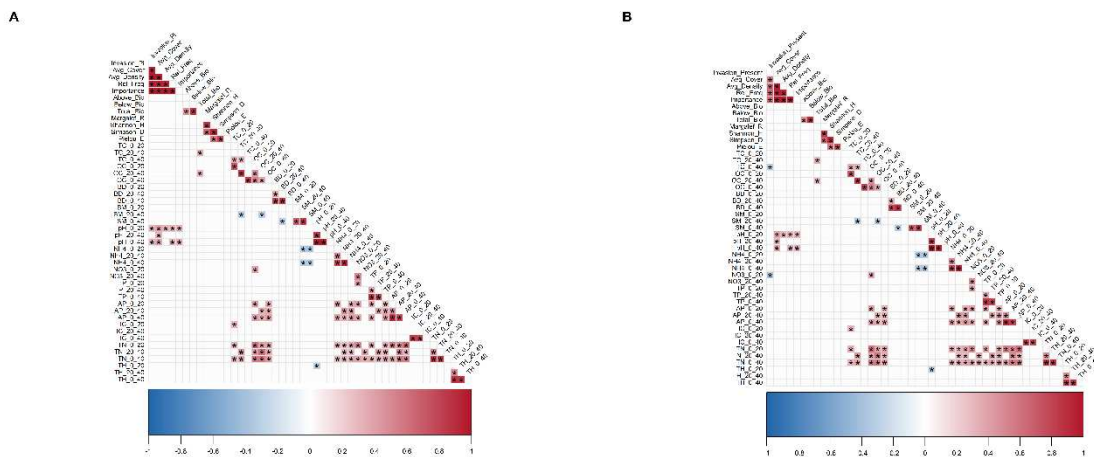


Note: median and IQR; whiskers: range; points: raw data. Asterisks indicate significant differences between groups (LMM, $p < 0.05$; see Methods). $n = 52$ (non-invaded), 47 (invaded).

Fig. 6 Boxplots of soil nitrate-nitrogen (NO₃⁻-N) in (A) 0–20 cm and (B) 20–40 cm layers.

3.4 Correlation Analysis between *A. philoxeroides* Invasion and Herbaceous Plant Species Diversity and Soil Nutrient Availability along the Shoreline of Hongze Lake Wetland

Invasion presence correlated positively with Shannon ($r = 0.270$) and Simpson ($r = 0.285$), and negatively with NO_3^- -N ($r = -0.367$) and TC ($r = -0.326$) ($p < 0.05$; Fig. 7). The relative abundance of *A. philoxeroides* (Pi) correlated strongly with its own dominance indices ($r > 0.94$) and soil pH ($r = 0.31$), but showed no significant correlation with diversity indices or other soil nutrients ($p > 0.05$; Fig. 7).



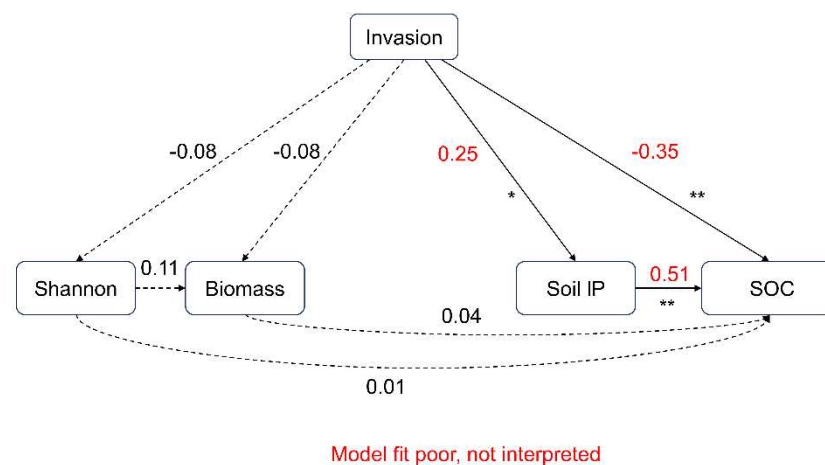
Note: Blue–red scale indicates negative–positive correlations; asterisks denote significant correlations (FDR-adjusted $p < 0.05$). Panel A: relative abundance of invasion (Pi); Panel B: presence/absence of invasion. Abbreviations: Bio, biomass ($\text{kg} \cdot \text{m}^{-2}$); TC, total carbon; SOC, soil organic carbon; BD, bulk density ($\text{g} \cdot \text{cm}^{-3}$); SM, soil moisture ($\text{g} \cdot \text{kg}^{-1}$); NH_4^+ -N, ammonium nitrogen; NO_3^- -N, nitrate nitrogen; TP, total phosphorus ($\text{g} \cdot \text{kg}^{-1}$); AP, available phosphorus ($\text{mg} \cdot \text{kg}^{-1}$); IC, inorganic carbon. Suffixes indicate soil layers; Above/Below/Total refer to biomass components. $n = 99$.

Fig. 7 Residual correlation heatmaps between invasion metrics and plant/soil variables

3.5 Potential Mechanisms of the Impact of *A. philoxeroides* Invasion on Soil Organic Carbon Content along the Shoreline of Hongze Lake Wetland

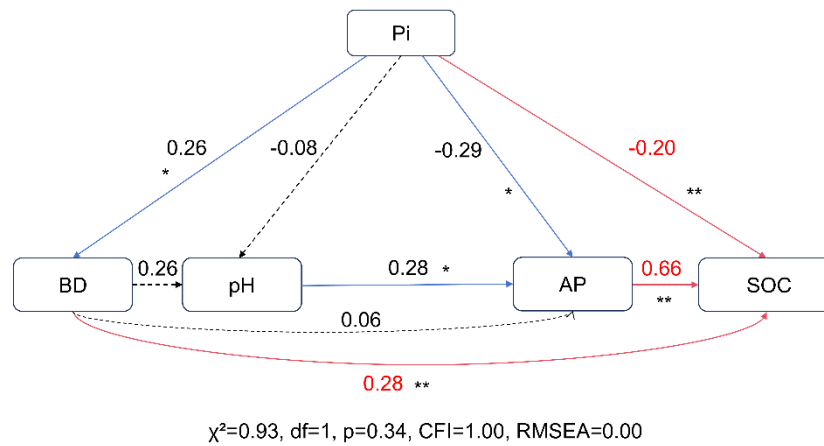
To identify pathways linking invasion to SOC, we constructed SEMs using Pi, SOC, bulk density, pH, and AP (Figs. 8, 9). The invasion presence/absence of *A. philoxeroides* model showed poor fit ($\chi^2=6.91$, $p=0.03$, RMSEA=0.16) and was not further interpreted (Fig. 8).

The proposed model showed an acceptable fit to the data (RMSEA = 0.00, CFI = 1.00; Fig. 9). The relative abundance of *A. philoxeroides* (Pi) had a direct negative effect on soil organic carbon (SOC; $\beta = -0.20$, $p < 0.001$). The key indirect pathway was influenced by AP: The relative abundance of *A. philoxeroides* reduced AP ($\beta = -0.29$, $p < 0.05$), which in turn served as the strongest positive predictor of SOC ($\beta = 0.66$, $p < 0.001$), yielding a significant indirect effect of -0.19 ($p < 0.001$). By contrast, the pathway linking Pi to SOC via bulk density (BD) was not statistically significant (indirect effect = -0.07 , $p = 0.07$), although Pi significantly increased BD ($\beta = 0.26$, $p = 0.01$) and BD significantly suppressed SOC ($\beta = -0.28$, $p < 0.001$). The total effect of Pi on SOC was -0.46 ($p < 0.001$).



Note: standardized coefficients shown; *, $p < 0.05$; **, $p < 0.01$. Dotted arrows indicate non-significant paths. The model fit was poor ($\chi^2=6.91$, $df=2$, $p=0.03$, RMSEA=0.16; see Table 7), so this model was not interpreted. $n=99$.

Fig 8. Path diagram of SEM examining effects of invasion presence (binary) on SOC.



294

295 Note: standardized coefficients shown; *, $p<0.05$; **, $p<0.01$. Solid arrows indicate significant

296 paths; dotted arrows are non-significant. Indirect effects were estimated by bootstrap (see Methods).

297 Model fit: $RMSEA=0.00$, $CFI=1.00$ (Table 7). $n=99$.

298

Fig 9. Path diagram of SEM with Pi as predictor of SOC.

4. Discussion

4.1 *A. philoxeroides* Invasion Altered Herbaceous Plant Community Structure but Did Not Affect SOC via the Biomass Pathway

Invasion induced marked restructuring of the herbaceous community, shifting from multi-species co-dominance to single-species dominance, consistent with previous observations that *A. philoxeroides* promotes community homogenization (Wu et al. 2022).

Floristic composition also shifted, with pantropical genera increasing while East Asian genera declined, possibly reflecting shared environmental adaptations (Muthukrishnan and Larkin 2020) or competitive exclusion of endemic lineages (Wu et al. 2024).

For α -diversity, Shannon and Simpson raw means were slightly higher in non-invaded quadrats, but after LMM correction for spatial autocorrelation, the invaded group showed significantly higher Shannon and Simpson indices, while Margalef was significantly reduced and Pielou showed no difference. This pattern exemplifies Simpson's paradox (Allison and Goldberg 2002), demonstrating the necessity of spatial correction. The results are better explained by environmental filtering (Kraft et al. 2015) and the driver-passenger model (Guillerme et al. 2020)—*A. philoxeroides* preferentially colonizes resource-rich patches with higher baseline diversity (passenger role) rather than actively altering diversity patterns (driver role)—than by a diversity-enhancing effect. The observed species richness decline is consistent with competitive exclusion (Jincheng and Sheng 2006), while the compensatory evenness increase following dominant species turnover buffered the Shannon index decline (Hillebrand et al. 2008).

Aboveground biomass declined while belowground biomass increased in invaded quadrats, though neither difference was significant, suggesting a potential allocation shift rather than a statistically robust effect. Notably, the indirect pathway from Shannon-Wiener index to SOC via biomass was not significant in the SEM ($p > 0.05$). Likewise, partial correlation analysis showed no significant Margalef–SOC association ($|r| < 0.25$, $p > 0.05$). Thus, the causal pathway—invansion altering diversity and thereby affecting SOC via biomass inputs—was not supported.

In summary, *A. philoxeroides* invasion significantly altered community composition and floristic structure, but total biomass did not differ between groups, and the diversity–biomass–SOC pathway was not significant. This indicates that invasion effects on SOC were not primarily achieved through suppression of biomass inputs, but rather through direct or indirect modification of soil physicochemical properties such as AP and bulk density (Wu et al. 2024). The SOC loss more plausibly stems from

intensified output processes (e.g., priming effects (Fasaeiyan et al. 2024) and nutrient-limitation-driven mineralization (Yin et al. 2018)).

4.2 Net effect of *A. philoxeroides* invasion on SOC: Statistically significant but with limited effect size

Soil pH, moisture, and bulk density showed no significant differences between invaded and non-invaded groups ($p > 0.05$), consistent with the view that invasive plant effects on soil properties vary among habitats (de Graaff et al. 2010). However, binary grouping has limited sensitivity; using continuous Pi in SEM revealed that Pi significantly increased bulk density ($\beta = 0.257, p = 0.008$), though the indirect effect on SOC via bulk density was not significant ($-0.072, p = 0.065$). This potential influence remains a preliminary clue requiring further validation.

In contrast, SOC changes were pronounced. In the 0–40 cm layer, TC and SOC decreased by 34.4% and 34.9%, respectively ($p < 0.05$). Variance partitioning showed invasion independently explained only 2.83% of SOC variation, while PCNM spatial variables explained 23.51%, indicating SOC was predominantly driven by spatial factors (hydrology, soil texture, micro-topography). Nevertheless, the 2.83% contribution remains ecologically meaningful, as Møller & Jennions (Møller and Jennions 2002) found core variables explain only 2.51–5.42% of variance on average in ecological meta-analyses. Since total biomass did not differ between groups, and the indirect pathway from plant diversity to soil organic carbon via aboveground biomass was non-significant in SEM, SOC loss is more plausibly attributed to enhanced decomposition output (Munro et al. 2024) rather than reduced biomass input.

Among measured nutrients, only NO_3^- -N showed significant between-group declines (0–20 and 20–40 cm; $p < 0.05$), but its correlation with SOC was weak ($|r| < 0.25$). Although LMM showed no significant group difference in AP ($p > 0.05$), AP decreased by 55.3% in invaded plots. This reflects the lower statistical power of LMM under high spatial variability (Al-Younis et al. 2025), whereas SEM using continuous Pi and multiple controls detected a significant negative effect of Pi on AP ($\beta = -0.285, p = 0.003$). Partial correlation further revealed a positive AP–SOC association ($r = 0.429, p < 0.05$), suggesting AP may mediate invasion effects on SOC. TN, NH_4^+ -N, TP, and SIC showed no significant differences and were excluded.

As this study used static observational data, the revealed associations reflect correlations rather than definitive causality; mechanisms require experimental validation. Although species richness declined, this did not translate into significant biomass reduction. Soil organic carbon loss is more plausibly

attributable to invasion-induced changes in soil micro-environment—enhanced microbial decomposition(Liao et al. 2008) or altered physicochemical properties(Wu et al. 2024)—rather than reduced biomass fluxes.

In summary, invaded plots exhibited marked depletion of SOC and NO_3^- -N, whereas effects on soil physical structure and stable nutrient pools were limited.

4.3 Mechanisms of *A. philoxeroides* Invasion Affecting SOC: A Synthesis Based on Partial Correlation Analysis and Structural Equation Modeling

Partial correlation analysis showed that soil available phosphorus (AP) was significantly positively correlated with SOC ($r = 0.429, p < 0.05$), with AP content reduced by 55.3% in invaded plots, suggesting a potential influencing role of AP in invasion-induced SOC change.

The well-fitted Pi model (RMSEA = 0.00, CFI = 1.00) revealed a significant direct negative effect of Pi on SOC ($\beta = -0.20, p < 0.001$), suggesting that root exudates may accelerate pre-existing SOC decomposition via priming effects (Chari and Taylor 2022), though experimental validation is needed. Total biomass did not differ significantly between the groups, and the indirect pathway from Shannon diversity to SOC via aboveground biomass was not significant. This further argues against reduced biomass input as the primary mechanism underlying SOC loss.

The indirect pathway via AP limitation was also significant. The relative abundance of *A. philoxeroides* reduced AP ($\beta = -0.29, p < 0.05$), and AP was the strongest positive predictor of SOC ($\beta = 0.66, p < 0.001$), yielding an indirect effect of -0.19 (95% CI: $[-0.31, -0.07], p < 0.05$)—comparable in magnitude to the direct effect (-0.20). This supports the co-metabolism hypothesis: P limitation induces microbial phosphatase secretion to mineralize organic P, concurrently decomposing the organic carbon skeleton (Jiang et al. 2026; Kokulan et al. 2025; Luo et al. 2022).

The bulk density pathway showed significant individual paths (Pi→BD: $\beta = 0.26, p = 0.01$; BD→SOC: $\beta = -0.28, p < 0.001$), but its overall indirect effect was non-significant ($-0.07, p = 0.07$), suggesting only a potential signal (Frene et al. 2024; Garcia-Franco et al. 2015). Notably, AP difference was non-significant in LMM between-group comparison due to high spatial variability reducing statistical power; the SEM, using continuous Pi and controlling multiple factors, more sensitively captured the AP gradient effect. This reflects differing sensitivities of the two approaches, not a contradiction.

Together, these results confirm that AP depletion is the primary indirect pathway, while the diversity–biomass pathway is excluded. This contrasts with Yang et al. (Yang et al. 2020) (SOC increase in rivers), underscoring that invasion effects on SOC are strongly habitat-dependent.

4.4 Integrated Path Model of *A. philoxeroides* Invasion

The Pi model (Fig. 8) showed a total effect of -0.46 on SOC ($p < 0.001$), comprising a direct effect of -0.20 and a total indirect effect of -0.26 . The AP depletion pathway was the dominant indirect route (indirect effect = -0.19 , $p < 0.001$), accounting for 41% of the total effect and operating via co-metabolism. The bulk density pathway showed only a potential signal (indirect effect = -0.07 , $p = 0.07$). The diversity–biomass pathway was not supported as a driver of SOC change.

In summary, invasion reduced SOC by two mechanisms: direct priming of existing SOC decomposition and indirect P-limitation-induced co-metabolism. Together these pathways explain the 34.9% SOC decline, while diversity changes were not critical drivers. The AP may serve as an early-warning indicator, and controlling invasion spread could mitigate topsoil carbon loss—though this requires experimental confirmation.

5. Conclusions

This study employed structural equation modeling to integrate the multiple pathways through which *A. philoxeroides* invasion affects SOC in the Hongze Lake wetland. The invasion significantly reduced surface SOC through both direct and indirect pathways. The direct pathway involved root exudates stimulating microbial decomposition of pre-existing soil organic matter via priming effects. Along the indirect pathway, the invasion depleted soil available phosphorus, which served as the strongest positive predictor of SOC. Invasion reduced species richness from 42 to 33 (21.4%); Margalef decreased significantly, while Shannon and Simpson increased after spatial correction, and Pielou showed no difference. The pathway from plant diversity through biomass to SOC was non-significant, confirming that invasion did not reduce SOC by suppressing biomass input, but rather by altering soil properties such as AP and bulk density. The observed association reflects preferential occupation of microhabitats rather than diversity-driven carbon regulation. In summary, *A. philoxeroides* invasion reduced SOC through two mechanisms: direct priming effects accelerating pre-existing SOC decomposition, and P limitation-induced co-metabolic processes that mineralize organic P while decomposing SOC.

6. Declarations

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6.2 *Competing* Interests

The authors have no relevant financial or non-financial interests to disclose.

6.3 *Data Availability*

The datasets generated during the current study are available from the corresponding author on reasonable request.

6.4 CRediT authorship contribution statement

Chengfeng Liu: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Visualization, Writing – original draft. **Yang Guo:** Investigation, Methodology, Resources. **Rui Sun:** Investigation, Methodology, Project administration. **Zhiwei Ge:** Funding acquisition, Methodology, Writing — Reviewing and Editing, Project administration, Resources, Supervision.

6.5 *Compliance* with Ethical Standards

6.5.1 Disclosure of potential conflicts of interest

The authors declare that they have no conflicts of interest that could influence the objectivity of this research.

6.5.2 Research involving Human Participants and/or Animals

This study does not involve human participants or animal experiments.

6.5.3 Informed consent

Yes.

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