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Plant Functional Diversity Drives Ecosystem Functions More Strongly than Species Diversity in East Dongting Lake Wetlands, China

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Abstract

As the relationship between plant diversity and ecosystem function has long been a contentious issue in ecological research, and wetlands globally are under severe threat, our study focused on the East Dongting Lake, a significant wetland in China. Subsequently, we employed correlation analysis and other refined methods to probe the linkage between plant species diversity, plant functional diversity and ecosystem functionality. Factor analysis was utilized to pinpoint the crucial influencing elements, and a random forest model was established to quantify and confirm the effects of various diversity components on the ecosystem. The findings indicated that forestland and marshland exhibited the highest levels of plant diversity, whereas cultivated land showed the lowest. Interestingly, an enhancement in plant community functional diversity was found to be more effective in boosting ecosystem functionality than an increase in species diversity. The ecosystem function of the East Dongting Lake wetland was driven mainly by the selection effect, which supported the “mass ratio hypothesis”. In addition, the degree of dominance, measured by the community-weighted mean, more effectively explained the ecosystem function of the wetland, therefore, the functional traits of dominant species should be prioritized in wetland management, restoration, and conservation.

Keywords: Wetland; East dongting lake; Functional diversity; Species diversity; Ecosystem function.
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1. Introduction

Biodiversity is a core component of ecosystems and makes a vital impact on maintaining ecosystem stability, productivity, and the provision of various ecosystem services.[1] However, human activities greatly threaten biodiversity.[2,3] Land use change is a key driver of plant community variation, as different utilization patterns (*e.g.*, cultivation, afforestation) alter habitat conditions such as soil fertility and hydrology, thereby affecting species composition and diversity.[4] Additionally, as the rate of global species extinction increases, how species loss affects ecosystem function has been a highly debated issue, and studies exploring the linkage between biodiversity and ecosystem productivity has become an extremely important topic in global ecology over the past 20 years.[5] Biodiversity can be divided into species diversity, functional diversity, and phylogenetic diversity.[6] Although various research has indicated that both species diversity and functional diversity have beneficial impacts on ecosystem functionalities,[7,8] the correlation between biodiversity and ecosystem function, *i.e.*, the relative importance of species diversity and functional diversity in maintaining ecosystem function, continues to be widely debated.[9] Numerous studies have acknowledged the contribution of species diversity to ecosystem function,[10,11] but recent studies have suggested that the functional traits of prominent species can exert a substantial influence on ecosystem functionality.[12-14] One study suggested that the effects of the two on ecosystem function are consistent,[7,15] whereas other studies suggested that they have relatively independent effects on ecosystem function.[13,16]

Research on the relationships between plant diversity and ecosystem functions has revealed two core maintenance mechanisms, including the selection effect and the complementary effect. The core idea of the selection effect is that in a community with a higher level of diversity, there may

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be more species that contribute highly to ecosystem functions, *i.e.*, dominant species. The functional traits of these dominant species dominate ecosystem functions, which is strongly supported by the research of Roscher *et al*.[14] According to the complementary effect, a highly diverse community often exhibits greater differences in functional traits. This difference can further promote the optimal utilization of resources and thus enhance ecosystem functions, which was depicted by Tilman *et al*.[17] and Cavanaugh *et al*.[7] There are two hypotheses regarding the mechanisms by which functional diversity affects ecosystem functions, namely the "mass ratio hypothesis" and the "diversity hypothesis." The "mass ratio hypothesis" holds that the functional traits of dominant species determine changes in ecosystem functions.[18] The "diversity hypothesis" suggests that differences in functional traits among species reduce resource niche overlap between species, increase resource utilization efficiency, and thereby enhance ecosystem functions.[17] Therefore, assessing the applicable conditions for determining the importance of selection effects and complementary effects in maintaining the relationship between functional diversity and ecosystem functioning has become one of the key issues of concern to community ecologists.[11,12]

In recent years, many ecologists have conducted relevant research in this field. Studies conducted outside China have focused mostly on North America and Europe,[19,20] while studies conducted in China have focused mostly on grasslands and woodlands.[21,22] In the study of plant diversity across different dimensions and ecosystem functions, there is relatively little research on natural wetlands.[23]

The Dongting Lake wetland stands as one of China's most crucial natural ecosystems and natural resource reserves, and it holds significant importance as a wetland resource globally. It plays a vital role in regulating climate, replenishing water sources, carbon sequestration and oxygen release,[24,25] regulating runoff, providing habitats for various species, and protecting plant diversity.[26] However, owing to a lack of scientific planning and management and the continuous increase in urbanization and industrialization in the lake area, the ecological system of the Dongting Lake wetland has been severely eroded, and many problems exist in the preservation and enduring management of the wetland.[27] Therefore, in this study, we investigated the Dongting Lake wetland and embarked on a comprehensive exploration of the interplay between the diverse facets of indigenous plant species and ecosystem functions across various dimensions, aiming to dissect the ecological system's structure and functionality. This endeavor aims to offer a scientific rationale for the preservation and sustainable management of the ecological system in the vicinity of the lake.

2. Study site and research methods

2.1 Site description

Dongting Lake stands as the second-largest freshwater lake in China and constitutes a vital lacustrine wetland ecosystem situated in the middle and lower reaches of the Yangtze River.[27] The research area, the East Dongting Lake Wetland, was situated in Yueyang City, Hunan Province, in the central part of southern China (28°44′–29°35′ N and 111°53′–113°5′ E). It is located at the confluence of the “Four Rivers” (the Xiang River, the Zi River, the Yuan River, and the Li River) in the south and discharges into the Yangtze River in the north, covering an area of about 1,327.8 km^2, with an annual lake capacity of 17.8 billion cubic meters. The lake area has a subtropical monsoon climate. The overall landform is a shallow basin-shaped plain with little undulations. The annual average temperature is approximately 17ºC, and the annual precipitation is around 1,200–1,400 mm. This area primarily has a wetland ecosystem, including lakes, rivers, swamps, and tidal flats. There are three types of vegetation, namely, wetland forests (plantations mainly composed of *Populus* × *euramericana* and natural forests mainly composed of evergreen mixed broad-leaved forests), wetland herbaceous vegetation (mainly composed of *Carex* spp. and *Phragmites australis*), and artificial wetland vegetation (paddy fields mainly planted with rice). The main soil types are fluvo-aquic soil and marsh soil.[28]

2.2 Research methods

2.2.1 Experimental design and field survey

Vegetation surveys and sample collection were conducted from 2022 to 2023, covering key stages of the plant growth cycle (including germination, leaf expansion, flowering, fruiting, and the peak growing period in August). A total of 6 survey frequencies were set to capture community dynamic changes, following the ecological monitoring protocols by Imanaliyeva *et al*.[29] and considering the phenological characteristics of plants in the study area.

To ensure the collection of samples effectively and their representativeness in spatial distribution, we classified the land types of East Dongting Lake into six types, including forestland, agricultural land, grassland, marshland, unused land, and construction land, according to the GB/T21010-2017 Classification of Land Use Status. In these areas, we established 6 types of plots with relatively little human disturbance, where plant community species, structure, and habitat composition are relatively uniform. Representative sampling points were set up in each type of plot for field

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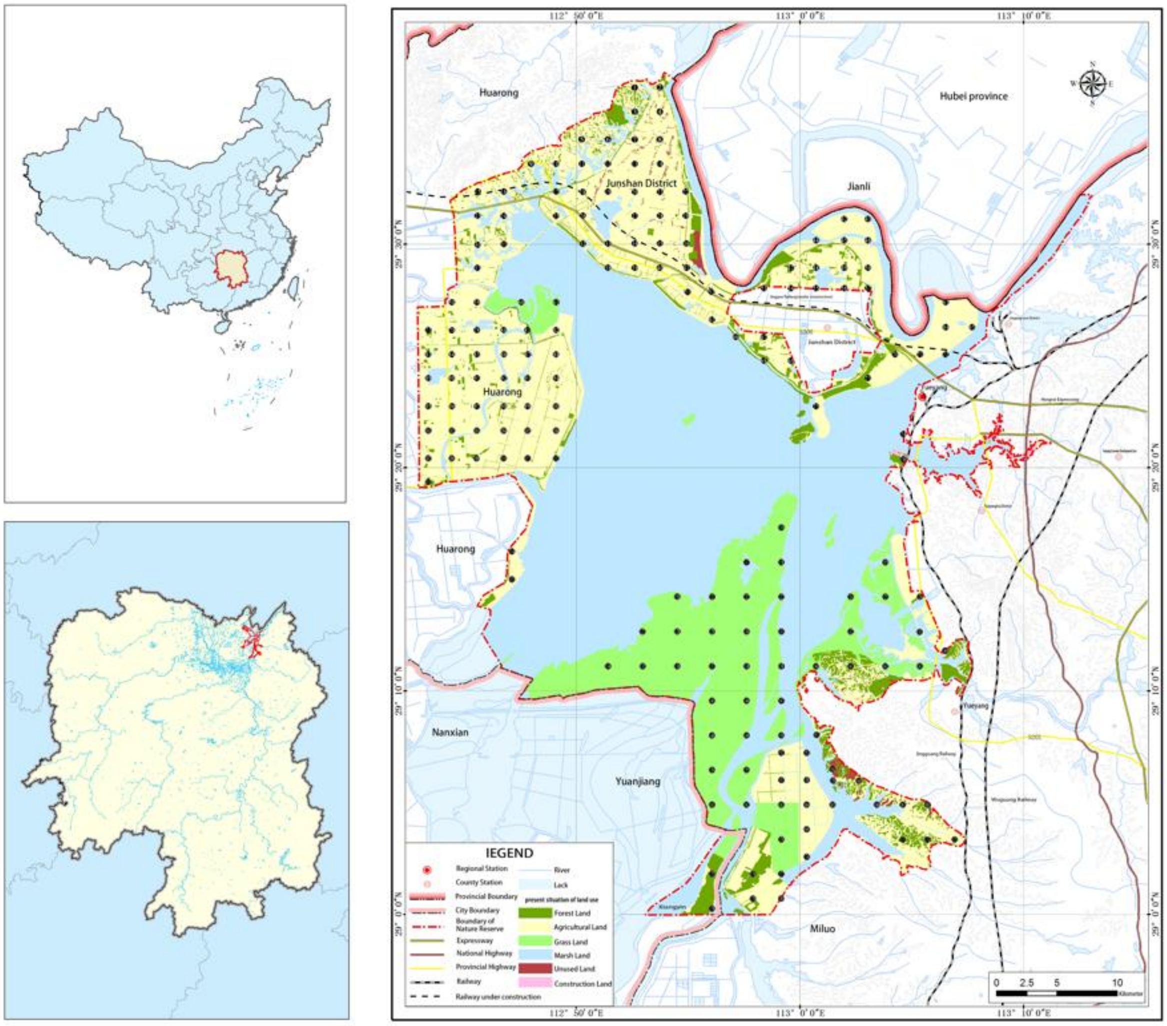


Fig. 1: Locations of sample sites in East Dongting Lake, China.

surveys, with a total of 180 sampling points (Fig. 1). Within each sampling point, 10 quadrats (1 m × 1 m) were systematically arranged following the vegetation survey standards of Imanaliyeva *et al*.,[29] with adjustments based on vegetation height and distribution density in the study area. Each quadrat was recorded three times to reduce errors, consistent with the above method. Quadrat surveys included community characteristics such as plant species, individual quantity, coverage, and frequency; meanwhile, terrain (slope, aspect), soil type, and surface disturbance within quadrats were recorded to provide basic data for analyzing the relationship between plant diversity and microhabitats. This resulted in 180 sampling points and 1,800 quadrats, ensuring representativeness across both broad habitat types and local community structures. These quadrats were used to determine plant traits, community characteristics, and soil physical-chemical properties.

For the types of plant communities, the main focus was on the *Miscanthus sacchariflorus* community, *Polygonum hydropiper* community, and *Carex* community, and the number of individual count, species richness, coverage, and frequency of each plant within the sample plot were recorded in detail. Representative plants (n = 3–5) were collected from each species in the sample plot, and five fully expanded and sun-exposed leaves were selected from each plant, placed in a sample bag, labeled, and transported to the laboratory. The soil sampling points were arranged in the same way as the vegetation sample points, the latitude, longitude, and elevation of each sample point were measured in the field using GPS, and the slope was measured using a slope meter. Referring to the experimental protocol of Zhang *et al*.[30] and combining the hydrological characteristics of the East Dongting Lake wetland, soil samples from the 0–20 cm soil layer within each quadrat were collected using a soil auger with a diameter of 3.8 cm. This soil layer depth is regarded as the core area where plant roots are mainly distributed, nutrients are enriched, and soil-plant material exchange is most active.[31] Five soil cores were taken from each quadrat (at the four corners and the center respectively) and mixed into one soil sample. Using clean, dust-free latex gloves, the samples were placed into clean polyethylene bags and sealed. All samples were uniformly placed into black plastic bags in order and transported back to the laboratory.

2.2.2 Determination and analysis of plant and soil factors

The aboveground plants collected were transported to the laboratory, and the leaf area (LA) was measured using a CanoScan LiDE700F scanner. The height (HA) was obtained through community investigations and referred to the Flora of China. The leaf length (LL) was measured by laying the leaves flat on a plane and measuring from the base to the tip of the leaves using a ruler or a Vernier caliper. These functional traits (LA, LL, HA) were selected based on their significant role in reflecting the acquisition of plant resources (such as light and space), environmental adaptation, and potential ecosystem processes (such as litter decomposition and carbon storage).[32] Since the differences in functional traits among species are greater than those within species and to avoid variations within species, the average value of the traits of 3–5 mature individuals of each species was adopted for representing the functional traits of that species. The measurement methods for all plant functional traits referred to those of Cornelissen *et al.*[33]

A total of 4 indicators were selected for the determination of ecosystem functions: soil pH, soil organic carbon (SOC), soil nitrate nitrogen (NO_3^--N), and soil available phosphorus (AP).[34] After being transported back to the laboratory, soil samples were air-dried naturally, gently crushed with a grinding rod to remove plant leaves, stones, *etc*. The samples were then ground in a mortar and passed through a 2-mm nylon sieve. The sieved soil samples were placed in containers for the determination of soil physical and chemical properties. For soil pH determination, a soil-water suspension with a ratio of 1:2.5 was prepared and measured using a Mettler-Toledo 320 instrument. SOC was quantified using an Analytik Jena HT1300 analyzer after removing soil calcium carbonate with hydrochloric acid. The level of NO_3^--N was determined by alkaline hydrolysis (GB7849-87). The content of AP was measured by the sodium bicarbonate extraction-molybdenum-antimony colorimetric method. All methods were referenced from previous protocols.[35-37] and integrated to a certain extent. The above indicators comprehensively reflect multiple ecosystem functions such as soil fertility, soil structure and nutrient retention capacity.

2.2.3 Data analysis methods

2.2.3.1 Calculation of diversity indices

Species diversity indices were selected from Margalef's richness index, Shannon-Wiener's diversity index, Simpson's diversity index, and Pielou's evenness index,[38] and functional diversity indices were selected from four main components: community-weighted mean trait value (CWM), functional richness (FR), functional evenness (FE) and functional divergence (FD) (Table 1). CWM represents the multiplicity and traits of dominant species;[39] functional richness indicates the size of the ecological space occupied by existing species;[40]

Table 1: Calculation methods for diversity indices.

Species diversity		Functional diversity	
Component	Calculation method	Component	Calculation method
Margalef's richness	$M = (S-1)/ln\,N$	Functional richness	$FR = \sqrt{\sum_{i=1}^{N}(X_{ia}-X_{ib})^2}$
Pielou's evenness	$J = H/ln\,S$	Functional evenness	$FE = \frac{\sum_{i=1}^{S}\left[min\left(P_{i'}\frac{1}{S-1}\right)\right]-\frac{1}{S-1}}{1-\frac{1}{S-1}}$
Shannon's diversity	$H = -\sum P_i\,ln\,P_i$	Functional divergence	$FD = \frac{\sum_{i=1}^{s} w_i\left(a-\frac{1}{s}\sum_{i=1}^{s} a\right)+\frac{1}{s}\sum_{i=1}^{s} a}{\sum_{i=1}^{s} w_i\left(a-\frac{1}{s}\sum_{i=1}^{s} a\right)+\frac{1}{s}\sum_{i=1}^{s} a}$ $a = \sqrt{\sum_{k=1}^{T}\left(x_{ik}-\frac{1}{v}\sum_{i=1}^{v} X_{ik}\right)^2}$
Simpson's diversity	$D = 1-\sum_{i=1}^{s} P_i^2$	Community-weighted mean	$CWM = \frac{\sum_i P_i \sum_{j=1}^{NIV_i}(t_{ij}/NIV_i)}{P_{cov\,er}}$

Note: S: total count of species; N: total population of all species; P_i: proportion of individuals of the ith species in the sample to the number of individuals of all species; X_{ia} X_{ib}:value of trait i for species a and b; $P_{i'}$: relative trait values for species i'; T: all functional traits; X_{ik}: position of species i on trait axis k; v: volume of functional space occupied by species i; w_i: relative abundance of species i; T_i: trait values for species i in the observed quadrats; NIV: number of individual values of traits for species i; t_{ij}: a given trait value j in species i; $P_{cov\,er}$: cumulative relative abundance values for the proportion of all species in a given community.

functional evenness measures the regularity of the distribution of the trait means of species in the trait space; and functional divergence characterizes the distance or degree of variation,[41] as these indices comprehensively characterize functional differences among communities.[42]

Referring to the experiment by Zhang *et al*.,[30] in this study, the "mass ratio hypothesis" characterizes functional diversity by CWM, while the "diversity hypothesis" characterizes functional diversity by FD.

2.2.3.2 Statistical analysis

Microsoft Excel 2021 was used to calculate all data. To determine species variety and functional diversity within the community, we utilized the "vegan" and "FD" packages in R version 4.1.3. SPSS 26.0 was used to perform Bartlett's test of sphericity on various ecosystem function indices for testing factor independence and avoiding collinearity issues among factors. The factor loading matrix was obtained using the dimensionality reduction factor analysis method. SPSS 26.0 and Origin 2021 were subsequently used to conduct Pearson correlation analyses to analyze the relationships between ecosystem functions and plant diversity, after which regression models were established. The random forest technique, implemented using the "random Forest" package in R, was employed to assess the comparative significance of various biodiversity facets in shaping ecosystem functionalities.

3. Results

3.1 Response of plant species diversity to various land utilization types

Our study established plots across six land use types; however, due to the extremely low proportion of sampling points in construction land and unused land (only 0.5%-1%), this section only discusses the response of plant species diversity to forest land, marsh land, agricultural land, and grass land.

One-way ANOVA revealed that Pielou's evenness, Shannon-Wiener's diversity, Simpson's diversity, and Margalef's richness varied significantly with land-use types in the quadrats.

For Pielou's evenness and Simpson's diversity: Marsh Land was the highest, followed by Forest Land, with Agricultural and Grass Lands being the lowest. Marsh and Forest Lands differed significantly from Agricultural/Grass Lands ($P<0.05$), and a significant difference was also observed between Marsh and Forest Lands ($P<0.05$).

For Shannon-Wiener's diversity: Forest Land was the highest, followed by Marsh Land, with Agricultural and Grass Lands being the lowest. Forest and Marsh Lands differed significantly from Agricultural/Grass Lands ($P<0.05$), and a significant difference was also found between Forest and Marsh Lands ($P<0.05$).

For Margalef's richness: Grass Land exhibited the highest richness, followed by Marsh and Forest Lands, with Agricultural Land being the lowest. Significance tests indicated that Grass, Marsh, and Forest Lands all differed significantly from Agricultural Land in richness ($P<0.05$), whereas no significant differences were detected between Grass Land and Marsh/Forest Lands, or between Marsh and Forest Lands ($P>0.05$). Specifically, Grass and Marsh Lands showed no significant difference ($P>0.05$) but were both significantly higher than Forest and Agricultural Lands ($P<0.05$); no significant difference was observed between Forest and Agricultural Lands ($P>0.05$) (Fig. 2).

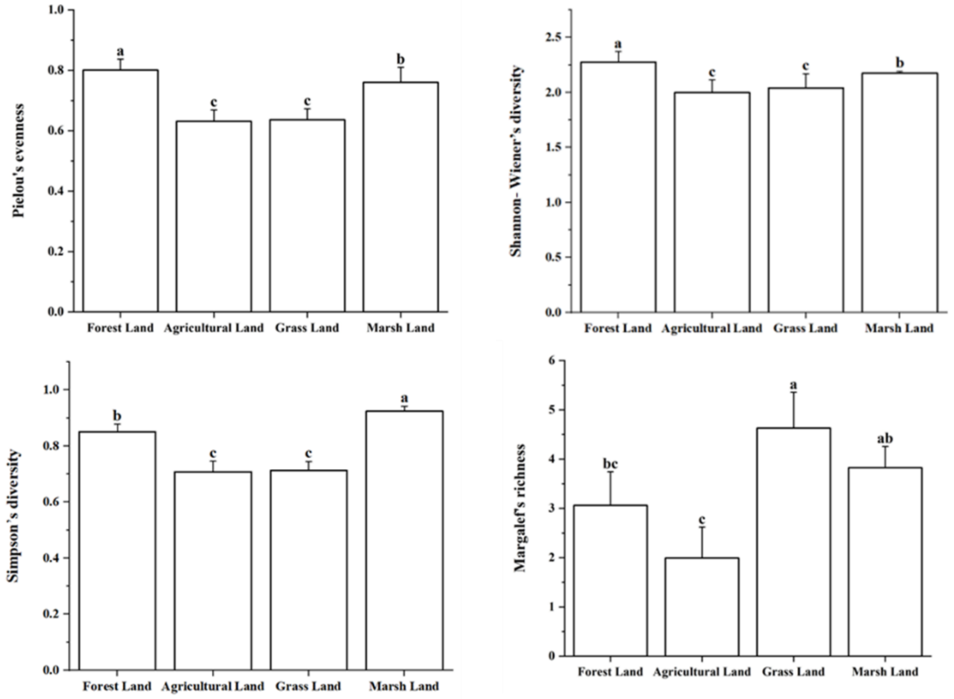


Fig. 2: Comparison of plant species diversity among different land use types.

Table 2: Factor loading matrix of species diversity and ecosystem functions.

Variables	Factors		
	f_1	f_2	f_3
Pielou’s evenness	0.394	0.161	0.034
Shannon-Wiener’s diversity	0.037	0.341	0.048
Simpson’s diversity	0.429	-0.005	0.037
Margalef richness	-0.311	0.303	0.039
pH	0.002	-0.043	0.495
SOC	0.064	0.129	0.424
NO_3-N	0.017	0.08	-0.449
AP	0.133	0.269	-0.134

Overall, the plant species diversity in the quadrats of the East Dongting Lake wetland was relatively high, and the species composition was rich. The diversity indices of the forestland and marshland in the quadrats were the best, which was consistent with the results of the plant investigations in East Dongting Lake conducted by Li *et al*.[43]

3.2 Factor analysis

The prerequisite for applying factor analysis is that there is a relatively strong correlation among various indices. Otherwise, common factors cannot be shared among the indices. Therefore, the SPSS 26.0 software was used to perform the Kaiser-Meyer-Olkin (KMO) test and Bartlett’s test of sphericity on the selected ecosystem function indices and diversity indices to evaluate the correlations. The results revealed that the KMO statistic was greater than 0.5, suggesting that factor analysis could be applied.[30] The result of Bartlett’s test of sphericity indicated that p = 0 (*i.e.*, less than 0.5). Hence, the hypothesis of independence among variables was rejected, demonstrating a correlation among the selected indices, and that variables were suitable for conducting factor analysis.

Subsequently, dimensionality reduction factor analysis was conducted. The initial factor loading matrix was rotated using the maximum variance method to obtain the factor loading matrix. According to the principle that the eigenvalue is greater than 1, three common factors were calculated and obtained.

For the species diversity indices (Table 2), common factor 1 was dominated by Pielou’s evenness and Simpson’s diversity, with positive correlations (loading = 0.394 and 0.429). Common factor 2 was dominated by Shannon-Wiener diversity and Margalef richness, with positive correlations (loading = 0.541 and 0.403). Common factor 2, associated with species richness and heterogeneity, showed lower loadings for Shannon-Wiener diversity (0.341) and Margalef richness (0.303), indicating their limited contribution to ecosystem function dynamics.

For the community-weighted mean trait value indices (Table 3), CWM (LL) and CWM (HA) exhibited a notable link with common factor 1 (loading = 0.574 and 0.457). while CWM (LA) also exhibited a significant association (0.466). These results highlight that dominant species’ traits are core drivers of ecosystem processes. Common factor 2, linked to SOC and pH, showed elevated loadings (0.556 and 0.484), reinforcing the tight coupling between CWM and key soil properties.

In the functional evenness (FE) and divergence (FD) indices (Table 4), common factor 1 revealed moderate correlations with FE (LA, 0.356) and FD (LA, 0.216), suggesting a secondary role of trait distribution and differentiation in supporting ecosystem functions—consistent

Table 3: Factor loading matrix of community-weighted mean and ecosystem functions.

Variables	Factors		
	f_1	f_2	f_3
CWM(LL)	0.574	-0.225	-0.026
CWM(LA)	0.466	0.207	0.061
CWM(HA)	0.457	-0.035	-0.032
pH	-0.068	0.484	-0.166
SOC	-0.09	0.556	0.166
NO_3-N	-0.001	-0.166	0.519
AP	-0.011	0.184	0.627

Table 4: Factor loading matrix of the functional evenness index and functional divergence index with ecosystem functions.

Variables	Factors		
	f_1	f_2	f_3
FE(LA)	0.356	0.259	0.219
FD(LA)	0.216	-0.036	-0.017
FE(LL)	-0.156	0.226	0.227
FD(LL)	-0.214	0.053	0.033
FE(HA)	0.278	0.211	0.185
FD(HA)	0.210	-0.075	-0.054
pH	-0.003	0.383	-0.207
SOC	-0.019	0.414	0.103
NO_3-N	0.023	-0.316	0.433
AP	0.005	0.028	0.569

with the primary influence of CWM.

Furthermore, significant correlations were also found among ecosystem functions. The NO_3^--N and AP contents were significantly correlated with each substrate factor 3 but weakly correlated with factor 1. Also, pH and SOC had relatively strong correlations with substrate factors 2 and 3 and had almost no correlation with factor 1 (Tables 2-4).

3.3 Correlations analysis

Building on the factor analysis, which suggested a stronger driving signal of functional diversity, especially CWM, on ecosystem functions, we used a correlation heatmap to compare the linear relationships between functional diversity (CWM, FE, FD), species diversity (Shannon, Simpson, *etc.*), and ecosystem functions (SOC, pH, *etc.*). The aim was to verify if functional diversity shows significantly stronger correlations than species diversity.

Collinearity diagnostics were performed prior to correlation analysis using the Variance Inflation Factor (VIF) implemented in the SPSS 26.0 software. The VIF values for all diversity indices and ecosystem function variables were calculated via linear regression models, with thresholds set at VIF < 5 indicating negligible collinearity.[44] After inspection, all variables satisfied this criterion, confirming that multicollinearity would not distort the Pearson correlation results.

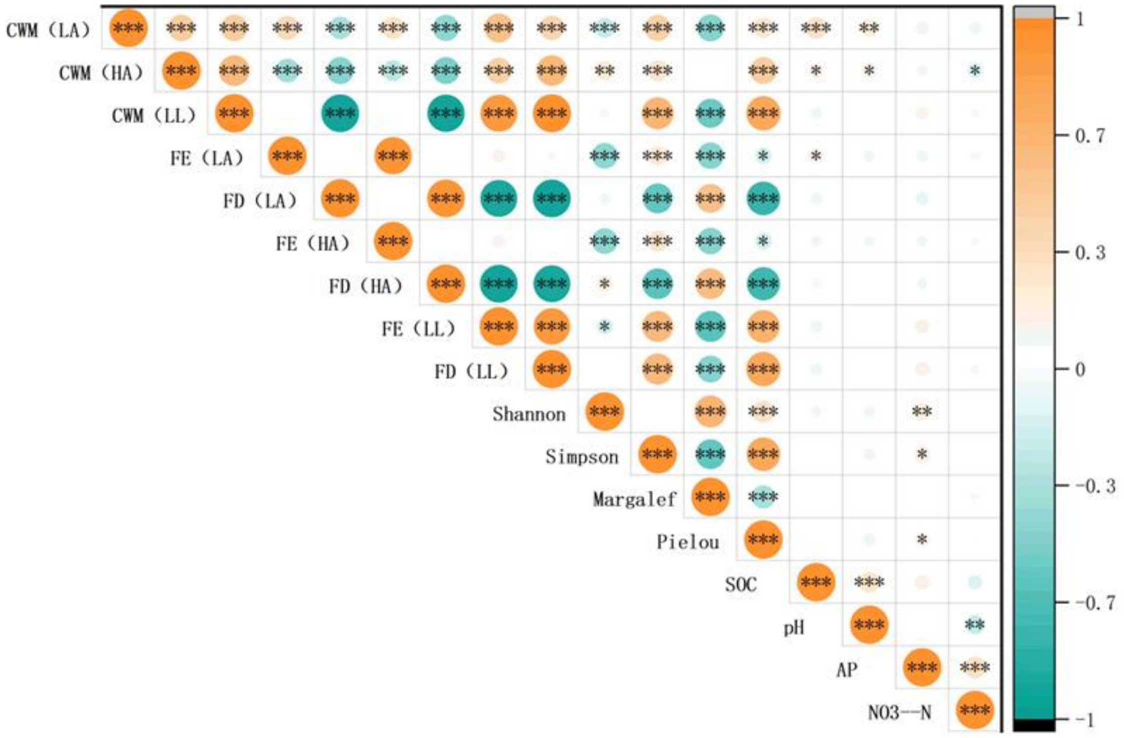


Fig. 3: Analysis of the correlation coefficient matrix among the indices of species diversity, functional diversity and ecosystem functions.

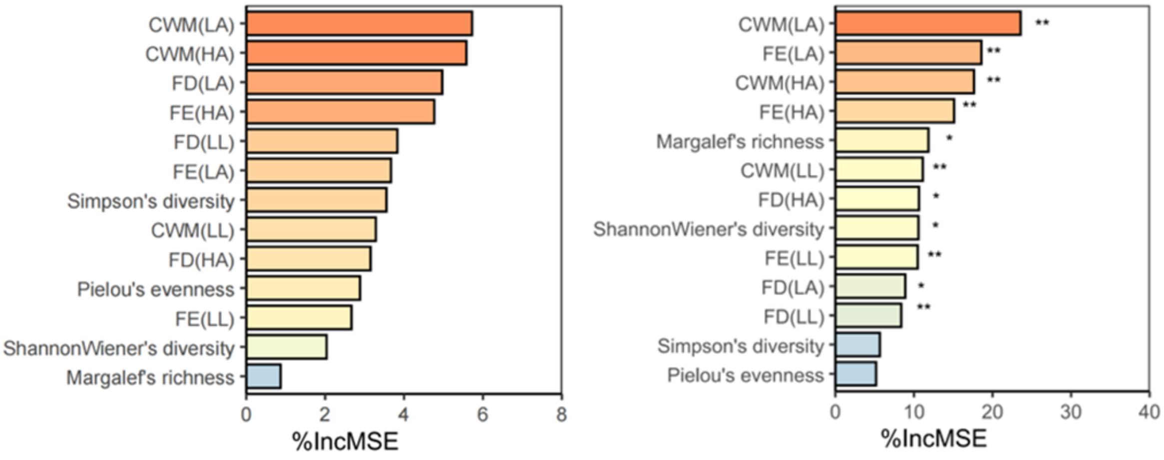
Note: (*) signifies a statistically significant difference at the P < 0.05 level, (**) suggest significance at P < 0.01, and (***) denote significance at P < 0.001.

Pearson correlation analysis of plant species diversity, functional diversity, and ecosystem functions in the study area (Fig. 3) revealed distinct association patterns: At the functional diversity level, CWM traits acted as core drivers: CWM (LA) exhibited a highly significant positive correlation with SOC ($P<0.001$) and a strongly significant positive correlation with pH ($P<0.01$, $r=0.6$); CWM (HA) showed significant positive correlations with both SOC and pH ($P<0.05$), while displaying a significant negative correlation with NO_3^--N ($P<0.05$, $r=0.3$). In contrast, FE(LA) only had a significant positive correlation with SOC ($P<0.05$), with a much weaker strength compared to CWM. At the species diversity level, only Shannon-Wiener's diversity showed a strongly significant positive correlation with SOC ($P<0.01$); Simpson's diversity and Pielou's evenness were each significantly positively correlated with AP ($P<0.05$). Other species diversity indices (*e.g.*, Margalef's richness) showed no significant associations with ecosystem functions, and the correlation coefficient is close to 0.

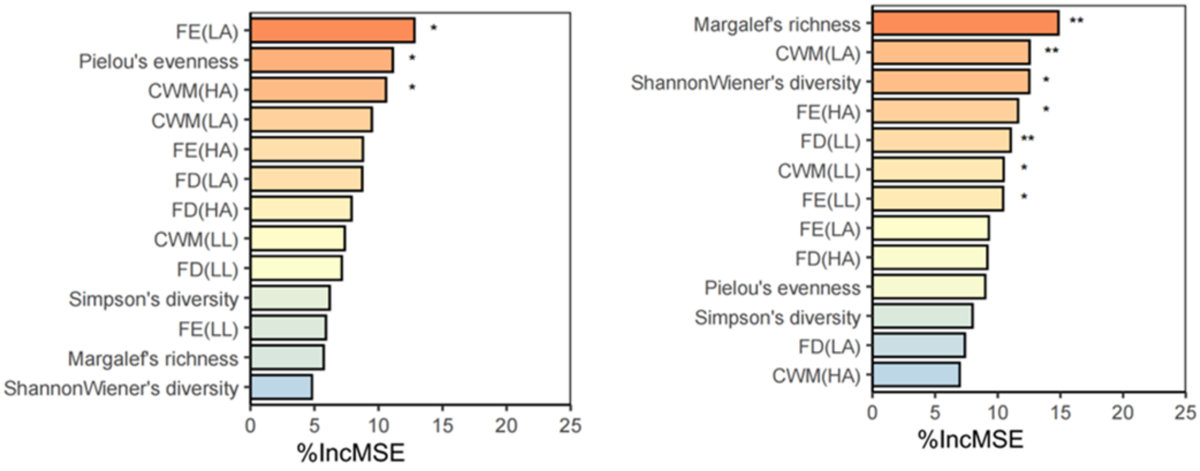
Collectively, functional diversity (especially CWM) exhibited broader and more significant correlations with ecosystem functions, which aligns well with the factor analysis conclusion that "functional diversity dominates ecosystem functions." In contrast, the contributions of species diversity were only sporadically observed, further confirming its limited role.

3.4 Model construction of wetland plant diversity and ecosystem functions

To analyze the influence of species diversity indices and functional diversity indices on plant diversity and ecosystem functions, we constructed a random forest model using the 'random Forest' package in R 4.1.3. This method quantifies independent contributions via permutation importance.[45] By randomly shuffling values of one predictor while holding others constant, it isolates the unique effect of each variable on ecosystem functions, controlling for covariate correlations. This model enabled the precise quantification of the contribution of both species diversity indices and functional diversity indices to the ecosystem functions.[30]



(a) pH (b) SOC



(c) NO_3^--N (d) AP

Fig. 4: Random forest model of plant diversity and ecosystem functions.

Note: (*) signifies a statistically significant difference at the $P < 0.05$ level, (**) suggest significance at $P < 0.01$, and (***) denote significance at $P < 0.001$.

The findings of the random forest method revealed the following (Fig. 4). Importance values represent independent contributions after accounting for inter-predictor correlations. In terms of the change in pH, each index had a relatively low effect, indicating that the roles of these plant diversity indices in the process of change in pH were relatively limited. The changes in SOC, CWM (LA), FE (LA), CWM (HA) and FE(HA) played important roles as key influencing factors, with importance values of 23.58%, 18.58%, 17.64% and 15.11%, respectively, which highlighted the different contributions of these indices to the dynamic changes in the SOC content. Among the influencing factors for the change in (NO_3^--N), FE (LA), Pielou's evenness and CWM (HA) were important influencing factors, with importance values of 12.81% ,11.12% and 10.59%respectively, indicating that these indices affected the process of NO_3^--N change. Regarding the change in AP, what is different from others is that Margalef's richness is the most important influencing factor, with an importance value of 14.84%. The next two are CWM(LA) and Shannon Wiener's diversity, with importance values of 12.54% and 12.52% respectively, all being significant.

As can be seen from the random forest model, the explanatory power of plant functional diversity for ecosystem function indicators far exceeds that of plant species diversity. For example, for SOC, the total importance value of plant functional diversity (124.42%) is 4.43 times that of species diversity (28.06%).

3.5 Linear relationships between key drivers and ecosystem functions

In the preceding analyses, factor analysis identified core factors with potentially significant impacts on ecosystem functions through dimensionality reduction; correlation heatmaps initially revealed the association patterns between plant diversity indices (species diversity and functional diversity) and ecosystem function indicators (*e.g.*, SOC, pH, AP). Furthermore, the random forest model quantified the relative importance of each factor to ecosystem functions, clarifying the key driving factors. To intuitively demonstrate the specific association strength, trends, and data distribution characteristics between these key drivers and ecosystem functions, this section selects 12 well-correlated combinations based on the above results. Pearson linear correlation analysis is used to construct scatter plots, focusing on presenting the linear relationships between representative species diversity indices, functional diversity indices, and core ecosystem function indicators. These visualizations provide empirical support for the in-depth discussion of ecological mechanisms in subsequent sections.

Based on species diversity dimension, Shannon-Wiener's

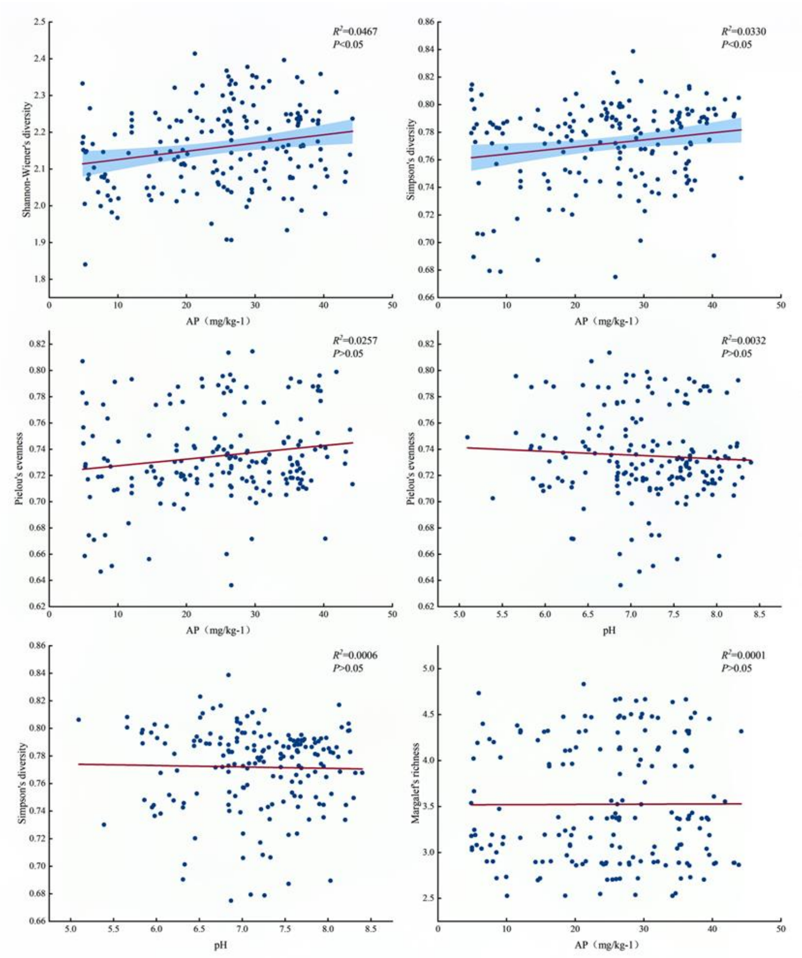


Fig. 5: Correlation analysis between species diversity and ecosystem functions.

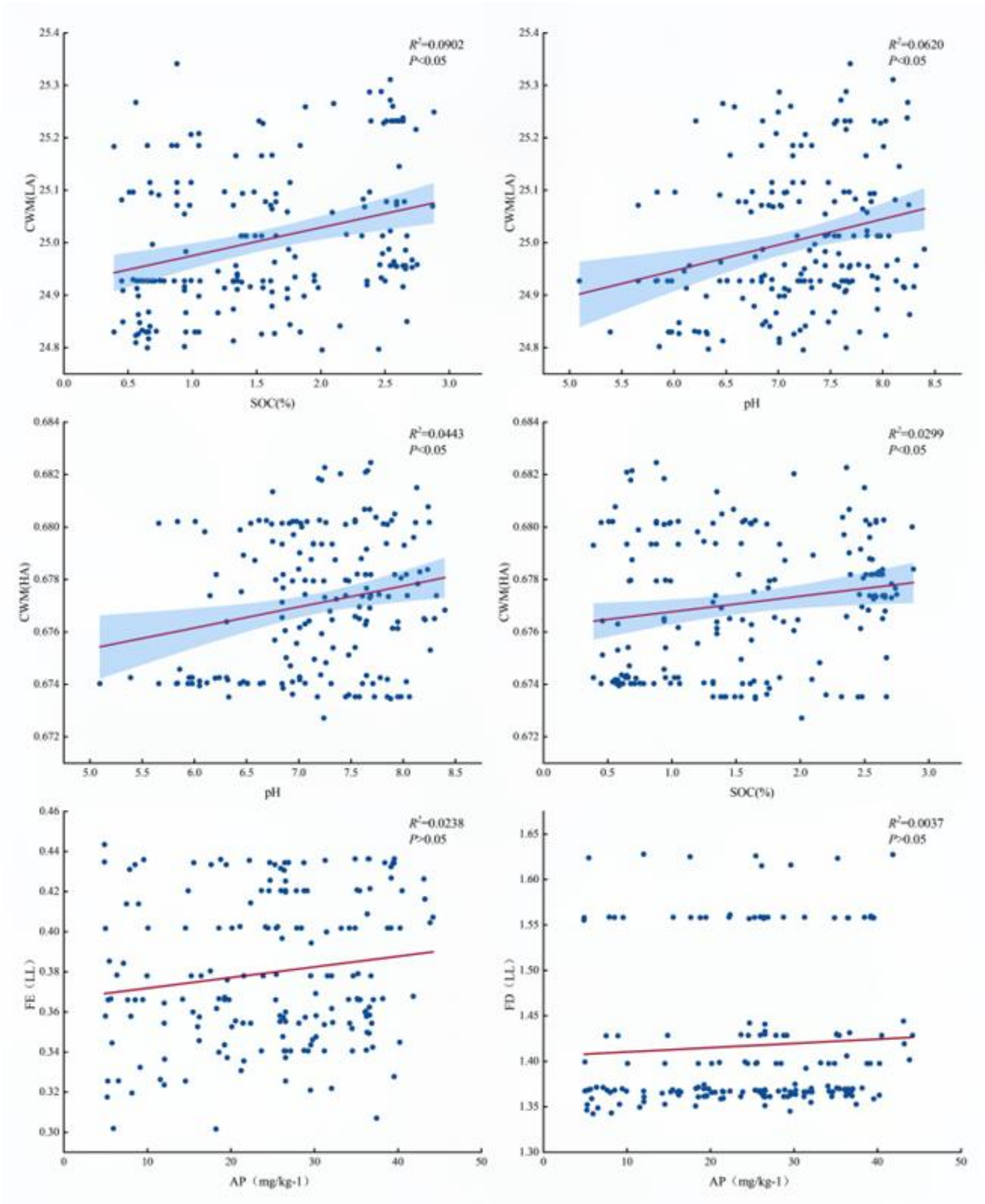


Fig. 6: Correlation analysis between functional diversity and ecosystem functions.

index showed a weak positive correlation with AP (R^2=0.0467, $P<0.05$), and Simpson's diversity index had a very weak positive correlation with pH (R^2=0.0330, $P<0.05$). Margalef's richness and Pielou's evenness showed no significant associations with AP or pH ($P>0.05$), with overall low explanatory power of species diversity for ecosystem functions($R^2<0.05$) (Fig. 5)

For functional diversity indices, CWM(LA) showed a significant positive correlation with SOC (R^2=0.0902, $P<0.05$);CWM(HA) exhibited a weak positive correlation with soil pH (R^2=0.0620, $P<0.05$);Although functional evenness FE(LL) and functional divergence FD(LA) were statistically significant with AP ($P<0.05$), their explanatory power was low ($R^2<0.05$) (Fig. 6).

4. Discussion

4.1 Responses and changes in plant species diversity to the environment

Soil is crucial for plant growth and has a fundamental effect on the growth, development, and succession of plants in terms of their structure and fertility level.[46] Changes in land use patterns can trigger changes in the structure and composition of plant communities, which in turn affect the types, quantities, and distributions of plants.[47] In the study area, forest land and marsh land exhibit relatively high species diversity indices. Agricultural land, which is intensively cultivated and managed by farmers, is subject to intense human selection and disturbance. This transforms continuously distributed ecosystem types into fragmented patches, reducing population density, pollen quantity, and pollination rates.[48] Such disturbances affect the formation and development of fruits and seeds, hinder seed dispersal and seedling development,[49] and ultimately result in low species richness. In contrast, grassland and forestland are less affected by human disturbance and almost unaffected by human activities.[50] The hydrological effects on marshland are weak, the habitat of marshland is stable, and the soil texture is fine. Marshlands have favorable conditions for the survival of species, thus leading to a relatively high level of species diversity.[51] The evenness index did not change significantly, possibly because most of the stable natural plots selected in this study were less affected by human interference and also because the ecosystems remained relatively stable under different environmental conditions. This finding also implied that under large-scale environmental changes, even if the species composition and ecological niches of the community change significantly, new species may emerge to maintain the balance of the ecosystem structure.[52]

4.2 Relationships between plant species diversity, functional diversity and ecosystem functions

In the research area of ecosystem functions, dominance (with CWM as an example) among the diversity indices effectively explained ecosystem functions, which showed that some features of dominant species were highly relevant to the ecosystem processes of the wetland under study. This discovery coincided with the research findings of Garnier *et al*.[39] Crucially, random forest analysis confirmed the dominant independent role of functional diversity over species diversity. This study revealed that both measures of evenness—Pielou’s evenness and FE—and indices of diversity—Shannon-Wiener’s and Simpson’s—displayed significant relationships with ecosystem functioning. This is due to the fact that the uniform distribution of species allows for the full exploitation of resources, and the complementary use of resources is capable of strengthening the functionality of the ecosystem. This result concurs with earlier research on the influence of diversity on temperate grassland ecosystems.[53]

In the present study, most of the studied ecosystem functions did not show an extremely notable correlation with richness, which was indicated by Margalef’s richness and FR. This finding contrasted with the research results of Zhang *et al*.,[54] who reported that the correlation between species richness and plant and ecosystem characteristics was greater than that between other taxonomic diversity indices. Richness reflects the niche space occupied by existing species. In general, the greater the richness, the more fully the niche space is occupied, the greater the community productivity, and the more stable the ecosystem functions.[17] Generally, functional richness is proportional to species richness. The species richness in the East Dongting Lake wetland might be significantly greater than that in the wetland studied by Zhang *et al*.[54] This is because, as Lohbeck *et al*.[55] noted, when traits are randomly distributed, more species mean a larger trait space. When species richness increases significantly and saturates, its effect on ecosystem functions is no longer significant, and the majority of rare species typically exert a minor role in maintaining ecosystem functions.[56]

Additionally, in this work, the plant functional diversity indices were strongly correlated with ecosystem functions. The functionality of ecosystems is notably enhanced by the increased variety of plant species, this phenomenon could potentially arise due to an augmentation in the quantity of species, which in turn elevates the variety of functional characteristics, conforming to the findings of Chanteloup and Bonis[12] and Fu *et al*.[13] The species diversity of the plant community cannot reflect the utilization of niche space;[57] compared to species diversity without a trait-based foundation, functional diversity derived from trait details showed a more pronounced correlation with ecosystem functions.

Compared with functional traits or phylogenetic diversity, the species diversity of plant communities cannot fully represent the utilization of niche space.[30] Plant functional traits are related to plants' resource utilization strategies.[57] At different spatial and temporal scales, coexisting species with different trait values may utilize distinct resources, thereby increasing the overall resource utilization efficiency of plant communities.[58] The conclusion that plant functional trait diversity can effectively enhance ecosystem multifunctionality has been confirmed in both controlled experiments and field survey experiments.[59] The role of high-level functional diversity in ecosystem functions is associated with high resource acquisition rate, high resource utilization efficiency, and temporal and spatial niche differences.[60] For example, increasing the functional diversity of plant traits, due to differences in plant size, leads to regular and spaced spatial distribution among plant individuals.[61] Such spatial distribution can maximize soil infiltration rate and heterogeneity,[62] thereby maximizing plant growth and ecosystem functions.

4.3 Potential ecological mechanisms

Based on the study by Zhang *et al*.,[54] we explained the ecological mechanisms represented by the eight diversity indices (Table 5). Referring to the conclusions of Yi *et al*.,[63] productivity significantly increases with the increase in the community-weighted mean (CWM) of maximum plant height, which supports the "mass ratio hypothesis" and demonstrates that the selection effect plays an important role in maintaining ecosystem productivity. When niche differentiation or mutual promotion occurs between species or groups, and thus ecosystem processes exceed the expected level of a single species or group, a complementary effect may emerge. Functional divergence (FD) is closely associated with synergistic effects and can serve as an indicator, highlighting its significance in the relationship between plant species and ecological performance, which is used to verify the complementary effect. This is also confirmed by the studies of

Table 5: Ecological mechanisms represented by the eight diversity indices.

Diversity indices	Dominance	Richness	Evenness	Divergence	Ecological mechanisms
Margalef's richness	-	+	-	-	Complementary effect
Pielou's evenness	-	-	+	-	Complementary effect
Shannon's diversity	-	+	+	+	Complementary effect
Simpson's diversity	-	+	+	+	Complementary effect
Functional richness	+	-	-	-	Complementary effect and Selection effect
Functional evenness	-	-	+	-	Complementary effect and Selection effect
Functional divergence	-	-	-	+	Complementary effect and Selection effect
Community-weighted mean	+	-	-	-	Selection effect

Table 6: Correlation coefficients between CWM, FD and ecosystem function indices.

	CWM（LL）	CWM（LA）	CWM（HA）	FD（LL）	FD（LA）	FD（HA）
pH	0.049	0.213**	0.153*	0.012	-0.02	-0.023
SOC	0.086	0.308***	0.15*	0.098	-0.082	-0.053
NO3--N	-0.044	-0.088	-0.15*	-0.054	-0.007	0.018
AP	0.123	0.121	0.077	0.141	-0.11	-0.07

Note: (*) signifies a statistically significant difference at the $P < 0.05$ level, (**) suggest significance at $P < 0.01$, and (***) denote significance at $P < 0.001$.

Mouchet *et al*.[64] and Fu *et al*.[13] In our study, the CWM, which characterizes the "mass ratio hypothesis", is important for maintaining ecosystem functions, whereas FD, which characterizes the "diversity hypothesis", has no significant impact on the ecosystem (Table 6). This is consistent with the conclusions of Roscher *et al*.[14] and Fu *et al*.,[13] indicating that the maintenance of ecosystem functions in the East Dongting Lake wetland is mainly driven by the selection effect. This conclusion contradicts the findings of Zhang *et al*.[30] in the Yellow River Delta wetland, which may be due to the fact that Zhang *et al*. considered multiple ecosystem functions simultaneously, leading to the maintenance of ecosystem functions in the Yellow River Delta being mainly driven by the complementary effect.

In this study, although the correlation between ecosystem functions and the richness index (represented by Margalef's richness) in terms of species diversity was not significant, the results of the Pearson analysis revealed a negative correlation. This negative correlation occurred probably because the richness index is measured by the number of species and fails to reveal the characteristics of the species, thus affecting ecosystem processing. To illustrate, this index treats all species as having the same contribution to ecosystem processing; however, from a functional perspective, these plants are not equivalent, which is consistent with the findings of Díaz and Cabido[57] and Mokany *et al*.[53] In addition, we also discovered a very significant positive correlation between ecosystem characteristics and the average trait value, which indicated that more vital ecosystem functions are linked to the dominant species that have higher trait values. Consequently, to maintain specific ecosystem functions in wetlands, key species and essential plant characteristics should take precedence instead of only concentrating on species quantity. This was also stated by Zhang *et al*.[54] This strategy aligns with the research concept of understanding how plants adapt to environmental stresses (such as drought, fire, and flooding) through specific organizational structures and functional traits. Protecting and restoring species with key adaptive traits is crucial for maintaining the resilience and functionality of ecosystems.[32]

5. Conclusion

To conclude, the plant species diversity level in the East Dongting Lake wetland is the greatest in the forestland and marshland and the smallest in the agricultural land, indicating that environmental factors significantly affect plant diversity.

Compared to the improvement in plant species diversity, the improvement in the plant community functional diversity level in the East Dongting Lake wetland can more effectively improve the functionality of the ecosystem. A high level of plant community functional diversity is the key to maintaining a high level of ecosystem functionality. Moreover, the dominance of the CWM is the most prominent, which indicates that ecosystem function is related mainly to the specific species traits of the dominant species, supporting the "mass ratio hypothesis". Therefore, the selection effect is the most important ecological mechanism in the restoration of the East Dongting Lake wetland, but the complementary effect guided by FD has a relatively limited impact on ecosystem functions to a certain extent.

This study, starting from the two dimensions of plant diversity, assessed the degree of its association with ecosystem functions in detail and provided a valuable reference for the management and restoration of the East Dongting Lake wetland. However, this study had certain limitations. For example, it focused only on species diversity and functional diversity and did not consider the influence of plant phylogenetic diversity on ecosystem functionality; soil microorganisms that interact with plants in nutrient cycling were not included; factors such as soil electrical conductivity and aboveground biomass were not considered. These factors need to be provided special attention in future research.

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Conflict of Interest

The authors declare no conflict of interest.

Supporting Information

Not applicable.

CRediT Statement

Jiayan Zhang: Conceptualization, Writing - Original draft. **Peiye Cheng:** Writing - Original draft, Data curation. **Yang Lin:** Methodology, Formal analysis. **Ye Li:** Resources, Visualization. **Ziqi Zheng:** Visualization, Validation. **Lu Qi:** Writing - Review & editing, Software. **Haoyu Zhang:** Writing - Review & editing, Funding acquisition.

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