

Which components of plant diversity are most correlated with ecosystem properties? A case study in a restored wetland in northern China

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ABSTRACT

The relationship between plant diversity and ecosystem services is a controversial topic in ecology that may be due, at least in part, to the variety of methods used to define and quantify diversity. This study examined the relationship between plant diversity and 11 ecosystem properties of a restored wetland in northern China by considering four primary components of diversity (dominance, richness, evenness, and divergence). Each diversity component was expressed by eight taxonomic and functional diversity indices respectively. Results showed that trait-based functional diversity had a stronger correlation with ecosystem processes than non-trait taxonomic diversity did. Among the four components of diversity, dominance (in terms of mean trait value index) was the best in explaining the variation in ecosystem processing. Richness and divergence also had significant correlations with ecosystem properties in some instances. By contrast, evenness had no significant correlation with most of the studied ecosystem properties. Our results indicated that wetland ecosystem properties are significantly related to certain traits of the dominant species. Thus, the dominant species and functional traits should be considered before the number of species in managing diversity and enhancing certain ecosystem functions of wetlands, especially in the case of conservation.

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1. Introduction

The past few decades have seen a rapid decline in global biodiversity, as well as a precipitous loss of ecosystem services (M.E.A., 2005), highlighting the critical need for a comprehensive understanding of the relationship between the two (Naeem et al., 1994; Chapin III et al., 2000; Hooper et al., 2005; Hillebrand and Matthiessen, 2009; MacDougall et al., 2013). However, the relationship between biodiversity and ecosystem services is still highly controversial (Schwartz et al., 2000; Kremen, 2005). While a number of studies have shown that the effect of species richness on ecosystem services is significantly positive (Engelhardt and Ritchie, 2001; Engelhardt and Ritchie, 2002 review in Balvanera et al., 2006 Zhu et al., 2012), the relationship is still highly controversial (Schwartz et al., 2000; Kremen, 2005). Indeed, several studies have argued against the existence of simple or

direct relationships between diversity and ecosystem function at all (Grime, 1997; Wardle et al., 1997; Schwartz et al., 2000; Thompson et al., 2005). Moreover, while some studies have suggested that ecosystem services are influenced by the diversity of all species (Tilman et al., 1997; Petchey and Gaston, 2002), others posit that the functional traits of the dominant species overwhelmingly affect ecosystem services (Grime, 1998; Mokany et al., 2008). Also, some evidence suggests that functional diversity is more significant than non-trait based diversity in providing ecosystem services (Symstad, 2000; Moonen and Bärberi, 2008). Clearly, the biodiversity/services debate requires a fundamental understanding of diversity and ecosystem services.

Diversity can be measured in a number of ways, and we propose that the variety of methods used to define and quantify diversity might be an important reason for the ecosystem 'biodiversity/services' debate. Diversity metrics quantify not only the number of species, but also the diversity of functional traits (Díaz et al., 2006). In addition to straightforward taxonomic diversity, the effects of functional diversity on ecosystem services have also drawn attention in recent years (Balvanera et al., 2006; Laliberté and

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Table 1

Four primary components of diversity and eight diversity indices applied as the expression of the components.

Component	Diversity indices			
	Taxonomic diversity	Calculation method	Functional diversity	Calculation method
Dominance			Mean trait value ^e	$MTV = \sum_{i=1}^{S'} p_i \times \ln x_i$
Richness	Species richness ^a	S	Functional group richness ^f	F
Evenness	Pielou's evenness ^b	$J = \left(-\sum_{i=1}^S p_i \times \ln p_i \right) / \ln S$	Functional regularity ^g	$FRO = \sum_{i=1}^{s-1} \min \left(\frac{EW_{i,i+1}}{\sum_{j=1}^S EW_{i,j+1}}, \frac{1}{S-1} \right)$
				$EW_{i,i+1} = \frac{x_{i+1} - x_i}{p_{i+1} + p_i}$ With
Divergence	Shannon's diversity ^c	$H' = -\sum_{i=1}^S p_i \times \ln p_i$	Functional divergence ^h	$FD = \sum_{i=1}^S p_i (\ln x_i - \ln X)^2$ with
	Simpson's diversity ^d	$D = 1 - \sum_{i=1}^S p_i^2$		$\ln X = \sum_{i=1}^S p_i \times \ln x_i$

S : number of all species; S' : number of dominant species; p_i : relative abundance of species i ; x_i : single functional trait value of species i .

^a Colwell, 2009,

^b Ricotta and Avena, 2003,

^c Shannon, 1948,

^d Simpson, 1949,

^e Garnier et al., 2004,

^f Tilman et al., 1997,

^g Mouillot et al., 2005,

^h Mason et al., 2003.

Legendre, 2010; Polley et al., 2013). Numerous diversity indices exist, but it has been generally measured using four primary components: dominance, richness, evenness, and divergence (Mason et al., 2005; Mokany et al., 2008). Dominance refers to the functional traits of the dominant species in a community, whereas richness, evenness and divergence refer to species number and functional traits of all species (Mason et al., 2005; Mokany et al., 2008). The four components of diversity can be measured by various taxonomic and functional diversity indices (Table 1). On the other hand, the labels of properties, processes, functions and services are helpful in understanding the ecosystem biodiversity/services debate. A cascade model summarized the distinction of these labels (Haines-Young and Potschin, 2010) (Fig. 1). Combination of many ecosystem properties, processes and functions could produce a particular ecosystem service, and may

also lead to the generation of other kinds of service outputs. Ecosystem services fundamentally are products of ecosystem properties. Thus, studying the relationship between diversity components and ecosystem properties might be more helpful to fundamentally understand the biodiversity/services debate.

Using these four components of diversity (dominance, richness, evenness, and divergence), this study focused on the correlations between diversity and 11 ecosystem properties in a restored wetland in North China. We hypothesize that the four components of diversity might have different correlations with ecosystem properties. The four components of diversity were measured using eight taxonomic and functional diversity indices. Correlations between diversity indices and ecosystem properties were analyzed using Pearson's correlation and factor analyses. Based on these results, we identified potential ecological mechanisms that would

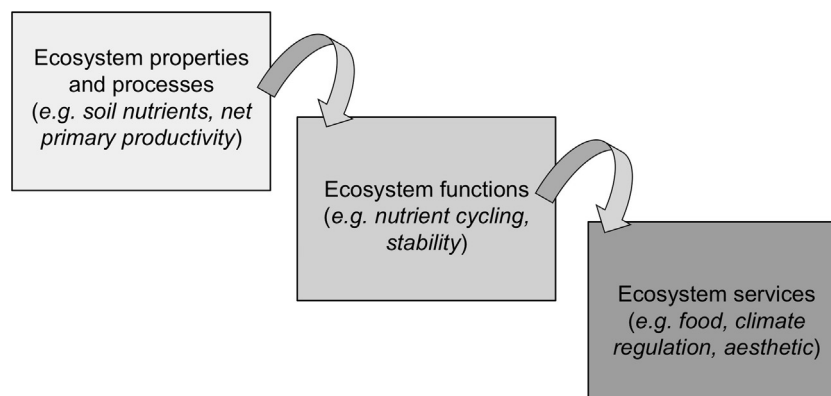


Fig. 1. Cascade model distinguishing ecosystem properties, processes, functions and services. (modified from Haines-Young and Potschin 2010).

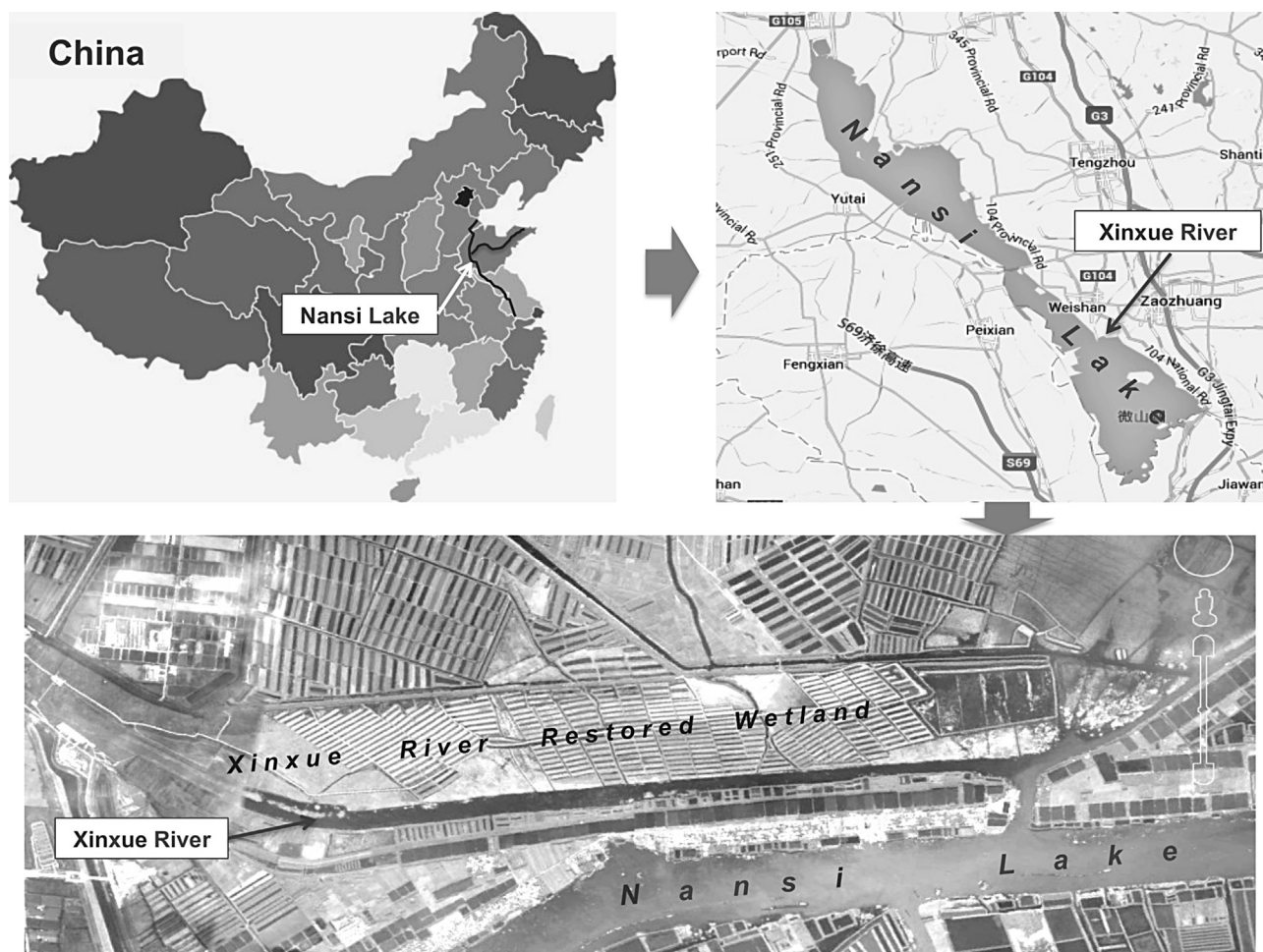


Fig. 2. Location of Xinxue river restored wetland in Nansi Lake, China.

support the observed relationships between diversity and ecosystem services. The aspect of the four primary components of diversity in our study might provide insight and contribute to a more comprehensive understanding of the relationship between diversity and ecosystem functions. Our study will also provide guidance on how to manage diversity and maximize ecosystem functions of wetland ecosystems, especially in the case of conservation.

2. Material and methods

2.1. Site description

The Xinxue river wetland was restored in 2004. This wetland has an area of 1330,000 m² and is located in Nansi Lake, Shandong Province, China (34° 45'N, 117° 09'E) (Fig. 2). The area has a temperate continental monsoon climate, annual average rainfall of 870 mm, and annual average temperature of 13.6 °C. Seedlings of 13 native species (e.g., *Nelumbo nucifera*, *Phragmites australis*, and *Typha orientalis*) were planted in the restored wetland in 2004 as pioneer species to facilitate vegetation restoration. This wetland is a flow-through system, and the water flowing into the wetland originates from the adjacent Xinxue river. The hydraulic residence time is 25 d. Water quality of wetland inflow has the following properties: $C_{(COD)} = 40 \text{ mg L}^{-1}$, $C_{(\text{ammonianitrogen})} = 2 \text{ mg L}^{-1}$, and $C_{(\text{totalphosphorus})} = 0.1 \text{ mg L}^{-1}$ (Lei et al., 2011). Water depth of the

wetland varies between 0 and 2 m over space. The wetland has been protected as a natural reserve since 2004 to exclude anthropogenic disturbance, thus enabling the full expression of plant traits and making the wetland a good subject for conducting research on relationships between diversity and ecosystem processes.

2.2. Field and laboratory methods

2.2.1. Abundance and functional traits

Fieldwork was conducted in late August 2011. Fourteen 30 m × 30 m sampling sites were selected to include the entire range of community types observed in the wetland. Six 1 m × 1 m quadrats were selected within each site through restricted randomization (Smith, 1983), for a total of 84 quadrats. Plants in each quadrat were sorted by species, and abundance, height, leaf area, and growth period were recorded. Seven plant functional traits were examined. These traits included height of adults (HA), leaf area of adults (LAA), maximum height (MH), maximum leaf area (MLA), life span (LS), life form (LF), and growth form (GF). LS was measured as categorical data with: 1 (annuals), 2 (biennials), and 3 (perennials). Similarly, life form was measured as categorical data as 1 (herb), 2 (shrub), and 3 (tree), whereas GF was categorized as 1 (submergent), 2 (floating), 3 (emergent), and 4 (others). Plant traits of height and leaf area were measured using

Table 2

Diversity components of eight indices and the ecological mechanisms they represent.

Diversity indices	Dominance	Richness	Evenness	Ecological mechanisms
Species richness (<i>S</i>)	–	✓	–	Complementary effect
Pielou's evenness (<i>J</i>)	–	–	✓	Complementary effect
Shannon's diversity (<i>H'</i>)	–	✓	✓	Complementary effect
Simpson's diversity (<i>D</i>)	–	✓	✓	Complementary effect
Mean trait value (MTV)	✓	–	–	Selection effect
Functional group richness (<i>F</i>)	–	✓	–	Complementary effect and selection effect
Functional regularity (FRO)	–	–	✓	Complementary effect and selection effect
Functional divergence (FD)	–	✓	✓	Complementary effect and selection effect

the protocol in [Cornelissen et al. \(2003\)](#). Plant traits of life form and growth form were derived from the database The Flora of China.

2.2.2. Ecosystem properties

The aboveground biomass of each quadrat was measured by clipping the plants 5 cm above the soil surface. The plants were then dried at 80 °C to a constant weight. The dried plants were weighted. Percent coverage of each quadrat was recorded. Meanwhile, soil samples were collected with 10 cm cores. In each quadrat, five cores were collected using an auger (5 cm diameter) to form a composite sample. Roots were manually removed when the samples were prepared in the laboratory. Soil moisture content, pH, clay, sand, silt, organic matter, ammonia nitrogen, total nitrogen, total phosphorus, available nitrogen, and available phosphorus were determined. Soil moisture was determined by drying the soil samples at 105 °C to a constant weight. Soil pH was determined using a PHS-3C pH meter (Leici, China) with a 1:2.5 suspension in H₂O. Distribution of soil particles was measured by using the micropipette method ([Miller and Miller, 1987](#)). Soil organic matter was determined by oxidation with potassium dichromate-titration of FeSO₄. Soil ammonia nitrogen was extracted with 1 mol/L KCl solution and was measured using a continuous flow analyzer (Skalar SAN++, the Netherlands). Total nitrogen was determined by using the Kjeldahl method ([Kirk, 1950](#)) and total phosphorus was determined using sodium hydroxide molten Mo-Sb colorimetry method ([Lu, 1999](#)). Available nitrogen in soil was measured using alkali N-proliferation method ([Lu, 1999](#)). Available phosphorus in soil was extracted with 0.5

mol/L NaHCO₃ and measured with molybdenum blue colorimetry ([Olsen et al., 1954](#)).

2.3. Data analysis methods

2.3.1. Calculation of diversity indices

Plant diversity generally has four primary components ([Table 1](#)), namely, dominance (abundance or traits of the most abundant species) ([McNaughton and Wolf, 1970](#)), richness (range, number of groups in community or how much trait space is filled), evenness (distribution, how organisms or trait values are spread out in groups or trait space), and divergence (variation, combination of richness, and evenness) ([Mason et al., 2005](#); [Mokany et al., 2008](#)) ([Table 1](#)). In this study, the four components of diversity were measured with eight taxonomic diversity and functional diversity indices ([Table 1](#)). With the use of the data on the abundance of all species, taxonomic diversity indices, including species richness, Pielou's evenness ([Ricotta and Avena, 2003](#)), Shannon's diversity, and Simpson's diversity, were calculated. With a combination of the species abundance of all species and plant trait values, functional diversity indices were calculated. These indices included the functional regularity index (FRO) ([Mouillot et al., 2005](#)) and functional divergence (FD) ([Mason et al., 2003](#)). Combining the abundance of dominant species and plant trait values, we calculated community weighted mean trait value ([Garnier et al., 2004](#)). The calculation equations for the diversity indices and the components they represent are shown in [Table 1](#). All trait data were standardized before being used to calculate diversity indices

Table 3Pearson's correlation analysis for diversity indices and ecosystem properties, showing the eight most-correlated ecosystem properties (*n* = 84).

Independent variable	Aboveground biomass	Soil moisture	Soil clay	Soil pH	SOM	STP	SAP	NH ₄ -N
Species richness	0.228 [*]	–0.496 ^{**}	–0.326 [*]	0.251	–0.273	0.199	–0.434 ^{**}	–0.456 ^{**}
Pielou's evenness	–0.065	–0.194	–0.395 ^{**}	–0.221	0.075	0.036	0.000	–0.185
Shannon's diversity	0.059	–0.413 ^{**}	–0.402 ^{**}	0.017	–0.180	0.101	–0.271	–0.379 ^{**}
Simpson's diversity	0.036	–0.334 [*]	–0.431 ^{**}	–0.068	–0.140	0.077	–0.196	–0.299 [*]
FRO (HA)	0.309 ^{**}	0.037	–0.106	0.014	0.065	–0.098	0.146	0.039
FRO (LAA)	–0.104	0.037	–0.178	–0.151	0.040	0.150	0.081	0.054
FRO (MH)	0.256 [*]	0.054	–0.165	–0.306 [*]	0.097	–0.173	0.186	0.075
FRO (MLA)	–0.213	–0.208	–0.191	–0.032	0.042	–0.010	–0.100	0.051
FD (HA)	0.089	–0.166	–0.125	–0.109	0.010	–0.113	–0.102	–0.263
FD (LAA)	–0.417 ^{**}	0.108	–0.254	–0.194	0.067	–0.106	–0.103	–0.176
FD (MH)	0.225	–0.340 [*]	–0.192	–0.120	0.017	–0.039	–0.189	–0.323 [*]
FD (MLA)	0.529 ^{**}	–0.200	–0.347 [*]	–0.356 [*]	0.040	–0.010	–0.090	–0.309 [*]
FD (LS)	–0.155	–0.175	–0.327 [*]	0.010	–0.107	0.032	–0.266	–0.240
FD (GF)	0.550 ^{**}	0.570 ^{**}	0.113	–0.544 ^{**}	0.301 [*]	–0.384 ^{**}	0.423 ^{**}	0.238
FD (LF)	–0.152	–0.269	–0.271	–0.113	0.032	0.000	–0.147	–0.211
Mean trait value (HA)	0.057	0.147	0.399 ^{**}	–0.071	0.243	0.022	0.281 [*]	0.109
Mean trait value (LAA)	0.393 ^{**}	–0.129	–0.103	–0.295 [*]	0.014	0.032	0.148	–0.229
Mean trait value (MH)	–0.193	–0.035	0.236	–0.010	0.076	–0.062	0.175	0.128
Mean trait value (MLA)	–0.119	–0.138	–0.075	–0.279 [*]	0.020	–0.063	0.087	–0.194
Mean trait value (LS)	–0.032	0.283 [*]	0.255	0.108	0.151	–0.047	0.210	0.264
Mean trait value (LF)	–0.231 [*]	–0.680 ^{**}	–0.234	0.440 ^{**}	–0.311 [*]	0.471 ^{**}	–0.464 ^{**}	–0.378 ^{**}
Mean trait value (GF)	0.041	0.320 [*]	0.430 ^{**}	0.065	–0.030	–0.328 [*]	0.310 [*]	0.284 [*]

Trait codes: HA: height of adults; LAA: leaf area of adults; MH: maximum height; MLA: maximum leaf area; LS: life span; LF: life form; GF: growth form.

Ecosystem property codes: SOM: soil organic matter; STP: soil total phosphorus; SAP: soil available phosphorus; NH₄-N: soil ammonia nitrogen.

^{*} *p* < 0.05.

^{**} *p* < 0.01.

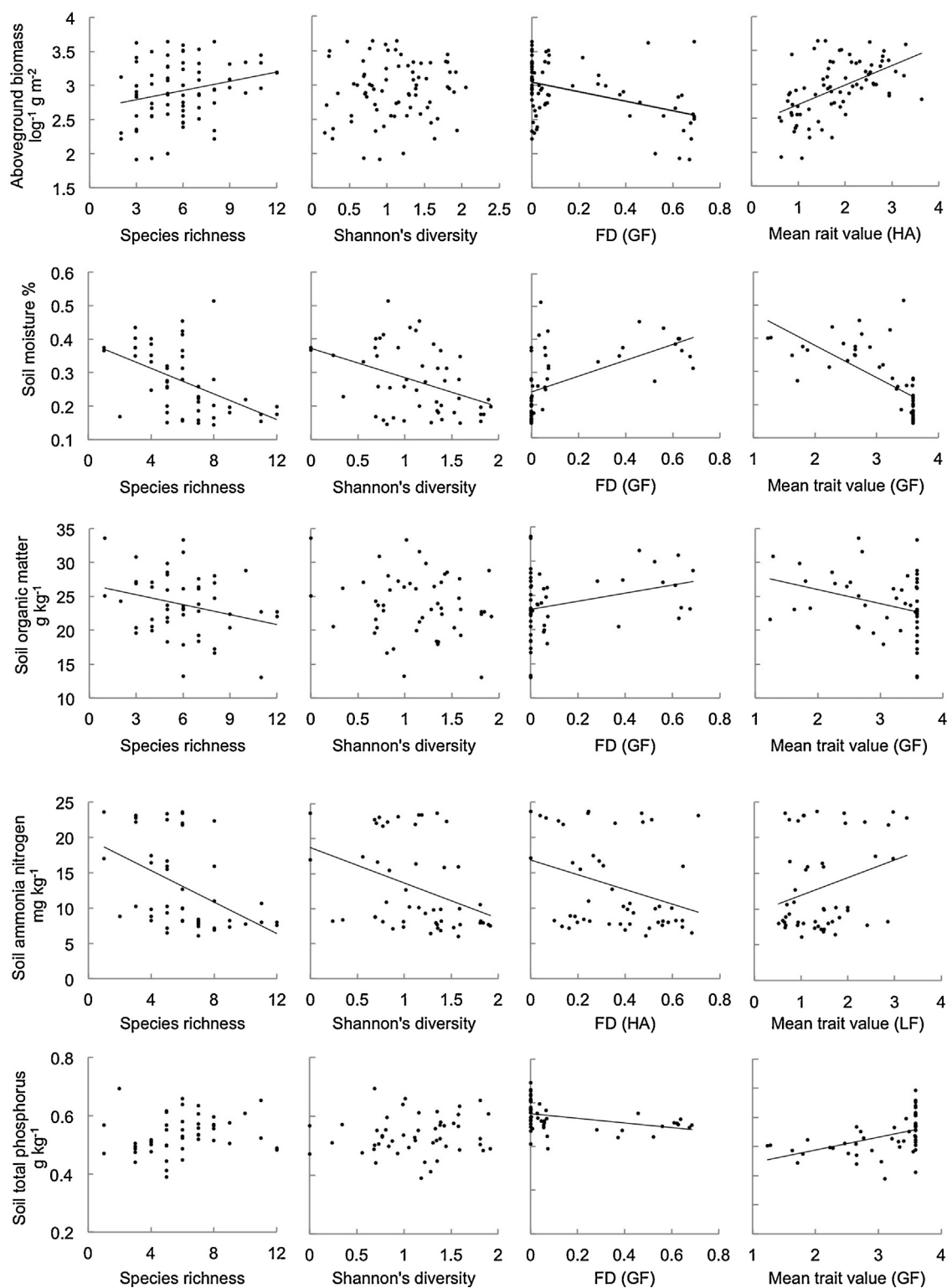


Fig. 3. Relationship between a range of diversity indices and ecosystem processes, showing the best-explained ecosystem processes with the best diversity indices.

(mean=0 and variance=1). All functional diversity indices were based on single trait instead of multiple traits. In measuring functional diversity using multiple traits, functional traits have been found to be trivially correlated (Mason et al., 2005), and the use of single trait avoids the calculation of spuriously high or low values of functional diversity.

2.3.2. Statistical analysis

Pearson's correlation and factor analyses were applied to examine the correlations between diversity indices and ecosystem functions. Factor analysis describes the variability among the observed correlated variables in terms of a potentially lesser number of unobserved variables called factors. Factors were

extracted using the principal component method, followed by varimax rotation (Reis et al., 2010). All statistical analyses were performed using SPSS Statistics 17.0.

3. Results

Pearson's correlation analysis showed the correlations between each diversity index and ecosystem properties (Table 3, Fig. 3). Among the taxonomic diversity indices, species richness had a positive correlation with aboveground biomass ($r = 0.228$, $p < 0.05$, and $n = 84$) and negative correlations with soil moisture, soil available phosphorus, and ammonia nitrogen ($r = -0.496$, -0.434 and -0.456 , respectively, $p < 0.01$, and $n = 84$). Shannon's diversity had significant negative correlations with soil moisture, clay, and ammonia nitrogen ($r = -0.413$, -0.402 , and -0.379 , respectively, $p < 0.05$, and $n = 84$). By contrast, Pielou's evenness had no significant correlation with all ecosystem properties, except for soil clay ($r = -0.395$, $p < 0.01$, and $n = 84$). Ecosystem properties in terms of soil pH, organic matter and total phosphorus had no significant correlations with any of the taxonomic diversity indices (Table 3).

Among the trait-based functional diversity indices, mean trait value was more related to six of the ecosystem processes compared with functional divergence or regularity indices (Table 3). Mean trait value (LF) was negatively related to soil moisture ($r = -0.680$, $p < 0.01$, and $n = 84$), and had significant correlations with all examined ecosystem properties. Mean trait value (LAA) had a significant positive correlation with aboveground biomass ($r = 0.393$, $p < 0.01$, and $n = 84$). Functional divergence (GF) was positively related to aboveground biomass and soil moisture ($r = 0.550$ and 0.570 , $p < 0.01$, and $n = 84$), but negatively related to soil pH ($r = -0.544$, $p < 0.01$, and $n = 84$) (Table 3). Functional divergence (LAA) had a significant negative correlation with aboveground biomass ($r = -0.417$, $p < 0.01$, and $n = 84$). Both functional divergence and mean trait value had significant correlations with all examined ecosystem processes. By contrast, FRO showed no significant correlation with the examined ecosystem properties, except for aboveground biomass and soil pH.

The results of factor analysis for correlations between diversity indices and the 11 ecosystem properties are presented in Tables 4–6 and are sorted based on taxonomic diversity indices, functional divergence, and mean trait value, respectively. Factors extracted from FRO were not presented because of their weak correlations with ecosystem properties. Moreover, three plant traits, which had no significant correlations with ecosystem properties in factor analysis, were removed. These three traits are

MH, MLA, and GF. The retained factors accounted for 66–71% of the total variance (Tables 4–6).

Among non-trait taxonomic diversity indices (Table 4), Shannon's diversity and Simpson's diversity had negative loadings (-0.66 and -0.67 , respectively) on factor 2 in their matrix. Furthermore, soil total phosphorus also had negative loadings on the same factor (loading = -0.49 and -0.46 , respectively). Available soil phosphorus, clay, and moisture content were all positively related to factor 2. Species richness also had a negative correlation with factor 2 (loading = -0.59), whereas available nitrogen, clay, and moisture content had strong, positive correlations on the same factor (loading = 0.80 , 0.72 , and 0.63 , respectively). Pielou's evenness had a negative correlation with factor 3 (loading = -0.49), but aboveground biomass was positively related to the same factor (loading = 0.82).

Among the functional divergence indices based on the four plant traits (Table 5), functional divergence (LF) and soil moisture had strong, negative correlations with factor 2 (loading = -0.89 and -0.48 , respectively). Moreover, aboveground biomass had a strong, positive correlation with the same factor (loading = 0.84). Functional divergence (HA) had a negative loading on factor 3 (loading = -0.56), whereas aboveground biomass had a positive loading on the same factor (loading = 0.75). Functional divergence (LS) had a negative correlation with factor 2 (loading = -0.58), whereas soil available phosphorus and soil clay had strong, positive correlations with the same factor (loadings = 0.75 and 0.76 , respectively). Among the mean trait value indices (Table 6), mean trait value (LF) and aboveground biomass had high loadings (0.82 and 0.85 , respectively) on factor 2, and soil pH and percent coverage also had relatively high loadings on the same factor (loadings = 0.56 and 0.66 , respectively). Mean trait value (HA) and aboveground biomass had positive correlations with factor 3 (loadings = 0.65 and 0.80 , respectively). Mean trait value (LS), available soil phosphorus, and clay content were positively related to factor 2 (loading = 0.59 , 0.76 , and 0.73 , respectively). Mean trait value (LAA) had a negative correlation with factor 3 (loading = -0.54), whereas aboveground biomass, soil pH, and percent coverage showed highly positive loadings on the same factor (loading = 0.77 , 0.62 , and 0.61 , respectively).

In addition, significant correlations were found among the ecosystem properties. Soil organic carbon, total nitrogen, available nitrogen, and ammonia nitrogen had significant positive correlations (loading ranged from 0.62 to 0.90) with factor 1 of each matrix. However, soil pH had negative correlations with factor 1 in all cases. Aboveground biomass and percent coverage had significantly high loadings in the same factor of each matrix. Soil

Table 4

Rotated factor loading matrix of factor analysis for ecosystem properties and taxonomic diversity indices ($n = 84$).

Variables	Species richness			Pielou's evenness			Shannon's diversity			Simpson's diversity		
	f_1	f_2	f_3	f_1	f_2	f_3	f_1	f_2	f_3	f_1	f_2	f_3
A-biomass	-0.06	-0.04	0.86	-0.11	-0.15	0.82	-0.16	0.14	0.82	-0.19	0.20	0.79
SOM	0.83	0.16	-0.24	0.84	0.12	-0.22	0.83	0.16	-0.21	0.84	0.14	-0.19
STN	0.90	0.07	0.02	0.90	0.02	0.09	0.87	0.18	0.07	0.87	0.18	0.09
STP	0.32	-0.64	0.32	0.27	-0.75	0.26	0.35	-0.49	0.56	0.32	-0.46	0.61
SAP	0.30	0.80	-0.01	0.35	0.76	0.08	0.23	0.77	-0.20	0.25	0.72	-0.27
SAN	0.80	0.23	-0.18	0.82	0.21	-0.13	0.79	0.27	-0.18	0.79	0.25	-0.17
NH ₄ -N	0.62	0.39	-0.30	0.66	0.35	-0.24	0.63	0.34	-0.32	0.64	0.30	-0.34
Clay/%	0.17	0.72	0.24	0.20	0.66	0.28	0.07	0.76	0.04	0.08	0.78	-0.01
Moisture	0.43	0.63	-0.41	0.51	0.64	-0.27	0.43	0.56	-0.50	0.46	0.50	-0.53
pH	-0.54	0.13	0.62	-0.56	0.12	0.62	-0.63	0.23	0.48	-0.65	0.28	0.44
% Cover	-0.23	-0.29	0.68	-0.28	-0.40	0.57	-0.28	-0.16	0.72	-0.30	-0.12	0.71
DI ^a	-0.14	-0.59	0.28	0.00	-0.11	-0.49	-0.19	-0.66	-0.09	-0.16	-0.67	-0.16
% Variance	27	49	68	29	49	66	28	49	68	29	49	68

Ecosystem property codes: A-biomass–aboveground biomass; SOM: soil organic matter; STN: soil total nitrogen; STP: soil total phosphorus; SAP: soil available phosphorus; SAN: soil available nitrogen; NH₄-N: soil ammonia nitrogen.

^a DI, diversity indices = species richness, Shannon's diversity or Simpson's diversity.

Table 5Rotated factor loading matrix of factor analysis for ecosystem processes and functional divergence indices ($n = 84$).

Variables	FD (HA)			FD (LAA)			FD (LS)			FD (LF)		
	f_1	f_2	f_3	f_1	f_2	f_3	f_1	f_2	f_3	f_1	f_2	f_3
A-biomass	−0.22	−0.07	0.75	−0.19	−0.12	0.75	−0.20	0.19	0.81	−0.09	0.84	0.07
SOM	0.84	0.12	−0.18	0.85	0.14	−0.13	0.83	0.15	−0.19	0.84	−0.23	0.11
STN	0.87	0.05	0.11	0.88	0.03	0.09	0.87	0.18	0.09	0.89	0.02	0.07
STP	0.27	−0.68	0.42	0.27	−0.70	0.37	0.34	−0.47	0.60	0.30	0.41	−0.64
SAP	0.32	0.80	0.07	0.32	0.77	0.05	0.23	0.75	−0.24	0.33	−0.09	0.78
SAN	0.83	0.25	−0.03	0.81	0.22	−0.09	0.79	0.27	−0.17	0.82	−0.16	0.21
NH ₄ –N	0.67	0.36	−0.19	0.68	0.37	−0.17	0.64	0.36	−0.30	0.64	−0.33	0.32
Clay/%	0.12	0.70	0.17	0.15	0.70	0.27	0.06	0.76	0.00	0.17	0.11	0.75
Moisture	0.52	0.62	−0.29	0.52	0.63	−0.28	0.45	0.56	−0.49	0.46	−0.48	0.55
pH	−0.64	0.17	0.51	−0.62	0.15	0.54	−0.66	0.24	0.44	−0.55	0.59	0.25
% Cover	−0.33	−0.31	0.65	−0.32	−0.35	0.64	−0.30	−0.15	0.70	−0.26	0.68	−0.23
DI ^a	−0.21	−0.27	−0.56	−0.14	−0.27	−0.61	−0.18	−0.58	−0.16	0.11	−0.89	0.18
% Variance	31	50	67	30	50	67	29	48	67	28	53	71

Trait codes see Table 3.

Ecosystem property codes see Table 4.

^a DI, diversity indices = FD (HA), FD (LAA), FD (LS) or FD (LF).**Table 6**Rotated factor loading matrix of factor analysis for ecosystem processes and mean trait value indices ($n = 84$).

Variables	Mean trait value (HA)			Mean trait value (LAA)			Mean trait value (LS)			Mean trait value (LF)		
	f_1	f_2	f_3	f_1	f_2	f_3	f_1	f_2	f_3	f_1	f_2	f_3
A-biomass	−0.26	−0.19	0.80	−0.13	−0.12	0.77	−0.19	0.18	0.80	−0.10	0.85	0.12
SOM	0.87	0.14	0.01	0.84	0.12	−0.20	0.85	0.16	−0.16	0.84	−0.23	0.11
STN	0.85	−0.01	0.12	0.90	0.06	0.12	0.87	0.14	0.10	0.89	0.04	0.09
STP	0.22	−0.76	0.25	0.28	−0.71	0.33	0.31	−0.50	0.59	0.31	0.45	−0.61
SAP	0.30	0.74	0.10	0.34	0.78	0.05	0.27	0.76	−0.22	0.31	−0.13	0.78
SAN	0.81	0.21	−0.04	0.81	0.22	−0.13	0.80	0.19	−0.19	0.81	−0.18	0.21
NH ₄ –N	0.70	0.37	−0.01	0.64	0.30	−0.33	0.65	0.35	−0.28	0.64	−0.34	0.31
Clay/%	0.14	0.67	0.44	0.17	0.66	0.18	0.10	0.73	−0.01	0.16	0.09	0.76
Moisture	0.54	0.64	−0.18	0.50	0.63	−0.32	0.48	0.55	−0.48	0.45	−0.52	0.53
pH	−0.69	0.07	0.39	−0.57	0.17	0.62	−0.65	0.26	0.44	−0.57	0.56	0.27
% Cover	−0.39	−0.43	0.51	−0.29	−0.37	0.61	−0.31	−0.13	0.71	−0.28	0.66	−0.17
DI ^a	0.23	0.21	0.65	−0.09	−0.36	−0.54	0.10	0.59	0.27	−0.12	0.82	−0.34
% Variance	32	52	67	29	49	67	29	49	67	28	52	71

Trait codes see Table 3.

Ecosystem property codes see Table 4.

^a DI, diversity indices = mean trait value (HA), (LAA), (LS) or (LF).

available phosphorus, clay, and moisture content showed strong positive correlations with the same factor in 10 of the 12 matrices.

4. Discussion

4.1. Relationship between different components of diversity and ecosystem processing

Among the four primary components of diversity, dominance (in terms of mean trait value index) is the best in explaining ecosystem properties (Tables 3 and 6, Fig. 3), indicating that certain traits of the dominant species are significantly related to ecosystem processes of the studied wetland. This result is consistent with Garnier et al. (2004), who found that mean trait value based on leaf traits was a significant aspect of net primary productivity, total soil carbon, and nitrogen during the succession. Mokany et al. (2008) also found that the mean trait value had the strongest correlations with ecosystem processes among the diversity indices. In this study, richness (represented by species richness) and divergence (represented by Shannon's diversity, Simpson's diversity, and functional divergence) also had significant correlations with ecosystem properties, which are consistent with the study examining the effects of diversity on aboveground net

primary production, soil moisture and litter decomposition rate in a temperate grassland (Mokany et al., 2008). In our study, evenness (represented by Pielous's evenness index and functional regularity index) had no significant correlation with most of the studied ecosystem properties.

On the other hand, species richness index (representing diversity component of richness) was more related to the ecosystem properties than any other index of taxonomic diversity, which is in contrast to the findings of Mokany et al. (2008), who found that species richness has weak correlations with most grassland ecosystem processes. One of the reasons for this difference might be that species richness in the wetland in our study was significantly lower than that in the grassland in the study of Mokany et al. (2008). When species richness is generally low, an increase in the number of species may significantly increase ecosystem processing. However, the increasing effect will saturate at high species richness. This finding is in concordance with curve B suggested by Schwartz et al. (2000), who hypothesized that ecosystem processing is effectively maximized by a relatively low diversity (Fig. 4). Meanwhile, when species richness is at a high level, most rare species do not materially contribute to ecosystem maintenance. In our study, functional diversity indices generally had stronger correlations with ecosystem properties

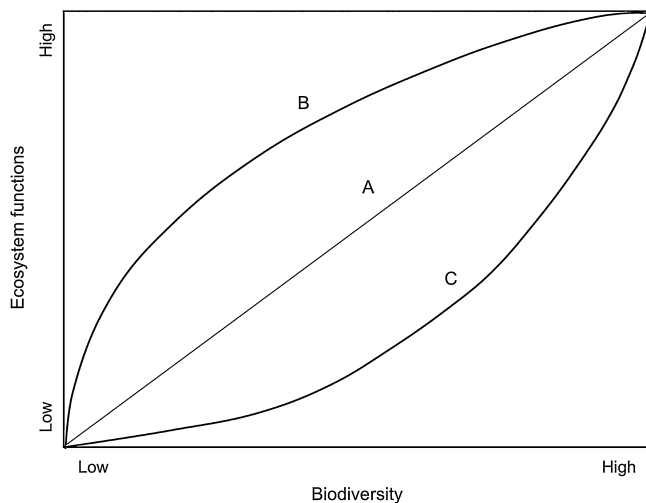


Fig. 4. Theoretical relationship between biodiversity and ecosystem functions. (after Schwartz et al., 2000).

than taxonomic diversity indices, which indicate that functional diversity based on trait information is more related to ecosystem processing than non-trait taxonomic diversity.

A major constraint of observational studies examining the relationship between diversity and ecosystem processes is the inability to isolate co-varying abiotic factors that may be responsible for observed correlations (Schwartz et al., 2000). In this study, factor analysis was used to examine the relationship between various diversity indices and ecosystem processing, as well as to identify how ecosystem processes interact as co-varying abiotic factors. The results of factor analysis showed significant correlations among ecosystem processes in some cases. For instance, soil organic matter had a significant correlation with soil total nitrogen and available nitrogen (Tables 4–6). Moreover, diversity indices also had significant correlations with most examined ecosystem properties, which indicate that diversity is considerably related to ecosystem processing. For instance, mean trait value (LF) and functional divergence (LF) (representing dominance and divergence) best explain biomass processing. Furthermore, functional divergence (LS) and mean trait value (LS) had significant correlations with soil available phosphorus, which might be related to the different growth strategies of the annual, biennial, and perennial plants during their life cycles (Blom and Voesenek, 1996). Annuals would uptake more nutrients than biennials and perennials because annuals usually germinate, flower, and die in one year. Moreover, taxonomic richness and divergence (representing richness and divergence) had significant correlations with total soil phosphorus, soil clay and soil moisture (Table 3).

4.2. Potential ecological mechanisms

Numerous hypotheses explaining the relationships between diversity and ecosystem processing have been established from experimental and theoretical studies. These hypotheses can be classified into two primary mechanisms: selection effect and complementarity effect (Loreau and Hector, 2001). The selection effect gives rise to correlations between diversity and ecosystem processing through interspecific competition, which causes the dominance of species with certain traits. In our study, the selection effect can be quantified by the diversity component of dominance in terms of mean trait value (Mokany et al., 2008) (Table 2). Additionally, plant trait-based functional diversity indices (FRO and FD) are also partially related to the selection effect (Table 2).

The complementarity effect occurs when the niche differentiation or facilitation between species or groups increases ecosystem processing above that expected from individual species or group (Loreau and Hector, 2001). The taxonomic or functional diversity indices applied in this work were all directly or indirectly related to the assessment of the complementarity effect to explain the relationship between diversity and ecosystem processing (Table 2). In our results, mean trait value had the most significant correlations with ecosystem processes and properties, which implies that the selection effect was dominant in assessing the relationship between diversity and ecosystem processes. Species richness, Shannon's diversity, Simpson's diversity, and functional divergence also exhibited significant correlations with the examined ecosystem properties in some instances, thus indicating that complementarity may serve as an important function in influencing wetland ecosystem processes. In this study, we suggest that the selection effect is generally stronger than the complementarity effect in the studied wetland.

In this study, most significant correlations between ecosystem properties and taxonomic diversity and functional divergence are negative (Fig. 3, Tables 4 and 5), as frequently reported in studies on natural communities (Díaz and Cabido, 2001; Mokany et al., 2008). The negative relationship is possibly caused by the fact that indices cannot reveal the species identities that affect ecosystem processing (Bengtsson, 1998). For instance, species richness uses the number of species as indicator, which suggests that all species equally contribute to ecosystem processing. However, the plants could not be considered as equivalent in terms of function. The positive/negative correlations between diversity and ecosystem processing might be closely related to the type of ecosystem properties and functional traits measured. Some ecosystem processes might be highly dependent on the existence of some particular species, whereas others might increase with the development of a particular trait value presented by all species. Moreover, we found most significantly positive relationships exist between ecosystem properties and mean trait value (Table 6). The positive relationship between mean trait value and ecosystem properties merely indicates that more significant ecosystem processes or properties are related to the dominance of species with higher trait values. Thus, the consideration of dominant species and plant functional traits should be prioritized over the species numbers in maintaining certain ecosystem functions of wetlands.

5. Conclusions

From the aspect of the four primary components of diversity, we found that dominance in terms of mean trait value is of primary importance in determining the correlations between diversity and ecosystem properties. This indicates that ecosystem properties are mainly related to particular species traits of dominant species. Thus, the selection effect might be the dominant ecological mechanism during the wetland restoration process. Moreover, richness and divergence also had significant correlations with ecosystem processing in some instances, which indicates that complementarity effects do exist and may partly influence ecosystem properties. Our results suggest that dominant species and plant functional traits should be considered over species numbers when managing diversity and certain ecosystem functions in a wetland ecosystem, especially in the restoration case. We believe that the aspect of the four primary components of plant diversity provides insight into the relationship between diversity and ecosystem functions, and can serve as a reference for the management of ecosystem diversity and services, especially in the case of wetland conservation and restoration.

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