

Assembly processes of waterbird communities across subsidence wetlands in China: A functional and phylogenetic approach

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Abstract

Aim: Although assembly processes have been studied in a wide range of taxa, determining assembly rules remains controversial, particularly in assemblages consisted of species with strong dispersal capacities. Moreover, few studies focused on communities in recently human-created habitats. We tested two prevailing but opposing hypotheses, environmental filtering and limiting similarity, in waterbird communities across subsidence wetlands created by underground coal mining in China, with an aim to better understand assembly processes in communities composed of highly mobile species in human-dominated landscape.

Location: The North China Plain.

Methods: We quantified taxonomic, functional and phylogenetic diversity of the waterbird assemblages in different seasons and compared the mean pairwise distances (MPD) and the mean nearest taxon distances (MNTD) with null models to examine whether co-occurring species were clustered or overdispersed on the functional dendrogram or phylogenetic tree. Independent contributions of multi-scale habitat variables therein were determined using a hierarchical partitioning method.

Results: We showed asynchronous patterns of seasonal dynamics among the multiple diversity metrics, with highest species diversity during autumn migration. Generally, the co-occurring species were functionally and phylogenetically clustered. Habitat variables had stronger effects on the functional structure than on the phylogenetic structure of the communities. The degree of functional clustering increased in older and larger wetlands, while the assemblages shifted from functional clustering to overdispersion with increasing habitat diversity, landscape connectivity and human disturbance.

Main conclusions: The waterbird assemblages were mainly structured by environmental filtering, and the assembly processes were significantly affected by habitat variables, with stronger effects on functional diversity. Our study highlights the

importance of environmental filtering and habitat variables in structuring assemblages dominated by species with high dispersal capacities and suggests that increasing habitat diversity and reducing disturbances will contribute to waterbird conservation in this human-dominated landscape.

KEYWORDS

assembly process, environmental filtering, functional diversity, phylogenetic diversity, subsidence wetland, waterbird assemblage

1 | INTRODUCTION

How biotic communities are assembled from regional species pool is one of the basic questions in ecology (Cornwell & Ackerly, 2009). In spite of other possible assembly processes (Weiher et al., 2011), two prevailing but opposing mechanisms are environmental filtering (Cornwell, Schwillk, & Ackerly, 2006) and limiting similarity (Chesson, 2000; MacArthur & Levins, 1967). Environmental conditions may act as filters selecting species with similar traits to survive the same local environment, resulting in a larger ecological similarity and closer phylogenetic relatedness among coexisting species than would be expected by chance (i.e., functional or phylogenetic clustering; Mouchet, Villeger, Mason, & Moullot, 2010). Alternatively, niche theory highlights the importance of interspecific competition in assembly processes, and thus, species with similar ecological characteristics or phylogenetic relatedness are prevented to stably co-exist (i.e., functional or phylogenetic overdispersion; MacArthur & Levins, 1967; Mouchet et al., 2010).

In the progress of exploring assembly mechanisms in biotic communities, multifaceted metrics have been increasingly advocated to quantify assemblage structures, that is, functional (FD) and phylogenetic diversity (PD), in addition to traditional measures of biodiversity such as species richness (SR) and taxonomic diversity (TD; Gómez, Bravo, Brumfield, Tello, & Cadena, 2010; Mouchet et al., 2010; Tucker et al., 2017). When using SR and TD to measure biodiversity, species are considered equally distinct, providing little information about ecosystem functions and phylogenetic relatedness of the co-occurring species (Sodhi & Ehrlich, 2010; Tschamntke et al., 2012). However, FD and PD consider species-specific functional traits and evolutionary histories, respectively, and may therefore lead to a better understanding of mechanisms driving assembly processes. FD measures variability in species traits linked to ecosystem functions and thus should provide insights into how species coexist along gradients of environmental variables (Barbaro, Giffard, Charbonnier, van Halder, & Brockerhoff, 2014; Mouchet et al., 2010). PD measures evolutionary differences among species in a community (Srivastava, Cadotte, MacDonald, Marushia, & Mirotnick, 2012), bridging gaps between ecological processes with long-term evolutionary potential of species (Sandel, 2018). These metrics are complementary, quantifying multiple dimensions of biodiversity, and therefore facilitate a comprehensive understanding of assembly processes (Pavoine & Bonsall, 2011).

Although assembly processes have been studied in a wide range of taxa from bacteria to plants and animals, the topic is still controversial (Pavoine & Bonsall, 2011; Stevens, Cox, Strauss, & Willig, 2003; Zak, Willig, Moorhead, & Wildman, 1994). Most of the studied communities comprise relatively sedentary species with low dispersal capacities. However, few studies have focused on assemblages dominated by taxa with high dispersal capacities, such as migratory waterbirds, that may assemble differently from sedentary taxa (Mendez et al., 2012; Wiens, 1992). Waterbirds with various biological and ecological characteristics perform a wide array of ecosystem functions, such as nutrient cycling, ecosystem engineering, and dispersal of seed, pathogens and invertebrates (Green & Elmberg, 2014; Sekercioglu, 2006). They are also one of the most conspicuous taxa sensitive to wetland degradations and are often used as bioindicators of environmental changes (Green & Elmberg, 2014). Therefore, waterbirds are an ideal species group to explore assembly processes and assess effects of habitat changes on biotic communities. Moreover, in the context of global losses and degradations of natural wetlands (Butchart et al., 2010; Kar, 2013), waterbirds have been increasingly found to use artificial wetlands as complementary habitats, such as paddy fields, aquaculture ponds and water reservoirs (Elphick, 2015; Navedo et al., 2012; Petchey, Evans, Fishburn, & Gaston, 2007). An understanding of waterbird responses to environmental variables and assembly processes in human-dominated landscape can increase the success of management and conservation actions of waterbirds (Thompson & Starzomski, 2007; Tschamntke et al., 2012).

Subsidence wetlands created by large-scale underground mining are unintended man-made wetlands, overlooked by the conservation community, but they harbour a large variety of flora and fauna species (Lewin, Spyra, Krodziewska, & Strzelec, 2015; Nawrot, Kirk, & Elliott-Smith, 2003; Townsend et al., 2009). China is rich in coal resources, and the annual production is approximately 50% of the worldwide total (Dong, Samsonov, Yin, Yao, & Xu, 2015). The massive underground coal mining has resulted in extensive land subsidence, estimated to be 1×10^6 ha as of 2011, with an annual increase of 7×10^4 ha (Hu et al., 2014). Because of high groundwater levels and abundant rainfall, subsidence land has been flooded in the North China Plain, one of the most important coal production areas in China. The newly created artificial wetlands are still expanding and have been found to be used by a wide range of waterbird species, especially by long-distance migrants from the East Asian–Australasian

Flyway (Li, Zhao, & Wang, 2019). These artificial wetlands have clear boundaries and vary in spatial complexity, providing good chances to explore assembly processes of communities dominated by migratory species in a human-modified landscape.

In this study, we quantified taxonomic, functional and phylogenetic diversity of waterbird communities in subsidence wetlands in the North China Plain. We tested for a seasonal effect and for independent contributions of multi-scale habitat variables to variations in the multifaceted biodiversity metric data. Because the waterbird communities are dominated by migratory species that can rapidly respond to environmental changes (Li et al., 2019), we hypothesized that the assemblages should predominantly be structured by environmental filtering. We expected stronger effects of habitat variables on functional structures on which environmental filtering directly operates. We also expected a shift from functional or phylogenetic clustering to overdispersion in the assemblages with increasing habitat diversity, as heterogeneous habitats provide more

ecological niches to be partitioned. With these analyses, we contribute to a better understanding of assembly processes in biotic communities, exemplified by waterbird communities dominated by migratory species in these expanding man-made wetlands.

2 | METHODS

2.1 | Study area

The study was carried out in the Huainan–Huaibei coal mining area, which occupies an area of $\sim 1.5 \times 10^6$ ha in the North China Plain (Figure 1, $32^\circ 44' - 33^\circ 44'N$, $116^\circ 02' - 117^\circ 31'E$). The landscape is dominated by agricultural lands of flat and occasionally undulating topography. This region is one of the 14 largest coal bases in China, producing $\sim 4.1\%$ of the national output (Hu et al., 2014). The massive underground mining has created large-scale ground deformation and land subsidence. The total subsidence area was more than

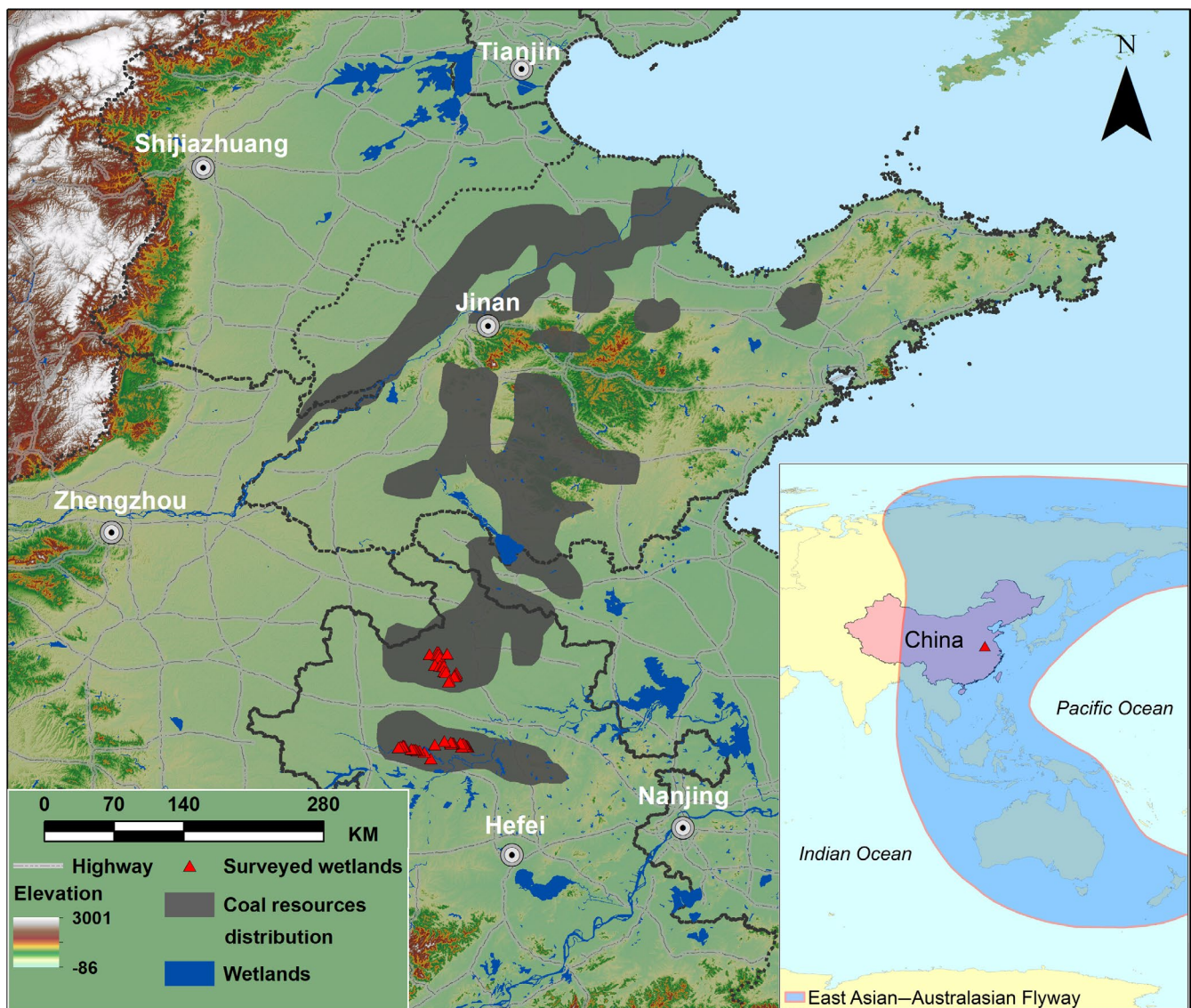


FIGURE 1 Subsidence wetlands surveyed for waterbirds in the Huainan–Huaibei coal mining area in China

30,000 ha in 2010, with an annual expansion of over 2,000 ha (Xie, Zhang, Yi, & Yan, 2013). Nearly half of the subsidence area has been flooded because of high groundwater levels and abundant rainfall, creating hundreds of independent wetlands of different sizes. These subsidence wetlands were created in different years, and many of them are still expanding due to the ongoing underground mining. They differ in a wide range of environmental attributes, which may influence biotic communities formed after waterlogging. These man-made wetlands are located within the East Asian–Australasian Flyway and have been found to harbour a wide array of migratory waterbird species (Li et al., 2019).

2.2 | Bird data

From September 2016 to July 2017, we carried out a total of 13 point-count waterbird surveys, each covering the same 55 subsidence wetlands. The total sampled area was 6,226 ha, accounting for ~40% of the subsidence wetlands in this region. These wetlands were selected randomly, representing a wide range of environmental conditions. Depending on the wetland area and accessibility, we placed 1–6 counting points along its boundary with unobstructed views of each wetland. We defined the areas within a radius of 1 km at each counting point as observation areas, and these areas were not overlapping to avoid double counting. The relatively small areas and clear boundaries of the wetlands guaranteed good detection of waterbirds, which is important when quantifying assemblage structures (Si et al., 2018).

Each field survey was completed within three clear and calm days, and the “look-see” total counting method (Delany, 2005) was employed by the same two experienced bird observers (CL & SY) to record waterbird species and abundance at each counting point. Waterbirds occurring within each observation area were identified to species level following Jetz, Thomas, Joy, Hartmann, and Mooers (2012), within 15 min, with the help of binoculars (10 × 42 WB Swarovski) and a telescope (20–60 × zoom ATM 80 Swarovski). We defined a waterbird species as a species that is “ecologically dependent upon wetlands” according to the Ramsar Convention (Gardner & Davidson, 2011). We only recorded waterbirds that used the sampled wetlands, ignoring those flying over. Species with less than

three records during all surveys were excluded from the following analyses.

According to the migration chronology of the waterbirds, we divided the field surveys into four periods: autumn migration (September–November 2016), wintering season (December 2016 to mid-February 2017), spring migration (late February–April 2017) and summer breeding season (May–August 2017). The season division allowed us to better understand the variations in the multiple diversity metrics under influence of assembly processes that vary among seasons. During each nonbreeding period, there were four surveys with breaks of minimally two weeks in between. These surveys were pooled in the analyses by summing the abundances of each species recorded in each wetland. We carried out only one survey in the summer breeding season (in July 2017). Therefore, we had four species × sites matrices, one in each period. Here, we considered a community as a pool of waterbird species co-occurring in a given wetland in each period.

2.3 | Habitat variables

We measured eight habitat variables at both local scale and landscape scale in each sampled wetland (Table 1). Wetland age (AG) was defined as the time (years) since waterlogging and was determined by comparing a time series of Landsat images (TM/ETM/OLI) acquired every 16 days from 1987 to 2016. Distance to human settlements (DH) was determined using high-resolution Google Earth maps. Area of each wetland (AW), area of open water (AO), area of aquatic vegetation (AA), habitat diversity (HD) and total area of wetlands (>1 ha) within a 5-km buffer area surrounding each wetland (TA) were calculated based on a land cover map interpreted from a Landsat OLI image, acquired on 2 September 2016. Detailed methods for the image interpretation can be found in Li et al. (2019). We used the inverse of Simpson's index as a proxy of HD:

$$HD = 1 / \sum_{i=1}^n p_i^2,$$

where p_i is the proportion of the wetland area occupied by the i th of n habitat types, that is, open water, aquatic vegetation and ground (Simpson, 1949). We also calculated Wetzel's (1975) shape index

TABLE 1 Habitat variables considered as potential predictors of waterbird diversity patterns in subsidence wetlands in the Huainan–Huaibei coal mining area in China

Variables	Description
AG (years)	Years since wetland creation
DH (km)	Shortest Euclidian distance from the boundary of each wetland to the nearest human settlement occupying an area >50 ha
AW (ha)	Area of each wetland
AO (ha)	Area of open water in each wetland
AA (ha)	Area of aquatic vegetation in each wetland
HD	Habitat diversity within each wetland
TA (ha)	Total area of wetland (>1 ha) within a 5-km buffer area surrounding each wetland
SW	Wetzel's (1975) shape index of wetlands. $SW = \text{Perimeter/circumference of a circle of equal area} : L / 2\sqrt{\pi \times A}$ (L: wetland perimeter, A: wetland area)

(SW) to quantify the irregularity of each wetland, as the amount of deviation from a perfect circle. There were no significant changes in habitat variables during field surveys, and thus, the same variables \times sites matrix was used in all analyses.

2.4 | Functional traits

Functional diversity may depend on arbitrary decisions on the selected traits, and there is no consensus on the selection of species characteristics to capture all functions of species. To facilitate meaningful comparisons among studies, the same suite of traits is suggested to be selected (Petchey & Gaston, 2006). We followed Petchey et al. (2007) and Jia, Wang, Zhang, Cao, and Fox (2018) to select four traits to measure the functional diversity of waterbird assemblages, comprising one continuous and three categorical attributes (Table 2). Body mass is correlated with species' required resource quantity and is a mean value for each species recorded in the literature. The categorical attributes, that is, main food type (vertebrates, invertebrates, plants), foraging method (pursuit, gleaning, pouncing, grazing, digging, scavenging, probing) and substrates (water, mud, vegetation), were treated as binary traits (0 or 1). Because a species may adopt more than one of them while feeding, these categorical traits are not mutually exclusive. Trait data were obtained from del Hoyo, Elliott, and Christie (2004–2011), del Hoyo, Elliott, and Sargatal (1992–2002) and the BTO database (<http://www.bto.org/aboutbirds/birdfacts>).

2.5 | Biodiversity metrics

For each wetland during each period, we defined species richness (SR) as the total number of species and calculated biodiversity

metrics, in the R packages *ape* and *picante* (Kembel et al., 2010; Paradis & Schliep, 2018), representing the divergence dimension for taxonomic (TD), functional (FD) and phylogenetic diversity (PD). TD was quantified using the Simpson index (Simpson, 1949) under the mathematical framework of Rao's quadratic entropy (Rao, 1982), which is defined as.

$$Q = \sum_{i=1}^S \sum_{j=1}^S p_i p_j d_{ij} \quad (1)$$

where d_{ij} is the distance between species i and j in a community containing a total of S species. The distances were weighted by the relative abundances of each species (p_i and p_j). The Rao index recognizes unequal differences between pairwise species by including d_{ij} which can be functional or phylogenetic distances. Rao's Q will reduce to Simpson diversity index when $d_{ij} = 1$ for all $i \neq j$, indicating that all species in the community are equally different (Botta-Dukat, 2005).

For FD, we first calculated functional dissimilarity between all pairs of species using the Gower metric, which is preferred when both categorical and continuous traits are used (Botta-Dukat, 2005), and then generated a dendrogram using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA; Swenson, 2014). For PD, we collected 2,000 phylogenetic trees covering all waterbird species in our study from BirdTree (<http://birdtree.org>), using the "Hackett" backbone (Hackett et al., 2008; Jetz et al., 2012), and summarized these trees to generate a 50% majority rule consensus tree using SumTrees (Sukumaran & Holder, 2010). Based on the functional dendrogram and phylogenetic tree, respectively, we calculated two metrics that were weighted by relative abundance: the mean pairwise distance (MPD) and the mean nearest taxon distance (MNTD) for both FD (hereafter functional MPD and MNTD) and PD (hereafter phylogenetic MPD and MNTD). MPD is calculated by averaging all

TABLE 2 Traits used to measure functional diversity associated with resource use, adapted from Petchey et al. (2007)

Trait types	Traits	Value type	Phylogenetic signal	p_{Brownian}	p_{random}
Resource quantity	Body mass	Continuous	$\lambda = 0.996$		<0.001
Main food type	Vertebrates	Binary	$D = -0.39$ ($N = 18$)	0.846	<0.001
	Invertebrates	Binary	$D = -0.27$ ($N = 23$)	0.772	<0.001
	Plants	Binary	$D = -0.32$ ($N = 17$)	0.799	<0.001
Main foraging method(s)	Pursuit	Binary	$D = -0.09$ ($N = 6$)	0.567	0.007
	Gleaning	Binary	$D = 0.02$ ($N = 28$)	0.454	<0.001
	Pouncing	Binary	$D = -1.05$ ($N = 12$)	0.991	<0.001
	Grazing	Binary	$D = -0.18$ ($N = 14$)	0.692	<0.001
	Digging	Binary	$D = 0.75$ ($N = 6$)	0.084	0.197
	Scavenging	Binary	$D = -2.43$ ($N = 2$)	0.906	0.002
	Probing	Binary	$D = 0.44$ ($N = 7$)	0.192	0.038
Main foraging substrate(s)	Water	Binary	$D = -0.48$ ($N = 35$)	0.875	<0.001
	Mud	Binary	$D = -0.14$ ($N = 19$)	0.671	<0.001
	Vegetation	Binary	$D = 1.04$ ($N = 9$)	0.007	0.522

Notes. Phylogenetic signals (D for binary traits and λ for body mass) were shown for functional attributes of the 51 waterbird species in the Huainan–Huaibei coal mining area in China. The N values in parentheses equal to the number of species exhibiting the given attributes. Both probabilities of $E(D)$ resulting from Brownian (p_{Brownian}) and random (p_{random}) phylogenetic structures were reported, and significant phylogenetic signals are in boldface.

pairwise functional or phylogenetic distances (branch lengths on the functional or phylogenetic dendrogram) among co-occurring species, representing an overall divergence of the community. MNTD quantifies the mean functional or phylogenetic distance between nearest neighbours, and it can describe the degree of terminal clustering among co-occurring species (Webb, 2000).

To examine whether co-occurring species in communities were clustered or overdispersed on the functional dendrogram or phylogenetic tree, we compared the observed MPD and MNTD in each wetland during each period with the corresponding mean value generated by null models by shuffling the tip labels of the trees (Swenson, 2014). In this process, 999 communities with species richness and occurrence frequencies equal to the observed communities were randomly generated using an independent swap algorithm, and metrics were calculated and averaged (Gotelli & Entsminger, 2001). The species pool used in the simulation process was defined as all species recorded during the given period. Standardized effect sizes were calculated for both MPD and MNTD as

$$\text{Standardized effect size} = (M_{\text{null}} - M_{\text{obs}}) / SD_{\text{null}} \quad (2)$$

where M_{obs} is the observed value of MPD and MNTD, M_{null} is the metric corresponding mean value of the 999 randomly simulated communities, and SD_{null} is the standard deviation of the simulated values. Standardized MPD and MNTD, also termed as nearest relative index (NRI) and nearest taxon index (NTI), respectively, quantify overall and terminal clustering of taxa on a tree. Both NRI and NTI indicate functional or phylogenetic clustering when >0 , while overdispersion generates values lower than 0 (Gómez et al., 2010; Webb, Ackerly, McPeck, & Donoghue, 2002).

2.6 | Phylogenetic signal

The use of PD to estimate ecosystem functioning of species depends highly on the strength of phylogenetic signals in functional traits (Srivastava et al., 2012). Phylogenetic signals measure the statistical dependence among species' traits associated with their phylogenetic relatedness, and significant phylogenetic signals indicate higher similarity than expected by chance among closely related species (Revell, Harmon, & Collar, 2008). We used the statistic D (Fritz & Purvis, 2010) to measure phylogenetic signals in categorical traits, with lower D values indicating a more conserved trait evolution (i.e., stronger phylogenetic signal). If D approaches 0, the trait is distributed as expected under the Brownian motion model of evolution (i.e., conserved trait evolution), and $D < 0$ suggests a highly clustered trait. A value of $D = 1$ or > 1 indicates that the trait is randomly distributed (i.e., no signal) or overdispersed on the phylogenetic tree.

We used the Pagel's λ (Freckleton, Harvey, & Pagel, 2002; Pagel, 1999) to measure phylogenetic signal in body mass, a continuous trait. A value of $\lambda = 0$ indicates no correlation between evolution in body mass and phylogeny. If body mass evolves according to Brownian motion along a phylogeny, λ will be equal to 1. A value of λ between 0 and 1 indicates that body mass has evolved according to a process in which the effect of phylogeny is weaker than in the

Brownian model (Pagel, 1999). The package *caper* was used to calculate and test the significances of the phylogenetic signals (Orme et al., 2018).

2.7 | Statistical analyses

The package *nlme* was used to perform repeated-measures ANOVA to test for seasonal differences in SR, TD, MPD and MNTD (Pinheiro, Bates, DebRoy, & Sarkar, 2018). Post hoc Tukey's test with a Bonferroni correction was used to compare metrics among the four periods. We used one-sample t test to determine whether NRI and NTI were significantly different from 0, which would be expected by chance. We employed a hierarchical partitioning method (Chevan & Sutherland, 1991; Mac Nally, 2002) to quantify independent contributions of habitat variables towards variations in NRI and NTI. In hierarchical partitioning, models containing all possible combinations of explanatory factors were considered in a hierarchy and goodness of fit (R^2) was calculated for each model. A randomization procedure with 1,000 iterations was performed to test the significance of the effect of each variable. The package *hier.part* was used to perform the hierarchical partitioning (Mac Nally, 2002; Nally & Walsh, 2004); all analyses were carried out in R 3.3.4.

3 | RESULTS

During the 13 field surveys, we recorded a total of 62 waterbird species across all sampled wetlands. After discarding species with less than three records, we obtained 51 species (i.e., 48 species in autumn, 44 in winter, 47 in spring and 18 in summer) which were used in the following analyses. **Phylogenetic signals were significantly related to body mass and most categorical traits, indicating strong phylogenetic niche conservatism (Table 2).**

Species richness (SR) was on average highest in autumn and lowest in summer with no difference between winter and spring ($F_{3,150} = 55.67, p < 0.001$). Taxonomic diversity (TD) was on average higher in autumn but no differences were found among other periods ($F_{3,150} = 6.00, p < 0.001$). Phylogenetic MPD was on average highest in autumn and lowest in summer, but there were no significant differences between autumn and spring, between winter and spring, and between winter and summer ($F_{3,150} = 8.94, p < 0.001$). Phylogenetic MNTD was highest in summer with no differences among other periods ($F_{3,150} = 17.30, p < 0.001$). Functional MPD was highest in autumn and spring, and lowest in summer ($F_{3,150} = 14.77, p < 0.001$), while functional MNTD was higher in winter and spring than those in autumn and summer ($F_{3,150} = 8.69, p < 0.001$; Figure 2).

Phylogenetic NRI was greater than 0 during all four periods. Phylogenetic NTI was greater than 0 in winter and spring, but not different from 0 during the other two periods. Functional NRI was not different from 0 in spring, but greater than 0 during the other periods. Functional NTI was greater than 0 in summer, but not different from 0 during the other three periods (Figure 3).

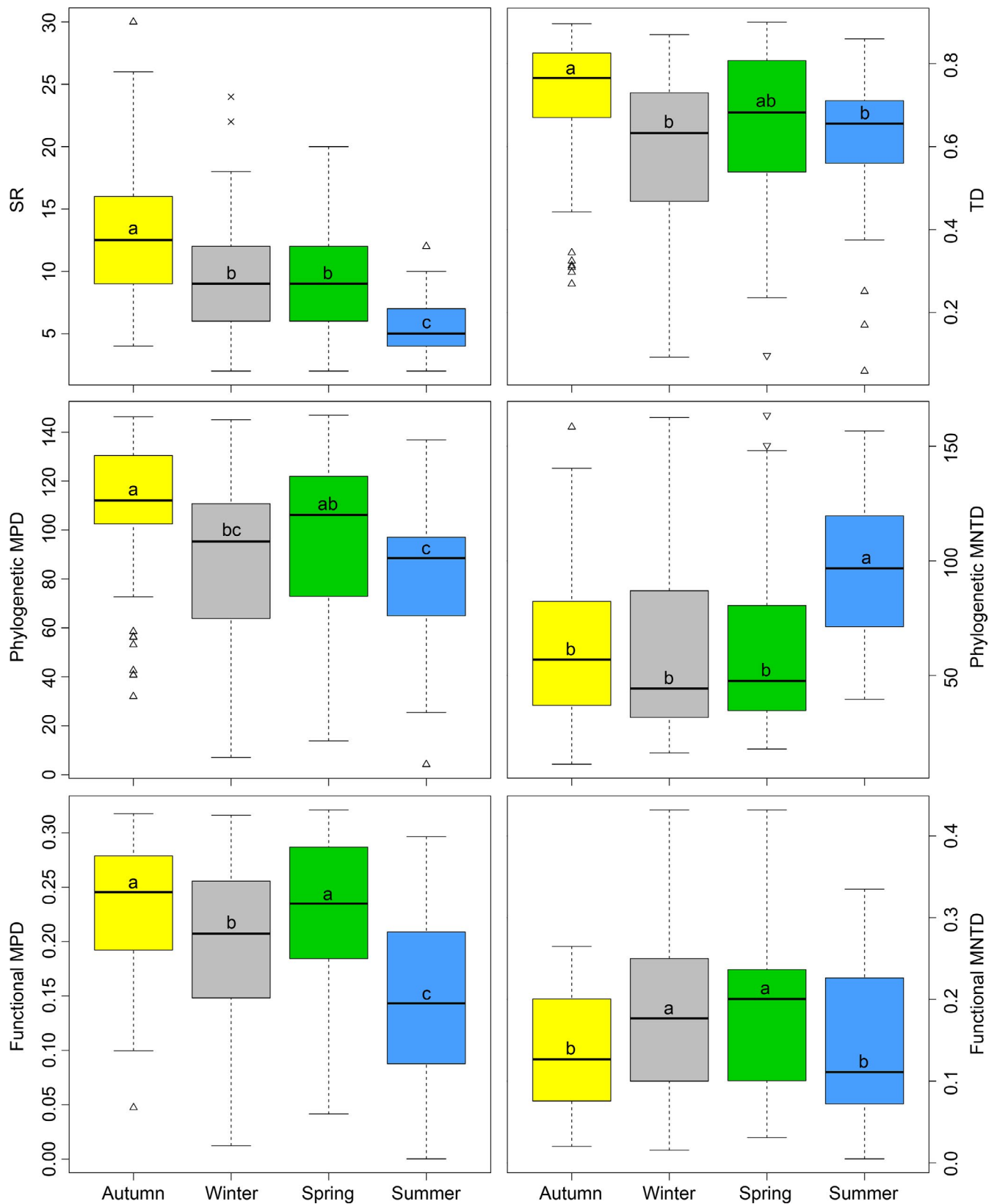
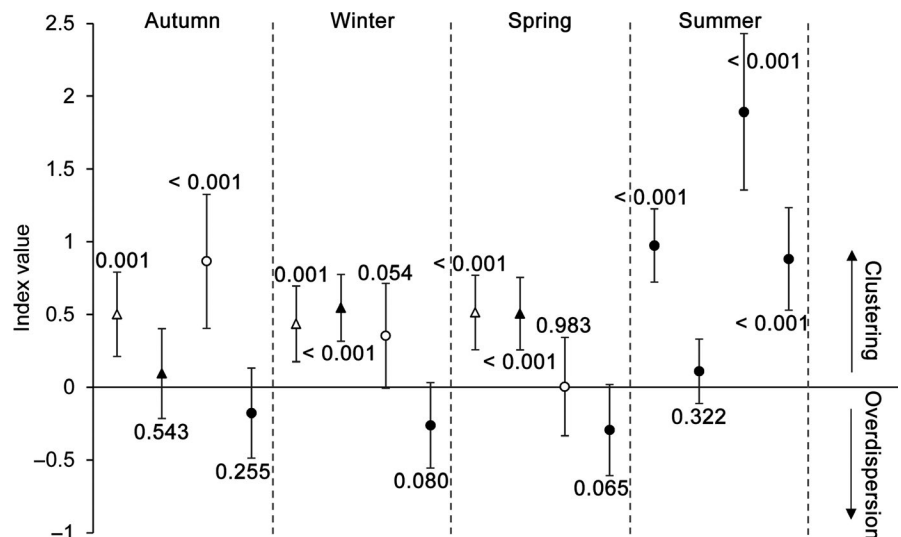


FIGURE 2 Seasonal differences in multiple biodiversity metrics of waterbird communities in subsidence wetlands in the Huainan-Huaibei coal mining area in China. Boxplots with the same letter indicate no significant difference as determined by post hoc Tukey's tests after the repeated-measures ANOVA. MPD: the mean pairwise distance; MNTD: the mean nearest taxon distance; SR: species richness; TD: taxonomic diversity

FIGURE 3 Standardized effect sizes of functional and phylogenetic diversity and their 95% confidence intervals (along with p -values of one-sample t tests) of waterbird communities in subsidence wetlands in the Huainan–Huaibei coal mining area in China. Open triangle: phylogenetically nearest relative index (phylogenetic NRI); filled triangle: phylogenetically nearest taxon index (phylogenetic NTI); open circle: functionally nearest relative index (functional NRI); filled circle: functionally nearest taxon index (functional NTI)



The proportions of variation explained by the variables with significant effects ranged from 10.4% to 53.4%. The selected habitat variables had stronger effects on the standardized effect sizes of functional diversity than on those of phylogenetic diversity (Table 3). We only found a negative effect of habitat diversity (HD) on phylogenetic NRI in autumn, and a negative effect of wetland age (AG) on phylogenetic NTI in winter. Wetland age (AG) was a positive predictor for functional NRI and NTI in all periods. Functional NTI in

winter was also positively affected by wetland area (AW), area of open water (AO) and distance to human settlements (DH), but negatively with area of aquatic vegetation (AA) in summer. As habitat diversity (HD) increased, functional NRI and NTI decreased in all periods except in winter. Total area of wetlands within a 5-km buffer area (TA) was a negative predictor for functional NRI in winter, but a positive predictor for functional NTI in summer. There was no effect of wetland shape (SW) on any biodiversity metrics.

TABLE 3 The independent contribution (%) of each habitat variable to variations of the multifaceted diversity metrics of waterbird communities in subsidence wetlands in the Huainan–Huaibei coal mining area in China

Period	Diversity metrics	R^2	AG	DH	AW	AO	AA	HD	TA	SW
Autumn	Phylogenetic NRI	0.132	6.13	1.39	−6.57	6.79	6.15	−61.56	2.62	−8.79
	Phylogenetic NTI	/	−11.76	−29.45	−13.59	−12.76	−6.03	2.78	−4.82	18.81
	Functional NRI	0.245	14.55	3.13	11.53	14.80	−7.40	−39.58	3.87	−5.15
	Functional NTI	0.310	21.96	5.92	10.32	13.23	−8.41	−27.71	10.19	−2.24
Winter	Phylogenetic NRI	/	19.08	−4.79	2.73	3.19	1.15	−3.48	−25.61	−39.97
	Phylogenetic NTI	0.112	−58.55	−0.81	−2.83	−3.06	4.01	10.38	−13.49	6.87
	Functional NRI	0.104	22.11	11.26	9.25	11.72	−7.09	−5.42	−30.65	−2.52
	Functional NTI	0.482	29.61	20.14	11.82	14.49	−8.68	−7.43	2.77	−5.07
Spring	Phylogenetic NRI	/	40.22	−2.16	9.92	10.34	8.30	−10.68	3.65	−14.73
	Phylogenetic NTI	/	−17.19	−9.83	5.32	4.14	6.81	10.09	0.88	45.75
	Functional NRI	0.117	35.23	11.47	11.77	12.95	1.38	−16.70	9.01	1.48
	Functional NTI	0.169	12.92	16.69	12.59	14.78	1.40	−19.01	11.69	−10.92
Summer	Phylogenetic NRI	/	−6.41	−6.59	17.96	15.48	42.27	−5.34	0.76	−5.19
	Phylogenetic NTI	/	−15.88	2.05	−14.41	−17.24	4.71	−4.12	40.66	−0.92
	Functional NRI	0.263	9.60	2.04	9.07	10.26	−6.08	−46.80	10.74	−5.42
	Functional NTI	0.534	1.21	2.58	7.03	8.20	−14.63	−39.56	25.28	−1.50

Notes. Negative correlations are indicated by a minus sign, and significant relationships ($p < 0.05$) are in boldface.

AG: wetland age; DH: shortest Euclidian distance from the boundary of each wetland to the nearest human settlement occupying an area >50 ha; AW: area of each wetland; AO: area of open water in each wetland; AA: area of aquatic vegetation in each wetland; HD: habitat diversity within each wetland; TA: total area of wetlands (>1 ha) within a 5-km buffer area surrounding each wetland; SW: Wetzel's (1975) shape index. NRI: nearest relative index; NTI: nearest taxon index.

4 | DISCUSSION

We found that species diversity of waterbird communities in subsidence wetlands was on average highest during the autumn migration period (Figure 2). In the context of natural wetland loss along the East Asian–Australasian Flyway (Kirby et al., 2008), the newly created subsidence wetlands provide important complementary staging habitats for the migratory waterbirds, particularly during their southward migrations when there are more birds due to the post-breeding population increase (Li et al., 2019). Seasonal patterns of functional and phylogenetic diversity measured by MPD were similar to SR and TD, indicating that overall functional and phylogenetic divergence of the communities increased with species enrichment in autumn. However, functional and phylogenetic MNTD were rather low in autumn, and were quite different from the other metrics, providing evidence of clustering along the functional or phylogenetic dendrogram for the co-occurring species in our sampled wetlands. MPD and MNTD are two divergence metrics of biodiversity, measuring the overall divergence and terminal clustering, respectively, and may differently respond to species enrichment (Webb, 2000). The asynchrony of different biodiversity facets found in our study and in previous studies (Che et al., 2018; Monnet et al., 2014) justifies measurement of both MPD and MNTD when quantifying divergence in species assemblages.

The positive values of NRI and NTI indicated that these waterbird communities were composed of species with similar functional traits and close phylogenetic relatedness, suggesting the predominant importance of environmental filtering in the assembly processes (Figure 3). Under this hypothesis, habitat variables act like filters to allow species with similar ecological traits to coexist, resulting in phylogenetic clustering with high niche conservatism (Webb et al., 2002). Our results contrasted with the expectation of the limiting similarity hypothesis that interspecific competition prevents coexistence of species with similar ecological niches or close relatedness (Chesson, 2000; MacArthur & Levins, 1967). Because of high dispersal capacities and rapid responses to environmental changes, waterbird communities should also be less likely determined by stochastic process or “priority effect,” whereby pioneer species largely influence the community development (Fukami, 2015; Lok, Overdijk, & Piersma, 2013). The relative importance of environmental filtering and limiting similarity in assembly processes is hypothesized to be scale-dependent, exemplified by shifts from functional or phylogenetic clustering to evenness in some mammal and plant assemblages with decreasing geographical scales (Bryant et al., 2008; Cardillo, Gittleman, & Purvis, 2008; Cavender-Bares, Kozak, Fine, & Kembel, 2009). Contrary to this hypothesis, we found functional and phylogenetic clustering at local scales, like those found in Neotropical forest birds (Gómez et al., 2010). This may be attributed to the fact that the many waterbird species largely rely on wetlands, resulting in strong waterbird-habitat associations (Cao & Fox, 2009), and the effect of environmental filtering may therefore be stronger than interspecific interactions, even at local scales. Besides, migration phenology differs among species and their temporary interactions are not stable in a given wetland compared to those among resident

taxa, particularly during migration periods, making limiting similarity less important in assembly processes (Kirby et al., 2008).

The assembly processes of these waterbird communities were mediated by habitat variables with different effects among seasons (Table 3). In general, the effects were stronger on the standardized effect sizes of functional metrics than on those of phylogenetic dimensions, suggesting that environment filtering on phenotypic traits were more prominent. Unlike the regional species pool, which is determined by broadscale and long-term colonization–extinction processes (Emerson & Gillespie, 2008; Ricklefs, 2006), species present in local communities vary in space and time, and select habitats in response to local ecological conditions. It is more prominent in assemblages dominated by migratory waterbirds, due to their large dispersal capacities and rapid responses to habitat changes. The environmental effects were also stronger on functional NTI than on functional NRI. Ecological processes may have very different effects on functional divergence depending on how they are measured. In contrast to functional NRI capturing the overall dissimilarity of the taxa, functional NTI is more sensitive to the distribution of lineages close to the tips of trees (Swenson, 2014). Therefore, NRI might be more influenced by factors that operated in the distant past, while NTI patterns are likely to reflect more recent changes (Che et al., 2018). This pattern provides further evidence for the importance of environmental filtering over a variety of temporal scales in assembly processes of assemblages comprised of mobile species.

As habitat diversity (HD) increased, functional NRI and NTI both decreased, indicating a shift from functional clustering to overdispersion in the waterbird communities. Under environmental filtering, more heterogeneous habitats may provide more diverse filters to allow species with various ecological requirements to coexist in these relatively independent habitats (Bradford & Kastendick, 2010; Mouchet et al., 2010). Overdispersion in functional space may facilitate the stability of biodiversity under environmental changes, maintaining phylogenetic diversity, given the high phylogenetic trait conservatism in case of local species losses (Arroyo-Rodríguez et al., 2012; Cavender-Bares, Ackerly, Baum, & Bazzaz, 2004). However, habitat diversity was relatively low in these subsidence wetlands, simplifying the phenotypic structure of the waterbird assemblages. This demands further investigation, because it may indicate limited ecosystem functioning and high vulnerability of the waterbird communities to the human-dominated environment. The role of habitat diversity in assembly processes can also explain why waterbird communities were more likely to be functionally clustered in larger and older wetlands with larger area of open water. Because underground coal mining is still ongoing, many subsidence wetlands are continuously expanding with wetland age (Xie et al., 2013). The regressive succession of aquatic vegetation and the increasing predominance of open water due to human modification for aquaculture result in relatively homogeneous habitats for waterbirds (Li et al., 2019), providing limited opportunities for resource partitioning. Similar to heterogeneous habitats, wetlands with better landscape connectivity can attract more waterbird species (Che et al., 2018), resulting in functional overdispersion, particularly in winter. However, waterbirds may rely

more on local environment during the breeding season when communities were functionally clustered (Wiens, 1992). Furthermore, the waterbird communities were more likely to be functionally clustered in wetlands far away from human settlements, indicating increased functional redundancy under lower disturbance levels. On the contrary, lower functional redundancy in more disturbed environments, such as reported in other empirical studies (Laliberté et al., 2010; Luck, Carter, & Smallbone, 2013), may increase vulnerability of communities to future disturbances (Naeem, 1998).

In conclusion, we found functional and phylogenetic clustering in waterbird communities in subsidence wetlands in the Huainan–Huaibei coal mining area, indicating the importance of environmental filtering in structuring assemblages dominated by species with high dispersal capacities. Habitat variables played important roles in the assembly processes, with stronger effects on functional diversity, which is more likely determined by ecological processes. The patterns in multiple biodiversity metrics were not synchronous, reflected by different responses to habitat variables and seasons. The assemblages somewhat shifted from functional clustering to overdispersion with increasing habitat diversity, which underlines the importance of environmental heterogeneity in maintaining functional and phylogenetic diversity. The subsidence wetlands provide complementary habitats for waterbirds migrating along the East Asian–Australasian Flyway; however, these waterbirds are facing a variety of threats that should be further studied (Li et al., 2019). In order to better manage and protect waterbirds in these man-made wetlands, we suggested (a) increasing habitat diversity and improving landscape connectivity within the wetland network, (b) reducing human disturbances and (c) systematically monitoring these waterbird communities along with the expansion of subsidence wetlands, with more emphasis on their early stages.

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DATA ACCESSIBILITY

All the raw data are accessible through the School of Resources and Environmental Engineering, Anhui University (contact: Chunlin Li; lichunlin1985@163.com).

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