

# Prioritizing landscapes for mitigating the impacts of onshore wind farms on multidimensional waterbird diversity in the Yellow Sea

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Handling editors: Zhi-Yun Jia and Zu-Shi Huang

## Abstract

Ongoing wind energy developments play a key role in mitigating the global effects of climate change and the energy crisis; however, they have complex ecological consequences for many flying animals. The Yellow Sea coast is considered as an ecological bottleneck for migratory waterbirds along the East Asian–Australasian flyway (EAAF), and is also an important wind farm base in China. However, the effects of large-scale onshore wind farms along the EAAF on multidimensional waterbird diversity, and how to mitigate these effects, remain unclear. Here we examined how wind farms and their surrounding landscapes affected multidimensional waterbird diversity along the Yellow Sea coast. Taxonomic, functional, and phylogenetic diversity of the waterbird assemblages, and mean pairwise distances and nearest taxon distances with null models were quantified in relation to 4 different wind turbine densities. We also measured 6 landscape variables. Multi-dimensional waterbird diversity (taxonomic, functional, and phylogenetic diversity) significantly decreased with increasing wind turbine density. Functional and phylogenetic structures tended to be clustered in waterbird communities, and environmental filtering drove waterbird community assemblages. Furthermore, waterbird diversity was regulated by a combination of wind turbine density and landscape variables, with edge density of aquaculture ponds, in addition to wind turbine density, having the greatest independent contribution to waterbird diversity. These results suggest that attempts to mitigate the impact of wind farms on waterbird diversity could involve the landscape transformation of wind farm regions, for example, by including high-edge-density aquaculture ponds (i.e., industrial ponds) around wind farms, instead of traditional low-edge-density aquaculture ponds.

**Key words:** East China coast, environmental filtering, mitigation measure, renewable energy, sustainable development, waterbird conservation.

The effects of wind farms on birds have received increasing attention from ecologists and conservation biologists worldwide (Thaker et al. 2018). These effects vary among different landscape structures and functional groups (Thaxter et al. 2017), and include both direct and indirect effects (Song et al. 2021; Xu et al. 2021). Direct effects include bird mortality caused by collisions with wind turbines and associated infrastructure (Janss 2000; Singh et al. 2015), whereas indirect impacts involve the spatial displacement of birds (Kelsey et al. 2018; Zhao et al. 2020). A case study showed that wind farms have caused fatalities in 12 bird species in the Yangtze River Delta (Zhang et al. 2022). These direct and indirect impacts will eventually affect the richness and abundance of birds (Gómez-Catasús et al. 2018), and have a cumulative impact on the diversity of species at both local and global scales (Masden et al. 2010). Creating a balance between wind farm

development and bird conservation, and mitigating the influences of wind farms on birds, are thus hot research topics.

Wind farm developments and planning mainly focus on wind resource distribution, energy demands, and land ownership (Li et al. 2020; Zhao et al. 2020), and thus tend to include regions with higher wind resources and land that can be obtained at lower cost. Local governments also encourage wind farm developments by providing subsidies and promoting renewable energy development in China. However, little attention has been paid to the landscape configuration of the candidate areas, and wind farms are always constructed in the boundary of the natural habitats, which are untested along the Yellow Sea coast (Li et al. 2020). Several studies have shown that 69% of waterbird species in China have been recorded at aquafarms (aquaculture ponds) (Cheng et al. 2022), whereas the upper tidal flats can support > 70% of

Received 9 October 2023; accepted 27 February 2024

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the foraging time of shorebirds (Mu and Wilcove 2020). It is therefore important to identify the key landscape elements related to the diversity of the target groups.

Current studies mainly focused on the effects of upland wind farms on raptors (Garvin et al. 2011), songbirds (Zwart et al. 2016), and waders (Veltheim et al. 2019), flatland wind farms on terrestrial birds (Winder et al. 2014), and offshore wind farms on seabirds (Warwick-Evans et al. 2018), however, few studies have examined the importance of onshore wind farms on waterbirds in coastal regions. Due to lower mortality rates among waterbird groups compared with raptors (Desholm 2009; Wang et al. 2015), the method based on traditional fatality seeking may underestimate the effects of onshore wind farms on waterbirds. In addition, tracking-based methods (satellite tracking, radio telemetry, and bluetooth telemetry) are limited to exploring single species in response to wind farms, whereas species identification is difficult using radar-based monitoring methods. Although some studies have examined the impacts of wind farms on the abundance of a single species or the total abundance of bird communities (Gómez-Catasús et al. 2018; Fernández-Bellon et al. 2019), studies on the contributions of the associated landscapes to the assembly of waterbird communities around onshore wind farms are lacking. This information could help to explain the mechanism responsible for maintaining the coexistence and diversity of different functional species under the long-term influence of wind farms.

Two main but opposing mechanisms affect bird assembly processes: environmental filtering and limiting similarity (Ding et al. 2013). Environmental conditions, landscape structure, vegetation status, and human activity, including wind farms, may act as environmental filters in community assemblages, by filtering species with similar characteristics in the local environment, leading to greater ecological similarity and closer phylogenetic relatedness among coexisting species than would be expected by chance (i.e., functional or phylogenetic clustering; Li et al. 2019). Alternatively, niche theory highlights the importance of interspecific competition in assembly processes, in which species with similar ecological characteristics or phylogenetic relatedness are prevented from stably coexisting (i.e., functional or phylogenetic overdispersion; MacArthur and Levins 1967). Functional diversity represents differences in traits and physiological characteristics associated with resource use and also reflects the adaptability of communities to environmental changes and pressure. Several studies have demonstrated significant differences in the susceptibilities of different bird species to wind turbines (Bright et al. 2009; Herreraalsina et al. 2013; Roemer et al. 2017), and wind farms could also act as barriers to disturb bird movements (Masden et al. 2009); however, waterbird assembly processes around the wind farm and the function of wind turbine in waterbird community assembly remain unclear.

The East Asian–Australasian flyway (EAAF) supports 19% of the world's threatened waterbird populations (Bamford et al. 2008), and is one of the busiest of the 9 global migratory waterbird flyways (Yang et al. 2020). The Yellow Sea region provides a crucial stopover and/or wintering site and a migration bottleneck for many shorebirds along the EAAF (MacKinnon et al. 2012; Studds et al. 2017). More than 50 million individuals of 490 species of migratory birds migrate along the EAAF annually. These waterbirds are

highly dependent on the inter-tidal wetland landscape outside the dykes and the artificial landscape inside the dykes (Zhao et al. 2020), and move between the areas inside and outside the dykes during migration and overwintering (Li et al. 2020). Meanwhile, the Yellow Sea coast is a crucial region for Chinese wind farm developments, due to its abundant wind resources and China's high energy demands, making it one of 7 gigawatt wind farm bases in China (Li et al. 2020). Numerous wind turbines are arranged at different density gradients along the dykes of the Yellow Sea coast. The Jiangsu coast of Yellow Sea is one of the gigawatt wind farm bases in China, with a total installed capacity of wind turbines >11.80 GW in 2021 (<http://www.cnenergynews.cn>). The landscape structure around the wind farms is complex, including aquaculture ponds, farmland, and inter-tidal zones, and the Yellow Sea coast is an ideal research platform for studying wind farm developments and waterbird conservation.

In this study, we used the Yellow Sea coast as study area to develop an approach to balance onshore wind farm developments and waterbird conservation at a landscape scale, including determining the community assemblages in relation to wind turbine density, and the identification of key landscape characteristics that might benefit waterbird diversity. We aimed to identify differences in the functional and phylogenetic structures of waterbird communities in relation to four categories of wind turbine density gradients. We also aimed to quantify the different landscape structures around each transect along the 4 wind turbine density gradients and explore the relationships among wind turbine density, landscape structure, and waterbird community structure. We hypothesized that there would be significant differences in multidimensional diversity (including taxonomic, functional, and phylogenetic diversity) among the 4 wind turbine density gradients, with the highest multidimensional diversity in regions with the lowest wind turbine density, due to the strong susceptibility of bird species to wind turbines (Bright et al. 2009; Herreraalsina et al. 2013; Roemer et al. 2017). We also hypothesized that waterbird communities would be shaped by wind farm development density-associated landscape characteristics, given that wind farms may affect waterbirds' selection of landscapes differently, depending on their functional traits and phylogenetic structure (Furness et al. 2013; Thaxter et al. 2017).

## Materials and Methods

### Study area and survey transect

We explored the effects of the landscapes associated with wind farms on multidimensional waterbird diversity in 4 categories of wind turbine density in China, using the following selection criteria for the study area: 1) region contains different multiple rows of wind turbines; 2) region contains stopover and/or overwintering site for waterbirds; and 3) region accessible for waterbird surveys, enabling field collection of waterbird community data. The Yellow Sea coast met the above 3 criteria and was thus chosen as the study region to assess the assembly process of waterbird communities around wind farms.

China's coast along the EAAF has a high capacity for wind farms (Resdm 2023), and the high levels of economic development, electricity demand, and population density mean that many wind farms have been constructed and are planned

along the Yellow Sea coast. Wind turbines along this coast are arranged in single or multiple rows, with an average of 3 rows. The installed capacity of a single wind turbine was 1.5–2.5 MW. The coast of the Yangtze River Delta includes a unique and typical pelitic beach along the Yellow Sea coast, as a result of sediment accumulation and deposition from the Yangtze and Old Yellow Rivers, as well as other small rivers (Zhao et al. 2023), leading to diverse biological resources (Tian et al. 2016).

The study area extended from the Guanhe estuary in Jiangsu Province in the north to the Yangtze River estuary in Shanghai in the south (119° 53' 40.64" to 121° 59' 2.98", 31° 30' 31.61" to 34° 25' 6.66") (Figure 1). The main habitat types in the study area were intertidal tidal flats, estuary areas, aquaculture ponds, farmland, and forest (Chen et al. 2016). Aquaculture ponds, farmland, and forest were mainly located inside the dykes, and intertidal tidal flats were located outside the dykes. Wind farms were distributed on the dykes and/or aquaculture ponds, farmland, and intertidal flats.

We first determined the accurate locations of the wind turbines by a combination of field surveys and landscape identification. We then selected 53 1-km transects according to the arrangement and scale of the wind turbines (Tan et al. 2021). The centers of the survey transects were  $\geq 4,000$  m apart, to reduce spatial autocorrelation (mean neighbor distance  $\pm$  standard error =  $8.322 \pm 2.070$  km; range = 4.281–81.143 km) (Song et al. 2021; Liu et al. 2024). We defined the wind turbine density of the transect according to the number of wind turbines within 3 km of the geometric center radius of the transect. We defined 4 wind turbine densities: control (no wind turbines,  $N = 7$ ), low density (1–15 turbines,  $N = 19$ ), medium density (16–30 turbines,  $N = 12$ ), and high density ( $>30$  turbines,  $N = 15$ ) (Supplementary Table S1). A total of 1,092 turbines were included in the study.

### Bird surveys

We carried out waterbird community surveys during high tide for a total of 138 days over 2 winter periods (December 2019 to February 2020; December 2020 to March 2021). We surveyed during the winter for several reasons. First, the waterbird communities are most diverse in winter, allowing better analysis of the different community compositions and distribution in response to coastal wind farm developments (Fan et al. 2020). Second, the spatial and temporal distributions of waterbird communities are relatively stable throughout the winter compared with the spring and autumn migratory periods, and third, the findings regarding wintering waterbird communities could be extrapolated to the spring and autumn migratory periods. The period from November to after February is considered to be relatively stable in terms of waterbird occurrence because waterbirds wintering on the East China coast reach peak numbers during this period (Zhao et al. 2020). Because the distribution and number of waterbirds might be influenced by the tidal cycle (Kuang et al. 2019), we started waterbird counts within 1 h before high tide to record all the waterbird species present. Counts were only performed on days without strong wind or heavy fog. Birds were identified and counted using binoculars (8 × 42, Kowa SV42-8) and a spotting scope (20–60×, Kowa TSN 773). Each transect was repeated 6 times and each survey lasted for 62 ( $\pm 1.26$ ) min (mean  $\pm$  standard error), and each survey period lasted 21–25 days, providing sufficient time to cover all 53 transects.

### Species trait data

Following Ding et al. (2013), we applied the measured species-level bird traits associated with resource use, feeding type, and foraging behavior to assess functional diversity, including 6 continuous traits (body mass, body length, bill length, dispersal ability, wing length, and wing span) and 2 categorical types (feeding guild, foraging behavior, and stratum) (Table 1). Body mass is widely considered to be one of the single most informative traits in animal species (Brown 1996), because large birds might require more resources, occupy higher trophic levels, and are more vulnerable to extinction than smaller birds (Gaston and Blackburn 1995). Feeding guild, foraging behavior, and stratum mainly reflect how birds search for and use food, and also include various aspects of resource use. Dispersal ability, wing length, and wing span are associated with the bird's maneuverability and athletic ability (Herreraalsina et al. 2013), which may reflect its ability to avoid obstacles and assess risks. Species with high dispersal capacity are thought to be better foragers and more able to cope with environmental stresses, such as food scarcity. Dispersal ability was calculated as follows:

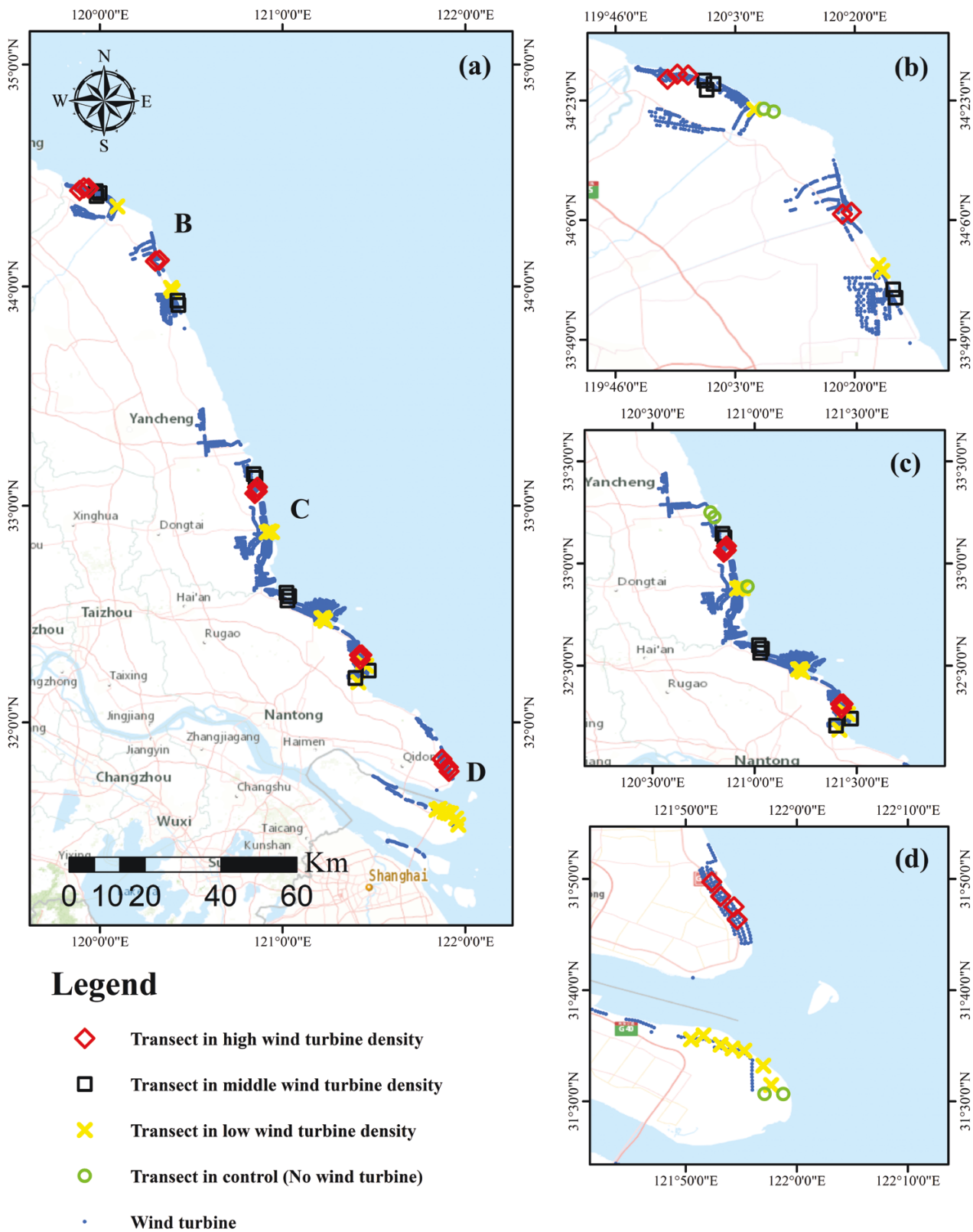
$$\text{Dispersal ability} = \frac{\text{wing length}}{\sqrt[3]{\text{body mass}}}$$

Trait data were obtained from the local literature (Sai 2017; Fan et al. 2020), and Handbook of the Birds of the World (HBW Alive <https://birdsoftheworld.org/bow/home>). Body mass, body size, dispersal ability, wing length, and wing span were averaged over multiple female and male characteristics of the species. Categorical attributes, i.e., feeding type (vertebrates, plants, invertebrates) and foraging behavior (diving, pecking, plunging, probing, and sweeping) were treated as binary traits (0 or 1); however, birds within a species could adopt more than one of these attributes while acquiring food, and these categorical traits were therefore not mutually exclusive (Bae et al. 2018; Ding et al. 2021a).

Phylogenetic signals of continuous traits were measured using Blomberg's  $K$  and Pagel's  $\lambda$ .  $K \leq 1$  represented a lower phylogenetic signal and less trait conservatism than expected from random evolution, whereas  $K > 1$  represented a high phylogenetic signal and stronger phylogenetic signals in trait data than expected from Brownian motion of trait evolution (Ackerly 2009). We also tested the significance of differences between the observed patterns of trait data and those expected by randomly shuffling species at the tips of the phylogeny (Blomberg et al. 2003). Similarly, we measured the phylogenetic signal of body mass using Pagel's  $\lambda$  compared with a Brownian model and Blomberg's  $K$ . If trait values were randomly distributed across the species,  $\lambda$  was close to 0, indicating a very weak signal, whereas  $\lambda$  close to 1 indicated a strong signal. We also tested the phylogenetic signal of categorical traits (feeding type and foraging behavior) using a "Fixed tree, character randomly reshuffled" model, as proposed by Maddison and Slatkin (1991).

### Biodiversity metrics

Bird communities along the Yellow Sea coast differ greatly between months and years during the winter (Fan et al. 2020). We therefore gathered and analyzed bird survey data in each transect and calculated the bird diversity for each transect, including taxonomic, functional, and phylogenetic diversity. Taxonomic diversity was calculated as the observed bird



**Figure 1** Distribution of wind farms and transects along the Yellow Sea coast. (A) whole study area; (B–D), survey regions corresponding to detailed images in (B–D).

species recorded within each transect, absolute functional diversity was estimated as functional richness (FRic) and FD (Petchey and Gaston 2002), and phylogenetic diversity was estimated as Faith's PD index (Faith 1992).

Functional diversity is the sum of the branch lengths of the functional dendrogram for species within a community (Petchey and Gaston 2002). We used UPGMA clustering methods based on the functional distance matrix to construct

**Table 1** Traits used to measure functional diversity and phylogenetic signals in wintering waterbirds along the Yellow Sea coast.

Trait type	Trait	Type	Range
Resource quantity	Body mass	Continuous	34–9,667
	Body length	Continuous	16–2,015
	Bill length	Continuous	13–198
	Dispersal ability	Continuous	16–48
	Wing length	Continuous	157–606
	Wing span	Continuous	37–235
Feeding type	Vertebrates, plants, invertebrates	Binary variable	—
Foraging behavior	Diving, pecking, plunging, probing, sweeping	Binary variable	—

a functional dendrogram of bird species and calculated dendrogram-based functional diversity in R using the function “pd” in the R package picante (Kembel et al. 2010). For phylogenetic diversity, we obtained 5,000 phylogenetic trees covering all the waterbirds occurring in our study area from BirdTree (<http://birdtree.org>), using “Hackett All Species.” We then estimated the Maximum Clade Credibility tree based on mean node heights using TreeAnnotator v1.10.4. Faith’s PD index was thus estimated as the sum of all branch lengths of the phylogeny connecting all species of each transect using the function “pd” in the R package picante (Ding et al. 2021a).

We calculated 2 metrics weighted by relative abundance: mean pairwise functional distance (MFD) based on the functional dendrogram and mean pairwise phylogenetic distance (MPD) based on the phylogenetic tree. Mean pairwise functional distance and mean pairwise phylogenetic distance were calculated by averaging all pairwise functional or phylogenetic distances (branch lengths on the functional or phylogenetic dendrogram), respectively, among co-occurring species, representing an overall divergence of the community (Webb et al. 2002), as follows:

$$\text{MFD or MPD} = \frac{\sum_i^n \sum_j^n \delta_{i,j}}{n} \quad (i \neq j)$$

where  $n$  is species richness in each transect,  $\delta_{i,j}$  is the pairwise functional (or phylogenetic) distance (Euclidean distance) between species  $i$  and species  $j$ .

We also determined if the functional and phylogenetic community structures differed from random expectations by comparing 999 randomized communities, generated by tip-shuffling across all taxa included in the distance matrix across the transect. In each randomization run, species richness was kept constant for communities within each wind turbine density, but tip labels in functional or phylogenetic distance matrix were shuffled. These randomizations were performed using the function `ses.mpd` in the R package picante (Kembel et al. 2010). We then calculated the standardized effect sizes (SES) of mean pairwise functional distance and mean pairwise phylogenetic distance for each transect as:

$$\text{SES} = \frac{\text{Obs} - \text{Exp}}{\text{SDexp}}$$

where Obs is the observed MFD or MPD, Exp is the mean of the 999 null communities, and SDexp is the standard deviation of the 999 simulated values. The SES values can then be used to quantify community assembly processes (i.e.,

environmental filtering or competition) when traits were conserved (i.e., with phylogenetic signals):  $\text{SES} < 0$  indicated that environmental filtering may drive community clustering, and if  $\text{SES} > 0$ , competitive exclusion may drive community overdispersion (Webb et al. 2002).

### Landscape interpretation and landscape variables

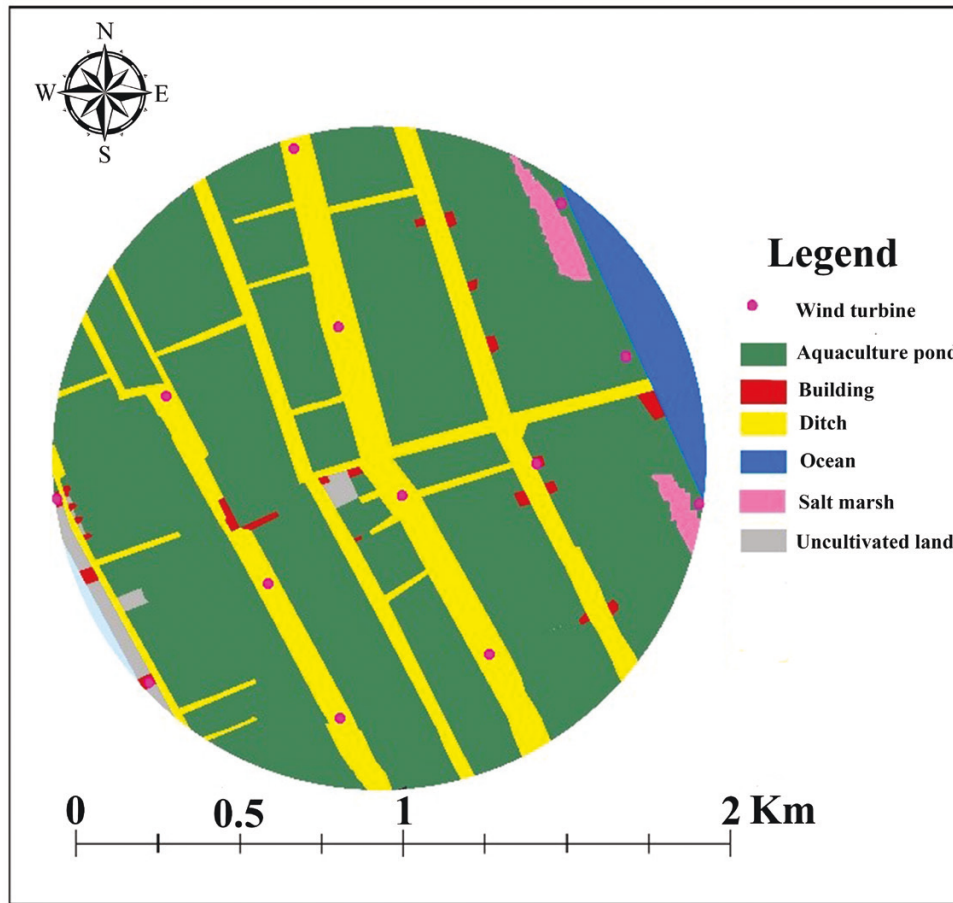
We used visual interpretation to determine the landscape contents with ArcGIS 10.2 (ESRI). Land-use data were obtained from satellite images in Google Earth and further corrected by drone aerial images and field surveys with a resolution of 0.5 m × 0.5 m (Hu et al. 2022a). We defined 11 land-cover types: aquaculture ponds, rivers, roads, farmland, ocean, tidal flats, salt marshes, forests, buildings, ditches, and uncultivated land (Figure 2).

We measured 6 potential landscape variables within 1 km of the geometric center radius of the transect (Yuan et al. 2014): landscape configuration heterogeneity, landscape compositional heterogeneity, area of tidal flats, area of farmland, area of aquaculture pond, and aquaculture pond-edge density (Table 2). Landscape configurational heterogeneity represents landscape fragmentation and reflects the dispersal and movement space of birds (Li et al. 2018), with higher landscape configurational heterogeneity representing lower potential dispersal space. We measured the edge density of the land-cover types within each landscape to determine the landscape configurational heterogeneity (Li et al. 2020). We also estimated the Shannon diversity index for all land-cover types, except buildings and roads, to determine the landscape compositional heterogeneity. Tidal flats represent a crucial habitat for shorebirds along the flyway (Ge et al. 2006) and we therefore calculated the TA in the study area, and because farmland can provide a food resource for wintering birds (Xie et al. 2019), we also calculated the area of farmland. The area of tidal flats and area of farmland were calculated as the proportions of tidal flats and farmland cover, respectively, in the landscape. Aquaculture ponds are a typical artificial landscape along the Yellow Sea coast and may provide essential foraging and resting resources for waterbirds (Jackson et al. 2020). However, the aquaculture ponds in the study area were different sizes, densities, and shapes, and we therefore calculated the aquaculture pond-edge density within each 1 km radius landscape to represent the pattern of aquaculture ponds.

### Statistical analyses

Significant differences in bird diversity (taxonomic, functional, and phylogenetic diversity) and landscape variables (landscape compositional heterogeneity, landscape configurational heterogeneity, area of farmland, area of tidal flats, area of aquaculture pond, and aquaculture pond-edge density) among the 4 wind turbine densities were analyzed by one-way ANOVA. If significant differences in bird diversities and landscape variables were detected among the different wind turbine densities, post hoc Games–Howell multiple comparisons were used to identify the crucial wind turbine density for bird (significantly higher bird diversity in one density compared with others) and landscape variables. In addition, the similarity of waterbird communities in each transect with different wind turbine densities were analyzed by non-metric multidimensional scaling (NMDS).

We analyzed the relationships between bird diversity and landscape variables using single-variable ordinary least



**Figure 2** Map of example landscape interpretation with radius of 1 km (Jiangsu Qidong on Yellow Sea coast).

**Table 2** Variables used in the study. The variables included 2 variables for landscape heterogeneity (composition and configuration), 3 variables for proportions of 3 land uses (tidal flats, aquaculture ponds, and farmland), and one variable for edge density (aquaculture pond-edge density).

Landscape variable	Description
Landscape configurational heterogeneity (LCFH)	Landscape edge density (ED) represents the landscape configurational heterogeneity. $ED = \frac{Fe}{Fs} * 10^6$ $Fe$ is the total edge length of all land cover types in the study area, $Fs$ is the area of the study area ( $m^2$ ).
Landscape compositional heterogeneity (LCPH)	Landscape Shannon diversity index (SHDI) represents the landscape compositional heterogeneity (LCPH); $SHDI = -\sum_{i=1}^m Pi \ln(Pi)$ where $Pi$ represent proportion of land use types that are available habitats for waterbirds.
Area of tidal flats (TA)	Proportion of tidal flats cover within 1 km of geometric center radius of the transect ( $m^2$ ).
Area of farmland (FA)	Proportion of farmland cover within 1 km of geometric center radius of the transect ( $m^2$ ).
Area of aquaculture ponds (AA)	Proportion of aquaculture pond cover within 1 km of geometric center radius of the transect ( $m^2$ ).
Aquaculture pond-edge density (APED)	Edge density of aquaculture ponds within 1 km of geometric center radius of the transect.

squares (OLS) and spatial auto-regressive error (SAR) models, and hierarchical partitioning (Li et al. 2019; Ding et al. 2021a). To allow direct comparison of regression coefficients or improve normality, we standardized all response variables and explanatory variables (standard deviation = 1 and mean = 0) before OLS regression or SAR analysis, and hierarchical partitioning using the R function “scale” (Ding et al. 2021a). We also used SAR for spatial autocorrelation by GeoDa 1.14 (Gao et al. 2020).

Hierarchical partitioning (Chevan and Sutherland 1991) was also used to qualify the explanatory variables that best

estimated the variation in each of the 3 dimensions of bird diversity. This method can effectively alleviate collinearity and has thus been commonly used to identify the most likely explanatory variables. We also selected models with high explanatory power but low variance inflation factor (VIF) values to reduce collinearity. VIF is a measure of collinearity among explanatory variables in the multiple linear regression model. All VIFs were <5 (Supplementary Table S2), i.e., below the cut-off value of 10 (Dormann et al. 2013). We performed a hierarchical partitioning analysis to reveal the relative importance of the selected variables (Dormann et al. 2013;

Ding et al. 2021a). The results of the hierarchical analyses of the selected variables were generally similar to those for the 7 variables used in the above analysis.

All calculations and analyses were performed in R 4.0.3 (R Core Team 2020) and GeoDa 1.14 (Anselin et al. 2006).

## Results

A total of 91,067 waterbirds representing 63 species were recorded across 138 days in 6 surveys during 2 winters (Supplementary Table S3 and Figure S1), including 4,816 individuals from 8 Ardeidae species, 40,689 individuals from 20 Charadriidae species, 26,726 individuals from 19 Anatidae species, 8,557 individuals from 8 Laridae species, and 10,279 individuals from 8 other species (Supplementary Figures S2 and S3). The top 5 most abundant waterbird species were Dunlin (*Calidris alpina*), Pied Avocet (*Recurvirostra avosetta*), Indian Spot-billed Duck (*Anas poecilorhyncha*), Eurasian Coot (*Fulica atra*), and Mallard (*A. platyrhynchos*), accounting for 18.51%, 12.63%, 10.25%, 9.35%, and 5.47% of the total abundance, respectively. Six species with 3,152 individuals were listed in the IUCN threatened species, and 12 species with 4,031 individuals were listed in the Red Book of China State Protected Species (Supplementary Table S3). Non-metric multidimensional scaling showed that survey samples within different wind turbine densities had similar waterbird communities (Supplementary Figure S4).

### Multidimensional diversity of waterbirds around onshore wind farms

Phylogenetic signals were significantly related to body mass, bill length, wing length, wind span, and foraging behavior. At the same time, body length, dispersal ability, and feeding type were only marginally significant (Supplementary Material, Table S4). Taxonomic, functional, and phylogenetic diversity, and mean pairwise functional distance and pairwise phylogenetic distance were highest in the control area and lowest in areas with high wind turbine density. The negative standardized effect sizes of functional diversity, phylogenetic diversity, mean pairwise functional distance, and mean pairwise phylogenetic distance indicated that waterbird communities tended to cluster, and environmental filtering may drive community clustering across different wind farm densities along the Yellow Sea coast (Figure 3). In addition, the standardized effect sizes of mean pairwise phylogenetic distance and mean pairwise functional distance in areas with medium and high wind turbine densities were  $< -1.96$ , which were significantly lower than the random value and indicated clustered in terms of phylogenetic structure.

There were significant differences among the 4 wind turbine densities in terms of taxonomic diversity ( $F = 8.706$ ,  $P < 0.001$ ), functional diversity ( $F = 7.058$ ,  $P < 0.001$ ), and phylogenetic diversity ( $F = 8.093$ ,  $P < 0.001$ ), but no significant difference in mean pairwise functional distance ( $F = 2.247$ ,  $P = 0.095$ ), mean pairwise phylogenetic distance ( $F = 1.055$ ,  $P = 0.377$ ), SES.FD ( $F = 0.619$ ,  $P = 0.606$ ), SES.PD ( $F = 0.379$ ,  $P = 0.769$ ), SES.MFD ( $F = 1.295$ ,  $P = 0.287$ ), or SES.MPD ( $F = 0.293$ ,  $P = 0.830$ ) (Supplementary Table S5). *Post hoc* multiple comparisons showed that taxonomic, functional, and phylogenetic diversity, and mean pairwise functional distance were significantly higher in the control area than in any of the other 3 wind turbine densities (Figure 3).

### Landscape characteristics around onshore wind farms

One-way ANOVA demonstrated significant differences in the landscape variables area of aquaculture pond ( $F = 3.311$ ,  $P = 0.028$ ) among the 4 wind turbine densities (Figure 4, Supplementary Table S6), weak differences in landscape configurational heterogeneity ( $F = 2.823$ ,  $P = 0.048$ ) and aquaculture pond-edge density ( $F = 2.778$ ,  $P = 0.051$ ), and no significant differences in landscape compositional heterogeneity ( $F = 0.303$ ,  $P = 0.823$ ), area of tidal flats ( $F = 1.186$ ,  $P = 0.157$ ), and area of farmland ( $F = 1.096$ ,  $P = 0.360$ ).

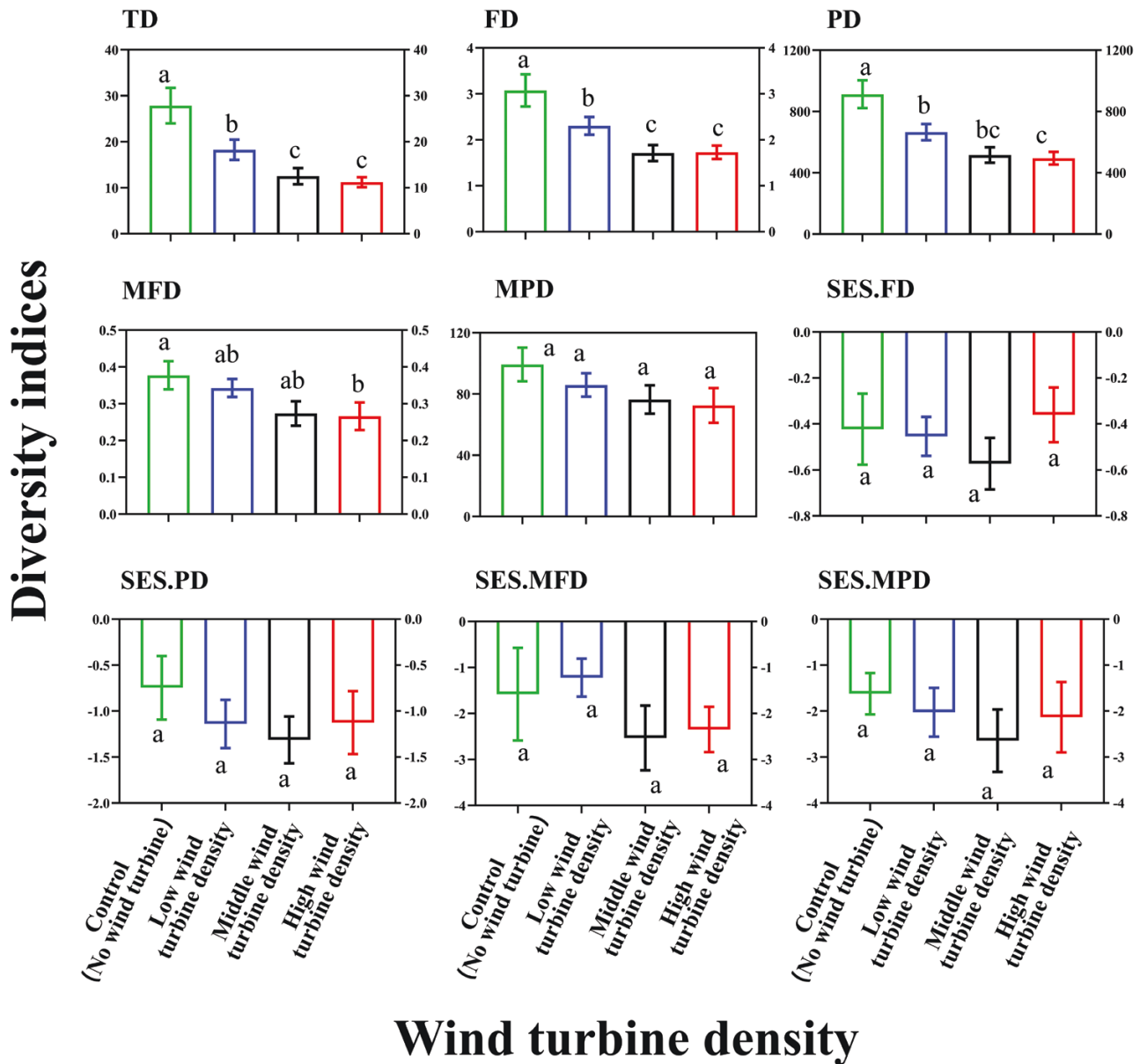
### Effects of wind farms and landscape characteristics on waterbird multidimensional diversities

Taxonomic, functional, and phylogenetic diversity were all significantly and positively influenced by the area of tidal flats and negatively influenced by wind farm, landscape configurational heterogeneity, aquaculture pond-edge density, and area of aquaculture ponds (Table 3). SES.FD, SES.PD, mean pairwise functional distance, mean pairwise phylogenetic distance were significantly and positively affected by landscape compositional heterogeneity and negatively influenced by the area of aquaculture pond (Table 3). SES.MFD was significantly and negatively influenced by landscape configurational heterogeneity, wind farm, aquaculture pond-edge density, area of tidal flats, and area of aquaculture ponds and SES.MPD was significantly and positively affected by landscape compositional heterogeneity, area of farmland, and area of aquaculture ponds (Table 3).

The hierarchical partitioning results showed that taxonomic diversity was best explained by wind turbine density (percentage of independently explained variance, 48.240%) and aquaculture pond-edge density (13.390%), functional diversity was best explained by wind turbine density (33.076%) and aquaculture pond-edge density (21.157%), and phylogenetic diversity was best explained by wind turbine density (50.167%) and area of aquaculture ponds (15.367%) (Figure 5, Supplementary Table S7). Landscape configurational heterogeneity had the highest independent contribution to explaining SES.PD (49.806%), mean pairwise phylogenetic distance (39.783%), and SES.MPD (47.446%), and area of farmland had the highest independent contribution to explaining SES.FD (34.538%) and SES.MFD (29.641%) (Figure 5, Supplementary Table S7).

## Discussion

Many studies have examined the effects of the absence/presence of wind turbines and distance to wind turbines on bird density and/or the abundance of one species (Shaffer and Buhl 2016; Fernández-Bellon et al. 2019); however, the present study aimed to investigate the effects of wind turbine density-associated landscape characteristics on multidimensional waterbird diversity. We found significant differences in taxonomic, functional, and phylogenetic diversity among 4 different wind turbine densities, with the highest diversity in areas with no turbines and the lowest diversity in areas with the highest wind turbine density (Figure 3), which supports our first hypothesis. Taxonomic, functional, and phylogenetic diversity were significantly higher in control areas (no wind turbines) than in areas with low, middle, and high wind turbine densities, suggesting that the density of wind turbines should be reduced in future wind farm planning and design. This result showing decreased diversity in relation to wind



**Figure 3** Waterbird diversity around onshore wind farms along the Yellow Sea coast. Different small letters above bars indicate  $P < 0.05$ .

Mean  $\pm$  standard error (SE). TD, taxonomic diversity; FD, functional diversity; PD, phylogenetic diversity; MFD, mean pairwise functional distance; MPD, mean pairwise phylogenetic distance; SES.FD, standardized effect size of FD; SES.PD, standardized effect size of PD; SES.MFD, standardized effect size of MFD; SES.MPD, standardized effect size of MPD.

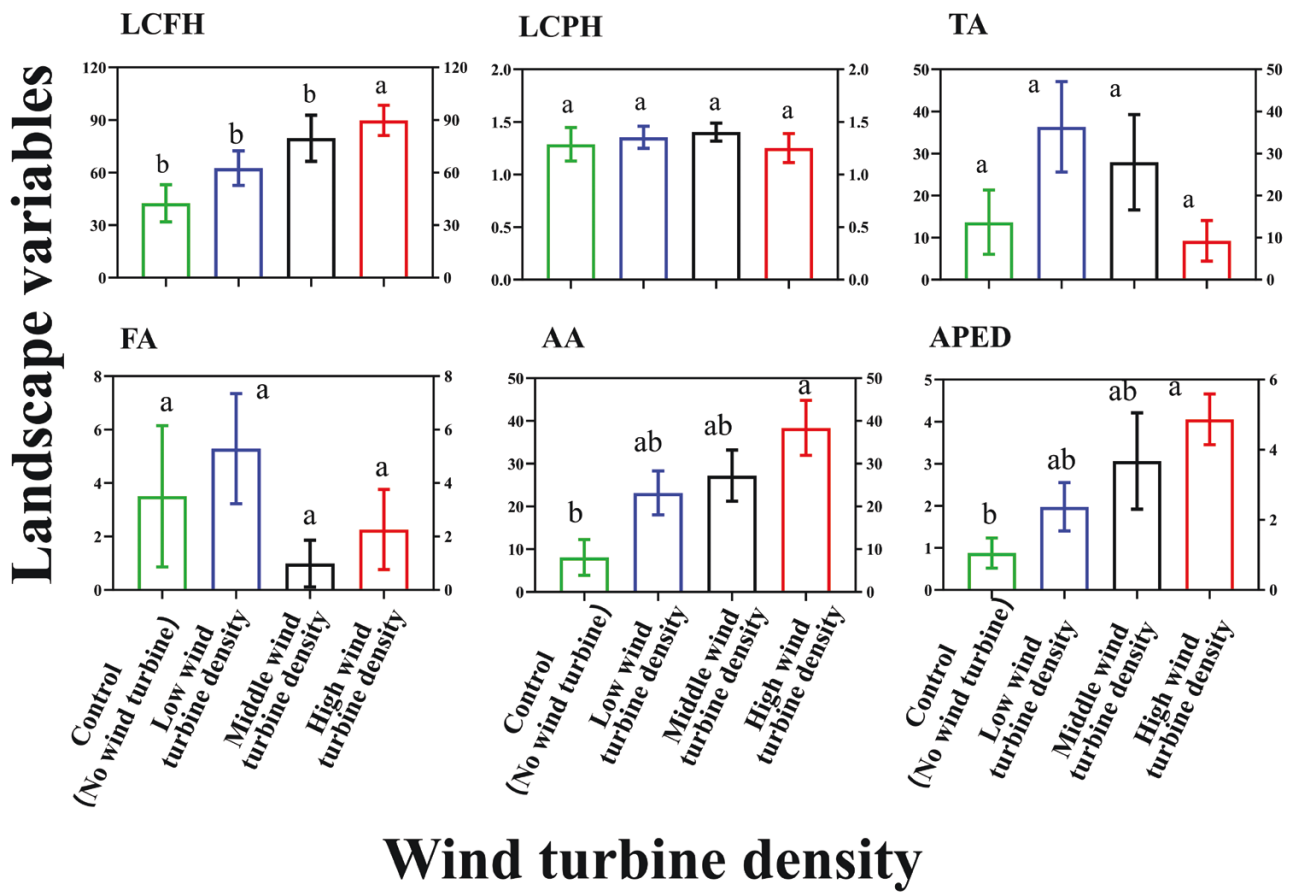
turbines corresponds with results for breeding shorebirds (Sansom et al. 2016) and breeding forest birds (Ding et al. 2021b). The current results thus help to demonstrate that onshore wind farms may decrease multidimensional waterbird diversity in the Yellow Sea region.

Taxonomic, functional, and phylogenetic diversity all decreased with increasing wind turbine density, and hierarchical partitioning also showed that wind turbine density had the greatest independent contribution to explaining taxonomic diversity (48.240%), functional diversity (33.076%), and phylogenetic diversity (50.167%, Figure 5, and Supplementary Table S7), suggesting that wind farms play a crucial role and have significant negative effects on waterbird diversity. These results were in accord with studies in marine and mountain ecosystems (Dohm et al. 2019; Heinänen et al. 2020). Discrepancies in birds' sensitivities in response to wind farms

may explain our results. Thaxter et al. (2017) showed that birds' collision risk varied among ecological groups, species, and landscapes and that species with good flexibility (small body weight and large wing area) were more likely to occur in wind farm areas (Herreraalsina et al. 2013), whereas sensitive or displaced populations tended to abandon areas close to wind farms or with high wind turbine densities (Kelsey et al. 2018; Dohm et al. 2019), and select harsher habitats with more competition or fewer resources (Meatley et al. 2019).

The negative values of SES.FD, SES.PD, SES.MFD, and SES.MPD (Figure 3) indicated that the studied waterbird communities included species with similar functional traits and close phylogenetic relatedness, suggesting the predominant importance of environmental filtering in the assembly processes. Under this hypothesis, habitat variables act as filters encouraging species with similar ecological traits to coexist, leading to





**Figure 4** Landscape variables at onshore wind farms along the Yellow Sea coast. Different small letters above bars indicate  $P < 0.05$ . Mean  $\pm$  standard error (SE). LCFH, landscape configurational heterogeneity; LCPH, landscape compositional heterogeneity; TA, area of tidal flats; FA, area of farmland; AA, area of aquaculture ponds; APED, aquaculture pond-edge density.

phylogenetic clustering with high niche conservatism (Li et al. 2019). Our result was inconsistent with the limiting similarity hypothesis, in which interspecific competition dominates community assemblages with similar ecological niches or close relatedness. Waterbirds show high dispersal ability and sensitivity to coastal wetland ecosystems (Li et al. 2019), which are less likely to be affected by stochastic processes. In contrast, however, our results were in agreement with assemblage patterns in artificial wetlands (Li et al. 2019). Waterbirds depend on wetlands, and the effect of environmental filtering may thus be stronger than the impacts of interspecific interactions.

In the current study, waterbird diversity was regulated by a combination of different landscape variables and wind turbine density (Table 3 and Figure 5), thus supporting our second hypothesis. Landscape configurational heterogeneity was negatively and significantly related to taxonomic, functional, and phylogenetic diversity (Table 3), suggesting that a higher landscape-edge density supported a lower multidimensional diversity of waterbirds. Along the Yellow Sea coast, the landscape inside dykes was dominated by artificial and modified habitats (e.g., aquaculture ponds, farmland) whereas that outside the dykes was mainly tidal flats (Li et al. 2020; Zhao et al. 2023). Higher landscape configurational heterogeneity in this region reflects a relatively high degree of fragmentation (Li et al. 2018; Xu et al. 2018), whereas waterbirds prefer vast stretches of habitats. We recommend that the impact of wind farms on waterbird diversity may be mitigated by the transformation of the landscape in regions with existing wind farms.

Aquaculture ponds are an important habitat for waterbirds along China's coast (Jackson et al. 2020). They exist within the dykes and have different edge densities, and include farmed fish, shrimp, or crabs (He et al. 2016; Peng et al. 2021). During the drying phase in winter, these ponds provide roosting spaces for waterbirds at high tide and places to recharge their energy (Li et al. 2020). In the current study, taxonomic, functional, and phylogenetic diversity were all significantly and negatively related to the edge density of aquaculture ponds (Table 3), which was the second most important independent factor affecting waterbird diversity, suggesting that aquaculture pond-edge density is a crucial landscape variable in the study area. Aquaculture pond-edge density is commonly associated with the management rights and construction patterns of the ponds. Along the Yellow Sea coast, ponds with a high edge density are industrial ponds with a homogeneous structure (small patch) and automatic operating mode (water storage and feeding) (Hu et al. 2022b), which are fragmented and unsuitable for perching, leading to lower waterbird diversity. Ponds with a low edge density are traditional ponds (large and free-range) managed by self-employed individuals, and contain mudflats and aquatic plants, and show low human disturbance, creating a semi-natural environment for waterbirds to roost, feed, and rest (Yang et al. 2013). The number of species and abundance of waterbirds were thus higher in areas with low-edge-density aquaculture ponds. High-edge-density ponds (i.e., industrial ponds) should thus be preferred and low-edge-density ponds

**Table 3** Responses of bird diversity to each variable along the Yellow Sea coast based on single-variable ordinary least squares regression and spatial auto-regressive models

		WF	LCPH	LCFH	APED	TA	FA	AA
TD	Coef <sub>OLS</sub>	-0.502	-0.021	-0.385	-0.524	0.241	0.042	-0.387
	R <sup>2</sup> <sub>OLS</sub>	0.313	0.000	0.158	0.162	0.059	0.000	0.192
	Coef <sub>SAR</sub>	-0.500	0.002	-0.364	-0.503	0.237	-0.009	-0.371
	AIC <sub>SAR</sub>	-13.929	5.477	-3.498	-3.781	1.694	5.474	-4.869
FD	Coef <sub>OLS</sub>	-0.446	0.024	-0.431	-0.605	0.214	0.166	-0.396
	R <sup>2</sup> <sub>OLS</sub>	0.263	0.000	0.220	0.241	0.047	0.005	0.217
	Coef <sub>SAR</sub>	-0.455	0.025	-0.414	-0.588	0.212	0.131	-0.380
	AIC <sub>SAR</sub>	-15.079	1.552	-11.147	-12.699	-1.645	0.847	-9.942
PD	Coef <sub>OLS</sub>	-0.425	0.108	-0.292	-0.431	0.224	0.090	-0.321
	R <sup>2</sup> <sub>OLS</sub>	0.288	0.011	0.112	0.139	0.068	0.008	0.171
	Coef <sub>SAR</sub>	-0.429	0.126	-0.275	-0.416	0.227	0.064	-0.309
	AIC <sub>SAR</sub>	-25.713	-8.495	-13.990	-15.606	-12.062	-7.798	-16.652
SES.FD	Coef <sub>OLS</sub>	0.039	0.292	-0.006	-0.187	-0.038	0.364	0.053
	R <sup>2</sup> <sub>OLS</sub>	0.002	0.056	0.000	0.000	0.000	0.101	0.004
	Coef <sub>SAR</sub>	-0.012	0.277	-0.012	-0.199	-0.083	0.387	0.634
	AIC <sub>SAR</sub>	0.627	-2.349	0.626	-0.862	0.184	-6.641	0.326
SES.PD	Coef <sub>OLS</sub>	-0.060	0.314	0.145	0.087	0.013	0.232	0.029
	R <sup>2</sup> <sub>OLS</sub>	0.000	0.092	0.016	0.000	0.000	0.043	0.002
	Coef <sub>SAR</sub>	-0.046	0.315	0.150	0.100	0.004	0.223	0.029
	AIC <sub>SAR</sub>	-11.567	-17.722	-13.426	-11.865	-11.360	-14.628	-11.445
MFD	Coef <sub>OLS</sub>	-0.343	0.429	-0.107	-0.353	0.198	0.425	-0.447
	R <sup>2</sup> <sub>OLS</sub>	0.105	0.099	0.000	0.047	0.023	0.100	0.206
	Coef <sub>SAR</sub>	-0.357	0.416	-0.079	-0.350	0.184	0.419	-0.481
	AIC <sub>SAR</sub>	11.147	11.937	17.830	15.315	16.440	12.006	6.156
MPD	Coef <sub>OLS</sub>	-0.225	0.616	0.099	-0.134	0.107	0.463	-0.292
	R <sup>2</sup> <sub>OLS</sub>	0.041	0.257	0.000	0.011	0.000	0.141	0.099
	Coef <sub>SAR</sub>	-0.238	0.615	0.113	-0.127	0.104	0.477	-0.317
	AIC <sub>SAR</sub>	8.798	-4.465	11.530	11.748	11.592	2.943	6.441
SES.MFD	Coef <sub>OLS</sub>	-0.207	-0.028	-0.365	-0.498	0.048	0.325	-0.280
	R <sup>2</sup> <sub>OLS</sub>	0.047	0.000	0.169	0.174	0.000	0.083	0.119
	Coef <sub>SAR</sub>	-0.218	-0.039	-0.366	-0.498	0.045	0.326	-0.290
	AIC <sub>SAR</sub>	-5.339	-1.628	-12.273	-12.624	-1.719	-7.071	-8.284
SES.MPD	Coef <sub>OLS</sub>	-0.043	0.353	0.067	-0.065	0.043	0.291	0.063
	R <sup>2</sup> <sub>OLS</sub>	0.000	0.128	0.008	0.004	0.004	0.084	0.007
	Coef <sub>SAR</sub>	-0.020	0.382	0.061	-0.060	0.054	0.272	0.046
	AIC <sub>SAR</sub>	-14.404	-24.525	-14.723	-14.556	-14.707	-19.666	-14.575

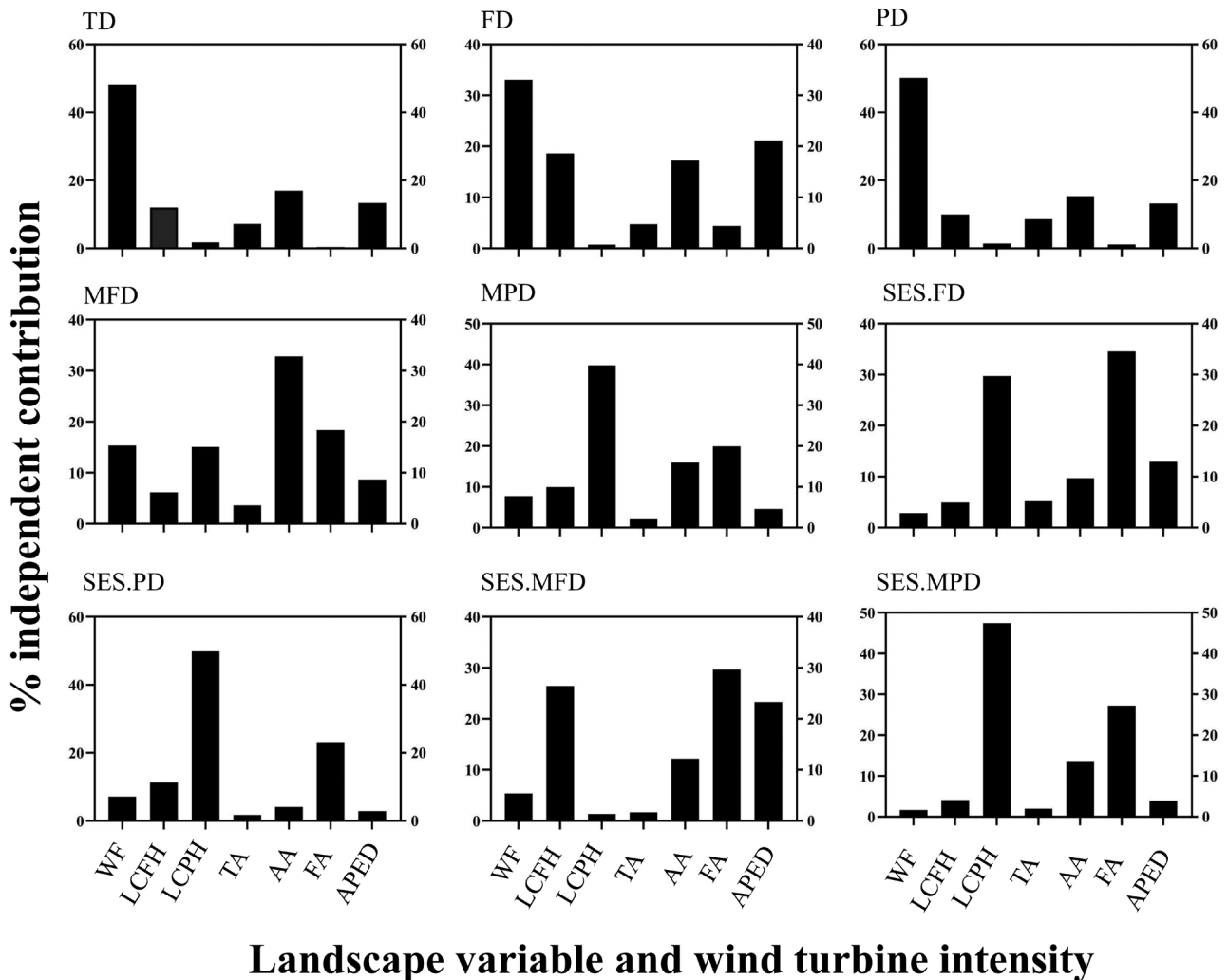
(i.e., traditional aquaculture ponds) should be avoided in the spatial planning of wind turbines along the flyway, to mitigate further direct effects (collision risk) and indirect effects of wind farms on waterbird conservation.

In this study, we showed that waterbird diversity decreased with increasing wind turbine density, and functional and phylogenetic structures tended to be clustered in waterbird communities in density gradient wind turbines. Waterbird diversity was regulated by the combination of wind turbine density and landscape variables, with the edge density of aquaculture ponds, in addition to wind turbine density, having the largest independent contribution to waterbird diversity. This study had some limitations, including the short-term data collection; however we conducted 6 rounds of waterbird surveys, providing extensive coverage of waterbird diversity at 4 wind turbine densities across 53 transects, and 3 waterbird

surveys in each season (6 times during 2 winters), to meet the standard technical specifications for synchronous waterbird surveys in China (Yuan et al. 2019), to help ameliorate this limitation. Future studies should include larger-scale survey and longer durations and should consider the effects of environmental variables (e.g., electric intensity, magnetic intensity, noise, wind speed, and temperature) impacted by wind farms.

## Acknowledgments

This study was financially supported by the Science and Technology Commission of Shanghai Municipality (No. 18DZ1205000), Natural Science Foundation of China (No. 31901099), Yangtze Delta Estuarine Wetland Ecosystem Observation and Research Station, Ministry of Education, Shanghai Science and Technology Committee



**Figure 5** Independent contributions of each variable derived by hierarchical partitioning to each dimension of biodiversity of waterbirds along the Yellow Sea coast. WF: wind farm; APED: aquaculture pond-edge density; TA: area of tidal flats; LCFH: landscape configurational heterogeneity; LCPH: landscape compositional heterogeneity; FA: area of farmland; TD: taxonomic diversity; FD: functional diversity; PD: phylogenetic diversity; MFD: mean pairwise functional distance; MPD: mean pairwise phylogenetic distance; SES.FD: standardized effect size of FD; SES.PD: standardized effect size of PD; SES.MFD: standardized effect size of MFD; SES.MPD: standardized effect size of MPD.

(ECNU-YDEWS-2022), Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Institute of Biodiversity Science, Fudan University (2023-FDU-KF-02), and Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration (SHUES-2023A04), “Pioneer” and “Leading Goose” R&D Program of Zhejiang (2024C02002). We thank Dr. Hanbin Xie from Shanghai Natural History Museum and Dr. Jinjin Du from World Natural Heritage site of Tiaozini Area for assistance in supporting the fieldwork. We also thank the editors and 3 anonymous reviewers for their helpful comments on the article.

### Conflict of Interest Statement

The authors declare that they have no conflict of interest.

### Author Contributions

S.Z.: investigation, formal analysis, writing—original draft. X.L.: review and editing. H.X., N.L., H.L., F.G., and X.S.,

investigation, resources. T.W., A.X., X.C., and B.L. supervision, conceptualization, methodology, writing—review and editing.

### Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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