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How waterbird communities respond to seasonal and environmental factors in rice fields adjacent to a Ramsar wetland

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ABSTRACT

Natural wetlands have been lost or degraded worldwide, negatively impacting waterbird populations. However, many species have capitalised on the creation of complementary habitats such as rice fields, a common and widespread type of artificial wetland. Despite the significance of rice fields as supplementary habitats for waterbirds, few studies have explored how waterbirds use these wetlands across seasons and how they respond to different local environmental factors. We surveyed waterbird communities in rice fields near Anhui Shengjin Lake National Nature Reserve, a Ramsar site, during the rice growing periods and the post-harvest periods from 2023 to 2024, to analyse the impact of environmental factors on the metrics of community diversity. We observed 15,085 waterbirds of 33 species in the rice fields, with diversity indices that were generally higher in rice fields inside the reserve than those outside the reserve in most periods. Waterbird densities peaked during the seedling and pre-wintering periods. Species richness, the Shannon-Wiener diversity index, and the densities of ducks and shorebirds were highest during the seedling period, while gull densities peaked in the flowering period. In contrast, goose densities were highest during the pre-wintering period. Rice fields with larger areas, irregular shapes, deeper water, higher drain density, and closer proximity to larger adjacent rice fields and Shengjin Lake supported higher waterbird densities and species richness. Human disturbances from main roads and settlements negatively affected waterbirds. However, during certain periods, waterbirds were attracted by human activities that may expose food resources in rice fields. These findings provide important implications for waterbird conservation in these artificial wetlands, which are of global significance given their important role in the context of worldwide wetland loss and degradations.

1. Introduction

As one of the most important ecosystems on Earth, wetlands provide critical habitats for waterbirds and other wetland-dependent species (Wang et al., 2022). However, since the 20th century, overexploitation has led to the loss of more than 50 % of the world's natural wetlands, with the remaining wetlands continuing to degrade (Oliver and Morecroft, 2014). The degradation and loss of wetlands have severely impacted wildlife that depend on these ecosystems, and this issue is not confined to specific regions but represents a global ecological crisis, thus deserving worldwide attention from research and conservation communities (Bai et al., 2015; Jia et al., 2018).

Waterbirds play crucial roles in wetland ecosystems by contributing to material cycling, energy flow, and enhancing the diversity of other taxa (Green and Elmberg, 2014). Due to their sensitivity to habitat changes, the community structure and species diversity of waterbirds often serve as important biological indicators of wetland health (Péron et al., 2013; Wang et al., 2018). The degradation and loss of natural wetlands often result in reduced food availability for waterbirds, which may lead to a decline in species diversity and drives some waterbird species to local extinctions (Aarif et al., 2014, 2021). In this context, many waterbird species have been found to change their distributions to

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neighbouring artificial wetlands in search of food resources, nesting and roosting sites (Wang et al., 2016; Nawaz et al., 2022; Byju et al., 2023). Despite significant human disturbance, global studies have shown that these artificial wetlands have become important compensatory habitats for waterbirds (Zou et al., 2017; Rusinque et al., 2021). Therefore, more attention should be paid on the high value and suitability of these man-made wetlands for the waterbirds.

Rice fields are one type of artificial wetland widely distributed around the world, and they can attract a variety of waterbird species, providing them with important compensatory habitats (Fujioka et al., 2001; Herring et al., 2019; Ali et al., 2020; Fraixedas et al., 2020). For example, rice fields may have shallow water areas and mudflats, which can provide abundant food resources for waterbirds (Maeda, 2001; Pernollet et al., 2017). Although rice fields attract waterbirds for feeding and resting, they are often subject to significant human disturbances (Elphick and Oring, 2003; Munira et al., 2014). Global studies have emphasized the vital role of rice fields as habitats for waterbirds, suggesting that scientifically managing these fields could offer a new approach to waterbird conservation (Czech and Parsons, 2002; Ma et al., 2010; Sesser et al., 2016). However, there is still limited knowledge regarding how waterbirds utilize these man-made wetlands during different seasons (e.g. how do bird densities and species diversity vary between the rice-growing season and post-harvest period?) and how do they respond to different local environmental factors (e.g. field area, water depth). Answering these questions will enhance our understanding of the ecological value of rice fields and provide a scientific basis for reconciling waterbird conservation with rice production at both regional and global levels.

In 2023, China's rice cultivation area reached 290,000 km^2, accounting for 22.7 % of the country's arable land (NBS, 2023). Amid the degradation and loss of natural wetlands, these rice fields may provide important alternative habitats for wetland organisms, as found elsewhere (Toral and Figuerola, 2010; Yu et al., 2019). The middle and lower reaches of the Yangtze River cover an area of 148,000 km^2 paddy fields and have long been an important region for rice production (Yang et al., 2015). The abundant natural wetlands in the region, particularly the numerous Yangtze-connected lakes, also provide critical breeding, staging, and wintering grounds for waterbirds migrating along the East Asian-Australasian Flyway, with the wintering period coinciding with the post-harvest fallow period of rice fields (Li et al., 2014; Fan et al., 2020). Due to intense human economic activities, however, this region has experienced significant degradation and loss of natural wetlands, which adversely affects waterbird populations (Li et al., 2015; Xu et al., 2022). Hence, many waterbirds increasingly move to the rice fields surrounding these human-disturbed natural wetlands (Li et al., 2019b; Zhou et al., 2020). A deeper understanding of how waterbirds utilize these artificial wetlands and how they respond to local environmental factors is crucial for improving the conservation and management of the waterbird communities. It may also provide valuable insights for waterbird conservation in other rice-growing regions globally, such as Southeast Asia and South America, while supporting the implementation of international conservation policies. Furthermore, this study can serve as a scientific basis for evaluating the potential for collaborative management of agricultural landscapes and natural wetlands, contributing to the integration of ecological agriculture and wetland conservation.

From 2023–2024, we conducted field surveys of waterbirds and environmental factors across 44 rice fields adjacent to the Anhui Shengjin Lake National Nature Reserve, a wetland of international importance designated under the Ramsar Convention (a Ramsar site) and a typical Yangtze-connected lake. The objectives of this study were to explore how waterbirds use these man-made wetlands across seasons and how they respond to different local environmental factors. We expected higher bird diversity indices in rice fields closer to the Shengjin Lake which is a main traditional wintering site for waterbirds in the middle and lower reaches of the Yangtze River (Wang et al., 2017). More species of waterbirds were hypothesized to be found during the seedling period when the prolonged flooding of these fields would promote the growth of small fish and invertebrates, providing abundant food resources for waterbirds (Amira et al., 2018). During the wintering period, many geese overwinter in Shengjin Lake and may forage in surrounding fields, and therefore would result in an expected higher bird density in these rice fields (Fox and Madsen, 2017). Additionally, we hypothesized that rice field area and water depth would positively impact waterbird community diversity. Larger rice fields offer more habitat space and food resources, supporting a greater diversity of species, while deeper water levels create a more stable environment, facilitating waterbird aggregation (Strum et al., 2013; Cheng et al., 2022). Our study may offer valuable insights into waterbird utilization of rice fields and their adaptation to seasonal changes, providing crucial scientific evidence for global wetland management and conservation.

2. Materials and methods

2.1. Study area

Shengjin Lake is a typical shallow-water lake, located in the floodplain of the middle and lower Yangtze River in eastern China and was designated as a National Nature Reserve in 1997 and a Ramsar site in 2015. It lies on the East Asian-Australasian Flyway and serves as a crucial breeding, stopover, and wintering grounds for tens of thousands of waterbirds each year (Li et al., 2019b). To restore and protect natural wetlands, the reserve management committee has implemented several conservation measures, including water level management to optimize waterbird habitats, regular ecological monitoring to assess waterbird populations and habitat conditions, regulation of agricultural activities and restriction of human disturbances, and replanting of native vegetation to improve water quality (Wang et al., 2024). Surrounding Shengjin Lake are numerous rice fields, largely the result of local efforts over the last century to reclaim land. Rice cultivation in this region follows a defined annual cycle: flooding and ploughing occur in April, planting starts in early May, flowering happens around July, and harvesting takes place in late September. After harvest, the fields are either left fallow or sown with rapeseed, with rice cultivation resuming the following year.

This study was conducted in the rice fields near the upper lake area of Shengjin Lake (30°33' ~ 30°40' N, 116°92' ~ 117°01' E, Fig. 1), which has the highest waterbird diversity and abundance in the lake (Li et al., 2019b). We selected 44 rice fields as sample plots (1.43–19.27 ha), with 24 located inside the reserve and 20 outside, varying in shape, size, and other environmental factors.

2.2. Bird counts

During 2023–2024, we conducted two waterbird surveys for each of the following six periods: rice seedling (RS, May), rice flowering (RF, July), early post-harvest (RH, October), pre-wintering (WP, November), mid-wintering (WM, January), and late-wintering (WL, March). To enhance survey accuracy, we established 1–3 observation points for each sample plot, considering the size, shape, and environment of the area to avoid duplicate observations. Each survey lasted approximately 15 minutes to ensure comprehensive recording of waterbirds within the plots. To standardise detectability, surveys were conducted during sunny, calm days (wind speed less than 14.4 km/h). Each survey was carried out by the same two experienced birdwatchers, using binoculars (10 × 42 WB Swarovski) and spotting scopes (20–60 × zoom Swarovski: ATM 80) with the "look-see" total count method (Delany, 2005). We recorded waterbirds within rice field boundaries and those flying out of the fields, excluding those flying over without landing (Delany, 2005). An index of community composition was obtained by pooling all waterbirds recorded during the two surveys per rice field per period. Based on the differences in waterbird resource utilization, the waterbirds were

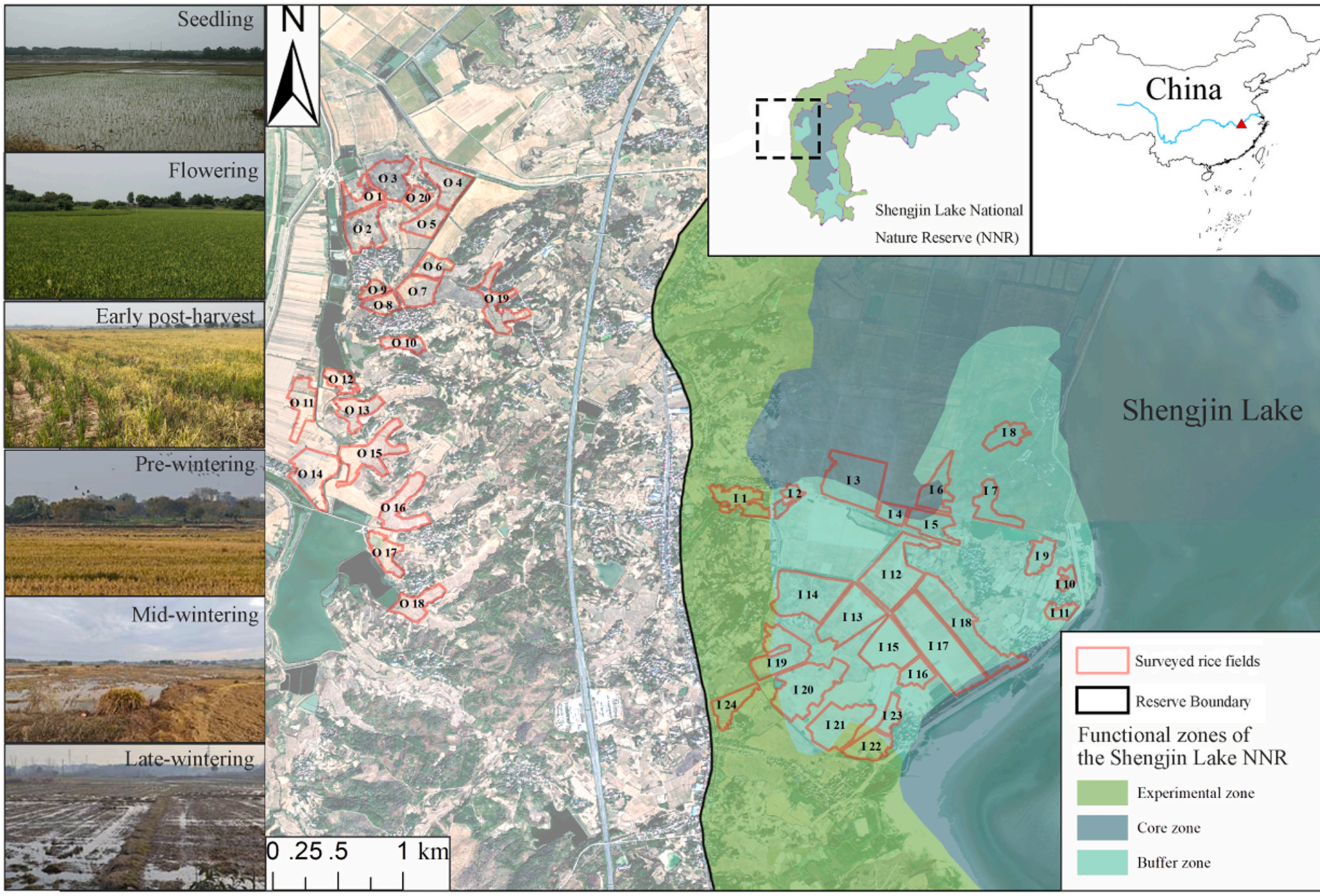

Fig. 1. Locations of 44 rice fields surveyed inside and outside Anhui Shengjin Lake National Nature Reserve near the upper lake area of Shengjin Lake. Experimental zone: designated for scientific research, monitoring, and sustainable development activities; Core zone: strictly protected area, prohibiting human activity to preserve natural ecosystems; Buffer zones: surrounding the core zone, allowing limited human activity to reduce impacts on the core zone.

classified into six guilds (Blondel, 2003): geese, ducks, gulls, large waders, shorebirds, and vegetation gleaners (waterbirds that primarily forage in wetland or aquatic vegetation, feeding on insects, small invertebrates, or plant seeds, and are commonly found in vegetated habitats such as marshes and lakes).

2.3. Habitat variables

Based on previous research (Wang et al., 2023), we identified 15 potential environmental and anthropogenic variables that might influence waterbird communities (Table 1). Among these, the field shape becomes progressively more irregular as the shape index increases. During each survey, we randomly selected 10 locations within each rice field to measure rice plant height and water depth, calculating their average values. We established a 200-m buffer zone around the edge of each rice field and quantified the remaining environmental factors through field surveys combined with Google Earth imagery. To assess the effect of human disturbance, we recorded the number of humans, automobiles, cultivators, and pumps within the boundaries of each field before the waterbird survey, with any subsequent occurrences being excluded from the records.

2.4. Data analyses

For each surveyed field, we aggregated the total number of waterbirds in each of the six periods to obtain a species × site matrix for each period. From these matrices, we calculated the bird density (D; Eq. (1)), richness (total number of species), the Shannon-Wiener index (H; Eq. (2)) and the density of birds in each guild per field for each period (Pielou, 1966; Spellerberg and Fedor, 2003):

$$D = n/AF \tag{1}$$

$$H = -\sum_{i=1}^{S} P_i \ln(P_i) \tag{2}$$

where n is the total number of waterbirds, AF is the area of each rice field, P_i is the proportion of the number of birds of species i to the total number of birds, and S is the total number of species.

We calculated the Global Moran's I to analyse whether the distribution of the data was spatially random and thus independent. The R package *sf* was used to read the spatial dataset, the *poly2nb* function was employed to compute the spatial weights matrix, and the *moran.test* function was used to calculate the Global Moran's I for each index during each period. The results indicated that the indices from different sites generally exhibited no spatial autocorrelation in most periods, with only a few showing weak autocorrelation (Table S1).

Prior to analysis, environmental factors were standardized using z-score. The two-way ANOVA was conducted to test the effects of season and location (inside vs outside the reserve) on density, richness, the Shannon-Wiener index and the density of birds in each guild. Post-hoc comparisons were performed using the *emmeans* package to explore interactions between different periods and locations.

We applied generalized linear mixed models (GLMMs) to test the effects of environmental variables on density, richness, the Shannon-Wiener index, and the density of birds in each guild for each period. Environmental factors were treated as fixed effects, and wetland ID as a

Table 1
Measured habitat variables and their descriptions.

Variables	Description	Range	Mean ± SE
Environmental			
PF (km)	Perimeter of each rice field	0.59 – 2.45	1.27 ± 0.07
AF (ha)	Area of each rice field	1.43 – 19.27	6.18 ± 0.62
SF	Shape index of each rice field. $SF = L/2\sqrt{\pi \times A}$ (L = PF; A = AF)	1.15 – 2.48	1.51 ± 0.05
DF (km/ha)	Total density of drains in each rice field. $DF = L/A$ (L= drain length; A = AF)	0.03 – 2.11	0.53 ± 0.07
DS (km)	Minimum distance from the boundary of each rice field to Shengjin Lake	0.05 – 4.95	2.29 ± 0.28
FZ (ha)	Total rice field area within the 200-m buffer zone of each rice field	1.89 – 35.14	12.62 ± 1.19
AH (m)	Average plant height of rice in each rice field	0 – 1.27	0.48 ± 0.02
AD (m)	Average depth of water in each rice field	0 – 0.20	0.03 ± 0.00
Anthropogenic			
DR (km)	Minimum distance from the boundary of each rice field to the nearest main road	0.02 – 2.47	1.18 ± 0.02
DA (km)	Minimum distance from the boundary of each rice field to the nearest residential area	0.01 – 0.46	0.15 ± 0.08
SZ (ha)	Total settlement area within the 200-m buffer zone of each rice field	0.00 – 8.40	2.13 ± 0.37
NH	Number of humans in each rice field during the survey period	0 – 26	1.12 ± 0.20
NA	Number of automobiles per field boundary during the survey period	0 – 5	0.05 ± 0.02
NC	Number of cultivators (machines) in each rice field during the survey period	0 – 1	0.03 ± 0.01
NP	Number of pumps in each rice field during the survey period	0 – 1	0.02 ± 0.01

random effect. A Poisson distribution was applied to species richness and a Gaussian distribution was used for the other data (Bolker et al., 2009). During the analysis, we addressed multicollinearity among environmental variables by calculating variance inflation factors (VIF). We removed the wetland perimeter with the highest VIF value (VIF > 20) and retained all remaining environmental factors with VIF values below 5 (Akinwande et al., 2015). We used backward elimination to remove non-significant terms ($P > 0.05$), ensuring that only significant factors were retained in the final models. We used separate GLMMs for each time period to account for significant seasonal variations in the regional species pool, particularly due to migratory waterbirds, allowing us to identify season-specific environmental factors influencing species presence; this approach aligns with similar studies (Li et al., 2019c; Almeida et al., 2020; Lee et al., 2025). All analyses were conducted in R (v. 4.3.2; R Core Team, 2024).

3. Results

3.1. Waterbird communities

During the 12 surveys conducted across 44 rice fields, we recorded a total of 15,085 waterbirds from 33 species in 4 orders and 8 families (Table S2). Among these species, three are listed on the IUCN Red List: White-naped Crane (*Antigone vipio*, VU), Hooded Crane (*Grus monacha*, VU), and Northern Lapwing (*Vanellus vanellus*, NT). Four species were classified as Key Protected Wild Animal Species in China: White-naped Crane (Class I), Hooded Crane (Class I), Common Crane (*Grus grus*, Class II), and White-fronted Goose (*Anser albifrons*, Class II).

3.2. Effects of environmental variables on waterbird community diversity

The waterbird density, species richness, and the Shannon-Wiener index were all influenced by seasonal changes, peaking during the seedling period (Fig. 2). All three diversity indices were influenced by both location (inside vs outside the reserve) and season, with a significant interaction between the two factors for bird density and the Shannon-Wiener index (Table S3). Inside the reserve, bird densities were higher during the seedling and pre-wintering periods than those during other periods (Fig. 2). Both inside and outside the reserve, richness and the Shannon-Wiener index were higher during the seedling period than those during other periods (Fig. 2). Overall, density, richness, and the Shannon-Wiener index were higher inside the reserve than those outside (Fig. 2).

Field area (AF) and water depth (AD) were positively correlated with each diversity index across multiple periods (Table 2). Specifically, during the seedling period, water depth (AD) was negatively correlated with bird density. Plant height (AH) was negatively correlated with each diversity index during the flowering period. Distance from the rice field to Shengjin Lake (DS) was negatively correlated with species richness during the wintering period and positively correlated with the Shannon-Wiener index during the seedling period. The area of rice fields within the buffer zone (FZ) and the number of humans (NH) were positively correlated with various diversity indices during the early post-harvest period. The number of humans (NH) was negatively correlated with species richness during the flowering and late-wintering periods. The area of settlements within the buffer zone (SZ) was negatively correlated with bird density and richness at different periods. Distance from the rice field to the nearest main road (DR), shape index (SF), drain density (DF), the number of cultivators (NC), and automobiles (NA) were positively correlated with various diversity indices across different periods (Table 2).

The full names of the variables are displayed in Table 1.

3.3. Effects of environmental variables on different guilds

The bird density in each guild was influenced by seasonal changes, peaking at different times: geese during the pre-wintering period, gulls during the flowering period, vegetation gleaners in the late-wintering period, and ducks, large waders, and shorebirds during the seedling period (Fig. 3). The density of birds in each guild was generally influenced by both location (inside vs outside the reserve) and season, with a significant interaction between the two factors (Table S3). Inside the reserve, the densities of ducks and shorebirds during the seedling period, the densities of gulls during the flowering period, and the densities of geese during the pre-wintering period were higher than those during other periods (Fig. 3). The densities of geese and large waders during the pre-wintering and mid-wintering periods, the densities of ducks and shorebirds during the seedling period, and the densities of gulls during the flowering period were higher inside the reserve than those outside (Fig. 3). No seasonal or locational effects were found for vegetation gleaners.

Field area (AF) was positively correlated with the density of geese and large waders during the pre-wintering period, as well as with the density of shorebirds during the late-wintering period (Table 3). During the seedling period, the density of multiple guilds was negatively affected by water depth (AD) and the area of settlements within the buffer zone (SZ). Distance from the rice fields to the nearest main road (DR) was negatively correlated with the density of ducks during the seedling period, while plant height (AH) was negatively correlated with the density of shorebirds during the flowering period. The area of rice fields within the buffer zone (FZ) was positively correlated with the density of shorebirds, and the number of humans (NH) was positively correlated with the density of large waders during the early post-harvest period. The number of humans (NH) was negatively correlated with the density of shorebirds during the late-wintering period. The shape index (SF), drain density (DF), the number of cultivators (NC), and automobiles (NA) were positively correlated with the density of various guilds across different periods (Table 3).

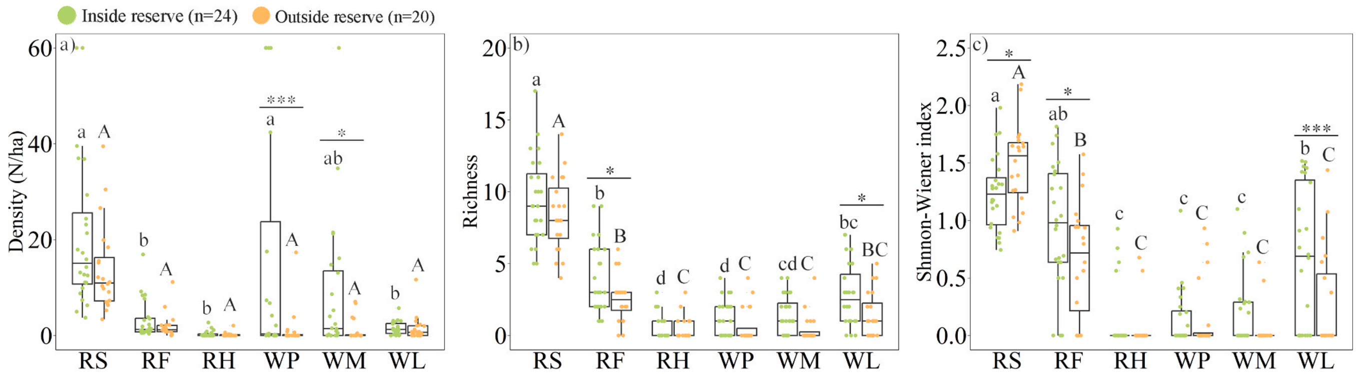

Fig. 2. Waterbird density (a), species richness (b), and Shannon-Wiener index (c) for each survey period in rice fields inside and outside the reserve near Shengjin Lake. The same lowercase letters indicate no significant difference in diversity indices between periods inside the reserve, and the same uppercase letters indicate no significant difference in diversity indices between periods outside the reserve ($P < 0.05$). The asterisk indicates significant difference in diversity index between inside and outside the reserve in that period (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). The number of sampling sites inside the reserve was 24, and outside the reserve was 20. RS = rice seedling period; RF = rice flowering period; RH = early post-harvest period; WP = pre-wintering period; WM = mid-wintering period; WL = late-wintering period; IS = inside the reserve; OS = outside the reserve.

The full names of the variables are displayed in Table 1.

4. Discussion

We recorded a large number of waterbirds, including a variety of protected species, in the rice fields near Shengjin Lake, a Ramsar site. We found that each waterbird diversity index was generally higher in the rice fields inside the Shengjin Lake Nature Reserve than those outside, likely due to their proximity to the main lake and the conservation measures implemented by the reserve (Li et al., 2019a). As a primary traditional wintering site for waterbirds in the middle and lower reaches of the Yangtze River, Shengjin Lake provides a core habitat for these birds. During the past several decades, Shengjin Lake experienced significant wetland loss and degradation (Li et al., 2015). Although the reserve management committee has implemented a series of conservation measures which have started to generate positive effects (Zhou et al., 2020; Wang et al., 2024), the waterbirds are frequently found to use the surrounding rice fields as their supplementary habitats (Wang et al., 2025). The spatial proximity of the rice fields within the reserve results in their more important supporting roles for the waterbirds than those outside the reserve, thus deserving more conservation attention.

We found that waterbird species richness and the Shannon-Wiener index were highest during the seedling period, likely due to the distinct ecological conditions of rice fields during this stage of growth. The seedling period, the earliest stage of rice growth, is characterized by prolonged flooding, providing ideal breeding, foraging, and roosting sites for waterbirds such as ducks (Pernollet et al., 2015). Additionally, the tender leaves and stems of rice attract small invertebrates, a crucial food source for waterbirds such as shorebirds (Amira et al., 2018). Gull density peaked during the flowering period, likely due to a surge in aquatic insects and other invertebrates, which attracted breeding gulls to forage (Wood et al., 2010). In contrast, at other times of the year, rice field conditions and hydrology may be less favourable for waterbirds. For example, during the early post-harvest period, fields are typically dry, making them less suitable for waterbirds that rely on shallow water habitats (Sesser et al., 2016). Based on these results, the seedling period can be considered a key period for farmland management and waterbird conservation, enhancing rice fields' capacity to support waterbird diversity and fully realizing their conservation value in agricultural landscapes.

During the pre-wintering period, waterbird density was high, due to the large number of geese migrating to Shengjin Lake each winter before dispersing to surrounding areas in search of food (Fan et al., 2020). At this time, leftover rice spikes and plant debris from harvested fields, along with reduced human activity, provide abundant food and suitable undisturbed habitat for geese (Navedo et al., 2015). This phenomenon has also been observed in rice fields across Europe and North America, highlighting the widespread role of rice fields as wintering habitats for geese (Fox and Abraham, 2017). Goose density during this period was higher than in other wintering periods, likely due to the seasonal decline in local bird populations as wintering waterbirds begin their northward migration at the end of winter (Ma et al., 2010). Furthermore, the depletion of residual food in these rice fields further diminishes their attractiveness to waterbirds (Toral and Figuerola, 2010). To enhance the ecological support capacity of these rice fields throughout the entire wintering period, we recommend implementing measures such as supplementary food provision to improve their sustained attractiveness and carrying capacity for waterbirds.

We found that rice fields with larger areas, more irregular shapes, deeper water, and higher drain density had higher waterbird diversity indices. Larger rice fields can offer more food and various microhabitats, attracting a greater variety of waterbird species (Li et al., 2019c; Cheng et al., 2022). During the pre-wintering period, larger fields also supported higher densities of geese and large waders. Fields with higher shape indices are more irregular and often have more field ridges, which not only offer perching and resting areas but also provide shade due to their elevated topography (Merken et al., 2015; Brandolin and Blendinger, 2016). Deeper water and higher drain density also positively influence waterbirds, as many large waders, shorebirds, and vegetation gleaners prefer foraging and roosting in these microhabitats (Valente et al., 2012; Sesser et al., 2018, Aarif et al., 2024). Higher drain density also increases the complexity of water habitats within the rice fields, offering waterbirds more diverse habitat choices (Strum et al., 2013). However, during the seedling period, ducks, large waders, and shorebirds prefer shallower fields, as deeper water can reduce foraging efficiency (Sulai et al., 2015). During the flowering period, fields with higher rice plants showed lower diversity indices and shorebird densities. This might be attributed to the reluctance of birds to forage in closed habitats which may obstacle their views for potential risks. We also acknowledge that this may to some extent be due to our observational bias due to lowered visibility. However, we had tried our best to increase observation time at various points during the surveys to enhance bird detectability. The post-harvest fields, rich in grain remnants, attract more waterbirds, with larger surrounding field areas further enhancing this effect through habitat connectivity (Xia et al., 2024). These findings highlight the importance of spatial structure and microhabitat management in rice fields. We recommend prioritizing the retention of larger, contiguous rice field patches in agricultural management, dynamically regulating water levels according to species-specific requirements, and optimizing drain layouts to enhance

Table 2

Results of GLMMs (coefficient and *P*-value) on the effects of environmental variables on waterbird density, species richness and the Shannon-Wiener index in rice fields near Shengjin Lake in different periods. Results show the final reduced model, after elimination of non-significant terms; variables that are not listed were not significant.

	Variables	Seedling		Flowering		Post-harvest		Pre-wintering		Mid-wintering		Late-wintering	
		Coefficient	*P*-value	Coefficient	*P*-value	Coefficient	*P*-value	Coefficient	*P*-value	Coefficient	*P*-value	Coefficient	*P*-value
Density	AF							20.072	< 0.001				
	DF			1.116	0.017								
	FZ					0.215	0.004						
	AH			- 1.947	< 0.001								
	AD	- 7.816	< 0.001			0.209	0.005					1.064	< 0.001
	DR									9.585	0.023		
	SZ	- 4.558	0.037										
	NH					0.208	0.010						
	NA					0.176	0.024						
Richness	AF	0.207	< 0.001	0.226	0.003	1.042	0.002	0.975	< 0.001	0.658	< 0.001	0.435	< 0.001
	SF			0.264	0.015			0.213	0.015	0.679	< 0.001		
	DF			0.263	0.002								
	DS							- 0.196	0.027	- 0.501	0.010		
	FZ							- 0.746	< 0.001				
	AH			- 0.412	< 0.001			0.174	0.035				
	AD					1.174	< 0.001			0.356	0.001	0.284	0.013
	SZ							- 0.433	< 0.001	- 0.689	0.006		
	NH			- 0.269	0.030	1.078	0.002					- 1.775	0.020
	NC			0.269	0.003								
Shannon-Wiener index	AF	0.208	< 0.001	0.254	< 0.001			0.261	< 0.001	0.132	< 0.001	0.295	< 0.001
	SF									0.064	0.037		
	DF			0.189	0.005								
	DS	0.204	< 0.001										
	FZ					0.097	0.002	- 0.170	< 0.001				
	AH			- 0.249	< 0.001								
	AD					0.113	< 0.001			0.177	< 0.001	0.165	0.024
	NH					0.112	0.001						

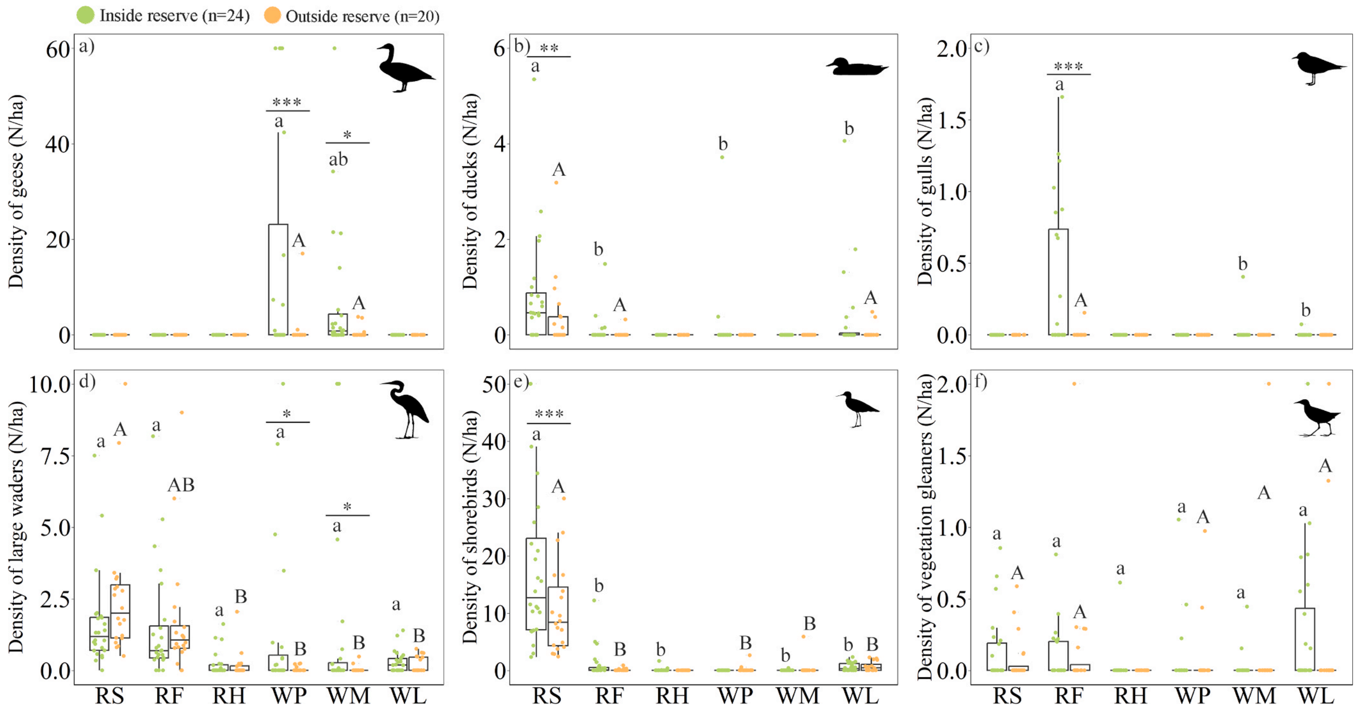

Fig. 3. Densities of geese (a), ducks (b), gulls (c), large waders (d), shorebirds (e), and vegetation gleaners (f) for each survey period in rice fields inside and outside the reserve near Shengjin Lake. The same lowercase letters indicate no significant difference in guild densities between periods inside the reserve, and the same uppercase letters indicate no significant difference in guild densities between periods outside the reserve ($P < 0.05$). The asterisk indicates significant difference in diversity index between inside and outside the reserve in that period (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). The number of sampling sites inside the reserve was 24, and outside the reserve was 20. RS = rice seedling period; RF = rice flowering period; RH = early post-harvest period; WP = pre-wintering period; WM = mid-wintering period; WL = late-wintering period; IS = inside the reserve; OS = outside the reserve.

the ecological functions of rice fields and promote waterbird conservation within agricultural landscapes.

Human disturbances such as activities on roads and in villages may drive waterbirds to seek rice fields farther from such disturbances (Yu et al., 2019). Interestingly, however, our results indicate that during certain periods, such as the seedling and early post-harvest periods, disturbances on rice fields caused by cultivators, automobiles, and humans can positively impact the densities of certain waterbird guilds. This is likely because these disturbances upturn the soil, exposing more food and thereby attracting waterbirds to forage (Fox, 2013; Pan et al., 2019). These agricultural activities, such as intermittent tilling and harvesting, are often localized, allowing waterbirds to avoid direct disturbance while still benefiting from the foraging opportunities created (Mcpeake, 2008). This spatial separation underscores an important perspective: under suitable conditions, agricultural practices and nature conservation can coexist. By rationally arranging the time of agricultural activities, we can achieve a win-win situation between waterbird conservation and agricultural production. Hence, future studies could focus on optimizing agricultural activities to achieve a balance between ecological conservation and agricultural development. Additionally, we recommend developing incentives for rice growers to integrate biodiversity into their management strategies, both within and outside the reserve, as a means of complementing existing regulatory framework (Mameno et al., 2021; Herring et al., 2022).

5. Conclusions

In 2023–2024, we observed that rice fields near Shengjin Lake, a Ramsar site, served as important supplementary habitats for numerous waterbirds. These fields attracted large numbers of waterbirds during the seedling and pre-wintering periods, especially during the seedling period, when species richness and the Shannon-Wiener diversity index were higher. We found that rice fields with larger areas, irregular shapes, deeper water, and higher drain density generally supported higher waterbird densities and species richness. Based on these findings, we recommend that rice field management consider water level regulation and optimized drain design to better meet the foraging and habitat needs of waterbirds. To mitigate human disturbances from main roads and nearby settlements, we suggest enhancing vegetation cover or creating buffer zones to reduce negative impacts on waterbird habitats. Additionally, during certain periods, agricultural activities that disturb the soil expose food resources in rice fields, benefiting waterbird foraging. Therefore, it is essential to evaluate agricultural practices and intensity in relation to their benefits for waterbirds, while balancing waterbird conservation and agricultural productivity. Although our study focused on rice fields at a local scale, it provides a case study of global significance in the context of global loss and degradation of natural wetlands. Future studies may benefit from comparing findings from similar studies across scales and investigate behavioural strategies of waterbirds in rice fields, such as food searching and breeding behaviours. Furthermore, we suggest conducting long-term monitoring of the waterbirds and environmental factors in these artificial wetlands to capture the temporal dynamics to inform timely conservation and management plans.

CRediT authorship contribution statement

Xinsheng Chen: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Chunlin Li:** Writing – review & editing, Writing – original draft, Validation, Methodology, Funding acquisition, Data curation, Conceptualization. **Willem F. de Boer:** Writing – review & editing, Writing – original draft, Methodology. **Yu Zheng:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Yu Chen:** Writing – review & editing, Writing – original draft, Methodology. **Yunwei Song:** Writing – review & editing,

Table 3
Results of GLMMs (coefficient and *P*-value) on the effects of environmental variables on the density of birds in each guild class in rice fields near Shengjin Lake in different periods. Results show the final reduced model, after elimination of non-significant terms; variables that are not listed were not significant.

	Variables	Seedling		Flowering		Post-harvest		Pre-wintering		Mid-wintering		Late-wintering	
		Coefficient	*P*-value	Coefficient	*P*-value	Coefficient	*P*-value	Coefficient	*P*-value	Coefficient	*P*-value	Coefficient	*P*-value
Goose	AF							18.831	< 0.001				
	DR									9.292	0.028		
Duck	AD	- 0.482	0.001										
	DR	- 0.358	0.017										
	SZ	- 0.347	0.019										
	NC			0.220	< 0.001								
Gull	DS			- 0.137	0.006								
	DR			0.196	< 0.001								
	NC			0.160	0.001								
Large wader	AF							1.221	< 0.001	1.511	< 0.001		
	DF					0.113	0.024						
	DS	0.636	0.017										
	AD	- 0.655	0.015			0.123	0.013					0.127	0.012
	NH					0.201	< 0.001						
	NA					0.164	0.002						
	NC	1.438	< 0.001										
Shorebird	AF											0.279	0.011
	SF							0.127	0.040	0.278	0.033		
	DF									0.263	0.043		
	DS											0.254	0.021
	FZ					0.105	0.005						
	AH			- 1.138	< 0.001								
	AD	- 7.016	0.001										
	SZ	- 4.137	0.049									- 0.261	0.015
	NH											- 0.225	0.030
Vegetation gleaner	FZ											- 0.548	0.018
	AD											0.860	< 0.001

Writing – original draft, Methodology. **Guangyao Wang:** Writing – review & editing, Methodology, Conceptualization. **Yong Zhang:** Writing – review & editing, Methodology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109778.

Data availability

Data will be made available on request.

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