

Semi-natural habitats enhance bird diversity in intensively managed farmlands in North China

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ABSTRACT

Agricultural intensification has caused substantial biodiversity loss in farmland worldwide. Although China's farmland accounts for a significant proportion globally, knowledge about farmland heterogeneity and biodiversity remains limited. We examined how semi-natural habitats and habitat heterogeneity affect bird diversity in the intensively managed, low-crop-diversity (wheat–maize rotation) farmland of Qihe County, Shandong Province, China. We applied a multi-scale approach that included patch-scale and transect-scale analyses at both local (100 m buffer) and broader local (200 m buffer) scales across 20 transects, with habitat data classified into eight types: cropland, woody vegetation, herbaceous vegetation, reed, bare ground, tomb (small, earthen mounds with spontaneous vegetation), water, and artificial infrastructure. Bird richness and abundance were recorded within 100 m on either side of each 500 m transect. At the patch scale, Semi-natural habitats—particularly tombs, woody vegetation, and reeds—supported higher bird richness and abundance. At both local and broader local scales, semi-natural habitats positively influenced bird richness, but their positive effect on abundance occurred only at the local scale; woody vegetation, herbaceous, and reed were most important locally, while at the broader scale, richness was mainly associated with woody vegetation, herbaceous, and bare ground. Habitat diversity (SHDI) positively affected species richness, edge density (ED) of semi-natural habitat had a positive effect on bird abundance, and mean patch size showed limited effects. These results indicate that biodiversity in intensively farmed landscapes can be enhanced through the management of semi-natural habitats and habitat heterogeneity, highlighting the importance of maintaining these habitats and improving landscape connectivity.

1. Introduction

To address the urgent challenges of climate change, ecological degradation, and environmental health issues, China launched the Beautiful China Initiative in 2013 (Qin et al., 2024). This initiative underscores the country's commitment to ecological civilization, including biodiversity conservation, as reaffirmed in international frameworks such as the Kunming-Montreal Global Biodiversity Framework (Convention on Biological Diversity, 2022). However, frameworks for evaluating progress in biodiversity protection remain vague (Guan et al., 2024), partly due to the inherent complexities and difficulties in measuring biodiversity (Qin et al., 2023). As a result, conservation

efforts often emphasize nature reserves and protected areas, while farmland is still primarily regarded as an economic resource for agricultural production.

Yet farmland plays a vital, if underappreciated, role in supporting biodiversity. Biodiversity contributes crucial ecosystem services such as pollination, soil fertility, and natural pest control (Albrecht et al., 2020; Martin et al., 2019), and many studies have shown that cultural agricultural landscapes can maintain significant species richness (Klein et al., 2025; Li et al., 2020a; Li et al., 2020b). This is especially relevant in China, which ranks third globally in cropland area (FAO, 2023), making its agricultural landscapes not only essential for national food security, but also critical for biodiversity conservation at a global scale.

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Globally, farmland biodiversity has declined mainly due to habitat loss, agricultural intensification, degradation and climate change, with farmland birds being the most prominent and well monitored indicator group (Attwood et al., 2009; Donald et al., 2006; Jeanneret et al., 2021; Stanton et al., 2018). Birds are key indicators of ecosystem health and biodiversity in agricultural landscapes (Fraixedas et al., 2020; Gregory et al., 2003), and provide critical ecosystem services, such as pest control, pollination, maintaining ecological balance (Boesing et al., 2017; Mayne et al., 2023; Sekercioglu, 2006; Whelan et al., 2008). While a few bird species may occasionally cause crop losses, their overall contributions far outweigh their negative impacts (Huang et al., 2023), making farmland bird protection crucial for sustainable agriculture and biodiversity conservation.

Importantly, non-protected farmlands also support a variety of bird species (Das et al., 2025; Li et al., 2020a; Li et al., 2020b; Mupepele et al., 2021). Despite the extensive farmland coverage in China, long-term trends of farmland bird populations remain poorly documented. However, an analysis of 78 sample areas representing diverse habitats of breeding birds, observed continuously from 2011 to 2017, revealed a decreasing trend in population density for 50% of the 556 bird species (Zhang, 2018). Agricultural landscapes, while often simplified and intensively managed, still provide important breeding, foraging, and sheltering opportunities, particularly when semi-natural habitats are present (Johnson et al., 2011; Li et al., 2020a; Li et al., 2020b).

The presence and quality of semi-natural habitats play a decisive role in maintaining farmland bird diversity. Semi-natural habitats, including linear elements, areal habitats and small patches (Herzog et al., 2017), are essential for enhancing biodiversity and supporting ecosystem services in agricultural landscapes (Dufлот et al., 2015; Olimpi et al., 2022; Šálek et al., 2022; Tarjuelo et al., 2020). These elements act as connecting corridors, stepping stones, nesting sites, and foraging grounds, especially for species with specific habitat preferences (Hietala-Koivu et al., 2004; Šálek et al., 2022). Bird communities are often closely linked to such features (Miller and Cale, 2000; Whittingham et al., 2009), making their integration into farmland management essential to achieving the goals of the Beautiful China Initiative.

Semi-natural habitats show a decreasing trend in agricultural landscapes across specific regions of China (Liu et al., 2024a, 2024b, Liu et al., 2019), despite their crucial role in maintaining biodiversity. Research on their ecological functions in Chinese farmland remains limited and regionally fragmented. Existing studies highlight the importance of non-crop habitats in enhancing bird diversity, particularly in southern China, where small fields with diverse crop types dominate (Lee et al., 2024, Lee et al., 2022; Lee and Goodale, 2018; Li et al., 2020b; Liao et al., 2020). Another form of semi-natural habitat in this region is the tomb (family graveyard). Tombs function as small, non-cultivated patches interspersed throughout the agricultural landscape of the North China Plain. These culturally significant features, being spared from routine farming activities, develop spontaneous vegetation, making them important refuges for biodiversity. Their great value as semi-natural habitats for plants was demonstrated in a study in Hebei Province, China (Gong et al., 2021). Similarly, the vegetation that grows in irrigation ditches has also been shown to benefit bird diversity by providing diverse habitats and enhancing resource availability (Hu et al., 2025; Lu et al., 2019). These findings underscore the critical role of semi-natural habitats across different agricultural regions in China, while also reflecting the limited scope of current research and the need for further exploration in other regions. At the policy level, China's biodiversity strategies remain focused on productivity and protected areas, lacking specific provisions for semi-natural habitats conservation—unlike EU frameworks that integrate such measures into agri-environmental schemes (Liu et al., 2022; Ministry of Agriculture and Rural Affairs of the People's Republic of China, 2021; Ministry of Ecology and Environment of the People's Republic of China, 2024). This underscores the need for further research on “everyday agricultural landscapes” in China, to provide a scientific basis for advice to the

administration on how to integrate semi-natural habitat conservation into agricultural landscape management (Li et al., 2020a; Li et al., 2020b; Liu et al., 2013).

The effects of habitat and landscape structures on biodiversity are scale-dependent (Benton et al., 2003; Wiens, 1989), necessitating multi-scale assessments to design effective conservation strategies. Bird diversity responds to these factors across patch (discrete, homogeneous habitat patches, e.g., woody vegetation or reed beds; Klein et al., 2023; Mühlner et al., 2012), field (Christina, 2012; Gonthier et al., 2014), landscape (Billeter et al., 2008; Gil-Tena et al., 2015; Reiley and Benson, 2019), and regional scales (Buchanan et al., 2017). While studies on farmland bird diversity in China have explored local and landscape scales (D. Li et al., 2020a; Li et al., 2020b; Liao et al., 2020), with some multi-scale research combining these two (Lee, 2022; Lee et al., 2022; Lee and Goodale, 2018), finer-scale analyses, such as patch and transect-based studies, remain rare. Based on this context, this study addresses this gap by employing a multi-scale approach to explore bird-habitat relationships across spatial extents. In this study, we incorporated habitat variables at the patch scale and two transect-buffer scales, defining the 100 m buffer as the local scale and the 200 m buffer as a broader local scale.

This study aims to assess the drivers of bird diversity in the intensively farmed North China Plain by investigating the effects of both local habitat types and habitat structure across multiple scales. We evaluated how bird species richness and abundance are influenced by: semi-natural habitats (woody and herbaceous vegetation, reeds, bare ground, water and tombs—classified as such and manifesting as small, earthen mounds with spontaneous vegetation), cropland and artificial infrastructure (paved/dirt roads, buildings) at the patch scale and within transect buffers at the local (100 m) and broader local (200 m) scales. In addition, we quantified local heterogeneity at both buffer scales using metrics of habitat composition and configuration. Our findings provide valuable insights for biodiversity conservation and management in Chinese agricultural landscapes.

2. Methods

2.1. Study area

This study was conducted in Qihe County, Shandong Province, China (36°24'37"-37°1'44"N, 116°23'28"-116°57'35"E), located in the lower plains of the Yellow River, a representative region of the North China Plain. The region experiences a temperate semi-humid monsoon climate, with an average annual temperature of 13.5 °C, annual precipitation of 622 mm, and a frost-free period of 217 days. The topography is characterized by a gentle slope, descending from southwest to northeast, with elevations between 19 and 35 m above sea level. Qihe County spans 1411 km², with 839.4 km² of cultivated land. Agricultural management is uniform and consists of a simple rotation of winter wheat followed by maize that alternate synchronously on virtually all parcels, yielding two harvests per year. The management practices for wheat and maize were evaluated using questionnaires completed by 30 farmers from 15 townships in Qihe County, and the results are summarized in Tables S1. On average, farmers apply 465 kg (+/- 196) of nitrogen per hectare and year (both crops combined) and count 7.0 (+/- 1.4) pesticide applications. The farmland is intersected by mostly unsealed irrigation ditches. During the irrigation period, the ditches contain water, but during the non-irrigation period, water levels are very low, or they fall completely dry. Woody vegetation, herbaceous vegetation, and reeds are also present within the farmland, though most of these habitats are concentrated in the ditches. Occasionally, tombs can be found as burial mounds in the middle of the fields, which are spared from labouring and cropping. The overall forest cover is approximately 35%, mainly consisting of planted willow (*Salix babylonica* L.) or poplar (*Populus* spp.) trees.

2.2. Transect selection

In this study, we selected twenty 1 km × 1 km sites as landscape units. Within each site, a 500 m transect line was chosen for field survey. The site selection process followed an adapted method from Pasher et al. (2013), using a land cover map (10 m resolution). This map was created through visual interpretation of 2019 remote sensing images (0.5 m resolution), obtained from a data-sharing platform (<http://www.rivemap.cn/>). Fragstats V4.2 (McGarigal et al., 2023) was used to compute habitat metrics.

The site selection process consisted of four main steps. Step 1: We

identified potential study areas where farmland covered 60% to 90% of the total land cover by using moving window analysis. Step 2: To capture landscape heterogeneity, we used Mean Patch Size as the key metric to capture variation in landscape configuration, since landscape composition was homogeneous due to the consistent rotation of winter wheat and summer maize. Step 3: Maximizing variation of Mean Patch Size to select a maximum extent for further analysis. According to the coefficients of variation (Fig. S1) for Mean Patch Size with increasing spatial extent, 1 km × 1 km was select as the maximum extent for analyses. Farmland in Qihe County is fragmented among smallholders, and this extent adequately encompasses multiple operational farm units.

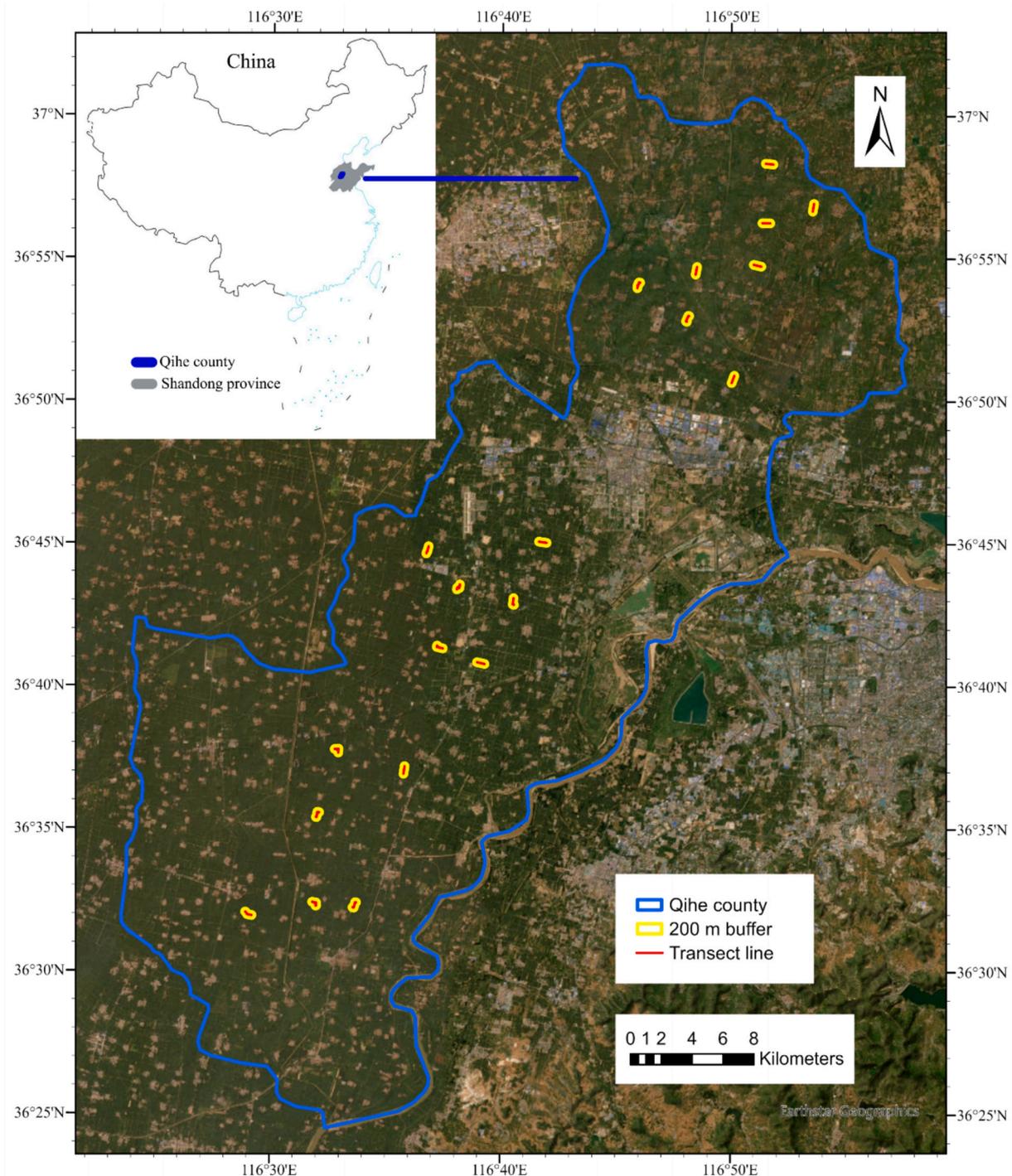


Fig. 1. Location of the study area and spatial distribution of the 20 bird survey transects in Qihe County, Shandong Province, China. The base maps were sourced from <https://www.tianditu.gov.cn/>.

Moreover, this scale aligns with previous studies in agricultural landscapes (Fahrig et al., 2015; Li et al., 2020b). Step 4: To avoid spatial autocorrelation, we ensured a minimum center-to-center distance of 2.6 km between sites. This distance threshold was determined based on a spatial autocorrelation analysis of the Mean Patch Size, where Moran's I fell below 0.4 (Fig. S2).

We used drone images captured in 2022 to identify a 500 m transect within each site and map the detailed land use. These transects were positioned along low-traffic roads or at the edges of farmland to ensure easy access on foot. All 20 selected transects (Fig. 1) were dominated by farmland, with varying proportions of semi-natural habitats (e.g., woody vegetation, reed beds, and herbaceous vegetation patches) embedded within the agricultural landscape. The presence of these habitat elements ensured representation of diverse structural types for examining bird-habitat relationships.

2.3. Data collection

2.3.1. Bird data

All bird surveys were conducted by a single observer to minimize potential bias introduced by multiple observers. Birds observed within 100 m on either side of the transect line were recorded following standard methods applied in previous field studies on birds (Assandri et al., 2016; Klein et al., 2023; Marcacci et al., 2020). Each transect was surveyed by an observer over approximately 30 min, allowing sufficient time to record all birds while maintaining a consistent pace. Each transect was surveyed three times in 2023: from 9 May to 20 May, from 4 June to 11 June, and from 27 June to 1 July. During the first survey, wheat was in the late growing season, with fields covered by uniform, tall, dense, and fully green vegetation. During the second survey, wheat had turned completely yellow and ceased growth but had not yet been harvested, resulting in dry, upright, golden-yellow standing crops with continuous cover. The third survey was conducted after large-scale wheat harvest, when most fields were open bare land with low stubble, and a few fields had been sown with summer crops (mainly maize), whose seedlings had emerged to about 20 cm, forming low, green vegetation patches. The order in which the 20 transects were surveyed was randomized to ensure that no single transect was consistently observed at the same time of day, reducing potential time-of-day biases. Surveys were conducted from sunrise to up to four hours after sunrise. Weather conditions during the surveys were generally favourable, with mostly sunny or partly cloudy skies and no precipitation, fog, or strong winds. During field surveys, the precise location of each bird detection was marked on a printed map. All observation points (Fig. 2) were subsequently digitized manually in ArcGIS Pro (Version 3.2.0, Esri Inc., 2023), allowing each record to be spatially linked to both the surrounding habitat categories and the specific habitat patch in which it occurred. Although flying birds were recorded during the surveys, they were excluded from further analysis to focus on stationary or foraging birds within the transects.

2.3.2. Habitat data

Detailed habitat data were collected within a 200 m buffer surrounding each transect (Fig. 2), extending beyond the 100 m bird survey range to capture broader local context. Using drone imagery and field surveys digitalized in ArcGIS Pro (Version 3.2.0, Esri Inc., 2023), habitats were initially classified into eight specific categories: Cropland, Woody vegetation, Herbaceous vegetation, Reed, Bare ground, Tomb, Water, and Artificial infrastructure (Table 1).

For the purposes of analysis, a dual habitat classification scheme was established to capture both broad- and specific-scale habitat effects. The broad habitat classification consisted of three categories—Cropland, Semi-natural habitat, and Artificial infrastructure—which allowed us to first evaluate the overall influence of semi-natural habitats on bird diversity. To further examine habitat effects at a finer resolution, the specific habitat classification included eight habitat types: Cropland,

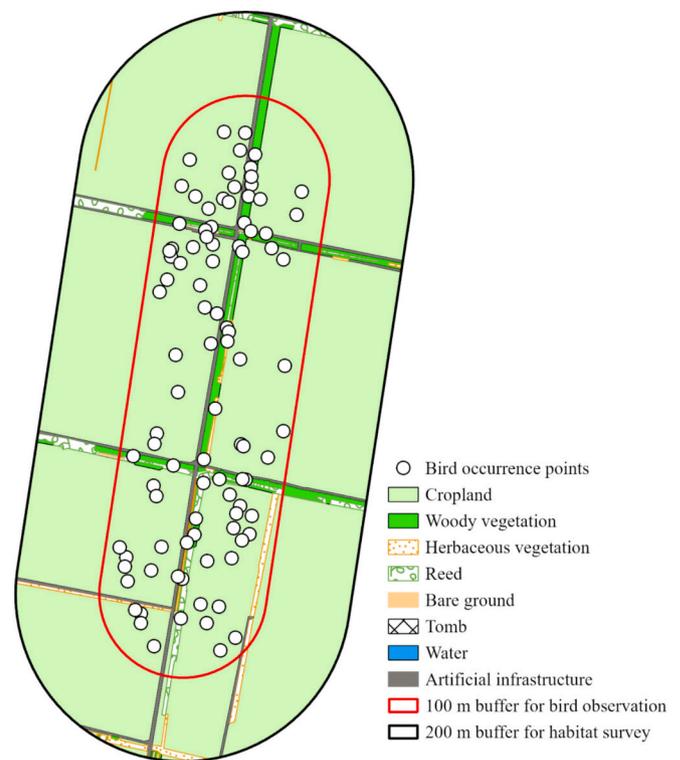


Fig. 2. Actual spatial distribution of habitat types and corresponding bird occurrence records along Transect 15 (1 of 20 study transects, 200 m buffer width) in Qihe county, Shandong province China.

Woody vegetation, Herbaceous vegetation, Reed, Bare ground, Tomb, Water, and Artificial infrastructure. Based on this specific classification, individual habitat patches were delineated in the digitalized habitat map as discrete, homogeneous areas of a single habitat type, represented as continuous polygons within the 200-m buffer. For the broad classification, all polygons corresponding to the six semi-natural habitat types (Woody vegetation, Herbaceous vegetation, Reed, Bare ground, Tomb, Water) were relabelled as Semi-natural habitat. Adjacent or contiguous semi-natural polygons were then merged into a single continuous semi-natural patch, while isolated semi-natural polygons remained as separate patches.

2.3.3. Habitat structure data

Based on broad habitat category, habitat composition and configuration metrics were calculated for each transect at both the 100 m and 200 m buffer scales. Landscape composition was quantified using the Shannon's Diversity Index (SHDI) (Lee and Martin, 2017; Liao et al., 2020), while habitat configuration was characterized by Edge Density (ED) (Klein et al., 2023; Liao et al., 2020) and Mean Patch Size (AREA_MN) (Fahrig et al., 2015; Frank et al., 2024) of semi-natural habitats. This subset of metrics was selected to represent complementary aspects of habitat structure while maintaining statistical parsimony given the limited sample size ($n = 20$ transects). As an initial screening step, pairwise Pearson correlations among all habitat structure metrics were examined, and all correlation coefficients were below $|0.7|$ (see Table S20) (Dormann et al., 2013), indicating no strong pairwise collinearity at the metric-selection stage.

2.4. Data analysis

Species richness was calculated as the total number of species detected across all three surveys for each transect and for each individual habitat patch (i.e., any species recorded at least once was included). Abundance was calculated as the total number of individuals

Table 1
Classification and description of mapped habitat types.

Broad habitat category	Specific habitat type	Description
Cropland	Cropland	Agricultural fields primarily planted with wheat or maize during the field survey, with a few patches of other crops such as garlic or scallions.
	Woody vegetation	Areas containing single trees or patches of woody vegetation.
	Herbaceous vegetation	Grass-dominated areas with non-woody plants, excluding reed or trees.
	Reed	Areas dominated by reed.
Semi-natural habitats	Bare ground	Open ground without any visible vegetation, neither grass, reed or trees.
		Bare ground occurs at the edges of cropland, in ditches, or alongside water bodies, but does not include other semi-natural habitats. Examples include soil patches along field margins or bare surfaces in ditches.
	Tomb	Family graveyards, typically appearing as a small, rounded earthen mound in or near cropland. They occur both as isolated patches and in clusters, with the latter forming larger, more complex semi-natural habitat islands. Spared from routine farming, these tombs support spontaneous herbaceous vegetation and, particularly in larger clusters, scattered trees. This varied structure provides critical refuge and resources for biodiversity. Tombs represent semi-natural habitat islands and are common features in rural agricultural landscapes in China.
	Water	Water bodies such as ponds, rivers, and water in ditches. Man-made structures and surfaces designed for human utility with minimal ecological function, including paved or dirt roads and buildings. These features are typically maintained through regular anthropogenic intervention and lack self-sustaining vegetation, distinguishing them from semi-natural constructs like vegetated ditches and tombs.
Artificial infrastructure	Artificial infrastructure	

observed across the three surveys for each transect and for each individual habitat patch. All statistical analyses were performed using software R version 4.4.1 (R Core Team, 2024).

2.4.1. Habitat and bird diversity at patch scale

Before conducting patch-scale analyses, each bird observation was spatially assigned to the habitat patch in which it occurred. Using the digitized bird locations and the habitat patch map, every detection was linked to a specific patch polygon. For each patch, we then calculated patch-scale bird species richness (the number of species recorded within the patch) and bird abundance (the total number of individuals recorded within the patch). These patch-scale biodiversity metrics, together with the corresponding habitat type of each patch, formed the basis of the patch-scale analysis.

We compared mean species richness among habitats using individual-based rarefaction and extrapolation curves (type = 1) following (Colwell et al., 2012). This approach estimates the expected number of species for a standardized number of individuals, allowing for comparisons among habitats with unequal sampling effort. The analysis was conducted for both the three broad habitat categories and the eight specific habitat types. The rarefaction curves show mean species richness and 95% confidence intervals for each habitat. All analyses were performed using the iNEXT package (Hsieh et al., 2016) in R.

At the patch scale, Generalized linear mixed models (GLMMs) with the “glmer” function of the lme4 package (Bates et al., 2022) were used

to assess the effects of broad habitat categories, and generalized linear models (GLMs) with the “glm” function of the stats package (Bates et al., 2022) were applied for the eight habitat types, on species richness and abundance. Species richness or abundance were used as the response variables, while habitat type was treated as an explanatory categorical variable, with cropland set as the reference level to allow comparison of other habitat types. Transect ID was included as a random effect to account for non-independence of patches within the same transect. The logarithm of patch area, log (area), was incorporated into the model using the “offset” function to adjust for patch size (Hilbe, 2011), to account for the species-area relationship. We evaluated model performances by checking dispersion (“dispersion_glm” function of the blmeco package, Korner-Nievergelt et al., 2015), zero-inflation, AIC, and residuals to select the most suitable model. In cases of overdispersion, negative binomial models were used instead of Poisson (Hilbe, 2011).

To assess potential spatial autocorrelation in patch-scale models, we applied a two-step diagnostic approach.

First, spatial autocorrelation in model residuals was evaluated using Moran's I based on transect centroid coordinates and inverse-distance spatial weights. This analysis tested whether residuals from the patch-scale models exhibited spatial structure at the level of transect centroids. No significant spatial autocorrelation was detected in the overall model residuals. Second, to account for potential within-transect spatial dependence, spatial autocorrelation was assessed separately for each transect by examining patch-level residuals within distance thresholds ranging from 100 to 500 m. Among the 20 transects, only 0–3 showed significant Moran's I values (see Tables S5, S7), indicating that spatial dependence was weak and not systematic across transects. In addition, patch-level spatial covariates were included in alternative model formulations to evaluate whether explicit spatial terms improved model performance. Model fit, assessed using R^2 , showed no meaningful improvement after including these spatial variables. Based on these diagnostics, spatial autocorrelation was considered negligible at the patch scale and was therefore not explicitly incorporated into the final models.

2.4.2. Habitat and bird diversity at local (100 m buffer) and broader local scale (200 m buffer)

At the local and broader local scale, we examined how the composition of different habitat types surrounding each transect affected bird diversity, with each transect serving as an independent sampling unit. The bird data comprised all species and individuals detected within 100 m on both sides of each transect. The corresponding habitat data were quantified by calculating the total area of each habitat type within two buffer distances – 100 m and 200 m - from each transect line.

Because cropland area was strongly correlated with the areas of other habitat types, we used principal component analysis (PCA) to summarize habitat composition into a reduced set of independent gradients at each scale and for each habitat classification scheme (three broad categories and eight specific habitat types). PCA was conducted on log-transformed (log (x + 1)) and standardized habitat-area variables.

Generalized linear models (GLMs) and their extensions were employed to relate bird species richness and abundance to the resulting PCA axes at both the local (100 m) and broader local (200 m) scales. Models including different numbers of PCA axes were compared using AIC and Nagelkerke R^2 (see Tables S9, S12, S15, S18), and the most parsimonious models were retained for inference. To account for differences in dispersion, Poisson models were initially fitted; negative binomial models were used for overdispersed data, and Generalized Poisson (GP, using VGAM package) models were evaluated for underdispersed data, following established procedures (Giuffrè et al., 2013; Harris et al., 2012; Muchika et al., 2020). Across scales, habitat composition was thus represented by continuous PCA-derived variables, whereas at the patch scale habitat types were treated as categorical variables with cropland as the reference category.

2.4.3. *Habitat structure and bird diversity at local (100 m buffer) and broader local (200 m buffer)*

To complement the habitat-area-based analysis, we further examined the influence of habitat structure on bird diversity the local (100 m) and broader local (200 m) scales. Key habitat composition and configuration metrics—SHDI, ED, and AREA_MN—were calculated within 100 m and 200 m buffers around each transect based on the three broad habitat categories: cropland, semi-natural habitats, and artificial infrastructure. SHDI reflects overall habitat heterogeneity across all three categories, while ED and AREA_MN specifically describe the configuration of the semi-natural habitat component. This approach provides a parsimonious yet ecologically meaningful characterization of habitat composition and structure relevant to bird richness and abundance.

To ensure comparability among variables measured on different scales and units, all landscape metrics were standardized using z-score transformation (mean-centered and scaled to unit variance) via the scale () function in R. prior to model fitting, variance inflation factors (VIF) were calculated to assess multicollinearity among local metrics. All VIF values were below 2 (Tables S21, S22), indicating low multicollinearity. Generalized linear models (GLMs) and their extensions were employed. Poisson regression models were initially fitted for bird species richness and abundance, with negative binomial models used for overdispersed data and Generalized Poisson models used for underdispersed data. This approach allowed us to rigorously assess the effects of habitat structure at the local and broader local scales on bird diversity while maintaining consistency with the habitat-area-based analyses.

3. Results

3.1. *Habitat and bird data*

All 20 transects were dominated by farmland (71.3% - 94.1% coverage; median = 90.3%) within the 200 m buffer, with semi-natural habitats (4.4% - 25.5%; median = 7.9%) and artificial infrastructure (0.9% to 5.5%; median = 1.7%) comprising the remaining area. Within the semi-natural habitats, woody vegetation (12.0% - 73.3%; median = 36.1%), reed (0.4% - 53.7%; median = 25.8%), and herbaceous vegetation (5.1% - 74.7%; median = 29.4%) were the predominant types. Other habitat elements occurred infrequently within semi-natural habitats: bare ground (0%–7.7%; median = 1.2%), water (0%–6.1%, median = 0.5%), and tombs (present in only 5 transects, max = 6.5%). Most of the semi-natural habitats were located in ditches (73.2%). The bird data included 2144 individuals from 36 species with Reed Parrotbill

(*Paradoxornis heudei*) as near threatened according to IUCN (2023) (Tables S2, S3). Along the transects, total bird species richness ranged from 7 to 18 bird species, and total abundance from 55 to 164 individuals. Patch characteristics, species richness and abundance across habitat categories are summarized in Table 2.

At patch scale, the rarefaction–extrapolation curves supported these habitat associations. Species richness was highest in semi-natural habitats, followed by cropland and artificial infrastructure (Fig. 3). When specific habitat types were considered (eight-class analysis), cropland and woody vegetation supported the highest observed richness, followed by reed and herbaceous vegetation, while bare ground, tomb, and water patches supported few species (Fig. 4).

3.2. *Habitat and bird diversity at patch scale*

Based on the patch scale model with three broad habitat categories—using cropland as the reference—both semi-natural habitats and artificial infrastructure supported significantly higher bird richness and abundance compared to cropland (Table S4). This pattern is consistent with the observed data, where both the richness-based (Fig. 5c) and abundance-based (Fig. 5a) violin plots show much higher bird densities in semi-natural habitats and artificial infrastructure compared with cropland. Among them, semi-natural habitats contributed the most to supporting bird diversity. The Marginal R² of the patch-scale model was 0.64 for species richness and 0.58 for abundance (Table S4), reflecting the contribution of fixed effects in the patch-scale models. The random effect of transect accounted for only a small portion of the variance, 0.05 in the richness model and with 0.03 in the abundance model (Table S4).

Based on the patch-scale model with eight habitat types—again using cropland as the reference—all seven other habitat types showed significantly higher predicted bird richness and abundance than cropland (Table S6). This pattern is consistent with the observed data, where violin plots show higher bird densities in all non-cropland habitats compared with cropland (Fig. 5b and Fig. 5d). Tomb showed the highest predicted bird richness and abundance. This was followed by woody vegetation, bare ground, reed, water, herbaceous vegetation, artificial infrastructure, and cropland, which exhibited progressively lower richness and abundance with smaller confidence intervals. The patch model (Table S5) for abundance (Marginal R²: 0.51) performed better than the patch model for richness (Marginal R²: 0.42).

Table 2
Bird counts and composition of habitat in the transects.

Specific habitat type	Bird counts in 100 m buffer		100 m buffer		200 m buffer
	Number of species	Number of individuals	Number of Patches	Habitat area per transect [ha] (Mean ± SE, Min–Max)	Habitat area per transect [ha] (Mean ± SE, Min–Max)
Cropland	24	977	193	11.31 ± 0.99 (7.73–12.55)	28.27 ± 2.31 (21.93–30.53)
Semi-natural habitats	32	1076	189	1.35 ± 0.83 (0.29–4.39)	3.09 ± 1.76 (1.45–7.85)
-Woody vegetation	21	624	275	0.55 ± 0.72 (0.13–3.31)	1.36 ± 1.38 (0.28–5.75)
-Herbaceous vegetation	16	196	253	0.42 ± 0.24 (0.02–1.15)	0.90 ± 0.52 (0.08–2.13)
-Reed	18	199	122	0.31 ± 0.25 (0.01–0.97)	0.67 ± 0.51 (0.03–2.12)
-Bare ground	4	28	35	0.04 ± 0.05 (0.00–0.17)	0.09 ± 0.15 (0.00–0.58)
-Tomb	4	12	16	0.01 ± 0.03 (0.00–0.12)	0.01 ± 0.03 (0.00–0.13)
-Water	3	17	19	0.04 ± 0.06 (0.00–0.23)	0.06 ± 0.10 (0.00–0.33)
Artificial infrastructure	7	91	43	0.30 ± 0.09 (0.16–0.56)	0.63 ± 0.31 (0.30–1.75)

Note: All values represent totals across 20 transects.

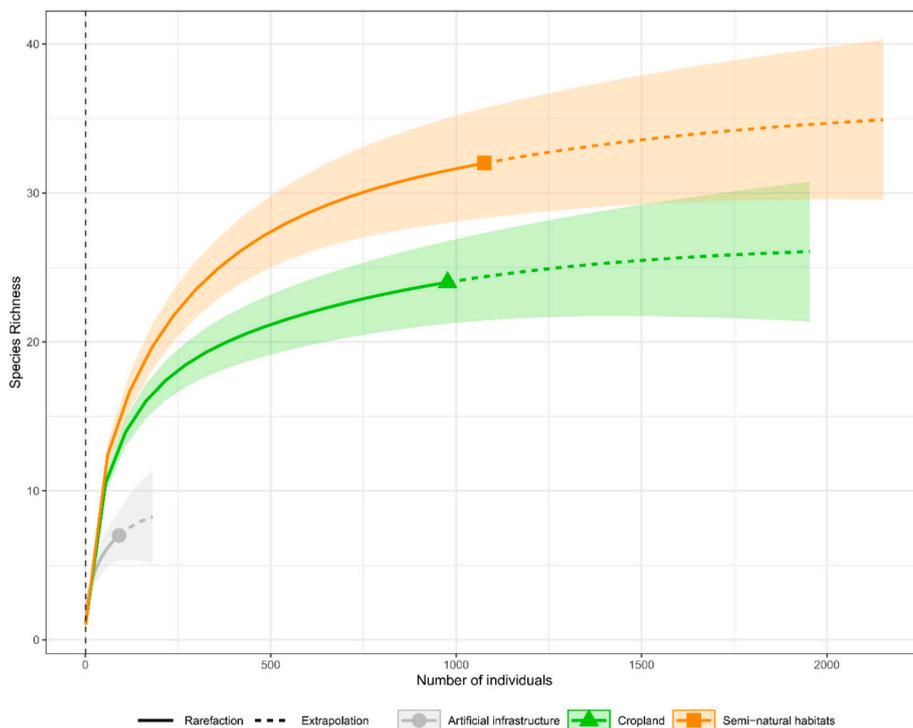


Fig. 3. Species accumulation curves for three broad habitat categories based on individual-based rarefaction, with 95% confidence intervals.

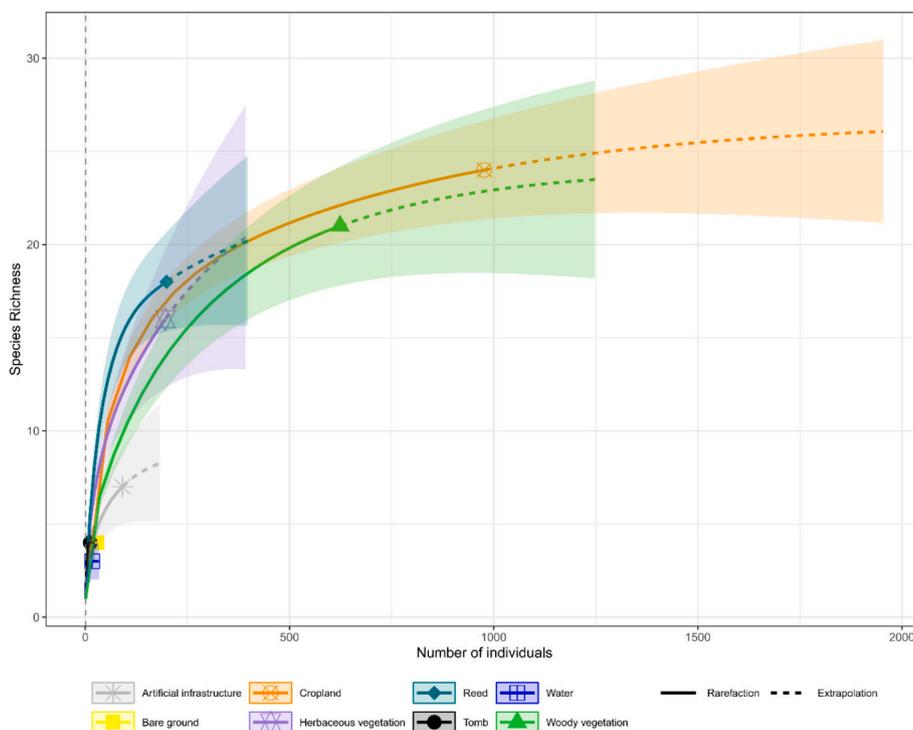


Fig. 4. Species accumulation curves for eight specific habitat types based on individual-based rarefaction, with 95% confidence intervals.

3.3. Habitat and bird diversity at local (100 m buffer) and broader local (200 m buffer) scales

At the local scale (100 m buffer), PCA of habitat composition based on three broad habitat categories (cropland, semi-natural habitats, artificial infrastructure) identified PC1 and PC2 as major axes of variation, explaining 70% and 25% of the total variance, respectively. PC1

contrasted cropland with semi-natural habitats and artificial infrastructure (main loadings: cropland = 0.65, semi-natural = -0.62, artificial = -0.44) (see Table S8), while PC2 contrasted semi-natural habitats with cropland and artificial infrastructure (main loadings: semi-natural = 0.43, artificial = -0.88, cropland = -0.19). GLMMs showed that PC1 was negatively associated with bird richness (Estimate = -0.09, $p < 0.01$) and abundance (Estimate = -0.08, $p < 0.05$) (see

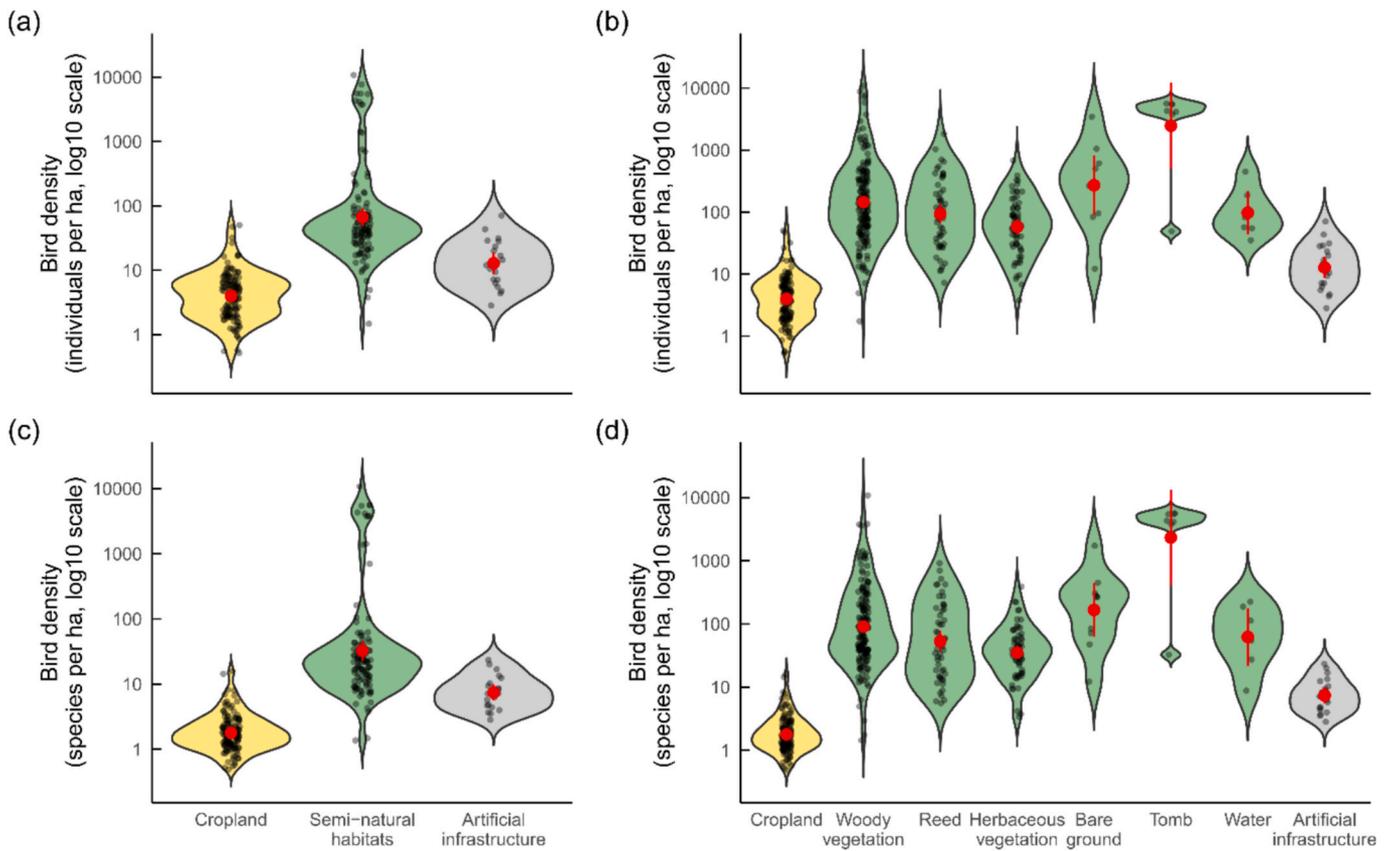


Fig. 5. Observed bird density for a) individuals and c) species across three broad habitat categories, and for (b) individuals and (d) species across eight specific habitat types at patch scale.

Fig. 6a, b), whereas PC2 was positively associated with both richness (Estimate = 0.14, $p < 0.01$) and abundance (Estimate = 0.14, $p < 0.01$) (see Table S10).

Based on eight specific habitat types (cropland, woody vegetation, herbaceous vegetation, reed, bare ground, tomb, water, artificial

infrastructure), PCA identified PC1 and PC2 as major axes, explaining 34% and 16% of the total variance, respectively. PC1 contrasted cropland with woody vegetation, water, and other semi-natural habitats (main loadings: cropland = 0.53, woody = -0.51, water = -0.36) (see Table S14), while PC2 contrasted herbaceous and reed vegetation with

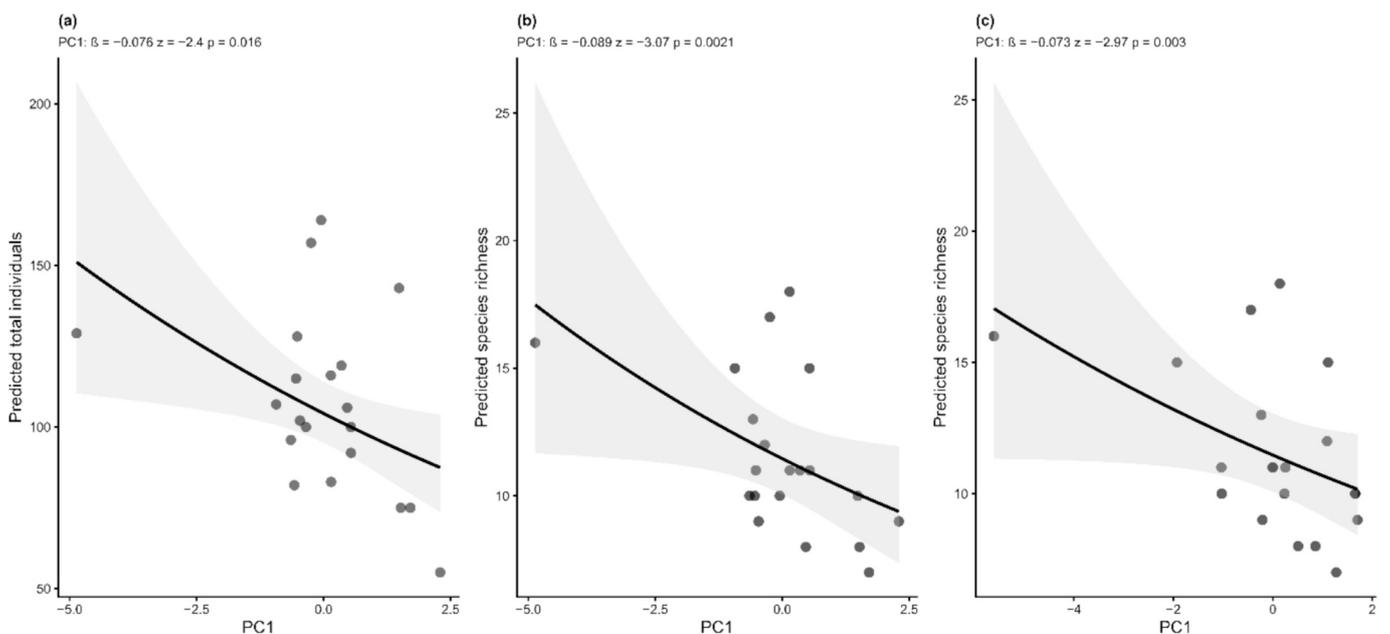


Fig. 6. Relationships at the local scale (100 m buffer) between the first principal component (PC1) and (a) bird abundance, (b) species richness (both analyzed for three broad habitat categories), and (c) bird species number (analyzed for eight specific habitat types). Shaded areas indicate 95% confidence intervals.

cropland, bare ground, and artificial infrastructure (main loadings: herbaceous = 0.69, reed = 0.42, bare ground = -0.40, artificial = -0.31, cropland = -0.25) (see Table S14). GLMMs showed that PC1 was negatively associated with bird richness (Estimate = -0.07, $p < 0.01$) (see Fig. 6c) but not abundance (Estimate = -0.03, $p = 0.27$), whereas PC2 was positively associated with both richness (Estimate = 0.12, $p < 0.01$) and abundance (Estimate = 0.14, $p < 0.001$) (see Table S16).

At the broader local scale (200 m buffer), PCA of three broad habitat categories identified PC1 as the dominant axis of variation, explaining 77% of the total variance. PC1 contrasted cropland with semi-natural habitats and artificial infrastructure (main loadings: cropland = -0.63, semi-natural = 0.61, artificial = 0.48) (see Table S11). GLMMs showed that PC1 was positively associated with bird richness (Estimate = 0.10, $p < 0.01$) but not abundance (Estimate = 0.05, $p = 0.22$) (see Table S13).

PCA based on eight specific habitat types at the broader local scale identified PC1 and PC2 as major axes of variation, explaining 39% and 19% of the total variance, respectively. PC1 contrasted woody vegetation, artificial infrastructure, and water with cropland (main loadings: woody = 0.47, artificial = 0.43, water = 0.34, cropland = -0.52) (see Table S17), while PC2 contrasted bare ground with herbaceous and reed vegetation (main loadings: bare ground = -0.63, herbaceous = 0.47, reed = 0.38, artificial = -0.32, cropland = -0.21) (see Table S17). GLMMs showed that PC1 was positively associated with bird richness (Estimate = 0.07, $p < 0.01$) but not abundance (Estimate = 0.02, $p = 0.46$), and PC2 showed marginal positive associations with richness (Estimate = 0.07, $p = 0.08$) and abundance (Estimate = 0.08, $p = 0.06$) (see Table S19).

3.4. Habitat structure and bird diversity at local (100 m buffer) and broader local (200 m buffer) scales

In the local (100 m) habitat structure analysis, ED of semi-natural habitats showed a significant positive effect on bird abundance ($\beta = 0.14$, SE = 0.06, $z = 2.54$, $p < 0.05$), while AREA_MN of semi-natural habitats exhibited a marginally positive effect ($\beta = 0.09$, SE = 0.05, $z = 1.88$, $p = 0.06$). In contrast, SHDI had no significant effect. For bird species richness in the local scale, SHDI exhibited a marginally significant positive effect ($\beta = 0.11$, SE = 0.06, $z = 1.83$, $p = 0.07$). In contrast, neither ED nor AREA_MN of semi-natural habitats showed significant effects (Table S21).

At the broader (200 m) scale, a different pattern emerged. ED of semi-natural habitats showed a significant positive effect on bird abundance ($\beta = 0.14$, SE = 0.07, $z = 2.05$, $p < 0.05$). In contrast, neither SHDI nor AREA_MN of semi-natural habitats showed significant effects. For bird species richness in the broader scale, SHDI exhibited a significant positive effect ($\beta = 0.14$, SE = 0.07, $z = 2.12$, $p < 0.05$). However, neither ED nor AREA_MN of semi-natural habitats showed significant effects (Table S22).

4. Discussion

Our results indicate that bird richness and abundance are influenced by habitat and landscape characteristics operating at multiple spatial scales. At the patch scale, semi-natural habitats have generally positive effects, highlighting their critical role in supporting farmland bird communities. At the local and broader local scales, the effects of habitat and landscape variables vary depending on spatial extents and surrounding landscape context. These findings underscore the importance of preserving and managing semi-natural habitats, and of considering scale-dependent responses when assessing biodiversity in intensively managed farmland.

4.1. Importance of semi-natural habitats at patch scale

Observed species richness was highest in semi-natural habitats (32

species) and lowest in artificial infrastructure (7 species). Species accumulation curves showed a similar pattern, with cumulative richness greatest in semi-natural habitats and lowest in artificial infrastructure. In contrast, patch-scale GLMMs that accounted for sampling effort and transect effects indicated higher patch-scale species richness and abundance (i.e., within-patch diversity) in both semi-natural and artificial habitats compared to cropland. This apparent discrepancy reflects the difference between cumulative and patch-scale diversity: while cropland supports more species overall due to its larger area and cumulative sampling, individual patches in semi-natural and artificial habitats provide higher-quality habitat for birds. These results align with previous studies highlighting the critical role of fine-scale habitat characteristics in agricultural landscapes (Martínez-Núñez et al., 2021; Pithon et al., 2016). Semi-natural habitats with heterogeneous microhabitats, which occurs predominantly in ditches, serves as key biodiversity reservoirs. While our study recorded only one near-threatened Reed Parrotbill, national distribution modelling reveals that farmland in China provides habitat for 220 bird species, including 39 nationally protected and 14 globally threatened ones, thus highlighting the critical importance of farmland bird conservation (Li et al., 2020a).

Among specific habitat types, tombs exhibited particularly high richness and abundance, reflecting their function as semi-natural habitat islands (Gong et al., 2021), a pattern consistent with the global importance of sacred sites as biodiversity refuges (Dudley et al., 2010; Löki et al., 2019). However, the wide confidence interval associated with tomb habitats indicates high variability, likely due to the small sample size (16 tomb patches out of 956 total patches analyzed) and limited area of tomb patches, which may lead to irregular bird usage patterns. Various semi-natural habitats provided critical resources: woody vegetation offered shelter and nesting sites (Heath, 2018; Rime et al., 2020), bare ground served as essential foraging areas (Schaub et al., 2010; Tagmann-Ioset et al., 2012), and reeds and water bodies supported habitat specialists (Amano et al., 2008; Gregory and Baillie, 1998; Wright et al., 2020). The species-accumulation curves also suggested that although reed habitats showed higher richness at low sampling effort, herbaceous vegetation may contain a larger potential species pool revealed under greater sampling intensity. This stands in stark contrast to the low diversity found in intensively managed cropland and artificial infrastructure, which are characterized by high disturbance and simplified structure (Battisti and Fanelli, 2011; Rime et al., 2020). Overall, these results emphasize that semi-natural habitats provide critical resources for birds at the patch scale, despite occupying only a small proportion (6–29%) of the landscape.

Rarefaction curves and patch-scale GLMMs capture different aspects of diversity. Rarefaction curves summarize cumulative species richness across all patches and individuals, giving more weight to extensive habitats like cropland. In contrast, patch-scale GLMMs account for sampling effort and transect effects to estimate diversity within individual patches, highlighting the higher quality and resource availability in semi-natural or tomb habitats.

4.2. Importance of semi-natural habitats at local (100 m buffer) and broader local (200 m buffer) scales

At the local and broader local scales, PCA-based analyses revealed clear scale-dependent effects of semi-natural habitats on bird richness and abundance, with the strongest and most consistent relationships observed within the 100 m buffer. At this scale, principal components representing gradients from cropland-dominated surroundings toward semi-natural habitats were positively associated with both richness and abundance, indicating that birds respond particularly strongly to habitat composition in the immediate vicinity of transects. This finding is consistent with previous studies showing that local habitat availability plays a crucial role in sustaining farmland bird communities and often outweighs broader landscape effects (Elsen et al., 2017; Marcacci et al., 2020; Perkins et al., 2003; Rösch et al., 2023).

When specific habitat types were considered through PCA, local-scale components characterized by higher contributions of herbaceous vegetation and reed relative to cropland and artificial infrastructure were positively associated with bird richness and abundance. These results highlight the functional importance of linear semi-natural vegetation, which in our study area predominantly occurs along ditches, in providing key foraging and nesting resources within intensively managed farmland. Similar positive effects of semi-natural vegetation elements, including woody and herbaceous habitats, have been widely documented in agricultural landscapes (De Frutos et al., 2015; Neilan et al., 2019; Tschumi et al., 2020). Rather than single habitat types acting independently, our results suggest that birds benefit from combinations of semi-natural elements that collectively enhance habitat complexity at fine spatial scales.

At the broader local scale (200 m buffer), habitat effects were generally weaker and more variable. PCA axes representing increased availability of semi-natural habitats relative to cropland were positively associated with species richness, whereas effects on abundance were limited or marginal. This pattern suggests that broader-scale habitat composition contributes primarily to species richness, while bird abundance remains more strongly linked to local resource availability, a scale-dependent response also reported in other farmland bird studies (De Frutos et al., 2015; Neilan et al., 2019).

Overall, PCA-based results indicate that the influence of semi-natural habitats declines with distance from survey transects and becomes increasingly dependent on habitat combinations rather than individual habitat types. While high-quality semi-natural patches consistently support bird richness and abundance at fine scales, broader-scale effects are weaker and mainly related to compositional heterogeneity. These findings emphasize the importance of conserving semi-natural habitat elements close to focal areas, while maintaining habitat diversity within 100–200 m to support farmland bird communities in intensively managed landscapes.

4.3. Importance of habitat structure at local (100 m buffer) and broader local (200 m buffer) scales

We found that bird richness and abundance at local and broader local scale were influenced by habitat structure, particularly the configuration of semi-natural habitats and compositional diversity of study area. Most semi-natural habitats in our study were linear, occurring along ditches, which likely enhanced their functional importance for birds by providing continuous corridors for movement, foraging, and nesting. ED of these linear habitats consistently had a positive effect on bird abundance at both local and broader local scales, highlighting that structurally complex interfaces, even when linear, facilitate resource access. Similar positive effects of ED on farmland birds have been reported in other agricultural landscapes, where increased habitat interfaces enhance foraging and nesting opportunities (Ekroos et al., 2019; Morelli et al., 2013; Šálek et al., 2021; Tschumi et al., 2020). Similar edge effects have also been reported at broader spatial extents. For example, studies at the 1 × 1 km scale show that higher edge density particularly benefits generalist and open-habitat species in productive landscapes, suggesting that the positive effects of ED observed at fine scales may extend to larger landscape contexts.

SHDI showed only a marginal effect at local scale but became a significant predictor of species richness at broader local buffer. This indicates that, while local linear habitats provide essential resources for abundance, a wider diversity of habitat types at broader scales is necessary to support a richer assembly of species with varying ecological requirements. These findings are consistent with previous studies showing that habitat diversity is more influential for species richness (Liao et al., 2020; Tscharnke et al., 2012). At broader spatial extents, non-crop landscape diversity has also been shown to positively affect total bird species richness and forest bird abundance at the 1 × 1 km scale, suggesting that the effects of SHDI may be more apparent at

broader spatial extents.

Mean patch area (AREA_MN) of semi-nature had limited effects in our study, suggesting that the linear configuration of semi-natural habitats may be more important than patch size alone at local and broader local scales. However, smaller fields of cropland often support higher bird diversity at 1 km × 1 km landscape scale (Fahrig et al., 2015).

5. Limitations

While our study provides important insights into bird–habitat relationships, several limitations should be noted. The study is based on a relatively small sample size, with three surveys conducted in a single year across 20 transects. Both temporal and spatial replication are limited, which may increase uncertainty in parameter estimates and reduce statistical power, potentially affecting the detection of weaker or context-dependent patterns. Nevertheless, the positive effects of semi-natural habitats on bird richness and abundance were consistently observed in the majority of analyses, suggesting that these results are robust despite the limited sampling. Future studies with additional years of surveys or more transects would help to validate and extend our findings, particularly for patterns that were less pronounced or non-significant in this study.

In this study, semi-natural habitats were classified into woody vegetation, herbaceous vegetation, reed, bare ground, and tombs to reflect key landscape features observed in the field. Bare ground differs from artificial structures such as roads, occurring mainly along field edges or ditches without vegetation, providing perching and foraging sites for birds. Reed habitats support specialist species and are common in ditches, with ecological functions distinct from woody and herbaceous vegetation. Tombs, often covered with grass and occasionally trees or shrubs, are widespread within cropland and serve as semi-natural habitat islands. Although tombs and bare ground patches are relatively few, potentially affecting model stability, their inclusion is ecologically justified as they support bird diversity and habitat heterogeneity. Overall, this classification is suitable for the study area and allows meaningful ecological interpretation of habitat effects on birds.

Patch sizes varied considerably in our study, and some categories—particularly tombs—were comparatively small. Tombs are relatively isolated patches within the agricultural matrix and have received increasing attention in recent studies in China, reflecting their potential ecological importance as stepping stones or refuges for birds. Small patch size may introduce additional variability and reduce the reliability of parameter estimates in patch-scale analyses. Nevertheless, patch types were defined based on repeated on-site explorations and capture the major habitat elements present in our study region, including these ecologically relevant tombs. While we recognize that boundary clarity and surrounding matrix features are important considerations, as highlighted by Klein et al. (2023), we retained these small patches in the analyses to reflect the full heterogeneity of the landscape in our study area. Future studies with larger sample sizes and additional characterization of matrix context could further validate and refine these findings.

6. Conclusion

Our study reveals that even the very intensively managed croplands of Qihe County, Shandong Province, which are dominated by only two crops that alternate in synchrony and that are highly fertilized and subject to intensive plant protection measures, host farmland bird populations. The multi-scale analysis highlights how the diversity and heterogeneity of ditch habitats contributes to maintaining farmland birds by offering different and complementary resources. Importantly, these habitats exist as part of the farming infrastructure and do not compete with core production areas. Although tombs were not widespread in our study transects, they demonstrated a notable role in bird conservation, consistent with previous research on their ecological

significance. The large differences in bird richness and abundance, indicate that even in intensively farmed anthropogenic landscapes, biodiversity can be fostered through an optimization of landscape and habitat characteristics, in this case even without losing production areas through context-sensitive management of semi-natural habitats and consideration of habitat heterogeneity.

This study provides clear implications for policy and land management. First, conservation strategies should not only focus on protecting semi-natural habitats but also intentionally integrate and manage these anthropogenic elements—particularly woody/herbaceous vegetation and reeds in ditches, as well as culturally significant tombs—through context-sensitive design in agricultural landscapes. Second, our results show that such semi-natural habitats can provide biodiversity benefits without compromising crop production. Therefore, land-use policies should promote habitat diversity and structural complexity (e.g., patch configuration and edge density) to support bird diversity. These recommendations complement existing guidelines for biodiversity conservation in farmland landscapes in China and offer practical measures for enhancing biodiversity without compromising agricultural productivity. Third, we recommend that biodiversity indicators—such as farmland bird index—be formally integrated into agricultural monitoring and evaluation frameworks. These measures complement existing guidelines and offer practical strategies for sustaining biodiversity in intensively managed agricultural landscapes.

CRedit authorship contribution statement

Hongyan Zheng: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Noëlle Klein:** Writing – review & editing, Visualization, Methodology. **Lili Wang:** Writing – review & editing, Supervision. **Sonja Kay:** Writing – review & editing, Methodology. **Felix Herzog:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Rongguang Shi:** Resources, Funding acquisition. **Rongle Liu:** Writing – review & editing, Supervision, Conceptualization. **Jan Bogaert:** Writing – review & editing, Supervision, Methodology, Conceptualization.

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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. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2026.114666>.

Data availability

Data will be made available on request.

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