ORIGINAL RESEARCH

Multiscale effects of habitat and surrounding matrices on waterbird diversity in the Yangtze River Floodplain

Boyu Gao · Peng Gong · Wenyuan Zhang · Jun Yang · Yali Si

Abstract

Context With the expansion in urbanization, understanding how biodiversity responds to the altered landscape becomes a major concern. Most studies focus on habitat effects on biodiversity, yet much less attention has been paid to surrounding landscape matrices and their joint effects.

Objective We investigated how habitat and landscape matrices affect waterbird diversity across scales in the Yangtze River Floodplain, a typical area with high biodiversity and severe human-wildlife conflict.

Methods The compositional and structural features of the landscape were calculated at fine and coarse scales. The ordinary least squares regression model was adopted, following a test showing no significant spatial autocorrelation in the spatial lag and spatial error models, to estimate the relationship between landscape metrics and waterbird diversity.

Results Well-connected grassland and shrub surrounded by isolated and regular-shaped developed area maintained higher waterbird diversity at fine scales. Regular-shaped developed area and cropland, irregular-shaped forest, and aggregated distribution of wetland and shrub positively affected waterbird diversity at coarse scales.

Conclusions Habitat and landscape matrices jointly affected waterbird diversity. Regular-shaped developed area facilitated higher waterbird diversity and showed the most pronounced effect at coarse scales. The conservation efforts should not only focus on habitat quality and capacity, but also habitat connectivity and complexity when formulating development plans. We suggest planners minimize the expansion of the developed area into critical habitats and leave buffers to maintain habitat connectivity and shape complexity to reduce the disturbance to birds. Our findings provide important insights and practical measures to protect biodiversity in human-dominated landscapes.

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Introduction

Anthropogenic landscape modification is the major cause of biodiversity loss (Fischer and Lindenmayer 2007; Guadagnin and Maltchik 2007), and is one of the most pressing challenges for ecologists and conservation biologists. Globally, urban and rural areas are developing rapidly (Andrade et al. 2018), vastly altering the landscape composition and structure of wildlife habitats and their surroundings. However, the influence on urban development is not ubiquitous for biodiversity and is instead dependent on landscape composition and configuration at local and regional scales (Andrade et al. 2018). Wetlands, as important biodiversity hotspots, maintain high biodiversity and biological productivity (Forbes 2000; Dudgeon et al. 2006; Green et al. 2017), and offer habitat for many threatened species (Green 1996; Dudgeon et al. 2006). Though some wetlands are under protection, human activities remain a threat to wetland biodiversity, resulting in degraded ecosystem services (Green 1996; Nassauer 2004; Galewski et al. 2011; Martínez-Abraín et al. 2016). For example, due to dryland development, such as for agriculture and urban construction, large numbers of natural wetlands are deteriorated (Nilsson et al. 2005; Niu et al. 2012). Waterbirds (e.g. swans, geese, ducks, and herons), that rely on wetland habitats are sensitive to the environmental change and are often regarded as important indicators of ecosystem health (Ogden et al. 2014). Nevertheless, populations of such important bird groups are declining globally, which calls for new strategies for conservation of both waterbirds and wetlands (Amano et al. 2018).

Habitat characteristics influence bird distribution, abundance and diversity (Paracuellos and Telleria 2004; Beatty et al. 2014). For example, Zhang et al. (2018) found that waterfowl prefer areas with well-connected waterbodies and wetlands. Neotropical migrants are more abundant in landscapes with a greater proportion of forest and wetland (Flather and Sauer 1996). Shorebird abundance is positively affected by wetland area and number of wetlands (Webb et al. 2010). Moreover, greater habitat patch

size, core area, edge and connectivity positively influence bird diversity (Wu et al. 2011). Nevertheless, the suitability of an area for birds depends on the condition of both habitat and the surrounding landscape matrix (Saab 1999; Guadagnin and Maltchik 2007; Elphick 2008; Perez-Garcia et al. 2014). For example, Morimoto et al. (2006) found that two woodland bird species prefer woodlands surrounded by agricultural areas over those surrounded by urban areas. Francesiaz et al. (2017) found that gulls prefer ponds surrounded by meadow and fallow land rather than woodland. Dallimer et al. (2010) found that the size of urban area and the amount of grassland patches affect the richness of moorland bird species in northern England. Nevertheless, studies investigating the effect of the landscape matrix have mainly considered the distance of the landscape matrix to habitats (Debinski et al. 2001; Summers et al. 2011), or the size and amount of the matrix (Guadagnin et al. 2009; Dallimer et al. 2010; Egerer et al. 2016). Thus, the effect of detailed characters (such as shape complexity and connectivity) of the surrounding landscape matrix on bird diversity are largely unknown.

Landscape metrics are frequently used to evaluate landscape pattern change (Riitters et al. 1995; Lausch and Herzog 2002), habitat characters (Mcalpine and Eyre 2002; Bailey et al. 2007), and linked to biodiversity (Bailey et al. 2007; Walz 2011; García-Llamas et al. 2018). Landscape metrics can be used to assess biodiversity at a higher and integrated level (Walz 2011) as higher environmental diversity leads to higher species diversity (Ricotta et al. 2003). These metrics can also capture biotic processes, such as immigration (Honnay et al. 2003) and biotic interactions (Simmonds et al. 2019). Numerous metrics have been proposed to quantify landscape composition, configuration and connectivity (Šímová and Gdulová 2012; Sklenicka et al. 2014), covering the patch size, dominance, shape complexity, fragmentation, connectivity, landscape diversity, contagion and aggregation (Mcgarigal and Marks 1995). We used these metrics to quantify the character of habitat and surrounding landscape matrices to investigate their effects on waterbird diversity.

Moreover, birds respond to their environment differently at different spatial scales and hence different conservation plans are needed across scales (Wiens 1989; Zhang et al. 2018). The surrounding environment tend to play a more important role at coarser scales as birds avoid areas highly disturbed by human activities

(Si et al. 2020), which often are a large component of landscape matrices (Herbert et al. 2018; Souza et al. 2019). However, the understanding of how landscape matrices affect bird diversity across spatial scales, in particular at coarse scales, is rather limited. Previous studies (Chan et al. 2007; Guadagnin and Maltchik 2007; De Camargo et al. 2018) investigating the effect of habitat and the surroundings on bird communities mainly focus on fine scales (500 m to 10 km). Considering that the maximum mean foraging flight distances of ducks and geese is 32. 5 km (Johnson et al. 2014) and is generally < 50 km (Ackerman et al. 2006; Si et al. 2011; Johnson et al. 2014), we chose the spatial scale > 10 km and < 50 km as the coarse scales to further investigate how the landscape features influence waterbird diversity.

This study investigates how habitat and landscape matrices affect waterbird diversity in the Yangtze River Floodplain across spatial scales using spatial and ordinary least squares regression models. We hypothesize that (1) habitat and landscape matrices jointly affect waterbird diversity, and (2) the effect of landscape matrices outweighs that of habitats at coarse scales.

Methods

Study area

The Yangtze River Floodplain (thereafter YRF, 28.3°–33.6° N, 112.2°–122.5° E; Fig. 1) is located in the humid subtropical climate zone. The annual average temperature ranges from 14 °C to 18 °C and average annual rainfall is from 1, 000 mm to 1, 400 mm (Xie et al. 2017; Wei et al. 2019). In this region, 11 Ramsar sites (wetlands of international importance, designated under the Ramsar Convention; http://www.ramsar.org) and 31 wetlands (including 10 national and 21 provincial-level wetlands) are designated as protected areas. A seasonal flood-drought cycle results in high water levels in spring and summer, followed by low water level in autumn and winter (Wei et al. 2019). Flooding brings nutrients and organic matter into the wetlands, during drought cycles as water levels decline, the large number of wetlands provide abundant feeding areas for waterbirds (Xu et al. 2017; Wei et al. 2019). YRF, as an important wintering area for local and migratory birds along the East Asian-Australasian Flyway, is composed of variable types of wetlands such as flooded wetlands, inland marshes, swamps and mudflats.

YRF is one of the Global 200 priority ecoregions for conservation identified by the World Wide Fund for Nature (Olson et al. 1998), and it provides habitat for about one million wintering waterbirds (Wang et al. 2017). Meanwhile, YRF, flowing through Shanghai and Hunan, Hubei, Jiangxi, Anhui and Jiangsu provinces, plays an important role in Chinese economy, agriculture and industry (Hollert 2013), support 29% of China's population (about 400 million) and produces more than 40% of the national GDP (Wang et al. 2017). Intensive human activities (such as agriculture, urbanization, land reclamation and conversion, etc.) in this region makes YRF one of the most critical and endangered ecoregions in the world (Olson and Dinerstein 2002). Thus, YRF is an appropriate region to explore how species diversity responds to the altered landscape patterns. There is an urgent need to generate sustainable development plans to solve the conflicts between economic development and biodiversity conservation in YRF.

Waterbird survey data

We obtained the waterbird survey data for 101 sites along YRF from The World Wide Fund for Nature (WWF; survey was carried out from 9 to 13 January 2011). This time of year was chosen because the distribution of wintering birds is relatively stable and concentrated. The survey sites where bird congregate were identified based on expert knowledge. Various methods were used to approach the survey sites. The survey team usually drove as close as possible and then walked on foot. Birds were counted by experienced field ornithologists from early morning and through the day using telescope, in at least two locations of one surveyed wetland. A total of 136 waterbird species were recorded during the survey. In some regions, only data at the county level was summarized and the counts corresponding to specific wetlands were not available. For example, the count in the Xingzi County (Jiangxi Province, China) is the sum of three wetlands. We excluded these records and only used data for sites with accurate geographical locations of a specific wetland and corresponding bird counts for further analyses (Fig. 1).
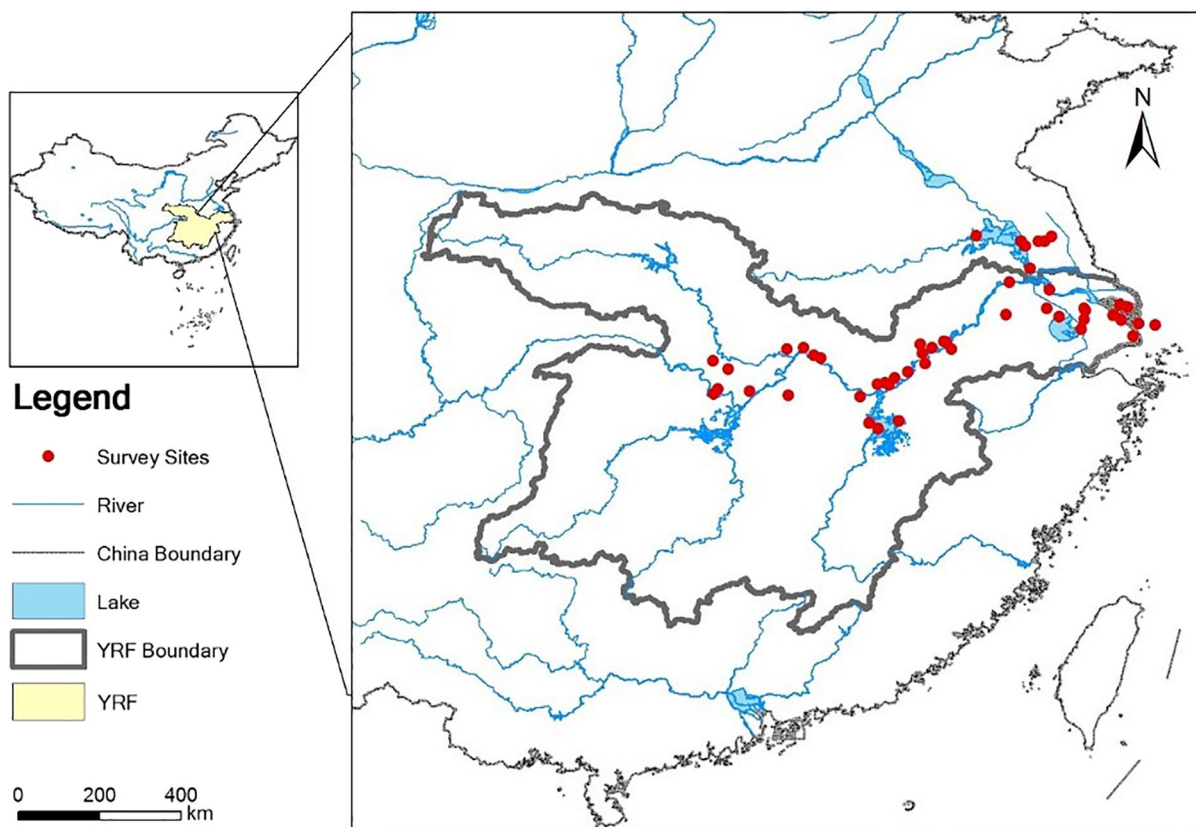
Fig. 1 Location of the Yangtze River Floodplain (YRF) and waterbird survey sites (red dots)

Land cover map

We used the aggregation land cover map of the finer resolution observation and monitoring of global land cover in 2010 (FROM-GLC-agg; http://data.ess.tsinghua.edu.cn; Yu et al. 2014) to calculate landscape metrics. According to the classification scheme of Li et al. (2016), we reclassified land cover map into nine types: cropland, forest, grassland, shrub, wetland, water, developed area and bareland. As wetlands are difficult to characterize by automatic classification (Yu et al. 2016), we replaced the water and wetland classifications in the FROM-GLC map with a 2008 wetland map generated based on human interpretation and multi-temporal imagery (Niu et al. 2012). Specifically, with the wetland map, 'water' is composed of recreational waters, artificial channels and fish farms, and 'wetland' includes shallow beaches, coastal marshes, estuary deltas, flooded wetlands and inland marshes. We then categorized land-use types into waterbird habitat (wetland, water, grassland, and shrub) and the surrounding landscape

matrix (cropland, forest, bareland, and developed area). Grassland and shrub were included as habitat because grass is a potential food resource for some waterbirds and shrub could be used for resting or roosting. Cropland was classified as the landscape matrix due to a limited number of observed waterbird species in this land cover type (12/136 species).

Waterbird diversity

The Shannon-Wiener index has been frequently used to measure species diversity (Macarthur 1955; Lin et al. 2011; Dronova et al. 2016). It combine richness and evenness and can be used to compare the species diversity among different sites (Payne et al. 2005; Lin et al. 2011). The index (Hill 1973) is calculated for each site by Eq. (1):

$$\text{H}' = -\sum_{i}^{s} P_i ln P_i \qquad (1)$$

where s is the total number of species and P_i is the proportion of individuals of species i to the total individuals of all species.

Landscape metrics at fine and coarse spatial scales

To quantify the habitat feature and landscape matrices, we generated circular buffers around the locations of sites at different spatial scales i.e., 5 km, 10 km, 20 km, 25 km, 40 km and 50 km, as the radii. We defined 5 km- and 10 km-scale as the fine scales (Forcey et al. 2011; Morelli et al. 2013), and scales larger than 10 km-scale as the coarse scales.

Landscape metrics were selected based on the life-history and ecological characteristics of waterbirds (Madsen 1985; Si et al. 2011; Li et al. 2017; Zhang et al. 2018). Table 1 lists the selected metrics covering multiple forms of patch size, dominance, shape complexity, fragmentation, connectivity, landscape diversity, contagion and aggregation (Mcgarigal and Marks 1995). For patch size and shape complexity, we also calculated their mean, minimum, maximum and standard deviation. Patch size includes patch area (PA) and patch core area (PCO), with a higher value indicating a larger patch. The core area represents the interior area of a patch after a user-specified edge buffer is eliminated. Smaller patches with greater shape complexity have a smaller PCO (Mcgarigal and Marks 1995; De Smith et al. 2007). Metrics for shape complexity include perimeter area ratio (PAR), shape index (SI) of each land cover type. Higher PAR and SI indicate greater shape complexity or greater deviation from regular geometry. Patch density (PD) and splitting index (SPI) (Green et al. 2017) represent the fragmentation level, while patch cohesion index (PCI) (Concepcion et al. 2016) indicates the connectivity level. Higher values of PD and SPI indicate more isolated patches, whereas higher PCI indicates more connected patches. Landscape Shannon index (LSHD) indicates the level of landscape diversity, with a higher value representing higher heterogeneity of patches in the landscape. Contagion index (CI) and aggregation index (AI; Li and Reynolds 1993) measure the extent of aggregation of patches for one particular land cover type. CI and AI increase if a landscape is dominated by large and well-connected patches. Landscape metrics were calculated in R 3.3.3 using the package 'SDMTools'. All metrics were standardized using z-score normalization transformation for the further analyses.

Statistical analyses

We first tested the influence of each landscape metric on waterbird diversity using univariate linear regression. Only significant metrics (p value < 0.05) were included (Forcey et al. 2011). A preselection was then carried out to exclude metrics with relatively high autocorrelation or high collinearity. Specifically, we used Moran's I to detect autocorrelation and metrics with a Moran's I larger than 0.5 or smaller than -0.5 were removed. We then use Variance Inflation Factors (VIF; Marquardt 1970) to diagnose collinearity. VIF measures the amount of multicollinearity in a set of multiple regression variables and tests the multiple correlation coefficient between one variable and the rest of variables. Specifically, we dropped the metric with relatively less impact (based on the result of the univariate linear regression), and repeated this process until VIFs of each variable were < 10. Considering the potential spatial dependency among survey sites, we used both spatial regressions (the spatial lag model SLM and the spatial error model SEM) and the Ordinary Partial Least Squares (OLS) regression. The non-significant metrics were removed, and variables kept in the final model were considered as key landscape metrics.

Two spatial autoregressive models were used to detect the level of spatial autocorrelation. A matrix of spatial weights W was calculated based on Euclidean distances between survey sites. The one is the spatial lag model (SLM) that adds a lag term of the dependent variable y into the OLS model. This model explains the spatial interaction between survey sites based on their proximity, as given by Eq. (2):

$$y = \beta X + \rho W y + \varepsilon \qquad (2)$$

where β is the correlation coefficient of the independent variable X, W is a spatial weights matrix indicating distance relationship between pairs of survey sites. ρ is the coefficient of the spatially lagged variable Wy on the matrix of weight W applied to response values from spatial neighbors of each survey site, and ε is the random error.

Table 1 Summary of the landscape metrics used for investigating the effect of habitat and surrounding matrices on waterbird diversity

Category	Landscape metrics	Abbreviation	Description
Patch size	Patch area	PA	Mean/Min/Max/SD PA: the average/smallest/largest/ standard deviation of all patch areas of a particular land cover type. SD PA indicates the level of deviation from the mean patch area for one particular land cover type
	Patch core area	PCO	Mean/Min/Max/SD PCO: the average/smallest/largest/standard deviation patch core area of a particular land cover type. SD PA indicates the level of deviation from the mean patch core area for one particular land cover type
Shape complexity	Perimeter area ratio of each land cover type	PAR	$\text{PAR} = \frac{p_j}{a_j}$, where p_j is the perimeter of patch j and a_j is the area of patch j.
			Mean/Min/Max/SD PAR: the average/smallest/largest/ standard deviation perimeter area ratio for one particular land cover type. SD PAR indicates the level of deviation from the mean perimeter area ratio for one particular land cover type
	Landscape shape index of land cover type	LSI	$\text{LSI} = \frac{0.25E}{\sqrt{A}}$, where E is the total edges of patches of one land cover type and A is the total landscape area
	Shape index of each patch	SI	Mean/Min/Max/SD SI: the average/smallest/largest/standard deviation shape index for one particular land cover type. SD SI indicates the level of deviation from the mean value of the shape index for one particular land cover type
Fragmentation	Patch density of each land cover type	PD	$\text{PD} = \frac{N_i}{A}$, where N_i is the total number of patches for the particular land cover type and A is the total landscape area
	Splitting Index	SPI	$\text{SPI} = \frac{A^2}{\sum_{i=1}^{m}\sum_{j=1}^{n} a_{ij}^2}$, aij is area of patch ij, A is total landscape area. The degree of patch isolation for one particular land cover type
Connectivity	Patch cohesion index	PCI	$\text{PCI} = 1 - \left(\sum_{j=1}^{m} p_j / \sum_{j=1}^{m} p_j \sqrt{a_j} \right)\left(1 - \frac{1}{\sqrt{A}}\right)^{-1}$, where m is the number of patches of each land cover type, a_j is area of patch, p_j is the perimeter of patch j and A is the total landscape area
Diversity	Landscape Shannon diversity index	LSHD	$\text{LSHD} = -\sum_{i}^{n} P_i ln P_i$, where n is the number of land cover types and Pi is the percentage of land cover i
Contagion	Contagion index	CI	$\text{CI} = \left[1 + \frac{\sum_{i=1}^{m}\sum_{k=1}^{m}\left[(P_i)\left(\frac{g_{ik}}{\sum_{i=1}^{m} g_{ik}}\right)\right]\left[ln(P_i)\left(\frac{g_{ik}}{\sum_{i=1}^{m} g_{ik}}\right)\right]}{2ln(m)} \right]$, where P_i is the percentage of patch type i, g_{ik} is the number of patch type i, and m is the number of land cover types in a buffer. High CI indicates large and well-connected patches
Aggregation	Aggregation index	AI	$\text{AI} = \frac{g_{ii}}{max \to g_{ii}}$, g_{ii} is the number of like adjacencies between pixels of patch i based on the single-count method. $max \to g_{ii}$ is the maximum number of like adjacencies between pixels of patch i based on the single-count method. The value of AI ranges from 0 to 1, and high AI means more aggregated patches

The other model is the spatial error model (SEM) that estimates the spatial autocorrelation existing in the regression residuals of the neighboring location (i.e. the spatial error) of the OLS model, as given by Eq. (3):

$$y = \beta X + \lambda W\epsilon + \mu \qquad (3)$$

where λ is the spatial autoregressive coefficient for the spatial error variable $W\epsilon$ and μ is the random factor of disturbances.

We fitted in total seven models for the fine (two models) and the coarse (five models) scales. The performance of OLS and spatial auto-regression

models were compared using Akaike Information Criterion (AIC). AIC, as a model selection criterion, has a sound likelihood framework, based on Kullback-Leibler information loss between estimates of the model and actual values and allows the comparisons among models (Burnham and Anderson 2004). A lower AIC value means better fit of the model, thus the model with the lowest AIC value is deemed as the best model. Spatial regressions were carried out in GeoDa and the other analyses in R 3.3.3 software.

Results

Waterbird diversity of the survey sites in the Yangtze River Floodplain measured by the Shannon-Wiener index is shown in Table S1. The Shannon-Wiener index values varies between 0 and 2.6877 (mean = 1.32 ± 0.69 SD). The highest waterbird diversity was found in the Poyang Lake Nature Reserve in Jiangxi Province, followed by Chen Lake and Liangzi Lake in Hubei province, while relatively lower Shannon-Wiener values occurred in Ge Lake in Jiangsu province, the Aquafarm of Jieshou Town in Anhui province and West Yangcheng Lake in Jiangsu province (Table S1).

At both fine and coarse scales, the p-value of λ in SLM and that of ρ in SEM were higher than 0.05, which indicated that no strong spatial autocorrelation was observed among survey sites. Thus, we retained OLS models to estimate the influence of landscape features on waterbird diversity (Table 2).

According to the coefficient of each significant metric (Table 2; Fig. 2), we found waterbird diversity was strongly associated with the surrounding landscape matrix at both fine and coarse scales, and the effect was stronger at the coarse scales. At fine scales, a higher waterbird diversity was associated with a lower connectivity of developed area (i.e., lower PCI, a negative effect). At coarse scales, developed area showed the most pronounced effect on waterbird diversity, i.e., habitats surrounded by developed area of regular shapes (i.e., higher LSI, a positive effect) tended to have a higher waterbird diversity (Fig. 2). In addition, regular-shaped croplands (i.e. higher LSI, Mean SI and SD SI; positive effects) and larger irregular-shaped forest patches (i.e. higher Min SI and Mean PCA; positive effects) facilitated a higher waterbird diversity.

Significant relationships between habitat features and waterbird diversity were found at both fine and coarse scales (Table 2). At fine scales, the important variables included patch density (PD) of grassland and SD shape index (SD SI) of shrub. Waterbird diversity was significantly higher in more connected grassland (i.e. lower PD, a negative effect) and more irregular-shaped shrub (i.e. higher SD SI, a positive effect). At coarse scales, the important variables were the landscape shape index (LSI), the splitting index of shrub, the Mean shape index (Mean SI) and aggregation index (AI) of wetland. Irregular-shaped and well-connected wetland (i.e. higher Mean SI and AI, a positive effect), as well as irregular-shaped shrub (i.e. higher LSI, a positive effect) contributed to a high waterbird diversity whereas the isolated shrub (i.e. higher SI, a negative effect) resulted in a low waterbird diversity.

Discussion

This study investigated the impact of habitat features and landscape matrices on waterbird diversity across spatial scales. At fine scales, well-connected habitats (grassland and shrub) surrounded by isolated and regular-shaped developed area helped maintain high waterbird diversity. At coarse scales, waterbird diversity was higher in areas where aggregated wetlands were surrounded by regular-shaped developed area and croplands, and large irregular-shaped forests. Developed areas consistently influenced waterbird diversity and showed the most pronounced effect at coarse scales. The landscape matrix in which wildlife habitat is embedded should be managed wherever possible (Prugh et al. 2008; Franklin and Lindenmayer 2009), especially when expanding the developed area.

Waterbird diversity was negatively correlated with fragmentated habitats (i.e., isolated grassland, regular and isolated shrub and unconnected wetland with regular boundaries). Well-connected grassland, shrub and wetland habitat provide important foraging and resting area for waterbirds (Stafford et al. 2009; Pearse et al. 2012). Connectivity, at both fine and coarse scales, is important for waterbird aggregation (Guadagnin and Maltchik 2007). At finer scales, well-connected habitats facilitate the movement of waterbirds between feeding and roosting sites (Elphick

Table 2 The influence of landscape features on waterbird diversity in the Yangtze River Floodplain at fine and coarse scales

Scale	Buffer	Model	Dependent variable: Shannon–Winner index of waterbirds			
		Independent variable	Coefficient	P-value	Adjust R^2 (OLS)	AIC (OLS)
Fine scale	5 km	− the PCI of developed area	− 0.490	0.024*	0.283	82.081
		− the PD of grassland	− 0.350	0.001**		
	10 km	− the SD SI of developed area	− 1.126	0.042*	0.514	30.311
		+ SD SI of shrub	3.179	0.003**		
Coarse scale	15 km	+ the LSI of shrub	0.053	0.013*	0.303	51.813
		− the LSI of cropland	− 0.004	0.008**		
	20 km	− the Mean SI of cropland	− 2.260	0.031*	0.233	77.635
		+ the Mean SI of wetland	1.442	0.005**		
	30 km	− the SD SI of cropland	− 0.810	0.029*	0.139	99.897
		+ the AI of wetland	0.106	0.031*		
	40 km	− the Mean SI of developed area	− 4.458	0.001**	0.235	97.674
		+ the Mean PCA of forest	1.567e-6	0.012*		
		+ the Min SI of forest	2.733	0.013*		
	50 km	− the Mean SI of developed area	− 2.887	0.015*	0.160	100.302
		− the SPI of shrub	− 1.123e-4	0.027*		

'+' means positive effects while '−' means negative effects

The credible interval of the estimate is 95%. *P < 0.05 (two-sided test), **P < 0.01 (two-sided test), ***P < 0.001 (two-sided test)

Landscape metrics: PCI patch cohesion index, PD patch density, SD SI standard deviation of shape index, LSI landscape shape index, Mean SI mean shape index, AI aggregation index, Mean PCA mean patch core area, Min SI minimum shape index, SPI splitting index

2008), which can reduce the costs due to shorter foraging flight distances. In addition, we found that waterbird diversity was lower in sites with regular-shaped shrub and wetland patches at coarser scales. In general, the regular and less complex patches are often associated with intensive human influnce (Mcgarigal and Marks 1995; Cunningham and Johnson 2011), whereas less disturbed patches are more complex (Krauss and Klein 2004). Furthermore, habitat patches with a higher shape complexity tended to have increased foraging resources (Andrade et al. 2018). Therefore, irregular-shaped shrub and wetland habitat helped to maintain a higher waterbird diversity due to the lower level of human disturbance and the higher level of potential food resources.

Developed area was the most critical factor influencing waterbird diversity, particularly at coarse scales. Though a previous study found that the presence of developed area negatively influenced waterbird richness (Rosa et al. 2003), we suggest that habitat surrounded by isolated or regular-shaped developed area can help to maintain higher waterbird diversity. Isolated developed area indicated a lower level of connectivity of surrounding patches, resulting in a higher connectivity of waterbird habitat patches (Pearce et al. 2007; Larsonab and Perrings 2013). In other words, well-connected surrounding landscape patches (i.e. developed area) indicated higher habitat degradation and fragmentation, which leads to a lower waterbird diversity. In particular, the effect of shape complexity of developed area was more prominent. Waterbird diversity decreased as the shape complexity of surrounding developed area increased. Surrounding developed patches with a more complex shape tended to have a longer border with the adjacent natural habitats, indicating a higher level of human disturbance (Gyenizse et al. 2014). Regular-shaped developed patches resulted in less disturbance to the habitat and hence support higher waterbird diversity.

Other landscape matrices, such as cropland and forest, also affected waterbird diversity. Regular-shaped cropland and larger irregular-shaped forest tended to facilitate a higher waterbird diversity. Similar to the developed area, regular-shaped cropland
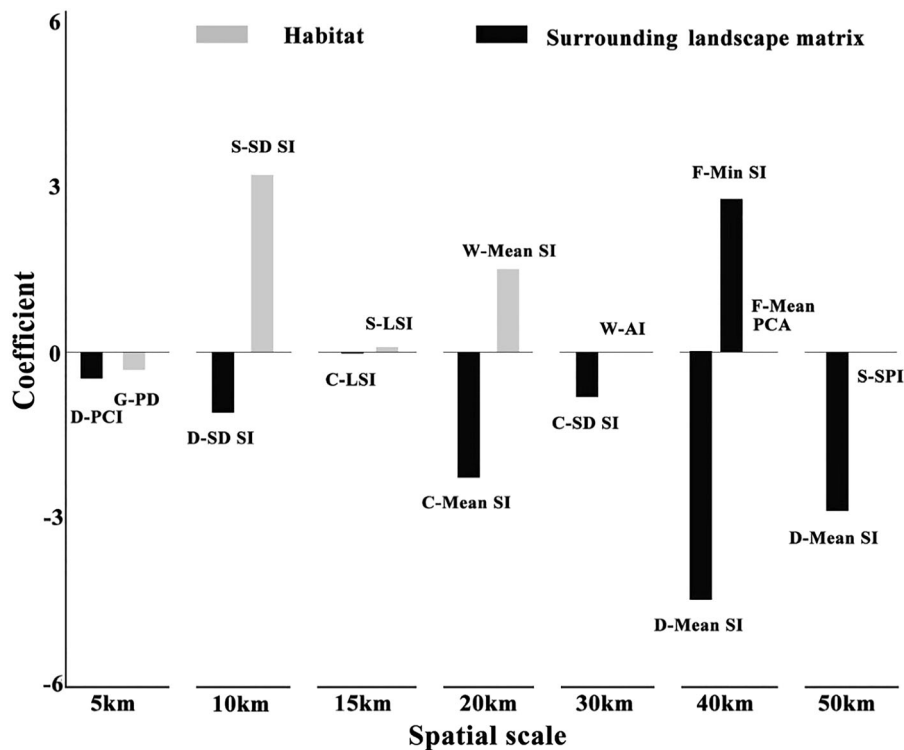
Fig. 2 Effects of landscape features on waterbird diversity along Yangtze River Floodplain. Black bars denote landscape matrices and grey bars denote habitat. The length of the bar depicts the coefficient of each metric representing the level of importance. Landscape metrics that have statistically significant values are displayed: D-PCI indicates the patch cohesion index (PCI) of developed area (D); G-PD means the patch density (PD) of grassland (G); D-SD SI indicates the standard deviation of shape index (SD SI) of developed area; S-SD SI means the SD SI of shrub (S); C-LSI indicates the landscape shape index (LSI) of cropland (C); S-LSI means the LSI of shrub; C-Mean SI indicates the mean shape index (Mean SI) of cropland; W-Mean SI means the Mean SI of wetland (W); C-SD SI indicates the SD SI of cropland; W-AI means the aggregation index (AI) of wetland; D-Mean SI indicates the Mean SI of developed area; F-Min SI means the minimum shape index (Min SI) of forest (F); F-Mean PCA means the mean patch core area (Mean PCA) of forest; D-Mean SI indicates the Mean SI of developed area; S-SPI means the splitting index (SPI) of shrub

indicated a lower level of habitat invasion and disturbance. Habitats surrounded by natural land tended to support more species due to relatively low human disturbance (Vandermeer and Carvajal 2001). Larger irregular-shaped forest patches could act as a buffer insulating core habitats from intensive human activities such as urban-rural development and agriculture expansion (Findlay and Houlahan 1997) thus facilitating a higher waterbird diversity.

We found that both habitat features and surrounding landscape matrices influenced waterbird diversity at fine scales, whereas at coarse scales the effect of the landscape matrix outweighed that of the habitat. At fine scales, waterbird diversity was facilitated by well-connected habitats surrounded by regular-shaped developed area. Whereas at coarse scales, the surrounding matrices (with the shape of developed area outperformed others) played the most important role in determining species diversity. The reason might be that initial habitat selection is mainly based on the appearance of the landscape (Moore and Aborn 2000), and birds tend to avoid regions with the habitat surrounded by well-connected landscape matrices. This kind of landscape tends to have more fragmented habitat patches and a relatively higher human disturbance. Among different types of landscape matrices, developed area had the most pronounced negative effect on waterbird diversity, probably because the level of human activity intensity is the highest in the developed area in comparison to other landscape matrices. We acknowledge that imperfect detection during surveys might negatively impact data quality

(false absences or false presence of species) and interpretation. We suggest increasing the number of surveys for each location in the future to further validate our findings.

Conclusion

Habitat features and landscape matrices jointly affected waterbird diversity, and the effect of the landscape matrix was more pronounced at coarse scales. Well-connected habitats (e.g. wetland, shrub and grassland) surrounded by isolated regular-shaped developed area and cropland, and large irregular-shaped forest helped maintain a higher waterbird diversity. Regular-shaped developed area was a critical factor that consistently facilitates a higher waterbird diversity across scales. Wetland managers should maintain well-connected habitats (wetland, grassland and shrub), and urban and rural landscape planners should minimize the expansion of developed areas to critical habitats and leave sufficient buffer to maintain the habitat connectivity and shape complexity in order to reduce the disturbance to birds. Our findings provide insights into understanding how waterbirds respond to altered landscapes and offer practical measures to help mitigate the human-bird conflicts in biodiversity hotspot areas.

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