

The effect of grain size on the relationship between urbanization and bird diversity

Jiayu Wu^a, Guanyi Chen^b, Corey T. Callaghan^c, Qiang Ren^{d,*}

^a Institute of Landscape Architecture, Zhejiang University, Hangzhou, 310058, Zhejiang Province, PR China

^b College of Agriculture and Biotechnology, Zhejiang University, Hangzhou, 310058, Zhejiang Province, PR China

^c Department of Wildlife Ecology and Conservation, University of Florida, Davie, FL, 33314-7799, 3205 College Avenue, USA

^d School of International Affairs and Public Administration, Ocean University of China, Qingdao, 266100, PR China

ARTICLE INFO

Handling Editor: J Peng

Keywords:

Urbanization

Birds

Taxonomic diversity

Functional diversity

Urban ecology

Grain

ABSTRACT

The intensifying urbanization markedly influences bird diversity, frequently with negative repercussions but also yielding mixed outcomes. Our hypothesis posits that the variability in results often arises from methodological choices in measuring both bird diversity and urbanization. We investigated whether the effects of urbanization on bird diversity are influenced by the grain size of the measurements. Selected urban areas in China from 2000 to 2020 were analyzed, and bird diversity distributions were derived from citizen science data. Urbanization levels rose by approximately 30%, resulting in the loss of around 17 urban bird species. Panel data analyses at different grain sizes showed that urbanization negatively affected bird diversity, while taxonomic diversity was more resilient at the grain size (1–10 km). Furthermore, our findings indicate a grain effect on the urbanization–bird diversity relationship, revealing instability at various measurement grains. Functional diversity requires finer grains (1 km), reflecting feature redundancy. Our analytical approach enhances understanding of the mechanisms and cross-grain relationships through which urbanization impacts bird communities, and underscores the significance of grain in urban ecology.

Funding

This work was supported by National Natural Science Foundation of China (NO.32271935), the Natural Science Foundation of Zhejiang Province (LY22E080013), Young Elite Scientists Sponsorship Program by CAST (2021QNRC001) and China Postdoctoral Science Foundation (2022M722968).

Declaration of interest statement

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.

1. Introduction

Global bird diversity is declining, with roughly 50% of bird populations decreasing and one out of every eight species in danger of extinction (Lees et al., 2022). Human activities, such as agricultural

intensification, climate change, and urban expansion, are well-documented as having negative impacts on bird populations (Lees et al., 2022). Over 50% of the global population currently resides in cities (UN, 2022), resulting in daily production of large volumes of waste and sound and light pollution. The global urban population is estimated to increase by 2–3 billion and the global urban area projected to increase by approximately 600,000–1,300,000 km², equivalent to an increase of 78%–171% from 2015 to 2050 (Huang, Li, Liu, & Seto, 2019). High development rates may have adverse effects on bird diversity. Consequently, quantifying how, and to what extent, urbanization impacts bird diversity is essential in mitigating biodiversity loss from future development (Marzluff, 2001).

The effects of urbanization on bird diversity have been widely researched (Marzluff, 2001; S. Chen & Wang, 2017; Isaksson, 2018; Filloy, Zurita, & Bellocq, 2019), with key findings that at a landscape scale, urbanization causes a decrease in taxonomic diversity of birds (Aronson et al., 2014; Blair, 1999; Sun et al., 2022), whereas at a habitat scale there is often a decrease in the functional diversity of birds (Luck, Carter, & Smallbone, 2013; Schütz & Schulze, 2015). Although most

* Corresponding author.

E-mail addresses: wujiayula@gmail.com (J. Wu), zacharychen315@gmail.com (G. Chen), c.callaghan@ufl.edu (C.T. Callaghan), renqiang@ouc.edu.cn (Q. Ren).

<https://doi.org/10.1016/j.apgeog.2023.103154>

Received 25 August 2023; Received in revised form 16 November 2023; Accepted 18 November 2023

Available online 29 November 2023

0143-6228/© 2023 Elsevier Ltd. All rights reserved.

studies have found that increasing levels of urbanization lead to a decrease in bird diversity (Clergeau, Croci, Jokimäki, Kaisanlahti-Jokimäki, & Dinetti, 2006; Clergeau, Jokimäki, & Savard, 2001; Sandström, Angelstam, & Mikusiński, 2006), there is also a contrasting perspective known as the moderate disturbance hypothesis. Suburban areas typically have low to moderate surface development, combined with significant green spaces, which increases habitat heterogeneity and attracts both native and exotic birds, ultimately leading to bird diversity peaking in suburban areas (Callaghan et al., 2019; Lepczyk et al., 2008). However, previous studies have primarily focused on a singular spatio-temporal grain size, with limited consideration given to a critical aspect of scale, namely the grain or spatial resolution of sampling. Therefore, the methodological choice of grain size could be one possible reason for the variation in previous research findings.

The concept of grain pertains to both the spatial and temporal dimensions, encompassing the spatial resolution and temporal interval used for data collection and analysis. Spatial grain involves sampling data at various spatial resolutions, ranging from local habitats to the broader landscape context. Temporal grain, on the other hand, encompasses the time interval and duration of data collection and analysis, enabling the capture of both short-term fluctuations and long-term trends in the dynamics of urbanization and its impact on bird diversity. The neglect of grain effects is due to three potential reasons: (1) previous studies utilized samples selected on different urbanization gradients to investigate bird diversity (Blair, 1996; Davis et al., 2012), and extrapolating such results to different spatial scales lacks meaning (Openshaw, 1984); (2) since ecological processes demonstrate varying behaviors, investigating scale effects involves limited opportunities for integrated data collection (Goodchild, 2011; Mandelbrot, 1967); (3) most urban bird studies were conducted on short-term intervals, thus limiting our understanding of how temporal processes affect urban bird diversity (Fidino & Magle, 2017).

Birds are recognized as valuable indicators of ecosystem health due to their sensitivity to habitat change (Chace & Walsh, 2006). Urban areas, hosting approximately 20% of known bird species (Aronson et al., 2014), play a significant role in supporting diverse bird communities (Kowarik, 2011; Savard, Clergeau, & Mennechez, 2000). Assessing bird diversity involves various indicators, with taxonomic diversity being the most commonly used measure, providing essential data on community structure, species interactions, and ecosystem stability (Balvanera et al., 2006; Losos & Ricklefs, 2009). Additionally, functional diversity, highlighting the ecological functions and characteristics of species, contributes to understanding biodiversity and can be measured using metrics such as functional diversity (FD) and functional dispersion (FD_{is}) (Laliberté & Legendre, 2010). The relationship between taxonomic diversity and functional diversity is complex and interdependent. Taxonomic diversity does not always correspond to functional diversity and vice versa. Depending on the species' function, the loss of a single species can significantly impact ecosystem functions and services (Balvanera et al., 2014; Flynn, Mirotnick, Jain, Palmer, & Naeem, 2011). Functional diversity can better predict the responses of bird communities to land use change than taxonomic diversity alone (Devictor et al., 2010). Therefore, incorporating functional diversity into biodiversity conservation and management strategies is essential.

There may be various mechanisms inherent in the effects of urbanization on biodiversity, but all are relatively grain-dependent (Nally & Quinn, 1998; Wheatley & Johnson, 2009). At larger biogeographic or macroecological scales, or at the regional or subregional levels (Clergeau, Jokimäki, & Snep, 2006), there is a broad positive correlation between urbanization and species diversity (Luck, 2007; Qizhi, Ying, Kang, & Qingfei, 2016), but at smaller habitat scales, human activities are negatively correlated with biodiversity. Most research has documented a decrease in bird taxonomic diversity at the habitat or landscape scale due to urbanization (Aronson et al., 2014; Callaghan et al., 2019; Meffert & Dzioc, 2013). Cities may function as extensive ecological filters, where bird communities that better adapt to urban

environments thrive while others decline gradually, resulting in an overall drop of bird taxonomic diversity. In contrast, moderate urbanization provides more food sources while reducing natural enemies, leaving remaining habitats, such as natural woodlands (Blair, 1996; Davis et al., 2012; Filloy et al., 2019) and therefore could lead to increases of taxonomic diversity of birds.

We devised a research framework to examine the impact of urbanization's grain on bird diversity. This framework was employed to evaluate two primary hypotheses: (1) that investigations of bird taxonomic diversity should be conducted at finer grain to more precisely characterize urbanization and yield more pronounced outcomes; and (2) that functional diversity displays more robust responses to urbanization when analyzed at a landscape or sub-regional grain. Our standardized framework relied on panel data and employed a panel linear model, with natural social variables as covariates, to elucidate the underlying mechanisms governing the responses of bird taxonomic diversity and functional diversity to urbanization indicators, specifically impervious surface coverage, nighttime light index, and population density, at three distinct grains. We assessed the following aspects: (1) the significance, direction, and magnitude of the effects of urbanization variables on bird diversity at different granular levels; (2) the resilience of urbanization variables and bird diversity variables to granular changes; (3) the optimal grain for capturing the relationship between urbanization variables and bird diversity; and (4) the exploration of spatial patterns in urban gradients and bird diversity (Fig. 1).

2. Data and method

2.1. Study area

China was selected as the principal study area for this research (Fig. 2) as the country is vast, encompassing both temperate and colder zones along the north-south axis, with differing levels of aridity and humidity in the east-west direction (Tregear, 2017). This could potentially influence how grain size can influence the relationship between bird diversity and urbanization. Furthermore, China has high levels of biodiversity and diverse natural habitats, with 1371 bird species present, representing approximately 15% of all worldwide bird species (Zheng, 2005). Secondly, China has undergone rapid urbanization and industrialization in recent decades, making it an appropriate candidate for investigating the implications of urbanization on biodiversity (Tian, Jiang, Yang, & Zhang, 2011). Lastly, China is situated along both the East Asia-Australasia and Central Asia-India migration routes for birds (Cox, 2010), with the high rate of industrialization and urbanization in China posing a severe threat to migratory birds passing through its eastern coastal regions (Liang et al., 2018; MacKinnon, Verkuil, & Murray, 2012).

We have chosen a temporal cross-section comprising 2000, 2010, and 2020, a period characterized by China's high urbanization growth, with the urbanization rate surging from 36.09% in 2000 to 63.89% in 2020, constituting an average annual increase of 1.39% (National Bureau of Statistics of China, n. d.). It is projected that China's urban population will increase by 292 million by 2050 (S. Chen & Wang, 2017).

2.2. Spatio-temporal cross-section

In this study, considering the potential biases in data sampling and the typical scale of urban areas within the study region, we employed a grain range that approximated a landscape scale, specifically ranging from 1 to 10 km. If we use a smaller habitat scale, it may result in a larger bias in the data and is better suited for study through the sample strip method. Conversely, employing a larger sub-regional scale could overlook the differences in intra-urban gradients. In this study, we used 1 km × 1 km, 5 km × 5 km, and 10 km × 10 km square grids as grain sizes to assess the variations and consistency in urbanization's influence on bird

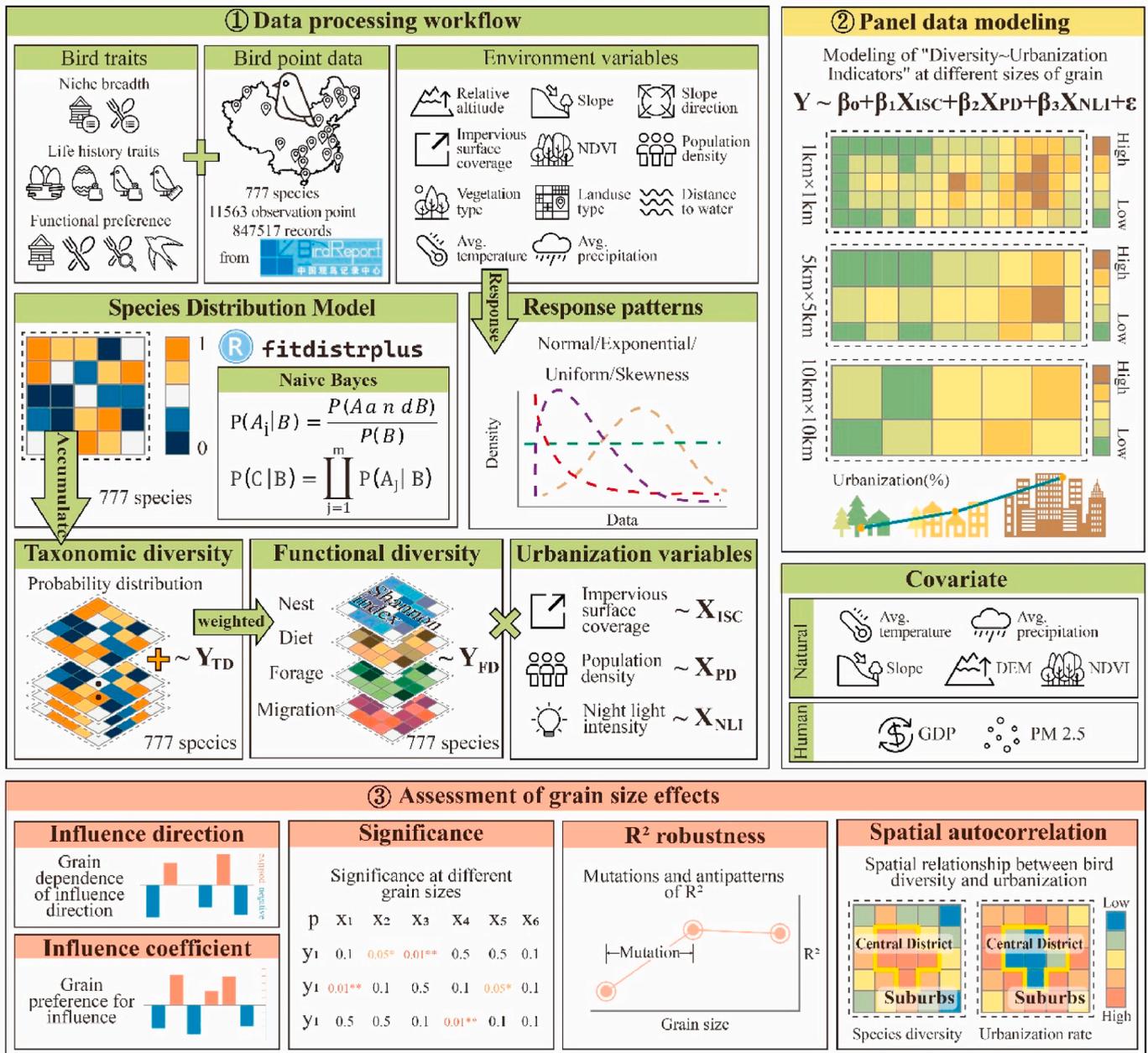


Fig. 1. Analytical Framework. This paper presents a comprehensive framework. (1) Data processing workflow: bird point data were obtained from the Citizen Science Database China Birding Report Center, and a species distribution model(SDM) was used to generate taxonomic diversity of birds. Functional diversity was calculated by overlaying the bird functional matrix. (2) Panel data modeling: Panel data modeling was performed using data from six seasons in three years, individually according to the grain. (3) Grain effects assessment: Analyses were carried out using a variety of statistics including coefficient magnitude and direction, significance, mutation and antimodal phenomena in R², and spatial correlation analysis.

diversity at varied spatial grains, with an aim to assess the influence of grain size on the relationship between urbanization and bird diversity.

2.3. Data sources

2.3.1. Bird data

Bird survey: We used the China Birding Records Center (<http://www.birdreport.cn>), which is currently the most extensive citizen science database on birds in China, containing over six million bird observations, with a coverage of over 94% of all of China's species. During birdwatching events, volunteer observers record the date, start time, end time, and number of individuals of each species encountered in addition to the species' names. A unique "report ID" is assigned to

each birdwatching event, which provides a summary of species, observation notes, and user information. Each report is submitted either through a mobile app or the website. The user manually georeferences each report, or GPS automatically georeferences it. The system scans the birding records, and if new distribution patterns are observed, the researchers review them further by uploading pictures or audio and text evidence before finalizing them.

We obtained bird observation data from the China Birdwatching Records Center for the period from January 2012 to December 2020. This period had the most extensive records, which reduced the possibility of differences between bird observation records and corresponding environmental variables. While it is acknowledged that the distribution of some species may have varied during this period, it is

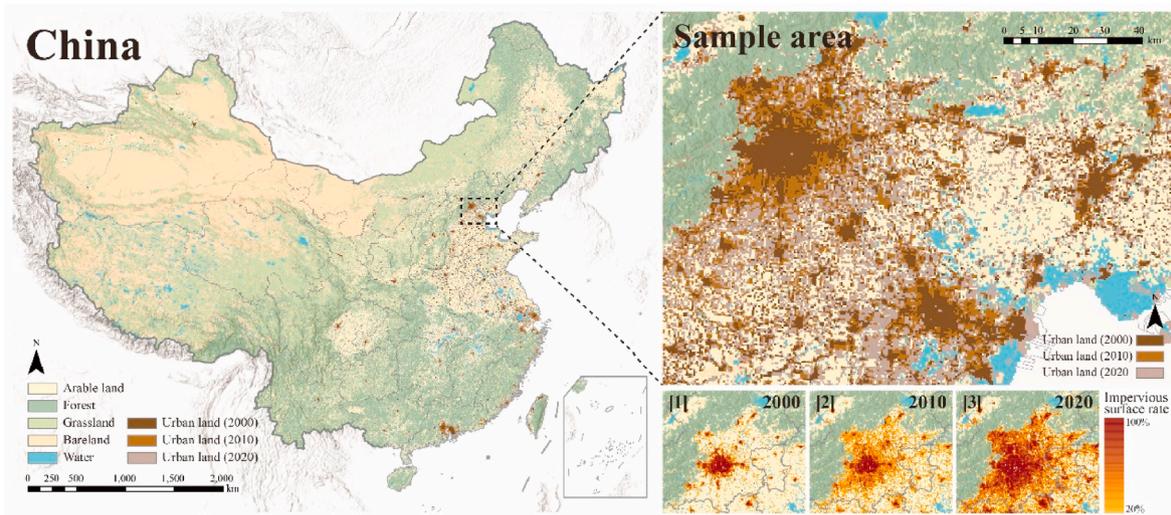


Fig. 2. Study area and urbanization in China. The map on the left provides a visual representation of the major areas of land use and urbanization in China. Additionally, the slice on the right illustrates the urban land dynamics in the Beijing-Tianjin-Hebei region (1 km × 1 km). It is worth noting that China has not yet experienced a reverse urbanization trend, as urban land continues to expand gradually.

worth noting that using a 10-year period, as recommended by the IUCN (Santini et al., 2019), is appropriate since it is considered a reliable and time-sensitive estimate of population distribution. To guarantee the precision of our predictions regarding bird distribution in China, we executed several procedures. This included validating species, excluding those with fewer than 50 observations since 2012, and filtering observations based on the geographical characteristics of the sites, focusing exclusively on inland areas while omitting data from border regions and the islands in the South China Sea. This process resulted in a total of 847, 517 observations of 777 species, with 11,563 sites recording multiple bird species (Fig. S1). The effective number of observations varied considerably among bird species. The species with the lowest number of observations was the yellow-billed egret (*Egretta eulophotes*, 56) and the highest was the bulbul (*Pycnonotus sinensis*, 18,986), with an average of 1090 ± 2175 observations.

Bird traits: We retrieved bird traits using three open source datasets; Ecological Archives E096-269 (Myhrvold et al., 2015), E095-178 (Wilman et al., 2014), and the World Bird Survival Handbook (<https://birdsoftheworld.org>). We summarized 19 life history and functional traits of birds, which were categorized into five groups based on their characteristics: forage preferences (n = 5), nesting preferences (n = 5), diet preferences (n = 4), and migration traits (n = 5) (Table S1). Our functional diversity metrics are primarily designed to measure the degree of ecological functional category features for all potential bird species within a grid, representing a mix of functional traits for bird species within a given region. In case of any missing trait, a comprehensive assessment was conducted based on the traits of closely related species within the same genus.

2.3.2. Urbanization data

To present a comprehensive understanding of urban development, we employ three urbanization indicators: impervious surface coverage, nighttime light, and population density (Fig. S2). The use of multiple indicators, instead of relying on representative ones, is motivated by the recognition that the impacts of urbanization on bird communities are diverse. The process of land development leads to the conversion of natural surfaces into impervious surfaces, such as roads, squares, and buildings (Collins et al., 2000). By utilizing nighttime light remote sensing data, we can effectively evaluate urban nighttime light pollution and ecological disturbance (Z. Chen et al., 2020). Furthermore, population density serves as a vital determinant and evidence of urbanization, directly reflecting the fundamental spatial pattern of urban

development (Qizhi et al., 2016).

Impervious surface coverage: The impervious surface data utilized in this research was procured from the impervious surface dataset of 30-m spatial resolution (1978–2017) in China (Gong, Li, & Zhang, 2019). We determined the impervious area in 2000, 2010, and 2017, and computed the proportion of impervious surface within 1 km × 1 km, 5 km × 5 km, and 10 km × 10 km square grids to form impervious surface coverage maps.

Nighttime light: In this study, we utilized long-term time series of nighttime light data with a spatial resolution of 500 m obtained from Suomi National Polar-orbiting Partnership-Visible Infrared Imaging Radiometer Suite (NPP-VIIRS) (Z. Chen et al., 2020) for the years 2000–2018. We resampled the data (BILINEAR) from the years 2001, 2011, and 2018 to achieve a spatial resolution of 1 km × 1 km, 5 km × 5 km, and 10 km × 10 km.

Population density: Annual population density data were obtained, of 1 km × 1 km spatial resolution for 2001, 2011 and 2019, from WorldPop (<https://www.worldpop.org/>) provided (Tatem, 2017). We cropped it to the study area and resampled it (BILINEAR) to 1 km, 5 km and 10 km spatial resolutions.

2.3.3. Environmental data

Different types of environmental variables were chosen to describe the physical and human geography of the study area, as summarized in Table 1. Eleven environmental variables were chosen for the species distribution model. We selected seven control variables to evaluate the impact of urbanization on bird diversity. The spatial resolution of all environmental variables was resampled to 1 km × 1 km, 5 km × 5 km, and 10 km × 10 km.

2.4. Generate bird diversity

Taxonomic diversity: In this study, species richness was used to characterize the taxonomic diversity of birds. We first matched the bird distribution data with local natural and environmental variables and calculated the species distribution probability for each bird species based on the naive Bayes classification principle. For each observation Y of bird species X, it can be represented as follows:

$$Y = \{B, A_{DEM}, A_{SLO}, A_{ASP}, A_{TMP}, A_{PRE}, A_{VEG}, A_{NDVI}, A_{Dwater}, A_{LU}, A_{POP}, A_{IMPRE}\}$$

Where B takes values of 0 or 1, with 1 indicating the presence of bird

Table 1
All environmental variables (including urbanization variables) and their role in the workflow.

Variables	Definition	Time/Physiological Season	SDM environmental variables	Urbanization × bird diversity Covariates	Urbanization × bird diversity Independent variable	Reference
Natural	Environment					
Dem	Relative elevation (m)	Stable	T	T		(https://www.resdc.cn)
Slope	Slope (degree)	Stable	T	T		
Aspect	Slope direction	Stable	T			
Tmp	Average temperature (C°)	2001A/2001B/2011A/2011B/2019A/2019B	T	T		(http://www.geodata.cn)
Pre	Average precipitation (mm)	2001A/2001B/2011A/2011B/2019A/2019B	T	T		(http://www.geodata.cn)
Veg	Vegetation type	Stable	T			(https://www.resdc.cn)
NDVI	Vegetation cover index	2001A/2001B/2011A/2011B/2019A/2019B	T	T		(https://www.resdc.cn)
Dwater	Distance from nearest water surface (m)	Stable	T			
Human	Environment					
Landuse	Land Use Type	2001/2011/2019	T			Sulla-Menashe and Friedl (2018)
GDP	Regional GDP	2000/2010/2019		T		(http://www.resdc.cn/DOI),2017.DOI:10.12078/2,017,121,102
PM	Respirable particulate matter (μg/m ³ /yr)	2001/2011/2018		T		(Hammer et al., 2020; van Donkelaar, Martin, Li, & Burnett, 2019)
ISC	Impervious surface coverage (%)	2000/2010/2017	T		T	Gong et al. (2019)
NLI	Nighttime light	2001/2011/2018			T	(Z. Chen et al., 2020)
PD	Population density (persons/km ²)	2001/2011/2019	T		T	(https://www.worldpop.org/)

species X in the selected grid cell, otherwise 0. Each A represents an environmental variable feature of Y. For each environmental variable feature, we computed the conditional probability estimate of observing bird species X given the value A_i, denoted as P(A_i|B). Bird’s responses to categorical environmental variables (ASP, VEG, and LU) typically exhibited multiple patterns. Therefore, we counted the proportion of observed records for each category, i.e.,

$$P(A_i|B) = \frac{P(A_i \text{ and } B)}{P(B)}$$

Depending on their diverse impacts on the selection of bird species, continuous environmental variables (DEM, SLO, ASP, TMP, PTR, NDVI, Dwater, POP, IMPRE) can lead to varied response patterns in birds, which could be characterized as stabilized, unimodal, or random. By assessing the AIC values of our model, we associated each bird species with specific response patterns to particular environmental variables (see Fig. S3). Subsequently, utilizing the response patterns, we employed the corresponding environmental variables for the respective years to forecast the likelihood of each bird species’ distribution in the study area for 2001, 2011, and 2019. Given the conditional independence of the environmental variable features, we applied the Bayesian theorem to derive, for each predicted grid cell C:

$$P(C|B) = \prod_{j=1}^m P(A_j|B)$$

In order to promote data stability, ensure consistent probability values across grid cells, and standardize the data, we applied a two-step process. First, we computed the natural logarithm of each grid cell value. Subsequently, we normalized these values. This procedure yielded bird species distribution probability distributions that range from 0 to 1, with values closer to 1 signifying a greater likelihood of the bird species’ presence in that grid.

Ultimately, we derived distribution probabilities (ranging from 0 to 1) for all 777 bird species within the designated study area. We summed the distribution probabilities of all birds present in each grid to obtain species richness to characterize the taxonomic diversity of birds. Finally,

a taxonomic diversity raster was produced for both breeding and non-breeding seasons in 2001, 2011, and 2019. The raster was created using spatial resolutions of 1 km × 1 km, 5 km × 5 km, and 10 km × 10 km (Fig. 3). The package “fitdistrplus” available in R version 4.0.2 was used for species distribution modeling (Delignette-Muller & Dutang, 2015; R Core Team, 2013).

Functional diversity: We classified the functional diversity of birds into four categories, including nesting diversity, diet diversity, forage diversity, and migration diversity. As an illustration, we calculated the weighted sum of nesting diversity in each study raster cell based on the probability of bird distribution data. Subsequently, we characterized nesting diversity by calculating the Shannon-Wiener index for the total number of distinct nesting preferences in each raster cell, using the following formula:

$$H = - \sum [(pi) \times \ln(pi)] \tag{1}$$

Defined nesting diversity using notation H and proportion of each nesting preference using notation pi. The Shannon-Wiener index ranges from 0 to 1, and when the number of nesting preferences in a study unit is larger or the proportion of each nesting preference is more even, the Shannon-Wiener index becomes close to 1 (Keylock, 2005). Four Shannon-Wiener indices were calculated to measure nesting diversity, diet diversity, forage diversity, and migration diversity. The overall bird functional diversity index was obtained by summing the four indices, reflecting the functional diversity of birds in the study unit, and indicating higher values indicate higher functional diversity. A raster map displaying the bird functional diversity was created for the breeding and non-breeding seasons of 2001, 2011, and 2019, with resolutions of 1 km × 1 km, 5 km × 5 km, and 10 km × 10 km (Fig. 4).

Six temporal sections were indicated using letters (a-f). The spatial resolution for ab/cd/ef are 10km/5km/1 km, respectively. The periods a [1], a[2], and a[3] correspond to 2019 non-breeding season, 2019 breeding season, and 2010 breeding season, respectively. a[1]-a[2] refers to seasonal variation, while a[2]-a[3] refers to interannual variation.

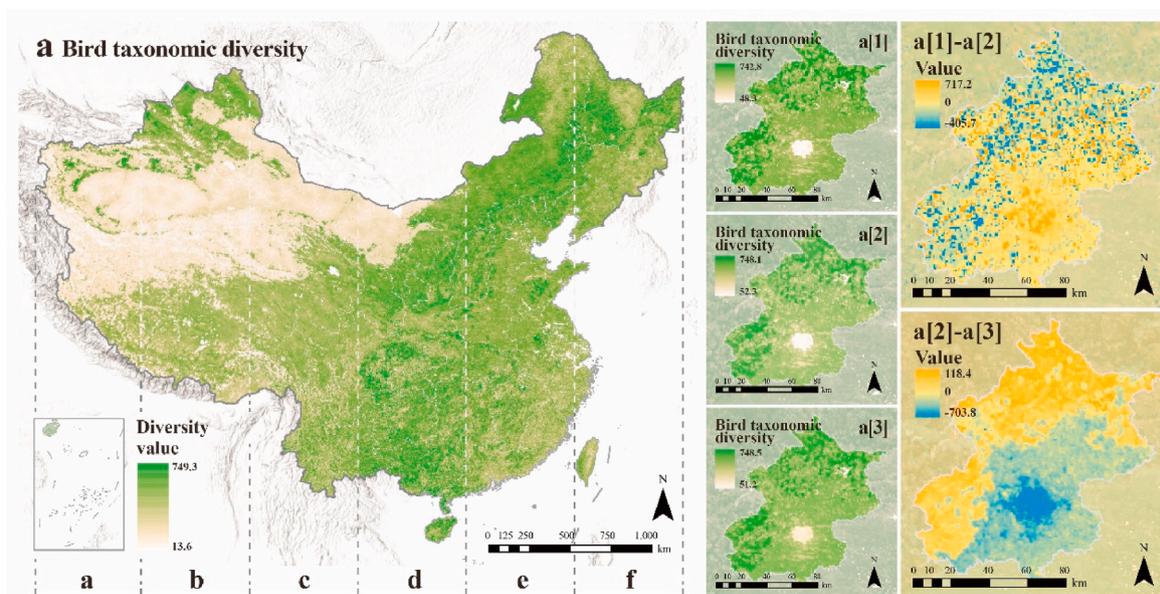


Fig. 3. Taxonomic diversity distribution of Chinese birds. The six sections of this study are denoted by letters (a–f) and have varying temporal and spatial resolutions. Sections ab, cd, and ef have spatial resolutions of 10 km, 5 km, and 1 km, respectively. The 2019 non-breeding season, 2019 breeding season, and 2010 breeding season are represented by a[1], a[2], and a[3], respectively, with a change between a[1] and a[2] indicating seasonal variation, and a change between a[2] and a[3] indicating interannual variation.

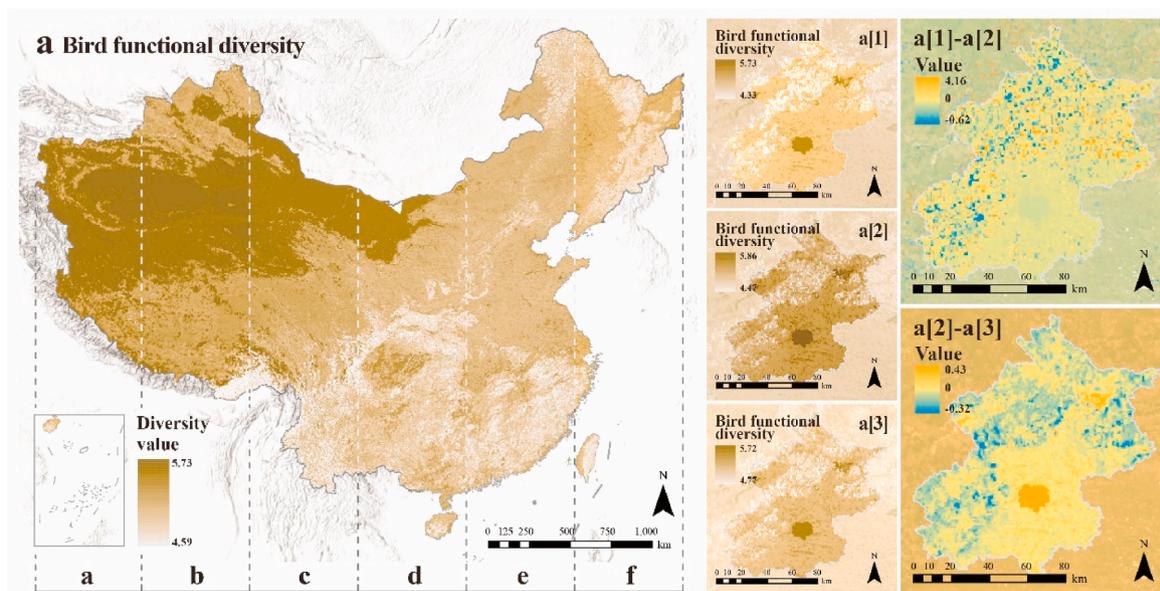


Fig. 4. Functional diversity distribution of birds in China.

2.5. Statistical analysis

2.5.1. Descriptive statistics

In this study, we utilized QGIS to generate a set of uniformly distributed grid points within the study area with grid resolutions of 1 km × 1 km, 5 km × 5 km, and 10 km × 10 km. At each grid point, raster values were extracted at its corresponding grain for each variable and organized into structured tables. As a result, a comprehensive dataset of environmental variables was obtained and used for subsequent data analysis and modeling.

In order to evaluate the discrepancies between the years for the bird diversity and the urbanization variables, we performed a descriptive statistics analysis on the response variables of bird taxonomic diversity

and bird functional diversity, along with the independent variables of impervious surface coverage, nighttime light intensity, and population density. These variables were tested for the significance of differences over time utilizing the Wilcoxon test (Gehan, 1965).

To assess the characteristics of urbanization and the distribution of bird diversity in China, and to evaluate the distributional differences and grain stability of these characteristics, we counted the number of study units at three spatial resolutions for high (80 ≤ ISC ≤ 100) - medium (80 ≤ ISC ≤ 100) - low (80 ≤ ISC ≤ 100) urbanization gradients and bird taxonomic diversity high (TD ≥ 500) - medium (200 ≤ TD ≤ 500) - low (0 ≤ TD ≤ 200) and assessed the potential patterns of their quantitative relationships with grain.

2.5.2. Modeling

In the same time section, the impacts of urbanization led to a spatial reconfiguration of bird communities with varying degrees of tolerance to urban environments. We applied a filtering process to the sampling units within each time section based on a criterion of impervious surface coverage equal to or exceeding 20%, delineating them as “urban areas”. Subsequently, we utilized the “plm” package in R to evaluate the significance of the temporal or bivariate effects within the predefined model (Croissant & Millo, 2008). Based on this assessment, we fitted a one-way individual effect model to the two response variables. To generate reliable parameter estimates, we introduced administrative regions as clustering variables and calculated cluster-robust standard errors.

To examine potential variations in the impacts of urbanization on bird diversity based on urbanization levels, specifically focusing on the distinctions between low and moderate areas along the urbanization gradient, we partitioned the gradient into two categories: suburban areas with impervious surface coverage ranging from 20% to 50%, and central urban areas with impervious surface coverage exceeding 50%. Subsequently, we conducted separate statistical analyses for each group of samples to examine differences in the effects of basal levels of urbanization on bird diversity.

We filtered the response variables for outliers (Z-Score ≥ 3) in all models and Calculated inter-variate correlations, variance inflation factors, significance of fixed and random effects, goodness of fit, and standardized regression coefficients for all models. Based on visual evaluation, all models satisfied the assumptions of normality and homoscedasticity of residuals. With the exception of generating bird diversity, subsequent data processing was performed using R version 4.1.2 (R Core Team, 2013).

2.5.3. Calculating the spatial correlation between bird diversity and urbanization gradients

To evaluate the spatial relationship between bird diversity and gradients of urbanization, we applied GeoDa’s global bivariate spatial autocorrelation and bivariate local Moran’s I to determine the spatial autocorrelation of the depressions in bird diversity with urbanization hotspots. Additionally, we conducted visual analysis to investigate how the spatial distribution and homogeneity of bird diversity are impacted by cities of varying geographical backgrounds.

3. Result

3.1. Urbanization and the loss of bird diversity

China has experienced significant growth in urbanization over the span of two decades (Fig. S5). All three urbanization variables have shown higher mean and median values, with impervious surface coverage increasing at a faster rate between 2010 and 2020 (18.1%–28.8%–47.9%). This increase indicates a rapid expansion of urban land (Ma, He, & Wu, 2016). However, nighttime light intensity (1.9–4.8–8.1) and population density (1708–1947–2142 persons/km²) exhibited higher growth rates between 2000 and 2010. This growth may be related to the large influx of population as well as the expansion of the real estate and service industries (Wang, Shi, & Zhou, 2020; Wu, 2022). It is important to note that in urban areas, the average population density has decreased over time (3450–2926–2142 persons/km²). This decrease suggests that the population is gradually transitioning from an agglomeration state in urban centers to a decentralized state that is more evenly distributed in central and suburban areas.

The overall taxonomic and functional diversity of birds experienced a decline over the 20-year period (Fig. S6), with a decrease in species richness of about 3.2% (17 species) and a slight decrease in functional diversity (0.32%). While it remained stable during the first decade, the second decade showed an increasing trend. Interestingly, for a single year, the overall distribution experienced a significant reduction at a

species richness of approximately 500, without regard for the breeding or non-breeding season. The functional diversity of birds demonstrated a single lower peak with various secondary peak values. This signifies that certain hotspots of functional diversity still exist in urban areas. Across years, the Wilcoxon test for each variable was statistically significant ($p < 0.001$). The temporal variation in bird diversity between the breeding and non-breeding seasons differed greatly in both urban and areas of urbanization influence. This disparity reflects the varying impacts of urbanization on birds across physiological seasons (La Sorte, Tingley, & Hurlbert, 2014, 2018). Between 2000 and 2010, both taxonomic and functional diversity increased in the non-breeding season, and in contrast, decreased in the breeding season, suggesting that birds during the breeding season are more susceptible to habitat alterations and external disturbances, which may increase their likelihood of being caught in ecological traps (Garmendia, Apostolopoulou, Adams, & Bormpoudakis, 2016). Overall, bird diversity during breeding season is more crucial for species survival, as it holds a high numerical value, but is more vulnerable to external factors, while bird diversity during the non-breeding season provides a better reflection of urban bird diversity conservation, with a lower numerical value but more tolerant to external stressors.

3.2. Optimal grains for coupling urbanization with bird diversity

Fig. 5 shows the results of the panel data model. Species richness is a stable response variable as evidenced by the significant and stable negative effect of urbanization variables on bird species richness. Habitat loss due to land use change remains the primary cause of the decline in bird species richness, which is further evidenced by the strong and stable negative effect of impervious surface cover, the dominant variable affecting species richness, across all grains. Nighttime light intensity displayed a significant and maximum effect at the 10 km grain, indicating a preference for large scales, possibly due to the large-scale influence of light sources. The effect of population density peaked at the 5 km grain.

Impervious surface coverage had a significant negative effect on the functional diversity of the birds, while nighttime lights had a negative effect on the 1 km grain and population density showed a positive effect on the 1 km and 5 km grains. Impervious surface coverage emerges as the most significant factor affecting functional diversity. In conclusion, the negative effect of urbanization on bird species richness was

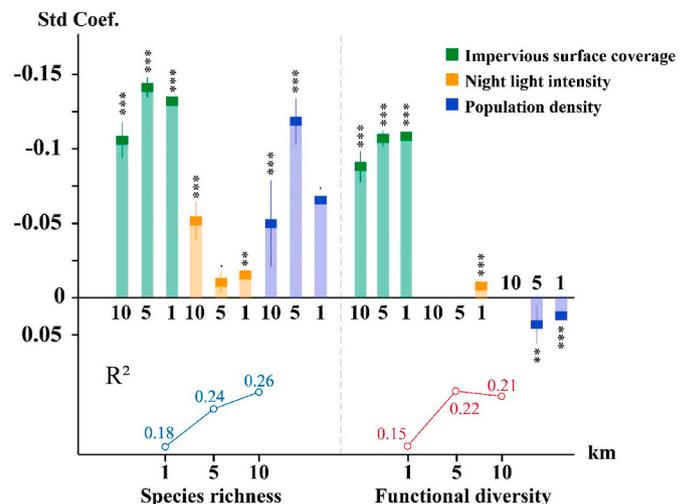


Fig. 5. Effect of grain size on the relationship between urbanization and bird diversity. The vertical line at the top of the bar graph represents the 95% confidence interval. The line graphs represent the change in the goodness of fit at different grain sizes. Significance level ($P \leq 0.001/0.01/0.05/0.1: ***/**/*./$)The original regression results are available in Table S3.

consistently and significantly observed at all landscape scales up to 10 km; however, for the functional diversity of birds, the 1 km grain was the most effective in detecting significant variables.

4. Discussion

4.1. Grain effects between “urban - bird” ecological community: importance and role

Using continental scale citizen science data across China, we tested the influence of grain on the bird diversity – urbanization gradient, summarized by two key findings. Firstly, grain had an effect on the impact of urbanization on bird diversity at the subcontinental range, meaning that changes in grain affected the level of consistency in results, including the significance, strength, and direction of effects. Second, variables associated with bird responses exhibited sensitivities and preferences at different grains (Fig. 5). Species richness supported a wider range of grain and possessed greater grain sensitivity than functional diversity. Urbanization variables also differed in impact at different grains. The results suggest that most urbanization variables have a negative effect on bird diversity. These variables include land usage conversion, disturbance from nighttime lighting, and human activities, which are in line with previous findings (Gagné, Sherman, Singh, & Meentemeyer, 2016; Kosicki, 2021; Rich & Longcore, 2013; Sun et al., 2022).

In general, our work supported other previous works. Numerous studies on ecological processes in urban birds have examined issues of scale or grain, for example, showing a clear grain dependence (from 50 km to global) in temporal changes in multiple metrics of bird taxonomic and functional diversity (Jarzyna & Jetz, 2018). Studies with a scale perspective have also shown that the homogenizing effect of cities on bird communities is scale-dependent, producing very different results at large and regional scales (Leveau, Jokimäki, & Kaisanlahti Jokimäki, 2017). Furthermore, research shows that the scale of urbanized areas has an impact on bird community structure: an increase in floor area is found to be negatively correlated with bird richness only in towns over 7000 inh (Garaffa, Filloy, & Bellocq, 2009).

4.2. Grain effects yield a partial explanation for the intermediate disturbance hypothesis

Urbanization is a human activity that causes disruption to the natural environment. We evaluated the rate of urbanization, using the rate of change of impervious surface between the two periods. The graphical representation of the urbanization gradient across various geographic areas has an apparent correspondence with the rate of urbanization, as observed over a span of time. Urban centers have a higher initial level of urbanization, which leads to a slower speed of urbanization; while suburban areas, as the main expansion areas of land, display a low initial level of urbanization and a comparatively faster speed of urbanization (Fig. S7).

Numerous studies have observed results endorsing the intermediate disturbance hypothesis. The studies suggest that species richness and total bird abundance reach their apex at intermediate levels of development (Blair, 1996; Lepczyk et al., 2008; McKinney & Lockwood, 2001). Our research findings indicate that the adverse impacts of urbanization on bird species richness remain steady, which agrees with the results of several other studies (Clergeau, Croci, et al., 2006; Clergeau et al., 2001; Sandström et al., 2006). Our findings imply that an intermediate disturbance between functional diversity and the urbanization gradient is more probable than taxonomic diversity (Table S4). This occurs because urbanization leads to greater habitat heterogeneity and provides multiple sources of food resources (Connell, 1978). This is in contrast to previous studies where disturbances from urbanization have reduced functional diversity (Matuoka, Benchimol, de Almeida-Rocha, & Morante-Filho, 2020; Sol et al., 2020). In the same temporal

cross-section, nighttime lighting at 5 km and 10 km grains in suburban areas caused a decline in taxonomic diversity but resulted in enhanced functional diversity. This phenomenon may be due to greater patch fragmentation in suburban areas than in urban centers, with blurring effects under large grain size sampling and natural surfaces. Alternatively, low to medium intensity urbanization pressure (in suburban areas) may act as a screening mechanism that eliminates local birds that are functionally homogenous. This leads to suburban areas becoming the point of extinction for local bird species and the entry point for exotic species into urban systems. This, in turn, alters the community structure of birds and facilitates functional traits (Blair & Johnson, 2008).

The majority of results from this study do not support the hypothesis that intermediate disturbance affects bird diversity through urbanization. The findings suggest that functional diversity is more likely to reach its maximum in areas with low levels of urbanization and potential intermediate disturbance. Possible explanations for this finding include the relatively crude approach to urban expansion in China, characterized by sprawl strategies such as large-scale land development and the construction of high floor-area-ratio housing (Souza et al., 2019; Wei & Ye, 2014). In contrast to many urbanization patterns in western countries where there is an abundance of sparse low- and medium-story housing, this development approach has a more severe environmental impact by altering the natural ground surface (Cui & Shi, 2012; Y. Tan, Xu, & Zhang, 2016). Additionally, this development lacks support for small private gardens which have been shown to increase urban green space penetration and provide habitat for birds (Blair, 1996; Croci, Butet, Georges, Aguejda, & Clergeau, 2008; Crooks, Suarez, & Bolger, 2004; Sandström et al., 2006), thereby missing a potential habitat mechanism in suburban and urban areas for birds. Further analysis is needed, including more precise measurements of urban gradients with spatio-temporal statistics, and dynamic identification of urbanization characteristics.

4.3. The spatial relationship between bird diversity and urbanization gradients reflects the operating mechanisms of urban ecosystems

The analysis of impervious surface coverage and bird species richness in Chinese urbanization using step-graded statistics reveals that the accuracy of the process is influenced by the grain of sampling employed. At a larger grain, urban centers' proportion is underestimated, and their growth rate overestimated, whereas suburban areas are overestimated, and their urbanization growth rate underestimated (Table S5). Notably, the ratio of “high-middle-low” bird species richness remained consistent irrespective of grain, and sampling within the 200–500 species range indicated spatial clustering centered on the heart of the urban area, with significant overlap. The proportion of such units increased gradually over two decades, indicating decreased bird diversity in central urban areas due to urbanization. Consequently, there are now more bird species in the suburban areas than in the original urban centers (Table S6).

Fig. 6 illustrates the analysis of spatial autocorrelation between bird diversity and urbanization. As the study grain reduced, the strength of spatial autocorrelation increased, indicating the presence of a grain effect. The outcomes showed a significant global spatial correlation (Moran's $I = -0.193$, $p < 0.001$) between impervious surface coverage (urbanization variable) and species richness. The significance of spatial autocorrelation increased from suburban to central urban areas, indicating the impact of urbanization intensity. The analysis of autocorrelation clustered at different gradients of urbanization. The urban centers illustrated a “high urbanization level-low species richness” trend, while the ring-like suburbs showed a “high urbanization level-high species richness” distribution. This distribution pattern might be linked to the existence of large urban green spaces in suburban blocks (Callaghan et al., 2019). Furthermore, the functional diversity showed a significant autocorrelation with impervious surface coverage, but correlation was weak.

The variation in physical geographic context and urbanization is a

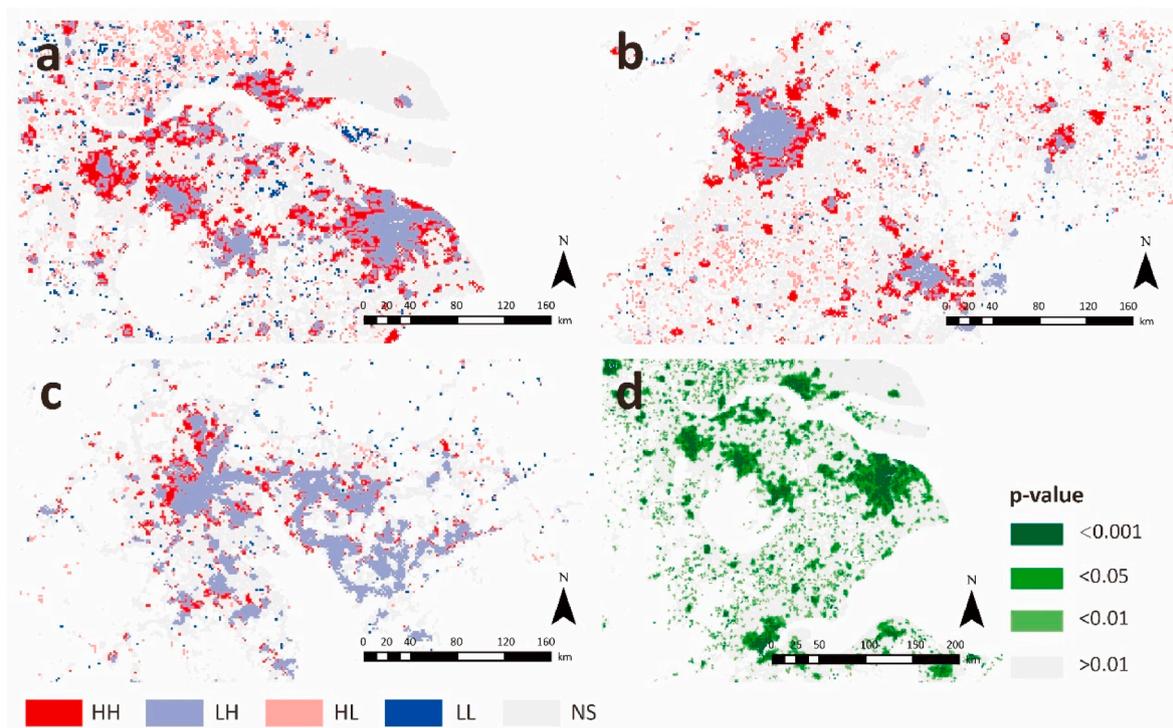


Fig. 6. Spatial autocorrelation of the urbanization variable (impervious surface coverage) with the taxonomic diversity of birds. a/b/c: spatial relationship between impervious surface coverage and taxonomic diversity of birds in the urban agglomerations of the Yangtze River Delta, the Beijing-Tianjin-Hebei, and the Pearl River Delta, and d: significance level of spatial autocorrelation related to the urbanization rate.

key factor in autocorrelated clustering differences across cities. Typically, urban centers present a “high urbanization level-low species richness” trend, whereas peri-urban areas display “high urbanization level-high species richness”. These phenomena generate diversity depressions or ecological islands (Chace & Walsh, 2006; M. Tan, Li, Xie, & Lu, 2005), which are more observable in cities with single-core tessellated expansion like Beijing and Zhengzhou. This effect becomes more pronounced with the growth of urban land. In urban areas with a more complicated natural context, such as the Yangtze River Delta urban agglomeration, the “high-high” clustering of suburban areas is relatively fragmented due to the influence of rivers, lakes, or mountains. For example, cities like Shanghai and Suzhou have natural features that break this pattern. Conversely, in densely populated urbanized areas like Guangzhou, Foshan, and Shenzhen in the Pearl River Delta (Fig. 6 a/b/c), where urban land is directly linked without the buffer of rural areas, the spatial clustering of “high urbanization level-low species richness” is more fragmented and the “high urbanization level-high species richness” pattern is less frequent.

4.4. Research limitations and future work outlook

Our findings highlight the grain effect of urbanization on bird diversity and underscore the importance of selecting the appropriate spatial scale for research. Given that bird communities exhibit behavior across multiple scales, it is essential to conduct multi-scale studies within urban environments (Fidino & Magle, 2017; Swan et al., 2021) and develop species-specific policies. Analyzing the intra- and inter-annual variations in how different bird species respond to urban environments can help identify crucial periods for maintaining urban avian diversity, thus enhancing the efficiency of conservation efforts (Marra, Cohen, Loss, Rutter, & Tonra, 2015; Zuckerberg, Fink, La Sorte, Hochachka, & Kelling, 2016).

Our study primarily focuses on the macroecological impacts of urbanization on bird diversity. However, it is worth acknowledging that our minimum grain size was 1 square kilometer, which did not fully

capture the local-scale effects of micro processes on avian communities, such as the support of fragmented urban green spaces for birds (Morales, Frei, Mitchell, Bégin-Marchand, & Elliott, 2022) or the interference of bright lights on migratory birds (Van Doren et al., 2017). We fully recognize the significance of local-scale research for urban planning and avian diversity conservation. Future research can investigate the differential impacts of urban development characteristics (such as scale, natural context, and urban form) on bird diversity, allowing for a more in-depth exploration of the interactions between urban features and avian diversity along an urbanization gradient.

5. Conclusion

By analyzing data from citizen science projects, we have unveiled the significant impact of spatial grain on the relationship between urbanization and bird diversity, affecting the strength, direction, and significance of these effects. We have demonstrated that the intermediate disturbance hypothesis is more applicable to functional diversity than taxonomic diversity, yet overall, urbanization’s influence on bird diversity remains constant. Our methodological workflow is globally applicable and opens doors to exploring broader ‘urban-ecological’ patterns, particularly the long-term spatial and temporal impacts of urbanization on biodiversity. In summary, this study underscores the pivotal role of spatial grain in understanding the effects of urbanization on bird diversity and emphasizes the necessity of considering spatial grain in future analyses of urbanization gradients and biodiversity.

Environmental data sources

Environmental data sources used in this study include Digital Elevation Model (DEM) data, vegetation type data, Normalized Difference Vegetation Index (NDVI) data, and Gross Domestic Product (GDP) data obtained from the Resource and Environment Science and Data Center, Chinese Academy of Sciences (<https://www.resdc.cn>). Slope and aspect data were calculated based on DEM data using Esri ArcMap. The

distance to the nearest water body data was derived from China's water system data (<https://www.resdc.cn>) using Esri ArcMap. Temperature and precipitation data were sourced from the National Earth System Science Data Center in China. Monthly averages were calculated for the breeding season (March–August) and non-breeding season (September–February) to obtain the corresponding annual averages for both seasons. NDVI data was divided into four quarterly periods: spring (March–May), summer (June–August), autumn (September–November), and winter (December–February). The quarterly data were synthesized for both breeding and non-breeding seasons (A and B). Land use type data were obtained from (Sulla-Menashe & Friedl, 2018). PM2.5 data were sourced from (Hammer et al., 2020; van Donkelaar et al., 2019). Impervious surface data were acquired from (Gong et al., 2019). Nighttime light data were obtained from (Z. Chen et al., 2020), and population data were sourced from worldpop (<https://www.worldpop.org/>).

Bird data sources

Bird data sources utilized in this research consist of bird sighting records from the China Birding Records Center (<http://www.birdreport.cn>). Bird trait data were collected from Ecological Archives E096-269 (Myhrvold et al., 2015), E095-178 (Wilman et al., 2014), and the World Bird Survival Handbook (<https://birdsoftheworld.org>).

Note

The data sources mentioned above have been utilized for this study. Proper citations and references have been provided for each data category.

CRedit authorship contribution statement

Jiayu Wu: Conceptualization, Funding acquisition, Supervision, Writing – review & editing. **Guanyi Chen:** Data curation, Formal analysis, Methodology, Validation, Writing – original draft. **Corey T. Callaghan:** Conceptualization, Writing – review & editing. **Qiang Ren:** Conceptualization, Supervision, Writing – review & editing.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apgeog.2023.103154>.

References

- Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., et al. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*, 281(1780), Article 20133330. <https://doi.org/10.1098/rspb.2013.3330>
- Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J., Nakashizuka, T., Raffaelli, D., et al. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9(10), 1146–1156.
- Balvanera, P., Siddique, I., Dee, L., Paquette, A., Isbell, F., Gonzalez, A., et al. (2014). Linking biodiversity and ecosystem services: Current uncertainties and the necessary next steps. *BioScience*, 64(1), 49–57.
- Blair, R. B. (1996). Land use and avian species diversity along an urban gradient. *Ecological Applications*, 6(2), 506–519. <https://doi.org/10.2307/2269387>
- Blair, R. B. (1999). Birds and butterflies along an urban gradient: Surrogate taxa for assessing biodiversity? *Ecological Applications*, 9(1), 164–170.
- Blair, R. B., & Johnson, E. M. (2008). Suburban habitats and their role for birds in the urban–rural habitat network: Points of local invasion and extinction? *Landscape Ecology*, 23, 1157–1169. <https://doi.org/10.1007/s10980-008-9267-y>
- Callaghan, C. T., Bino, G., Major, R. E., Martin, J. M., Lyons, M. B., & Kingsford, R. T. (2019). Heterogeneous urban green areas are bird diversity hotspots: Insights using continental-scale citizen science data. *Landscape Ecology*, 34(6), 1231–1246. <https://doi.org/10.1007/s10980-019-00851-6>
- Chace, J. F., & Walsh, J. J. (2006). Urban effects on native avifauna: A review. *Landscape and Urban Planning*, 74(1), 46–69. <https://doi.org/10.1016/j.landurbplan.2004.08.007>
- Chen, S., & Wang, S. (2017). Bird diversities and their responses to urbanization in China. In *Ecology and conservation of birds in urban environments* (pp. 55–74). Springer.
- Chen, Z., Yu, B., Yang, C., Zhou, Y., Yao, S., Qian, X., et al. (2020). An extended time-series (2000–2018) of global NPP-VIIRS-like nighttime light data. In *Harvard dataverse* (V3 ed.). <https://doi.org/10.7910/DVN/YGIVCD>
- Clergeau, P., Croci, S., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., & Dinetti, M. (2006). Avifauna homogenisation by urbanisation: Analysis at different European latitudes. *Biological Conservation*, 127(3), 336–344.
- Clergeau, P., Jokimäki, J., & Savard, J. L. (2001). Are urban bird communities influenced by the bird diversity of adjacent landscapes? *Journal of Applied Ecology*, 38(5), 1122–1134.
- Clergeau, P., Jokimäki, J., & Snep, R. (2006). Using hierarchical levels for urban ecology. *Trends in Ecology & Evolution*, 21(12), 660–661. <https://doi.org/10.1016/j.tree.2006.09.006>
- Collins, J. P., Kinzig, A., Grimm, N. B., Fagan, W. F., Hope, D., Wu, J., et al. (2000). A new urban ecology: Modeling human communities as integral parts of ecosystems poses special problems for the development and testing of ecological theory (Vol. 88, pp. 416–425), 5.
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs: High diversity of trees and corals is maintained only in a nonequilibrium state. *Science*, 199(4335), 1302–1310.
- Cox, G. W. (2010). *Bird migration and global change*. Island Press.
- Croci, S., Butet, A., Georges, A., Aguejedad, R., & Clergeau, P. (2008). Small urban woodlands as biodiversity conservation hot-spot: A multi-taxon approach. *Landscape Ecology*, 23, 1171–1186. <https://doi.org/10.1007/s10980-008-9257-0>
- Croissant, Y., & Millo, G. (2008). Panel data econometrics in R: The plm package. *Journal of Statistical Software*, 27(2), 1–43.
- Crooks, K. R., Suarez, A. V., & Bolger, D. T. (2004). Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biological Conservation*, 115(3), 451–462.
- Cui, L., & Shi, J. (2012). Urbanization and its environmental effects in Shanghai, China. *Urban Climate*, 2, 1–15.
- Davis, A. Y., Belaire, J. A., Farfan, M. A., Milz, D., Sweeney, E. R., Loss, S. R., et al. (2012). Green infrastructure and bird diversity across an urban socioeconomic gradient. *Ecosphere*, 3(11). <https://doi.org/10.1890/ES12-00126.1.art105>
- Delignette-Muller, M. L., & Dutang, C. (2015). fitdistrplus: An R package for fitting distributions. *Journal of Statistical Software*, 64, 1–34.
- Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. *Ecology Letters*, 13(8), 1030–1040.
- van Donkelaar, A., Martin, R. V., Li, C., & Burnett, R. T. (2019). Regional estimates of chemical composition of fine particulate matter using a combined geoscientific-statistical method with information from satellites, models, and monitors. *Environmental Science and Technology*, 53(5), 2595–2611. <https://doi.org/10.1021/acs.est.8b06392>
- Fidino, M., & Magle, S. B. (2017). Trends in long-term urban bird research. In E. Murgui, & M. Hedblom (Eds.), *Ecology and conservation of birds in urban environments* (pp. 161–184). Springer International Publishing. https://doi.org/10.1007/978-3-319-43314-1_9
- Filloley, J., Zurita, G. A., & Bellocq, M. I. (2019). Bird diversity in urban ecosystems: The role of the biome and land use along urbanization gradients. *Ecosystems*, 22(1), 213–227. <https://doi.org/10.1007/s10021-018-0264-y>
- Flynn, D. F., Mirotnick, N., Jain, M., Palmer, M. I., & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. *Ecology*, 92(8), 1573–1581.
- Gagné, S. A., Sherman, P. J., Singh, K. K., & Meentemeyer, R. K. (2016). The effect of human population size on the breeding bird diversity of urban regions. *Biodiversity & Conservation*, 25, 653–671.
- Garaffa, P. I., Filloley, J., & Bellocq, M. I. (2009). Bird community responses along urban–rural gradients: Does the size of the urbanized area matter? *Landscape and Urban Planning*, 90(1–2), 33–41. <https://doi.org/10.1016/j.landurbplan.2008.10.004>
- Garmendia, E., Apostolopoulou, E., Adams, W. M., & Bormpoudakis, D. (2016). Biodiversity and green infrastructure in Europe: Boundary object or ecological trap? *Land Use Policy*, 56, 315–319.
- Gehan, E. A. (1965). A generalized Wilcoxon test for comparing arbitrarily singly-censored samples. *Biometrika*, 52(1–2), 203–224.
- Gong, P., Li, X., & Zhang, W. (2019). 40-Year (1978–2017) human settlement changes in China reflected by impervious surfaces from satellite remote sensing. *Science Bulletin*, 64(11), 756–763. <https://doi.org/10.1016/j.scib.2019.04.024>
- Goodchild, M. F. (2011). Scale in GIS: An overview. *Geomorphology*, 130(1), 5–9. <https://doi.org/10.1016/j.geomorph.2010.10.004>
- Hammer, M. S., van Donkelaar, A., Li, C., Lyapustin, A., Sayer, A. M., Hsu, N. C., et al. (2020). Global estimates and long-term trends of fine particulate matter concentrations (1998–2018). *Environmental Science and Technology*, 54(13), 7879–7890. <https://doi.org/10.1021/acs.est.0c01764>
- Huang, K., Li, X., Liu, X., & Seto, K. C. (2019). Projecting global urban land expansion and heat island intensification through 2050. *Environmental Research Letters*, 14(11), Article 114037. <https://doi.org/10.1088/1748-9326/ab4b71>
- Isaksson, C. (2018). Impact of urbanization on birds. In D. T. Tietze (Ed.), *Bird species: How they arise, modify and vanish* (pp. 235–257). Springer International Publishing. https://doi.org/10.1007/978-3-319-91689-7_13
- Jarzynna, M. A., & Jetz, W. (2018). Taxonomic and functional diversity change is scale dependent. *Nature Communications*, 9(1). <https://doi.org/10.1038/s41467-018-04889-z>. Article 1.

- Keylock, C. (2005). Simpson diversity and the Shannon–Wiener index as special cases of a generalized entropy. *Oikos*, 109(1), 203–207.
- Kosicki, J. Z. (2021). The impact of artificial light at night on taxonomic, functional and phylogenetic bird species communities in a large geographical range: A modelling approach. *Science of the Total Environment*, 780, Article 146434.
- Kowarik, I. (2011). Boston, USA. *Novel urban ecosystems, biodiversity, and conservation. Selected papers from the conference urban environmental pollution: Overcoming obstacles to sustainability and quality of life (UEP2010), 20-23 June 2010* (Vol. 159, pp. 1974–1983). <https://doi.org/10.1016/j.envpol.2011.02.022>, 8.
- La Sorte, F. A., Fink, D., & Johnston, A. (2018). Seasonal associations with novel climates for North American migratory bird populations. *Ecology Letters*, 21(6), 845–856.
- La Sorte, F. A., Tingley, M. W., & Hurlbert, A. H. (2014). The role of urban and agricultural areas during avian migration: An assessment of within-year temporal turnover. *Global Ecology and Biogeography*, 23(11), 1225–1234.
- Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299–305.
- Lees, A. C., Haskell, L., Allinson, T., Bezeng, S. B., Burfield, I. J., Renjifo, L. M., et al. (2022). State of the world's birds. *Annual Review of Environment and Resources*, 47(1), 231–260. <https://doi.org/10.1146/annurev-environ-112420-014642>
- Lepczyk, C. A., Flather, C. H., Radeloff, V. C., Pidgeon, A. M., Hammer, R. B., & Liu, J. (2008). Human impacts on regional avian diversity and abundance. *Conservation Biology*, 22(2), 405–416.
- Leveau, L. M., Jokimäki, J., & Kaisanlahti Jokimäki, M. L. (2017). *Scale dependence of biotic homogenisation by urbanisation: A comparison of urban bird communities between central Argentina and northern Finland* (21). <https://doi.org/10.1515/eje-2017-0011>
- Liang, J., Xing, W., Zeng, G., Li, X., Peng, Y., Li, X., et al. (2018). Where will threatened migratory birds go under climate change? Implications for China's national nature reserves. *Science of the Total Environment*, 645, 1040–1047.
- Losos, J. B., & Ricklefs, R. E. (2009). *The theory of island biogeography revisited*. Princeton University Press.
- Luck, G. W. (2007). A review of the relationships between human population density and biodiversity. *Biological Reviews*, 82(4), 607–645. <https://doi.org/10.1111/j.1469-185X.2007.00028.x>
- Luck, G. W., Carter, A., & Smallbone, L. (2013). Changes in bird functional diversity across multiple land uses: Interpretations of functional redundancy depend on functional group identity. *PLoS One*, 8(5), Article e63671. <https://doi.org/10.1371/journal.pone.0063671>
- MacKinnon, J., Verkuil, Y. I., & Murray, N. (2012). IUCN situation analysis on East and Southeast Asian intertidal habitats, with particular reference to the Yellow Sea (including the Bohai Sea). *Occasional Paper of the IUCN Species Survival Commission*, 47.
- Ma, Q., He, C., & Wu, J. (2016). Behind the rapid expansion of urban impervious surfaces in China: Major influencing factors revealed by a hierarchical multiscale analysis. *Land Use Policy*, 59, 434–445.
- Mandelbrot, B. (1967). How long is the coast of Britain? Statistical self-similarity and fractional dimension. *Science*, 156(3775), 636–638. <https://doi.org/10.1126/science.156.3775.636>
- Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E., & Tonra, C. M. (2015). A call for full annual cycle research in animal ecology. *Biology Letters*, 11(8), Article 20150552.
- Marzluff, J. M. (2001). Worldwide urbanization and its effects on birds. *Avian Ecology and Conservation in an Urbanizing World*, 19–47. https://doi.org/10.1007/978-1-4615-1531-9_2
- Matuoka, M. A., Benchimol, M., de Almeida-Rocha, J. M., & Morante-Filho, J. C. (2020). Effects of anthropogenic disturbances on bird functional diversity: A global meta-analysis. *Ecological Indicators*, 116, Article 106471. <https://doi.org/10.1016/j.ecolind.2020.106471>
- McKinney, M. L., & Lockwood, J. L. (2001). Biotic homogenization: A sequential and selective process. *Biotic Homogenization*, 1–17. https://doi.org/10.1007/978-1-4615-1261-5_1
- Meffert, P. J., & Dziock, F. (2013). The influence of urbanisation on diversity and trait composition of birds. *Landscape Ecology*, 28(5), 943–957. <https://doi.org/10.1007/s10980-013-9867-z>
- Morales, A., Frei, B., Mitchell, G. W., Bégin-Marchand, C., & Elliott, K. H. (2022). Reduced diurnal activity and increased stopover duration by molting Swainson's Thrushes. *Ornithology*, 139(2), ukab083. <https://doi.org/10.1093/ornithology/ukab083>
- Myhrvold, N. P., Baldrige, E., Chan, B., Sivam, D., Freeman, D. L., & Ernest, S. M. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles: Ecological Archives E096-269. *Ecology*, 96(11), 3109–3109.
- Nally, R. M., & Quinn, G. P. (1998). Symposium introduction: The importance of scale in ecology. *Australian Journal of Ecology*, 23(1), 1–7.
- Openshaw, S. (1984). Ecological fallacies and the analysis of areal census data. *Environment and Planning A: Economy and Space*, 16(1), 17–31. <https://doi.org/10.1068/a160017>
- Qizhi, M., Ying, L., Kang, W., & Qingfei, Z. (2016). Spatio-temporal changes of population density and urbanization pattern in China(2000–2010). *China City Planning Review*, 25(4), 8–14.
- R Core Team, R. (2013). *R: A language and environment for statistical computing*.
- Rich, C., & Longcore, T. (2013). *Ecological consequences of artificial night lighting*. Island Press.
- Sandström, U., Angelstam, P., & Mikusiński, G. (2006). Ecological diversity of birds in relation to the structure of urban green space. *Landscape and Urban Planning*, 77(1–2), 39–53.
- Santini, L., Butchart, S. H., Rondinini, C., Benítez-López, A., Hilbers, J. P., Schipper, A. M., et al. (2019). Applying habitat and population-density models to land-cover time series to inform IUCN Red List assessments. *Conservation Biology*, 33(5), 1084–1093.
- Savard, J.-P. L., Clergeau, P., & Mennechez, G. (2000). Biodiversity concepts and urban ecosystems. *Landscape and Urban Planning*, 48(3), 131–142. [https://doi.org/10.1016/S0169-2046\(00\)00037-2](https://doi.org/10.1016/S0169-2046(00)00037-2)
- Schütz, C., & Schulze, C. H. (2015). Functional diversity of urban bird communities: Effects of landscape composition, green space area and vegetation cover. *Ecology and Evolution*, 5(22), 5230–5239. <https://doi.org/10.1002/ece3.1778>
- Sol, D., Trisos, C., Múrria, C., Jeliakov, A., González-Lagos, C., Pigot, A. L., et al. (2020). The worldwide impact of urbanisation on avian functional diversity. *Ecology Letters*, 23(6), 962–972. <https://doi.org/10.1111/ele.13495>
- Souza, F. L., Valente-Neto, F., Severo-Neto, F., Bueno, B., Ochoa-Quintero, J. M., Laps, R. R., et al. (2019). Impervious surface and heterogeneity are opposite drivers to maintain bird richness in a Cerrado city. *Landscape and Urban Planning*, 192, Article 103643.
- Sulla-Menashe, D., & Friedl, M. A. (2018). *User guide to collection 6 MODIS land cover (MCD12Q1 and MCD12C1) product* (Vol. 1, p. 18). Reston, Va, Usa: Usgs.
- Sun, B., Lu, Y., Yang, Y., Yu, M., Yuan, J., Yu, R., et al. (2022). Urbanization affects spatial variation and species similarity of bird diversity distribution. *Science Advances*, 8(49), Article eade3061. <https://doi.org/10.1126/sciadv.ade3061>
- Swan, C. M., Brown, B., Borowy, D., Cavender-Bares, J., Jeliakov, A., Knapp, S., et al. (2021). A framework for understanding how biodiversity patterns unfold across multiple spatial scales in urban ecosystems. *Ecosphere*, 12(7), Article e03650. <https://doi.org/10.1002/ecs2.3650>
- Tan, M., Li, X., Xie, H., & Lu, C. (2005). Urban land expansion and arable land loss in China—a case study of Beijing–Tianjin–Hebei region. *Land Use Policy*, 22(3), 187–196.
- Tan, Y., Xu, H., & Zhang, X. (2016). Sustainable urbanization in China: A comprehensive literature review. *Cities*, 55, 82–93.
- Tatem, A. J. (2017). WorldPop, open data for spatial demography. *Scientific Data*, 4(1), 1–4.
- Tian, G., Jiang, J., Yang, Z., & Zhang, Y. (2011). The urban growth, size distribution and spatio-temporal dynamic pattern of the Yangtze River Delta megalopolitan region, China. *Ecological Modelling*, 222(3), 865–878.
- Tregear, T. R. (2017). *A geography of China*. Routledge.
- UN. (2022). *World population prospects 2022: Summary of results*.
- Van Doren, B. M., Horton, K. G., Dokter, A. M., Klinck, H., Elbin, S. B., & Farnsworth, A. (2017). High-intensity urban light installation dramatically alters nocturnal bird migration. *Proceedings of the National Academy of Sciences*, 114(42), 11175–11180.
- Wang, X., Shi, R., & Zhou, Y. (2020). Dynamics of urban sprawl and sustainable development in China. *Socio-Economic Planning Sciences*, 70, Article 100736.
- Wei, Y. D., & Ye, X. (2014). Urbanization, urban land expansion and environmental change in China. *Stochastic Environmental Research and Risk Assessment*, 28, 757–765.
- Wheatley, M., & Johnson, C. (2009). Factors limiting our understanding of ecological scale. *Ecological Complexity*, 6(2), 150–159.
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals: *Ecological Archives* E095-178. *Ecology*, 95(7). <https://doi.org/10.1890/13-1917.1>, 2027–2027.
- Wu, F. (2022). Land financialisation and the financing of urban development in China. *Land Use Policy*, 112, Article 104412.
- Zheng, G. (2005). *A checklist on the classification and distribution of the birds of China*. Geological Publishing House.
- Zuckerberg, B., Fink, D., La Sorte, F. A., Hochachka, W. M., & Kelling, S. (2016). Novel seasonal land cover associations for eastern North American forest birds identified through dynamic species distribution modelling. *Diversity and Distributions*, 22(6), 717–730.