

ECOLOGY

Urbanization affects spatial variation and species similarity of bird diversity distribution

Bin Sun^{1,2,3,4}, Yonglong Lu^{1,3*}, Yifu Yang^{3,5}, Mingzhao Yu³, Jingjing Yuan¹, Ran Yu^{1,5}, James M. Bullock⁶, Nils Chr. Stenseth⁷, Xia Li⁸, Zhiwei Cao¹, Haojie Lei¹, Jialong Li¹

Although cities are human-dominated systems, they provide habitat for many other species. Because of the lack of long-term observation data, it is challenging to assess the impacts of rapid urbanization on biodiversity in Global South countries. Using multisource data, we provided the first analysis of the impacts of urbanization on bird distribution at the continental scale and found that the distributional hot spots of threatened birds overlapped greatly with urbanized areas, with only 3.90% of the threatened birds' preferred land cover type in urban built-up areas. Bird ranges are being reshaped differently because of their different adaptations to urbanization. While green infrastructure can improve local bird diversity, the homogeneous urban environment also leads to species compositions being more similar across regions. More attention should be paid to narrow-range species for the formulation of biodiversity conservation strategies, and conservation actions should be further coordinated among cities from a global perspective.

INTRODUCTION

Cities are arguably the newest ecosystem type on the planet, while urbanization is a complex and dynamic historical process, both in China and globally (1–4). Escalating urbanization is evidenced by an increasing urban population and impervious surface area and brings a series of economic, social, and environmental problems (5). Urbanization causes shifts in species composition, diversity, and community structure (6) and is one of the main drivers of the rapid decline and extinction of many native species due to habitat loss and degradation (7). Specific threats are through rapid expansion of human populations, habitat fragmentation, environmental pollution, and non-native invasive species (8). Although there are many studies on how urbanization affects ecological patterns and processes (9–11), there is limited knowledge about the spatial and temporal distribution of the impacts of urbanization on biodiversity. Our understanding of the relationships between urbanization and biodiversity remains insufficient, especially in the Global South (12–14).

Biodiversity is vital for maintaining ecosystem health and achieving the sustainable development goals (SDGs) (8, 15, 16). The world's governments have promised to abide by the Convention on Biological Diversity and other international agreements to reduce biodiversity loss. However, little attention has been paid to urban biodiversity, an essential aspect of SDG11 (17). It is of great importance to maintain urban ecological diversity and to improve

the urban environment (7, 18, 19), especially for the delivery of SDG15 (life on land).

Vertebrates are important in urban food webs (7, 20, 21), and their spatial behaviors can be heavily modified in urban ecosystems (22). Birds are an important indicator of urban ecological status and are among the main animal groups that survive in the urban environment (23–25). According to a report by the Intergovernmental Science–Policy Platform on Biodiversity and Ecosystem Services, 3.5% of birds had become extinct by 2016 (26). However, it suggested that the extinction risks for birds and other vertebrates would have been at least 20% greater without conservation action in recent decades. Therefore, it is important to study bird biodiversity and its protection in the context of urbanization. Some studies have shown that the isolation and fragmentation of their habitats have adversely affected urban birds (27–30), and their biodiversity in cities has declined, leading to the homogenization of bird communities. However, other studies have indicated that moderate urbanization can help increase bird abundance and species diversity, through increased availability of resources and reduced predators (31–33). There is a lack of spatiotemporal data to assess how rapid urbanization affects bird distributions at large scales. In this context, our hypothesis is that urban expansion may have opposing effects on the distribution of widespread and narrow-range birds, and highly homogeneous urban environments may help recover local biodiversity while increasing species similarity across regions.

To test the above hypotheses, we combined three data sources comprising the China Bird Watching Record Center, eBird, and Global Biodiversity Information Facility (GBIF) to obtain high-precision bird distribution information across China (34, 35). Species distribution models (SDMs) were used to simulate the potential climatic distribution of each bird, and the observed/potential range size ratio [range filling (RF)] was used to evaluate the impact of human activities relating to urban expansion on the distribution of birds. With detailed data on night lighting, impervious surfaces, vegetation coverage, and other information characterizing urbanization, we aimed to test our hypotheses and address knowledge gaps concerning the impacts of urbanization on bird distribution (36).

¹State Key Laboratory of Marine Environmental Science and Key Laboratory of the Ministry of Education for Coastal Wetland Ecosystems, College of the Environment and Ecology, Xiamen University, Fujian 361102, China. ²Sino-Danish College, University of Chinese Academy of Sciences, Beijing 100049, China. ³State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100085, China. ⁴University of Chinese Academy of Sciences, Beijing 100049, China. ⁵School of Environmental and Natural Resources, Renmin University of China, Beijing 100872, China. ⁶UK Centre for Ecology and Hydrology, Wallingford, Oxon OX10 8BB, UK. ⁷Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, 03160 Oslo 3, Norway. ⁸East China Normal University, Shanghai 200241, China.

*Corresponding author. Email: yllu@xmu.edu.cn, yllu@rcees.ac.cn

Because China is the fastest urbanizing country and a notable contributor to global green growth (37), this research is relevant for emerging economies that aim to protect biodiversity during the process of rapid urbanization.

RESULTS AND DISCUSSION

Prefecture-level spatial distribution of bird biodiversity

Using bird observation data from 2000 to 2020 and the checklist on the classification and distribution of the birds of China (38), we found that rapid urbanization has not brought about a radical change in the distribution patterns of birds in sub-biogeographic regions at the national level (Fig. 1, A and B). Species richness was significantly correlated between the observation data and checklist in sub-biogeographic regions [coefficient of determination (R^2) = 0.89, $P < 0.01$; fig. S1]. There are more observed bird species in southwest and eastern China, while less in northeast and north China. The spatial distribution of bird species is similar to that of wider biodiversity in China (39), which shows latitudinal gradients. However, the distribution of some birds has changed. The distribution areas of 404 bird species (table S1), of a total of 1338 species, have expanded compared to the bird checklist (38). Most of the 404 species are widely distributed and can be observed in more than 20 prefectures (fig. S2). At the prefecture level, the number of bird species observed in Dehong Dai and Jingpo Autonomous Prefecture and Baoshan is significantly higher than that in other prefectures, which may be related to the high species richness in Southwest China (Fig. 1C) (15). More bird species were observed in southeastern coastal cities, probably because the climate of coastal areas is warm and suitable for birds to overwinter. To ensure the accuracy of bird diversity data at the prefecture level,

we excluded prefectures with poor data in the following analysis. Taking into account the differences in the observation records for each prefecture (fig. S3), we used the calculation method for sample coverage rate of communities (40), assuming that the bird distribution was well sampled if the average increase in the number of bird species observed in the recent 10 observations was within 1%. A total of 247 prefectures passed through data quality control (Fig. 1D). The well-sampled prefectures are found in every region of China, which suggests that they can be used to reflect the prefecture-level spatial distribution pattern of birds in China.

A total of 66 threatened bird species, comprising the “Critically Endangered” (CR), “Endangered” (EN), and “Vulnerable” (VU) from China’s Red List categories (41), are found in coastal cities including Shanghai, Tangshan, Qinhuangdao, Wenzhou, Tianjin, and Yancheng, accounting for 50.77% of China’s threatened bird species, while the number of threatened species in Central and Western China is relatively low (Fig. 2A). In contrast to the spatial distribution of all bird species, the number of threatened birds in Southwest China is not large, despite it being the hot spot for bird diversity. In terms of the bird threatened species index, there is a great difference between prefectures, with the maximum value of more than 9% and some prefectures having no threatened birds (Fig. 2B). The threatened species index of eastern prefectures, which are urbanization hot spots, is significantly higher than that of central and western prefectures, and the highest threatened species index values are in eastern coastal cities such as Dongying, Shanghai, Tianjin, and Qingdao (Fig. 2B). Because threatened birds mostly comprise migratory species, their distribution has strong seasonal variability. In spring and summer, the threatened bird species are mainly found in northeast China and the coastal zone of northern China (Fig. 2, C and D). In autumn, the

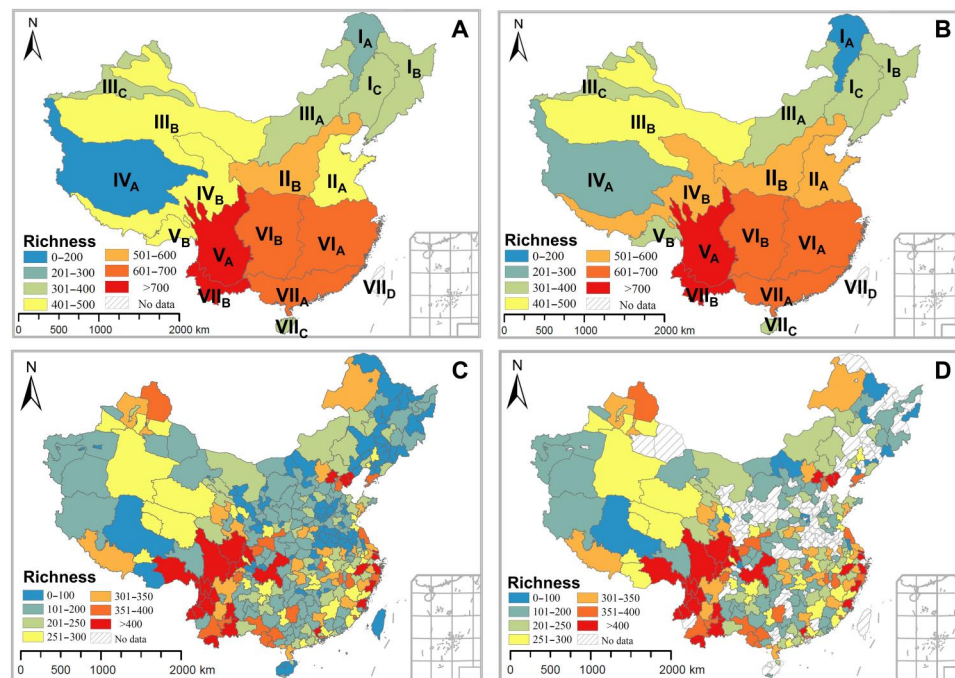


Fig. 1. Distribution pattern of birds in China. (A) Bird distribution pattern in sub-biogeographic regions based on “a checklist on the classification and distribution of the birds of China (Third Edition).” (B) Bird distribution pattern in sub-biogeographic regions based on integrated multisource bird watching data. (C) Bird distribution pattern at the prefecture level. (D) The cities for which bird distribution at the prefecture level was well sampled.

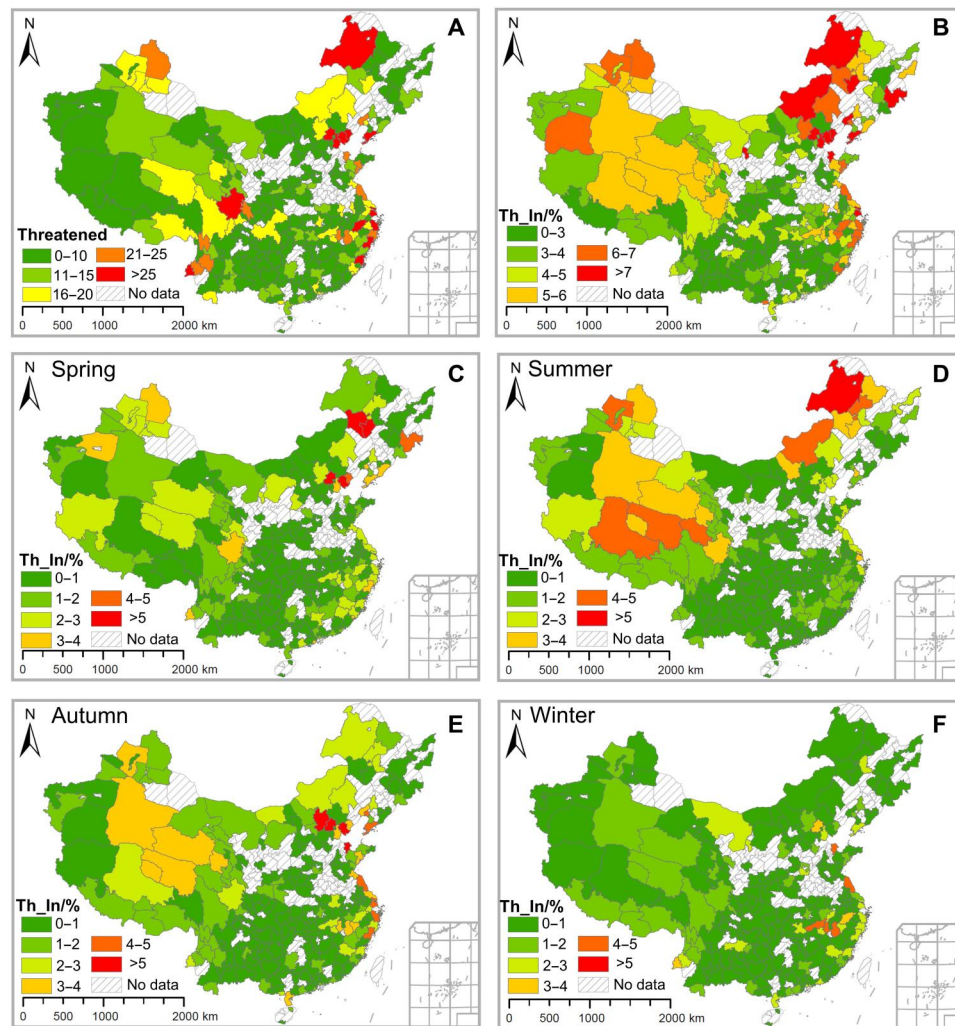


Fig. 2. Prefecture-level spatial variation in threatened bird numbers. (A) Distribution of numbers of threatened species at the prefecture level. (B) Distribution of the threatened species index (Th_In, %) at the prefecture level throughout the year. (C) Distribution of threatened species index at the prefecture level in spring. (D) Distribution of threatened species index at the prefecture level in summer. (E) Distribution of threatened species index at the prefecture level in autumn. (F) Distribution of threatened species index at the prefecture level in winter.

coastal areas become the most popular locations (Fig. 2E). The hot spots in winter appear in the middle and lower reaches of the Yangtze River Fig. 2F.

Habitats of threatened birds are constrained by continuing urbanization

Urbanized areas can be characterized in terms of nighttime light and large areas of manufactured impervious surfaces. The spatial distribution of urban expansion is closely related to environmental conditions and economic development. In China, the Bohai Rim, the Yangtze River Delta, and the Pearl River Delta have had the most significant urban expansion. According to the SDMs, many of the hot spots of urban expansion are spatially significantly correlated with the hot spots of climatically based potential ranges of threatened birds (Fig. 3A and fig. S4) (42).

Both artificial lights and impervious surfaces adversely affect bird diversity. For birds that migrate at night, artificial lights affect avian orientation (43). Taking nocturnal migratory birds as

an example, millions of birds die from hitting buildings, especially city buildings and communication towers that are brightly lit at night. The most influential factors in predicting fatal bird strikes include the nocturnal migrating birds' size, light intensity/brightness, and wind conditions (44). More generally, artificial light at night can disrupt a wide range of bird behaviors, including sleep patterns and breeding dates (45). Hot spots of potential distributions of threatened birds, such as Bohai Rim, Yangtze River Delta, and Middle Reaches of Yangtze River (Fig. 3, C, E, and G), have shown large increases in the area affected by nighttime light, and light intensity is also increasing.

The negative impacts of impervious areas on birds reflect the loss of food resources, shelter, and nest sites. In this study, the changes in impervious areas were calculated at the prefecture level from 2000 to 2018. China has shown a large growth in impervious area over the past two decades (fig. S5). The total impervious area of China was 195,185 km² in 2018, an increase of 132% relative to 2000. Most impervious surfaces are located in the three potential hot spots for

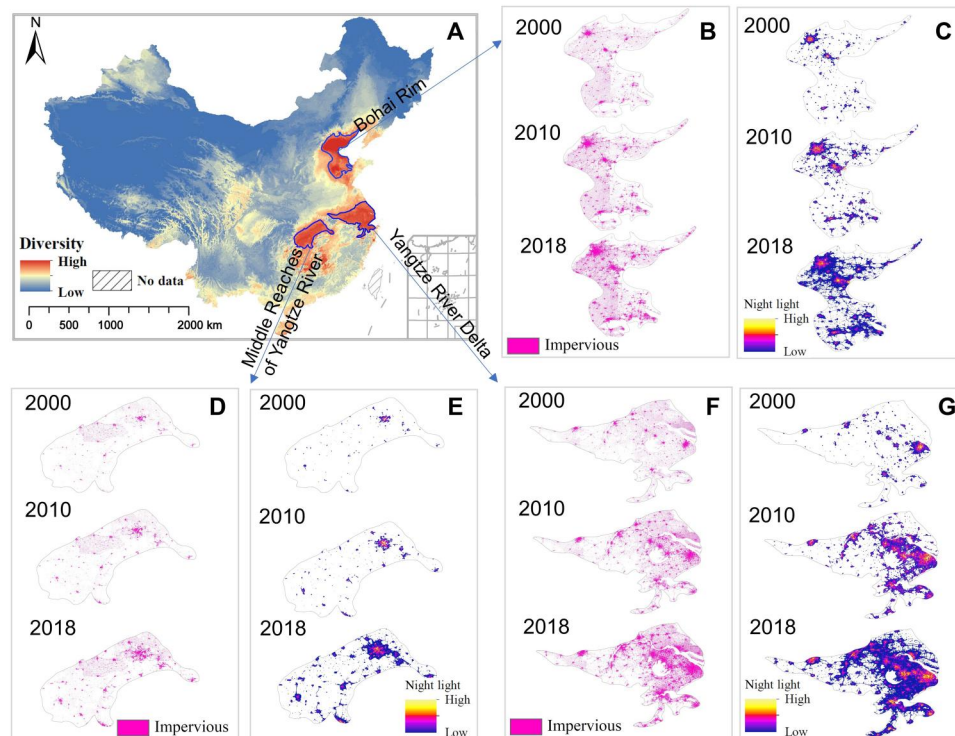


Fig. 3. Threatened bird species' hot spots have seen dramatic increases in impervious area and nighttime light from 2000 to 2018. (A) Hot spots of potential distributions of threatened bird species, including Bohai Rim, Yangtze River Delta, and Middle Reaches of Yangtze River. (B) The impervious paved area of the Bohai Rim in 2000, 2010, and 2018 at 30-m spatial resolution. (C) Changes in nighttime light intensity of the Bohai Rim from 2000 to 2018 at 500-m spatial resolution. (D) The impervious area of the Middle Reaches of Yangtze River in 2000, 2010, and 2018. (E) Changes in nighttime light intensity of the Middle Reaches of Yangtze River from 2000 to 2018. (F) The impervious area of the Yangtze River Delta in 2000, 2010, and 2018. (G) Changes in nighttime light intensity of the Yangtze River Delta from 2000 to 2018.

threatened birds (Fig. 3, B, D, and F). From 2000 to 2018, the impervious areas of these hot spots increased by 124.5, 212.0, and 172.0%, respectively. The proportion that is impervious surface in the Yangtze River Delta has been close to a quarter, reaching 24.3%. Because of habitat being constrained by continuing urbanization, the RF by threatened birds is 0.29 lower than that of other species.

Attributing the effects of urbanization on bird distributions

For the locations for which we had bird distribution data at yearly intervals, the corresponding land cover types were extracted at 500-m spatial resolution from the MCD12Q1 V6 product (<https://earthengine.google.com/>) according to the coordinates and year of the locations with the presence of birds and reclassified in terms of the preference by different birds for the land cover type ["preferred land cover type" (PLCT)] (table S3). There were significant differences in PLCT for different orders (Fig. 4C). For Passeriformes, the largest avian order, the PLCT comprises forest, followed by grassland and urban and built-up land. The PLCT of the second largest order Charadriiformes is wetland. With rapid urbanization, different types of land cover change idiosyncratically, which has a filtering effect on the distribution of birds. Consistent with the large-scale expansion of impervious surfaces, the birds whose PLCTs are urban and built-up lands can likely survive in urban environments. Their RF is 0.68, which is significantly higher than those of other species (Fig. 4A). The birds whose PLCTs are wetlands and forest are more likely to suffer from habitat loss under urbanization, with RFs of 0.44 and 0.41,

respectively. For many threatened birds, the PLCT is wetland (Fig. 4D), and this negative filtering effect will continue as urbanization progresses.

When the actual distribution area is larger than the potential range based on the SDMs, we consider that the distribution area has expanded, and the number of prefectures the range has expanded into is used as a proxy for the species adaptability. We found that this adaptability was significantly positively correlated with a species distribution range (Fig. 4B). Birds with narrow ranges may also expand to some degree but generally have lost range area. Ultimately, human activities have opposing effects on the distributions of large-range and narrow-range birds. This pattern is consistent with the impacts of human activities on plant distribution (46). Species with narrow ranges are more vulnerable and should be given more attention in biodiversity conservation planning. In addition, there remain some species with small distribution ranges that have not been listed as threatened species. To fill this gap, future research should focus on the assessment of their distribution and abundance.

Bird composition is more similar across regions under urbanization

The expanding urban environment not only increases the potential distribution area of birds adapted to the urban environment but also reduces the differences in bird species between regions. A between-city bird similarity network (BSN) was constructed by using both the bird distribution information based on SDMs and bird watching

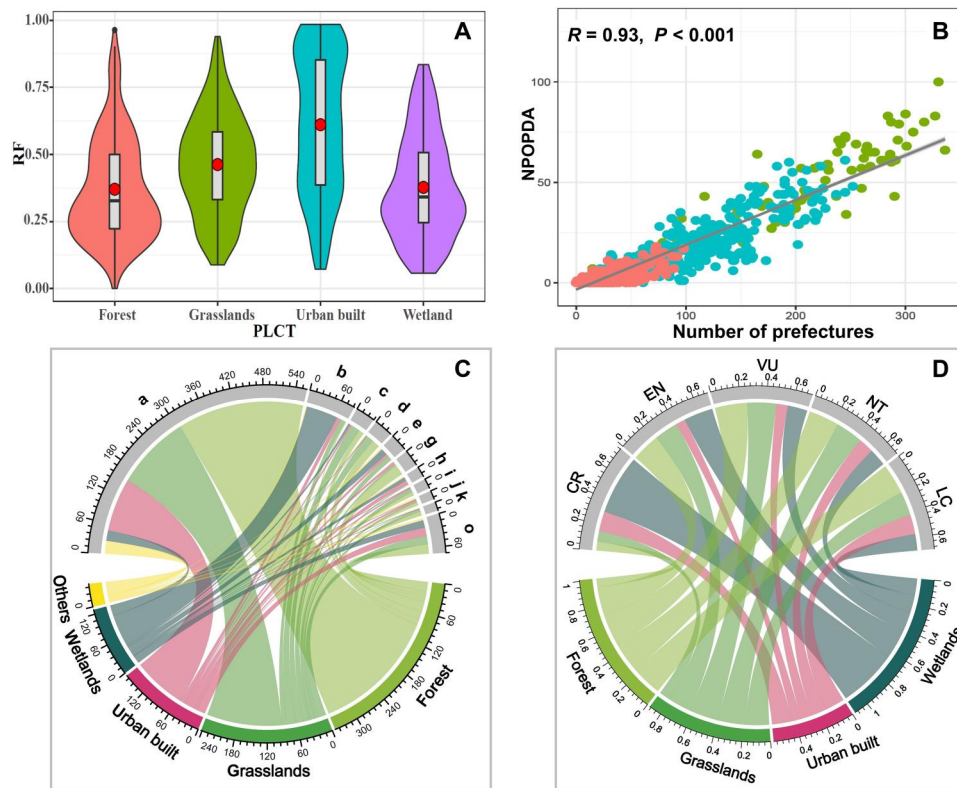


Fig. 4. The impact of urbanization on RF. (A) The preferred land cover types (PLCTs) of individual bird species divided into four types: forest, grassland, urban built-up land, and wetland. The shapes present the distribution of RF. The red dots in (A) represent the average RF value. Birds usually have a smaller RF if their PLCT is forest or wetland. Birds that can adapt to the urban environment have the largest mean RF, indicating that they are less affected by human activities. (B) Each dot represents a bird species. The horizontal axis represents the number of prefectures where the bird species are currently found (number of prefectures). The vertical axis represents the number of prefectures outside the potential distribution area (NPOPDA). Green dots indicate that the bird's range is expanding, which accounted for 7.24%. The red dots indicate that disappearance from the potential distribution is larger than NPOPDA, and the area is shrinking. Human activities have opposite effects on the distribution of widespread and narrow-range birds. (C) Bird's PLCT for different order. Numbers represent the number of species. (a) Passeriformes, (b) Charadriiformes, (c) Accipitriformes, (d) Galliformes, (e) Anseriformes, (g) Piciformes, (h) Pelecaniformes, (i) Columbiformes, (j) Coraciiformes, (k) Strigiformes, and (o) others. (D) Bird's PLCT for different Red List categories. Numbers represent the preference of each category of birds for different PLCTs.

observations, which represent the BSN undisturbed and disturbed by urban expansion, respectively. The former BSN has a strong regional clustering feature, and different regions are independent of each other (Fig. 5, B and D). When only focusing on species whose PLCTs are urban and built-up lands, this pattern is more obvious, forming three subnetworks: the Bohai Rim, the Yangtze River Delta, and the Pearl River Delta. The average clustering coefficient of the BSN based on observation data is 0.51. In contrast, the average clustering coefficient of the BSN based on SDMs is 0.62. The smaller average clustering coefficient indicates stronger links between regions, especially for bird species that can adapt to urban environments. Their similarity network is integrated and spatially highly consistent with the hot spots of urbanization in China (Fig. 5, A and C). The expansion of highly homogeneous urban environments may lead to narrowing differences in bird composition between regions, which is a challenge to the maintenance of bird diversity.

Bird similarity and geographic distance between cities show a negative correlation (47); using a similarity network based on SDMs (Fig. 5D), distant cities retain a high similarity in urbanization hot spots (Fig. 5C), which implies that the distance effect is weakened under urbanization. The quality of urbanized areas can

be improved by building more green infrastructure, which offers an opportunity for restoring urban biodiversity (48, 49). The normalized difference vegetation index is a widely used proxy for urban green infrastructure and has been found to be related to bird species richness (50). Thirty-two percent of the world's built-up areas that are showing significant greening are located in China, especially concentrated in several city clusters including the Beijing-Tianjin-Hebei region, the Yangtze River Delta, and the Pearl River Delta (37). As the core cities of the three city clusters, Beijing, Shanghai, and Guangzhou have significantly higher bird diversity than surrounding cities. This implies that the construction of green infrastructure plays a positive role in maintaining urban bird diversity (51). However, this human-dominated greenness also increased species similarity between cities, as illustrated by comparisons of BSNs based on SDMs (table S4). Although the construction of green infrastructure can help to protect bird diversity, it also reduces the differences between regions. Therefore, for biodiversity conservation, in addition to paying attention to local species diversity, it is necessary to coordinate conservation planning at larger scales.

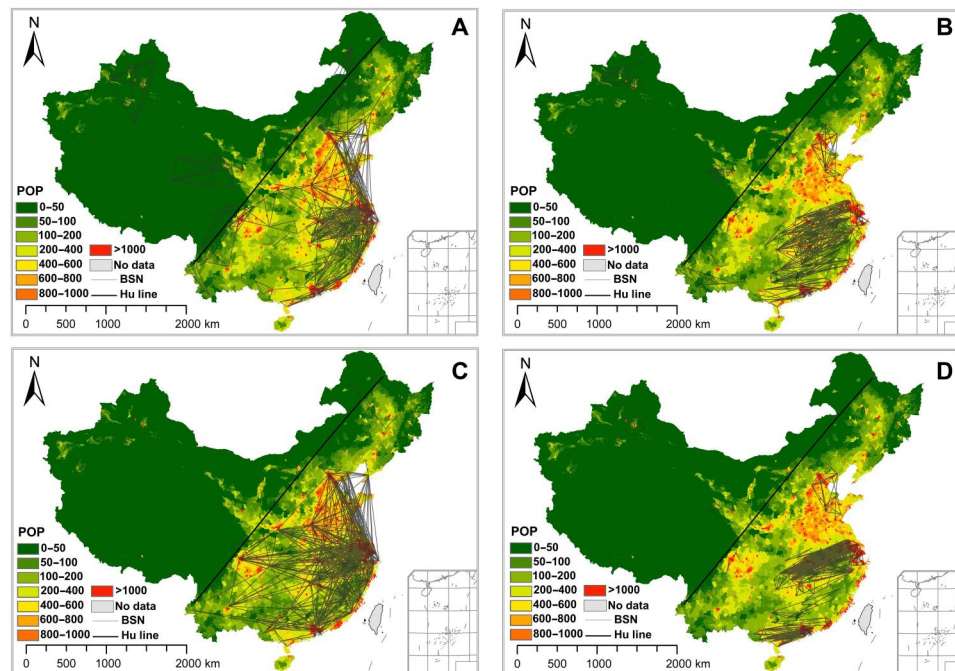


Fig. 5. Bird similarity network. (A) All BSNs based on birdwatching data. The data comprised population spatial distribution data on a 1-km grid in China in 2015. The values represent the population (POP) within that grid extent. East of the Hu line (black solid line) is a hot spot of diversity. At the same time, the similarity of birds is higher, and the regions with high population density are closely connected. (B) All BSNs based on SDMs. The data comprised bird spatial distributions based on SDMs. (C) Similarity network based on birdwatching data for birds whose PLCTs are urban and built-up lands. (D) Similarity network based on SDMs for birds whose PLCTs are urban and built-up lands.

Conservation case studies of mitigating the effects of urbanization on bird diversity

Urbanization effects can sometimes be reversed by conservation and restoration measures. For example, in 1984, the city of Panjin was established in the Liaohe delta in northeastern China for oil extraction. It is also an important habitat and breeding ground for waterbirds along their migration routes in East Asia (fig. S6) (52, 53). From 1986 to 2000, the natural wetland decreased by 726.4 km², of which the tidal flat wetland decreased by 52.86% (54). Because of habitat loss, only about 10 pairs of red-crowned cranes *Grus japonensis* were observed breeding in the whole Liaohe River Delta in 2005, less than one-third of the number in 1998 (55). Because of fragmentation of the habitat, the Liaohe River Delta could only support up to 39 pairs of red-crowned cranes in 2002 (56). In 2015, the government launched the “Return the Wetland” project. By 2020, about 57.3 km² wetland had been restored, and all oil extraction facilities in the core area of the reserve had been phased out. With the restoration of the wetland ecosystem, bird diversity has gradually recovered. According to the China Coastal Waterbird Census Report (57, 58), the number of waterbird species increased from 94 in 2005–2011 to 112 during 2012–2019, and the number of threatened waterbird species increased from 8 to 14.

The coastal wetland of Yancheng is an important breeding and wintering ground for migratory birds in East Asia and Australia (fig. S7) (52, 59). With rapid urbanization, the natural wetlands in Yancheng have gradually decreased and fragmented (60), threatening the survival and reproduction of wild animals such as wild Père David’s deer and red-crowned Crane (61, 62). Meanwhile, the emissions from human activities also have an adverse impact on the

environment, leading to the reduction of wetland biodiversity (63). To improve the environmental quality of coastal wetlands for biodiversity conservation, Yancheng Tiaozini wetland, as the core area of migratory bird habitat (phase 1) in the Huanghai and Bohai seas, was listed as the 14th World Natural Heritage in China in 2019. In the past 2 years, 22 new bird species have been observed in Tiaozini wetland, and the total number of bird species has reached 410.

Because of their mobility, birds can actively seek suitable habitats to offset the impacts of human activities. This ability makes it possible to maintain regional bird diversity by establishing protected areas in nonurbanized core areas of city clusters. For example, Yancheng city has become an important node for the maintenance of bird diversity in the Yangtze River Delta through active protection measures. Other city clusters are maintaining regional biodiversity through similar measures, but it should be noted that these measures may alter local bird composition, which may adversely affect interspecific interactions. On the other hand, whether the maintenance of regional biodiversity can achieve biodiversity conservation targets at the national level should also be considered.

Threatened birds are mostly migratory ones, and their distribution has strong seasonal differences. Because of high overlaps with urbanized hot spots, the distribution ranges of these bird species are shrinking. The results support the hypothesis that the homogenized urban environment has opposing effects on the distribution of widespread and narrow-range birds and eventually increasing birds’ similarity across regions. For widespread birds, most can adapt to the urban environment and have larger RF. As urbanization is undertaken with greater care, more green infrastructure has

been created, which can improve the local bird diversity, but it may have little effect on the restoration of bird diversity from the global perspective. Ultimately, green infrastructure may lead to increased bird similarity across regions. Future biodiversity conservation strategies should pay more attention to coordinating local and global aims and strengthen the protection of narrow-range species. It should be noted that here, we only consider changes in the distribution of birds, which may also trigger other adverse effects, such as changes in interspecific interactions.

METHODS

Species distribution at the prefecture level

The bird list used is mainly derived from the China Bird Report (CBR) Checklist of Birds of China v8.0 (2020) (64) and the checklist on the classification and distribution of the birds of China (38). The list was improved using GBIF (65) and eBird (66). Only species with observation records in mainland China from 2000 to 2020 were retained as the bird list used for this study (table S5).

We classified threatened species as those in the CR, EN, and VU International Union for Conservation of Nature Red List categories. The ratio of threatened species to the total number of species is defined as the threatened index.

To obtain the bird distribution data at the prefecture level, we first downloaded the bird species list for each prefecture from the CBR (67), then obtained the bird distribution by prefecture based on the longitude and latitude of bird observations in GBIF and eBird, and lastly integrated the above data to get the actual bird list for each prefecture (table S6). To ensure that the data are reliable at the prefecture level, we used the calculation method for sample coverage rate of communities (40), assuming that the bird distribution was well sampled if the average increase in the number of bird species observed in the recent 10 observations was within 1%. A total of 247 prefectures passed through the above data quality control (Fig. 1D).

Species potential distribution based on SDMs

Using the stacked SDMs package “ssdm” (68), we predicted the potential distributions of species with more than 50 records across China. We selected five modeling algorithms: maximum entropy, random forest, generalized additive model, generalized linear model, and support vector machines. Thirty percent of the data were randomly selected for cross-validation, which were repeated five times, and those with an area under the curve greater than 80% were used to find a consensus (69). The SDMs for all 1021 species with more than 50 records had good performance and were used for further analyses (fig. S8 and table S7). The environmental variables for fitting SDMs were extracted by principal components (95%) from 19 bioclimatic variables (bio1 to bio19) and elevation at a 30-s resolution from WorldClim 2 (70). All analyses were run using the R-3.6.3 powered by the Aliyun cloud server (www.aliyun.com).

Encroachment of bird habitats by urbanization

The urbanization process is represented by changes in nighttime lights and impervious area over time. Overlay analysis of the spatial distribution of bird diversity with nighttime lights and impervious surfaces is used to obtain the encroachment of bird habitats by urbanization. Specifically, three hot spot areas of potential

distribution of threatened bird species were identified using SDMs (Fig. 3A). Then, the nighttime lights and impervious surfaces were extracted according to the boundary of the hot spot area and ultimately used to analyze the continued encroachment of bird habitats by urbanization.

Range filling

Because the most reliable and most resolved bird distribution data currently available are based on prefecture-level cities in China, for further analysis, we counted the number of birds potentially distributed in prefectures based on GeoPandas (<https://geopandas.org/>). We used RF, the ratio of actual to potential distribution areas, to assess the impact of human activities on bird distributions (46). Furthermore, we assessed whether RF varied with the PLCTs, avian order, and Red List category.

Bird similarity network

We defined the bird similarity of two cities as the ratio of the shared to summed overall species numbers. The network formed by the connection of city pairs with bird species similarity is defined as the BSN. The similarities of all pairs of well-sampled cities were calculated and sorted, and the top 500 city pairs by similarity value were selected to build the BSN with Arcgis 10.6. The average clustering coefficient was calculated by NetworkX 3.0 (<https://networkx.org/>).

Supplementary Materials

This PDF file includes:

Figs. S1 to S8
Tables S3 and S4

Other Supplementary Material for this manuscript includes the following:

Tables S1, S2, and S5 to S7

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Urbanization affects spatial variation and species similarity of bird diversity distribution

Bin Sun, Yonglong Lu, Yifu Yang, Mingzhao Yu, Jingjing Yuan, Ran Yu, James M. Bullock, Nils Chr. Stenseth, Xia Li, Zhiwei Cao, Haojie Lei, and Jialong Li

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