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ORIGINAL ARTICLE

# Urbanization drives biotic homogenization of the avian community in China

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## Abstract

Urbanization-driven biotic homogenization has been recorded in various ecosystems on local and global scales; however, it is largely unexplored in developing countries. Empirical studies on different taxa and bioregions show conflicting results (i.e. biotic homogenization vs. biotic differentiation); the extent to which the community composition changes in response to anthropogenic disturbances and the factors governing this process, therefore, require elucidation. Here, we used a compiled database of 760 bird species in China to quantify the multiple-site $\beta$-diversity and fitted distance decay in pairwise $\beta$-diversities between natural and urban assemblages to assess whether urbanization had driven biotic homogenization. We used generalized dissimilarity models (GDM) to elucidate the roles of spatial and environmental factors in avian community dissimilarities before and after urbanization. The multiple-site $\beta$-diversities among urban assemblages were markedly lower than those among natural assemblages, and the distance decays in pairwise similarities in natural assemblages were more rapid. These results were consistent among taxonomic, phylogenetic, and functional aspects, supporting a general biotic homogenization driven by urbanization. The GDM results indicated that geographical distance and temperature were the dominant predictors of avian community dissimilarity. However, the contribution of geographical distance and climatic factors decreased in explaining compositional dissimilarities in urban assemblages. Geographical and environmental distances accounted for much lower variations in compositional dissimilarities in urban than in natural assemblages, implying a potential risk of uncertainty in model predictions under further climate change and anthropogenic disturbances. Our study concludes that taxonomic, phylogenetic, and functional dimensions elucidate urbanization-driven biotic homogenization in China.

**Key words:** $\beta$-diversity, compositional dissimilarity, distance decay, generalized dissimilarity modeling

## INTRODUCTION

Understanding how biodiversity patterns change in response to human-altered environments is one of the research highlights in global change biology and biodiversity conservation (McGill *et al.* 2015; Johnson & Munshi-South 2017). Biotic homogenization refers to

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the replacement of native and unique endemic species by already widespread and/or non-native species (McKinney & Lockwood 1999) and the processes by which ecosystems lose their biological uniqueness (Olden & Rooney 2006). The processes underlying biotic homogenization are generally associated with biological invasion and local extirpation due to human-driven introductions (Capinha *et al.* 2015; Liu X *et al.* 2021), landscape conversion (Sol *et al.* 2017; Liang *et al.* 2019; Liu *et al.* 2022), and climate change (Zwiener *et al.* 2017; Saladin *et al.* 2020). Most empirical studies have recorded biotic homogenization among multiple taxa in various ecosystems, from the local to the global scale (Villeger *et al.* 2011; Godet *et al.* 2015; Ibáñez-Álamo *et al.* 2017; Monchamp *et al.* 2017; Nowakowski *et al.* 2018; Finderup Nielsen *et al.* 2019; Daru *et al.* 2021; Yang *et al.* 2021). However, some previous studies have yielded different results (i.e. biotic differentiation; e.g. Sfair *et al.* 2016; Collins *et al.* 2017; Hensley *et al.* 2019), implying variations in the factors governing biodiversity changes, thus emphasizing the need for further assessment of these processes.

Urbanization can cause local extirpation and promote the expansion of generalist species, thus likely homogenizing regional communities (McKinney 2006; Davey *et al.* 2012). Nevertheless, previous studies have largely focused on the decline in taxonomic similarity, ignoring non-equivalent phylogenetic and functional relationships between species (Olden *et al.* 2018). For example, whether a species is sustained in a community depends on the degree to which the species niche matches the local climate conditions (Zwiener *et al.* 2018). In general, cities favor generalist species adaptable to heterogeneous and fluctuating urban environments (Evans *et al.* 2011). When urban communities filter out a subset of species with specific biological and ecological attributes from regional pools, taxonomic similarity among communities may increase over time (i.e. taxonomic homogenization). If communities are replaced by species with a high redundancy of functional traits or clustered distribution in the phylogeny, such taxonomic homogenization may trigger functional and/or phylogenetic homogenization (Olden & Rooney 2006). Therefore, compared with taxonomic facets, exploring changes in functional and phylogenetic facets can provide more insight into the reorganization of evolutionary history and ecosystem functioning due to urbanization (Gagic *et al.* 2015).

Beta ($\beta$) diversity quantifies the differences in species composition between communities, which has widely been used to indicate how community composition changes along geographical and environmental gradients (Socolar *et al.* 2016; Rolls *et al.* 2023). This metric can measure the difference in $\beta$-diversity between natural and human-mediated communities (e.g. rural vs. urban; native vs. introduced), providing a useful approach to reveal the potential mechanisms underlying the human-mediated changes in community composition (Ding *et al.* 2017; La Sorte *et al.* 2018; Liu X *et al.* 2021). In addition, quantifying the difference in $\beta$-diversity at different temporal intervals can determine whether biological communities become biotic homogenization or heterogenization (Mori *et al.* 2015; Socolar *et al.* 2016; Marcacci *et al.* 2021). Based on a decline in $\beta$-diversity over time, for example, previous studies have recorded that human activities have caused geographically distinct communities to become more similar in the last decades (Capinha *et al.* 2015; Monchamp *et al.* 2017). Nevertheless, most previous studies have been conducted in Europe and North America, and there is still limited evidence on how increasing urbanization homogenizes biotic communities on a large scale in developing countries.

China harbors rich biodiversity owing to its topographic heterogeneity and diverse climatic conditions. In recent decades, China has experienced rapid socioeconomic growth, which not only promotes urbanization but has also caused a substantial decline in biodiversity and reorganized biogeographic patterns (Liu *et al.* 2022; Sun *et al.* 2022). Therefore, China is an ideal place to explore how anthropogenic disturbances and climatic gradients alter urban biodiversity. Here, we used a Chinese database comprising 760 bird species to: (a) assess the degree to which urbanization influences taxonomic, phylogenetic, and functional similarities among bird communities and (b) unravel the relative contributions of geographical distance and environmental factors in shaping bird assemblages before and after urbanization.

Specifically, we hypothesized that the compositional similarities among urban communities would be higher than those among natural communities, given that urbanization drives biotic homogenization (H1). Because urban environments are likely to filter out species characterized by a combination of phylogenetically inherited traits, we hypothesized that the extent of phylogenetic and functional homogenization among avian communities would be stronger than that at the taxonomic level (H2). Given the highly human-induced environmental change within cities, we hypothesized that the relative contribution of geographical distance and environmental factors in shaping bird communities would decrease after urbanization (H3).

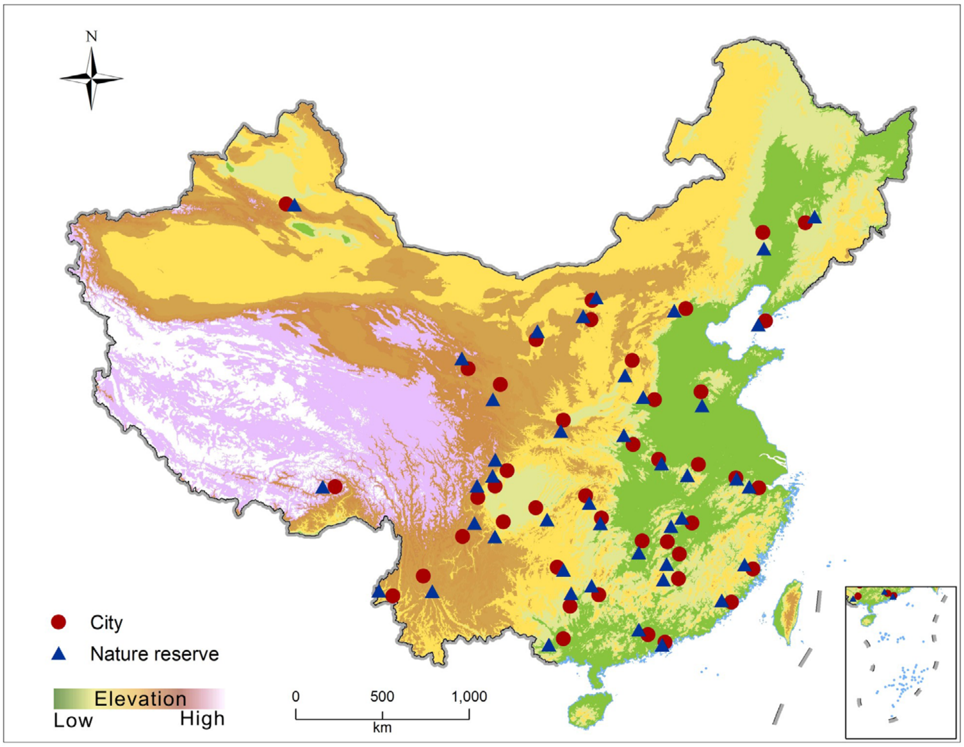

**Figure 1** Geographical distribution of the natural and urban avian communities included in this study. The red circles indicate the location of cities, and the blue triangles represent the location of corresponding nature reserves.

# MATERIALS AND METHODS

## Species data

To explore the changes in the similarity of the avian community due to urbanization, we assembled urban bird checklists and used regional lists of birds from the nearest nature reserves as baselines. Bird checklists for the cities were compiled from published papers and the China Bird Recording Center (Dataset S1, Supporting Information). We confined the bird checklists to the university campuses or academic institutions because of their relatively high biodiversity, many naturalists, and biodiversity inventory studies (Liu J *et al.* 2021). We conducted an exhaustive literature search for urban bird checklists in China, including ISI Web of Science, Google Scholar, and the China National Knowledge Infrastructure (CNKI; http://cnki.net) in September 2022, based on combinations of the following keywords in English or Chinese: "bird," "avian," "avifauna," "university," "campus," and "college." Each paper from this search was reviewed and checked for inclusion in a bird checklist in the field study. This resulted in 64 articles comprising 70 campus avifauna samples from 48 cities. In the search of the China Bird Recording Center, we used the keywords "university," "campus," and "college" to search and download 12 365 reports in September 2022. Reports with fewer than five species or suspicious records were excluded. To assess the extent of avian community changes caused by urbanization, we included the avian communities in nature reserves within a 100-km radius as the baseline (Fig. 1). Bird checklists for nature reserves were compiled using published faunal data, regional checklists, and online databases. When there were many nature reserves within a 100-km radius of a city, we used only the nature reserve with the highest species richness of birds recorded, such that a nature reserve, in this case, is considered one sampling site in a city.

We combined all intraspecific taxa with their species and standardized the species names and higher taxonomic nomenclature according to Jetz *et al.* (2012). We excluded predominately pelagic and marine species, as well as non-breeding migrant species. Nocturnal species (e.g. owls and nighthawks) were also excluded. Furthermore, we verified species checklists using BirdLife International and NatureServe (http://www.birdlife.org) and only considered areas where a species was extant or probably extant, native, resident, or occurred regularly during the breeding season. The most comprehensive dated phylogenies available from Jetz *et al.* (2012) for birds ($n = 9993$) were obtained using the Hackett family-level backbone (http://vertlife.org/phylosubsets). We downloaded a set of posterior distributions of trees ($n = 1000$) online and obtained the maximum clade credibility phylogenies for downstream analysis using the "maxCladeCred" function in the R package "phangorn" (Schliep 2011). We used eight morphological traits (including body size, shape of the beak, tarsus, wing, and tail) for each species, which were most likely to represent the most important dimensions of the avian niche (Stewart *et al.* 2022). These morphological traits were obtained from a recently published global bird dataset (Tobias *et al.* 2022). After combining distributional, phylogenetic, and functional data, the dataset comprised 760 avian species from 43 cities and their corresponding nature reserves (Dataset S1, Supporting Information). This resulted in 548 bird recording reports in China, with a median value of 6 reports per city and 25% and 75% quartiles of 1 and 14 reports, respectively (Table S1, Supporting Information). The median range size of nature reserves was 252.1 km$^2$, with 25% and 75% quartiles of 117.7 km$^2$ and 470.5 km$^2$, respectively.

## Multiple-site *β*-diversity

To evaluate the overall change in community composition between sites (i.e. biotic homogenization or heterogenization) at a national scale, we calculated the multiple-site $\beta$-diversities of all assemblages across nature reserves and cities using the R package "betapart" (Baselga & Orme 2012). We used only the Simpson dissimilarity ($\beta_{\mathrm{SIM}}$), the turnover (i.e. replacement) of species between sites, because this metric represents a true substitution of species without the influence of differences in species richness between sites (Baselga 2010). Thus, the Simpson dissimilarity could reduce effects resulting from variation in species–area relationships, colonization pressure, or sampling efforts (Capinha *et al.* 2015). For taxonomic composition, the multiple-site $\beta$-diversity uses information on the total number of species in all sites and the number of species unique to each site (Baselga 2010). For phylogenetic composition, multiple-site $\beta$-diversity was calculated using a phylogenetic tree, where shared and unique branch lengths were used instead of shared and unique species (Leprieur *et al.* 2012). Functional multiple-site $\beta$-diversity was calculated using a similar method, replacing the phylogenetic tree with a functional trait-based dendrogram (Petchey & Gaston 2002). The dendrogram was generated using the unweighted pair group method with the arithmetic mean (UPGMA) from a Gower dissimilarity distance matrix. The cophenetic correlation coefficient was 0.78, indicating a suitable UPGMA performance in transferring the original distance matrix into dendrograms.

Given that compositional similarity generally decreases with spatial distance, we sub-sampled sites outside a minimum distance of 200 km to account for spatial autocorrelation. Furthermore, we randomly subsampled 70% of the sites (30 out of 43 sites) to account for the effect of the number of sites on the multiple-site beta diversity (Baselga 2013). We also performed these analyses by subsampling 60% and 80% of site numbers to verify our results. We repeated this procedure 1000 times and computed the mean values of the multiple-site $\beta$-diversity among the natural and urban communities, respectively. We used paired *t*-tests to assess the overall change in community composition between sites (i.e. biotic homogenization or heterogenization) based on the difference in multiple-site $\beta$-diversities among natural and urban communities.

## Pairwise *β*-diversity

To explore the patterns and drivers of compositional dissimilarity between natural and urban communities, we calculated the pairwise $\beta$-diversity based on the presence–absence comparisons between each pair of avian communities using Simpson's dissimilarity index ($\beta_{\mathrm{sim}}$). $\beta_{\mathrm{sim}}$ is a widely used index for community dissimilarity because it presents the turnover component of the overall $\beta$-diversity, which is rarely affected by differences in species richness (Koleff *et al.* 2003):

$$\beta_{\mathrm{sim}} = \frac{\min(b, c)}{a + \min(b, c)}$$

where $a$ is the number of shared taxa, and $b$ and $c$ are the numbers of taxa unique to each community (Baselga 2010).

We further incorporated phylogenetic tree and functional trait-based relationships among species into the quantification of phylogenetic ($\mathrm{P}\beta_{\mathrm{sim}}$) and functional ($\mathrm{F}\beta_{\mathrm{sim}}$) pairwise $\beta$-diversity (Graham & Fine 2008), respectively. These indices calculate pairwise phylogenetic or functional dissimilarity between two communities by replacing shared and unique species with shared and unique branch lengths, respectively (Leprieur *et al.* 2012):

$$\mathrm{P}\beta_{\mathrm{sim}}\ \mathrm{or}\ \mathrm{F}\beta_{\mathrm{sim}} = \frac{\min\left(\mathrm{PD}_{\mathrm{Total}} - \mathrm{PD}_k,\ \mathrm{PD}_{\mathrm{Total}} - \mathrm{PD}_j\right)}{\mathrm{PD}_k + \mathrm{PD}_j - \mathrm{PD}_{\mathrm{Total}} + \min\left(\mathrm{PD}_{\mathrm{Total}} - \mathrm{PD}_k,\ \mathrm{PD}_{\mathrm{Total}} - \mathrm{PD}_j\right)}$$

where $\mathrm{PD}_j$ and $\mathrm{PD}_k$ are the total branch lengths of the communities $j$ and $k$, respectively; $\mathrm{PD}_{\mathrm{Total}}$ is the total branch length of a phylogenetic tree or functional trait-based dendrogram containing all species present in both $j$ and $k$ communities.

## Analyses

To explore the association between changes in avian similarity and geographical distance, we fitted a single-predictor generalized linear model using a negative power law function. The geographical distance between pairs of avian communities was calculated using the function "earth.dist" in the R package "fossil" (Vavrek 2011). We calculated and compared the halving distance to quantify the turnover rate of each similarity index between the natural and urban communities. The halving distance represents the distance at which a given similarity value is predicted to decrease by 50% (Soininen *et al.* 2007; König *et al.* 2017). In addition, we compared the slopes of natural and urban communities from regressions of compositional similarity and log-transformed geographical distance. To investigate the underlying factors in natural and urban communities, we performed generalized dissimilarity modeling (GDM) using the R package "gdm" (Fitzpatrick *et al.* 2022). Compared with classical linear matrix regression (e.g. the Mantel test), GDM can account for the nonlinear relationship between compositional dissimilarity and environmental distance, representing ecologically realistic relationships (Ferrier *et al.* 2007). In addition, this model can evaluate variations in the rate of compositional turnover along individual environmental gradients and in geographical spaces (Fitzpatrick *et al.* 2013). In this analysis, environmental dissimilarity and geographical distance were the predictor variables, and community composition was the response variable. The fit of each GDM was measured using the percentage of explained variance (Ferrier *et al.* 2007), and the variable importance with respect to compositional similarity was estimated using the total height of the transformation function curve (Fitzpatrick *et al.* 2013; König *et al.* 2017). The shape of the curve reflects the rate of change in compositional similarity along environmental or geographical gradients (Ferrier *et al.* 2007; Fitzpatrick *et al.* 2013). We estimated the parameter uncertainty of the fitted I-spline of each predictor in the "plotUncertainty" function and tested the significance of each predictor using the Monte Carlo permutation procedure in the "gdm.varImp" function (Ferrier *et al.* 2007). To explore whether variable importance differed between natural and urban communities, the height of each predictor was linearly rescaled to ensure that their sum equaled the proportion of deviance explained by the model (König *et al.* 2017). The climate data were derived from the WorldClim dataset (version 2.0; 2.5 arc min spatial resolution; Fick & Hijmans 2017). We conducted a principal component analysis (PCA) based on temperature-related variables (BIO 1–BIO 11) and precipitation-related variables (BIO 12–BIO 19) and used the first ordination axis in the PCA to calculate temperature and precipitation dissimilarity among communities. The elevation data were based on a digital elevation model derived from the National Centres for Environmental Information (https://www.ngdc.noaa.gov/mgg/global/relief/ETOPO1/data/).

# RESULTS

## $\beta$-diversity patterns in the avian communities

By subsampling 70% of all sites across China 1000 times, the mean values of multiple-site $\beta$-diversity of urban communities were 0.855, 0.772, and 0.768 for the taxonomic, phylogenetic, and functional dimensions, respectively, which were lower than those in the natural communities (0.873, 0.792, and 0.807, respectively; paired *t*-test, $P < 0.001$; Fig. 2). This finding is consistent with the result from subsampling 60% and 80% of site numbers as thresholds (Fig. S1, Supporting Information). The distance decays in pairwise taxonomic, phylogenetic, and functional similarities were best fitted by the power-law models ($R^2 = 0.22$–$0.50$, $P < 0.01$). Taxonomic similarity declined by 50% every 844 km for urban communities and by 50% every 1007 km for natural communities (Fig. 3). The relationship between taxonomic $\beta$-diversity and log-transformed distance also revealed

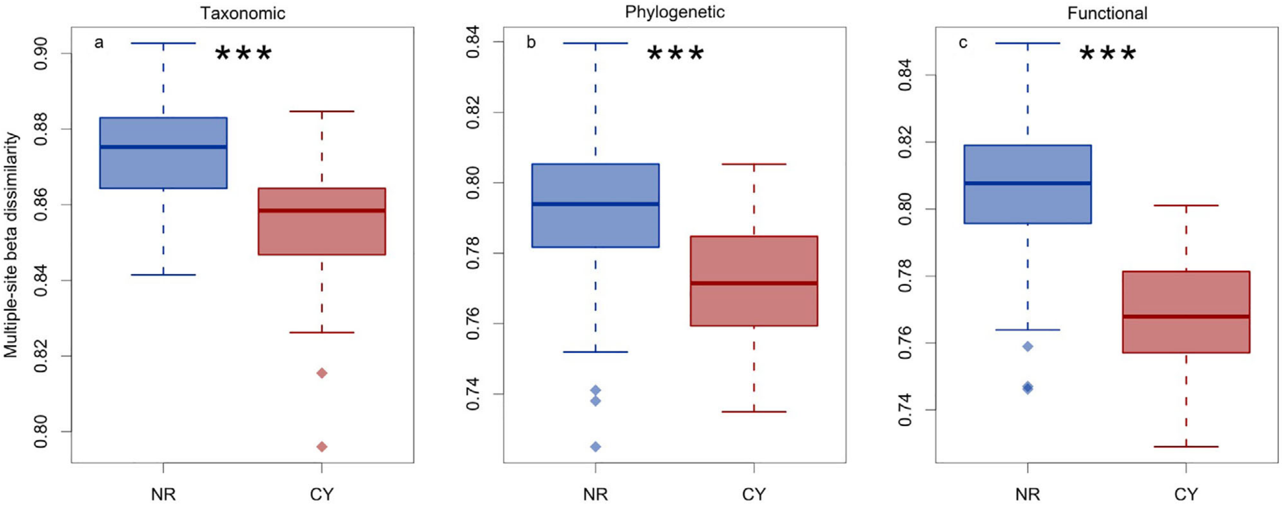

**Figure 2** Overall $\beta$-diversity of natural and urban avian communities in China. Multiple-site $\beta$-diversity was measured by (a) taxonomic, (b) phylogenetic, and (c) functional facets using Simpson's index. Boxes show the median, 25th, and 75th percentiles of 1000 resamplings. Asterisks indicate significant differences of multiple-site $\beta$-diversity between natural and urban avian communities (paired *t*-test, $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$) NR, nature reserve; CY, city.

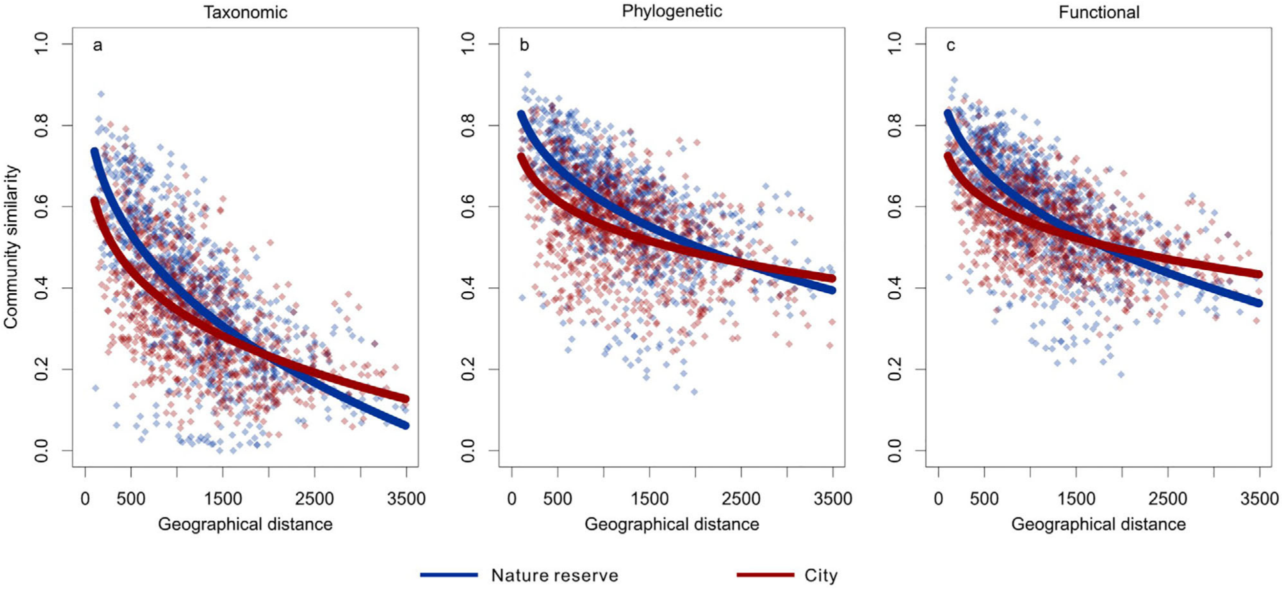

**Figure 3** Distance decay of compositional similarity across natural and urban avian communities. Points represent pairwise similarities between avian communities within nature reserves (blue) and cities (red). Solid curves indicate distance decay of similarity relationships with exponential fits.

that the compositional similarity in natural communities (slope = −0.20, 95% CI = [−0.22, −0.19]) decayed more quickly than those among urban communities (slope = −0.15, 95% CI = [−0.16, −0.13]; Fig. 3; Fig. S2, Supporting Information). The curves of phylogenetic and functional groups exhibited similar patterns; that is, the distance decays of phylogenetic similarity (DS/2: NR = 1012 km; CY = 815 km) and functional similarity (DS/2: NR = 1025 km; CY = 796 km) were more rapid among natural than among urban communities (Fig. 3). Taken

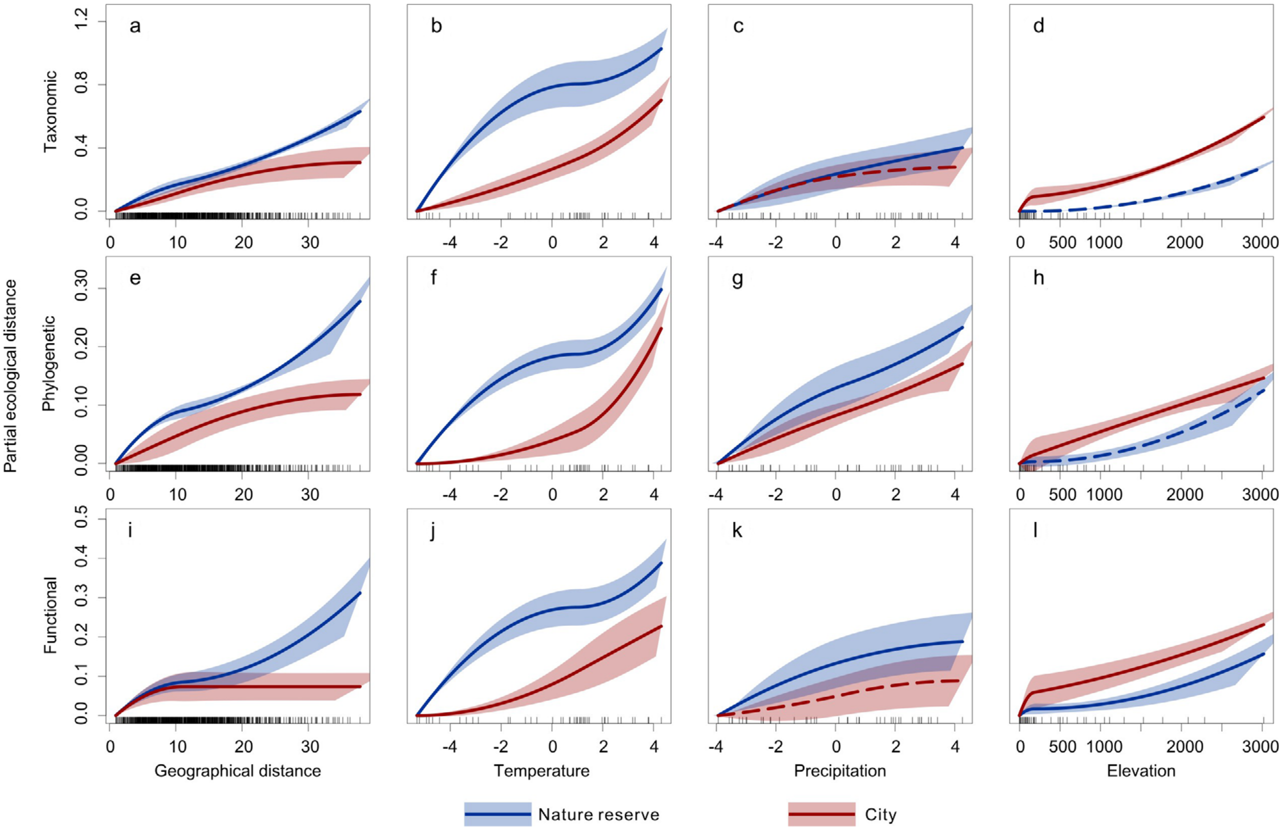

**Figure 4** Fitted I-splines for variables underlying the compositional dissimilarity across natural and urban avian communities. Plots on rows are subsets measured by (a–d) taxonomic, (e–h) phylogenetic, and (i–l) functional $\beta$-diversity matrices. The curves show that the rate of compositional similarity varies along the geographical and environmental gradients; the shaded area shows the confidence bands calculated using 100 times bootstrapping on 70% subsampling of the dataset. The maximum height of each curve indicates the relative importance of each predictor, quantified by summary of the coefficients of the I-splines from generalized dissimilarity models. The solid curves indicate the significant predictors and dashed curves indicate the nonsignificant predictors based on Monte Carlo permutation analyses.

together, these results indicated that avian communities in cities exhibited lower taxonomic, phylogenetic, and functional $\beta$-diversity (i.e. more homogenization) than in natural communities.

## Predictors of natural and urban communities

The fitted I-splines from the GDMs showed that temperature and geographical distance were the dominant predictors of compositional dissimilarity among the natural communities (Fig. 4a,b), followed by precipitation and elevation (Fig. 4c,d; Table S2, Supporting Information). Geographical distance, temperature, and precipitation were correlated with compositional dissimilarity, as revealed by Monte Carlo permutation analyses ($P < 0.001$). However, for urban communities, the relative importance of geographical distance declined, and the I-splines tended to be stable when the geographical distance reached a threshold (Fig. 4a). In addition, the effect of elevation increased and exhibited a strong correlation with community dissimilarity among avian assemblages in the cities ($P < 0.001$; Fig. 4d). These trends were also documented in the phylogenetic (Fig. 4e–h) and functional (Fig. 4i–l) compositional dissimilarities.

The relative importance of each predictor variable differed in the compositional dissimilarity between the natural and urban communities (Fig. 5). Overall, geographical and environmental distance accounted for 56.10–69.87% of the variation in the compositional dissimilarities among natural communities, whereas their explained variations decreased to 29.10–46.47% in urban communities (Fig. 5; Table S2, Supporting

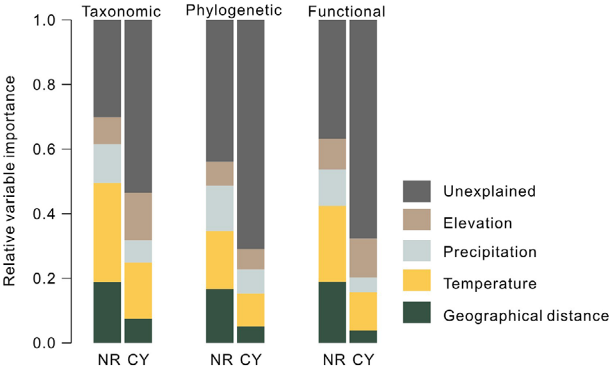

**Figure 5** Relative importance of potential factors shaping taxonomic, phylogenetic, and functional $\beta$-diversity across natural and urban avian communities. NR, nature reserve; CY, city.

Information). For example, in natural communities, the unique deviances of geographical distance, temperature, and precipitation in explaining taxonomic dissimilarity were 18.86%, 30.69%, and 11.97%, respectively, whereas these deviances decreased to 7.55%, 17.38%, and 6.86%, respectively, after urbanization. In contrast, the relative importance of elevation (14.68%) and unexplained variation (53.53%) in the compositional dissimilarity of urban communities were higher than the natural communities (elevation: 8.35%; unexplained variation: 30.13%). The predictive power of geographical and environmental distances exhibited a greater decline in the functional (30.9%) and phylogenetic (27.0%) dimensions than in the taxonomic (24.4%) dimension (Table S2, Supporting Information).

## DISCUSSION

The study showed that urban avian communities exhibited lower multiple-site dissimilarities (Fig. 2) and a slower distance decay of community similarity (Fig. 3) than natural communities. These results support the hypothesis (H1) that urbanization has caused the biotic homogenization of bird assemblages across China. This is not surprising, as biotic homogenization has been widely observed across China in other taxonomic groups, such as terrestrial plants (Wang *et al.* 2021; Qian & Qian 2022), aquatic macrophytes (Ding *et al.* 2019), and fish (Liu *et al.* 2017; Xiang *et al.* 2023). Liang *et al.* (2019) documented the biotic homogenization of bird communities induced by land-use change in Inner Mongolia, China. By comparing the compositional similarities of avian assemblages between natural and urban communities across China, our study provides empirical evidence of a homogenization trend at the national scale.

This study suggests that urbanization-driven biotic homogenization is a multifaceted process involving a decline in taxonomic, phylogenetic, and functional similarity among communities (Luck & Smallbone 2011). Urbanization might act as an environmental filter for specialist species, whereas generalist species with specific traits (e.g. smaller size, wider feeding habits, and wider ecological niches) have a greater ability to sustain themselves in urban environments and become urban dwellers (La Sorte *et al.* 2018; Callaghan *et al.* 2019; Santini *et al.* 2019; Palacio 2020). Therefore, the loss of specialist species reduces the functional and phylogenetic richness, resulting in phylogenetic and functional homogenization (Davey *et al.* 2012). Nevertheless, we found that taxonomic similarities showed faster distance decay than phylogenetic and functional similarities (Fig. 3), which is inconsistent with the second hypothesis of this study (H2). A potential explanation for this is that the study covered a large spatial extent and comprised a large species pool, which led to functional redundancy owing to a greater number of species than the corresponding functional traits (Cooke *et al.* 2019). The greater the functional redundancy in the community, the higher the probability that the replaced species would be functionally redundant in the species pool (Swenson *et al.* 2011). A recent global study compiling 148 datasets from terrestrial, freshwater, and marine groups found that distance decay of taxonomic similarities was often stronger than functional decay (Graco-Roza *et al.* 2022), which supports our findings.

Although geographical distance had consistent effects on both natural and urban communities, its effect was lower in urban than in natural communities (Figs 4,5). This suggests that urbanization reduced the effect of geographical distance on biological turnover. This is likely because urbanization can filter out some specialist species and retain a fraction of generalist species that can persist in urban environments (Silva *et al.* 2016). Alternatively, human activities break down geographical barriers and facilitate the spread of some species (e.g. species with strong dispersal capacity). This is consistent with other studies that have demonstrated the lower importance of geographical distance in the compositional dissimilarity of communities after invasion on a global scale (Liu X *et al.* 2021). Thus, it is expected that, compared to natural communities, the turnover rate of community dissimilarity among cities will become increasingly slower along the geographical distance and reach a lower height on the transformation function curve. Apart from geographical distance, temperature and precipitation also had weaker explanatory power for compositional similarity in urban than in natural communities (Figs 4,5). Precipitation became a nonsignificant predictor of taxonomic and functional dissimilarities in urban communities (Fig. 4). Both of these results are consistent with the third hypothesis (H3). Temperature- and precipitation-related variables are critical for structuring native avian communities (Curley *et al.* 2022). However, in cities, because of greenhouse gas emissions and land-use changes, the variation in temperature and precipitation conditions in different cities might have diminished, thus weakening the explanatory power of compositional similarity in urban communities.

Unexpectedly, elevational dissimilarity, which explained the minimum variance in community dissimilarity in natural communities, emerged as a significant predictor of urban community dissimilarities (Figs 4,5). This is presumably because the extent of urbanization varies across China, wherein cities at higher elevations are less urbanized than those in the lowlands (Guan *et al.* 2018). Furthermore, high elevations are often characterized by severe cold and oxygen deficiency, which have a limiting effect on most birds and play an important role in structuring avian communities (He *et al.* 2022; Yao *et al.* 2022). In this context, urbanization may promote the homogeneity of climatic conditions in cities and exacerbate the environmental conditions caused by elevation differences. Therefore, compared to natural communities, the relative role of climatic conditions in the turnover rate of urban compositional dissimilarities decreased whereas that of elevational dissimilarities increased.

The study revealed that geographical distance and environmental dissimilarity jointly explained approximately 60% of the total $\beta$-diversity patterns of the natural communities (Fig. 5). This result is largely consistent with other studies on avian communities (Wayman *et al.* 2021; Lazarina *et al.* 2022). The relative effects of geographical distance and climatic dissimilarity declined after urbanization, and the unexplained proportion of community dissimilarity increased (Fig. 5). This confirms the considerable reorganization of avian communities induced by urbanization, suggesting more unmeasured effects (e.g. biotic interactions) on structuring the urban avian community (Czeglédi *et al.* 2020). Furthermore, this pattern highlights the potential for unpredictable trends in bird assemblies in urban communities across China. As urban communities continue to change with warming climates and increasing human disturbance, future studies should jointly evaluate the role of geographical and environmental distances in shaping natural and human-disturbed communities in specific regions to enhance the predictive power of the factors underlying human-driven biotic changes.

This study has several limitations, and the results should be interpreted with caution. First, we only evaluate the effect of urbanization on biotic homogenization and not the relative contributions of other factors that could potentially drive community assemblage changes, such as human-driven introductions (Capinha *et al.* 2015; Liu X *et al.* 2021) and climate change (Zwiener *et al.* 2017; Saladin *et al.* 2020). Second, the present study assessed the biotic homogenization using the "space-for-time" method (França *et al.* 2016), which compares the $\beta$-diversities of avian assemblages between natural and urban communities (Morelli *et al.* 2016). Ideally, biotic homogenization or heterogeneity should be determined by temporal changes in the $\beta$-diversities of species assemblages. Nevertheless, using the temporal $\beta$-diversities method to assess urbanization-driven biotic homogenization is challenging because of the lack of data on avian communities before urbanization (La Sorte *et al.* 2018). Third, spatial bias in the available data may have influenced the results. For example, bird observation data recorded in eastern China were much higher than those from western China. This bias may exaggerate the decline in $\beta$-diversities of avian assemblages (i.e. biotic homogenization) due to the unbalanced level of urbanization between eastern and western China. Thus, biodiversity monitoring networks comprising long-term observations (Xu *et al.* 2022) and more spatially comprehensive coverage would better assess large-scale biotic changes across China during the Anthropocene.

## CONCLUSIONS

As cities are consistently expanding, understanding how urbanization influences present-day biological communities is crucial. However, given the lack of long-term and large-scale observational data, assessing the extent to which community composition changes and the factors governing this process are extremely challenging, particularly in developing countries. Here, we provide empirical evidence—from taxonomic, phylogenetic, and functional perspectives—that urbanization has driven the national-scale biotic homogenization of avian biodiversity in China. The increase in taxonomic similarity was stronger than that of phylogenetic and functional similarities, indicating that species loss might be subsampled non-randomly from the regional pool based on functional traits and phylogenetic positions. Notably, the explanatory power of geographical distance and climatic factors in compositional dissimilarities decreased after urbanization, implying a potential risk of uncertainty in model predictions under further climate change and anthropogenic disturbance. Future studies should fill the data gaps using a recently established national-scale biodiversity monitoring network to reinforce our understanding of patterns and trends in community changes in response to anthropogenic disturbances and climate change.

## ACKNOWLEDGMENTS

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

### DATA AVAILABILITY STATEMENT

Data regarding species occurrences, functional traits, phylogenetic trees, and relevant environmental variables were derived from different datasets, as described in the Materials and Methods section. The data that support the findings of this study are available in the supporting information of this article.

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## SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1** Numbers of university campuses and avian species checklists of each city used in this study.

**Table S2** Relative importance of space and environment in shaping biological dissimilarities of natural and urban avian communities using generalized dissimilarity model.

**Figure S1** Overall $\beta$-diversity of natural and urban avian communities in China based on different thresholds of subsampling site numbers.

**Figure S2** Distance decay ($\log_{10}$-transformed) of compositional similarity across natural and urban avian communities.

**Dataset S1** Bird checklists.

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