

Urbanization alters the geographic patterns of passerine plumage color in China

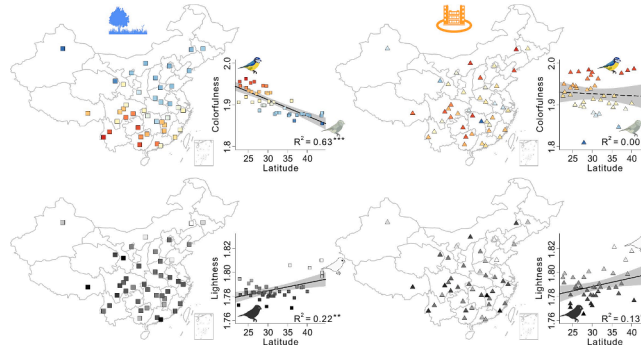
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HIGHLIGHTS

- The color space of urban birds was reduced compared to non-urban species.
- Urbanization influenced the homogenization of bird plumage color in China.
- Urbanization altered the latitudinal gradients in avian colorfulness diversity.
- We recommend urban design to consider how landscape changes affect animal coloration.

GRAPHICAL ABSTRACT



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ABSTRACT

Urbanization has altered natural landscapes and serves as an environmental filter that selects species with specific traits. Coloration is an important trait associated with biotic interactions and thermoregulation, enabling species' survival and reproductive success. However, few studies have focused on how species coloration changes in response to urbanization. Here, we used 547 passerine bird species from 42 cities and their corresponding non-urban communities in China to test whether urban species are darker and if they have duller plumage colors than their non-urban counterparts. Furthermore, we examined whether and how urbanization influences avian plumage color homogenization and the extent to which urbanization has altered the strength of the color–latitude geographic pattern in passerine birds across China. We found a 3.2% loss in the coloration space of birds after urbanization, although there were no significant differences in the individual dimensions of colorfulness and lightness between urban and non-urban birds. Avian communities in cities exhibited more plumage color homogenization than those in non-urban communities. There were significant latitudinal gradients in plumage colorfulness and lightness in non-urban communities, but these correlations were weaker in urban communities. Non-urban communities that were more colorful and lighter tended to be duller and darker in urban environments, and vice versa. Our results provide national-scale evidence that urbanization has led to reduced color diversity, increased color-based community similarity, and altered geographic patterns of avian plumage color gradients in China. These findings provide new insights into how rapid human-induced environmental changes have affected animal coloration during the Anthropocene.

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1. Introduction

Urbanization alters landscapes and creates a series of threats to biodiversity (Johnson & Munshi-South, 2017; Hahs et al., 2023), including natural habitat loss, artificial light, noise, pollution, traffic networks, and food deficiencies (Cabrera-Cruz et al., 2019; Verrelli et al., 2022). These environmental pressures not only reduce species richness (Piano et al., 2020) but also exert a profound influence on the evolutionary and functional aspects of biodiversity (Sol et al., 2017; La Sorte et al., 2018; Marcacci et al., 2021). In recent decades, most empirical studies have revealed that urbanization is an environmental filter for selecting multiple traits for urban species or populations among a variety of taxa from local to global scales (Callaghan et al., 2019; Hahs et al., 2023; Neate-Clegg et al., 2023; Zhong et al., 2024). However, few studies have focused on the divergence in species coloration between rural and urban communities (Turak et al., 2022; Salmón et al., 2023; Leveau, 2024), limiting our ability to comprehensively understand the phenotypic shifts in species in response to human activity.

Changes in species coloration within anthropogenic habitats have long attracted the attention of evolutionary and conservation biologists (Delhey & Peters, 2016; Johnson & Munshi-South, 2017). One of the most well-known examples is the variation in the gray gradient of peppered moths with notable urban–rural gradients (Kettlewell, 1955). This is probably because birds selectively prey on typical melanic morphs of these species (Steward, 1977), and varying coloration patterns provide a selective advantage in urban and rural environments. In addition to changes in the expression of melanin, which produces dark colors (e.g., gray, black, and brown) in animals (i.e., urban melanism), urbanization-driven changes in carotenoid-based coloration (e.g., yellow, orange, and red colors) – the so-called urban dullness phenomenon – have also been widely documented (Eeva et al., 2009; Biard et al., 2017; Salmón et al., 2023). A recent review provided evidence that, despite taxonomic and geographic biases, urban animals generally show darker coloration and duller plumage colors than their rural counterparts among multiple taxonomic groups such as insects, amphibians, reptiles, and birds (Leveau, 2021). In addition to the phenomena of urban melanism and urban dullness, animals in urban areas exhibit complicated changes in response to stressful environments. For example, along the urban–rural gradients within central Argentina, urban exploiters had uniform plumage lightness to enhance camouflage, whereas avoiders had high plumage lightness variations to enhance conspicuous signaling for intraspecific and interspecific communications (Leveau & Ibáñez, 2022). These changes have eventually resulted in urbanization-induced homogenization of bird color (Leveau, 2019).

These divergences in the color of species or populations between urban and rural communities reflect the natural selection pressure exerted by urbanization (Johnson & Munshi-South, 2017). Coloration is highly correlated with sexual signaling, antipredator deterrence, thermoregulation, and camouflage (Cuthill et al., 2017), enabling the survival and reproductive success of urban species (Salmón et al., 2023). Therefore, in the context of biodiversity loss and global climate change, it is of particular importance to evaluate how urbanization has reshaped the geographic patterns of animal coloration (Delhey et al., 2019). Previous studies have been confined to intra- and inter-specific comparisons of animal coloration in some lineages and have mainly been conducted at small spatial scales (Leveau, 2021; Leveau, 2024), which emphasize the need for further assessment of urbanization-driven changes in species coloration patterns across larger spatial scales.

Birds are among the most colorful and well-studied groups of animals in the field of urban biodiversity (Patankar et al., 2021). Based on the previously observed phenomena of urban melanism and dullness, urbanization favors darker and less colorful bird species (Leveau, 2021). Therefore, we hypothesize that the lightness and colorfulness of avian communities are lower in urban areas than that in non-urban communities (Hypothesis 1). Given that cities generally have high environmental similarities, urbanization can select for species with a

combination of specific traits, causing taxonomic, functional, and phylogenetic homogenization at regional and global scales (Ibáñez-Alamo et al., 2017; Liang et al., 2019; Deng et al., 2024). Therefore, we hypothesize that plumage color similarities are higher among urban bird communities than that among non-urban communities, exhibiting urbanization-driven homogenization of avian plumage color (Hypothesis 2). Furthermore, we predict that regardless of whether avian coloration has become darker, duller, or more uniform in lightness, the geographic pattern of avian coloration altered by urbanization will exhibit different patterns within the natural ecosystem. Recent global studies have documented a latitudinal gradient in avian colorfulness, showing that tropical species are more colorful than temperate species (Cooney et al., 2022; Senior et al., 2022). Given that urbanization has profoundly changed the climate, habitats, and visual conditions of cities, we hypothesize that the latitudinal coloration gradient is weaker among urban birds than among their non-urban counterparts (Hypothesis 3).

To test these hypotheses, we compiled a dataset that included 547 passerine bird species from 42 cities and their corresponding non-urban communities to explore how urbanization changes the geographic patterns of avian coloration in China. Specifically, we measured the coloration space occupied by species to compare the colorfulness and lightness of birds in urban and non-urban communities. We then investigated whether urbanization influenced the homogenization of avian plumage color by measuring multiple-site and pairwise indices of color-based similarities among bird assemblages in urban and natural areas. Finally, we assessed whether latitudinal gradients in avian coloration varied between non-urban and urban communities and evaluated the extent of this change relative to the baseline avian coloration of non-urban communities.

2. Methods

2.1. Bird observation data

Checklists of bird species in urban areas were compiled from published articles and bird recording reports. In this study, we only included bird checklists recorded at university campuses or academic institutes because university campuses are widely distributed throughout China and represent critical components of biodiversity in urban environments (Wang et al., 2021). In addition, university campuses not only have clear boundaries, similar building structures, and green spaces (Zhang et al., 2018) but also host many active naturalists who have conducted comprehensive biodiversity sampling, thus providing comparable data among cities (Liu et al., 2021). We carried out an intensive literature search for Chinese campus bird checklists in September 2022 using the ISI Web of Science, Google Scholar, and the China National Knowledge Infrastructure (CNKI; <http://cnki.net>), based on combinations of the following keywords in English or Chinese: “bird”, “avian”, “avifauna”, “university”, “campus”, and “college”. Each article obtained was reviewed to determine whether it included a field study bird checklist. To complement our database, we also included bird recording reports from the China Bird Recording Center (CBRC; <http://www.birdreport.cn/>), which were searched and downloaded in September 2022, based on the following keywords in Chinese: “university”, “campus”, and “college”. These procedures resulted in 67 published papers and 12,365 bird recording reports.

To identify potential non-urban avian communities in each city, we used the avian checklists of nature reserves within a radius of 100 km as a baseline (Fig. S1 in Supplementary Data 1). Bird checklists for nature reserves were compiled from faunal books, regional checklists, and online databases (<http://www.zrbhq.cn/>). When there were many nature reserves within a 100 km radius of a city, we used only the nature reserve with the highest recorded bird species richness to maximize the sampling completeness. After combining the non-urban and urban checklists, we retained 42 cities and their corresponding nature reserves. To reconcile the taxonomic inconsistencies among the different datasets,

we standardized the species names and higher taxonomic nomenclature according to Jetz et al. (2012). We focused on passerine birds and excluded predominantly pelagic and marine species as well as non-breeding migrant species. This refinement yielded a dataset of 547 passerine species, belonging to 160 genera and 42 families (Supplementary Data 2).

2.2. Plumage color

The plumage color of each passerine bird was extracted from the database provided by Cooney et al. (2022), which represents the most comprehensive available dataset of avian colorfulness. This dataset quantified plumage coloration based on > 140,000 calibrated visible and ultraviolet light photographs of male and female museum specimens of 4,527 passerine species (Cooney et al., 2022). We used the number of occupied color loci to quantify plumage colorfulness because this metric is less sensitive to noise, outliers, and large ‘gaps’ in color space occupation that can bias colorfulness estimates (Cooney et al., 2022). The plumage lightness of each species was quantified by averaging pixel lightness values from images in the Handbook of the Birds of the World (Delhey et al., 2021). For each image plate, the red–green–blue (RGB) values for all pixels were extracted and then transformed into the CIE-LAB color space, which included the amount of achromatic (lightness or darkness) and chromatic (hue and saturation) color components. We used the achromatic component per species and the average plumage lightness for sexually dimorphic species. Methodological details on the measurement of plumage colorfulness and lightness have been described by Cooney et al. (2022) and Delhey et al. (2021). To test the robustness of our results among different methods for quantifying bird colors, we used alternative measurements of plumage color (Dale et al., 2015) and lightness (Delhey et al., 2019).

2.3. Plumage color space

To assess whether urbanization altered the coloration of birds, we conducted a functional space overlap analysis to compare the breadth and position of coloration spaces between birds in natural and urban areas. This method is analogous to analyses that quantify the dynamics of climatic niches (Broennimann et al., 2012). To facilitate the interpretation of the results, we used the colorfulness and lightness of birds as the two dimensions of the coloration space. We measured the coloration space of non-urban and urban bird species using the ‘ecospat.grid.clim.dyn’ function in the R package “ecospat” (Di Cola et al., 2017). This function projected the densities of species occurrences along two gridded gradients of colorfulness and lightness at a resolution of 100×100 cells, and then measured the avian coloration space using the kernel smooth density method (Broennimann et al., 2012). To quantify the difference in avian coloration between non-urban and urban birds, we calculated the overlap of the coloration space (i.e., the proportion of cells that were common between the urban and non-urban birds) using Schoner’s D metric via the ‘ecospat.niche.overlap’ function. Schoner’s D metric ranges from 0 to 1, with smaller values indicating a lower overlap. In addition, we used the Wilcoxon rank-sum test to evaluate differences in the dimensions of colorfulness and lightness of bird species between natural and urban environments.

2.4. Homogenization of plumage color

To assess whether avian coloration was more similar in urban communities than in non-urban communities, we calculated the multiple-site beta dissimilarities (β_{SIM}) of all assemblages in cities and the corresponding species pools using the R package ‘betapart’ (Baselga & Orme, 2012). The β_{SIM} value reflects the turnover components of total compositional heterogeneity within a species pool of several sites (Baselga, 2013). We calculated the β_{SIM} using a color-based dendrogram (Petchey & Gaston, 2002) based on information on shared branch

lengths in all sites considered together and the branch lengths unique to each site (Leprieur et al., 2012). Plumage color and lightness were used to measure pairwise color distances between species based on Gower’s distance. We then used the unweighted pair group method with arithmetic mean (UPGMA) to generate a color-based dendrogram of the color distance matrix using the R package ‘picante’ (Kembel et al., 2010). The cophenetic correlation coefficient was 0.73, which indicated good performance of the UPGMA in transferring the original distance matrix into dendrograms. In this analysis, we used Simpson’s dissimilarity index, as it indicates species turnover (i.e., replacement) between sites and therefore represents a true substitution of species without the influence of differences in species richness between sites (Baselga, 2010). We randomly resampled 70 % of the sites (30 out of 42 sites) 1,000 times and calculated the mean values of the β_{SIM} among the urban and non-urban communities. We used a paired *t*-test to assess the overall change in community composition between sites (i.e., biotic homogenization or heterogenization) based on the difference in β_{SIM} between the urban and non-urban communities.

Furthermore, we evaluated coloration homogenization after urbanization by fitting the decay curves of the color-based similarity to the geographic distance. We used the halving distance (i.e., the distance after which a given similarity value was predicted to decrease by 50 %) as a measure of turnover rate (König et al., 2017). We calculated the pairwise beta dissimilarity between each pair of avian communities using Simpson’s dissimilarity index (β_{sim}). Color-based relationships between species were incorporated into quantifying pairwise beta dissimilarities (Graham & Fine, 2008). These indices calculate the pairwise dissimilarity between two communities by replacing shared and unique species with shared and unique branch lengths, respectively (Leprieur et al., 2012), as follows:

$$\beta_{sim} = \frac{\min(PD_{Total} - PD_k, PD_{Total} - PD_j)}{PD_k + PD_j - PD_{Total} + \min(PD_{Total} - PD_k, PD_{Total} - PD_j)}$$

where PD_j and PD_k are the total branch lengths of the communities j and k , respectively. PD_{Total} is the total branch length of a color-based dendrogram containing all the species present in both j and k communities.

2.5. Latitudinal gradient in avian coloration

To explore whether urbanization influences the strength of geographic patterns in avian colorfulness, we compared the coloration–latitude correlations of passerine bird species using the avian communities recorded in cities versus those recorded in natural environments. Colorfulness scores and lightness per site were measured using the median values of all species within each avian community. We then fitted univariate linear regression models using the median values of colorfulness scores and lightness as response variables, and latitude per avian community as a predictor. Given the potential spatial autocorrelation in the residuals of the linear regression models, we used linear mixed models (LMMs) to formally assess the coloration–latitude correlation. In the LMMs, we specified the correlation structure using the ‘corExp’ function in the R package ‘nlme’ (Pinheiro et al., 2023) to account for spatial autocorrelation between the proximate sites. Furthermore, we tested whether the colorfulness and lightness of avian communities differed between the subtropical and temperate zones in China.

Finally, we evaluated how urban–rural differences in avian coloration were related to baseline avian color within rural environments. For each urban–rural comparison, we calculated the log-transformed response ratio (LRR) by dividing the median value of avian coloration in urban areas (C_{CY}) by that in the nearest nature reserve (C_{NR}), and then we applied the natural logarithm ($LRR = \log(C_{CY}/C_{NR})$). An $LRR > 0$ indicates an increase in coloration, whereas an $LRR < 0$ indicates a decrease in coloration in urban environments. We then regressed the

LRR against avian coloration in rural environments.

3. Results

3.1. Plumage color space

Our results did not show significant differences in the individual dimensions of avian colorfulness and lightness between non-urban and urban birds (Wilcoxon rank-sum test, $P > 0.05$; Fig. 1). Our data also revealed a high overlap in the coloration space for non-urban and urban birds according to the density of species occurrence (Schoener's $D = 0.664$; Fig. 1). However, niche equivalency and similarity tests showed that the coloration spaces of birds in non-urban and urban communities were neither equivalent ($P = 1$) nor more similar ($P = 0.091$) than expected by chance. These results indicated that when colorfulness and lightness were combined in a coloration space, coloration differences emerged between non-urban and urban birds. The dynamics of the coloration space analysis further showed that this difference was caused by the coloration loss of urban birds (unfilling 3.2 %) instead of an increase in coloration (expansion 0 %; Fig. 1).

3.2. Color-based community similarity

The mean value of multiple-site color-based β_{SIM} was 0.858 for urban communities, which was lower than that observed for non-urban communities (0.869; paired t -test, $P < 0.001$; Fig. 2a). Distance decays in pairwise color-based similarities were best fitted with power-law models ($R^2 = 0.29$ for non-urban communities; $R^2 = 0.12$ for urban communities; $P < 0.01$ for both). Halving distance analyses revealed that color-based similarity declined by 50 % every 949 km for urban communities,

which was lower than that for non-urban communities (50 % every 1,146 km; Fig. 2b). The slope of the fitted linear model between color-based similarity and log-transformed distance was -0.064 (95 % CI = $[-0.075, -0.052]$) for urban communities and -0.086 (95 % CI = $[-0.096, -0.070]$) for non-urban communities, supporting a slower distance decay in color-based similarity after urbanization (Fig. S2 in Supplementary Data 1). These results indicated that avian communities in cities had a higher similarity in plumage coloration than avian communities in nature reserves (i.e., biotic homogenization). Based on alternative measures of colorfulness and lightness, the multiple-site color-based β_{SIM} also indicated urbanization homogenization of avian plumage color (Fig. S3a in Supplementary Data 1), but there were no significant differences in distance decays in the pairwise similarity (Fig. S3b in Supplementary Data 1).

3.3. Latitudinal gradients in plumage color

Univariate linear regression models showed pronounced latitudinal gradients in the plumage colorfulness ($R^2 = 0.63$, $P < 0.001$; Fig. 3a) of passerine birds in non-urban communities, with subtropical birds significantly more colorful than their temperate counterparts (Wilcoxon rank sum test, $P < 0.05$; Fig. S4a in Supplementary Data 1). However, in urban communities, the plumage colorfulness of the species did not show a significant latitudinal gradient ($P > 0.05$; Fig. 3b), nor did the plumage colorfulness between subtropical and temperate communities ($P > 0.05$; Fig. S4b in Supplementary Data 1). The lightness–latitude correlation was significant ($R^2 = 0.22$, $P < 0.01$; Fig. 3b) in non-urban communities and much lower in urban communities ($R^2 = 0.13$, $P = 0.02$; Fig. 3d). These patterns were consistent with the results of an alternative measure of avian plumage colorfulness and lightness (Fig. S5

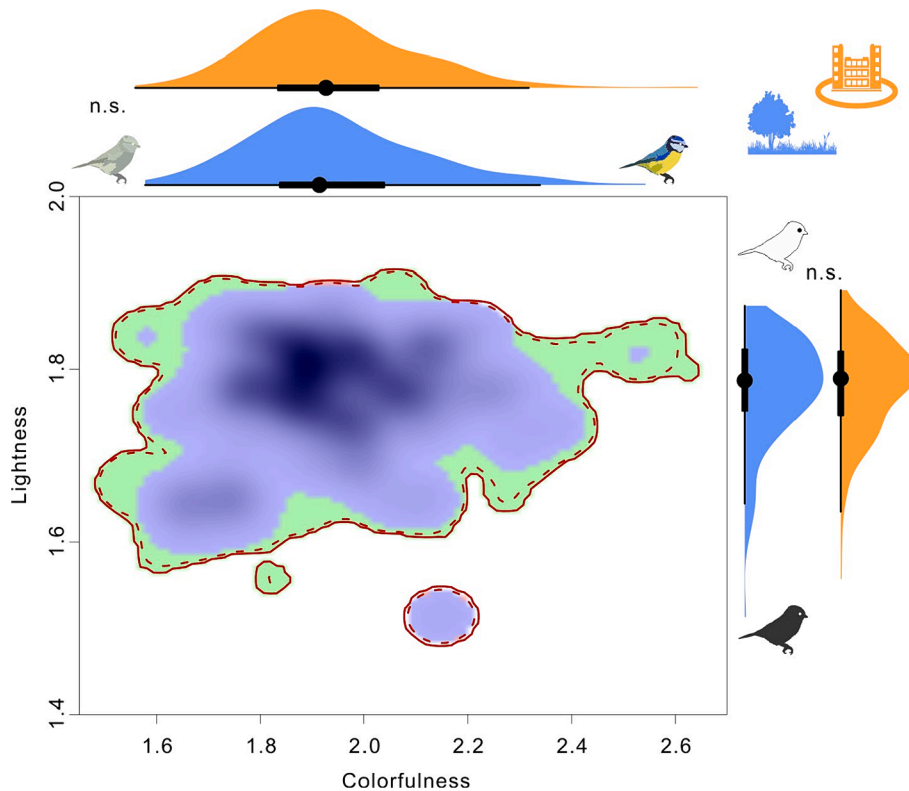


Fig. 1. Differences in bird plumage color between urban and non-urban communities. Violin plots show the difference in (a) colorfulness and (b) lightness between urban (orange) and non-urban (blue) communities. Asterisks indicate the level of significant differences evaluated by the Wilcoxon rank-sum test (n.s., $p > 0.05$). (c) The coloration space occupied by avian species recorded in urban and non-urban communities. The solid and dashed contour lines indicate 100 % and 75 % of the background environment. Blue area indicates coloration space occupied by species in both urban and non-urban communities (i.e., stability); green area indicates coloration space occupied by the species in natural but not in urban environments (i.e., unfilling). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

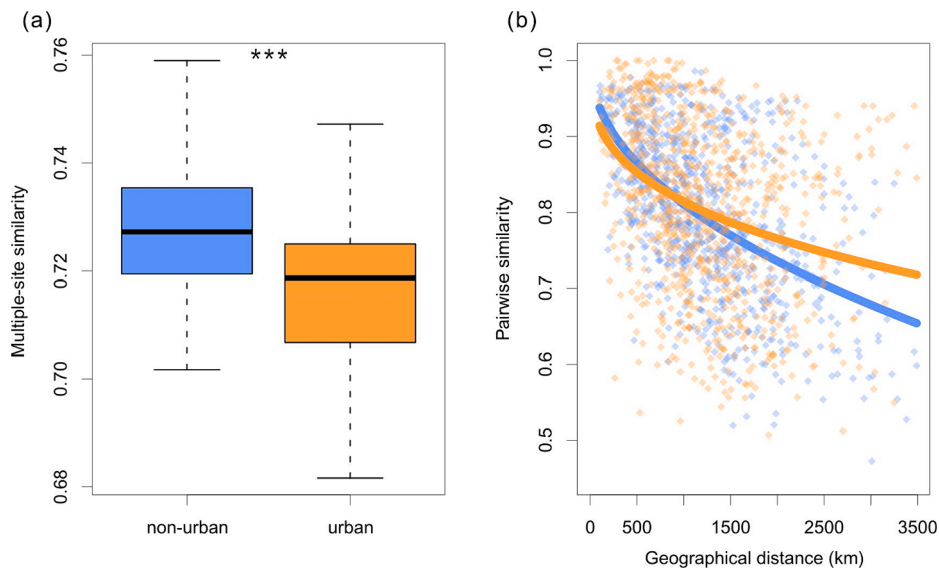


Fig. 2. The color-based beta diversity between urban and non-urban bird communities in China. (a) Boxplots showing the median and 25th and 75th percentiles of 1,000 resamplings of color-based, multiple-site beta dissimilarity. Asterisks indicate significant differences between urban (orange) and non-urban (blue) avian communities (paired *t*-test, ****p* < 0.001). (b) Distance decay of color-based similarity across urban and non-urban avian communities. Points represent pairwise similarities between avian communities within nature areas (blue) and cities (orange). Solid curves indicate distance decay of similarity relationships with exponential fits. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

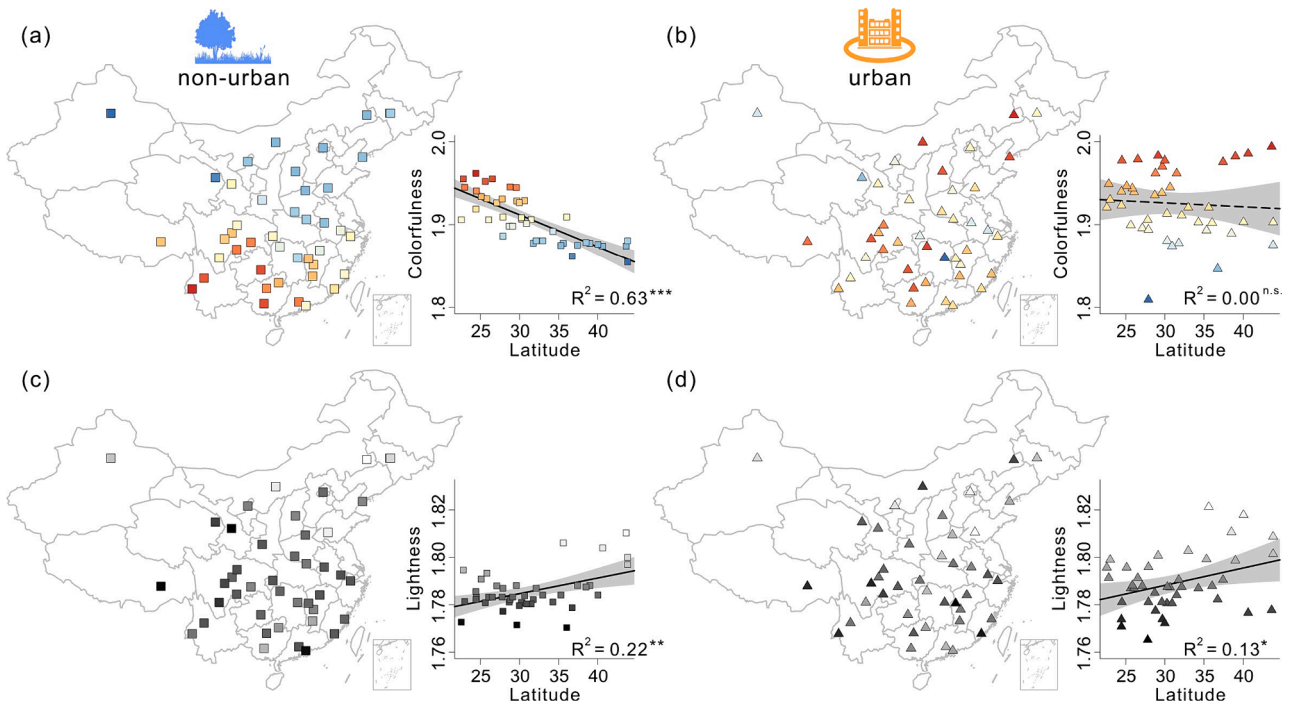


Fig. 3. Geographic patterns of the avian colorfulness and lightness within urban and non-urban communities in China. The latitudinal gradient in bird plumage colorfulness in (a) non-urban and (b) urban communities. The color gradient indicates the colorfulness of avian communities; red indicates high colorfulness and blue indicates low colorfulness. The latitudinal gradient in bird plumage lightness in (c) non-urban and (d) urban communities. The gray gradient indicates the lightness of avian communities; black indicates darkness and white indicates brightness. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

in Supplementary Data 1). After accounting for spatial autocorrelation, the latitudinal gradients in colorfulness and lightness remained valid for the non-urban communities (*P* < 0.05). However, this gradient in colorfulness was not observed (*P* > 0.726) among urban communities, and the lightness gradient was only marginally valid (*P* > 0.042; Table S1 in Supplementary Data 1). We found that the LRR was negatively correlated with both colorfulness ($R^2 = 0.15$, *P* < 0.05) and

lightness ($R^2 = 0.17$, *P* < 0.01) for avian communities in natural environments (Fig. 4). This indicated that avian communities in natural environments that were more colorful and lighter were duller and darker in urban environments, whereas avian plumages were more colorful and brighter in cities when the plumage color of non-urban communities was dull or dark.

4. Discussion

By compiling a dataset of 547 bird species from 42 cities and their corresponding non-urban communities in China, we did not observe significant differences in the individual dimensions of colorfulness and lightness between non-urban and urban bird communities. However, the coloration space of birds in urban environments was reduced by 3.2 % compared with that in rural environments. Multiple-site and pairwise indices of color-based similarities revealed that avian communities in cities exhibited greater homogenization of plumage color than those in non-urban communities. We documented significant latitudinal gradients in plumage colorfulness and lightness in non-urban communities, but these correlations were weaker in urban communities. Interestingly, non-urban communities that were more colorful and lighter tended to be duller and darker in urban environments. These results suggest that urbanization reduces color diversity, increases the color similarity of avian communities, and alters the geographic patterns of plumage color in China.

Our results provide empirical evidence that urbanization induces the loss of bird plumage color in China (Fig. 1), which is not surprising because urban communities are generally subsets of their corresponding species pools. There is growing evidence that birds in urban areas are characterized by a range of traits that enable them to persist in the city (Hahs et al., 2023), such as small body size (Zhong et al., 2024), habitat generalism (Callaghan et al., 2019), and behavioral flexibility and innovation (Santini et al., 2019; Sayol et al., 2020). As urban areas are typically characterized by impervious surfaces, such as asphalt pavement and concrete buildings, birds with dull and/or gray plumage may have a survival advantage in cities owing to the better thermoregulation and camouflage (Delhey et al., 2023). However, there were no significant differences in the colorfulness or lightness of birds between urban and rural environments (Fig. 1), indicating that urban bird species are neither darker nor duller than their non-urban counterparts. This finding is inconsistent with our Hypothesis 1 and previous reports on the ‘urban melanism’ and ‘urban dullness’ phenomena (Jacquin et al., 2013; Sal-món et al., 2023). One possibility is that urbanization has contributed to greater uniformity in the color of avian plumage. Urban environments retain species with uniform colorfulness and lightness and filter out species with distinctive coloration, such as those that are outliers in the coloration space (Leveau & Ibáñez, 2022). Another possibility is that the effect of urbanization on avian plumage coloration may be neutral in that bird species filtered out by urbanization were evenly distributed along the individual dimensions of the colorfulness and lightness gradients. In addition, our study focused on the overall changes in plumage

color at a national scale. Because the environmental filters for selecting avian traits (e.g., plumage color) vary with city characteristics (Cosen-tino & Gibbs, 2022; Neate-Clegg et al., 2023; Zhong et al., 2024), city-level variations in coloration gain and loss may result in mutual compensation within China.

Our results showed that urban communities had lower multiple-site dissimilarities and a slower distance decay of community similarity than those of their non-urban counterparts (Fig. 4). These results provide evidence for our Hypothesis 2 that urbanization drives the homogenization of bird plumage color in China. Previous studies have recorded biotic homogenization caused by urbanization among a wide range of taxa from the local to global scales (Morelli et al., 2016; Marcacci et al., 2021; Wang et al., 2021; Sidemo-Holm et al., 2022; Deng et al., 2024), but few have focused on changes in color-based community similarity (Leveau, 2019). The increase in community similarity was generally attributed to the fact that urbanization has acted as an environmental filter for some specialist species and has promoted the expansion of generalists (Evans et al., 2011; Aronson et al., 2016). Given that our data did not show significant differences in avian colorfulness and lightness between urban and non-urban communities (Fig. 1), such an increase in color-based similarity in urban communities might result from similar plumage coloration shared by specialists and/or generalists (i.e., the gain and loss of species have non-random plumage colorations). Therefore, urban areas not only contain a subset of species relative to rural areas, but also retain species with more similar coloration than that expected by chance (Leveau, 2019), which eventually results in the homogenization of the plumage color of urban birds.

Our study documented significant latitudinal gradients in plumage colorfulness and lightness in non-urban communities across China. This pattern is consistent with previous global scale studies showing that tropical species are more colorful than temperate species (Cooney et al., 2022; Senior et al., 2022). However, the colorfulness of avian plumage in urban communities did not show a significant latitudinal gradient (Fig. 3a, b), and the lightness–latitude correlation in urban communities was weaker than that in non-urban communities (Fig. 3c, d). This indicates that urbanization contributed to greater uniformity in the plumage color of bird communities at a national scale, which is consistent with our Hypothesis 3. Furthermore, the magnitude of the change in plumage colorfulness was greater than that in lightness (Fig. 3). Plumage lightness is strongly correlated with large-scale patterns of climatic conditions, such as rainfall and temperature (Delhey et al., 2019). Although urbanization alters the lightness–latitude correlations in avian plumage, such a gradient still exists. However, unlike melanins, carotenoids cannot be synthesized by birds and must be

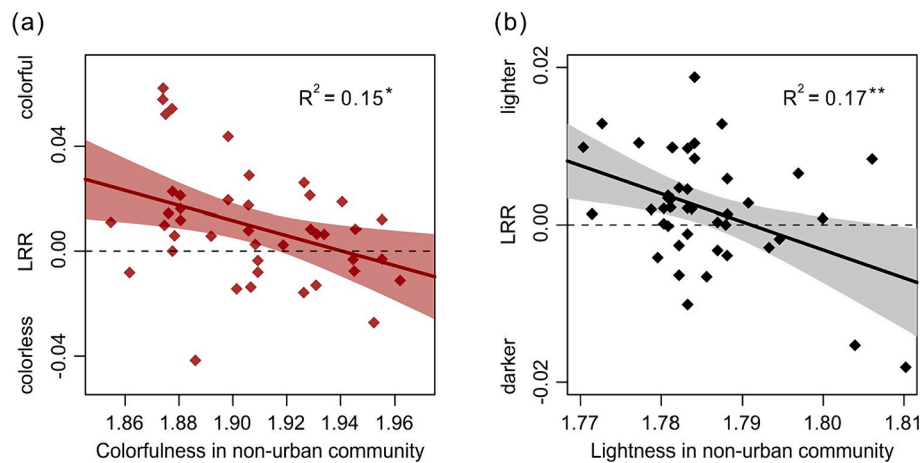


Fig. 4. Correlations between log response ratios (LRR) and (a) colorfulness and (b) lightness of avian communities in natural environments. The solid lines represent the fitted linear models and the shaded areas are the 95% confidence intervals of these models. An LRR greater than zero indicates an increase in colorfulness/lightness within an urban community, whereas an LRR lower than zero indicates a decrease in colorfulness/lightness within an urban community.

obtained from food (Barreira & García, 2019), and the limited availability of plant-derived dietary carotenoids in urban areas limits the occurrence of species with carotenoid-based colors (Biard et al., 2006; Willink & Wu, 2023). Therefore, urbanization might have a stronger impact on latitudinal gradients in plumage colorfulness than that on latitudinal gradients in plumage lightness.

Interestingly, we found a considerable negative correlation between plumage coloration variation along urban community gradients and that along non-urban community gradients (Fig. 4). This finding implies that for non-urban communities where avian plumage is more colorful and lighter, bird species had duller and darker plumage in urban environments. However, in cases where avian plumage was dull or dark in non-urban communities, there was more colorful and brighter plumage color in urban communities. This shift in coloration variation confirms that the uniform plumage color of bird communities is driven by urbanization (Leveau & Ibáñez, 2022). This is likely because in more colorful communities, which are located in subtropical zones, urban dullness may be favorable for blending into anthropogenic backgrounds, such as bricks and concrete (Kreling, 2023), allowing birds to thrive in stressful environments with a high risk of predation. Furthermore, the food available in cities are generally low in nutrition and high in carbohydrate content. Large urban–rural differences in the accessibility of plant-based dietary carotenoids in the subtropical zone could enhance this difference in coloration (Biard et al., 2006; Willink & Wu, 2023). In contrast, in temperate zones, carotenoid-rich plants in urban areas can provide additional food that improves the carotenoid-based color of urban species (Baldassarre et al., 2022). Birds in urban areas with more colorful and brighter plumage compared to their non-urban counterparts would increase conspicuous signaling for intra- and inter-specific communication in temperate zones (Delhey & Peters, 2016). A previous study in the Argentinian Pampas documented that bird species living in wooded environments of urban parks were more colorful than those in open habitats of rural areas (Leveau, 2024), which corroborates our results. These findings add new insights on changes in animal coloration in response to urban environments. Traditionally, harsh environmental conditions in cities were thought to act as an environmental filter in selecting species with specific coloration (e.g., urban melanism and urban dullness). However, our results suggest that urbanization-driven coloration changes are not unidirectional and that the extent to which animal coloration changes is environment-dependent.

This study had several limitations that should be considered in future studies. First, the plumage colorfulness used in this study was originally measured using the photographs of museum specimens (Cooney et al., 2022), and the plumage lightness was obtained from bird image plates in books (Delhey et al., 2021). Although we performed sensitivity analyses based on alternative measurements of plumage colorfulness and lightness (Dale et al., 2015; Delhey et al., 2019), there is a need to reconcile differences in the methods for measuring plumage reflectance in future analyses. Furthermore, our results on urbanization-driven changes in plumage coloration were mainly based on colorfulness and lightness. Some adaptations of plumage color, such as changes in reflectance of ultraviolet light (Tringali & Bowman, 2015) or color patch patterns (Senar et al., 2014), might also reflect the effect of urbanization on birds; however, this information was not considered in the present study because of a lack of data completeness and accessibility (Delhey et al., 2023). Finally, we compared the geographic patterns of avian plumage color between non-urban and urban communities rather than investigating the changes in coloration of the same communities before and after urbanization along a time slice. Although this “space-for-time” method has been widely used in previous studies (Leveau, 2019; Leveau & Ibáñez, 2022; Salmón et al., 2023), future studies should provide more direct evidence of bird coloration changes during the Anthropocene from long-term biodiversity observations.

5. Conclusions

Understanding biotic changes in response to human-induced environmental pressures is essential for promoting sustainable human coexistence with wildlife. Despite cases of urbanization-driven changes in animal traits, to our knowledge, this study is the first national assessment of how urbanization drives changes in avian coloration across China. We conclude that urbanization induces a loss of bird plumage color despite the absence of significant changes in the individual dimensions of colorfulness and lightness. Such coloration loss and increasing community compositional similarities further trigger avian plumage color homogenization in urban areas and disrupt the coloration–latitude correlations at a national scale. Taken together, these results highlight the importance of evaluating the extent to which urbanization acts as an environmental filter for avian plumage coloration and restructures the geographic patterns of colorfulness diversity gradients. These findings provide some implications for urban design based on biodiversity protection. For example, urbanization exerts filtering effects on the presence of colorful bird species owing to urban–rural differences in the availability of dietary carotenoids and habitat openness. To improve bird color diversity in cities, it is crucial to design bird-friendly landscapes by creating closed habitats and planting native fruit trees as sources of carotenoids. Future studies should explore the spatial variation in avian plumage color interacting with previously reported traits, such as body size, diet, habitat, and behavioral innovation, to better understand the trade-offs between morphological and behavioral responses of species to urbanization.

6. Data accessibility statement

The data supporting the findings of this study are available in the [Supplementary file](#).

ORCID iD authorship contribution statement

Jiehua Yu: Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Haoting Duan:** Writing – review & editing, Data curation. **Baoming Zhang:** Writing – review & editing, Data curation. **Ludan Zhang:** Writing – review & editing, Data curation. **Jiekun He:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data supporting the findings of this study are available in the [Supplementary file](#).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2024.105101>.

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