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RESEARCH ARTICLE

Does building height influence bird diversity in urban landscapes?

Cristina del Pilar Buenaño-Mariño · Jackson Barratt Heitmann · Juan A. García-Esparza · Brittany M. Mason · Corey T. Callaghan

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Abstract
Context Urbanization impacts biodiversity through changes in horizontal and vertical structures. While impervious cover is well-studied, the role of building height remains underexplored at a broad scale.
Objectives This study aimed (1) to assess whether building height differed statistically from impervious cover and NDVI in explaining bird diversity in cities, and (2) to assess the impacts of building height in conjunction with seven predictor variables: impervious cover, bare, trees, grass, water, shrub and scrub and NDVI.
Methods We combined land cover data with an open-access building footprints data. We analyzed over 1 million eBird checklists from 298 cities in the United States. For objective one seven models were evaluated for each city (1) building height, (2) impervious cover, (3) NDVI, (4) building height and impervious cover, (5) building height and NDVI, (6) impervious Cover and NDVI, and (7) building height, impervious Cover and NDVI. For objective two we use model 7 and the rest of the predictor variables to assess the impact of building height. For both objectives, we compared model results by ecoregion.
Results Building height, impervious cover, and NDVI were the best single predictors of bird species richness in 10.7%, 10.4%, and 12.4% of cities, respectively. However, the combined model including all three variables performed best in 25.8% of cities, underscoring the complementary influence of vertical and horizontal urban structures in cities. Species richness was positively related to shrub/scrub and water cover, highlighting the importance of these habitats for urban biodiversity.
Conclusions Our research advances landscape ecology by incorporating vertical urban structure into biodiversity models, providing new insights into the multidimensional impacts of urbanization on bird communities. Findings underscore the need for context-specific strategies integrating green infrastructure to promote avian diversity in cities.

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C. d. Buenaño-Mariño (✉) · J. A. García-Esparza (✉)
Department of Mechanical Engineering and Construction, Jaume I University, Castellón de la Plana, Spain
e-mail: buenano@uji.es

J. A. García-Esparza
e-mail: juan.garcia@uji.es

J. Barratt Heitmann · B. M. Mason · C. T. Callaghan (✉)
Department of Wildlife Ecology and Conservation, Fort Lauderdale Research and Education Center, Institute of Food and Agricultural Sciences, Davie, FL, USA
e-mail: c.callaghan@ufl.edu

J. Barratt Heitmann
e-mail: j.barrattheitmann@ufl.edu

B. M. Mason
e-mail: bmason1@ufl.edu

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Introduction

Human activity is continually transforming natural spaces, converting natural habitat into anthropogenically-dominated areas (Lee et al. 2019; Yang et al. 2023; Jokimäki and Ramos-Chernenko 2024; Maseko et al. 2024). Such habitat transformation and associated habitat loss leads to biodiversity declines (Díaz et al 2019; Šálek et al. 2020; Ding et al. 2023; Kroc et al 2024; Paniagua-Villada et al. 2024). Increasing urbanization, with its inherent complexity and diverse land use patterns, highlights the need to understand how wildlife persists and responds to the various forms of impervious cover (Šálek et al. 2020; Ding et al. 2023). However, urbanization does not affect species equally; while some species persist and even thrive in urban environments (MacGregor-Fors et al. 2022; Yang et al. 2023) others are negatively impacted in human-dominated landscapes (Benedetti et al. 2023).

For birds in particular, diversity metrics (e.g., species richness and abundance) tend to be positively related to vegetation cover, while being negatively affected by high-density urban areas and intense human activity (MacGregor-Fors and Schondube, 2011; Yu et al. 2025). Given the growing complexity of urban ecosystems and the sensitivity of birds to urbanization (Pena et al. 2023), many studies focus on birds due to their potential role as indicators of ecosystem health (Smits and Fernie 2013; Beninde et al. 2015) and their visibility in urban landscapes. Most of the research of birds in cities have investigated the importance of green area availability (Buron et al. 2022; Yang et al. 2022a, b), the structure and height of vegetation (Ding et al. 2023; Hao et al. 2024), the size of urban parks (Kumari et al. 2024), the effect of habitat fragmentation (Carvajal et al. 2018) on bird diversity and the role of bird traits in shaping urban bird communities (Neate-Clegg et al. 2023; Ibáñez-Álamo et al. 2024; Alba et al. 2025). Our knowledge of the factors that shape bird communities in urban areas is largely influenced by studies focusing on how bird diversity responds along an urbanization gradient (Concepción et al. 2016; Lee et al. 2019; Šálek et al. 2020; Xie et al. 2020; Yang et al. 2023) and within and among green areas (MacGregor-Fors and Schondube, 2011). In general, bird diversity declines along an urbanization gradient (Filloy et al. 2019; Korányi et al. 2021; Callaghan et al. 2023). However, this signal is not consistent across all studies, with some evidence of species diversity increasing in some urban environments (Leveau and Leveau 2016; Mbiba et al. 2021; Maseko et al. 2024). Although much attention has been paid to the impacts of various forms of land cover and vegetation on bird diversity in urbanized landscapes, few have considered the 3-dimensional nature of cities.

Land cover is often a remotely sensed predictor variable in landscape ecology studies on bird biodiversity in urban landscapes, creating a two-dimensional representation of the landscape; for instance, a given pixel is classified as either impervious cover or some other land cover type (Petersen et al. 2022; Davis et al. 2023; Huang et al. 2023; Wei et al. 2024). Simultaneously, proxies for vegetation cover are also used, for example the Normalized Difference Vegetation Index (NDVI) is widely used as it provides a standardized and globally available measure of vegetation cover and can be an effective predictor of urban bird diversity (Benedetti et al. 2023; Fairbairn et al. 2025). While remote sensing often captures two-dimensional features, digital surface or elevation models are increasingly used to assess vertical structure, including vegetation and building height (Merkens et al. 2023; Fairbairn et al. 2025). The most common feature throughout the urban landscape are buildings—the locations humans erect within urban environments for dwelling and other uses. The height and heterogeneity of buildings introduce additional complexity to urban environments. The relationship between birds' use of this complex three-dimensional space comprising buildings of varying heights can offer insights into avian behavior, community dynamics, and practical applications for urban planning (Mikami et al. 2022). In densely built areas, limiting the construction of very tall buildings and relegating them to less densely populated zones is often recommended to mitigate urban heat island effects (Shen et al. 2024). This spatial heterogeneity in building height can also affect airflow (Sützl et al. 2021), shade distribution, and microclimates, further impacting local ecosystems (Zhou and Chen 2021; Lin et al. 2023). There is a growing amount of research investigating the relationship between birds and buildings, mostly related to window collisions (Kummer et al. 2016; Riding et al. 2020; Scott et al. 2023; Chen et al. 2024) and roof gardens (Wang et al. 2017; Belcher et al. 2019).

For instance, the number of high-rise buildings has been found to affect the vertical space utilization of urban birds (Przybylska et al. 2012; Mikami et al. 2022). Additionally, there may be a positive relationship between building height and species abundance in northern Mexico (MacGregor-Fors and Schondube, 2011), while taller building heights could be a stronger factor in describing avian species presence than the amount of built-up structure at the landscape scale (Lee et al. 2019). Furthermore, Yang et al. (2022a, b) observed a negative correlation between bird flight resistance and building height, and others have found a variable relationship between species richness and the average height of buildings (Leveau and Leveau 2016; Pena et al. 2023). However, the research which has focused on bird diversity and various components of buildings within cities has been limited to relatively small scales, for instance focusing on a single city (Leveau and Leveau 2016; Souza et al. 2019; Titoko et al. 2019; Petersen et al. 2022; Pena et al. 2023), a handful of cities (Campbell et al. 2022; Benedetti et al. 2023), or only a few species (Przybylska et al. 2012). Therefore, a broad-scale understanding is needed to fully quantify the relationship between bird diversity and building height within cities.

Our overall objective was to fill this research gap by understanding how building height affects bird diversity. Specifically, our first objective was to assess if building height—a three-dimensional representation of the urban environment—was statistically different in terms of its explanatory power of bird diversity compared to impervious cover and Normalized Difference Vegetation Index (NDVI). Our second objective was then to assess the impacts of building height in conjunction with the six types of land cover—water, trees, grass, shrub and scrub, impervious cover, and bare—on bird diversity within cities, as identified in previous studies (Benedetti et al. 2023; Davis et al. 2023; Huang et al. 2023; Wei et al. 2024). Here, we included NDVI as a predictor. We hypothesize that a lower average building height will positively influence bird species richness due to the absence of vertical obstacles and shorter flying distances between nesting and foraging areas. We explore these two objectives across the continental United States by leveraging eBird citizen science data (Wood et al. 2011). By integrating a biological perspective and proposing spatial construction solutions, we aim to contribute to alleviating the conflict between urban development and biodiversity conservation (Yang and Cui 2022).

Methodology

City and building data

We used the U.S. Census Bureau urban areas shapefile to delineate cities in the continental United States—referred to as cities hereafter (U.S. Census Bureau 2023). This shapefile contains urban area delineations that represent densely populated land cover including residential, commercial, and other nonresidential urban land uses. There are 2645 urban areas delineated in the U.S. Census Bureau urban areas shapefile that meet the minimum requirements of having either a minimum population of 5000 and/or a housing unit count of 2000 units. This data is available for free download (see more information here: https://catalog.data.gov/dataset/urban-areas2).

After downloading the cities data, we compared data availability between these urban shapefiles and building height information from Bing Maps, which contains global building height footprints (https://github.com/microsoft/GlobalMLBuildingFootprints?tab=readme-ov-file). For inclusion in analysis, a city had to be included in both the U.S. Census Bureau's shapefile and the Bing Maps data catalog. Large conurbations were excluded because they often encompass multiple cities and metropolitan areas, which could introduce confounding factors and skew the results. To assess whether this exclusion omitted important information about building height, we modeled the distribution of building heights in all cities with at least 70% coverage of building height data. We focused on the 99th percentile of building height, which captures the distribution of tall buildings while minimizing the influence of outliers. Although this metric had a statistically significant relationship with the number of buildings ($p < 0.001$), the explanatory power was very weak ($R^2 = 0.016$), indicating that the number of buildings explains only 1.6% of the variation in tall building heights across cities (Supplementary Material Fig. A1). Therefore, the exclusion of conurbations is unlikely to bias our results.

We also filtered our city and building dataset to only include cities from the contiguous United States to maximize the presence of eBird data and ensure sufficient coverage of building height data. We required that at least 70% of the buildings in each city had building height data available from Bing Maps. This threshold was chosen to balance data completeness while ensuring we had an adequate number of cities eligible for analysis. After imposing these filters, we had 551 cities in the contiguous US that had 70% building height data completeness (see more details about further filtering in Sect. "eBird data").

Land cover data

We used Google Earth Engine (GEE; Benedetti et al. 2023; Tian et al. 2023; Paniagua-Villada et al. 2024) to extract Dynamic World land cover information from 551 cities at all unique eBird sampling locations (Brown et al. 2022; see Sect. "eBird data"). We calculated the percentage of land cover data within a 250 m buffer of each eBird sampling location. The 250 m buffer area represents the local habitat complexity, which is an important factor determining bird species richness (Lim and Sodhi 2004; Weyland et al. 2012; Silvetti et al. 2023). We extracted nine land cover types from the Dynamic World dataset within the 250 m buffer around each eBird sampling location (Brown et al. 2022) using GEE, averaged with the *ee.mean.reducer* function from 01/01/2022 to 12/31/2022. Pixel grain was set to 25 m resolution to reduce computing time for the number of unique eBird sampling locations. We found that the 25 m pixel resolution had an $R^2 = 1$ at 10 m and 30 m resolution respectively, meaning we felt comfortable reducing computing time without sacrificing data granularity (Supplementary Material Figs. A2, A3). We removed three of the land cover types, crops, flooded vegetation, and snow/ice land cover due to their limited relevance in our study area and for having incredibly small land cover proportions (Foody 2002; Radford et al. 2005). Instead, we focus on the more prevalent land cover types (water, trees, grass, shrub and scrub, impervious cover, and bare) across the entire spatial scale of our study for our specific research objectives. We also calculated NDVI measurements in GEE using *MODIS* satellite imagery (MODIS/006/MOD13Q1) from 01/01/2022 to 12/31/2022 using the *ee.MeanReducer* function at 250 m resolution—the native resolution for the *MODIS* dataset (Didan 2021). We also appended the EPA Level I Ecoregion to each eBird sampling location to control for larger landscape effects at the biome level (US EPA 2015). You can see our harmonizing protocol for the building height data, land cover, and eBird data in Sect. "Harmonizing environmental data with eBird data within cities".

eBird data

eBird is a semi-structured community science platform launched in 2002 by the Cornell Lab of Ornithology (Sullivan et al. 2009; Wood et al. 2011). eBird has been widely used in research focused on birds and urban environments (Carmona et al. 2013; La Sorte et al. 2017; Callaghan et al. 2021; Campbell et al. 2022; Godoy et al. 2024) since it has over 1.3 billion bird observations globally. We downloaded stationary eBird checklists from 551 cities within the United States, submitted from 01/01/2019 to 06/30/2024. All available data within the selected temporal window were used, without separating records by specific period such as the breeding season (Callaghan et al. 2021; Aznarez et al. 2022; Hao et al. 2024). Similarly, no distinction was made between resident and migratory birds in the analysis, in order to capture the annual variation in diversity (Belcher et al. 2019; Benedetti et al. 2023). To refine our dataset for subsequent analysis, we implemented a filtering process based on eBird checklist completeness. The previous 551 cities were filtered to meet the criteria of having at least 100 eBird checklists and 50 geographically unique eBird sampling locations. As a result of this filtering, the dataset was reduced to 298 cities (Fig. 1).

We selected checklists that had one observer to remove duplicate checklists submitted by groups of two or more eBird users and filtered checklists to be at least 5 min in duration, but no longer than 240 min in duration (Callaghan et al. 2017). We only included stationary checklists to ensure observations could be associated with the 250 m land cover buffer containing our predictor variables of interest. The above filtering steps help to ensure comparability among eBird checklists and help to minimize potential outliers

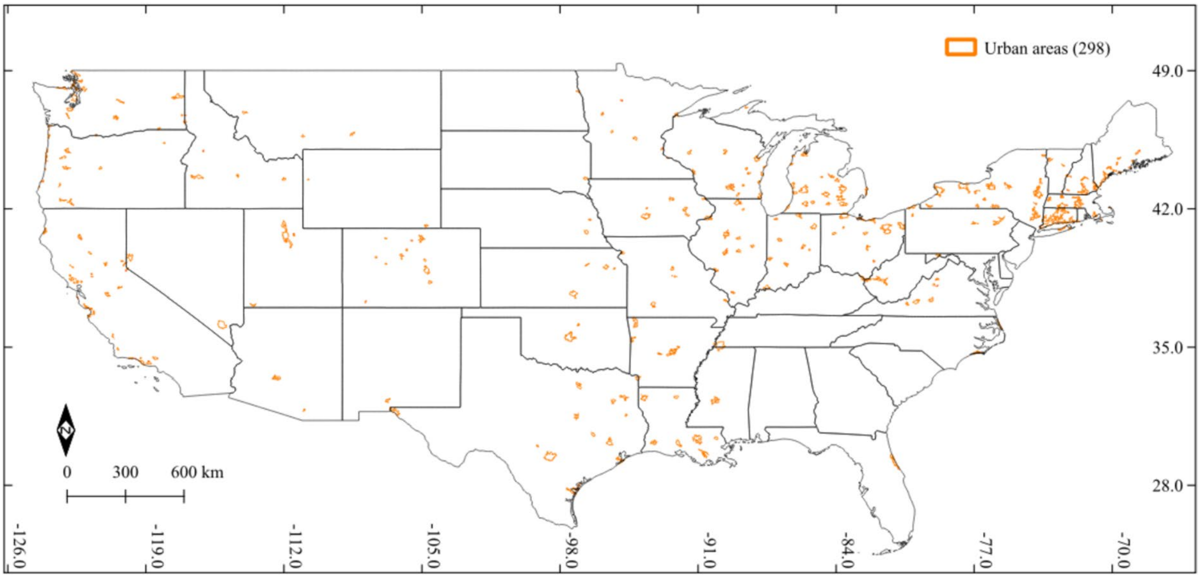

Fig. 1 Map of the study area showing the urban areas selected from the United States after applying the filtering criteria, which included a minimum of 100 eBird checklists from 50 geographically unique locations

in the dataset. We calculated species richness at the checklist level. Checklists could come from the same eBird sampling location but were treated as independent units of replication.

Harmonizing environmental data with eBird data within cities

We combined land cover data with the open-access building footprints database to extract habitat attribute variables for each checklist (Callaghan et al. 2021). Using 250 m buffers around eBird hotspots, we calculated the following: (1) mean building height and (2) land cover proportions for NDVI, impervious cover, grass, shrub and scrub, trees, water, and bare (Fig. 2).

Statistical model

Our analysis focused on variations in bird diversity within city boundaries rather than comparisons among cities. This approach allowed us to isolate the effects of building height and urban land cover on bird communities while controlling broader regional differences, providing a clearer understanding of urban-scale ecological patterns. Importantly, each city was treated as an independent unit in our modeling framework to ensure that predictions reflect localized relationships between urban structures and bird diversity, minimizing cross-city biases. All analyses were performed within the R statistical environment (R Core Team 2018). Statistical significance was interpreted following the guidelines of Muff et al. (2022).

For the first objective—quantifying the explanatory power of building height compared with impervious cover and NDVI—we conducted a comparative analysis of bird species richness across the cities using Generalized Additive Models (GAMs; Zhao et al. 2014; Yan et al. 2020; Ding et al. 2023). We chose to use GAMs so that we could account for the known, non-linear impact of latitude and longitude on species richness (Field et al. 2008), as well as the possible non-linear relationship between survey duration and species richness. Survey duration was modeled using a cubic regression spline with a basis dimension of 15. Geographic coordinates (latitude and longitude) were modeled using a two-dimensional thin plate spline with a basis dimension of 30 (Wood 2003). These basis dimensions were selected based on exploratory models using data from all cities and assessing the estimated degrees of freedom (EDF) using the gam.check() function from the *mgcv* package in R (Wood 2011). The mean building height, percent impervious cover, and NDVI were treated

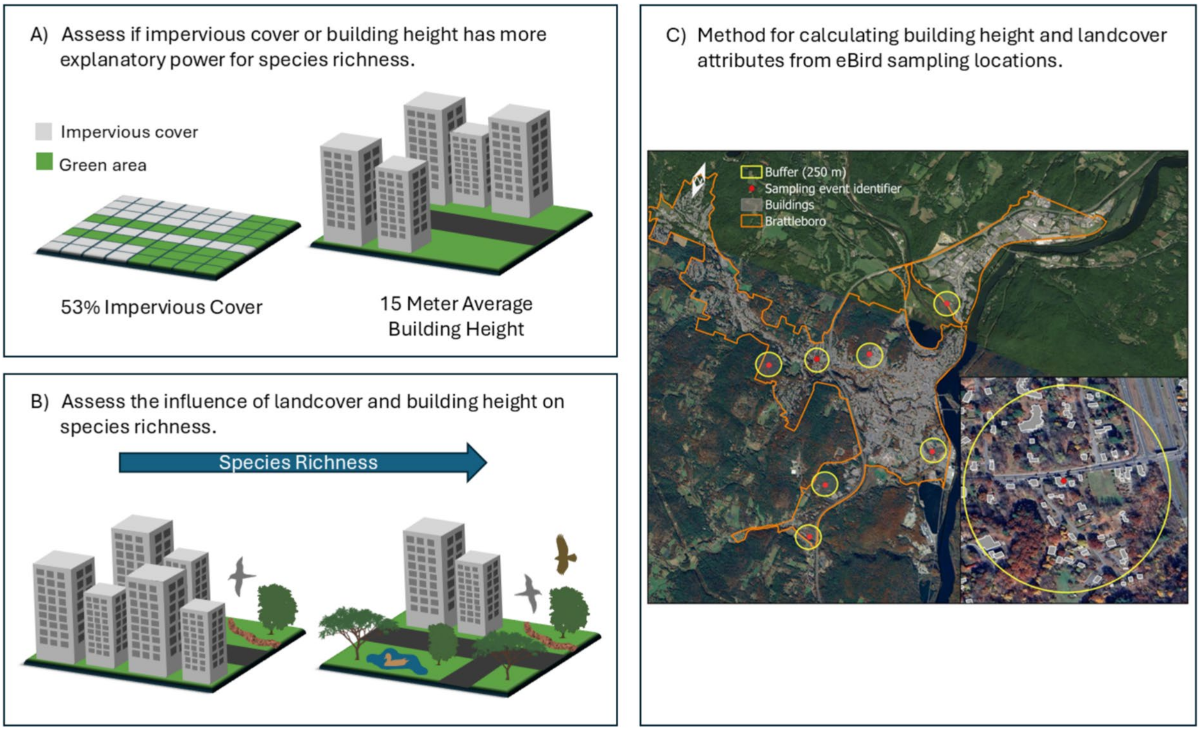

Fig. 2 Conceptual diagram of paper objectives and methods. **A** Explanatory power of building height and impervious cover on bird richness. **B** Hypothetical expectations of species richness response to mean building height. **C** Example of an urban area and one 250 m land cover buffer. Brattleboro, VT

as linear terms based on data exploration (Supplementary Material Fig. A4) and previous research (Souza et al. 2019). For objective one seven models were evaluated for each city (1) building height, (2) impervious cover, (3) NDVI, (4) building height and impervious cover, (5) building height and NDVI, (6) impervious Cover and NDVI, and (7) building height, impervious Cover and NDVI.

For the second objective, we used model percent impervious cover and mean building height to assess the impacts of building height in conjunction with seven predictor variables—water, bare, trees, grass, impervious cover, shrub and scrub, and NDVI—on urban bird richness. This approach allows for the evaluation of how the vertical structure of cities, together with the composition of different land cover types, influences bird communities across urban environments.

For both objectives, GAMs were fitted using the mgcv package in R (Wood 2011). To design the model for each city, we first ran model tests using data from all cities and then tested the model on randomly selected cities. To avoid multicollinearity, we assessed correlations among all predictor variables using a correlation matrix (Supplementary Material Fig. A5), and found no concerning correlations, including between impervious cover and building height ($r = -0.21$, $p\text{-value} < 0.001$). Although statistically significant, the weak correlation indicates both variables can be included in the same GAM (Zhao et al. 2014).

For the second objective, we created a model with the predictor variables built, impervious cover, bare, grass, shrub and scrub, water, tree cover, and NDVI. These variables were included as linear terms in the model, as they are expected to have a linear relationship with species richness based on data exploration (Supplementary Material Fig. A4) and previous research (Souza et al. 2019). We incorporated smooth terms for survey duration using a cubic regression spline with a basis dimension of 20, and for geographic coordinates using a two-dimensional thin plate spline with a basis dimension of 50 (Wood 2003). These basis dimensions were selected based on model testing, during which we evaluated the effective degrees of freedom. The values differ from those used in the first objective to accommodate the increased model complexity resulting from the inclusion of additional predictor variables. Modeling these predictors linearly also facilitates direct comparison of coefficient estimates across cities.

Our response variable, species richness, was positively skewed for most cities, so we specified a Gamma distribution and a log link function in the GAM. The models were fitted using Restricted Maximum Likelihood (REML) estimation, as recommended by Wood (2004). We used the *gam.check* function from the *mgcv* package (Wood 2011), on data from all cities and randomly selected cities, to test key assumptions, including the basis dimensions selection, residual distribution, and independence of residuals. In all cases, our distribution selection met model assumptions.

Model performance was evaluated using model weight because it balances model fit and complexity, which was calculated by comparing the three models for each city based on the Akaike Information Criterion (AIC). Because model weights within each model were non-normally distributed, we used the Pairwise Wilcoxon Rank Sum Test to compare the distribution of model weights. For objective 2, we compared the model estimates and p-value by city using a t-test. We additionally conducted a supplemental analysis by replacing mean building height in the model with the standard deviation of building height, to test whether a greater mix of short and tall buildings was similarly related to total richness. We expected a similar result because mean building height and the standard deviation of building height were moderately correlated (Pearson's $r = 0.54$). For both objectives, we compared model results by ecoregion as this may influence the relationship between species richness and landscape variables.

Data analysis and availability

Relevant code and data necessary to reproduce these analyses are available here: https://doi.org/10.5281/zenodo.17436509.

Results

We had 298 cities that met our criteria for inclusion. In these cities, there were a total of 1,063,603 bird checklists. We found that building height showed little variability between checklists (mean = 4.8 ± 0.7 SD m; Supplementary Material Fig. A6).

Objective 1: impact of building height on bird species richness

Of the 298 cities, 10.4% indicated that the model with only impervious cover information was the best model, 10.7% for building height, 12.4% for NDVI, 11.4% for the combination of building height and impervious cover, 19.5% for the combination of impervious cover and NDVI, and 25.8% for the model with building height, impervious cover, and NDVI. The analysis revealed varying patterns across cities, with different models performing best in different cities.

The best-performing models for each city, determined by the lowest AIC values, showed deviance explained values ranging from 0.07 to 0.64 (mean = 0.31), indicating substantial variation in the explanatory power of urban structure variables for bird species richness (Fig. 3; Supplementary Material Fig. A7). When comparing the difference between the deviance explained in the lowest performing model compared to the best performing model for each city, we found that it ranged from 0.0001 to 0.07 (median = 0.007). This indicates that the choice of urban structure variables does not have a strong influence on the deviance explained.

Based on Wilcoxon tests, we found that all models were significantly different from one another, with two exceptions: there was no evidence of a difference between the NDVI-only model and the impervious cover-only model ($p = 0.635$), and no evidence of a difference between the NDVI + building height model and the impervious cover + building height model ($p = 0.561$). Full pairwise comparisons are provided in Supplementary Table A1. For the models with a single predictor variable, we found strong evidence that the average model weight of the building height-only model was lower than that of the impervious cover-only model and the NDVI-only model.

In all cases, we found very strong evidence that the combined models outperformed the single-variable

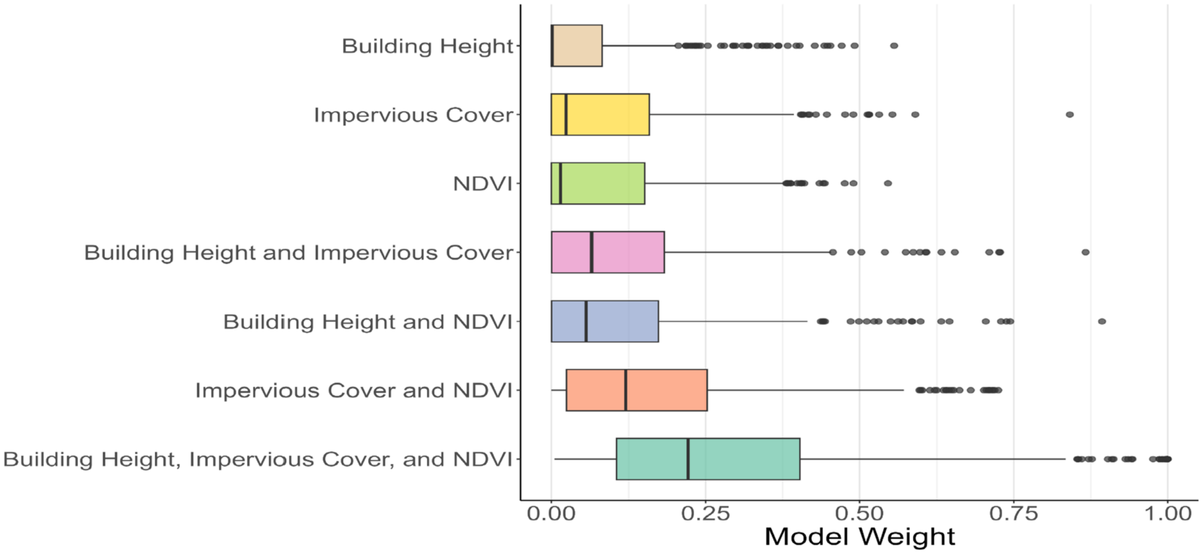

Fig. 3 Boxplot of model weights for 298 cities, calculated using a Generalized Additive Model, comparing seven model types where species richness is the response variable. The y-axis indicates all combinations of predictor variables tested. Pairwise Wilcoxon tests indicate that, with two exceptions, all models are significantly different from one another. To see the distribution of model weights, see Supplementary Material Fig. A8

models. Specifically, we found very strong evidence that the impervious cover + NDVI model had a higher average model weight than both the impervious cover + building height model and the NDVI + building height model. Finally, we found very strong evidence that the model including all three urban structure variables—building height, impervious cover, and NDVI—had the highest average model weight (Mean = 0.320, SE = 0.017) compared to all other models ($p < 0.001$ for all comparisons). In a supplementary analysis where we compared model weights for each ecoregion, we found similar trends (Supplementary Material Fig. A8).

Objective 2: drivers of bird diversity within cities

From the 298 GAM models calculated for each city, we examined the percentage of cities with significant (p-value < 0.05) positive or negative trends for each variable. These results are presented in Table 1.

We used a t-test to assess whether there was an overall significant tendency for cities to exhibit positive or negative trends for each variable. We found no significant trends for bare, grass, trees, or impervious cover. However, we found strong evidence of a significant negative relationship between species richness and mean building height (Mean = −0.011, SE = 0.004; Fig. 4), and a significant positive relationship between species richness and NDVI (Mean = 0.019, SE = 0.007). Additionally, we found very strong evidence of a significant positive relationship between species richness and both scrub/shrub and water. We repeated this analysis using the standard deviation of building height, rather than the mean, to test whether a greater mix of short and tall buildings was similarly related to total richness (Supplementary Material Fig. A11). This analysis also

Table 1 Percentage of cities with significant (p-value < 0.05) positive or negative trends for eight predictor variables

	Negative trend − (%)	Positive trend + (%)
Mean building height	24.2	12.1
Impervious cover	22.8	20.8
NDVI	14.1	27.2
Trees	19.8	23.5
Water	14.1	27.2
Shrub and scrub	13.4	34.2
Grass	19.8	17.1
Bare	27.9	14.8

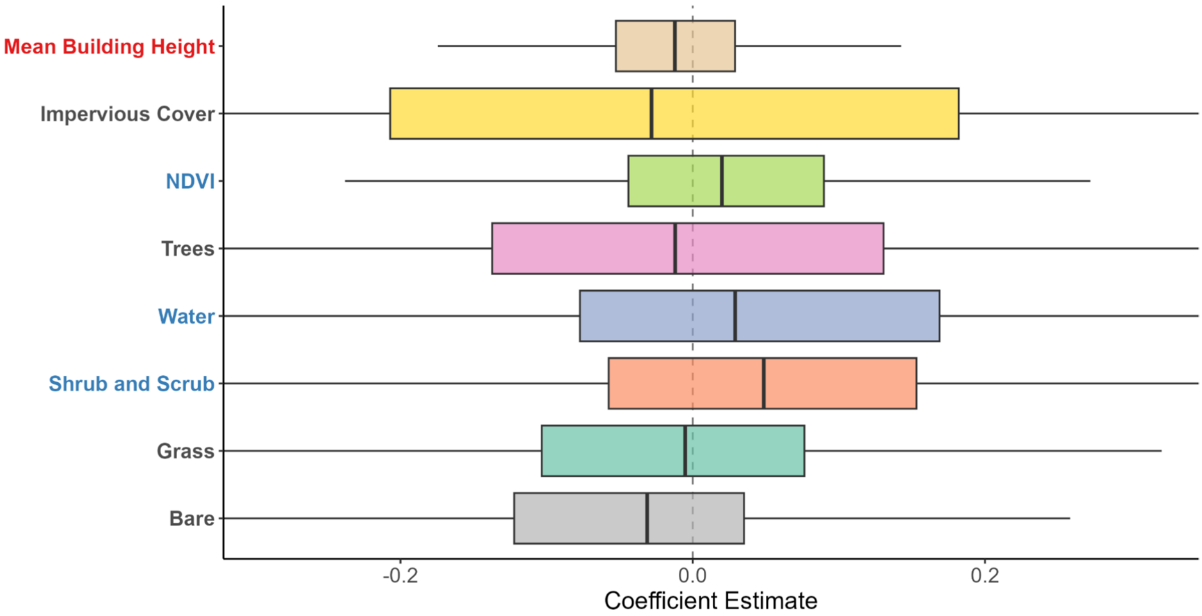

Fig. 4 Coefficient estimates from Generalized Additive Models fit for 298 cities where species richness is the response and predictor variables include bare, grass, shrub and scrub, water, trees, impervious cover, and mean building height variables. The color of the y-axis labels indicates whether the mean coefficient estimate was significantly different from zero: blue represents significantly positive trends, while red indicates significantly negative trends. For this visualization, 188 outliers above coefficient estimate were excluded. To see the plot with outliers see Supplementary Material Fig. A10

revealed a negative relationship between total richness and building height variability (Mean = -0.016, SE = 0.005, $p < 0.005$).

We additionally examined whether these trends varied by ecoregion (Fig. 5). The number of cities per ecoregion ranged from 9 to 79, limiting statistical power in some cases. Nevertheless, we found several significant relationships. In the Western Cordillera, we found moderate evidence of a negative relationship between species richness and bare area. There was strong evidence that shrub and scrub cover was positively associated with species richness in both the Marine West Coast Forest and the Mixed Wood Plains. For water cover, we found moderate evidence of a positive relationship with species richness in the Cold Deserts and strong evidence of a positive relationship with species richness in the Central USA Plains. In Mediterranean California, there was moderate evidence that NDVI was positively associated with species richness.

We also found moderate evidence of a negative relationship between impervious cover and species richness in the Mississippi Alluvial and Southeast USA Coastal Plains. Finally, mean building height showed contrasting relationships: moderate evidence of a negative association in the Mixed Wood Plains and moderate evidence of a positive association in the Ozark/Ouachita–Appalachian Forests. All other ecoregion–landscape variable combinations were not significantly different from zero, through limited sample sizes (≤cities in all but one ecoregion) many have reduced statistical power to detect additional trends.

Discussion

The impact of building height on bird species richness

Using > 1 million eBird checklists from 298 urban areas across the United States, we found strong evidence that the model including all three urban structure variables—building height, impervious cover, and NDVI—had the highest average model weight compared to the other models. Building height alone was the best predictor in 10.7% of cities. Pena et al. (2023) similarly found that building height is an important predictor variable; specifically, average

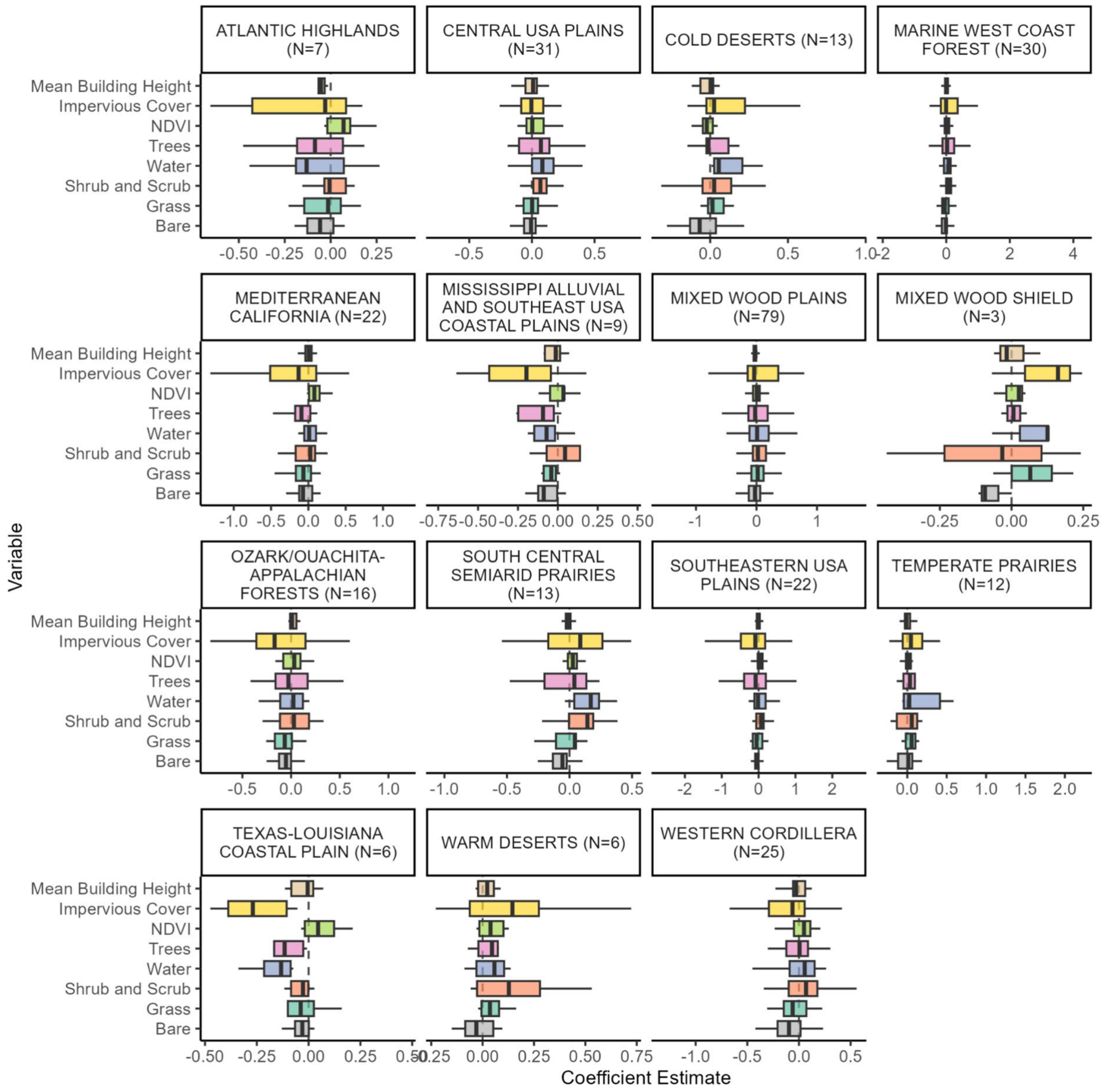

Fig. 5 Coefficient estimates from Generalized Additive Models fit for 298 cities and grouped by ecoregion, where species richness is the response and predictor variables include bare, grass, shrub and scrub, water, trees, impervious cover, NDVI and mean building height predictor variables. The number of cities in each ecoregion is provided in the individual plot titles

building height accounted for 16.6% of the variation in species occurrences in their study, which was conducted in a Brazilian metropolis. Our analysis extends this perspective by testing building heights across 298 cities in the USA. Impervious cover alone performed best in 10.4%, and NDVI in 12.4%. This finding demonstrates the complex nature of urban environments and their impact on bird species richness. The fact that building height improved the model in the first objective of our study highlights its relevance.

Our research incorporated building height information, which helped to enrich models of bird species richness in urban areas, providing a more comprehensive understanding of habitat availability and the effects of urban structure. In areas where land cover data is partial or unavailable, building height serves as a proxy to infer urban structure characteristics, although its effectiveness depends on the specificities of urban contexts. Mean building height showed contrasting relationships—a negative association in the Mixed Wood Plains and a positive association in the Ozark/Ouachita–Appalachian Forests. This suggests that while building height may not be a universal predictor of species richness across all urban environments, it should be considered as an important variable in some ecoregions.

Drivers of bird diversity within cities

Our examination with the eight predictor variables corresponds to earlier studies emphasizing that land cover is a fundamental driver of urban biodiversity (Cristaldi et al. 2023; Zhao et al. 2023). The strong positive association of shrubs and scrub (34.2% of cities showing a significant positive trend), followed by NDVI and water (with 27.2% both), suggests that green and blue infrastructure plays a crucial role in maintaining avian diversity in cities. This result is not surprising, as shrub cover has been positively correlated with bird species richness in several studies (Ortega-Álvarez and MacGregor-Fors 2009; MacGregor-Fors and Schondube, 2011; Mühlbauer et al. 2025). This aligns too with previous research highlighting the importance of heterogeneous green spaces in providing food, shelter, and nesting opportunities for urban bird communities (Threlfall et al. 2017; Wang et al. 2017; Aznarez et al. 2022).

Our findings reinforce the well-documented negative impact of urbanization on biodiversity (Belcher et al. 2019; Benedetti et al. 2023; Kroc et al. 2024). Bare areas, typically associated with highly urbanized environments, were generally linked to lower species richness. Although the median coverage of bare areas across sites was relatively low (5%), these zones were often cleared, intensively managed urban spaces (e.g., sports fields as observed in Google Earth) lacking vegetation structure. Such conditions likely limit their suitability for bird communities. Therefore, the observed negative association is ecologically plausible, despite the potential for model overfitting in large datasets. We found that the effects of urbanization on bird communities are highly context dependent. The wide range of deviance explained values (0.07–0.64) further supports this heterogeneity, indicating that while urban structure plays a role, its influence varies considerably across different urban landscapes (Fig. 3; Supplementary Material Fig. A8). In particular, the mixed effects observed across cities with trees and impervious cover (see Table 1) indicate that the influence of these features varies geographically.

The results of Objective 2 varied by ecoregion, highlighting distinct ecological influences on species richness. Factors such as climate, building characteristics (Morelli et al. 2021; Buenaño et al. 2023; Leveau 2025) and local species composition are likely to interact with green space characteristics to modulate avian diversity patterns. Sample sizes varied across ecoregions (9 to 79 cities), limiting statistical power in some cases. Nonetheless, these results provide meaningful insight into geographic variation in bird responses to landscape characteristics. While mean building height had a relatively low impact on species richness compared to land cover variables overall, its significant effect in a substantial number of cities suggests that it represents a structural dimension of the urban landscape distinct from vegetation and impervious cover. Moreover, in certain urban contexts, buildings may provide resources or conditions that benefit specific species, particularly those adapted to urban environments (Mak et al. 2021; Sarkar and Bhadra 2022; Buenaño-Mariño et al. 2025).

Limitations and future work

The limited variability in building height data represents a constraint on our models—most of the building height data was between 2 and 3 stories (calculated by dividing building height by 2.74 m, or 9 ft., as the average floor-to-floor height; mean = 4.8 ± 0.7 SD m; Supplementary Material Fig. A6). Even when examining maximum building height within buffers, we found the mean to be 8.7 ± 3.1 m. Moreover, the distribution of building height is significantly skewed, with relatively few instances of taller buildings. Additionally, our analysis is currently restricted by the availability of building height data (e.g., resulting in sparser coverage in the southern US). As more comprehensive height datasets become available through open access repositories, future large-scale studies will greatly benefit. These limitations could mean that the effects of building height on species richness are potentially underestimated, particularly in areas with taller buildings.

Additionally, biases in the eBird dataset may exacerbate this issue, as users tend to sample more frequently in areas with higher green space and are less likely to survey locations dominated by tall buildings (Grade et al. 2022). Given that areas with tall buildings were relatively underrepresented in our dataset, future research could specifically target the influence of building height on species richness and determine at what threshold average building height becomes a more significant factor. This could be achieved through targeted sampling or the use of alternative datasets with greater building height variability. To mitigate these limitations, we recommend carefully assessing the distribution of building height data prior to conducting statistical analyses, thereby addressing potential biases arising from data skewness. Another limitation of our study related to the eBird dataset is that we used the entire temporal window without distinguishing between resident and migratory species. While this approach is consistent with previous studies (Belcher et al. 2019; Benedetti et al. 2023; Hao et al. 2024), it may obscure seasonal or migratory patterns and the specific drivers of species richness associated with different periods or bird groups. Future research should address these aspects by applying temporal filters or analyzing resident and migratory species separately, which would allow for a more detailed understanding of the ecological processes influencing avian diversity throughout the year.

Conclusions

The inclusion of building height in urban bird diversity studies provides determinant insights into the vertical dimension of urban habitats analysis; a factor largely overlooked in previous research (Wang et al. 2017; Lee et al. 2019; Mikami et al. 2022). This vertical component likely captures key ecological drivers, such as nesting opportunities and predator avoidance (MacGregor-Fors and Schondube, 2011; Mikami et al. 2022). Our results indicate that incorporating building height alongside traditional urbanization metrics significantly enhances our understanding of avian diversity patterns in cities. The varying influence of vegetation types, water bodies, and bare ground across cities highlights the context-dependent nature of urban ecology. Interestingly, while urbanization features like building height often showed negative associations with species richness, the effects were not uniform across all urban contexts, suggesting that the impact of urbanization on bird diversity is complex and multifaceted. Rather than proposing building height as the sole predictor of species richness, we introduce it as a complementary explanatory variable that warrants further exploration.

Author contributions All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by BMM, JBH, CTC, and CdPBM. The first draft of the manuscript was written by CdPBM, BMM, and JBH. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability Relevant code and data necessary to reproduce these analyses are available here: https://doi.org/10.5281/zenodo.17436509.

Declarations

Conflict of interest The authors declare no competing interests.

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