

Research Paper

Historical park planning is associated with modern-day patterns of bird diversity in cities

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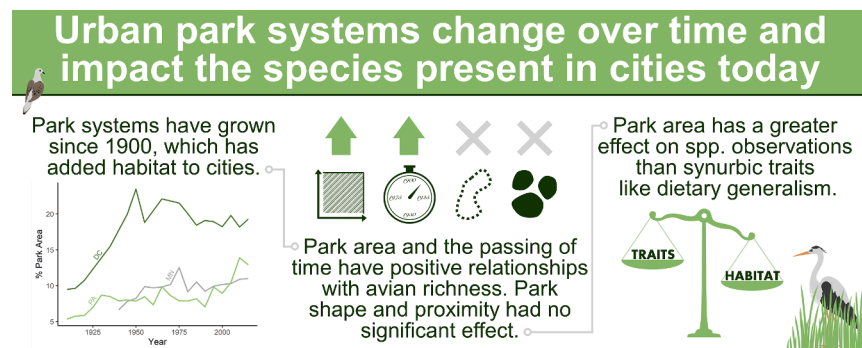
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HIGHLIGHTS

- Parks make up a large proportion of habitat available to wildlife in urban areas.
- Historical planning decisions have shaped the size, total amount, and configuration of urban green spaces.
- Green space area had a positive association with avian diversity metrics.
- Green space shape and connectivity also impacted biodiversity but with mixed results and to a lesser extent.
- Urban planners can support urban biodiversity by adding and preserving green space.

GRAPHICAL ABSTRACT



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ABSTRACT

Land use planning directly governs the location, size, and shape of urban parks, which can act as habitat refuges for wildlife. Thus, land use planning decisions made decades, or even centuries, ago likely affects modern day habitat availability for wildlife in cities. We sought to understand the role of these historical decisions on avian diversity between 1900 and 2020 to inform future biophilic urban planning efforts. We digitized historical maps of three mid-sized temperate U.S. cities — Washington (DC), Minneapolis (MN) and Pittsburg (PA) — in five-year increments between 1900 and 2020, and calculated landscape metrics of each city's park system over time. Historical Christmas Bird Count data in each city were used to estimate species and functional diversity metrics over the same 120-year period as a function of historical landscape metrics. Our results lend further support to the species-area relationship, as total greenspace area had the greatest positive relationship with species richness, functional divergence, and observations of species in different functional groups. Greenspace shape and connectivity also influenced some biodiversity metrics, but to a lesser degree than greenspace area. These findings demonstrate that historical land use decisions have a strong influence on the modern-day patterns of avian diversity in urban areas, which may help explain apparent differences in species assemblages across otherwise similar cities. As such, we suggest cities prioritize the establishment and protection of greenspaces to ensure lasting conservation of species across urban landscapes.

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1. Introduction

Urbanization acts as a filter such that some wildlife species adapt to urban living with relative ease while others face substantial challenges and run the risk of extirpation (Aronson et al., 2016; McKinney & Lockwood, 1999). In general, the species which are well-adapted to urban environments tend to have lower body mass, less discriminate diets, and higher fecundity than rural-restricted species (Neate-Clegg et al., 2023; Rega-Brodsky et al., 2023; Santini et al., 2019). As a result, much of the existing literature on patterns of urban biodiversity argues that traits like these pre-dispose some species to urban living. Yet, while such traits are correlated with a species' urban adaptability (Evans et al., 2011; Kark et al., 2007; Santini et al., 2019; Weiss et al., 2023), the traits themselves are not the filters. Instead, life history traits interact with aspects of the urban environment in ways that encourage the success of some species and limit the success of others (Andersson & Colding, 2014; M. F. J. Aronson et al., 2016; Tratalos et al., 2007).

While ecological processes such as succession continue to take place in urban greenspaces, ultimately the form and composition of these spaces are the result of human-driven processes. For the purpose of our study, we define greenspace as a sanctioned park, cemetery, or golf course. Zoning and land use policies largely dictate the spatial organization of modern cities, including the placement of greenspaces (Twinnam, 2020). In this way, humans have directly shaped the availability of habitat across urban areas and implicitly established the resulting landscape-level filters which control species diversity (M. F. J. Aronson et al., 2016; E. M. Wood et al., 2023). Greenspace abundance, configuration, and management differ across cities, and thus may filter species differently (Fidino et al., 2021). The configuration of park systems, which account for much of the planned greenspace in cities, is dependent on local geography and history. While the role of geography is often considered when assessing the relationship between park systems and biodiversity, the influence of history has received considerably less attention (Foster et al., 2003; Norton et al., 2016).

In the United States, early post-colonial urban development embraced rectilinear street grids which facilitated concentrated development and subsequent overcrowding (Boeing, 2021; LaGrand, 2020; Loughran, 2020). The urban planning profession was created in response, and parks were formally introduced to urban landscapes to create a place for residents to relax outside of their homes (Brinkley & Vitiello, 2014; Loughran, 2020). Romanticization of spacious rural living prompted the creation of sprawling parks, such as Central Park in New York City, that resembled pastures rather than native ecosystems (Crawford, 1905; Gobster, 2007).

Public opinion shifted in the early 1900's to value thoughtful landscaping, which included increased planting of trees and maintenance of semi-natural landscapes (Freestone, 2011; LaGrand, 2020; Peterson, 1976; Szczygiel, 2003). At the same time, urban planners shifted away from designing networks of large isolated parks and instead focused on connected networks of smaller neighborhood parks that could be more easily accessed by residents (Crawford, 1905; Freestone, 2011; Ignatieva et al., 2011). Communities of color and low economic standing were both systematically excluded in the expansion of such systems, however, leading to disproportionate greenspace availability in wealthy white neighborhoods (Schell et al., 2020; E. M. Wood et al., 2023). Naturalistic conditions were restored to some parks during the environmental era of the 1960's and 70's through the deliberate reintroduction of native plant species (Daniels, 2009). Each of these historical developments incrementally contributed to the mosaic of semi-connected parks of varying size and management intensity typical of American cities today (Fig. 1).

Despite the clear relationship between historical land use planning and modern-day park systems, the extent to which these historical decisions impact modern patterns of species diversity is largely unknown (Ramalho & Hobbs, 2012). Our understanding of this phenomenon is limited, at least in part, because of the paucity of data required to explore such research questions. Historical land use is often poorly

documented, and few datasets chronicle trends in species diversity over long periods of time (Lister et al., 2011; Magurran et al., 2010). Fortunately, systematic long-term monitoring schemes exist for some taxa (e. g., Christmas Bird Counts) and can provide rare insight into historical dynamics (Magurran et al., 2010). Similarly, municipalities have been inadvertently documenting historical changes in their urban form via routine mapping. Although these maps were not intended to document iterative urban change, they can serve as an invaluable data source for contemporary scholars seeking to understand the consequences of historical decisions. As such, there are clear opportunities to explore the role of historical land use on biodiversity over time by joining these two data sources.

In this study we leverage archived bird surveys and municipal maps from three U.S. cities to perform a longitudinal assessment of the relationship between urban park configuration and avian diversity over the last 120 years. The three cities — Washington (DC), Minneapolis (MN), and Pittsburgh (PA) — share a similar development age (≥ 200 years old), area ($< 180 \text{ km}^2$), and human population density ($\sim 2,000\text{--}4,000$ people/ km^2 ; United States Census Bureau, 2020). Additionally, these cities all contain at least one large river, are not coastal cities, and experience seasonality (Lisovski et al., 2017). By investigating the role of historical land use and urban planning on avian diversity, we aim to increase our understanding of the mechanistic roles of urban form and avian traits in the formation of urban species assemblages. Specifically, we analyze the relationships that overall greenspace availability, shape, and connectivity have with avian diversity indices and the number of observations of species within specific functional groups between 1900 and 2020. Such knowledge can provide insight into biophilic urban design, which is becoming increasingly crucial in the face of unprecedented global urbanization and commensurate biodiversity loss (Collins et al., 2021; Garrard et al., 2018; Kay et al., 2022; Magle et al., 2012).

2. Methods

2.1. Study areas

2.1.1. Minneapolis, Minnesota (MN)

The city of Minneapolis was established in 1867 and was built over the Dakota village of *Héyáta Othúnjwe*, and the Dakota and Ojibwe homelands (Beane, 2014; K. Carlson & John, 2015; K. M. Carlson, 2012). Minneapolis was built to harness the power of the Mississippi River and, as such, land adjacent to the river was intensely developed for industrial use (Anfinson et al., 2003). Likewise, a comprehensive survey process resulted in a uniform street grid that left relatively little designated open space (Atwater, 1893). The Minneapolis Board of Park Commissioners was formed in 1883 and began preserving undeveloped land across the city (History of the Grand Rounds, 1999). The City's park system grew increasingly linear, however, as it became an early adopter of the greenway concept. The greenway eventually grew to encircle the City and became an early example of a successfully implemented greenway system (Fábos, 2004). In the 1980's and 90's, efforts began to remove invasive plants from parks and restore native vegetative communities (Ford, 2015; Friberg, 1998). Today, Minneapolis contains approximately 16.38 km^2 of protected greenspace managed by local, state, and federal agencies (Fig. 1).

2.1.2. Pittsburgh, Pennsylvania (PA)

The Lenape settlement of Shannopin's Town is known to have existed, and the Seneca village of Diondega is believed to have existed within the borders of modern-day Pittsburgh (Sipe, 1930; Swauger, 1977). The area was then developed by French military forces in the 1750's, followed by English then American military expansions (Sipe, 1930). The modern city of Pittsburgh grew up around the military fort with relatively little urban planning, and limited recreational greenspace was intentionally preserved. Instead, four of Pittsburgh's major parks were donated by philanthropists rather than planned by the

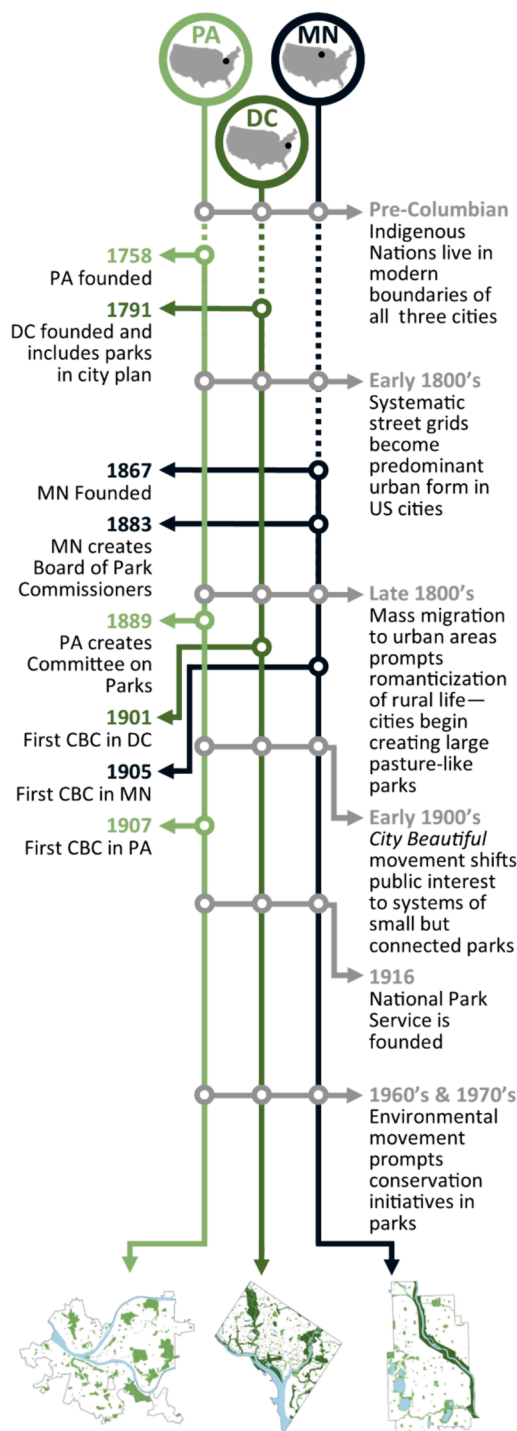


Fig. 1. Timeline of greenspace system development across Pittsburgh, PA (left), Washington, DC (center), and Minneapolis, MN (right). Dotted lines act as figure breaks and substitute for time periods too long to depict here. Colored hollow circles and arrows signify a city-specific development, whereas gray hollow circles and arrows signify a national trend which influenced all three cities. Maps in the top of the figure depict the location of each city within the contiguous USA. Maps in the bottom of the figure depict the current system of greenspace. Light green polygons represent locally managed greenspaces, whereas dark green polygons represent federally managed greenspaces. Blue polygons represent open water. Acronyms used in the figure are as follows: Pittsburgh, Pennsylvania (PA), Washington, DC (DC), Minneapolis, Minnesota (MN), United States of America (US), Christmas Bird Count (CBC). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

municipality (Pittsburgh Department of City Planning, 2012). The Pittsburgh Committee on Parks was established in 1889 and, already having a handful of spacious parks, devoted its efforts to developing smaller neighborhood parks (Freestone, 2011; Maxwell, 1985). Compared to other US cities, Pittsburgh was an early adopter of conservation-oriented park management and completed its first ecological assessment in 1947 (Maxwell, 1985). The City adopted its first comprehensive plan in 2013 and is now committed to connecting its previously isolated greenspaces via a planned network of green ways (Pittsburgh Department of City Planning, 2013). Today, the city contains 19.51 km² of protected greenspace managed by local and state agencies (Fig. 1).

2.1.3. Washington, District of Columbia (DC)

The city of Washington was built over Nacotchtank, the city and agricultural lands of the Anacostan People (Burr, 1920; R. L. Humphrey & Chambers, 1977; McFadden-Resper & Williams, 2005). The modern city's street system was intentionally planned to include both rectilinear and diagonal streets whose intersections would form triangular parcels which, alongside rectangular plazas and the National Mall, created an early park system (Berg, 2008; Schroder, 2021). While the rest of the country was developing small and manicured neighborhood parks, congress authorized the preservation of a 7.1 km² park through the center of Washington which bore a unique mandate that its native flora be preserved (Rock Creek Park Enabling Act, 1890; Carruthers et al., 2009). In 1901, Congress commissioned a study of the city's park system which ultimately resulted in an enlargement of the National Mall and established a plan to create a greenway system connecting the abandoned Civil War battlements (Finnigan, 2012; Hines, 1991; Peterson, 1976; Vernon, 2014; Witt, 2005). The greenway was never completed, but the parcels acquired for the plan remain as parks today (Finnigan, 2012). While Washington began systematically considering the ecological state of its parks in the 1960's, many remain dominated by non-native manicured vegetation (Capital Space: A Park System for the Nation's Capital, 2010; The Nation's Capital: Policies Plan for the Year, 2000, 1961). Currently, Washington contains approximately 34.2 km² of protected greenspace managed by local and federal agencies (Fig. 1).

2.2. Historic landscape and independent variables

We obtained park system maps between 1900 and 2019 for Washington (DC), Pittsburgh (PA), and Minneapolis (MD) from historical archives, libraries, and online databases (Supplemental Material 2). A single park system map was obtained for every five-year period for each city and was assumed to be representative of the park system during this timeframe. When multiple maps were available for the same city during the same period, the map with higher resolution (digital) or smaller scale (print) was selected to obtain the most accurate park shapes. We scanned and imported maps to ArcMap 10.8 (ESRI, 380 New York Street, Redlands, CA 92373). Once imported, author DH overlaid historical city maps on the current street grid of each respective city and georeferenced the historical map using major intersections that existed over the entire study period. Once georeferenced, the greenspaces were digitized by manually drawing polygons over land that was identified as park space, cemeteries, golf courses, and all other public lands (Fig. 2). Military bases and educational campus were not included as greenspaces as they were not consistently labeled over the years. Individual structures within these lands were not always represented and are thus not identified in this dataset. Similarly, because some maps did not depict street width, all parks with a linear orientation that were bisected by streets were drawn as if the street was not present and the park was continuous.

We imported completed park shapefiles into v 4.2.2 of R (R Core Team, 2021) and converted polygons to 20 × 20 m rasters with the 'sf' and 'raster' packages (Fig. 2; Hijmans, 2023; Pebesma, 2018). We used a 20 × 20 m resolution for two reasons. First, larger resolutions are not sufficient to detect changes in urban park systems over time (Qian et al.,

2015). Second, the varying resolutions of historical landscape data may bias year-to-year changes in metrics due to varying degrees of cartographic detail indicating changes in greenspace shape which were actually present in previous years but not documented under a coarser scale. Although we included any park that was depicted in our historical maps, we were beholden to the inclusion criteria of the cartographers of the era, and thus cannot report a consistent minimum mapping unit. We used the ‘landscapemetrics’ package (Hesselbarth et al., 2019) to calculate various landscape metrics which described the total area of greenspace and average shape and connectivity of patches within each city during each time period (Table 1). Pair-wise Pearson correlation coefficients were calculated for all variables, and variables with $r \geq |0.70|$ were removed (Wei & Simko, 2021). After removing colinear landscape variables, the following variables remained: proportion of the city which is greenspace, representing habitat availability; mean greenspace edge-interior ratio, representing the edge-effect imposed by complexity of shape; and clumpiness index of greenspaces, representing habitat connectivity.

To control for additional factors that may impact avian diversity, we included survey year to reflect the passing of time (Fernández-Juricic, 2000; Nielsen et al., 2014), human population density (Fontana et al., 2011; Gagné et al., 2016), and mean winter temperature (Lehikoinen et al., 2016; Reif et al., 2010) as continuous variables. Human population density was calculated by dividing each city’s population by its area using data from the U.S. Census Bureau archives (specific publications are listed in Supplemental Material 2). Because the U.S. census is only conducted every ten years, no census records existed for survey periods which did not include a decadal year (e.g., 1945–1949). In these instances, we averaged the census counts before and after the survey. We used mean winter temperature to align with our bird survey data. Mean winter temperature was calculated by taking the mean daily temperature between the months of December through February of all weather stations within a 50-km buffer of each city center. Temperature readings were obtained using the ‘rnoaa’ package (Chamberlain, 2023) and were averaged so a single value was representative of each five-year survey period’s mean winter temperature.

2.3. Historical bird diversity

We queried historical bird observations from Christmas Bird Count survey records (National Audubon Society, 2020). The Christmas Bird Count, an annual survey of birds between December 14 and January 5, has taken place in each city (at least intermittently) since 1901 (DC),

Table 1

Potential landscape variables considered for analysis. Traits were ultimately selected for parsimony and lack of collinearity.

Variable	Justification	Metric	Unit	Used in final analysis?
Area of greenspace	Species-area relationship states that spaces with more habitat area will support more species	Proportion of greenspace	percent	yes
		Greenspace area	m ²	no
		Mean greenspace area	m ²	no
Shape of greenspace	The <i>single-large or several-small</i> (SLOSS) debate suggests that intact systems will support more species than fragmented systems	Edge-interior ratio	unitless	yes
Configuration of greenspaces	Theory of island biogeography states that patches with greater connectivity (less isolation) will support more species	Clumpiness index	unitless	yes
		Mean nearest neighbor	m	no
		Effective mesh size	m ²	no

1907 (PA) and 1941 (MN). Christmas Bird Count records contain the number of individuals observed of each species detected during each survey year and the survey effort (people per survey). The Christmas Bird Count is volunteer-driven, and thus likely biased towards conspicuous species. Additionally, the survey is biased towards granivorous and frugivorous species, since insectivorous species migrate to warmer regions during the survey period. Likewise, Christmas Bird Count surveys occur within a 12-km radius of a center point, which expands the possibly surveyed area beyond the boundaries of our study cities. It is possible that our bird data, despite being centered in our study cities, contain records from neighboring suburbs whose landscape metrics are not captured in this analysis. Despite these limitations, the longevity of the Christmas Bird Count provides an invaluable record of resident bird species since 1900. Because surveys do not overlap in space, concurrent surveys from cities which contain multiple surveys were collapsed into a single dataset with combined effort. Similarly, we combined data from each annual survey within each five-year period to achieve city-specific cumulative species counts for every five-year period. The periods used to coalesce these surveys match those used in the collection of our

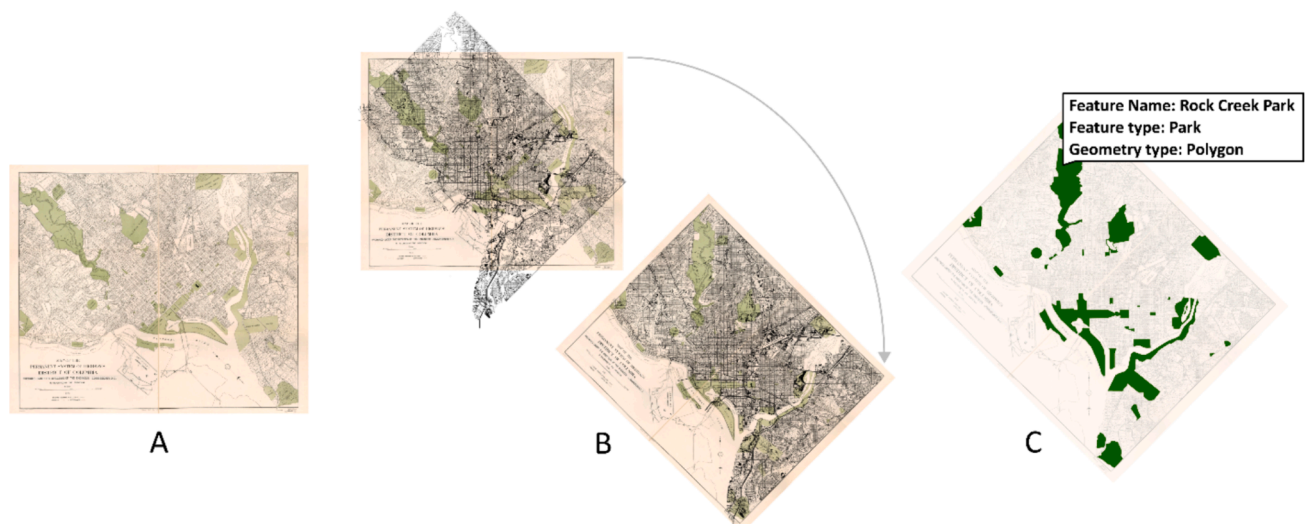


Fig. 2. Visualization of the map digitization process, including (A) obtaining the map, (B) georeferencing the map by aligning it with the current street grid, and (C) tracing each park to create a digital polygon shapefile. Map reprinted from the United States Library of Congress, Geography and Map Division.

historical maps.

While numerous diversity indices are available, we chose to use species richness, species diversity (Shannon-Wiener Index), functional richness, and functional divergence, which is an index of functional diversity and describes the dissimilarity of traits present in a community. We did not analyze species or functional evenness since this measure is already considered in measures of species diversity and functional divergence. While species richness and functional richness were positively correlated, we analyzed them separately to differentiate the impacts of our variables on various biological levels. Species richness was calculated by summing the number of unique species observed during each survey period in each city. Shannon's Diversity Index was calculated using the 'vegan' package (Oksanen et al., 2022). Functional richness and functional divergence were each calculated using the 'FD' package (Laliberté & Legendre, 2010). The 'FD' package uses continuous life history traits to compute functional indices in multidimensional space using a distance-based framework. Under this framework, functional richness is defined as the volume of the convex hull formed by the species' points in trait-space. Functional divergence, which represents the magnitude of dissimilarity of traits across the community, is contrived from the distribution of functional units in multi-dimensional trait-space irrespective of the number of dimensions (i.e., species and traits) of the community's total niche space (Laliberté & Legendre, 2010; Mouchet et al., 2010; Petchey & Gaston, 2002). We chose to use these measures of functional richness and divergence because they are not linearly correlated with species richness and do not require the arbitrary categorization of species into discrete functional groups. We used the following life history traits to calculate functional richness and divergence: diet breadth, foraging breadth, range size, body mass, and clutch size (trait justifications provided in Supplemental Material 3). Trait data was reported for each species in Wilman, et al. (2014) and Tobias and Pigot (2019), and was accessed using the 'traitdata' package (RS-eco, 2022). These traits were also used to categorize species into trait-specific functional groups to assess the dual roles of life history traits and environmental characteristics on species persistence. To do so, we first scaled all traits to have mean of 0 and standard deviation of 1 to allow for direct comparison of model results. Following this, we labeled any species whose trait value was within one standard deviation of the mean as having an average trait value. Species whose trait values differed from the mean trait value by more than one standard deviation were labelled as belonging to a functional group whose trait value is greater or less than average, respectively. This categorization resulted in three groups per functional trait: less than average (e.g., dietary specialists, small-ranged species, etc.), average, and greater than average (e.g., dietary generalists, large-ranged species, etc.). To create trait-specific survey data we summed observations of all species in each trait-specific functional group.

We accounted for variation in survey effort by including the number of Christmas Bird Count participants as an additional parameter in each model. Survey participants were summed across all surveys within each five-year period. When participant data was missing, the arithmetic mean of the nearest two surveys was used to impute this missing value. All independent variables were scaled by subtracting each value by the city-specific mean, then dividing by the dataset-wide standard deviation (Gallo et al., 2022).

2.4. Data analysis

We fitted a series of generalized linear mixed models in a Bayesian framework to assess how species richness, species diversity, functional richness, and functional divergence (dependent variables) varied as a function of the various covariates we calculated. Our models estimated each of these dependent variables as a function of survey year, survey effort, human population density, mean winter temperature, and all landscape metrics. Local species pools govern the species available, and differ between cities. We accounted for this in our models by including a

random intercept for each city. This approach allowed us to maintain the assumption that birds across all three cities share similar responses to our independent variables, but the intercept value for each dependent variable (e.g., species richness, functional divergence, etc.) differs between cities. We modeled species richness using Poisson regression because our data consisted of species count data, and used a linear model with the dependent variables logged to model species diversity and functional richness because our data consisted of positive non-integers. Functional divergence values were bounded between 0 and 1, which necessitated the use of a beta regression model.

We used the same model structure to model life history traits, but used the number of observations of individuals from each functional group as the dependent variable. Data from all three trait-specific functional groups (e.g., dietary specialist, average dietary breadth, and dietary generalist) were included in the same model with a categorical variable to identify the functional group each data point belonged to. We used the average group (e.g., average dietary breadth) as the reference category for this analysis, comparing the number of observations of birds from less than average and greater than average functional groups to the number of observations of birds with the average value for the respective functional trait.

We assigned each intercept term and all parameters vague normal priors with a mean of zero and a standard deviation of 1,000. Hyperpriors were similarly assigned the same vague normal priors when possible or were otherwise assigned uniform priors between 0 and 100 if the term was constrained to positive values (e.g., variance terms). Each model was fitted using the 'runjags' package (Denwood, 2016) and consisted of 4 MCMC chains of 500,000 iterations and a 250,000-iteration burn-in. To reduce autocorrelation within each chain, every fifth iteration was retained. Upon convergence, each MCMC chain's Gelman-Rubin statistic was checked to ensure it was less than 1.10, and each chain's traceplot was visually inspected for adequate mixing (Gelman et al., 2000). Additionally, a visual inspection of posterior predictive plots was made to ensure that estimated results generally matched those of the actual dataset indicating a proper model fit, and visual inspections of residual plots were made to ensure that residuals did not present obvious patterns such as regular oscillation, etc. (Kruschke, 2015). We considered a variable to have a significant effect if its 95 % credible interval did not overlap zero. Model diagnostics are available in Supplemental Material 4.

3. Results

Christmas Bird Count surveys during our time periods yielded a total of 4,555,450 observations of 235 species across a total of 268 survey years. Survey effort increased substantially in all three cities between the first and last survey period (DC = 7 – 905 people; MN = 22 – 328; PA = 7 – 806), and consequently so did the number of species (DC = 48 – 147 species; MN = 38 – 82; PA = 10 – 101) and individual birds observed (DC = 1,445 – 165,122 individuals; MN = 2,665 – 53,335; DC = 379 – 153,809). Most birds fell within 1 standard deviation of the mean for each functional trait (Table 2).

We obtained 22 historical landscape records for DC (18 maps, 4 shapefiles), 19 records for Minneapolis (10 maps, 9 shapefiles) and 16 records for Pittsburgh (14 maps, 2 shapefiles; Supplemental Material 2). Together, these yielded a sample size of 55 data points for models assessing diversity indices, and a minimum of 150 data points for each model assessing functional traits. Over time, all three cities increased their proportional park area (Figs. 3 & 4; DC = 9.48 % – 19.29 %; MN = 6.65 % – 11.01 %; PA = 5.35 % – 12.91 %). In addition to increased park area, parks in all three cities became more convoluted in shape (Fig. 4; DC = 0.05 – 0.11 change in edge-interior ratio; MN = 0.03 – 0.07; PA = 0.01 – 0.11) and more evenly distributed across the city (Fig. 4; DC = 0.97 – 0.90 change in clumpiness index; MN = 0.93 – 0.89; PA = 0.97 – 0.91). Washington and Minneapolis experienced warmer winters since the surveys began (DC = 1.75 – 3.87 °C; MN = –7.47 –

-6.98 °C), but Pittsburgh’s mean winter temperature has decreased (-0.23 – -0.72 °C).

3.1. Avian richness and diversity

Avian species richness was most strongly positively correlated with survey year ($\beta = 0.20$, 95 % BCI = 0.11 – 0.29), followed by greenspace area ($\beta = 0.18$, 95 % BCI = 0.10 – 0.27) and survey effort ($\beta = 0.12$, 95 % BCI = 0.04 – 0.19). Species richness was strongly negatively correlated with mean winter temperature ($\beta = -48.3$, 95 % BCI = -70.74 – -25.95). Credible intervals for greenspace edge-interior ratio ($\beta = 0.01$, 95 % BCI = -0.06 – 0.06), greenspace clumpiness ($\beta = 0.06$, 95 % BCI = -0.02 – 0.14), and human population density ($\beta = -5.08$, 95 % BCI = -13.28 – 3.19; Table 3) all contained zero. Intercept values — which indicate what each city’s dependent variable value would be if all independent variables were held at their mean value, here representing differences in each city’s unique initial species pool — were similar across the three cities, but were slightly higher in DC ($\beta_0 = 4.59$, 95 % BCI = 4.54 – 4.65) compared to Minneapolis ($\beta_0 = 4.23$, 95 % BCI = 4.16 – 4.30) and Pittsburgh ($\beta_0 = 4.02$, 95 % BCI = 3.97 – 4.08).

Shannon’s diversity index, which describes the degree to which species are evenly represented in the community by considering both species richness and evenness, was most strongly positively associated with human population density ($\beta = 15.56$, 95 % BCI = 5.09 – 25.93) followed by survey year ($\beta = 0.19$, 95 % BCI = 0.08 – 0.30). Diversity was negatively associated with greenspace area ($\beta = -0.15$, 95 % BCI = -0.27 – -0.02), greenspace edge-interior ratio ($\beta = -0.02$, 95 % BCI = -0.11 – 0.07), and clumpiness ($\beta = 0.06$, 95 % BCI = -0.05 – 0.17), mean winter temperature ($\beta = -11.34$, 95 % BCI = -38.95 – 16.56), and survey effort ($\beta = 0.07$, 95 % BCI = -0.02 – 0.16; Table 3) all had credible intervals which overlapped zero. Estimated intercepts were similar across all three cities (DC $\beta_0 = 0.87$, 95 % BCI = 0.81 – 0.94; MN $\beta_0 = 0.85$, 95 % BCI = 0.78 – 0.92; PA $\beta_0 = 0.85$, 95 % BCI = 0.80 – 0.90).

3.2. Functional richness and diversity

Avian functional richness, which represents the quantity of functional groups present in the community, was positively associated with survey year ($\beta = 0.81$, 95 % BCI = 0.34 – 0.1.28). Greenspace area ($\beta = -0.02$, 95 % BCI = -0.50 – 0.46; Fig. 5), edge-interior ratio ($\beta = 0.12$, 95 % BCI = -0.27 – 0.51), clumpiness ($\beta = 0.29$, 95 % BCI = -0.17 – 0.76), mean winter temperature ($\beta = -13.83$, 95 % BCI = -69.61, 34.64) and survey effort ($\beta = 0.07$, 95 % BCI = -0.34 – 0.47; Table 3) all contained zero in their 95 % credible intervals. Estimated intercepts

Table 2

Summary of functional trait groups for the 235 species detected during Christmas Bird Counts in Washington DC, Pittsburg, and Minneapolis between 1900 and 2019. Each species belongs to either the below-average, average, or above-average functional group for each of the five functional traits.

Trait	Mean value and standard deviation	Number of species with value lower than one standard deviation from mean	Number of species with value within one standard deviation from mean	Number of species with value greater than one standard deviation from mean
Diet breadth	2.85 (SD = 1.21)	28	186	18
Foraging breadth	2.19 (SD = 0.91)	51	163	18
Mass	605.46 (SD = 1350.23)	0	218	14
Clutch size	1.53 (SD = 0.42)	31	163	38
Home range size	15.73 (SD = 0.89)	29	166	37

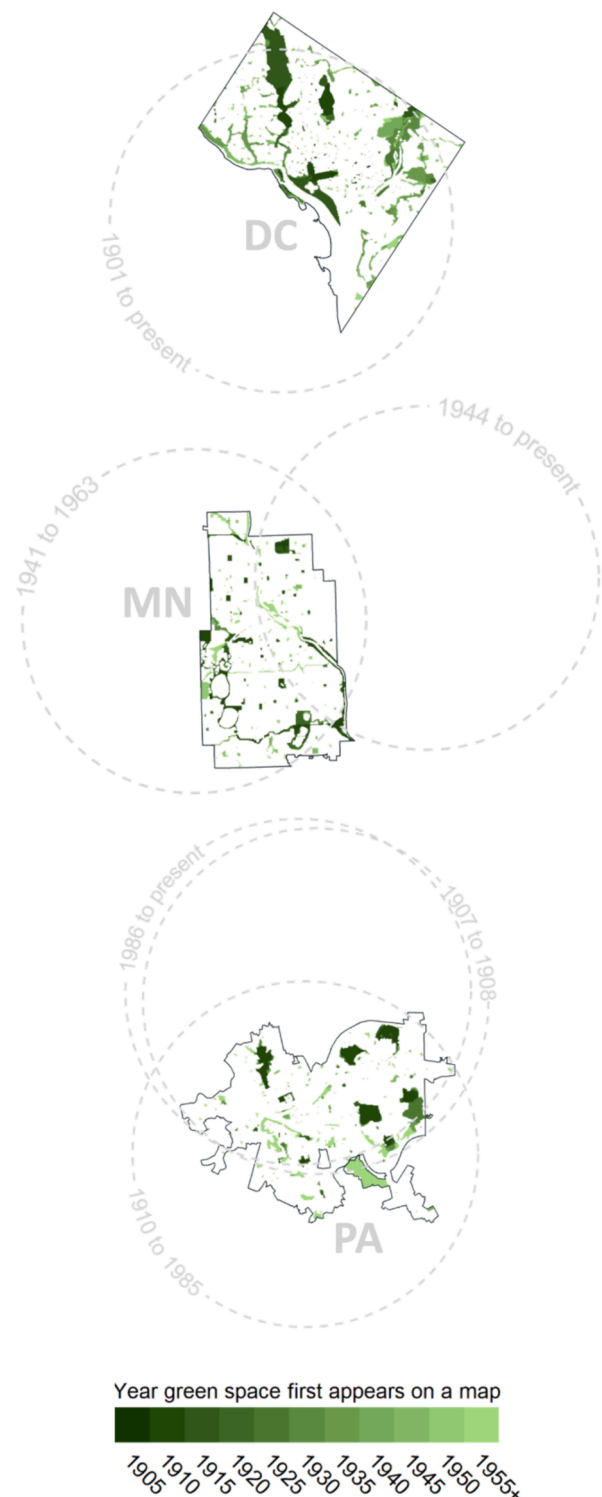


Fig. 3. Growth of park systems over time where a greenspace’s color represents the first year it appears on a map. Grey circles around the cities indicate the spatial extent of the bird surveys. Each survey circle has a radius of 12-km. Initials signify the District of Columbia (DC), Pittsburgh (PA) and Minneapolis (MN).

were similar, but highest for DC ($\beta_0 = 3.72$, 95 % BCI = 3.39 – 4.05) compared to Minneapolis ($\beta_0 = 3.47$, 95 % BCI = 3.13 – 3.82) and Pittsburgh ($\beta_0 = 2.90$, 95 % BCI = 2.64 – 3.17).

Functional divergence, which describes the variation in functional traits across the community, was positively associated with greenspace

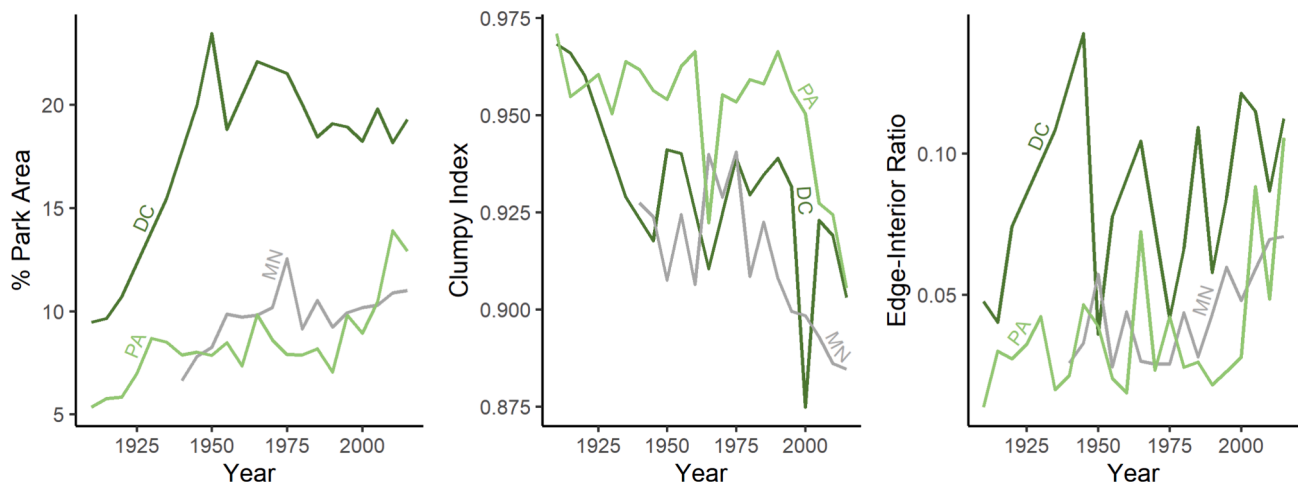


Fig. 4. Graphs of change in greenspace area, shape, and distribution over time. Initials signify the District of Columbia (DC), Pittsburgh (PA) and Minneapolis (MN).

Table 3

Parameter estimates and 95% credible intervals for models predicting diversity indices. Parameters whose credible intervals do not overlap zero are bolded.

Dependent variable	Parameter	Mean	95 % Credible Interval	
			Lower	Upper
Species richness	Percent park area	0.19	0.10	0.27
	Edge-interior ratio	0.01	-0.06	0.07
	Clumpiness index	0.06	-0.02	0.14
	Regional temperature	-48.35	-70.74	-25.95
	Population density	-5.08	-13.28	3.20
	Year	0.20	0.11	0.29
	Survey effort	0.16	0.04	0.19
Species diversity	Percent park area	0.87	0.81	0.94
	Edge-interior ratio	0.85	0.78	0.92
	Clumpiness index	0.85	0.80	0.90
	Regional temperature	-0.15	-0.27	-0.02
	Population density	-0.02	-0.11	0.07
	Year	0.06	-0.05	0.17
	Survey effort	-11.34	-38.95	16.56
Functional richness	Percent park area	3.72	3.39	4.05
	Edge-interior ratio	3.48	3.14	3.82
	Clumpiness index	2.90	2.64	3.17
	Regional temperature	-0.02	-0.50	0.46
	Population density	0.12	-0.27	0.51
	Year	0.29	-0.17	0.76
	Survey effort	-13.83	-69.61	42.14
Functional divergence	Percent park area	0.72	0.32	1.12
	Edge-interior ratio	0.03	-0.28	0.35
	Clumpiness index	0.01	-0.36	0.38
	Regional temperature	-21.75	-73.25	30.24
	Population density	-43.14	-72.58	-13.61
	Year	0.01	-0.34	0.36
	Survey effort	-0.23	-0.51	0.06

area ($\beta = 0.72$, 95 % BCI = 0.32 – 1.12; Fig. 5) and negatively associated with human population density ($\beta = -43.14$, 95 % BCI = -72.58 – -13.61). Greenspace edge-interior ratio ($\beta = 0.03$, 95 % BCI = -0.28 – 0.35) and clumpiness ($\beta = 0.01$, 95 % BCI = -0.36 – 0.38), mean winter temperature ($\beta = -21.75$, 95 % BCI = -73.25 – 30.24), survey year ($\beta = 0.01$, 95 % BCI = -0.34 – 0.36) and survey effort ($\beta = -0.23$, 95 % BCI = -0.51 – 0.06; Table 3) all had 95 % credible intervals which contained zero. The estimated intercept was highest in DC (mean = 1.88, 95 % BCI = 1.61 – 2.15), but values for Minneapolis (mean = 1.44, 95 % BCI = 1.20 – 1.69) and Pittsburgh (mean = 1.44, 95 % BCI = 1.25 – 1.62) were similar.

3.3. Life history traits

Regarding the life history models, model coefficients for non-trait variables were the same across all functional trait models (Table 4), and indicated a positive correlation, regardless of trait group, with greenspace area ($\beta = 0.72$, 95 % BCI = 0.722 – 0.727), survey year ($\beta = 0.42$, 95 % BCI = 0.419 – 0.425), survey effort ($\beta = 0.19$, 95 % BCI = 0.187 – 0.192), and park clumpiness ($\beta = 0.10$, 95 % BCI = 0.096 – 0.100), and a negative correlation with mean winter temperature ($\beta = -52.099$, 95 % BCI = -52.841 – -51.355), human population density ($\beta = -11.210$, 95 % BCI = -11.520 – -10.900), and edge-interior ratio ($\beta = -0.056$, 95 % BCI = -0.057 – -0.054; Table 4).

The analysis of dietary functional groups revealed a strong negative correlation between the number of observations of a species and both dietary specialization (*less than average group* $\beta = -4.558$, 95 % BCI = -4.570 – -4.545) and dietary generalization (*greater than average group* $\beta = -0.028$, 95 % BCI = -0.030 – -0.026), when compared against the average dietary breadth. Similarly, we were less likely to observe birds with either larger ($\beta = -2.851$, 95 % BCI = -2.855 – -2.847) or smaller ($\beta = -3.418$, 95 % BCI = -3.423 – -3.413) foraging breadths, relative to species with an average foraging breadth. Species with above-average dispersal capabilities were less likely to be observed ($\beta = -0.232$, 95 % BCI = -0.233 – -0.230), as were species with below-average dispersal capabilities ($\beta = -2.638$, 95 % BCI = -2.642 – -2.633). Birds with clutch sizes above ($\beta = -1.828$, 95 % BCI = -1.831 – -1.825) and below ($\beta = -1.356$, 95 % BCI = -1.359 – -1.354) the average clutch size were also less likely to be observed. Finally, species with greater than average body mass were less likely to be observed ($\beta = -2.899$, 95 % BCI = -2.903 – -2.895; Table 4) when compared to the average body mass. No birds had a body mass which was one standard deviation less than average.

4. Discussion

Cities, and the species which inhabit them, change over time as a function of urban planning and land use decisions (Dunn et al., 2022; Fahey et al., 2012; Fidino et al., 2022; Roman et al., 2018). Our analysis sought to understand how these land use decisions impact avian diversity in cities. Overall, we observed that increasing greenspace was associated with greater species richness and greater numbers of observations of birds regardless of their functional traits. Yet, while richness and abundance increased, the proportion of park area in a city was negatively correlated to species diversity, which indicates that some species disproportionately increased in abundance and drove species evenness down (La Sorte et al., 2023). Park connectivity and shape were also associated with abundance but the magnitudes of these

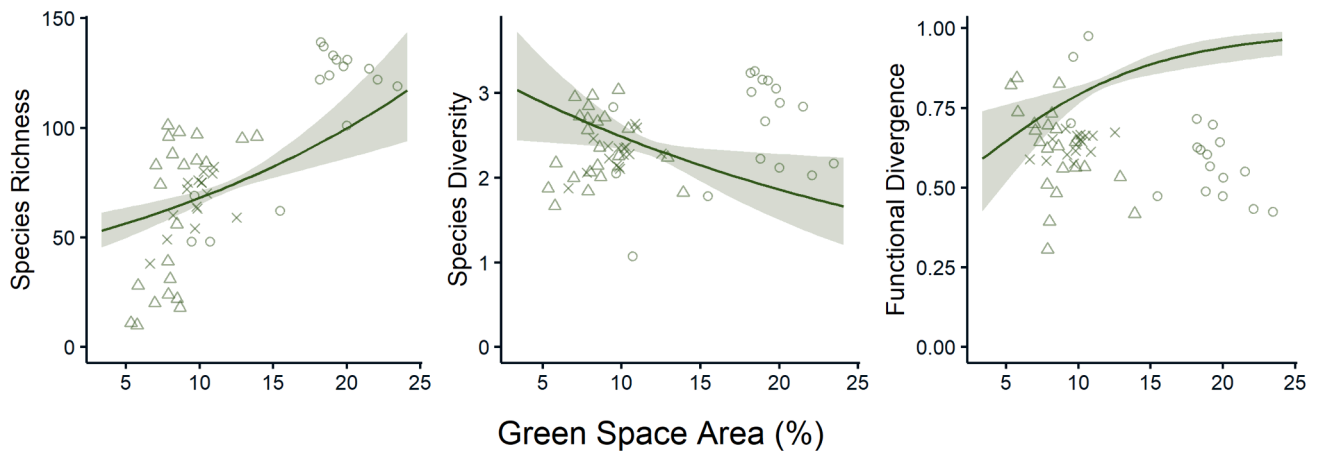


Fig. 5. Effect of proportional park area on species richness, species diversity, and functional divergence. Mean predicted value is depicted as a dark line, while 95% credible intervals are depicted as a shaded polygon. Points depict observed data from our three study cities, where circles represent data from Washington (DC), x's represent data from Minneapolis (MN), and triangles represent data from Pittsburgh (PA). Note that y-axes differ between graphs.

relationships were considerably less than that of park area. Likewise, park area had a larger effect than some functional traits, suggesting that habitat availability may filter even the most urban-adapted species. Because our findings corroborate the validity of the species-area relationship within urban areas (Nielsen et al., 2014; Rosenzweig & Ziv, 1999), we echo calls for continued creation and preservation of urban greenspace to achieve species conservation in cities (Apfelbeck et al., 2020; Garrard et al., 2018; Rosenzweig, 2003).

The species-area relationship posits that patches with greater area will contain a greater number of species compared to smaller patches (MacArthur & Wilson, 1967; Rosenzweig & Ziv, 1999; Williams, 1943). This concept similarly applies to urban habitats, indicating that cities with greater cumulative habitat will contain more species than cities with less cumulative habitat (Beninde et al., 2015; Davis & Glick, 1978; Dunn et al., 2022). The distribution of habitat within a city can further impact biodiversity, with systems comprised of fragmented and isolated patches tending to have lower biodiversity due to reductions in core habitat, genetic flow, and probability of recolonization after local extinction (Haddad et al., 2015; Nielsen et al., 2014). Habitat fragmentation, understood here as patch edge-interior ratio, and lack of connectivity between patches are common features of urban park systems and threaten urban biodiversity (Nielsen et al., 2014; Norton et al., 2016). However, our analyses revealed that park fragmentation and connectivity were not significant predictors of any avian diversity metric. Furthermore, the effect of total habitat area was notably larger than connectivity or fragmentation for all avian functional groups (7 and 12 times larger, respectively). These findings further support the notion that habitat availability, not configuration, drives urban avian assemblages (Dale, 2018).

While increasing overall park area had a positive correlation with species richness and functional divergence, our analysis revealed a negative correlation between park area and species diversity. Because diversity indices consider both richness and evenness, the addition of a low-abundance species will increase richness but lower diversity if the site is still dominated by individuals of only a few species (Morris et al., 2014). Furthermore, greenspaces vary widely in both form and function, and the species supported by greenspaces differ based on how the space is managed (M. F. Aronson et al., 2017; Gallo et al., 2017; Sandström et al., 2006). We suggest future studies explore species turnover and beta diversity in response to a changing park system to better understand changes in community composition over time (Fidino et al., 2022).

Particular traits (Evans et al., 2011; Santini et al., 2019), or flexibility within particular traits (Weiss et al., 2023) can pre-dispose a species for success in urban environments. Our findings support the notion that specific traits confer an advantage to some species and demonstrate that

species were observed less frequently if their traits deviated from the average trait value, even if the deviation is conventionally considered advantageous (e.g., dietary generalism). This is likely because the mean trait values in our analysis were derived from species assemblages that have endured generations of anthropogenic pressures and whose traits may already reflect urban optimality. In this way, our analysis supports previous claims that ideal trait combinations can contribute to urban exploitation. Our analysis further suggests, however, that such traits do not exclusively determine urban success.

Traits such as dietary generalism and large dispersal ability are generally considered helpful to species persistence in urban areas (Cove & Pease, 2021; Neate-Clegg et al., 2023; Pentead, 2021; Santini et al., 2019). Yet, we found these traits to be disadvantageous to birds and the strengths of effect for these traits ($\beta = -0.03$ and -0.23 , respectively) were less than that of greenspace area ($\beta = 0.72$), and for diet generalists, less than that of greenspace clumpiness ($\beta = 0.1$). These findings indicate that landscape features have an equal, if not greater, effect on filtering urban species compared to life history traits – further indicating that thoughtfully planned networks of urban greenspace have the potential to overcome inherent self-limiting factors for some species.

In addition to functional traits and landscape features, our findings emphasized the role of time in the formation of avian communities. Avian species richness and diversity, functional richness, and total observations of birds in every functional group each had a positive association with the survey year. One possible explanation for these phenomena is that the rise of environmental awareness has produced greater environmental regulations which have positively benefited bird communities (Taylor et al., 2005; K. A. Wood et al., 2019). Simultaneous increased survey efforts have also likely contributed to a larger, and thus more representative sample in later years, although this was controlled for in our analysis. An ecological explanation for the relationship between survey year and avian diversity and abundance is that habitats take decades to mature into a complex state that can support a greater breadth of ecological niches (Gilhen-Baker et al., 2022; Roman et al., 2017). Again, future studies should explore species turnover and beta diversity to identify any changes in species assemblages across time or seasons (e.g., La Sorte et al., 2023).

There are undoubtedly limitations to using historical bird data and historical maps. First, our historical park data relied on the judgments of cartographers, who depicted park systems to differing degrees of detail depending on the purpose of the map or their perceptions of the greenspace (Monmonier, 1991). Additionally, our model investigated changes in greenspace availability, but we could not assess greenspace composition or quality. Changes in landscaping trends or temporary repurposing of parks would likely impact wildlife communities, but

Table 4

Parameter estimates and 95% credible intervals for models predicting observations of individual from functional groups. Parameters whose credible intervals do not overlap zero are bolded.

Dependent variable	Parameter	Mean	95 % Credible Interval		
			Lower	Upper	
Functional group: clutch size	Percent park area	0.72	0.72	0.73	
	Edge-interior ratio	-0.06	-0.06	-0.05	
	Clumpiness index	0.10	0.10	0.10	
	Regional temperature	-52.10	-52.84	-51.36	
	Population density	-11.21	-11.52	-10.90	
	Year	0.42	0.42	0.42	
	Survey effort	0.19	0.19	0.19	
	Clutch size above the mean value	-1.83	-1.83	-1.83	
	Clutch size below the mean value	-1.36	-1.36	-1.35	
	Functional group: diet breadth	Percent park area	0.72	0.72	0.73
Edge-interior ratio		-0.06	-0.06	-0.05	
Clumpiness index		0.10	0.10	0.10	
Regional temperature		-52.10	-52.84	-51.36	
Population density		-11.21	-11.52	-10.90	
Year		0.42	0.42	0.43	
Survey effort		0.19	0.19	0.19	
Diet breadth above the mean value		-0.03	-0.03	-0.03	
Diet breadth below the mean value		-4.56	-4.57	-4.54	
Functional group: foraging breadth		Percent park area	0.72	0.72	0.73
	Edge-interior ratio	-0.06	-0.06	-0.05	
	Clumpiness index	0.10	0.10	0.10	
	Regional temperature	-52.10	-52.84	-51.36	
	Population density	-11.21	-11.52	-10.90	
	Year	0.42	0.42	0.42	
	Survey effort	0.19	0.19	0.19	
	Foraging breadth above the mean value	-2.85	-2.86	-2.85	
	Foraging breadth below the mean value	-3.42	-3.42	-3.41	
	Functional group: body mass	Percent park area	0.72	0.72	0.73
Edge-interior ratio		-0.06	-0.06	-0.05	
Clumpiness index		0.10	0.10	0.10	
Regional temperature		-52.10	-52.84	-51.35	
Population density		-11.21	-11.52	-10.90	
Year		0.42	0.42	0.42	
Survey effort		0.19	0.19	0.19	
Body mass above the mean value		-2.90	-2.90	-2.90	
Functional group: home range size		Percent park area	0.72	0.72	0.73
		Edge-interior ratio	-0.06	-0.06	-0.05
	Clumpiness index	0.10	0.10	0.10	
	Regional temperature	-52.10	-52.84	-51.36	
	Population density	-11.21	-11.52	-10.90	
	Year	0.42	0.42	0.42	
	Survey effort	0.19	0.19	0.19	
	Home range size above the mean value	-0.23	-0.23	-0.23	
	Home range size below the mean value	-2.64	-2.65	-2.63	

those changes were not reflected on maps of the era. Furthermore, our analysis assumed that designated greenspace was the only available urban habitat. This assumption is false, as birds regularly make use of private greenspaces, abandoned lots, etc. However, historical records offer little insight into the availability of privately-owned urban habitat and limit our ability to study the contribution of these habitat over time.

An additional constraint imposed by our historical data is that the Christmas Bird Count occurs during the winter and at a spatial scale larger than our study cities. Winter conditions in temperate regions greatly reduce resource availability, prompting many bird species to migrate in search of food. While supplemental resources and the urban heat island effect have encouraged some species to remain in cities through the winter (Bonnet-Lebrun et al., 2020), urban avian species

richness and functional divergence have still been found to decline in winter months (La Sorte et al., 2023). By using data collected in the winter, our dataset likely underrepresents species from functional groups which cannot sustain themselves in temperate winters such as insectivores. Furthermore, the tendency for some species to form larger flocks during the winter (e.g., South and Pruett-Jones, 2000) may increase their visibility to observers and cause them to be disproportionately represented in the data. However, these trends may not hold true in the less-temperate cities which host migrating birds or otherwise do not encourage seasonal flock behavior. Finally, Christmas Bird Counts take place within a circle with a ~ 12-km radius. While survey circles were approximately centered on each of our study cities, some observations were made from outside city boundaries and were influenced by neighboring landscapes that were not accounted for in our analysis. Despite these limitations, we believe that our approach provides strong insight into historical trends in urban biodiversity and the legacies of park planning.

Urbanization has contributed to substantial habitat degradation and destruction globally (Haddad et al., 2015; Liu et al., 2016). However, urbanization also has the potential to slow or reverse the global extinction crisis if cities are planned with conservation in mind (Ives et al., 2016; Soanes & Lentini, 2019). Research shows that urban form has consequences on biodiversity, and can thus be planned to accommodate human needs while minimizing habitat and species loss (Andersson & Colding, 2014; Lynch, 2019; Tratalos et al., 2007; J. E. Humphrey et al., 2023). We acknowledge that the establishment of large new nature reserves and corridors in urban areas are not likely, at least immediately. Rather, systems of preserved greenspace are more likely to grow incrementally as property becomes available (Qian et al., 2015). We recommend that urban planners do not discount this method of park system growth, as our analysis suggests that the total area of greenspace has a greater impact on the conservation of species than greenspace connectivity or fragmentation, and that the incremental growth of park systems in our study cities (mean growth of 0.16 km² per year) contributed to long-term gains in biodiversity. We do, however, still recommend that connectivity be maintained and fragmentation and edges minimized when possible – especially for the sake of species with lower dispersal abilities (Beninde et al., 2015; Elliot et al., 2014; Lynch, 2019). Similarly, it is important to recognize that cities are different from one another in form, and presumably function. As such, further investigations into landscape-level differences between cities may further illuminate mechanisms of urban biodiversity and contribute to biophilic cities.

5. Conclusions

Habitat availability in urban areas is dictated by human decisions, and is the product of the urban planning processes (Fahey et al., 2012; Roman et al., 2018). While some life-history traits clearly advantage certain species in urban areas, our analysis found that the physical landscape plays just as large a role in filtering species. Here, we demonstrate that urban planning decisions which maximize the area of greenspace will have an outsized effect on avian richness and diversity, with greenspace shape and connectivity having less of an effect. Although minimizing the edge-interior ratio and maintaining connectedness between greenspaces are of obvious importance, our results demonstrate that the addition of any greenspace will contribute to a biophilic city. Modern park systems are the manifestation of historical urban planning efforts that were meant to benefit humans but have inadvertently benefited wildlife. Contemporary urban planners can continue this legacy by expanding systems of greenspace to further serve humans and wildlife alike.

CRedit authorship contribution statement

Daniel J. Herrera: Writing – review & editing, Writing – original

draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Mason Fidino:** Writing – review & editing, Methodology, Formal analysis. **David Luther:** Writing – review & editing, Methodology. **Jennifer M. Mullinax:** Writing – review & editing, Methodology. **Travis Gallo:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization.

Data availability

Data available in data repository at https://github.com/Dan-Herrera/Legacy_Effects_of_Park_Planning/.

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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.2024.105132>.

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