

The public–private divide and seasonal variation shape bird diversity in greenspaces of two neighboring midwestern USA cities

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HIGHLIGHTS

- Private yards provided habitat for birds in two neighboring cities.
- Private yards had less bird diversity than public parks in the summer.
- Private and public lands had equally diverse but distinct communities in the winter.
- Land cover and season explained differences in bird diversity between the two cities.
- Heterogeneous landscapes with both land sparing and land sharing maximize bird diversity.

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ABSTRACT

Greenspaces are increasingly valued for supporting biodiversity in urbanized landscapes. Previous research efforts have emphasized the importance of public land such as parks and nature preserves for biodiversity, yet private yards in residential neighborhoods also have great potential for species conservation. Our study considered the importance of adjacent public and private greenspaces for urban bird diversity. We surveyed birds in public parks ($n = 39$) and private yards ($n = 41$) distributed across neighboring twin cities (Champaign and Urbana) in Illinois, USA, to assess potential differences in bird diversity across: (1) the public–private divide; (2) seasons (winter vs. summer); and (3) the two cities. We found a seasonal interaction across the public–private divide. In summer, communities in private yards were a subset of those found in public parks, whereas in winter, both private yards and public parks hosted equally diverse yet distinct species assemblages. Between the two cities, Urbana supported greater bird diversity and a distinct species assemblage compared to the warmer, more urbanized city of Champaign. Our results demonstrate that both public parks and private yards play key roles in supporting native bird diversity, but also highlight that these roles can shift across seasons. Furthermore, we show that neighboring cities within the same conurbation can differ substantially in bird community structure and diversity. Our findings reinforce the importance of maintaining heterogeneous landscape mosaics and combining land sparing and land sharing approaches to maximize bird diversity in urban areas.

1. Introduction

As the human population continues to increase in size and shift towards urban centers (Acuto et al., 2018; United Nations, 2018), conserving urban biodiversity has become an issue of global importance (Aronson et al., 2017; Knapp et al., 2021). In recent decades, urban

greenspaces (i.e., vegetated areas including but not limited to grass, flowers, bushes, or trees; adapted from Lachowycz & Jones, 2013) have been highlighted for their critical role in mitigating the impacts of accelerating urbanization on native biodiversity (Beninde et al., 2015; Lepczyk et al., 2017). For example, urban greenspaces can serve as reservoirs of local biodiversity, supporting more diverse communities

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than the surrounding built environment and even threatened or endangered species (Ives et al., 2016; MacGregor-Fors et al., 2016; Soanes & Lentini, 2019). These green spaces can also stimulate positive human-wildlife interactions and provide a variety of other ecological and cultural ecosystem services (Aerts et al., 2018; Carr et al., 2022; Fuller et al., 2007). Although urban systems do provide habitat for wildlife species, populations may not be healthy or even of conservation value if these urban areas are ecological traps (reviewed in Zúñiga-Palacios et al., 2021). Nevertheless, the protection and conservation of effective green spaces will be crucial for promoting sustainable social-ecological systems and maintaining nature's contributions to people in urban areas (Aerts et al., 2018; Díaz et al., 2018; Soulsbury & White, 2015).

Whereas public green spaces such as parks and nature preserves have received widespread attention in the literature, private green spaces (i.e., areas that are not accessible to the general public) such as residential yards or other personal property are becoming increasingly appreciated for their contribution to supporting native biodiversity (Campos-Silva & Piratelli, 2021; Gaston et al., 2005; Goddard et al., 2010; Loram et al., 2007; Lerman et al., 2023). For example, a recent comparison of bird community structure in six metropolitan areas of the USA found that, within a given city, private yards supported more species-rich bird communities than public parks, though many of these species were generalists and overall, parks supported more species of conservation concern (Lerman et al., 2021a). Likewise, moderately developed urban areas and private yards have been shown to support similar or greater mammal diversity than remnant natural areas (Parsons et al., 2018; van Helden et al., 2020). Because private yards comprise a substantial proportion of available habitat in urban areas (e.g., 36–47 %; Loram et al., 2008) and the majority of human-wildlife interactions take place close to home (United States Fish & Wildlife Service, 2018), addressing the relative value of adjacent public and private green spaces is a first step towards effectively conserving urban biodiversity and informing future land management decisions (Aronson et al., 2014; Cubino et al., 2020; Lerman et al., 2021a,b).

In addition to the public–private axis, the efficacy of green spaces as reservoirs of biodiversity may also vary on a seasonal basis. Among birds, for example, the majority of studies have focused on characterizing bird communities in a single season, usually the breeding season (e.g., Ferenc et al., 2014; Ciach & Fröhlich, 2017; Dale, 2018). However, most bird communities change seasonally with the influx or efflux of migrants, and resident bird species can also change their behavior and habitat use seasonally (Petit, 2000; Wagner, 1981). Especially in temperate regions that experience cold winters, supplemental feeding by householders and thermoregulatory benefits from urban heat island effects (Deilami et al., 2018; Mohajerani et al., 2017) could shift the cost-benefit ratio from public to private green spaces, resulting in equivalent or higher diversity in private yards (Jones & Reynolds, 2008; Chamberlain et al., 2009). Consistent with this hypothesis, bird diversity in a Mediterranean city in France increased in suburban areas and decreased in adjacent natural areas during the winter (Caula et al., 2008). Among overwintering Blackcaps (*Sylvia atricapilla*) in Ireland and Great Britain, individuals that shifted habitats into private yards with supplemental feeding during particularly cold periods exhibited better body condition than rural conspecifics that were not supplementally fed (van Doren et al., 2021). Finally, data from Project FeederWatch, a continent-wide network of bird feeders observed across North America, have demonstrated that colonization rates of urban areas by overwintering birds increase sharply during the harshest winter weather (Latimer & Zuckerberg, 2021). Taken together, these findings suggest that private yards may increase in value during energetically challenging periods due to the benefits of supplemental feeding.

Thirdly, cities themselves vary in the way they are designed and how well they support urban biodiversity. Cities span orders of magnitude in human population size and employ varied management practices, which in turn serve as ecological filters that dictate which species can persist (Andrade et al., 2021; Aronson et al., 2016; Uchida et al., 2021;

MacGregor-Fors et al., 2022). Factors such as city age, total greenspace area, landscape configuration, vegetation structure, and regional species pool can be important determinants of biodiversity in urban green spaces (Aronson et al., 2017; Beninde et al., 2015; Norton et al., 2016). Indeed, management strategies and land use policies consistently emerge as determinants of biodiversity between cities and across taxonomic groups (Baycan-Levent & Nijkamp, 2009; Beninde et al., 2015; Warren et al., 2011). Given the ecological, psychological, and economic benefits of increased biodiversity (de Groot et al., 2010; Fuller et al., 2007; Pimentel et al., 1997), identifying the urban areas where biodiversity is highest and the land management strategies that maximize biodiversity can serve as a blueprint for optimizing human-wildlife interactions and creating wildlife-friendly cities (Polasky et al., 2008).

Although some studies have characterized urban bird community structure across multiple seasons (e.g., Caula et al., 2008) or multiple cities (e.g., Lerman et al., 2021a), none to our knowledge has explored how these dynamics might differ between public parks and private yards. Integrating these three factors will reveal their relative importance as predictors of bird diversity and broaden our understanding of the forces shaping urban biodiversity patterns.

To address this knowledge gap, we compared bird communities between public parks and private yards in two neighboring (twin) cities (Champaign and Urbana) in Illinois, USA in winter and summer. We made four predictions about how bird diversity would differ across the public–private divide, cities, and seasons: (1) bird diversity would be greater in public parks than private yards; (2) bird diversity would be greater in the city of Urbana than in the more densely populated Champaign; (3) bird diversity would be higher in summer than in winter, and relative patterns across the public–private divide and cities would vary seasonally; and (4) patterns of bird diversity across the public–private divide, cities, and seasons would be associated with a suite of proximate environmental variables related to vegetation, development intensity, forest cover, and land surface temperature.

2. Methods

2.1. Study site and historical land management practices

We conducted this research in Champaign (population ~ 88,000, ~60 km²) and Urbana (population ~ 38,000, ~31 km²), two neighboring (twin) cities with a shared border located in east central Illinois, USA. Urbana was founded in 1822 and originally called “Big Grove,” referring to a ~ 26 km² area of oak-dominated hardwood forest (Buck, 2016) that encompassed most of modern-day Urbana. Champaign was then established in the 1850s to accommodate the advent of a newly constructed railroad that passed through east central Illinois, two miles west of Urbana (Buck, 2016). Over time, the cities grew together into a connected conurbation, but differences in level of urbanization and population size have persisted (Supplementary Table S1). Urbana is designated as a Tree City USA (Arbor, 2022), with 11,000 street trees, 4,000 park trees, and more than 100,000 trees in privately-owned yards (City of Urbana, 2021). Urbana also has more than twice as much public greenspace area (653 ha vs. 276 ha; Supplementary Table S1, S2) despite having 16 fewer public parks than Champaign.

The Champaign and Urbana Park Districts manage most of the public parks and several additional facilities (e.g., recreation centers, aquatic centers) in their respective cities, and differ substantially in their overall approach to land management (i.e., their prioritization of biodiversity and nature conservation). The Champaign Park District focuses on managing smaller areas and providing infrastructure for human recreation, including paved trails, playgrounds, and picnic areas (www.champaignparks.com). In contrast, the Urbana Park District has a longer history and a more explicit focus on conservation and restoration. Over time, the Urbana Park District prioritized establishing large pieces of land that allowed for a stronger focus on environmental preservation and nature-oriented activities such as hiking, birdwatching, and wildlife

viewing (www.urbanaparks.org). Thus, we expected these differences in management priorities to have important impacts on bird community structure in the two cities.

2.2. Selection of public parks and private yards

We selected 80 greenspaces located in public parks ($n = 39$) and private yards ($n = 41$), distributed across the metropolitan areas and the immediate surroundings of Champaign ($n = 41$: 16 public parks, 25 private yards) and Urbana ($n = 39$: 23 public parks, 16 private yards; Fig. 1). For public park selection, we first created a database of all local parks and natural areas ($n = 102$, Supplementary Table S2). We focused on medium- to large-sized parks, and thus excluded all greenways (linear greenspaces; $n = 5$) and parks < 5 ha in size ($n = 43$), resulting in 54 public parks (range: 5–191 ha) from which we randomly selected 39 parks (72%) for bird sampling (see below). The 39 public parks included 21 neighborhood parks (i.e., parks embedded within residential neighborhoods or local communities), nine natural areas, four university greenspaces, three golf courses, and two cemeteries (Supplementary Table S2). We initially tested for and found no significant differences in bird diversity metrics between neighborhood parks and any other types of greenspaces (i.e., cemeteries, golf courses, and university greenspaces; Tukey's pairwise post-hoc tests, all $p > 0.05$), so we combined these groups and considered them all public parks in our subsequent analyses. Although several natural areas were outside of the city limits of Champaign and Urbana, we chose to include them in our study since they served as important greenspaces in the context of the regional landscape. For private yard selection, we divided the entire metropolitan area of the two cities in 1-mi^2 ($\sim 2.59\text{ km}^2$) polygons and used a random coordinate generator to randomly select one to two yards per polygon. All sites were separated from each other by at least 300 m to ensure spatial independence. Within each site, we established bird

monitoring locations (hereafter, points). For public parks, we assigned the number of points per park based on park area, as follows: one point for parks between 0 and 50 ha in size ($n = 27$), two points for parks between 50 and 150 ha in size ($n = 11$), and three points for parks larger than 150 ha ($n = 1$), resulting in 52 points. For private yards, we conducted one point count per yard, resulting in 41 points, and a cumulative total of 93 points in the 80 public parks and private yards.

2.3. Point counts and bird identification

To characterize bird community structure across cities, the public–private divide, and seasons, we conducted 10-minute, 50 m-distance point counts (Ralph et al., 1995) at each of the 93 points in winter (January–February) and summer (June–July) 2022. Prior to starting data collection in both seasons, expert observers ($n = 3$) conducted simultaneous, triple-blind point counts ($n = 9$) to test for interobserver variation in bird detection and identification. Pairwise comparisons of observers' species accumulation curves revealed strong similarity in species detection among observers that was indicative of minimal interobserver variation in detection probability (Ralph et al., 1995): we present a single example here (Supplementary Fig. S1). During the point counts, we recorded detections of every bird species seen or heard, the number of individuals per species, and the distance (in meters) and direction of the observed individuals. A detection consisted of any time an individual of a particular species was seen or heard during a point count. A single detection, for example, could consist of observing multiple individuals of a given species. We classified a species as 'rare' in a given season if it was detected in $n \leq 10$ point counts during that season.

In each season, each point was visited and surveyed five times to provide replication and ensure that sampling was sufficient to detect the majority of species at any given point. Observers rotated between points, and each point was visited by all observers at least once per season.

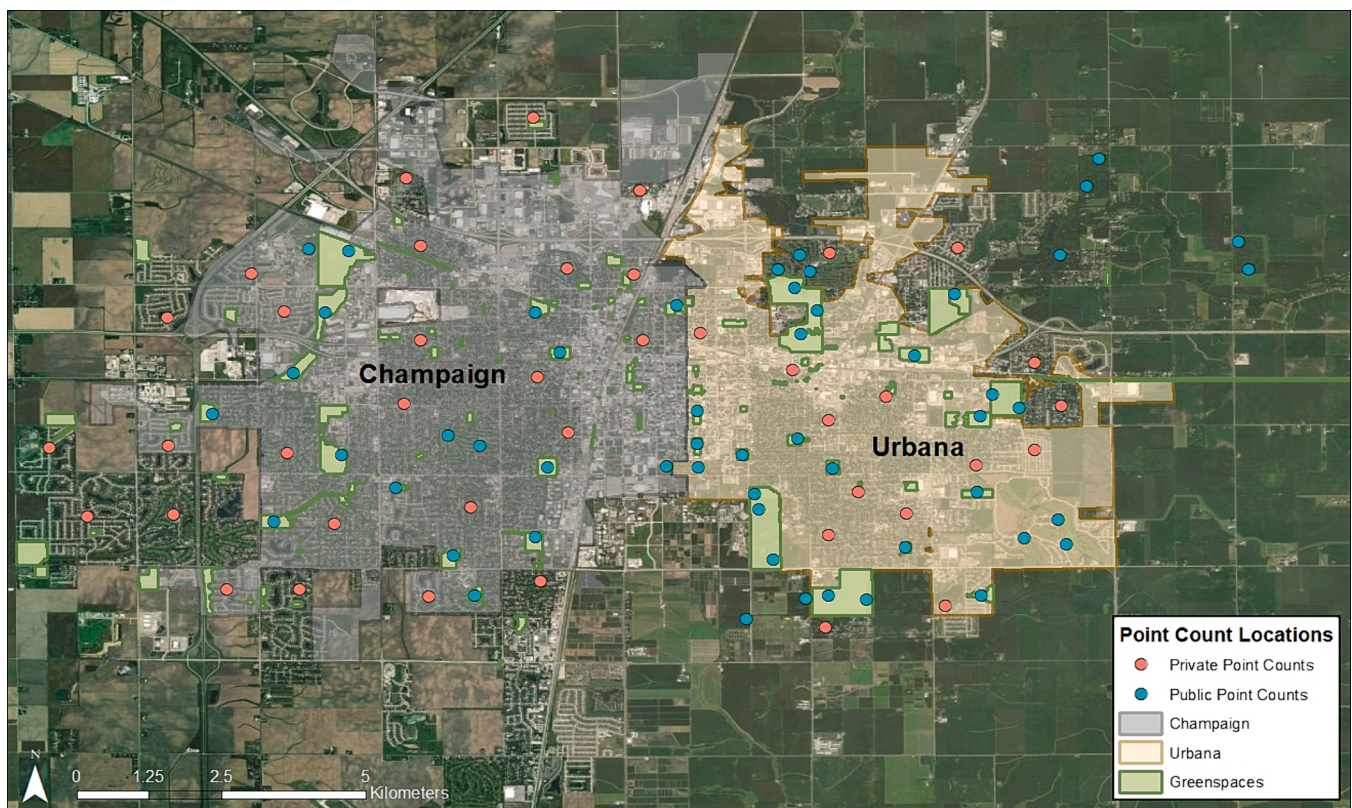


Fig. 1. Satellite imagery of the metropolitan areas of Champaign (gray shading) and Urbana (green shading). Point count locations for the 80 greenspaces are indicated by blue circles (public parks and natural areas, $n = 39$) and red circles (private yards, $n = 41$), respectively. Public greenspaces are outlined in green. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Thus, we conducted a total of 930 point counts across the entire survey: 93 points (53 public + 40 private) * five replicates * two seasons.

2.4. Environmental data

To explore the influence of land cover and temperature on bird diversity, we spatially matched eight land cover variables at each of the 80 greenspaces. We selected seven land cover variables from the U.S. Geological Survey (USGS) National Land Cover Database (NLCD) from 2019 (30-m resolution) relevant to our urban study system, including developed open space, developed low intensity, developed medium intensity, developed high intensity, agriculture (cultivated crops and pasture/hay), forested land, and impervious surface (Dewitz, 2021). To capture further heterogeneity of urban land cover, we selected an eighth landcover variable, tree canopy coverage, provided by the U.S. Forest Service as part of the National Land Cover Database (Yang et al., 2018). We also matched two land surface temperature (LST) variables, which we calculated with the online global Land Surface Temperature Estimation tool (Parastatidis et al., 2017) by taking the median LST of each point count location for the summer (June–July) and winter (January–February) to coincide with the bird surveys. To integrate each of the eight environmental and two LST variables with each of the 80 greenspaces, we placed a 200 m buffer around each greenspace (a common buffer for studies of land cover and avian habitat use; see Smallwood and Wood, 2023) and calculated the percentage of each land cover within the boundary. We used the R packages ‘rgeos’ (Bivand & Rundel, 2021) to calculate the buffer and ‘raster’ (Hijmans, 2022) for the land cover extraction procedure.

We tested for and found high multicollinearity among the 10 predictor variables in our dataset (Supplementary Table S3). We therefore used Principal Component Analysis as a variable reduction technique to account for high collinearity among the eight land cover variables (following Grade et al., 2021) using the *prcomp* function in R. Although temperature is related to land cover factors such as impervious surface, we excluded the LST variables from the PCA to account for differences in temperature variation between the summer and winter months across the urban landscape. We retained three components describing distinct features of the environment, which accounted for 93 % of the total variation in the original data (Supplementary Table S4). We named PC1 as “Vegetation” to describe the positive loadings of forest, tree canopy, and open space land cover variables and negative loadings of impervious surface, and development intensity. PC2 further separated the various development intensities, with positive loadings for medium and high development intensity and a negative loading for low intensity development. Thus, increases along PC2, or “Development” represent increasing development intensity. PC3 distinguishes between forested land cover with tree canopy and developed open space that largely encompassed grassy lawns. We used the name “Forest” for PC3 to describe increasing forest cover and decreasing grass cover with positive values. With this variable reduction technique, we had a total of five environmental variables for our statistical analysis to represent the urban landscape: LST in Winter, LST in Summer, Vegetation, Development, and Forest (Supplementary Table S5).

2.5. Statistical analyses

We conducted all statistical analyses in the R programming environment (R Core Team, 2022). To test whether we achieved sufficient sampling depth of the bird community at each survey point, we generated species accumulation curves in both summer and winter for all 93 point count locations using the *specpool* function in the ‘vegan’ package (Oksanen et al., 2022). We compared four different coverage-based species richness estimators that have been shown to yield reasonably precise estimates independent of spatial sampling grain: the Chao1, Jackknife1, Jackknife 2, and bootstrap estimators (Hortal et al. 2006). We also calculated one incidence-based species estimator using the *ice*

function in the ‘fossil’ package (Vavrek, 2011). We used multiple metrics of diversity in addition to species richness so that we did not present a uni-dimensional view of diversity (following Morin, 2009 and Morris et al., 2014). Specifically, we used the *diversity* function in the ‘vegan’ package to calculate the Shannon (H') and Simpson's (D_1) diversity indices. We then manually calculated Pielou's evenness index (J) following Oksanen et al. (2022), where $J = H' \div \log(\text{species richness})$.

Given the significance of greenspace area as an important predictor of bird diversity (e.g., Schütz and Schulze, 2015), we tested for and found significant associations between all four bird diversity metrics and public greenspace area (in hectares) in both winter ($F_{1,36} = 16.8$, $p = 0.002$, $R^2 = 0.32$ and summer ($F_{1,36} = 52.4$, $p < 0.0001$, $R^2 = 0.59$; Supplementary Fig. S2). To ensure that systematic differences in greenspace area were not the primary factor driving differences between the two cities, we ran a linear regression with city as the predictor variable and greenspace area as the response variable and found no significant differences between Champaign and Urbana in greenspace area ($F_{1,36} = 1.61$, $p = 0.21$, $R^2 = 0.04$). Therefore, we did not include greenspace area as a predictor variable in subsequent models.

Because urban areas in temperate North America are often dominated by non-native bird species (e.g., Murthy et al., 2016), we initially tested for the influence of species origin on the conclusions of the statistical analyses. Non-native species made up ~ 37 % of all detections, >99 % of which were European Starling (*Sturnus vulgaris*) and House Sparrow (*Passer domesticus*). When we removed non-native species and re-ran analyses, we obtained qualitatively similar results, and thus, we opted to lump all species together given that analyses with and without non-native species yielded similar conclusions, and best reflected the bird communities.

To test for the relative importance of season (winter vs. summer), land use type (public vs. private), and city as predictors of variation in diversity metrics, we created a global linear model (we tested for and found no evidence of non-linearity) for each of the four diversity metrics (species richness, H' , D_1 , and J) including all three terms and their interactions as predictor variables and the respective diversity metric as the response variable. We then used the *dredge* function in the ‘MuMIn’ package (Barton, 2009) to test all possible nested model subsets of the global model for the respective diversity metric and ranked models using Akaike's information criterion for small sample sizes (AICc). We considered all models within 2.0 ΔAICc as equivalent in explanatory power to the top model. We report the β estimates and standard errors for each parameter in the top model (as indicated by lowest AICc score) below. We used Tukey's post-hoc tests to quantify differences between treatment groups for all three predictor variables.

Additionally, to explore differences in community structure between public parks and private yards, and across the two cities of Urbana and Champaign, we conducted a non-metric multidimensional scaling (NMDS) analysis using the *metaMDS* function in the ‘vegan’ package (Oksanen et al., 2022). We removed species that were only seen in a single site to account for rare species that are often not accurately placed in multivariate analysis (McCune et al., 2002). We omitted outliers of extremely large flocks of certain species [e.g., Canada Goose (*Branta canadensis*); European Starling] only seen on a single point count to make sure that individual observations unrepresentative of a given site's ecological community did not disproportionately influence community structure (McCune et al., 2002). We calculated the NMDS with a Bray-Curtis distance using a square-root transformation on the site by species abundance matrix (Kruskal, 1964) in the ‘vegan’ package (Oksanen et al., 2022) for bird communities in both seasons. For both the winter and summer ordinations, a three-axis solution was needed to reduce the stress below an acceptable threshold of 0.2 (Clarke, 1993). First, we ran univariate linear regressions to test for direct differences in the five environmental variables between Champaign and Urbana and across the public–private divide. We then used the *envfit* function in the ‘vegan’ package to fit the five environmental variables (Summer LST, Winter LST, Greenspace [PC1], Development [PC2], and Forest [PC3]) to the

ordination plot to explore the bird community’s relationships with land use (public versus private) and city management regime (Urbana versus Champaign) in multivariate space in both winter and summer. We used the *p.adjust* function to apply Bonferroni corrections for multiple comparisons before assessing relationships between the five environmental variables and the predictor variables of interest.

3. Results

3.1. Overview of the Champaign-Urbana bird community

We recorded 2,549 detections of 6,387 individual birds of 47 species in the winter and 5,742 detections of 10,524 individuals of 86 species in the summer, for a total of 8,291 detections of 16,911 individuals of 100 species across the two seasons (Supplementary Table S6). The extrapolation of species accumulation curves indicated that our sampling depth of the Champaign-Urbana bird community was sufficient in both seasons: the estimated winter and summer species pools were 50–71 species and 90–101 species, respectively (Supplementary Table S7). There were no significant differences between the five different species richness estimators in winter (Supplementary Fig. S3a) or summer (Supplementary Fig. S3b).

The winter bird community was dominated by 15 common species (13 resident, two migratory) that comprised nearly 90 % (2,324 of 2,549) of all detections (Supplementary Fig. S4a). Nearly half of the species detected in winter (23 of 47) were relatively rare (i.e., detected in ≤ 10 point counts; Supplementary Table S6). Eleven of the 15 most abundant resident species in winter were also in the top 15 most abundant species in the summer (Supplementary Fig. S4b, Supplementary Table S6), including species such as Northern Cardinal (*Cardinalis cardinalis*), House Sparrow, and House Finch (*Haemorrhous mexicanus*). Lastly, we recorded two detections of an Illinois state-endangered species, Black-crowned Night-Heron (*Nycticorax nycticorax*) – one each at two public parks in Champaign.

3.2. Predictors of variation in bird diversity

The top models from our AIC analyses were consistent across all four diversity metrics (species richness *S*, Shannon diversity index *H'*, Simpson diversity index *D*₁, and the Pielou evenness index *J*). For species richness and the Pielou evenness index *J*, the top models included the predictor variables of city, season, land use type, and an interaction between season and land use type (Table 1, Supplementary Table S8). For the Shannon Diversity Index *H'* and the Simpson Diversity index *D*₁, the top models ($\Delta\text{AICc} \leq 2$) included city and season or city, season, and land use type (Supplementary Table S8). In all top models (e.g., species richness *S* intercept: $\beta \pm \text{SE} = 17.3 \pm 0.9$), season (e.g., species richness *S*: $\beta \pm \text{SE} = -7.1 \pm 1.1$) was the most important predictor, followed by the season*land use type interaction (e.g., species richness *S*: $\beta \pm \text{SE} = -4.4 \pm 1.6$), land use type (e.g., species richness *S*: $\beta \pm \text{SE} = 3.5 \pm 1.2$), and finally city (e.g., species richness *S*: $\beta \pm \text{SE} = 3.3 \pm 0.8$). In all cases,

Table 1
Top models explaining variation in bird species richness of the Champaign-Urbana bird community. For each model, the terms are listed, as well as the degrees of freedom (df), R-squared (*R*²) values, Akaike’s information criterion (AICc), changes in Akaike’s information criterion values (ΔAICc) relative to the top model, and model weight.

Model terms	Model df	Model <i>R</i> ²	AICc	ΔAICc	Model weight
City + Land use type + Season + Land use type*Season	6	0.51	986.9	0.00	0.88
City + Land use type + Season	5	0.48	992.2	5.21	0.06
City + Season	4	0.47	992.5	5.56	0.05

diversity metrics were higher in the summer than the winter (Fig. 2a) and higher in Urbana than Champaign (Fig. 2b). In winter, the top 10 most species-rich greenspaces were all located in Urbana (Supplementary Fig. S5), seven of which were public and three of which were private. Of the top 10 most species-rich greenspaces in summer (Supplementary Fig. S5), eight were public, only two were private, and nine were in Urbana compared to only one in Champaign.

3.3. Differences in bird community structure across the public–private divide, seasons, and cities

Similar to the AIC models, NMDS ordination with a three-axis solution for both the winter (NMDS stress = 0.16, Non-metric *R*² = 0.98, Linear *R*² = 0.84) and summer (NMDS stress = 0.14, Non-metric *R*² = 0.98, Linear *R*² = 0.93) revealed differences in bird community structure between public parks and private yards, as well as an interaction between season and land use type (Fig. 3). For the 28 % (24/86) of species recorded during the summer that were ecologically rare, all were solely detected in public parks and were absent from private yards, whereas only one introduced species (Eurasian Collared-Dove, *Streptopelia decaocto*) was detected solely in private yards (Supplementary Table S6). The majority (~56 %, 36 species) of the remaining 62 species were more abundant in public parks, ~27 % (17/62) were of relatively equal abundance across the public–private divide, and only ~ 15 % (9/62) were more abundant in private yards, eight of which were in the top 15 most abundant species. The total number of bird detections in winter was roughly equal between public parks (51 %; *n* = 2,956) and private yards (49 %; *n* = 2,786).

In the winter, public parks and private yards harbored distinct bird communities and supported similar levels of bird diversity (Fig. 3). Eleven rare species were solely detected in public parks, whereas the introduced Eurasian Collared-Dove, and the rare Fish Crow, (*Corvus ossifragus*) and Merlin, (*Falco columbarius*) were solely detected in private yards (Supplementary Table S6). Eleven species were of relatively equal abundance across the public–private divide, 11 species were more abundant in public parks, and 11 species were more abundant in private yards (Supplementary Table S6). The total number of bird detections in winter was higher in private yards (56 %; *n* = 1,424) than in public parks (44 %; *n* = 1,125).

The NMDS analysis further highlighted interesting trends in city management for bird community composition, independent of season. Of the 100 total species detected across both seasons, 30 ecologically rare species were exclusively detected in Urbana. In contrast, only six rare species were unique to Champaign. Of the remaining 64 species, 13 (20 %) had relatively similar abundances between the two cities, 40 (63 %) were more abundant in Urbana, and only 11 (17 %) were more abundant in Champaign. Of those 11 species, all were generally urban tolerant including two waterfowl species (Canada Goose; Mallard, *Anas platyrhynchos*), four aerial insectivores (Barn Swallow, *Hirundo rustica*; Chimney Swift, *Chaetura pelagica*; Purple Martin, *Progne subis*; Northern Rough-winged Swallow, *Stelgidopteryx serripennis*), a raptor (Cooper’s Hawk, *Accipiter cooperii*), two sparrows (Chipping Sparrow, *Spizella passerina*, House Sparrow), American Crow (*Corvus brachyrhynchos*), and American Robin (*Turdus migratorius*; Supplementary Table S6). The total number of detections was higher in Urbana (57 %; *n* = 4,753) than Champaign (43 %; *n* = 3,538).

3.4. Associations between temperature, land cover, and bird community structure

Linear regressions revealed clear differences between the five environmental variables across cities and the public–private divide. Urbana was characterized by denser vegetation (PC1: *F*_{1,78} = 13.7, *p* = 0.0004, *R*² = 0.15) and lower temperatures (LST: *F*_{1,78} = 15.3, *p* = 0.0002, *R*² = 0.16) than Champaign, although development (PC2) and forest cover (PC3) did not differ significantly between the two cities (both *p* > 0.05).

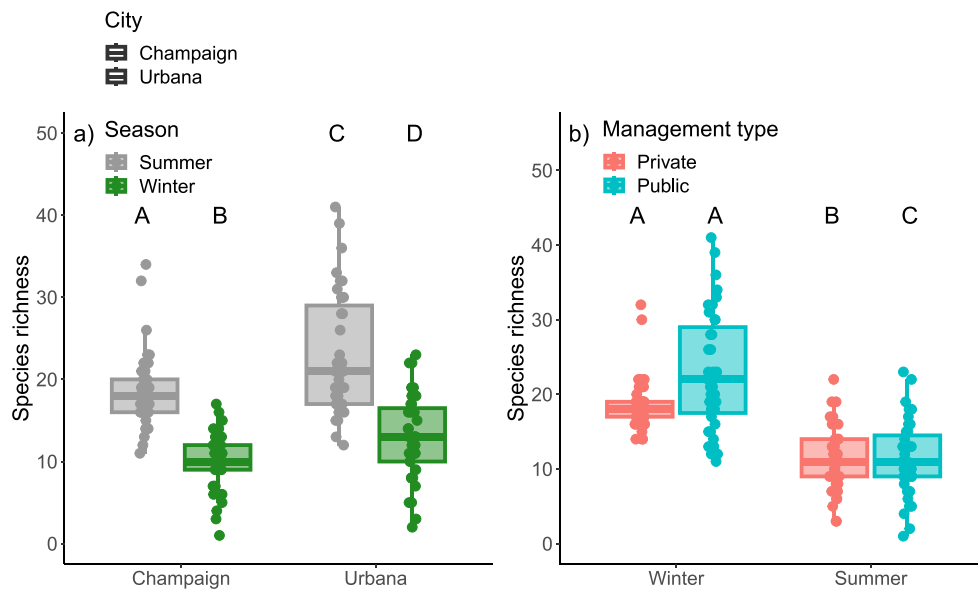


Fig. 2. Seasonal differences in bird species richness between a) public (blue, $n = 39$) and private (red, $n = 41$) greenspaces and b) Champaign and Urbana in winter (gray, January-February) and summer (green, June-July) 2022 in the Champaign-Urbana metropolitan area. Letters indicate significant differences in species richness among treatment groups as determined by a Tukey's post-hoc test ($\alpha = 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

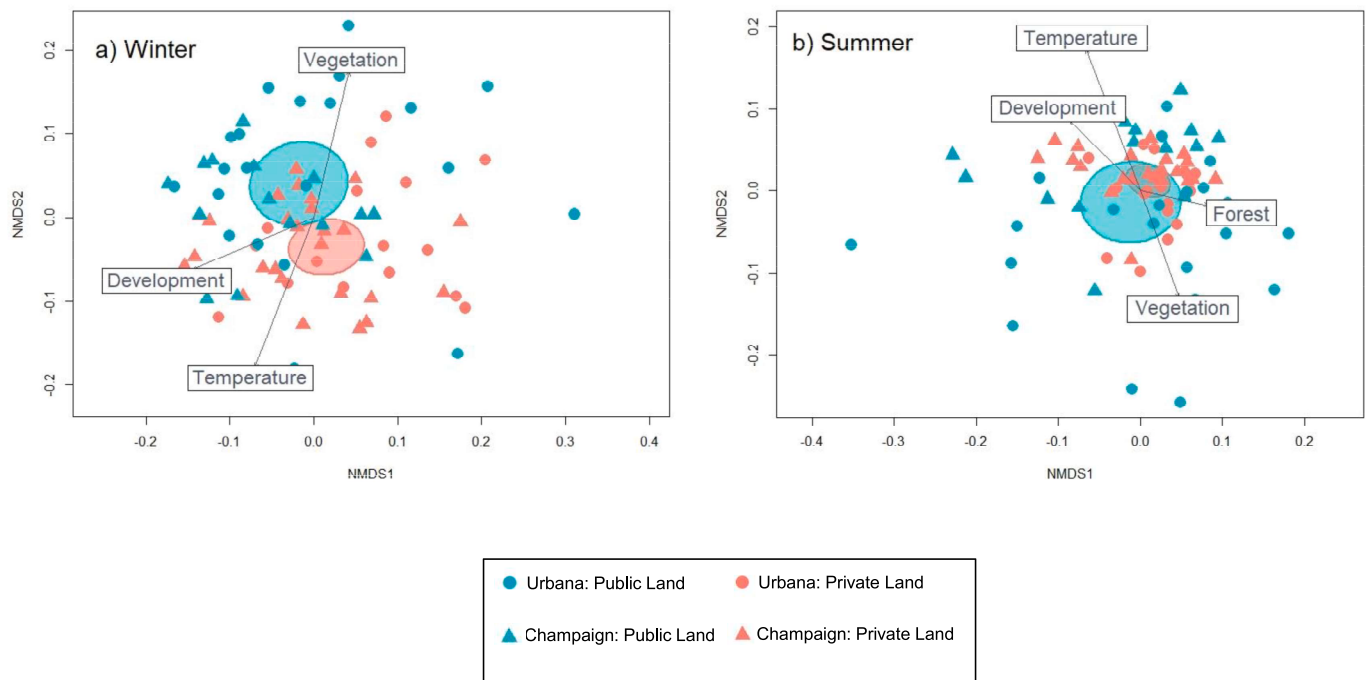


Fig. 3. Non-metric dimensional scaling (NMDS) of a) winter and b) summer bird communities for axes 1 and 2 of the 3-axis solution. Points represent the bird community at respective point count locations in the cities of Champaign (triangles) and Urbana (circles) as well as public (blue) and private (red) land uses. Standard error ellipses with a 99 % confidence interval are shown for the mean of public versus private sites in multivariate space. Arrow vectors represent environmental variables that had significant effects on community structure ($\alpha = 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Similarly, public parks were characterized by denser vegetation ($F_{1,78} = 25.8$, $p < 0.0001$, $R^2 = 0.25$), lower forest cover ($F_{1,78} = 15.3$, $p = 0.0002$, $R^2 = 0.16$), and lower temperatures ($F_{1,78} = 18.7$, $p < 0.0001$, $R^2 = 0.19$) than Champaign, but did not differ significantly in development ($p > 0.05$).

The analysis of environmental data showed that these differences in land surface temperature, vegetation, and development intensity were

also reflected in differences in bird community composition (Table 2). In the ordination separating public versus private land use (NMDS 2,3), the bird community in public parks was associated with significantly more vegetation and cooler temperatures than the bird community in private yards in both winter and summer. The bird community in public parks was also associated with significantly less urban development than that of private yards (NMDS 2,3) but not the amount of forested land cover.

Table 2

Associations between environmental variables and bird community structure based on the three-axis Non-metric dimensional scaling (NMDS) ordinations. Bold indicates significant associations ($\alpha = 0.05$).

Environmental Variable	Season	NMDS 1,2	NMDS 2,3	NMDS 1,3
City (Urbana vs Champaign)	Summer	$R^2 = 0.09$, $P = 0.002$	$R^2 = 0.17$, $P = 0.001$	$R^2 = 0.05$, $P = 0.020$
	Winter	$R^2 = 0.06$, $P = 0.008$	$R^2 = 0.03$, $P = 0.087$	$R^2 = 0.05$, $P = 0.020$
Land use (Public vs Private)	Summer	$R^2 = 0.02$, $P = 0.155$	$R^2 = 0.03$, $P = 0.096$	$R^2 = 0.02$, $P = 0.260$
	Winter	$R^2 = 0.10$, $P = 0.001$	$R^2 = 0.11$, $P = 0.001$	$R^2 = 0.02$, $P = 0.239$
Land Surface Temperature (LST), Summer	Summer	$R^2 = 0.52$, $P = 0.004$	$R^2 = 0.44$, $P = 0.004$	$R^2 = 0.12$, $P = 0.048$
Land Surface Temperature (LST), Winter	Winter	$R^2 = 0.46$, $P = 0.004$	$R^2 = 0.40$, $P = 0.004$	$R^2 = 0.10$, $P = 0.088$
Vegetation	Summer	$R^2 = 0.29$, $P = 0.004$	$R^2 = 0.29$, $P = 0.004$	$R^2 = 0.10$, $P = 0.048$
	Winter	$R^2 = 0.40$, $P = 0.004$	$R^2 = 0.37$, $P = 0.004$	$R^2 = 0.03$, $P = 1.000$
Development	Summer	$R^2 = 0.22$, $P = 0.004$	$R^2 = 0.09$, $P = 0.014$	$R^2 = 0.14$, $P = 0.032$
	Winter	$R^2 = 0.31$, $P = 0.004$	$R^2 = 0.04$, $P = 0.908$	$R^2 = 0.27$, $P = 0.004$
Forest	Summer	$R^2 = 0.11$, $P = 0.050$	$R^2 = 0.02$, $P = 1.000$	$R^2 = 0.12$, $P = 0.048$
	Winter	$R^2 = 0.01$, $P = 1.000$	$R^2 = 0.03$, $P = 1.000$	$R^2 = 0.02$, $P = 1.000$

Land surface temperature as well as two environmental variables (vegetation and development) were related to differences in bird community composition between the two cities (Table 2). All three variables were significant in the NMDS ordination (NMDS 1,3) that differentiated the bird communities between Champaign from Urbana, with the Champaign bird community being associated with warmer temperatures, greater development intensity, less forest cover, and less vegetation than the Urbana bird community.

4. Discussion

By assessing bird diversity in public parks and private yards, and across two seasons in two neighboring cities, we demonstrated the importance of the public-private divide and seasonal interactions for shaping urban bird community structure in the twin cities of Champaign-Urbana, Illinois, USA. We found that public parks supported higher bird diversity in summer, but private yards harbored distinct and equally diverse bird communities in winter, thereby increasing regional diversity. By sampling twin cities that share a similar macroclimate and regional context, we were better able to understand how environmental factors influence bird community structure. We found that the city of Urbana, which was characterized by lower development intensity, cooler temperatures, and greater forest cover, supported higher biodiversity than Champaign in both seasons. These results indicate that a city's current approach to land management and the broader historical context that has influenced development patterns over time can have major implications for bird diversity and community structure. Our findings reinforce the idea that both public parks and private yards can serve as important bird habitats when supported by resource management and individual stewardship behaviors, respectively.

We documented a seasonal shift in the relative importance of public parks and private yards for bird diversity. During the summer, public parks supported significantly higher bird diversity and far more ecologically rare species and habitat specialists than private yards. For example, forest-dependent species such as Tufted Titmouse (*Baeolophus bicolor*), Barred Owl (*Strix varia*), and Acadian Flycatcher (*Empidonax*

virescens) and grassland/prairie specialists such as Eastern Meadowlark (*Sturnella magna*), Field Sparrow (*Spizella pusilla*), and Ring-necked Pheasant (*Phasianus colchicus*) were almost exclusively found in forest and prairie fragments on public lands and were absent in private yards. In contrast, private yards supported more urban-tolerant, resident, and generalist species across seasons, such as House Sparrow, House Finch, and American Crow. These results are consistent with a large body of literature demonstrating the importance of "land sparing," or the retention of concentrated greenspaces such as forest remnants or large urban parks, for urban wildlife (Caryl et al., 2016; Dale, 2018; Soga et al., 2014; Sushinsky et al., 2013), and in particular for specialist bird species (Lerman et al., 2021a). In winter, however, private yards equaled public parks in overall species richness and other diversity metrics and supported higher abundances of birds. The relatively increased value of private yards for winter bird communities reinforces the importance of "land sharing," or mixed-use residential neighborhoods with interspersed greenspaces, for urban bird diversity (Belaire et al., 2014; Ibáñez-Álamo et al., 2020). Overall, our findings echo the conclusions of other studies that have simultaneously quantified bird diversity in adjacent public and private greenspaces; namely, that heterogeneous urban landscapes that combine land sparing and land sharing approaches are key to creating bird-friendly cities (Ibáñez-Álamo et al., 2020; Lerman et al., 2021a). Nevertheless, because we only sampled birds in two seasons, future studies that sample across the full annual cycle will be necessary to fully understand how seasonality interacts with the private vs. public dichotomy.

Because our study was observational, we were unable to pinpoint the mechanisms underlying the dynamics of bird community structure. However, our spatial environmental data analysis found key differences in land cover and surface temperatures between public parks and private yards. Across seasons, public parks had higher vegetation cover and higher forest cover than private yards. Several studies have similarly shown that higher forest cover and vegetation greenness are associated with increases in bird species richness and diversity in urban areas and across seasons (Bino et al., 2008; Leveau et al., 2018, 2020; Rega-Brodsky & Nilon, 2017). Land surface temperatures were also cooler on average in public parks compared to private yards in both seasons. We posit that these differences in land cover and temperatures likely explain the seasonal differences in bird community structure between public and private greenspaces. In summer, public parks have cooler temperatures and higher primary productivity than private yards, as well as fewer year-round anthropogenic threats (e.g., outdoor cats, windows, introduced or invasive species; Galbraith et al., 2015; Gehrt et al., 2013; Hager et al., 2013), and are thus likely more beneficial for breeding birds. Conversely, private yards provide greater shelter, warmer temperatures, and more reliable supplementary food resources via bird feeders (e.g., Jokimäki & Suhonen, 1998; Rinner & Hussain, 2011), in winter. Thus, private yards support similar bird species richness and higher abundances than public parks in winter, although it is important to acknowledge the negative implications of bird-feeding, including altered community structure and disease transfer (Galbraith et al., 2015, 2017). Consistent with our hypothesis, similar winter influxes of birds into private yards have been documented in several other studies (e.g., Caula et al., 2008; Latimer & Zuckerberg, 2021), and linked to the density of bird feeders and supplementary food resources (van Doren et al., 2021). We were unable to test this idea because we relied on landscape-level spatial analyses, but we recommend that future studies collect the necessary yard- or neighborhood-specific temperature or feeder density data to evaluate this hypothesis.

Our comparison of two adjacent cities that share similar macroclimates and geographic attributes provided a unique opportunity to isolate the effects of historical land use and current land management practices on bird community structure. Champaign has double the human population size and covers twice as much geographic area as Urbana (www.champaignil.gov, www.urbanainilinois.us). These differences arose early in these cities' histories when the population of

Champaign exploded following the re-routing of the railroad two miles west of Urbana, and have persisted to the present day. Our results may also be attributable to the cities' different management strategies for public parks. On one hand, public parks in Champaign are predominantly smaller in size and contain more developed facilities (e.g., playgrounds, paved trails). To manage these greenspaces, the Champaign Park District has prioritized actions such as controlled burns and invasive plant species management rather than biodiversity conservation (D. Olson, Champaign Park District land manager, personal communication). On the other hand, Urbana includes larger parcels of land with more intact ecosystems that are maintained with guidance from formal management plans. The Urbana Park District is working towards a 5 %–10 % limit of any one species/genus in its parks, a concentration on conserving large native trees, and plans for sustaining the tree canopy in remnant old growth forests (D. Liebert, Urbana Park District land manager, personal communication). The agency has facilitated annual prairie seed collections, invasive species management and planned burns to increase the diversity and abundance of native flora in managed prairies. Moreover, there are management plans for the signature natural areas in Urbana that detail historical bird community baselines and dictate how these unique habitats should be managed to maintain robust native bird communities (<https://www.urbanaparks.org/>).

We observed clear and strong differences in bird community structure that were independent of the public–private divide or season. In both seasons, Urbana harbored a significantly more diverse bird community than Champaign, including far more ecologically rare species and habitat specialists as well as higher overall bird abundance. Champaign sites were associated with warmer temperatures in both seasons, and greater development intensity, as well as less vegetation, more open space, and reduced forest cover relative to Urbana sites in the winter. As a result, urban-tolerant species such as European Starling, House Sparrow, American Crow, and Canada Goose were far more abundant in Champaign than Urbana. The more depauperate bird community observed in Champaign may be due to the increased level of urbanization and development, higher population density, and less intensive natural area management. These results are consistent with a large body of literature that has demonstrated increasing biotic homogenization as human population density increases and urbanization intensifies (DeVictor et al., 2007; Groffman et al., 2017; Latta et al., 2013; Murthy et al., 2016). More broadly, our findings support the conclusions of several recent syntheses emphasizing the primary importance of land management practices in determining biodiversity potential in heterogeneous urban areas (Aronson et al., 2017; Baycan-Levent & Nijkamp, 2009; Beninde et al., 2015).

4.1. Management implications

Our study highlights the importance of maintaining heterogeneous urban areas to maximize bird diversity, and indicates that both public parks (land sparing) and private yards (land sharing) play key and complementary roles in supporting robust bird communities throughout the annual cycle (Ibáñez-Álamo et al., 2020; Lerman et al., 2021a). The unique environmental conditions associated with private yards (i.e., higher temperatures and more abundant food resources) have the potential to shape bird behavior, local distributions, and ultimately, patterns of community structure (Lerman et al., 2021a; Paker et al., 2014; van Doren et al., 2021). Therefore, personal environmental stewardship decisions in private yards, such as bird feeding, sowing native plant species, and providing artificial nesting opportunities, are essential for maintaining robust urban bird communities (Belaire et al., 2014; Lerman and Warren, 2011) and supporting urban biodiversity in general (Cubino et al., 2020; Goddard et al., 2017; Lerman et al., 2023; Larson et al., 2022). More importantly, providing bird-friendly habitat in yards can not only enhance local species richness, but also deepen the connection between humans and birds (Andrade et al., 2022; Brock et al., 2021; Cox & Gaston, 2016; Dayer et al., 2019). It is important to

mention, however, that these findings represent only two seasons (winter and summer) from one pair of cities. Further studies from other sites will be needed to determine whether these management implications for Champaign-Urbana, Illinois are applicable in other localities.

In addition to private stewardship decisions, we show that historical land use trends and current land management practices are both important predictors of bird community structure in public parks. In our study, the most diverse parks included the two largest patches of remnant prairie and the four largest forest fragments, all of which were located in the city of Urbana. Thus, cities that prioritize preservation of large tracts of native habitat, are more likely to retain diverse bird communities and less likely to undergo biotic homogenization (e.g., Mörtberg, 2001; Palmer et al., 2008). The more intensive management of Urbana lands has yielded positive impacts on grassland and prairie bird populations and communities (Davis et al., 2000; Lengyel et al., 2023). Similarly, efforts to remove invasive vegetation and restore native plants have been shown to benefit native birds (Catling, 2005; Narango et al., 2017, 2018). Given that natural forest remnants and prairie ecosystems are irreplaceable refuges for native biodiversity (e.g., Lepczyk et al., 2017), we encourage the continued protection and restoration of these areas, especially around urban centers.

CRedit authorship contribution statement

Henry S. Pollock: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Carena J. van Riper:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. **Devin J. Goodson:** Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Susannah B. Lerman:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – original draft, Writing – review & editing. **Mark E. Hauber:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

Data availability

Data will be made available on request.

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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.2024.105060>.

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