









Residential yard management and landscape cover affect urban bird community diversity across the continental USA

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Abstract. Urbanization has a homogenizing effect on biodiversity and leads to communities with fewer native species and lower conservation value. However, few studies have explored whether or how land management by urban residents can ameliorate the deleterious effects of this homogenization on species composition. We tested the effects of local (land management) and neighborhood-scale (impervious surface and tree canopy cover) features on breeding bird diversity in six US metropolitan areas that differ in regional species pools and climate. We used a Bayesian multiregion community model to assess differences in species richness, functional guild richness, community turnover, population vulnerability, and public interest in each bird community in six land management types: two natural area park types (separate and adjacent to residential areas), two yard types with conservation features (wildlife-certified and water conservation) and two lawn-dominated yard types (high- and low-fertilizer application), and surrounding neighborhood-scale features. Species richness was higher in yards compared with parks; however, parks supported communities with high conservation scores while yards supported species of high public interest. Bird communities in all land management types were composed of primarily native species. Within yard types, species richness was strongly and positively associated with neighborhood-scale tree canopy cover and negatively associated with impervious surface. At a continental scale, community turnover between cities was lowest in yards and highest in parks. Within cities, however, turnover was lowest in high-fertilizer yards and highest in wildlife-certified yards and parks. Our results demonstrate that, across regions, preserving natural areas, minimizing impervious surfaces and increasing tree canopy are essential strategies to conserve regionally important species. However, yards, especially those managed for wildlife support diverse, heterogeneous bird communities with high public interest and potential to support species of conservation concern. Management approaches that include the preservation of protected parks, encourage wildlife-friendly yards and acknowledge how public interest in local birds can advance successful conservation in American residential landscapes.

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INTRODUCTION

Urbanization has a homogenizing, or converging effect whereby ecological form and function among cities are more similar to each other than to the native ecosystems that they replaced (Groffman et al. 2014, Hall et al. 2016, Wheeler et al. 2017). This homogenizing force can lead to more depauperate native animal communities in urban ecosystems (Czech et al. 2000, McKinney 2006). For birds, urbanization results in communities that are similar across cities (Devictor et al. 2007, Luck and Smallbone 2011), less taxonomically diverse (Aronson et al. 2014, Batáry et al. 2018), and less evolutionarily distinct (Morelli et al. 2016, Ibáñez-Álamo et al. 2017, Sol et al. 2017, LaSorte et al. 2018) compared with those found in natural areas. However, most urban bird communities still include primarily locally native species (Aronson et al. 2014), and cities can provide important habitats for threatened species (Ives et al. 2016, Soanes and Lentini 2019). Yet, urban areas tend to support habitat- and diet-generalist bird species at the expense of specialists (Evans et al. 2011, 2018, Leveau 2013, Concepción et al. 2015, Joyce et al. 2018) and these losses can have significant impacts on species diversity in cities (Sol et al. 2020). These community patterns suggest that food resources and/or nesting habitat may ultimately limit species occupancy in urban landscapes, and that restoring these features may improve local bird community diversity (Beninde et al. 2015, Lepczyk et al. 2017).

Because most studies of urban bird communities have focused on the differences between urban and non-urban sites (e.g., Aronson et al. 2014, Sorte et al. 2014, Morelli et al. 2016, Ibáñez-Álamo et al. 2017, Sol et al. 2017), they have yet to fully account for the variation of habitats embedded within a particular city, limiting our understanding of *how* to manage local features for biodiversity. Zooming in from a landscape to a local (e.g., household) perspective reveals a tremendous amount of landscape heterogeneity within urban areas (Cadenasso et al. 2007). Socioeconomic processes are major drivers of management and preferences (Avolio et al. 2015). In addition, legacies of systemic racism, for example, redlining, further define differences in types and amount of vegetation such as canopy cover, their associated land management and subsequent ecological patterns and processes (Avolio et al. 2020, Schell et al. 2020). Landscaping preferences for colorful and showy plants, and those easy to maintain also influence landscape heterogeneity (Larson et al. 2016, Avolio et al. 2018, Cavender-Bares et al. 2020). Studies have exposed differences between urban and peri-urban green spaces in their ability to support local biodiversity; specifically, rural lands and large natural parks (e.g., National Forest

lands, large county parks with native vegetation and other protected open spaces) have higher bird diversity compared with other land-use types embedded within the urban matrix (Chace and Walsh 2006). However, both “land sparing” for example, protecting local natural habitat and “land sharing” (e.g., managing developed land as habitat) strategies can be integrated in urban planning (Sushinsky et al. 2013, Ibáñez-Álamo et al. 2020). Yet, few studies have explored whether harnessing the collective efforts of householder management has the potential to improve urban conservation efforts beyond efforts reliant on government agencies or non-government organizations alone (Derby Lewis et al. 2019, Soanes and Lentini 2019). Therefore, determining which land uses and management strategies support diverse species assemblages will help to inform conservation plans to curb negative impacts of development on biodiversity in urban areas.

In urban areas, private residential yards (from this point forward “yards”) represent a substantial portion of urban green spaces (36–47%; Loram et al. 2008), and contain the majority of plant biomass, including a mix of native and introduced plant and animal species (Nowak et al. 2001, Donnelly and Marzluff 2004, Loram et al. 2007). Households manage yards in diverse ways (Goddard et al. 2017). For example, management decisions include whether to garden for wildlife, plant native plants, maintain lawns, or fertilize and irrigate plants (Goddard et al. 2013, Larson et al. 2016), and can vary between neighborhoods and within a city (Polisky et al. 2014, Locke et al. 2019). Variation in management can drive heterogeneity in bird habitat quality within cities, influencing community assembly, diversity, and species turnover among yards (Daniels and Kirkpatrick 2006, Lerman and Warren 2011, Belaire et al. 2014). However, the vast majority of studies have been limited in scope, focusing on a single species (e.g., Narango et al. 2017), a single city (e.g., Goddard et al. 2013), or a single dichotomy of landscape management such as the use of native vs. non-native plants (Burghardt et al. 2009). Studies conducted at continental scales that investigate multiple taxa and assess the broad variations in land management across scales are necessary to address the generalizability of these patterns (Heffernan et al. 2014). Furthermore, the methods for how we assess biodiversity patterns (i.e., bird diversity metrics such as taxonomic richness, phylogenetic and functional diversity) have importance for understanding biodiversity conservation.

Different diversity metrics present unique aspects of biodiversity, and in combination provide a more complete description of the bird community (McGill et al. 2015, Ibáñez-Álamo et al. 2017), especially when considering differences related to species identity within the

local community. For example, species richness (i.e., total number of species per unit area) can be similar between a residential yard and a natural park, or yards might have higher richness than parks because they contain both native and exotic vegetation, which may support a broader array of species (Marzluff 2005, 2017, Lerman and Warren 2011). Yet the bird communities in each are composed of different species that vary in identity and functional traits such as dietary specialization. For example, yards may be more likely to contain non-native and generalist species, over native and specialist ones. This distinction is important when considering relationships between ecosystem function and biodiversity as function may be primarily driven by the particular traits of species that occupy a habitat, rather than by taxonomic diversity per se (Cadotte et al. 2017). Similarly, yards can support comparable species richness but exhibit more homogenized communities (i.e., similar species composition in yards across cities) relative to the native ecosystems that these yards have replaced (Socolar et al. 2016) meaning that, at scales larger than a single parcel (i.e., the metropolitan area), species richness could be reduced.

In addition to the above biodiversity metrics, considering the conservation status or public interest of a particular species can help to develop conservation strategies aimed at improving urban biodiversity (Schuetz and Johnston 2019). For example, species differ in their vulnerability to urban development because of habitat specializations, limited distributions or regional population trends (Nuttall et al. 2003), which might be independent of functional traits. In addition, public interest in a species (e.g., “popularity” based on Google searches as per Schuetz and Johnston 2019) may help make the biodiversity crisis relevant to decision makers and stakeholders (Hiron et al. 2018) with implications for enhancing the conservation value of residential landscapes.

Here, we tested for differences in the breeding bird community among different urban land management types including public parks and private yards. The parks included two types of sites: interstitial areas that abut residential lands and protected reference areas located at the edges of metropolitan areas. Both park types had unmanaged natural vegetation. The yards included those managed for lawns (i.e., high or low-fertilizer inputs), or yards managed for conservation (i.e., wildlife or water) across six major US metropolitan regions (Baltimore, MD; Boston, MA; Miami, FL; Minneapolis-St. Paul, MN; Phoenix, AZ; Los Angeles, CA), which differed in regional bird communities, climate, and ecological biomes (Trammell et al. 2016). Because birds respond at scales larger than an individual parcel, we considered neighborhood-scale (1 km) effects of land cover within our models by simultaneously assessing relationships between bird communities and tree canopy cover and impervious surface (from this point forward neighborhood-scale features). We (1) modeled bird species occupancy using multiregion

hierarchical community occupancy models that accounted for detection (Kéry and Royle 2016, Sutherland et al. 2016), and (2) used estimated predictions of occupancy for each species at each site to test whether estimated species richness, functional traits, conservation score, public interest score and community turnover differed within and across cities for the different land management types and land cover. We predicted that, controlling for neighborhood-scale features, wildlife-certified management would support higher bird species richness and higher turnover among yards relative to yards managed as lawns or for water conservation. We further predicted that levels of richness and turnover in wildlife-certified yards would be comparable with those in parks. We also predicted that wildlife-certified yards and parks would support species with higher conservation scores and public interest. Our empirical study expands upon previous work by explicitly testing bird community responses to multiple land management regimes at a continental scale with the goal to advance our understanding of the generalizability of urban bird patterns.

MATERIALS AND METHODS

Study sites

We selected six Metropolitan Statistical Areas (from this point forward “cities”) across the continental USA that represented different climates and ecological biomes: Baltimore, MD (BAL; Southeastern USA Plains), Boston, MA (BOS; Mixed Wood Plains), Los Angeles, CA (LA; Mediterranean California), Miami, FL (MIA; Everglades), Minneapolis-St. Paul, MN (MSP; Temperate Prairies/Mixed Wood Plains), and Phoenix, AZ (PHX, Warm Deserts; Trammell et al. 2016; Ecological Region Level II, <https://www.epa.gov/eco-research/ecoregions-north-america>). Within each city, we sampled two different land uses (public parks and private yards) and within these two land uses, six management types (two park types and four yard types).

For the parks, the two management types included reference sites ($n = 4$ or 5 per city) and interstitial sites ($n = 4$ or 5 per city). We selected the reference sites in parks or preserves within or near each city that were composed of native vegetation and minimally managed. Additional selection criteria included sites where we could secure permission or sites that coincided with long-term monitoring as part of the Long-Term Ecological Research (LTER) network. The reference sites represented the historical vegetation types for each city, including oak/tulip poplar forest (BAL), northern hardwood forest (BOS), coastal sage scrub (LA), pine rockland and subtropical hardwood hammock (MIA), tallgrass prairie/oak savanna/mixed hardwood forest (MSP), and Sonoran desert (PHX). We identified candidate interstitial sites across each city using prior knowledge of locations of greenways and the edges of

unmanaged natural vegetation that share at least one border with a residential neighborhood. Interstitial areas that matched our criteria included: patches of natural vegetation within the city (e.g., edges of public open space or unmanaged parks, edges of public trails, public wooded areas behind homes), or patches of natural vegetation at the edge of the city, at the interface with suburban residential land, and at least 50 m². We then randomly selected four or five sites per city.

To maximize our regional-scale inference based on a limited sample size per city, for our yard site selection process, we controlled for some of the variation inherent in residential landscapes that might confound bird community structure (Lerman and Warren 2011, Belaire et al. 2014). We limited the census block groups from which we selected potential sites using Tapestry Segmentation data in ArcGIS (ESRI 2017) which categorizes US neighborhoods into 67 distinct lifestyle groups based on market research (“LifeModes”; Grove et al. 2006). As we aimed to sample yards from detached, single-family housing stock, with similar housing density, and occupied by residents with relatively similar median household income (US\$45,000 in MIA to US\$105,000 in BOS; range reflects regional variation), we targeted the “Urban Periphery,” “Metro Cities,” and “Suburban Periphery” urbanization groups ($n = 22$ LifeModes). We included houses that were at least 10 yr old to avoid immature vegetation of very new developments (Loss et al. 2009), and at least 0.5 km away from a park, golf course, or other open spaces to reduce the influence of non-residential habitat features (e.g., water features, large tracts of land). We used these criteria when selecting the four yard types: two yard types included lawn-dominated management and two yard types included conservation management.

The two lawn-dominated yards included “high-input lawns” ($n = 4$ per city; yards with at least 75% of the front or back yard pervious area covered in turfgrass for which homeowners self-reported either contracting with a lawn-care company that applied fertilizer or self-applied comparably consistent rates of fertilizer), and “low-input lawns” ($n = 4$ per city; yards with at least 75% of the front or back yard pervious area covered in turfgrass, with “do it yourself” yard care and no fertilizer application within the last year). Within the census block groups identified by the above criteria, we randomly selected 50 parcels per city and visually assessed yard type using Google imagery. We then sent fliers that described the project to the randomly selected lawn-dominated households and provided a link to an online questionnaire. We asked whether the household used a lawn-care company, whether the lawn had received fertilizer in the past year, and whether they would like to “opt in” to the study. For households who opted in, we then randomly selected four yards per city for each lawn category.

The two conservation yards included “wildlife-certified” ($n = 4$ per city; yards certified as a wildlife

habitat through the National Wildlife Federation’s (NWF) certification program (<https://www.nwf.org/Garden-for-Wildlife/Certify>) that included food, water, cover, breeding locations and sustainable practices), and “low-impact on hydrology” ($n = 4$ per city; yards with hydrological features, for example, rain gardens in temperate or tropical BAL, MIA and MSP, or drought-tolerant landscaping in arid LA and PHX). BOS did not have a hydrological treatment because of the difficulty of identifying yards with these features in yards in this city. All sites were at least 1 km from other sites. For wildlife-certified yards, we contacted the NWF for a list of addresses for certified yards for each city that met the yard selection criteria above. The NWF contacted households, provided a description of the study, asked whether the yard still contained habitat features and whether the household would like to participate in the study. For households who opted in, we then randomly selected four yards per city. For the low-impact on hydrology yards, we contacted water districts for each municipality and asked for a list of at least 25 addresses for parcels that have received a rebate for installing a hydrology feature (rain garden or xeriscape). In instances when we were unable to get addresses from the water districts or when the municipality did not have a rebate program, we used Google Earth to find homes with visible rain garden-like structures in the front yard or back yards. We sent fliers to all homes fitting the criteria, with a questionnaire about the presence of the hydrology feature and an option to opt in to the research. We then randomly selected four yards per city for inclusion. Mean parcel size for all yard types was 0.1052 (± 0.0728 standard deviation [SD]) ha. See Appendix S1 for additional detail on the site selection workflow and examples of the yards.

We emphasize that the study design aimed to compare the bird communities in each yard and park management type and not to test the effects of specific activities within a management type (e.g., community responses to fertilizer application). This study design was used as part of a broader assessment of yard management and the impacts on biodiversity, ecosystem function, and social governance (www.residentialmacrosystems.com).

Bird surveys

At each site, a trained observer conducted two limited 50-m radius, 10-min point count surveys (Ralph et al. 1993) divided into three intervals of 3 min and 20 s each during the breeding season (Mar–Apr for PHX and LA, Apr–May for MIA, and Jun–Jul for BAL, BOS and MSP). Counts were conducted in 2017 for PHX, BAL, BOS and MSP, and in 2018 for LA and MIA. For the yards, the center of the point count survey was in front of the house in a location that maximized yard coverage, including the backyard. In the interstitial and reference sites, the point was randomly centered within the other data collection areas. During the count, every individual

bird visually or aurally detected was identified, assigned a distance category from the observer (0–10 m, 10–20 m, 20–30 m, 30–40 m, 40–50 m), a cardinal direction, and for the yard sites, whether it was located within the focal yard. As the point counts covered a 50-m radius area (7,854 m²), we also observed birds in neighboring yards that may have had different yard management from the focal yard. Although the 50-m did not capture the entirety of the parks, we aimed to make relative comparisons among the different sites within a comparable area.

All visits were conducted within four hours of sunrise, on days of low wind, and no precipitation. We conducted two visits per site, separated by at least 10 days between surveys. Our three intervals during each of the two visits resulted in six repeated counts in which we used to model detection of individuals (e.g., Chandler et al. 2011, Hill and Lloyd 2017). We chose this method over collapsing counts to site visits to maximize available data to inform detection probabilities while minimizing number of visits to private land (for efficiency) and time between visit (for site closure; Rota et al. 2009). Models run using the closure method did not produce results that were meaningfully different from those using six repeated counts. Because we were primarily interested in species using the habitat in the yards, we excluded species with large home ranges that were not territorial to the immediate site, such as raptors and scavengers (e.g., hawks, Accipitridae; vultures, Cathartidae, 0.39% of observations), wading birds (e.g., herons, Ardeidae, 0.29% of observations), and aerial foragers (e.g., swifts, Apodidae, 1.40%). We also excluded observations of birds that could not be identified to species (i.e., unknowns, 0.04% of observations) and migratory species observed in regions for which they are not known to breed (e.g., American redstart, *Setophaga ruticilla*, in Miami, 4.50%). See Appendix S2 for more information on processing the final bird observation data set.

Neighborhood-scale land cover

We accounted for neighborhood-scale features not represented by the differences in our land management types as these features also contributed to local bird communities by facilitating or restricting colonization (Lerman and Warren 2011). As proxies for the degree of surrounding urbanization and habitat availability, we used % impervious surface and % tree canopy within a 1 km buffer surrounding each point count location (Daniels and Kirkpatrick 2006, Strohbach et al. 2013, Evans et al. 2017). These two variables were derived from national maps of land cover surface for the conterminous United States in 2011 at 30 m² resolution as part of the National Land Cover Data (NLCD) set (Homer et al. 2015) (<https://www.mrlc.gov/nlcd2011.php>). The canopy cover represented the percentage of the tree canopy's vertical projection that covers the ground. We used R package *raster* (Hijmans 2018) to create buffers and extract surface values from all 30 m × 30 m pixels

within the 1 km-radius buffer in which each pixel was assigned a % impervious surface and % tree canopy. We then took the mean value of all pixels within the buffer for both impervious surface and tree cover separately for each location.

We inspected for potential multicollinearity between impervious surface, tree canopy, and land management type. Impervious surface was moderately correlated with tree canopy ($R^2 = 0.33$), and the variation inflation factor (VIF) was 1.12, suggesting that including both terms would not introduce problems with multicollinearity (Zuur et al. 2010). Similarly, when comparing the land management types with impervious surface and tree canopy, VIF was 1.37 and 1.00, respectively; therefore, we included all three terms in our model. Both tree canopy and impervious surface were centered and standardized to the grand mean (across all cities) prior to analysis (Kéry and Royle 2016).

Statistical analysis

Community occupancy model.—To predict species occupancy among the six management types and our neighborhood-scale features, we used a Bayesian hierarchical community occupancy model (Kéry and Royle 2016, Devarajan et al. 2020, Tingley et al. 2020). This method produces estimates of occupancy for each species that allowed for inference on both site-level community richness and composition and accounted for imperfect detection. We modeled occupancy of species k in site i within city c as a Bernoulli process in which occupancy was a function of the land management type of the site, as well as covariates for the degree of surrounding impervious surface and tree canopy cover. In our model, observation of a species was conditional on occupancy probability (ψ : probability an individual resides in the site), inclusion probability (ω : the probability a species resides in the city) and detection probability (p the probability that an individual is detected by the surveyor given ψ), the latter included a covariate of calendar date to allow detection to vary over the season due to intrinsic variation in activities that influence detection (e.g. singing frequency over the breeding season; Tingley and Beissinger 2013, Kéry and Royle 2016).

To account for differences in the total species assemblages among the six cities, we integrated a multiregion component to the community model (Sutherland et al. 2016). This model structure allowed the estimation of species richness of different regions (i.e., γ -diversity) that varied in potential species pools due to intrinsic environmental features such as ecological biome and climate. In the model, each city had its own community assemblage that we modeled separately but compared via our common parameter of interest, the land management types (i.e., the two park and the four yard types) and the neighborhood-scale land cover variables (impervious surface and tree canopy). By incorporating a multiregion community model, species information and variance can

be shared across both sites and regions (Sutherland et al. 2016). This approach allowed us to estimate city (e.g., BOS, BAL, PHX, etc.) and site-specific (e.g., one of four sampled wildlife-managed yards in a given city) community species pools, determine the effect of land management within each city, and make region-wide inferences about the general trend of land management and land cover across all six cities, the latter being our primary scale of inference. In a hierarchical multispecies occupancy model, species information and variance is shared across the community and improves estimates of rarely detected species (Kéry and Royle 2016). In a multiregion model, information is also shared across regions, improving estimates for species that are possible within a region but never detected (Sutherland et al. 2016). Because some species do not have distributions that overlap all six cities, we also modified the inclusion parameter (w) by a 0/1 binary modifier for whether a species could be observed in a given city based on visually assessing range maps in eBird, the Cornell Laboratory of Ornithology's online citizen science bird observation repository (<https://www.ebird.org>) (Sullivan et al. 2009). In this way, occupancy estimates for species that would never be expected to occur in a region were always zero. For example, our model only allowed Abert's towhee (*Melospiza aberti*) to be estimated for sites within Phoenix, AZ as this bird had an inclusion parameter of zero in all other cities because its distribution did not overlap the boundaries of those cities. Because true richness within a site could also include species that were never detected by any observer but may still be present, we also modeled occupancy using augmented communities (Dorazio and Royle 2005) such that a "hypercommunity" included all species observed as well as additional, non-observed species with detection rates of zero. This method extends our scope of inference beyond the species observed at least once across the six cities to estimate true richness. We augmented the region-wide (i.e., across all cities) species pool to include an extra 50 hypothetical species that could be present within all sites of each city to account for the possibility that species were present but never observed.

Our occupancy model is composed of two hierarchical levels:

Level 1. Detection process: detection as a function of date

$$Y_{cijk} \sim \text{Bernoulli}(Z_{cik}, p_{cijk})$$

where Y is whether or not a species was observed for species k in city c at site i and visit j . This follows a Bernoulli distribution where Z_{cik} is a latent variable representing the true occurrence state of species k in site i within city

c conditional on occupancy (ψ) and p is the probability of successful detection (given occupancy). Detection (p) is a function of a logit-linear model that includes a random intercept a for species k in city c , and covariates of linear date and quadratic date on detection to allow relationships with date to be non-linear.

$$\text{logit}(p_{cijk}) = a_{ck} + \text{date}_{ck} + \text{date}_{ck}^2$$

Level 2. Occupancy process: Species presence as a function of local land management and neighborhood-scale land cover

$$Z_{cik} \sim \text{Bernoulli}(w_{ck} * \psi_{cik})$$

where the predicted occupancy of species k in city c at site i (Z_{cik}) follows a Bernoulli distribution and where w_{ck} is the inclusion parameter that a species k is present in city c and ψ_{cik} is the expected occupancy (ψ) as a function of the logit-linear model:

$$\text{logit}(\psi_{cik}) = \beta \text{impervious}_{ck} + \beta \text{impervious}_{ck}^2 + \beta \text{tree canopy}_{ck} + \beta \text{tree canopy}_{ck}^2 + \alpha \text{land management}_{cikt}$$

where land management type t is one of the six treatments: high-input lawn, low-input lawn, water conservation, wildlife-certified, reference parks and interstitial parks. The term impervious is the mean % impervious surface and tree canopy is the mean % tree canopy in the 1 km buffer. The squared terms allow relationships with impervious and tree canopy to also be non-linear. The effect of land management was modeled as both a community (i.e., region-specific) and species-specific mean response (μ) to land management type t as a normal distribution (N) pulled from a global (i.e., all regions) mean and precision. We accounted for within-city inherent variability between sites of land management type t by modeling a site-specific response of each species (i), in each city to each land management type (Gallo et al. 2017), which was informed by a mean response of that species to a management type.

$$\mu_{\text{global}_t} \sim \text{Logistic}(0, 1)$$

$$\mu_{\text{community}_{ct}} \sim N(\mu_{\text{global}_t}, \tau_t)$$

$$\mu_{\text{species}_{ckt}} \sim N(\mu_{\text{community}_{ct}}, \tau_{ct})$$

$$\alpha_{\text{land management}_{cikt}} \sim N(\mu_{\text{species}_{ckt[c]}}, \tau_{ckt[c]})$$

In our model, occurrence and detection could vary by region and by species within a region, such that a given species k could have different responses within each region to date, land cover, or land management. For all occupancy hyperparameters, we specified a weakly

informative logistic (0,1) prior distribution (Northrup and Gerber 2018) and non-informative Gamma (0.1,0.1) prior distributions for precision.

Model specifications and assessing fit.—We fitted our model to estimate posterior distributions for each parameter using a Markov Chain Monte Carlo (MCMC) method implemented in JAGS v.4.3.0 (Plummer 2003). We ran 300,000 iterations with a 25,000-iteration adaption phase, 25,000 burn-in, six parallel chains, and a thinning interval of 10. This analysis was conducted with parallelization via the *jagsUI* package (Kellner 2018) using R version 3.5.1 (R Core Team 2018). We assessed chain convergence by confirming that the Gelman-Rubin diagnostic statistic (R-hat) was <1.1 (Gelman and Rubin 1992), visually inspecting traceplots, and ensuring sufficient number of effective samples. We also considered model fit using a posterior predictive check based on a chi-square discrepancy (Kéry and Royle 2016).

Derived community metrics.—*1. Species and functional guild richness.*—To determine which site-level responses to use in comparisons with management types, impervious surface, and tree canopy, we used the occupancy estimates for each species from the posterior draws of the MCMC runs. We include the posterior distributions of occupancy parameters for each species in each city in Appendix S3. Using estimates from these parameters, we derived several community metrics. For the estimated total species pool for each metropolitan area (γ -diversity), we summed the city-specific inclusion parameter w . For the estimated species richness of each site (α -diversity) at each iteration we summed the occupancy of all predicted species (the presence or absence of a species; Z -matrix) as site richness and took the mean richness and SD of all iterations.

We were also interested in whether some land management types may filter species of functional guilds that are more sensitive to habitat quality. To look at species richness within functional guilds, we used the predicted presence/absence of each species in each land management type at each iteration. We then grouped species by guild attributes and considered the number of species within the following functional guilds in each site: insectivorous diet, migratory behavior, and origin (native or non-native). We acquired diet from the EltonTraits 1.0 database (Wilman et al. 2014) and origin and migratory behavior from Rodewald (2017).

2. Conservation scores.—Because species differ in their sensitivity to land-use conversion (i.e., habitat loss and alteration from residential development; Blair 1996), we assessed whether the “conservation score” of the bird community differed between the land management types. To quantify, we used the Partners in Flight Avian Conservation Assessment Database

(Will et al. 2019) to assign each species a score based on its population status, distribution range, and life history traits (Smith et al. 2013). Each species was assigned an ordinal value between 1 and 5 in increasing conservation importance, where 1 represented species of low concern and 5 represented highest concern (e.g., endangered species, see Nuttle et al. 2003 for specific criteria for the index). Non-native species (e.g., introduced to the United States) were assigned a value of zero. For each iteration, we multiplied the Z -matrix (presence/absence of a species) by the conservation index for each species and calculated the summed conservation score of the bird community at a site. We then derived a posterior mean conservation score and SD across all iterations for each site of each land management type.

3. Public interest scores.—We were also interested in whether public interest in bird communities varied by land management types. We defined public interest as a desire to learn more about observed bird species by members of the public. To measure public interest in a bird species, we used the “popularity” index for North American birds from Schuetz and Johnston (2019). In short, they defined the “popularity” of a bird species as the residuals of a regression between interest in a bird species (i.e., how often the full common name of a bird is searched for based on Google trend data, <https://trends.google.com>) and how often that bird species is encountered via data from complete checklists (i.e., all birds seen, including common species) submitted to eBird (Sullivan et al. 2009). Positive scores indicate that a bird was searched for more often than predicted from encounter rates (see Schuetz and Johnston 2019 for additional details). For example, species that are colorful, large and charismatic, visit feeders or provide cultural service often have high public interest (Schuetz and Johnston 2019). We recognize that Google searches of bird species names may only sample a subset of the US population that encounters birds, and search trends do not contain qualitative information about why a species was searched. However, this method provides the most accessible and comprehensive measure of public interest in individual bird species at a national scale. The popularity index ranged from -1.56 (Abert’s towhee, *Pipilo aberti*) to 3.56 (Wild Turkey, *Meleagris gallopavo*) and distribution of these scores was unaffected by the exclusion of species not well sampled by point counts prior to analysis. At each iteration, we multiplied the Z -matrix by the popularity index for each species at each site and determined the summed popularity of the bird community. For species that were missing from the Schuetz and Johnston (2019) archived data (six species, mostly Psittacidae), we substituted the mean popularity for the family (see supplemental material for species). For each site, we derived the posterior mean community popularity and SD.

4. Community turnover.—To determine whether some land management types contained a more heterogeneous bird community than others, we compared city-wide turnover in community composition (i.e., β -diversity) among land management types within and across cities. We used our Z -matrix for each site to estimate a metric of community turnover based on presence-absence data (i.e., Sørensen–Dice index, S) (Koleff et al. 2003, Kéry and Royle 2016) between all site pairs within a given management type. For example, turnover between bird communities in site $i = a$ and site $i = b$ of management type (t) “wildlife yard” in city c were compared as:

$$S_{cti} = 1 - \frac{2 * \sum_{ct=1}^{ab} Z_{cti=a}, Z_{cti=b}}{N_{cti=a} + N_{cti=b}}$$

where N is the number of species in the community. High S values indicated high community turnover (e.g., bird communities were more heterogeneous across sampled areas) and low values indicated low community turnover (e.g., bird communities were more homogenous across sampled areas). Species observed in more than one city could also contribute to continental-wide homogenization; therefore, we also looked at S indices between species assemblages within a land management type and across different cities as well (e.g., pairwise comparison of a wildlife yard in BOS with a wildlife yard in PHX). We also calculated species accumulation curves for the six land management types at a continental scale to link how species richness scaled with community turnover. Using the Z -matrix from our occupancy model, we first randomized the order of sites, and then calculated the total supported species, given the number of additional species, from 1 to 20 sites, for each land management type. We did this for each iteration from the model, determined the mean total species over all iterations, and plotted a smoothed logistic curve to visually assess differences in species richness as sampled locations increased.

Community difference models for hypothesis tests.—We tested whether community species richness (α -diversity), functional guild richness (i.e., insectivore, migratory, native origin), conservation and public interest score, and turnover differed among our six land management types and explored the relationships with neighborhood-scale impervious surface and tree canopy percentages. For each site, we used the mean posterior community measure (\bar{Y} ; i.e., species richness, etc.) as the response variable in a separate, complementary Bayesian linear mixed model. To account for uncertainty in our estimates of species richness from the prior occupancy model, we propagated uncertainty of each derived community measure by including the posterior estimates of the reciprocal squared standard error as a residual component in the second model ($\frac{1}{\sigma^2}$; Kéry and Royle 2016). For all comparisons except for continental-wide turnover, we included city as a

random effect in the model. The model for continental turnover did not include any random effects because comparisons were made across cities. We assumed that each city would have a specific trend in relation to each of our parameters; therefore, we allowed both slopes and intercepts to be random and pulled from a region-wide hyperparameter.

$$\mu\beta_{\text{region}} \sim N(\mu, \tau)$$

$$\beta_{\text{city}} \sim N(\mu\beta_{\text{region}}, \tau)$$

$$\begin{aligned} Y_{\text{species richness}} &\sim \alpha 5_{\text{city(land management)}} * \text{land management}_{\text{site}} \\ &+ \beta 1_{\text{city}} * \text{impervious}_{\text{site}} + \beta 2_{\text{city}} * \text{impervious}_{\text{site}}^2 \\ &+ \beta 3_{\text{city}} * \text{tree canopy}_{\text{site}} + \beta 4_{\text{city}} * \text{tree canopy}_{\text{site}}^2 \\ &+ \varepsilon_{\text{site}} \end{aligned}$$

The same model structure was used for subsequent models of insectivore richness, migratory species richness, native species richness, community turnover and conservation, and public interest scores. We assessed distributions of each of our responses using histogram shaped QQ plots and used different error distributions for our separate models appropriate to the response of interest that also accommodated our estimates of precision. Species richness, community turnover, and public interest scores were normally distributed and modeled using a normal distribution (function *dnorm*) with a mean and SD for each site for each metric. Insectivore richness, migratory bird richness, non-native bird richness and conservation scores were bounded by zero and were modeled using a log-normal distribution (function *dlnorm*) with a mean value and the log of the SD for each site. To make model predictions along our neighborhood-scale variables, we used values in between the minimum and maximum values observed for the city to avoid extrapolating past values that were not trained by the data. Community difference models were fitted using the same MCMC techniques with parallelization described above in the occupancy model. We ran 500,000 iterations with a 250,000-iteration adaptation phase, 250,000 burn-in, three parallel chains, and a thinning interval of 10. We assessed chain convergence again using R-hat, traceplots, and effective sample sizes and checked model fit using the chi-square statistic.

RESULTS

Summary

During our 2017–2018 surveys we observed 8,127 individuals of 161 bird species. After discarding observations of species that did not meet our criteria (Appendix S2), we analyzed occupancy of 118 bird species in 151 sites across the six cities with a total of 906 sampling occasions in our final analysis. Of the 118 species, 57 were insectivores, 65 were migratory, and 12 were non-native. The most common conservation score was 1 and

the average popularity score was 0.06 ± 0.70 . For a full account of all species detected, their associated functional traits and diversity scores, see Appendix S4: Table S1. Estimated city species pools (γ -diversity) were higher than those observed (BAL estimated 34, CI: 32–42; observed 32; BOS estimated 49, CI: 39–61; observed 36; LA estimated 49, CI: 44–56; observed 42; Miami estimated 36, CI: 29–43; observed 25; MSP estimated 51, CI: 47–56; observed 46; PHX estimated 40, CI: 35–48; observed 32; Appendix S3: Fig. S1).

Metacommunity occupancy models

Hyperparameters from our occupancy models indicated that, across cities, both neighborhood-scale and local-scale variables influenced the occupancy of the metacommunity, albeit with high uncertainty due to variance across the community (Appendix S3: Figs. S2–S6). Occupancy was negatively influenced by impervious surface at both low (impervious: -1.71 ± 1.71 SD, 90% CI $-3.91, 0.40$) and high (impervious²: mean: -1.80 ± 1.50 SD, 90% CI $-3.73, -0.01$) impervious cover, however credible intervals of the relationship with low impervious surface cover overlapped zero (Appendix S3: Fig. S2). There was negligible influence of tree canopies on occupancy at low (tree canopy: 0.42 ± 1.68 , 90% CI $-1.62, 2.53$) and high (tree canopy²: -1.13 ± 1.81 , 90% CI $-3.42, 1.06$) canopy cover (Appendix S3: Fig. S3). For both variables, relationships between neighborhood cover and occupancy varied among species and among cities. For example, at the city scale, negative relationships with impervious surface were most apparent for BAL, and BOS at low impervious cover and BOS at high impervious cover (Appendix S3: Fig. S2). Positive relationships between tree canopy and occupancy were most apparent in MSP and LA (Appendix S3: Fig. S3). Across cities, mean occupancy of the metacommunity was highest in high-input lawns (0.48) and lowest in interstitial parks (0.09). For species-specific occupancy for each land management type in each city, and

relationships with neighborhood-scale land cover, see Appendix S3: Figs. S8–S31.

Derived community metrics

Species richness.—At a continental scale, species richness was linearly and inversely related to impervious surface cover (Table 1, Fig. 1a) such that approximately 2.5 species were lost for each 10% increase in impervious surface. A negative relationship was apparent in five out of six cities with a positive relationship in PHX (Appendix S5: Fig. S1). There was no effect of tree canopy cover on species richness (Table 1, Fig. 1b; Appendix S5: Fig. S2). After accounting for neighborhood-scale (1 km) impervious surface and tree canopy cover across cities, yards, particularly both lawn types, had more species than both park types across cities (Table 2, Fig. 2a). With few exceptions, these patterns held in all cities (Appendix S5: Fig. S3).

Functional guild richness.—Across cities, we found weak linear negative relationships between impervious surface and both insectivore and migratory bird richness (Table 1; Appendix S5: Figs. S4, S5, S9, S10) and a weak positive linear relationships for insectivorous birds with tree canopy (Table 1; Appendix S5: Figs. S6, S7, S11, S12). Approximately one insectivore and 1.5 migratory birds were lost for every 20% increase in impervious surface and one insectivore gained for every 10% increase in tree canopy. For insectivorous birds, negative relationships of impervious surface were most apparent in MSP and LA, and positive relationships between tree canopy observed in MSP, BOS and BAL. For migratory birds, negative relationships of impervious surface were most apparent in MSP, BOS and BAL. We found differences in guild richness among the land management types for insectivores but not for migratory birds after controlling for neighborhood-scale variables (Table 2; Appendix S5: Figs. S8, S13). Both park types had more insectivores,

TABLE 1. Mean β estimate \pm SD across all cities for the entire bird community in relation to the two land cover variables including both linear and quadratic terms.

Response	Impervious surface	Impervious surface ²	Tree canopy	Tree canopy ²
Species Richness	-2.03 ± 1.10 ($-3.32, -0.75$)	0.51 ± 0.78 ($-0.41, 1.37$)	-0.11 ± 1.10 ($-1.40, 1.12$)	-0.44 ± 0.83 ($-1.37, 0.53$)
Insectivore Richness	-0.14 ± 0.14 ($-0.31, 0.03$)	0.01 ± 0.14 ($-0.16, 0.17$)	0.17 ± 0.21 ($-0.07, 0.41$)	-0.17 ± 0.19 ($-0.39, 0.05$)
Migratory Bird Richness	-0.16 ± 0.14 ($-0.33, 0.01$)	0.00 ± 0.13 ($-0.15, 0.15$)	0.13 ± 0.18 ($-0.08, 0.35$)	-0.10 ± 0.19 ($-0.32, 0.12$)
Non-native Richness	-0.03 ± 0.25 ($-0.32, 0.26$)	-0.09 ± 0.16 ($-0.27, 0.10$)	-0.13 ± 0.29 ($-0.46, 0.20$)	0.14 ± 0.24 ($-0.14, 0.43$)
Conservation Score	-0.17 ± 0.14 ($-0.33, -0.01$)	0.02 ± 0.12 ($-0.12, 0.16$)	0.08 ± 0.18 ($-0.13, 0.29$)	-0.12 ± 0.17 ($-0.32, 0.08$)
Public Interest Score	0.11 ± 0.51 ($-0.48, 0.71$)	-0.06 ± 0.33 ($-0.44, 0.34$)	1.87 ± 2.06 ($-0.41, 4.19$)	0.20 ± 0.84 ($-0.50, 0.92$)

Note: Parameters in bold have 80% credible intervals that do not overlap 0.

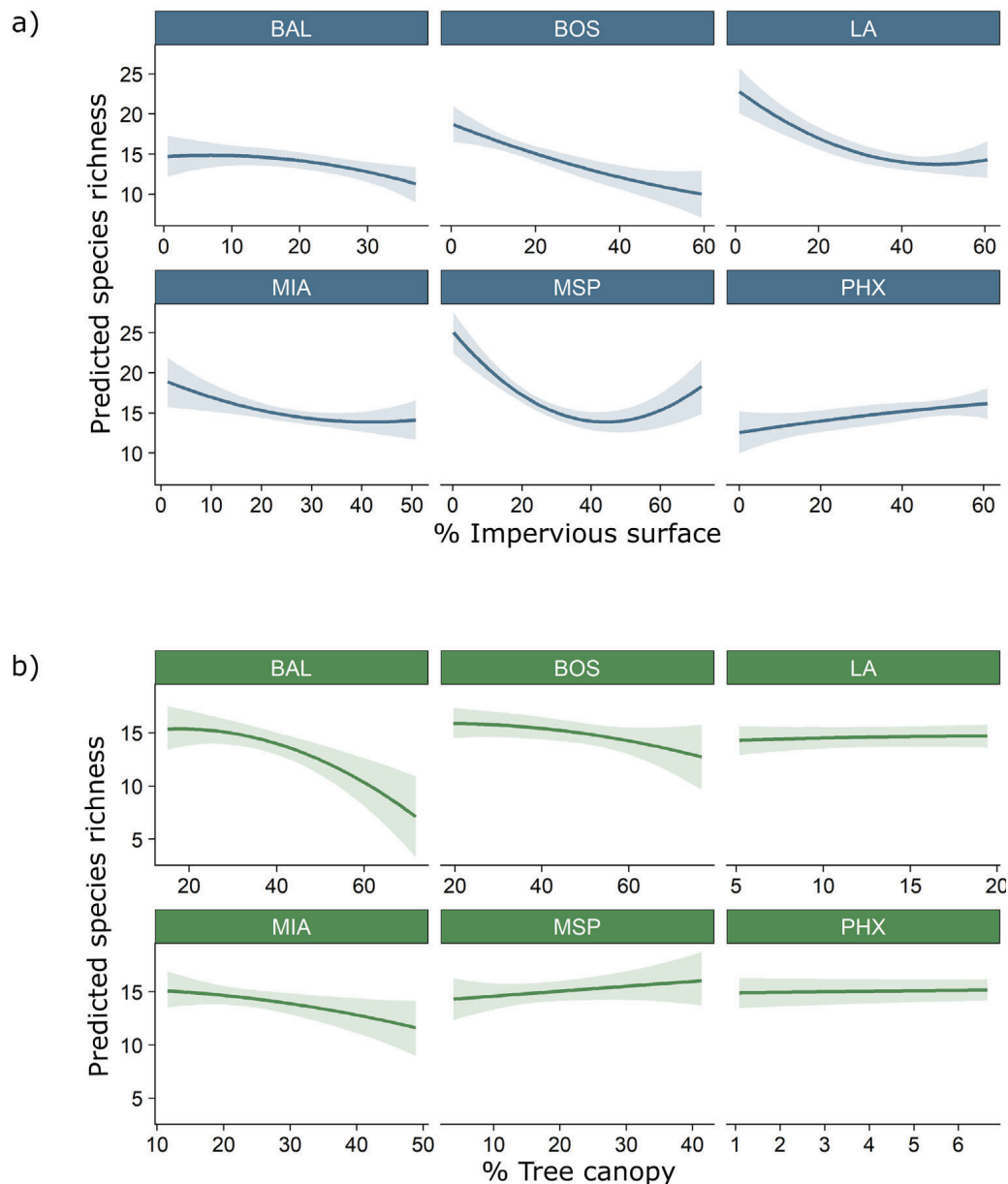


FIG. 1. Model-predicted relationships between species richness (α diversity) and (a) % impervious surface and (b) % tree canopy cover in the six major metropolitan areas. Gray shading is the 90% credible interval of estimated species richness. Predictions were made over the range of impervious surface and tree canopy values sampled in each city.

but similar numbers of migratory species, compared with yards (Fig. 2b, c, respectively). For non-native species, there were no clear relationships with neighborhood-scale land cover variables (Table 1), however non-native species increased with impervious surface in BAL (Appendix S5: Figs. S14–S18). Yards were estimated to have higher richness of non-native species (Fig. 2d); however, numbers of non-native species were generally low, and communities in all land management types were composed of primarily native bird species (Table 2; Appendix S6: Table S1).

Community conservation score.—We found a negative linear relationship between impervious surface and the bird community conservation scores, but no clear relationship between tree canopy and conservation score when accounting for impervious surface and land management type surrounding a site (Table 1, Fig. 3). Relationships with impervious surface resulted in a 6-point loss in the score for every 30% increase in impervious surface; the equivalent of losing six “species not at risk,” three “species of low concern,” two “species of moderate concern,” or 1.5 “species of high concern” (Nuttall et al.

TABLE 2. Mean estimate \pm SD across all cities for the entire bird community in each land management type.

Response	Reference	Interstitial	High-input lawn	Low-input lawn	Water conservation	Wildlife certified
Species Richness	13.55 \pm 1.68	14.88 \pm 1.22	16.46 \pm 1.03	16.19 \pm 0.66	15.49 \pm 0.78	15.34 \pm 1.05
Insectivore Richness	6.04 \pm 1.24	6.52 \pm 1.27	5.26 \pm 1.22	5.43 \pm 1.24	4.88 \pm 1.22	5.14 \pm 1.25
Migratory Bird Richness	7.69 \pm 1.26	7.83 \pm 1.24	7.69 \pm 1.18	8.06 \pm 1.20	7.65 \pm 1.22	7.63 \pm 1.25
Non-native Richness	0.21 \pm 3.78	0.39 \pm 3.04	2.43 \pm 1.31	2.35 \pm 1.31	2.90 \pm 1.37	2.38 \pm 1.23
Conservation Score	17.20 \pm 1.23	17.80 \pm 1.25	15.44 \pm 1.23	16.02 \pm 1.20	15.41 \pm 1.19	15.39 \pm 1.25
Public Interest Score	4.27 \pm 0.93	3.30 \pm 1.01	5.59 \pm 0.46	6.13 \pm 0.52	6.25 \pm 0.57	5.89 \pm 0.52
Community turnover (within cities)	0.36 \pm 0.01	0.41 \pm 0.01	0.29 \pm 0.01	0.34 \pm 0.01	0.32 \pm 0.02	0.39 \pm 0.01
Community turnover (across cities)	0.95 \pm 0.002	0.93 \pm 0.002	0.78 \pm 0.003	0.80 \pm 0.003	0.76 \pm 0.003	0.77 \pm 0.003

Notes: Values are the mean of the posterior distribution of the effective samples, for each parameter. The richness values (Species, Insectivore, Migratory, and Non-native) are the predicted mean number of species for each land management type across all sites and cities. The conservation and public interest scores are the means of the summed scores for each species in the community where higher values indicate a higher cumulative conservation/public interest score of the community. Values in bold are the land management types that were estimated to have the greatest richness or scores of that diversity metric. See Fig. 2 for distributions of the differences relative to the means and Appendix S5 for more specific information about the relationships within each city.

2003). However, negative relationships with impervious surface were not consistent and only apparent in LA, BOS, and BAL while conservation scores increased with tree canopy only in MSP (Appendix S5: Figs. S19–S21). Controlling for neighborhood-scale land cover, we found that interstitial parks supported bird communities with higher conservation scores compared with communities within most yard types (Table 2, Fig. 2e). Nonetheless, all management types supported species of conservation concern (i.e., scores >4 , highest scores for non-endangered species). For instance, we recorded Allen's Hummingbird (*Selasphorus sasin*) in all six management types in LA, Wood Thrush (*Hylocichla mustelina*) in wildlife-certified yards and interstitial sites in BAL and in reference sites in BOS and BAL; California Thrasher (*Toxostoma redivivum*), Oak Titmouse (*Baeolophus inornatus*), and Wrentit (*Chamaea fasciata*) in LA interstitial sites; Boat-tailed Grackle (*Quiscalus major*) in water conservation yards in MIA; Willow Flycatcher (*Empidonax traillii*) in reference sites in MSP and Gilded Flicker (*Colaptes chrysoides*) in reference sites in PHX (Appendix S6: Tables S1–S6). For a full list of all predicted species occupancies in each management type for each city, see Appendix S6.

Community public interest score.—There were no consistent relationships between the public interest of the bird community and impervious surface (Table 1), however, public interest increased strongly with impervious surface in LA and with tree canopy in LA and PHX (Appendix S5: Figs. S22–S25). Public interest scores also differed among the land management types (Table 2). All yard types had a bird community with a higher public interest score compared with the communities within parks; yet among yard management types, we found little difference in the mean popularity of the bird community (Fig. 2f; Appendix S5: Fig. S26). The most popular birds found throughout the six cities and

in all management types included Mourning Dove (*Zenaidura macroura*) and European Starling (*Sturnus vulgaris*). In addition, Blue Jay (*Cyanocitta cristata*), Northern Cardinal (*Cardinalis cardinalis*), and American Robin (*Turdus migratorius*) were ubiquitous throughout the relatively humid cities of BAL, BOS, MIA and MSP. In the arid, western cities of LA and PHX, the most popular bird was Common Raven (*Corvus corax*), which was predicted to occur only in the parks. The species with the most popular score, Wild Turkey (*Meleagris gallopavo*), was only recorded in the low management yards in BOS.

Community turnover across and within cities.—When comparing community composition across the continent, all yard types had lower site-to-site turnover compared with both park types, regardless of management (Table 2, Fig. 4). Turnover across cities differed among yard types but mean differences were negligible compared with the wide difference between yards and parks (Fig. 4a). Within cities, however, turnover among sites differed based on land management (Table 2). High-input lawns had the lowest site-to-site turnover (i.e., more homogenized bird communities) compared with all other yard types and parks. Interstitial park sites, followed by reference parks and wildlife-certified yards, had the highest within-city turnover (Fig. 4b; Appendix S5: Fig. S27) indicating that when scaled to larger areas, reference parks, interstitial parks and wildlife-certified yards supported the greatest number of species (Fig. 4).

DISCUSSION

We assessed the differences in bird communities among multiple land management types across six major metropolitan areas to reveal general patterns of urban bird community assembly across the United States. After accounting for detection and regional differences in

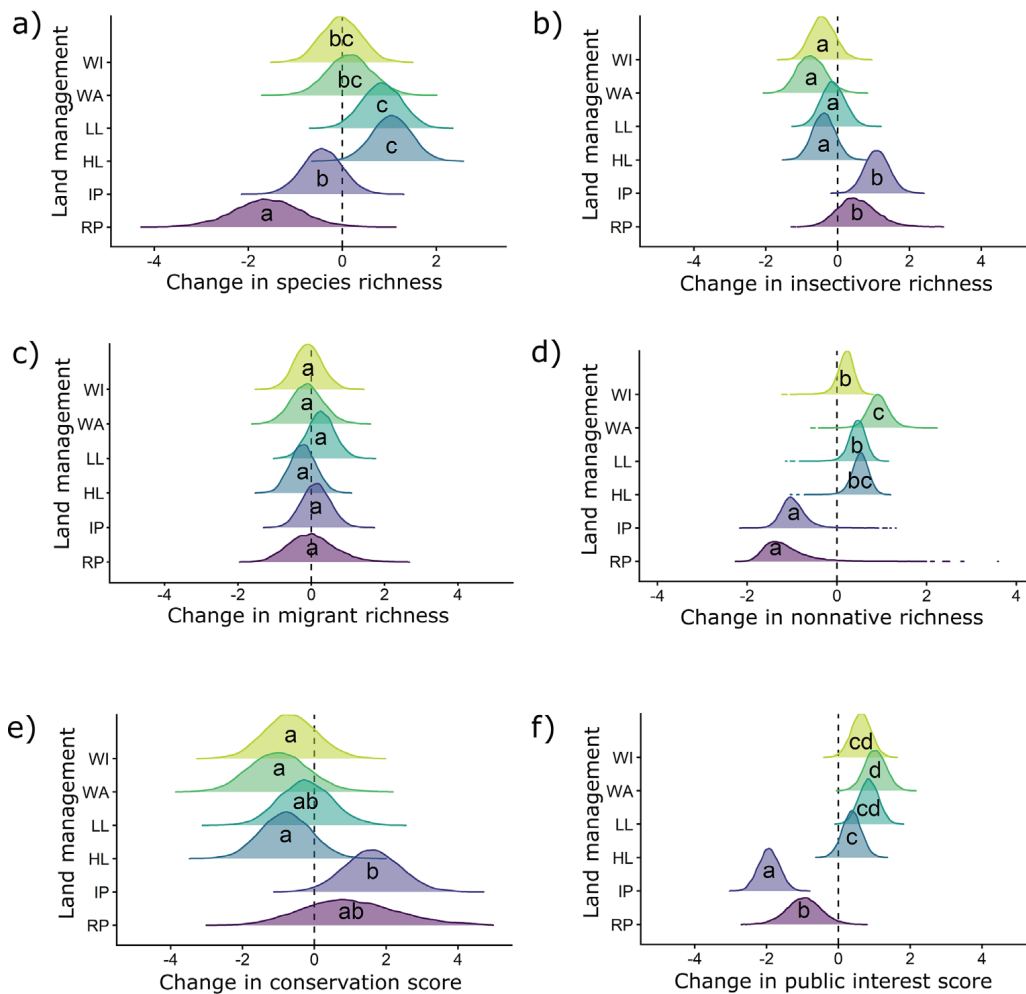


FIG. 2. Posterior distributions of change in richness relative to the mean for (a) Species Richness, (b) Insectivore Richness, (c) Migratory Bird Richness, (d) Non-native Richness, (e) Conservation Scores, and (f) Public Interest Scores for each land management type across all six cities for the entire bird community controlling for impervious surface and tree canopy. Different letters represent that the 90% credible interval of the difference in distributions between two treatments does not overlap zero. Vertical dotted line at zero represents the mean. WI = wildlife-certified yard, WA = water conservation yard, LL = low-input lawn, HL = high-input lawn, IP = interstitial park, RP = reference park.

species pools, we found that, at a continental scale, species richness was strongly related to neighborhood-scale features (i.e., impervious surface and canopy cover) and broad land-use categories (e.g., parks vs. yards) but not strongly related to specific yard management types. When controlling for neighborhood-scale features, species composition differed among the land management types (i.e., parks vs. yards). Parks supported more native species, more insectivores and communities with higher conservation value, while yards supported higher richness overall and taxa with higher public interest scores. Parks and yards supported similar richness and migratory species. We found strong support for differences in biological homogenization between scales; at a continental scale, yards exhibited lower site-to-site turnover compared with parks. However, at a city scale, species compositional turnover was related to yard management types such that the lowest turnover occurred in lawn-

dominated yards, while turnover among wildlife-certified yards was higher than other yard types and comparable with parks. Therefore, although supporting relatively fewer species at a single site, when scaled to larger areas across the city, reference parks, interstitial parks and wildlife-certified yards supported the greatest number of bird species.

Neighborhood-scale features

Our finding that minimizing neighborhood-scale impervious surface can positively affect species diversity concurred with recent studies that landscape-scale variables serve as strong predictors of bird diversity (Lerman et al. 2014, Schütz and Schulze 2015, Batáry et al. 2018, but see: Callaghan et al. 2018). Unique to our study, we showed that these relationships can be generalized across ecological biomes and, to a lesser degree, land

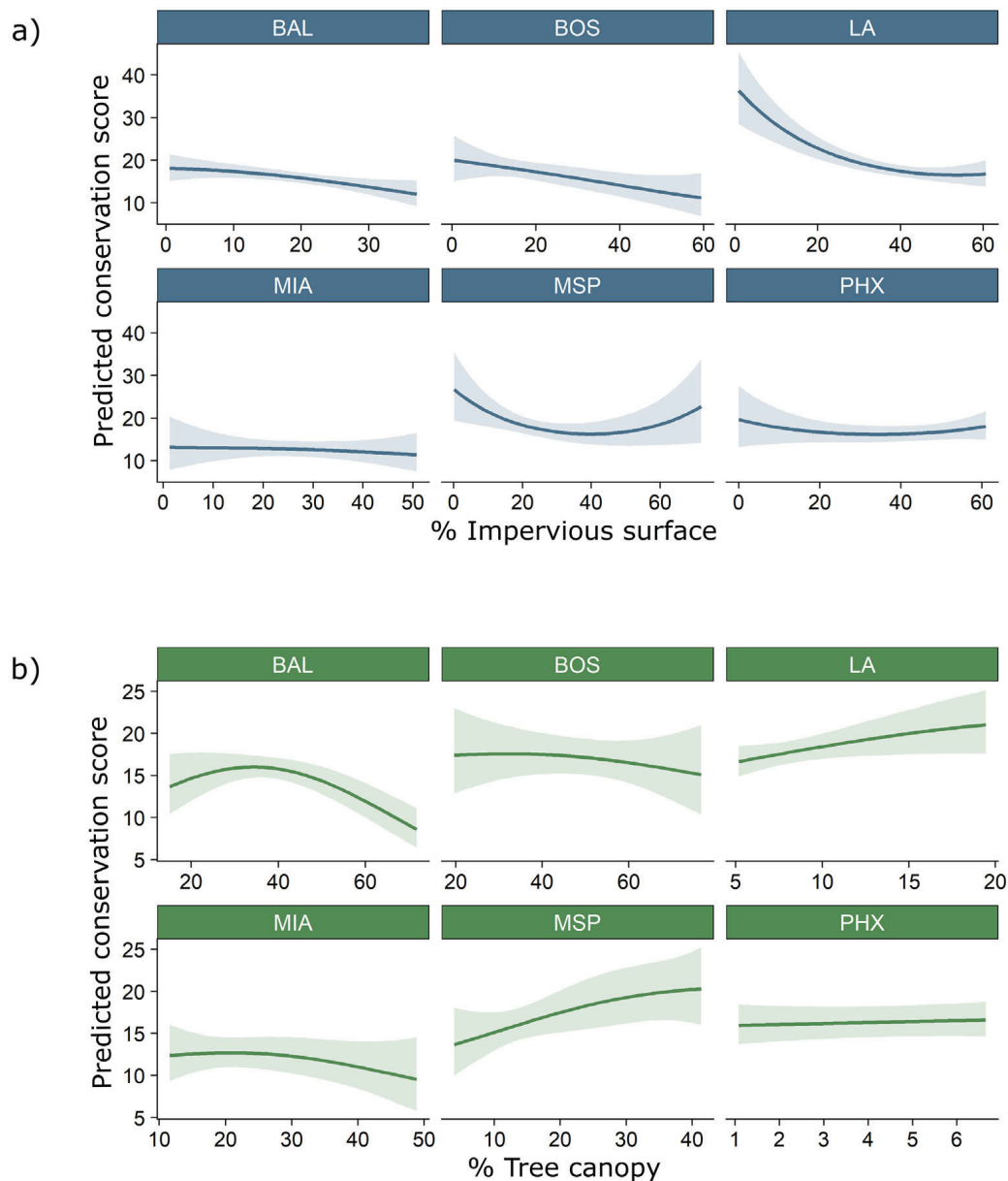


FIG. 3. Model-predicted relationships between predicted conservation scores and (a) impervious surface and (b) tree canopy in our six cities. Gray shading is the 90% credible interval of the estimated conservation score. Predictions were made over the range of impervious surface and tree canopy values sampled in each city.

management types. We acknowledge that we only identified the management type in the focal yard and not neighboring yards or at the neighborhood scale. Nonetheless, when comparing yard management types at the individual yard-scale, we did find consistent patterns, suggesting that the focal yards were likely to have had proximate influence on the full survey area. Overall, we found stronger effects of impervious surface on bird communities than for tree canopies. The effects of impervious surfaces on bird communities are complex. In addition to loss of habitat, other negative effects of impervious surfaces (e.g., roads, pavement, buildings)

include road noise (Goodwin and Shriver 2010, Klingbeil et al. 2020), higher pollution (Roux and Marra 2007), and more artificial light (Ciach and Fröhlich 2017). Impervious surface may also fragment habitat and limit dispersal, even with the presence of an intact mature canopy, because of anthropogenic mortality hazards (Evans et al. 2017, Adalsteinsson et al. 2018). The negative effects of impervious surface (and of urbanization as a whole) may not be fully mitigated by increases in tree canopies alone.

While continental-scale relationships with the canopy appeared to trend positive, relationships were not clear,

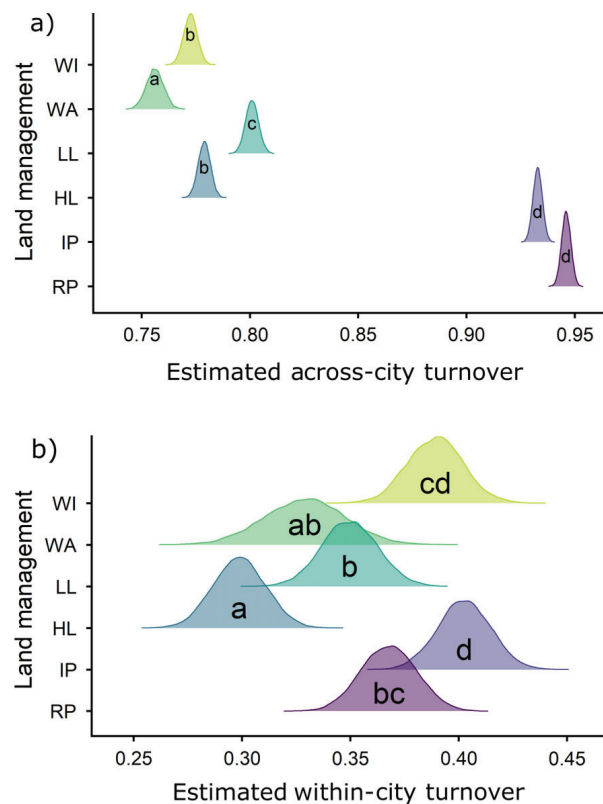


FIG. 4. Posterior distribution of (a) across city and (b) within-city community turnover of land management types across the six cities. Different letters represent that the 90% credible interval of the difference in distributions between two treatments does not overlap zero. WI = wildlife-certified yard, WA = water conservation yard, LL = low-input lawn, HL = high-input lawn, IP = interstitial park, RP = reference park.

and city-specific relationships between bird diversity and increasing canopy cover were linearly positive in some cities, but had diminishing returns or no relationship in others (Fig. 1). This pattern may reflect that, in all cities, our neighborhood-scale metric of canopy cover did not account for the presence of non-native or low quality trees, which can influence habitat quality by reducing the availability of food resources for habitat specialists (Narango et al. 2018, 2020). For example, high tree canopy cover may occur because of the increased presence of popular non-native trees (Avolio et al. 2015), which can strongly increase generalist and non-native bird species richness, albeit at the reduced occupancy of desert specialists and regional species of conservation concern (Warren et al. 2019). These relationships can be particularly striking in arid cities that naturally have low tree densities (e.g., Los Angeles and Phoenix). Similarly, in temperate/tropical cities where we observed some evidence of relationships with tree canopies (Baltimore, Boston, Minneapolis-St. Paul, and Miami; Fig. 1), increases in canopy cover may not necessarily increase species richness, but induce a functional turnover from forest habitat generalists to forest habitat specialists (Blair and Johnson 2008, LaSorte et al. 2018). For

example, we documented positive relationships between tree canopy and insectivorous species, but only in Baltimore and Minneapolis-St. Paul (Appendix S5: Fig. S7). Future research could better address the nature of these functional relationships at a finer resolution. Taken together, our results suggested that relationships between canopy cover and urban avian biodiversity are complex and contingent on multiple factors that should be considered in assessment and conservation efforts.

Heterogeneity in local management

The macroecological relationships between local management and bird diversity were most evident in the coarse-scale land-use difference between parks and yards. Although the yards had higher estimated species richness (Fig. 2a), both park types had higher between-site turnover (i.e., less homogenized communities; Fig. 4) and were composed of the most habitat-specialist, native species, and species with high conservation scores (Fig. 2b–e). The higher continental-wide turnover in the bird community in parks across our six cities reflected differences in regionally specific species pools from which we calculated our estimates. The lower turnover we found in yards (compared with parks) was evidence for a continental-scale ecological homogenization (Groffman et al. 2014) of avian communities, similar to that observed for plant (Pearse et al. 2018), soil (Trammell et al. 2020), hydrography (Steele et al. 2014) and microclimate (Hall et al. 2016) variables. Interstitial parks, i.e., the fragmented green spaces adjacent to residential areas, were comparable with reference natural areas regarding species richness, turnover, and functional guild richness across cities. We recognize that species presence does not equate to species fitness, which may be lower in smaller habitat fragments because of the negative consequences of edge effects or invasive species (Fischer and Lindenmayer 2007). Alternatively, species presence in interstitial parks could signify a lag between habitat degradation and when species are actually lost (e.g., extinction debt; Tilman et al. 1994). When scaling up from a local city scale to the entire continent, parks unequivocally sustain higher bird diversity because they disproportionately preserve regionally appropriate species pools. Our results lend further support to the idea that preserving parkland greenspace in urban areas reduces ecological homogenization at a continental scale. Our simultaneous investigation of land management across six cities demonstrated the essential role that urban parks play in supporting more specialist species and are consistent with a “land-sparing” approach to urban bird conservation (Sushinsky et al. 2013, Dale 2018, Ibáñez-Álamo et al. 2020).

Differences in heterogeneity between fine scale land management (i.e., wildlife-certified vs. lawn-dominated yards) were more apparent within cities rather than across cities (Fig. 4b). Although our results did not support our richness and conservation score predictions

in wildlife-certified yards, we did observe some strong differences among the four yard management types in species turnover and community composition at a continental scale. The bird communities in high-input lawns were more homogenized than bird communities in all other yard types and were mostly composed of urban generalists and some non-native species. The high dominance of lawn limited the plant biomass and vegetation structure within a parcel, which can reduce the availability of resources for birds (Bormann et al. 2001, Belaire et al. 2014, Lerman et al. 2018). Therefore, landscape management that prioritizes the “high-input” lawn aesthetic (Robbins 2007) may serve as a filter by limiting the local urban species pool to species that can utilize this novel resource (Aronson et al. 2016) and/or supplemental food (Galbraith et al. 2015) and, therefore, increase biotic homogenization within urban areas (McKinney 2006) despite high species richness. In addition, low turnover in high-input lawns may result from increased dispersal of urban-generalist and non-native species, given that lawn management is ubiquitous across most US cities (Milesi et al. 2005, Polsky et al. 2014). Conversely, at a city scale, yards with low-input lawn management and wildlife-certified features appear to partially mitigate homogenization by increasing turnover at least within cities (Fig. 4b). This may be explained in part by the decreased occupancy of non-native species in these yard types (Appendix S6: Tables S1–S6) in combination with a more complex yard management design (Widows and Drake 2014, Murthy et al. 2016) or high heterogeneity between yards of similar landscaping styles. This suggests that, in addition to protecting parks, wildlife-certified yards have the potential to contribute to avian conservation by supporting high species richness, reducing homogenization and supporting species that have high public value at the local scales.

Potential values of land sharing for bird conservation

Our results point toward an additional important contribution of wildlife-certified yards to biodiversity within a “land-sharing” approach (i.e., yards as habitat); supporting high species diversity and species valued by the public. Although the species detected in yards had lower conservation scores than parks, they had higher public interest scores (Fig. 1f; Appendix S4 and S6). Human interactions with biodiversity differ between yards and parks (Barbosa et al. 2007), and these interactions, particularly with birds, have implications for human well-being (Fuller et al. 2007). However, it remains unclear whether these scores reflect a cause or an effect. To contextualize, householders might manage their yards to attract the species they like (i.e., causal relationship with public interest scores; Goddard et al. 2013, Belaire et al. 2016). Alternatively, householders may like the birds in their yards because these are the

most familiar species (i.e., an effect of the scores; Lerman and Warren 2011, Belaire et al. 2015). If the former, then efforts to engage the public in managing their yard for species of conservation concern will face additional challenges because this action requests the public to manage for “less popular” species (Belaire et al. 2016). If the latter, then improving yard management to support more species of conservation concern could have positive effects as the public becomes more aware of regional native fauna through interactions in yards (Dunn et al. 2006). Land sharing provides opportunities for increased exposure to diverse bird communities, and can strengthen connections with nature (Luck et al. 2011, Sushinsky et al. 2013) and ultimately lead to more conservation action (Hughes et al. 2018). However, recognizing the complex feedbacks, and the importance of the cultural, in addition to ecological, services birds provide (Robinson 2019) becomes essential for successful conservation in residential landscapes. Although the public interest score might not fully reflect a cause or effect for management, the value of this metric is that it provides an entry point into an initial assessment of interest in (and perhaps interaction with) individual bird species, and highlights the opportunities for expanding conservation partners and future interdisciplinary collaborations between social scientists and ecologists.

Contrary to our prediction, wildlife-certified yards, after controlling for neighborhood-scale features and ecological differences across cities, did not necessarily support higher bird richness, insectivores, or species of conservation concern when compared with other yard designs. Our results might reflect the broader spatial scales in which these yards interact, the scale at which birds respond, and/or the specific habitat features within the wildlife-certified yards. Although we investigated habitat at local (i.e., parcel) and neighborhood (i.e., 1 km) scales, we probably did not capture the variation found at intermediate scales, that is, the collective-effect of multiple neighboring yards (Goddard et al. 2010). It is important to note that our point counts encompassed a 50-m radius, and therefore included multiple parcels adjacent to the wildlife-certified yards (~7 parcels). Yards adjacent to the wildlife-certified parcels were not certified as wildlife habitat (personal communication NWF), although they might have included wildlife features. Nonetheless, wildlife-certified yards probably exist as isolated habitat islands within a matrix of lawn-dominated yards (i.e., a tidy aesthetic and simplified structure; Robbins 2007) reducing habitat quality or colonization.

The wildlife-certified yards in our study included food sources (e.g., fruit-producing plants, bird feeders), water features, vegetative cover, and nesting locations (e.g., dense shrubs, nest boxes), and presumably managed with sustainable gardening practices (e.g., refrained from chemical applications). However, these recommendations do not necessarily include resources that have the most relevance to habitat quality (Gaston et al. 2005).

For example, some wildlife-certified yards may have lacked native plants, (an option, not a requirement for certification), that supply important insect prey and fruit (Narango et al. 2018, Gallinat et al. 2020), or nesting locations free from domestic pets (Marra 2019). It is also important to note, sample size was limited to four wildlife-certified yards per city ($n = 24$), and therefore might not have captured all the variation in this management type both within and across cities. Still, these yards had enhanced plant diversity (Padullés Cubino et al. 2020) that may have contributed in part to the higher turnover in species communities between wildlife-certified yards relative to other yard types. Alternatively, high heterogeneity may be a result of increased opportunities for more diverse bird species using these yards, but lower site occupancy due to exogenous factors (e.g., colonization). In either case, these results suggested that wildlife-certified yards could support more diversity at regional (i.e., the metropolitan area) scales, and when in aggregate.

Our bird diversity results suggest a synergistic, and possibly interactive, role that wildlife-certified yards can play in conjunction with park preservation. By increasing heterogeneity among yards, wildlife-friendly landscaping, although homogenized at a continental scale, can support higher diversity at a city scale compared with traditional yard management (e.g., lawns). Wildlife-certified yards also have the capacity to support sensitive guilds as in insectivorous and migratory species, although the inclusion of the most imperiled species (i.e., those with high conservation scores) may be context dependent. Although not an objective of this study, we posit that the inclusion of wildlife-certified yards could have positive ecological interactions with local parkland by increasing connectivity and reducing edge effects. We suggest that future studies investigate whether the location, frequency and spatial configuration of wildlife-certified yards might lead to stronger responses from the bird community (Lepczyk et al. 2017). For example, locating wildlife-certified yards adjacent to parks and other protected green spaces, in combination with certifying multiple adjacent yards within a neighborhood might increase patch size and connectivity across the urban matrix, and therefore bird diversity (Goddard et al. 2010, Gilroy et al. 2014). Furthermore, research that explores the consequences of full adoption of wildlife-certified yards across the metropolitan area might elucidate the scale in which we can detect differences in conservation scores.

CONCLUSION

Our study tested how urban bird diversity responds to multiple yard management designs and neighborhood landscape features at a continental scale. Although we did not study every biome, nor were the cities evenly distributed in the geographical and environmental space, the study sites are representative of other cities within

similar ecosystems and, therefore, by standardizing methods and randomly sampling cities we can make inferences about bird communities in cities beyond our sampling. We suggest future investigations include additional locations to help refine our conclusions. Moreover, by including multiple diversity metrics such as species richness, functional guild richness and turnover, conservation and public interest scores, we elucidated the complex ways in which the urban bird community responds to different urban management strategies.

Our results clearly demonstrated the importance of parks and other “unmanaged” spaces for supporting diverse communities with species of conservation concern. Yet yards, with their high species richness and high public interest scores, have clear potential to contribute services that are both cultural and ecological. Backyard birds are the species with which the public interacts (DeStefano and DeGraaf 2003), and these interactions increase both interest in and support for conservation action (Hiron et al. 2018). Given the sharp declines of North American birds, including widespread species with high public interest scores (Rosenberg et al. 2019), assessing urban bird communities and how changes at the individual parcel level scale up to continental scales has consequences for evaluating the impacts of future urban expansion and conservation of avian biodiversity. Wildlife-certified yards have the potential to contribute to city-scale heterogeneity and potentially mitigate the ecological homogenization of American residential landscapes.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2455/full>

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Data (Lerman and Narango 2020) are available from the EDI Data Portal: <https://doi.org/10.6073/pasta/712f1faf17c92b6b7508c35ae33c6bfd>.