



RESEARCH ARTICLE

Heterogeneous urban green areas are bird diversity hotspots: insights using continental-scale citizen science data

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Abstract

Context Urbanization fragments and destroys natural landscapes, generally decreasing bird diversity. While in some cases bird diversity continuously decreases in response to urbanization, in others a non-linear response is evident, with peak bird diversity observed at intermediate levels of urbanization. But many studies previously investigating this pattern are spatially or temporally constrained.

Objectives In this study, we analyzed the impacts of urbanization on bird diversity, stratified to native and exotic species. We specifically investigated the

differences in bird diversity between natural and urban green areas.

Methods We used eBird citizen science data (> 4,000,000 bird-survey lists) and remotely-sensed landcover data, throughout the contiguous United States of America.

Results We found a non-linear response to urbanization for both species richness and Shannon diversity. There was distinctly greater bird richness and Shannon diversity in urban green areas compared to natural green areas. Our observed response is likely explained by an increase in habitat heterogeneity of urban green areas compared with natural green areas.

Conclusions Our work highlights the importance of diverse urban green areas for supporting bird diversity in urban areas. We recommend that urban planning should focus on maintaining high habitat

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heterogeneity in urban green areas to promote greater bird diversity.

Keywords eBird · Citizen science · Urbanization · Intermediate disturbance hypothesis · Habitat heterogeneity · Species richness · Shannon diversity

Introduction

More than half (54%) of the world's human population lives in urban areas (United Nations 2014), projected to increase to 60% by 2030 (United Nations Population Fund 2007). Impacts of urbanization on native flora and fauna are complex, driving high rates of local extinction (McKinney 2002) but also creating refugia for rare or threatened species (Madre et al. 2014; Ives et al. 2016). Supporting high urban biodiversity (Dearborn and Kark 2010) is critical for ecosystem services (e.g., social relations and good health, supply of food and fibre, regulation of local and global climate change; Luederitz et al. 2015), with measurable benefits for physical and psychological well-being (Fuller et al. 2007; Cocker et al. 2013; Carrus et al. 2015; Hedblom et al. 2017). Understanding complex interactions between urbanization and biodiversity is paramount for management of biodiversity within constantly evolving urban ecosystems (Savard et al. 2000; Marzluff et al. 2008; Goddard et al. 2010).

Birds are sensitive to habitat change (Chace and Walsh 2006) and are therefore often used as indicators of environmental change (Kushlan 1993; Blair 1999, Sekercioglu et al. 2012). They are relatively easily detected, compared with other taxa, and attract many wildlife hobbyists. As a result, the effects of urbanization on bird biodiversity are relatively well understood (e.g., Blair 1996; Marzluff et al. 2001; Chace and Walsh 2006; Bino et al. 2008; Aronson et al. 2014; Beninde et al. 2015; Lepczyk et al. 2017b). Total bird abundance usually increases while species richness decreases with intensifying urbanization (Chace and Walsh 2006), often non-linearly (Blair 1996; McKinney 2002; Tratalos et al. 2007), with the highest species richness frequently observed within intermediate levels of urbanization (Blair 1996; Germaine et al. 1998; Tratalos et al. 2007; Batáry et al. 2018). However, in some circumstances there are no apparent diversity trends along urban gradients (Chamberlain

et al. 2017), and in others, trends are inconsistent (Garaffa et al. 2009). The non-linear response to urbanization is akin to the intermediate disturbance hypothesis, with peak biodiversity at intermediate levels of disturbance (Connell 1978), with “disturbance” portrayed by the relative level of urbanization (e.g., Lepczyk et al. 2008). These intermediate levels of disturbance are generally some form of urban green area (e.g., remnant native habitat, parks, golf courses, cemeteries), but underlying mechanisms explaining such peaks in biodiversity are complex. Urban green areas are likely more fragmented and include multiple types of habitats within one area (e.g., a golf course frequently includes forested patches, water bodies, and open areas), than comparable natural green areas (e.g., a homogenous forest or grassland), potentially resulting from aesthetic landscape planning in developing urban green areas (i.e., constructed water bodies, wetlands or riparian areas associated with parks). Given the strong relationship between species diversity and habitat diversity (e.g., Recher 1969; Tews et al. 2004), with different assemblages of bird species associated with increased habitat types (Online Appendix Fig. S1), it is likely that urban green areas have high species diversity, based on the diversity of niches they provide due to habitat heterogeneity (e.g., Fahrig et al. 2019).

Urban environments commonly encourage the establishment of exotic bird species (McKinney 2006), whereby exotic species often increase richness and diversity (Green 1984; Blair 1996; van Heezik et al. 2008), sometimes at the expense of native species, which in part can lead to biotic homogenization (McKinney and Lockwood 1999). Few species can dominate urban bird communities, with lower overall species richness, relative to communities in surrounding natural vegetation (Chace and Walsh 2006). This is likely from synanthropy of many exotic species (Blair and Johnson 2008; Sol et al. 2017), but also the ability of some native species to thrive in urban environments (Major and Parsons 2010). In overall assessment of taxonomic diversity, numbers of exotic species within cities tends to be smaller than native species (Aronson et al. 2014). It is therefore important when assessing biodiversity responses to urbanization, to investigate exotic and native species separately (van Heezik et al. 2008). Understanding different habitat requirements of exotic and native birds can guide design of urban landscapes,

minimizing impacts of urbanization, maintaining native bird diversity (Eraud et al. 2007) and sustaining ecosystem function (Hunter and Luck 2015; Luederitz et al. 2015).

Our understanding of the effects of urbanization gradients on both native and exotic bird diversity are generally based on constrained spatial (i.e., a single city; Gavareski 1976; Lancaster and Rees 1979) or temporal survey effort, sometimes focused on breeding seasons (Blair 1996), single years (van Heezik et al. 2008) or relatively few observations (Germaine et al. 1998; Blair 1999; van Heezik et al. 2008). Spatiotemporal constraints limit generalities of our understanding of the effects of urbanization on ecological patterns and mechanisms. The development of general theory has depended primarily on qualitative and descriptive reviews (e.g., Chace and Walsh 2006; Marzluff 2016) or meta-analyses (e.g., Batáry et al. 2018). The burgeoning field of citizen science (e.g., Devictor et al. 2010; Kobori et al. 2015) offers broad-scale empirical datasets, for testing theory at spatiotemporal scales previously unexplored. For example, recent citizen science data has produced new insights into the associations of North American forest bird species with landcover types (Zuckerberg et al. 2016), migration turnover variability in urban areas (La Sorte et al. 2014), effects of anthropogenic drivers on bird diversity in cities (Aronson et al. 2014), and phylogenetic associations between bird families and urban areas (Lepczyk et al. 2017a, b). Such datasets can also cost-effectively explore the impacts of urbanization on biodiversity and outcomes of conservation strategies (Kobori and Primack 2003; Evans et al. 2005; McCaffrey 2005; Cooper et al. 2007; Kobori et al. 2015). Promisingly, some citizen science data has been found to be as reliable as those collected by practicing scientists (Oldekop et al. 2011; Hoyer et al. 2012; Aceves-Bueno et al. 2017; Callaghan et al. 2017).

We used *c.* 4.4 million bird-surveys from the eBird database (Sullivan et al. 2009) to test how bird biodiversity varied along an implicit urbanization gradient, using satellite-derived landcover classes across the contiguous United States of America. We investigated three biodiversity metrics at the level of bird-surveys, separately for native and exotic bird species: species richness, Shannon diversity, and overall abundance. We investigated whether bird biodiversity responses generally followed the

intermediate disturbance hypothesis, where disturbance is reflected in our implicit urbanization gradient, at a sub-continental scale. We then explored possible mechanisms that could explain differences in bird biodiversity in urban green areas, relative to non-urban green areas. We predicted that the surrounding habitat heterogeneity would be higher for bird-surveys within urban green areas compared with natural green areas, resulting in an increase in biodiversity metrics with associated bird-surveys. We then investigated, via a clustering analysis, whether the number and structure of species assemblages (i.e., clusters), differed between urban green areas and natural green areas (Online Appendix Fig. S1), and hence whether differences in the number of species assemblages could be a mechanism explaining any associations with habitat heterogeneity.

Methods

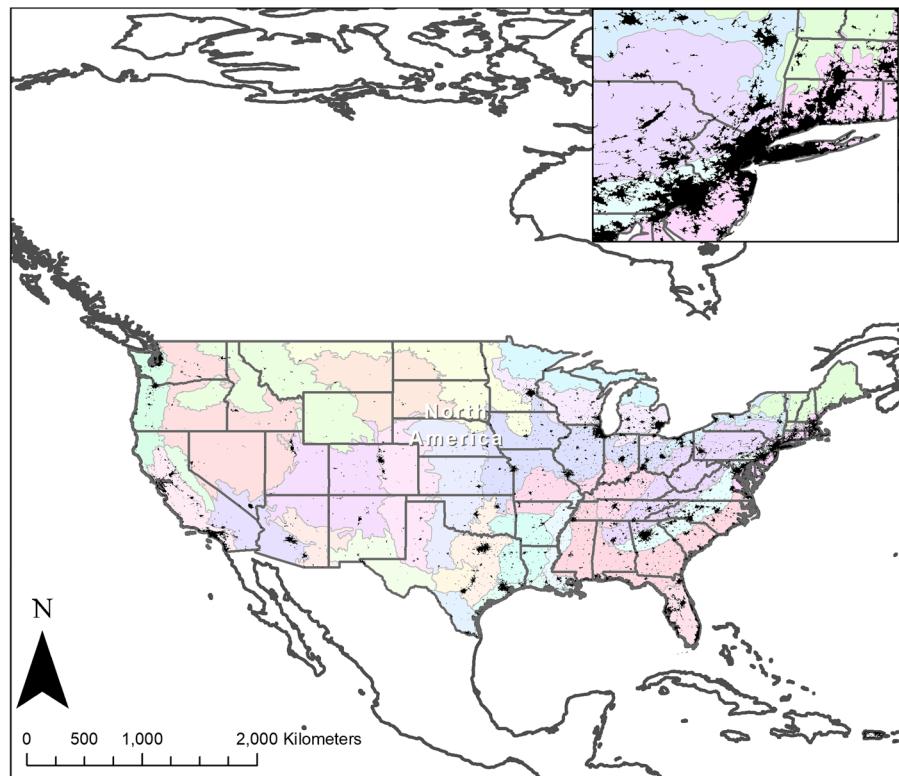
Study area

We used data spanning the entirety of the contiguous United States of America (USA; Fig. 1), where about 600 bird species regularly occur, including a few exotic species, with some regions being ‘hotspots’ for exotic species (i.e., southern California, south Florida, and parts of Texas; Avery and Tillman 1999). We stratified the area using Bird Conservation Regions (hereafter: BCRs), representing biogeographic regions with similar bird communities (US NABCI Committee 2000a, b).

Landscape analysis

We used the National Land Cover Dataset (NLCD 2011), with a 30 m spatial resolution, representing 20 landcover classes (Homer et al. 2015), of which we aggregated 15 (some were only applicable to Alaska, outside the scope of this study) (*sensu* Bonter et al. 2010) to represent six major landcover types along an urbanization gradient: Natural green area, Agriculture, Urban green area, Open-urban, Low-intensity developed, and Medium/high-intensity developed (Table 1). ‘Natural green area’ and ‘Urban green area’ were differentiated from ‘Green area’ (aggregated emergent herbaceous wetlands, woody wetlands, open water, shrub/scrub, deciduous forest,

Fig. 1 Spatial extent of the study across contiguous USA, showing the colored Bird Conservation Regions (<http://nabci-us.org/resources/bird-conservation-regions-map/>; see link for associated legend of BCRs), and measure of urbanization, based on 2014 census data (black areas). The inset shows a zoomed in portion illustrating the extent of urban habitat



evergreen forest, and mixed forest), by overlaying a measure of urbanization. We used the United States Census Bureau's map of urban area (United States Census Bureau 2014; Fig. 1), which defines urban areas throughout the United States, relying on a definition based on population density and other land-use characteristics to identify densely developed territory (see more here: <https://www.census.gov/geo/reference/urban-rural.html>).

Bird surveys

We used the eBird dataset, a large citizen science dataset, housed at the Cornell Lab of Ornithology (Sullivan et al. 2009; Wood et al. 2011; Sullivan et al. 2014), with greater than 600 million global bird observations (Sullivan et al. 2017). Volunteer observers record the species seen while birding, start time, date, duration, distance covered, and number of individuals of each species. A 'checklist' provides this information from an individual observer, submitted via the eBird app or website. Each eBird checklist, regardless of observation protocol (see below), is georeferenced by the user. Volunteer experts develop

regional filters on the distribution and maximum number of individuals for each species as a quality control (Wood et al. 2011). When counts or identifications trigger thresholds, the record is flagged for further scrutiny by an expert reviewer. eBird data provide a unique source of ecological data, differing from that of structured citizen science projects (Callaghan et al. 2018a, b), and have been used in > 220 peer-reviewed publications. When biases are accounted for (see below) eBird can provide valuable data for understanding ecological patterns (Sullivan et al. 2014; La Sorte et al. 2018a).

We downloaded the eBird basic dataset (version ebd_relNov-2017: <https://ebird.org/data/download>), consisting of observations between January 1st, 2010 and November 31st, 2017. The checklists were overlaid with landcover classes and BCRs and all observations not associated with a landcover class or BCR (i.e., erroneously plotted points, or pelagic observations) were omitted from analyses. eBird checklists were included according to the following criteria: (1) only complete checklists were included (all birds seen and/or heard); (2) a travel distance < 2.5 km; (3) recording duration of 5–240 min; and (4) followed the

Table 1 Six aggregated landcover classes used in the analyses to investigate bird species diversity based on the 2011 National Land Cover dataset (NLCD 2011)

Landcover classes from NLCD 2011	Aggregated landcover class
Emergent herbaceous wetlands	Natural green area/Urban green area ^a
Woody wetlands	Natural green area/Urban green area ^a
Open water	Natural green area/Urban green area ^a
Shrub/scrub	Natural green area/Urban green area ^a
Deciduous forest	Natural green area/Urban green area ^a
Evergreen forest	Natural green area/Urban green area ^a
Mixed forest	Natural green area/Urban green area ^a
Cultivated crops	Agriculture
Pasture/hay	Agriculture
Grassland/herbaceous	Agriculture
Developed open space	Open-urban
Barren land	Open-urban
Developed, low intensity (20–49% impervious surface)	Low intensity developed
Developed, medium intensity (50–79% impervious surface)	Medium/high intensity developed
Developed, high intensity (80–100% impervious surface)	Medium/high intensity developed

^aNatural Green Area and Urban Green Area were split from a broad category, ‘Green Area’, by overlaying the spatial data with the 2014 United States Census Bureau cartographic boundary file (United States Census Bureau 2014), which served as a measure for urban habitat

‘stationary’, ‘travelling’, or ‘exhaustive’ protocols, removing any incidental checklists (see Sullivan et al. 2014). The objective of this approach was to filter the sampling events to the ‘best quality’ lists, limiting the undue leverage that outliers of distance or time would have on the results (*sensu* La Sorte et al. 2014). Following filtering, there were 4,358,517 checklists which were spatially intersected with the aggregated landcover classes (defined above; Table 1).

Statistical analysis

Each checklist was treated as an independent survey, accounting for temporal and spatial autocorrelation. For each checklist, three biodiversity response variables were calculated for exotic and native bird species, separately: (1) species richness, the total number of species on a checklist; (2) effective Shannon diversity $\left[\text{i.e., } H' = e \left(- \sum_{i=1}^R p_i \ln p_i \right) \right]$, the exponential transformation applied to the standard Shannon diversity index (Jost 2006; Leinster and Cobbold 2012); and (3) total abundance, the total number of individuals reported on each checklist. The latter two were only applied to checklists with abundance estimates for

each species; if observers reported ‘presence only’ for a single species, that checklist was excluded from analysis for Shannon diversity and abundance but included for species richness. Vagrants and seabirds were eliminated from potential analyses (see Online Appendix Table S1 for a list of species analysed and their exotic or native classification).

We then fitted Generalized Additive Models (GAMs; Wood 2006) separately to each response variable, and for native and exotic species, testing the association between the response variables and the aggregated landcover classes. GAMs extend Generalized Linear Models where the linear predictor is given by both traditional parametric terms, plus a sum of some set of smooth functions of the covariates, increasing the flexibility of linear models by modelling unknown non-linear relationships with multiple predictors, including continuous and categorical linear terms. After initial exploration of alternative error distributions (e.g., Poisson, Tweedie), where models were developed and compared using the deviance explained of the models; all models were fitted using log-transformed response variables with a Gaussian distribution. This was a pragmatic decision, given that our large sample sizes reduced the importance of error

distribution choice (Ghasemi and Zahediasl 2012), and we aimed to keep the response variable consistent among models allowing the added advantage of keeping the estimates and effect sizes on the same scale. GAMs were fitted using a quadratically penalized likelihood approach, and the smoothing parameters were estimated via Generalized Cross Validation. This controlled the trade-off between model complexity and model fit.

To account for the possible temporal autocorrelation and non-independence of eBird checklists, we included a smooth term (cyclic cubic regression spline) for week of the year in the models. This also allowed us to investigate changes in diversity throughout the full annual cycle (Marra et al. 2015). To account for possible spatial autocorrelation, we included latitude and longitude as smooth terms (thin plate regression spline). To account for the effect of survey effort, varying among checklists, we included another smooth term of effort (survey duration, minutes) per checklist (thin plate regression spline). We also included BCRs as a random effect (parametric terms penalized by a ridge penalty) to account for inherent differences in bird diversity among BCRs, that was not of interest in this analysis. We used the *bam* fitting function in the 'mgcv' package (Wood 2004), within the R statistical environment (R Core Team 2016). Inclusion of a smooth term for temporal autocorrelation allowed us to investigate empirical relationships of predicted biodiversity metrics in response to the urbanization gradient, after accounting for temporal autocorrelation. We further wanted to make inferences about temporal effects on biodiversity metrics as they related to the landcover classes. To do this, we refitted the same models, but fitted the smooth term (cyclic cubic regression spline) for week 'by' each of the categorical landcover classes, allowing specific smooths to be visualized and interpreted for each of the landcover classes in our analysis.

To test for differences in habitat heterogeneity within urban green areas and natural green areas, we used the previously assigned classifications of all eBird checklists in the associated aggregated landcover classes. Each point was then given a 5 km buffer using Google Earth Engine (Gorelick et al. 2017) and within these buffers the number of pixels of each of the original 15 landcover classes (Homer et al. 2015) was counted (Table 1). We calculated Shannon entropy, $-\sum_{i=1}^n P(x_i) \ln P(x_i)$, where $P(x_i)$ was the proportion

of pixels in class i , as the measure of habitat heterogeneity of each buffer's habitat pixel counts. Any buffers not completely within our study area were eliminated. Habitat heterogeneity was calculated for a total of 1,772,327 eBird checklists (1,157,641 in natural green area and 614,686 in urban green area). We tested for significance between habitat heterogeneity in urban green area and natural green area using a t test. We then assessed whether there was a positive relationship between habitat heterogeneity of a given eBird checklist and bird biodiversity (species richness and effective species diversity).

To explore whether there was a difference in the structure of bird assemblage data between urban green and natural green areas, we used a cluster analysis. First we created a matrix where the rows (or the 'sites') summarised species' observations (columns) for each unique locality (i.e., any unique checklist), separately for each BCR. The proportion of checklists on which a bird was reported, for a given locality (some unique localities have many submitted checklists) was the response variable in the matrix. We then used k-means clustering, a non-hierarchical method (Hartigan and Wong 1979), to cluster the species composition data from the checklists into distinct bird assemblage clusters. The analysis was stratified to each BCR. K-means clustering required a priori specification of the number of clusters, and we chose the best number by minimising the Akaike Information Criterion (AIC), which performs well for ecological community classifications (Lyons et al. 2016). Each checklist thus had membership to a 'bird assemblage cluster', and clusters were assigned independent of the corresponding landcover designations of the checklist data.

To assess differences in the structure of the bird assemblage data between urban and natural green areas, we calculated Shannon entropy for urban and natural green areas on the distribution of site membership to each cluster. For each BCR, we derived two entropy values, for urban and natural green, describing the degree of spread of sites among clusters. We then performed a two-way t test to test whether there were significant differences in urban versus natural green areas. In addition, we qualitatively assessed whether each cluster could be described as either an 'urban' or 'natural' assemblage. We also visually investigated the proportional difference between number of sites which belonged to urban and natural green areas for each cluster. Finally, to determine whether particular clusters

were contributing more than others to bird diversity, we calculated the total species richness assigned to each cluster and plotted this against the calculated proportional differences.

Results

A total of 4,357,492 checklists were included in the analyses, of which 2,017,881 (46%) had exotic species and 4,354,327 (99%) contained native species. For analyses of effective species diversity and species abundance 3,910,314 checklists were included; of which 1,773,563 checklists (45%) had exotic species and 3,907,235 checklists (99%) had native species. The overall mean \pm SD checklists per BCR was $219,731 \pm 228,867$ (Online Appendix Table S2) with the largest number of checklists originating from the New England Mid-Atlantic Coast (944,367) and the fewest from Badlands and Prairies (18,139). The landcover class with the most checklists was natural green area (1,680,016 and 1,501,707 for species richness and species diversity/abundance respectively) while the fewest originated in medium/high-intensity developed area (558,519 and 499,836 for species richness and species diversity/abundance respectively; Table 2).

Bird diversity patterns in response to an urbanization gradient

Abundance

All parametric predictors in the models were significant ($p < 0.001$), reflecting the large sample size. As a result, we focused on empirical patterns of predicted

abundances and effect sizes – effect sizes are shown in parentheses. Our smoothed terms for temporal autocorrelation (week), spatial autocorrelation (latitude and longitude), and effort (minutes per checklist) were significant for both native (Deviance explained = 21.7%) and exotic abundance (Deviance explained = 8.8%) models (see Online Appendix Table S3 for full model outputs). The predicted abundance of native species on a checklist (Fig. 2a) was lowest in medium/high intensity developed, followed by open-urban, low-intensity developed, and natural green area. The highest predicted native abundance on a checklist was found in urban green area, followed by agriculture. The effect size for native species abundance for urban green area (64.45) was greater than natural green area (60.07), while the effect size for agriculture (67.05) was significantly greater than all other landcover classes, aside from urban green area (Online Appendix Fig. S2). Overall predicted abundance on a checklist of native species was also $\sim 9 \times$ higher than for exotic species.

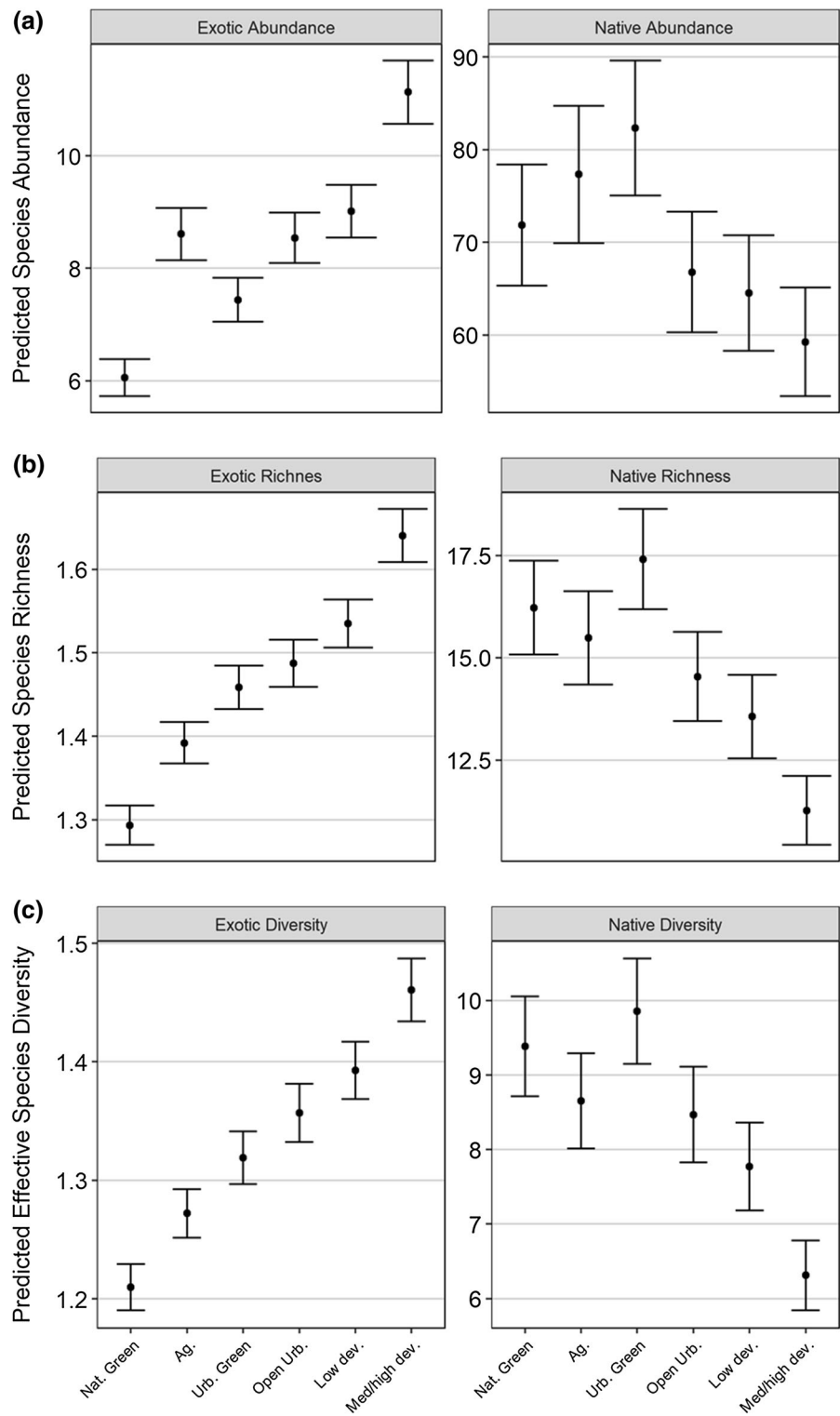
These patterns for native bird species contrasted to those of exotic bird species abundance. The predicted abundance of exotic species on a checklist (Fig. 2a) generally increased along our urbanization gradient: the lowest predicted abundance was in natural green area and the highest in medium/high intensity developed. There was a slight peak of predicted abundance in agriculture. Similarly, the effect sizes showed a similar general trend to the empirical predicted patterns, but the confidence intervals for all effect sizes overlapped (Online Appendix Fig. S2). Both exotic and native abundances were intra-annually variable: decreasing in abundance on a checklist during the spring and highest during the winter

Table 2 Number of eBird checklists (1 January 2010–31 November 2017), per six landcover types

Landcover	Total number of checklists used in analyses	
	Species richness	Species diversity and species abundance ^a
Natural green area	1,680,016	1,501,707
Agriculture	1,057,787	950,346
Urban green area	1,071,179	932,292
Open-urban	1,234,717	1,106,609
Low-intensity developed	769,999	690,008
Medium/high-intensity developed	558,510	499,836

^aFewer checklists were used for species diversity and species abundance because abundance estimates were not available for every species observed

Fig. 2 Mean (\pm standard error) predicted model results for **a** species abundance, **b** species richness, and **c** effective species diversity in response to six landcover classes for both exotic and native species. *Nat. Green* natural green area, *Ag.* agriculture, *Urb. Green* urban green area, *Open-urb.* open-urban, *Low Dev.* low-intensity developed, *Med/high Dev.* medium/high-intensity developed. Responses were predicted from Generalized Additive Models and represented the total response variable observed on a given eBird checklist. See Online Appendix Table S3 for full model details and Online Appendix Fig. S2–S4 for parameter estimates (effect sizes) corresponding to each of the 6 model results. Note the different scales on the y-axes



(northern hemisphere). These intra-annual temporal patterns were similar for all landcover classes (Online Appendix Fig. S5).

Species richness

All parametric predictors in the native species richness model were significant ($p < 0.001$), reflecting the large sample size, but not in the exotic species richness model. Our smoothed terms for temporal autocorrelation (week), spatial autocorrelation (latitude and longitude), and effort (minutes per checklist) were significant for both native (Deviance explained = 37.8%) and exotic species richness (Deviance explained = 8.4%) models (see Online Appendix Table S3 for full model outputs). Predicted native species richness generally decreased in response to the urbanization gradient (Fig. 2b): predicted native species richness was lowest in medium/high intensity developed, followed by low-intensity developed, and open-urban. The highest predicted native species richness was in urban green area, followed by natural green area, and agriculture. The effect sizes for native species richness (Online Appendix Fig. S3) were similar to empirical predicted results: medium/high intensity developed (11.91) was less than the other landcover classes, and although no significance in effect sizes existed among the other landcover classes, urban green area (14.77) had a stronger effect size than natural green area (13.97).

The patterns for exotic species contrasted those of native species richness: predicted exotic species richness generally increased in response to the urbanization gradient, with the lowest predicted exotic richness in natural green area and the highest in medium/high intensity developed. We note that the difference in predicted exotic species richness across the urbanization gradient had a relatively low magnitude of increase (i.e., 1.65 in medium/high intensity developed and 1.28 in natural green area). The effect sizes for the exotic species richness model all overlapped and showed no discernible trends (Online Appendix Fig. S3). Both exotic and native species richness were intra-annually variable: increasing in richness on a checklist during the spring period and another slight peak in the fall period. These intra-annual temporal patterns were similar for all landcover classes (Online Appendix Fig. S6).

Species diversity

All parametric predictors in the models were significant ($p < 0.001$), reflecting the large sample size. Our smoothed terms for temporal autocorrelation (week), spatial autocorrelation (latitude and longitude), and effort (minutes per checklist) were significant for both native (Deviance explained = 35.7%) and exotic effective species diversity (Deviance explained = 7.9%) models (see Online Appendix Table S3 for full model outputs). Predicted native effective species diversity on a checklist was lowest in medium/high intensity developed and highest in urban green area (Fig. 2c). Generally, predicted native species diversity decreased with increasing urbanization. Urban green area had a higher predicted native species diversity than natural green area. Although there were no significant differences in landcover effect sizes for native effective species diversity, there was a similar pattern to empirical predicted results (Online Appendix Fig. S4). The effect size was lowest for medium/high intensity developed (6.64) and urban green area (8.52) had a stronger effect size than natural green area (7.99).

These empirical patterns for exotic effective species diversity contrasted to those of native effective species diversity. Predicted exotic effective species diversity generally increased with urbanization (Online Appendix Fig. S4): the highest predicted effective species diversity was in medium/high intensity developed landcover and the lowest was in natural green area. There were no discernible or significant trends in effect sizes for the exotic effective species diversity model, but the strongest effect size was in medium/high intensity developed (1.47), contrasting with the lowest in natural green area (1.20). Both exotic and native effective species diversity were intra-annually variable (Online Appendix Fig. S7): for both response variables there was a distinct peak in the spring followed by a moderate peak in the fall. Temporal trends among landcover classes were generally consistent, but for exotic effective species diversity, the strongest temporal signal was in medium/high intensity developed and the lowest in natural green area.

Potential drivers of biodiversity metric differences

Mean habitat heterogeneity in urban green areas (1.76 ± 0.27 sd, $N = 614,684$) was significantly

greater than in natural green areas (1.42 ± 0.51 sd, $N = 1,157,636$; Fig. 3; $t = 566.33$, $df = 1,772,300$, $p < 0.001$). Overall, there was a positive relationship between native species richness on an eBird checklist and the surrounding habitat heterogeneity of an eBird checklist, but this was stronger for natural green areas than urban green areas. There was minimal influence of habitat heterogeneity on exotic species richness of an eBird checklist (Online Appendix Fig. S8). For effective species diversity, there was a positive relationship between native effective species diversity on an eBird checklist and the corresponding habitat heterogeneity for those checklists in urban green areas, contrasting with a negative relationship for those eBird checklists assigned to natural green areas. There was also a positive relationship between exotic effective species diversity on an eBird checklist and habitat heterogeneity in urban areas, but a slightly negative relationship for natural green areas (Online Appendix Fig. S9).

The number of distinct bird assemblage clusters per BCR ranged from 4 (Chihuahuan Desert & Edwards Plateau) to 30 (Appalachian Mountains), with a mean of 14.2 ± 7.8 sd (Online Appendix Fig. S10). Overall, entropy of site membership to the clusters was not significantly different between urban green areas

(2.89 ± 1.02 sd), compared to natural green areas (3.02 ± 1.02 sd, Fig. 4; $t = -0.48$, $df = 56$, $p = 0.632$). Proportional differences between clustered sites in urban and natural green areas, were almost evenly split, with only some clusters trending towards “natural green assemblages” or “urban green assemblages” (Online Appendix Fig. S11). Similarly, there was little difference between the total species richness of a given cluster and its proportional difference, although if a cluster was strongly associated with urban green areas, it tended to have higher species richness values (Online Appendix Fig. S12).

Discussion

This study demonstrated, at a continental scale, that native bird species richness, effective species diversity, and species abundance generally decreased in response to an urbanization gradient (sensu Blair 1996), while exotic bird species richness, effective species diversity, and abundance generally increased with urbanization. Bird responses to varying urban gradients have been well studied (Beissinger and Osborne 1982; Clergeau et al. 1998; Blair 1999; Cam et al. 2000; Crooks et al. 2004; Filloy et al. 2019), albeit with different definitions of urban gradients (cf Blair 1996; Crooks et al. 2004; Filloy et al. 2019) and

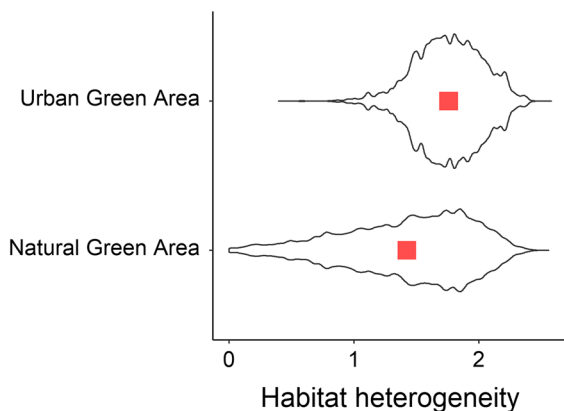


Fig. 3 The distribution (violin plot) of habitat heterogeneity (i.e., Shannon entropy of underlying habitat pixel values in a given 5 km buffer surrounding an eBird checklist) for 1,157,641 and 614,686 buffers in natural green and urban green areas, respectively. The red box represents the overall mean. The habitat heterogeneity is significantly greater in urban green areas than natural green areas ($t = 566.33$, $df = 1,772,300$, $p < 0.001$). The violin plot draws the kernel density distribution, showing the distribution of data points: the widest area represents the mode(s)

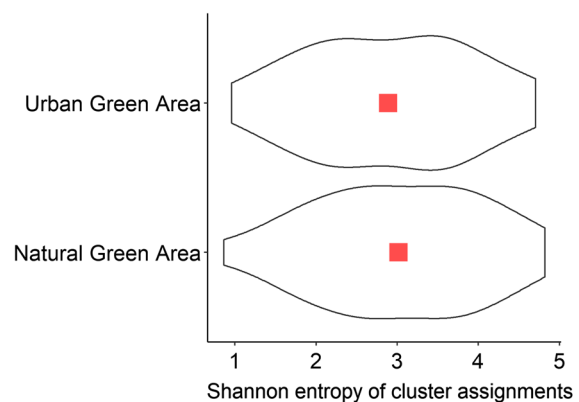


Fig. 4 The distribution (violin plot) of Shannon entropy for the number of bird assemblage clusters for each of urban green area and natural green area. The red box represents the overall mean. There was no significant difference between the number of species assemblages from urban green and natural green areas ($t = -0.93$, $df = 55.9$, $p = 0.356$). The violin plot draws the kernel density distribution, showing the distribution of data points: the widest area represents the mode(s)

different definitions of urban environments (McIntyre et al. 2000). But we took analysis to a continental scale using large spatial-scale citizen science data and, importantly, added explanatory power by associating a remotely-sensed landcover map (Homer et al. 2015) in a reproducible workflow. Our broad-scale results support the conclusions of previous studies (Gavareski 1976; Lancaster and Rees 1979; Beissinger and Osborne 1982; Cam et al. 2000), adding to our generalized understanding based on more local studies. Our analysis found that bird biodiversity patterns varied between different metrics of biodiversity, whether species were native or exotic, and with landcover changes.

Although urbanization increases establishment of exotic bird species (McKinney 2006) and we found that exotic bird species biodiversity metrics increased with urbanization, native bird species still dominated highly urbanized areas for all three biodiversity metrics (Fig. 2). Even in the medium/high intensity developed landcover, our models predicted respectively 590%, 330%, and 440% increases of native to exotic species richness, effective species diversity, and abundance, aligning with current global understanding (Aronson et al. 2014). Importantly, there was a non-linear relationship between diversity and categorical levels of urbanization (Jokimäki and Suhonen 1993; Blair 1999; Marzluff 2016; Batáry et al. 2018), contrasting findings that negative-impact of urbanization on bird diversity is constant (Clergeau et al. 2001, 2006; Sandström et al. 2006).

Urbanization is an ecological disturbance, with the intermediate disturbance hypothesis providing a useful conceptual tool to frame the impacts of urbanization gradients and spatial heterogeneity on bird communities (Lepczyk et al. 2008), even though it usually also incorporates temporal heterogeneity (Connell 1978). High levels of urbanization equated to low levels of bird biodiversity compared with low levels of urbanization, while intermediate levels of urbanization (i.e., urban green area) provided the highest levels of bird biodiversity (Fig. 2). These results conform to the intermediate disturbance hypothesis, likely resulting from intermediate levels of urbanization providing high levels of habitat heterogeneity (Fig. 3) and thus resources (Connell 1978). Our analysis categorically assigned landcover classes to an implicit urbanization gradient which requires more analysis including development of

continuous measures of the urban gradient and investigation of what role spatial heterogeneity plays in reducing species dominance, reflecting the intermediate disturbance hypothesis.

We identified intra-annual changes in biodiversity responses, accounted for in the systematic part of our modelling (Online Appendix Table S3). There was a distinct peak in biodiversity metrics throughout the spring, probably reflecting migration (La Sorte et al. 2014). This was generally consistent among landcover classes, suggesting that our empirical analysis (Fig. 2) also picked up temporal biological processes. The extent of intra- and inter-annual differences in bird biodiversity responses to urbanization (La Sorte et al. 2014; Marra et al. 2015; Zuckerberg et al. 2016; La Sorte et al. 2018c) could be further examined by explicitly identifying important times of year for bird biodiversity, allowing for better management and conservation of urban bird biodiversity.

Our results have implications for understanding responses of ecological processes to urbanization, useful for conservation and management. Urbanization fragments (Crooks et al. 2004) and alters energy flow and nutrient cycling (Alberti 2005), which can increase habitat heterogeneity (i.e., different remnant and constructed habitat types). This habitat variability was reflected in increased bird biodiversity, given the relationship between species diversity and habitat diversity (e.g., Recher 1969; Tews et al. 2004). We compared bird biodiversity between urban and natural green areas (i.e., the same aggregated landcover classes over USA) and found that native bird species richness, effective species diversity, and abundance were much higher in urban green areas than natural green areas, probably reflecting increased habitat heterogeneity in the former (Fig. 3). Also, remnant habitats (Fahrig et al. 2019) within urban areas are important for conservation, providing similar macroecological functions to their natural counterparts (Pautasso et al. 2010), with high productivity (Shochat et al. 2006). Thus, urban planners should maintain high diversity of vegetation types within urban green areas, promoting high native bird biodiversity. Although not detected in our study, such habitat heterogeneity in urban green areas can also favor generalists (Shochat et al. 2006; Callaghan et al. 2019), potentially contributing to functional or phylogenetic homogenization (Devictor et al. 2007; Sol et al. 2017; La Sorte et al. 2018b). But further work to

confirm these broad-scale patterns are necessary to further aid urban planning and conservation within cities.

We focused on macroecological patterns of bird biodiversity in response to an urbanization gradient which could not fully address local-scale influences of underlying processes, fundamental to urban planning and conservation within cities. However, our results provide an opportunity to further explore fine-scale processes and patterns impacting bird biodiversity in urban green areas. For example, our analysis did not address the continuity or quality of habitat within natural and urban green areas (Beninde et al. 2015; Fahrig et al. 2019), and increased bird biodiversity in urban green areas could reflect degradation of natural green areas. Moreover, we ‘lumped’ all urban green areas, but future work should examine the differences between urban green areas (e.g., pollution (including noise and light at night), predators (including domestic pets), wildlife feeding) and what aspects of urban green areas are beneficial for diverse assemblages of native species (Beninde et al. 2015; Lepczyk et al. 2017a; Callaghan et al. 2018a, b). And also important to consider is how these features interact along urbanization gradients, and how this influences species-specific responses, likely to be different for exotic and native species (van Heezik et al. 2008). For example, larger urban green areas may have increased importance for bird diversity within highly developed parts of a city than less developed parts, due to island habitat effects (Beninde et al. 2015). We recommend future research and planning should investigate city and climate-specific bird responses to urbanization gradients, relating these gradients to fine scale habitat features (e.g., trees, water, and habitat diversity), providing tailored management and planning priorities (Melles et al. 2003). Lastly, future research should explore whether urban green areas are ecological traps (Garmendia et al. 2016) and how this interacts with patch-size dynamics, investigating whether this differs between native and exotic species. Ultimately, our analysis provided a broad-scale assessment, with some relevance for fine-scale patterns helpful for urban planners.

We predicted that increased habitat heterogeneity in urban green areas, compared with natural green areas, would result in an increase in the number of distinct bird assemblages; or that there would be a number of unique ‘urban’ and ‘non-urban’

assemblages (Online Appendix Fig. S1). But this was not the case: bird assemblages were mostly similar between urban and natural green areas (Fig. 4). However, the clusters that could be associated with urban green areas tended to have greater richness (Online Appendix Fig. S12), suggesting that the species’ pool of urban green assemblages was larger than those from natural green areas, confirming our empirical patterns. This result may be an artefact of the spatial scale of heterogeneity, coupled with the spatial scale of eBird checklists. There may also be biases associated with the intersection of eBird checklists with the underlying landcover classes, but these biases are likely systematic and were accounted for by considering spatial autocorrelation. It is likely that the eBird surveys within urban green areas sampled birds across a range of distinct habitats—and associated bird assemblages—owing to the absence of distinctly urban or natural green clusters. More research is required to investigate the affinities between cluster analysis of eBird data and its ability to characterize distinct assemblages. Our results provide a basis for this work, and exploration of the explicit drivers of bird community assembly in urban and natural areas.

Conclusions

The size of a city (Fuller and Gaston 2009; Beninde et al. 2015) and amount of remnant vegetation within a city (Parsons et al. 2003; Aronson et al. 2014) are critical for bird biodiversity: larger cities with more remnant vegetation have greater bird biodiversity. We provide a further generalizable trend: urban green areas—frequently a form of remnant vegetation—are rich in bird biodiversity compared with natural green areas, driven by habitat heterogeneity. This pattern was elucidated at a continental scale, using over 4 million bird-survey lists, confirming previous studies, and generalizing the responses of bird biodiversity to urbanization. Furthermore, our methodological workflow is potentially applicable for global landcover classes (e.g., Arino et al. 2012), providing subsequent opportunities for investigating broad ecological patterns (Morelli et al. 2016; Zuckerberg et al. 2016; Sol et al. 2017), especially within urban ecosystems (La Sorte et al. 2014, 2018a, c). There is a clear need for conservation of urban green areas (Dearborn and Kark 2010; Ives et al. 2016), focusing on preserving

biodiversity (United Nations Environment Programme 2007). Our results suggest that increasing and maintaining habitat heterogeneity of urban green areas is critical for the future maintenance of bird biodiversity in urban areas.

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Data accessibility All data used for our analyses are open-access from their original sources – eBird data, map of BCRs, and map of NLCD 2011 – but the necessary code and filtered data used to produce the GAMs which formed the main component of the analysis are available here: <https://doi.org/10.5281/zenodo.3246994>. Other larger data files are available upon request.

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