esa ECOSPHERE

The effects of local and landscape habitat attributes on bird diversity in urban greenspaces

Corey T. Callaghan,[1,†] Richard E. Major,[1,2] Mitchell B. Lyons,[1] John M. Martin,[1,3] and Richard T. Kingsford[1]

[1]Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, UNSW Sydney, Sydney, New South Wales 2052 Australia
[2]Australian Museum Research Institute, Australian Museum, 1 William Street, Sydney, New South Wales 2010 Australia
[3]Royal Botanic Gardens and Domain Trust, Mrs Macquaries Road, Sydney, New South Wales 2000 Australia

Citation: Callaghan, C. T., R. E. Major, M. B. Lyons, J. M. Martin, and R. T. Kingsford. 2018. The effects of local and landscape habitat attributes on bird diversity in urban greenspaces. Ecosphere 9(7):e02347. 10.1002/ecs2.2347

Abstract. Contrasting trajectories of biodiversity loss and urban expansion make it imperative to understand biodiversity persistence in cities. Size-, local-, and landscape-level habitat factors of greenspaces in cities may be critical for future design and management of urban greenspaces in conserving bird biodiversity. Most current understanding of bird communities in cities has come from disparate analyses of single cities, over relatively short time periods, producing limited understanding of processes and characteristics of bird patterns for improved biodiversity management of the world's cities. We analyzed bird biodiversity in 112 urban greenspaces from 51 cities across eight countries, using eBird, a broadscale citizen science project. Species richness and Shannon diversity were used as response variables, while percent tree cover, percent water cover, and vegetation index were used as habitat predictor variables at both a landscape (5 and 25 km radius) and local-scale level (specific to an individual greenspace) in the modeling process, retrieved using Google Earth Engine. Area of a greenspace was the most important predictor of bird biodiversity, underlining the critical importance of habitat area as the most important factor for increasing bird biodiversity and mitigating loss from urbanization. Surprisingly, distance from the city center and distance from the coast were not significantly related to bird biodiversity. Landscape-scale habitat predictors were less related to bird biodiversity than local-scale habitat predictors. Ultimately, bird biodiversity loss could be mitigated by protecting and developing large greenspaces with varied habitat in the world's cities.

Key words: avian; biodiversity; citizen science; eBird; mixed-models; species richness; species–area relationship; urban ecology.

Received 6 June 2018; accepted 8 June 2018. Corresponding Editor: Paige Warren.

† **E-mail:** c.callaghan@unsw.edu.au

Introduction

Continued global urbanization is contributing to global biodiversity loss. Consequently, there are calls for improved understanding of urban biodiversity (Marzluff et al. 2008, McDonnell et al. 2009), reflecting its importance for human well-being (Fuller et al. 2007) and as an indicator of environmental change (Dearborn and Kark 2010). Conservation of urban biodiversity, as with all conservation, requires the application of traditional biodiversity concepts such as scale, hierarchy, and fragmentation effects (Savard et al. 2000, Faeth et al. 2011), relevant to survey methods. Birds are easy to survey, sensitive to environmental change (Croci et al. 2008, Ferenc et al. 2014*a*), and popular with non-scientific public (Cocker et al. 2013, Hedblom et al. 2017), making an excellent focal taxon for studying ecological patterns and mechanisms within urban ecosystems (Cramp 1980, Marzluff 2016), enabling assessment at a global scale.

Cities can support high densities of some native bird species, compared with the density of these species in the surrounding landscapes (Fuller et al. 2008). Broadly, composition of bird communities changes with gradients of urbanization (La Sorte et al. 2014, Sol et al. 2014, Beninde et al. 2015), driven by different abiotic and biotic variables: Species richness decreases with increasing urbanization, and bird abundance and density increase with urbanization (Blair 1996, Germaine et al. 1998, Chace and Walsh 2006, Sandström et al. 2006, van Heezik et al. 2008). Species biodiversity in individual cities has been attributed to the overall amount of remnant native vegetation within a city (Parsons et al. 2003, Aronson et al. 2014, 2016) and the city's area (Fuller and Gaston 2009). Urban greenspaces (e.g., woodlots, parks, gardens, vegetation corridors, golf courses, and cemeteries) are key biodiversity hotspots within cities (Khera et al. 2009), as they make up most vegetation cover in a city (Fuller et al. 2010*a*, Tryjanowski et al. 2017) and serve multiple uses, including biodiversity conservation (Ives et al. 2016). However, greenspace infrastructure greatly varies both within (Davies et al. 2008) and among cities (Fuller and Gaston 2009).

Habitat characteristics within greenspaces are critical for urban bird biodiversity (Chace and Walsh 2006, McKinney 2008), with a positive relation between native vegetation and native bird species richness (Chace and Walsh 2006). Bird diversity is commonly predicted by a myriad of urban greenspace characteristics (Mörtberg and Wallentinus 2000, Chamberlain et al. 2004, 2007, Sandström et al. 2006, Fuller et al. 2008, van Heezik et al. 2008, Palmer et al. 2008, Khera et al. 2009, Carbó-Ramírez and Zuria 2011, Fontana et al. 2011, Ferenc et al. 2014*a*). For example, greenspace area (Chamberlain et al. 2007, Palmer et al. 2008, Khera et al. 2009, Carbó-Ramírez and Zuria 2011, Svein 2018), diversity of vegetation (Böhning-Gaese 1997, Evans et al. 2009, Khera et al. 2009), vegetation density (Sandström et al. 2006, Khera et al. 2009), amount of green area within a city (Hedblom and Söderström 2010), and presence of water bodies (Chamberlain et al. 2007) explain much of the variation in bird biodiversity in urban greenspaces.

Most current understanding of patterns of bird biodiversity within urban greenspaces has come from investigations of particular habitat associations, such as woodland bird species (Ferenc et al. 2014*a*); particular functional groups (Sandström et al. 2006, Chamberlain et al. 2007); or comparisons between non-native and native species (van Heezik et al. 2008). The predominant spatial extent has generally been a single city (Mörtberg and Wallentinus 2000, Sandström et al. 2006, Chamberlain et al. 2007, Palmer et al. 2008, Khera et al. 2009, Carbó-Ramírez and Zuria 2011, Ferenc et al. 2014*a*), with high variation in the number of greenspaces investigated, ranging from 17 (Jokimäki and Suhonen 1993) to 474 (Hedblom and Söderström 2010). There are also inevitable temporal limitations, due to the large amount of effort involved in bird surveys, with temporal scales often covering a single breeding season (Mörtberg and Wallentinus 2000, Fuller et al. 2008, Khera et al. 2009) or a single year (Palmer et al. 2008, Carbó-Ramírez and Zuria 2011). Such studies have greatly added to our understanding and knowledge of urban greenspace characteristics (Chace and Walsh 2006), but the opportunity for global generalization, using individual greenspaces as a sampling unit, is consequently limited given the limited temporal and spatial scales.

Fortunately, broadscale citizen science (Cooper et al. 2007, Bonney et al. 2009, 2014, Kobori et al. 2015) can provide large temporal and spatial coverage of bird biodiversity (McCaffrey 2005, La Sorte et al. 2018). Sightings may be disproportionately biased toward cities (Kelling et al. 2015), but this provides unique opportunities to investigate ecological patterns of bird biodiversity in urban environments (McCaffrey 2005, Callaghan and Gawlik 2015, Callaghan et al. 2018). Arguably, eBird (Sullivan et al. 2009, 2014) is the world's largest global citizen science project with over 500 million observations, submitted by more than 250,000 participants (Sullivan et al. 2017). It therefore may have the potential to provide the data necessary for a global analysis of the relationships between urban greenspaces and bird biodiversity, enabling an additional method for elucidating such generalizable patterns and processes.

We investigated the relationships between urban greenspaces and bird biodiversity, measured using species richness and Shannon diversity, two commonly employed biological diversity metrics (Magurran 1988), at 112 greenspaces and 51 cities across eight countries. Our study focused on broadscale habitat variables that predict overall bird biodiversity (cf., La Sorte et al. 2014), calculated over a four-year period, while accounting for differences throughout the year. This study differs from those studies which investigate the overall role of urban bird communities throughout the urban matrix (La Sorte et al. 2014, Morelli et al. 2016, Lepczyk et al. 2017*b*, Batáry et al. 2017), as we are particularly focused on the relationship between distinct urban greenspaces and bird diversity. We examined the importance of habitat variables both within a greenspace and within the surrounding landscape of a greenspace (Major et al. 2001, Melles et al. 2003), based on multi-temporal satellite imagery, using Google Earth Engine (Gorelick et al. 2017). We test the ability of eBird data to address long-standing hypotheses for urban greenspaces, and discuss the potentials and limitations of said data. Specifically, we investigated the relationship between (1) greenspace area and bird biodiversity; (2) habitat complexity (water, tree, and vegetation cover) and bird biodiversity; (3) the quantity of habitat in the landscape and local bird biodiversity; and (4) waterbirds and landbirds in their responses to habitat variables.

Methods

Bird surveys

Bird data were collected in eBird checklist format, whereby an observer submits a list of birds seen or heard at a given location, over a user-determined duration and survey area (see Wood et al. 2011 and Sullivan et al. 2014, 2017). The submitted list of species and counts are auto-checked against predetermined filters for expected metrics, based on the spatiotemporal coordinates of the survey site. Conflicting data are reviewed by regional experts. We used only those eBird checklists in which an individual observer submitted a list of all birds seen or heard, and depending on the statistical analysis, we applied additional filters for survey area and location—see *Predictor variables and response variables*. eBird data are accessible to any researchers or practitioners (Sullivan et al. 2014). We downloaded the eBird basic dataset (version ebd_relFeb-2017), 1 January 2013–2031 December 2016, chosen for this recent period when eBird data were richest, with relatively high sample size and potentially less bias. We used post-2010 satellite imagery which ensured that the imagery and derived explanatory variables matched the timing of the eBird surveys and the habitats used by the birds.

Study sites

Starting with the 1,022 most populated cities of the world (Demographia World Urban Areas 2016), we used R statistical software (R Core Team 2017) to return the coordinates (lat/long) of each city using ggmap (Kahle and Wickham 2017). For every locality (i.e., eBird location) in the eBird data with >250 filtered checklists (Callaghan et al. 2017), we returned the nearest city (using the geosphere package; Hijmans 2016), excluding any locality that was >20 km from the city center. Only greenspaces which were eBird hotspots (see http://help.ebird.org/customer/portal/articles/1006824-what-is-an-ebird-hotspot) were included in the analysis; that is, personal locations were disregarded. For each remaining greenspace, we visually inspected the greenspace using ArcMap 10.3 (ESRI 2016) and included it in our working data set if it met the following three criteria: (1) The greenspace was completely surrounded by urban/built up area (i.e., suburbs, housing districts, major roads/highways, or sealed urban area; (2) the greenspace was not directly adjoined by another greenspace; and (3) the greenspace was not adjoining a major water body (i.e., river, lake, or ocean). For five greenspaces, there were multiple "hotspot pins" within that greenspace, and so they were aggregated to one location for the purpose of analysis. The boundary of each greenspace was manually delineated using ArcMap 10.3 (ESRI 2016) to calculate the projected area.

Predictor variables and response variables

Greenspace-level and landscape-level predictor variables were calculated for each greenspace, where the latter was represented by three buffers around the greenspace of 5, 15, and 25 km. These potential buffer sizes were chosen to incorporate any potential changes in the habitat attributes at different landscape scales, relevant to the birds

(Radford et al. 2005). Average percent tree cover, water cover, and enhanced vegetation index (EVI) values were calculated for each greenspace and its buffers using Google Earth Engine (Gorelick et al. 2017). Tree and water datasets were derived globally, from multi-temporal time series of both MODIS and Landsat satellite imagery, at a 30 m resolution (see Sexton et al. 2013). We calculated an average annual composite (2013–2016) EVI which approximates vegetation and canopy structure (Huete et al. 2002), an improved version of NDVI which better accounts for the structural variation of the canopy. Distance to the coast and city center were, respectively, calculated using rgeos package (Bivand and Rundel 2017) and the geocode function from ggmap, which relies on Google maps (Kahle and Wickham 2017). Some areas lacked sufficient satellite data for the global tree cover map, requiring removal of two greenspaces from our analysis. These predictor variables were chosen as they have been used in previous analyses of bird biodiversity within urban ecosystems (e.g., Chace and Walsh 2006 and references within), and because we assessed patterns on a global scale which restricted the spatial resolution for which predictor variables were available.

We performed two types of analyses on the data (*Statistical analyses*). For the first analysis, the response variable was greenspace species richness, calculated from all checklists at that greenspace. This can be thought of as an overall richness for each greenspace. In addition to the greenspace species richness model, we modeled proportional species richness at each greenspace, which was the proportional species richness relative to all species within a 100 km buffer of the greenspace in the corresponding time frame (cf., Cam et al. 2000). This was done to account for known latitudinal gradients of species richness and ensure robustness of our results. Further, overall species richness was split between landbird and waterbird classification (Appendix S1: Table S1) and both were modeled separately. We calculated species richness using all available checklists (i.e., no additional filtering conditions were applied to the data) across the full annual cycle as we were interested in the cumulative richness at a given greenspace.

We then modeled the relationship between predictor variables and both species richness and Shannon diversity for each individual checklist. This can be thought of as each greenspace having repeated measures. Before this analysis of individual checklists, the dataset was filtered further, according to the following criteria (sensu Callaghan et al. 2017): (1) Where multiple observers contributed to and submitted a checklist, it was only counted once; (2) checklists were excluded if they recorded a travel distance > the perimeter of the associated greenspace; (3) checklists were excluded if they recorded an area search > the area of the associated greenspace; (4) checklists were included only if the recording duration was 5–240 min; and (5) checklists were included only if they followed the stationary, traveling, or exhaustive protocols (see Sullivan et al. 2014). Species richness was calculated as the total number of species on a checklist. For Shannon diversity, any checklists which included an X (an X signifies presence and does not provide an abundance estimate) were eliminated, and Shannon diversity was calculated using the diversity function, from the vegan package (Oksanen et al. 2016).

Statistical analyses

*Overall species richness.—*After exclusion of greenspaces that failed to meet the aforementioned criteria, 112 greenspaces from 51 cities among eight countries were included in this analysis (Appendix S2: Table S1). We employed a linear mixed-effects model (Bolker et al. 2009), in a multimodel selection framework (sensu Grueber et al. 2011). Before modeling, exploratory data analysis of predictor variables (Grueber et al. 2011) revealed relatively high collinearity between the 15 km buffer values (i.e., EVI, tree, and water variables) and the 5 and 25 km buffer values. Accordingly, the 15 km buffer values were excluded from analyses (Cade 2015). Before modeling, we also scaled and centered predictor variables, to ensure commensurate and interpretable results among models (Cade 2015). City and country were treated as random effects, as they represented just a sample of the possible greenspace choices and would contain local variation that is of low intrinsic interest. By treating each city as a random effect, this allowed for valid comparisons among cities, despite an inherent difference in bird communities among cities. In order to ensure the richness patterns were not solely an effect of sampling effort, we included an offset in the models for total number of checklists for each greenspace.

We employed model averaging where all possible subset models of a global model were fitted, and all top models with ΔAIC $\leq$ 3 included in a full model-averaging process (Grueber et al. 2011). This resulted in a list of predictor variables with their relative importance (hereafter RI) to the models, their inclusion proportion (0–1) in the top models (Grueber et al. 2011). Predictor variables whose confidence intervals did not overlap zero were considered significant. Model assumptions (i.e., normality and heteroscedasticity) were assessed after modeling, and R^2 values (Nakagawa and Schielzeth 2013, Nakagawa et al. 2017) for each of the global models were calculated by averaging the R^2 values among the respective top selected model-set. Analyses were carried out using R statistical software (R core team 2017). The lme4 package (Bates et al. 2015) was used for model-fitting, and the MuMIn package was used for model-averaging (Bartoń 2009). Four models were fitted (1) using standard species richness as the response variable; (2) proportional species richness as the response variable; (3) landbird richness as the response variable; and (4) waterbird richness as the response variable.

*Repeated measured analyses.—*The second analysis used the same general framework with the same predictor variables, but as a repeated-measures analysis (Baayen et al. 2008) in which an observer's visit was assumed to be an independent sample. This analysis was done to standardize survey effort among greenspaces with different numbers of checklists, albeit that overall richness begins to asymptote below the 250 checklist threshold (Callaghan et al. 2017) that we imposed on the dataset. This analysis provided rigor to the results from our previous analysis. Given we were interested in habitat associations, and not changes in the full annual cycle, we accounted for the inherent differences among greenspaces by treating month and greenspace as nested random effects. Duration of a checklist (mins) was included in the model as an offset (Bates et al. 2015). Any greenspaces with <50 viable checklists (see *Methods* above for criteria) were excluded from this analysis.

See Appendix S3 for a list of the six different models included in the analysis as well as associated notes about the response variables and sample sizes.

Results

We analyzed 112 greenspaces from 51 cities and eight countries (Appendix S2: Table S1), with broad representation of cities from four continents, despite a bias toward North American cities (eBird originated in New York State, USA). On average, there were 2.19 greenspaces per city in the analysis, with a range from 1 to 7 (Appendix S2: Table S1). The final dataset comprised 104,318 checklists where the mean $\pm$ standard deviation (SD) number of checklists per greenspace was 931 $\pm$ 1847 (range: 256–17,905). The mean $\pm$ SD area of a greenspace was 130.8 $\pm$ 172.6 (range: 3.014–813.5) hectares (Appendix S4: Fig. S1).

The mean $\pm$ SD species richness per greenspace was 138.0 $\pm$ 39.5, ranging from a low of 38 species in Dixie Woods, Toronto, Canada, to a high of 248 species in Central Park, New York, USA. The city with the highest overall mean species richness (236) and highest mean landbird species richness (168) was New Orleans, USA, while the highest mean waterbird richness (69) was found in Ciudad Juarez, Mexico (Fig. 1). Conversely, the city with the lowest overall mean species richness (57) and lowest mean waterbird species richness (3) was Belgrade, Serbia, while the lowest mean landbird richness (51.5) was in London, UK (Fig. 1).

In terms of explaining this variation in species richness and Shannon diversity, predictor variables included in our models accounted for a substantial proportion of the variation in the response variables. Among the six different analyses, the top models (i.e., those with ΔAIC $\leq$ 3) accounted for between 44% (repeated-measures species richness) and 76% (overall landbird species richness) of variation (Tables 1–6). Area of a greenspace was significantly positively related to overall species richness (Fig. 2, Table 1), and it was the most important variable, reflected in its inclusion in all 73 top models (RI: 1.00; Table 1). The amount of tree cover within a greenspace was also important in predicting species richness (RI: 0.85; Table 1), while water cover within a greenspace was relatively unimportant (RI: 0.33; Table 1). Distance to the coast and distance from

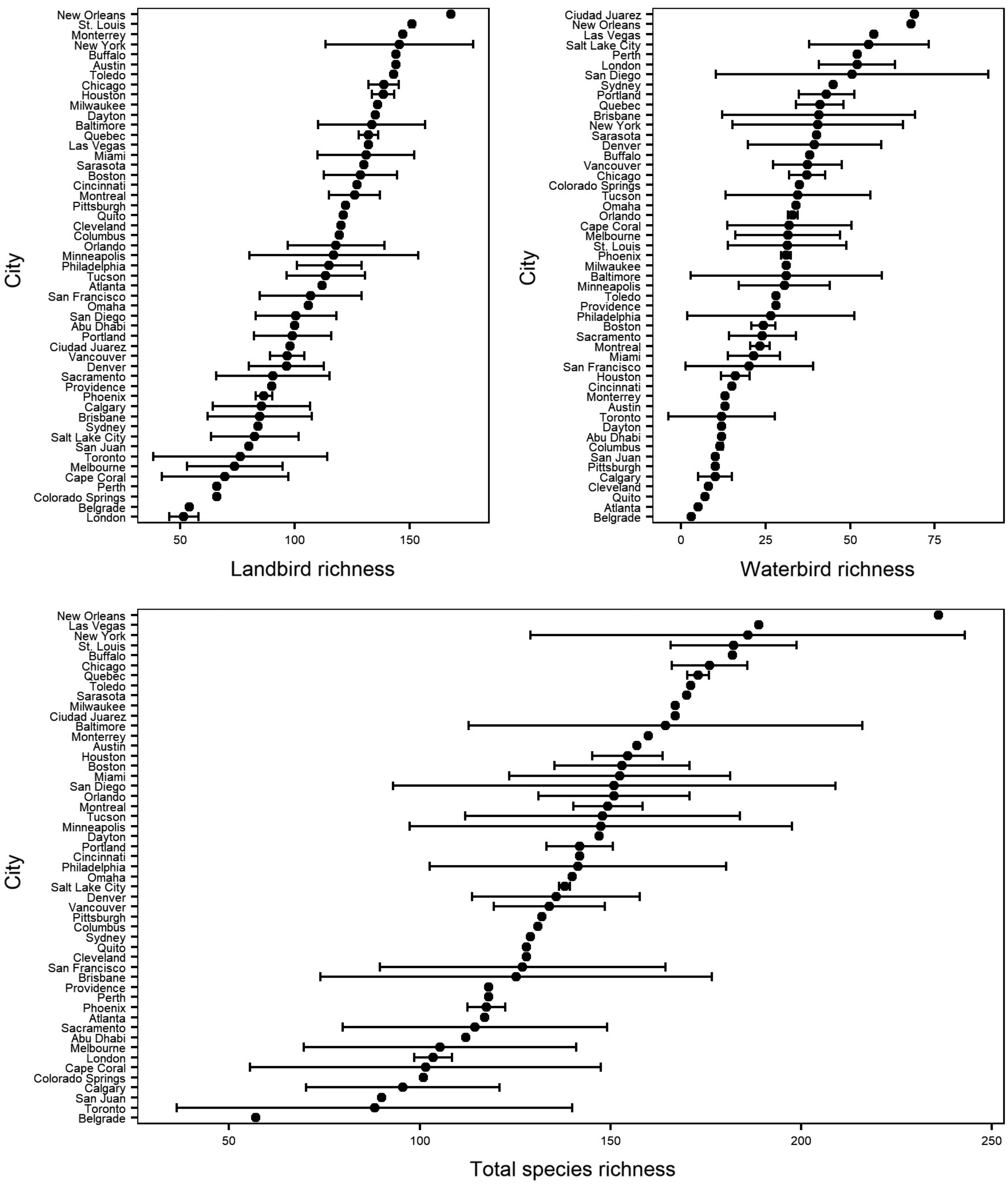

Fig. 1. The 51 cities included in the analysis, ranked by mean (±SD) overall species richness (bottom panel), landbird species richness (top left panel), and waterbird species richness (top right panel), 2013–2016. Some cities had only one greenspace included in the analysis; hence, their SDs are not shown (see Appendix S2: Table S1 for a detailed list of greenspaces and associated cities).

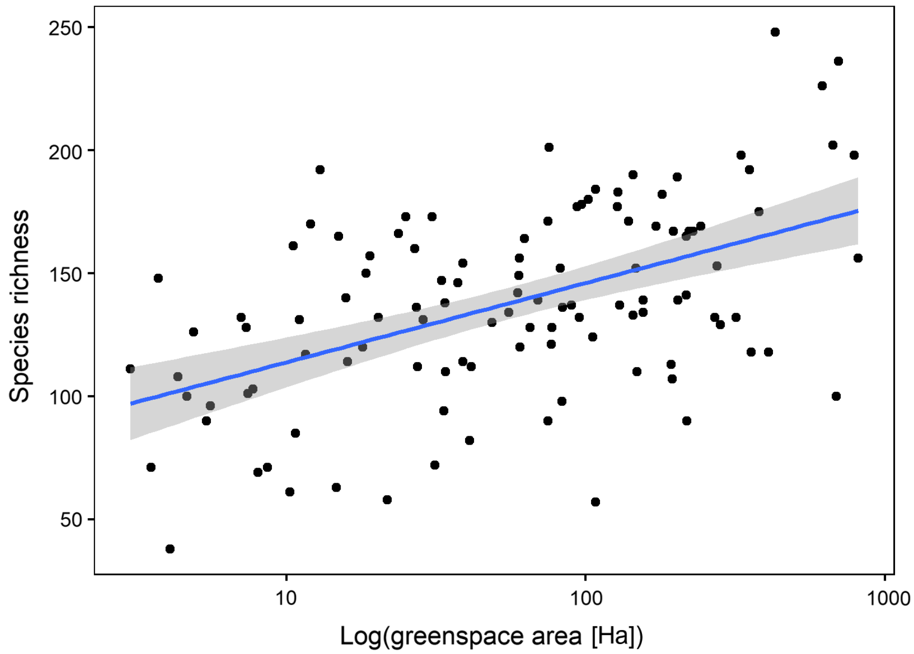

Fig. 2. Relationship between overall species richness (the total species richness at a site, as derived from eBird data between 1 January 2013–2031 December 2016) and greenspace area, the most important and positive predictor at 112 urban greenspaces, in 51 cities.

the city center were not contributors to explaining variance, with a RI of 0.06 for each (Table 1).

While accounting for the species pool for a given greenspace (i.e., proportional species richness model; Appendix S3), area of the greenspace remained significantly positive (RI: 1.00; Table 2), along with tree cover within a greenspace (RI: 1.00; Table 2). Landscape predictors (tree and water cover within 25 km and tree cover within 5 km) were least related (Table 2) but distance to

Table 1. Variable estimates, standard errors, 95% confidence intervals, and relative importance of the predictor variables in the averaged model results, which predicted species richness at 112 greenspaces from 51 cities across eight countries.

Variable	Estimate	Standard error	Confidence interval	Relative importance
(Intercept)	119.98	10.61	98.94, 141.02	–
Area (ha)	16.69	3.06	10.64, 22.75	1.00
Percent tree, greenspace	6.34	4.51	−2.55, 15.23	0.85
Percent water, greenspace	1.21	2.39	−3.51, 5.93	0.33
Percent water, 5 km buffer	1.30	2.67	−3.96, 6.56	0.30
EVI, 5 km buffer	−1.49	3.12	−7.64, 4.65	0.28
EVI, 25 km buffer	−1.36	3.29	−7.83, 5.11	0.25
EVI, greenspace	−0.82	2.29	−5.32, 3.69	0.21
Percent tree, 5 km buffer	−0.79	2.57	−5.86, 4.29	0.16
Percent water, 25 km buffer	−0.09	1.89	−3.82, 3.64	0.10
Percent tree, 25 km buffer	−0.21	1.38	−2.94, 2.52	0.08
Distance to coast (km)	0.09	1.03	−1.95, 2.13	0.06
Distance from city (km)	0.08	0.83	−1.55, 1.72	0.06

Notes: EVI, enhanced vegetation index. Variables are ranked by their relative importance across 73 models which were model-averaged. Mean R^2 (±SD) for top models was 0.60 ± 0.02 and 0.22 ± 0.01 for conditional and marginal R^2, respectively.

Table 2. Variable estimates, standard errors, 95% confidence intervals, and relative importance of the predictor variables in the averaged model results, which predicted proportional species richness at 112 greenspaces from 51 cities across eight countries.

Variable	Estimate	Standard error	Confidence interval	Relative importance
(Intercept)	0.329	0.031	0.267, 0.391	–
Area (ha)	0.046	0.008	0.029, 0.062	1.00
Percent tree, greenspace	0.028	0.011	0.006, 0.050	1.00
Distance to coast (km)	0.021	0.015	−0.010, 0.051	0.80
EVI, greenspace	0.007	0.010	−0.027, 0.014	0.42
Percent water, 5 km buffer	0.002	0.006	−0.010, 0.015	0.22
EVI, 25 km buffer	−0.003	0.009	−0.021, 0.014	0.21
Percent water, greenspace	0.001	0.004	−0.007, 0.010	0.16
EVI, 5 km buffer	−0.001	0.006	−0.012, 0.010	0.13
Distance from city (km)	−0.000	0.001	−0.006, 0.005	0.10
Percent tree, 25 km buffer	−0.001	0.005	−0.010, 0.009	0.09
Percent water, 25 km buffer	0.000	0.004	−0.008, 0.009	0.09
Percent tree, 5 km buffer	−0.000	0.004	−0.008, 0.008	0.08

Notes: EVI, enhanced vegetation index. Proportional species richness was calculated as the species richness at a greenspace divided by the species richness within 100 km buffer of the greenspace. Variables are ranked by their relative importance across 43 models which were model-averaged. Mean R^2 (±SD) for top models was 0.67 ± 0.02 and 0.22 ± 0.02 for conditional and marginal R^2, respectively.

the coast was positively related to proportional species richness, with a RI of 0.80. When species richness was considered separately for landbirds and waterbirds, both response variables were still positively related to greenspace area (Fig. 3, Tables 3, 4). Water within a greenspace was positively related to waterbird species richness, but negatively related to landbird species richness (Fig. 3, Tables 3, 4). Conversely, waterbirds were negatively associated with tree cover within a greenspace (Table 3), while landbirds showed a positive association (Table 4).

After filtering checklists for the repeated-measures analysis of species richness, there were 61,123 checklists among 102 greenspaces across 50 cities and seven countries, with an average of 599 ± 1273 (range: 55–11,878) checklists per greenspace. The model-averaging procedure, using a repeated-measures model, showed that area of a greenspace was again significantly related to species richness (RI: 1.00; Table 5). Water cover within the greenspace was also significant and important (RI: 1.00), whereas tree cover within a greenspace (RI: 0.23) and tree cover within the landscape (5 km, RI: 0.36 and 25 km, RI: 0.13) were all weakly related (Table 5).

After filtering checklists for the repeated-measures analysis of species diversity, there were 44,452 checklists among 101 greenspaces across 49 cities and six countries with an average 440 ± 820 (range: 59–7,722) checklists for each greenspace. Model-averaged results again showed area to be the most important predictor variable, significantly and positively related to species diversity (RI: 1.00; Table 6). The EVI within a 5 km buffer was also important and significant and positively related to species diversity (RI: 1.00; Table 6). Further, the amount of tree cover within a greenspace and within 5 km of a greenspace were positively associated with species diversity and included in more than half of the top models (Table 6). Conversely, water within a greenspace and within 5 km of a greenspace was relatively unimportant for species diversity (Table 6).

Discussion

With considerable loss of biodiversity partly driven by increasing urbanization, there is a need to understand which characteristics of urban greenspaces might be preserved or manipulated to improve biodiversity conservation outcomes (Lepczyk et al. 2017*a*). We identified a positive relationship between greenspace area and bird biodiversity (Fig. 2, Tables 1–6), supporting previous results across multiple taxa (Goddard et al.

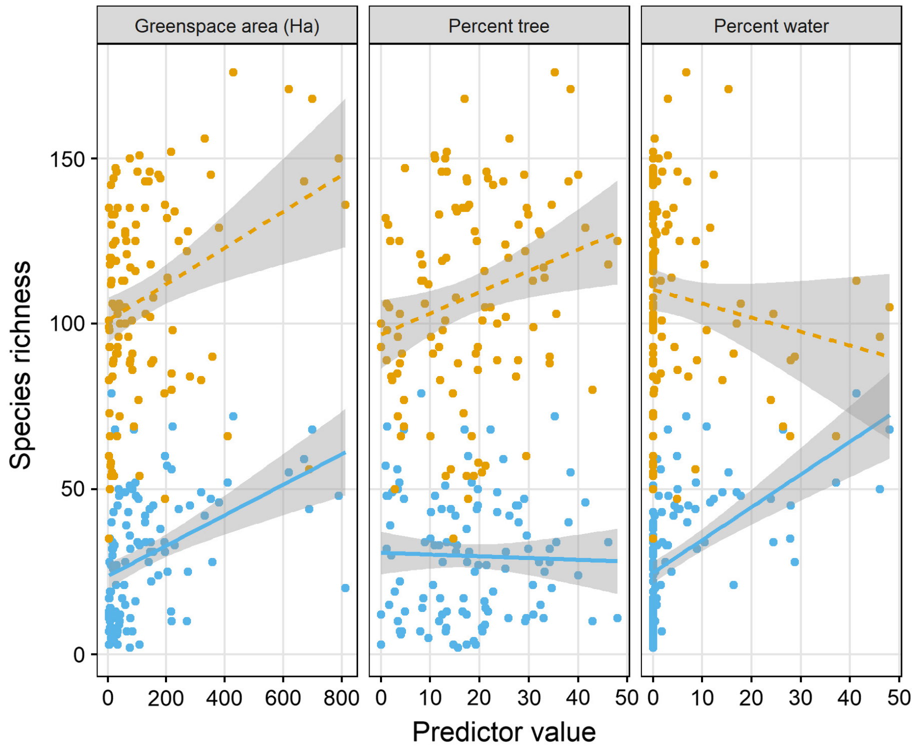

Fig. 3. Relationships between three predictor variables (i.e., greenspace area, percent tree cover, and percent water cover) and waterbird (blue) and landbird (gold) species richness among 112 urban greenspaces from 51 cities (2013–2016).

Table 3. Variable estimates, standard errors, 95% confidence intervals, and relative importance of the predictor variables in the averaged model results, which predicted waterbird species richness at 112 greenspaces from 51 cities across eight countries.

Variable	Estimate	Standard error	Confidence interval	Relative importance
(Intercept)	30.028	1.531	26.991, 33.064	–
Area (ha)	7.416	1.315	4.807, 10.024	1.00
Percent tree, 5 km buffer	−3.989	1.798	−7.550, −0.428	1.00
Percent water, greenspace	8.621	1.304	6.035, 11.208	1.00
Percent water, 5 km buffer	0.479	1.116	−1.719, 2.677	0.25
Distance from city (km)	0.354	0.922	−1.464, 2.172	0.22
Percent tree, 25 km buffer	0.285	1.149	−1.981, 2.551	0.13
EVI, 5 km buffer	0.051	0.675	−1.284, 1.387	0.10
Percent water, 25 km buffer	0.067	0.480	−0.881, 1.015	0.07
Distance to coast (km)	−0.061	0.488	−1.027, 0.901	0.06
EVI, greenspace	0.008	0.356	−0.697, 0.714	0.06
EVI, 25 km buffer	−0.005	0.412	−0.821, 0.811	0.06
Percent tree, greenspace	−0.001	0.469	−0.930, 0.928	0.06

Notes: EVI, enhanced vegetation index. Variables are ranked by their relative importance across 13 models which were model-averaged. Mean R^2 (±SD) for top models was 0.56 ± 0.01 and 0.45 ± 0.00 for conditional and marginal R^2, respectively.

Table 4. Variable estimates, standard errors, 95% confidence intervals, and relative importance of the predictor variables in the averaged model results, which predicted landbird species richness at 112 greenspaces from 51 cities across eight countries.

Variable	Estimate	Standard error	Confidence interval	Relative importance
(Intercept)	93.264	10.333	72.775, 113.752	–
Area (ha)	8.323	2.201	3.960, 12.687	1.00
Percent tree, greenspace	9.376	2.799	3.830, 14.922	1.00
Percent water, greenspace	−2.136	2.403	−6.870, 2.599	0.59
EVI, 5 km buffer	−1.804	2.905	−7.526, 3.919	0.41
EVI, 25 km buffer	−1.292	2.761	−6.731, 4.147	0.28
Percent water, 5 km buffer	0.227	1.126	−1.996, 2.450	0.13
Distance from city (km)	−0.251	1.034	−2.290, 1.789	0.13
Percent tree, 25 km buffer	−0.292	1.375	−3.007, 2.422	0.11
EVI, greenspace	−0.115	1.045	−2.179, 1.948	0.09
Percent water, 25 km buffer	0.113	1.210	−3.007, 2.422	0.09
Percent tree, 5 km buffer	−0.087	1.069	−2.204, 2.030	0.08
Distance to coast (km)	0.065	0.830	−1.578, 1.709	0.06

Notes: EVI, enhanced vegetation index. Variables are ranked by their relative importance across 45 models which were model-averaged. Mean R^2 ($\pm$SD) for top models was 0.76 $\pm$ 0.01 and 0.15 $\pm$ 0.01 for conditional and marginal R^2, respectively.

2010, Beninde et al. 2015), but relationships between diversity and habitat features were less striking (Tryjanowski et al. 2017).

Area was the only predictor that was consistently significant across all analyses, for species richness, standardized species richness, and species diversity. This supports the long-standing species–area relationship (Schoener 1976, Lomolino 2000), generalizable to greenspaces within cities (Goddard et al. 2010, Ferenc et al. 2014*b*). Positive relationships between bird biodiversity and greenspace size, based on localized studies, identify a threshold of greenspace area of 10–35 ha for most urban bird diversity (Fernández-Juricic and Jokimäki 2001, Chamberlain et al. 2007). It is difficult to dissociate this relationship from that of habitat complexity/quality and greenspace area (Holtmann et al. 2017). For

Table 5. Variable estimates, standard errors, 95% confidence intervals, and relative importance of the predictor variables in the averaged model results, which predicted species richness within a checklist (N = 61,123) at 102 greenspaces from 50 cities across seven countries. Duration per checklist, in minutes, was included in the model as an offset.

Variable	Estimate	Standard error	Confidence interval	Relative importance
(Intercept)	19.742	1.980	15.861, 23.622	–
Area (ha)	2.505	0.701	1.131, 3.879	1.00
Percent water, greenspace	0.983	0.405	0.190, 1.777	1.00
EVI, 5 km buffer	1.777	0.980	−0.143, 3.697	0.90
Percent water, 25 km buffer	0.851	0.822	−0.759, 2.461	0.68
EVI, 25 km buffer	−0.405	0.920	−2.209, 1.398	0.41
Percent tree, 5 km buffer	0.306	0.566	−0.803, 1.414	0.36
Distance from city (km)	0.153	0.332	−0.497, 0.804	0.31
Percent tree, greenspace	0.180	0.452	−0.706, 1.067	0.23
Percent water, 5 km buffer	−0.153	0.444	−1.023, 0.717	0.19
Percent tree, 25 km buffer	−0.067	0.336	−0.726, 0.592	0.13
EVI, greenspace	0.068	0.298	−0.517, 0.652	0.13
Distance to coast (km)	−0.010	0.130	−0.264, 0.245	0.06

Notes: EVI, enhanced vegetation index. Variables are ranked by their relative importance across 42 models which were model-averaged. Mean R^2 ($\pm$SD) for top models was 0.44 $\pm$ 0.004 and 0.05 $\pm$ 0.004 for conditional and marginal R^2, respectively.

Table 6. Variable estimates, standard errors, 95% confidence intervals, and relative importance of the predictor variables in the averaged model results, which predicted Shannon diversity within a checklist (N = 44,452) at 101 greenspaces from 49 cities across six countries.

Variable	Estimate	Standard error	Confidence interval	Relative importance
(Intercept)	2.208	0.103	2.007, 2.410	–
Area (ha)	0.118	0.041	0.038, 0.198	1.00
EVI, 5 km buffer	0.174	0.058	0.061, 0.287	1.00
Percent tree, 25 km buffer	−0.086	0.070	−0.224, 0.051	0.78
Percent tree, greenspace	0.057	0.053	−0.047, 0.160	0.70
Distance from city (km)	0.028	0.029	−0.029, 0.085	0.64
Percent water, 25 km buffer	0.043	0.051	−0.057, 0.143	0.54
Percent tree, −5 km buffer	0.050	0.063	−0.074, 0.173	0.53
Distance to coast (km)	−0.030	0.040	−0.107, 0.048	0.50
EVI, 25 km buffer	−0.042	0.062	−0.163, 0.079	0.48
EVI, greenspace	0.018	0.035	−0.050, 0.086	0.36
Percent water, greenspace	0.001	0.014	−0.020, 0.026	0.15
Percent water, 5 km buffer	−0.001	0.014	−0.027, 0.030	0.10

Notes: Duration per checklist, in minutes, was included in the model as an offset. EVI, enhanced vegetation index. Variables are ranked by their relative importance across 126 models which were model-averaged. Mean R^2 (±SD) for top models was 0.49 ± 0.005 and 0.08 ± 0.007 for conditional and marginal R^2, respectively.

example, small greenspaces can support a surprising amount of bird diversity (Carbó-Ramírez and Zuria 2011, Matthies et al. 2017), given high-quality habitat. Indeed, we found considerable variation in species richness in relation to greenspace area (Figs. 2 and 3), where several small greenspaces had proportionately higher species richness (i.e., were in the upper left-hand corner of Fig. 2), potentially indicative of high habitat quality. Conversely, some large greenspaces supported surprisingly low bird diversity (Figs. 2 and 3), likely reflecting their poorer habitat quality and diversity. We did not assess habitat quality within the greenspaces, a limitation which could be further investigated in the future as large datasets continue to improve in their granularity of habitats. A greenspace's avifauna is inherently influenced by the potential regional species (Szlavecz et al. 2010), and our results are robust as we show the positive relationship between proportional species richness and greenspace area (Table 2) in addition to species richness.

Although area was the most important variable, the nature of the greenspace was also significant, supporting the general understanding that increased areas of specific habitats are related to increases in diversity of the bird habitat specialists (Donnelly and Marzluff 2004, Holtmann et al. 2017). The relative amount of water within a greenspace was positively related to waterbird richness and negatively related to landbird richness. Contrastingly, the percentage of tree cover within the greenspace exhibited the opposite relationship (Fig. 3). Waterbirds may rely not only on the presence of water within a greenspace, but also the extent of water cover, while there are dependencies on tree cover for landbirds. Our study considerably extends similar more local results for urban greenspaces (Chace and Walsh 2006, Goddard et al. 2010, Lepczyk et al. 2017*a*), underlining not only the importance of area but also the value of varied habitat for the persistence of bird biodiversity in urban greenspaces (Fitzsimons et al. 2011).

We analyzed both the overall species richness at a greenspace and a random sample of richness and Shannon diversity at a greenspace, in the form of single surveys, which served as repeated random samples in repeated-measures analyses. Greenspace area was a significant predictor of the overall richness as well as richness determined through the repeated-measures analysis, but the analyses provided somewhat differing results for other predictor variables. Using a repeated-measures approach of species richness per checklist, percent water cover was an important predictor of species richness, but not important for overall species richness for the duration of the study period (cf. Tables 1, 5). This is likely an artifact of the detectability differences between waterbirds and landbirds. Waterbirds would probably be detected more easily and quickly, thereby increasing their occurrence probability in a random sample survey compared to landbirds. In contrast, for tree cover, birders continue to observe more species (i.e., transient or vagrant species) over a long period of time, reflected in overall species richness (Callaghan et al. 2017) but detect only a finite diversity within a greenspace during a specified time. Aside from the importance of area, there were no clear patterns in the analysis of repeated measures for species diversity (Table 6).

The connectivity of urban greenspaces and the location of a given urban greenspace in the urban matrix are also important for local biodiversity (Lepczyk et al. 2017*a*). For instance, urban density (Matthies et al. 2017) and distance from the city core (Carbó-Ramírez and Zuria 2011) are generally positively related to biodiversity within greenspaces. Further, despite uncertainty surrounding the importance of landscape variables to predict local species richness at a greenspace (Lepczyk et al. 2017*a*), there is evidence that landscape context is critical (Prevedello and Vieira 2010). We found that distance from the city center and distance from the coast were not important predictors. We also found that habitat within a greenspace was more important than habitat within the urban landscape (in 5 and 25 km buffers), confirming a general pattern that local factors are critical for biodiversity (Donnelly and Marzluff 2004, Evans et al. 2009, Williams and Winfree 2013, Lepczyk et al. 2017*a*). We did not dissociate the relationship between patch size and habitat quality and diversity (Lepczyk et al. 2017*a*) but our selection of greenspaces that were isolated within an urban matrix implies that all greenspaces analyzed had better habitat quality than the immediate surrounding landscape. These results suggest that processes within a greenspace may be more important than landscape processes, highlighting the importance of local management. However, many studies have investigated bird communities in response to the urban matrix as a whole (La Sorte et al. 2014, Morelli et al. 2016, Lepczyk et al. 2017*b*, Batáry et al. 2017), but this study was specifically focused on the role of urban greenspaces that reside within the urban matrix.

Understanding the relationships between biodiversity and urban greenspaces is critical for the management of urban greenspaces (Semple and Weins 1989), especially for conservation (Ibáñez-Álamo et al. 2016, Ives et al. 2016). Specifically, this understanding can enhance the planning, protection, and development of future greenspaces—including those within rapidly developing cities (particularly in rapidly Westernizing countries). This is especially important given increasing urbanization of the human population (United Nations 2014), with a concomitant increase in stakeholder competition for urban greenspaces (Azadi et al. 2011). We found no relationship between habitat heterogeneity and greenspace area (Appendix S5: Fig. S1), suggesting that the greatest conservation outcomes for bird biodiversity would come through establishment and protection of larger urban greenspaces (Fig. 2), with the corollary that these need to be planned for in developing cities and also maintained and preserved in developed cities.

Although we used a global dataset to identify general predictors of urban bird diversity, the global coverage was not sufficiently large to generalize patterns of variation among particular geographical regions. We found only 112 greenspaces (manually delineated and checked), which met our criteria for inclusion in the analyses. Thus, limitations of eBird currently include a bias toward North American cities. Importantly, our analysis showed how easily repeatable analyses could use readily available global datasets, allowing for inclusion of many more greenspaces in future analyses. In many areas, there is a significant increase in eBird submissions (Wood et al. 2011, Callaghan et al. 2018), improving the value of the eBird dataset for elucidating biogeographical patterns of bird diversity (La Sorte et al. 2014, Zuckerberg et al. 2016). Future approaches could use these data to investigate overall biodiversity metrics, with sufficient data, where minor errors by individual observers (i.e., data quality) become less important. Lastly, increasingly advanced remote-sensing technologies and the advent of volunteered geographic information (Stehman et al. 2018) are improving the spatial resolution and inference of habitat attributes. These data, linked with broad-scale empirical data (i.e., the big-data era in ornithology La Sorte et al. 2018), such as eBird, can be pivotal for investigating urban bird ecology and conservation.

We clearly identified patterns of bird biodiversity, positively related to greenspace area, supporting the results of many single-site studies and systematic reviews (Chace and Walsh 2006, Marzluff 2016, Lepczyk et al. 2017*a*, Svein 2018), but over a longer temporal and broader spatial scale than the majority of previous studies to investigate the specific instance of greenspace size related to bird biodiversity. Broadscale citizen science data, collected by volunteer birdwatchers (Wiersma 2010, Wood et al. 2011, Callaghan et al. 2017), can powerfully demonstrate generalized patterns of biodiversity (McCaffrey 2005, Wei et al. 2016, Zuckerberg et al. 2016), with clear conservation implications. The methods described herein could serve as a focal point for future urban greenspace research using eBird. We recommend that when planning for future urban development, including both setting aside greenspace and protecting existing greenspace from incremental reduction, priority should be given to larger urban greenspaces and for existing greenspaces, increasing the diversity and naturalness of the habitats (Fuller et al. 2010*b*).

Acknowledgments

We thank the countless volunteers who contribute data to eBird and the eBird team at the Cornell Lab of Ornithology for curating the data and making it freely available to researchers. We are also grateful to Dr. Paige Warren and two anonymous referees for constructive comments which improved this manuscript.

Literature Cited

Aronson, M. F. J., et al. 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proceedings of the Royal Society B 281. https://doi.org/10.1098/rspb.2013.3330

Aronson, M. F. J., et al. 2016. Hierarchical filters determine community assembly of urban species pools. Ecology 97:2952–2963.

Azadi, H., P. Ho, E. Hafni, K. Zarafshani, and F. Witlox. 2011. Multi-stakeholder involvement and urban green space performance. Journal of Environmental Planning and Management 54. https://doi.org/10.1080/09640568.2010.530513

Baayen, R. H., D. J. Davidson, and D. M. Bates. 2008. Mixed-effects modelling with crossed random effects for subjects and items. Journal of Memory and Language 59:390–412.

Bartoń, K. 2009. MuMIn: multi-model inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn

Batáry, P., K. Kurucz, M. Suarez-Rubio, and D. E. Chamberlain. 2017. Non-linearities in bird responses across urbanization gradients: a meta-analysis. Global Change Biology 12:3218–3221.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beninde, J., M. Veith, and A. Hochkirch. 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. Ecology Letters 18:581–592.

eBird Basic Dataset. 2016. Version: ebd_relNovember-2016. Cornell Lab of Ornithology, Ithaca, New York, USA.

Bivand, R., and C. Rundel. 2017. rgeos: Interface to Geometry Engine – Open Source (GEOS). R package version 0.3-23. https://CRAN.R-project.org/package=rgeos

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 5:506–519.

Böhning-Gaese, K. 1997. Determinants of avian species richness at different spatial scales. Journal of Biogeography 24:49–60.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127–135.

Bonney, R., C. B. Cooper, J. Dickinson, S. Kelling, T. Phillips, K. V. Rosenberg, and J. Shirk. 2009. Citizen science: a developing tool for expanding science knowledge and scientific literacy. BioScience 59:977–984.

Bonney, R., J. L. Shirk, T. B. Phillips, A. Wiggins, H. L. Ballard, A. J. Miller-Rushing, and J. K. Parrish. 2014. Next steps for citizen science. Science 343: 1436–1437.

Cade, B. 2015. Model averaging and muddled multimodel inferences. Ecology 96:2370–2382.

Callaghan, C. T., and D. E. Gawlik. 2015. Efficacy of eBird data as an aid in conservation planning and monitoring. Journal of Field Ornithology 86:298–304.

Callaghan, C. T., M. B. Lyons, J. M. Martin, R. E. Major, and R. T. Kingsford. 2017. Assessing the reliability of avian biodiversity measures of urban greenspaces using eBird citizen science data. Avian Conservation and Ecology 12:12.

Callaghan, C. T., J. M. Martin, R. E. Major, and R. T. Kingsford. 2018. Avian monitoring – comparing structured and unstructured citizen science. Wildlife Research 45:176–184.

Cam, E., J. D. Nichols, J. R. Sauer, J. E. Hines, and C. H. Flather. 2000. Relative species richness and community completeness: birds and urbanization in the mid-Atlantic states. Ecological Applications 10:1196–1210.

Carbó-Ramírez, P., and I. Zuria. 2011. The value of small urban greenspaces for birds in a Mexican city. Landscape and Urban Planning 100:213–222.

Chace, J. F., and J. J. Walsh. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning 74:46–49.

Chamberlain, D. E., A. R. Cannon, and M. P. Toms. 2004. Associations of garden birds with gradients in garden habitat and local habitat. Ecography 27:589–600.

Chamberlain, D. E., S. Gough, H. Vaughn, J. A. Vickery, and G. F. Appleton. 2007. Determinants of bird species richness in public green spaces. Bird Study 54:87–97.

Cocker, M., D. Tipling, J. Elphick, and J. Fanshawe. 2013. Birds and people. Jonathan Cape, London, UK.

Cooper, C. B., J. Dickinson, T. Phillips, and R. Bonney. 2007. Citizen Science as a Tool for Conservation in Residential Ecosystems. Ecology and Society 12:11.

Cramp, S. 1980. Changes in the breeding birds of inner London since 1900. Proceedings of the International Ornithological Congress 17:1316–1320.

Croci, S., A. Butet, A. Georges, R. Aguejdad, and P. Clergeau. 2008. Small urban woodlands as biodiversity conservation hot-spot: a multi-taxon approach. Landscape Ecology 23:1171–1186.

Davies, R. G., O. Barbosa, R. A. Fuller, J. Tratalos, N. Burke, D. Lewis, P. H. Warren, and K. J. Gaston. 2008. City-wide relationships between green spaces, urban land use and topography. Urban Ecosystems 11:269. https://doi.org/10.1007/s11252-008-0062-y

Dearborn, D. C., and S. Kark. 2010. Motivations for conserving urban biodiversity. Conservation Biology 24:432–440.

Demographia World Urban Areas. 2016. Demographia world urban areas 12th annual edition: 2016:04. Demographia. http://www.demographia.com/db-worldua.pdf

Donnelly, R., and J. M. Marzluff. 2004. Importance of reserve size and landscape context to urban bird conservation. Conservation Biology 18:733–745.

ESRI. 2016. ArcGIS desktop: Release 10.3. Environmental Systems Research Institute, Redlands, Clifornia, USA.

Evans, K. L., S. E. Newson, and K. J. Gaston. 2009. Habitat influences on urban avian assemblages. Ibis 151:19–39.

Faeth, S. H., C. Bang, and S. Saari. 2011. Urban biodiversity: patterns and mechanisms. Annals of the New York Academy of Sciences 1223:69–81.

Ferenc, M., O. Sedláček, and R. Fuchs. 2014*a*. How to improve urban greenspace for woodland birds: site and local-scale determinants of bird species richness. Urban Ecosystems 17:625–640.

Ferenc, M., O. Sedláček, R. Fuchs, M. Dinetti, M. Fraissinet, and D. Storch. 2014*b*. Are cities different? Patterns of species richness and beta diversity of urban bird communities and regional species assemblages in Europe. Global Ecology and Biogeography 23:479–489.

Fernández-Juricic, E., and J. Jokimäki. 2001. A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. Biodiversity Conservation 10:2023–2043.

Fitzsimons, J. A., M. J. Antos, and G. C. Palmer. 2011. When more is less: Urban remnants support high bird abundance but diversity varies. Pacific Conservation Biology 17:97–109.

Fontana, S., T. Sattler, F. Bontadina, and M. Moretti. 2011. How to manage the urban green to improve bird diversity and community structure. Landscape and Urban Planning 101:278–285.

Fuller, R. A., and K. J. Gaston. 2009. The scaling of green space coverage in European cities. Biology Letters 5:352–355.

Fuller, R. A., K. N. Irvine, P. Devine-Wright, P. H. Warren, and K. J. Gaston. 2007. Psychological benefits of greenspace increase with biodiversity. Biology Letters 3:390–394.

Fuller, R. A., J. Tratalos, P. H. Warren, R. G. Davies, A. Pepkowska, and K. J. Gaston. 2010*a*. Environment and biodiversity. Pages 75–103 *in* M. Jenks and C. Jones, editors. Dimensions of the sustainable city. Springer, London, UK.

Fuller, R. A., E. McDonald-Madden, K. A. Wilson, J. Carwadine, H. S. Grantham, J. E. M. Watson, C. J. Klein, D. C. Green, and H. P. Possingham. 2010*b*. Replacing underperforming protected areas achieves better conservation outcomes. Nature 466:365–367.

Fuller, R. A., P. H. Warren, P. R. Armstrong, O. Barbosa, and K. J. Gaston. 2008. Garden bird feeding predicts the structure of urban avian assemblages. Diversity and Distributions 14:131–137.

Germaine, S. S., S. S. Rosenstock, R. E. Schweinsburg, and W. S. Richardson. 1998. Relationships among breeding birds, habitat, and residential development in greater Tucson, Arizona. Ecological Applications 8:680–691.

Goddard, M. A., A. J. Dougill, and T. G. Benton. 2010. Scaling up from gardens: biodiversity conservation in urban environments. Trends in Ecology and Evolution 25:90–98.

Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. Google Earth Engine: planetary-scale geospatial analysis for everyone. Remote Sensing of Environment 202:18–27.

Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699–711.

Hedblom, M., I. Knez, and B. Gunnarsson. 2017. Bird diversity improves the well-being of city residents. Pages 287–306 *in* Ecology and conservation of birds in urban environments. Springer, Cham, Switzerland.

Hedblom, M., and B. Söderström. 2010. Landscape effects on birds in urban woodlands: an analysis of 34 swedish cities. Journal of Biogeography 37:1302–1316.

Hijmans, R. J. 2016. geosphere: spherical trigonometry. R package version 1.5-5. https://CRAN.R-project.org/package=geosphere

Holtmann, L., K. Philipp, C. Becke, and T. Fartmann. 2017. Effects of habitat and landscape quality on amphibian assemblages of urban stormwater ponds. Urban Ecosystems. https://doi.org/10.1007/s11252-017-0677-y

Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, and L. G. Ferreira. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment 83:195–213.

Ibáñez-Álamo, J. D., E. Rubio, Y. Benedetti, and F. Morelli. 2016. Global loss of avian evolutionary uniqueness in urban areas. Global Change Biology 23:2990–2998.

Ives, C. D., et al. 2016. Cities are hotspots for threatened species. Global Ecology and Biogeography 25:117–126.

Jokimäki, J., and J. Suhonen. 1993. Effects of urbanization on the breeding bird species richness in Finland: a biogeographical comparison. Ornis Fennica 70:71–77.

Kahle, D., and H. Wickham. 2017. ggmap: spatial visualization with ggplot2. R Journal 5:144–161.

Kelling, S., D. Fink, F. A. La Sorte, A. Johnston, N. E. Bruns, and W. M. Hochachka. 2015. Taking a 'Big Data' approach to data quality in a citizen science project. Ambio 44:601–611.

Khera, N., V. Mehta, and B. C. Sabata. 2009. Interrelationships of birds and habitat features in urban greenspaces in Delhi, India. Urban Forestry and Urban Greening 8:187–196.

Kobori, H., et al. 2015. Citizen Science: a new approach to advance ecology, education, and conservation. Ecological Research 31:1–19.

La Sorte, F. A., C. A. Lepczyk, J. L. Burnett, A. H. Hurlbert, M. W. Tingley, and B. Zuckerberg. 2018. Opportunities and challenges for big data ornithology. Condor: Ornithological Applications 120:414–426.

La Sorte, F. A., M. W. Tingley, and H. A. Hurlbert. 2014. The role of urban and agricultural areas during avian migration: an assessment of within-year temporal turnover. Global Ecology and Biogeography 23:1215–1224.

Lepczyk, C. A., M. F. J. Aronson, K. L. Evans, M. A. Goddard, S. B. Lerman, and S. Macivor. 2017*a*. Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. BioScience 67:799–807.

Lepczyk, C. A., F. A. La Sorte, M. F. J. Aronson, M. A. Goddard, I. MacGregor-Fors, C. H. Nilon, and P. S. Warren. 2017*b*. Global patterns and drivers of urban bird diversity. Pages 13–33 *in* E. Murgui and M. Hedblom, editors. Ecology and conservation of birds in urban environments. Springer International Publishing, Cham, Switzerland.

Lomolino, M. V. 2000. Ecology's most general, yet protean pattern: the species-area relationship. Journal of Biogeography 27:17–26.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, USA.

Major, R. E., F. J. Christie, and G. Gowing. 2001. Influence of remnant and landscape attributes on Australian woodland bird communities. Biological Conservation 102:47–66.

Marzluff, J. M. 2016. A decadal review of urban ornithology and a prospectus for the future. Ibis 159:1–13.

Marzluff, J. M., E. Shulenberger, W. Endlicher, M. Alberti, G. Bradley, C. Ryan, C. ZumBrunnen, and U. Simon, editors. 2008. Urban ecology: an international perspective on the interaction between humans and nature. Springer, New York. New York, USA.

Matthies, S. A., S. Rüter, F. Schaarschmidt, and R. Prasse. 2017. Determinants of species richness within and across taxonomic groups in urban green spaces. Urban Ecosystems. https://doi.org/10.1007/s11252-017-0642-9

McCaffrey, R. 2005. Using citizen science in urban bird studies. Urban Habitats 3:70–86.

McDonnell, M. J., A. Hahs, and J. Breuste, editors. 2009. Ecology of cities and towns: a comparative approach. Cambridge University Press, New York, New York, USA.

McKinney, M. L. 2008. Effects of urbanization on species richness: a review of plants and animals. Urban Ecosystems 11:161–176.

Melles, S., S. Glenn, and K. Martin. 2003. Urban bird diversity and landscape complexity: species-environment associations along a multiscale habitat gradient. Conservation and Ecology 7:5.

Morelli, F., Y. Benedetti, J. D. Ibáñez-Álamo, J. Jokimäki, R. Mänd, P. Tryjanowski, and A. P. Møller. 2016. Evidence of evolutionary homogenization of bird communities in urban environments across Europe. Global Ecology and Biogeography 25:1284–1293.

Mörtberg, U., and H. G. Wallentinus. 2000. Red-listed forest bird species in an urban environment–assessment of green space corridors. Landscape and Urban Planning 50:215–226.

Nakagawa, S., P. C. D. Johnson, and H. Schielzeth. 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. Journal of the Royal Society Interface 14:20170213.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Oksanen, J. F., et al. 2016. vegan: Community ecology package. R package version 2.4-1. https://CRAN.R-project.org/package=vegan

Palmer, G. C., J. A. Fitzsimons, M. J. Antos, and J. G. White. 2008. Determinants of native avian richness in suburban remnant vegetation: implications for conservation planning. Biological Conservation 141:2329–2341.

Parsons, H., K. French, and R. E. Major. 2003. The influence of remnant bushland on the composition of suburban bird assemblages in Australia. Landscape and Urban Planning 66:43–56.

Prevedello, J. A., and M. V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation 19:1205–1223.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Radford, J. Q., A. F. Bennett, and G. J. Cheers. 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. Biological Conservation 124:317–337.

Sandström, U. G., P. Angelstam, and G. Mikusiński. 2006. Ecological diversity of birds in relation to the structure of urban green space. Landscape and Urban Planning 77:39–53.

Savard, J. L., P. Clergeau, and G. Mennechez. 2000. Biodiversity concepts and urban ecosystems. Landscape and Urban Planning 48:131–142.

Schoener, T. W. 1976. The species-area relationship of terrestrial isopods (Isopoda; Oniscidea) from the Aegean archipelago (Greece): a comparative study. Global Ecology and Biogeography Letters 5: 149–157.

Semple, S. A., and J. A. Weins. 1989. Bird populations and environmental changes: Can birds be bio-indicators? American Birds 43:260–270.

Sexton, J. O., et al. 2013. Global, 30-m resolution continuous fields of tree cover: Landsat-based rescaling of MODIS Vegetation Continuous Fields with lidar-based estimates of error. International Journal of Digital Earth, 6:427–448.

Sol, D., C. González-Lagos, D. Moreira, J. Maspons, and O. Lapiedra. 2014. Urbanisation tolerance and the loss of avian diversity. Ecology Letters 17: 942–950.

Stehman, S. V., C. C. Fonte, G. M. Foody, and L. See. 2018. Using volunteered geographic information (VGI) in design-based statistical inference for area estimation and accuracy assessment of land cover. Remote Sensing of Environment 212:47–59.

Sullivan, B. L., T. Phillips, A. A. Dayer, C. L. Wood, A. Farnsworth, M. J. Iliff, I. J. Davies, A. Wiggins, D. Fink, and W. M. Hochachka. 2017. Using open access observational data for conservation action: a case study for birds. Biological Conservation 208:5–14.

Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling. 2009. eBird: a citizen-based bird observation network in the biological sciences. Biological Conservation 142:2282–2292.

Sullivan, B. L., et al. 2014. The eBird enterprise: an integrated approach to development and application of citizen science. Biological Conservation 169:31–40.

Svein, D. 2018. Urban bird community composition influenced by size of urban green spaces, presence of native forest, and urbanization. Urban Ecosystems 21:1–14.

Szlavecz, K., P. Warren, and S. Pickett. 2010. Biodiversity on the urban landscape. *In* R. Cincotta and L. Gorenflo, editors. Human population. Ecological studies (analysis and synthesis), volume 214. Springer, Berlin, Heidelberg, Germany.

Tryjanowski, P., F. Morelli, P. Mikula, A. Krištín, P. Indykiewicz, G. Grzywaczewski, J. Kronenberg, and L. Jerzak. 2017. Bird diversity in urban green space: a large-scale analysis of differences between parks and cemeteries in Central Europe. Urban Forestry & Urban Greening 27:264–271.

United Nations. 2014. World urbanization prospects: the 2014 revision. United Nations Publication, New York, New York, USA.

van Heezik, Y., A. Smyth, and R. Mathieu. 2008. Diversity of native and exotic birds across an urban gradient in a New Zealand city. Landscape and Urban Planning 87:223–232.

Wei, J. W., B. P. Y. Lee, and L. B. Wen. 2016. Citizen science and the urban ecology of birds and butterflies – A systematic review. PLoS ONE. https://doi.org/10.1371/journal.pone.0156425

Wiersma, Y. F. 2010. Birding 2.0: citizen science and effective monitoring in the Web 2.0 world. Avian Conservation and Ecology 5:13.

Williams, N. M., and R. Winfree. 2013. Local habitat characteristics but not landscape urbanization drive pollinator visitation and native plane pollination in forest remnants. Biological Conservation 160:10–18.

Wood, C., B. Sullivan, M. Iliff, D. Fink, and S. Kelling. 2011. eBird: engaging Birders in Science and Conservation. PLoS Biology 9:e1001220.

Zuckerberg, B., D. Fink, F. A. La Sorte, W. M. Hochachka, and S. Kelling. 2016. Novel seasonal land cover associations for eastern North American forest birds identified through dynamic species distribution modelling. Diversity and Distributions 22:717–730.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2347/full