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Research Paper

Area is the primary correlate of annual and seasonal patterns of avian species richness in urban green spaces

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ABSTRACT

Urban green spaces (UGS) often support diverse bird assemblages. Current evidence suggests large UGS that are circular in shape and contain abundant tree canopy cover will support more bird species independent of UGS isolation. Here, we use bird occurrence information from the eBird citizen-science database over an 18-year period (2002–2019) to estimate annual and seasonal patterns of avian species richness in well-surveyed New York City green spaces. Area was the strongest correlate of annual (n = 102 UGS) and seasonal species richness (n = 43 UGS), whereas shape and isolation lacked significant relationships. Increasing area by 50% resulted in an 11.5% increase in annual and an 8.2% increase in seasonal species richness. There was no evidence that these relationships contained an upper limit. Tree canopy cover was weakly correlated with annual species richness. The richness of nocturnally migrating species was strongly correlated with area in the spring and autumn, especially for non-passerine species. The species richness of nocturnally migrating passerines was strongly correlated with tree canopy cover in the spring, where a 50% increase in canopy cover resulted in a 23.3% increase in species richness. Our findings emphasize the broad importance of area, the value of tree canopy cover for spring migrants, and the limited relevance of shape and isolation. Efforts to enhance area and tree canopy cover will increase the number of resident and migratory bird species, which will likely increase the number of other area-sensitive forest taxa that occur in urban environments.

1. Introduction

Urbanization broadly affects the taxonomic, phylogenetic, and functional diversity of bird assemblages through a variety of processes including habitat loss and the introduction of non-native species (Aronson et al., 2014; Ibáñez-Álamo, Rubio, Benedetti, & Morelli, 2017; La Sorte et al., 2018; Sol, Bartomeus, González-Lagos, & Pavoine, 2017). A critical feature of cities that provides habitat for birds are urban green spaces (UGS), primarily urban parks. Much work has emphasized the importance of UGS size, shape, isolation, and tree canopy cover as factors effecting the occurrence of birds and other taxa (Beninde, Veith, & Hochkirch, 2015; Dale, 2018; Nielsen, van den Bosch, Maruthaveeran, & van den Bosch, 2014). However, few studies have tested these factors in combination for multiple UGS simultaneously, and many questions remain regarding how to plan, design, and manage UGS for biodiversity conservation.

The geographic location of cities determines how bird assemblages within UGS are defined across the annual cycle. For cities located in temperate regions of the Northern Hemisphere, species richness is lowest during the non-breeding season and highest during spring and autumn migration (La Sorte, Tingley, & Hurlbert, 2014). The majority of species that conduct seasonal migration within this region are nocturnal migrants, and UGS provide critical stopover habitat for these species during daylight hours (Dale, 2018; Mehlman et al., 2005). How the structure and composition of bird assemblages, including the presence of nocturnal migrants during seasonal migration, are defined across the full annual cycle within UGS has not been explored, and how these patterns are related to UGS features has not be documented.

Here, we use bird occurrence data from the eBird citizen-science program (Sullivan et al., 2014) compiled within New York City (NYC) over an 18-year period (2002–2019) to estimate annual and seasonal species richness of birds within well-surveyed NYC green spaces. NYC green spaces are known to host large numbers of migratory bird species during spring and autumn migration (Chapman, 1906), and stopover

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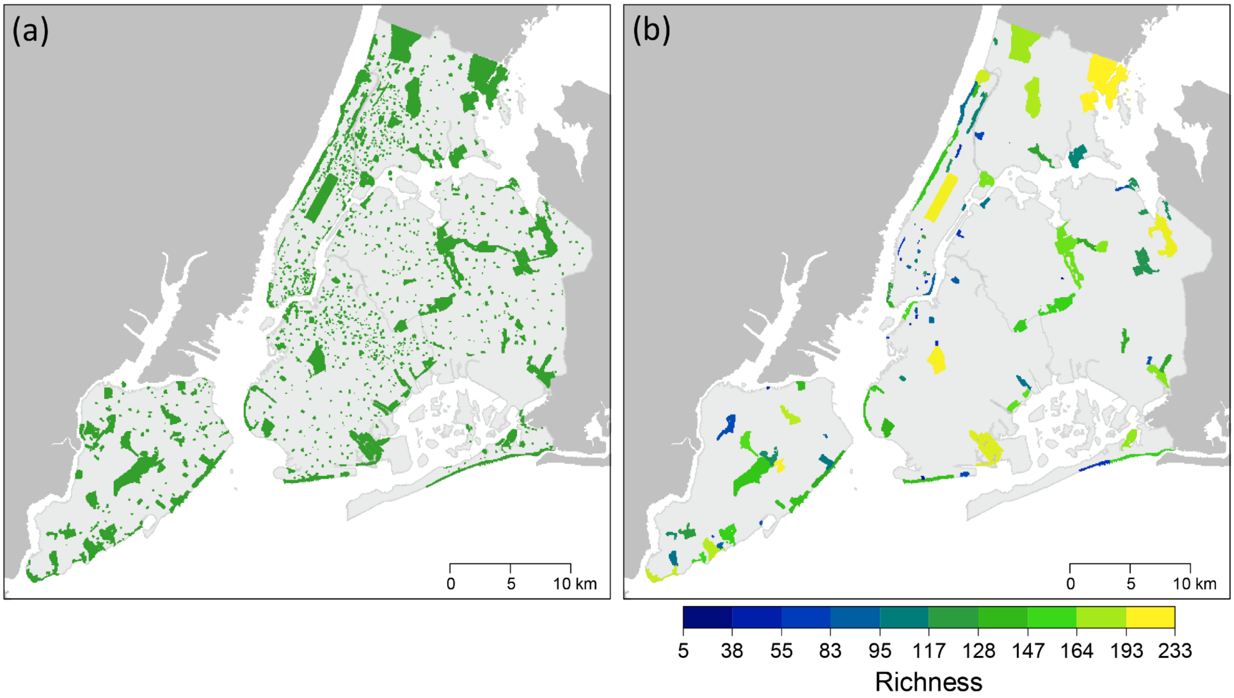

Fig 1. The New York City metropolitan area with the five boroughs of NYC shown in light gray. (a) The 1481 NYC green spaces considered in the analysis and (b) the predicted annual species richness at 102 NYC green spaces. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

visits by migrants at NYC green spaces can span several days (Seewagen, Slayton, & Guglielmo, 2010). Our first objective is to document the survey completeness (Lobo et al., 2018) of annual and seasonal bird assemblages within NYC green spaces. For well surveyed NYC green spaces, we then determine how annual and seasonal estimates of species richness are correlated with UGS area, shape, isolation, and tree canopy cover. Lastly, we assess how these features are correlated with the richness of nocturnally migrating passerine and non-passerine species during spring and autumn migration.

Through the species-area relationship (Lomolino, 2000), we expect larger NYC green spaces to host more species annually and seasonally. Area has been identified as a central predictor of species richness for birds and other taxa in UGS (Beninde, Veith, & Hochkirch, 2015). Evidence for birds, however, is based primarily on breeding assemblages with little consideration given to survey completeness (Dale, 2018; Nielsen et al., 2014). We also expect larger UGS to contain more nocturnally migrating species in the spring and autumn. Nocturnal migrants often conduct morning flights where they search for suitable stopover habitat just after sunrise (Chernetsov, 2006; Tuck, Gesicki, & Bingman, 2018; Wiedner et al., 1992). For migrants that occur in cities, larger UGS would presumably provide stronger visual cues for migratory birds searching for suitable stopover habitat. We expect UGS that are more circular in shape to host more species during the breeding and non-breeding seasons through a reduction of edge effects and the presence of additional forest interior species (Mason, Moorman, Hess, & Sinclair, 2007). We expect this same outcome during migration based on the stronger visual cues that circular UGS would provide for migratory birds independent of flight direction.

Many studies have emphasized the negative affect of UGS isolation on birds and other taxa (Beninde, Veith, & Hochkirch, 2015). With birds, however, the evidence is largely equivocal, suggesting that isolation may have a limited effect for highly mobile taxa (Dale, 2018; Nielsen et al., 2014). We expect UGS with greater tree canopy cover to host more species through the presence of additional forest interior species. Evidence supporting this prediction has been acquired primarily for breeding birds with little consideration given to survey completeness (Beninde, Veith, & Hochkirch, 2015; Dale, 2018). We expect tree canopy cover to provide a stronger visual cue for migratory birds during morning flight, the majority of which are forest specialists. By testing these expectations, our goal is to determine which features promote avian species richness across the annual cycle, including nocturnal migrants that occur inadvertently in cities during spring and autumn migration. These results will address fundamental gaps in our knowledge of the patterns and correlates of urban bird diversity, and provide a much needed full annual cycle perspective (Marra, Cohen, Loss, Rutter, & Tonra, 2015). Our findings will inform urban conservation planning, design and management, not only for NYC but also for other large cities situated within the Northeastern United States.

2. Methods

2.1. New York City green spaces

We acquired a polygon coverage of New York City green spaces from the NYC Planimetrics database through the NYC Department of Information Technology & Telecommunications (DoITT). The data were created in March 2019 and were last updated February 2019. We downloaded the data from the NYC OpenData portal (https://data.cityofnewyork.us/). We only considered UGS polygons that were classified as Community Park, Flagship Park, Garden, Historic House Park, Jointly Operated Playground, Nature Area, Neighborhood Park, Playground, Triangle/Plaza, or Waterfront Facility. We exclude UGS polygons that were classified as Buildings/Institutions, Cemetery, EventArea, Lot, Mall, Parkway, Recreation Field/Courts, Retired, Strip, Tracking, or Undeveloped. This process resulted in a total of 1481 NYC green spaces for analysis (see Fig. 1a).

We acquired land cover information for the 1481 NYC green spaces from the New York City Landcover 2010 spatial dataset gridded at a 3-ft spatial resolution. We downloaded the data from the NYC OpenData portal (https://data.cityofnewyork.us/). The land-cover dataset was developed as part of the NYC Urban Tree Canopy Assessment conducted by the University of Vermont Spatial Analysis Laboratory in

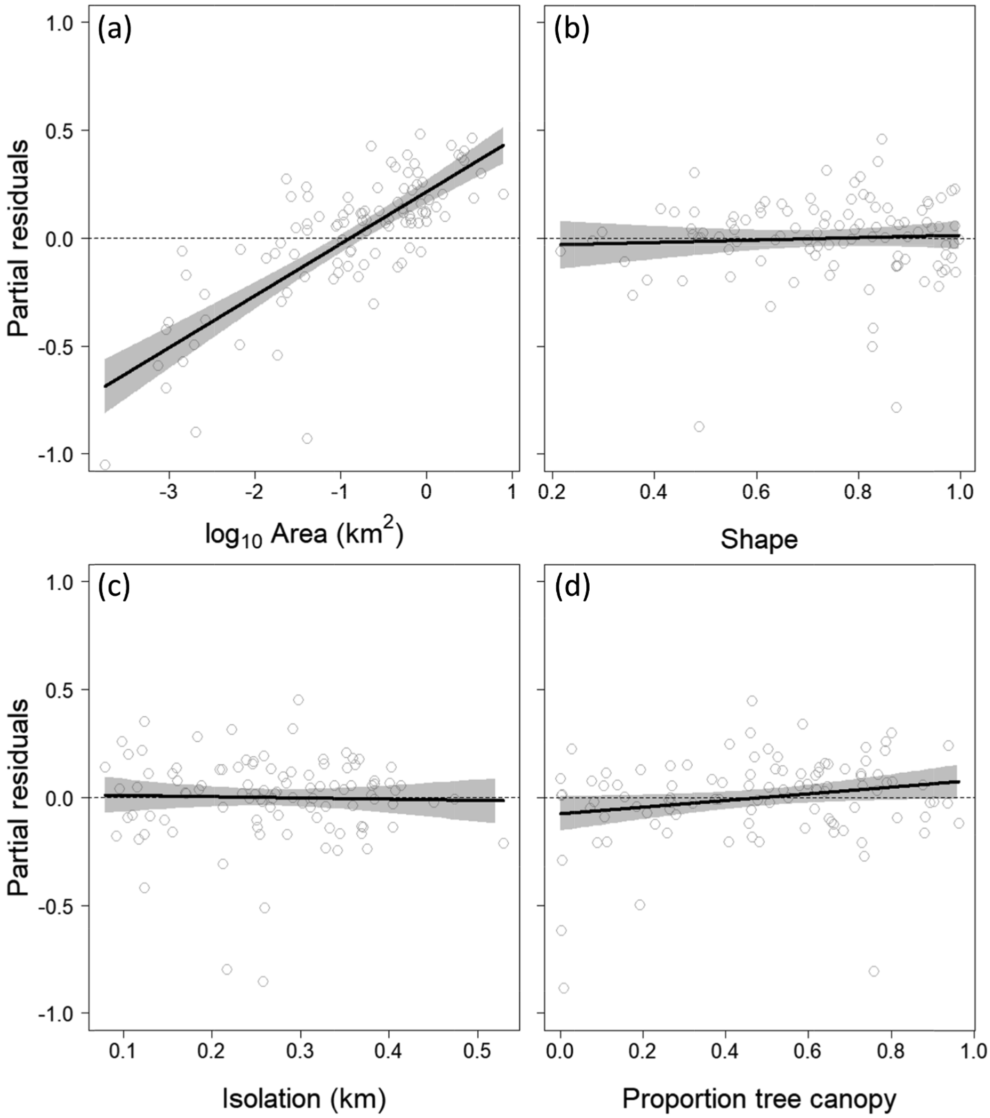

Fig. 2. Partial residuals with 95% confidence bands from the ordinary least-squares regression of predicted annual species richness by four features of 102 New York City green spaces. The features include (a) area, (b) shape, (c) isolation, and (d) proportion tree canopy cover. Isolation is the mean distance to other NYC green spaces within a 2-km buffer of the boundary. For the shape index, values approaching zero indicate elongated and values approaching one indicate circular.

collaboration with the New York City Urban Field Station. The land-cover dataset contains seven classes: (1) tree canopy, (2) grass/shrub, (3) bare earth, (4) water, (5) buildings, (6) roads, and (7) other paved surfaces. The dataset was created using a top down mapping perspective where the tree canopy class was given precedence over other land-cover classes. We calculated the proportion of total surface area containing tree canopy cover for each NYC green space.

We estimated the geometric shape of each of the NYC green space using an orthogonal linear transformation. We first converted the NYC green space polygons to gridded coverages using the 3-ft resolution land-cover dataset. We then applied a two-dimensional principle component analysis (PCA) to the x and y coordinates of the grid cell centers that occurred in each NYC green space. This approach fits a two-dimensional ellipsoid to the data where the first axis (first principle component) contains the greatest variance and the second axis (second principle component) is perpendicular to the first. The PCA was conducted using a singular value decomposition of the centered data matrix of grid cell coordinates. We defined our shape index as the ratio of the square root of the eigenvalue from the second principle component divided by the square root of the eigenvalue from the first principle component. The eigenvalues estimate the variance for the two principle components or the variance of the major and minor axes of the two-dimensional ellipse generated by the PCA. Values approaching zero indicate elongated green spaces and values approaching one indicate circular green spaces.

We estimated the isolation of each of the NYC green spaces using the following procedure. We first aggregated the 3-ft resolution gridded coverage of the NYC green space polygons to a 99-ft resolution. We applied this step to increase the efficiency of the analysis after it was determined finer spatial resolutions generated similar isolation estimates. We then calculated the distance between all 1481 NYC green space within the 99-ft resolution gridded coverage. Using a 2-km buffer around each NYC green space, we calculated the average distance between the NYC green spaces that occurred within the buffer, which defined our estimate of isolation for each green space. We selected a 2-km buffer size based on the spatial extent and geography of NYC (see Fig. 1a).

2.2. Survey completeness of bird occurrence

We acquired bird occurrence information for the NYC metropolitan area from the eBird citizen-science dataset (Sullivan et al., 2014). The

Table 1
Summary statistics from ordinary least-squares regression of estimated annual and seasonal species richness within New York City green spaces by four features: area, shape, isolation, and tree canopy cover.

Season[a]	Feature	Coef.	t	P[b]	partial R^2
Annual	Area	0.266	12.80	< **0.001**[c]	0.628
Annual	Shape	0.065	0.61	0.544	0.004
Annual	Isolation	0.174	1.39	0.167	0.020
Annual	Canopy cover	0.186	2.26	**0.026**[c]	0.050
Spring	Area	0.144	6.08	< **0.001**[c]	0.493
Spring	Shape	0.143	1.84	0.074	0.082
Spring	Isolation	0.025	0.13	0.895	0.000
Spring	Canopy cover	0.093	1.51	0.140	0.057
Summer	Area	0.249	6.30	< **0.001**[c]	0.511
Summer	Shape	0.160	1.23	0.226	0.038
Summer	Isolation	0.202	0.64	0.529	0.011
Summer	Canopy cover	−0.031	−0.30	0.767	0.002
Autumn	Area	0.153	7.18	< **0.001**[c]	0.576
Autumn	Shape	0.137	1.95	0.059	0.091
Autumn	Isolation	−0.001	−0.01	0.996	0.000
Autumn	Canopy cover	−0.029	−0.53	0.603	0.007
Winter	Area	0.224	7.51	< **0.001**[c]	0.598
Winter	Shape	0.168	1.71	0.096	0.071
Winter	Isolation	0.172	0.72	0.477	0.013
Winter	Canopy cover	−0.056	−0.72	0.479	0.013

[a] Annual species richness estimates were made at 102 NYC green spaces and seasonal species richness estimates were made at 43 NYC green spaces. [b] P values < 0.05 are shown in bold. [c] P-value < 0.05 after applying the Benjamini-Hochberg adjustment for multiple comparisons.

eBird program was initiated in 2002 and contains bird observations in checklist format where species detected by sight or sound are recorded by one or more observers during a sampling event. Volunteer eBird observers select from a number of predefined sampling protocols where sampling effort is defined by the observer using the parameters specific to each sampling protocol. We compiled bird occurrence information from all available eBird checklists within the NYC area from 1 January 2002 to 25 November 2019. The data were queried on 26 November 2019 and included all sampling protocols, all levels of sampling effort, and either designation (yes/no) for the field “all observations reported.” We only considered observations that were identified as valid by the eBird review process (Sullivan et al., 2014), and we combined observations in grouped checklists into single checklists. We removed species from the checklists that were vagrants, eruptive migrants, or pelagic seabirds.

We compiled the eBird checklists within the 1481 NYC green spaces by intersecting the geographic coordinates of the eBird checklists with the locations of the NYC green space polygons. This procedure resulted in 349,490 checklists across 342 NYC green spaces containing 5,079,773 observations of 306 species. We selected checklists for analysis for each NYC green space using the following procedure. We retained all checklists that used incidental or stationary sampling protocols. We selected area protocol checklists where the survey area was less than the area of the NYC green space. We selected traveling protocol checklists where the length traveled was less than the 99% quantile of the distribution of distances between the centers of all the grid cell pairs located in each NYC green space (gridded at a 3-ft resolution). This procedure resulted in a total of 101,489 checklist across 322 NYC green spaces containing 1,432,183 observations of 270 species. We classified the 270 species as migratory or non-migratory and the migratory species as nocturnal or diurnal migrants following Horton et al. (2019) (Appendix A Table A1).

We calculated survey completeness of the bird occurrence information in each of the 322 NYC green spaces at two temporal resolutions, annual and seasonal, for all years combined (2002–2019). We calculated survey completeness using the approach described by Lobo et al. (2018). Survey completeness estimates the ability of survey inventories to capture the full assemblage of species that are expected to occur at a given location during a given time (Colwell, & Coddington, 1994), and is defined as the percentage of observed species richness captured by predicted species richness (Lobo et al., 2018). Here, we estimate predicted species richness and survey completeness for each NYC green space based on the final slope of the relationship between the number of observed species and the number of database records, which we use as a surrogate of survey effort. The species accumulation curves were calculated using the exact estimator of Ugland, Gray, & Ellingsen (2003). We defined the four seasons for our analysis as spring (March-May), summer (June-August), autumn (September-November), and winter (December-February). We removed poorly surveyed NYC green spaces from our annual and seasonal analyses based on the default parameter recommendations from Lobo et al. (2018): the ratio between the number of occurrence records and the number of observed species was < 3, the slope of the species accumulation curve was > 0.3, and survey completeness was < 50.

We $\log_{10}$ transformed NYC green space area and our estimates of annual and seasonal species richness to improve their distributional properties and reduce the influence of outliers in our analysis. We tested for differences in our estimates of seasonal species richness among NYC green spaces using one-way ANOVA. We examined the seasonal species-area relationship across the NYC green spaces using ordinary least-squares regression, and we tested for differences in intercept and slope among seasons using ANOVA of nested model pairs.

We examined the relationship between predicted annual and seasonal species richness and the four UGS features (size, shape, isolation, and tree canopy) using ordinary least-squares regression. We displayed the regression results using partial residuals. We used the same procedure to examine the relationship with the species richness of nocturnally migrating passerine and non-passerine species during the spring and autumn. To ensure that species composition of nocturnally migrating species was adequately represented, we only considered NYC green spaces where survey completeness was > 80 after removing poorly surveyed NYC green spaces (the ratio between the number of occurrence records and the number of observed species was < 3, and the slope of the species accumulation curve was > 0.3) (Lobo et al., 2018). All analyses were conducted in R version 3.6.1 (R Development Core Team, 2020). We used the KnowBR package to implement the survey completeness analysis (Lobo et al., 2018). We control Type-I error and the false discovery rate in our multiple comparisons using the Benjamini-Hochberg adjustment (Benjamini, & Hochberg, 1995) available in the p.adjust function (R Development Core Team, 2020).

3. Results

3.1. *Annual species richness*

The 1481 NYC green spaces had a combined surface area of 79.8 km^2, or *ca.* 10% of the total surface area of NYC (Fig. 1a). A total of 211 NYC green spaces contained enough bird occurrence information to estimate annual survey completeness. After removing poorly surveyed NYC green spaces, 102 were available for analysis whose area represented *ca.* 78% of the total surface area encompassed by the 1481 NYC green spaces (Fig. 1b). Predicted annual species richness for the 102 NYC green spaces had a range from 5 to 233 species (Fig. 1b & Appendix A Table A2). The top five NYC green spaces with the highest estimates of annual species richness were Pelham Bay Park, Prospect Park, High Rock Park, Central Park, and Alley Pond Park (Fig. 1b, Appendix A Table A2).

Predicted annual species richness at the 102 NYC green spaces displayed contrasting relationships with the four UGS features (Fig. 2, Table 1). After removing the contributions from the other features, area displayed a strong positive relationship (Fig. 2a, Table 1). Shape (Fig. 2b, Table 1) and isolation showed no relationships (Fig. 2c, Table 1), and tree canopy cover displayed a significant positive relationship (Fig. 2d, Table 1). When the relationship with area was

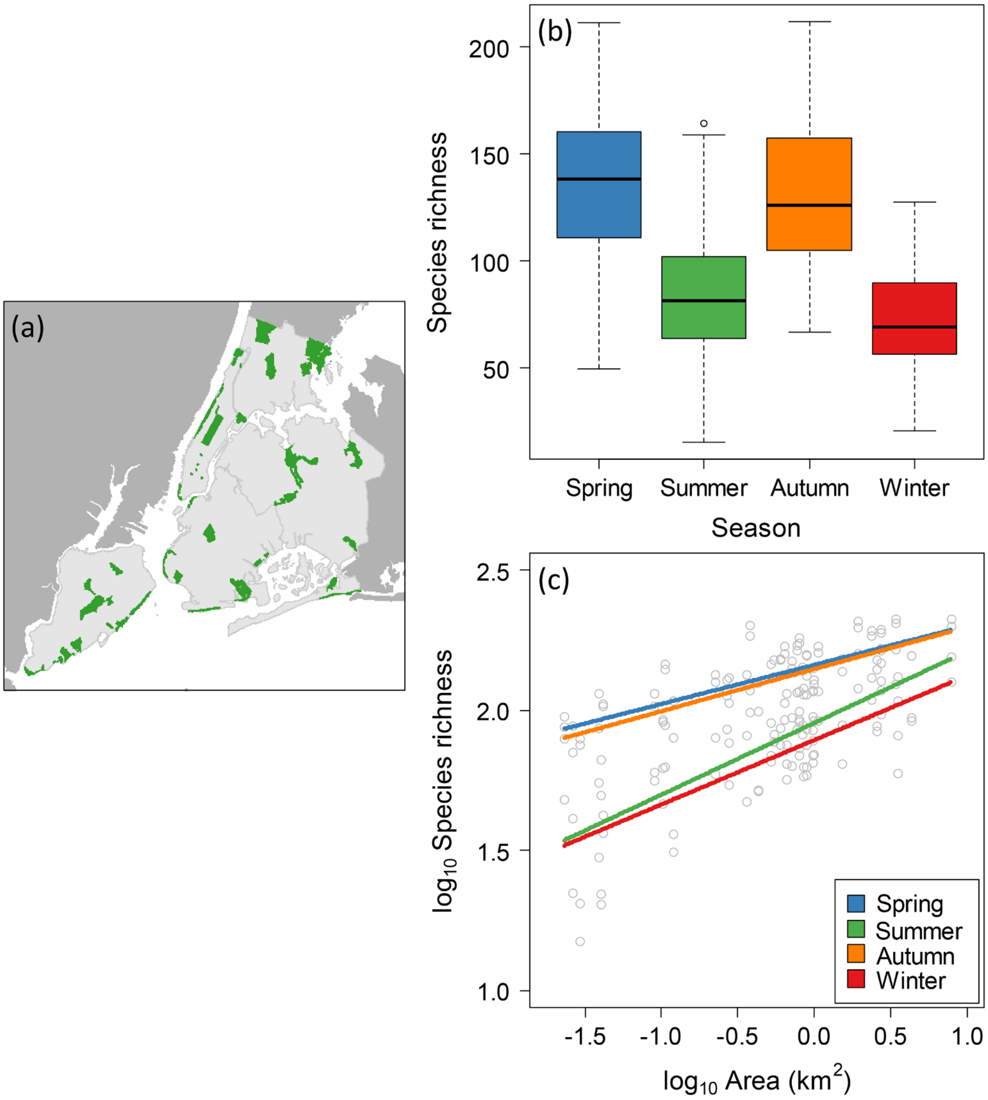

Fig. 3. (a) The 43 New York City green spaces considered in the seasonal species richness analysis. (b) Species richness predicted by season for the 43 NYC green spaces. (c) The relationship between area and species richness predicted by season for the 43 NYC green spaces. The fitted lines are from ordinary least-squares regression. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

examined alone, a 50% increase in area was associated with an 11.5% increase in annual species richness (Appendix A Fig. A1). There was no evidence that the species-area relationship was non-linear (Appendix A Fig. A1). When the relationship with tree canopy cover was examined alone, a 50% increase in canopy cover was associated with a 2.9% increase in annual species richness.

3.2. Seasonal species richness

From the 1481 NYC green spaces, 198 contained enough bird occurrence information to estimate survey completeness for at least one season. After removing poorly surveyed NYC green spaces, 43 were available for analysis where seasonal species richness estimates were available for all four seasons (Fig. 3a). Predicted species richness differed on average across the four seasons (one-way ANOVA, $F_{3,168} = 38.14$, $P < 0.001$; Fig. 3b). Predicted species richness was highest on average during the spring and autumn (Fig. 3b), which did not differ on average between the two seasons (Welch two-sample t-test, $t_{84} = 0.708$, $P = 0.481$). Predicted species richness was lowest on average during the summer and winter (Fig. 3b), which did not differ on average between the two seasons (Welch two-sample t-test, $t_{79} = 1.70$, $P = 0.093$). When compared to winter estimates, species richness increased by 12 species on average during the summer (16%), increased by 59 species on average during the autumn (94%), and increased by 65 species on average during the spring (104%; Fig. 3b). Across the four seasons, the top three NYC green spaces with the highest estimates of species richness varied: Central Park was included in all four seasons, Prospect Park and Pelham Bay Park were included in three seasons, and High Rock Park and Marine Park were included in one (Appendix A Table A3).

When the relationship with area was examined alone by season, all four seasons presented positive relationships (Fig. 3c). The intercepts differed among seasons (ANOVA, $F_{3,167} = 58.25$, $P < 0.001$), and the slopes did not differ among seasons (ANOVA, $F_{3,164} = 0.35$, $P = 0.792$; Fig. 3c). On average, a 50% increase in area was associated with an 8.2% increase in seasonal species richness.

When examined relative to the four UGS features, after removing the contributions from the other features, area displayed a strong positive relationship with predicted seasonal species richness for all four seasons (Fig. 4a, Table 1). Shape (Fig. 4b), isolation (Fig. 4c) and tree canopy cover (Fig. 4d) did not present significant relationships during any season (Table 1).

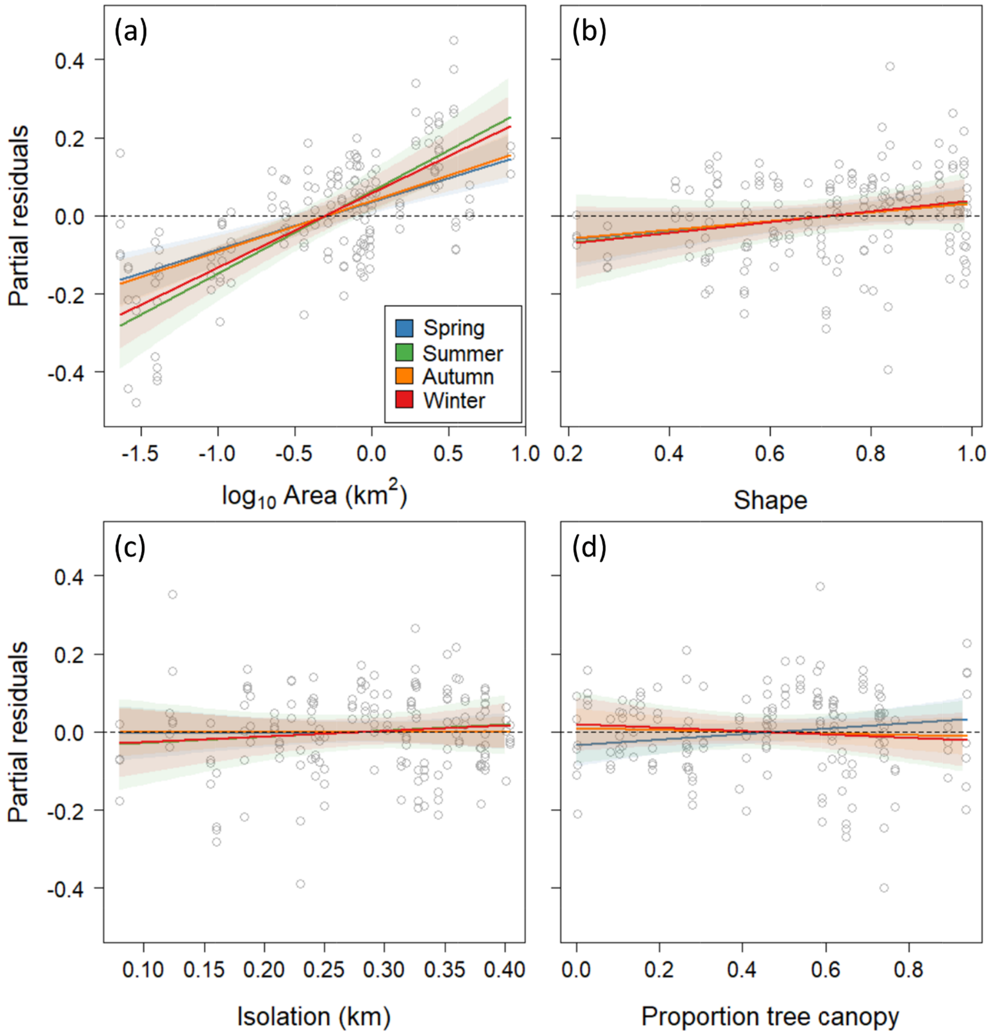

Fig. 4. Partial residuals with 95% confidence bands from the ordinary least-squares regression of predicted seasonal species richness by four features of 43 New York City green spaces. The features include (a) area, (b) shape, (c) isolation, and (d) proportion tree canopy cover. Isolation is the mean distance to other NYC green spaces within a 2-km buffer of the boundary. For the shape index, values approaching zero indicate elongated and values approaching one indicate circular. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Species richness of nocturnal migrants

After removing poorly surveyed NYC green spaces, our analysis of nocturnally migrating species included 44 NYC green spaces for the spring and 41 NYC green spaces for the autumn. When the species richness of nocturnally migrating passerines was examined relative to the four UGS features, after removing the contributions from the other features, area displayed a strong positive relationship during both the spring and autumn (Fig. 5a, Table 2). Shape (Fig. 5b, Table 2) and isolation (Fig. 5c, Table 2) did not present significant relationships during both the spring and autumn. Tree canopy cover presented a significant positive relationship during the spring and no relationship during the autumn (Fig. 5d, Table 2). When area was examined alone, a 50% increase in area resulted in an 11.3% increase in the number of nocturnally migrating passerines in the spring and a 5.0% increase in the number of nocturnally migrating passerines in the autumn. When tree canopy cover was examined alone, a 50% increase in canopy cover resulted in a 23.3% increase in the number of nocturnally migrating passerines in the spring.

When the species richness of nocturnally migrating non-passerine species was examined relative to the four UGS features, after removing the contributions from the other features, area displayed a strong positive relationship during both spring and autumn (Fig. 6a, Table 2). Shape (Fig. 6b, Table 2), isolation (Fig. 6c, Table 2), and tree canopy cover (Fig. 6d, Table 2) did not present significant relationships during the spring or autumn. When area was examined alone, a 50% increase in area resulted in a 21.9% increase in the number of nocturnally migrating non-passerines in the spring and a 22.6% increase in the number of nocturnally migrating non-passerines in the autumn.

4. Discussion

Using bird occurrence information compiled by citizen scientists across a large number of well-surveyed NYC green spaces, our analysis identified UGS area as the strongest correlate of annual and seasonal species richness, and the species richness of nocturnally migrating passerines and non-passerines in the spring and autumn. There was no evidence that these relationships contained an upper limit, suggesting that avian species richness within NYC green space are not approaching an asymptote based on UGS area. These findings expand upon previous UGS research where area has been broadly identified as an important correlate of species richness of birds and other taxa (Beninde, Veith, & Hochkirch, 2015; Dale, 2018; Nielsen et al., 2014). Shape and isolation presented little evidence for significant relationships with annual or seasonal species richness or the species richness of nocturnally migrating species. Tree canopy cover did present a weak positive

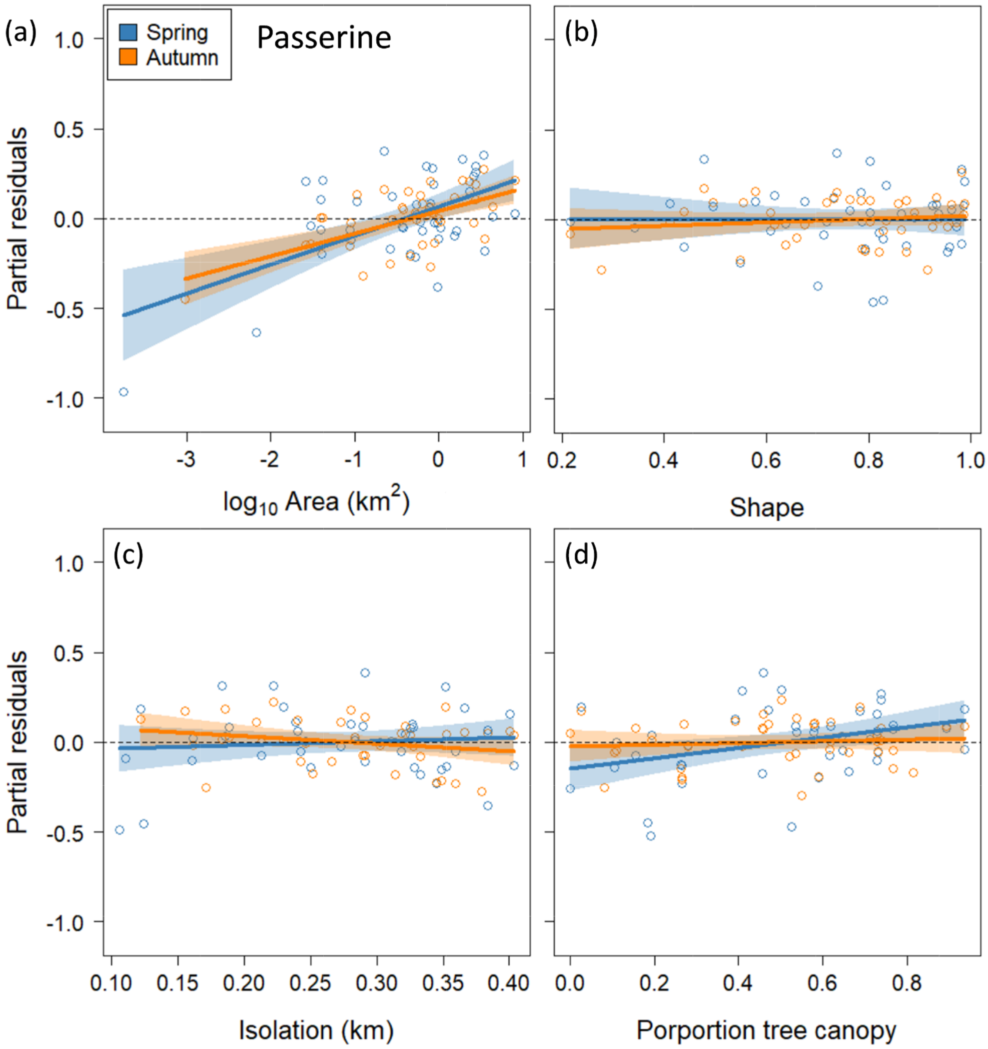

Fig. 5. Partial residuals with 95% confidence bands from the ordinary least-squares regression of the number of nocturnally migrating passerine bird species by four features of New York City green spaces during the spring and autumn. The features include (a) area, (b) shape, (c) isolation, and (d) proportion tree canopy cover. Isolation is the mean distance to other NYC green spaces within a 2-km buffer of the boundary. For the shape index, values approaching zero indicate elongated and values approaching one indicate circular. The analysis includes 44 NYC green spaces during the spring and 41 NYC green spaces during the autumn. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Summary statistics from ordinary least-squares regression of spring and autumn species richness of nocturnally migrating passerine and non-passerine species within New York City green spaces by four features: area, shape, isolation, and tree canopy cover.

Passerine	Season[a]	Feature	Coef.	t	P[b]	partial R^2
Yes	Spring	Area	0.241	5.79	< **0.001**[c]	0.468
Yes	Spring	Shape	−0.014	−0.08	0.934	0.000
Yes	Spring	Isolation	0.314	0.71	0.484	0.013
Yes	Spring	Canopy cover	0.332	2.58	**0.014**[c]	0.149
Yes	Autumn	Area	0.138	4.75	< **0.001**[c]	0.385
Yes	Autumn	Shape	0.117	1.01	0.318	0.028
Yes	Autumn	Isolation	−0.473	−1.55	0.130	0.063
Yes	Autumn	Canopy cover	0.051	0.56	0.582	0.008
No	Spring	Area	0.450	6.41	< **0.001**[c]	0.526
No	Spring	Shape	0.220	0.90	0.373	0.022
No	Spring	Isolation	0.849	1.32	0.196	0.045
No	Spring	Canopy cover	−0.342	−1.80	0.080	0.080
No	Autumn	Area	0.471	8.63	< **0.001**[c]	0.674
No	Autumn	Shape	0.205	0.94	0.353	0.024
No	Autumn	Isolation	1.217	2.12	**0.041**	0.111
No	Autumn	Canopy cover	−0.205	−1.17	0.249	0.037

[a] Spring richness estimates were made at 44 NYC green spaces and autumn species richness estimates were made at 41 NYC green spaces. [b] P-values $<$ 0.05 are shown in bold. [c] P-value $<$ 0.05 after applying the Benjamini-Hochberg adjustment for multiple comparisons.

relationship with annual species richness and strong positive relationship with the richness of nocturnally migrating passerines in the spring. Our findings for shape did not follow our expectations, suggesting circular UGS do not support greater numbers of bird species annually, seasonally, or during migration. Our findings for isolation largely followed our expectations, supporting the conclusion that bird occurrence in UGS, including during migration, is not effected by UGS isolation (LaPoint, Balkenhol, Hale, Sadler, & van der Ree, 2015). Collectively, our findings indicate that, independent of shape and isolation, maximizing area will enhance annual and seasonal species richness, and maximizing tree canopy cover will enhance annual species richness and, in particular, the presence of nocturnally migrating passerines that occur in cities during spring migration.

Our findings emphasize the value of UGS as source of breeding and wintering habitat and of stopover habitat during migration. There is the possibility, however, that UGS may represent sink habitats (Pulliam, 1988) where survival and fitness are lower relative to similar habitats outside of the city (Chamberlain et al., 2009; de Satgé et al., 2019; Lepczyk, Aronson, et al., 2017; Reynolds, Ibáñez-Álamo, Sumasgutner, & Mainwaring, 2019). Habitat quality within UGS may also be adversely affected by higher parasitism and toxicant load (Murray et al., 2019) and enhanced predation pressures (Eötvös, Magura, & Lövei, 2018; Vincze et al., 2017). Migratory birds face a number of unique threats when entering urban environments during migration, primary among them are fatal collisions with buildings or other elevated illuminated structures (Lao et al., 2020; Longcore et al., 2013; Loss, Will,

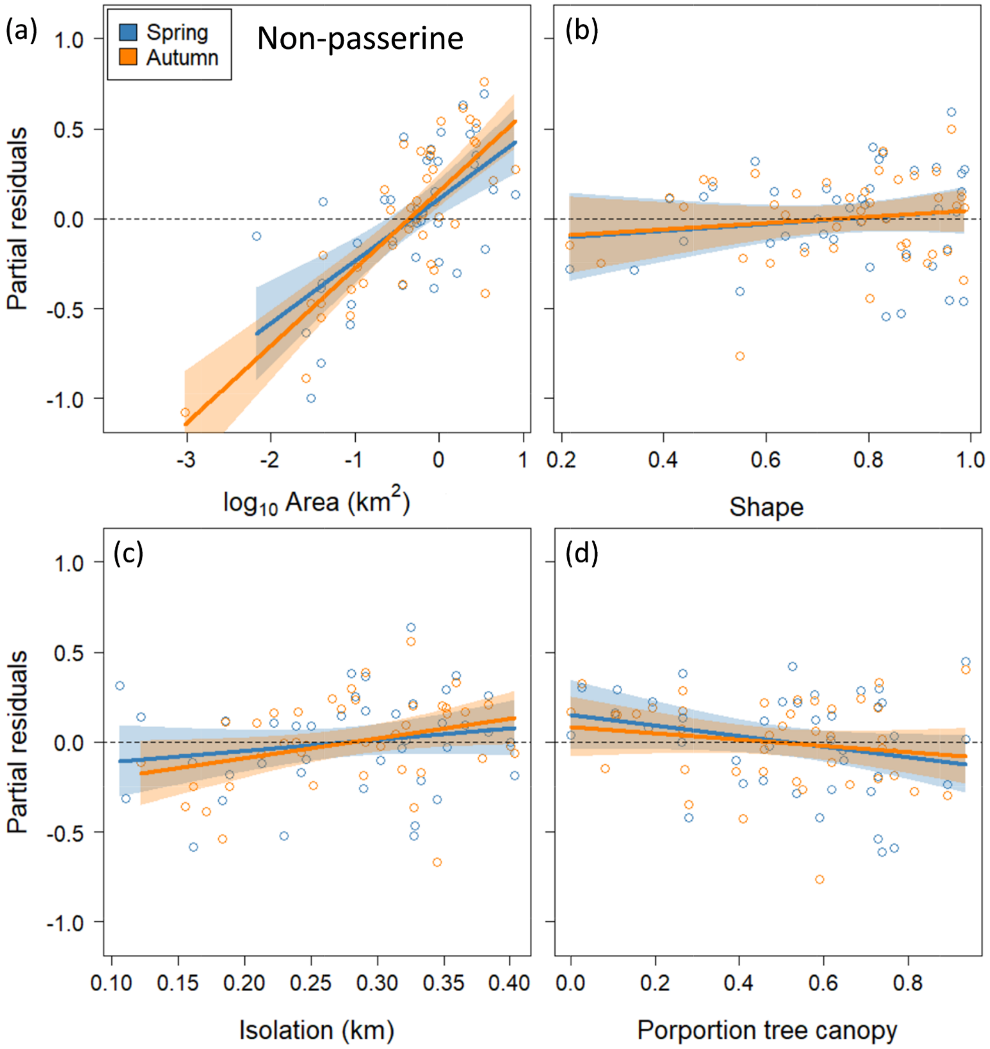

Fig. 6. Partial residuals with 95% confidence bands from the ordinary least-squares regression of the number of nocturnally migrating non-passerine bird species by four features of New York City green spaces during the spring and autumn. The features include (a) area, (b) shape, (c) isolation, and (d) proportion tree canopy cover. Isolation is the mean distance to other NYC green spaces within a 2-km buffer of the boundary. For the shape index, values approaching zero indicate elongated and values approaching one indicate circular. The analysis includes 44 NYC green spaces during the spring and 41 NYC green spaces during the autumn. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Loss, & Marra, 2014). A central factor promoting the occurrence of nocturnal migrants within urban areas is artificial light at night (ALAN), which interferes with the ability of migrants to navigate effectively at night (Gauthreaux, & Belser, 2006). The risk generated by urban sources of ALAN add to the many challenges and threats inherent to long-distance migration (Rushing et al., 2017; Sergio et al., 2019). UGS may therefore represent a sink habitat (Delibes, Ferreras, & Gaona, 2001) for nocturnal migrants that occur inadvertently in urban areas. However, there is evidence that migratory birds can efficiently replenish their energy stores in UGS (Seewagen, & Slayton, 2008), emphasizing the need to better understand how ALAN and UGS act in a combination to affect the survival of nocturnal migrants.

Our analysis identified tree canopy cover as an important predictor of the occurrence of nocturnally migrating passerines in the spring. The majority of the nocturnal migratory passerines that occur in the NYC region are forest insectivores. The emergence of insects in the spring is synchronized with the emergence of green vegetation (Feeny, 1970, 1976; van Asch, & Visser, 2007), which may provide a visual cue for migrants searching for stopover sites in the city. The senescence of deciduous vegetation may reduce the relevance of tree canopy cover as a visual cue in the autumn. The ability of some insectivorous migrants to expand their diets to include fruits and seeds in the autumn (Bairlein, 1990; Bairlein, & Gwinner, 1994; Berthold, 1976), a behavior that has been documented for migratory species in the NYC region (Parrish, 1997, 2000; Smith et al., 2007), may also reduce the relevance of tree canopy cover in the autumn.

To support urban bird populations, our findings highlight the broad importance of area, the importance of tree canopy cover, especially during spring migration, and the limited relevance of shape and isolation. Increasing area and tree canopy cover will therefore support the occurrence of more resident and migratory bird species, which will likely benefit other area-sensitive forest taxa that occur in UGS (Beninde, Veith, & Hochkirch, 2015). These conclusions were derived using occurrence information, and the abundance of the majority of the species considered in our analysis is likely lower than the abundance of the few non-native and human commensal bird species that occur in high abundance (Lepczyk, La Sorte, et al., 2017) in the world's cities (Aronson et al., 2014). Additional work is needed to assess how the patterns and correlations documented in this study are affected by the addition of abundance information.

5. Conclusions

Based on our findings, when considering urban bird diversity, it is less critical where the UGS is located or if it is circular or elongated, but how large the UGS is and the extent of tree canopy cover within the UGS. Citizen science programs create unique opportunities to monitor and study the natural systems that occur in UGS while increasing human interactions with the natural environment (Bonney et al., 2009; Dickinson, Zuckerberg, & Bonter, 2010). There is broad evidence that the physical and mental health of the human inhabitants of a city are enhanced through access to UGS (Ayala-Azcárraga, Diaz, & Zambrano, 2019; Larson, Jennings, & Cloutier, 2016; Sturm, & Cohen, 2014), increasing the importance of understanding the interconnectedness of UGS form and function. The high density of humans provides a rich source of potential volunteers, and if maintained over time, citizen science programs can provide an increasingly more detailed and rigorous source of information on UGS or other urban features. When implemented across multiple cities over time, questions can be addressed in a more comprehensive fashion. These efforts will inform urban planning and design that will directly support local and regional conservation objectives, which in turn will benefit human wellbeing.

CRediT authorship contribution statement

Frank A. La Sorte: Conceptualization, Methodology, Formal analysis, Writing - original draft. **Myla F.J. Aronson:** Conceptualization, Writing - review & editing. **Christopher A. Lepczyk:** Conceptualization, Writing - review & editing. **Kyle G. Horton:** Conceptualization, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2020.103892.

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