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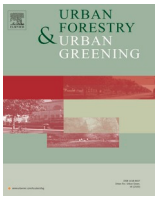

Multi-scale responses of bird species to tree cover and development in an urbanizing landscape

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ABSTRACT

Landscape change is an ongoing process for even the most established landscapes, especially in context to urban intensification and growth. As urbanization increases over the next century, supporting bird species' populations within urbanizing areas remains an important conservation challenge. Fundamental elements of the biophysical structure of urban environments in which bird species likely respond include tree cover and human infrastructure. We broadly examine how tree cover and urban development structure bird species distributions along the urban-rural gradient across multiple spatial scales. We established a regional sampling design within the Oak Openings Region of northwestern, Ohio, USA, to survey bird species distributions across an extensive urbanization gradient. Through occupancy modeling, we obtained standardized effects of bird species response to local and landscape-scale predictors and found that landscape tree cover influenced the most species, followed by landscape impervious surface, local building density, and local tree cover. We found that responses varied according to habitat affiliation and migratory distance of individual bird species. Distributions of short-distance, edge habitat species located towards the rural end of the gradient were explained primarily by low levels of urbanization and potential vegetative and supplemental resources associated with these areas, while forest species distributions were primarily related to increasing landscape tree cover. Our findings accentuate the importance of scale relative to urbanization and help target where potential actions may arise to benefit bird diversity. Management will likely need to be implemented by municipal governments and agencies to promote tree cover at landscape scale, followed by residential land management education for private landowners. These approaches will be vital in sustaining biodiversity in urbanizing landscapes as urban growth expands over the next century.

1. Introduction

Landscape change is an ongoing process for even the most established landscapes, especially in context to urban intensification and growth (Grimm et al., 2008; Nowak and Greenfield, 2018). With urbanization comes land conversion and replacement of native vegetation with human infrastructure (e.g., buildings, asphalt, and pavement), including significant losses in biodiversity (Aronson et al., 2014; McKinney, 2002). Global land area consumed by urbanization could increase by a factor of 1.8–5.9 over the next century (Gao and O'Neill, 2020). However, many studies have shown that a wide variety of native bird species can still persist in urban environments, especially when vegetation is optimally integrated into the urban landscape (Archer et al., 2019; Chace and Walsh, 2006; Ibáñez-Álamo et al., 2020). Determining the conditions supporting bird species' populations under accelerating urban growth remains an important conservation challenge (Hostetler et al., 2005; Lerman and Warren, 2011; Pennington and Blair, 2011).

A commonly observed feature of urban and community lands is tree cover co-occurring with development (Brown et al., 2005; Martin et al., 2008; Nowak and Greenfield, 2012; Radeloff et al., 2005). Trees provide important functional services, improving air and water quality (Berland and Hopton, 2014), sequestering carbon, and modulating the heat island effect (Park et al., 2017). The mechanisms responsible for urban tree cover include direct urban planning actions (e.g., planting street trees and residential landscaping) (Eisenman et al., 2021), but also major development trends of expanding urban growth into forested or mixed-woodland settings over the last half century (Brown et al., 2005;

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Lepczyk et al., 2007; Martin et al., 2008; Radeloff et al., 2005). The latter trend occurs largely at the expense of native forest cover, though. Indeed, there has been a rapid increase in scholarly work on urban tree planting over the last decade (Eisenman et al., 2021). The important implication is that urban and community development often coincides with changes in tree cover (Nowak and Greenfield, 2012), typically resulting in a tree canopy that is mostly composed of fragmented mixes of isolated stands and scattered trees (Nyland et al., 1986; Zipperer et al., 2012), possibly limiting conservation value to urban bird communities (Ibáñez-Álamo et al., 2020). Furthermore, recent assessments have shown that urban and community tree cover (estimated at around 35% of the land area on average) has declined by upwards of one percent over a recent five-year period, while impervious surfaces have increased by roughly the same amount over the same period (Nowak and Greenfield, 2018, 2012). Nonetheless, it would seem that trees along with human infrastructure (e.g., buildings and impervious surfaces) collectively form key elements of the biophysical structure of many urban landscapes. To anticipate continued change and evaluate potential conservation opportunity, urban studies might broadly consider examining bird species associations with variation in tree cover relative to infrastructure (e.g., buildings and impervious surfaces) across the urbanizing landscape (Ibáñez-Álamo et al., 2020).

Trees provide vital foraging, nesting, and roosting (e.g., cavities) resources to urban and residential bird communities (Barth et al., 2015; Lerman and Warren, 2011; Wood and Esaian, 2020). Bird community associations with increasing tree cover under moderate levels of urbanization have been observed in a variety of ecoregional contexts and among studies conducted within focal habitat patches or the built matrix alike (Belaire et al., 2014; DeGraaf and Wentworth, 1986; Donnelly and Marzluff, 2006; Green and Baker, 2003; Hostetler and Holling, 2000; Hostetler and Knowles-Yanez, 2003; Lerman and Warren, 2011; Taylor et al., 2016). Generally speaking, woodlots and parks often function as biodiversity hotspots in urban areas (Fernandez-Juricic and Jokimaki, 2001). In addition, bird abundance and diversity (often measured along a gradient of urban-to-rural land uses) often peaks with increasing tree cover under moderate levels of urbanization in the matrix, though typically favoring granivores and residents over insectivores and migrants (Blair, 1996; Emlen, 1974; Kluza et al., 2000; Poague et al., 2000), and especially discouraging forest interior and Neotropical migrants in particular (Fraterrigo and Wiens, 2005; Kluza et al., 2000; Lumpkin and Pearson, 2013; Rodewald and Bakermans, 2006). Bird species occurring within the urban or residential matrix are thought to be encouraged by certain vegetative characteristics (e.g., open lawns and diverse native and ornamental residential landscaping) or human food subsidies (e.g., bird feeders) associated with residential development (Atchison and Rodewald, 2006; Belaire et al., 2014; Narango et al., 2017). On the other hand, urbanization is known to fragment forested habitats (Friesen et al., 1995; Lumpkin and Pearson, 2013) and increase nest predation and brood parasitism rates of species typically associated with the forest interior (Jokimäki et al., 2020, 2005; Jokimäki and Huhta, 2000; Lepczyk et al., 2003; Robinson et al., 1995). Thus, bird species associations among urban and community lands are complex, incorporating specific life history traits (e.g., migration distance) and direct and indirect responses to urbanization.

An important aspect of any bird-habitat study is scale, as birds tend to respond to habitat variation simultaneously across a range of spatial scales (Cunningham and Johnson, 2006; Wiens, 1989). However, scale at city to regional levels may be especially important to urban areas due to the highly heterogeneous and disturbed nature of the urbanization process, given differences in the extent to which humans (from individual landowners to municipal governments and agencies) influence bird habitats in relation to scale (Cam et al., 2000; Donnelly and Marzluff, 2006; Hostetler and Holling, 2000; McCaffrey and Mannan, 2012; Pennington and Blair, 2011). Thus, scale-dependent relationships may be particularly informative to management planning within cities and larger community regions (Belaire et al., 2014; Goddard et al., 2010; Kinzig et al., 2005; Lerman and Warren, 2011; Pennington and Blair, 2011). As such, determining the appropriate scale to which bird species respond to the biophysical structure of urban areas is essential to ensuring that conservation and management plans are applied at the correct scale (Lerman and Warren, 2011; Pennington and Blair, 2011).

Numerous multiscale studies of urban bird communities have identified the importance of habitat variation at both local and broader landscape scales (Donnelly and Marzluff, 2006; Hostetler and Holling, 2000; Jokimäki, 1999; McCaffrey and Mannan, 2012; Melles et al., 2003; Pennington and Blair, 2011; Taylor et al., 2016). However, it has been suggested that certain aspects of bird community structure (such as diversity and richness) may be more strongly associated with urban habitat at finer scales (Evans et al., 2009). While it is possible that landscape-scale responses vary by region or study design (Clergeau et al., 2001), it is also likely that discrepancies result from improper applications of scale, particularly when the incorrect scale is incorporated in the analysis (Jackson and Fahrig, 2014). In particular, few studies have considered more than one landscape size (Hostetler and Holling, 2000; Pennington and Blair, 2011), often using a single spatial extent (e.g., 1-km buffer) to represent the landscape scale for all species. It may be appropriate to consider a greater range of possible landscape sizes as different bird species may respond to similar biophysical measures but within entirely different landscape scales (Jackson and Fahrig, 2014).

In this study, we broadly examine how tree cover and urban development are associated with bird species distributions along the urban-rural gradient. We identify two essential development variables we expect to influence birds at multiple spatial scales: local building density and landscape-scale impervious surface cover. We hypothesized that habitat affiliation (forest, edge or shrubland, and neither forest nor edge) and migration strategy (Neotropical migrant, short-distance migrant, and permanent resident) (Rodewald et al., 2016) also influence bird species responses to these features. Specifically, we ask the following question: what is the relative importance of tree cover (extent and configuration) and urban development on birds at multiple spatial scales in urbanizing landscapes and do responses vary by habitat affiliation or migration strategy? To answer this question, we use occupancy modeling to compare the effects (directionality and significance of each variable) and identify the features and scales at which birds respond most strongly in an urbanizing area. In addition, we developed a bird community map to spatially interpret the distribution of community variation relative to tree cover and urban development and facilitate an understanding of how bird communities are structured across the urbanizing landscape.

2. Methods

2.1. Study area

Our study area was the 478-km^2 Oak Openings Region of northwestern Ohio, USA (Fig. 1). The region refers to a historic pocket of globally rare Midwestern oak (*Quercus* spp.) savanna that was once more common in the surrounding region (Nuzzo, 1986). Dominant vegetation at the time of Euro-American settlement (1817–1836) included oak savanna and woodlands, collectively 66% of the original area, followed by wet prairie (27%) and other vegetation types (Brewer and Vankat, 2004). Tree density likely averaged 14–90 stems ha^{-1} in these woodlands, in contrast to 155 stems ha^{-1} in the surrounding forest (Brewer and Vankat, 2004). Dominate tree species were white (*Quercus alba*) and black oak (*Q. velutina*). Following settlement, the original vegetation was drastically altered by drainage, fire suppression, and conversion to agricultural and urban land uses (Mayfield, 1989, 1988). Presently, the Oak Openings is dominated by urban development (39% of the area) and row-crop production (27%; Schetter and Root, 2011). These land-use types are largely arranged along a strong geographic urban-rural gradient, spanning from the metropolitan area of the City of Toledo

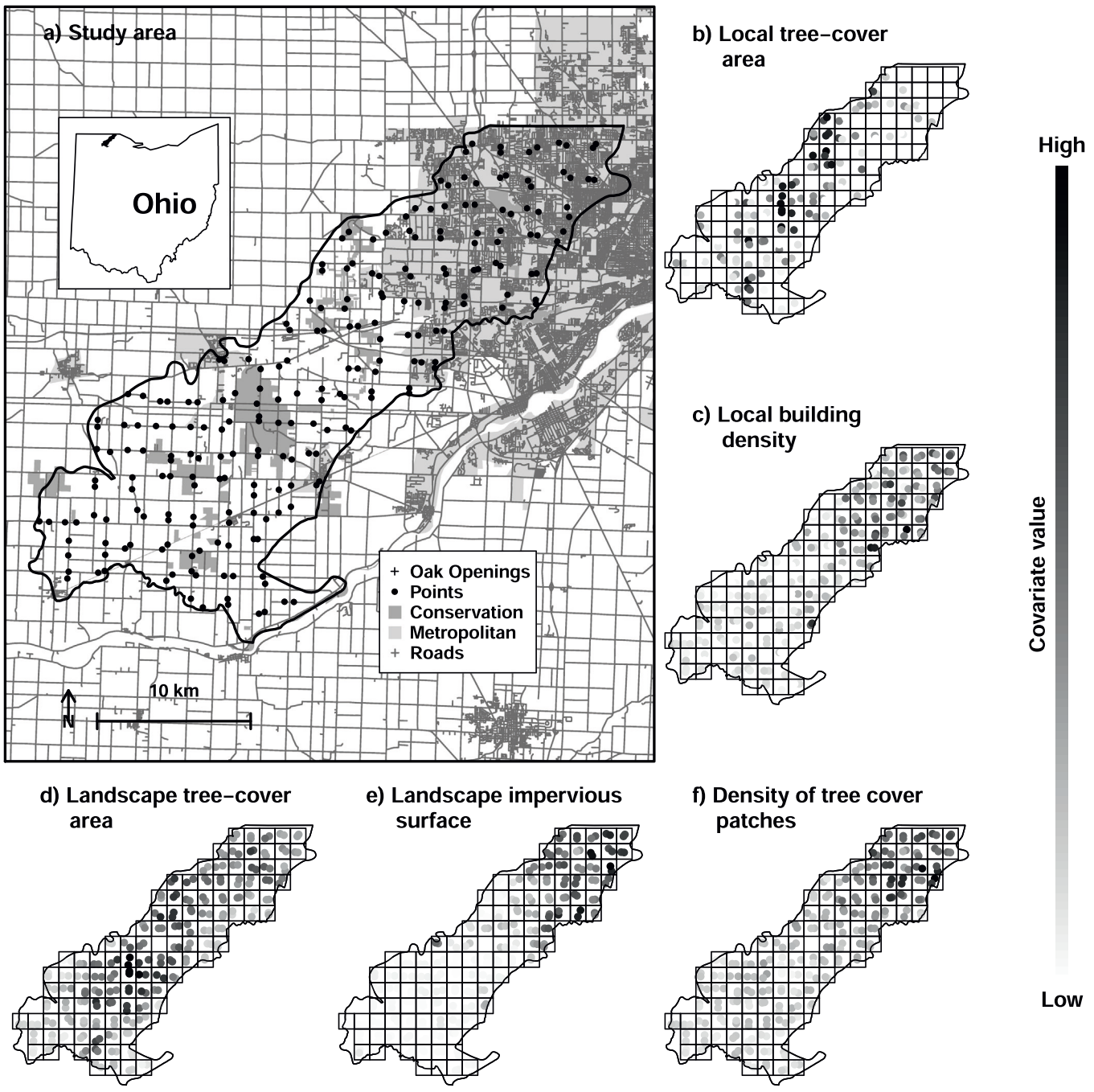

Fig. 1. The distribution of bird survey points within the study area, the Oak Openings Region of northwestern Ohio, USA (a), including variation in local- and landscape-scale tree cover and urban variables (b-f). Values of landscape variables are displayed at the 1,000-m radius landscape scale. Overlaid on variable maps is the two-km by two-km grid pattern used to spatially-distribute bird survey locations across the region.

(including a population of 270,871 people in 2020) in the north towards a largely agricultural area dominated by rural housing towards the south. The largest share of conservation lands, including the preeminent Oak Openings Preserve Metropark, occur in the middle to lower half of the region.

2.2. Bird occurrence

We conducted breeding bird surveys using the point count method from 230 fixed-width (100-m) point count stations. To develop a spatially-balanced study design, we applied a two-km by two-km block design across the region, then randomly positioned three to five survey points (≥250 m apart) along tertiary roads or residential streets with minimal traffic within each block. We surveyed points within blocks in numerical order until two points were completed per block. Each point was surveyed twice, including two weeks between visits, in routes in random sequence beginning 0.5 hr before sunrise to 1030 EST, and on precipitation-free and low wind days (<19 km hr^{-1}). Survey routes were alternated to ensure points were visited at different times in the morning over the survey period. Surveys were conducted from 23 May to 2 July 2013, including all detections ≤ 100 m from point center. From the original count data, we generated species detection/no detection histories for each survey point. Each survey lasted 6.25 min and we included a one-min adjustment period to allow birds to acclimate to observer presence, following protocols established in the second Ohio Breeding Bird Atlas (Rodewald et al., 2016). Only birds actively using

the habitat, i.e., perching in vegetation, on the ground, or aerial insectivores (e.g., swallows and swifts) observed foraging on insects in flight, within 100 m from point center during the 6.25 min surveys were used to indicate species presence for each survey point and we excluded flyovers from analysis. A laser rangefinder was used to determine whether birds were located within the survey point. Ambient temperature (°C) during surveys was recorded with a digital thermometer following each survey to be used as variable in the statistical analysis. We assigned each bird species to one of three habitat categories (forest [36% of species], edge or shrubland [44%], and neither forest nor edge [19%]) and one of three migration categories (Neotropical migrant [36%], short-distance migrant [28%], and permanent resident [36%]) following Freemark and Merriam (1986); Rodewald et al. (2016).

2.3. Tree canopy cover and urban development

Tree cover and urban development were measured locally and within landscapes surrounding each survey point (Table 1). Locally (≤ 100 m from point center), tree-canopy cover area was photo-interpreted, by sketching over 0.5-m resolution aerial photographs provided by the National Agriculture Imagery Program (NAIP, https://www.fsa.usda.gov/FSA, accessed 9 April 2013) in the field during survey visits. Percent tree cover area was then estimated within each point using 0.5-cm dot transparency grids. Similarly, we measured local building density by counting the numbers of residential houses, commercial buildings, etc., ≤ 100 m from point center. At the landscape scale, we selected two products provided in raster format at 30-m resolution by the 2011 National Land Cover Database (NLCD; https://www.mrlc.gov/, accessed 5 November 2016). These were the United States Forest Service-generated percent tree canopy cover and urban imperviousness estimates (Coulston et al., 2012). These data were averaged among a set of buffer radii ranging from 500 m to 2000 m at 250-m increments to provide percentages of tree cover and impervious surface within different landscape sizes (~0.8–12.6 km^2 in size) surrounding each survey point. This allowed us to select the best landscape size for each variable most correlated with the occurrence of each species (Holland et al., 2004; Jackson and Fahrig, 2012). These scales were shown to be influential to bird species response to urbanization in another study (Dunford and Freemark, 2005). We also characterized the spatial configuration of tree-cover area, including edge-density (m/ha), mean patch area (ha), mean nearest-neighbor distance (m), patch density (no./km^2), and patch cohesion (ranges 0–100; measures physical connectedness of patches). Original data on percentages were reclassified into a discrete map of canopy/no canopy using cells ≥ 50% canopy for use in configuration calculations. We tested for collinearity among all variables and landscape sizes, and selected patch density as the final configuration variable as it was the least correlated variable with tree canopy cover area ($r = 0.17 – 0.63$).

Table 1
Variables used to model bird species occurrence relative to variation in tree cover and urbanization intensity at local and landscape scales.

Variable	Mean (SD)	Description
A) Local		
Tree-cover area	18.49 (27.37)	percent area of tree cover within 100 m of survey point
Building density	1.97 (1.97)	density (no./ha) of houses, barns, commercial, and other structures within 100 m of survey point
B) Landscape scale‡		
Tree-cover area	29.44 (16.46)	percent area of tree cover in the landscape
Impervious surface	11.01 (13.9)	percent area of impervious surface in the landscape
Density of tree cover patches	11.12 (8.2)	density (no./ha) of tree cover patches in the landscape

‡Landscape-scale variables measured within buffer radii, 500–2000 m; displayed here are values at the 1000 m scale.

2.4. Data analysis

We built single-season occupancy models for all landbird species detected in ≥ 10% of survey points (MacKenzie et al., 2006, 2002). Occupancy modeling is a hierarchical modeling framework that accounts for imperfect detection, which can negatively influence model results if left unadjusted. Specifically, these models simultaneously estimate species probability of detection (p) and probability of occurrence (ψ), including the incorporation of survey- and site-level variables on p and ψ, respectively. Our analytical approach was to evaluate the relative influence of site-level variables, multiscale tree cover and urban development, by fitting a model of similar structure to each bird species and evaluating the direction, relative effect size, and statistical significance of each variable on ψ, relative to all species and habitat and migratory groupings. The detection model included three survey-level covariates, min. from sunrise, Julian date, and temperature (°C), that we expected to influence p via effects on bird activity over the survey period. All survey- and site-level variables were standardized by subtracting by the mean and dividing by the standard deviation to assist in the numerical optimization algorithm, control for potential residual correlation, and facilitate comparisons in effect sizes between variables, corresponding to one standard deviation change in response to each variable (Smith et al., 2009). In addition, before fitting the final occupancy models, we determined the best-fit landscape size for each landscape variable (Holland et al., 2004; Jackson and Fahrig, 2014, 2012; Miguet et al., 2016). Therefore, for each species we determined the spatial extent (i.e., buffer radii 500–2000 m) that best explained variation in species occurrence using the coefficient of determination according to the likelihood-ratio test (R^2_{LR}) (Fig. 2). The R^2_{LR} was evaluated as the improvement in model fit for each landscape variable and scale combination relative to the null model (intercept only for ψ) (Magee, 1990).

Full occupancy models were fit, and standardized parameter estimates were extracted for each species. We removed problematic site-level variables one at a time when models failed to converge or provided unreasonable solutions (i.e., unrealistically large effect sizes). We expected the presence of spatial autocorrelation, which has the tendency to inflate Type I errors (Legendre, 1993). We tested for spatial autocorrelation using a residual index proposed by Moore and Swihart (2005). This index estimates site-level residuals by subtracting the probability of at least one detection from the naïve occupancy rate of each species (i.e., one for at least one detection and zero for no detections at a given site). Using these residuals, we calculated Moran's I at 1000, 2000, and 3000 m lag distances and evaluated significance at the 0.05 level using a running Bonferroni correction (Lichstein et al., 2002). When spatial autocorrelation was detected, we calculated the "weighted-average" spatial autocovariate also presented in Moore and Swihart (2005) and elsewhere (e.g., Dormann et al., 2007) as an additional site-level variable and reran the model. Significance of each site-level variable was assessed via a likelihood ratio test of the full model versus a reduced model without that variable. We evaluated variable significance at both 0.05 and 0.10 levels. Occupancy models were fit with the *unmarked* package (Fiske and Chandler, 2011) in the R statistical analysis environment (https://cran.r-project.org/).

We developed a map of bird community composition on the basis of a two-dimensional nonmetric multidimensional scaling (nMDS) ordination (Kruskal, 1964), including Jaccard's dissimilarity for binary data, and the naïve occupancy rate (i.e., presence to include at least one detection and absence as no detections) as response values, as the ordination cannot easily accommodate the detection process. We fit variable vectors to the ordination to assist in our interpretation, where the direction and length of vectors correspond to the linear change and degree of correlation (R^2) of variables to each axis (Oksanen et al., 2018). The final community map used continuous color values as an

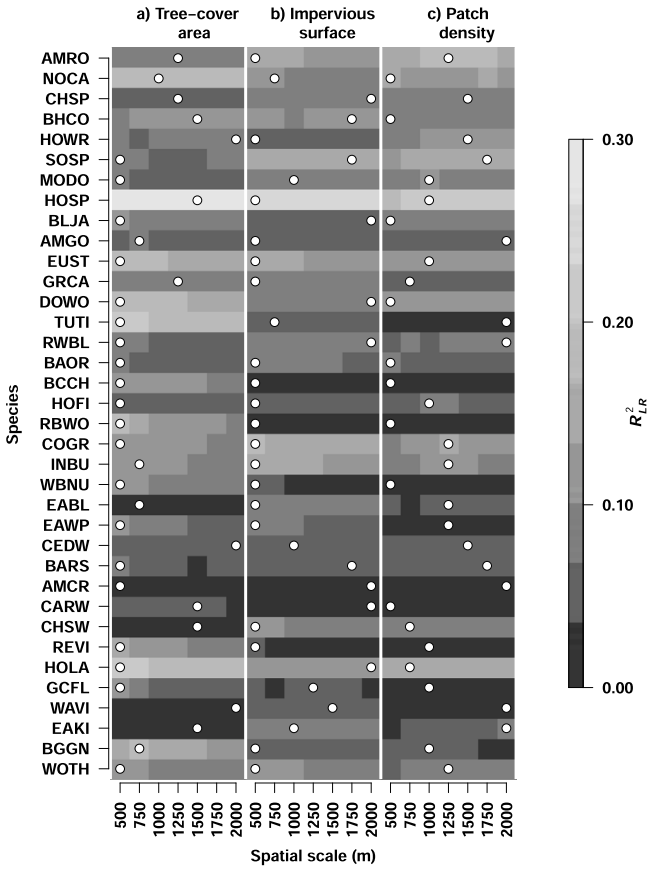

Fig. 2. Variation in explanatory power of landscape variables on 36 bird species occurrences at landscape extents (i.e., buffer radii) 500–2000 m. Dots correspond to scales that explain the most variation selected for analysis for each variable. Species acronyms (codes) are formatted from the first two letters of English common names, e.g., American Robin = AMRO (see also Table 2).

expression of the species composition of the bird community among sites by translating axis dimensions into channels of color and combining into a RGB color composite (Adams et al., 2019; Baldeck et al., 2013; Thessler et al., 2005). Specifically, the first and second nMDS axes were allocated to the green and blue channels, respectively, whereas the red channel was arbitrarily fixed at a value of 255 (full expression in the digital 8-bit RGB color scheme). To visualize regional variation in bird community composition, the final color values of each point were then mapped according to their locations within east/west subblocks within the regional sampling design. We produced ordination biplots, displaying species scores and 90% ellipses surrounding habitat and migratory groupings, to provide a legend and facilitate the matching of color values on the map to their respective species compositions on the ordination. Functions provided in the *vegan* package (Oksanen et al., 2018) in R were used in the ordination analysis.

3. Results

We recorded 7014 detections of 96 species over the course of the study (see Supplementary Material Table S1 for a complete list of species and scientific names throughout). Our final data set included 36 landbird species detected in ≥ 10% of survey points (Table 2). We grouped 13 species within the forest habitat group, 16 within the edge or shrubland group (hereafter we simply refer to as the edge group), and seven within the neither forest nor edge group. Migratory groupings included 13 Neotropical migrants, 10 short-distance migrants, and 13 permanent residents. Species displayed substantial variation in the spatial scale of response to specific landscape variables, both within and across different species (Fig. 2). For example, American Robins responded most strongly to tree canopy cover and configuration (i.e., density of tree canopy patches) within the 1250-m buffer, while responses to impervious surface were strongest within the 500-m buffer. In contrast, Black-capped Chickadee responses were strongest within the 500-m buffer of the three landscape variables.

Overall, the occurrence of 34 of the 36 bird species were associated with at least one site-level variable according to variable significance evaluated at $P < 0.05$ and $P < 0.10$ levels (Table 2). Seventy-two percent ($n = 26$) of species included significant effects of landscape-scale tree-cover area, and the majority (65%; $n = 17$) of these responses were positive (Fig. 3). In contrast, 33% ($n = 12$) of species responded significantly to landscape-scale impervious surface, of which 11 of these responses were negative (Chimney Swift was the only species to respond positively). The density of tree canopy patches included significant effects among 22% ($n = 8$) of models, of which all were positive. Twenty-seven percent ($n = 10$) of species responded significantly to local tree-cover area. Thirty-one percent ($n = 11$) of species responded significantly to local building density, including nine and two species with positive and negative effects, respectively.

The forest habitat group displayed significantly positive responses to local and landscape-scale tree-cover area and negative responses to landscape-scale impervious surface (Fig. 4). Species among the edge group included species that responded both positively and negatively to local tree-cover area, building density, and landscape-scale tree-cover area. However, all significant responses were negative relative to landscape-scale impervious surface in this group. Species among the neither forest nor edge group displayed significantly-negative responses to local and landscape-scale tree-cover area. The majority of Neotropical migrants responded positively to tree-cover area at both scales and negatively to landscape-scale impervious surface. Short-distance migrants tended to respond positively to local building density and negatively to landscape-scale tree-cover area and impervious surface. Resident species responded positively to local building density and local and landscape-scale tree-cover area and negatively to landscape-scale impervious surface.

The bird community map is displayed in Fig. 5. The nMDS ordination converged on a final solution capturing a total of 72% of the variation in the original compositional distances within two ordination dimensions. The legend illustrates the color values of individual species distributions within the ordination, as well as the color ranges (90% ellipses) of each habitat and migratory grouping. Habitat and migratory groupings overlap within the ordination, reflecting both similarities and transitions in species assemblages between groups. The purple hues correspond to large portions of the forest habitat group, while the purple-to-red trends reflect transitions between Neotropical migrants and resident species. Spatially, these communities were largely located within the center of the region where tree-cover area is greatest. Variable vectors fitted to the ordination illustrate strong correlations between tree-cover area and these species groups. The neither-forest-nor-edge habitat group and short-distance migrants were associated with orange, yellow, and green color trends on the map. Orange color values that especially dominate the Toledo Metropolitan area reflect large concentrations of synanthropic species, such as Chimney Swift, House Sparrow, and House Finch, associated with increases in building density and impervious surface in accordance with variable vectors on the ordination. The edge habitat group associated with light blue and pink hues displays a large prominence within the lower rural section of the region, corresponding to land uses dominated by low-density rural housing and agriculture.

4. Discussion

We found tree cover and urban development to be important predictors of breeding bird occurrence including effects at different scales. The presence of scale-specific responses mirrors findings from other studies (McCaffrey and Mannan, 2012; Melles et al., 2003; Pennington

Table 2
Bird species and standardized effect sizes from single-season occupancy models relative to variation in tree cover and urbanization intensity at local and landscape scales.

Species (code)	Local tree-cover area	Local building density	Landscape tree-cover area	Landscape impervious surface	Density of tree cover patches	Habitat	Migration
American Robin (AMRO)	0.68	3.58*	-0.75	0.13	2.69*	E	S
Northern Cardinal (NOCA)	1.29#	3.77	-0.14	0.42	2.18#	E	R
Chipping Sparrow (CHSP)	-0.84*	0.87*	0.89*	-0.93*	-0.63	E	S
Brown-headed Cowbird (BHCO)	-0.39	0.37	0.80*	-1.27*	0.84*	E	S
House Wren (HOWR)	0.06	1.93*	0.38	-1.26*	0.52	E	N
Song Sparrow (SOSP)	0.35	-0.10	-0.87*	-0.73#	-0.10	E	S
Mourning Dove (MODO)	0.25	1.60*	-0.65*	-0.13	0.12		S
House Sparrow (HOSP)	-1.09*	1.44*	-0.81*	0.05	-0.14		R
Blue Jay (BLJA)	-0.22	0.11	0.87*	-0.05	0.30	F	R
American Goldfinch (AMGO)	-0.67	1.53*	0.90	.	.	E	S
European Starling (EUST)	-0.11	0.69	-0.90*	0.19	0.13		R
Gray Catbird (GRCA)	.	-0.64#	1.22*	-0.16	-0.38	E	N
Downy Woodpecker (DOWO)	1.00	-0.83	1.33*	0.64	1.27#	F	R
Tufted Titmouse (TUTI)	1.12*	0.34	2.13*	-0.27	-0.75	F	R
Red-winged Blackbird (RWBL)	-0.08	-0.26	-0.54*	-0.92#	0.43	E	S
Baltimore Oriole (BAOR)	.	-0.06	0.57	-2.02*	2.77*	E	N
Black-capped Chickadee (BCCH)	0.81	0.91	1.05*	-1.36*	0.64	F	R
House Finch (HOFI)	0.55	3.47*	-1.16*	0.66	3.36*		R
Red-bellied Woodpecker (RBWO)	2.21*	-0.26	3.56*	0.34	-0.92	F	R
Common Grackle (COGR)	-1.04#	1.87*	-1.13*	-0.32	0.90	E	S
Indigo Bunting (INBU)	1.68*	0.42	-0.24	-1.01#	-0.02	E	N
White-breasted Nuthatch (WBNU)	0.31	0.24	1.61*	-1.20#	1.26	F	R
Eastern Bluebird (EABL)	-0.42	1.28*	0.69#	-2.54*	-0.28	E	R
Eastern Wood-Pewee (EAWP)	1.50#	-0.98	3.09*	-0.58	-0.38	F	N
Cedar Waxwing (CEDW)	.	0.81	0.95*	5.48	1.64	E	S
Barn Swallow (BARS)	-0.67	-0.85	-2.75*	-2.53#	0.32*		N
American Crow (AMCR)	-0.46	0.28	0.56#	-0.70	0.05	F	R
Carolina Wren (CARW)	-0.05	.	0.16	-1.31	3.38*	F	R
Chimney Swift (CHSW)	-0.71	0.40	0.45	3.38*	-0.31		N
Red-eyed Vireo (REVI)	0.37	-0.70	1.34*	-0.10	0.14	F	N
Horned Lark (HOLA)	-1.29*	-2.41*	-1.32*	-0.41	-1.42		S
Great Crested Flycatcher (GCFL)	.	-2.75	6.50*	-1.41	.	F	N
Warbling Vireo (WAVI)	-0.15	-0.38	0.21	-1.06	0.48	E	N
Eastern Kingbird (EAKI)	-0.55	0.15	0.59	-1.97	-0.67	E	N
Blue-gray Gnatcatcher (BGGN)	0.08	-0.63	1.67*	0.45	-0.78	F	N
Wood Thrush (WOTH)	2.99*	-1.46	1.06*	-3.64	0.34	F	N

Note: Ellipses specify variables removed from occupancy models either due to model convergence errors or unreasonable effect sizes; statistical significance is based on the likelihood ratio test of a full vs. reduced model without the variable; habitat designations include F = forest species, E = shrubland or edge species, and blank indicates species neither forest nor edge; migration designations include N = Neotropical migrant, S = short-distance migrant, and R = permanent resident; scientific names found in Supplementary Material Table S1.
* $P < 0.05$; # $P < 0.10$.

and Blair, 2011). Birds also displayed varying responses to measurements taken within different landscape sizes (i.e., ~0.8 – 12.6 km^2), supporting the testing of multiple spatial extents rather than selecting one size to represent the landscape scale of all species (Hostetler and Holling, 2000). Tree cover and urban features significant at local and landscape scales were also relevant to species' habitat and migratory groupings, but, in general, many species collectively responded strongly to landscape tree cover.

Landscape-scale tree cover was the most influential variable examined in this study, including positive effects for the majority of species (65% of species with significant responses and 67% of all species combined). Tree cover was likely incorporated into primary sources of habitat for the one-third of species belonging to the forest habitat group (bluish hues on the community map). In addition, landscape tree cover is known to influence foraging opportunities (Barth et al., 2015; Wood and Esaian, 2020) and facilitate matrix dispersal for a variety of species (Arroyo-Rodríguez et al., 2020; Betts et al., 2021; DeMars et al., 2010). Regardless, the results are important because they are not exclusively based on large contiguous forest patches but incorporate a greater variety of tree cover within the broader landscape. Previous work has shown that indiscriminate sources of tree cover (i.e., synthesizing tree cover across residential, park, and woodland settings) may similarly influence community structure at landscape scales (Smith et al., 2014; Taylor et al., 2016). In other words, landscape tree cover may integrate to emulate much larger core areas for forest-sensitive species (e.g., Wood Thrush, other Neotropical migrants) (Taylor et al., 2016).

We found fewer species responded significantly to local tree cover. However, responses were largely consistent between scales. There is variation with respect to the relative importance of scale in tree cover measurements (Belaire et al., 2014; Donnelly and Marzluff, 2006; Hostetler and Holling, 2000; Luther et al., 2008; McCaffrey and Mannan, 2012; Pennington and Blair, 2011). Variation in landscape size and

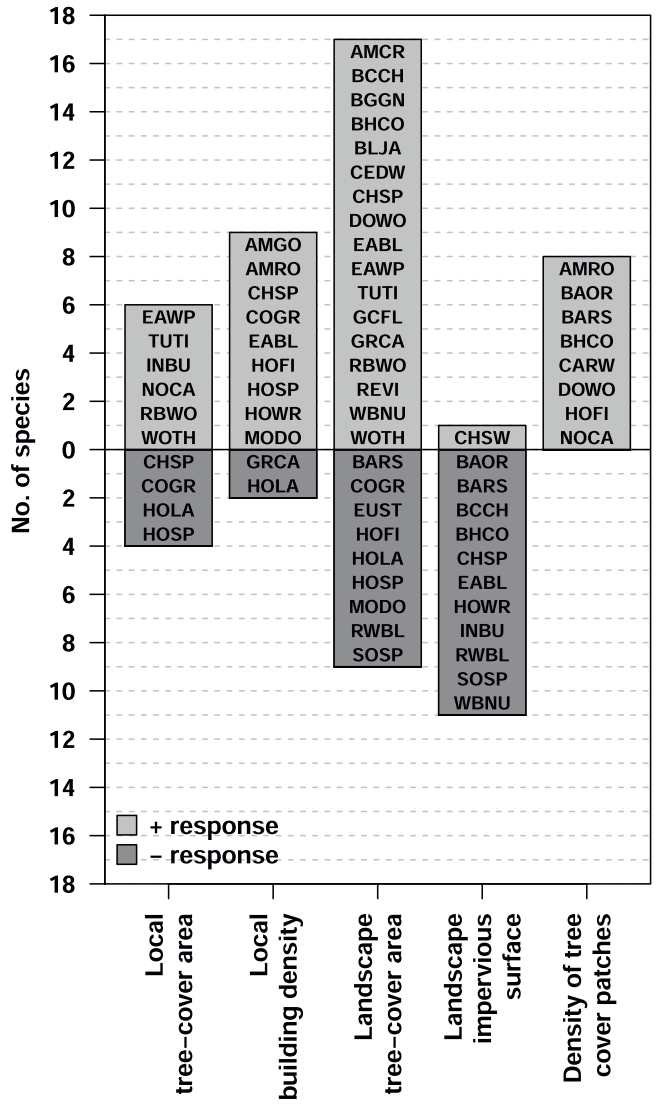

Fig. 3. The direction and number of bird species with significant effects to tree cover and urban variables, based on single-season occupancy models. Species with significant effects are displayed within bars. Species acronyms (codes) are formatted from the first two letters of English common names, e.g., American Robin = AMRO (see also Table 2).

spatial terminology could influence interpretations. In addition, unlike responses observed at landscape scales, bird may display more variability in response to local tree cover and depend on other local factors, as bird community structure and composition have been shown to vary across different urban treed habitats, such as parks and cemeteries (Tryjanowski et al., 2017). These subtle differences in tree conditions are not easily inferred from remotely-sensed data to test at the landscape scale. However, we suspect that the overall length of the urban-rural gradient in this study could also be prone to detecting greater effects of landscape tree cover when such relationships exist. Moreover, it is difficult to disentangle the limited support for patch density in this study. It is possible that the observed patterns emerged from a subset of patchy landscapes despite tree cover area and configuration being statistically uncorrelated. Still though, comparable studies have reported similar effects of tree cover area relative to spatial configuration (Donnelly and Marzluff, 2006).

The majority of significant responses to urban development features were largely dissimilar between scales. Significant responses to building density were largely positive (82% of species with significant responses), whereas responses to landscape impervious surface were largely negative (92% of species with significant responses). These differences could reflect inherent differences in measurement scales between local vs. landscape measurements. For example, impervious surface appeared to represent more effectively the overall urban-rural gradient across the study area (Fig. 1). In such case, measurements of impervious surface taken at the landscape scale likely better synthesized a myriad of unmeasured factors, including subtle changes in habitat, artificial light, and noise pollution, known to the influence urban bird communities (Liordos et al., 2021b, 2021a). Building density alone only represented a portion of this variation (possibly including unique responses) and appeared to also capture different development patterns at the local scale, particularly towards the rural-end of the study area.

In the case of separating out the effects of local building density from overall urban development, residential housing likely incorporated a range of potential responses, including the presence of bird feeders (Ibáñez-Álamo et al., 2020; Jokimäki, 1999). Some species may have also been attracted to lawns or other cleared spaces due to different foraging opportunities or residential landscaping (Belaire et al., 2014; Melles et al., 2003). Differing responses to urban predictors were also generally represented by large number of similar species within the short-distance migrant and edge habitat species groups (corresponding to the orange, yellow, and green color trends on the map) restricted to areas of low levels of urbanization associated with agriculture and other open, rural land uses. Thus, these responses also likely incorporated some the differences in development patterns inherent to these measurements. Land uses of this type represent much less of a habitat discontinuity for these species relative to more intense urbanization (Gilbert and Ferguson, 2019; Schlossberg et al., 2011). Many of these responses were also among species (e.g., Mourning Dove, Barn Swallow, Red-winged Blackbird, etc.) responding negatively to landscape tree cover. We suspect some of the relationships were also the result of agricultural land uses tending to reduce tree cover in our region (Nowak and Greenfield, 2012). For other species, it is still well-established that building presence often degrades local forest habitat (Friesen et al., 1995; Lumpkin and Pearson, 2013). Future studies might consider examining whether different building types (e.g., single-family homes or large commercial dwellings) or building features (e.g., building height and area) influences urban bird communities (Liordos et al., 2021a; MacGregor-Fors and Schondube, 2011).

The remaining effect sizes for urban variables were relatively weak in comparison, possibly attributed to many species being detected across large segments of the urban-rural gradient. Specific life history traits of these species, such as omnivorous diets (e.g., Cedar Waxwing and American Robin), cavity nesting (e.g., woodpeckers), or multi-brooded nesting attempts (e.g., Northern Cardinal), are considered traits that promote some level of urban adaptability (Callaghan et al., 2019; Chace and Walsh, 2006). The map clearly illustrates community change across the region, broadly agreeing with the common understanding that bird composition and structure respond to changes in urbanization (Aronson et al., 2014; Chace and Walsh, 2006). However, on the basis of relative importance, it would appear that birds may respond more strongly to vegetation relative to urban predictors (Lerman and Warren, 2011; Mills et al., 1989). Furthermore, our finding that tree cover was more important than development intensity is similar to results found in other studies (Fletcher and Hutto, 2008; Taylor et al., 2016). In such case, urban planners might find vegetation management to be a particularly important strategy to conserving urban bird communities.

The relationships described here are based entirely within the breeding season. Factors influencing species' interactions within the urban environment vary at different times of the annual cycle (Atchison and Rodewald, 2006; Ibáñez-Álamo et al., 2020; Leveau et al., 2021). Many migratory species are known to use urban areas as stopover habitat (Archer et al., 2019). In particular, bird-building collisions are now considered a leading cause of migrant mortality (Loss et al., 2014). Collisions by nocturnal migrants are facilitated by large glass surfaces that reflect vegetative cover when located near vegetation sources (Loss

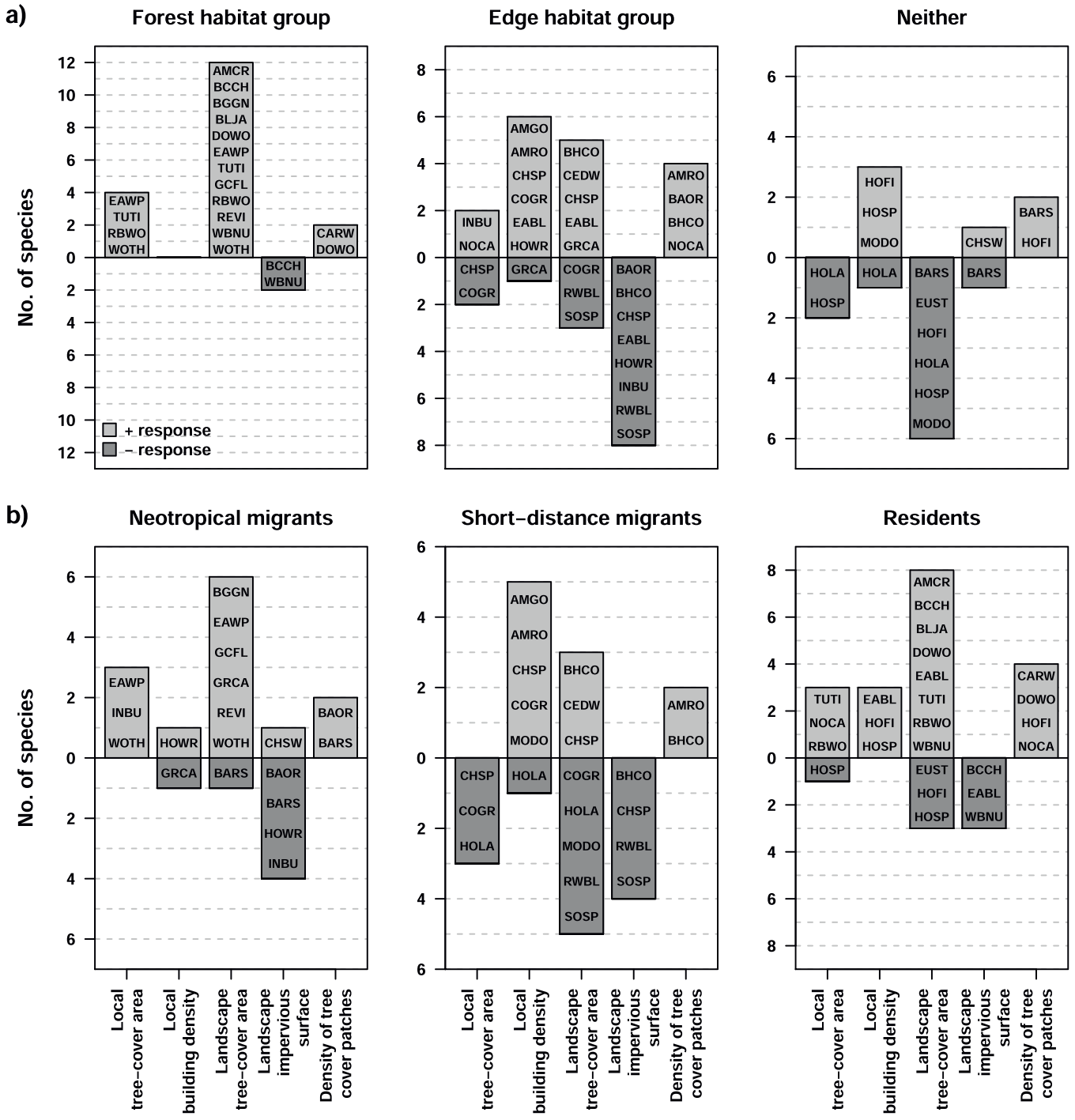

Fig. 4. The direction and number of bird species with significant effects to tree cover and urban variables relative to habitat and migration groupings. Species with significant effects are displayed within bars. Species acronyms (codes) are formatted from the first two letters of English common names, e.g., American Robin = AMRO (see also Table 2).

et al., 2019). Urban greening efforts may reduce bird collisions by removing surface reflectivity near vegetated areas or reducing night light pollution (Loss et al., 2019). These considerations may be essential in ensuring that urban tree cover is beneficial and not harmful to the full annual cycle of birds.

Regional land acquisition and vegetation management are important to the restoration of the Oak Openings (Abella et al., 2017, 2007; Martin and Root, 2020). Though there are few recognized obligate oak savanna bird species (Red-headed Woodpecker being one species but detected at too few sites to be considered for analysis), many bird species have been shown to respond positively to oak savanna restoration. At least 80% of bird species responding positively to restoration in another study showed strongly positive associations with increasing landscape tree cover in this study (Brawn, 2006). Our results suggest that improving landscape tree cover surrounding restoration may facilitate the conservation of regional bird diversity while restoring this unique ecosystem.

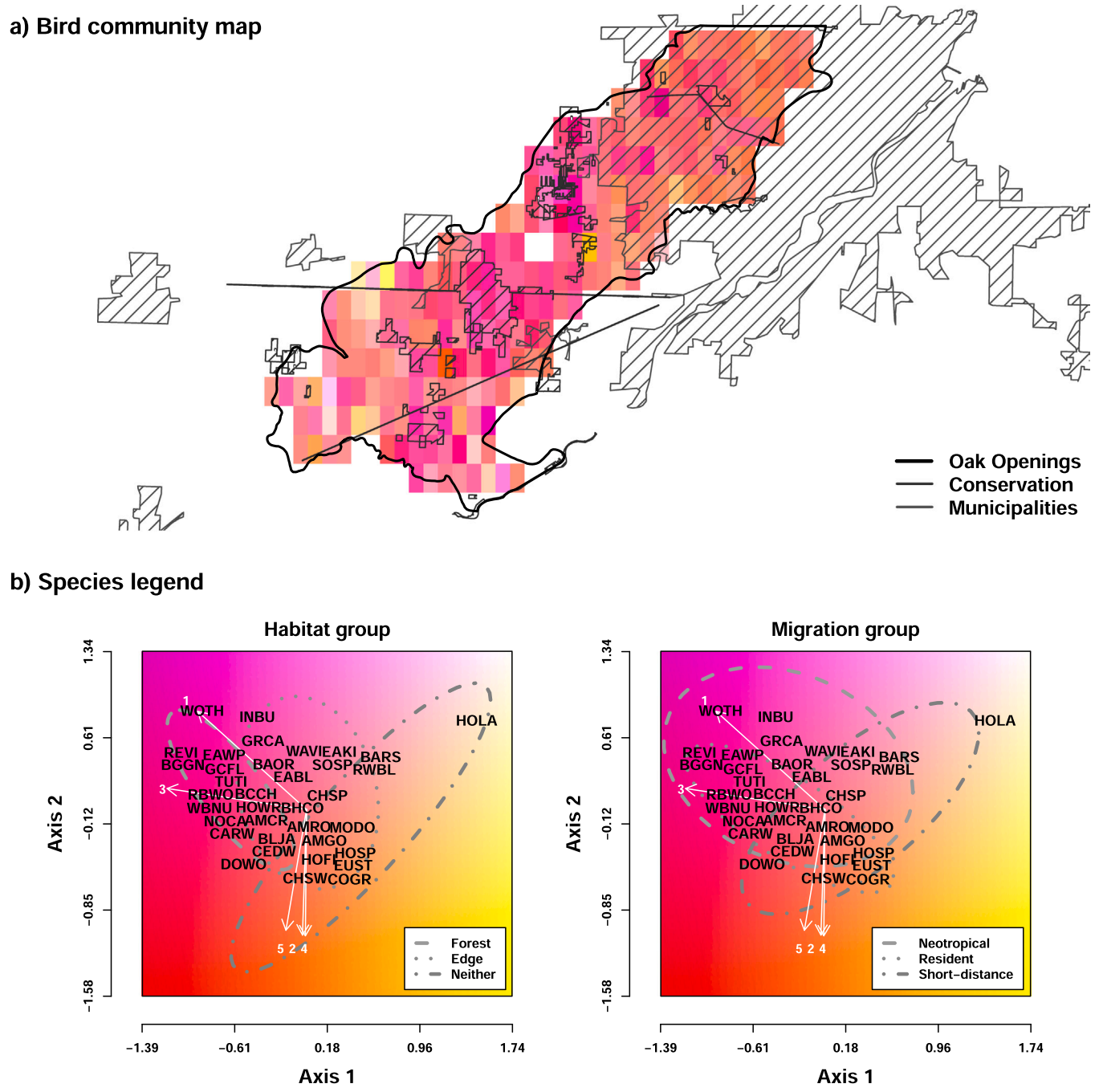

Fig. 5. Community map of 36 bird species displayed at one-km by two-km scale relative to the study's regional sampling design (a). Differences in community composition corresponds to species positions in the related color space by transforming axes of a two-dimensional non-metric multidimensional scaling (nMDS) ordination in channels of color (b). The color space is defined by nMDS axis scores (axis 1, green; axis 2, blue; including a default value of 255 in red). Vectors on the species legend correspond to the direction and correlation of variable vectors (1 =local tree-cover area; 2 = local building density; 3 = landscape-scale tree-cover area; 4 =landscape-scale impervious surface; and 5 = density of tree cover patches) relative to species associations along nMDS axes. Species acronyms (codes) are formatted from the first two letters of English common names, e.g., American Robin = AMRO (see also Table 2).

In addition, reducing the overall spread of urbanization into these sensitive areas will likely have maximum benefits to collections of edge and shrubland bird species (as shown by the strongly negative responses to urbanization in this study). We cannot easily distinguish the influence of individual tree species in this study, while bird communities are known to affiliate with different tree assemblages (Adams and Matthews, 2019; Rodewald, 2003; Wood et al., 2012; Wood and Esaian, 2020). Therefore, future work may consider incorporating species-level tree information (Belaire et al., 2014; Bourne and Conway, 2014; Dekeukeleire et al., 2019). The application of iTree (www.itreetools.org) and other urban forest assessment tools could also provide improved tree statistics over remotely-sensed canopy coverage estimates (Lerman et al., 2014). Our extensive sampling of bird communities from roadsides likely had no influence on the responses observed in this study, especially considering our overall landscape focus (McCarthy et al., 2012). An orientation towards a more patch-level focus, however, could have provided a much larger sample of more patch-sensitive or rare species and perhaps augmented the overall sample size of bird species considered for analysis. In addition, our methods are biased against nocturnal species and future studies may consider nocturnal

surveys to provide a more comprehensive picture of potential bird responses to urbanization. This deeper focus, in combination with incorporating additional response values (e.g., abundance or breeding success), could enhance the overall results of this study.

Our findings suggest that the extent of tree cover on the landscape is a powerful predictor of bird species distributions across regional urban-rural gradients. We accentuate the importance of scale in disentangling the relative importance of fundamental elements of the biophysical structure of urban areas and where potential actions may arise to benefit bird https://www.oakopenings.orgdiversity. Tree cover assessments taken at large spatial scales can play an important role in regional bird diversity conservation goal setting and action. Our findings may be of interest to growing tree planting initiatives (Eisenman et al., 2021), including that of the Green Ribbon Initiative (https://www.oakopenings.org), a partnership of local conservation organizations utilizing tree planting to improve landscape connectivity of the Oak Openings. In addition, positive associations of many bird species with local building density suggests that landowner education and outreach can be important to inform residents of their role in supporting bird communities in urban environments. These approaches working in combination may be key to sustaining urban biodiversity as urban growth is expected to intensify in the coming decades.

CRediT authorship contribution statement

Bryce Adams: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft. **Karen Root:** Conceptualization, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare no competing interests.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2022.127601.

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