Differential response of migratory guilds of birds to park area and urbanization

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Abstract

Variation in species richness and density of native birds in urban parks and greenspaces ("parks") is often substantial. Understanding why differences exist, and whether all migratory guilds are equally affected, is poorly known. We surveyed breeding bird communities in 48 undeveloped forested parks in Portland, Oregon, USA, to determine the contributions of park area, shape, connectivity, landscape composition surrounding parks, and differences in structure/composition of local habitat to variation in richness and density of residents, long-distance migrants, and short-distance/partial migrants. Migratory guilds responded differently to environmental factors. Richness and density of long-distance migrants increased with park area and abundance of small (< 10 cm DBH), mostly native, tree species. Resident richness also increased with the abundance of small trees. However, resident and short-distance/partial migrant richness was independent of park area, and resident density declined with increasing area. Park shape, connectivity, and landscape composition did not influence richness or density of any migratory guilds, possibly because of relatively high tree cover in Portland's landscape. Separate analyses of forest-dependent species of all migratory guilds revealed that area was the primary contributor to variation in density of residents and long-distance migrants, structural habitat features contributed to variation in density of residents but not long-distance migrants, and that density of long-distance migrants declined with elongated park shape. Few forest-dependent species existed in parks below 10 ha, and their minimum area requirements for maintaining populations were estimated to be 30 to 40 ha. Without such parks most long-distance migrants would likely disappear from Portland's landscape.

Introduction

Attempts to better understand and mitigate the negative effects of urbanization on wildlife have grown in response to rapidly increasing human populations (Steffen et al. 2015), the continuing expansion of megacities (Seto et al. 2012;

Kennedy et al. 2014), and recognition that urbanization represents a major extinction threat (McDonald et al. 2008; Seto et al. 2012). As cities expand beyond present boundaries into surrounding semi-natural habitats, the potential, and need, to incorporate reserves for native species will both grow. Studies of birds have been at the forefront of urban ecology (Marzluff et al. 2001), but our understanding of what structures avian systems is still wanting because of the many potential sources of variation in urban settings, and regional differences in their importance (Lerman et al. 2021).

Answering the question of what drives variation in species richness and abundance among urban avian communities is complicated because it requires consideration of the geometry (i.e., size and shape) of the park itself and other factors operating from the higher landscape to the lower local level (Nielsen et al. 2014). For instance, species richness of birds

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regularly increases with park area (Crooks et al. 2001; Husté et al. 2006; Ikin et al. 2013; Myczko et al. 2014; Huang et al. 2015; Kang et al. 2015; Maseko et al. 2020; de Groot et al. 2021; but see Cooper and Walters 2002, Martensen et al. 2008), while elongated fragments that contain relatively high amounts of edge has been associated with low species richness (Natuhara and Imai 1999) and low nest success and/or survival of fledglings (Batáry and Báldi 2004; Shipley et al. 2013). Regardless of geometry, parks are not true islands and land use in a park's surrounding landscape (i.e., the "matrix") can either ameliorate or exacerbate negative effects of shrinking park area, habitat fragmentation, and isolation (Taylor et al. 2016, Amaya-Espinal et al. 2019, Spake et al. 2020). The negative effects of highly developed matrices may arise from several sources, including inhibition of dispersal movements among parks (Martensen et al. 2008; Tremblay and St. Clair 2011), support of synanthropic species that may also use parks and compete with native habitat specialists (Donnelly and Marzluff 2004; Rodewald and Bakermans 2006; Oliver et al. 2011; Canedoli et al. 2018; Amaya-Espinel et al. 2019), or increase in depredation of birds and/or their nests by mesopredator species that increase in response to the absence of large predators in urban environments (Fischer et al. 2012; but see Rodewald et al. 2011). On a more local level, species richness of parks often responds strongly to variation in structural vegetation complexity (Myczko et al. 2014; Rush et al. 2014; Kang et al. 2015), habitat diversity (Donnelly and Marzluff 2004; Cornelis and Hermy 2004), or floristic composition (Husté et al. 2006; Shwartz et al. 2008; Paker et al. 2014; Huang et al. 2015; Taylor et al. 2016).

However, because birds vary greatly in nesting, feeding, and migratory ecology we should not expect all species to respond equally to urbanization (Concepción et al. 2015; Callaghan et al. 2020). For example, urbanization adversely affects nesting site specialists (Callaghan et al. 2020) and the ground nesting guild typically suffers in urban settings presumably because of elevated rates of nest predation from mesopredators and/or domestic/feral animals (Chace and Walsh 2006). Noninsectivorous passerines and raptors often fare well in cities, in part, because of elevated food supplies resulting from either direct (Robb et al. 2008; Plummer et al. 2019) or indirect (Chace and Walsh 2006) supplementation by humans, respectively. Migratory behavior represents a fundamental difference in life history among birds, but our understanding of how different migratory guilds respond to urbanization is limited and lacks consistency. Park and Lee (2000) reported that, relative to migrants, richness of resident bird species increased more quickly with park area and that larger parks supported twice the number of residents as migrant species. Husté and Boulinier (2007) found equal rates of increase in richness of residents and migrants with

area, but that residents were again more diverse. By contrast, Taylor et al. (2016) reported that resident bird species richness responded to vegetation composition within parks but was independent of park area, whereas area was the best predictor of migrant species richness. In general, negative responses to urbanization appear stronger in long-distance migrants than other species (e.g., Friesen et al. 1995, Hennings and Edge 2003, Rodewald and Bakermans 2006), possibly because the small population size of the former may lead to more frequent local extirpation (Husté and Boulinier 2007). Given the poor state of the world's birds (Lees et al. 2022), declining populations of many migrant species in Europe (Sanderson et al. 2006; Both et al. 2010) and North America (Rosenberg et al. 2019), and that urban growth is inevitable, urban greenspaces must be better planned to conserve migrant birds (see also Rodewald et al. 2013).

Portland, Oregon (USA), is the 26th largest city in the US (~ 666,500 in 2022) http://worldpopulationreview.com/us-cities/), is growing rapidly (600,000 + more people are expected by 2035; METRO 2015), but also supports an extensive park system (4740 ha, 13.7% of city land area). Most of the system (3206 ha [68%]) is maintained as natural areas or otherwise undeveloped parks (no development beyond trails), and individual patches range from ~ 1 to 2064 ha. We surveyed breeding bird communities in 48 sites to evaluate affects of park geometry and connectivity, landscape composition, and local (within-park) habitat structure and floristic composition on richness and abundance of bird species associated with upland forest habitats. Based on past literature (see above) we hypothesized that (1) species richness and density of bird populations would increase with park area and eclipse all other factors as the primary source of variation in bird community structure for all migratory guilds (defined below), and that (2) given Portland's high tree cover (~ 30%), high structural habitat/floristic diversity within parks would have a greater positive influence on birds than high park connectivity or favorable landscape composition. Furthermore, because conservation planning requires estimates of species-specific minimum area requirements, (3) for those species that are most dependent on forested parks, we attempt to identify minimum area needs (sensu Robbins et al. 1989).

Methods

Study area, site selection, and site properties

We sampled birds and vegetation in 48 second growth parks located in the northern Willamette, Sandy, and lower Columbia river watersheds in the greater Portland metropolitan area (city center: 45.52 N, -122.68 W). The region is

Table 1 Description of the variables used in the analysis of among park variation in species richness and density of birds from 2003 in Portland, OR (USA). Description of each principal component (PC) axis (left to right) reflects negative to positive scores. Percentages refer to the portion of total variation accounted for by each PC axis. Details of principal component analyses in Electronic Supplementary Materials

Variable	Description
Park area (ha)	Area contained within political boundary of parks or legal border of privately owned land
Shape	Shape of park reflects compactness and amount of "edge"; equals 1.0 for a perfectly square patch and increases as patch shape becomes more complex and elongate
Connectivity	Distance to greenspaces within 1000 m area around parks weighted by the area of specific greenspace
LandPC1	PC1 from analysis of landscape in 500 m buffer around each park; contrast of abundant low urban (i.e., residential home) development and high human population density grading into sites with high forest cover with low residential development and low human population density; 53.9%
TreePC1	PC1 of canopy analysis; Contrast of forests dominated by angiosperm trees with few individuals in the largest size class grading into coniferous forest (mostly Douglas-fir) of the largest trees (≥ 60 cm DBH); 20.3%
TreePC2	PC2 of canopy analysis; Gradient of increasing number of trees of primarily native species in smallest size class (< 10 cm DBH); 19.0%
TreePC3	PC3 of canopy analysis; Gradient of increasing volume of coarse woody debris; 12.7%
TreePC4	PC4 of canopy analysis; Contrast of forests with few medium/large trees and abundant red alder with forests having abundant big-leaf maple and trees in second largest size class (30–60 cm DBH); 7.4%
HbShPC1	PC1 of herb/shrub layer; Contrast of forests with deep and abundant litter on forest floor with forests having soil surface composed primarily of moss and/or bare soil; 15.9%
HbShPC2	PC2 of herb/shrub layer; Contrasts of forests with abundant medium shrub (1–2 m high) cover with English ivy below grading into forests with little shrub cover or English ivy, but abundant snowberry;12.8%
HbShPC3	PC3 of herb/shrub layer; Contrasts of forests with abundant low (0–1 m) shrub cover dominated by salal, thimbleberry and trailing blackberry that grade into forests with little shrub but abundant herbaceous plant cover; 11.6%
HbShPC4	PC4 of herb/shrub layer; Abundant medium (1–2 m) and high (2–3 m) shrub cover (primarily of salmon berry) but little low (0–1 m) shrub cover or English ivy contrasted with forests with little medium or high shrub cover but abundant low shrub cover dominated by English Ivy; 10.8%

characterized geologically by broad alluvial flats punctuated by scattered volcanic buttes that rise to low hills in the west and south of the Willamette and Columbia rivers, respectively. Elevation ranges from 20 to 250 m. Climate is characterized by cool, wet winters (December: 4.7º C and 13.9 cm precipitation) and warm, dry summers (August: 20.8º C and 1.7 cm precipitation**)**. Later seral-stage vegetation is dominated by shade tolerant conifers including western hemlock (*Tsuga heterophylla*), grand fir (*Aibes grandis*), and western red cedar (*Thuja plicata*), but earlier seral-stage Douglas fir (*Pseudotsuga menziesii*) and big-leaf maple (*Acer macrophyllum*) now dominate the mainly second growth stands throughout the study area.

Parks were selected by stratified random sampling to represent the full range of possible areas (< 1 to 2,000 ha). All sites contained multistory forest with ≥ 50% canopy closure and limited development. All but one (Oxbow Regional Park) fell within Portland's urban growth boundary, and 42 of 48 were city parks. The other six were privately owned parcels. Sites were delimited by roads and adjacent urban development (i.e., the presence of buildings, impervious surfaces, or intensively maintained vegetated habitats), rather than ownership or parcel boundaries (for details see Supplementary Information [SI]). Park area, shape and connectivity (Table 1) were extracted using ArcGIS and FRAGSTATS (McGarigal and Marks 1995) from data provided by Portland's METRO Regional Services' RLIS database (Metro 2004). All analyses utilized digitized 2001 aerial photographs of the greater Portland metropolitan region with a pixel resolution of 3.05 m. Details are provided in the SI.

Landscape composition: quantification and analysis

We quantified landscape composition (undeveloped forest, developed forest and total forest [= undeveloped + developed], light urban development, heavy urban development, total urban development [light + heavy], and open spaces without trees), human population density, and street density in the 500 m buffer surrounding each park (see SI). We then subjected these data to a principal component analysis (PCA) to identify the main gradients of landscape variation across Portland for the purpose of testing for avian responses to differences in landscape structure. Principal component 1 (LandPC1) accounted for 54% of the variation in landscape structure and described a gradient in which more urbanized landscapes (negative scores) that were characterized by high residential development and high population density were replaced by landscapes with increasing dominance of trees, low residential development, and low human population density in the 500 m buffer surrounding each park (positive scores; Table 1). Full details of PCA are provided in the SI.

Quantification and analysis of vegetation

We sampled vegetation in 2003 at 2 to 16 plots per park (total = 279), with larger parks having a greater number of plots to capture potentially greater vegetation diversity. Plots were randomly located (ArcGIS and Garmin 12XL GPS units; ± 10 m) within parks and associated with either vegetation sampling alone, bird point count stations, small mammal traplines, or amphibian pitfall arrays. In some cases, the plots associated with amphibian surveys were moved up to 10 m to accommodate pitfall installation. At all but the smallest parks, points were located at least 100 m away from forest edge and 200 m from one another.

Vegetation structure and composition at each plot were measured in 10 m radius circles. We identified most plants to species, and measured diameter breast height (DBH) of all trees with DBH > 2.5 cm. We also counted the number and estimated the volume (cross-sectional area x length) of all snags (standing dead tree) and logs (fallen dead tree) > 10 cm diameter. Subsamples of vegetation of the shrub and herbaceous layers, and forest floor were taken from two perpendicular transects that crossed through the center of the circle. Canopy closure was also estimated visually along the same two transects (see SI for full details).

Modified importance values (IV) were calculated for all tree species at all 279 points. Total coniferous and angiosperm IVs, along with canopy closure, number of trees in four size classes (< 10 cm, 10.1–30 cm, 30.1–60 cm, and > 60 cm), total volume of logs and snags (= coarse woody debris), tree species richness (3 classes: native, exotic, and

total), and IV of the four most dominant trees in the data (2 conifers: Douglas-fir, western red cedar; 2 angiosperms: big-leaf maple, red alder [*Alnus rubra*]) were used in a PCA to describe forest tree structure. Eigenvalues of the first four PCs exceeded 1.0, and in total, they accounted for 59.4% of the variation in the data. The gradients in forest structure that they represent are described in Table 1. Similarly, we used proportional ground cover (i.e., bare ground, moss, leaf litter, small woody debris, herbs), litter depth, shrub density (3 layers: 0–1 m, 1.1-2 m, and 2.1-3 m), and proportional contribution to the shrub layer of eight common species in a PCA to describe the structure of the forest floor and understory. Eigenvectors of the first four PCs also exceeded 1.0 and accounted for 51.1% of variation. Descriptions of the gradients described by the shrub to forest floor PCA variables are provided in Table 1 (see SI for full detail). Plot-level PCA scores were averaged within each park to calculate park-level averages for all eight PCA axes.

Avian surveys: richness and abundance

Avian migratory activity drops sharply by late May in Portland and therefore surveys were conducted between 15 May and 18 July, 2003, to avoid sampling transiting migrants; our surveys thus represent samples of the breeding bird communities. All surveys were conducted by one person (DCB) between sunrise and 1100 h on days without rain and little to no wind. Three counts were made at all survey points over the course of the season. Point count locations (1–6 per park) were randomly selected, and all points within a park were surveyed on a single day, but survey times at any given point were changed between survey dates to minimize potential effects of time of day on results. All points were located ≥ 50 m from the park edge and ≥ 150 m from one another. A few small sites were not wide enough to accommodate points ≥ 50 m from a site edge, so points were located as far from edges as possible. Species accumulation curves for all 48 sites individually (Fig. 1a), and for the system in its entirety (Fig. 1b), indicated that 3 surveys were sufficient to describe avian community composition.

We used the variable circular plot method (Bibby et al. 2000) to record all birds heard or seen out to 50 m. Ten-minute point counts were made following a 1-min period of quiet to allow birds to return to normal activity; flyovers were not included. To minimize double-counting, determination of multiple conspecifics was based on detection of counter-singing or simultaneous visual and/or aural detection along with mapping detections on data sheets in concentric circles at survey points (0–10 m, 10–25 m, 25–50 m). To avoid double-counting birds that fell between adjacent points that were relatively close to each other, mapped locations were

Fig. 1 Absolute (a) and standardized (b) species accumulation curves in which total number of new species detected are plotted against survey number for all 48 parks. Standardized plots were based on Z-scores calculated for each park based on its mean and standard deviation of number of new species. The lines in (a) and (b) are the predicted number of new species obtained from asymptotic regression of cumulative number of new species against survey number
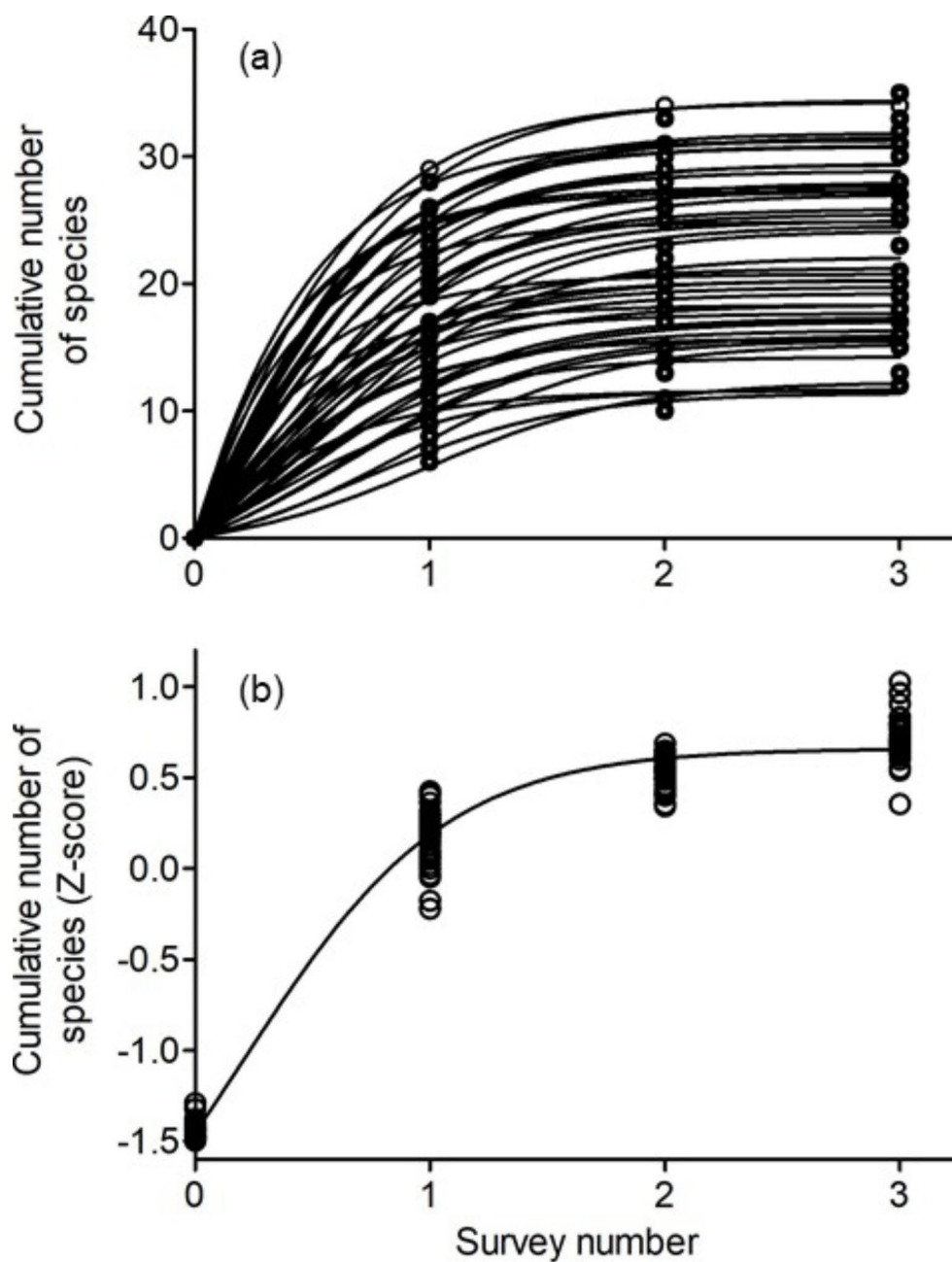
compared in the field to assign individuals that fell between points to the nearer station.

Spot mapping is the most accurate estimator of avian abundance (Notes 1970). Hamel's (1984) comparison of spot mapping estimates of abundance to counts made using the variable circular plot method showed that biasing abundance estimates from the variable circular plot method upward better approximated spot mapping estimates of abundance. Therefore, at each point count location our index of abundance of each species was the average of the two highest of the three counts made, which we averaged across all survey locations within each park to obtain an

average abundance for each species. Absence of a species from a park was treated as an abundance of zero.

Analysis of avian species richness and density

Abundance measured within a specified area represents density and henceforth we use density to describe number of individuals detected by point counts. We omitted from our analyses all aerial insectivorous birds and rare species. Aerial insectivores (swifts and swallows) are wide ranging, forage above the canopy, and cannot be associated with a particular point in the forest. Rare species were those whose

95% confidence interval (CI) for average density, computed across all 48 parks, included zero (Appendix 1). Species classified as rare were raptors (Red-tailed Hawk and Cooper's Hawk; all scientific names in Appendix 1), species that do not breed in the habitats in which we conducted our work, are irruptive, or were never detected at more than two sites (and at low density). For purposes of analysis, we classified species as belonging to 1 of 3 migratory guilds (Appendix 1). Year-round residents are present throughout the year, long-distance migrants overwinter primarily south of the border of the United States (i.e., Nearctic-Neotropical migrants), while short-distance/partial migrants exhibit intermediate behavior. We relied on Birds of the World accounts (Rodewald 2022) and personal experience in this system to classify all species to migratory category.

Park area and other variables that deviated from a Gaussian distribution were transformed (log_{10}) prior to analysis. The quadratic of park area was included in all analyses as preliminary inspection of data indicated frequent nonlinearity in the relationship between park area and the response variables. All predictor variables (Table 1) were z-transformed to enable direct comparisons of coefficients (Schielzeth 2010), and the quadratic of park area was taken after standardization of area (Schielzeth 2010). Variance inflation factors in analyses were almost always below 2.0, rarely exceeded 3.0, and never approached 10 (Quinn and Keough 2002).

We used generalized linear models with a Poisson distribution and log link function to identify the drivers of variation in species richness (i.e., cumulative number of different species). Number of survey points per park was included as an offset to account for differences in sampling intensity. All variables were added to the model, and then removed by backward elimination by removing the variable with the highest P-value at each step until a final set of competitive models ($\Delta AICc \leq 2$) was obtained. Models within 2 AIC_c units that added a parameter without improving model deviance were not included in the final set to ensure that ΔAIC_c values were not the result of uninformative parameters (Arnold 2010). If the number of competitive models exceeded two we report model averaged parameter estimates for all variables retained by the models, but report original model output if only 1 or 2 competitive models existed. Model averaged coefficients were considered "significant" if their 85% confidence intervals did not include zero (Arnold 2010). Poisson regression does not generate a formal R^2 but a pseudo-R^2 was calculated as the difference in deviance between the null model (i.e., no predictor variables) and the fitted model divided by the null model's deviance. We also used best subsets regression analysis to examine variation in density of the three migrant guilds in relation to the same set of predictor variables (Table 1). As

for the Poisson regressions, we used an information theoretic approach to identify top models. Explained variation is reported as an adjusted R^2 (R^2_{adj}).

Although we do not report them here, we also conducted individual analyses of density of all species using best subsets regression analysis. From these analyses we identified a set of forest-dependent species that we define as species with positive coefficients (at $P \leq 0.10$) between their density and either park area or area^2. For these species we performed separate best subsets regression analyses on the summed density of forest-dependent species belonging to the three migratory guilds using the predictors described in Table 1. Our objective was to remove area effects and identify other important determinants of density in the ecologically sensitive forest-dependent species that are most at risk in urban landscapes. For similar reasons we also calculated minimum area requirements (MAR) for the forest-dependent species using generalized linear models with a binomial distribution and logit link function to model presence/absence of each species in relation to park area. For species that reached an asymptote (100% probability of occurrence) within our range of park areas we used park area at 50% of the area at the asymptote to be a conservative estimate of minimum area needed to sustain populations (Robbins et al. 1989). For species for which probability of occurrence continued to increase within the bounds of our study (~ 2000 ha), we used park area at 50% of the probability of occurrence exhibited at 2000 ha as our estimate of MAR (Robbins et al. 1989). We then compared MAR in relation to body mass and migratory behavior to discern if MAR varied predictably with either variable.

We used STATISTIX version 9 (Analytical Software, Tallahassee, Florida, USA) for basic summary statistics, least squares regressions, PCAs, and best subsets regression analyses and JMP Pro 12 (SAS Institute Inc., Cary, North Carolina, USA) for generalized linear models of species richness and calculation of MARs. Statistics are reported as mean $\pm$ SE, with statistical significance accepted at $P \leq 0.05$.

Results

Excluding aerial foragers, we recorded 41 regularly occurring and 17 rare species. Of the regularly occurring species, most were residents (49%), followed by long-distance migrants (32.0%), and short-distance/partial migrants (19%). Rare species included 2 raptors, and 3, 4, and 6 resident, long-distance migrant, and short-distance/partial migrant native species, respectively, and two invasive species (European Starling and House Sparrow; see Appendix 1 for a full list of species).

Fig. 2 Species richness of (a) resident species in relation to TreePC2 and (b) long-distance migrants as a function of park area in 48 parks in Portland, Oregon, in 2003. Richness in both (a) and (b) is the residual after accounting for the offset (number of sample points per park), and for long-distance migrants it also reflects the statistical removal of positive influences of TreePC2 on richness. TreePC2 and park area are both standardized to a mean of zero and standard deviation of 1.0. Positive scores on TreePC2 represent an increase in the abundance of small, mostly native, trees
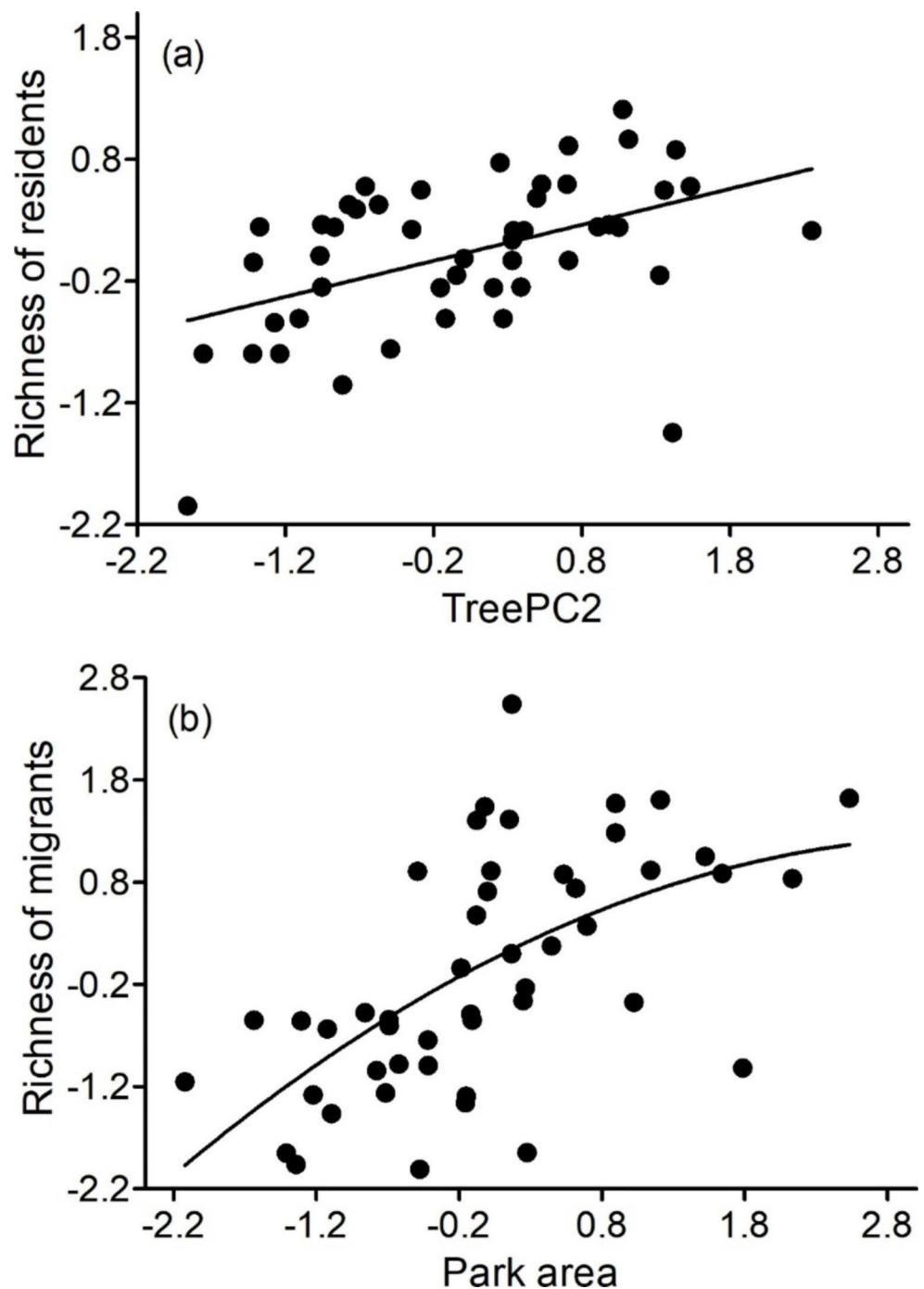
Determinants of richness. – Analysis of resident species richness yielded two competitive models (Table 2). TreePC2 appeared in both and showed that richness increased with greater abundance of small (DBH < 10 cm), mostly native, trees (Fig. 2a). The presence of HbShPC4 in the top model suggested resident richness possibly increased as the understory shifted from medium/high to low shrub cover where English ivy (*Hedera helix*) was abundant, but HbShPC4's 95% CI included zero (Table 2). Among long-distance migrants, park area was the main contributor to variation in

species richness followed by TreePC2 (Table 2). The negative quadratic for park area reflected a decelerating increase in species richness with park area (Fig. 2b). The top models for residents and long-distance migrants reduced the deviance for variation in richness by 34% and 55%, respectively. By contrast, our analysis accounted for little if any of the among park variation in species richness of short-distance/partial migrants (Table 2).

Determinants of density. – Two competitive models emerged from our analysis of variation in resident density.

Table 2 Top models ($\Delta AICc \leq 2$) accounting for variation in species richness of birds in 48 parks from Portland, OR, in 2003. Data analyzed separately for resident species, long-distance migrants, and short-distance/partial migrants

Variable	Coefficient (SE; P)	Lower 95% CI	Upper 95% CI	$\Delta AICc$	Pseudo-R^2
RESIDENTS		Residents			
TreePC2	0.078 (0.041; 0.060)	-0.002	0.158	0.000	0.345
HSPC4	0.064 (0.042; 0.124)	-0.018	0.146		
TreePC2	0.085 (0.041; 0.038)	0.005	0.165	0.083	0.222
LONG-DISTANCE MIGRANTS					
Area	0.645 (0.119; <0.001)	0.420	0.886	0.000	0.548
Area^2	-0.153 (0.061; 0.007)	-0.278	-0.039		
TreePC2	0.168 (0.086; 0.049)	0.001	0.336		
SHORT-DISTANCE/PARTIAL MIGRANTS					
TreePC4	0.103 (0.075; 0.170)	-0.044	0.250	0.000	0.085

A negative quadratic of park area and TreePC2 appeared in both, indicating that the density of residents was greater in small parks and where smaller, mainly native, trees, were abundant (Table 3; Fig. 3a and c). The positive correlation of density with TreePC3 in the top model suggested residents were more abundant where coarse woody debris was common, but TreePC3's 95% CI overlapped zero (Table 3). Density in both competitive models of long-distance migrant density indicated that density increased steadily with park area (Table 3; Fig. 3b), and was greater in parks with abundant medium and high shrub cover where little English ivy was present (HbShPC4; Fig. 3d; Table 3), and where the ground surface was comprised of more moss or bare soil than plant litter (HbShPC1; Table 3). The appearance of TreePC2 in the top model again suggested that density tended to be higher in parks where smaller, mainly native trees were abundant, but TreePC2's 95% CI included zero (Table 3). For short-distance/partial migrants, our single competitive model indicated that density was likely greater in parks embedded within a landscape comprised of
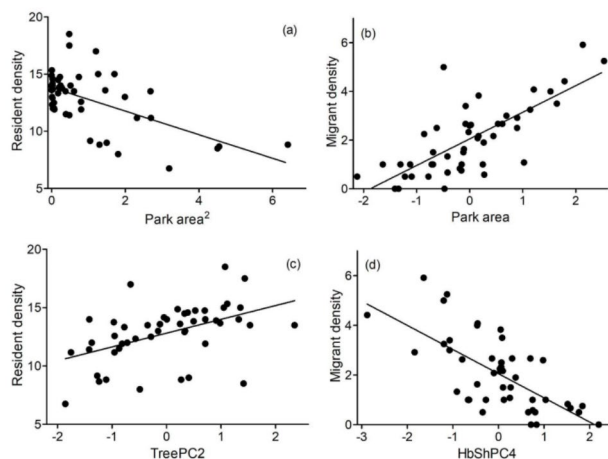
Fig. 3 Variation in density (mean number of individuals of all species/point count/park) for resident species (a and c) and long-distance migrants (b and d). All predictor variables are standardized to a mean of zero and standard deviation of 1.0. Density declined with the quadratic of area for residents (a) but increased with area in long-distance migrants (b). Resident density was also greater in parks where small, mostly native trees (TreePC2) were abundant, while long-distance migrants were denser in parks with abundant medium to high shrub cover (HbShPC4). Statistically significant least squares regression line describing the relationship between density and the predictor variables plotted

fewer trees and more residential development (LandPC1; Table 3). However, LandPC1's 95% CI included zero.

Forest-dependent species: habitat and minimum area requirements. – The proportion of species that were forest-dependent (i.e., density increased with increasing park area or area^2) was roughly twice as great for long-distance migrants (0.54 [7 of 13]) as for residents (0.25 [5 of 20]; $X^2 = 2.83$, df = 1, $P = 0.093$); short-distance/partial migrants were intermediate (0.38 [3 of 8]).

Multiple species exhibited abrupt increases in density when park area reached 10 ha (Fig. 4), and separate analyses of migratory guilds revealed that the strength of the relationship between density and area differed among them. Although weaker in resident ($R^2 = 0.512$, $P < 0.001$) than long-distance migrants ($R^2 = 0.721$, $P < 0.001$), second-order polynomial regression with a positive coefficient for the quadratic term provided the best fit for both, indicating that density tended to exhibit an accelerating increase with area. Density of short-distance/partial migrants, on the other hand, exhibited only a weak increase with the square of park area ($r^2 = 0.066$, $P = 0.077$).

Best subsets regression analysis of density yielded 3, 7, and 6 competitive models for residents, long-distance migrants, and short-distance/partial migrants, respectively (all model results in the Supplementary Materials). Model averaged coefficients for forest-dependent residents confirmed the area affects, but showed also that density varied with all four variables describing tree community structure

Table 3 Top models (ΔAIC ≤ 2) accounting for variation in average density of birds per point count in 48 parks from Portland, OR, in 2003. Results of best subsets regression analysis reported separately for resident species, long-distance migrants, and short-distance/partial migrants. Models ranked by ΔAICc, with explained variation reported after adjusting for number of variables in the model (R^2_{adj})

| Variable	Coefficient (SE; P)	Low 95% CI	High 95% CI	ΔAICc	R^2_{adj}
RESIDENTS		Residents			
Area^2	-0.933 (0.204; <0.001)	-1.333	-0.533	0.000	0.459
TreePC2	1.039 (0.298; 0.001)	0.455	1.623		
TreePC3	0.463 (0.295; 0.123)	-0.115	1.041		
Area^2	-0.987 (0.204; <0.001)	-1.387	-0.587	0.121	0.441
TreePC2	0.871 (0.282; 0.004)	0.318	1.424		
LONG-DISTANCE MIGRANTS					
Area	1.166 (0.200; <0.001)	0.774	1.558	0.000	0.698
TreePC2	0.258 (0.157; 0.108)	-0.050	0.566		
HbShPC1	0.352 (0.134; 0.012)	0.089	0.615		
HbShPC4	-0.418 (0.146; 0.007)	-0.704	-0.132		
Area	0.949 (0.152; <0.001)	0.651	1.247	0.298	0.687
HbShPC1	0.291 (0.131; 0.031)	0.034	0.548		
HbShPC4	-0.496 (0.141; 0.001)	-0.772	-0.220		
SHORT-DISTANCE/PARTIAL MIGRANTS					
LandPC1	-0.240 (0.145; 0.105)	-0.524	0.044	1.341	0.036

(Table 4). The mean explained variation (R^2_{adj}) of the three models increased to 0.657 (range = 0.644 to 0.672) from 0.512 for area affects alone, suggesting an important contribution of local habitat structure to richness of residents. Density was greater in parks in which large conifers (mainly Douglas-fir) were dominant (TreePC1), small (< 10 cm DBH) and mostly native tree species (TreePC2) and coarse woody debris (TreePC3) were abundant, and where red alder and trees < 30 cm DBH were common (TreePC4; Table 4).

Analysis of forest-dependent, long-distance migrants showed that density was greater in rounder and less elongated parks (i.e. low score for Shape) and where shrubs were abundant 1–3 m above ground and English ivy was an uncommon ground cover (Table 4). The R^2_{adj} of the 7 competitive models averaged 0.757 (range = 0.749 to 0.766), an addition of only 0.036 to the variation accounted for by area alone (i.e. 0.721). TreePC2 and HbShPC1 were also found in some of the competitive models of the forest-dependent, long-distance migrants but their 85% confidence intervals included zero (Table 4). For short-distance/partial migrants, adding other predictors to the best subsets regression of density did not substantially raise the explained variation

(mean adjusted R^2_{adj} = 0.138, range = 0.113 to 0.185) above that due solely to park area (R^2_{adj} = 0.066). Greater density was found in parks in which big-leaf maple and trees in the 3rd largest size class (30–60 cm DBH) were abundant, but confidence intervals of two other variables found in competitive models, both measures of shrub density, included zero (Table 4).

MAR calculated using Robbin et al.'s (1989) graphical method could not be determined for the Pine Siskin, but the average area of parks in which they were found was large (35.4 ± 19.23 ha, n = 6). Of the remaining 14 forest-dependent species, MAR averaged 48.9 ± 16.80 ha (95% CI = 12.6 ha to 85.2 ha [Table 5]). MAR did not differ between long-distance migrants and other species ($t = 0.70$, df = 12, $P = 0.499$), and increased with body mass (coefficient = 0.785 ± 0.261 SE, $r^2 = 0.430$, df = 12, $P = 0.011$) in identical manner in long-distance migrants and other species (ANCOVA: $F_{body\ mass}$ = 7.69, $P = 0.018$, $F_{migrant\ category}$ = 0.00, $P = 0.947$). The area of the three smallest parks in which each species was detected (Table 5) all correlated with MAR, with the weakest relationship being that with the smallest park (log-log analysis, $r = 0.524$, df = 12, $P = 0.054$)
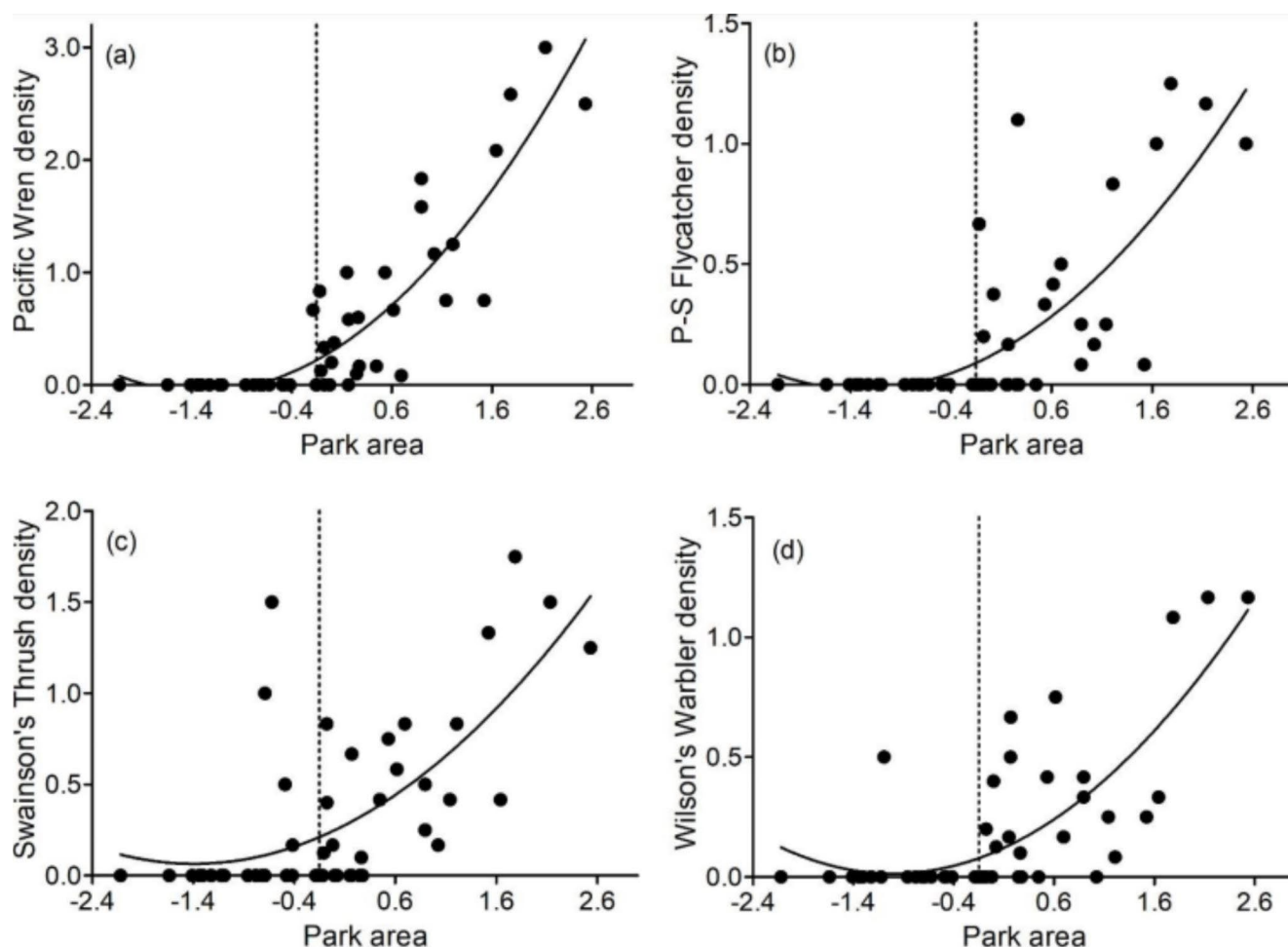
Fig. 4 Representative plots of density (mean number of individuals/point count/park) for (a) the Pacific Wren, a resident species, and three species of long-distance migrants, the (b) Pacific-slope Flycatcher, (c) Swainson's Thrush, and (d) Wilson's Warbler. Data were collected in 2003 from 48 parks in Portland, Oregon. Park area is standardized to a mean of zero and standard deviation of 1.0. The dashed vertical line in all four plots is located at an area equal to 10 ha. Statistically significant second-order polynomial plots of abundance versus park area plotted for all species

and the strongest with the largest of the three ($r = 0.830$, $df = 12$, $P < 0.001$). Thus, while individuals of forest-dependent species occurred in parks below their MAR, the ability of said parks to predict MAR waned steadily as the size of these parks declined.

Discussion

The importance of park area

In general, forest park area has a positive influence on species richness of birds in urban settings (Crooks et al. 2001; Husté et al. 2006; Ikin et al. 2013; Myczko et al. 2014; Huang et al. 2015; Kang et al. 2015; Maseko et al. 2020; de Groot et al. 2021). However, and contrary to our expectations (Park and Lee 2000; Husté and Boulinier 2007), area effects were not expressed uniformly across migrant guilds. Species richness of long-distance migrants rose with increasing park area, but then reached an asymptote between 50 and 100 ha, suggesting that parks exceeding 100 ha may yield diminishing returns for increasing richness of long-distance migrants. Richness of neither residents nor short-distance/partial migrants varied with park area. Robbins et al. (1989) documented the same difference between long-distance Nearctic-Neotropical migrants and residents/short-distance migrants breeding in nonurban habitat fragments in forests of eastern North America.

Density of short-distance/partial migrants was also independent of area, while that of resident and long-distance migrants declined and increased with park area, respectively. The latter observation suggests large parks were not only preferred by long-distance migrants, but that quality and quantity of habitat for migrants was greatest in the largest parks. What constitutes high "quality" is not clear, but large parks typically have less edge habitat, which may

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Table 4 Model averaged standardized coefficients (standard error in parentheses) and 85% confidence intervals from analyses of variation in density of forest-dependent breeding birds in 48 parks in Portland, OR, belonging to 1 of 3 migratory guilds. Predictor variables included park area, shape, and connectivity, and axes that describe variation in landscape structure surrounding parks, and variation in the structure and composition of the tree canopy and understory within parks (see Table 1). Separate analyses are reported for residents (n = 5 species), long-distance migrants (n = 7 species), and short-distance/partial migrants (n = 3 species). Predictor variables with 85% CI (see Arnold 2010) that excluded zero are highlighted in bold font. Number in parentheses following migratory guild name indicates the number of competitive models (i.e. ΔAICc ≤ 2.0) resulting from the analysis of each guild, while frequency refers to the number competitive models in which each variable appeared

Migratory guild	Predictors	Frequency	Estimate (SE)	85% CI
Residents (3)	**Area**	**3**	**2.406 (0.542)**	**1.613 to 3.200**
	Area^2	**2**	**0.264 (0.165)**	**0.023 to 0.506**
	TreePC1	**3**	**0.966 (0.274)**	**0.565 to 1.377**
	TreePC2	**3**	**0.904 (0.321)**	**0.434 to 1.374**
	TreePC3	**2**	**0.459 (0.264)**	**0.074 to 0.844**
	TreePC4	**2**	**-0.323 (0.234)**	**-0.726 to -0.039**
Long-distance migrants (7)	**Area**	**7**	**3.569 (0.605)**	**2.684 to 4.454**
	Area^2	**6**	**0.336 (0.186)**	**0.064 to 0.608**
	Shape	**4**	**-0.623 (0.355)**	**-1.144 to -0.103**
	HbShPC4	**4**	**-0.467 (0.274)**	**-0.868 to -0.067**
	TreePC2	3	0.268 (0.216)	-0.049 to 0.584
	HbShPC1	1	0.009 (0.012)	-0.009 to 0.027
Short-distance/partial migrants (6)	**TreePC4**	**6**	**0.668 (0.302)**	**0.226 to 1.110**
	Area^2	**4**	**0.243 (0.146)**	**0.030 to 0.457**
	HbShPC2	4	0.258 (0.179)	-0.004 to 0.520
	HbShPC4	3	0.276 (0.205)	-0.023 to 0.576

Table 5 Area of forest cover at which probability of occurrence (P) was maximum and then at 50% of maximum (minimum area requirement) for forest-dependent birds breeding in 2003 in parks and greenspaces in Portland, Oregon. Body mass and area of the three smallest fragments in which each species was detected also given, along with designation as resident (R), long-distance migrant (LD) or short-distance/partial migrant (SDP) as superscript

Species	Body mass (g)	Area (ha) of max P	Area (ha) at 50% of P_{max}	Area (ha) of three smallest fragments		
				1st	2nd	3rd
Chestnut-backed Chickadee[R]	10.0	>2,000	7.5	0.6	1.4	3.2
Dark-eyed Junco[R]	18.0	>2,000	10.0	1.7	3.7	3.7
Hutton's Vireo[R]	11.3	>2,000	14.5	3.7	5.6	10.9
Pacific Wren[R]	9.0	36.3	12.6	9.6	10.9	11.1
Pileated Woodpecker[R]	303.0	>2,000	159.2	49.4	71.7	91.5
Black-throated Gray Warbler[LD]	8.5	30.2	6.0	3.7	4.2	6.2
Olive-sided Flycatcher[LD]	33.2	>2,000	161.2	17.9	42.6	71.7
Orange-crowned Warbler[LD]	9.0	>2,000	9.0	5.4	9.6	13.1
Pacific-slope Flycatcher[LD]	10.0	223.9	25.9	10.9	11.7	14.1
Swainson's Thrush[LD]	31.0	794.3	18.1	3.7	4.2	5.4
Western Tanager[LD]	30.3	>2,000	10.0	1.2	1.4	2.7
Wilson's Warbler[LD]	6.9	=2,000	28.2	1.8	11.7	13.5
Cedar Waxwing[SDP]	32.0	>2,000	55.0	0.3	1.0	4.2
Purple Finch[SDP]	26.0	>2,000	167.0	18.5	71.9	113.6

result in lower rates of nest predation and offspring mortality (Batáry and Báldi 2004; Shipley et al. 2013). Low nest failure rated may be critical for long-distance migrants that have short breeding seasons and limited time to replace failed nests before fall migration (e.g. Mumme et al. 2021). Declining density of residents with increasing park area may be, at least in part, related to preferences for earlier successional habitats and more omnivorous diets that enable them to either directly (i.e. bird feeders) or indirectly exploit supplemental foods provided by humans (Robb et al. 2008; Plummer et al. 2019) in the surrounding landscape.

The absence of an area effect on richness and abundance of short-distance/partial migrant group might be disregarded as a sampling artifact as the number of species involved was small. The same cannot be said for residents given they comprised 20 of the 41 species in the sample. Limiting the number of point counts to a maximum of six per site likely did not lead to an underestimate of richness in large parks because Donnelly (2002) showed that species richness did not increase with more than six points in surveys conducted in urban forest fragments in Seattle, Washington (USA) in habitat similar to Portland. We suggest the failure to detect area effects for residents was partially an artifact of the method of analysis. Number of survey points and park area were highly correlated ($r = 0.859$, $P < 0.001$), and inclusion of number of survey points as an offset may have eliminated the possibility of detecting weak to moderate positive influences of area on resident species richness. Indeed, removal of the offset resulted in a positive relationship between species richness and park area ($P < 0.001$); Donnelly and Marzluff (2004) likewise saw a diminution of area effects when bird species richness of parks was rarefied. However, the fact that the density of residents in our study declined with increasing area suggests that most residents tended to avoid heavily forested habitat, and an area effect on species richness, if it existed, was likely weak. By contrast, that long-distance migrants exhibited greater richness as park area increased (Fig. 1b), despite the offset, emphasizes the importance of park area for migrants that overwinter largely south of the United States.

Landscape versus local habitat effects

Landscape structure (LandPC1), while possibly influencing the density of short-distance/partial migrants, had no relationship with species richness or density of residents, long-distance migrants, or forest-dependent species. The absence of landscape effects contradicts many published studies from urban landscapes (Nielsen et al. 2014; Huang et al. 2015; Reider et al. 2018; Amaya-Espinel et al. 2019), and is likely a consequence of, first, the importance of park area in the Portland system, and second, the city's generally high tree cover (METRO 2015). The absence of an influence of connectivity on either richness or abundance in our study is not uncommon in birds (Crooks et al. 2001; Donnelly and Marzluff 2006; Radford et al. 2005; Husté et al. 2006; Ikin et al. 2013; Kang et al. 2015; Maseko et al. 2020). In large nonurban landscapes, richness of woodland species declined steadily but slowly until a precipitous drop in richness began when landscape tree cover declined to 10% (Radford et al. 2005)Tremblay and St. Clair (2011) also reported that 20–40% canopy cover proved adequate for successful movement of nonurban adapted forest birds in the urban landscape of Calgary, Alberta. At 30% average tree cover (METRO 2015), Portland's landscape probably does not present strong barriers to avian dispersal, and

this is especially true of the portions of Portland where we worked; landscape canopy cover surrounding the 48 sites averaged nearly 40% out to a distance of 1 km (M. T. Murphy, unpubl. data).

As predicted, the influence of habitat structure and floristic features on species richness and density surpassed that of landscape composition, connectivity, and in most cases, park shape. TreePC2 played a particularly prominent role as it was a primary correlate of species richness for residents and long-distance migrants (in the latter case after removal of area effects), and for the density of residents, in particular the forest-dependent species (and possibly also the full guild of long-distance migrants, Table 3). The positive coefficients in all of these relationships indicated that richness and abundance were greater in parks with abundant smaller, and mostly native, tree species. The importance of TreePC2 may relate to the relatively greater invertebrate prey abundance in younger early seral stage forests where light levels, angiosperm leaf area, and herbivory are greater than in mature conifer stands (Shaw et al. 2006; Campbell and Donato 2014).

By contrast, only forest-dependent residents responded to variation in TreePC1 and TreePC3. The increase in density of forest-dependent residents with TreePC1 and TreePC3 indicated that populations were densest in parks dominated by large conifers in which coarse woody debris was abundant. Habitat descriptions (Rodewald 2022) of the forest-dependent residents in our sample (Table 5) repeatedly note their association with large trees (most often conifers), coarse woody materials, and dense, closed canopies. These features describe the oldest and most mature forests in the Portland system, and represents a mid-successional sere for Pacific Northwest forests (Franklin and Dyrness 1988). The importance of these structural habitat features for species that are year-round occupants is thus perhaps not surprising. On the other hand, TreePC4 described a gradient in the abundance of angiosperm trees in which red alder was replaced by larger big-leaf maple. Alder is abundant in earlier stage successional forests and is commonly associated with riparian zones (Franklin and Dyrness 1988), a habitat that enhances diversity and abundance of numerous taxa (e.g. Sabo et al. 2005).

Unlike the forest-dependent residents, their long-distance migrant counterparts exhibited no association with tree community structure. Instead, park area and shape were the primary factors driving their abundance. Indeed, the only habitat feature that varied consistently with the abundance of long-distance migrant was the density of shrubs 1 to 3 m aboveground (i.e. HbShPC4). With only one major exception (sword fern [*Polystichum munitum*]), all shrubs in the Portland system were angiosperms, and others have detected a positive association between species richness

and/or density of birds with angiosperms (Myczko et al. 2014; Taylor et al. 2016). Greater avian richness and density in urban parks with abundant shrub cover is not uncommon (Donnelly and Marzluff 2004; Myczko et al. 2014; Paker et al. 2014), presumably because shrubs provide foraging substrates for leaf-gleaning insectivores, nesting substrates, and/or cover for shrub and ground nesting birds. High shrub cover along HbShPC4 was also associated with low abundance of invasive English ivy as a ground cover. The importance of HbShPC4 may thus stem not only from the addition of an important habitat feature (i.e. shrubs), but also because of the absence of a noxious invasive species. The absence of any strong relationships between short-distance/partial migrant density and our multiple predictors may reflect the ecological and behavioral variability of this group that, for the most part, represents species that do not fit into the far more discrete categories of resident or long-distance migrant.

In summary, our results suggest that landscape composition had no, or at best a weak, influence on community structure of birds breeding in forest fragments in Portland, and that variation in species richness and density were a consequence primarily of differences in park area (especially for long-distance migrants), but also local habitat structure, and floristic composition (especially for residents). Taylor et al. (2016) reported similar findings from a rural-urban landscape in Michigan (USA); migrant richness was most dependent on the area of forest patches while species richness of resident species was unrelated to forested park area and was instead dependent on the proportion of vegetation that was deciduous. Unlike us, however, Taylor et al. (2016) reported that migrant species richness increased with tree cover in the immediate landscape surrounding the focal patch. Resident and migrant birds thus appear to respond differently to urbanization, but more work is needed from additional urban landscapes to establish the generality of this conclusion (see also Lerman et al. 2021).

Minimum area requirements of forest-dependent species

Multiple species, but mostly long-distance migrants, showed striking increases in density beginning at a park area of ~ 10 ha (Fig. 4). Similar patterns have been described previously for urban greenspaces (Chamberlain et al. 2007 and review by Nielsen et al. 2014). Natuhara and Imai (1999), for instance, noted that insectivores were rarely found in greenspaces below 10 ha, while Rodewald and Bakermans (2006) identified insectivory as an important property of area sensitive species in riparian urban forests. Maseko et al. (2020) noted that, although bird species of all diet categories responded positively to park area, insectivorous birds

exhibited the strongest relationship. Most forest-dependent species in our study were also strict insectivores, and thus, smaller parks may not support insect communities productive enough to sustain the most insectivorous bird species. Robbins et al.'s (1989) assertion that 10 ha was a threshold below which few forest-dependent species bred in semi-natural forests from eastern North America suggests that 10 ha is a critical threshold not restricted to urban environments.

Despite the apparent importance of 10 ha as a threshold, it fell below the MAR of most forest-dependent species (Table 5). In addition, density increased steadily with area for many of these species (e.g., Fig. 4). MAR represents the area at which a species' probability of occurrence is at 50% of maximum for that system, and Robbins et al. (1989) viewed it as a conservative estimate of minimum area needed to sustain breeding populations. All forest-dependent species were found in parks below their MAR (Table 5), but it is important to recognize that the presence of a species in a habitat does not demonstrate that it is a self-sustaining population (e.g., Bartos Smith et al. 2016); local extinction is a likely fate of forest-dependent species in these locations (e.g., Husté and Boulinier 2007). MAR of forest-dependent species averaged nearly five times larger than 10 ha, and although MAR increased with body size, even some of the small species had MARs in excess of 10 ha (Table 5). Radford et al. (2005) emphasized that thresholds are "points of instability" below which systems are likely to fail rapidly and therefore minimum thresholds should be avoided. Richmond et al. (2015) further stressed that thresholds may vary with landscape structure. However, the identification of 10 ha as a critical size for forest-dependent species from different locations and habitats (Robbins et al. 1989; Nielsen et al. 2014, present study) suggests a true threshold below which declines of forest-dependent species are inevitable. Given this, species with larger MARs should be the drivers of policy if the goal is to maintain intact communities of birds in forested urban parks.

Summary and recommendations

Avian communities within forest fragments in Portland, Oregon, were dominated by resident species, but among the largest parks, richness of residents and long-distance migrants were roughly equal. If management goals are to restore the landscape's avifauna, or more realistically, prevent further erosion, we make several recommendations: (1) Expansion of the park system should prioritize acquisition of the largest forest fragments possible. Forest-dependent species, many of which are long-distance migrants, do not have meaningful presence in parks below 10 ha and most forest-dependent species will likely disappear from the

landscape unless multiple parks of a minimum size of 30 to 40 ha, and possibly 50 ha, are retained. Donnelly and Marzluff (2004) arrived at a similar figure (42 ha) for nearby (280 km) Seattle, WA. (2) Within-habitat features of parks were important secondary contributors to avian species richness and density and thus parks must remain undeveloped to maintain complex vegetation structure. (3) Floristics were also important as, with the exception of short-distance/partial migrants, richness and/or density of species were higher in forests where there was high diversity of mainly small native tree species (TreePC2). (4) Mature coniferous forests are associated with the Pacific Northwest region (Franklin and Dyrness 1988) and our closest approximation to these forests yielded the highest density of forest-dependent, resident species. Providing for such forests is thus essential, but maintenance of forests at diverse seral stages is desirable to provide for species dependent on earlier successional stages. (5) While park area was the dominant predictor of density of forest-dependent resident and long-distance migrant species, park shape proved important as well for the forest-dependent, long-distance migrants, suggesting that long and thin parks should be avoided. And finally, (6) habitat connectivity and landscape composition had the least influence on density and species richness of birds, but this was likely because Portland's landscape has abundant tree cover. In this system, maintenance of high landscape tree cover is likely essential for maintenance of high species richness and density.

Data Availability (data transparency) If accepted all data will be made available through Dryad.

Declarations

Conflict of interest/Competing interests None.

Ethics approval No animals were handled and therefore not required.

Consent to participate Full consent to conduct research in parks within the Portland Metropolitan area were given by Metro Regional Services, City of Portland, Oregon State Parks, Tualatin Hills Park and Recreation District, City of Lake Oswego, City of West Linn, Riverview Cemetery Association, Lake Oswego High School, Clackamas County, City of Durham, City of Troutdale, City of Gresham, Mt. Scott Church of God, Lake Oswego United Church, and Three Rivers Land Conservancy.

References

Amaya-Espinel JD, Hostetler M, Henríquez C, Bonacic C (2019) The influence of building density on Neotropical bird communities in small urban parks. Landsc Urban Plan 190:103578

Arnold TW (2010) Uninformative parameters and model selection using Akaike's Information Criterion. J Wildl Manag 74:1175–1178

Bartos Smith S, McKay JE, Richardson JK, Shipley AA, Murphy MT (2016) Demography of a ground nesting bird in an urban system: Are populations self-sustaining? Urban Ecosyst 19:577–598

Batáry P, Báldi A (2004) Evidence of an edge effect on avian nest success. Con Biol 18:389–400

Bibby JC, Burgess ND, Hill DA, Mustoe S (2000) Bird Census Techniques (2nd edition). Academic Press, London

Both C, Van Turnhout CAM, Bijlsma RG, Siepel H, Van Strien AJ, Foppen RPB (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proc Roy Soc B 277:1259–1266

Callaghan CT, Benedetti Y, Wilshire JH, Morelli F (2020) Avian trait specialization is negatively associated with urban tolerance. Oikos 129:1541–1551

Campbell JL, Donato DC (2014) Trait-based approaches to linking vegetation and food webs in early-seral forests of the Pacific Northwest. For Eco Manag 324:172–178

Canedoli C, Manenti R, Padoa-Schioppa E (2018) Birds biodiversity in urban and periurban forests: environmental determinants at local and landscape scales. Urban Ecosyst 21:779–793

Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urban Plan 74:46–69

Chamberlain DE, Gough S, Vaughan H, Vickery JA, Appleton GF (2007) Determinants of bird species richness in public green spaces. Bird Study 54:87–97

Concepción ED, Moretti M, Altermatt F, Nobis MP, Obrist MK (2015) Impacts of urbanization on biodiversity: the role of species, mobility, degree of specialization and spatial scale. Oikos 124:1571–1582

Cooper CB, Walters JR (2002) Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. Con Biol 16:471–478

Cornelis J, Hermy M (2004) Biodiversity relationships in urban and suburban parks in Flanders. Landsc Urban Plan 69:385–401

Crooks KR, Suarez AV, Bolger DT, Soule ME (2001) Extinction and colonization of birds on habitat islands. Con Biol 15:159–172

de Groot M, Flajŝman K, Mihelĉ T, Vilhar U, Simonĉĉ P, Verliĉ A (2021) Green space area and type affect bird communities in a South-eastern European city. Urban For Urban Green 63:127212

Donnelly RE (2002) Design of habitat reserves and settlements for bird conservation in the Seattle Metropolitan area. PhD Dissertation. University of Washington, Seattle

Donnelly R, Marzluff JM (2004) Importance of reserve size and landscape context to urban bird conservation. Con Biol 18:733–745

Donnelly R, Marzluff JM (2006) Relative importance of habitat quantity, structure, and spatial pattern to birds in urbanizing environments. Urban Ecosyst 9:99–117

ESRI (1999) ArcGIS 8.2. ESRI, Redlands, California, USA

Fischer JD, Cleeton SH, Lyons TP, Miller JR (2012) Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. Bioscience 62:809–818

Franklin JF, Dyrness CT (1988) Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR, USA

Friesen LE, Eagles PFJ, Mackay RJ (1995) Effects of residential development on forest-dwelling Neotropical migrant songbirds. Con Biol 6:408–414

Hamel PB (1984) Comparison of variable circular-plot and spot-mapping censusing methods in temperate deciduous forests. Ornis Scand 15:266–274

Hennings LA, Edge WD (2003) Riparian bird community structure in Portland, Oregon: habitat, urbanization, and spatial scale patterns. Condor 105:288–302

Huang Y, Zhao Y, Li S, von Gadow K (2015) The effects of habitat area, vegetation structure and insect richness on breeding bird populations in Beijing urban parks. Urban For Urban Green 14:1027–1039

Husté A, Selmi S, Boulinier T (2006) Bird communities in suburban patches near Paris: determinants of local richness in a highly fragmented landscape. Ecoscience 13:249–257

Husté A, Boulinier T (2007) Determinants of local extinction and turnover rates in urban bird communities. Ecol Appl 17:168–180

Ikin K, Beaty RM, Lindenmayer DB, Knight E, Fischer J, Manning AD (2013) Pocket parks in a compact city: how do birds respond to increasing residential density? Landsc Ecol 28:45–56

Kang W, Minor ES, Park CR, Lee D (2015) Effects of habitat structure, human disturbance, and habitat connectivity on urban forest bird communities. Urban Ecosyst 18:857–870

Kennedy CA, Ibrahim N, Stewart I, Facchini A, Mele R (2014) Developing a multilayered indicator set for urban metabolism studies in megacities. Ecol Indic 47:7–15

Lees A, Haskell L, Allison T, Bezeng SB, Burfield IJ, Renjifo LM, Rosenberg KV, Viswanathan A, Butchart SM (2022) State of the world's birds. Ann Rev Env Res 47:1

Lerman SB, Narango DL, Avolio ML, Bratt AR, Engebretson JM, Groffman PM, Hall SJ, Heffernan JB, Hobbie SE, Larson KL, Locke DH, Neill C, Nelson KC, Cubino JP, Trammell TLE (2021) Residential yard management and landscape cover affect urban bird community diversity across the continental USA. Ecol Appl 31:e02455

Martensen AC, Pimentel RG, Metzger JP (2008) Relative effects of fragment size and connectivity on bird community in the Atlantic rain forest: implications for conservation. Biol Con 141:2184–2192

Maseko MST, Zungu MM, Ehlers Smith DA, Ehlers Smith YC, Downs CT (2020) Effects of habitat-patch size and patch isolation on the diversity of forest birds in the urban-forest mosaic of Durban, South Africa. Urban Ecosyst 23:533–542

Marzluff JM, Bowman R, Donnelly R (2001) Avian Ecology and Conservation in an Urbanizing World. Kluwer, Academic Press

McDonald RI, Kareiva P, Forman RTT (2008) The implications of current and future urbanization for global protected areas and biodiversity conservation. Biol Con 141:1695–1703

McGarigal K, Marks BJ (1995) FRAGSTATS: spatial analysis program for quantifying landscape structure. U.S. Forest Service General Technical Report PNW 351

METRO (2004) Regional land information system metadata viewer http://mazama.metro-region.org/metadata.Metro Regional Services, Portland, Oregon, USA

METRO (2015) 2014 Urban growth report: investing in our communities 2015–2035

Mumme RL, Mulvihill RS, Norman D (2021) High-intensity flight feather molt and comparative molt ecology of warblers of eastern North America. Ornithology 138:ukaa072. https://doi.org/10.1093/ornithology/ukaa072

Myczko Ł, Rosin AM, Skórka P, Tryjanowski P (2014) Urbanization level and woodland size are major drivers of woodpecker species richness and abundance. PLoS ONE 9:e94218

Natuhara Y, Imai C (1999) Prediction of species richness of breeding birds by landscape-level factors of urban woods in Osaka Prefecture, Japan. Biodiv and Con 8:239–253

Nielsen AB, van den Bosch M, Maruthaveeran S, van den Bosch CK (2014) Species richness in urban parks and its drivers: a review of empirical evidence. Urban Ecosyst 17:305–327

Notes, A. F. (1970) Recommendations for an international standard for a mapping method in bird census work. Audubon Field Notes 24:722–726

Oliver AJ, Hong-Wa C, Devonshire J, Olea KR, Rivas GF, Gahl MK (2011) Avifauna richness enhanced in large, isolated urban parks. Landsc Urban Plan 102:215–255

Paker Y, Yom-Tov Y, Alon-Mozes T, Barnea A (2014) The effect of plant richness and urban garden structure on bird species richness, diversity and community structure. Landsc Urban Plan 122:186–195

Park CR, Lee WS (2000) Relationship between bird species composition and area in breeding birds of urban woods in Seoul, Korea. Landsc Urban Plan 51:29–36

Plummer KE, Risely K, Toms MP, Siriwardena GM (2019) The composition of British bird communities is associated with long-term garden bird feeding. Nat Comm 10:2088

Quinn G, Keough M (2002) Experimental design and data analysis for biologists. Cambridge University Press

Radford JQ, Bennett AF, Cheers GJ (2005) Landscape-level thresholds of habitat cover for woodland-dependent birds. Biol Con 124:317–337

Reider IJ, Donnelly MA, Watling JI (2018) The influence of matrix quality on species richness in remnant forest. Landsc Ecol 33:1147–1157

Richmond S, Jenkins E, Couturier A, Cadman M (2015) Thresholds in forest bird richness in response to three types of forest cover in Ontario, Canada. Landsc Ecol 30:1273–1290

Robb GN, McDonald RA, Chamberlain DE, Bearhop S (2008) Food for thought: supplementary feeding as a driver of ecological change in avian populations. Front Ecol Environ 6:476–484

Robbins CS, Dawson DK, Dowell BA (1989) Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildl Monogr 103:3–34

Rodewald AD, Bakermans MN (2006) What is the appropriate paradigm for riparian forest conservation? Biol Cons 128:193–2000

Rodewald AD, Kearns LJ, Shustack DP (2011) Anthropogenic resource subsidies decouple predator-prey relationships. Ecol Appl 21:936–943

Rodewald AD, Kearns LJ, Shustack DP (2013) Consequences of urbanizing landscapes to reproductive performance of birds in remnant forests. Biol Cons 160:32–39

Rodewald P (ed) (2022) Birds of the World: https://birdsoftheworld.org/bow/home.Cornell Laboratory of Ornithology, Ithaca, NY

Rosenberg KV, Dokter AM, Blancher PJ, Sauer JR, Smith AC, Smith PA, Stanton JC, Panjabi A, Helft L, Parr M, Marra PP (2019) Decline of the North American avifauna. Science 366:120–124

Rush SA, Romito T, Robison TL Avian diversity in a suburban park system: current conditions and strategies for dealing with anticipated change. Urban Ecosyst 17:45-60 Sabo JL, Sponseller R, Dixon M, Gade K, Harms T, Herrernan J, Jani A, Katz G, Soykan C, Watts J, Welter J (2005) Riparian zones increase regional species richness by harboring different, not more, species. Ecology 86:56–62

Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, van Bommel FPJ (2006) Long-term population declines in Afro-Palearctic migrant birds. Biol Conserv 131:93–105

Seto KC, Güneralp B, Hutyra LR (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proc Nat Acad Sci USA 109:16083–16088

Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. Methods Ecol Evol 1:103–113

Shaw DC, Ernest KA, Rinker HB, Lowman MD (2006) Stand-level herbivory in an old-growth conifer forest canopy. Western North Am Nat 66:473–481

Shipley AA, Murphy MT, Elzinga AH (2013) Residential edges as ecological traps: postfledging survival of Spotted Towhees in an urban park. Auk 130:501–511

Shwartz A, Shirley S, Kark S (2008) How do habitat variability and management regime shape the spatial heterogeneity of birds within a large Mediterranean urban park? Landsc Urban Plan 84:219–229

Spake R, Soga M, Kawamura K, Cooke RS, Yamaura Y, Eigenbrod F (2020) Regional variability in landscape effects on forest bird communities. Landsc Ecol 35:1055–1071

Steffen W, Broadgate W, Deutsch L, Gaffney O, Ludwig C (2015) The trajectory of the Anthropocene: the great acceleration. Anthropocene Rev 2:81–98

Taylor JJ, Lepczyk CA, Brown DG (2016) Patch and matrix level influences on forest birds at the rural-urban interface. Landsc Ecol 31:1005–1020

Tremblay MA, St. Clair CC (2011) Permeability of a heterogeneous urban landscape to the movements of forest songbirds. J Appl Ecol 48:679–688