Differential Response of Migratory Guilds of Birds to Urbanization

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Abstract

Species richness and density of native fauna in urban parks and greenspaces (“parks”) is often lower than in surrounding areas. Understanding the causes of these differences requires a hierarchical approach that integrates factors across multiple scales. In 2003 we surveyed bird communities in 48 forested parks in Portland, Oregon, USA, to identify the relative contributions of park size, shape, and connectivity, landscape composition, and variation in local habitat to differences in richness and density of long-distance migrant, short-distance/partial migrant, and resident birds. All surveyed parks contained highly structured understories comprised primarily of native vegetation and lacked development beyond trails. The bird guilds responded differently to environmental factors. Richness and density of long-distance migrants increased with park area and the abundance of small, mostly native, tree species. Resident species richness also increased with the abundance of small trees. Richness of residents and short-distance migrants was independent of park area, and resident density declined with increasing park area. Park shape, connectivity, and landscape composition did not contribute to differences in richness or density of different migratory guilds. Most long-distance migrants were forest-dependent species. An analysis of all forest-dependent species of all migratory guilds suggested that few exist in parks below 10 ha, and minimum area requirements for maintaining populations of forest-dependent species are 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 increased in response to rapidly increasing human populations (Steffen et al. 2015), the continuing growth 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 their present boundaries into the surrounding semi-natural habitats, the potential and need to incorporate reserves for native species will both grow.

Urban habitats present unique challenges for wildlife, including exotic, and often invasive, species, high levels of sound, light, and air pollution, and the potential for lethal impacts with vehicles and built structures. However, the principal challenges from urbanization are those posed by agriculture and timber extraction. They include reduction and fragmentation of natural habitat (i.e., greenspaces), increased isolation of greenspaces, and habitat degradation within greenspaces (see reviews by Chace and Walsh 2006, Nielsen et al. 2014).

Attempts to understand the drivers of variation among avian communities in urban spaces must consider factors that operate from the landscape to the local level (Nielsen et al. 2014). Land use in the matrix surrounding greenspaces can influence avian communities by supporting synanthropic species that may also use greenspaces and compete with native habitat specialists (Blair 1996, Donnelly and Marzluff 2004, Rodewald and Bakermans 2006, Oliver et al. 2011, Canedoli et al. 2018), while

mesopredator release due to the absence of large predators can elevate predation rates (Fischer et al. 2012). The ability to disperse through the urban matrix may also affect native urban bird populations. However, presumably because of their high vagility, greenspace area regularly surpasses patch/fragment connectivity (i.e., isolation = low connectivity) as a determinant of differences in avian species richness in urban spaces (Crooks et al. 2001, Husté et al. 2006, Ikin et al. 2013, Kang et al. 2015; but see Cooper and Walters 2002, Martensen et al. 2008). Greenspace shape also has the potential to influence species richness. Elongated fragments, for example, contain relatively high amounts of edge habitat that has been associated with low species richness (Natuhara and Imai 1999) and low reproductive and/or survival rates (Batáry and Báldi 2004, Shipley et al. 2013). Many bird species have narrow habitat requirements, and therefore species richness and abundance often increase with structural vegetation complexity (Myczko et al. 2014, Rush et al. 2014, Kang et al. 2015), and habitat (Donnelly and Marzluff 2004, Cornelis and Hermy 2004) and floristic diversity (Husté et al. 2006, Shwartz et al. 2008, Paker et al. 2014).

Notwithstanding the results highlighted above, we know relatively little about how different guilds of birds respond to urbanization. For example, differences in migratory behavior mark fundamental differences in life history among temperate-zone breeding birds, but we know little about how different migratory guilds respond to urbanization. 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 resident as migrant species, while Husté and Boulinier (2007) found equal rates of increase in richness with area, but that again, residents were more diverse. 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). The small population size of urban migrant populations may lead to more frequent local extirpation (Husté and Boulinier 2007). Given that many migrant bird species in both Europe (Sanderson et al. 2006, Both et al. 2009) and North America (Rosenberg et al. 2019) are declining, and that urban growth is inevitable, urban greenspaces need to be better planned for the conservation of migrant avian species (see also Rodewald et al. 2013).

Portland, Oregon (USA), is the 27th largest city in the US (~662,000 in 2021) (<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 birds in 48 of the system's parks to evaluate the effects of landscape composition, distance from city center, park geometry (size, shape, connectivity), and local (within-park) habitat structure and floristic composition on the richness and abundance of bird species associated with upland forest habitats. We expected that (1) park area would eclipse all other factors as the primary source of variation in bird community structure for all migratory guilds, and (2) that given Portland's high tree cover (~30%), structural habitat/floristic diversity within parks would have greater influence on birds than park connectivity or landscape composition. We further expected (3) that long-distance migrants would exhibit lower richness (Park and

Lee 2000, Hennings and Edge 2003) and abundance (Park and Lee 2000, Hennings and Edge 2003, Hulsé and Bouliner 2007, Rodewald and Bakermans 2006) than residents regardless of park area. Lastly, because conservation planning requires estimates of species-specific minimum area requirements, 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 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: 4.7° C and 13.9 cm precipitation) and warm, dry summers (August: 20.8° 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 $\geq 50\%$ 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), and distance from downtown Portland, 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. Greater distance to city center likely reflects decreasing anthropogenic influences on landscape composition and increasing proximity of park to habitats with native fauna. We therefore used Google Maps to measure the shortest distance between each park and city center (DistPDX; Table 1).

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. We then subjected these data to a principal component analysis (PCA) to identify the main gradients of landscape variation across Portland. Principal component 1 (LandPC1) accounted for 54% of the variation in landscape structure and described a gradient in which more urbanized landscapes (negative scores) were replaced by landscapes with increasing dominance of trees 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 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 number and estimated 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, herbaceous layer, 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, 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. In total they accounted for 59.4% of the variation in the data and the gradients in forest structure that they reflect are described in Table 1. Similarly, we used percent ground cover (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 percent 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 in these data 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 by late May in Portland and therefore surveys were conducted between 15 May and 18 July, 2003, to avoid sampling transiting migrants. All surveys were conducted by one person (DCB) between sunrise and 1100 hours on days without rain and little to no wind. Three counts were made at all survey points over the course of the season, and at times that were rotated to avoid sampling points at the same time of day. Point count locations (1-6 per park) were randomly selected, and all points within a park were surveyed on a single day. 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.

We used the variable circular plot method (Bibby et al. 2000) to record all birds heard or seen out to 50 m; birds estimated to be beyond 50 m were noted but not used in analyses. 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 at a point, determination of multiple conspecifics was based on detection of counter-singing or simultaneous visual and/or aural detection along with mapping of detections on data sheets in concentric circles around survey points (0-10 m, 10-25 m, 25-50 m, >50 m). To avoid double-counting birds that fell between adjacent points that were relatively close to each other, mapped locations were 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 (Audubon Field Notes 1970), and Hamel's (1984) comparison of spot mapping estimates of abundance to counts made using the variable circular plot methods 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 raptors, 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 for average density, computed across all 48 parks, included zero (Appendix 1). Species classified as rare were those that do not breed in the habitats in which we conducted our work, are irruptive, were never detected at more than two sites (and at low density), or were only detected at the single site located outside of the Urban Growth Boundary (Common Raven; scientific names given in Appendix 1).

Avian richness and density for three groups of birds based on migratory behavior were then made in relation to landscape composition, distance to city center, park geometry, and habitat structure (Table 1). The three migratory categories were residents (year-round occupation of sites), long-distance migrants

(overwinter primarily south of the border of the United States; Nearctic-Neotropical migrants), and short-distance/partial migrants. We relied on Birds of North America accounts (Rodewald 2018) 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. 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 selection until a final set of competitive models ($\Delta AIC_c \leq 2$) 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). Given recent concerns regarding interpretability of model averaged coefficients (Cade 2015), we interpret results primarily for the top model but supplemented by input from other competitive models. 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 area². We performed best subsets regression analyses on the summed density of forest-dependent species using the predictors described in Table 1. We expected that park area would be the main determinant of density. Our objective was thus to remove the area effect and identify other important determinants of density in this ecologically sensitive group that is most at risk in the urban landscape. For similar reasons we also calculated minimum area requirements (MAR) for 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.

Results

Excluding raptors and aerial foragers, we recorded 41 regularly occurring and 15 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 3, 4, and 6 residents, long-distance, 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).

Determinants of richness. – Analysis of resident species richness yielded two competitive models (Table 2). TreePC2 appears in both and shows that richness increased as the abundance of small, mostly native, trees increased (Fig. 1a). The presence of HbShPC4 in the top model suggested that resident richness might increase as the understory shifted from medium/high to low shrub cover where English ivy was abundant. However, HbShPC4's 95% CI included zero (Table 2). Park area was the primary contributor to variation among parks in long-distance migrant richness, followed by TreePC2 (Table 2). The negative quadratic term for park area reflected a decelerating increase in species richness with park area (Fig. 1b), indicative of a point of diminishing returns in the relationship between park area and richness of long-distance migrants. 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 of the among park variation in species richness of short-distance/partial migrants (Table 2).

Determinants of density. – The density of residents was greater in small parks and where smaller, mainly native, trees, were abundant (Table 3 and Fig. 2a and 2c). Long-distance migrant density increased steadily with park area (Table 3 and Fig. 2b), and was greater in parks with abundant medium and high shrub cover where little English ivy was present (HbShPC4; Fig. 2d, Table 3), and where moss or bare soil were common (HbShPC1; Table 3). Density also tended to be higher in parks where smaller, mainly native trees were abundant, but the 95% CI for TreePC2 included zero (Table 3). For short-distance/partial migrants, our single competitive model indicated that density tended to increase with increasing distance of the park from Portland city center, and possibly in parks with a more developed landscape (LandPC1; Table 3).

Forest-dependent species: habitat and minimum area requirements. – The proportion of species that were forest-dependent (i.e., density increased with increasing park area) was roughly twice as great for

long-distance migrants (0.54 [7 of 13]) compared to residents (0.25 [5 of 20]; $\chi^2 = 2.83$, $df = 1$, $P = 0.093$); short-distance/partial migrants were intermediate (0.38 [3 of 8]). Analysis of total density of the 15 forest-dependent species indicated that, as expected, park area was the most important determinant of density in all three competitive models (Table 4); area effects alone accounted for just over three-quarters of the variation in density ($R^2_{adj} = 0.775$). Indeed, multiple species exhibited abrupt increases in density when park area reached 10 ha (Fig. 3). The addition of forest habitat structure, landscape composition, or park shape raised the explained variation to between 85% and 87% (Table 4). TreePC1, TreePC2, TreePC3, DistPDX, and HbShPC2 appeared in all models, indicating that the density of forest-dependent species was greater in parks with abundant angiosperms in the tree canopy (TreePC1), where small, primarily native trees (TreePC2) and coarse woody debris (TreePC3) were abundant, in parks further from city center (DistPDX), and where medium shrub cover (1-2 m above ground) and English ivy were abundant (HBSHPC2). Shape appeared in 2 of 3 models and indicated that forest-dependent species tended to be less dense in parks of elongated shape. HbShPC3 appeared only in the top model, and it indicated that density increased as low shrub cover was replaced by abundant herbaceous cover.

MAR 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 $48.9 (\pm 16.80$ 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 three smallest parks in which each species was detected (Table 5) all correlated significantly with MAR, with the weakest relationship being that with the smallest park (log-log analysis, $r = 0.524$, $df = 12$, $P = 0.054$) 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 well below their MAR, the ability of said parks to predict MAR waned steadily as the size of these parks declined.

Discussion

Contrary to 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 at an area of between 50 to 100 ha, suggesting that parks exceeding 100 ha in area 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. In addition, density of resident species in Portland declined with park area while that of migrants increased steadily. This observation suggests that large parks were not only preferred by long-distance migrants, but that quality and quantity of habitat for migrants increased in the largest parks.

The absence of an area effect on richness 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 habitat similar to ours. 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 positive relationships 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 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.

The absence of an effect of landscape structure (LandPC1) on either richness or density of any migrant group (except possibly for density of short-distance/partial migrants) or the forest dependent species was striking and contrary to many published studies from urban landscapes (Nielsen et al. 2014). This may be a consequence of the overriding importance of park area in the Portland study system, and the generally high tree cover of Portland. High tree cover in the matrix likewise probably explains the weak to nonexistent influence of connectivity on the avian species that we detected, which 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). In large nonurban landscapes, richness of woodland species declined steadily but slowly until a precipitous drop in richness began when landscape tree cover dropped to 10% (Radford et al. 2005). Tremblay and St. Clair (2011) also reported that 20% to 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, 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 (e.g., see figure 1 of Bartos Smith et al. 2016); canopy cover of the landscape surrounding the 48 parks averaged nearly 40% out to a distance of 1 km (M. T. Murphy, unpubl. data). Distance to city center (DistPDX) was included as a separate (albeit coarse) measure of probable landscape influences, the assumption being that sites far from the city center would have a higher proportion of suitable habitat in the landscape. However, only amongst the short-distance/partial migrants and forest dependent species did distance to city center appear to have an influence on community characteristics, and in both, abundances were greater with increasing distance from city center.

As predicted, the influence of habitat structural and floristic features on species richness largely surpassed that of park shape and connectivity. TreePC2 played a particularly prominent role as it was a primary correlate of species richness for residents and long-distance migrants (after removal of area

effects), and for the density of residents, forest-dependent species, and possibly also long-distance migrants. The positive coefficients indicated that richness and abundance were greatest in parks with abundant smaller, and mostly native, tree species. By contrast, only forest dependent species appeared to respond to variation in TreePC1 and possibly TreePC3. The importance of TreePC2 may relate to the relatively greater invertebrate (i.e., prey) abundance in younger early seral stage forests where light levels, angiosperms leaf area, and herbivory are greater than in mature conifer stands (Shaw et al. 2006, Campbell and Donato 2014).

Greater avian richness and density in urban parks with abundant shrub cover has been reported previously (Donnelly and Marzluff 2004, Myczko et al. 2014, Paker et al. 2014), and we likewise found that abundant medium (1-2 m: HbShPC2) to high (2-3 m: HbShPC4) shrub cover was associated with higher density of forest dependent species and long-distance migrants. The association of avian density with high shrub cover likely exists because shrubs provide foraging substrates for leaf-gleaning insectivores, nesting substrates, and/or cover for shrub and ground nesting birds.

Minimum area requirements of forest species

Several species in Portland showed striking increases in density at park area of ~10 ha (Fig. 3). Similar patterns have been described previously for urban greenspaces (Chamberlain et al. 2007 and review by Nielsen et al. 2014). Natuhara and Imai (1999) noted insectivores were rarely found in greenspaces below 10 ha and thus that smaller parks may not support the insect community needed to support these species. Most forest-dependent species from Portland are also strict insectivores. Rodewald and Bakermans (2006) also identified insectivory as an important property of area sensitive species in riparian urban forests, while 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 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. 3). MAR represents the area at which a species probability of occurrence is at 50% of maximum for that system. 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 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 they should be avoided. Species with larger MARs should thus 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, the richness of long-distance migrants was nearly as great as residents. 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 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 richness and/or abundance of resident, long-distance migrant, and forest-dependent species were higher in forests where there was high diversity of mainly small native tree species (TreePC2). (4) Although coniferous forests are typically associated with the Pacific Northwest region (Franklin and Dyrness 1988), forest-dependent species were most abundant in forests with a high angiosperm tree component (TreePC1) comprised of mainly native species (TreePC2). Maintenance of forests at diverse seral stages is thus desirable. And finally, (5) habitat connectivity and landscape composition had the least influence on density and species richness of birds, but this was likely only because much of 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.

Declarations

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Conflict of interest/Competing interests – None

Availability of data and material (data transparency) – If accepted all data will be made available through Dryad

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

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Tables

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
DistPDX	Shortest distance from each parks to Portland (PDX) city center (45.52 N, -122.68 W)
LandPC1	PC1 from analysis of landscape in 500 m buffer around each parks; contrast of high urban and high human population density grading into high forest cover and low human population density; 53.9%
TreePC1	PC1 of canopy analysis; Contrast of coniferous forest (mostly Douglas-fir) of largest trees (≥ 60 cm DBH) grading into forests dominated by angiosperm trees with few individuals in the largest size class; 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%

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; <i>P</i>)	Lower 95% CI	Upper 95% CI	ΔAICc	Pseudo- R^2
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)	0.4202	0.8863	0.000	0.548
Area ²	-0.153 (0.061; 0.007)	-0.2783	-0.0393		
TreePC2	0.168 (0.086; 0.049)	0.0007	0.3363		
Short-distance/partial migrants					
TreePC4	0.103 (0.075; 0.170)	-0.0445	0.2500	0.000	0.085

Table 3 Top models ($\Delta\text{AIC} \leq 2$) 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					
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		
Area ²	-0.987 (0.204; <0.001)	-1.387	-0.587	0.705	0.451
TreePC1	-0.403 (0.301; 0.189)	-0.993	0.187		
TreePC2	0.940 (0.285; 0.002)	0.381	1.499		
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					
Distance PDX	0.291 (0.143; 0.048)	0.011	0.571	0.000	0.062

LandPC1	-0.240 (0.145; 0.105)	-0.524	0.044	1.341	0.036
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Table 4 Top models accounting for variation in total density of forest-dependent species in 48 parks from Portland, OR, in 2003. Competitive models, those within 2 AICc of top model (ΔAICc) and with all variables included in the model significant at $P < 0.10$, are reported. All predictor variables were standardized (mean = 0, SD = 1.0) and thus coefficients can be compared directly to assess strength of relationship to total abundance

Variable	Coefficient (SE; P)	Low 95% CI	High 95% CI	ΔAICc	R^2_{adj}
Area	2.010 (0.241; <0.001)	1.538	2.482	0.000	0.867
Area ²	0.423 (0.105; <0.001)	0.217	0.629		
Shape	-0.379 (0.192; 0.056)	-0.755	-0.003		
DistPDX	0.431 (0.146; 0.006)	0.145	0.717		
TreePC1	0.328 (0.150; 0.035)	0.034	0.622		
TreePC2	0.735 (0.220; 0.002)	0.304	1.166		
TreePC3	0.314 (0.165; 0.064)	-0.009	0.637		
HbShPC2	-0.378 (0.153; 0.018)	-0.678	-0.078		
HbShPC3	0.365 (0.207; 0.086)	-0.041	0.771		
Area	2.093 (0.248; <0.001)	1.607	2.579	0.379	0.860
Area ²	0.432 (0.107; <0.001)	0.222	0.642		
Shape	-0.366 (0.197; 0.071)	-0.752	0.020		
DistPDX	0.491 (0.146; 0.002)	0.205	0.777		
TreePC1	0.434 (0.142; 0.004)	0.156	0.712		
TreePC2	0.461 (0.160; 0.006)	0.147	0.775		
TreePC3	0.303 (0.169; 0.081)	-0.028	0.634		
HbShPC2	-0.338 (0.155; 0.035)	-0.642	-0.034		
Area	1.807 (0.200; <0.001)	1.415	2.199	1.236	0.852
Area ²	0.440 (0.110; <0.001)	0.224	0.656		
DistPDX	0.458 (0.149; 0.004)	0.166	0.750		
TreePC1	0.451 (0.146; 0.004)	0.165	0.737		

TreePC2	0.498 (0.164; 0.004)	0.177	0.819
TreePC3	0.370 (0.170; 0.035)	0.037	0.703
HbShPC2	-0.300 (0.158; 0.065)	-0.610	0.010

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		
				1 st	2 nd	3 rd
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

Figures

Figure 1

Figure 1

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.

Figure 2

Figure 2

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.

Figure 3

Figure 3

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.

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