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Relative importance of habitat quantity, structure, and spatial pattern to birds in urbanizing environments

Roarke Donnelly · John M. Marzluff

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Abstract Urbanization reduces the quantity of native vegetation and alters its local structure and regional spatial pattern. These changes cause local extirpations of bird species associated with native vegetation and increases in the abundance and number of bird species associated with human activity. We used 54–1 km^2 landscapes in the Seattle, Washington, USA metropolitan area to determine (1) the relative importance of habitat quantity, structure, and pattern to bird diversity and abundance and (2) whether housing developments can be managed to mitigate the negative impacts of urbanization on forest bird diversity. In general, bird species richness was high and many native forest species were retained where urban landcover comprised less than 52% of the landscape, tree density (especially that of evergreens) remained at least 9.8 trees/ha in developments, and forest was at least 64% aggregated across the landscape. These results suggest that the quantity, structure, and pattern of forested habitat affected breeding bird diversity in urbanizing landscapes. However, habitat pattern appeared less influential than other habitat attributes when results from all community- and population-level analyses were considered. Conservation of native birds in reserves can be supplemented by managing the amount, composition, structural complexity, and—to a lesser extent—arrangement of vegetation in neighborhoods.

Keywords Bird · Conservation · Fragmentation · Landscape · Pattern · Urban · Vegetation

Introduction

As Earth's human population grows, it becomes more concentrated in and around urban centers (Berry, 1990; Vitousek et al., 1997; United Nations, 1999). Even developed nations with

R. Donnelly (✉) · Present address:
Biology Department, Oglethorpe University, 4484 Peachtree Rd. NE, Atlanta, GA 30319, USA
e-mail: rdonnelly@oglethorpe.edu

R. Donnelly · J. M. Marzluff
Box 352100, Environmental Science and Resource Management, College of Forest Resources, University of Washington, Seattle, WA 98195-2100, USA

relatively stable human populations, such as the USA, are characterized by sprawling urban areas, as personal preferences, economics, and incentives increase development in suburbs and at the suburban/exurban interface (Berry, 1990; Ewing, 1994; Wang and Moskovits, 2001; see Marzluff et al., 2001a for standard definitions of urbanization levels). This development degrades, converts, and fragments native vegetation (Marzluff, 2001; Marzluff and Ewing, 2001; McKinney, 2002). Degradation alters the local structure of native habitat structure, reduces habitat quality for many native species and increasing habitat quality for many early-successional and non-native species. Conversion reduces habitat quantity. Fragmentation alters habitat spatial pattern. Although "natural" disturbances alter native habitat in similar ways, urbanization involves a severe initial disturbance that is maintained by manmade materials (e.g., pavement) or by frequent, low-severity disturbances (e.g., lawn mowing; Blair, 1996). Not surprisingly, urbanization has dramatic effects on bird communities and their constituent populations (Marzluff, 2001; Marzluff et al., 2001b; Chace and Walsh, 2006).

Urbanization alters the composition of bird communities by increasing the fitness of synanthropic species (associated with humans; Johnston, 2001) and decreasing the fitness of species associated with native habitat. As urbanization proceeds, synanthropic species colonize and increase in abundance by taking advantage of new anthropogenic habitats, supplemental food (Nuorteva, 1971; Lancaster and Rees, 1979), and nest sites. These species achieve unusually high abundances, decreasing community evenness (Pitelka, 1942; Beissinger and Osborne, 1982). Native species associated with early successional habitats may increase in abundance at moderate levels of disturbance (Marzluff, 2005). Species associated with mature, native habitats decline and suffer local extinction due to demographic mechanisms (increased brood parasitism and increased risk of nest predation Wilcove, 1985; Major et al., 1996) and behavioral mechanisms such as area sensitivity (Whitcomb et al., 1981). Richness may increase with urban development, decrease with development, or peak at intermediate levels of development depending on the losses of mature habitat species relative to the gains in synanthropic and early-successional species (Opdam et al., 1984; Blair, 1996; Marzluff, 2005).

Our knowledge of avian responses to urbanization is deficient, from a conservation perspective, in two important ways. First, the *relative* impact of habitat quantity, structure, and pattern on birds is contentious in fragmented systems (Harrison and Bruna, 1999; Lichstein et al., 2002) and unknown where fragments sit within an urban matrix (Marzluff, 2001; Miller and Hobbs, 2002). To our knowledge, no single study or collection of studies has investigated the relative impact of these three habitat attributes in one developed region. Thus, their importance for conservation must, at best, be inferred from studies of multiple regions with potentially confounding factors. Second, the degree to which residential development can supplement traditional bird conservation in reserves is uncertain (Donnelly and Marzluff, 2004). These two deficiencies have lead to general landscape planning guidelines for wildlife conservation (Knight, 1990; Soulé, 1991; Shafer, 1997) that are largely based on island biogeographical and metapopulation theory (Haila, 2002). These guidelines stress the landscape-scale quantity and pattern of native habitat and ignore variation in local-scale habitat structure that is dictated by the type of residential development.

To conserve birds in urbanizing areas, urban planners and natural resource managers need conservation guidelines that address the deficiencies described above and provide specific targets for resources amenable to management. To begin developing these guidelines for the Pacific Northwest, we conducted an empirical field study of breeding songbirds in the rapidly urbanizing Seattle metropolitan area (Washington, USA). We determined the relative influence of habitat quantity, structure, and pattern to bird communities and populations. We use our results to hypothesize how housing developments can be managed to mitigate the negative impacts of urbanization on forest bird diversity.

Methods

Study area

The Seattle metropolitan area ($47^\circ, 40'$ N; $122^\circ, 20'$ W) is located within the Western Hemlock (*Tsuga heterophylla*) Zone of the Pacific Northwest (Franklin and Dyrness, 1988), where forest cover was dominant before European settlement (Booth, 1991). The metropolitan area was composed of a large business district on the east side of the Puget Sound that was surrounded by residential developments and satellite business districts. Immigration and, to a lesser extent, intrinsic growth over the last 25 years fueled residential development (Puget Sound Regional Council, 1997) in existing suburbs and at the suburban/exurban interface (Robinson et al., 2005). This development created landscapes that varied in habitat quantity, structure, pattern, and age (Fig. 1).

Site selection

We used stratified random sampling to select 54 sites/landscapes representing the range and combination of habitat quantity (estimated with percent urban landcover) and habitat pattern (estimated with mean urban patch size, forest aggregation). We chose 1 km^2 as the standard landscape size because it was comparable to the size of typical residential developments and territories of common synanthropic nest predators like the American Crow (*Corvus brachyrhynchos*; Marzluff et al., 2001c). We quantified habitat quantity and pattern by converting 1998 LANDSAT satellite images to a four-class landcover with 30×30 m pixels based on impervious surface and vegetation (following Botsford, 2000; forest = 59% of 356377 ha classified, urban forest = 19%, urban = 11%, other = 11%). Forest was $\geq$70% trees and $<$ 20% impervious surface (e.g., pavement). Urban forest was $\geq$ 25% trees and 20–60% impervious surface. Urban was $\geq$ 60% impervious surface. Other was $\geq$ 75% open water or bare soil. Within each landscape, we estimated the representation of each landcover class and the size of urban patches (i.e., continuous urban area calculated with 8-neighbor rule; see McGarigal et al., 2002 for best description of method) using the Geographic Resource Analysis Support System and the r.le add-on programs (Baker, 1997; Alberti et al., 2001) and the forest connectivity using the Aggregation Index produced by Fragstats 3.1 (McGarigal et al., 2002). The Aggregation Index is a proportion equal to the number of pixels adjacent to pixels of the same class (forest) divided by the maximum possible number of same class adjacencies. Higher index values indicate that forest fragments are large given the amount of forest on the landscape. We identified a set of landscapes below 1000 m in elevation that represented a range of landcover composition and connectivity by superimposing a grid of 1 km^2 cells on the classified landcover. For each cell, we calculated landcover composition and connectivity. We visited each landscape in the set to select those that were predominately single family residential, similar in forest structure and composition, and without extensive agricultural activity.

Selected landscapes spanned the available range of habitat quantity and pattern variables in the study area. Urban landcover ranged from 4–77% with a mean ($\pm$ SE) of 36 ± 3. Urban patch size ranged from 0–89 ha with a mean of 12 ± 3. Forest aggregation ranged from 0–0.96 with a mean of 0.70 ± 0.03. We could not include some combinations of variables, such as

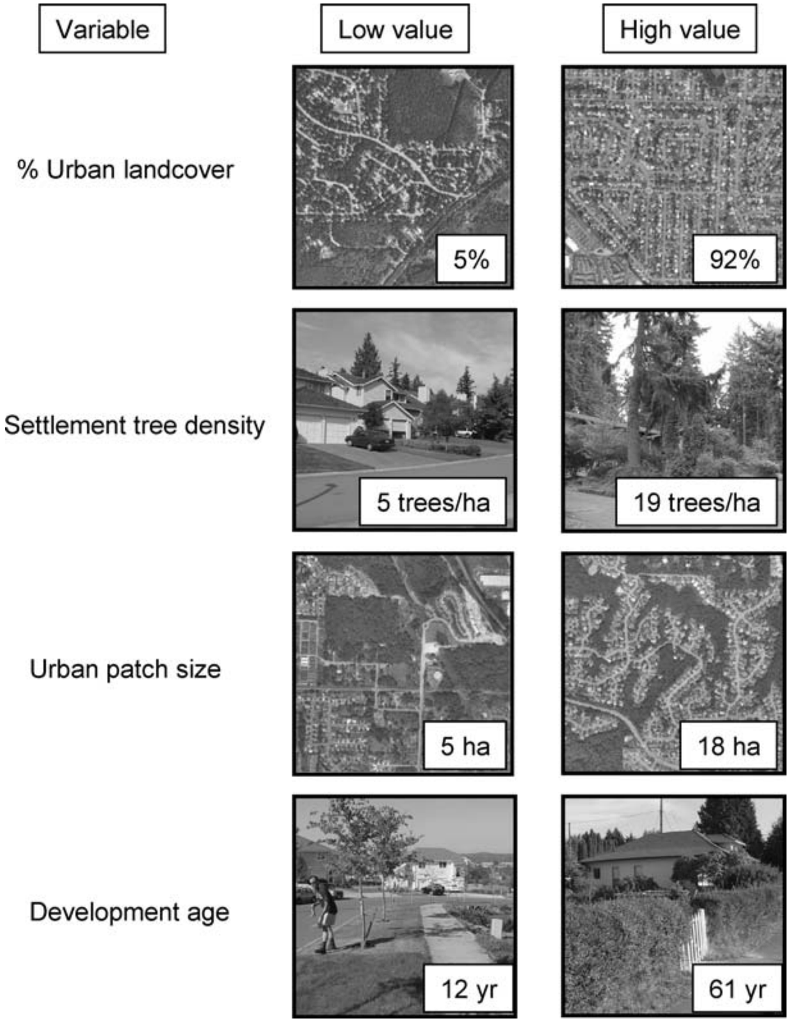

Fig. 1 Photographs of study sites taken from the air (1 km^2) and ground showing ranges of habitat quantity (percent urban landcover), one element of habitat structure (tree density in development), one element of habitat pattern (urban patch size), and development age. All statistics except percent urban landcovers are means

low percent urban landcover/high mean urban patch size, because they did not exist. After we completed field work in 2001, we controlled for age of development/habitat fragmentation within each landscape by calculating mean development age from county parcel data. We expressed age as the average number of years elapsed between development and 2001. This variable ranged from 9–85 yr with a mean of 30 ± 2 for all landscapes.

Bird surveys

We conducted four fixed-radius (50 m) point count surveys of breeding birds in each landscape between 17 April and 28 July 2001. We (R.D. and two assistants that he trained) recorded all birds that we detected in or just above the canopy by sight or sound during 10 min at each point. We surveyed a total of eight points in each landscape. Forty landscapes had enough forest (i.e., classified as forest landcover) to survey two points in contiguous forest with greater than 50 m between circle edges. In those forty landscapes, we surveyed six points in development (i.e., areas not classified as forest landcover). In the 14 remaining landscapes, we located all survey points in development. We allocated more effort to development than forest because a previous study in the same region indicated that birds and vegetation were more variable in development (Donnelly and Marzluff, 2004). All points were > 150 m apart, with the exception of a few forest points where we maximized separation within the only forest fragment that existed on the landscape. We did not conduct more than four surveys per landscape because less than two new species were detected in forests with increased effort (Donnelly, 2002).

We investigated patterns of species richness, Shannon evenness (Magurran, 1988), percent of bird species found in large exurban reserves, and species relative abundance using a subset of observed birds. We did not consider migrant birds that did not breed in our study area or birds that ranged over large areas because our survey technique was unable to reliably assess their abundance. We defined native forest bird species as the species found in large exurban reserves in the Seattle, WA metropolitan area (Donnelly and Marzluff, 2004). All other species were defined as synanthropic and generally appeared on Johnston's (2001) list of synanthropic species. By comparing birds present in the reserves to bird species found in our 54 landscapes, we estimated the percent of native forest species ($n = 19$, Appendix 1) retained and the number of synanthropic species ($n = 28$, Appendix 1) gained following development. We expressed species relative abundance in forested and settled portions of the landscape as the mean number of individuals per point averaged over four surveys. This calculation method prevented young of the year and migrating individuals from inflating abundances.

We present results from bird surveys conducted in 2001 at 54 field sites. These sites represent most of the possible combinations of habitat quantity, structure, and pattern. Because an analysis of one year's data could be misleading if bird abundance varied considerably among years, we assessed annual variation at a subset of the 54 sites surveyed in 2001 ($n = 17$). Four sites in completely forested landscapes were surveyed in 1999, 2001, and 2003. Thirteen sites in landscapes with 5–84% forest of variable structure and arrangement were surveyed in 2000, 2001, and 2003. We combined all 17 sites into a single, repeated-measures analysis of covariance to assess the relative importance of percent forest (a covariate that estimated habitat quantity) and year (a measure repeated three times per site) for each of 57 bird species individually. Combining observations from 1999 at completely-forested sites with those from 2000 at sites with less forest (i.e., < 85%), while not ideal, allowed a conservative test of our study design; it could accentuate habitat x year interactions, thereby invalidating inferences from a single year of bird surveys.

Bird abundance appeared much more sensitive to habitat than to year. On average, variation in bird abundance attributable to variation in percent forest among sites was 46 times greater than variation within sites among years (SE = 14.4; median difference = 6.4× greater). Variation in bird abundance attributable to variation in percent forest was 29 times greater than variation attributable to the interaction of year and percent forest (SE = 9.1, median difference = 3.6× greater). Eight species varied substantially ($p < 0.10$) among years, but only the Northern Flicker had a significant ($p < 0.05$) year by percent forest interaction. All other species responded consistently to variation in the amount of forest in the landscape in each of the three years, even if their abundance was greater in some years than in others. Because our results for Northern Flickers may not be generalized beyond 2001, we deleted them from all subsequent analyses of relative abundance. Based on the repeated measures analysis, the 2001 data were suitable for generating plausible relationships between habitat attributes and populations of all species other than flickers, as well as plausible relationships between habitat attributes and bird communities.

Vegetation surveys

We quantified habitat structure (i.e., composition and structural complexity of local vegetation) surrounding all bird survey points in 2000 (28 landscapes) or 2001 (26 landscapes). Centered on each point, we marked two circular plots covering 0.02 and 0.08 ha. Within the smaller plots, we (1) identified all plants, (2) visually estimated the percent vertical cover of all ground/forb and shrub species, and (3) estimated the horizontal and vertical cover with a Moosehorn (a tool that functions like a spherical densiometer; Garrison, 1949) from 1.5 m above ground at the cardinal directions. Within the larger plots, we counted the number of individuals representing all tree species and the number of snags. From these data, we calculated 12 vegetation indices. For the ground and shrub strata, we calculated the total percent vertical cover, percent cover by exotic species, total horizontal cover in the four cardinal directions (shrub strata only), and species diversity. For the canopy, we estimated tree density, snag density, percent exotic trees, percent evergreen trees, and total canopy closure in the four cardinal directions. To summarize the indices by site, we averaged values across survey points within the same habitat type (i.e., forest or development).

Statistical analyses

We completed all statistical analyses using the Statistical Package for Social Sciences 10.1.3 (2001) and quantified community nestedness using a randomization program called Nest1 (Lomolino, 1996). We used two-tailed tests and $\alpha = 0.05$. To meet the assumptions of parametric tests, we used four types of transformations: log (number of trees, development age), power (number of snags), exponential (urban patch size), and arcsine square root (urban landcover, forest aggregation, total vegetation covers, individual plant covers, community evenness, native forest species retention). In cases where normality could not be achieved through transformation, we used non-parametric tests. We report all means $\pm$ SE.

We tested the relative effects of habitat quantity, structure, pattern, and age on bird communities and their constituent populations using regression analysis. We considered all explanatory variables noted in the methods above (e.g., two habitat pattern variables: forest aggregation and mean urban patch size), except those related to habitat structure. For each portion of the landscape, we considered only the habitat structure variables with the greatest potential to influence birds. We used a two-step procedure to define these subsets of the original 12 measured variables. Based upon previous study of bird communities in metropolitan Seattle (Donnelly and Marzluff, 2004), we identified local vegetation metrics that were most likely to affect the community in developments (percent ground cover, percent exotic ground cover, percent shrub cover, percent exotic shrub cover, tree number, percent exotic trees, percent evergreen trees, percent canopy closure) and forests (percent exotic ground cover, ground cover diversity, percent shrub cover, shrub cover diversity, horizontal shrub cover, percent evergreen trees, snag number, percent canopy closure). Using backwards stepwise regression (P-value $= 0.10$ to remove), we further reduced these sets of vegetation variables to those correlated with the bird communities in each portion of the landscape (i.e., forest and development) without considering other habitat attributes. For example, all vegetation variables considered during analysis of bird species richness in developments were correlated with richness without consideration of habitat quantity, pattern, or age. All subsequent analyses at the population level considered the same subset of habitat structure variables.

We averaged regression models (Burnham and Anderson, 1998) to test the relative effects of habitat quantity, structure, pattern, and age on four bird community metrics: species richness, evenness, native forest species retention, and synanthropic species gain. For each explanatory variable considered in development and forest, this method provided a regression coefficient, coefficient SE, and coefficient weight. These statistics were unconditional, meaning that they were derived from all models rather than the model producing the best fit. Unconditional statistics may produce more precise and less biased estimates of explanatory variable effects than conventional stepwise regression analyses (Burnham and Anderson, 1998). We considered a variable to be relatively important and its coefficient to be different than zero if its weight was large and the 95% confidence interval failed to include zero, respectively. Because model averaging did not quantify the absolute explanatory power of models, we calculated R^2_{adj} for models including all significant variables using the least squares method. If R^2_{adj} was <0.15, we considered all variables in the model, even those with the greatest weights, to be poorly associated with the community metric and drew limited conclusions from those relationships. We used average regression models with R^2_{adj} >0.15 to reduce the set of potentially explanatory habitat variables in subsequent community analyses. We explain variation in species richness with native forest species retention or synanthropic species gain if (1) richness was significantly correlated with retention or gain, (2) the average regression models had $R^2_{adj} > 0.15$ (e.g., forest richness model and forest retention model), and (3) average regression models shared explanatory variables with similar coefficient signs.

In order to explain mechanisms underlying relationships between bird communities and habitat, we analyzed relationships between bird population abundance and habitat quantity, structure, pattern, and age. We considered these analyses exploratory because, compared with community composition, we had fewer hypotheses regarding how species would respond. Since model averaging is not appropriate for exploratory analyses (Burnham and Anderson, 1998), we used forward stepwise regression to develop population models (P-value = 0.05 to enter and 0.10 to remove). For species that were either absent or present at very low density, we used forward logistic regression (see Donnelly, 2002 for detailed list). We transformed explanatory variables before submitting them to the selection criteria, when species showed curvalinear responses.

We estimated where bird species switched from present to absent (occurrence thresholds) along gradients of important habitat variables using regression and nestedness analysis. When it was possible to estimate a threshold with respect to one habitat variable using both methods, we interpret only the results of the regression method. Regression was used to estimate thresholds for variables found in significant forward regression models of abundance. We did not investigate thresholds with respect to development age or measures of habitat structure, other than tree density and percent evergreen trees, because these variables were not as amenable to management. For habitat variables that were amenable to management, we regressed relative abundance on each untransformed habitat variable and plotted the 95% confidence interval around the regression line. We defined the threshold as the intersection of the lower bound of the confidence interval with the x-axis (i.e., zero abundance). Species affected by the variable did not necessarily show thresholds of occurrence within the variable's range. When enough species showed thresholds with respect to one habitat variable (≥ 4 species in forest and development combined), we averaged thresholds by species classification

Table 1 Average regression models of bird community metrics for development and forest. Retention and gain refer to native forest species and synanthropic species, respectively. Retention in the forest could not be modeled. We estimated model fit with R^2_{adj} by entering variables in averaged models into multiple linear regressions. We did not attempt to interpret models with $R^2_{adj} < 0.15$ due to poor fit. The order of coefficients weights corresponds to coefficient order in the model

Portion of landscape	Metric	Average model	Coefficient weight	R^2_{adj}
Development	Richness	23 − 0.13 Urban landcover + 9.8 Tree density − 0.20 Canopy closure	0.67, 0.93, 0.88	0.59
	Evenness	62 − 2.9 Urban patch size − 0.037 Exotic tree	0.66, 0.69	0.53
	Retention	37 − 0.20 Urban landcover + 14 Tree density	0.73, 0.95	0.66
	Gain	17 + 0.12 Exotic ground cover − 0.13 Canopy closure	2.6, 2.6	0.01
Forest	Richness	24 − 0.13 Canopy closure	0.96	0.17
	Evenness	74 − 2.6 Ground diversity	0.87	0.10
	Gain	5.1 − 0.11 Canopy closure + 2.9 Ground diversity	0.94, 0.92	0.32

(native forest or synanthropic species). Averaging the thresholds allowed us to generalize the effect of the habitat variable across bird species.

Where bird species retention or gain appeared to explain bird species richness, we used nestedness analysis (Atmar and Patterson, 1993) to estimate an occurrence threshold with respect to each variable shared by models for forest and shared by models for development. Nested communities are those in which less speciose communities tend to be proper subsets of more speciose communities. In other words, if a community is perfectly nested, species found in a community of species richness n are also found in all communities with richness $> n$. If communities were nested by a habitat variable meeting the above criteria, we (1) superimposed a threshold of occurrence curve on the presence/absence matrix ordered by the habitat variable (Fig. 4; for methods, see Lomolino, 1996 and Donnelly and Fleishman in review), (2) estimated the species-specific thresholds using the intersections of the curve with each row, and (3) averaged the species-specific thresholds.

Results

Bird communities

Communities in developments were richer and less even than those in forests. We detected a mean of 23.0 ± 0.7 bird species in developments and 14.9 ± 0.6 in forests. However, the number of species in developments and forests appeared similar when we controlled for sampling effort with rarefaction (Gotelli and Entsminger, 2002; mean rarefied richness: development = 13.2 ± 0.36, forest = 12.6 ± 0.38; $t_{92} = 1.1$, $P = 0.27$). Evenness averaged 0.81 ± 0.007 in developments and 0.89 ± 0.005 in forests ($t_{92} = 8.1$, $P < 0.001$).

Community attributes were associated with habitat quantity and structure more often than habitat pattern or age (Table 1). In our best regression models ($R^2_{adj} > 0.15$), at least one aspect of habitat structure, typically an attribute of the canopy or ground vegetation, was related to each community metric. Conversely, habitat pattern was only associated with development evenness and age was not associated with any community metric. Bird species richness in developments decreased with urban landcover and development canopy closure and increased with development tree density (Table 1, Figs. 2(a)–(c)). Richness decreased with canopy closure in forest (Fig. 2(d)). The ability of individual variables to

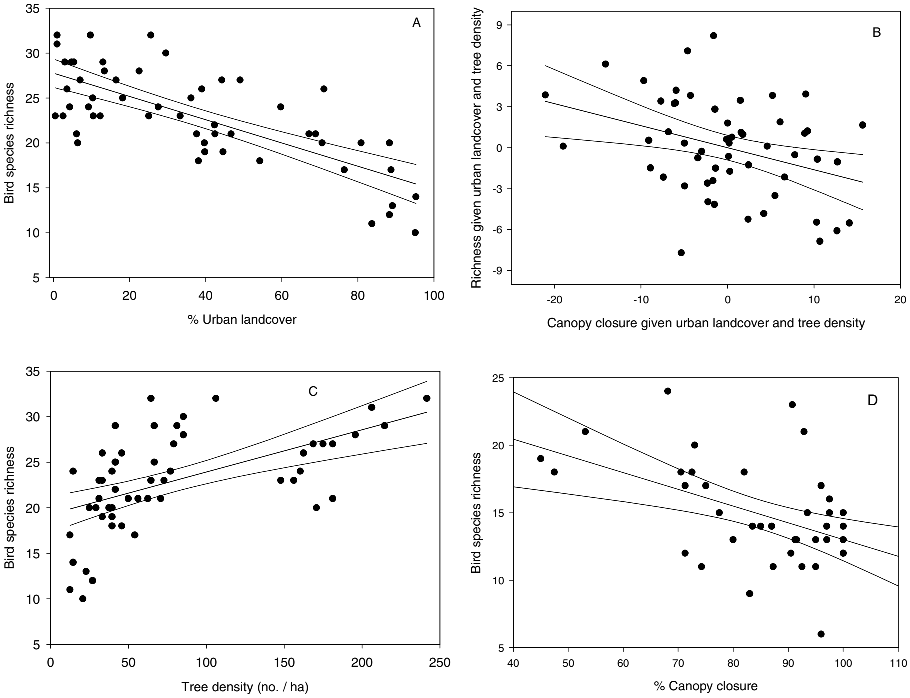

Fig. 2 Relationship of bird species richness to (a) habitat quantity and (b and c) structure in development and (d) habitat structure in forest. Canopy closure in development is depicted as a partial regression plot rather than a direct plot because the relationship was not clear without removing the effects of the other gradients. Each panel has a regression line with a 95% confidence interval

explain richness varied little within average regression models (all regression coefficient weights within 10% of maximum weight), with one exception. Urban landcover explained less variation in development richness compared to other significant variables. Evenness in development declined with urban patch size and percent exotic trees (Table 1; Fig. 3(a)). Again, the explanatory variables explained similar amounts of variation in the response variable.

Richness increased with species retention in development and with species gain in forest. Richness and species retention in development were positively correlated ($r = 0.82$, $P < 0.001$, $n = 54$), decreased with urban landcover, and increased with tree density (Table 1). Richness and species gain in forest were positively correlated ($r = 0.76$, $P < 0.001$, $n = 40$) and decreased with canopy closure.

Bird populations

Habitat quantity, structure, and age were correlated with the relative abundance of more species in developments than habitat pattern. Urban landcover, development age, and the percent evergreen trees were related to the abundance of more species in development than expected by chance ($\chi^2_{11} = 21.5$, $P < 0.05$; Table 2). Synanthropic species increased and native forest species decreased as urban landcover became more common (10 of 11 species with urban landcover in their relative abundance models). Synanthropic species decreased

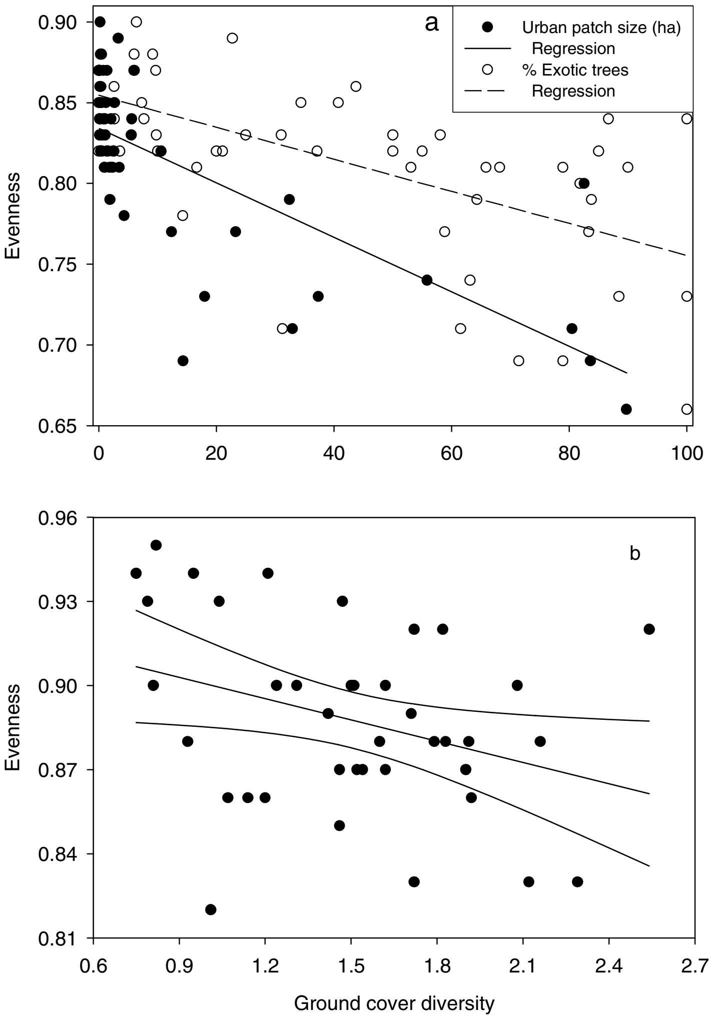

Fig. 3 Relationship of bird evenness to habitat structure and pattern in (a) development and (b) forest. Regression lines are bounded by the 95% confidence interval where possible

and native forest species increased as evergreen trees became more common in the canopy (7 of 8 species). Development age did not have a consistent effect on the abundance of native forest or synanthropic species.

We estimated the average vegetation values at which native forest species tended to switch from present to absent within landscapes. Most species tended to be absent from communities with $>52 \pm 7.6\%$ urban landcover (development: American Robin 83%, Brown Creeper 43%, Chestnut-backed Chickadee 68%, Hairy Woodpecker 42%, Western Tanager 42%; Forest: Wilson's Warbler 36%; see Appendix 1 for scientific names), $<23 \pm 3.4\%$ evergreen trees in the canopy (development: Chestnut-backed Chickadee 20%, Golden-crowned Kinglet 19%, Winter Wren 32%, Dark-eyed Junco 22%), $<0.64 \pm 0.039$ forest aggregation (development: Pacific-slope Flycatcher 0.69, Winter Wren 0.52; forest: Swainson's Thrush 0.68, Pacific-slope Flycatcher 0.67), and $<9.8 \pm 1.6$ trees/ha ($n = 10$ species; see Fig. 4

Table 2 Relative abundance models for development and forest from forward stepwise regressions. The numerator and denominator degrees of freedom associated with the F statistic were equal to the number of estimated parameters minus one and 39 (the number of sites with $< 10\%$ forest) minus the number of estimated parameters, respectively. All models were linear except those for pine siskins in development and hairy woodpeckers in forest. These models were logistic and are accompanied below by Cox and Snell R^2 and χ^2 statistics. Forest aggregation is abbreviated as For. Aggr. within models. See methods for transformations to explanatory variables. An asterisk indicates that the abundance of the species at 17 of the 54 sites contributing to the regression varied among years but did not depend on the combination of year and habitat

Species	Linear model	R^2_{adj}	F	P
DEVELOPMENT				
American Crow	−0.35 + 1.2 Development age − 0.61 Tree density	0.30	9.0	< 0.01
American Robin	1.5 − 0.013 Urban landcover	0.21	11.0	< 0.01
Band-tailed Pigeon	0.32 − 0.19 Development age	0.09	4.5	0.04
Barn Swallow	0.035 − 0.0044 Evergreen tree + 0.0079 Exotic ground cover	0.22	6.2	< 0.01
Bewick's Wren	−0.50 + 0.38 Development age + 0.0052 Exotic shrub cover	0.38	12.6	< 0.001
Black-capped Chickadee	0.040 + 0.61 Development age − 0.013 For. Aggr.	0.43	15.5	< 0.001
Black-headed Grosbeak	−0.34 + 0.0068 For. Aggr.	0.22	11.8	< 0.01
Black-thrtd. Gray Warbler	−0.034 + 0.057 Tree density	0.18	9.3	< 0.01
Brown Creeper	−0.15 − 0.0025 Urban landcover + 0.26 Development age + 0.00084 Canopy closure − 0.0032 Exotic ground cover	0.43	8.0	< 0.001
Brown-headed Cowbird	−0.066 + 0.0066 Exotic ground cover	0.14	7.0	< 0.02
Bushtit	−0.037 + 0.013 Urban landcover	0.12	6.0	<0.02
Chestnut-backed Chickadee	0.14 − 0.010 Urban landcover + 0.41 Development age + 0.0052 Evergreen tree	0.52	14.5	< 0.001
Dark-eyed Junco	2.3 − 0.0062 Urban landcover − 0.69 Development age − 0.018 For. Aggr. + 0.0073 Evergreen tree	0.34	7.6	< 0.001
Downy Woodpecker	0.036 − 0.0011 Shrub cover	0.17	8.6	< 0.01
European Starling	−0.73 + 0.041 Urban landcover + 0.044 Exotic shrub cover	0.47	18.1	< 0.001
Golden-crowned Kinglet*	−0.59 + 0.0031 Evergreen tree	0.19	9.9	< 0.01
Hairy Woodpecker	0.10 − 0.0023 Urban landcover	0.20	10.7	< 0.01
House Finch*	−0.089 + 0.025 Urban landcover + 0.011 Exotic tree cover	0.53	22.7	< 0.001
House Sparrow	−2.3 + 3.2 Development age − 0.025 Canopy closure – 0.015 Evergreen tree	0.57	17.6	< 0.001
Pacific-slope Flycatcher	−0.11 + 0.0087 For. Aggr.− 0.016 Exotic shrub cover	0.48	18.4	< 0.001
Pine Siskin*	−2.3 − 3.7 Urban patch size	0.25	11.3	< 0.01
Purple Finch	0.052 − 0.00097 Urban landcover − 0.011 Exotic ground cover + 0.011 Ground cover + 0.0073 Exotic shrub cover − 0.0073 Shrub cover	0.61	13.0	< 0.001
Red Crossbill	0.054 + 0.0034 Evergreen tree − 0.004 Exotic ground cover	0.25	7.3	< 0.01
Rock Dove	−0.097 + 0.0064 Urban landcover	0.21	10.8	< 0.01
Rufous Hummingbird	−0.054 + 0.0034 Canopy closure	0.22	11.6	< 0.01
Song Sparrow	0.15 + 0.54 Tree density − 0.0058 Evergreen tree − 0.0031 Exotic tree	0.50	13.9	< 0.001
Spotted Towhee*	−0.041 − 0.37 Urban patch size	0.40	26.0	< 0.001
Swainson's Thrush	0.030 + 0.43 Tree density − 0.012 Exotic shrub cover	0.37	16.7	< 0.001
Violet-green Swallow*	2.1 − 2.2 Development age + 0.032 Exotic ground cover + 3.0 Exotic shrub cover	0.48	12.9	< 0.001
Western Tanager	0.077 − 0.068 log Urban landcover	0.23	6.7	< 0.01
Wilson's Warbler	−0.032 + 0.0034 Canopy closure	0.22	11.9	< 0.01
Winter Wren	−0.56 + 0.0085 For. Aggr. − 0.0086 Exotic shrub cover + 0.0046 Ground cover + 0.0022 Evergreen tree	0.70	22.9	< 0.001
FOREST				
American Crow	1.6 − 0.017 Canopy closure	0.10	4.7	< 0.04
American Robin	−0.74 − 0.59 Urban patch size + 0.65 Shrub diversity	0.29	7.8	< 0.01
Band-tailed Pigeon	0.09 − 0.0018 Evergreen tree	0.19	9.2	< 0.01
Bewick's Wren	−0.235 + 0.0091 Urban landcover + 0.0098 Exotic ground cover	0.28	7.4	< 0.01
Black-capped Chickadee	0.10 + 0.012 Exotic ground cover	0.16	7.5	0.01
Black-throated Gray Warbler	−0.11 + 0.060 Snag density + 0.0027 Exotic ground cover	0.31	8.7	< 0.01

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Table 2 *(Continued)*

Species	Linear model	R^2_{adj}	F	P
Bushtit	0.94 − 0.011 Canopy closure	0.15	7.1	< 0.01
Cassin's Vireo	−0.056 − 0.019 Snag density + 0.0014 For. Aggr.	0.25	6.6	< 0.01
Dark-eyed Junco	1.5 − 0.019 Horizontal shrub cover − 0.50 Shrub diversity + 0.27 Ground diversity	0.57	16.0	< 0.001
Hairy Woodpecker	10.3 − 0.015 For. Aggr.	0.20	7.9	< 0.01
House Finch*	−0.81 + 0.77 Development age	0.10	4.6	< 0.04
Olive-sided Flycatcher	−0.055 + 0.049 Ground diversity	0.10	4.8	< 0.04
Pacific-slope Flycatcher	−0.19 − 0.31 Ground diversity + 0.015 For. Aggr.	0.35	10.0	< 0.001
Pine Siskin*	−0.18 + 0.20 Ground diversity	0.14	6.6	< 0.02
Rock Dove	−0.33 + 0.0083 Shrub cover	0.12	5.5	< 0.03
Spotted Towhee*	1.8 − 0.016 Canopy closure	0.17	8.1	< 0.01
Swainson's Thrush	−0.43 − 0.53 Shrub diversity + 0.013 Horizontal shrub cover + 0.018 For. Aggr.	0.32	6.2	< 0.01
Violet-green Swallow*	−0.42 + 0.015 Shrub cover	0.10	4.7	< 0.04
Western Tanager	−0.60 − 0.12 Urban patch size + 0.0046 Canopy closure + 0.12 Shrub diversity	0.33	6.5	< 0.01
Wilson's Warbler	−0.067 − 0.0048 Urban landcover + 0.0059 Horizontal shrub cover	0.30	8.2	< 0.01
Winter Wren	0.85 − 0.35 Ground diversity	0.15	6.9	< 0.02

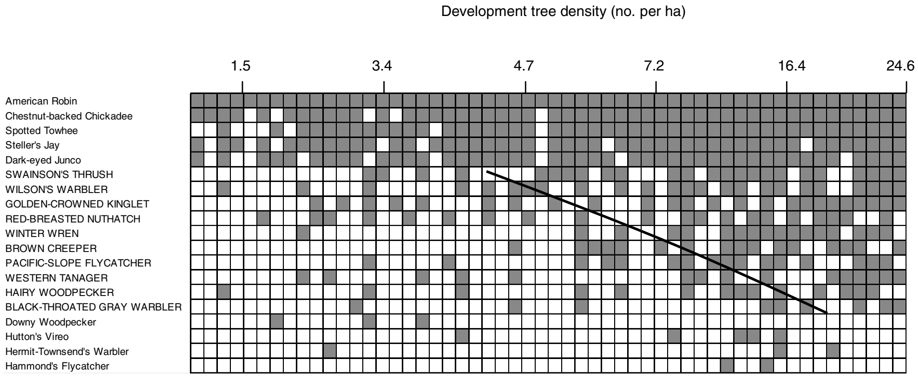

Fig. 4 Native forest species retention in development. Columns represent communities ranked by tree density in development. Rows represent species ordered to maximize presences in the upper right and absences in the lower left. Filled and unfilled squares indicate presence and absence, respectively. The intersection of the superimposed occurrence threshold curve with a column indicates a species-specific threshold of occurrence, or the tree density where a species tended to switch from present to absent. We applied this curve to species (names in all capitals) that established a consistent presence across the region (> 5 communities) and, yet, were not present at almost all sites (< 45 communities)

for species-specific thresholds). We calculated all thresholds using the regression method, except for the tree density threshold. Native forest birds in developments were nested by tree density (% of perfect nesting by tree density = 12.6, P <0.02), so we calculated the threshold for this explanatory variable using a presence/absence matrix (Fig. 4). We do not report average thresholds for native forest species with respect to urban patch size or thresholds for synanthropic species with respect to any habitat attributes due to small sample sizes (<3 species showing thresholds using regression method), large standard errors associated with the means calculated from small samples, and lack of nestedness with respect to these variables.

Discussion

Relative importance of habitat structure

Despite emphasis on habitat quantity and pattern by guidelines for wildlife conservation in urban systems (Knight, 1990; Soulé, 1991; Shafer, 1997), recent theoretical, meta-analytical, and empirical studies contend that habitat quantity is more important than habitat pattern, especially for mobile species like birds (Fahrig, 1997; Bunnell, 1999; Harrison and Bruna, 1999; Lichstein et al., 2002; Alberti and Marzluff, 2004) and that habitat structure is as important as habitat pattern in fragmented systems (Thomas et al., 2001). Our study of birds in the Pacific Northwest corroborates these recent findings and suggests that we should refine conservation priorities for this region.

Songbird communities in the Seattle metropolitan region were more closely allied with estimates of habitat quantity and structure (i.e., urban landcover and local vegetation) than estimates of habitat pattern (i.e., urban patch size and forest aggregation). The mobility of birds may explain the relatively small effect of pattern (Alberti and Marzluff, 2004). For example, synanthropic species may be more adept at dispersing through forest than at breeding in forest. Native forest species may be more adept at dispersing through development than breeding in development, unless the development has low urban landcover and high tree density. If those conditions are met, developments may retain native bird species and keep bird species diversity high. Several other studies have documented and discussed similar effects of urban landcover and native vegetation structure on the retention of native bird species and bird species richness (Penland, 1984; Germaine et al., 1998; Marzluff, 2005). Richness in forested portions of neighborhoods was less sensitive to retention of native forest birds. Instead, it was high where canopies were open and many synanthropic species were present. Only the evenness of bird communities in developments was influenced by habitat pattern. This community metric increased as urban patches decreased in size and exotic trees became rare.

Together, the models of species richness, retention, and gain suggest that we can increase retention of native forest bird species and decrease gain of synanthropic bird species by limiting urban landcover, maintaining tree density in development, and maintaining canopy closure in forest. With regard to tree density, it is important to note that dense stands of young trees ($<$70 yrs old) will conserve different bird species than will retention of older stands. Many sensitive native bird species (e.g., Black-throated Gray Warbler, Brown Creeper) are associated with older stands (Donnelly, 2002) that have greater tree species diversity and distribute more foliage over a greater vertical range (Oliver and Larson, 1996). Young stands will also conserve some sensitive native birds that use early-successional, human-dominated landscapes (e.g., Swainson's Thrush, Willow Flycatcher).

Songbird populations also appeared to be more closely related to habitat quantity and structure than habitat pattern. Species relative abundance was more often correlated with indices of habitat quantity and structure than habitat pattern. Moreover, native forest species exhibited thresholds of occurrence along gradients of these variables. Native forest species tended to be present when neighborhoods had significant tree cover ($>$9.8/ha), urban landcover did not dominate the landscape ($<$52%), canopies contained abundant evergreen trees ($>$23%), and forest was not highly fragmented ($>$64 aggregated).

It is possible that our study design was more likely to detect a stronger relationship between birds and habitat structure and than between birds and habitat quantity or pattern. Habitat quantity and pattern were estimated at the landscape scale, while habitat structure and bird metrics were estimated at local scales replicated many times in each landscape. Thus, the spatial scales of sampling for birds and habitat structure appear to match better than the spatial sampling scales for birds and the other habitat attributes. Yet, habitat pattern can have a greater influence on fragment occupancy by birds than habitat structure in highly fragmented landscapes (Cooper and Walters, 2002). Furthermore, we show that habitat quantity was very important to bird communities and populations, despite being measured at the landscape scale, and that habitat pattern was important to bird community evenness in developments and to the abundance of some bird species. We conclude that the study design had little effect on our results; habitat pattern was less important to birds than habitat quantity and structure in this region at this time.

Value of managing development for bird conservation

Residential developments in the Seattle metropolitan region can contribute to bird conservation. Forest reserves provide habitat for native forest species, unless they are small and located in highly urbanized landscapes (Donnelly and Marzluff, 2004). Therefore, they will always be a conservation priority. We show, however, that manipulation of housing development attributes can mitigate the negative impacts of urbanization on forest bird diversity and supplement bird conservation in reserves. We can encourage greater retention and abundance of native forest species outside reserves by building residential developments that minimize impervious surface and maximize retention of trees, especially those that are evergreen. Rather than applying this single neighborhood design over large areas, we suggest varying development design within and among landscapes to increase regional diversity of birds in urbanizing landscapes (Blewett and Marzluff, 2005). Such control of development may only be possible where state growth management acts are already in place.

Natural resource management and policy

Recommendations

Because urbanization systematically degrades habitat for native forest species and converts it to habitat for synanthropic species, we need conservation guidelines that focus on native forest species. Contrary to extant, general conservation guidelines (Knight, 1990; Soulé, 1991; Shafer, 1997), our data suggest that (1) habitat quantity and structure were at least as important as habitat pattern to bird communities and populations and (2) development had considerable potential to supplement bird conservation in forest reserves. Based on these conclusions, we propose the following management approach with specific management targets for 1 km^2 landscapes in the Pacific Northwest. This scheme is a starting point that should be updated as the underlying bird-habitat relationships are tested with new sets of landscapes, with different metropolitan areas in the Pacific Northwest, and across multiple years.

Policy makers can help conserve native forest birds at large (10–100 km^2) and small spatial scales (0.2–1.5 ha). At large scales, we recommend that county and city policy makers use a two-step process to maintain less than 52% urban landcover and greater than 64% forest aggregation, ideally creating forest patches of at least 42 ha (Donnelly and Marzluff, 2004). First, they should limit forest conversion and fragmentation by adopting ordinances that limit the amount of clearing/grading and that aggregate native growth protection areas within and among developments. Second, they should create ordinances protecting management thresholds from subsequent development or subdivision that would significantly increase urban landcover or decrease forest aggregation. As development pressure increases, these ordinances will be challenged with litigation and politics. Therefore, it will probably be necessary for state policy makers to add the management thresholds to criteria for evaluating regional growth plans, such as those required by Washington state's Growth Management Act.

At small spatial scales, we recommend that state, county and city policy makers provide incentives for small property owners to retain or restore neighborhood canopies to at least 9.8 trees/ha and at least 23% evergreen trees. The threshold for tree density is an average, meaning that densities will vary among yards and that some yards must have much higher densities than 9.8 trees/ha to realize conservation benefits. Existing incentives for these management activities include, but need not be limited to, certification of properties as wildlife sanctuaries, tax breaks for protection or restoration of native vegetation, and provision of saplings for canopy restoration. Homeowners and land managers can also contribute to bird conservation at an intermediate scale by incorporating the recommendations for small and large scales into policies for homeowners associations and public lands.

The recommendations in the preceding paragraph should *not* be applied to all landscapes, because landscape homogeneity of this type would (1) create low density development over a large area and (2) dramatically reduce the regional abundance of all synanthropic and early-successional species (Blewett and Marzluff, 2005). The first outcome is undesirable, because it disperses the negative effects of urbanization on biodiversity across a large area. The second outcome is undesirable, because some synanthropic species are native species that require early-successional habitat; they benefit from the creation of landscapes that do not simultaneously meet all management thresholds for native forest species. Providing some heterogeneity of landscapes will help preserve native forest species, native synanthropic species, and regional bird diversity (Pyle, 1980; Bunnell, 1999; Blewett and Marzluff, 2005).

Where, then, do we manage for native forest species? Management thresholds for native forest species should be applied to landscapes where: forests are relatively mature (>60 years), forests contain diverse habitat (Donnelly and Marzluff, 2004), forests contribute to forest size in adjacent landscapes, infrastructure increasing development pressure (e.g., highway corridors) is minimal, and residential development is primarily single-family. We include the last qualifier because greater human density in multi-family neighborhoods may negatively impact native forest birds at lower values of urban landcover relative to single-family neighborhoods despite its distribution over similar area.

Metropolitan Seattle's youth and considerable forest cover suggest that the relative importance of habitat quantity, structure, and pattern to birds could change with time. As developments mature, landscaping creates or restores habitats for birds that were absent just after development (Munyenyenbe et al., 1989) and long-term isolation of forest reserves causes bird communities to relax (Soulé et al., 1988). In our study area, development age was related to species abundance, but unrelated to species richness, gain, or retention. The lack of relationships suggested that landscaping had not increased habitat structure and that isolation was too recent or offset by demographic rescue by native forest birds from large/nearby forest reserves (Brown and Kodric-Brown, 1977). Development age and habitat pattern may become increasingly important to bird communities as landscaping matures and we continue to convert forest to development. If Andren (1994) and Fahrig (1998) are correct, this change will not occur until Seattle is less than 40% forested.

Appendix 1. Bird species names

Common name	Scientific name
SYNANTHROPIC SPECIES	
American crow	*Corvus brachyrhynchos*
Anna’s hummingbird	*Calypte anna*
Band-tailed pigeon	*Columba fasciata*
Bewick’s wren	*Thryomanes bewickii*
Black-capped chickadee	*Poecile atricapillus*
Black-headed grosbeak	*Pheucticus melanocephalus*
Brown-headed cowbird	*Molothrus ater*
Bushtit	*Psaltriparus minimus*
Cassin’s vireo	*Vireo cassinii*
Cedar waxwing	*Bombycilla cedrorum*
European starling	*Sturnus vulgaris*
House finch	*Carpodacus mexicanus*
House sparrow	*Passer domesticus*
MacGillivray’s warbler	*Oporornis tolmiei*
Northern flicker	*Colaptes auratus*
Olive-sided flycatcher	*Contopus cooperi*
Orange-crowned warbler	*Vermivora celata*
Pine siskin	*Carduelis pinus*
Purple finch	*Carpodacus purpureus*
Red crossbill	*Loxia curvirostra*
Red-winged blackbird	*Agelaius phoeniceus*
Rufous hummingbird	*Selasphorus rufus*
Song sparrow	*Melospiza melodia*
Violet-green swallow	*Tachycineta thalassina*
Warbling vireo	*Vireo gilvus*
Western wood peewee	*Contopus sordidulus*
Willow flycatcher	*Empidonax traillii*
Yellow-rumped warbler	*Dendroica coronata*
NATIVE FOREST SPECIES	
American Robin	*Turdus migratorius*
Black-throated Gray Warbler	*Dendroica nigrescens*
Brown Creeper	*Certhia americana*
Chestnut-backed Chickadee	*Poecile rufescens*
Dark-eyed Junco	*Junco hyemalis*
Downy Woodpecker	*Picoides pubescens*
Golden-crowned Kinglet	*Regulus satrapa*
Hairy Woodpecker	*Picoides villosus*
Hammond’s Flycatcher	*Empidonax hammondi*
Hermit-Townsend’s Warbler	*Dendroica spp.*
Hutton’s Vireo	*Vireo huttoni*
Pacific-slope Flycatcher	*Empidonax difficilis*
Red-breasted Nuthatch	*Sitta canadensis*

(*Continued on next page)*

(Continued)

Common name	Scientific name
SYNANTHROPIC SPECIES	
Spotted Towhee	*Pipilo maculatus*
Steller's Jay	*Cyanocitta stelleri*
Swainson's Thrush	*Catharus ustalatus*
Western Tanager	*Piranga ludoviciana*
Wilson's Warbler	*Wilsonia pusilla*
Winter Wren	*Troglodytes troglodytes*

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References

Alberti M, Botsford E, Cohen A (2001) Quantifying the urban gradient: linking urban planning and ecology. In: Marzluff JM, Bowman R, Donnelly R (eds) Avian ecology and conservation in an urbanizing world, Kluwer Academic Publishers, Norwell, pp. 89–116

Alberti M, Marzluff JM (2004) Ecological resilience in urban ecosystems: linking urban patterns to human and ecological functions. Urban Ecosyst 7:241–265

Andren H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366

Atmar W, Patterson BD (1993) The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia 96:373–382

Baker WL [online] (1997) The r.le Programs. Version 2.2. <http://www.baylor.edu/~grass/gdp/terrain/r_le_22.html> (6 June 1997)

Beissinger SR, Osborne DR (1982) Effects of urbanization on avian community organization. Condor 84:75–83

Berry BJL (1990) Urbanization. In: Turner BL, Clark WC, Kates RW, Richards JF (eds) Earth as transformed by human action, Cambridge University Press, New York, pp. 103–119

Blair RB (1996) Land use and avian species diversity along an urban gradient. Ecological Appl 6:506–519

Blewett CM, Marzluff JM (2005) Effects of urban sprawl on snags and the abundance and productivity of cavity-nesting birds. Condor 107:677–692

Booth DE (1991) Estimating prelogging old-growth in the pacific northwest. J Forestry 89:25–29

Botsford ER (2000) Development of a modified land composition classification methodology utilizing LANDSAT thematic mapping and ancillary data. M.S. thesis, University of Washington, Seattle

Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. Ecol 58:445–449

Bunnell FL (1999) What habitat is an island? In: Rochelle JA, Lehmann LA, Wisniewski J (eds) Forest Fragmentation: wildlife and management implications, Brill, Boston, pp. 1–31

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach, 1st edn. Springer-Verlag, New York, NY

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

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

Donnelly R (2002) Design of Habitat reserves and settlements for bird conservation in the seattle metropolitan area. Ph.D. dissertation, University of Washington, Seattle
Donnelly R, Fleishman E (In review) Application of nestedness analysis to biodiversity conservation in urbanizing areas. Landscape and Urban Planning
Donnelly R, Marzluff JM (2004) Importance of reserve size and landscape context to urban bird conservation. Conserv Biol 18:733–745
Ewing RH (1994) Characteristics, causes, and effects of sprawl: a Literature review. Environ Urban Issues 305:1–15
Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. J Wildl Manage 61:603–610
Fahrig L (1998) When does fragmentation of breeding habitat affect population survival. Ecological Modelling 105:273–292
Franklin JF, Dyrness CT (1988) Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis
Garrison GA (1949) Uses and modifications for the "Moosehorn" crown closure estimator. J Forestry 47:733–734
Germaine SS, Rosenstock SS, Schweinsburg RE, Richardson WS (1998) Relationships among breeding birds, habitat, and residential development in greater Tucson, Arizona. Ecological Applications 8:680–691
Gotelli NJ, Entsminger GL [online] (2002) EcoSim: null models software for ecology. Version 7.0. <http://homepages.together.net/∼gentsmin/ecosim.htm> (9 September 2002)
Haila Y (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. Ecolo Appl 12:321–334
Harrison S, Bruna E (1999) Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22:225–232
Johnston RF (2001) Synanthropic birds of north America. In: Marzluff JM, Bowman R, Donnelly R (eds) avian ecology and conservation in an urbanizing world, kluwer academic publishers, Norwell, pp. 49–68
Knight RL (1990) Ecological principles applicable to the management of urban ecosystems. In: Webb EA, Foster SQ (eds) Perspectives in urban ecology, denver museum of natural history and thorne ecological institute, Denver, pp. 24–34
Lancaster RK, Rees WE (1979) Bird communities and the structure of urban habitats. Canadian Journal of Zool 57:2358–2368
Lichstein JW, Simons TR, Franzreb KE (2002) Landscape effects on breeding songbird abundance in managed forests. Ecol Appl 12:836–857
Lomolino ML (1996) Investigating causality of nestedness of insular communities: selective immigrations or extinctions. J Biogeogr 23:699–703
Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press, Princeton
Major RE, Gowing G, Kendal CE (1996) Nest predation in Australian urban environments and the role of the Pied Currawong, *Strepera graculinaation,* in Australia. Australian J Ecol 21:399–409
Marzluff JM (2001) Worldwide urbanization and its effects on birds. In: Marzluff JM, Bowman R, Donnelly R (eds) avian ecology and conservation in an urbanizing world, kluwer academic publishers, Norwell, pp. 19–48
Marzluff JM (2005) Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. Urban Ecosyst 8:157–177
Marzluff JM, Bowman R, Donnelly R (2001a) An historical perspective on urban bird research: trends terms, and approaches. In: Marzluff JM, Bowman R, Donnelly R (eds) Avian ecology and conservation in an urbanizing world, kluwer academic publishers, Norwell, pp. 1–18
Marzluff JM, Bowman R, Donnelly R (eds) (2001b) Avian ecology and conservation in an urbanizing world. kluwer academic publishers, Norwell
Marzluff JM, McGowan KJ, Donnelly R, Knight RL (2001c) Causes and consequences of expanding American crow populations. In: Marzluff JM, Bowman R, Donnelly R, (eds) Avian ecology and conservation in an urbanizing world, kluwer academic publishers, Norwell, pp. 331–364
Marzluff JM, Ewing K (2001) Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. Restoration Ecol 9:280–292
McGarigal K, Cushman SA, Neel MC, Ene E [online] (2002) Spatial Pattern Analysis Program for Categorical Maps, FRAGSTATS 3.1. <http://www.umass.edu/landeco/research/fragstats/fragstats.html> (5 May 2002)
McKinney ML (2002) Urbanization biodiversity, and conservation. Biosci 52:883–890
Miller JR, Hobbs RJ (2000) Conservation where people live and work. Conservation Biology 16:330–337
Munyenyembe F, Harris J, Hone J (1989) Determinants of bird populations in an urban area. Australian J Ecol 14:549–557

Nuorteva P (1971) The synanthropy of birds as an expression of the ecological cycle disorder caused by urbanization. Annales Zoologici Fennici 8:547–553

Oliver CD, Larson BC (1996) Forest stand dynamics. John Wiley and Sons, New York

Opdam P, van Dorp D, ter Braak CJF (1984) The effect of isolation on the number of woodland birds in small woods in the Netherlands. J Biogeogr 11:473–478

Penland ST (1984) Avian responses to a gradient of urbanization in seattle, Washington. Ph.D. dissertation, University of Washington, Seattle

Pitelka RA (1942) High population of breeding birds within an artificial habitat. Condor 44:172–174

Puget Sound Regional Council (1997) Urban centers in the central puget sound region: a baseline summary and comparison. Puget sound regional council, seattle

Pyle RM (1980) Management of nature reserves, In: Soulé ME, Wilcox BA (eds) Conservation Biology: an Evolutionary-ecological Perspective, Sinauer, Sunderland, pp. 319–327

Ralph CJ, Geupel GR, Pyle P, Martin TE, Desante DF (1993) Handbook of field methods for monitoring Landbirds. U.S. Department of agriculture, forest service, pacific southwest research station, Albany. general technical report PSW-GTR-144

Robinson L, Newell JP, Marzluff JM (2005) Twenty-five years of sprawl in the Seattle region: growth management responses and implications for conservation. Landscape and Urban Planning 71:51–72

Rosenstock S, Anderson D, Giesen K, Leukering T, Carter M (2002) Landbird counting techniques: current practices and an alternative. Auk 119:46–53

Shafer CL (1997) Terrestrial nature reserve design at the urban/rural interface. In: Schwartz MW (ed) Conservation in highly fragmented landscapes, Chapman and Hall, New York, pp. 345–378

Soulé ME (1991) Land use planning and wildlife maintenance: guidelines for conserving wildlife in urban landscapes. Journal of the American Planning Association 57:313–323

Soulé ME, Bolger DT, Alberts AC, Wright J, Sorice M, Hill S (1988) Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2:75–92

Statistical Package for Social Sciences (2001) SPSS 10.1.3. SPSS, Chicago

Thomas JA, Bourn NAD, Clarke RT, Stewart KE, Simcox DJ, Pearman GS, Curtis R, Goodger B (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proce Royal Soc of Lond B268:1791–1796

United Nations (1999) The state of the world population 1999 – 6 Billion, a time for choices. United Nations, New York

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. Sci 277:494–509

Wang Y, Moskovits DK (2001) Tracking fragmentation of natural communities and changes in land cover: applications of LANDSAT data for conservation in an urban landscape. Conserv Biol 15:835–843

Whitcomb RF, Robins CS, Lynch JF, Whitcomb BL, Klimkiewicz MK, Bystrak D (1981) Effects of forest fragmentation on avifauna of the eastern deciduous forest. In: Burgeos R, Sharpe D (eds) Forest Stand Dynamics in Man-dominated Landscapes, Springer-Verlag, New York, pp. 125–205

Wilcove DS (1985) Nest predation in forest tracts and the decline of migratory songbirds. Ecol 66:1211–1214