

**HABITAT INTERACTIONS STRUCTURING SONGBIRD COMMUNITIES
ACROSS FOREST-URBAN EDGES**

By

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ABSTRACT OF THE DISSERTATION

HABITAT INTERACTIONS STRUCTURING SONGBIRD COMMUNITIES ACROSS THE FOREST-URBAN ECOTONE

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Urban habitats vary greatly in the resources they provide for birds and other wildlife. Few species entirely avoid either human or forest habitats and for species that regularly utilize both, the two habitat types (forest and urban) may interact in complex ways to shape the animal communities at the forest-urban ecotone. I studied habitat relations to songbird community structure across the urban-forest edge in a heavily urbanized watershed in the New York metropolitan region. My research was designed to provide specific knowledge about the natural and human-built habitat components that maintain avian richness and abundance. I found that mature, intact forests with large trees and greater vertical complexity were the most valuable to birds breeding in and migrating through urban forests. Also, shrubby habitats along forest edges bolstered bird richness because they provide habitat for specialized shrub-nesting species. In my study, urban forests of a broad range of sizes and habitat conditions were associated with increased bird diversity in adjacent human habitats up to at least 0.2 Km from their edges.

A high density of large trees in the urban matrix was related to increased avian richness outside the forest in urban neighborhoods. Also, a high density of large trees in the urban matrix was associated with higher richness and abundance of breeding and migrating birds inside adjacent forests. Because residential areas have the highest density as well as variety of large trees relative to other types of urban land use, they also contain the greatest richness of birds.

This study demonstrates that local habitat is very important in structuring the bird community both inside forests as well as in the urban matrix but adjacent habitat also affects bird community structure. Forest area and isolation are relatively unimportant in shaping bird communities at the forest-urban ecotone. These findings suggest a wide-range of conservation practices, including forest preservation, management of shrubby edges, and planting and caring for a variety of long-lived trees in urban neighborhoods, that would maintain a rich bird community in urban regions.

DEDICATION

To my parents, Robert and Mary MacDonald,
and my son, Gavin

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INTRODUCTION

Humans are having a tremendous impact on ecological processes (Vitousek 1997). Urbanization is one type of human activity that has received a lot of attention among ecologists and conservationists; its effects on plant and animal communities, especially birds, have been well documented (Marzluff 2001; Valiela and Martinetto 2007). Urbanization is linked to a general decline in biological diversity and increasing biotic homogenization whereby many native species are lost but a few, often exotic, species remain (McKinney and Lockwood 1999). Also, urbanization patterns and its effects are of concern because of an increase in per capita land consumption associated with development in rural areas away from city centers (i.e., urban sprawl; Burchell et al. 1998) and also a world-wide trend of urban immigration and expansion (United Nations 2006). Metropolitan regions of the northeastern United States are a heterogeneous mosaic of residential, commercial, industrial, recreational and other human-created habitat types along with remnants of forests and other natural habitats (Alberti et al. 2001; Cadenasso et al. 2007). These habitats vary greatly in the resources they provide for birds and other wildlife. We may be able to improve urban planning practices and management to better preserve biological diversity in areas undergoing urbanization as well as in heavily urbanized regions by studying which components of natural and built habitats are successfully support species diversity in an already-urbanized region.

I studied habitat relations to songbird community structure across forest-urban edges in a heavily urbanized watershed in the New York metropolitan region. My research was designed to provide specific knowledge about the natural and human-built habitat components that maintain a rich and abundant community of birds. I chose to study birds because they comprise a large proportion of the animal species in the region. Also, they are more likely to represent present land use conditions than other animal groups that are limited to movement on land. Perhaps most importantly, they are an accessible, charismatic component of urban biodiversity and a large portion of the public enjoys watching and feeding birds (U. S. Department of Interior et al. 2001).

My study is organized into the following three chapters, which each address the breeding birds in the urban matrix, in forests, and Neotropical migrants moving through forests, respectively:

1. Breeding songbirds in the urban matrix: Local land use and forest effects. I

related urban land use type and components of built habitat to richness and abundance of songbirds in the urban matrix. I explored whether urban forest reserves enhance richness and abundance of breeding songbirds in the adjacent urban matrix and how far that effect extends away from forests. The main hypotheses of Chapter 1 are as follows:

- a. Land use types vary in their effects on bird community structure due to underlying differences in habitat structure.

- b. Bird richness and density in urban areas adjacent to forests are higher than in urban areas away from forests.
- c. Characteristics of adjacent forest habitat as well as forest stand-level characteristics (e.g., forest area) also influence the bird community outside the forest but are not as important as characteristics of local land use.
- d. The effects of forest proximity, forest habitat and stand-level characteristics, and local urban land use vary in importance by species and guild.

By describing community-level patterns of bird richness and abundance as well as patterns at the guild- and species-level, potential mechanisms could be identified and appropriate conservation and management goals could be prescribed given the urban context.

2. Breeding songbirds in urban forests: forest habitat and adjacent land use effects.

I studied the effects of local forest habitat, stand-level features, and adjacent urban land use on breeding songbird communities in forests. The main hypotheses of Chapter 2 are as follows:

- a. Richness and abundance of the bird community in forests varies with land use along the forest edge due to direct and indirect effects of adjacent urban habitat.

- b. Local forest characteristics are more important than specific habitat characteristics outside the forest in determining richness and density of birds.
- c. The relationship of richness with land use varies when urban avoiders (species that rarely leave the forest) and urban exploiters (species that use forest and urban habitats) were compared. Urban avoiders should be less influenced by adjacent land use characteristics than urban exploiters because they are mainly affected indirectly by land use whereas urban exploiters in the forest may be influenced both directly and indirectly.
- d. Forest stand-level characteristics such as area, heterogeneity and forest habitat composition (i.e., % wetland) also affect richness and abundance because some forest species would not be found in smaller forests.

3. Urban forests as *en route* habitat for Neotropical migrants: Forest habitat and adjacent land use effects. I studied the effects of local forest habitat quality and adjacent urban land use on the community of migrating songbirds during spring of 2004.

The main hypotheses of Chapter 3 are as follows:

- a. Local forest habitat quality is most important in determining richness, abundance, and the presence of individual migrant species in forests because of its direct effects on the community.

- b. The importance of local habitat parameters does not vary much with the type of land use along the forest edge unless urban land use somehow alters the features of forest habitat that are most important in structuring the bird community.
- c. Forest stand-level characteristics, especially area and isolation from other forests, would have little effect on richness and abundance of birds.

Improving biological diversity in urban neighborhoods and opportunities to encounter charismatic components of diversity such as birds has direct benefits to human health, sense of well being, and child development (Rohde and Kendle 1994). Exposure to biological diversity in cities is linked to positive perceptions of environmental health within the urban population, which fosters both an appreciation for nature and the will to protect it (Turner et al. 2004). The United Nations (2006) reports that in 1950, 29% of the global population (732 million people) lived in urban areas. By 2030, 60% of the global population (4.9 billion people) will be urban dwellers. If we do not implement planning and management practices to preserve species diversity in urban regions, we risk having a majority of the human population living in biologically impoverished cities with little or no connection to natural, diverse ecosystems. With this in mind, conservation scientists need to be able to provide guidelines to policy-makers, landowners and other stakeholders as to how we can maintain biologically rich ecosystems in urban regions.

CHAPTER 1

Breeding songbirds in the urban matrix:

Local land use and forest effects

Abstract: Bird communities in built habitats in the urban matrix are potentially shaped by the local environment as well as adjacent natural areas. I studied the effects of forest proximity, forest characteristics and local (transect-level) habitat on songbird community structure in the urban matrix of a large, heavily urbanized watershed in the New York metropolitan region. I found that the structure of bird communities in the urban matrix was related to the local variety and density of large trees as well as proximity to forests. Avian richness and abundance was highest in residential areas and parks because of a wide variety and/or density of large trees and lowest in apartment complexes and commercial-industrial areas, which lack these traits. Among all land use types, areas at 0.025 and 0.2 Km of forest edge had a higher richness and abundance of birds than areas ≥ 350 meters from forests. Also, characteristics of adjacent forest habitat, especially a low density of ground and shrub vegetation, were positively associated with richness and abundance of birds outside the forest. This is likely due to forest areas in residential areas, where birds are richest because of high tree density, also having more open shrub layers along the edge. Forest area and other stand-level metrics had little detectable effect on bird communities outside the forest, which indicates that forests of a broad range of sizes and habitat composition are of value to birds in the urban matrix. Implications for local and regional conservation planning and habitat management to maintain bird diversity in urban regions are discussed.

Introduction

Metropolitan regions are a heterogeneous mosaic of residential, commercial, industrial, recreational and other human-created habitat types along with remnants of forests and other natural habitats (Alberti et al. 2001; Cadenasso et al. 2007). Urban habitats typically form the background landscape or urban matrix and natural habitats such as forests exist as patches or corridors embedded within (Forman 1995). Few species entirely avoid either human or forest habitats and for species that regularly utilize both, the two habitat types (forest and urban) may interact in complex ways to shape the bird community at the forest-urban boundary (Burgess and Sharpe 1981). Therefore, avian richness and abundance outside urban forests, within the urban matrix, is potentially affected by both local habitat as well as forests. The increase in variety and abundance of resources at the forest-urban boundary should allow for the persistence of some species in an otherwise lacking urban habitat and thereby enhance local bird richness and abundance in what amounts to a classic edge-effect (Odum 1971).

This study explores several questions about the importance of local- and larger-scale habitat features in maintaining bird diversity in urban landscapes. Specifically, does maintaining forest habitat in the urban landscape bolster avian richness and/or abundance outside the forest in man-made habitats? How far does this “forest effect” extend into the urban matrix? Do characteristics of the forest such as habitat composition and structure and forest area change this effect? How do forest characteristics compare in importance with the effects of local land use in shaping bird community structure?

There is ample evidence that local habitat characteristics, especially woody vegetation structure, are important in shaping bird communities in urban environments (Goldstein et al. 1986; Tzilkowski et al. 1986; DeGraaf and Wentworth 1986; Fernandez-Juricic 2000a; Fernandez-Juricic 2000, Hennings and Edge 2003, White et al. 2005, Donnelly and Marzluff 2006). Avian richness and abundance also vary when compared among gross land use types, which are usually defined as distinct points along a gradient from natural (e.g., forest) to most urban (e.g., city centers; Blair 1996, Clergeau et al. 1998, McDonnell and Pickett 1990). Along such gradients, bird richness generally decreases with increasing intensity of urbanization because many urban habitat types lack the resources needed by more specialized species (review in Marzluff 2001; Devictor et al. 2007). In other studies, overall bird diversity and abundance peak at the midpoint of a gradient between natural habitat and most developed (Blair 1996, Clergeau et al. 1998). At extreme levels of urbanization (i.e., city centers), composition and diversity of bird communities become very similar due to a pattern of native species loss and dominance of European Starling, House Sparrow, and Rock Dove (Clergeau 1998, Blair 1996, 2001, Bezzel 1985, McKinney and Lockwood 1999).

The urban matrix influences the bird community within urban forests, as demonstrated by studies showing a negative relationship between bird diversity and richness in natural areas with increasing adjacent urbanization (Rottenborn 1999; Tilghman 1987; Friesen et al. 1995; Lindsay et al. 2002; Donnelly and Marzluff 2004). While there have been many studies that related surrounding urban land use to bird community characteristics in urban forests, only a few studies have attempted to look at

how forests might in turn influence the structure of the bird community in the urban matrix. Melles et al. (2003) found that forest cover within a 500-meter radius of survey points increased the likelihood of finding many species in residential areas. DeGraaf and Wentworth (1986) found that abundance of insectivores in three residential areas was negatively correlated with distance to the edge of the nearest woodlot. In a similar study, Munyenyembe et al. (1989) studied the structure of suburban bird communities in relation to distance from remnant vegetation. They found that forest, woodland, and grassland species declined with increasing distance from habitat remnants. However, in another study looking at the scale at which adjacent habitats influence bird diversity, Clergeau et al. (2001) found that bird richness was not related to bird richness in adjacent landscapes at local and regional scales. Each of these studies also found a strong influence of local habitat characteristics on bird community structure.

To my knowledge, there have been no studies that controlled or replicated distance from forest in relation to avian richness and abundance. Furthermore, few studies have looked at subtle differences in habitat effects among urban land use types within the urban gradient. Using a large, heavily urbanized watershed in the New York metropolitan region, I explored whether urban forest reserves enhance richness and abundance of breeding songbirds in the adjacent urban matrix and how far that effect might extend. I hypothesized that bird richness and abundance in urban areas adjacent to forests should be higher than in urban areas away from forests. Also, urban land use types should vary in their effects on the bird community because of underlying differences in habitat structure. Furthermore, characteristics of adjacent forest habitat as

well as forest stand-level characteristics (e.g., forest area) should also influence the bird community outside the forest but not as much as characteristics of local land use. Finally, the effect of forest proximity, forest habitat and stand-level characteristics, and local land use should vary in importance by species and guild. By describing patterns of richness and abundance as well as patterns at the guild- and species-level, I could identify potential mechanisms and suggest appropriate conservation and management goals given the urban context.

Methods

Study Area: The Arthur Kill is a tidal strait and major deepwater shipping channel separating New Jersey from Staten Island, a borough of New York City (Figure 1). My study was limited to the portion of the watershed in New Jersey. The Arthur Kill and its six major tributaries drain an area of 337 km² (130 mi²) in Essex, Middlesex, and Union counties, NJ (Greiling 1993) in the Piedmont physiographic province. The mean population density among the 3 counties in the watershed is 1,775 people/Km² (4,597 people/ mi²), which is four times the state average and fifty-eight times the national average (U.S. Census Bureau 2000, <http://factfinder.census.gov>). The U.S. Census Bureau uses a minimum population density of about 386 people/km² (1,000 people/mi²) among its criteria for designating an area as urban.

The watershed contains approximately 4,395 ha. (10,860 acres) of forest, 1,136 ha. (2,808 acres) of which is forested wetland (New Jersey Department of Environmental Protection 2002). Various types of urban land use cover approximately 35,906 ha.

(88,722 acres). Forty-one percent of the watershed is used for single-family, two-family, and multi-family housing. Despite its reputation as a center of industry, only 18 percent of the land is in commercial or industrial use. Another six percent is recreational land, ballfields, and cemeteries, developed parks, and natural areas. The remainder falls into various categories including forest, open water, wetlands, and transportation corridors. Several cities, including Newark, Irvington, Orange, and Elizabeth are in the northern and eastern portion of the watershed. The western portions contain mainly single-family residential development. A few study sites fell just outside the southern boundary of the watershed.

I chose a sample of 21 hardwood forests that included most of the forests ≥ 6 ha in the watershed. Forests ranged in size from 6.02 ha. (14.87 acres) to 133.47 ha. (329.80 acres) with a mean of 46.87 ha. (115.81 acres, SD 97.91; Figure 1, Appendix A). All of the forests contained a significant deciduous forested wetland component (range 41% to 100% of total area). These and other forests in northeastern New Jersey are extremely variable hydrologically in large part due to historical alterations via ditching and draining activities (Ehrenfeld et al. 2003). The dominant tree species in the forested wetlands are red maple (*Acer rubrum* L.), pin oak (*Quercus palustris* L.), and sweetgum (*Liquidambar styraciflua* L.). Common shrubs are arrowwood viburnum (*Viburnum dentatum* L.), spicebush (*Lindera benzoin* L.), and sweet pepperbush (*Clethra alnifolia* L.). See Ehrenfeld (2005) for a detailed botanical description of forested wetlands in the region.

I placed a total of 167 transects parallel to forest edges at approximately 25 meters ($n=37$) and 200 meters ($n=33$) and at ≥ 350 meters (and up to ~ 4 Km; $n=97$) from forest ($n=97$) within the urban matrix (Figure 2; Appendix B). Transects at 25 and 200 meters from forest were not randomly placed because they were chosen based on particular forest sites and land use types. However, the transects located ≥ 350 meters from forests were randomly selected with the only criteria that those < 350 meters from a forest were not included. Most large forests had transects along 2 edges when it was possible to locate transects > 200 meters apart along noncontiguous edges (Appendix A). Because local vegetation and bird communities vary greatly within the same forest (Inman et al. 2002, Sallabanks et al. 2000) I felt that this did not constitute pseudoreplication. Thirty-three transects located 25 meters outside the forest in the urban matrix were paired with transects 25 meters inside the adjacent forest edge. Each transect was categorized into one of four land use categories based on the dominant land use type (apartment and condominium, hereinafter apartment, $n=21$; commercial-industrial, $n=36$; park, $n=16$; and one- or two-family residential, hereinafter residential, $n=94$; Appendix B). A few transects randomly located ≥ 350 meters from forest contained mixed land use. In these cases, land use was categorized as the type covering $>50\%$ of the transect length. A transect length of 161 meters was used because the use of a car odometer greatly aided in rapidly locating transects in urban land types (a distance of 0.1 mile on the odometer corresponds to 161 meters). The accuracy of this method for determining transect length was verified by pacing the length of several transects.

Avian Surveys: Transects were walked at a slow, even pace and all birds seen and heard within approximately 25 meters on either side and 25 meters past the end points were identified and counted (Bibby et al. 1992). A total transect width of 50 meters represents the approximate distance between houses on opposite sides of typical suburban streets in the study area. Backyards were likely under-sampled in residential areas because in many cases buildings obscured visual sightings and observations were made using songs and calls of birds. Surveys were conducted from sunrise to 9 am on days without precipitation or high winds from 25 May to 15 July. Birds that flew over the transect area were noted but not counted unless they took off or landed within 25 meters. Transects were sampled only once in 2002 and repeated 2-3 times in 2003 and 2004, respectively.

Habitat Structure and Composition: Because of the large number of environmental variables that could potentially affect bird community structure, I attempted to develop methods that would allow me to rapidly sample aspects of the forest and urban environment that have been related to bird parameters in other studies. Local (i.e., transect survey area), urban habitat variables were measured along all transects at 25 (n=35) and 200 meters (n=29) from the forest and along a sample of 74 transects ≥ 350 meters from forest (Appendix C). Percent cover of tree canopy, lawn, building, and paved surface were estimated along each urban transect using 4X6 inch photographs taken at each end of the transect. I counted the number of cells (1 in^2) in a grid that were filled at least >50% by a particular cover type. In order to increase the effectiveness of this technique in describing the amount of lawn cover, I made an additional count of cells occupied by any amount of lawn. Counts were made of coniferous and deciduous shrubs

(height <3 meters), trees in the 3-10-meter height range (small), and the ≥ 11 -meter height (large) categories along the entire transect length. Trees were identified to species. The number of pedestrians (including cyclists), automobiles (including motorcycles) and trucks (including buses) were counted for intervals of 3 minutes at the conclusion of each bird survey along transects in 2003 only and an average (#/minute) was calculated for each category.

Along transects at 25 meters into the adjacent forest, I measured various aspects of habitat structure and composition as well as human disturbance (Appendix D). The number of ditch, stream, snag, trail, garbage, and standing water encounters were recorded while walking the entire transect length. In addition, 0.5m^2 plots were set up at 20-meter intervals along transects. At each plot, foliage density at the shrub and ground layers was measured using the distance it took for 50% of a board (black and white check pattern) to be obscured by foliage using modified methods of Bibby et al. (1992) and MacArthur and MacArthur (1961). Observations were made by a stationary person at each plot as a second person walked slowly away with the board held at heights of 0.5 m, 1.0 m, and 2.0 m toward the edge and toward the center of the site, respectively. Percentage cover of tree canopy was determined by looking straight up and down with a spotting tube (James and Shugart 1970). Leaf litter depth was measured at 3 random locations within the plot. Diameters at breast height (d.b.h.) of the 4 nearest trees with a circumference ≥ 20 cm were measured, distance from center of plot to tree measured, and species recorded (Cottam and Curtis 1956). These metrics were used to generate mean d.b.h. and mean distance from transect to large trees (a proxy for tree density). A transect

was assigned a dominant tree species (i.e., species with the highest relative abundance), and the proportion of the five most common tree species (from all forest sites) was calculated for each transect. Tree species richness was measured as an overall number of species and as the number of exotic tree species. Species comprising $\geq 10\%$ of the shrub layer (within a 10m^2 plot) and ground vegetation (within 0.5m^2 plot) were recorded (Ralph et al. 1993). Overall species richness of shrub and herbaceous plants as well as richness of exotic species in each category were calculated. At the center point in each plot, I recorded visibility beyond the forest edge.

At the forest stand-level, I calculated total area, number of patches representing different types of forest and wetland, and percent wetland using 2002 land use-land cover data obtained from New Jersey Department of Environmental Protection (New Jersey Department of Environmental Protection 2002).

Data Analysis: I limited the study to Passeriformes (perching birds), Columbiformes (pigeons and doves) and Piciformes (woodpeckers) because these groups comprise typical members of the songbird community along the forest-urban boundary. Birds observed outside the dates during which they could be assumed to be breeding in New Jersey were excluded from subsequent analyses (Walsh, 1993). Species present at $< 5\%$ of the urban transects were removed from guild- and species-level analyses but retained in the measure of overall richness and abundance (Table 1).

I calculated species richness of birds (number of species) and mean daily abundance of birds (number of individuals) by combining all observations in a year. I assigned species to a nesting location guild based on Ehrlich et al. (1988; Table 1). Nesting location guilds included deciduous tree-nesters, shrub-nesters, snag-nesters, conifer-nesters, ground-nesters and building-nesters. The building-nester guild was comprised of European Starling, House Sparrow, and Rock Dove, all of which are exotic species in North America that tend to nest on man-made structures in urban areas (Melles et al. 2003). I calculated number of species (richness) in each guild. I did not include a diet guild in the analyses because most of the species feed heavily on insects during the breeding season (Stiles 1980).

Alpha was set at 0.05 for individual analyses. Where I performed multiple iterations of a similar test (e.g., analysis of variance, regressions), I adjusted the α -level to a “table-wide” α -level using the sequential Bonferonni method (Rice 1989). This accounted for the group-wide increase in the type I error rate with simultaneous-inference tests. All statistical analyses were completed using Statistical Package for the Social Sciences (SPSS 14.0, 2005) with the exception of Canonical Correspondence Analysis (CCA), which was done using PC-ORD ver. 5.07 (McCune and Mefford 1999). In some cases, data were transformed in order to meet the basic assumptions of normality and equal variance inherent in many parametric tests.

Land Use and Forest Proximity: I tested the effects of forest proximity and land use on community- and guild-level metrics using analysis of variance (ANOVA) with forest

proximity and land use as main effects and species richness, mean daily abundance, and number of species in each nesting guild as response variables. Because transects located 25 meters and 200 meters from the forest were not independent of one another, they were each compared with the random transects located ≥ 350 meters from the forest in separate ANOVAs. This allowed for investigation into whether forest effects existed at 25 meters from the forest as well as whether they extended at least up to 200 meters. *Post hoc* tests were used to determine which levels of significant main effects and interactions were different in general linear models. Hochberg's GT2 was the method used for comparisons among main effects because it is robust to differences in sample sizes among treatments (Sokal and Rohlf 1981).

Following the methods of Donnelly and Marzluff (2004), I ran a second iteration of each GLM on bird parameters that included only the 200 and ≥ 350 meter transects with land use as the main effect. I included habitat parameters such as vegetation and components of the built environment as covariates in models. If the inclusion of a habitat covariate in a model removed the significance of a main effect, I concluded that the covariate was a potential mechanism by which the main effect was influencing the bird community.

CCA is a constrained ordination technique that selects the best linear combinations (i.e., best weights) of environmental variables that maximize the dispersion of species scores (Jongman et al. 1995). I employed CCA to describe patterns in mean daily abundance of individual species in terms of patterns in environmental variables

measured along urban transects at 200 and ≥ 350 meters away from forest. In each analysis, I excluded species that were present at < 3 transects. Data were standardized to a mean of zero and unit variance before being entered into the analyses. I described major local, urban influences on bird community patterns and its relationship to land use by focussing on transects located 200 and ≥ 350 meters from forest. The analysis produced 3 axes, with Axis 1 describing the largest variance in bird abundance, Axis 2 describing the next largest amount while remaining uncorrelated with Axis 1, and so on. The amount of variance explained by each of the 3 axes and overall variance was used to determine the strength of the species-environment relationship in each analysis.

Biplots of species scores on canonical Axes 1 and 2 were used to visually explore patterns in species abundance in relation to important urban habitat characteristics. I tested whether transect scores on the 3 axes could predict overall richness and abundance of birds using stepwise regression analysis. At each step in the analyses, an F-statistic was calculated for each variable in the model. Variables having $p < 0.05$ were allowed to enter models and variables were removed if their significance level became $p < 0.10$ as other variables were entered into the model (Rodewald and Matthews 2005).

In a separate biplot based on the same species-environment data, I plotted transects coded for land use type to explore how land use type is related to bird-habitat patterns. I used multivariate analysis of variance (MANOVA) with land use type as main factors and transect scores on each axis as response variables to see how well land use was related to the axes.

Finally, in order to determine which species were making the largest contribution to higher richness and the relative effects of land use, distance and land use *distance, I entered all of the species mean daily abundance data into a MANOVA. I also ran *a posteriori* univariate ANOVAs for each of the main effects. Post hoc comparisons among groups were made using Hochberg's GT2 (land use) and multiple comparisons (distance, Bonferonni adjusted).

Bird-habitat relations at the forest-urban boundary: In a second set of analyses, I determined whether bird community patterns on the urban side of the boundary were most influenced by local urban parameters, adjacent forest and/or stand-level parameters by focussing on transects 25 meters outside forest and 25 meters inside forest. Biplots of species scores on CCA Axes 1 and 2 from each analysis (Urban, Forest, Stand) and the amount of variance explained from each analysis were used to explore whether patterns in bird abundance were related local urban, adjacent forest, and/or stand-level variables. I also entered variables from each of the analyses with intra-set correlations ≥ 0.30 into a CCA representing combined local, adjacent and stand-level habitat. I related scores of individual transects on Urban, Forest, Stand, and Combined axes to overall bird richness and density, and to richness in each nesting guild using stepwise linear regressions.

Results

Forty-four species of birds within the focal taxa (Passeriformes, Columbiformes, and Piciformes) were found among all transects in the urban matrix and were used to calculate species richness, mean daily abundance and richness in each of the nesting guilds. Table 1 provides a breakdown of each species and the proportion of sites occupied depending on land use type and forest proximity, respectively. Twenty-nine of these species were present at $\geq 5\%$ of the transects and were used for guild- and species-level analyses (Table 1). The dominant nesting guilds in the urban matrix were deciduous tree nesters (45% of total species) and shrub nesters (21%; Table 1).

Species richness for all urban transects combined was lower in 2002 (mean=6.74) than in 2003 (mean=9.54; $t=-8.836$, $p<0.001$) and 2004 (mean=8.68; $t=-6.742$, $p<0.001$). Richness also differed between 2003 and 2004 ($t=2.2909$, $p=0.004$). I attributed the large difference between richness in 2002 and other years to differences in the number of times sampled among years and not to differences in species composition (birds were only sampled once in 2002). Therefore, I decided to combine transects into one overall measure of species richness but I standardized overall richness to what it would be if an equal number ($n=5$) of observations had been made for each transect. Mean daily abundance was higher in 2002 (mean=23.65) than in 2003 (mean=19.96) or 2004 (mean=20.26; $t=4.051$, $p<0.001$ and $t=3.538$, $p=0.001$, respectively) but did not differ between 2003 and 2004. Because the pattern in bird abundance in 2002 differed from

that in subsequent years, I combined daily abundances in 2003 and 2004 into one overall mean daily abundance and excluded 2002.

House Sparrow and European Starling were nearly ubiquitous in the urban matrix, occupying 98% and 97% of transects, respectively. Furthermore, they tended to exist in large numbers. In order to remove the effect of these species on overall abundance, they were removed from the overall metric of mean daily abundance. Richness and abundance of birds in each guild were highly correlated once House Sparrow and European Starling were removed (Pearson correlation from 0.627 to 0.870, all $p < 0.01$). In order to avoid redundancy in the analyses, species richness, not abundance, for each nesting guild was the only metric used in guild-level analyses. Richness of conifer-nesters and ground-nesters and nest parasites were not analyzed because each included only one or two species once the rare species were removed.

Land use effect on the bird community: Species richness, the richness of all nesting guilds except building nesters, and mean daily abundance varied with land use type (Table 2, Fig. 3). Mean daily abundance in residential areas was higher than in commercial-industrial and apartment areas. Parks and residential areas had a higher overall bird richness and richness of snag-nesters than apartments and commercial-industrial areas (Table 2; Fig. 3 and Fig. 4c). Residential areas had more deciduous-nesting species than commercial-industrial areas and apartments and more shrub-nesting species than all other land use types (Fig. 4a and 4b). The richness of building nesters did not differ among land use types (Fig 4d).

The association of land use with species richness and abundance was largely explained by underlying differences in vegetation structure, in particular the number of large deciduous and coniferous trees, the amount of building cover, and disturbance by people (Table 3; Appendix C). Number and variety of large, deciduous trees were particularly important correlates of species richness (Figure 5). The relationships between land use and deciduous tree-nesting birds and shrub-nesters were not significant when models for these guilds included one or more environmental covariates, especially richness and density of large deciduous trees. However, land use type remained important in models of overall richness and abundance of birds and the richness of snag-nesters even when specific habitat characteristics affecting these metrics were included as covariates in the models probably because other factors that are potentially associated with land use, e.g., predation and competition, noise, etc. were not measured.

CCA of species-environment data from transects 200 and ≥ 350 meters away from the forest showed that environmental variables explained 25% of the variance in the species data (Table 4). A biplot of species scores on axes 1 and 2 was used to explore underlying patterns in species distribution (Figure 6a). The vectors represent the importance of each environmental variable (length of arrow) and its correlation with other variables and axes (angle between variables and axes, respectively; Jongman et al. 1995). Axis 1 represents a gradient of urban intensity with high tree cover and low built cover on the low end and high built cover low tree cover on the high end. Axis 2 represents a gradient of high lawn cover at the low end to high paved cover at the high

end. The location of individual species relative to the arrows and the axes reveals which factors are most influencing the abundance of that species. Most bird species in guilds other than building-nesters fall on the end representing lower urban intensity. Transect scores on Axis 1 were highly associated with species richness ($R^2=0.61$, $p<0.001$; Figure 7) and mean daily abundance ($R^2=0.34$, $p<0.001$). This means that both richness and abundance decreased with urbanization intensity.

In a second biplot comprised of the same environmental variables and bird species data, individual transects were plotted by land use type (Figure 6b). Along the urban gradient axis (Axis 1), residential areas fall out at the low development extreme and commercial-industrial areas fall out at the higher end. Apartments are located in the center (mean) for this axis. On Axis 2, parks form a cluster at the low end representing high lawn cover. The scores of transects on Axis 1 and Axis 2 were related to land use type ($F=12.095$, 3 df, $p<0.001$; $F=44.076$, 3 df, $p<0.001$, respectively). When the two biplots (Figures 6a and 6b) are compared, it is clear that the majority of birds are more abundant (i.e., more likely to be present) in residential areas, similar to the findings from the ANOVA of land use type (Tables 2 and 3). Residential areas have a high density and richness of large deciduous trees, which are features that favor higher richness of birds in the urban matrix.

Forest proximity effects on the bird community: Overall richness and abundance of birds and the richness of deciduous tree- and shrub-nesters were higher at transects located 25 meters from the edge of forests than at transects located ≥ 350 meters from the

forest edge (Table 2; Figure 3). Overall species richness and the richness of deciduous tree- nesters remained higher at transects located at 200 meters from the edge compared to ≥ 350 meters from edge (Table 2). However, abundance and richness of shrub-nesters did not remain higher at 200 meters than at ≥ 350 meters from forests, indicating the affinity of this guild for habitat along forest edges. Snag-nester richness was not affected by forest proximity. Richness of building-nesters was negatively associated with forest proximity when transects at 25 meters from forest were compared with those ≥ 350 meters away. The influence of forest on overall richness and the richness of deciduous tree-nesters remained significant even when large deciduous trees were included as covariates in models (Table 3). This suggests that even when highly suitable habitat is present in the urban matrix (i.e., many large trees), the positive benefits of forest habitat on species richness is not completely replaced.

Distance from forest was potentially confounded with the amount of built cover on Axis 1 of the CCA for transects located 200 and ≥ 350 meters from forests as denoted by the small angle between their vectors in the biplot (Figure 6b). This was likely due to the influence of several transects in the ≥ 350 meter group that represented the *extreme* of urbanization (i.e., highly built-up city centers), which is a land use type not usually found immediately adjacent to forests. In order to test whether the forest effect was “real” and not just due to the inclusion of these extreme transects in the sample ≥ 350 meters from forests, I removed 19 transects that contained high levels of built cover not comparable to those found adjacent to forests (i.e., mean number of cells containing built cover > 2). I then used the remaining transects at the low to mid-level of urban intensity to see if forest

proximity was still related to increased richness and abundance. I used GLM with distance (200 vs. ≥ 350 meters from edge) and land use as main effects, and richness and mean daily abundance as response variables, respectively. Distance remained a significant factor in both the model of species richness ($F=15.463$, 1 df, $p<0.001$) and mean daily abundance ($F=7.145$, 1 df, $p<0.009$). Land use also remained important in richness and abundance models ($F=18.232$, 3 df, $p<0.001$; $F=7.615$, 3 df, $p<0.001$, respectively).

Species-level relationships to land use and forest proximity: Land use, distance from forest, and the interaction of land use and distance were all related to mean daily abundance patterns among individual species (Wilks' $\lambda=0.168$, $F=2.705$, 87 df, $p<0.001$; Wilks' $\lambda=0.557$, $F=2.633$, df=29, $p<0.001$; Wilks' $\lambda=0.358$, $F=1.357$, 87 df, $p<0.05$, respectively). Seventeen species had significant associations with land use; sixteen of which were predominantly higher in park or residential areas (Table 5). Eight species were higher near forest (Rock Dove is the only species lower near forest). Four species abundances were related to the interaction of land use and distance (i.e., the slope of the relationship to land use was dependent on the proximity of forest and vice versa). Hairy Woodpecker and Yellow Warbler were found almost exclusively at transects 25 and 200 meters from forests as compared to those farther away (Table 1). In addition, all of the rare species that were excluded from the species and guild-level analyses were found predominantly along transects immediately adjacent to forests as well as a small proportion of those 200 meters from the forest (Table 1). Most of the rare species found along urban transects are either forest-associates (e.g., Eastern

Wood-pewee, Wood Thrush) or edge habitat specialists (Yellow Warbler, Indigo Bunting).

Bird-habitat relations at the forest-urban boundary: CCA of species-environment data at transects 25 meters outside the forest and data from adjacent forests, where the effects of forest and urban habitat would be expected to be strongest, showed that urban habitat features as well as some features of adjacent forest were important in structuring the bird community (Figure 8; Appendices C and D). Urban and Forest axes explained a much larger % variance (~26%, respectively; all axes combined) than the Stand-level axes (~10%; Table 6). I focus on explaining the biological meaning of axes 1 and 2 in each analysis. Urban Axis 1 represented the reverse of the urban intensity gradient seen in Axis 1 from the CCA of transects 200 and >350 meters from the forest. On this axis high built cover, low tree cover (high urban intensity) is at the lower end and high tree cover with low building cover (low urban intensity) is at the high end. Urban Axis 2 is a gradient of increasing tree richness, shrub density, large conifer density and lawn cover (a gradient of vegetation richness). Forest Axis 1 is a gradient of increasing shrub and ground layer density and increasing richness of exotic plants. Forest Axis 2 is a plant richness gradient with areas of bare ground and low richness of exotics on the low end and deep leaf litter with a higher herbaceous plant cover and high richness of exotic plants on the high end. Stand Axis 1 is a gradient of decreasing area and wetland cover. Stand Axis 2 is a gradient of increasing isolation.

When the important variables (i.e., those with ≥ 0.30 intra-set correlation) from each analysis (Urban, Forest, Stand) were simultaneously entered into a CCA of combined

habitat variables, several Urban and Forest variables remained important on Combined axes 1 and 2 (Table 6; Fig 8a). The three Combined CCA axes explained 31.5% of the variance in species abundance. Combined Axis 1 is an urban intensity-understory density gradient, with high building cover and few trees in adjacent urban areas and a dense ground and shrub layer in forests at the low end, and low building cover, many large trees in adjacent urban habitats and a more open ground and shrub layer with a high richness of exotic plants in forests at the high end. Combined Axis 2 is dominated by mainly urban parameters and represents a gradient of vegetation richness. High shrub cover, tree richness, large conifer density and lawn cover are at the low end and decrease along the gradient. Stand-level variables were only included in Combined Axis 3.

In the bi-plot of Combined Axes 1 and 2, it appears that most of the deciduous-nesting species clustered around points on the end of Combined Axis 1 that represented an open ground and shrub layer and high exotic plant richness in the forest with large street trees and low building cover (Figure 8a). This group also seemed to cluster in the area of Combined Axis 2 that represented high richness of street trees, high densities of shrubs and large conifers, and high lawn cover. However, the MANOVA comparing scores of deciduous-nesting species to all other species on axes from all levels of analysis did not result in a significant difference between deciduous tree-nesting species and all other species ($p > 0.05$).

Finally, when I entered transect scores on axes 1, 2, and 3 from each CCA analysis (Urban, Forest, Stand, Combined) into stepwise regressions to test the relative importance

of local urban, adjacent forest and stand-level variables on overall richness and abundance and the richness of individual nesting guilds, several patterns were evident (Tables 7 and 8). Urban Axis 1 and Combined Axis 1 were related to species richness. Combined Axis 2 and Urban Axis 2 were related to mean daily abundance. Deciduous tree-nester richness was related to Urban Axis 2, shrub-nesters were related positively to Combined Axis 1, and snag-nesters were related to Urban Axis 1 and Combined Axis 1. Building-nesters were related to Combined Axis 1. In summary, most community and guild parameters are positively influenced by a combination of mainly local, urban habitat characteristics, especially those representing the low building/high tree cover end of the urban gradient. Overall abundance is an exception in that it is most heavily influenced by the urban gradient representing increased vegetation richness (associated with residential areas). Also, overall richness, shrub-nester richness, and snag-nester richness are associated with edge characteristics; they are richer in urban areas where there is a low shrub density in adjacent forests. Building-nesters are the only group that is associated with the built up-low tree cover end of the gradient where forest edges are closed and they are also associated with smaller forests.

Land use type affected the scores of transects on Combined axes 1 and 2 (Wilks' $\lambda=0.131$, $F=9.535$, 3 df, $p<0.001$). Parks had higher scores than apartment commercial-industrial transects on Combined Axis 1 ($F=6.751$, 3 df, $p=0.001$), which means that parks had more trees outside the forest and a more open ground and shrub layer along the edge than those land use types. Commercial-industrial transects had higher scores than residential and apartment and parks had higher scores than residential

transects on Combined Axis 2 ($F=18.009$, 3 df, $p<0.001$). This means that commercial-industrial areas and parks had lower cover of planted shrubs outside forests than the other land use types.

Discussion

Bird communities in the urban matrix are shaped by both local characteristics of land use as well as proximity to forests. The broad range of niche space associated with a high variety and density of large trees is the likely explanation for high richness and density near forests as well as in urban areas containing a lot of trees (i.e., residential areas and parks). Local, urban habitat was most important in predicting community-level and species abundance patterns outside the forest but characteristics of adjacent forest habitat, especially low density of the ground and shrub layer did contribute to higher richness in shrub-nesters outside the forest. This is likely because these species prefer residential areas, which other studies have shown to have lower shrub density at the edge (Cutway 2004). Another possibility that was not investigated here is that when shrub density is low in forests, some shrub-nesting species use adjacent urban areas with a lot of shrub cover for nesting. Forest area and other stand-level metrics had little detectable effect on bird communities outside the forest. It is also possible that size effects would have been detected had smaller forests (i.e., <14 ha.) been included in the study. Hundreds of forest patches in the watershed are under 10 ha. However, the lack of an effect of area and isolation coupled with the importance of local habitat attributes outside

the forest indicates that a rather broad range of forest sizes and forest habitat composition are of value to birds in the urban matrix.

Land Use: Richness and abundance of deciduous trees and/or their correlates (i.e., decreased built and lawn cover) are the habitat features most influencing patterns of richness and abundance of birds. Because richness and abundance of trees are highly correlated with each other (Pearson correlation=0.607, $p \leq 0.01$, Figure 5) it is difficult to tease apart which of these factors is directly affecting birds. It is possible that deciduous nesters respond more to richness while snag nesters respond more to number of trees. It is likely that the positive effect of richness and density of tall trees in urban habitats on the richness and abundance of birds is a result of increased food resources and nesting sites associated with increased complexity. Also, a higher richness of trees and the presence of certain tree species are correlated with a higher diversity of insects (Southwood 1961) and a greater spread in flowering and fruiting phenology. Cavity-nesting species may be absent or in low abundance locally because of a shortage of older trees with cavities or because of competition with European Starling and House Sparrow in more urban areas (Rottenborn 1999, Walcott 1974; Blewett and Marzluff 2005). However, Koenig (2003) did not find a negative effect of European Starling on native cavity-nesting birds.

Forest Proximity: The peak in overall bird richness immediately outside forests is partly due to the presence of species of birds that are forest specialists and only occasionally leave the forest (i.e., species present at <5% of the urban transects; Table 1).

While some area sensitive, forest songbirds have been shown to move extensively among forest patches others avoid crossing gaps (Desrochers and Hannon 1997; Norris and Stutchberry 2001; Fraser and Stutchberry 2003). Thus, not all species in the forest are found in urban areas adjacent to forests. Also, a few species that are able to utilize suitable urban habitats as well as forests were nonetheless found at significantly higher rates near forests (Table 1). This group included several species that are typically rare or absent in the urban matrix away from forests but are typical of forest and/or forest edge habitats (i.e., Hairy Woodpecker, Yellow Warbler, Carolina Wren). Blewett and Marzluff (2005) also found that Hairy Woodpecker is dependent upon a high amount of forest cover in suburban landscapes. The peak in bird abundance at the forest-urban boundary supports the explanation that birds are responding to the broader range and higher availability of nesting and foraging resources found at the intersection of forest and urban habitats than would otherwise be found in either habitat type alone; a well-documented ecological phenomenon known as the edge-effect (Odum 1971) or complementation and supplementation of habitat (Dunning et al. 1992).

In addition to providing nesting and food resources for birds in adjacent urban habitats, other potential mechanisms by which forest enhances richness of birds in the urban matrix may occur without the need for direct interaction between birds and forest habitat. Many birds will settle and develop home ranges and territories near their natal range (Sutherland et al. 2000). Therefore, the increase in bird richness near forests could be a result of individuals leaving source habitat in forests that is already occupied by

conspecifics and settling in adjacent urban habitat but not necessarily continuing to rely on the adjacent forest habitat (i.e., as part of its home range).

It is easy to assume that forests are providing resources to birds in an otherwise lacking urban matrix but urban habitats may also provide resources lacking in adjacent forests. For example, it appears that shrub-nesters may be more abundant in urban habitats with high densities of shrubs just outside forests when the forest contains a low density of herbaceous plants and shrubs. In addition, food resources such as bird feeders and other forms of supplemental feeding are responsible for increased richness and abundance of birds (Cicero 1989). Supplemental bird feeding may aid in overwinter survival of some species and in turn may have effects on population and community structure that spill over into the breeding season (Brittingham and Temple 1988).

A high density of birds does not always indicate that the habitat is of high quality (Van Horne 1983). If the adjacent urban habitat is marginal, it may be a sink for the bird population in adjacent forests that are contributing dispersing individuals to the habitat (Donovan et al. 1995). Also, nest predators and parasites may be at higher concentrations at forest edges and in forests bordered by suburbs so that birds attracted to these areas actually have lower fitness as compared to birds in areas away from forests (Wilcove 1985, Gates and Gysel 1978, Trine 1998; Chace et al. 2003; Marzluff et al. 2007). In fact, Blair (2004) demonstrated that nest predation is lower in more intensely urban areas. Survival of individuals and reproductive success were not studied here so I mention this to help qualify how my results should be interpreted.

Nonetheless, forests are increasing bird richness and abundance up to at least 0.2 Km from forests and this effect declines at some point after 0.2 Km. Munyenyembe et al. (1989) found that bird richness declined up to 0.2 Km from woodland edge and then continued to decline at a rapid rate up to 0.4 Km. Mean daily abundance declined rapidly up to 0.4 Km. I did not compare richness and abundance between the 25 meter and 200 meter matrices so I am unable to comment on the rate at which richness and abundance decline.

Both forest proximity and local land use characteristics structure bird communities in the urban matrix via differences in the amount and variety of mature trees available to birds. Although a high richness and abundance of trees in local urban habitats may override some of the negative effects associated with being far from forest, it will not totally replace the positive effect on bird richness and abundance found on the urban side of the forest-urban boundary. These findings agree with DeGraaf and Wentworth (1986) in that overall species richness and several individual species seem to benefit from naturally forested areas even when a lot of trees are present within the urban matrix.

Figure 1. Map of the Arthur Kill Watershed in New Jersey depicting the extent of forest cover in green. The red dots denote forests included in the study.

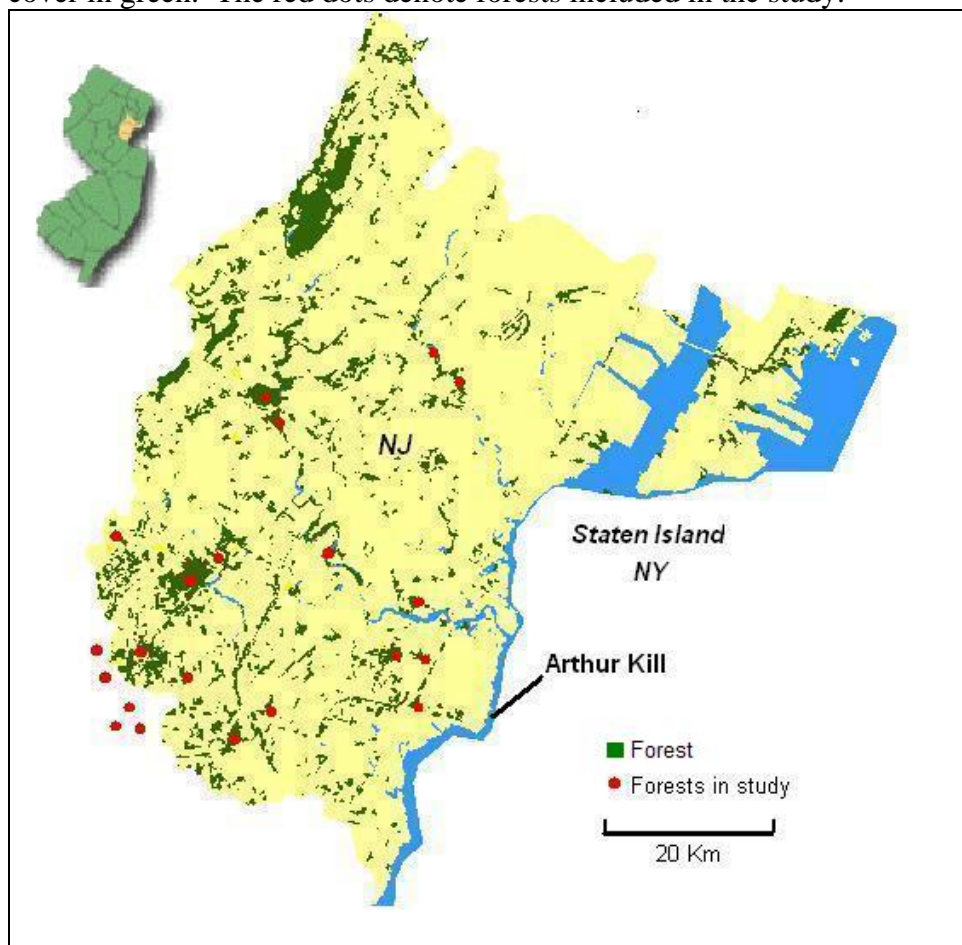


Figure 2. Diagram of transect locations in forests and adjacent urban land use relative to forest edge (picture not to scale).

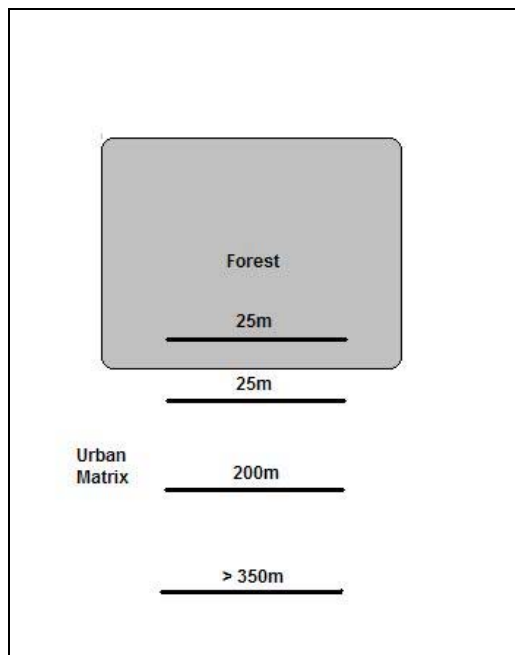


Figure 3. Mean species richness and mean daily abundance of birds (± 2 S.E.) in each land use type (a. and b.) and at each distance from forest edge (c. and d.). Error bars with the same letter above denote categories on each graph that are not different based on post hoc comparisons using Hochberg's GT2 ($p < 0.05$).

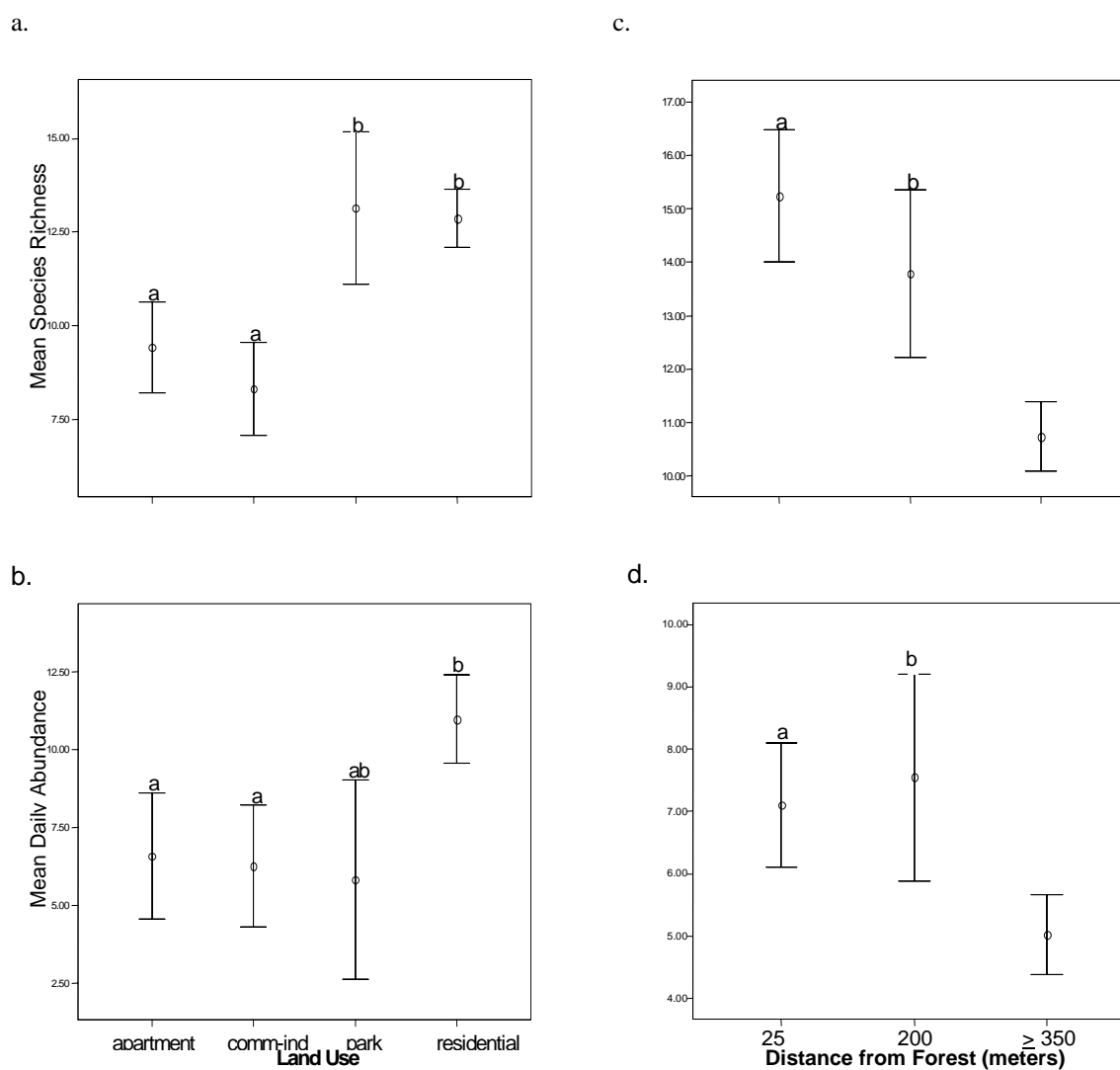
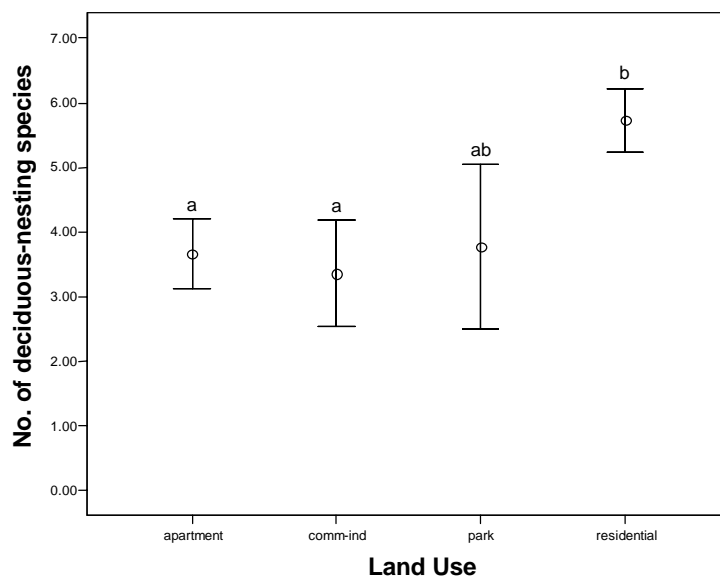


Figure 4 (a.-d.). Mean number of species (± 2 S.E.) in each nesting guild within each land use type. Error bars with the same letter above denote categories within each guild that are not different based on post hoc comparisons using Hochberg's GT2 ($p < 0.05$).

a.



b.

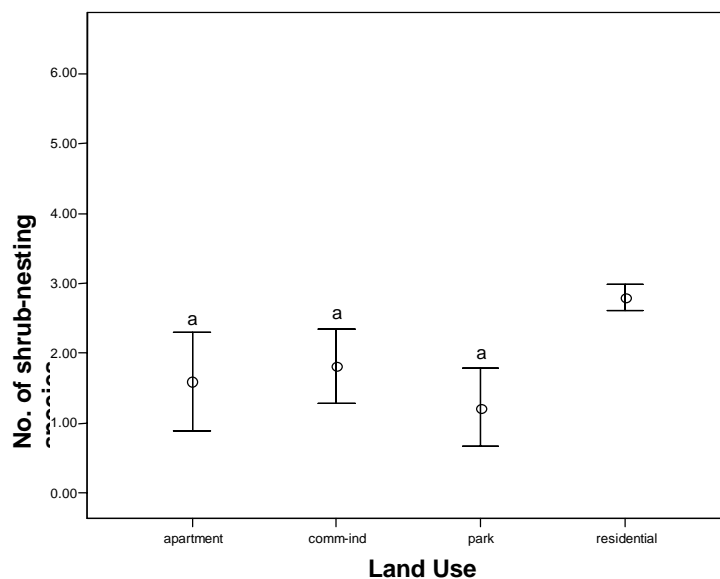
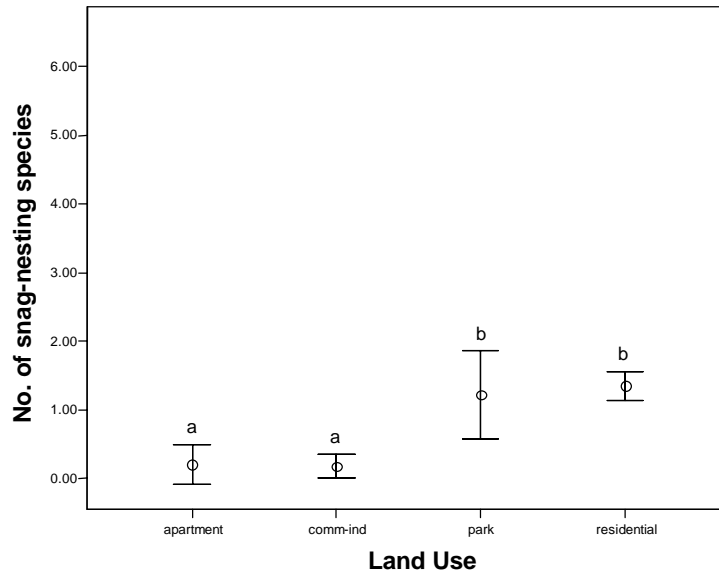


Figure 4, continued.

c.



d.

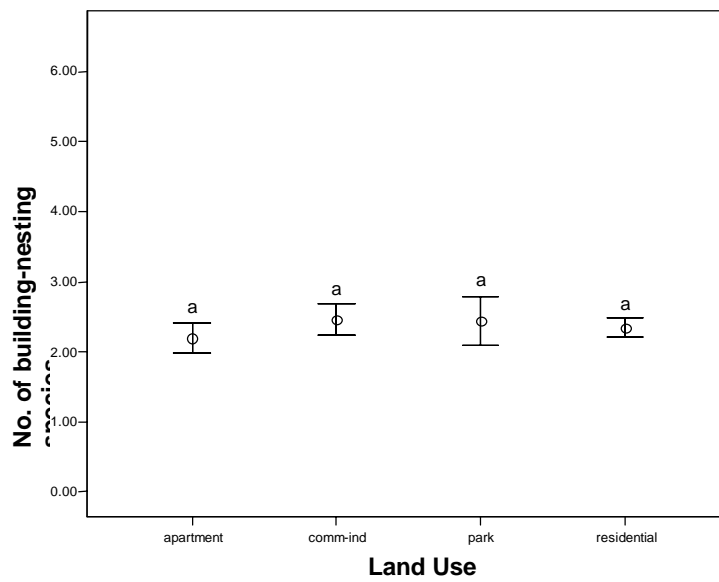


Figure 5. Relationship of bird richness to the richness and number of large trees along urban transects of different land use types (all transects).

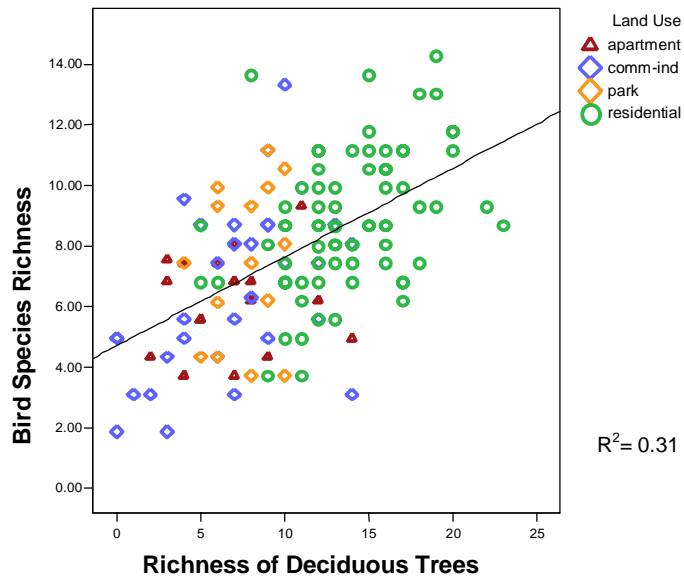
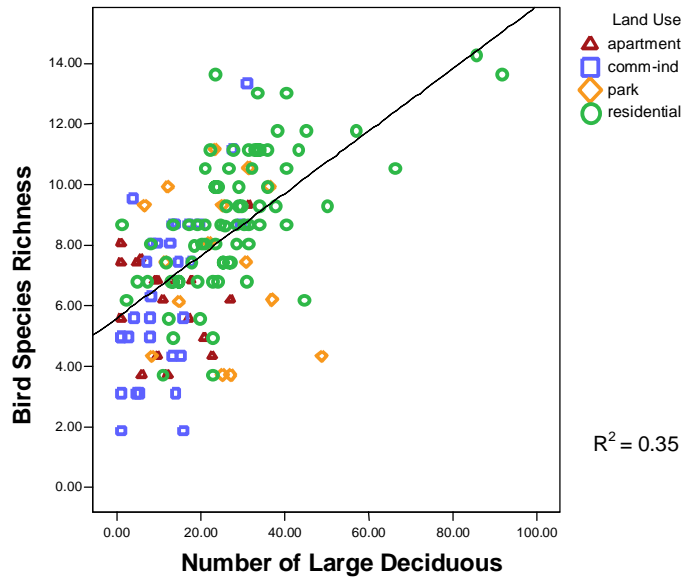


Figure 6. Bi-plot containing important environmental gradients from CCA of urban variables (at 200 and ≥ 350 meters from forest) related to structure in the bird community and species scores coded for nest location guild (a.) and transect scores coded for land use (b.). Nest location color codes: deciduous-tree-nesters (green), shrub-nesters (blue), snag-nesters (orange), and building-nesters (red).

a.

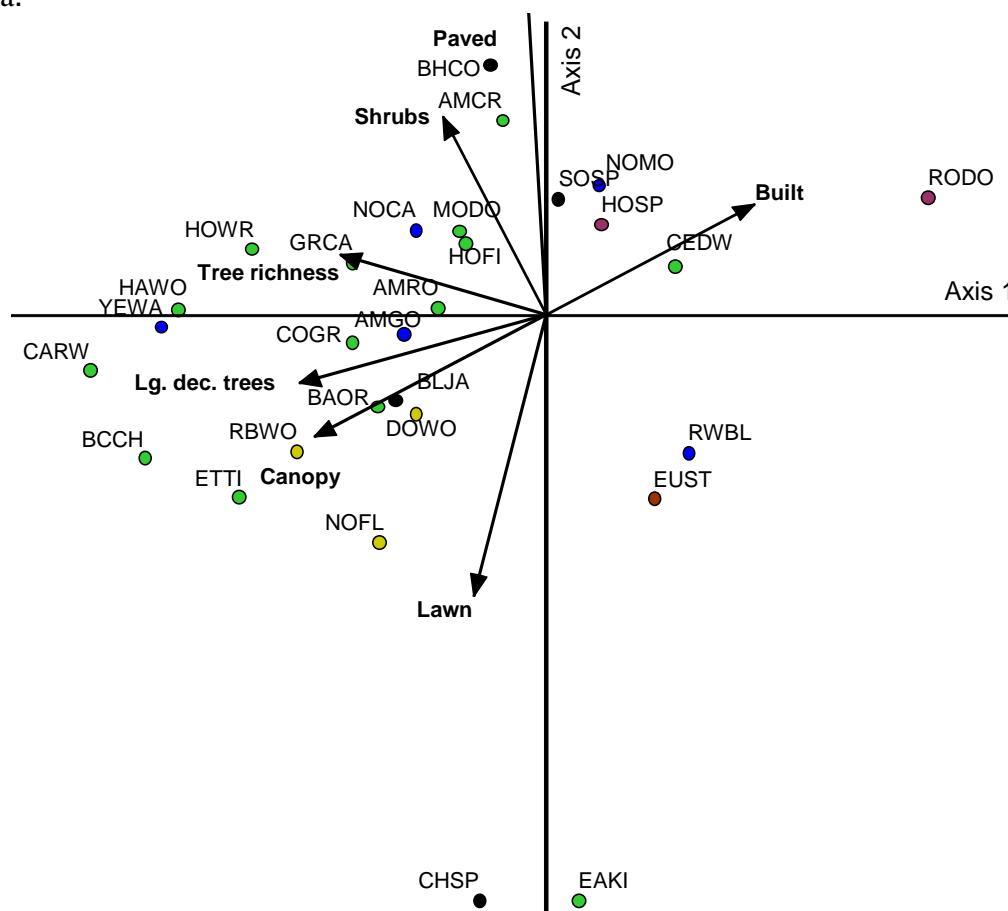


Figure 6, continued.

b.

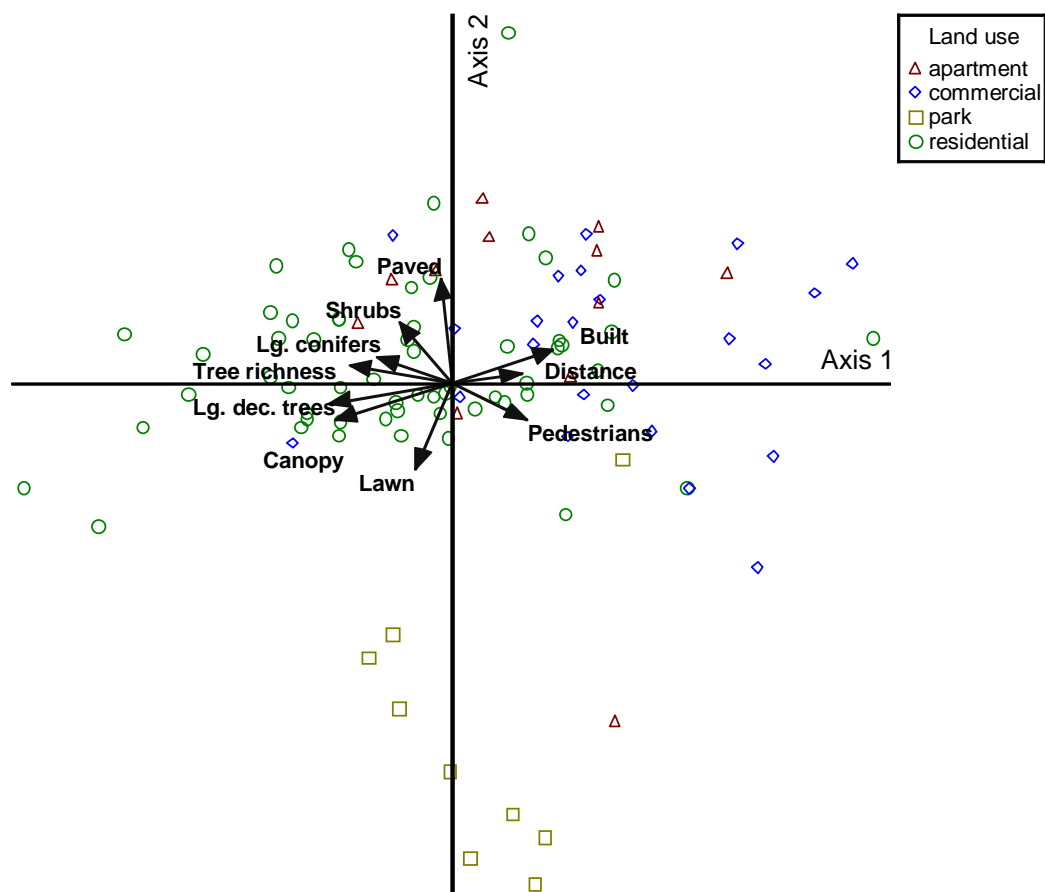
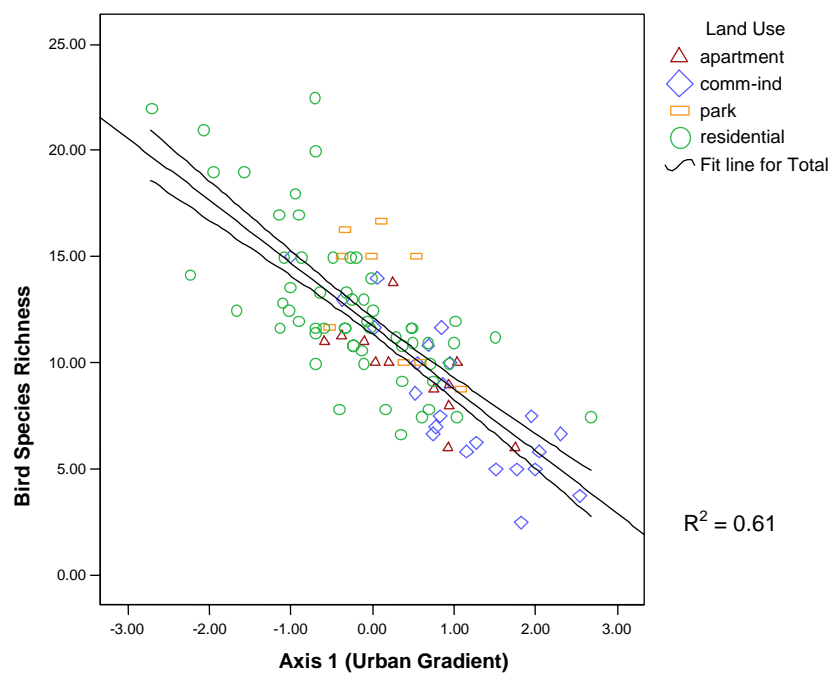


Figure 7. Relationship (mean and 95% confidence interval) of species richness (a) and mean daily abundance (b) of birds to CCA Axis 1, a gradient of increasing urban intensity, derived from species and environmental variables at 200 and ≥ 350 meters from forest.

a.



b.

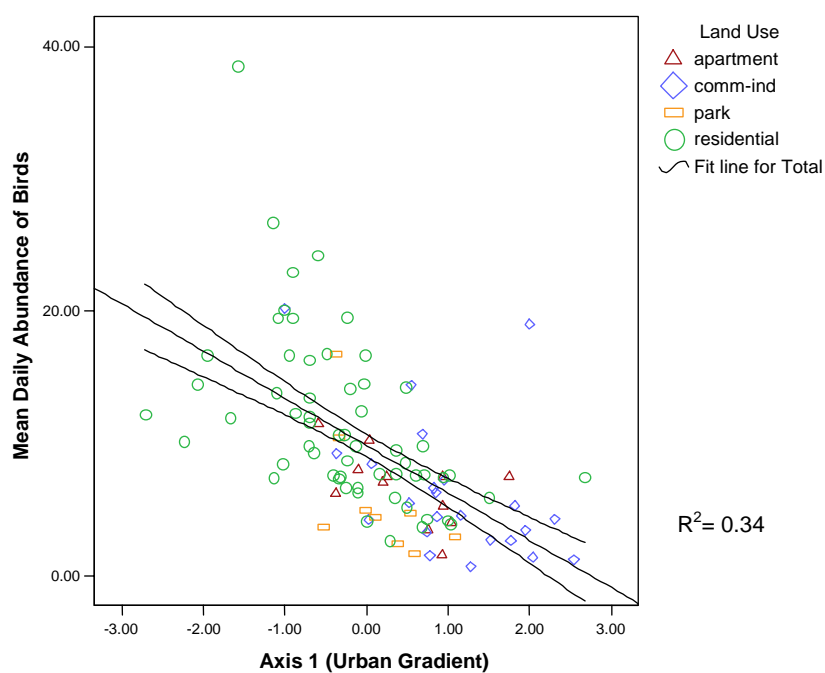


Figure 8. Bi-plot containing important environmental gradients from Combined Axis 1 of CCA of bird abundance and environmental variables (from 25 meters outside the forest and 25 meters inside the forest) related to structure in the bird community and species scores coded for nest location guild (a.) and transect scores coded for land use (b.). Nest location color codes: deciduous-tree-nesters (green), shrub-nesters (blue), snag-nesters (orange), and building-nesters (red).

a.

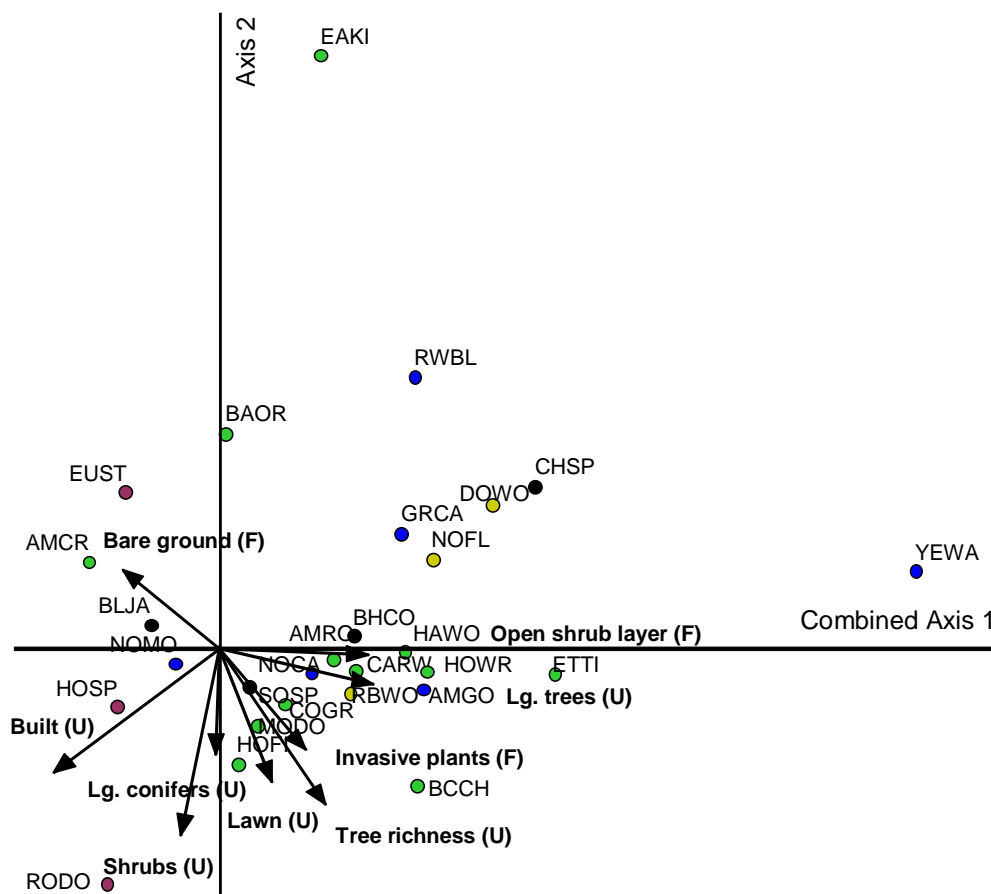


Figure 8, continued.

b.

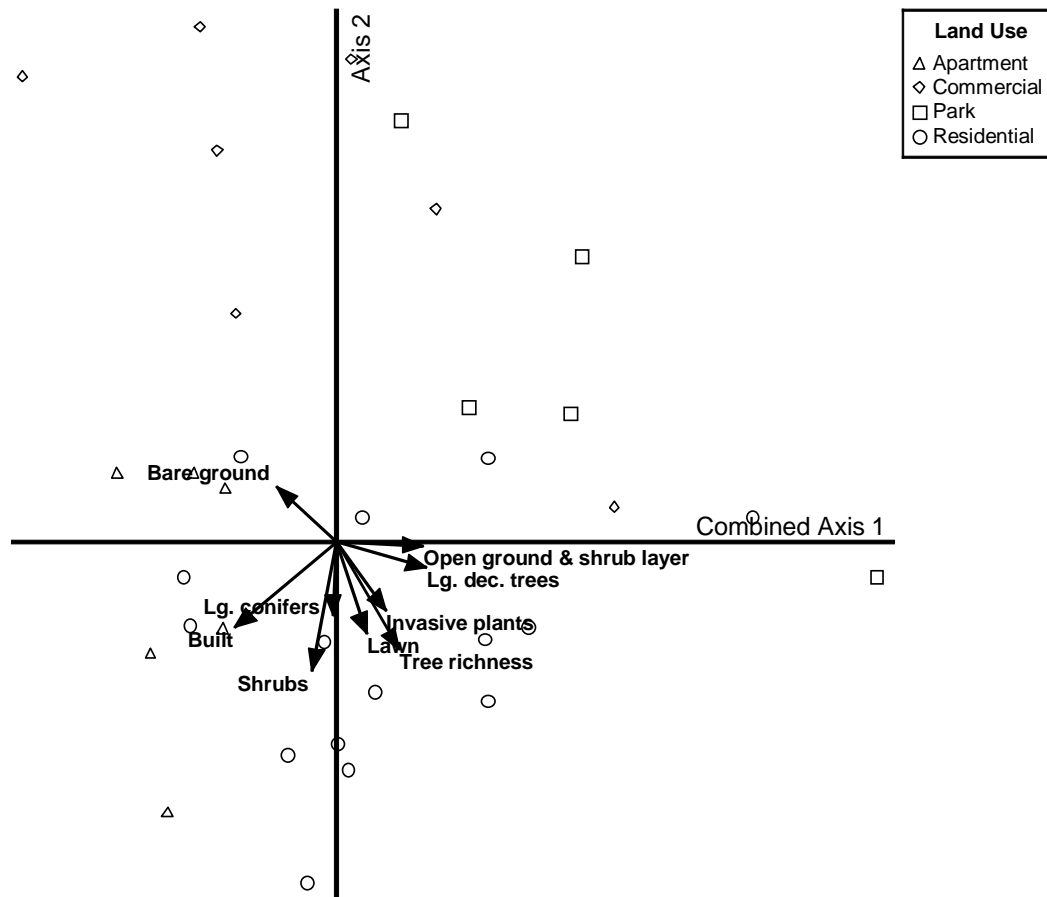


Table 1. Common and Latin name and alpha code of species found in the study. Species are organized into guilds by nesting substrate. Proportion of transects occupied by land use type and at increasing distance from forest for each species are given.

Species by Nesting Guild	Alpha code	Proportion of transects occupied (land use type)				Proportion of transects occupied (meters from forest)		
		residential	park	apartment	comm-industrial	25	200	≥350
Deciduous tree-nesters								
Hairy Woodpecker <i>Picoides villosus</i>	HAWO	0.17	0.19	0.05	0.08	0.32	0.24	0.03
Great-crested Flycatcher <i>Myiarchus crinitus</i> *	GCFL	0.03	0.06	0.00	0.00	0.05	0.03	0.01
Eastern Wood-pewee <i>Contopus virens</i> *	EAWP	0.01	0.31	0.00	0.03	0.14	0.03	0.01
Eastern Kingbird <i>Tyrannus tyrannus</i>	EAKI	0.04	0.25	0.00	0.17	0.11	0.12	0.06
Warbling Vireo <i>Vireo gilvus</i> *	WAVI	0.01	0.13	0.00	0.00	0.05	0.00	0.01
Yellow-throated Vireo <i>Vireo flavifrons</i> *	YTVI	0.00	0.06	0.00	0.00	0.03	0.00	0.00
American Crow <i>Corvus brachyrhynchos</i>	AMCR	0.15	0.06	0.10	0.14	0.19	0.06	0.13
Black-capped Chickadee <i>Poecile atricapilla</i>	BCCH	0.30	0.06	0.10	0.06	0.22	0.27	0.16
Eastern Tufted Titmouse <i>Baeolophus bicolor</i>	ETTI	0.44	0.31	0.10	0.06	0.19	0.39	0.31
White-breasted Nuthatch <i>Sitta carolinensis</i> *	WBNU	0.06	0.06	0.00	0.00	0.05	0.09	0.02
House Wren <i>Troglodytes aedon</i>	HOWR	0.44	0.00	0.05	0.11	0.24	0.30	0.28
Carolina Wren <i>Thryothorus ludovicianus</i>	CARW	0.20	0.00	0.05	0.06	0.16	0.21	0.09
American Robin <i>Turdus migratorius</i>	AMRO	0.98	0.94	0.95	0.81	1.00	0.97	0.90
Wood Thrush <i>Hylocichla mustelina</i> *	WOTH	0.01	0.06	0.00	0.00	0.03	0.03	0.00
Cedar Waxwing <i>Bombycilla cedrorum</i>	CEDW	0.10	0.06	0.19	0.14	0.05	0.18	0.11
Scarlet Tanager <i>Piranga olivacea</i> *	SCTA	0.02	0.00	0.00	0.00	0.00	0.06	0.00
Rose-breasted Grosbeak <i>Pheucticus ludovicianus</i> *	RBGR	0.01	0.13	0.00	0.00	0.03	0.03	0.01

Species by Nesting Guild	Alpha code	Proportion of transects occupied (land use type)				Proportion of transects occupied (meters from forest)		
		resident ial	park	apartme nt	comm-ind	25	200	≥350
Deciduous tree-nesters, cont.								
Common Grackle <i>Quiscalus quiscula</i>	COGR	0.91	0.88	0.86	0.61	0.92	0.88	0.79
Baltimore Oriole <i>Icterus galbula</i>	BAOR	0.39	0.25	0.19	0.19	0.30	0.52	0.25
Orchard Oriole <i>Icterus spurius</i> *	OROR	0.01	0.00	0.00	0.03	0.03	0.00	0.01
House Finch <i>Carpodacus mexicanus</i>	HOFI	0.76	0.56	0.43	0.53	0.70	0.67	0.62
Mourning Dove <i>Zenaida macroura</i>	MODO	0.95	0.56	0.90	0.64	0.86	0.94	0.79
Shrub-nesters								
Red-eyed Vireo <i>Vireo olivaceus</i> *	REVI	0.03	0.13	0.00	0.06	0.05	0.06	0.00
Northern Mockingbird <i>Mimus polyglottos</i>	NOMO	0.82	0.25	0.57	0.58	0.49	0.73	0.74
Gray Catbird <i>Dumetella carolinensis</i>	GRCA	0.73	0.50	0.33	0.58	0.84	0.61	0.56
Brown Thrasher <i>Toxostoma rufum</i> *	BRTH	0.03	0.00	0.00	0.03	0.00	0.09	0.01
Yellow Warbler <i>Dendroica petechia</i>	YEWA	0.04	0.19	0.10	0.06	0.14	0.18	0.00
Common Yellowthroat <i>Geothlypis trichas</i> *	COYE	0.03	0.06	0.05	0.06	0.11	0.03	0.02
Indigo Bunting <i>Passerina cyanea</i> *	INBU	0.00	0.06	0.00	0.06	0.08	0.00	0.00
Red-winged Blackbird <i>Agelaius phoeniceus</i>	RWBL	0.07	0.25	0.05	0.19	0.22	0.03	0.10
Northern Cardinal <i>Cardinalis cardinalis</i>	NOCA	0.88	0.44	0.43	0.42	0.68	0.70	0.68
American Goldfinch <i>Carduelis tristis</i>	AMGO	0.29	0.38	0.14	0.22	0.43	0.27	0.20
Snag-nesters								
Northern Flicker <i>Colaptes auratus</i>	NOFL	0.37	0.63	0.14	0.08	0.38	0.42	0.24
Red-bellied Woodpecker <i>Melanerpes carolinus</i>	RBWO	0.47	0.38	0.14	0.08	0.49	0.45	0.24
Downy Woodpecker <i>Picoides pubescens</i>	DOWO	0.53	0.38	0.00	0.11	0.30	0.36	0.38
Conifer-nesters²								
Blue Jay <i>Cyanocitta cristata</i>	BLJA	0.59	0.44	0.52	0.25	0.59	0.52	0.44

Species by Nesting Guild	Alpha code	Proportion of transects occupied (land use type)				Proportion of transects occupied (meters from forest)		
		residential	park	apartment	commercial	25	200	≥350
Conifer-nesters, cont.								
Fish Crow <i>Corvus ossifragus</i> *	FICR	0.01	0.00	0.00	0.00	0.03	0.00	0.00
Chipping Sparrow <i>Spizella passerina</i>	CHSP	0.05	0.25	0.00	0.03	0.08	0.09	0.04
Building-nesters								
European Starling <i>Sturnus vulgaris</i>	EUST	0.97	0.88	1.00	1.00	0.95	0.97	0.98
House Sparrow <i>Passer domesticus</i>	HOSP	0.99	0.94	1.00	0.94	0.95	0.97	0.99
Rock Dove <i>Columba livia</i>	RODO	0.36	0.25	0.19	0.39	0.11	0.18	0.86
Ground-nesters²								
Eastern Towhee <i>Pipilo erythrophthalmus</i> *	EATO	0.01	0.00	0.00	0.00	0.00	0.03	0.00
Song Sparrow <i>Melospiza melodia</i>	SOSP	0.54	0.25	0.62	0.56	0.65	0.64	0.43
Nest Parasite²								
Brown-headed Cowbird <i>Molothrus ater</i>	BHCO	0.46	0.25	0.43	0.33	0.70	0.52	0.26

*Species present at <5% of the total transects.

Table 2. Influence of distance from forest and land use on bird communities and guilds based on GLMs.

Species or Community Response	(25m vs. ≥ 350 m)			(200m vs. ≥ 350 m)		
Community	Factor	F	P	Factor	F	P
Species Richness	Distance*	49.016	<0.001	Distance*	10.768	0.001
	Land Use*	12.152	<0.001	Land Use*	20.558	<0.001
Mean Daily Abundance ^a	Distance*	14.559	<0.001	Distance	7.450	0.007
	Land Use*	7.822	<0.001	Land Use*	8.777	<0.001
Nesting Guilds						
Deciduous Nester	Distance*	9.105	0.003	Distance*	10.884	0.001
	Land Use*	10.168	<0.001	Land Use*	9.874	<0.001
Shrub Nester	Distance*	13.822	<0.001	Distance	0.711	0.401
	Land Use*	7.285	<0.001	Land Use*	10.713	<0.001
Snag Nester Richness	Distance	6.185	0.014	Distance	5.167	0.025
	Land Use*	12.893	<0.001	Land Use*	18.951	<0.001
Building Nester	Distance*	15.695	<0.001	Distance	2.712	0.102
	Land Use	1.157	0.329	Land Use	0.511	0.675

^a Combined 2003 and 2004 data, European Starling and House Sparrow excluded.

^b Log₁₀-transformed

* Factor or covariate is significant at the table-wide α -level, $p \leq 0.004$.

Table 3. GLMs of species richness, mean daily abundance and richness in each nesting guild to land use and distance from forest (main effects) and important environmental parameters as covariates.

Species or Community Response	Main effects (200 vs 350 only)			Covariates		
Community	Factor	F	P	Parameter	F	P
Species Richness	Distance*	14.653	<0.001	- Built*	9.705	0.002
	Land Use*	6.006	0.001	+ Lg. dec. trees*	12.992	0.001
Mean Daily Abundance ^a	Distance	3.636	0.060	+ Lg. conifers*	12.114	0.001
	Land Use*	9.657	<0.001			
Nesting Guilds						
Deciduous Nester	Distance*	16.355	<0.001	+ Canopy*	30.506	<0.001
	Land Use	0.838	0.477	+ Lg. dec. trees*	8.132	0.005
	Interaction	3.449	0.020	- Pedestrians* ^b	8.308	0.005
Shrub Nester	Distance	1.669	0.200	+ Tree richness*	24.269	<0.001
	Land Use	1.843	0.145	+ Sm. dec. trees* ^b	7.601	0.007
				+ Lg. conifers* ^b	13.131	<0.001
				- Pedestrians*	8.367	0.005
Snag Nester Richness	Distance	1.845	0.178	+ Lg. dec. trees*	22.195	<0.001
	Land Use*	4.781	0.004	- Pedestrians ^b	6.481	0.013
Building Nester	Distance	2.236	0.138	- Lg. dec. trees	15.879	<0.001
	Land Use	3.680	0.015	- Lawn ^b	7.528	0.007

^a Combined 2003 and 2004 data, European Starling and House Sparrow excluded.

^b Log₁₀-transformed

* Factor or covariate is significant at the table-wide α -level, $p \leq 0.008$.

Table 4. Bird-habitat relations in the urban matrix (200 and >350 meters from forest). CCA of urban environmental variables highly associated (intra-set correlation ≥ 0.30) with CCA axes 1, 2, and 3, respectively, of the analysis of bird species and local, urban variables, including distance from forest edge in order of decreasing importance. % variance explained in the bird species abundance data are given for each axis and for all axes combined (total).

	Environmental Variables with Intra-set Correlation ≥ 0.30 with each CCA axis	
	Positive Correlation	Negative Correlation
Axis 1	Built Pedestrians Distance Trucks	Lg. dec. trees Canopy Tree richness Lg. conifers Shrubs
(% Variance=15.7)		
Axis2	Paved Shrubs	Lawn
(% Variance=6.1)		
Axis 3	Lg. dec. trees	Shrubs Lawn
(% Variance=3.2)		
Total		
(% Variance=25.0)		

Table 5. Results of MANOVA with land use and distance as main effects and species mean daily abundance as response variables.

Species	Significance of Main Effects		
	Land Use	Distance	Interaction
HAWO	*	**	*
EAKI	-	-	-
AMCR	-	-	-
BCCH	**	-	-
ETTI	**	-	-
HOWR	**	-	-
CARW	-	-	-
AMRO	**	***	-
CEDW	-	-	-
COGR	**	-	-
BAOR	-	-	*
HOFI	*	-	-
MODO	**	-	-
NOMO	*	-	-
GRCA	*	*	-
YEWA	***	**	***
RWBL	-	*	-
NOCA	***	-	-
AMGO	-	***	-
NOFL	*	-	-
RBWO	**	-	-
DOWO	**	-	-
BLJA	-	-	-
CHSP	-	-	-
EUST	*	-	-
HOSP	***	-	**
RODO	-	*	-
SOSP	-	*	-
BHCO	-	**	-

*p<0.05, **p<0.01, ***p<0.001

Table 6. Bird-habitat relations at the forest-urban boundary (transects located 25 meters from forest). Results of four separate CCAs describing the relative importance of local (urban) variables, adjacent (forest) variables, stand-level (forest) variables, and urban and forest (combined) variables, respectively, in explaining bird species abundance patterns just outside the forest. Environmental variables with high correlations (intra-set correlation ≥ 0.30) with CCA axes 1, 2, and 3, respectively, are listed in order of importance. The percentage of the variance in bird species abundance data are given for each axis and for all axes combined (total), for each CCA.

	Important Environmental Variables (4 separate CCAs)							
	Urban		Forest		Stand		Combined	
Axis 1	-Built +Tree richness +Lg. dec. trees		+ Open shrub & ground layers -Bare ground +Exotic plants		-% Wetland -Area +Isolation		-Built +Lg. dec. trees +Open shrub & ground layers +Isolation +Tree richness -Bare ground +Litter depth	
	% Var.	12.3	% Var.	13.0	% Var.	4.5	% Var.	15.4
Axis 2	+Tree richness +Shrubs +Lawn +Lg. con. trees +Lg. dec. Trees		+Litter depth +Exotic plants +Herbaceous richness		+Isolation		-Shrubs -Tree richness -Lawn -Built -Lg. conifers -Exotic plants	
	% Var.	8.6	% Var.	6.9	% Var.	4.0	% Var.	8.9
Axis 3	+Lg. dec. trees		+Bare ground +Litter depth -Herbaceous richness -Exotic plants -Stream		-Area -% Wetland		+Lg. dec. trees -% Wetland -Area +Bare ground +Tree richness	
	% Var.	5.4	% Var.	6.4	% Var.	1.5	% Var.	7.3
Total	% Var.	26.4	% Var.	26.3	% Var.	10.0	% Var.	31.5

Table 7. Relationship of community- and guild-level metrics to the first 2 axes from 3 separate CCAs of local, adjacent, and stand-level habitat variables. Scores of transects on CCA axes were calculated and then entered into a stepwise regression as independent variables with community- and guild-level metrics as response variables to assess the relative importance of each type of each habitat, local, adjacent, and stand.

Avian Response Variable	Stepwise Regressions of Habitat Variables on Several Avian Response Variables			
	R ²	Urban	Forest	Stand
Species Richness	0.25	Urban Axis1* p=0.002	-	-
Mean daily abundance	0.21	Urban Axis 2* p=0.005	-	-
Deciduous tree-nesters	0.27	Urban Axis 2* p=0.007 Urban Axis 1 p=0.042	-	-
Shrub-nesters	0.13	Urban Axis 1 p=0.023	-	-
Snag-nesters	0.34	Urban Axis 1* p=0.002 Urban Axis 2 p=0.026	-	-
Building-nesters	0.31	-	Forest 1 p=0.020	Stand 2 p=0.033

* Significant at the table-wide α -level, $p \leq 0.008$.

Table 8. Relationship of community- and guild-level metrics to 3 axes from a single All Habitat CCA combining all local, adjacent, and stand-level habitat variables with intra-set correlations >0.30 . Scores of transects on Combined CCA axes were calculated and then entered into a stepwise regression as independent variables with community- and guild-level metrics as response variables.

Avian Response Variable	Stepwise Regressions of CCA Combined Scores on Avian Response Variables	
	R^2	Variables included in model
Species Richness	0.23	Combined Axis 1* p=0.008 Combined Axis 3 p=0.033
Mean daily abundance	0.35	Combined Axis 2* p=0.001 Combined Axis 1 p=0.038
Deciduous tree-nesters	0.10	Combined Axis 2 p=0.039
Shrub-nesters	0.25	Combined Axis 1* p=0.002
Snag-nesters	0.33	Combined Axis 1* p=0.001 Combined Axis 3 p=0.013
Building-nesters	0.23	Combined Axis 1* p=0.003

* Significant at the table-wide α -level, $p \leq 0.008$.

CHAPTER 2

Breeding songbirds in urban forests:

Forest habitat and adjacent land use effects

Abstract: I studied the effects of adjacent land use and local forest habitat on bird communities of urban forests in the New York metropolitan region. The structure of avian communities in urban forests was not related to the type of adjacent urban land use or to the size of the forest. Instead, birds responded to specific habitat characteristics along forest edges as well as characteristics of adjacent urban habitats that varied *within* each land use category. Shrub-nesters and some urban avoiding, forest species accounted for most of the differences among forest bird communities and the factors affecting these groups also affected overall richness. Mature and/or intact forests with more closed ground and shrub layers near the edge and few shrubs outside the forest had the highest richness of birds because they supported more shrub-nesters and urban avoiding species. Lower lawn, paved, and built cover and higher tree cover in adjacent urban habitats was associated with occupation by some urban avoiders. Both urban exploiters and urban avoiders were most influenced by adjacent urban habitat, which suggests that urban habitat adjacent to forest affects the bird community in both direct and indirect ways. These findings support the important contribution that forests of all sizes make to overall bird diversity in urban regions. Maintaining shrubby habitats along forest margins and dense edges for shrub-nesting species and large trees in adjacent urban habitat for urban avoiding species are some recommendations.

Introduction

In metropolitan regions of the northeastern United States, the urban matrix surrounding forests is extremely heterogeneous because human-created habitats vary in vegetation structure and composition, intensity of management, amount of impervious surface, and human density (Alberti et al. 2001, Cadennasso et al. 2007). Few species of birds are limited to either human or forest habitats and for species that regularly utilize both, the two habitat types (forest and urban) may interact in complex ways to shape the bird community at the forest-urban boundary (Burgess and Sharpe 1981). Furthermore, species that rarely leave the forest may be impacted by surrounding land use in direct and indirect ways. Many studies have compared bird community structure among points along a gradient of urbanization (i.e., urban to rural) or among forests surrounded by different levels of urban intensity. Few have looked at how bird communities of natural areas *within* an urban matrix might vary with urban land use type (e.g., residential, commercial-industrial) along the edge. Specifically, does the type of adjacent urban land use matter? How do local forest characteristics compare with the effects of habitat outside the forest in shaping the bird community? Does forest area play a role? Which component(s) of the bird community varies most with land use and habitat characteristics? What are the most important habitat characteristics maintaining high bird richness at the forest-urban boundary? Studies that increase our understanding of which habitat features maintain species richness in urban regions improve our ability to preserve and manage forests in urban landscapes.

Habitat at the local scale is important in shaping bird community patterns in urban forests (Clergeau et al. 2001, Tilghman 1987). Bird communities vary locally within the same forest and among forest types (Inman et al. 2002, Sallabanks et al. 2000). In general, most studies show that increasing horizontal and vertical complexity in forests increases the number of species in the forest (e.g., MacArthur and MacArthur 1961). Biological processes at higher spatial scales, such as forest area, degree of isolation, and landscape-level habitat heterogeneity could play an additional role in shaping communities in urban forests (Freemark and Merriam 1986, Tilghman 1987, Melles et al. 2003, Donnelly and Marzluff 2004).

Urbanization intensity adjacent to forests may also affect bird community structure. Increasing urbanization is associated with decreased bird diversity and richness and a decline in several sensitive groups including Neotropical migrants, foliage and bark gleaning insectivores, cavity- and ground-nesting species in urban forests and an increase in resident, edge-associated species (Donnelly and Marzluff 2004, Rottenborn 1999, Tilghman 1987, Friesen et al. 1995, Dowd 1992, Lindsay et al. 2002, Smith and Schaefer 1992, Hennings and Edge 2003). Density of birds in urban forests shows varying responses to urbanization (Rottenborn 1999). In a comparison between bird communities in a forest prior to development of a natural area along its borders, Hostetler et al. (2005) found that bird richness and guild abundance did not change post-development because the development retained local habitat features such as high tree cover and natural buffers. Bird communities in small forests may be more susceptible than those in large

forests to the effects of adjacent urbanization. Isolation from other forests further compounds this effect (Donnelly and Marzluff 2004).

Land use in urban regions varies greatly at small spatial scales (Cadenasso et al. 2007) and it remains to be shown whether distinct urban land use types along forest edges exert different effects on the bird community within forests. The mechanisms by which adjacent urban land use shapes the bird community in forests may act on bird populations in positive and negative, direct and indirect ways. About 25% of North American bird species are synanthropic to some degree in that they are able to persist in areas of human settlement (Johnston 2001). Blair (2001) referred to this group as “urban exploiters.” The urban exploiter component of the forest community is potentially most directly affected by adjacent land use because they are more likely to be found using resources in the urban habitat outside the forest. On the other hand, several species in the forest community fall into the group of “urban avoiders” in that they are forest specialists that seldom cross over into urban habitats. The effects of adjacent land use on urban avoiders would likely be indirect such as via modifications to forest habitat (e.g., changes in plant composition, edge structure, level of human disturbance and density of nest predators and large herbivores). They may also be indirectly affected by land use via changes in interspecific interactions because of changes in composition and density of the urban exploiters. In summary, the richness and abundance of urban exploiters within the forest bird community should reflect habitat features in the surrounding landscape more than the group of urban avoiders. Both groups should be directly affected by characteristics of

the local forest habitat but urban avoiders should be more tightly coupled to local forest characteristics, as well as those at the forest stand-level, than urban exploiters.

Comparing the response of these two groups to different habitat characteristics provides an opportunity to assess the relative importance of local forest habitat and adjacent urban land use in shaping the bird community. Also, exploring patterns in richness of specific nesting guilds may elucidate mechanisms by which local and adjacent land use are influencing community structure. Finally, because species vary greatly in their habitat requirements and behavior, it is important to also explore the relationship of local versus adjacent habitat to individual species responses (Lynch and Wigham 1984, Holmes et al. 1986).

Using a heavily urbanized watershed in the New York metropolitan region, I studied the effects of adjacent land use on bird communities in forests. I predicted that richness and abundance of the bird community in the forest would vary with land use along its edges. However, I predicted that local forest characteristics would be more important than specific habitat characteristics outside the forest in determining richness and abundance of birds. I also predicted that this relationship would vary when urban avoiders and urban exploiters were compared. Urban avoiders should be less influenced by adjacent land use characteristics than urban exploiters because they are mainly affected indirectly by land use whereas urban exploiters in the forest may be influenced both directly and indirectly. Finally, I predicted that forest stand-level characteristics such as area, heterogeneity and forest habitat composition (i.e., % wetland) would also

affect richness and abundance because some forest species would not be found in smaller forests and because bird species might be at higher densities in smaller forests.

Methods

Study Area: The Arthur Kill is a tidal strait and major deepwater shipping channel separating New Jersey from Staten Island, a borough of New York City (Figure 1). My study was limited to the portion of the watershed in New Jersey. The Arthur Kill and its six major tributaries drain an area of 337 km² (130 mi²) in Essex, Middlesex, and Union counties, NJ (Greiling 1993) in the Piedmont physiographic province. The mean population density among the 3 counties in the watershed is 1,775 people/Km² (4,597-people/ mi²), which is four times the state average and fifty-eight times the national average (U.S. Census Bureau 2000, <http://factfinder.census.gov>). The U.S. Census Bureau uses a minimum population density of about 386 people/km² (1,000 people/mi²) among its criteria for designating an area as urban.

The watershed contains approximately 4,395 ha. (10,860 acres) of deciduous forest and shrubland, 1,136 ha. (2,808 acres) of which is forested wetland. Various types of urban land use covers approximately 35,906 ha. (88,722 acres; New Jersey Department of Environmental Protection 2002). Forty-one percent of the watershed is used for single-family, two-family, and multi-family housing. Despite its reputation as a center of industry, only 18 percent of the land is in commercial or industrial use. Another six percent is recreational land, ballfields, and cemeteries. The remaining land use-land

cover falls into various other categories, including forests, open water, wetlands, and transportation corridors. Several cities, including Newark, Irvington, Orange, and Elizabeth are in the northern and eastern portion of the watershed. The western portions contain mainly single-family residential development. A few study sites fell just outside the southern boundary of the watershed.

I chose a sample of 21 hardwood forests that included most of the forests ≥ 6 ha in the watershed. Forests ranged in size from 6.02 ha. (14.87 acres) to 133.47 ha. (329.80 acres) with a mean of 46.87 ha. (115.81 acres, SD 97.91, Figure 1, Appendix A). All of the forests contained a significant deciduous forested wetland component (range 41% to 100% of total area). These and other forests in northeastern New Jersey are extremely variable hydrologically in large part due to historical alterations via ditching and draining activities (Ehrenfeld et al. 2003). The dominant tree species in the forested wetlands are red maple (*Acer rubrum* L.), pin oak (*Quercus palustris* L.), and sweetgum (*Liquidambar styraciflua* L.). Common shrubs are arrowwood viburnum (*Viburnum dentatum* L.), spicebush (*Lindera benzoin* L.), sweet pepperbush (*Clethra alnifolia* L.), common blackberry (*Rubus* sp.), and multiflora rose (*Rosa multiflora*). Common herbaceous species are poison ivy (*Toxicodendron radicans*), catbrier (*Smilax rotundifolia*), Virginia creeper (*Parthenocissus* sp.), Japanese honeysuckle (*Lonicera japonica*), Jack-in-the-pulpit (*Arisaema* sp.), skunk cabbage (*Symplocarpus foetidus*), spotted touch-me-not (jewelweed; *Impatiens capensis*), garlic mustard (*Alliaria petiolata*), Japanese knotweed (*Polygonum cuspidatum*), jumpseed (*Polygonum virginianum*), Canada mayflower (*Maianthemum canadense*), Japanese stilt grass (*Microstegium vimineum*), clearweed

(*Pilea pumila*), hayscented fern (*Dennstaedtia punctilobula*), sensitive fern (*Onoclea sensibilis*), and cinnamon fern (*Osmunda cinnamomea*). See Ehrenfeld (2005) for a detailed botanical description of forested wetlands in the region.

I placed transects at approximately 25 meters inside the forest (n=33; 12 residential, 6 apartment, 9 commercial-industrial, 6 park; Figure 9; Appendix B). In larger forests, I also placed transects 100 meters inside the forest (n=13; 2 residential, 4 apartment, 5 commercial-industrial, 2 park). Transects were parallel to the forest edge. Each forest site had between one and four transects placed at 25 meters inside as long as transects were at least 200 meters apart and not located along a contiguous edge (Appendix A). Because local vegetation and bird communities vary greatly within the same forest (Inman et al. 2002, Sallabanks et al. 2000) I felt that this did not constitute pseudoreplication. Transects were also placed 25 meters outside the forest. A transect length of 161 meters was chosen because the use of a car odometer aided in rapidly locating transects in urban land types and I wished to have the same transect length in the forests as I did outside the forests. I verified the validity of this method of delineating transect length along several transects. A distance of 0.1 mile on the odometer corresponds to 161 meters. A few transects were < 161 meters in length because the forest edge was not long enough to accommodate the full length.

Avian Surveys: Transects were walked at a slow, even pace and all birds seen and heard within 25m on either side and 25m past the end points were identified and counted. Surveys were conducted from sunrise to 9 am on days without precipitation or high winds

from 25 May to 15 July. Birds that flew over the transect area were noted but not counted within the boundaries of the transect unless they took off or landed within the 25 meters. Transects were sampled once in 2002 and repeated 2-3 times in 2003 and 2004. At transects located 25 meters outside the forest, backyards were likely under-sampled in residential areas because in many cases buildings obscured visual sightings and observations were made using songs and calls of birds.

Habitat Structure and Composition: Because of the large number of environmental variables that are known to affect bird community structure, I attempted to develop methods that would allow me to rapidly sample aspects of the forest and urban environment that have been related to bird parameters in other studies. At transects 25 meters into the forest, I measured various aspects of transect-level, hereinafter local-level, forest habitat structure and composition as well as human disturbance (Appendix D). The number of ditch, stream, snag, trail, garbage, and standing water encounters were recorded while walking the entire transect length. In addition, 0.5m² plots were set up at 20-meter intervals along transects. At each plot, foliage density at the shrub and ground layers was measured using the distance it took for 50% of a board (black and white check pattern) to be obscured by foliage using modified methods of Bibby et al. (1992) and MacArthur and MacArthur (1961). Observations were made by a stationary person at each plot as a second person walked slowly away with the board held at heights of 0.5 m, 1.0 m, and 2 m toward the edge and toward the center of the site, respectively. Percentage cover of tree canopy was determined by looking straight up and down with a spotting tube (James and Shugart 1970). Leaf litter depth was measured at 3 random locations

within the plot. Diameters at breast height (d.b.h.) of the 4 nearest trees with a circumference ≥ 20 cm were measured, distance from center of plot to tree measured, and species recorded (Cottam and Curtis 1956). These metrics were used to generate mean d.b.h. and mean distance from transect to large trees (a proxy for tree density).). A transect was assigned a dominant tree species (i.e., species with the highest relative abundance), and the proportion of the four most common tree species (from all forest sites) was calculated for each transect. Tree species were counted as the overall number of species (richness) as well as the number of exotic tree species. Species comprising $\geq 10\%$ of the shrub layer (within a 10m^2 plot) and ground vegetation (within 0.5m^2 plot) were recorded (Ralph et al. 1993). Overall species richness of shrub and herbaceous plants as well as richness of native and exotic species in each category were calculated. At the center point in each plot, I recorded visibility beyond the forest edge.

At the forest stand-level, I calculated total area, number of patches representing different types of forest and wetland cover types, and percent wetland using 2002 land use-land cover data obtained from New Jersey Department of Environmental Protection.

Adjacent urban habitat variables were measured along all transects at 25 meters from the forest (Appendix C). Percent cover of tree canopy, lawn, building, and paved surface were estimated along each urban transect using 4X6 inch photographs I took at each end of the transect. I counted the number of cells (1 in^2) in a grid that were filled at least $>50\%$ by a particular cover type. In order to increase the effectiveness of this technique in describing the amount of lawn cover, I made an additional count of cells

occupied by any amount of lawn. Counts were made of coniferous and deciduous shrubs (height <3 meters), trees in the 3-10-meter height range (small), and the ≥ 11 -meter height (large) categories along the entire transect length. Trees were identified to species and the richness of trees counted. The number of pedestrians (including cyclists), automobiles (including motorcycles) and trucks (including buses) were counted for intervals of 3 minutes at the conclusion of each bird survey along transects in 2003 only and an average (#/minute) was calculated for each category.

Data Analysis: Species other than Passeriformes (perching birds), Columbiformes (pigeons and doves), Piciformes (woodpeckers), and Cuculiformes (cuckoos) were not counted. Also, birds recorded outside the “safe dates” for breeding were excluded from subsequent analyses (Walsh, 1993). Species were assigned to a nesting location guild based on Ehrlich et al. (1988; Table 9). These included deciduous tree-nesters, shrub-nesters, conifer-nesters, snag-nesters and ground-nesters. I did not include a diet guild because most of the bird species feed on insects during the breeding season (Stiles 1980). In order to categorize species based on urban sensitivity, species present at <10% of a larger sample of transects including those located at 25 meters from forest but also at 200 and ≥ 350 meters (n=137 transects; see Chapter 1) were categorized as “urban avoiders” and the rest were grouped as “urban exploiters” (Table 9).

Alpha was set at 0.05 for individual analyses. Where I performed multiple iterations of a similar test (e.g., regressions), I adjusted the α -level to a “table-wide” α -level using the sequential Bonferonni method (Rice 1989). This accounted for the group-

wide increase in the type I error rate with simultaneous-inference tests. All statistical analyses were completed using Statistical Package for the Social Sciences (SPSS 14.0, 2005) with the exception of Canonical Correspondence Analysis (CCA), which was done using PC-ORD ver. 5.07 (McCune and Mefford 1999) . In some cases, data were transformed in order to meet the basic assumptions of normality and equal variance inherent in many parametric tests.

The effects of land use on community- and guild-level metrics were tested using analysis of variance (ANOVAs). Adjacent land use type (residential, apartment, commercial-industrial, park) was the main effect, and species richness, mean daily abundance, and richness of each nesting and urban sensitivity guild in the forest were community- and guild-level response variables.

Post hoc tests were used to determine which levels of significant main effects and interactions were different in ANOVAs. Hochberg's GT2 method was used for comparisons among land use effects because it is robust to differences in sample sizes among treatments (Sokal and Rohlf 1995).

CCA is a constrained ordination technique that selects the best linear combinations (i.e., best weights) of environmental variables that maximize the dispersion of species scores (Jongman et al. 1995). I employed CCA to describe patterns in mean daily abundance of individual species in terms of patterns in environmental variables. I focussed on transects located 25 meters inside the forest to determine whether bird

community patterns on the forest side of the forest-urban boundary were most influenced by local forest parameters, adjacent urban parameters and/or stand-level forest parameters and which were most important. I also combined environmental variables (those with intra-set correlations ≥ 0.30) from each of these analyses into one Combined CCA to see how the combined effects of environmental variables from each category would relate to bird patterns. Data were standardized to a mean of zero and unit variance before being entered into the analyses. Each analysis produced 3 axes, with axis 1 being a linear combination of environmental variables describing the largest variance in bird abundance, axis 2 describing the next largest amount while remaining uncorrelated with axis 1, and so on. The amount of variance explained by each of the 3 axes and overall was used to determine the strength of the species-environment relationship in each analysis and to compare the importance of forest, urban, stand, and combined variables. Variance is the best method for assessing the strength of the axes.

Biplots of species scores and transects coded by land use type on Combined Axes 1 and 2 were used to visually explore patterns of bird abundance (e.g., guild patterns) and land use in relation to important habitat characteristics. I entered scores on transects from the 3 types of variables (Forest, Urban, Stand), 3 axes each, into stepwise regression analyses to see which ones best predicted overall bird richness, mean daily abundance, and the richness in each guild. I also entered scores on Combined Axes 1 and 2 into a stepwise regression analysis to see how well these would predict the various bird community and guild metrics (i.e., how well the environmental variables important to overall bird community structure would also explain larger, community-level patterns).

At each step in the analyses, an F-statistic was calculated for each variable in the model. Variables having $p < 0.05$ were allowed to enter models and variables were removed if their significance level became $p < 0.10$ as other variables were entered into the model. This helped in determining how much a particular guild was contributing to overall richness.

I used multivariate analysis of variance (MANOVA) to compare species scores from guilds with significant associations with particular CCA axes to the scores of all other species to see whether the effect of habitat on a particular guild was significantly different than on the rest of the species. Finally, I tested whether land use types differed depending on transect scores on axes from Forest, Urban, Stand, and Combined CCAs using MANOVA.

Because CCA is a constrained ordination, it may or may not coincide with the “pure,” unconstrained gradient in the bird community. To see how well the patterns depicted by the species-environment gradient represent important overall gradients in the community, I conducted Principal Components Analysis on the species abundance data. Finally, I compared mean richness and abundance between transects 25 and 100 meters into the forest using t-tests .

Results

Forty-five species were detected among the focal bird taxa (Table 9). Most of the species were deciduous tree nesters (50% of species) or shrub nesters (23%; Table 9), similar to the proportions found outside the forest. Forty percent (n=16) of the species were urban avoiders and the rest were urban exploiters (Table 9). Avian richness did not differ among years so individual years were combined into one metric of overall species richness. Mean daily abundance in 2002 (17.48 ± 1.78) was higher than in 2004 (mean 12.34 ± 0.96 ; $t=2.452$, $p=0.022$) but not 2003 (13.41 ± 1.45 $p>0.05$). Mean daily abundance did not differ between 2003 and 2004 ($p=0.032$) so they were combined into one overall mean daily abundance. I excluded mean daily abundance in 2002 from further analyses. Furthermore, transect length was not related to species richness ($R^2 = -0.003$) or to mean daily abundance ($R^2 = 0.003$) so I did not standardize these metrics to transect length. However, I standardized overall richness to what it would be if an equal number (n=5) of observations had been made for each transect because of a large effect of number of observations.

Orchard Oriole, Veery, Black-billed Cuckoo, Yellow-billed Cuckoo, and Rock Dove were excluded from the species- and guild-level analyses because they were present at <5% of the forest transects. Species present at < 3 sites (25 meters into forest from edge) were excluded from canonical correspondence analysis. They included Northern Mockingbird, Fish Crow, Rock Dove, Black and white warbler, Ovenbird, Veery, Yellow-throated Vireo, Yellow-billed Cuckoo, and Orchard Oriole.

The forest-urban boundary: Adjacent land use was not associated with species richness, mean daily abundance, or richness in any of the guilds in urban forests (GLM, all $p > 0.05$). CCAs showed that particular habitat attributes at the forest-, urban-, and stand-levels were related to bird community structure. Table 10 provides a description of important variables (≥ 0.30 intra-set correlation, species-environment) on the 3 axes resulting from separate CCAs of Forest, Urban, Stand and Combined variables, respectively. These axes are the best linear combination of environmental variables related to the structure of the bird community. Forest Axis 1 is an axis describing an open understory and big trees on the low end and a closed understory and small trees on the other extreme. Forest Axis 2 is an axis of increasing forest maturity and wetness. Urban Axis 2 is a gradient of increasing number of large trees and lower built cover. Stand Axis 1 is a gradient of decreasing forest area and wetland cover. Stand Axis 2 is a gradient of decreasing area and increasing wetland composition.

When the variables with ≥ 0.30 intra-set correlations from each of these analyses were entered into the combined CCA the result was a Combined Axis 1 that includes both urban and forest variables. It is a gradient of closed forest understory and few large trees outside the forest to a more open understory in the forest with a lot of large trees outside. Combined Axis 2 is a gradient of increasing urban shrubs and decreasing forest maturity. Forest, Urban and Combined analyses explained a similar amount of variance (~ 21-25%; Table 10), with adjacent Urban axes explaining the highest among the 3 groups. Stand-level axes explained only ~12% of the variance in bird abundance data.

In the stepwise linear regressions relating community and guild-level metrics to transect scores on axes of Urban, Forest, and Stand CCAs, respectively, species richness, the richness of urban exploiters, urban avoiders, and shrub nesters were negatively associated with Urban Axis 1 (gradient of increasing lawn and shrub) in regression models (Table 11). In addition to Urban Axis 1, urban avoiders were positively related to Urban Axis 2 (gradient of decreasing urban intensity). Shrub-nesters were also positively related to Forest Axis 2 (gradient of increasing forest maturity) and were the only group to include any forest metrics in the regression model. Stand-level axes did not predict any of the community- or guild-level metrics. In a second set of stepwise regressions in which I entered the Combined axes, overall richness and richness of urban avoiders and shrub-nesters were all negatively related to Combined Axis 2 (a gradient of increasing urban shrubs and decreasing forest maturity; Table 12). However, when the table-wide alpha-level ($P \leq 0.006$) was applied, only Urban Axis 1 was significant in models of shrub-nester richness and Combined Axis 2 in models for urban avoider richness.

A biplot of species scores on the Combined Axes was used to look for relationships between species and environment that might emerge at the guild-level as well as to see how these trends relate to land use type (Figure 10, a and b). The length of the vectors represent the importance of each environmental variable and the angle relative to the axes and to other vectors represents the strength of its correlation. The closer a species lies to the head of vector arrows, the more it is influenced by the environmental variable represented by that arrow.

Shrub-nesters were clearly clustered at the low end of Combined Axis 2 and possibly combined Axis 1, with the exception of Red-eyed Vireo and American Goldfinch. I tested whether scores of shrub-nesting species differed from other species scores on the Combined axes and on all other axes using MANOVA. Shrub-nesting species did not differ from other species in the overall MANOVA (Wilks' $\lambda=0.648$, $F=1.134$, 12 df, $p>0.05$). However, there were significant differences between shrub-nesters and other species in individual comparisons on Urban Axis 1 and Combined Axis 2 ($F=5.796$, 1df, $p=0.021$; $F=5.468$, 1 df, $p=0.025$). This indicates that shrub-nesters are associated with more mature and/or intact forests that are adjacent to urban areas with few shrubs and low lawn and paved cover.

Urban avoiders as a group differed from urban exploiters (Wilks' $\lambda=0.402$, $F=3.103$, 12 df, $p=0.008$) along Urban Axis 1, Urban Axis 2, and Combined Axis 2 ($F=4.363$, 1df, $p=0.044$; $F=11.106$, 1df, $p=0.002$; $F=15.613$, 1 df, $p<0.001$). The response to Urban Axis 1 and Combined Axis 2 is likely heavily influenced by the shrub-nesters, many of which comprise the urban avoider group, because they are most influenced by the maturity of the forest and the number of shrubs outside the forest. Urban exploiters scored very low on Urban Axis 2 whereas urban avoiders scored high on this axis, which coincides with urban avoiders preferring adjacent urban habitats with large trees and low built areas (the low extreme of the urban gradient). The importance of large urban trees as reflected in the inclusion of Urban Axis 2 is probably an indication that other urban avoiding species, besides shrub-nesters, are affected by the adjacent

urban habitat. However, when individual variables from Urban axis 2 were entered into stepwise regressions on richness of urban avoiders, none were significant, which indicates a high variability among urban avoider species in their response to these attributes.

Although I was unable to demonstrate a relationship between land use and bird community parameters using ANOVAs, I wanted to see how land use might relate to the major environmental gradients (CCA axes) associated with abundance patterns of individual bird species. When transects coded by land use type were included on the biplot, associations between land use and individual species responses, which may not be apparent when community-level parameters are studied, may be inspected (Figure 5b.). Commercial-industrial areas and apartments appear to lie at the low end of Combined Axis1 (gradient of decreasing understory density in forest and increasing number of large trees outside the forest) while parks and residential areas are largely associated with the high end of this axis. Commercial-industrial areas and parks also appear to cluster at the low end of Combined Axis 2. MANOVA of transect scores on each of the CCA axes indicated that land use differed along Combined Axis 1 ($F=6.176$, $df3$, $p=0.003$) but none of the others. Parks had higher scores (i.e., had more open forest understories and were surrounded by more large trees and lawn) than apartment and commercial-industrial areas (Hochberg's GT2 $p=0.026$ and $p=0.019$). Residential areas had higher scores on this axis than commercial-industrial areas ($p=0.038$). Therefore, differences among land use types were largely attributable to differences in large trees outside the forest and a more open forest understory.

Shrub-nesters appear to cluster next to areas of commercial-industrial land use on the biplot. Although land use *per se* did not separate out along Combined Axis 2 in the MANOVA or the bi-plot, there does appear to be a trend of low shrub cover adjacent to forests and larger d.b.h. in forests with commercial-industrial and park areas adjacent to them in the bi-plot. To further investigate whether differences exist in shrub cover among land use types, I ran a MANOVA using the original environment variables. Number of planted shrubs was much higher in residential and apartment areas than in commercial-industrial areas and parks just outside the forest ($F=19.092$, df_3 , $p<0.001$; Hochberg, all $p<0.001$). Forest maturity and density of shrub and ground layer in the forest did not differ among land use types (both $p>0.05$).

Finally, I tested the ability of the CCA axes to predict overall species richness inside the forest. Both Urban Axis 1 and Combined Axis 2 were related to richness ($R^2=0.108$, $p=0.046$; $R^2=0.110$, $p=0.044$, respectively) but not mean daily abundance (density) of birds in the forest. Because shrub-nesters and urban avoiders are the groups that are structured most obviously by differences in habitat, they are likely comprised of the species that provide the added edge in overall richness. In fact, of the five shrub-nesting species that are also urban avoiders, density of four species (i.e., Yellow Warbler, Common Yellowthroat, Brown Thrasher, Indigo Bunting) was positively correlated with overall species richness (Pearson correlations from 0.427 to 0.461, all $p<0.05$).

Species-level relationships to land use and forest proximity: In the PCA, principal component 1 (PC1) explained 11.3% of the variance in the density of individual species

and principal component 2 (PC2) explained 9.4%. Most of the species with very high loadings (i.e., ≥ 0.50) on PC1 were shrub-nesting species that were also urban avoiders (Table 13). This confirmed that the CCA had described a true gradient in the bird community and could therefore be useful in predicting community-level richness and density patterns. Patterns in species loadings on subsequent principal components were less easy to interpret.

Species relationships to the edge: Species richness at 25 meters inside the forest (mean 18.444 ± 0.704 S.E.) was higher than richness outside the forest (15.495 ± 0.641 ; $t=4.541$, $p<0.001$) and they were not correlated (Pearson correlation, $p>0.05$). Bird density inside the forest (mean 12.36 ± 0.684 S.E.) was lower than outside the forest (20.577 ± 1.528 ; $t=5.787$, $p<0.001$). Density inside the forest was correlated with density outside the forest (Pearson correlation = 0.408, $p<0.05$).

Also, mean species richness at 100 meters inside the forest (16.18 ± 2.93) was not different than at 25 meters inside the forest ($t=1.834$, $p>0.05$). Bird density at 100 meters inside the forest (10.59 ± 4.42) was not different than at 25 meters inside the forest ($t=1.325$, $p>0.05$).

Discussion

The type of land use adjacent to urban forests did not affect the bird community inside the forest. Instead, birds responded to a combination of forest characteristics and

adjacent urban habitat that varied somewhat *within* land use categories. Urban avoiding species, especially those that are shrub-nesters, were most responsible for variation in bird community structure and made an important contribution to species richness. More mature and/or intact forests with many large trees and few shrubs (i.e., parks) in adjacent urban habitats had the highest overall richness of birds. More mature forests have larger, less dense trees and a more developed shrub understory, which means they have greater vertical complexity. These findings generally agree with those of other studies that demonstrate an increase in bird richness due to the broader range of resources that comes with increasing habitat complexity (MacArthur and MacArthur 1961, Roth 1976). The lack of a significant effect of land use type on richness is perplexing given the differences in habitat structure among the land use types and the strong relationships between land use type and bird richness and density outside the forest (see Chapter 1). There were gradients in combined forest and adjacent land use structure that were related to land use type but that gradient was not the one most important to shrub-nesters and urban avoiding species in forests. Also, no single land use type had a perfect combination of characteristics that benefit all species at once. For example, many parks are adjacent to large, mature forests. They often contain large trees and low shrub cover but they also have relatively high lawn cover; a characteristic negatively associated with bird richness. Also, high tree density outside the forest edge may not allow enough light to penetrate to the forest edge. Thus, a dense shrub layer along the edge may not be present.

Richness of urban avoiders was influenced positively by a low number of shrubs and a high density of large trees in the adjacent urban habitat. Hennings and Edge (2003)

and Hostetler et al. (2005) also found that urban tree cover and native vegetation surrounding forests were the most important features for maintaining native breeding birds in the forest. It is likely that high tree density in the adjacent urban habitat is either providing resources for some forest-dependent birds crossing over from the forest edge (e.g., Eastern Wood-pewee) or is buffering the forest edge from the negative effects of adjacent urban land use.

Both urban exploiters and urban avoiders were apparently heavily influenced by adjacent urban habitat. These findings suggest that direct exploitation of resources outside the forest, as would have been suggested if the urban exploiters responded more to adjacent urban habitat than the urban avoiders, is not the sole way in which birds are affected by adjacent urban habitat. The relationship of urban avoiders to habitat outside the forest likely reflects more complex indirect pathways by which adjacent habitat is affecting birds. Perhaps there are differences in forest understory and the density of large trees outside that forest not captured in this study. For instance, Cutway (2004) found that forests adjacent to residential areas had more open edge structure than forests in industrial areas. Also, some other pathways for indirect effects of adjacent habitat on the forest bird community that were not measured are likely having some effect. The lack of a strong effect of specific forest characteristics alone reflects the highly variable, species-specific nature of bird-habitat relationships, including behavioral differences. This also explains the low R^2 values (i.e., <0.30) for most of the models of community and guild metrics. Also, variables that were not measured here are likely contributing heavily to bird richness and density. Some of these variables may include predation (Wilcove 1985,

Haskell et al. 2001), competition, herbivore density, supplemental feeding and other local and landscape-scale habitat features (e.g., forest shape).

Shrub-nesters make an important contribution to bird diversity in urban regions and they are a group of species that is generally declining in North America (Askins 2002). It is likely that this guild reflects edge structure as most (with the exception of Red-eyed Vireo, Northern Cardinal, and Gray Catbird) are forest edge-associated specialists. Edges of mature forests surrounded by low shrub cover appear to be a preferred habitat type among shrub-nesters that are also urban avoiders (Yellow Warbler, Indigo Bunting, Brown Thrasher, and Common Yellowthroat). Sites where edges are only intermittently managed by people (e.g., commercial-industrial areas, roadsides, utility rights-of-way, train tracks) as well as shrubby vegetation strips of various widths along the margins of forest sites favor shrub-nesters. In general, a dense, shrubby edge or a gradual edge maintained around forest perimeters increase the value of that forest in maintaining overall bird richness. Furthermore, this is habitat for several Neotropical migrants during migration (Petit 2000).

It is surprising that richness of birds inside and outside the forest were not correlated given the important effect of adjacent urban habitat. Bird density outside the forest was, however, correlated with density in the forest. One possible explanation for the lack of a connection in species richness across the boundary is that many urban exploiting species move into the forest from the surrounding landscape and bolster richness and density there, whereas the same is not true for urban avoiding species

moving into the adjacent urban areas. Also, forest habitat is supplementing richness of urban avoiding species (Chapter 1).

It was also somewhat surprising that forest stand-level features had no detectable effect on species richness and density or on individual species despite the fact that all or most of the species I categorized as urban avoiders are also area-sensitive (Robbins et al. 1989). If I had included smaller forest patches in my study, I might have detected an area effect. Another explanation for the lack of a relationship with forest area is that many forest-breeding species have already undergone declines, especially in the urban core of New Jersey, and the remaining assemblage is comprised of those species less affected by area (Whitcomb et al. 1981, Walsh et al. 1999). I found that several bird species that are specialized to forest habitat remain a stable component of the forest bird community in this heavily urbanized watershed. However, there are several species that are very rare (e.g., Veery) or lacking entirely (e.g., Kentucky Warbler) in the forests studied even though they breed in forests north, south, and west of the study area (Walsh et al. 1999). This loss of several members of the regional breeding bird species with urbanization is similar to the findings of Devictor (2006). The finding that forest stand-level features were not important in explaining richness supports the importance of local forest features and adjacent urban habitat in determining the richness of the bird community inside the forest edge. However, I should caution that I did not measure fitness in this study. Birds in relatively small urban forests may be using marginal habitats that are actually population sinks because such factors as greater risk of predation and nest parasitism

result in decreased individual fitness (Wilcove 1985, Gates and Gysel 1978, Trine 1998, Chace et al. 2003, Marzluff et al. 2007).

In summary, forests support a higher level of bird diversity in urban landscapes than would otherwise be there. The size of forests and the type of urban land use surrounding them do not appear to influence this relationship. Instead, forest maturity as well as the density of large trees and shrubs in the surrounding urban areas make the difference in which urban-avoiding species, especially shrub-nesters, will be found there. These characteristics seem to vary somewhat among land use types but not enough to be statistically significant. This research demonstrates the important role that adjacent habitat might play in shaping the forest bird community and potential improvements that might be made in managing these habitats such as maintaining large, native trees and decreasing the amount of lawn, pavement and buildings around them. It also provides several management goals for habitat improvement within urban forests and around the perimeter to increase the number of bird species there. These include managing forests for dense shrub and herbaceous layers and maintaining shrubby edge habitats. It seems that the latter can be easily accomplished by decreasing the intensity and/or frequency of management such as mowing along edges. Also, shrubby habitats at the periphery of forests should be afforded protection as rare habitats that are important in maintaining bird diversity. Finally, planting and caring for native, long-lived trees in urban habitat will bolster bird diversity in forests as well as in the urban matrix.

Figure 9. Diagram of transect locations in forests and adjacent urban land use relative to forest edge (picture not to scale).

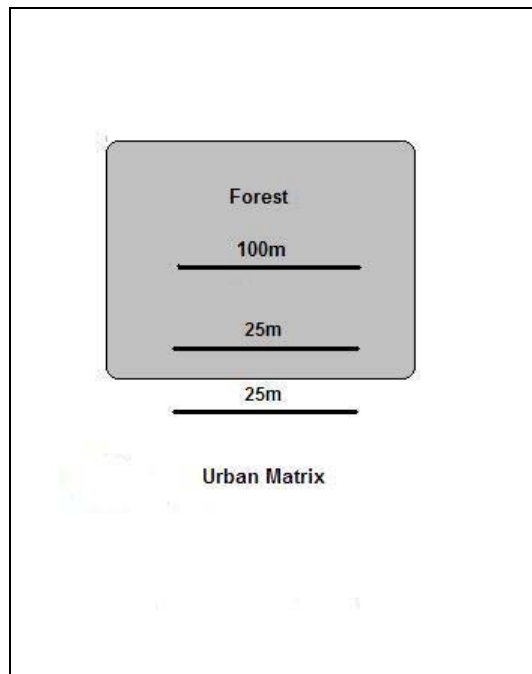


Figure 10a. Biplot of species scores (shrub-nesters in blue) on Combined Axis 1 and Combined Axis 2, representing the combination of forest, urban, and stand-level variables that best explain patterns in the abundance of individual bird species.

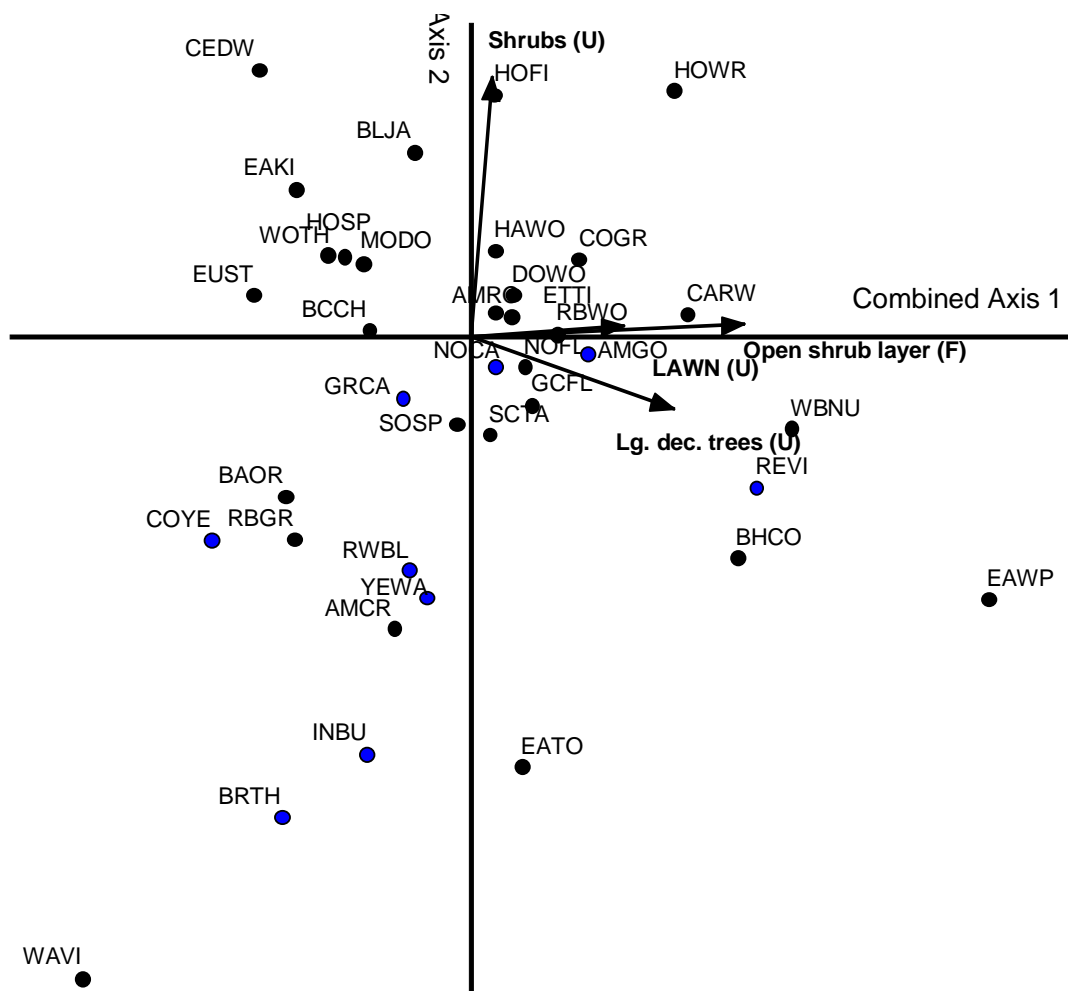


Figure 10b. Biplot of transect scores, coded by land use type, on Combined Axis 1 and Combined Axis 2, representing the combination of forest, urban, and stand-level variables that best explain patterns in the abundance of individual bird species.

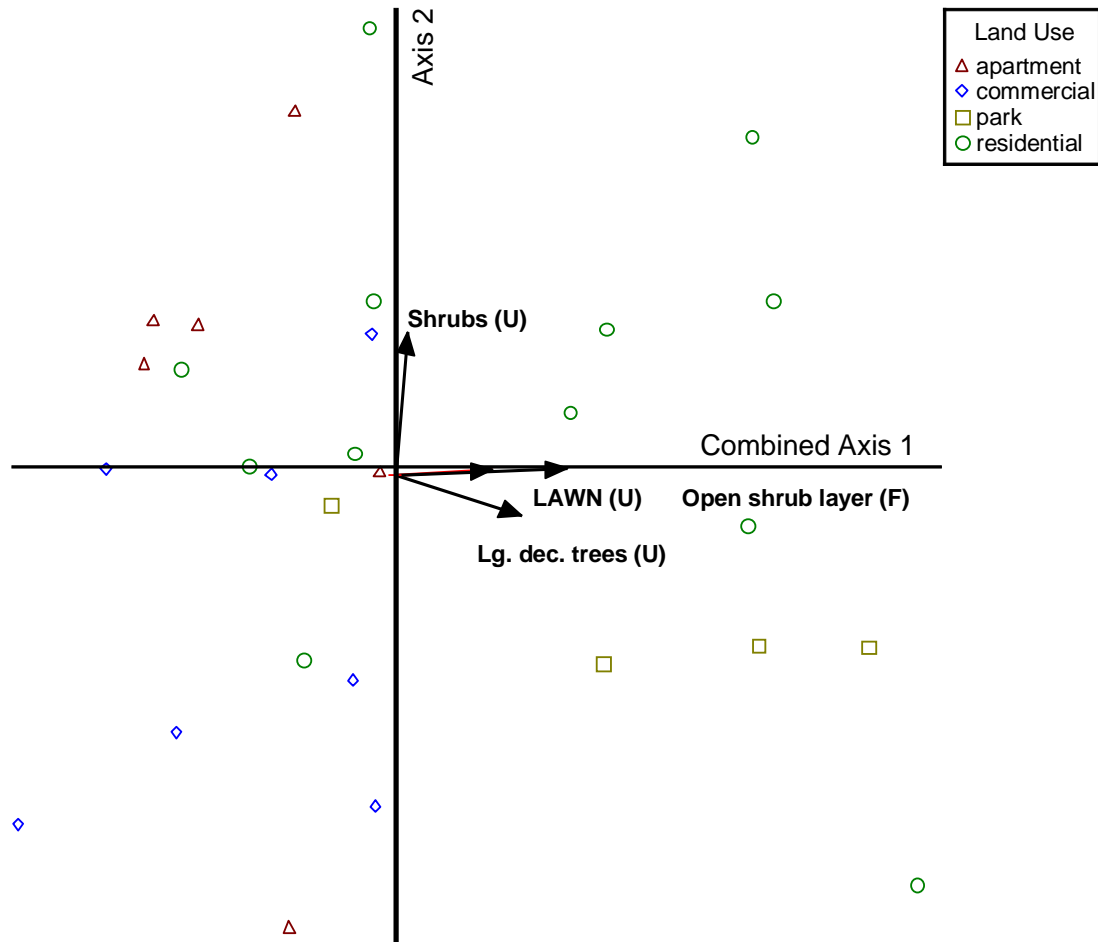


Table 9. Species detected in urban forests, the nesting and foraging guild they occupy, and the proportion of sites, inside at 25 and 100 meters from the edge and outside the forest in the urban matrix.

Species by Nesting Guild	Alpha Code	Proportion of transects occupied in relation to forest edge		
		25 meters inside	100 meters inside	Urban (outside forest) ⁴
Deciduous tree-nesters				
Hairy Woodpecker <i>Picoides villosus</i>	HAWO	0.73	1.00	0.14
Great-crested Flycatcher ^A <i>Myiarchus crinitus</i>	GCFL	0.55	0.46	0.02
Eastern Wood-pewee ^A <i>Contopus virens</i>	EAWP	0.18	0.38	0.04
Eastern Kingbird ^A <i>Tyrannus tyrannus</i>	EAKI	0.09	0.00	0.08
Warbling Vireo ^A <i>Vireo gilvus</i>	WAVI	0.09	0.00	0.02
Yellow-throated Vireo ^A <i>Vireo flavifrons</i>	YTVI	0.06	0.08	0.01
American Crow <i>Corvus brachyrhynchos</i>	AMCR	0.15	0.08	0.13
Black-capped Chickadee <i>Poecile atricapilla</i>	BCCH	0.48	0.62	0.20
Eastern Tufted Titmouse <i>Baeolophus bicolor</i>	ETTI	0.79	0.85	0.30
White-breasted Nuthatch ^A <i>Sitta carolinensis</i>	WBNU	0.33	0.23	0.04
House Wren <i>Troglodytes aedon</i>	HOWR	0.09	0.00	0.28
Carolina Wren <i>Thryothorus ludovicianus</i>	CARW	0.58	0.23	0.13
American Robin <i>Turdus migratorius</i>	AMRO	1.00	1.00	0.93
Wood Thrush ^A <i>Hylocichla mustelina</i>	WOTH	0.70	0.92	0.01
Cedar Waxwing <i>Bombycilla cedrorum</i>	CEDW	0.15	0.00	0.11
Scarlet Tanager ^A <i>Piranga olivacea</i>	SCTA	0.12	0.00	0.01
Rose-breasted Grosbeak ^A <i>Pheucticus ludovicianus</i>	RBGR	0.09	0.31	0.02
Common Grackle <i>Quiscalus quiscula</i>	COGR	0.91	0.85	0.84
Baltimore Oriole <i>Icterus galbula</i>	BAOR	0.67	0.31	0.31
Orchard Oriole ^A <i>Icterus spurius</i>	OROR	0.03	0.00	0.01

Species by Nesting Guild	Alpha Code	Proportion of transects occupied in relation to forest edge		
		25 meters inside	100 meters inside	Urban (outside forest) ⁴
Deciduous tree-nesters, cont.				
House Finch <i>Carpodacus mexicanus</i>	HOFI	0.12	0.08	0.65
Mourning Dove <i>Zenaida macroura</i>	MODO	0.15	0.00	0.84
Black-billed Cuckoo ^A <i>Coccyzus erythrophthalmus</i>	BBCU	0.00	0.08	0.00
Yellow-billed Cuckoo ^A <i>Coccyzus americanus</i>	YBCU	0.03	0.08	0.00
Shrub-nesters				
Red-eyed Vireo ^A <i>Vireo olivaceus</i>	REVI	0.52	0.62	0.02
Gray Catbird <i>Dumetella carolinensis</i>	GRCA	0.97	0.85	0.63
Brown Thrasher ^A <i>Toxostoma rufum</i>	BRTH	0.18	0.00	0.02
Yellow Warbler ^A <i>Dendroica petechia</i>	YEWA	0.27	0.00	0.07
Common Yellowthroat ^A <i>Geothlypis trichas</i>	COYE	0.27	0.46	0.04
Indigo Bunting ^A <i>Passerina cyanea</i>	INBU	0.15	0.00	0.02
Red-winged Blackbird <i>Agelaius phoeniceus</i>	RWBL	0.24	0.23	0.11
Northern Cardinal <i>Cardinalis cardinalis</i>	NOCA	0.94	0.85	0.68
American Goldfinch <i>Carduelis tristis</i>	AMGO	0.42	0.46	0.26
Snag-nesters				
Northern Flicker <i>Colaptes auratus</i>	NOFL	0.97	0.85	0.31
Red-bellied Woodpecker <i>Melanerpes carolinus</i>	RBWO	0.97	1.00	0.34
Downy Woodpecker <i>Picoides pubescens</i>	DOWO	0.76	0.77	0.36
Conifer-nesters				
Blue Jay <i>Cyanocitta cristata</i>	BLJA	0.85	1.00	0.49
Building-nesters				
House Sparrow <i>Passer domesticus</i>	HOSP	0.48	0.31	0.98
Rock Dove <i>Columba livia</i>	RODO	0.00	0.08	0.32
European Starling <i>Sturnus vulgaris</i>	EUST	0.45	0.00	0.97

Species by Nesting Guild	Alpha Code	Proportion of transects occupied in relation to forest edge		
		25 meters inside	100 meters inside	Urban (outside forest) ⁴
Ground-nesters				
Veery ^A <i>Catharus fuscescens</i>	VEER	0.03	0.08	0.00
Ovenbird ^A <i>Seiurus aurocapillus</i>	OVEN	0.06	0.08	0.00
Eastern Towhee ^A <i>Pipilo erythrophthalmus</i>	EATO	0.09	0.00	0.01
Song Sparrow <i>Melospiza melodia</i>	SOSP	0.30	0.08	0.52
Nest Parasite				
Brown-headed Cowbird <i>Molothrus ater</i>	BHCO	0.36	0.15	0.41

^A Urban Avoider species (present at <10 % of transects outside forest).

Table 10. Habitat variables with ≥ 0.30 intra-set correlation, species-environment from four separate CCAs: 1. Forest only (F), 2. Urban only (U), 3. Stand only (S), and 4. Combined.

Important Environmental Variables (4 separate CCAs)								
	Forest		Urban		Stand		Combined	
Axis 1	-Open ground and shrub layers -Dbh -Ditch -Litter depth		+Shrubs +Lawn +Paved -Truck		-% Wetland -Area +Isolation		+Open shrub & ground layers (F) +Lg. dec. trees (U) +Lawn (U) -% Wetland (F)	
	% Var.	10.4	% Var.	9.9	% Var.	6.0	% Var.	9.0
Axis 2	+Dbh +Standing water +Trail +Tree distance +Exotic shrubs -Litter depth		+Lg. dec. trees -Built +Pedestrians -Shrubs		-Area +% Wetland -Heterogeneity		+Shrubs (U) -Dbh (F)	
	% Var.	7.0	% Var.	7.9	% Var.	3.4	% Var.	6.9
Axis 3	+Streams +Dbh -Tree distance -Bare ground +Herb richness +Tree richness		- Lg. conifers		-Heterogeneity -Area -% Wetland +Isolation		+Shrubs (U) +Lg. dec. trees (U)	
	% Var.	5.2	% Var.	6.9	% Var.	2.7	% Var.	5.4
Total	% Var.	22.7	% Var.	24.6	% Var.	12.1	% Var.	21.3

Table 11. Relationship of community- and guild-level metrics to 3 axes from 3 separate CCAs of forest, urban, and stand-level habitat variables. Scores of transects on CCA axes were calculated and then entered into a stepwise regression as independent variables with community- and guild-level metrics as response variables to assess the relative importance of each type of each habitat, local, adjacent, and stand.

Avian Response Variable	Stepwise Regressions of Habitat Variables on Several Avian Response Variables			
	R ²	Forest	Urban	Stand
Species Richness	0.108	-	-Urban Axis 1 (p=0.046)	-
Mean daily abundance	-	-	-	-
Urban avoiders	0.231	-	-Urban Axis 1 (p=0.015) Urban Axis 2 (p=0.033)	-
Urban exploiters	0.106	-	-Urban Axis 1 (p=0.047)	-
Deciduous-nesters	-	-	-	-
Ground-nesters	-	-	-	-
Shrub-nesters	0.324	+Forest Axis 2 (p=0.045)	-Urban Axis 1 (p=0.003)*	
Snag-nesters	-	-	-	-

* Significant at the table-wide α -level, $p \leq 0.006$.

Table 12. Relationship of community- and guild-level metrics to 3 axes from a single All Habitat CCA combining all local, adjacent, and stand-level habitat variables with intra-set correlations >0.30 . Scores of transects on Combined CCA axes were calculated and then entered into a stepwise regression as independent variables with community- and guild-level metrics as response variables.

Avian Response Variable	Stepwise Regressions of CCA Combined Scores on Avian Response Variables	
	R ²	Variables included in model
Species Richness	0.110	- Combined Axis 2 ($p=0.044$)
Mean daily abundance	-	-
Urban avoiders	0.252	- Combined Axis 2 ($p=0.003$)*
Urban exploiters	-	-
Deciduous-nesters	-	-
Ground-nesters	-	-
Shrub-nesters	0.204	- Combined Axis 2 ($p=0.008$)
Snag-nesters	-	-

Significant at the table-wide α -level, $p \leq 0.006$.

Table 13. Coefficients of individual species on principal component 1 (PC1) from the PCA of mean daily abundance for individual species. Only species with coefficients of ≥ 0.3 included. * denotes species with a very high loading on the axis (>0.5).

Species	PC1
EAWP	-.373
AMCR*	.581
ETTI	.383
WBNU	-.390
WAVI*	.497
REVI*	-.457
YEWA*	.599
COYE*	.592
INBU*	.742
EATO	.346
BRTH*	.656
EUST*	.487
BAOR*	.458

CHAPTER 3

Urban forests as *en route* habitat for Neotropical migrants:

Forest habitat and adjacent land use effects

Abstract: I studied the effects of local forest habitat quality and adjacent urban land use on the community of migrating songbirds during spring of 2004 in a large urban watershed in northern New Jersey. I found that many species of Neotropical migrant birds use urban forests in heavily urbanized portions of the New York metropolitan region as *en route* stopover habitat during spring migration. Richness and density of migrating birds are positively associated with forest maturity. Bird richness is especially influenced by the habitat features of more mature forests, including larger trees, greater vertical complexity of the vegetation, and higher richness of herbaceous plant species. Forests with residential land use adjacent to them had a higher density of migrating songbirds than those abutted by commercial-industrial areas, which indicates that land use is affecting the community of birds migrating through forests in spring.

Introduction

Neotropical migrant songbirds are of conservation concern because habitat loss taking place on their wintering and breeding ranges as well as along their migration routes is believed to be causing decline in some species (Terborgh 1992, Moore 2000). High energetic demands during migration require that species be able to quickly find and select *en route* habitats in which they can rapidly meet their high energetic needs with relatively low risk of mortality (Petit 2000). Major migration routes often coincide with

areas that are also heavily used by people such as coastlines and river valleys (Barrow et al. 2000). Birds migrating through eastern North America must cross large, heavily urbanized areas where important stopover habitats such as forests and shrublands are highly fragmented and surrounded by urban land use of varying value to birds.

Migrants face many challenges while migrating through urban regions but they possess characteristics that may make them less vulnerable to urbanization and fragmentation effects than they would be on their breeding grounds. The nature of migration requires that species undertaking it be adapted to exploiting new, unpredictable habitats along their migration routes (Petit 2000). There is ample evidence that many species of Neotropical migrant songbirds use a broader range of microhabitats during migration than they do in other seasons. Also, many species use highly disturbed habitats on their wintering grounds. There is much to be learned about migrant distribution and patterns of richness in urban regions. This includes basic knowledge about forest structure that favors a high richness and density of migrants. Also, the possible effects of adjacent urban habitat on birds within the forest are not clear.

Neotropical migrant songbirds prefer forest and shrubland as *en route* habitat over other habitat types during migration (Simons et al. 2000). They select among sites based on local habitat features including insect prey abundance during spring and fruit abundance during fall, high structural complexity, and vegetation maturity and composition (Barrow et al. 2000, Petit 2000, Rodewald and Matthews 2005). Studies have shown varying effects of factors at higher-scales, such as forest area and degree of

isolation, on richness and density of migrants (Cox 1988, Yahner 1983, Martin 1980).

Density and richness of migrating songbirds is possibly highest in small, isolated habitats (Petit 2000). While many Neotropical migrant birds are sensitive to area on their breeding grounds, they may not be as sensitive to habitat size during migration because some of the negative effects of small forest size such as increased frequency of nest predation and nest parasitism are not at work during migration (Petit 2000).

Urbanization intensity adjacent to forests may also affect bird community structure. Increasing urbanization is associated with decreased diversity and richness of songbirds overall, especially among Neotropical migrants, breeding in forests (Tilghman 1987, Dowd 1992, Smith and Schaefer 1992, Friesen et al. 1995, Rottenborn 1999, Lindsay et al. 2002, Hennings and Edge 2003, Donnelly and Marzluff 2004). Density of breeding songbirds in urban forests has shown varying responses to urbanization (Rottenborn 1999). Communities of migrating songbirds using forests as stopover habitat may not be as affected by urban land use outside the forest. Rodewald and Matthews (2005) found that communities of Neotropical migrants using forests as stopover habitat were not affected by the level of urbanization within 1 Km. In a comparison between bird communities in a forest prior to development of a natural area along its borders, Hostetler et al. (2005) found that richness and abundance of migrating birds did not change much because the development retained local habitat features such as high tree cover and natural buffers.

Land use in urban regions varies greatly at small spatial scales (Cadenasso et al. 2007) and it remains to be shown whether different urban land use types (e.g., residential, commercial-industrial) along forest edges have different effects on the community of migrating songbirds within forests. The mechanisms by which adjacent urban land use potentially shapes the community of migrating songbirds in the forest may act in positive and negative, direct and indirect ways in addition to the effect of habitat loss and fragmentation. For example, forests surrounded by urban areas with a high density of trees may appear larger and more attractive to birds; a direct effect of urban habitat. An example of an indirect effect is that adjacent urban land use modifies the habitat in the forest in ways that alter its quality and affects migrants' decisions to settle there. Because species vary greatly in their habitat requirements, it is important to explore the relationship of local vs. adjacent habitat to individual species responses in addition to larger, community-level parameters (Lynch and Wigham 1984, Holmes and Sherry 1986, Petit 2000).

Using a heavily urbanized watershed in the New York metropolitan region, I studied the effects of local forest habitat quality and adjacent urban land use on the community of migrating songbirds during spring of 2004. I predicted that local forest habitat quality would be most important in determining richness, abundance, and the presence of individual species in forests because of its direct effects on the community. I also predicted that the importance of local habitat parameters would not vary much with the type of land use along the forest edge unless the land use somehow alters the features of forest habitat that are most important in structuring the bird community. Finally, I

predicted that forest stand-level characteristics, especially isolation from other forests, would result in higher densities and perhaps richness of birds, but this effect would be small relative to forest and urban habitat.

Methods

Study Area: The Arthur Kill is a tidal strait and major deepwater shipping channel separating New Jersey from Staten Island, a borough of New York City (Figure 1). The watershed includes some of the most heavily urbanized areas in the Boston-to-Washington megalopolis. My study was limited to the portion of the watershed in New Jersey. The Arthur Kill and its six major tributaries drain an area of 337 km² (130 mi²) in Essex, Middlesex, and Union counties, NJ (Greiling 1993) in the Piedmont physiographic province. The mean population density among the 3 counties in the watershed is 1,775 people/Km² (4,597 people/ mi²), which is four times the state average and fifty-eight times the national average (U.S. Census Bureau 2000, <http://factfinder.census.gov>). The U.S. Census Bureau uses a minimum population density of about 386 people/km² (1,000 people/mi²) among its criteria for designating an area as urban.

The watershed contains approximately 4,395 ha. (10,860 acres) of forest, 1,136 ha. (2,808 acres) of which is forested wetland (New Jersey Department of Environmental Protection 2002). Various types of urban land use covers approximately 35,906 ha. (88,722 acres). Forty-one percent of the watershed is used for single-family, two-family, and multi-family housing. Despite its reputation as a center of industry, only 18 percent

of the land is in commercial or industrial use. Another six percent is recreational land, ballfields, and cemeteries, developed parks, and natural areas. The remainder falls into various categories including forest, open water, wetlands, and transportation corridors. Several cities, including Newark, Irvington, Orange, and Elizabeth are in the northern and eastern portion of the watershed. The western portions contain mainly single-family residential development. A few study sites fell just outside the southern boundary of the watershed.

I chose a sample of 21 hardwood forests that included most of the forests ≥ 6 ha in the watershed. Forests ranged in size from 6.02 ha. (14.87 acres) to 133.47 ha. (329.80 acres) with a mean of 46.87 ha. (115.81 acres, SD 97.91; Figure 1, Appendix A). All of the forests contained a significant deciduous forested wetland component (range 41% to 100% of total area). These and other forests in northeastern New Jersey are extremely variable hydrologically in large part due to historical alterations via ditching and draining activities (Ehrenfeld et al. 2003). The dominant tree species in the forested wetlands are red maple (*Acer rubrum* L.), pin oak (*Quercus palustris* L.), and sweetgum (*Liquidambar styraciflua* L.). Common shrubs are arrowwood viburnum (*Viburnum dentatum* L.), spicebush (*Lindera benzoin* L.), and sweet pepperbush (*Clethra alnifolia* L.). See Ehrenfeld (2005) for a detailed botanical description of forested wetlands in the region.

I placed transects at approximately 25 meters (n=27; 10 residential, 5 apartment, 7 commercial-industrial, 5 park) and 100 meters (n=11; 1 residential, 3 apartment, 5 commercial-industrial, 2 park) inside the forest parallel to the forest edge (Figure 9).

Each forest site had between one and four transects placed at 25 meters inside as long as transects were at least 200 meters apart and not located along a contiguous edge (Appendix A). Because local vegetation and bird communities vary greatly within the same forest (Inman et al. 2002, Sallabanks et al. 2000) I felt that this did not constitute pseudoreplication. Transects were also placed 25 meters outside the forest. I used a transect length of 161 meters because the use of a car odometer greatly aided in locating transects in urban land types (a distance of 0.1 mile on the odometer corresponds to 161 meters). The accuracy of this method for determining transect length was verified by pacing the length of several transects.

Avian Surveys: Transects were walked at a slow, even pace and all birds seen and heard within 25m on either side and 25m past the end points were identified and counted. Surveys were conducted from sunrise to 9:30 am on days without precipitation or high winds. Birds that flew over the transect area were noted but not counted within the boundaries of the transect unless they took off or landed within the 25 meters. Transects were sampled three times with 7-day periods in between samples from 29 April to 20 May 2004.

Habitat Structure and Composition: Because of the large number of environmental variables that could have an effect on bird community structure, I attempted to develop methods that would allow me to rapidly sample aspects of the forest and urban environment that have been related to bird parameters in other studies. At transects 25 meters into the forest, I measured various aspects of transect-level, hereinafter local-level,

forest habitat structure and composition as well as human disturbance (Appendix D). The number of ditch, stream, snag, trail, garbage, and standing water encounters were recorded while walking the entire transect length. In addition, 0.5m² plots were set up at 20-meter intervals along transects. At each plot, foliage density at the shrub and ground layers was measured using the distance it took for 50% of a board (black and white check pattern) to be obscured by foliage using modified methods of Bibby et al. (1992) and MacArthur and MacArthur (1961). Observations were made by a stationary person at each plot as a second person walked slowly away with the board held at heights of 0.5 m, 1.0 m, and 2 m toward the edge and toward the center of the site, respectively. Percentage cover of tree canopy was determined by looking straight up and down with a spotting tube (James and Shugart 1970). Leaf litter depth was measured at 3 random locations within the plot. Diameters at breast height (d.b.h.) of the 4 nearest trees with a circumference ≥ 20 cm were measured, distance from center of plot to tree measured, and species recorded (Cottam and Curtis 1956). These metrics were used to generate mean d.b.h. and mean distance from transect to large trees (a proxy for tree density). A transect was assigned a dominant tree species (i.e., species with the highest relative abundance), and the proportion of the four most common tree species (from all forest sites) was calculated for each transect. Tree species were counted as the overall number of species (richness) as well as the number of exotic tree species. Species comprising $\geq 10\%$ of the shrub layer (within a 10m² plot) and ground vegetation (within 0.5m² plot) were recorded (Ralph et al. 1993). Overall species richness of shrub and herbaceous plants as well as richness of native and exotic species in each category were calculated. At the center point in each plot, I recorded visibility beyond the forest edge.

At the forest stand-level, I calculated total area, number of patches representing different types of forest and wetland cover types, and percent wetland using land use-land cover data obtained from New Jersey Department of Environmental Protection (2002).

Adjacent urban habitat variables were measured along all transects at 25 meters from the forest (Appendix C). Percent cover of tree canopy, lawn, building, and paved surface were estimated along each urban transect using 4X6 inch photographs I took at each end of the transect. I counted the number of cells (1 m^2) in a grid that were filled at least $>50\%$ by a particular cover type. In order to increase the effectiveness of this technique in describing the amount of lawn cover, I made an additional count of cells occupied by any amount of lawn. Counts were made of coniferous and deciduous shrubs (height <3 meters), trees in the 3-10-meter height range (small), and the ≥ 11 -meter height (large) categories along the entire transect length. Trees were identified to species and the richness of trees counted. The number of pedestrians (including cyclists), automobiles (including motorcycles) and trucks (including buses) were counted for intervals of 3 minutes at the conclusion of each bird survey along transects in 2003 only and an average (#/minute) was calculated for each category.

Data Analysis: Species other than Neotropical migrant Passeriformes (perching birds), and Cuculiformes (cuckoos) were not counted. Also, only individuals recorded outside the “safe dates” for breeding were included in subsequent analyses (Walsh, 1993).

Alpha was set at 0.05 for individual analyses. Where I performed multiple iterations of a similar test (e.g, regressions), I adjusted the α -level to a “table-wide” α -level using the sequential Bonferonni method (Rice 1989). This accounted for the group-wide increase in the type I error rate with simultaneous-inference tests. All statistical analyses were completed using Statistical Package for Social Sciences (SPSS 14.0, 2005) with the exception of Canonical Correspondence Analysis (CCA), which was done using PC-ORD ver. 5.07 (McCune and Mefford 1999) . In some cases, data were transformed in order to meet the basic assumptions of normality and equal variance inherent in many parametric tests.

The effects of land use and distance from edge on community- and guild-level metrics were tested using analysis of variance (ANOVA) with adjacent land use type (residential, apartment, comm-industrial, park) as the main factor, and species richness and highest daily abundance, both log-transformed, as the response variables. I chose high abundance in order to avoid the smoothing effects that averaging abundance has on this highly fluctuating assemblage of species.

Post hoc tests were used to determine which levels of significant main effects were different. Hochberg’s GT2 method was used for comparisons among land use effects because it is robust to differences in sample sizes among treatments (Sokal and Rohlf 1995). In a second set of analyses, habitat variables at the local, adjacent, and stand-levels were entered into GLMs as covariates. This analysis was limited to the transects at 25 meters from the edge because the measures of shrub density using the

distance to 50% checkerboard cover was complicated by distance of the transect from edge. In addition, individual transects located 100 meters from the edge were paired with one at 25 meters from the edge. Thus, the two distances were not independent of one another. Instead, community metrics were compared between samples at 25 meters and 100 meters from the edge using t-tests with the understanding that the assumption of independence of samples was violated.

In order to see which species were responsible for any land use and/or covariate effects, I entered the species high abundance data (for those at ≥ 3 sites) into a multivariate analysis of variance (MANOVA). The test of whether bird high abundance varies in multivariate space was Wilks' Lambda, which is a multivariate F-value used to test the strength of the main effect.

CCA is a constrained ordination technique that selects the best linear combinations (i.e., best weights) of environmental variables that maximize the dispersion of species scores (Jongman et al. 1995). I employed CCA to describe patterns in density of individual bird species in terms of patterns in environmental variables. I focussed on transects located 25 meters inside the forest to determine whether the community of migrating songbirds in urban forests were most influenced by local forest parameters, adjacent urban parameters and/or stand-level forest parameters and which were most important. I also combined environmental variables (those with intra-set correlations ≥ 0.30) from each of these analyses into one Combined CCA to see how the combined effects of environmental variables from each category would relate to bird patterns. Data

were standardized to a mean of zero and unit variance. Each analysis produced 3 axes, with axis 1 being a linear combination of environmental variables describing the largest variance in bird density, axis 2 describing the next largest amount while remaining uncorrelated with axis 1, and so on. The amount of variance explained by each of the 3 axes and overall was used to determine the strength of the species-environment relationship in each analysis and to compare the importance of forest, urban, stand, and combined variables. Variance is the best method for assessing the strength of the axes.

Biplots of species scores and transects coded by land use type on All Habitat Axes 1 and 2 were used to visually explore areas where species might be clustering as well as outliers in relation to environmental variables. I entered transects scores on axes from the 3 types of variables (Forest, Urban, Stand), into stepwise regression analyses to see which ones best predicted overall migrant richness and density. I also entered scores on Combined Axes 1 and 2 into a stepwise regression analysis to see how well these would predict richness and density. At each step in the analyses, an F-statistic was calculated for each variable in the model. Variables having $p < 0.05$ were allowed to enter models and variables were removed if their significance level became $p < 0.10$ as other variables were entered into the model. Finally, I tested whether land use types differed depending on transect scores on axes from Forest, Urban, Stand, and Combined CCAs using MANOVA.

Results

Forty-eight species of Neotropical migrant songbirds were found using the forests as *en route* stopover habitat. Forty-two of the species were found at transects 25 meters inside the forest. Two of these species, American Robin and Grey Catbird, were excluded from further analyses because they are nearly ubiquitous as breeding species in the forests and they have a winter range that overlaps with the study area (Walsh et al. 1999). Therefore, forty species were retained for calculating overall richness and high abundance and 23 species (those present at >3 transects) were used in MANOVAs and CCAs (Table 1).

Mean species richness was 10.96 (\pm 3.69, standard deviation). Mean high abundance was 14.11 (\pm 5.59). Species richness and high abundance of migrating songbirds were highly correlated (Pearson correlation = 0.944, $p < 0.01$) because each observation usually consisted of one individual of a species.

Land use type did not affect migrant richness ($F=2.828$, 3 df, $p=0.061$) but it did affect density (high abundance; $F=3.133$, df 3, $p=0.045$). Residential areas had a higher density of migrating birds than commercial-industrial areas ($p=0.045$). D.b.h. of forest trees was the only significant covariate in GLMs for both richness and density ($F=13.495$, 1df, $p=0.001$, and $F=9.783$, 1 df, $p=0.005$). Increasing d.b.h., a proxy for age of trees, was highly positively related to richness and density of migrating birds when included as covariates in models relating land use to richness and density ($R^2=0.465$ and $R^2=0.331$,

respectively). D.b.h. alone accounts for 31% of the variance in migrant richness (Figure 11). None of the urban or stand-level habitat parameters were significant. Land use and d.b.h. were not related to density (high abundance) of individual species (Wilks' $\lambda < 0.001$, $F = 4.453$, 3.843 df, $p = 0.082$; Wilks' $\lambda = 0.005$, $F = 8.371$, 1 df, $p = 0.267$, respectively).

Table 15 provides a description of important variables (≥ 0.30 intra-set correlation, species-environment) on the 3 axes resulting from separate CCAs of Forest, Urban, Stand and Combined variables, respectively. These axes are the best linear combination of environmental variables related to the structure of the bird community. Forest Axis 1 is a gradient of decreasing wetness and decreasing herbaceous plant cover. Forest Axis 2 is a gradient of increasing forest maturity and increasing vertical complexity. Urban Axis 3 is a gradient of decreasing use by people. Urban Axis 1 is a gradient of decreasing lawn and tree cover and increasing building cover. Urban Axis 2 represents increasing pedestrian and automobile traffic and decreasing tree richness. Urban Axis 3 is a gradient of decreasing truck and automobile traffic. Stand Axis 1 is a gradient of decreasing size/% wetland and increasing isolation. Stand Axis 2 is a gradient of increasing isolation. Stand Axis 3 is a gradient of decreasing % wetland. Combined Axis 1 is a gradient of increasing herbaceous plant cover and richness, increasing forest area/% wetland, and increasing streams in the forest with more built cover and lower vegetation in the surrounding landscape. Combined Axis 2 is a gradient of increasing forest maturity, vertical complexity and herbaceous richness. It is also an axis of decreasing presence of ditches. Combined Axis 3 is a gradient of increasing isolation, density of

forest shrubs, and exotic plant richness in the forest with increasing automobile traffic and decreasing number of planted shrubs in the surrounding urban landscape.

Local forest characteristics accounted for the highest proportion of the variance (i.e., 29.7%) in density of individual species of the three types of habitat variables, forest, urban, and stand (Table 15). Urban land use also explained a high level of variance (24%) in individual species abundance patterns. The CCA of combined forest, urban, and stand variables explained 37.7% of the variance in individual species abundance patterns, largely due to the many variables with intra-set correlation values ≥ 0.30 .

Stepwise regression using transect scores from the 3 axes associated with Forest, Urban, and Stand CCAs, respectively, as independent variables showed that none of these axes was related to overall richness and density of the migrating songbird community. However, the stepwise regression using only the scores on the Combined axes showed that Combined Axis 2 (gradient of increasing forest maturity, vertical complexity, and plant richness) was the only axis related to overall species richness ($F=4.445$, 1 df, $p=0.047$, $R^2=0.135$) but not density. Ten species scores were positive on Combined Axis 2 indicating that they are associated with more mature and structurally complex (i.e., intact) forest (Table 16).

The bi-plot of species on Combined CCA Axes 1 and 2 shows wide variation in species responses to individual variables (Figure 12). Patterns were not apparent. Land use was related to transect scores on the axes derived from Urban, Forest, and Stand

analyses (Wilks' Lambda=0.032, $F=1.960$, 46.707 df, $p=0.016$). Apartment areas scored higher than residential areas on Urban Axis 1 ($p=0.003$), which is an urban gradient of increasing building cover and decreasing tree and lawn.

Mean richness at 25 meters inside forest (10.758 ± 3.651) was not different from richness at 100 meters inside forest (10.000 ± 4.153 ; $t=0.528$, 36 df, $p=0.601$). Also, mean high abundance at 25 meters inside the forest (14.000 ± 5.445 SD) was not different from abundance at 100 meters into forest (12.000 ± 4.775 ; $t=0.813$, 36df, $p=0.422$).

Discussion

Many species of Neotropical migrant birds use urban forests in heavily urbanized portions of the New York metropolitan region as *en route* stopover habitat during spring migration. Richness and density of migrating birds are positively associated with forest maturity. Bird richness is especially influenced by the habitat features of more mature forests, including larger trees, greater vertical complexity of the vegetation, and higher richness of herbaceous plant species. Forests with residential land use adjacent to them had a higher density of migrating songbirds than those abutted by commercial-industrial areas, which indicates that land use is somehow affecting the bird community. However, land use had little to no detectable effect on overall richness of migrating songbirds. The lack of a strong effect of land use on migrant richness was also found in other studies (Rodewald and Matthews 2005, Hostetler et al. 2005).

Forest size, isolation, and wetland composition were not important predictors of richness and density of migrants relative to forest maturity in this study. This was somewhat expected given that migrants are not as sensitive to area effects as they may be on the breeding range. Also, other studies have shown that migrant richness is higher in upland forests than in riparian forests in an urban landscape (Rodewald and Matthews 2005). This study did not show this relationship. Instead, the lack of a relationship between percent wetland and richness or density suggests that forest wetland composition in this region is not an important predictor of bird diversity. Wetland status is the major regulatory impetus for protecting many types of habitat. This disconnect between science and policy as it relates to protecting biodiversity needs to be addressed.

The lack of higher richness at 25 meters as compared to 100 meters from the edge was a bit of a surprise given that migrants are known to congregate closer to the edge where food abundance (i.e., arthropods) is higher (Jokimaki et al. 1998). If I had surveyed birds in the forest interior of larger sites I might have detected an effect of distance from edge. However, the farthest I sampled into the forest was 100 meters, which may have still constituted edge habitat for many species.

Migrant species exhibit large inter-annual fluctuations in their numbers and distribution (e.g., Hagan et al. 1992). This makes it difficult to base important conservation decisions solely on the results of studies conducted in only one field season, such as this one. However, the relationship of forest maturity and vegetation complexity to migrant richness in urban forests is supported by other studies (Barrow et al. 2000,

Petit 2000, Rodewald and Matthews 2005). Therefore, I feel confident that these findings are useful in supporting the need to protect forests and plan for future forests in this and other urban regions.

Figure 11. Migrant richness in relation to d.b.h. of forest trees. Line of best fit and 95% confidence interval.

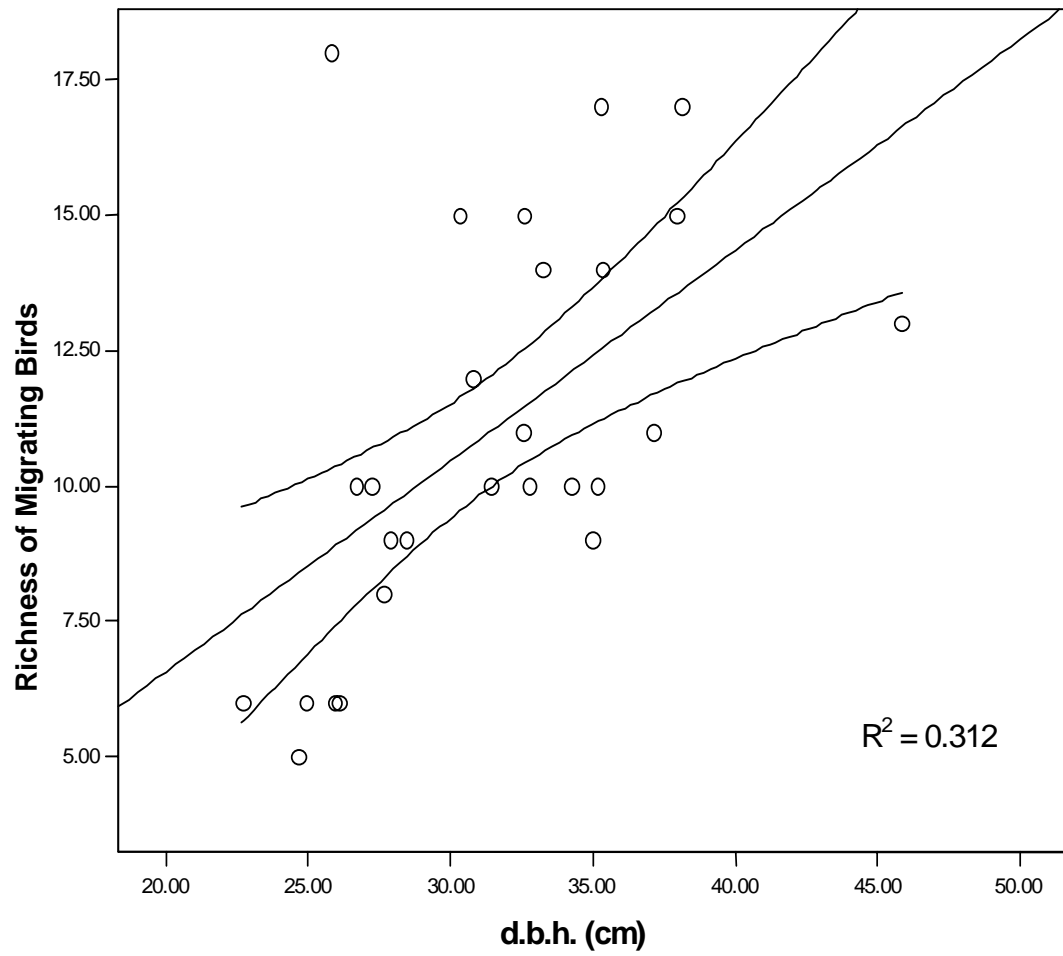


Figure 12. Bi-plot showing migrant distribution in relation to Combined Axes 1 and 2.

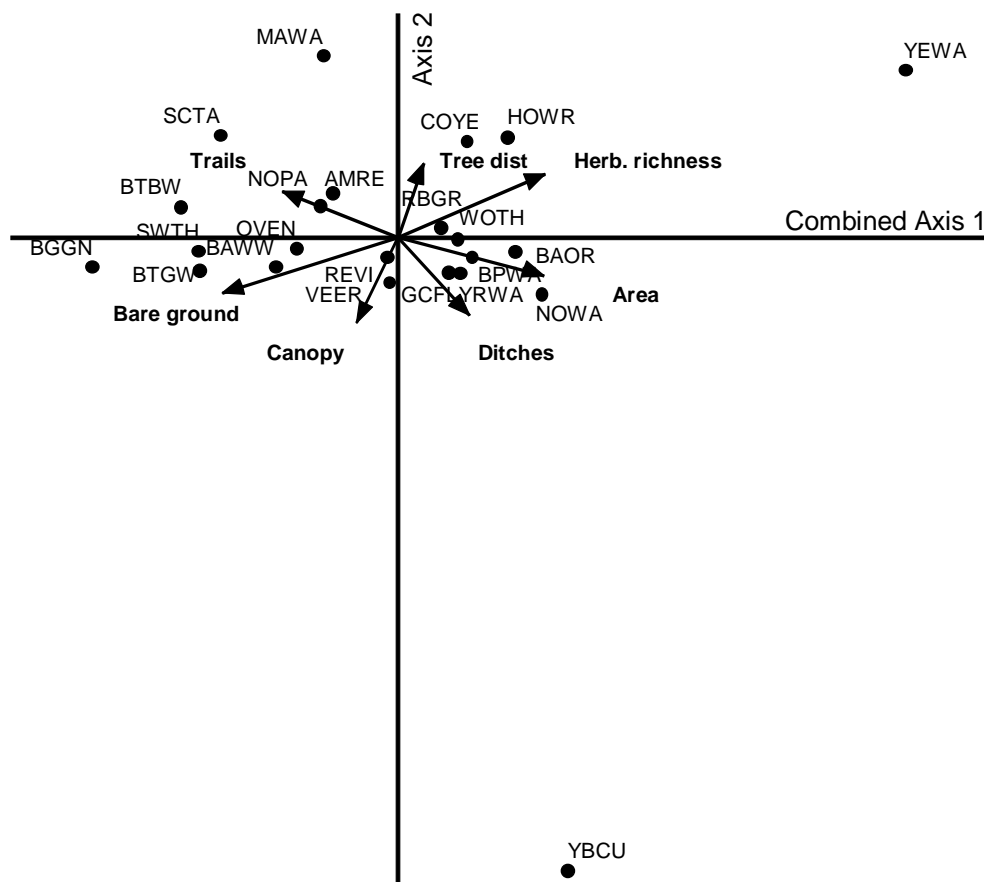


Table 14. Mean (\pm S.E.) high abundance of Neotropical migrant species in urban forests bordered by different types of land use. Means are based on observations at transects located 25 meters from the forest edge.

Species	Alpha Code	Land Use			
		Apartment	Comm-ind.	Park	Residential
Eastern Wood-pewee <i>Contopus virens</i>	EAWP	0	0	0.2 \pm 0.4	0.1 \pm 0.3
Great-crested Flycatcher <i>Myiarchus crinitus</i>	GCFL	0.2 \pm 0.4	0.4 \pm 0.5	0.2 \pm 0.4	0.4 \pm 0.5
Eastern Kingbird <i>Tyrannus tyrannus</i>	EAKI	0	0.3 \pm 0.8	0	0
Warbling Vireo <i>Vireo gilvus</i>	WAVI	0	0	0.4 \pm 0.5	0
Blue-headed Vireo <i>Vireo solitarius</i>	BHVI	0.2 \pm 0.4	0	0	0
White-eyed Vireo <i>Vireo griseus</i>	WEVI	0.2 \pm 0.4	0	0	0
Red-eyed Vireo <i>Vireo olivaceus</i>	REVI	0.2 \pm 0.4	0.4 \pm 0.5	0.6 \pm 0.5	0.9 \pm 0.3
Yellow-throated Vireo <i>Vireo flavifrons</i>	YTVI	0	0	0.2 \pm 0.4	0
House Wren <i>Troglodytes aedon</i>	HOWR	0.4 \pm 0.5	0.2 \pm 0.5	0.2 \pm 0.4	0.3 \pm 0.4
Ruby-crowned Kinglet <i>Regulus calendula</i>	RCKI	0.2 \pm 0.4	0	0	0.1 \pm 0.3
American Robin <i>Turdus migratorius</i>	AMRO	-	-	-	-
Wood Thrush <i>Hylocichla mustelina</i>	WOTH	1.6 \pm 0.9	1.1 \pm 0.9	1.8 \pm 1.3	1.4 \pm 1.1
Veery <i>Catharus fuscescens</i>	VEER	0	0.4 \pm 0.5	0.6 \pm 0.5	0.7 \pm 0.7
Swainson's Thrush <i>Catharus ustulatus</i>	SWTH	0	0.3 \pm 0.8	0.6 \pm 0.5	0.8 \pm 0.8
Gray-cheeked Thrush* <i>Catharus minimus</i>	GCTH	-	-	-	-
Blue-gray gnatcatcher <i>Poliophtila caerulea</i>	BGGN	0	0	0.2 \pm 0.4	0.3 \pm 0.5
Gray Catbird <i>Dumetella carolinensis</i>	GRCA	-	-	-	-
Northern Parula <i>Parula americana</i>	NOPA	0.4 \pm 0.5	0.3 \pm 0.5	0.4 \pm 0.5	0.9 \pm 0.6
Blue-winged Warbler* <i>Vermivora pinus</i>		-	-	-	-
Nashville Warbler <i>Vermivora ruficapilla</i>	NAWA	0	0	0	0.2 \pm 0.4
Yellow Warbler <i>Dendroica petechia</i>	YEWA	0.6 \pm 0.5	0	0.4 \pm 0.5	0
Chestnut-sided Warbler <i>Dendroica pensylvanica</i>	CSWA	0	0	0	0.1 \pm 0.3

Species	Alpha Code	Land Use			
Magnolia Warbler <i>Dendroica magnolia</i>	MAWA	0.4±0.9	0	0	0.4±0.7
Black-throated Blue Warbler <i>Dendroica caerulescens</i>	BTBW	0.4±0.9	0.3±0.5	0.6±0.9	0.8±0.6
Blackburnian Warbler <i>Dendroica fusca</i>	BLWA	0.2±0.4	0	0	0.1±0.3
Yellow-rumped Warbler <i>Dendroica coronata</i>	YRWA	2.0±1.7	1.1±0.9	1.8±2.2	2.5±1.2
Black-throated Green Warbler <i>Dendroica virens</i>	BTGW	0	0.2±0.5	0.6±0.9	0.80±0.6
Blackpoll Warbler <i>Dendroica striata</i>	BPWA	1.0±0.7	1.0±1.2	1.0±0.0	1.6±1.1
Worm-eating Warbler <i>Helmitheros vermivora</i>	WEWA	0.2±0.4	0	0	0.1±0.3
Black-and-white Warbler <i>Mniotilta varia</i>	BAWW	0	0.5±0.5	0.6±0.5	0.7±0.5
American Redstart <i>Setophaga ruticilla</i>	AMRE	0.4±0.5	0	0.6±0.5	0.7±0.7
Ovenbird <i>Seiurus aurocapillus</i>	OVEN	0.4±0.5	1.0±0.6	0.8±0.8	1.2±0.9
Northern Waterthrush <i>Seiurus noveboracensis</i>	NOWA	0.6±0.5	0.4±0.5	0.6±0.5	0.5±0.7
Louisiana Waterthrush <i>Seiurus motacilla</i>	LOWA	0	0	0	0.1±0.3
Common Yellowthroat <i>Geothlypis trichas</i>	COYE	0.8±0.8	0.4±0.5	0.4±0.5	0.6±1.0
Wilson's Warbler <i>Wilsonia pusilla</i>	WIWA	0.2±0.4	0	0	0
Canada Warbler <i>Wilsonia canadensis</i>	CAWA	0.2±0.4	0.1±0.4	0	0
Hooded Warbler <i>Wilsonia citrina</i>	HOWA	0	0	0	0.1±0.3
Scarlet Tanager <i>Piranga olivacea</i>	SCTA	0.4±0.5	0.4±0.5	0	0.3±0.5
Rose-breasted Grosbeak <i>Pheucticus ludovicianus</i>	RBGR	0	0	0.6±0.9	0.5±0.7
Indigo Bunting <i>Passerina cyanea</i>	INBU	0	0.1±0.4	0	0
Eastern Towhee <i>Pipilo erythrophthalmus</i>	EATO	0.4±0.5	0	0	0
Baltimore Oriole <i>Icterus galbula</i>	BAOR	0.6±0.9	1.0±0.6	0.6±0.5	0.8±0.9
Orchard Oriole <i>Icterus spurius</i>	OROR	-	-	-	-
Yellow-billed Cuckoo <i>Coccyzus americanus</i>	YBCU	0.2±0.4	0.1±0.4	0	0.1±0.3

*at 100 meters from edge only.

Table 15. Habitat variables with ≥ 0.30 intra-set correlation, species-environment from four separate CCAs: 1. Forest only, 2. Urban only, 3. Stand only, and 4. Combined (all habitat)

	Important Environmental Variables (4 separate CCAs)							
	Forest (F)		Urban (U)		Stand (S)		Combined	
Axis 1	+Bare ground -Herb richness -Streams -Exotic plants -Standing water		-Lawn +Built -Lg. dec. trees -Tree richness -Auto		-Area +Isolation -% wetland		-Bare ground (F) +Herb richness (F) +Area (F) +Built (U) -Lawn (U) +Stream (F) -Isolation (S) -Trail (F) -Lg. dec. trees (U) +% wetland (S)	
	% Var.	11.1	% Var.	9.6	% Var.	6.9	% Var.	13.9
Axis 2	-Open shrub layer -Canopy -Litter depth -Ditches +Tree distance +Trail +Herb richness		+Pedestrians -Truck -Tree richness +Auto +Lawn		+Isolation		-Canopy (F) -Ditch (F) +Tree distance (F) +Herb richness (F) -Open shrub layer (F)	
	% Var.	10.2	% Var.	7.8	% Var.	2.6	% Var.	12.3
Axis 3	-Trail -Exotic plants -Garbage -Open shrub layer		-Truck -Auto		-% Wetland		+Isolation (S) +Auto (U) -Open shrub layer (F) -Shrubs (U) +Exotic plants (F)	
	% Var.	8.4	% Var.	6.5	% Var.	1.6	% Var.	11.4
Total	% Var.	29.7	% Var.	24.0	% Var.	11.1	% Var.	37.7

Table 16. Scores derived from linear combinations of habitat variables on Combined Axis 2, CCA, for 23 migrating songbirds.

Species	Score
GCFL	-0.18
REVI	-0.10
HOWR	0.51
WOTH	-0.01
VEER	-0.23
SWTH	-0.07
BGGN	-0.15
NOPA	0.16
YEWA	0.85
MAWA	0.92
BTBW	0.15
YRWA	-0.19
BTGW	-0.17
BPWA	-0.10
BAWW	-0.15
AMRE	0.23
OVEN	-0.05
NOWA	-0.29
COYE	0.49
SCTA	0.52
RBGR	0.04
BAOR	-0.07
YBCU	0.54

CONCLUSION

Birds in North America are facing large declines in numbers due to many causes, including habitat loss from urbanization (Valiela and Martinetto 2007). Measures need to be taken to improve the value of urban landscapes for birds. In my study, forests with older, larger trees and a high density of shrub and ground vegetation near the edge have the highest richness of breeding songbirds as well as spring migrants. Also, adjacent habitats have important effects on bird communities. Forests of a broad range of sizes and habitat conditions bolster bird diversity in adjacent urban habitats up to at least 0.2 Km from their edges. I found that a high density of large trees in the urban matrix is the one critical habitat component for increasing bird richness outside the forest in urban neighborhoods as well as richness and density of breeding and migrating birds in adjacent forest. Because residential areas have the highest density as well as variety of large trees relative to other types of urban land use, they also contain the greatest richness of birds. Parks in the Arthur Kill watershed also support a high diversity of birds because they typically have a high density of large trees. These findings suggest a wide-range of conservation practices, including forest preservation, management of shrubby edges, and planting and maintaining a variety of large, long-lived trees in urban neighborhoods, which would maintain a rich bird community in urban regions.

In long-developed metropolitan regions, remnant forests are relatively small and isolated yet they provide breeding habitat for many migrant and resident birds that would otherwise not be found there (Robinson et al. 1997, Brawn et al. 2002, Hodgson et al.

2006, Platt and Lill 2006). Despite the importance of urban forest habitats to birds and other wildlife as well as the ecosystem services they provide (e.g., flood control, carbon sequestering), they are given little protection beyond that afforded by laws protecting wetlands (Turner et al. 1995, Bolund and Hunhammar 1999, Harrison and Davies 2002). Policies and innovative strategies at several tiers of government and private stakeholders are needed that provide direct protection of forested areas as rare, threatened habitat in urban regions. Large-scale stakeholder initiatives in the New York metropolitan region already recognize the value of remaining forests (e.g., New York/New Jersey Harbor Estuary Program) and protection of these places are among the top conservation priorities. The mechanisms for achieving this goal are somewhat opportunistic in nature and require some form of flexibility in the regulatory and planning process. While a thorough review of land conservation practice is outside the scope of this paper, I offer examples of some common approaches.

Most of the current approaches to conservation by governments and conservation organizations take advantage of various types of economic incentives (e.g., grants, tax cuts, streamlined permit approval) to partners that cooperate in purchasing or setting aside natural areas. In the eastern part of the Arthur Kill watershed, many “brownfield” re-development projects on previously industrial land are undertaken by developers with a high level of support from state and federal agencies in exchange for mitigation of often hazardous waste materials on the site (NY/NJ Baykeeper 2006). Unfortunately, most of these re-development projects plan for building outside the original industrial footprint into valuable natural habitats on the properties. State and federal agencies along with

local conservation groups have been successful at encouraging some developers to preserve existing natural habitats as part of the site plan in exchange for permit approval.

Another form of economic incentive is in the form of grants for towns that update their Master Plan to include open space preservation, enlist an open space tax and seek matching funds from state agencies (i.e., Green Acres) to purchase forests (Association of New Jersey Environmental Commissions 2002). Also, municipalities may employ various innovative local planning tools such as local ordinances (e.g., control on housing density), transfer of development rights, overlay permits, variances, etc., which can restrict development in certain ecologically important locations while channelling it into places where it would have less ecological impact (e.g., town centers; Association of New Jersey Environmental Commissions 2002, Daly and Nolan 1996). This would also require more flexibility in applying land use decisions within municipal governments than sometimes exists. For example, in some cases local ordinances that require large lot sizes may conflict with the desire to build housing in more concentrated areas while setting aside forests and other open space.

In addition to forest preservation, there are many opportunities for forest restoration in the region, including large, inactive landfills, many of which are covered by naturally regenerating forest and shrublands of value to birds and other wildlife. Also, forest preservation should coincide with forest management. This includes maintaining natural shrubby edges along forests instead of continually removing vegetation right up to the forest edge. This would be undertaken by residents with backyards abutting forests as

well as by grounds maintenance crews and landscaping companies that manage areas adjacent to forests along public roads and in commercial areas, parks, and apartment complexes. In addition, management of deer populations may be required, especially in areas where deer are in high density such as in the more suburban areas of the watershed that have a more forested landscape. Because these areas are also heavily populated, techniques for deer management other than hunting need to be investigated.

Much can be done from a local management perspective for birds in the built environment by simply increasing the number and variety of large, native trees. Thousands of trees in New York City and adjacent areas in New Jersey, including in the study area, have been removed because of infestations with Asian long-horned beetle (*Anoplophora glabripennis*) and the U. S. Department of Agriculture (USDA) recently announced the treatment of approximately 100,000 trees in the region with an insecticide (USDA 2007). Many areas throughout the Arthur Kill watershed are denuded of large trees (personal observation). However, Staten Island, a borough of New York City in the eastern portion of the watershed, actually had a 33% increase in street trees between 1995 and 2005 (New York City Department of Parks and Recreation 2007). Several of the largest cities in the region are taking part in tree-planting initiatives. New York City plans to plant a million trees throughout all five boroughs (<http://www.milliontreesnyc.org>). The City of Newark Shade Tree Operations and Engineering Department is working with the New Jersey Tree Foundation to plant trees throughout the city (<http://www.njtreefoundation.org>). Urban reforestation projects need to focus on planting a large variety of native, long-lived trees in order to increase richness

and density of birds as well as provide other services that benefit people such as shade, clean air, and aesthetically pleasing neighborhoods. Targets for such management practices are commercial-industrial areas and apartment complexes because they presently lack many of the habitat resources supporting bird diversity. Other targets are to increase the variety of trees in parks, which would be a management goal enacted at mainly the municipal and county levels.

State and non-profit sources of funding exist to aid municipalities in undertaking tree-planting projects (e.g. New Jersey Tree Foundation and Million Trees NYC). The State of New Jersey encourages formation of local shade tree commissions and protects them from liability due to property damage from trees under the New Jersey Shade Tree and Community Forestry Act. Education and outreach to municipalities and individual landowners regarding how to develop and implement an urban forestry plan, which includes resources for selecting appropriate tree species, is a priority for various government agencies and conservation groups (e.g., USDA and National Arbor Day Foundation). The Tree City USA award given to municipalities who take part in a community forestry program has been successful in encouraging tree planting and care in municipalities across the United States (Rosenow and Yager 2000).

In conclusion, bird diversity in urban regions may be greatly enhanced by preserving and managing intact forests with dense, shrubby perimeters as well as by increasing tree cover in urban neighborhoods. Increasing the diversity of bird species where people live and work benefits people indirectly via bird predation on insect pests

that may result in less damage to trees, lawns, and gardens (Strong et al. 2000). Birds are also important agents of seed dispersal in eastern deciduous forests (Stiles 1980), which has important implications for natural and human-facilitated forest regeneration.

Improving biological diversity in urban neighborhoods and opportunities to encounter components of diversity has direct benefits to human health, sense of well-being, and child development (Rohde and Kendle 1994). Exposure to biological diversity is, in turn, linked to positive perceptions of environmental health within the urban population, which fosters both an appreciation for nature and the will to protect it (Turner et al. 2004).

Birds are an accessible, charismatic component of urban biodiversity and a large portion of the public enjoys watching and feeding birds (U. S. Department of Interior et al. 2001). Therefore, they are an important target for conserving biological diversity in urban regions.

APPENDIX A: List of 21 forests used in study including location, number of transects within the forest, area, number of patches of different habitat classification, % of area that is wetland, and distance to the nearest forest patch.

ID	USGS Quad	Town	No. of transects at 25 and 100 m into forest	Area (ha.)	No. patches of habitat	Wetland (%)	Distance to nearest forest (meters)
01	Perth Amboy	Edison	4	28.24	10	72	110
02	Perth Amboy	Iselin	1	10.23	7	69	87
03	Perth Amboy	Edison	2	12.42	6	67	225
04	Plainfield	Edison	2	10.07	8	74	175
05	Plainfield	Edison	4	68.58	12	92	77
06	Perth Amboy	Scotch Plains	4	133.47	22	78	32
07	Roselle	Westfield	3	104.64	18	88	427
08	Perth Amboy	Woodbridge	3	29.57	12	68	384
09	Perth Amboy	Scotch Plains	2	15.32	4	79	447
10	Perth Amboy	Scotch Plains	1	18.05	11	70	60
11	Plainfield	Piscataway	1	14.01	1	100	52
12	Plainfield	S. Plainfield	4	86.94	19	100	139
13	Plainfield	S. Plainfield	2	31.31	13	100	96
14	Perth Amboy/Arthur Kill	Linden	2	15.69	4	92	153
15	Perth Amboy/Arthur Kill	Carteret	1	6.02	3	68	1,329
16	Perth Amboy/Arthur Kill	Port Reading	1	8.43	2	77	422
17	Plainfield	S. Plainfield	1	6.65	7	100	73
19	Perth Amboy	Rahway	1	15.13	6	41	214
20	Elizabeth	Hillside	1	25.26	7	57	107
21	Elizabeth	Hillside	1	15.49	13	95	68
22	Roselle	Cranford	5	42.82	19	78	427

APPENDIX B: Number of transects in each land use x distance category included in study. Numbers in parentheses are those at which habitat was also sampled.

Distance relative to forest edge	Apartment	Comm-ind	Park	Residential	Total
-100 (forest)	4	5	2	2	13
-25 (forest)	6	9	5	13	33 (33)
25 (urban)	6	8	7	16	37 (35)
200 (urban)	7	6	2	18	33 (29)
≥350 (urban)	8	22	7	60	97 (73)
Total	31	50	23	109	213 (170)

APPENDIX C: Summary of variables from transects (n=137) in the urban matrix.

Habitat Variable	Land Use	Mean	Std. Deviation	N
LAWN (mean # cells/24)	apartment	6.0556	2.92499	18
	comm-ind	4.6167	3.60479	30
	park	11.5357	3.58128	14
	residential	7.1600	2.17660	75
	Total	6.9051	3.33736	137
PAVED (mean # cells/24)	apartment	9.1944	3.05893	18
	comm-ind	8.9333	2.91469	30
	park	3.1071	3.26507	14
	residential	9.6933	1.62725	75
	Total	8.7883	3.04000	137
BUILT (mean # cells/24)	apartment	2.4444	1.55193	18
	comm-ind	1.4333	1.71572	30
	park	.0357	.13363	14
	residential	1.0400	1.40405	75
	Total	1.2080	1.54068	137
Tree Cover (mean # cells/24)	apartment	3.7778	2.88109	18
	comm-ind	3.3167	2.73699	30
	park	8.5357	3.15902	14
	residential	7.5200	2.96425	75
	Total	6.2117	3.53591	137
Pedestrians (per minute)	apartment	1.2991	1.34509	18
	comm-ind	1.5456	3.19646	30
	park	2.0452	2.91027	14
	residential	.9713	1.97492	75
	Total	1.2499	2.33756	137
Automobiles (per minute)	apartment	1.8306	2.01886	18
	comm-ind	6.9939	7.91288	30
	park	.8321	1.95877	14
	residential	4.3753	10.16646	75
	Total	4.2523	8.60887	137
Trucks (per minute)	apartment	.0917	.24450	18
	comm-ind	.8394	.99618	30
	park	.0000	.00000	14
	residential	.3300	.88656	75
	Total	.3765	.84885	137
Small dec. trees	apartment	8.5768	9.14904	18
	comm-ind	5.2034	5.50508	30
	park	3.4479	4.89190	14
	residential	4.5189	3.41981	75
	Total	5.0925	5.25793	137

Appendix C, Cont.

Habitat Variable	Land Use	Mean	Std. Deviation	N
Large dec. trees	apartment	11.2696	8.97928	18
	comm-ind	10.5515	8.24590	30
	park	22.5507	12.16233	14
	residential	26.7795	15.50689	75
	Total	20.7560	14.99260	137
Small conifers	apartment	2.6915	3.57758	18
	comm-ind	1.9255	3.45381	30
	park	.0000	.00000	14
	residential	2.9117	3.58408	75
	Total	2.3693	3.45404	137
Large conifers	apartment	7.7295	9.11416	18
	comm-ind	3.5611	8.52716	30
	park	1.5972	2.48106	14
	residential	5.3915	4.52785	75
	Total	4.9101	6.35162	137
Shrubs	apartment	69.8344	37.49396	18
	comm-ind	30.3876	35.30179	30
	park	4.3478	12.64962	14
	residential	53.9993	23.91769	75
	Total	45.8355	33.32914	137
Tree richness	apartment	6.78	3.246	18
	comm-ind	6.77	4.116	30
	park	7.43	1.910	14
	residential	13.80	3.687	75
	Total	10.69	4.952	137

APPENDIX D: Summary of variables from transects located 25 meters into the forest.

- a. Mean and standard deviation of forest habitat variables measured along 33 transects at 25 meters from the edge with different types of urban land use adjacent to them.

Habitat Variable	Land Use	Mean	Std. Deviation	# transects
Ditch (#Ditch/length)	apartment	.0031	.00520	6
	comm-ind	.0007	.00207	9
	park	.0055	.00546	5
	residential	.0010	.00244	13
	Total	.0020	.00377	33
#Stream / Length	apartment	.0021	.00507	6
	comm-ind	.0025	.00741	9
	park	.0039	.00567	5
	residential	.0032	.00706	13
	Total	.0029	.00639	33
#StandingWater / Length	apartment	.0438	.01419	6
	comm-ind	.0297	.02465	9
	park	.0319	.03522	5
	residential	.0248	.02119	13
	Total	.0307	.02353	33
#Trail / Length	apartment	.0067	.00835	6
	comm-ind	.0015	.00302	9
	park	.0158	.01969	5
	residential	.0115	.01390	13
	Total	.0085	.01266	33
#Snag / Length	apartment	.1194	.06268	6
	comm-ind	.1127	.05811	9
	park	.1131	.08224	5
	residential	.1279	.05769	13
	Total	.1200	.05999	33
#Garbage / Length	apartment	.0553	.05506	6
	comm-ind	.0348	.02996	9
	park	.0829	.10731	5
	residential	.0427	.04968	13
	Total	.0489	.05764	33
Herbaceous species	apartment	6.5000	3.27109	6
	comm-ind	2.5556	2.00693	9
	park	4.6000	2.96648	5
	residential	4.6923	2.75029	13
	Total	4.4242	2.90506	33

Appendix D, Table a.,
Cont.

Habitat Variable	Land Use	Mean	Std. Deviation	# transects
Exotic herb. species	apartment	1.5000	1.04881	6
	comm-ind	.5556	1.01379	9
	park	1.6000	1.14018	5
	residential	1.3077	1.65250	13
	Total	1.1818	1.33357	33
# bare ground (no herbs)	apartment	2.6667	1.36626	6
	comm-ind	4.5556	2.74368	9
	park	2.2000	2.68328	5
	residential	3.8462	1.95133	13
	Total	3.5758	2.29170	33
Shrub species	apartment	3.3333	.81650	6
	comm-ind	2.2222	1.39443	9
	park	2.0000	.70711	5
	residential	2.6154	1.12090	13
	Total	2.5455	1.14812	33
Exotic shrub species	apartment	.5000	.54772	6
	comm-ind	.1111	.33333	9
	park	.4000	.54772	5
	residential	.5385	.66023	13
	Total	.3939	.55562	33
Tree species	apartment	9.0000	1.41421	6
	comm-ind	9.4444	3.97213	9
	park	9.2000	1.92354	5
	residential	8.6923	2.59437	13
	Total	9.0303	2.70976	33
Exotic tree species	apartment	.0000	.00000	6
	comm-ind	.1111	.33333	9
	park	.4000	.54772	5
	residential	.3846	.65044	13
	Total	.2424	.50189	33
Total exotic species	apartment	2.0000	1.26491	6
	comm-ind	.7778	1.39443	9
	park	2.4000	1.81659	5
	residential	2.1538	1.95133	13
	Total	1.7879	1.72767	33
#human settlement visible	apartment	8.0000	1.54919	6
	comm-ind	5.6667	2.44949	9
	park	5.4000	3.57771	5
	residential	8.0000	1.77951	13
	Total	6.9697	2.48099	33

Appendix D, Table a.,
Cont.

Habitat Variable	Land Use	Mean	Std. Deviation	# transects
Ground and shrub openness toward edge (at .5 meters from ground)	apartment	15.2500	5.25495	6
	comm-ind	14.7969	5.16295	9
	park	25.4736	13.81885	5
	residential	18.9308	6.01838	13
	Total	18.1255	7.86119	33
Shrub openness toward edge (at 1.0 meter from ground)	apartment	16.9028	5.45916	6
	comm-ind	16.1176	6.99146	9
	park	26.4569	12.87662	5
	residential	18.8229	4.93844	13
	Total	18.8926	7.65500	33
Shrub openness toward edge (at 2.0 meters from ground)	apartment	17.2222	6.08854	6
	comm-ind	15.7138	7.61349	9
	park	25.7042	13.13324	5
	residential	19.5821	4.44731	13
	Total	19.0256	7.74921	33
Ground and shrub openness toward center (at 0.5 meter from ground)	apartment	25.0046	17.76832	6
	comm-ind	19.6378	8.60253	9
	park	32.6358	29.57267	5
	residential	27.2920	11.87895	13
	Total	25.5983	15.78059	33
Shrub openness toward center (at 1.0 meter from ground)	apartment	26.7269	17.58881	6
	comm-ind	20.5885	7.90695	9
	park	30.2369	23.22759	5
	residential	26.8674	11.18471	13
	Total	25.6400	13.77071	33
Shrub openness toward center (at 2.0 meters from ground)	apartment	25.3241	16.70431	6
	comm-ind	19.6836	9.02313	9
	park	27.5989	18.98344	5
	residential	28.8025	12.49290	13
	Total	25.5007	13.49690	33

Appendix D, Table a.,
Cont.

Habitat Variable	Land Use	Mean	Std. Deviation	# transects
d.b.h.	apartment	30.4146	6.52475	6
	comm-ind	28.8405	4.02374	9
	park	33.6384	7.57565	5
	residential	30.7678	3.99234	13
	Total	30.6129	5.11677	33
Tree distance (mean distance of 4 nearest trees from center of each plot; higher number is lower density)	apartment	4.2756	1.66861	6
	comm-ind	3.8201	.73377	9
	park	4.3808	1.05486	5
	residential	3.7976	1.52629	13
	Total	3.9790	1.28238	33
% tree canopy (spot tube)	apartment	71.3426	15.55549	6
	comm-ind	75.7564	5.74369	9
	park	79.4600	10.85689	5
	residential	74.9327	6.54955	13
	Total	75.1905	9.08942	33
Litter depth (mean of 3 measures/plot)	apartment	.7500	.30974	6
	comm-ind	1.3815	.42077	9
	park	1.1995	.48284	5
	residential	1.1428	.70282	13
	Total	1.1451	.56488	33

APPENDIX D, cont.

- b. Tree species composition (mean relative abundance and standard deviation) along transects 25 meters from the edge in forests with different types of land use adjacent to them.

Habitat variable	Land Use	Mean	Std. Deviation	N
% red maple	apartment	.4633	.18359	6
	comm-ind	.2978	.30683	9
	park	.2133	.19480	6
	residential	.3042	.19916	12
	Total	.3148	.23357	33
% pin oak	apartment	.0517	.08377	6
	comm-ind	.2722	.21644	9
	park	.1717	.20459	6
	residential	.1633	.28446	12
	Total	.1742	.22962	33
% ash species	apartment	.1283	.09390	6
	comm-ind	.0556	.06692	9
	park	.0517	.10815	6
	residential	.0442	.05838	12
	Total	.0639	.08043	33
% sweetgum	apartment	.2267	.22853	6
	comm-ind	.0911	.09804	9
	park	.2983	.33379	6
	residential	.2967	.20852	12
	Total	.2282	.22558	33

APPENDIX D, cont.

- c. Dominant tree species along transects 25 meters from the edge in forests with different types of land use adjacent to them.

Land Use	Dominant tree species	# transects
apartment	ash	1
	red maple	3
	sweetgum	2
	Total	6
comm-ind	red maple	3
	pin oak	4
	sweetgum	1
	tulip poplar	1
park	Total	9
	red maple	2
	pin oak	1
	sweetgum	3
residential	Total	6
	maple-sweetgum	1
	red maple	3
	pin oak	2
Total	sweetgum	6
	Total	12
	ash	1
	maple-sweetgum	1
	red maple	11
	pin oak	7
	sweetgum	12
	tulip poplar	1
	Total	33

APPENDIX D, cont.

- d. Common and Latin names of plant species (herbaceous plants, shrubs, and trees) surveyed along forest transects 25 meters from the edge. Herbaceous plant species are those counted in 1-m² plots and tree and shrub species are those counted in 10-m² plots and in measures of d.b.h..

Herbaceous plants	
garlic mustard*	<i>Alliaria petiolata</i>
great ragweed	<i>Ambrosia trifida</i>
Jack-in-the-pulpit	<i>Arisaema sp.</i>
false nettle	<i>Boehmeria cylindrica</i>
enchanter's nightshade	<i>Circaea quadrisulcata</i>
Asiatic dayflower *	<i>Commelina communis</i>
hayscented fern	<i>Dennstaedtia punctilobula</i>
white snakeroot	<i>Eupatorium rugosum</i>
eastern joe-pye weed	<i>Eupatorium rugosum</i>
wintergreen	<i>Gaultheria procumbens</i>
white avens	<i>Geum canadense</i>
English ivy *	<i>Hedera helix</i>
spotted touch-me-not	<i>Impatiens capensis</i>
ivy-leaved mourning glory*	<i>Ipomoea simplex</i>
cardinal flower	<i>Lobelia cardinalis</i>
Japanese honeysuckle*	<i>Lonicera japonica</i>
moneywort*	<i>Lysimacha nummularia</i>
Canada mayflower	<i>Maianthemum canadense</i>
Japanese stilt grass*	<i>Microstegium vimineum</i>
Indian pipe	<i>Monotropa uniflora</i>
sensitive fern	<i>Onoclea sensibilis</i>
cinamon fern	<i>Osmunda cinnamomea</i>
pachysandra*	<i>Pachysandra sp.</i>
Virginia creeper	<i>Parthenocissus sp.</i>
wild kidney bean	<i>Phaseolus polystachios</i>
pokeweed	<i>Phytolacca americana</i>
clearweed	<i>Pilea pumila</i>
halberd-leaved tearthumb	<i>Polygonum arifolium</i>
Japanese knotweed*	<i>Polygonum cuspidatum</i>
lady's thumb*	<i>Polygonum persicaria</i>
common cinquefoil	<i>Potentilla simplex</i>
buttercup	<i>Ranunculus sp.</i>
crow's feet	<i>Ranunculus sp.</i>
poison ivy	<i>Rhus radicans</i>
dewberry	<i>Rubus flagellaris</i>
catbrier	<i>Smilax rotundifolia</i>
goldenrod	<i>Solidago sp.</i>
skunk cabbage	<i>Symplocarpus foetidus</i>
New York fern	<i>Thelypteris noveboracensis</i>
jumpseed	<i>Tovara virginiana</i>
stinging nettle*	<i>Urtica dioica</i>
violet	<i>Viola sp.</i>
fox grape	<i>Vitis labrusca</i>
Chinese wisteria*	<i>Wisteria sinensis</i>

APPENDIX D, Table d.,cont.

Shrubs	
Japanese barberry*	<i>Berberis thunbergii</i>
buttonbush	<i>Cephalanthus occidentalis</i>
sweet pepperbush	<i>Clethra alnifolia</i>
laurel	<i>Laurel sp.</i>
privet*	<i>Ligustrum sp.</i>
spicebush	<i>Lindera benzoin</i>
swamp azalea	<i>Rhodendron viscosum</i>
multiflora rose*	<i>Rosa multiflora</i>
black raspberry	<i>Rubus sp.</i>
lowbush blueberry	<i>Vaccinium angustifolium</i>
highbush blueberry	<i>Vaccinium corymbosum</i>
mapleleaf viburnum	<i>Viburnum acerfolium</i>
arrowood viburnum	<i>Viburnum dentatum</i>

Trees	
box-elder	<i>Acer negundo</i>
Norway maple*	<i>Acer platanoides</i>
red maple	<i>Acer rubrum</i>
silver maple	<i>Acer saccharinum</i>
tree-of-heaven*	<i>Ailanthus altissima</i>
serviceberry	<i>Amelanchier canadensis</i>
yellow birch	<i>Betula alleghaniensis</i>
black (sweet) birch	<i>Betula lentata</i>
Gray birch	<i>Betula populifolia</i>
ironwood	<i>Carpinus caroliniana</i>
bitternut hickory	<i>Carya aquatica</i>
shagbark hickory	<i>Carya ovata</i>
mockernut hickory	<i>Carya tomentosa</i>
American chestnut	<i>Castanea dentata</i>
catalpa*	<i>Catalpa speciosa</i>
silky dogwood	<i>Cornus amomum</i>
flowering dogwood	<i>Cornus florida</i>
gray dogwood	<i>Cornus racemosa</i>
American beech	<i>Fagus grandifolia</i>
white ash	<i>Fraxinus Americana</i>
green ash	<i>Fraxinus pennsylvanica</i>
common witch hazel	<i>Hamamelis virginiana</i>
butternut	<i>Juglans cinerea</i>
sweetgum	<i>Liquidambar styraciflua</i>
tulip poplar	<i>Liriodendron tulipifera</i>
crabapple	<i>Malus coronana</i>
white mulberry*	<i>Morus alba</i>
black gum (tupelo)	<i>Nyssa sylvatica</i>
sycamore	<i>Platanus occidentalis</i>
eastern cottonwood	<i>Populus deltoides</i>
big-tooth aspen	<i>Populus grandidentata</i>
sweet cherry	<i>Prunus avium</i>
black Cherry	<i>Prunus serotina</i>
white oak	<i>Quercus alba</i>
swamp white oak	<i>Quercus bicolor</i>
pin oak	<i>Quercus palustris</i>

APPENDIX D, Table d.,cont.

red oak	<i>Quercus rubra</i>
black oak	<i>Quercus velutina</i>
buckthorn*	<i>Rhamnus sp.</i>
black willow	<i>Salix nigra</i>
Elderberry	<i>Sambucus canadensis</i>
sassafras	<i>Sassafras albidum</i>
American basswood	<i>Tilia americana</i>
American elm	<i>Ulmus Americana</i>
slippery elm	<i>Ulmus rubra</i>
smooth blackhaw	<i>Viburnum prunifolium</i>
blackhaw	<i>Viburnum prunifolium</i>

* Exotic species

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